

*Proceedings of the International Conference
on Tropical Oceanography*

INSTITUTE OF MARINE SCIENCES, UNIVERSITY OF MIAMI
1 RICKENBACKER CAUSEWAY, MIAMI, FLORIDA 33149

STUDIES IN
TROPICAL
OCEANOGRAPHY
No. 5



This volume may be referred to as:

Stud. trop. Oceanogr. Miami 5: xx + 847 pp.

October, 1967

EDITORIAL COMMITTEE
for this Number

Frederick M. Bayer

C. P. Idyll

James I. Jones

F. F. Koczy

Arthur A. Myrberg

C. Richard Robins

F. G. Walton Smith

G. L. Voss

E. J. Ferguson Wood

Albert C. Jensen

Proceedings
of the
International Conference
on
Tropical Oceanography

November 17-24, 1965

Miami Beach, Florida

*The Friedrich Frans Koczy
Memorial Volume*



October • 1967

Published by the University of Miami
INSTITUTE OF MARINE SCIENCES



FRIEDRICH FRANS KOCZY
Vienna, Austria, June 16, 1914
Honolulu, Hawaii, April 16, 1967

Friedrich Frans Koczy

Dr. Friedrich Frans ("Fritz") Koczy, a native of Vienna, Austria, did his graduate work at the famed Institut für Radiumforschung and obtained his Ph.D. in Physics and Mathematics from the University of Vienna in 1939. In the same year he joined the staff of the Oceanographic Institute of Göteborg, Sweden, where he spent the war years. He married the former Gunvor Bresky of Göteborg in 1944. He was in charge of the conversion of the ALBATROSS from a training ship for cadets to an oceanographic research vessel and participated as scientist in her world-wide cruise of 1947-1948. He joined the staff of the Board of Fisheries of Sweden in 1948 and in 1955 went back to the Oceanographic Institute.

In 1957, Fritz Koczy joined the faculty of the Institute of Marine Sciences (then the Marine Laboratory) of the University of Miami and was appointed chairman of the Division of Physical Sciences. In his new capacity, he was largely responsible for the highly successful development of the Division, including the construction of a new building especially designed for research in oceanography and marine geology. He taught courses in oceanography and was a member of the Graduate Council and the Research Council of the University.

Fritz Koczy's area of research covered the entire field of oceanography. He became chairman or member of various national committees appointed to deal with oceanographic problems, and to these he contributed his vast knowledge, his consummate skills, and his Viennese wit.

It can be said, in the truest sense, that his loss is an irreplaceable one for the Institute, the University, and the nation.

Cesare Emiliani

PREFACE

Oceanography, as a science, is generally considered to have its roots with the Challenger Expedition. It was not only the first expedition to include all sciences necessary for complete understanding of the ocean, but was also a tropical expedition. However, the emphasis on the tropics was replaced by a growing interest in northern waters, particularly the Arctic and the Northwestern Atlantic. As a result, oceanography became the study of cold-water areas during the summertime, because only during summer was it possible to investigate these rather unkind waters with the size and type of ships available.

When Hans Pettersson organized the Swedish Deep-Sea Expedition which crossed the Equator sixteen times, he made history. As Roger Revelle once said, "He did demonstrate that good oceanography can be done in tropical waters." In the last 20 years, we have seen intensification of the exploration of the tropics. Expeditions organized by "POFI," Scripps Institute of Oceanography and the Institute of Marine Sciences concentrated their efforts on tropical areas. International large-scale expeditions of several nations, such as the International Indian Ocean Expedition and I.C.I.T.A. devoted their time solely, or principally, to the equatorial regions.

Since the Institute of Marine Sciences and the Laboratory of the Bureau of Commercial Fisheries in Miami are the only laboratories in the United States which border directly on tropical waters, it was our choice that the general theme of the meeting held at the occasion of their dedication would be concerned with the entire field of oceanography as related to tropical areas.

This volume contains most of the invited papers and a part of the unsolicited papers. Because of the delay in receiving the manuscripts the printing was delayed. We are sorry and apologize for this, but we wanted to include all of the principal papers given during the conference. However, we failed to achieve this goal as some of the papers are still missing and we can only hope they will be published somewhere else.

The National Science Foundation and the Geophysical Branch of the Office of Naval Research, in recognition of its value, have sponsored this conference. Our sincere thanks go to these agencies for the funds that guaranteed the high quality of this conference. We further wish to thank all who have contributed to the preparation of the meeting—among them, those of the Faculty of the Institute of Marine Sciences who have supported

the conference preparation with advice and organized some of the seminars. The work of the staff of the Institute of Marine Sciences, who devoted much extra time before, during, and after the conference, must be specially acknowledged.

I am thankful for the work done by the editor of the Bulletin of Marine Science and by Mrs. G. A. Marmol, editorial secretary, in carrying out the tedious editorial work. The efforts by the printer are specially acknowledged, since they have done their utmost to speed up the printing of the volume.

F. F. Koczy

TABLE OF CONTENTS

Equatorial Current Systems

BRUCE A. TAFT: Equatorial Undercurrent of the Indian Ocean, 1963.

Abstract	3
Introduction	3
Winds	4
Velocity and Temperature Distributions	6
Salinity Distribution	11
Pressure Distribution along the Equator	12
Meridional Circulation	14
Acknowledgements	14
References	14

J. C. SWALLOW: The Equatorial Undercurrent in the Western Indian Ocean in 1964.

Abstract	15
Introduction	15
Methods	18
Observations	21
Wind Stress	34
Acknowledgements	36
References	36

MIZUKI TSUCHIYA: Distribution of Salinity, Oxygen Content, and Thickness at 160 cl/t of Thermosteric Anomaly in the Intertropical Pacific Ocean.

Abstract	37
Introduction	37
Oxygen and Salinity	39
Thickness	40
Conclusion	40
Literature Cited	41

Tectonic History of the West Indies Island Arc

JOHN D. MILLIMAN: Guyot-like features in the Southeastern Bahamas:

A Preliminary Report.

Abstract	45
Introduction	45
Bahamian Studies	45
Discussion	52
Conclusions	54
Acknowledgements	54
References	54

GABRIEL DENG0: Geological Structure of Central America.	
Abstract	56
Introduction	56
Physical Features	57
Tectonic History	61
Pacific-Caribbean Fracture Pattern	66
References	70
THOMAS W. DONNELLY: Some Problems of Island-Arc Tectonics, with Reference to the Northeastern West Indies.	
Abstract	74
Introduction	74
Geological Limitations of the Problem	75
Nature of the Deep Fundamental Deformative Force	77
Recent Seismicity of the Northeastern West Indies	80
The Problem of Continental Drift	85
Conclusion	86
Acknowledgements	87
References	87
JOHN EWING, MANIK TALWANI, MAURICE EWING, AND TERENCE EDGAR: Sediments of the Caribbean.	
Abstract	88
Introduction	88
The Basins	91
The Ridges	94
The Margins	96
Discussion	98
Conclusions	101
Acknowledgements	101
References	101
ALFREDO MENÉNDEZ V. DE V.: Tectonics of the Central Part of the Western Caribbean Mountains, Venezuela.	
Abstract	103
Introduction	103
The Tectonic Belts	104
Cordillera de la Costa Tectonic Belt	104
The Cauagua-El Tinaco Tectonic Belt	110
Rock Units	111
Major Structures	115
The Paracotos Belt and the Villa de Cura Block	119
The Mountain Front	124
Tectonic Evolution	126
Acknowledgements	128
Bibliography	128

Carbonate Sedimentation

KARL M. WILBUR AND NORIMITSU WATABE: Mechanisms of Calcium Carbonate Deposition in Coccolithophorids and Molluscs.	
Introduction	133
Calcification in Coccolithineae	133
Calcium Carbonate Deposition in Molluscs	143
Concluding Remarks	150
References	151
HENRY D. ISENBERG, STEVEN D. DOUGLAS, LEROY S. LAVINE, AND HENRY WEISSFELLNER: Laboratory Studies with Coccolithophorid Calcification.	
Abstract	155
Introduction	156
Defined Medium	156
Mineral Effect on Growth	158
Biphasic Nature of Coccolithogenesis	158
Action of Carbonic Anhydrase Inhibitor; Light	160
Nutrition and Calcification	162
Chemical Constitution of Coccoliths	169
Fine Structure Studies	172
References	177
P. K. WEYL: The Solution Behavior of Carbonate Materials in Sea Water.	
Abstract	178
Introduction	178
Experiments	
The Solution Kinetics of Calcite in Sea Water by the Saturometer Technique	178
The Solution Kinetics of Calcite in Different Waters by the Saturometer Technique	180
Flow Experiment	182
Field Experiment D	187
Apparatus and Procedure for Experiment E	188
Dolomitization, First Experiment	191
Dolomitization, Second Experiment	193
Solubility of Carbonate Minerals in Sea Water	196
The Solubility of Iceland Spar Calcite in Calcium Bicarbonate Solution	197
Solubility of Iceland Spar Calcite in Calcium-Magnesium Bicarbonate Solution	200
Solubility of Magnesian Calcites in Calcium-Magnesium Bicarbonate Solution	201
Solubility of Aragonite in Calcium-Magnesium Bicar-	

bonate Solution	203
Solubility of Dolomites in Calcium and Magnesium Bi-carbonate Solutions	203
Interpretation of the Experimental Results	205
1. The Carbonate Particle Suspended in Sea Water	210
2. The Carbonate Particle in the Sediment	211
3. The Carbonate Particle at the Sediment-Sea Water Interface	211
Acknowledgements	212
Appendix: A Simple Theory of the Solubility of Impure Solids	213
List of Symbols	227
References	228
TERRELL N. ANDERSEN, BRYANT A. MINER, ELLA DIBBLE, AND HENRY EYRING: Electrolytic Reduction of Carbon Dioxide on Lead Cathodes.	
Abstract	229
Introduction	229
Experiments	230
Results	231
Discussion	236
Acknowledgement	243
References	243
Nutrient Cycles in Tropical Waters	
JOHANNES KREY: The Vertical Distribution of Microbiomass in Northern and in Tropical Seas.	
Abstract	247
Introduction	247
Materials and Methods	247
Results	252
Discussion	256
References	258
H. ROTSCHI: On some Characteristics of the Distribution of Nutrient Salts in the Equatorial and South Tropical Pacific Ocean.	
Abstract	260
Introduction	260
Hydrological Outline	260
Relative Distribution of the Various Nutrient Salts	261
References	272
MARY BELLE ALLEN: Nannoplankton and the Carbon Cycle in Tropical Waters.	
Abstract	273

Introduction	273
Materials and Methods	274
Results	275
References	278
WILLIAM H. THOMAS: The Nitrogen Nutrition of Phytoplankton in the Northeastern Tropical Pacific Ocean.	
Abstract	280
Introduction	280
Methods	281
Results and Discussion	284
References	289
E. F. CORCORAN: Distribution of Copper and Iron in Tropical Sea Water.	
Abstract	290
Introduction	290
Methods	292
Discussion	293
Conclusions	301
Acknowledgements	303
References	303
A. A. ALEEM AND N. DOWIDAR: Phytoplankton Production in Relation to Nutrients along the Egyptian Mediterranean Coast.	
Abstract	305
Introduction	305
Area Investigated	306
Methods	307
Climatic Aspects	307
Flow of Nile Water into the Mediterranean Sea	308
Seasonal Changes in Physical and Chemical Characteristics of the Water	310
Periodicity of the Phytoplankton Community	314
Magnitude of the Phytoplankton Production During the Nile Flood	321
Literature Cited	322
MAYNARD M. NICHOLS: Organic Production and Phosphate in an Arid Coastal Lagoon.	
Introduction	324
Description of Area	324
Procedures	327
Results of Observations	327
Discussion	329
Summary	331
References	331

Economics of Tropical Fisheries

ANTHONY D. SCOTT: Fisheries Development and National Economic Development.

Abstract	335
Introduction	335
Economic Development	335
Needed Conditions in Fisheries	342
Conclusions	344
References	345

JOHN L. DIBBS: Development of Traditional and Large-Scale Industrial Fisheries in the Tropical Waters of Africa.

Abstract	346
Introduction	346
Ghana	346
Nigeria	351
Other English-speaking Countries of West Africa	352
French-speaking Countries of West Africa	352
Regional Surveys and Research	354
Comparative Australian Development	354
The Western Indian Ocean and East African Coast from the Somali-Kenya Border to Mozambique	356
The Future Needs of African Countries for Development of Traditional and Large-Scale Fisheries	360
Conclusion	362

JAMES A. STORER: Aspects of Fisheries in the Developing Philippines Economy.

Abstract	363
Introduction	363
Economic Development	363
Population Growth	364
Philippine Fisheries	365
Fishing Vessels	369
Fishing Establishments	370
Government Aid	370
Investment in Fisheries	371
Shoreside Facilities	372
Conclusion	373
References	374

JAMES A. CRUTCHFIELD: Marketing as a Constraint on Fishery Development in Tropical Countries.

Abstract	375
Introduction	375

Constraints in Fishery Development	375
Marketing Survey	376
Communication and Transportation	378
Technical Advances	378
Monopolistic Markets	379
Fishery Cooperatives	380
Conclusion	381

WILLIAM F. ROYCE: Decision Problems in Fisheries

Abstract	382
Introduction	382
Fishery Policies	382
Fishery Development	384
Fishery Decisions	385
Research Strategy	385
Conclusion	386
References	387

High Seas Fisheries

ALFREDO FREYRE: Fishery Development in Perú.

Abstract	391
1. Introduction	391
2. Background Information	391
3. Sea Industries in Perú	393
4. Comparison of Fish Landings in Perú and Japan	400
5. Peruvian Exports of Fishery Products During 1955/1964 ..	400
6. Fishery Contribution to Human Consumption	403
7. Fishery Contribution to the Industrial Development of the Country	405
8. Research and Training in Oceanography and Fishing	406
9. Social and Labor Legislation	408
10. Future Prospects	408
11. Bibliography	410

T. KAMENAGA: Development of Japanese High-Sea Fisheries.

Abstract	412
General Aspects	412
Tuna Fisheries	414
The Present Situation and Problems Involved	418
Future Prospect of these Problems	422

H. KASAHARA: Fishery Development on the West Coast of Africa.

Abstract	423
Introduction	423
Resources	423

Development of Fisheries	427
Foreign Activities and their Effects	434
MARIO RUIVO AND ADAM BEN-TUVIA: Trends in World High Seas Fisheries and Potential Exploitation of Living Resources of the Sea.	
Abstract	437
Catch, Potential Catch, and Distribution of Resources	437
Research Trends Associated with High Seas Fisheries Expansion	446
Conclusions	449
References	451
OSCAR GUILLÉN: Anomalies on Peruvian Sea during March and April 1965.	
Abstract	452
Introduction	452
Description of Hydrographic Conditions	456
Comparison of Normal and Abnormal Conditions on Peruvian Sea	459
Conclusions	462
References	464
PHILIP M. ROEDEL: Recent Developments in the Fisheries of California.	
Abstract	466
Introduction	466
The Research Program	466
Results	467
Discussion	468
Conclusions	469
References	470

Deep-Sea Biology

N. B. MARSHALL: The Organization of Deep-Sea Fishes.	
Abstract	473
References	478
BENT HANSEN: The Taxonomy and Zoogeography of the Deep-Sea Holothurians in the Evolutionary Aspects.	
Abstract	480
Introduction	480
Variation in Taxonomic Characters	480
Bathymetrical Distribution	481
Geographical Distribution and Variation	484
The Hadal Fauna	493

On the Evolution of the Higher Taxa	498
Conclusion	500
References	500
DONALD F. SQUIRES: The Evolution of the Deep-Sea Coral Family	
Micrabaciidae.	
Abstract	502
Introduction	502
Acknowledgements	503
Systematic Summary	503
Adaptations of the Micrabaciidae	506
Evolution of the Micrabaciidae	508
Summary	509
Literature Cited	509
GILBERT L. VOSS: The Biology and Bathymetric Distribution of	
Deep-Sea Cephalopods.	
Abstract	511
Introduction	511
The Deep Sea	513
Bathymetric Distribution and General Habitat	515
The Epipelagic Fauna	517
Mesopelagic Fauna	519
The Bathypelagic Fauna	520
The Abyssopelagic Fauna	522
The Littoral Benthic Fauna	523
The Mesobenthic Fauna	523
The Bathybenthic Fauna	524
The Abyssobenthic Fauna	525
Adaptations to Life in the Deep Sea	526
The Derivation of the Deep-Sea Fauna	531
Literature Cited	533
Behavior Patterns in Tropical Waters	
WOLFGANG WICKLER: Specialization of Organs having a Signal	
Function in some Marine Fish.	
Abstract	539
Introduction	539
Appendix	547
References	548
NEAL R. FOSTER: Trends in the Evolution of Reproductive Behavior	
in Killifishes.	
Abstract	549
Introduction	549
Evolution of Killifishes	550
Behavior of Killifishes	553

Discussion	562
Acknowledgements	565
Literature Cited	565

Varied Approaches in Marine Zoogeography

JOHN C. BRIGGS: Relationship of the Tropical Shelf Regions.	
Abstract	569
Introduction	569
East Pacific Barrier	569
New World Land Barrier	570
Mid-Atlantic Barrier	571
Old World Land Barrier	572
The Suez Canal	573
The Cape of Good Hope	573
Discussion	574
Summary	575
Acknowledgements	576
References	576
RICHARD H. ROSENBLATT: The Zoogeographic Relationships of the Marine Shore Fishes of Tropical America.	
Abstract	579
References	586
Appendix	588
ALFRED W. EBELING: Zoogeography of Tropical Deep-Sea Animals.	
Abstract	593
Introduction	593
Method	593
Zonal Component of Distributions	594
Meridional Component of Distributions	602
Vertical, Temporal, and Microgeographical Components of Distributions	606
Conclusions	608
Literature Cited	609
GEORGE S. MYERS: Zoogeographical Evidence of the Age of the South Atlantic Ocean.	
Abstract	614
Introduction	614
Stability <i>versus</i> Continental Drift	615
Old and New Evidence on Fish Dispersal	616
New Evidence on Fish Evolution	616
Africa and South America	617
Age	618
Conclusions	620
Literature Cited	620

ZACH M. ARNOLD: Biological Clues in Interpreting the Biogeography
of the Foraminifer *Nubecularia lucifuga* DeFrance.

Abstract	622
Introduction	622
Materials and Methods	624
Observations	624
References	631

Ecology of Tropical Organisms

DIETRICH B. E. MAGNUS: Ecological and Ethological Studies and
Experiments on the Echinoderms of the Red Sea.

Abstract	635
Introduction	635
<i>Ophiocoma scolopendrina</i> (Lamarck)	636
<i>Heterometra savignyi</i> (J. Müller)	644
Partnerships with <i>Diadema setosa</i> (Leske)	650
Acknowledgements	660
References	660

JOHN E. RANDALL: Food Habits of Reef Fishes of the West Indies

Abstract	665
Introduction	667
Acknowledgements	668
Methods	669
Food Habits	673
Orectolobidae	673
Carcharhinidae	673
Dasyatidae	675
Myliobatidae	675
Elopidae	676
Clupeidae	676
Dussumieridae	678
Synodontidae	679
Muraenidae	680
Opichthidae	681
Congridae	682
Belonidae	683
Hemiramphidae	684
Fistulariidae	686
Aulostomidae	686
Holocentridae	687
Mugilidae	692
Sphyraenidae	692
Atherinidae	694

Serranidae	695
Grammistidae	706
Grammidae	707
Cirrhitidae	707
Apogonidae	708
Priacanthidae	709
Pempheridae	710
Emmelichthyidae	711
Lutjanidae	711
Pomadasyidae	719
Sparidae	731
Kyphosidae	734
Gerreidae	736
Sciaenidae	738
Mullidae	740
Branchiostegidae	742
Rachycentridae	743
Echeneidae	743
Carangidae	744
Scombridae	752
Pomacentridae	754
Labridae	763
Scaridae	775
Bothidae	782
Gobiidae	783
Blenniidae	784
Clinidae	787
Opisthognathidae	788
Scorpaenidae	789
Dactylopteridae	792
Ephippidae	792
Chaetodontidae	794
Acanthuridae	799
Balistidae	803
Monacanthidae	807
Ostraciontidae	812
Tetraodontidae	818
Canthigasteridae	819
Diodontidae	820
Antennariidae	824
Ogcocephalidae	825
Discussion of Food Organisms	825
Plants	825
Animals	828
Literature Cited	840

Equatorial Current Systems

HENRY M. STOMMEL

Convener

The following papers were delivered at the Conference but have not been received for publication:

GERHARD NEUMANN: Equatorial Currents in the Atlantic Ocean with Special Consideration of the Gulf of Guinea During Equalant I and II.

ALLAN R. ROBINSON: A Theory of Equatorial Undercurrent.

EQUATORIAL UNDERCURRENT OF THE INDIAN OCEAN, 1963¹

BRUCE A. TAFT

Scripps Institution of Oceanography

ABSTRACT

An intensive program of direct measurement of current velocity and water properties was carried out along the Equator in the Indian Ocean from ARGO during the periods June 28 to September 24, 1962 and February 16 to May 15, 1963.

The Equatorial Undercurrent was measured at the end of the northeast monsoon on meridional sections at 61° E (March 1963) and 92° E (April 1963) and at six stations on the Equator from longitudes 53° to 92° E during March-April 1963.

Observations during the southwest monsoon in 1962 did not indicate the presence of the undercurrent.

INTRODUCTION

The Equatorial Undercurrent had been firmly established by 1962 as a major component of the equatorial circulation in the Atlantic and Pacific oceans. At that time the current velocity structure at the Equator in the Indian Ocean was not known. Since the equatorial wind system and sea-surface currents of the Indian Ocean differ so markedly from the other oceans, it was expected that it also differs with respect to the subsurface undercurrent. During the LUSIAD expedition to the Indian Ocean in 1962-1963, ARGO of the University of California, Scripps Institution of Oceanography was used for a 6-month study of the current velocity structure near the Equator. The program was undertaken to determine whether or not the undercurrent was present during one or both phases of the Indian Ocean monsoon. A full discussion of the results of the LUSIAD current studies is given by Taft & Knauss (In Press).

During two 3-month periods, current velocity and hydrographic measurements were made from ARGO at four meridional sections across the Equator, two on the western side of the ocean and two on the eastern side of the ocean, and on a zonal section along the Equator. The locations of the sections during the February 16 to May 15, 1963 survey are given in Figure 1. Meridional sections were made at 85° E (February), 61° E (March), 92° E (April), and 53° E (May). Except for the 53° E section, where the southernmost station was at 4° S, hydrographic measurements were made from 5° N to 5° S. The distance between hydrographic stations was 0.5° latitude from 3° N to 3° S and 1° between 3° and 5° North and South. Vertical distributions of the current velocity from the sea surface to 400 m were determined at 1° intervals from 2° N to 2° S. On the

¹Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

section along the Equator (late March-early April) hydrographic stations were made every 2° of longitude and current measurements were made at the longitudes of the meridional sections. During the other survey, conducted from June 28 to September 24, 1962, a zonal section along the equator was made in July and then followed by meridional sections at 53° and $62^{\circ} 20' E$ in August and at 79° and $89^{\circ} E$ in September. The distribution of hydrographic and current-measurement stations on these sections was the same as for the February to May 1963 survey.

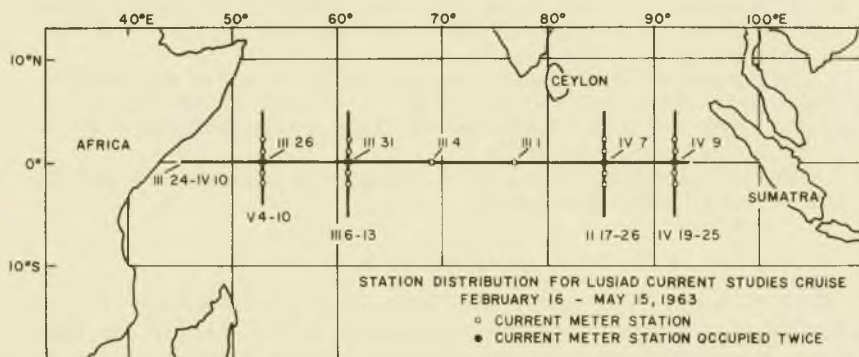
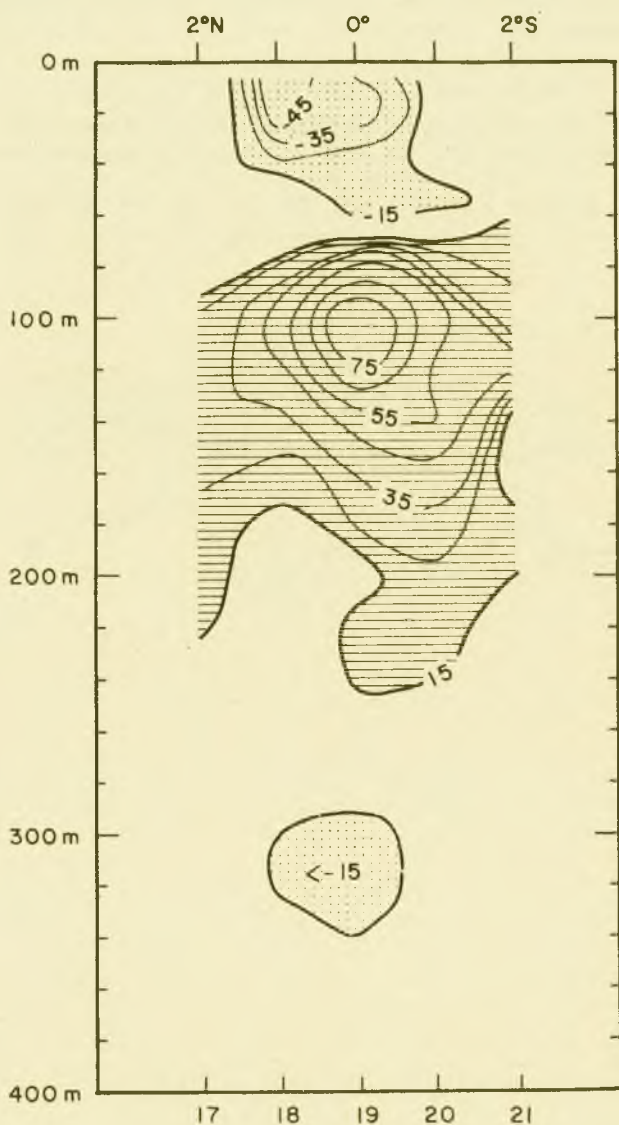


FIGURE 1. Station distribution on LUSIAD current studies cruise, February 16-May 15, 1963. The heavy lines denote hydrographic sections. The dates at the end of each section line indicate the period during which the section was made (Roman numerals refer to months). Current-meter stations are indicated by open circles if occupied once and by filled circles if occupied twice. The additional dates of occupancy for single current-meter stations on the Equator are also given.

Most of the current measurements were made with a telemetering Savonius-rotor current meter suspended from ARGO. Ship movement was determined by radar ranges and bearings on a reference buoy moored at each current-measurement station. Vertical current profiles were usually determined from an average of six individual lowerings of the meter over a period of 18 to 24 hours. Taft & Knauss (In Press) estimate the average axis of the 90 per-cent confidence ellipse for the average current velocity at a given depth to be 8 cm/sec. In general, velocity components less than 15 cm/sec are not considered to be reliably estimated.

WINDS

Wind observations during February and March 1963 (85° and $61^{\circ} E$ sections) were representative of the northeast monsoon. The transition between monsoon phases appeared to take place, at least on the eastern side of the ocean, during April. At the time of the $53^{\circ} E$ section in May the southwest monsoon appeared to be weakly established on the western side of the ocean.



$U(92^\circ\text{E}, Y, Z)$ APRIL 1963

FIGURE 2. Meridional distribution of zonal velocity component (cm/sec) at 92°E (April 20-25, 1963). Regions of east components >15 cm/sec are indicated by horizontal lines and regions of west components <-15 cm/sec are indicated by light dots. Vertical exaggeration $\times 3690$.

The southwest monsoon was well developed during the period of the July to September 1962 survey.

VELOCITY AND TEMPERATURE DISTRIBUTIONS

92° E (April 1963).—Measurements made at the 92° E meridional section show the closest resemblance to sections across the undercurrent in the

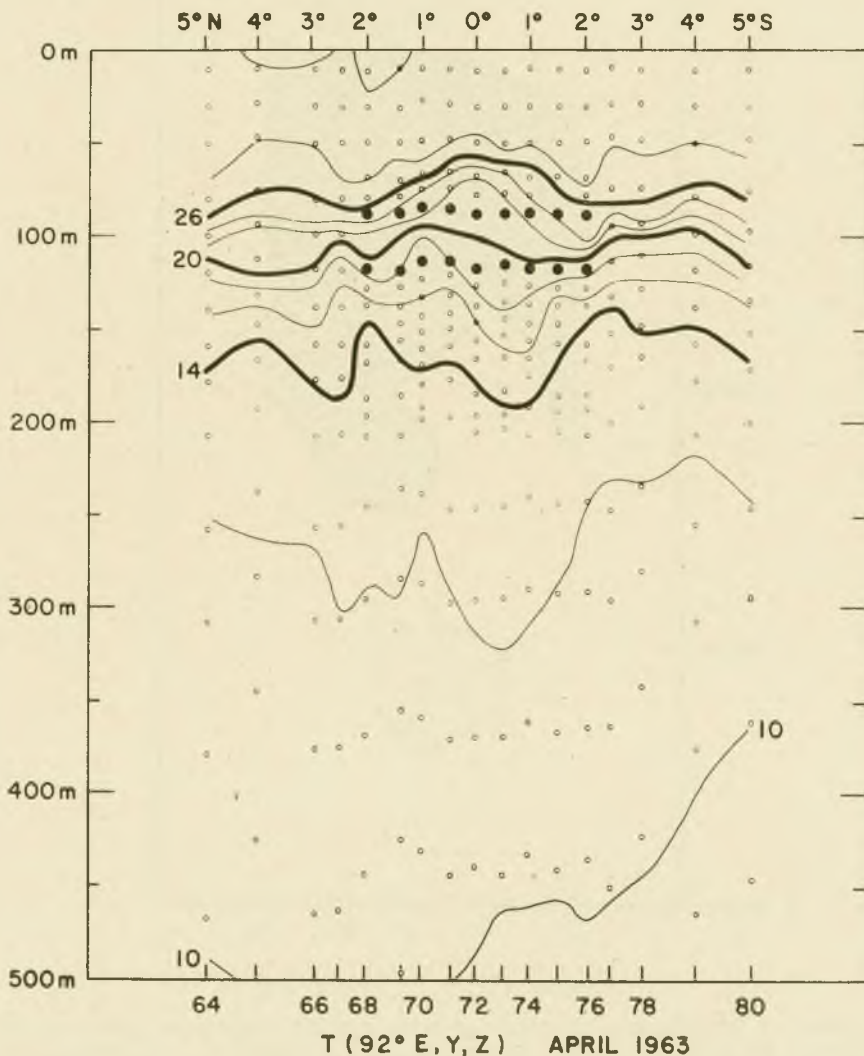


FIGURE 3. Meridional distribution of temperature (°C) at 92° E (April 19-25, 1963). Depths of observation are indicated by circles. The sampling interval between the filled circles is approximately 5 m. Vertical exaggeration $\times 3690$.

central Pacific and Atlantic. The distribution of the zonal velocity component at 92° E is given in Figure 2. The surface current was westward and of magnitude less than 50 cm/sec. At about 60 m there was a transition from westward to eastward flow; below the transition the east component increased with depth to a maximum value of 80 cm/sec at 100 m at the Equator. The thickness of the region of eastward flow was 125 to 150 m and the distribution of the east component of velocity was roughly symmetrical with respect to the Equator. Magnitudes of the meridional velocity components associated with the eastward flow were less than 20 cm/sec and did not present a recognizable pattern.

The temperature distribution at 92° E (Figure 3) shows that the depth of the surface layer was about 60 m. The depth of transition between the west and east velocity components coincided with the top of the thermocline and the undercurrent core lay below the maximum vertical temperature gradient in the thermocline. Isotherms in the upper thermocline were found at shallower depths near the Equator than north and south of the Equator. Conversely, isotherms in the middle thermocline deepened in the vicinity of the Equator. Thus the core of the undercurrent at 92° E was located in a region where the vertical temperature gradient was a minimum relative to conditions away from the Equator. Montgomery (1962) has summarized observations of the equatorial spreading of isotherms in the thermocline and its relationship to the equatorial undercurrent in the Pacific and Atlantic. However, in contrast to the usual case in the central Pacific (Cromwell, 1953), isotherms found in the thermocline away from the Equator at 92° E do not rise to the sea surface at the Equator.

61° E (March 1963).—The undercurrent was also present on the section at 61° E. Surface currents with strong west components (<85 cm/sec) were measured at all stations (Figure 4). At the top of the thermocline, which varied in depth from 90 m at 2° N to 30 m at 1° S, the current became eastward and the east component increased to a maximum value in the middle of the thermocline. The maximum east component of 60 cm/sec was located at 80 m on the Equator but the distribution of the east component was not symmetrical with respect to the Equator; stronger east components were measured at 2° N than at either 1° N or 1° S. Beneath the maximum of east current in the upper thermocline there was a deeper maximum with its largest value of 35 cm/sec located on the Equator. Although the relationship between these two maxima is not clear, the lower maximum will not be treated as an extension of the undercurrent. Meridional velocity components associated with the undercurrent were less than 15 cm/sec. Spreading of the thermocline at the Equator occurred on the 61° E section.

Steadiness of Undercurrent at 61° and 92° E.—Current measurements were made on two occasions at both 0° 61° E and 0° 92° E during the March-April period (Fig. 1). Vertical distributions of the zonal velocity

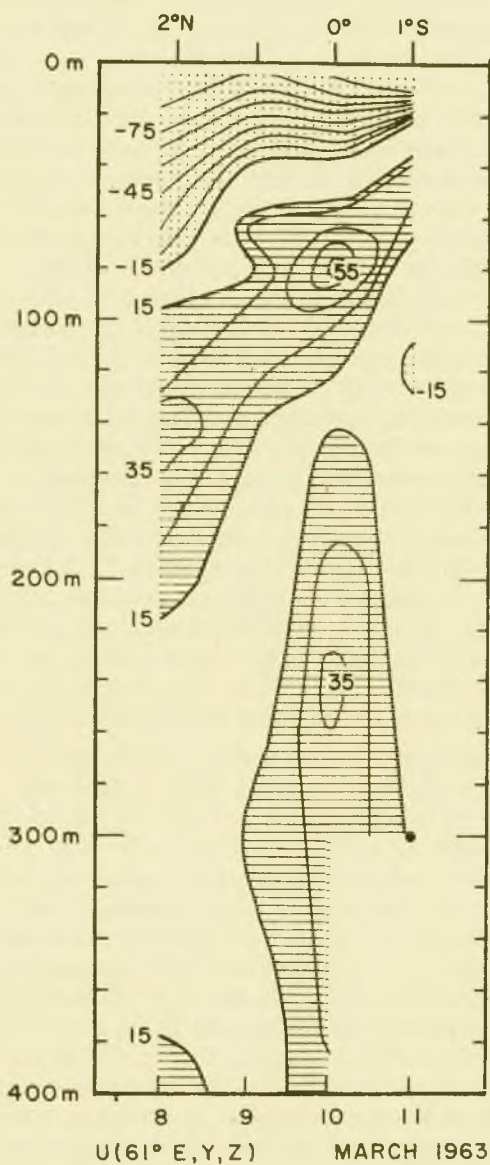


FIGURE 4. Meridional distribution of zonal velocity component (cm/sec) at 61°E (March 7-12, 1963). Regions of east components >15 cm/sec are indicated by horizontal lines and regions of west components <-15 cm/sec are indicated by light dots. Vertical exaggeration $\times 3690$.

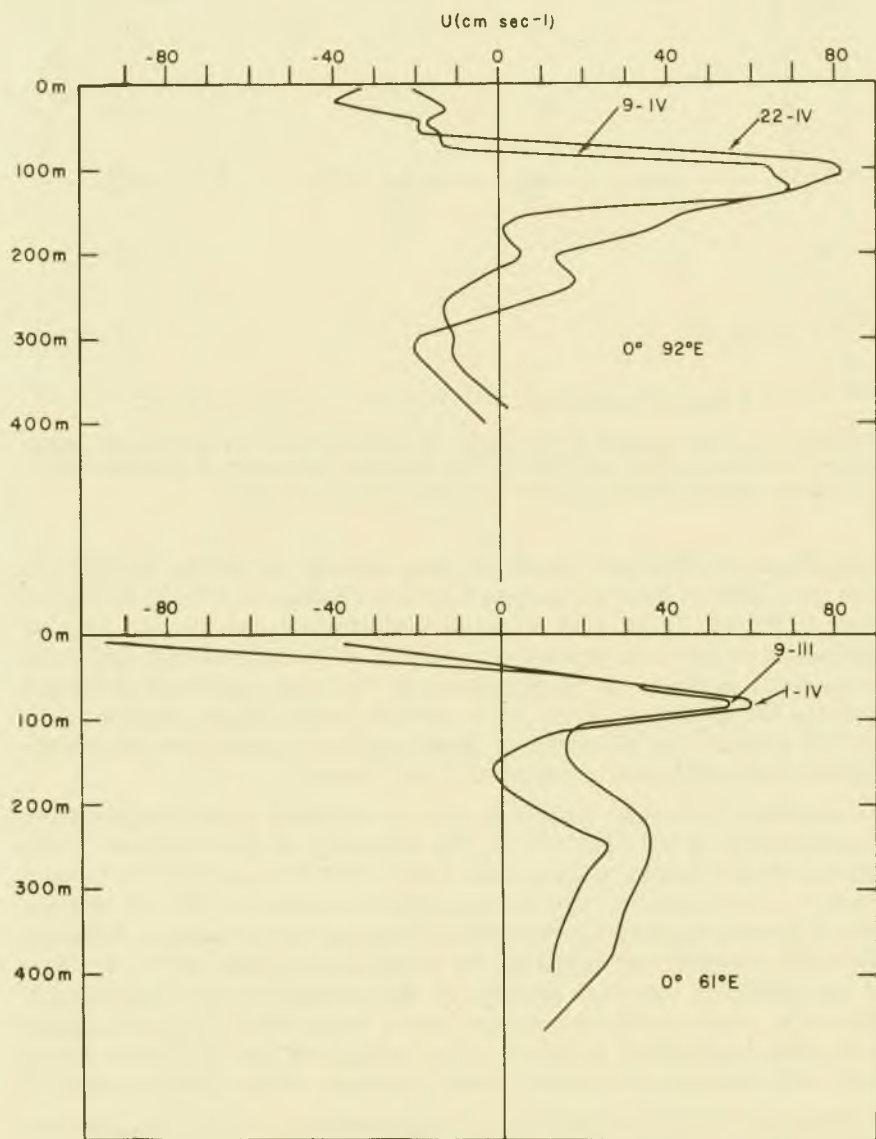


FIGURE 5. Vertical profiles of zonal velocity component on successive occupancies of stations at $0^\circ 61^\circ \text{E}$ and $0^\circ 92^\circ \text{E}$.

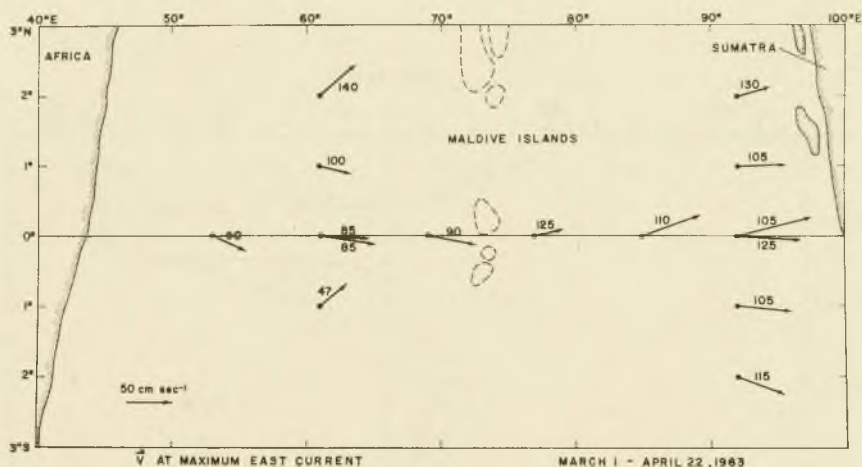


FIGURE 6. Current vectors at the depth of maximum east component of undercurrent (March 1-April 22, 1963). The length of the vector is proportional to the current speed. Depth in meters is entered by each vector.

components for both occupancies of these stations are plotted in Figure 5. The time interval between occupancies was 23 days at $0^{\circ} 61^{\circ} \text{E}$ and 13 days at $0^{\circ} 92^{\circ} \text{E}$. In both cases the undercurrent was present and the differences between the profiles in the region of the undercurrent are of the same order as the error of measurement. The only significant difference between the profiles at either station occurs in the deeper portion of the 61°E station. The similarity of these profiles suggests that the undercurrent was stable over a period of 2 to 3 weeks.

Longitudinal Extent of Undercurrent.—In addition to the undercurrent measurements at 61° and 92°E , the undercurrent also appeared to be present on the Equator at longitudes of 53° , 69° , 77° , and 85°E . Current vectors at the depth of the undercurrent maximum for the 15 stations where the undercurrent was indicated are represented in Figure 6. Although the largest speeds were found on the easternmost section at 92°E , there is no significant east-west gradient of the strength of the undercurrent. Since the observations were taken over a rather long period of almost 2 months, longitudinal variation of the strength of the undercurrent may have been obscured by shorter period variations within this time interval.

Summary of LUSIAD Undercurrent Measurements.—1. The undercurrent was an ocean-wide feature in the Indian Ocean in 1963 during the last month of the northeast monsoon (March) and the month of transition between monsoon phases (April).

2. The undercurrent did not appear to be present at 85°E in late February. Between late February and early April at $0^{\circ} 85^{\circ} \text{E}$ the east

current component in the thermocline increased from less than 15 to 65 cm/sec. The period of set up of the undercurrent on the eastern side of the ocean was therefore less than 45 days.

3. The undercurrent at the Equator, once it was set up, was stable over a period of at least 2 to 3 weeks.

4. The maximum east component of the undercurrent measured on LUSIAD was 80 cm/sec at 92° E. Eastward volume transport at 92° E was 11×10^6 m³/sec. On the western side of the Indian Ocean the undercurrent during March 1963 was roughly half as strong as that measured by Swallow (1964) approximately 1 month later during 1964. The strength of the Indian Ocean Undercurrent during 1963 was substantially less than that previously reported for the central Atlantic (Metcalf, Voorhis, & Stalcup, 1962) and the central Pacific (Knauss, 1960). Tsuchiya (1961) reports values of the eastward flow of the undercurrent in the western Pacific which are comparable to those observed on LUSIAD.

5. Decrease of the vertical temperature gradient in the thermocline at the Equator at 61° and 92° E suggests at least a tendency for the meridional components of pressure force and Coriolis force to be in balance in the undercurrent.

6. In several basic respects measurements during the southwest monsoon, *i.e.*, July-September 1962 and May 1963, differ from those made during March-April 1963. First of all, there is no *clear* evidence of the undercurrent. In contrast to the undercurrent observations, the following conditions were observed during the period of the southwest monsoon:

(a) currents in the thermocline, particularly on the western side of the ocean, had west components;

(b) current velocity on the Equator was unsteady;

(c) relatively large meridional velocity components occurred in the thermocline at the Equator; and

(d) intensification of the vertical temperature gradient occurred at the Equator rather than weakening of the temperature gradient. It should be pointed out that every section during the southwest monsoon did not show all of the above properties. Relatively strong east components (>50 cm/sec) were measured in the thermocline during September 1962 on the eastern side of the ocean but the unsteadiness of the velocity and the large associated meridional components do not seem to be representative of the undercurrent.

SALINITY DISTRIBUTION

Throughout the period of the LUSIAD measurements there was a salinity maximum in the thermocline. The distribution of salinity along the Equator in March-April 1963 is shown in Figure 7. Values of salinity at the maximum decrease, and the depth of the maximum increases, from west to east. The depth of the salinity maximum roughly coincides with the depth of the core of the undercurrent.

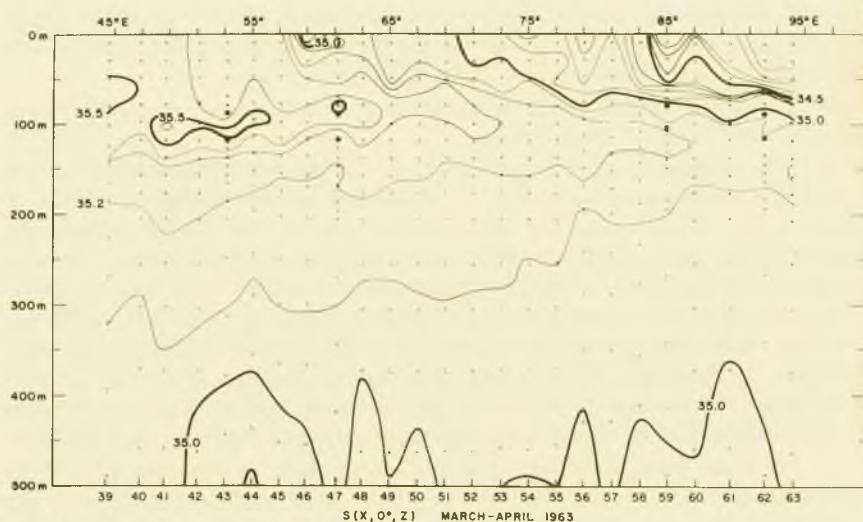


FIGURE 7. Zonal distribution of salinity (per mil) along equator (March 24-April 10, 1963). Depths of observation are indicated by circles. The sampling interval between the filled circles is approximately 5 m. Vertical exaggeration $\times 8840$.

During the period of the undercurrent measurements, the salinity maximum on the eastern side of the ocean was isolated in the meridional plane and thus dependent on the eastward transport of the undercurrent for its maintenance. The value of the salinity at the maximum and the thickness of the maximum are positively correlated with the measured strength of the undercurrent (Taft & Knauss, *In Press*). The relationship between the undercurrent and the salinity distribution along the Equator in the Indian Ocean thus appears to be analogous to that observed in the Atlantic (Metcalf, *et al.*, 1962).

PRESSURE DISTRIBUTION ALONG THE EQUATOR

Measurements of the density distribution along the Equator in the central Pacific and Atlantic have shown that the sea surface slopes up toward the west relative to deep isobars and the vertical integral of the longitudinal component of pressure force and the westward component of wind stress are approximately in balance (Arthur, 1960). The magnitude of the eastward pressure force in the Pacific decreases with depth to one-half of the surface value in the thermocline so that at the undercurrent core the pressure force is directed eastward and is of magnitude 2×10^{-5} dyne/gm.

The pressure distribution along the Equator in the Indian Ocean differs radically from that of the other oceans. Distributions of the geopotential

anomaly of selected isobaric surfaces relative to 400 db at the Equator determined from density measurements on the March-April section are shown in Figure 8. The sea-surface slopes up toward the east in the central and eastern Indian Ocean, *i.e.*, opposite to the sea-surface slope in the central Atlantic and Pacific. The magnitude of the slope is estimated to be 2×10^{-8} . On both sides of the ocean there is a reversal of the sign of the slope of the isobars in the thermocline. The reversal of the sign of the slope occurs at deeper depths on the eastern side of the ocean than on the western side. At the depth of the undercurrent core, *i.e.*, 85 m at 61° E and 110 m at 92° E (Fig. 6), the isobaric surfaces slope down toward the east. The longitudinal component of pressure force at the undercurrent core is of the same sign and magnitude as in the other oceans, even though the pressure distribution in the surface layer is totally different.

The close association of the undercurrent and an eastward pressure force has been demonstrated in all oceans. During the northeast monsoon the zonal component of wind stress at the Equator in the Indian Ocean is small and probably westward and is therefore not opposite in direction to

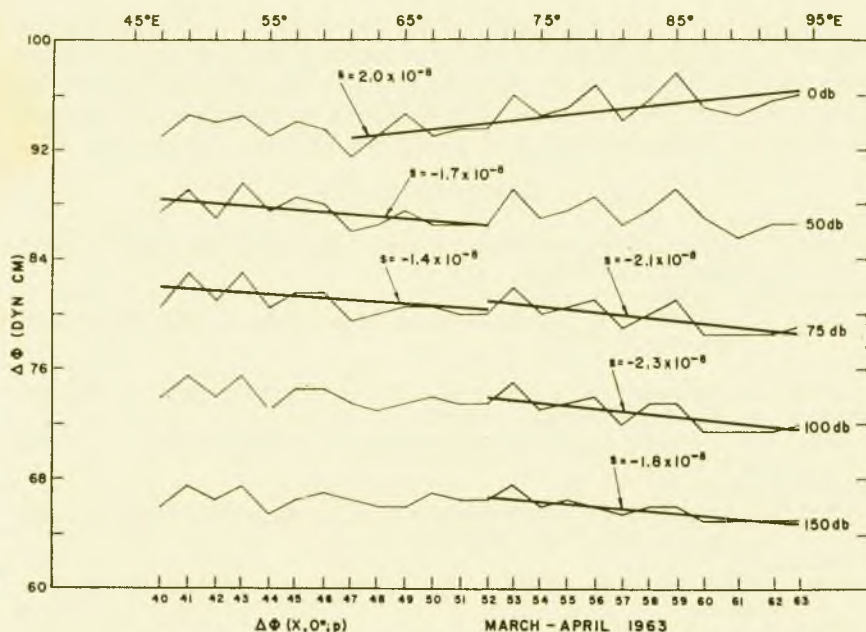


FIGURE 8. Zonal distribution of geopotential anomaly ($\Delta\Phi$) of selected isobaric surfaces (0, 50, 75, 100, 150 db) along the Equator relative to 400 db (March 24-April 10, 1963). The zero point of the values of the geopotential anomaly has been adjusted so that all five isobaric surfaces can be conveniently represented. Linear regression equations fitted to the data (s = slope) are shown by the heavy lines.

the pressure force at the sea surface. The observed vertical distribution of longitudinal component of pressure force must be maintained by the general equatorial circulation and cannot be related solely to the wind. The reversal of the sign of the pressure force is dependent on the presence of the undercurrent. On the zonal equatorial section in July 1962, when the undercurrent was not present, the sea surface sloped up to the east relative to 400 db but there was no reversal of the slope of the isobars in the thermocline.

MERIDIONAL CIRCULATION

Meridional circulation associated with the undercurrent could not be ascertained from the current measurements. Distributions across the Equator of temperature, dissolved oxygen, and inorganic phosphate did not suggest either upwelling or strong vertical mixing at the equator. The meridional circulation in the undercurrent appears to differ, at least in intensity if not in mode, from that inferred from hydrographic data in the Pacific.

ACKNOWLEDGEMENTS

LUSIAD was a joint expedition of the University of California and the University of Rhode Island. The current studies portion of the expedition was under the direction of Dr. John A. Knauss of the Narragansett Marine Laboratory, University of Rhode Island, Kingston. Primary sponsors were the Office of Naval Research and the National Science Foundation.

REFERENCES

- ARTHUR, R. S.
1960. A review of the calculation of ocean currents at the equator. *Deep-Sea Res.*, 6: 287-297.
- CROMWELL, TOWNSEND
1953. Circulation in a meridional plane in the central equatorial Pacific. *J. Mar. Res.*, 12: 196-213.
- KNAUSS, J. A.
1960. Measurements of the Cromwell Current. *Deep-Sea Res.*, 6: 265-286.
- METCALF, W. G., A. D. VOORHIS, AND M. C. STALCUP
1962. The Atlantic equatorial undercurrent. *J. geophys. Res.*, 67: 2499-2508.
- MONTGOMERY, R. B.
1962. Equatorial Undercurrent observations in review. *J. oceanogr. Soc. Japan*, 20th Ann. Vol.: 487-498.
- SWALLOW, J. C.
1964. Equatorial Undercurrent in the western Indian Ocean. *Nature*, 204: 436-437.
- TAFT, B. A. AND J. A. KNAUSS
In Press. The Equatorial Undercurrent of the Indian Ocean as observed by the LUSIAO expedition. Part I: Velocity structure and associated distribution of properties. *Bull. Scripps Instn. Oceanogr.*
- TSUCHIYA, MIZUKI
1961. An oceanographic description of the equatorial current system of the western Pacific. *Oceanogr. Mag.*, 13: 1-30.

THE EQUATORIAL UNDERCURRENT IN THE WESTERN INDIAN OCEAN IN 1964

J. C. SWALLOW

*National Institute of Oceanography,
Wormley, Godalming, Surrey, U.K.*

ABSTRACT

Observations of the equatorial undercurrent, made by the RRS *DISCOVERY* in the western Indian Ocean in March-June 1964, are described and compared with those of the R/V *ARGO* in the previous year. An attempt is made to relate the differences in strength of the undercurrent in the two years to the differences of wind stress, on the lines suggested by the undercurrent theory of Robinson.

INTRODUCTION

During March-June 1964, the RRS *DISCOVERY* occupied north-south sections in the western Indian Ocean in longitudes 58°E and 67.5°E . The sections extended to 20°S , and the station spacing varied from 90 miles to 30 miles (166 km to 55 km). One of the routine observations at each station was the measurement of relative currents from the surface down to a depth of 200 m, using direct-reading current meters. One reason for making these current measurements at every station was the finding by Knauss & Taft (1964) that in the early months of 1963 the equatorial undercurrent was only weakly developed in the western Indian Ocean. They found eastward currents in the thermocline generally less than 50 cm/sec, with the maximum not necessarily at the Equator. It seemed questionable whether such relatively weak flow was a significant equatorial feature; might there not be weak undercurrents of comparable speed at other latitudes?

It came as a pleasant surprise, therefore, to find a strong equatorial undercurrent in March 1964 at 58°E , and again in April at 67.5°E . These were certainly closely related to the Equator, as may be seen in Figures 1 and 2. Here are shown the currents observed at 10 m and 100 m depth, relative to 200 m. Although 100 m did not coincide with the core of the undercurrent, it falls conveniently within the thermocline in this range of latitudes, and 200 m is deep enough to be well below the steepest temperature gradients. The relative currents observed within 3° of the Equator were markedly stronger and more coherent in direction than those observed elsewhere, and although the near-surface current reversed between the two sections, there was a consistent eastward relative flow at 100 m suggestive of an undercurrent. These figures and the two following ones are from rough plots made on board ship. Vectors taken from the smoothed relative profiles would show minor differences, but the same essential features.

Later in the year, however, there were strong relative currents in other

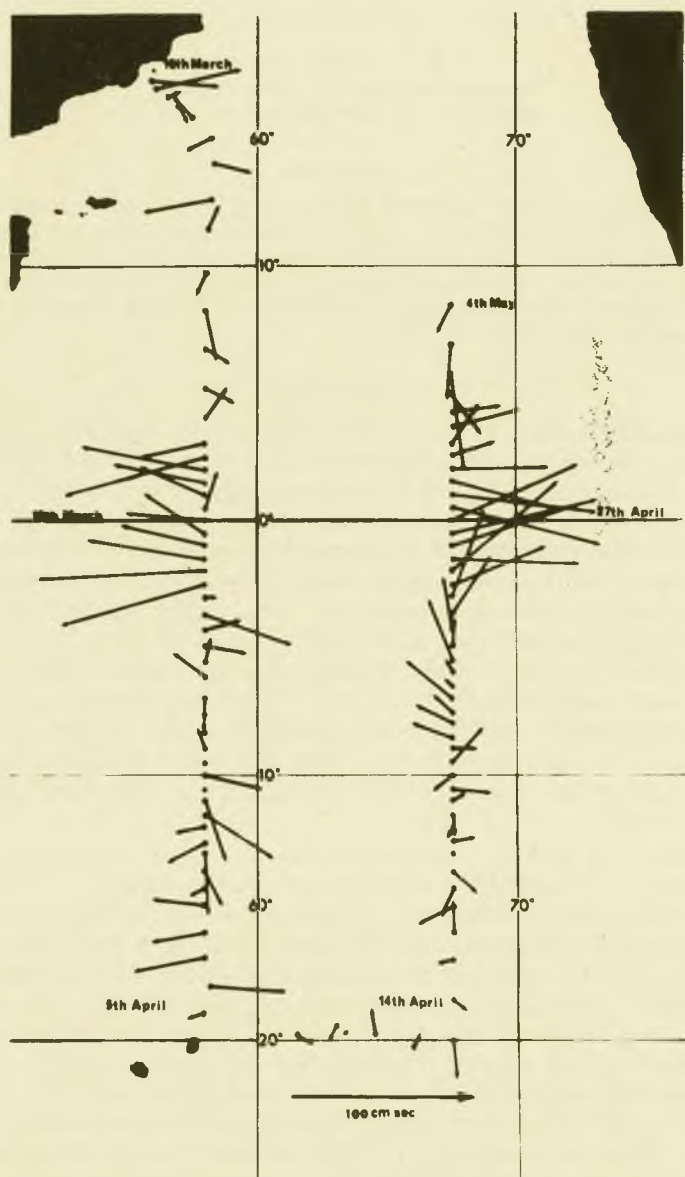


FIGURE 1. Currents at 10 m relative to 200 m, March-May 1964.

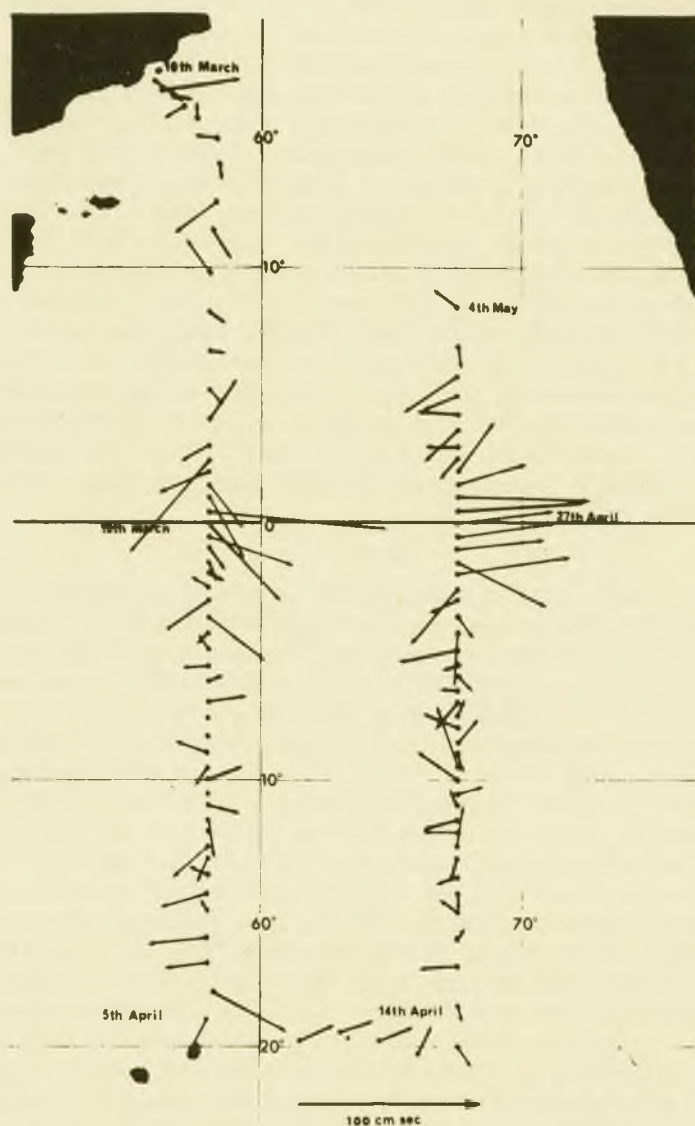


FIGURE 2. Currents at 100 m relative to 200 m, March-May 1964.

latitudes. Figures 3 and 4 show the observations made in May-September 1964, during the southwest monsoon season. The south equatorial current was much more clearly marked, and at 100 m along the Equator the relative currents were weaker and less zonal in character. The equatorial undercurrent had become weaker and was only intermittently present.

At certain stations on three of the trans-equatorial sections, the ship's movement over the ground was observed by radar relative to an anchored buoy, and the relative current measurements could be converted to true currents. A preliminary account of some of these measurements was published soon after they were made (Swallow, 1964). The profiles of current have been revised now that all the observations have been processed, and are described below. Some changes may be noticed, in particular the maximum speeds are of the order of 100 cm/sec instead of the 120 cm/sec published earlier. These changes have come about partly through averaging all the observations at each station where repeated measurements were made, and partly because some of the drogue observations used earlier had not been properly corrected for wind drag and near-surface current shear. However, the main features are substantially unchanged, with the undercurrent significantly stronger than in the same season of the previous year.

METHODS

For the relative current measurements, a pair of propeller-type direct reading current meters was used (Cartwright & Woods, 1963). One meter was kept near the surface, nominally at 10 m depth, while the other was lowered and read at 10 m intervals until a depth of 200 m was reached. Check readings were made at 40 m intervals on the way up. A simple depth gauge (a bourdon tube driving a potentiometer) and temperature-salinity probe (Cox & Moorey, 1962) were attached just above the deep current meter, and their signals were brought up the armoured electric cable from which the meter was suspended. The accuracy of the current meter readings has been discussed elsewhere (Swallow & Bruce, 1966) in relation to some measurements made later in the Somali current, where the weather conditions were somewhat worse than on these equatorial sections.

Conversion of the relative current profiles to "true" currents was done in three different ways, of varying accuracy. The most satisfactory method was to anchor a buoy and determine the ship's movement relative to it during the current measurements. Care had to be taken to check the relative position of the buoy by repeated brief echo-sounding surveys, since taut moorings with submerged buoyancy were not available. Two or more sets of current meter readings were made at each anchored buoy station, the results have been combined and mean curves drawn for the zonal and meridional components as functions of depth, at each station. Although some of the possible sources of error are difficult to estimate, it seems unlikely that these mean curves would be in error by more than 20 cm/sec.

However, in some cases there seem to have been substantially larger real changes of current (see, for example, Fig. 6). Most probably undetected real fluctuations of current are a more serious source of error than instrumental and navigational inaccuracies, in attempting to use these measurements as an indication of mean flow during the period of occupation of the section.

Buoys were anchored at relatively few stations, because of time limitations. At some other stations, a telemetering current meter, lent by the Chr. Michelsen Institute and the Geophysical Institute, Bergen, was used to provide a deep reference for the relative current measurements. It was

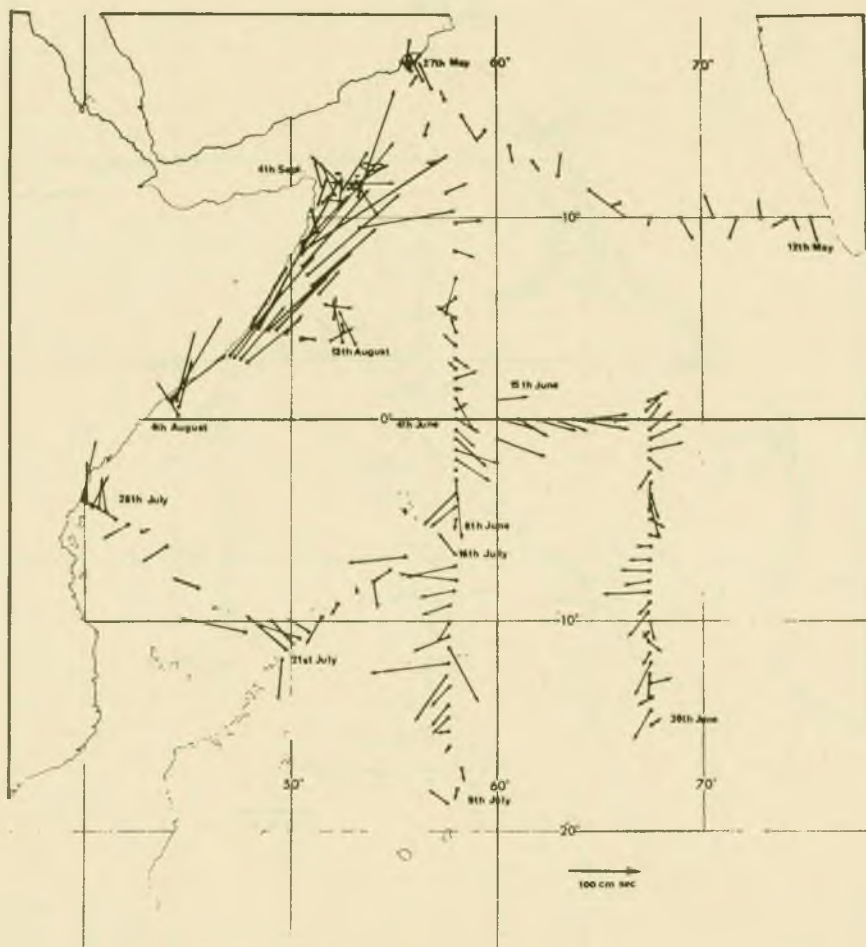


FIGURE 3. Currents at 10 m relative to 200 m, May-September 1964.

more convenient to use at depths of several hundred metres than the direct reading current meters mentioned above, which needed a six-core screened electric cable in addition to the strain-bearing cable. The mean difference of current observed between the meter at 10 m depth and the Bergen meter at three or four depths in the range 500-1500 m was taken as a measure of the near-surface current. Besides the uncertainty of the relative current measurements themselves (estimated to be about 15 cm/sec) an error was incurred in ignoring any movement of the deep water itself. Observations with neutrally-buoyant floats at 1000 m depth at

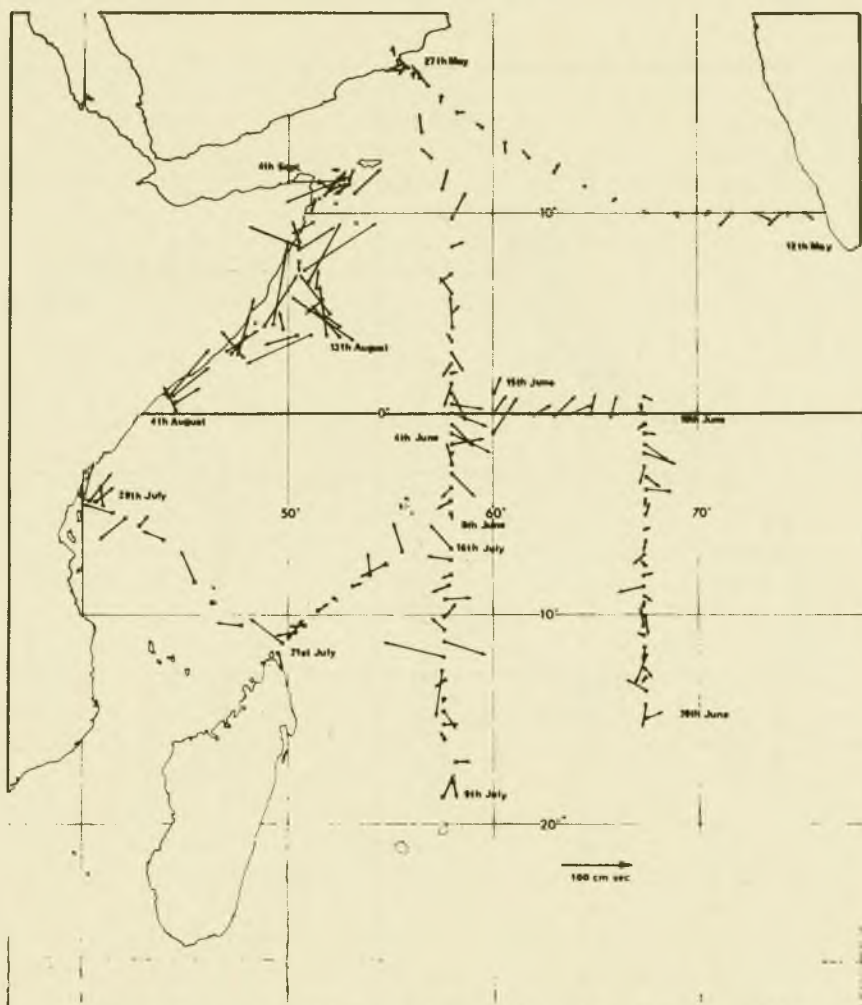


FIGURE 4. Currents at 100 m relative to 200 m, May-September 1964.

anchored-buoy stations suggested that this error might be about 10 cm/sec.

Elsewhere, the relative current profiles have been fitted to surface currents deduced in the usual way from dead-reckoning and celestial navigation, and of course the validity of combining observations averaged over such different periods of time depends very much on the steadiness of the current.

At most of the anchored buoy stations, small drogues were used to supplement the near-surface current measurements. Comparison with the 10 m currents deduced from the shallow current meter showed systematic errors amounting to 9 cm/sec in the March section on 58°E, and 12 cm/sec on 67.5°E in April. These discrepancies were always in the sense of the drogue having leeway, at about 1/60th of the wind speed. An observation of drogue movement relative to a dye marker had suggested a wind factor of 1/240, and the drogue observations had been corrected on that basis, but it seems possible that this observation may have been falsified by current shear in the near-surface layer and that a larger correction would be more appropriate. In the current profiles described below, only the current meter observations have been used at the anchored buoy stations. It may be worth pointing out, in support of the shallow current-meter readings, that the fluxgate compass used in the direct-reading current meters is less liable to error due to the presence of the ship, than a compass needle would be.

OBSERVATIONS

58°E, March 1964.—Approaching the Equator from the north, the first signs of strong relative currents came at 2.5°N, and at 1.5°N there was the first indication of an eastward flowing undercurrent. At 1°N a buoy was anchored and observations were made there on 18-19 March, with the undercurrent clearly present. Then, thinking the undercurrent might not last long, it seemed best to make a quick section across the Equator to 1.5°S, doing only a single cast of water bottles to 350 m and a relative current profile to 200 m, every 30 miles (55 km). Returning to the Equator by 20 March, a buoy was anchored for more current measurements. Continuing the section southwards, two more anchored buoy stations were occupied at 1°S and 2.5°S on 22 and 23 March. Some of the current vectors observed are shown in Figure 5. The core of the undercurrent was close to 75 m and the strong eastward flow within 1° of the Equator at that depth can be clearly seen. Solid current arrows are those observed relative to anchored buoys, dotted ones were obtained by fitting the current profiles to surface currents derived from the navigation. The westward surface currents show a tendency to diverge from about 1°S, and the vectors in the undercurrent tend to converge, but there was a considerable scatter in some of the repeated observations. This variability can be

seen in Figure 6. Changes of about 40 cm/sec could occur within a few hours in the eastward speed of the undercurrent at the Equator, but it was not seen to be weaker than 80 cm/sec. From the temperature-salinity probe observations, stronger current was associated with a deepening of the isotherms and density surfaces. In Figure 6, the two curves of thermohaline anomaly were drawn from the hydrographic data using the T-S probe observations as a guide in interpolation. The difference between the two curves is equivalent to a dynamic height change of 5.5 cm at the Equator. Repeating the shallow stations on the way south, a systematic increase in dynamic height of the sea surface relative to 300 decibars was found, suggesting a longer-period fluctuation of perhaps several days, though the possibility of aliasing from more rapid fluctuations cannot be ruled out.

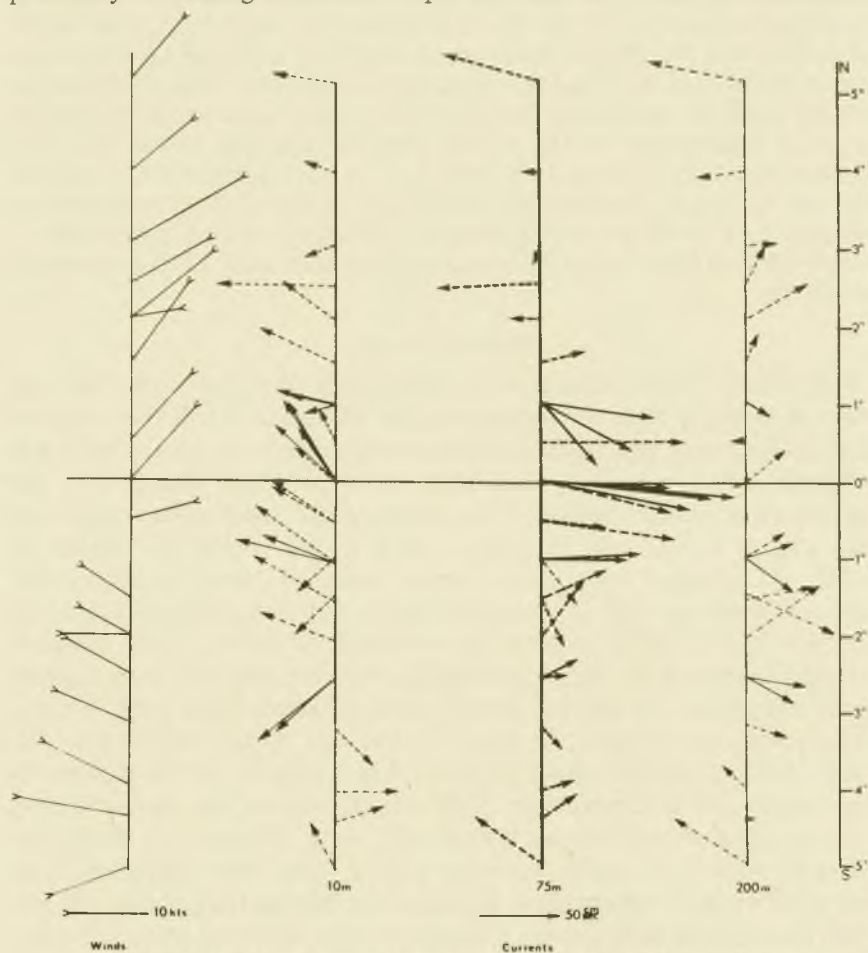


FIGURE 5. Wind and current vectors, 58°E, 16-24 March 1964.

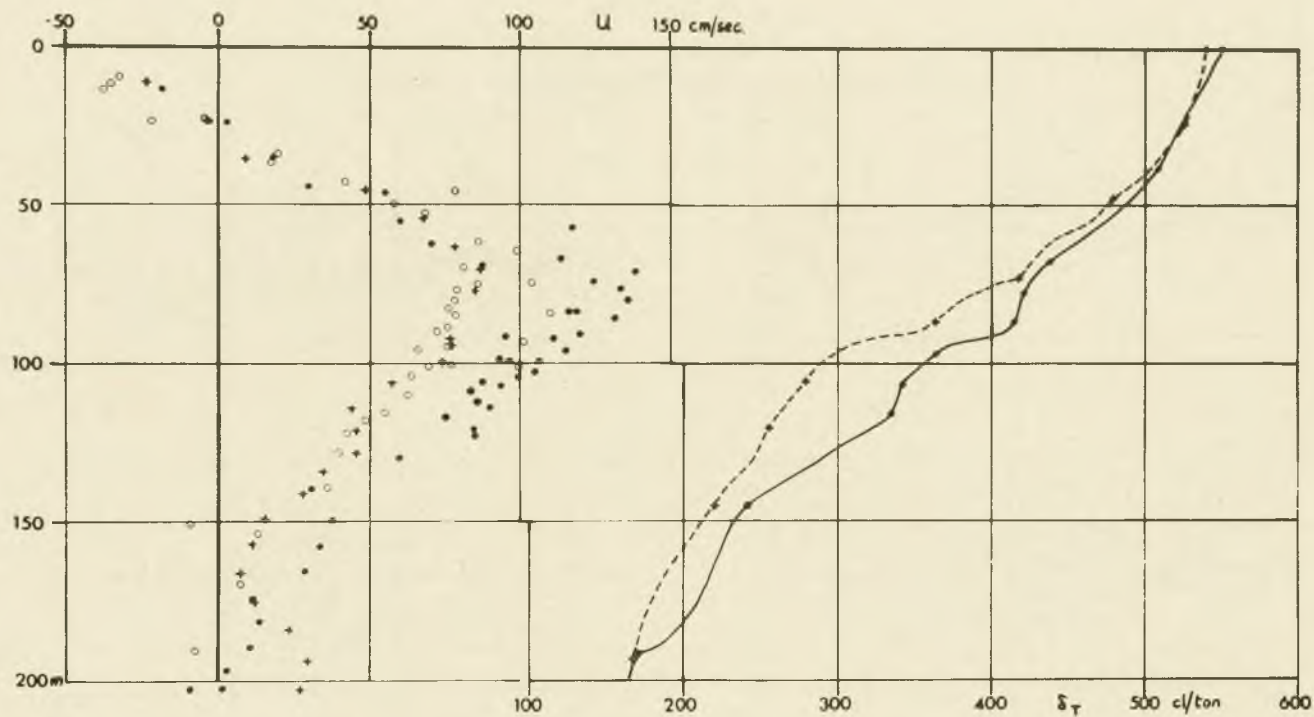
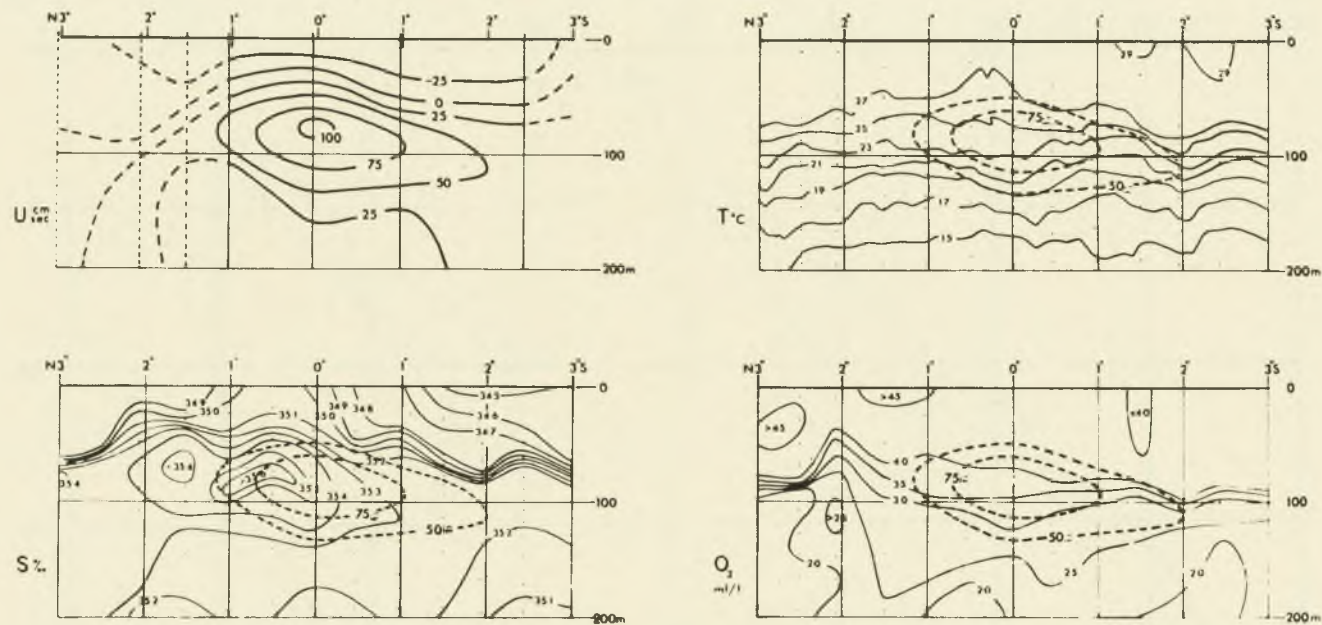


FIGURE 6. Eastward component of current, and thermohaline anomaly, at repeated stations at 0° , 58°E : + 19 March 1964; o, • 21 March 1964.



Using the mean currents at each anchored buoy station, and omitting the observations at the shallow stations between the Equator and 1.5°S , the profiles of current, temperature, salinity and dissolved oxygen shown in Figure 7 have been constructed. In the profile of eastward component of current, the solid contours are based only on the observations at the anchored buoy stations. Taking the 50 cm/sec speed contour as drawn here, the transport within it is 14 million m^3/sec —about half the corresponding value for the Pacific undercurrent (Knauss, 1960). In the temperature profile, there is some spreading of the isotherms associated with the current core, particularly between the Equator and 1°N . A similar slight spreading can be seen in the oxygen isopleths, and there is a clearly marked core of high salinity, slightly deeper than and a little to the north of the undercurrent core. Although the subsurface salinity maximum extended northward from the Equator on this 58°E section, no values as high as those at 0.5°N and 1°N were observed in it, except at $9^{\circ}38'\text{N}$. North of that, salinities exceeded 36‰ at the surface. The temperature-salinity curves shown in Figure 8 make it seem likely that the high-salinity water in the undercurrent came from the northern part of the Arabian Sea, but the isolation of the maximum near the Equator suggests that it was not due to direct southward spreading. More probably this high-salinity water had moved southwestward down the East African coast during the preceding 3 months, and then travelled along the Equator in the undercurrent. Thus, the strength and isolation of the salinity maximum associated with the undercurrent lends support to the idea of the existence of the undercurrent as a continuous feature in the early months of the year.

Further support for the continuity of the undercurrent came from an observation made by HMS OWEN two weeks after the above equatorial section was completed. On 7 April, 1964, on passage from Mauritius to

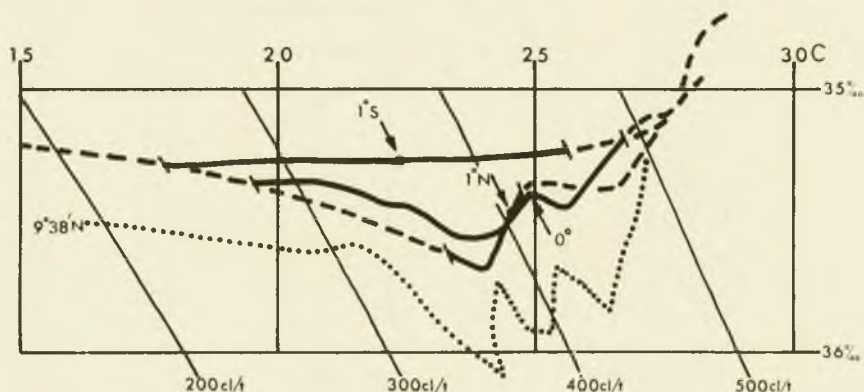


FIGURE 8. T-S curves, 58°E , March 1964. Heavy lines indicate water within 50 cm/sec speed contour of equatorial undercurrent.

Aden, the OWEN had the good fortune to find a seamount on the Equator in longitude $55^{\circ}40'E$ and succeeded in anchoring on top of it. There was very little wind or surface current, but an Ekman meter lowered to 50 fathoms (91m) indicated an eastward current of 90 cm/sec, with much weaker currents above and below.

The winds experienced near the Equator on $58^{\circ}E$ in March, shown in Figure 5, do not seem capable of generating the observed strong undercurrent. They were relatively light, of the order of 10 knots, with little resultant zonal stress and a marked change of direction across the Equator. This suggests that perhaps the undercurrent does not respond to rapid changes of wind and that mean wind stresses over longer periods should be considered.

$67.5^{\circ}E$, April-May 1964.—On this section (Fig. 9 and 10) the local

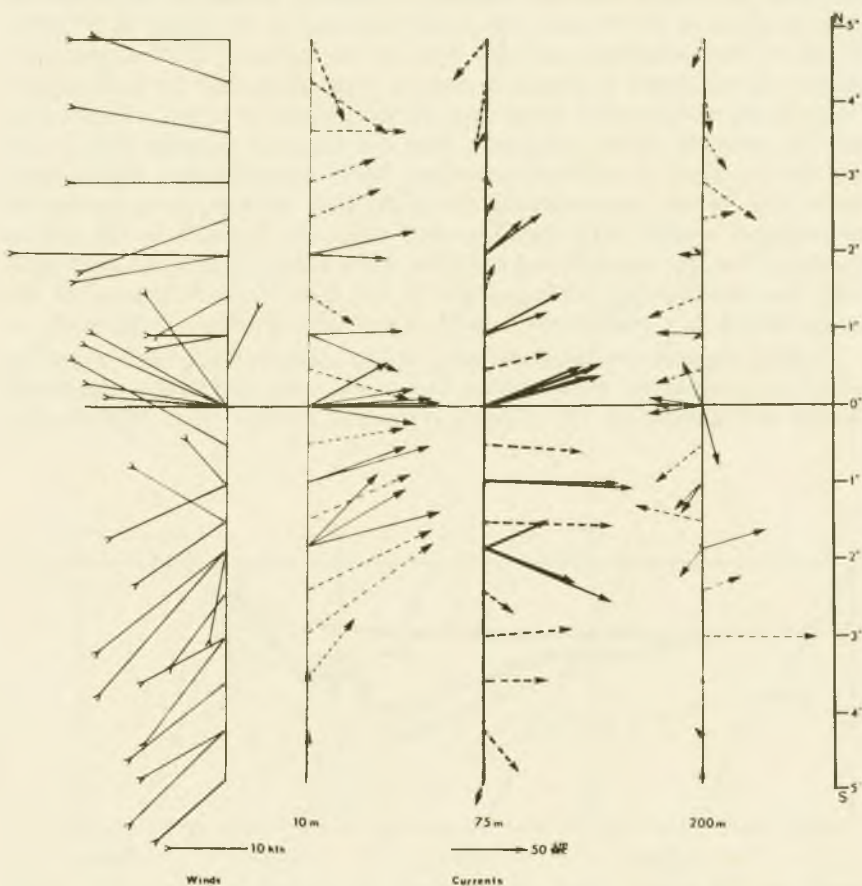


FIGURE 9. Wind and current vectors, $67^{\circ}30'E$, 23 April-3 May 1964.

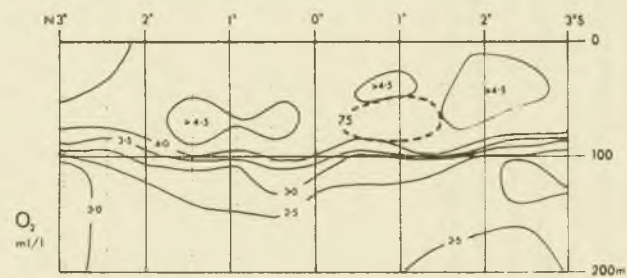
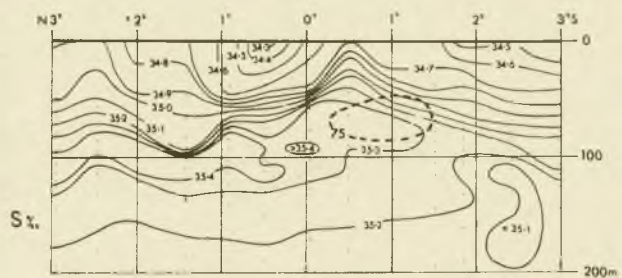
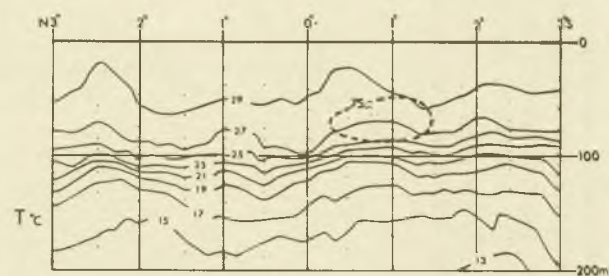
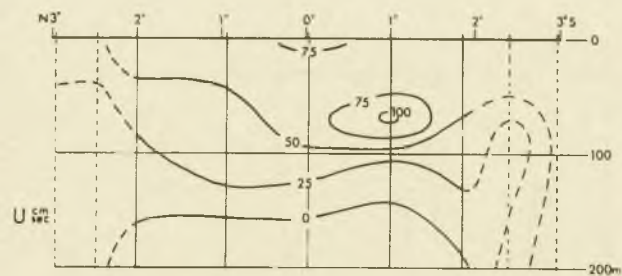


FIGURE 10. Vertical profiles, $67^\circ 30'$ E, 24 April-2 May 1964.

winds were stronger and directed more steadily eastward. The surface current was also eastward, with a marked tendency to converge towards the Equator. At the Equator and 1°S , the undercurrent was consistently present as a subsurface maximum of eastward flow, but only at 1°S did it exceed the surface current, reaching 100 cm/sec at 70 m depth at that station.

At 2°S , three very different profiles were recorded, two showing a subsurface eastward maximum but the third having a steady gradient. As

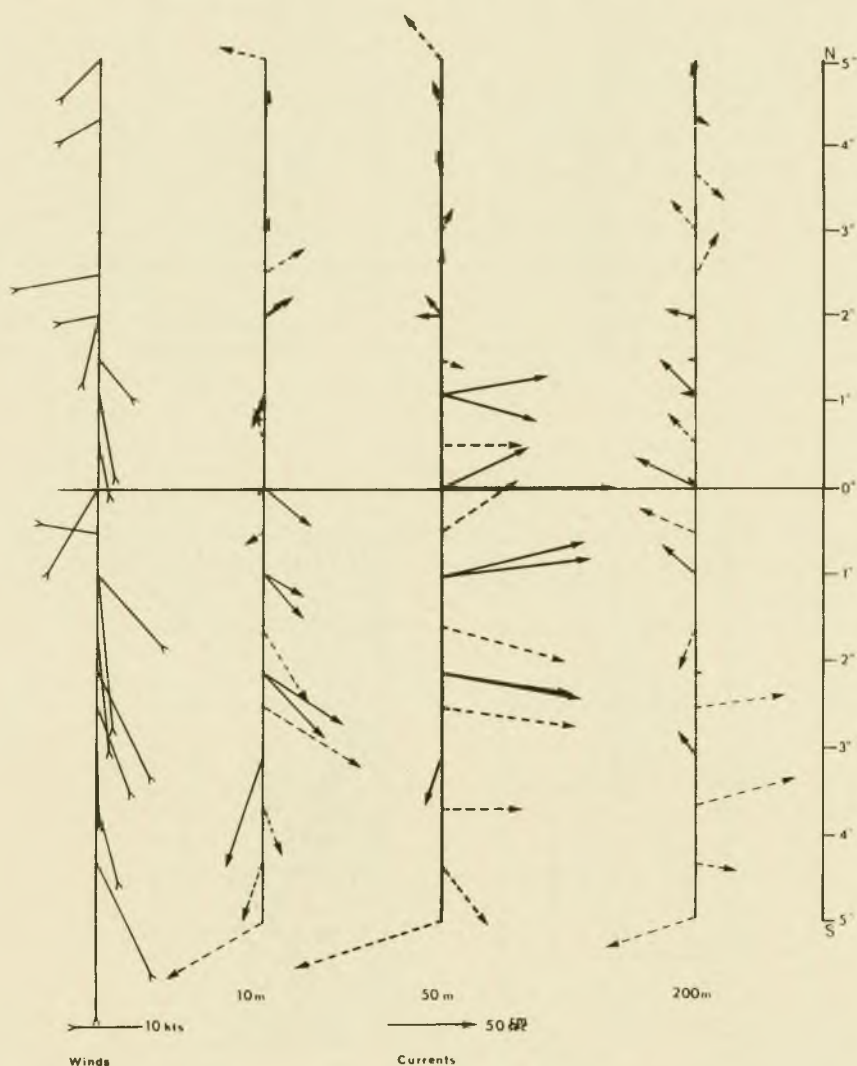


FIGURE 11. Wind and current vectors, 58°E , 31 May-8 June 1964.

in Figure 5, the solid current arrows in Figure 9 represent observations relative to anchored buoys. The convergence in the surface current was matched by a divergent tendency in the undercurrent, and if conditions are assumed to be uniform along the Equator, a vertical velocity of the order of 5×10^{-3} cm/sec may be derived, between the surface and the undercurrent. This is similar in magnitude to the values obtained by Knauss (1966) for the Pacific undercurrent, but in the present case the vertical motion is downwards. There is nothing, however, in the profiles of Figure 10 to suggest downward motion towards the undercurrent core; the reverse might be inferred from the temperature and salinity contours between the Equator and 1° S. The salinity maximum was less marked than on the previous section, with no significant isolated core near the Equator. Some spreading of the deeper isotherms can be seen near 1° N, but perhaps it would be better described as a narrowing at 2° N and 2° S, and it does not seem to be related to the undercurrent core. Currents at 200 m, though variable, were mainly westward near the Equator.

58°E, June 1964.—Measurements were made relative to anchored buoys at 1° intervals from 2° N to 3° S, during 2-7 June. The winds (see Fig. 11) were mainly from the south, and the surface currents were either weak or directed towards the south and southeast, against the wind. The undercurrent was still present, but somewhat weaker and shallower, and was distinctly asymmetrical about the Equator, with maximum eastward speed at 50 m depth at 1° S. At 200 m, westward flow was again observed. Some deeper observations in the range 400-1500 m showed insignificant currents, with nothing comparable to the strong westward flow found by the VITYAZ in the southwest monsoon of 1962 (Neyman, 1964).

In the profiles shown in Figure 12, there was some spreading of the isotherms and oxygen isopleths associated with the undercurrent at the Equator. The subsurface salinity maximum was less marked than it had been in March, and salinities in the core of the undercurrent were much lower. This would be expected, even if the undercurrent were continuous at this time, since by June, the Somali current would have reversed direction bringing relatively low-salinity water towards the Equator.

58°-67.5°E, 13-20 June 1964.—Part of the section on 58° E was re-occupied on 13-14 June, and this was followed by short sections at 60° E and 67.5° E, with stations along the Equator between the latter two sections. Profiles of the eastward component of current are shown in Figure 13. Buoys were not anchored, because of shortage of time; instead, the Bergen current meter was used to provide a deep reference for the relative currents in the upper 200 m.

Comparing the short section on 58° E with that made some 10 days earlier, a strengthening of the eastward component of surface current at 2° S and 1° S had destroyed the subsurface maximum, although there was still an eastward flow at 50 m depth and the deeper isotachs showed little

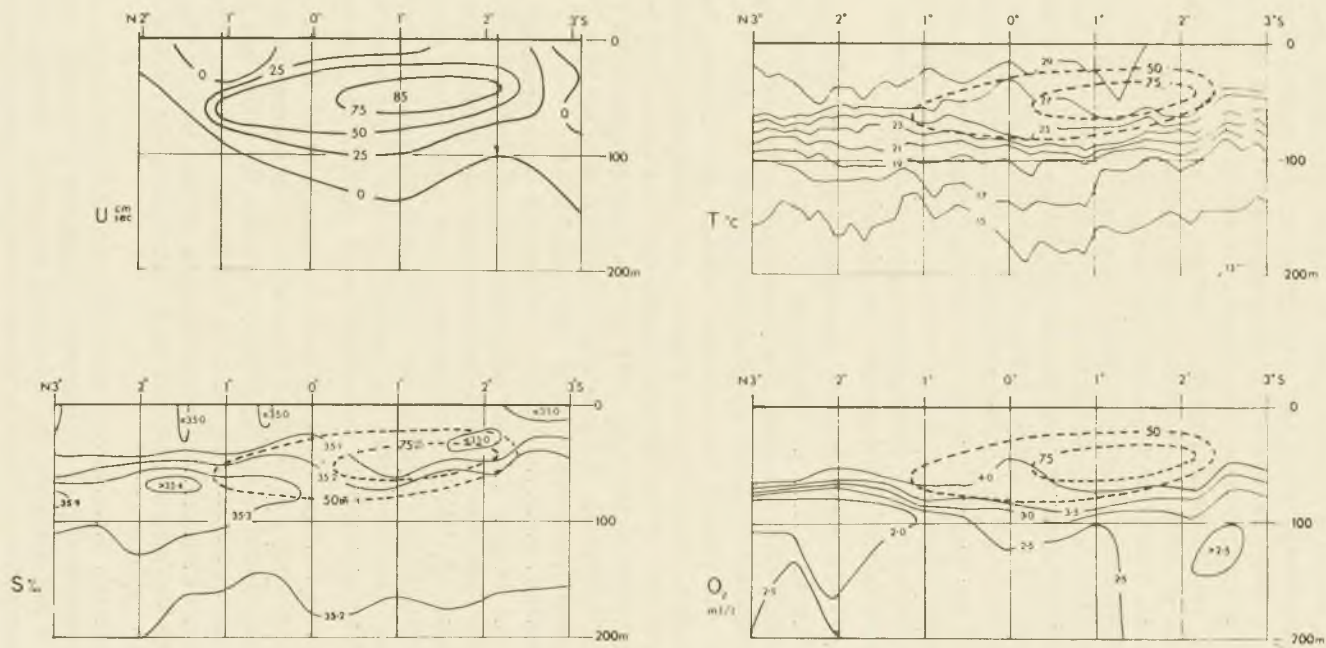


FIGURE 12. Vertical profiles, 58°E, 1-7 June 1964.

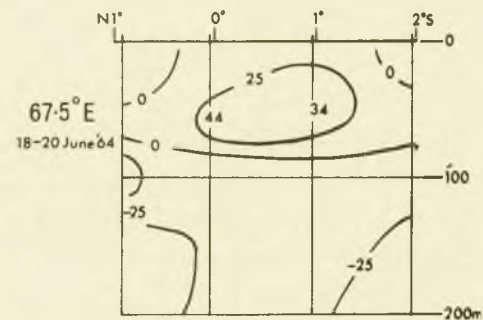
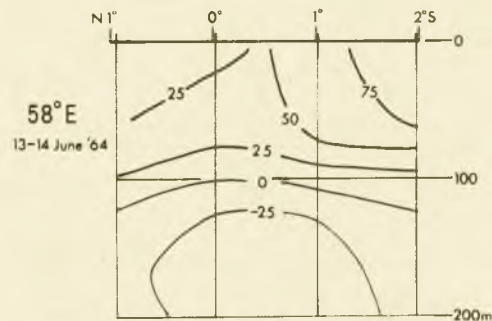
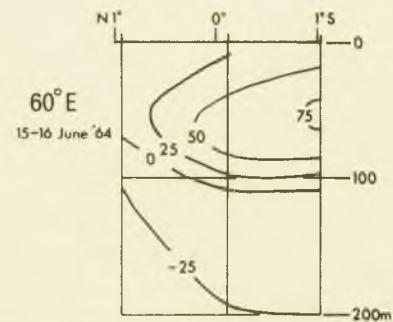
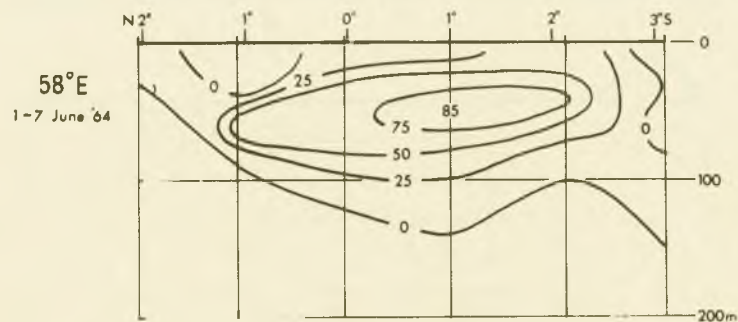


FIGURE 13. Eastward components of current on four equatorial sections, June 1964.

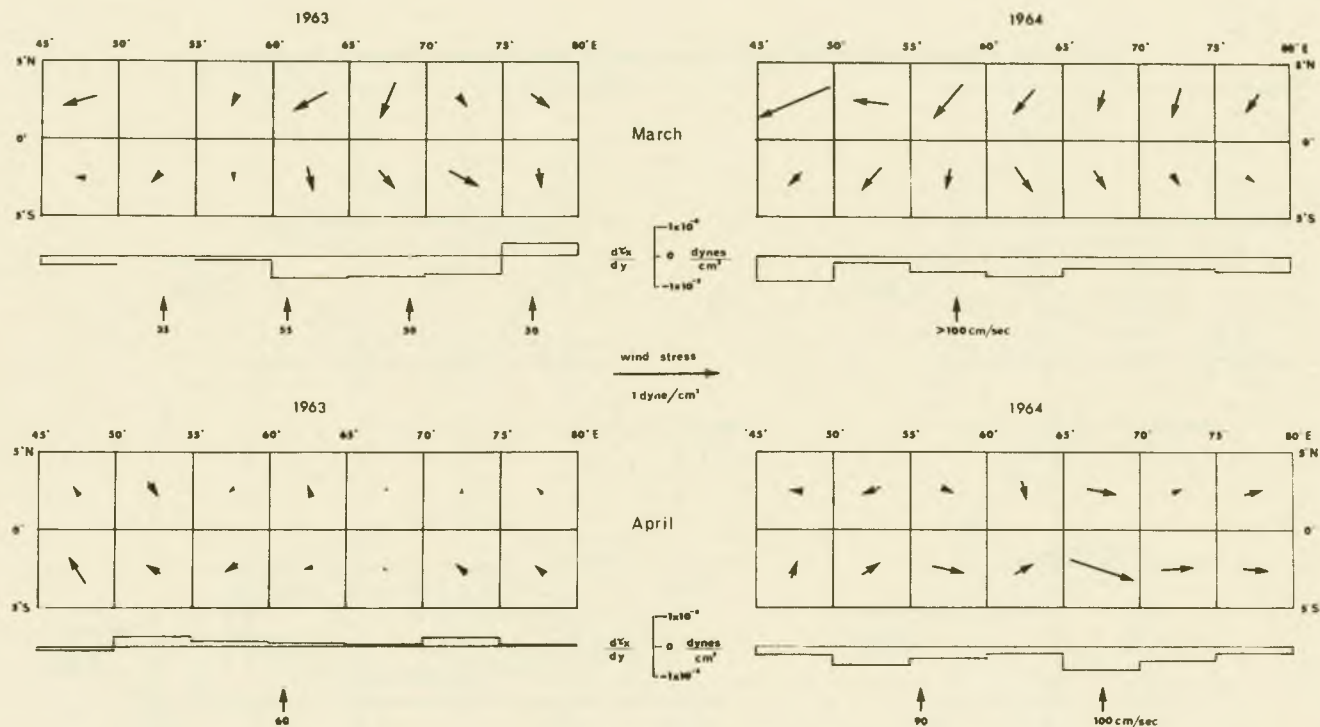


FIGURE 14. Comparison of wind stress vectors for March and April 1963 and 1964. Where an undercurrent was observed, its speed is shown at the appropriate longitude.

change. Winds were light southerly and seemed incapable of having caused the change of surface current at 2°S and 1°S. On 60°E, however, an undercurrent was found, quite similar to that at 58°E earlier in the month. Although the section did not go far enough south, the maximum speed observed was again at 50 m depth and to the south of the Equator. Currents decreased along the Equator, and at the same time the wind increased from the southeast. At 67.5°E, the undercurrent was much weaker, with a maximum speed of 44 cm/sec. On all three of these short sections, westward flow was again observed at 200 m depth.

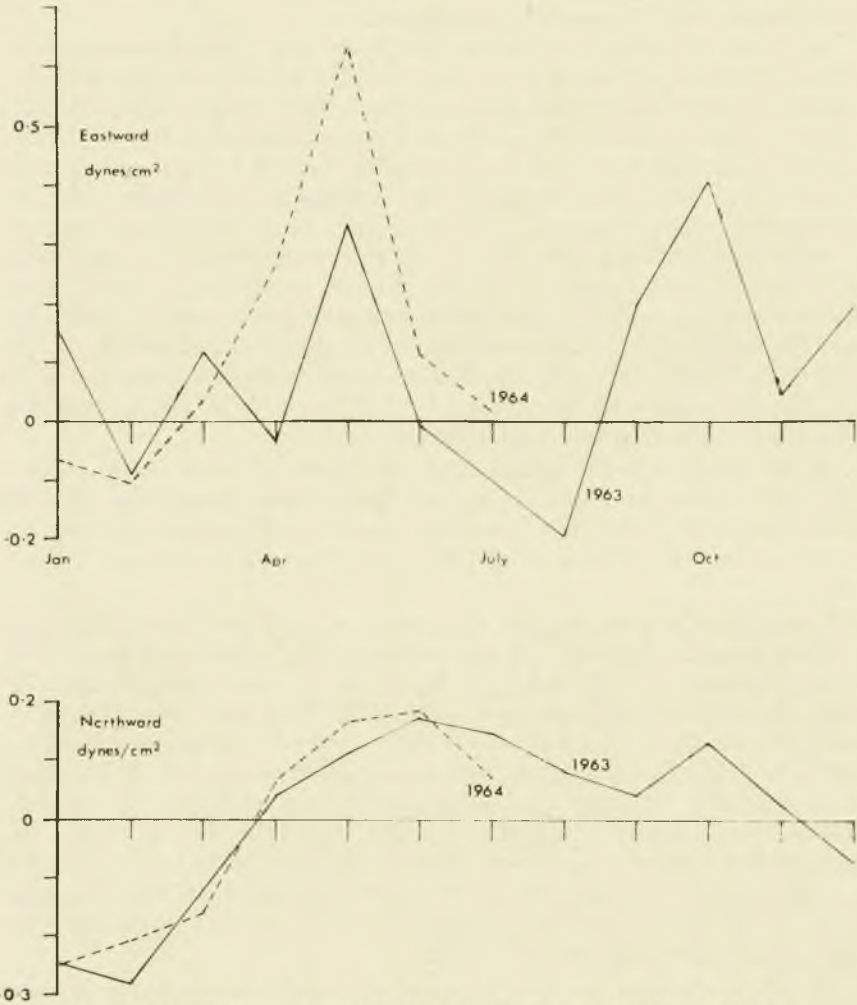


FIGURE 15. Wind stress at Gan, Maldives Islands, (0°41'S, 73°09'E).

WIND STRESS

The equatorial undercurrent as described above was stronger in March and April 1964 than it had been in 1963, and one may hope to relate this to differences of wind stress. Robinson (1966) has shown that an eastward undercurrent should be generated by zonal components of wind stress, and should tend to be destroyed by meridional components. He has also shown that a north-south gradient of zonal wind stress should tend to destroy an eastward undercurrent and should cause it to be displaced from the Equator. On these grounds, the winds shown in Figure 5 are unlikely to have generated the strong undercurrent found in March 1964, and a wider longer-term average has been considered.

In Figure 14, mean wind stresses are plotted for 5° quadrangles for the months of March and April 1963 and 1964. These were derived from ships' weather reports collected and made available by the International Meteorological Centre, Bombay. The method of converting these winds to stresses differed somewhat from that used by Hidaka (1958). Wind speeds were squared, resolved into eastward and northward components, and the components averaged for each 5° quadrangle. These were then converted to wind stress assuming $\tau = .0015 \rho u^2$ (τ = wind stress, ρ = air density, u = wind speed), since by far the greater proportion of winds were weaker than 20 knots. The mean number of observations per 5° quadrangle was 26, but there were wide variations, with none at all centered on 2.5°N , 52.5°E in March 1963. The distribution within each area was often quite irregular in space and time, and one may question to what extent the differences of wind stress are significant.

Some support can be gained from the curves of wind stress at Gan (Fig. 15). These have been calculated from hourly observations of wind at a fixed station, and show the same qualitative differences between the two years as may be seen in the ships' data between longitudes 70° and 80°E .

During March, in both years there was a distinct southward component of stress across the equator, the mean values for the whole area shown being 0.16 dynes/cm^2 in 1963 and 0.18 dynes/cm^2 in 1964. Zonal components were variable, but somewhat more scattered in 1963 than 1964. The mean value for the whole area was zero in 1963, and 0.12 dynes/cm^2 westward in 1964. This difference should tend to favour the production of an undercurrent in 1964. The westward component of stress was greater in comparison to the southward component between longitudes 45° to 60°E . The mean values over that area alone were 0.06 southward and 0.13 westward in 1963, and 0.20 southward and 0.29 westward in 1964. Thus the zonal wind stress was appreciably greater in 1964, though the southward component seems unfavourably large.

In April, eastward components of wind stress were markedly stronger in 1964 than in 1963, while the meridional components were weak in both

years. The mean values for the whole area shown are 0.05 dynes/cm² northward and 0.06 westward in 1963, and 0.01 southward and 0.16 eastward in 1964. These differences of wind stress are consistent with the currents observed in the two years. It may be noted that the 1964 wind stress was quite similar to the mean for April given by Hidaka (1958), suggesting that 1963 was abnormal and that the undercurrent observed in 1964 may perhaps be typical of most years.

Wind stresses for May and June 1964 are shown in Figure 16. In the eastern part of the area, the wind stress in May was similar to that of April, but a strong northward stress (southwest monsoon) appeared on the western side. This increased and spread eastwards during June, when the undercurrent became more variable. The north-south gradient of zonal wind stress, which had been small and variable but generally negative

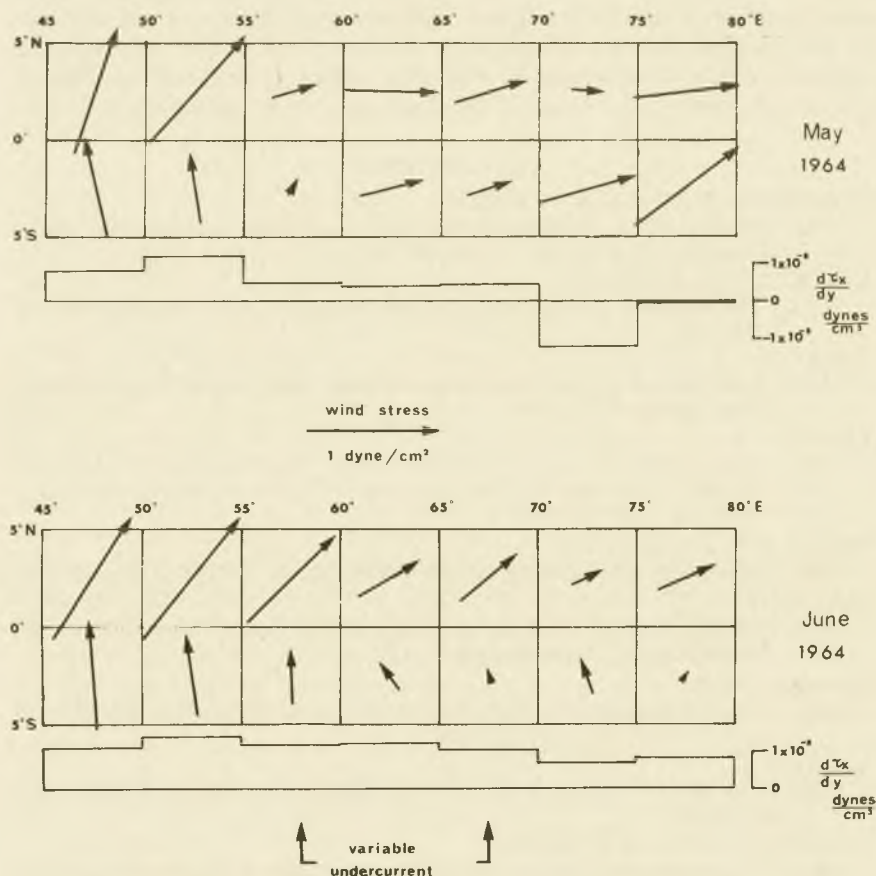


FIGURE 16. Wind stress vectors for May and June 1964.

during March and April 1964, became positive and increased in magnitude during May and June, consistent with the observed displacement of the undercurrent towards the south on 58°E between March and June.

ACKNOWLEDGEMENTS

The work at sea described above involved the co-operation of many persons and organizations and to all of these I am greatly indebted. The provision of equipment by the Fisheries Laboratory, Lowestoft, and by the Geophysical Institute, Bergen, is gratefully acknowledged.

The observations of the undercurrent made by HMS OWEN were communicated to me by the commanding officer, Commander D. W. Haslam R.N., and I am grateful to him and to the Hydrographer of the Navy for permission to refer to them. The wind data at Gan were made available by the Meteorological Office, and the ship's weather observations were supplied by the International Meteorological Centre. I am indebted to Mr. H. Charnock for advice about the treatment of the wind data, in addition to his contributions to the observations at sea, and to Miss J. Cleeve and Mr. C. L. Gulliver for their help with computation.

REFERENCES

- CARTWRIGHT, D. E. AND A. J. WOODS
1963. Measurements of Upper and Lower Tidal Currents at Banc de la Chapelle. *Dt. hydrogr. Z.*, 16: 64-76.
- COX, R. A. AND J. MOOREY
1962. The portable salinity/temperature bridge. N.I.O. Internal Report, No. C4.
- HIDAKA, K.
1958. Computation of the Wind Stresses Over the Oceans. *Rec. oceanogr. Wks. Japan*, 4: 77-123.
- KNAUSS, J. A.
1960. Measurements of the Cromwell Current. *Deep-Sea Res.*, 6: 265-286.
1966. Further measurements and observations in the Cromwell current. *J. Mar. Res.*, 24: 205-240.
- KNAUSS, J. A. AND B. A. TAFT
1964. Equatorial Undercurrent of the Indian Ocean. *Science*, 143: 354-356.
- NEYMAN, V. G.
1964. On the Structure of Zonal Currents in the Equatorial Region of the Indian Ocean. *Okeanologiya*, 5: 920.
- ROBINSON, A. R.
1966. An investigation into the wind as the cause of equatorial undercurrent. *J. Mar. Res.*, 24: 179-204.
- SWALLOW, J. C.
1964. Equatorial Undercurrent in the Western Indian Ocean. *Nature*, 204: 436-437.
- SWALLOW, J. C. AND J. G. BRUCE
1966. Current Measurements off the Somali Coast during the Southwest Monsoon of 1964. *Deep-Sea Res.*, 13: 861-888.

DISTRIBUTION OF SALINITY, OXYGEN CONTENT, AND THICKNESS AT 160 cl/t OF THERMOSTERIC ANOMALY IN THE INTERTROPICAL PACIFIC OCEAN¹

MIZUKI TSUCHIYA

Department of Oceanography, The Johns Hopkins University

ABSTRACT

By the use of observations from various ships during 1952-1960, maps showing the distribution of salinity, oxygen content, and *thickness* are prepared for the surface of constant thermosteric anomaly of 160 cl/t (temperature about 10° to 13°C) in the entire intertropical Pacific Ocean between 20°N and 20°S. The quantity used for *thickness* is the thickness of the layer from 155 to 165 cl/t. One of the most striking features of the distribution is the narrow and pronounced high-oxygen belt along the equator. The amount of water with thermosteric anomaly near 160 cl/t increases eastward along the equator. It seems probable that this increase is compensated by equatorward meridional flow from the south, where water has almost the same salinity as at the equator.

INTRODUCTION

The purpose of this paper is to present three maps showing the distribution of salinity, oxygen content, and *thickness* on the surface of constant thermosteric anomaly of $\delta_T = 160$ cl/t in the intertropical Pacific Ocean. The term *thickness* stands for the thickness of the layer between 155 and 165 cl/t. This quantity gives a measure of the amount of water with thermosteric anomaly near 160 cl/t and also gives a measure of hydrostatic stability. To a good approximation, the thickness is inversely proportional to hydrostatic stability.

The 160-cl/t surface is one of a series being studied. The other surfaces are $\delta_T = 120, 200, 300,$ and 400 cl/t. Maps have been drawn for each surface to show depth, and acceleration potential as well as salinity, oxygen, and thickness. The whole work is being prepared for publication elsewhere. The present paper is confined to some results concerning the 160-cl/t surface.

This work is based on data taken from various ships in various seasons during 1952-1960. No effort has been made to cover the region with stations occupied in one particular season. However, the seasonal variations of properties were checked by the use of available data, and it turned out that the seasonal or irregular variations of properties on the 160-cl/t surface were as small as the range of uncertainty due to interpolations involved in the analysis.

¹Contribution No. 99 of Chesapeake Bay Institute and Department of Oceanography, The Johns Hopkins University. This study was supported by National Science Foundation Grant GP 2443.

The 160-cl/t surface in the area studied lies close to or a little below the bottom of the thermocline in the region where the bottom of the thermocline can be distinctly defined. The depth of the 160-cl/t surface ranges from 100 m near 16° S, 77° W to 524 m near 20° N, 130° E. The depth along the equator is greater than 250 m near the eastern and western boundaries and less than 200 m between 135° W and 110° W.

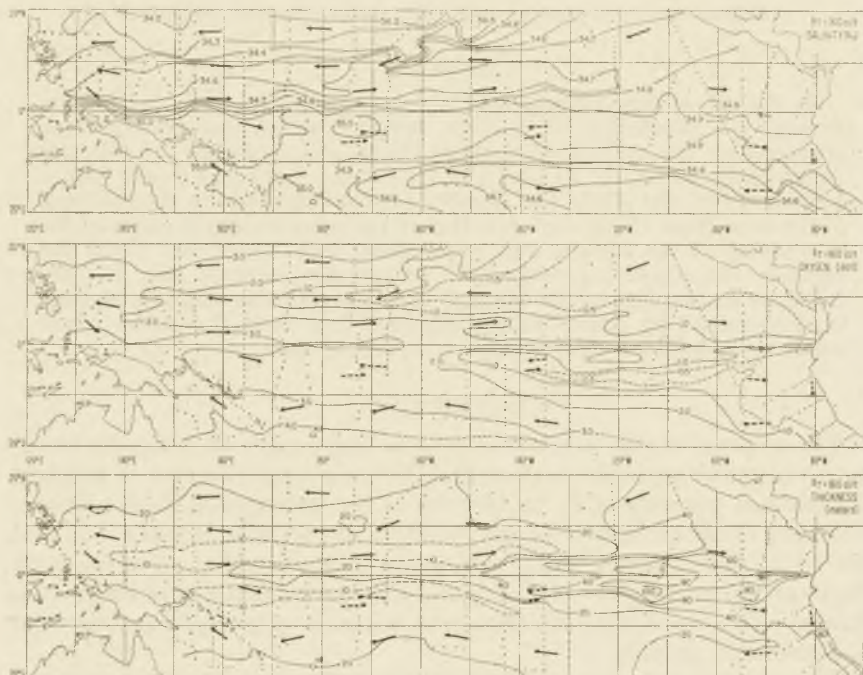


FIGURE 1. Salinity (top) and oxygen content (middle) on the surface of constant thermosteric anomaly of 160 cl/t and the thickness of the layer between 155 and 165 cl/t (bottom). The identical arrows on the three maps indicate the direction of geostrophic flow inferred from contours of acceleration potential relative to the 1000-db surface. The length of a shaft is not proportional to speed. Broken shafts denote flows of uncertain nature.

The distributions of salinity, oxygen content, and thickness are shown in Figure 1. The identical arrows drawn at some selected positions on the three maps indicate the direction of geostrophic flow inferred from contours of acceleration potential relative to the 1000-db surface. Because temperature on a surface of constant thermosteric anomaly is uniquely defined by salinity, the salinity map in Figure 1 can be alternatively interpreted as the temperature map. The values of temperature that correspond to the values of salinity contoured on the map are tabulated in Table 1.

OXYGEN AND SALINITY

One striking feature of the maps is the pronounced high-oxygen belt extending along the equator from 150° E all the way east to the coast of Ecuador. The high-oxygen belt is related to the marked oxygen-isopleth troughing, which can be seen near the bottom of the thermocline on meridional sections crossing the equator. Oxygen in the high-oxygen belt decreases eastward from a value greater than 3.0 ml/liter at 150° E to a value a little above 1.0 ml/liter near the coast of Ecuador. This decrease suggests that the high-oxygen belt is maintained by the transport of high-oxygen water in the Equatorial Undercurrent. Oxygen is perhaps also contributed to the high-oxygen belt by mixing of underlying water with the overlying water rich in oxygen (Knauss, 1960). Thus, the high-oxygen belt indicates the existence of the Equatorial Undercurrent, although the 160-cl/t surface lies well below the velocity core of the Undercurrent; the velocity core is found at about $\delta_T = 300$ cl/t (Montgomery & Stroup, 1962).

TABLE 1

SALINITY-TEMPERATURE CORRESPONDENCE ON THE 160-cl/t SURFACE

Salinity (‰)	34.2	34.3	34.4	34.5	34.6	34.7	34.8	34.9	35.0
Temperature (°C)	9.5	9.9	10.4	10.8	11.2	11.7	12.1	12.5	12.9

Water in the westernmost region north of the equator is too low in both salinity and oxygen to supply water near the equator, where the salinity is as high as 34.9 to 35.0‰ and oxygen exceeds 3.0 ml/liter. This saline and high-oxygen water near the equator has not come from the far west, either; salinity and oxygen at $\delta_T = 160$ cl/t in the Halmahera Sea are appreciably less than 34.9‰ and 3.0 ml/liter, respectively (Postma, 1958). Therefore, the primary source of Equatorial Undercurrent water with thermosteric anomaly near 160 cl/t appears to be in the Coral Sea or near the Solomon Islands, where the water is rich enough in oxygen and has almost the same salinity as at the equator.

The passages between New Guinea and New Britain, and between New Britain and New Ireland, are certainly too narrow to transmit all the Undercurrent water, unless the currents are extraordinarily strong. Therefore, some water in the Coral Sea may pass through northern passages among the Solomon Islands to feed the Undercurrent, or some water near the Solomon Islands outside the Coral Sea may take part in feeding the Undercurrent. In order to clarify this point, further observations in the region are required.

Far downstream, the oxygen values east of 100° W are higher on the north side than on the south side of the equator. Note that the area of water with oxygen exceeding 0.5 ml/liter is much greater to the north of the equator than to the south. This suggests that more Equatorial Under-

current water, which is rich in oxygen, is discharged toward the north than toward the south, though high-oxygen water transported by the North Equatorial Countercurrent might contribute, to some extent, to the higher oxygen values north of the equator.

THICKNESS

The thickness map shows a pronounced maximum along the equator at all longitudes. The maximum represents the less stable layer which lies near the bottom of the thermocline and is associated with the equatorial troughing of isotherms. Temperature at the equator is about 13°C on the 160-cl/t surface. Thus, the great thickness near the equator indicates a dominance of water with temperature of about 13°C and with salinity of about 34.9‰. This type of water forms the flux mode of the Equatorial Undercurrent (Montgomery & Stroup, 1962) and has been described by Stroup (1961) and by Montgomery & Stroup (1962) under the name of Equatorial 13°C Water.

West of 160°E the maximum thickness is less than 20 m. Eastward from 160°E it gradually increases to reach 40 m at about 150°W . As the maximum thickness increases more rapidly farther eastward from 150°W than in the western region, the maximum belt suddenly increases in its meridional extent; thickness greater than 40 m can be observed within about 5° of the equator between 140°W and 100°W . Between 135°W and 105°W , a maximum appears on either side of the equator, and at the equator thickness shows a secondary minimum. The greatest thickness along the equator is found at about 100°W , and from there thickness decreases eastward but is still as thick as 60 m even near the coast of Ecuador. East of the Galápagos Islands the maximum belt diminishes again in meridional extent.

As stated above, thickness increases eastward along the equator from less than 20 m at 150°E to about 90 m at 100°W (most of the increase occurs to the east of 150°W). In other words, the amount of water with thermocline anomaly near 160 cl/t and with salinity of about 34.9‰ increases downstream (eastward) along the equator. On the other hand, direct current measurements by Knauss (1960) indicate that between 140°W and 100°W the zonal component of the current velocity at $\delta_T = 160\text{ cl/t}$ is almost constant at about 20 cm/sec along the equator. Therefore, this downstream increase in the flux of water must be compensated by equatorward meridional flow. Since salinity north of the equator is appreciably lower than at the equator while salinity south of the equator is almost the same as at the equator, it seems probable that the compensating flow takes place from the south of the equator.

CONCLUSION

The salinity and oxygen distributions suggest that the source of Equatorial Undercurrent water is in the Coral Sea or near the Solomon Islands.

East of about 150°W , there appears to be a meridional flow into the Equatorial Undercurrent from the south. In the far east, evidence indicates that more Equatorial Undercurrent water is discharged toward the north than toward the south.

LITERATURE CITED

KNAUSS, J. A.

1960. Measurements of the Cromwell Current. *Deep-Sea Res.*, 6: 265-286.

MONTGOMERY, R. B. AND E. D. STROUP

1962. Equatorial waters and currents at 150°W in July-August 1952. *Johns Hopkins Oceanogr. Stud.*, 1: 68 p.

POSTMA, H.

1958. Chemical results and a survey of water masses and currents. *Snellius Expedition*, 2, part 8: 116 p., Leiden.

STROUP, E. D.

1961. The distribution of Equatorial 13°C water in the eastern Pacific. Presented at the symposium on Equatorial Circulation in the Pacific, 28 August 1961, Tenth Pacific Science Congress, Honolulu.

Tectonic History of
The West Indies Island Arc

H. H. HESS
Convener

The following papers were delivered at the Conference but have not
been received for publication:

GEORGES PARDO: Stratigraphy and Structure of Central Cuba.

ROBERT J. HURLEY: Geological Studies of the West Indies.

H. H. HESS: Speculation on Caribbean History.

GUYOT-LIKE FEATURES IN THE SOUTHEASTERN BAHAMAS: A PRELIMINARY REPORT¹

JOHN D. MILLIMAN

Institute of Marine Science, University of Miami

ABSTRACT

Several guyot-like features have been investigated in the southeastern Bahamas. The easternmost, Gerda Guyot (22°02'N, 73°08'W), shoals to a depth of 670 m. Dredge samples indicate that it is (at least) capped with a manganese-encrusted, recrystallized, pelagic limestone, with little or no unconsolidated sediment cover.

On Hogsty Plateau, east of Hogsty Reef (21°40'N, 73°50'W), there are three guyot-like features; all have relatively flat tops at depths concordant with Gerda Guyot. Another possible guyot lies 38 km west of Hogsty Reef.

The geologic history of the southeastern Bahamas is better understood in light of these findings. In contrast to other known guyots, these features may well be submerged banks whose immediate foundation is non-volcanic. It is thus quite possible that these "guyots" are constructional rather than erosional features.

INTRODUCTION

The submarine geomorphic features, guyots, were first reported by H. H. Hess in 1946. Named in honor of the 19th century geographer Arnold Guyot, they are defined simply as flat-topped sea-mounts; no mention of origin is made.

Most reported guyots are in the Pacific Ocean, the majority being on the Darwin Rise (Menard, 1964); only a few have been reported in the Atlantic Ocean (Heezen *et al.*, 1959; Pratt, 1963). In a recent paper, Bullis & Roe (1965) report a probable guyot (Colmer Knoll) east of the Yucatan Peninsula; to the author's knowledge, it is the first guyot reported in the Caribbean.

The occurrence of several guyots in the southeastern Bahamas is the subject of this paper.

BAHAMIAN STUDIES

For several years the author has been engaged in research on Hogsty Reef (21°40'N, 73°50'W), an atoll in the southeastern Bahamas (Figs. 1, 2, 3). In the course of a 1964 bathymetric survey (G6426; Fig. 2) of the Hogsty area, several flat-topped submarine features were studied, most all of which had been indicated by previous soundings published on navigation charts. These features were further studied during a subsequent cruise in 1965 (G6522). Each mount is discussed separately in the following paragraphs.

¹Contribution No. 792 from the Institute of Marine Science, University of Miami.



FIGURE 1. Southeastern Bahamas and Surrounding Area.

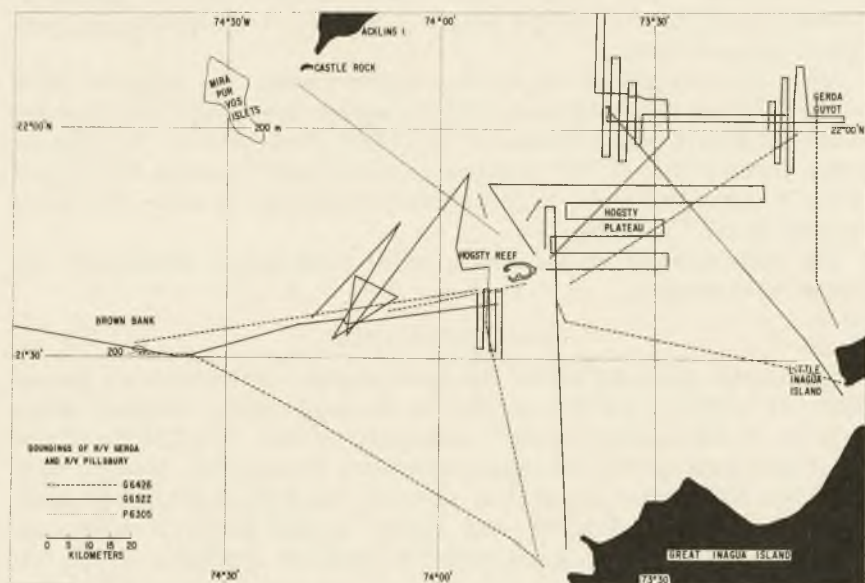


FIGURE 2. Bathymetric Tracks in the Hogsty Reef Area.



FIGURE 3. Bathymetry of the Hogsty Reef Area.

Gerda Guyot ($22^{\circ}02'N$, $73^{\circ}08'W$) lies 67 km northeast of Hogsty Reef (Fig. 3). It was named by the author in honor of R/V GERDA, from the Institute of Marine Science, University of Miami. The relief of Gerda Guyot exceeds 2200 m on its east and south sides, and 1600 m on its north and west sides (Figs. 4, 5). The top, which is remarkably flat at depths of 670 to 690 m, extends about 8 km E-W, and 7 km N-S. On the southwest corner the top shoals to 540 m. The outer margins of the flat top, with slopes of about 5° , break sharply at between 800 and 900 m, with slopes often greater than 20° .

In 1965 several attempts were made to sample the unindurated sediments and the rock substrate. It was only on the last attempt that any rock sample was obtained. This sample, recovered from the northern edge of the flat top, consisted primarily of an indurated, recrystallized Pleistocene *Globigerina*-Pteropod ooze; much of this limestone was encrusted with a manganese coating. One cetacean bone, partially replaced by manganese, was also recovered. No volcanics nor shallow-water limestone were in the sample.

Judging from the difficulty in recovering bottom samples from Gerda Guyot, it is assumed that the guyot's top is practically devoid of loose sediments, currents probably being sufficient to sweep the top clean. In this respect it is similar to other guyots studied (Hamilton, 1956; Hamilton & Rex, 1954; Pratt, 1963).

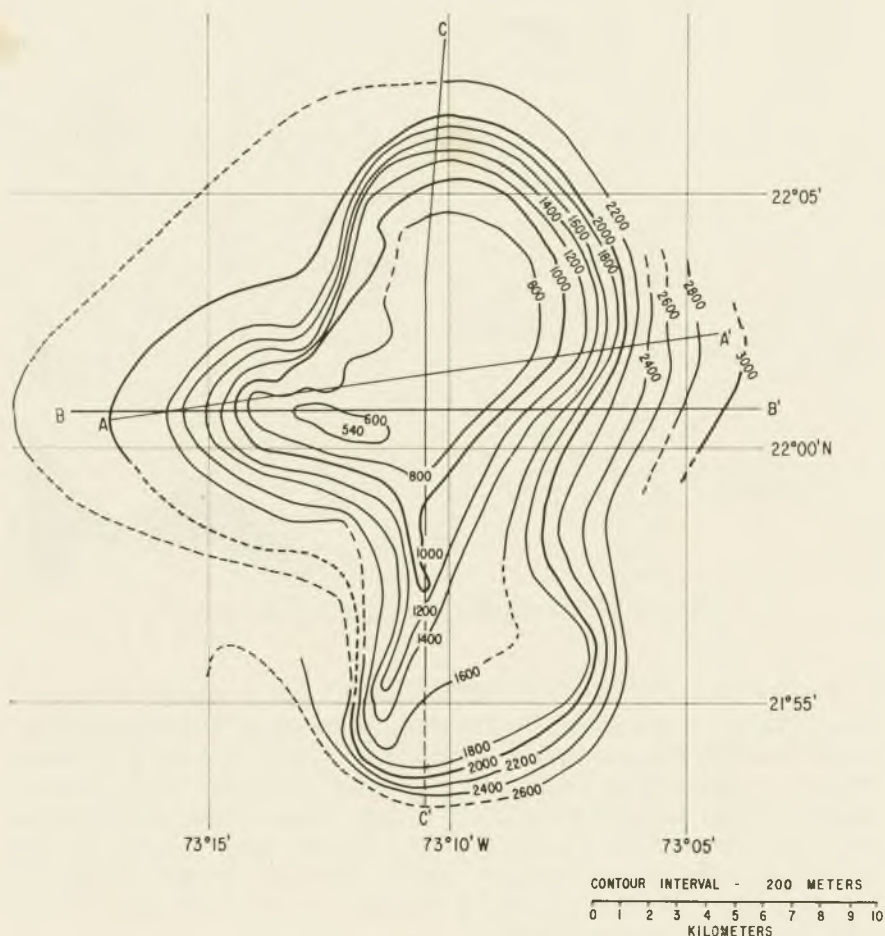


FIGURE 4. Plan of Gerda Guyot.

Extending about 40 km east and north from Hogsty Reef is a platform, which has been named Hogsty Plateau (Figs. 3, 6). It is connected to Hogsty Reef by a saddle, about 1400 m in depth. Most of the plateau is shoaler than 1000 m.

Located on this plateau are three rather flat-topped features, each rising about 200 to 300 m above the plateau. All three shoal to about the same depths (780, 760, 820 m) as Gerda Guyot. This feature, Hogsty Plateau, is remarkably similar to Sylvania Guyot, which is connected to Bikini Atoll in the Marshall Islands (Emery *et al.*, 1954).

The southern most rise on Hogsty Plateau has an extremely flat top (Fig. 7); the other two features have hummocky tops. The upper slopes

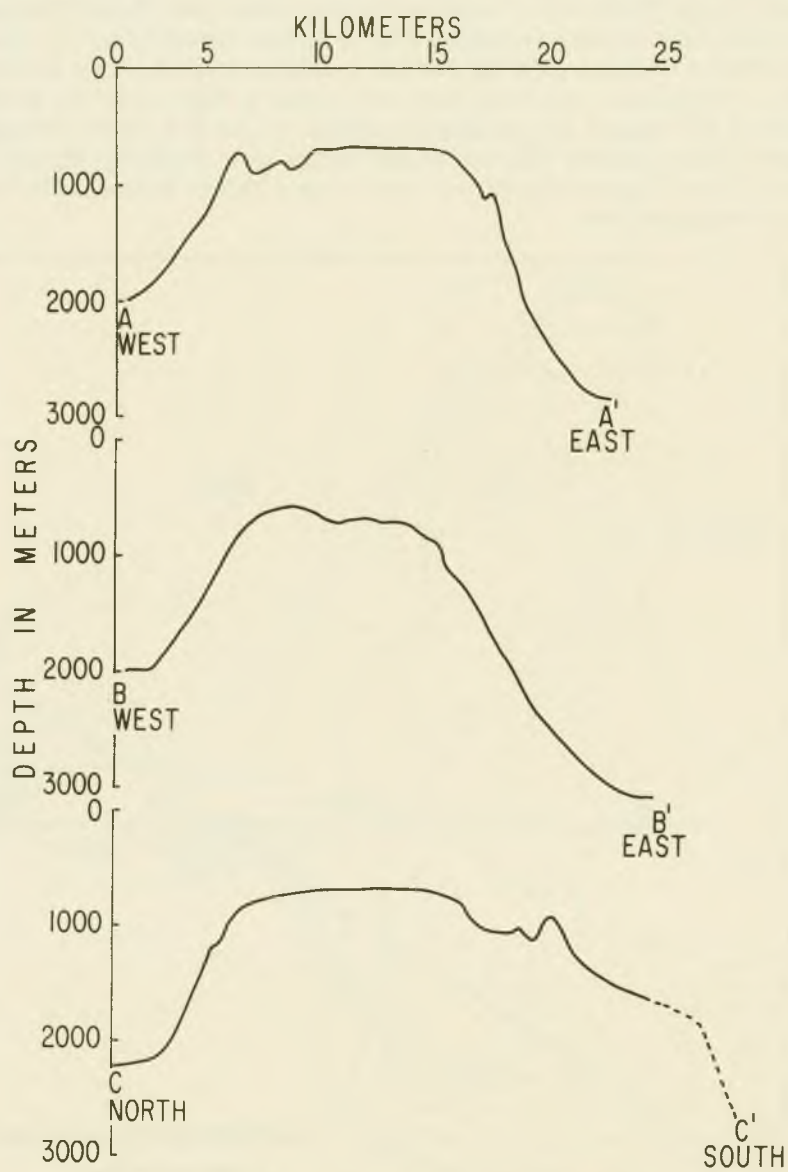


FIGURE 5. Profiles of Gerda Guyot. Vertical Scale $\times 5$.

of these features are somewhat less steep than the slopes of Gerda Guyot, although the lower slopes of Hogsty Plateau sometimes exceed those of Gerda Guyot. Thus far no samples have been taken from Hogsty Plateau.

Twenty-nine km west of Hogsty Reef is another mount (Fig. 3), which rises from a depth of 2000 m, and has a definite break in slope at about 900 m. Not enough soundings have been made to define fully the bathymetry of this mount, but soundings supplied by the U.S. Naval Oceanographic Office indicate that this mount shoals to a seemingly flat top at about 720 m. Figure 8 shows one cross section of this feature made during a bathymetric run.

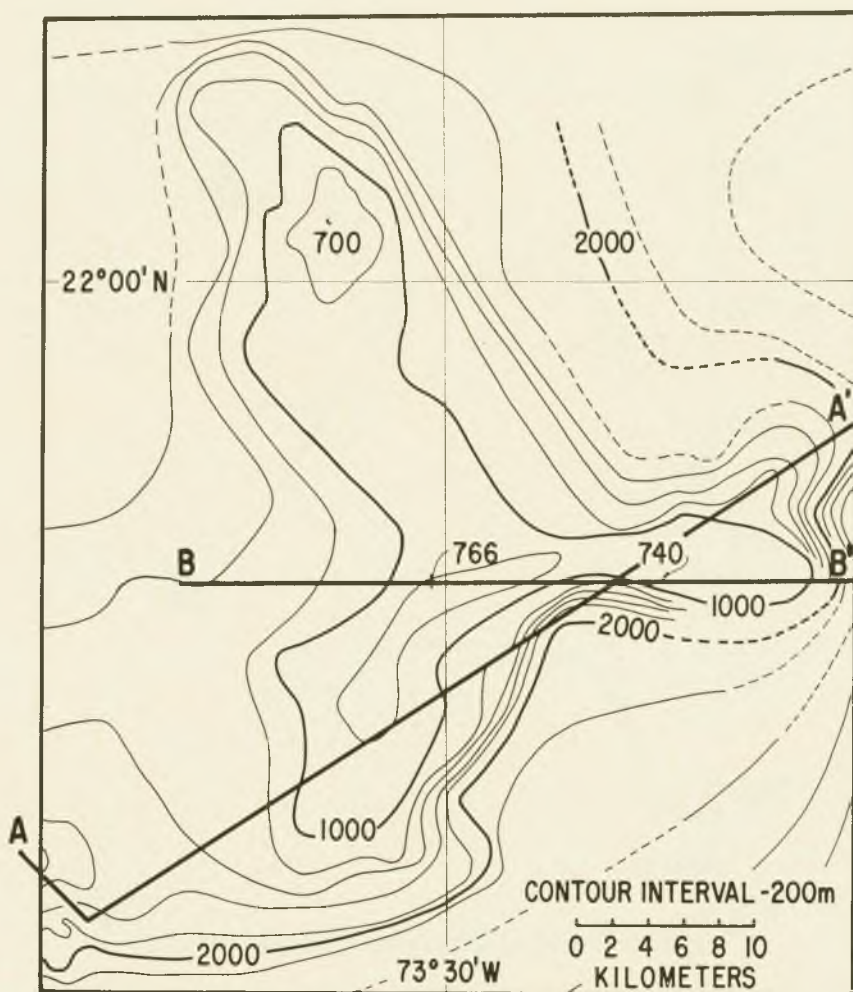


FIGURE 6. Plan of Hogsty Plateau.

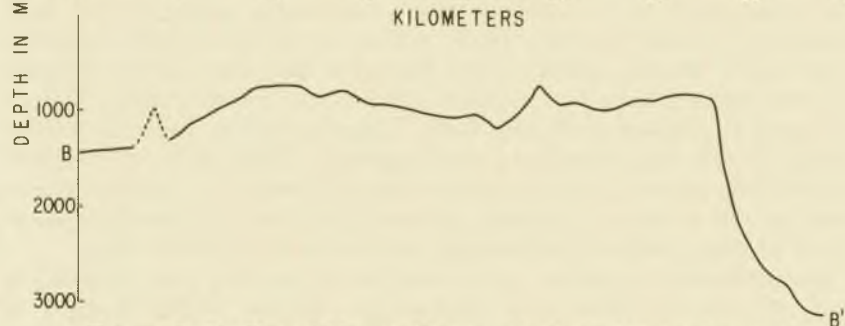
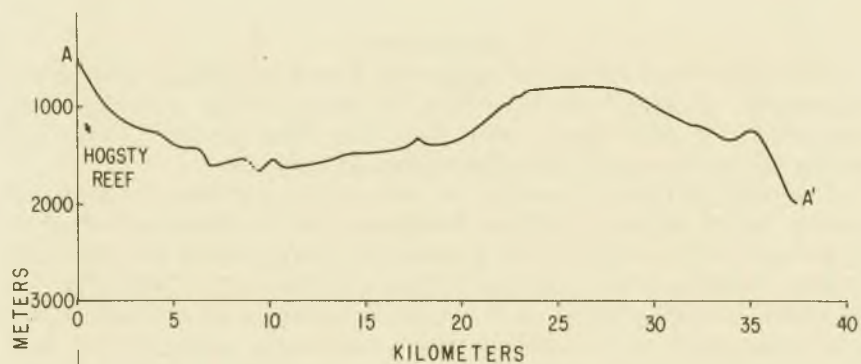


FIGURE 7. Profiles of Hogsty Plateau. Vertical exaggeration $\times 5$.

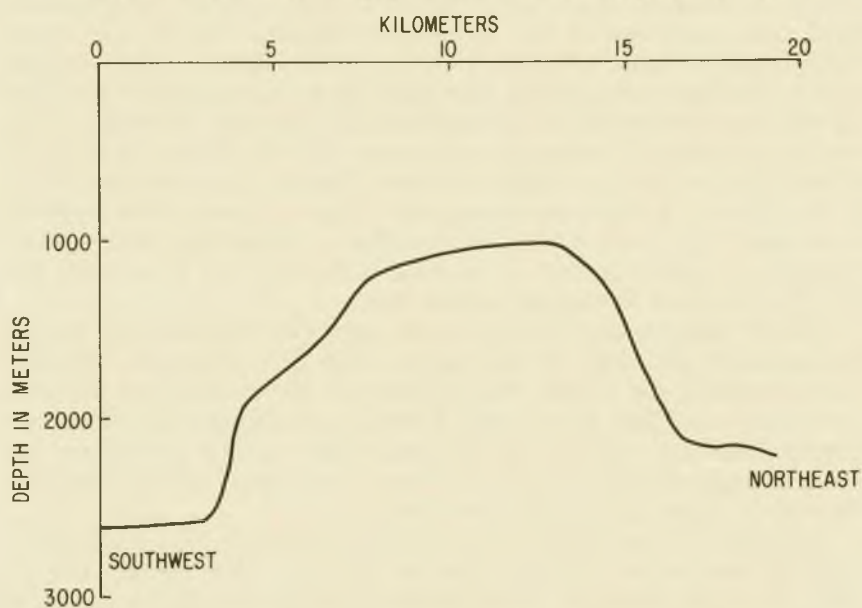


FIGURE 8. Crossing of a possible guyot ($21^{\circ}36'N$, $74^{\circ}09'W$) west of Hogsty Reef.

DISCUSSION

Although several alternative suggestions have been offered, erosion and subsequent subsidence are believed to be the processes involved in the formation of guyots (Hess, 1946; Hamilton, 1956; Menard, 1964). All guyots heretofore studied have been planated volcanoes.

Certainly the relatively concordant peaks of the southeastern Bahamian guyots would suggest a uniform subsidence, but a subsidence of what? Schuchert (1935), arguing from geomorphic analogy, stated that the southeastern Bahamas were a volcanic island arc, convex to Cuba (Fig. 1). However at Andros Island, in the northern Bahamas, an exploratory well penetrated 4500 m of "shallow-water" carbonates ending in the mid-Cretaceous (Newell & Rigby, 1957). Cuba, on the other hand, has had a more active tectonic history, with Mesozoic and some lower Tertiary volcanics present; but the northern parts of the island contain a thick sequence of Tertiary carbonate beds, quite similar to those at Andros Island (Pardo, 1965; personal communication). Thus one is left with two possible hypotheses: A. an immediate volcanic foundation of these guyots (and the rest of the southeastern Bahamas); B. that the immediate foundation of these guyots is sedimentary, probably of carbonate origin.

Several lines of evidence would tend to support the latter hypothesis. First, no volcanics have been obtained in samples (either dredged or cored) in the southeastern Bahamas; however this might be due to the paucity of sampling in the area. Secondly, some magnetic investigations have been made east of the southeastern Bahamas by the U.S. Naval Oceanographic Office (Bracey & Avery, 1963; Bracey, 1963, unpubl. rept.). Although these sections were generally in waters deeper than 1500 m, and thus not directly on the shallow banks, no high anomalies, which one would expect for volcanoes, were seen.² Thirdly, bottom photographs taken at Hogsty Reef, in depths of about 1600 m, show no signs of volcanic outcrops. In fact one photograph (Fig. 9) shows three probable shoal-water type corals in the rock, oriented in similar directions, perhaps indicating a growth position. It is possible that this rock is a slump feature, but its large size argues against this.

Thus it would appear, mainly on circumstantial evidence, that at least the immediate basement of these guyots, and the southeastern Bahamas, is non-volcanic. One might thus suspect that the southeastern Bahamas were once comprised of a series of banks (possibly atolls) whose carbonate deposition was able to keep pace with regional subsidence. For some unexplained reason several of these banks sank too fast and thus became the guyot-like features now seen.

This type of origin would indicate that these features have a completely different genesis than the other guyots that have been studied. For the latter have been shown to be truncated volcanoes, with only a superficial

²Recent magnetometer studies on Gerda Guyot (IMS Cruise P 6603) showed only slight topographic anomalies, thus supporting this hypothesis.



FIGURE 9. Outcrop with three *Montastrea*-like corals (see arrows). Photograph taken at Hogsty Reef at a depth of about 1600 m.

reef coating (Hamilton, 1956); in other words, erosional features. The tops of the Bahamian guyots however may well be constructional (*i.e.*, sedimentary) features with thick (perhaps greater than 800 m) reef deposits.

Much more work must be done in this area, especially in geophysical measurements and additional sediment and rock sampling, however, before any concrete theory of the origin of these features can be made.

I might mention one other observation. The dominant depths of the Blake Plateau (700-900 m) are strikingly similar to those of the guyots. While the under-lying geology of these two features may be different, it is possible that they do represent a common time of subsidence. Judging from the fossils recovered from the Andros Well, together with those on the Blake Plateau, the horizon of -700 m to -800 m is Miocene in age. If this time horizon continues into the southeastern Bahamas, then it is possible that the subsidence of the guyots occurred at a similar time.

CONCLUSIONS

It is concluded that the immediate foundation of the guyots in the southeastern Bahamas is non-volcanic, and therefore that all are constructional features rather than truncated volcanic islands. By correlating time horizons in the Blake Plateau and the Andros Well with the 700 m to 800 m depth of the guyots, it seems possible that the flat-topped mounts were formed during the mid-Tertiary by a relatively rapid subsidence.

It has long been assumed that undersea mountains were, by necessity, volcanic in origin. In areas bordering continents this need not be the case. Black *et al.* (1964) report several seamounts off the Iberian coast, which they hypothesize were continentally deposited. Also, the southeastern Bahamian guyots are seen to be related to a regional subsidence of a basically continental area (Talwani *et al.*, 1960). It might be expected that as our geophysical and sampling techniques improve, other such non-volcanic mounts shall be found.

ACKNOWLEDGEMENTS

The author is grateful to C. Emiliani of the Institute of Marine Science, University of Miami; N. D. Newell, Department of Geology, Columbia University; and K. O. Emery, Woods Hole Oceanographic Institution, for their suggestions and helpful comments. Financial support was given by the National Science Foundation Grant GP-5012 and the Office of Naval Research Contract Nonr 4008(02).

REFERENCES

- BLACK, M., M. N. HILL, A. S. LAUGHTON, AND D. H. MATTHEWS
1964. Three non-magnetic seamounts off the Iberian coast. *Quart. J. geol. Soc. London*, 120: 477-517.

- BRACEY, D. R.
1963. Geologic interpretation of marine magnetic data in an area off the southern Bahama Islands. U. S. Naval Oceanogr. Office, Informal Rept. (M-7-63): 1-8. (Unpublished manuscript.)
- BRACEY, D. R. AND O. E. AVERY
1963. Magnetic survey off the southern Bahamas. U. S. Naval Oceanogr. Office, Tech. Rept. (TR-160): 1-29.
- BULLIS, H. R. AND R. B. ROE
1965. Colmer Knoll—A new feature in the Yucatan Channel approaches. *Bull. Mar. Sci.*, 15 (3): 612-615.
- EMERY, K. O., J. I. TRACEY, JR., AND H. S. LADD
1954. Geology of Bikini and nearby atolls. U. S. Geol. Surv. prof. Paper, 260-A: 1-265.
- HAMILTON, E. L.
1956. Sunken islands of the Mid-Pacific Mountains. *Geol. Soc. Amer., Memoir*, 64: 1-97.
- HAMILTON, E. L. AND R. W. REX
1954. Lower Eocene phosphatized globigerina ooze from Sylvania Guyot. U. S. Geol. Surv. prof. Paper, 260-W: 785-797.
- HEEZEN, B. C., M. THARP, AND M. EWING
1959. The floors of the oceans. I. The North Atlantic. *Geol. Soc. Amer., Spec. Paper*, 65: 1-122.
- HESS, H. H.
1946. Drowned ancient islands of the Pacific Basin. *Amer. J. Sci.*, 244: 772-791.
- MENARD, H. W.
1964. Marine geology of the Pacific. New York, McGraw-Hill Book Co., 271 p.
- NEWELL, N. D. AND J. K. RIGBY
1957. Geological studies on the Great-Bahama Bank. *In* Regional Aspects of Carbonate Deposition, Soc. Econ. Paleont. Mineral., Spec. Publ. 5: 13-72.
- PARDO, G.
1965. Stratigraphy and structure of central Cuba (abs.). Internatl. Conf. Trop. Oceanogr., Nov. 17-24, 1965, Miami Beach, Fla.
- PRATT, R. M.
1963. Great Meteor Seamount. *Deep-Sea Res.*, 10: 17-25.
- SCHUCHERT, C.
1935. Historical geology of the Antillean-Caribbean region. New York, John Wiley & Sons, Inc., 811 p.
- TALWANI, M., J. L. WORZEL, AND M. EWING
1960. Gravity anomalies and structure of the Bahamas. *Trans. Second Carib. Geol. Conf., Mayagüez, Puerto Rico*: 156-160.

GEOLOGICAL STRUCTURE OF CENTRAL AMERICA

GABRIEL DENGÓ

Instituto Centroamericano de Investigación y Tecnología Industrial, Guatemala

ABSTRACT

Two major units of different geological structure and history are recognized in Central America—a northern one which is considered part of the North American continent, and a southern one which presents features similar to some Pacific areas. Gravity and seismic data, as well as geological evidence, point out different crust types under the two units.

The tectonic history of northern Central America can be traced as far as mid-Paleozoic time, when a marginal geosyncline existed south of a foreland platform which occupied approximately the present Yucatan Peninsula. Of special interest is a wide belt of serpentinites that essentially parallels major faults along the Bartlett Trough trend.

The narrow southern Central American isthmus developed during Jurassic or Early Cretaceous time, as an oceanic-type island arc built on a ridge of oceanic crust, separating the Caribbean Sea from the Pacific Ocean, and extending from the southern part of northern Central America to northwestern Colombia.

Without attempting to establish a regional stress pattern, it is concluded that, through its tectonic history, the region was broken up into individual blocks which moved relative to each other. These blocks are bounded by fairly straight faults of different ages and origin some of which lie along the trends of major fracture zones of the Pacific and the Caribbean. It is questionable, however, that the Pacific and Caribbean fracture zones are continuous.

INTRODUCTION

Several regions of the world have been especially attractive to geological investigators because of their complexity and the diversity of problems encountered when attempting to unravel their tectonic history. The Caribbean region has been a classical one in this respect. Some of the theories regarding the tectonics of the region, in particular of the West Indies island arc, have been developed on the basis of geological and geophysical studies in the eastern Caribbean, with only partial considerations of the western Caribbean and Central America.

The purpose of this paper is to summarize the structural features and tectonic history of Central America, and to point out their relations to the Caribbean, as well as the major problems encountered in establishing these relationships. In order to accomplish this aim, the eastern equatorial Pacific, whose major tectonic trends have influenced the structure of Central America, must also be taken into account.

The author's views on the tectonic history of Central America have been presented recently in two papers, one dealing with the tectonic and igneous activity of the southern portion (Dengo, 1962b), and the other concerning the structural evolution of the northern part (Dengo & Bohnenberger, In

Press). Selected bibliographies in both papers cover the most important recently published information, as well as some of the early classical investigations. No attempt is made here to review the literature and the specific details of the geology of the area. The references cited are mainly those that deal with the major tectonic features and problems of the area, or with data not discussed in the above-mentioned papers.

The courtesy of Mr. Julio Monges Caldera, of the Instituto de Geofísica, Universidad Nacional Autónoma de México, in securing geophysical information is acknowledged, as well as the constructive criticism of my colleagues at the Instituto Centroamericano de Investigación y Tecnología Industrial, Mr. Otto Bohnenberger and Mr. Enrique Levy. Mr. William Hunter has kindly helped in the revision and correction of the text.

PHYSICAL FEATURES

Topography.—Central America is defined here as the land and continental shelf area which extends from the Isthmus of Tehuantepec in Mexico

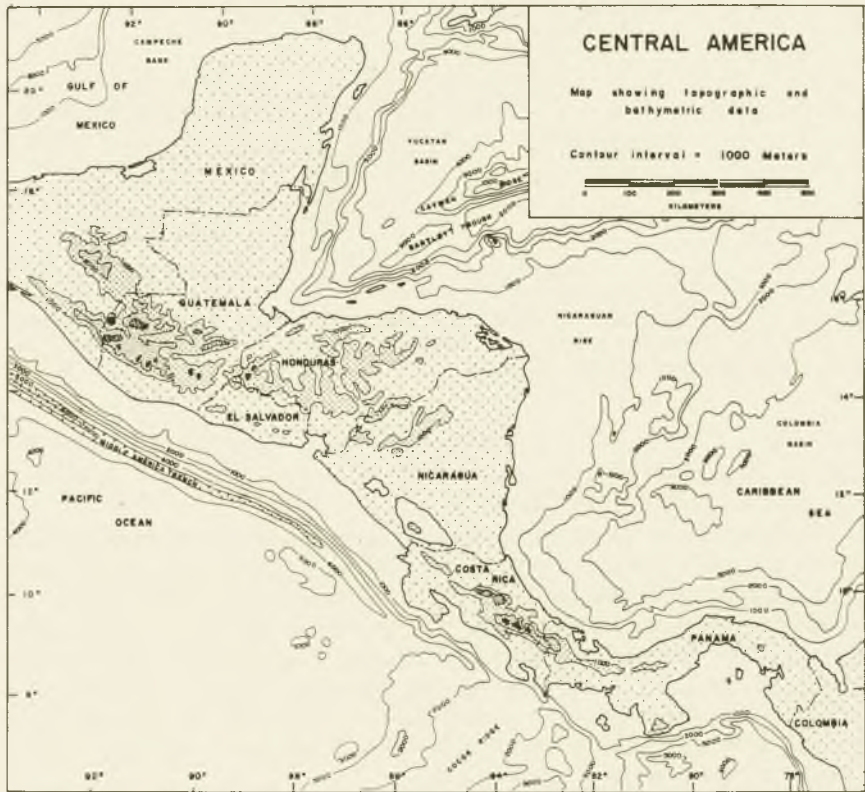


FIGURE 1. Topographic and bathymetric data for the Central America area.

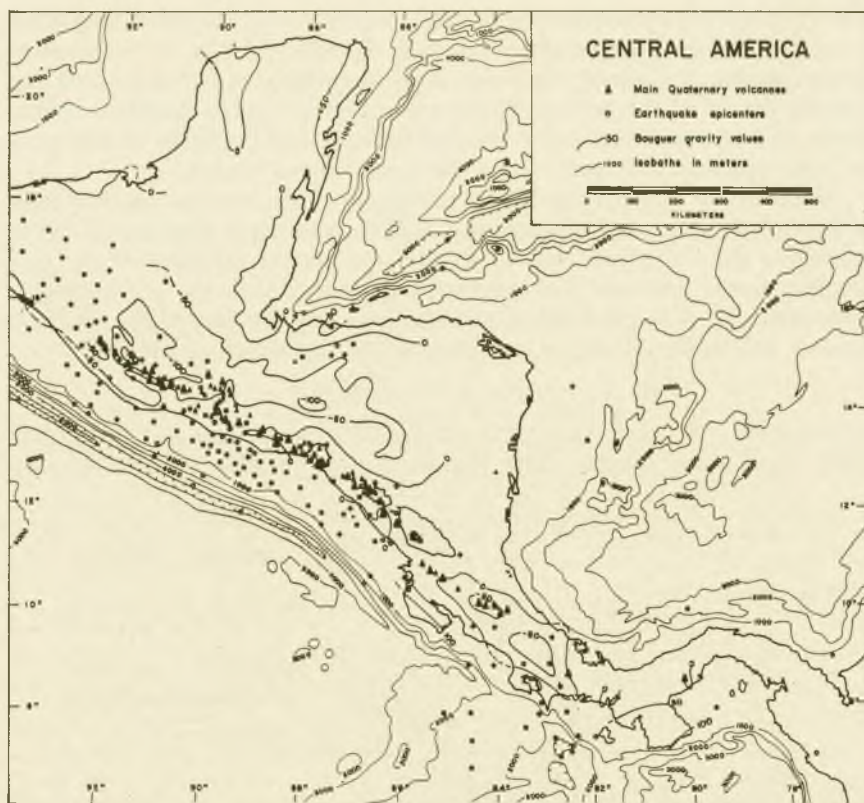


FIGURE 2. The Central American area with bathymetric data. The locations of the main Quaternary volcanoes and earthquake epicenters are shown together with Bouguer gravity values.

east- and southeastwards to the Atrato lowland in Colombia. Its geographical location, political divisions, as well as its terrestrial and submarine topography are shown in Figure 1.

The most salient terrestrial topographic features are the highlands (with elevations from 1,000 to slightly over 4,000 m), of the north-central part of the region, which extend from Chiapas, Mexico, across Guatemala, to Honduras and northern Nicaragua. North of the highlands is an extensive area of lower mountain ranges and lowlands, which includes the Yucatan Peninsula, continues northward as the submarine Campeche Bank, and terminates in the Campeche Escarpment in the Gulf of Mexico. This lowland area is separated from the Yucatan Basin (over 4,000 m deep), to the east, by a steep submarine scarp.

South and east of the highlands an extensive area of lower but rugged

topography comprises a large part of Honduras and Nicaragua. It continues to the east as a coastal plain and into the Caribbean as an extensive submarine bank less than 1,000 m deep, known as the Nicaraguan Rise or Mosquito Bank.

Another prominent terrestrial topographic feature in the southern portion of Central America is the highland area of central Costa Rica and eastern Panama (with altitudes from 1,000 m to 3,000 m). To the east of this highland a hilly lowland constitutes most of Panama and northwestern Colombia. This part of Central America is situated between the Cocos Ridge, which is a high area of the Pacific floor (generally less than 2,000 m deep), and a deep part of the Caribbean known as the Colombia Basin (more than 3,000 m deep) which separates the Nicaraguan Rise from South America.

The most prominent marine features in the areas adjoining Central America are the elongated deeps known as the Bartlett Trough (or Cayman Trench) in the Caribbean, and the Middle American Trench in the Pacific. The Bartlett Trough (with depths of more than 6,000 m), bounds the Nicaraguan Rise on the north and separates it from an elongated high called the Cayman Ridge. The Middle American Trench parallels the Pacific coast of Mexico and Central America. Its deepest portion (6,660 m) lies opposite the highest mountains (over 4,000 m). A chain of Quaternary volcanoes (Fig. 2), parallels the southern (Central American) part of the trench. On the ocean side of the trench lies the Guatemalan Basin with a general depth of over 3,000 m.

Geophysics.—The geological structure of Central America is now better understood as result of the geophysical information obtained both on land and at sea.

The Bouguer gravity values on the mainland (Woollard & Monges Caldera, 1956; Monges Caldera *et al.*, 1962) shown in Figure 2, closely correspond with the main topographic features, that is, the higher negative anomalies lie over the highland areas. They also give an indication of some of the main structural elements. The gravity minimum in western Guatemala (-100 to -150 mgal) corresponds to an area of granitic basement near the surface, and of granitic intrusive rocks. The larger area around this anomaly, marked by the -50 mgal contour, that extends from Chiapas to Central Honduras and northern Nicaragua, probably indicates the sub-surface extent of the granitic basement. The negative anomaly (-50 mgal) in southeastern Costa Rica corresponds to an area of Tertiary granodiorite intrusions of the Talamanca Range. These negative values should also correspond with the thicker parts of the crust, since it is generally accepted that the surface elevation, the Bouguer anomalies and the thickness of the crust are closely related (Woollard, 1959).

The higher Bouguer positive anomalies (over + 100 mgal) are found in the southern portion of Central America and correlate with areas such

as the Nicoya and Azuero peninsulas, underlain by a basement of basalt and other basic rocks.

The chain of Quaternary volcanoes does not reveal any apparent relation to any of the Bouguer anomalies on land. The main part of it, from southeastern Guatemala to northwestern Costa Rica, lies over an area of gravity values slightly above or below zero mgal.

The marine gravity information on both sides of the southern portion of Central America does not show any important anomalies over the Cocos Ridge (Vening Meinesz, 1960). On the Caribbean side there is a fairly large (-58 mgal) isostatic negative anomaly, north of Colón, Panama. The author does not know of any gravity surveys made over the entire length of the Middle American Trench, but the available adjusted gravity information shows negative anomalies along parts of it (Vening Meinesz, 1948).

Two types of seismic information are available for parts of the region, that derived from earthquakes (Gutenberg & Richter, 1954; Schulz, 1963; Figueroa, 1963), and that obtained by refraction methods at sea (Worzel & Schurbet, 1955; Ewing, Antoine, & Ewing, 1960; Shor & Fisher, 1961). Continuous seismic profiles carried recently by the Lamont Geological Observatory in the western Caribbean, and work now in progress off the Pacific coast of Nicaragua and Costa Rica, by Scripps Institution of Oceanography, should contribute to a better knowledge of the geophysical aspects of the region.

The earthquake epicenters shown in Figure 2 have been taken from the works of Schulz and Figueroa. The epicenters are located mostly along the Pacific, and to a lesser extent along the Bartlett Trough in the Caribbean. Those on the Pacific side may be grouped in three categories, according to the depths of their foci: (1) very shallow earthquakes associated with active faults on the mainland, particularly with a graben known as the Nicaragua Depression; (2) shallow earthquakes with foci between 30 and 70 km deep generally located near the edge of the Pacific Continental Shelf or in the Middle American Trench; and (3) intermediate focus earthquakes between 70 and 120 km deep and occasionally deeper but not exceeding 250 km, and aligned parallel to the trench but closer to the coast or inland. The intermediate and shallow earthquakes are associated with a fault zone that dips under the continent (Benioff, 1954). No deep focus earthquakes (over 300 kms deep) have been registered in the area, and no intermediate focus earthquakes have been recorded in the southern portion (Costa Rica-Panama) of Central America. The earthquakes that originate in this southern part present characteristics that suggest a different type of basement than the northern area (Schulz, personal communication).

The following conclusions were obtained from the marine seismic studies in areas bordering or near Central America:

- (1) A section normal to the Middle American Trench, off Guatemala

- (Fisher, 1961; Shor & Fisher, 1961) shows that the thickness of of the crustal layer (depth below sea level to the M discontinuity) is 9 km in the Pacific Basin, 16 km under the trench and 17 at the shelf. The crust becomes thicker toward the land.
- (2) A section over the Campeche Bank (Worzel & Schurbet, 1955) shows the crustal layer to be 17 km thick north of the Campeche Escarpment, 18 to 25 km thick from the edge of the shelf to the coast line, and to thicken southward under the Yucatan Peninsula.
 - (3) A structural section across the western Caribbean (Ewing, Antoine, & Ewing, 1960) indicates crustal thickness of 10 km under the Cayman Ridge, 6 to 8 km under the Bartlett Trough, more than 20 km in the Nicaraguan Rise, and 15 to 18 km in the Colombia Basin.

The previously summarized geophysical information permits certain conclusions regarding the nature of the crust in different parts of Central America and nearby marine areas. The northern portion, including the Nicaraguan Rise, is underlain by continental crust. This is corroborated by the known geology (Dengo & Bohnenberger, In Press) that shows the existence of a crystalline basement of Lower or Middle Paleozoic rocks. The southern portion (southern Nicaragua to northwestern Colombia), on the other hand, is underlain by a crust of intermediate thickness on the Caribbean side, similar to that of the Colombia Basin, and by a thinner crust probably of oceanic type, on the Pacific side. These implications regarding the nature of the crust are also supported by the geological facts (Dengo, 1962b) which demonstrate that the southern area has a basement largely made up of Mesozoic basic rocks.

On this basis, the region is considered to consist of two major geological provinces, Northern Central America and Southern Central America, whose tectonic histories have been different at least until mid-Tertiary time, when extensive volcanic activity was common to both areas. The younger features such as the development of the Middle American Trench and the Quaternary volcanic chain are also common to both provinces.

TECTONIC HISTORY

Northern Central America.—The geological differences between the northern and southern portions of Central America were recognized long ago (Vaughan, 1918; Wooding, 1928; Schuchert, 1935; Sapper, 1937), establishing that Northern Central America is part of the North American Continent. The structural boundary of this continent is considered by some authors (*i.e.*, L. King, 1962: 584), to lie along central Nicaragua and the southern continental slope of the Nicaraguan Rise.

The earlier episodes of the geological history of this part of the region are poorly known. It is possible, however, to trace it as far back as

mid-Paleozoic time. A land platform is considered to have existed at the present position of the Yucatan Peninsula and the Campeche Bank, which was the source for the sediments deposited in a marginal geosyncline, along its southern edge. Open sea existed immediately south of the geosyncline. We cannot determine how far the geosyncline extended toward the Caribbean, but it probably occupied part of the present Nicaraguan Rise (Meyerhoff, 1966).

The Paleozoic geosyncline was strongly deformed, metamorphosed, and intruded by several large granite plutons that extend across Northern Central America from Chiapas to the Caribbean coast. Rubidium-strontium dating of some of these metamorphic rocks indicates a probable Devonian age for the metamorphism and granitic intrusions (McBirney & Bass, In Press).

Upper Pennsylvanian to Lower Permian (Wolfcampian-Leonardian) sedimentary rocks that constitute a clastic wedge, were unconformably deposited over the metamorphic and granitic complex. Both suites of rocks were folded during Late Permian to Early Triassic times. This episode was followed by uplift and emergence of an extensive land area that occupied the present position of Northern Central America and the Nicaraguan Rise. The Late Paleozoic-Early Mesozoic orogenic movements and subsequent uplift, correspond to the orogenic phase of the Jaliscoan geotectonic cycle of Mexico (Guzmán & de Cserna, 1963) and to the Nevadan orogeny of North America (Eardley, 1954). Large longitudinal faults along the crest of the uplift marked the beginning of such features as the Bartlett Trough and the Cayman Ridge. It is possible, however, that some of these regional faults were controlled by older lines of weakness, as they separate parts of somewhat different geological history, at least since the Paleozoic episodes of metamorphism. This faulting resulted also in localized sedimentation along a narrow trough in Central Honduras where Late Triassic-Early Jurassic sediments were deposited (Mills, *et al.*, in preparation). Another event of importance after the uplift was the localized volcanic activity in Chiapas, Mexico.

Another regional depositional event started with widespread sedimentation of continental red beds, partly restricted to narrow fault troughs, during Late Jurassic and Early Cretaceous time. Subsidence of the area resulted in the formation of several large islands in its southern part and a large depositional area to the north, which was part of the extensive Mexican miogeosyncline. The general subsidence of Northern Central America, was contemporaneous with the tectonic activity in the open ocean area to the south, where a volcanic island arc was being formed in the position that now occupies Southern Central America. This is the oldest tectonic episode that was common to both parts of the region.

In the geosyncline, the basal Late Jurassic clastic rocks were followed by deposition of a great thickness of carbonates and evaporites that range

in age from Neocomian to Senonian (Santonian). Shallow deposition along smaller basins south of the geosyncline (southeastern Guatemala, Honduras, and northern Nicaragua) was characterized by limestones and subordinate clastic rocks of Aptian-Albian age.

Post-Albian pre-Senonian disturbances affected the southern portion of Northern Central America and were accompanied by intrusion of granitic and granodioritic rocks which now crop out from southern Guatemala to northern Nicaragua, and probably occupy part of the Nicaraguan Rise. This disturbance had little or no effect on the main geosyncline in Chiapas and northern Guatemala.

During Late Cretaceous (Campanian to Maestrichtian) to early Eocene times, the entire area of Northern Central America was subject to orogenic movements (Laramide) of different intensities, accompanied by contemporaneous sedimentation of clastic rocks in restricted areas. Intense faulting and folding took place along the axis of the geosyncline, while less severe movements affected the areas to the south (southeastern Guatemala to northern Nicaragua) and only mild deformation occurred in the north (Yucatan Peninsula).

There is evidence of Late Cretaceous volcanic activity in parts of Honduras and Nicaragua. It has been also assumed that Late Cretaceous to Eocene volcanic activity was localized along some of the now submerged ridges of the western Caribbean (Ewing, Antoine, & Ewing, 1960).

Renewed uplift and emergence followed during late Eocene and Oligocene times, leaving some restricted basins such as that of Campeche in Mexico, and Mosquitia in southeastern Honduras and northeastern Nicaragua. Except for the above-mentioned basins, Miocene and Pliocene marine sedimentation in Northern Central America was restricted to small embayments along fault troughs, such as that of the lower Polochic and Motagua valleys in Guatemala. Tertiary terrestrial sediments, localized in downfaulted basins, are fairly widespread, particularly in the area from central Guatemala to northern Nicaragua.

Extensive deposits of rhyolite tuffs, ignimbrites, and basalt flows, covered a large area in southern Guatemala, El Salvador, Honduras, and north-central Nicaragua. The volcanic activity occurred mainly during the Miocene and Pliocene epochs, although there seems to have been older volcanism in central Nicaragua (McBirney & Williams, 1965).

Separate consideration should be given to a wide zone of serpentinites and serpentinitized peridotites that crops out from Chiapas, Mexico, to the Bay Islands, off the coast of Honduras in the Caribbean. Their distribution follows essentially the wide zone of faulting related to the Bartlett Trough. It has been suggested by McBirney (1963) that these rocks represent mantle material emplaced along large fault zones. This possibility is partly supported by the presence of such rocks as eclogite, along the same zone. The fact that the mantle is found below a thin oceanic crust in the Bartlett

Trough, also gives support to this suggestion. The age of emplacement of the serpentinites is not known, but there is evidence that they were exposed to the surface prior to Maestrichtian sedimentation, that is, during the early deformational stages of the Laramide orogeny, and that they were remobilized during subsequent movements of the fault zone. The spacial relationships between a major zone of faulting and the serpentinites suggest that both are genetically related and that the original episode of emplacement may have been older than Cretaceous, perhaps contemporaneous with the Paleozoic tectonic disturbances.

Several attempts have been made to relate the tectonic history of Northern Central America with that of the Greater Antilles (Schuchert, 1935; Hess, 1938; Hess & Maxwell, 1953; Woodring, 1954). The relationships with the Cayman Ridge, Bartlett Trough, and the Nicaraguan Rise are apparently simple, although a complete correlation with Jamaica presents several problems. A correlation with Cuba and with the poorly known history of the Yucatan Basin is more difficult, and still remains as one of the major geological problems of the Caribbean region.

Southern Central America.—The history of Southern Central America began with the formation of an island arc built over a ridge of the ocean floor, as a result of movement of the Caribbean crust toward the Pacific ocean. Prior to the formation of the arc, both oceans were connected by the "Caribbean Mediterranean," as it was designated by Schuchert (1935). In fact, the western Caribbean, as stated by King (1962, p. 584) "may truly belong to the Pacific realm." The original form of the arc did not conform with the present sigmoidal shape of the isthmus. It was probably a simple open arc, concave to the Caribbean side, which extended from the southern edge of Northern Central America to the northwestern part of South America, essentially along the present position of the peninsulas of Nicoya, Osa, Azuero, and Garachiné. The present shape of the isthmus, in particular the arcuate form of Panama concave to the south, is the result of later tectonic deformation. These islands were formed during the span from Late Jurassic to Early Cretaceous, and, as it is supported by the present geological information, there is no evidence of any older land masses in this area, contrary to what has been postulated in several paleogeographic maps. It is difficult to establish whether there was some kind of marine trench associated with the island arc.

The combined processes of concomitant volcanism, erosion, and sedimentation, resulted in a complex association of igneous and sedimentary rocks, basalt agglomerates, cherts, siliceous limestones and graywakes. Some outcrops of red mudstones and manganiferous cherts were probably deep-sea sediments, and some of the older highly-altered basalts are considered to represent exposures of the oceanic crust. A similar association of rocks, along the western coast of northern South America, has been interpreted as a eugeosynclinal facies (Jacobs, Bürgl, & Conley, 1963),

and is considered to be no older than the Callovian stage of the Jurassic.

This suite of igneous and sedimentary rocks was deformed and even slightly metamorphosed, during mid-Cretaceous times, prior to the deposition of Campanian-Maestrichtian sediments. It is possible that this deformation corresponds with the tectonic episodes responsible for the intrusion of granite plutons in the central part of Northern Central America. Faulting of large displacement, along the trend of the Clipperton fracture zone of the Pacific floor, took place at this time, exposing the serpentinized peridotite that now forms a large part of the Santa Elena peninsula in northern Costa Rica. The peridotite has been interpreted to be an outcrop of the mantle, brought up on the up-thrown block of a fault (Dengo, 1962a), in a similar situation as that of Saint Paul's Rock in the Atlantic (Hess, 1955).

During Late Cretaceous to Eocene, a depositional trough was located on the concave (Caribbean) side of the arc, representing the northernmost extension of the Bolivar Geosyncline of northwestern South America (Nygren, 1950). The main source of sediments were the volcanic islands, and to a lesser extent the distant land areas of Northern Central America and of northwestern South America. Concomitant orogenic movements (Laramide), during this time span, produced local unconformities and folding and resulted in fragmentation of the trough and its separation from the Bolivar Geosyncline. Volcanic activity, prevailing of andesitic type, continued during Late Cretaceous to Eocene, with gradual shifting of the active centers to the east.

Tertiary marine sedimentation, with local oscillations, continued in the main part of the Bolivar Geosyncline along the western coast of South America from Peru to Colombia, while in Southern Central America it was localized in small basins. The Caribbean sea and the Pacific Ocean continued to be connected by several openings.

Volcanic activity and local tectonic disturbances, during Late Tertiary, culminated with granodiorite intrusions (late Miocene) along the axis of the isthmus. Uplift of a large part of the area resulted in the separation of the Caribbean and the Pacific. This episode was followed by rapid sedimentation of thick boulder conglomerates during Pliocene. The late Miocene-Pliocene volcanism was characterized by basalt and andesite rocks, in contrast to the rhyolite-basalt volcanism that took place contemporaneously in Northern Central America. These differences in composition of the volcanic rocks are probably related to the different crustal structure and composition of both portions of the region. Petrological studies now in progress by Howel Williams and A. R. McBirney will define more closely the relationships between the different igneous rock associations and the geological structure.

Pacific Marginal Zone.—Along the Pacific coast of Mexico and Central America, from the Islas Tres Marias to the Nicoya Peninsula, extends a

narrow and deep depression called the Middle American Trench. Descriptions and maps of the topography of this trench have been presented by Heacock & Worzel (1955) and Fisher (1961). The trench presents two parts of somewhat different topography and structure, marked by its intersection with the Tehuantepec fracture zone (Menard & Fisher, 1958). The southeastern part of the trench, in contrast to the northwestern portion, is separated from the main land by a wider continental shelf, is parallel to a chain of Quaternary volcanoes on land and is underlain by a thicker crust.

The structural interpretation made by Fisher (1961) based on refraction seismic data, indicates that this trench may be compared with other trench-island arc systems of the Pacific, even if it is shallower and located along a continental border. He did not find indications of a crustal downbuckle or tectogene. The negative gravity anomalies associated with it have been interpreted by Vening Meinesz (1948) as an indication that the continent is riding over the sea, perhaps also incidental to strike slip movements. Benioff (1954) interpreted the seismic data to indicate a fault complex dipping under the continent at an angle of 39° . A similar interpretation, although considering a lower angle, has been presented by Schulz & Weyl (1960). From these indications, it has been established that the trench was formed almost perpendicular to regional compression.

Quaternary volcanic activity in Central America is essentially restricted to the Pacific margin, with some exceptions of isolated cones on the Atlantic side. The chain of Quaternary volcanoes is located on the line of maximum bending of the upthrown block along the large zone of thrust faulting associated with the trench (Benioff, 1954). The axial part of this upbent block is marked by a graben of large proportions, usually referred to as the Nicaraguan Depression, which extends from southeastern Guatemala to Costa Rica, where it crosses the isthmus to the Caribbean side (Williams, McBirney, & Dengo, 1964; McBirney & Williams, 1965). Across Guatemala the graben loses its identity, is intersected by several small northward trending grabens, and seems to continue to the Mexican border as a single line of faulting. Quaternary volcanic rocks are mostly andesites in the southern province and andesite, rhyolite, and basalt in northern Central America.

The structural features along the Pacific marginal zone, namely the trench, volcanic chain, and parallel fault zones are very young and were probably developed during Late Tertiary and Quaternary times. They are all part of the last episode of the tectonic history of the region, and constitute its most actively tectonic zone, as it is evidenced by several active volcanoes and by frequent seismic shocks.

PACIFIC-CARIBBEAN FRACTURE PATTERN

Several explanations have been proposed in regard to the major fracture pattern of the larger region that includes the Caribbean, Central America,

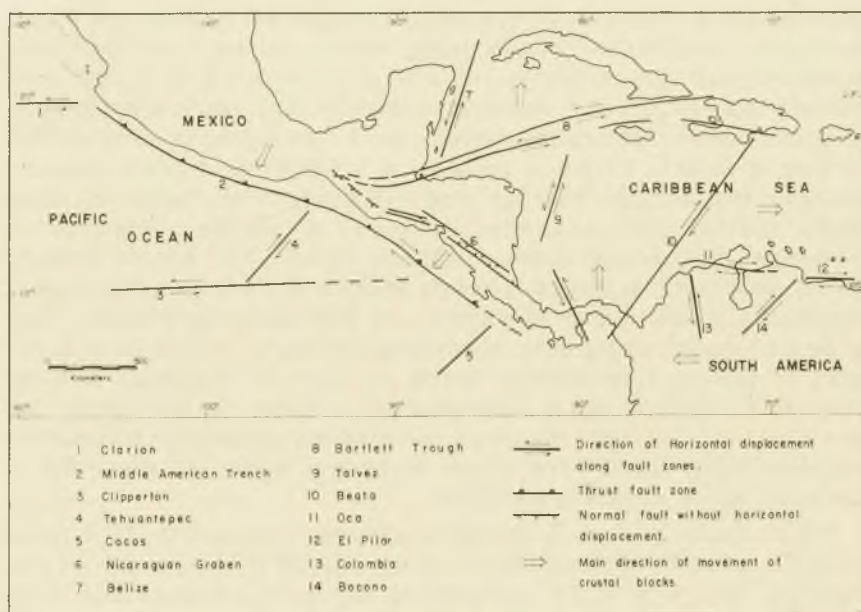


FIGURE 3. Pacific and Caribbean fracture zones.

and the adjoining part of the eastern equatorial Pacific. The fact that some of the major fracture zones in the Caribbean and the Pacific lie apparently along the same trends, has led several authors to believe that they are genetically related and that, therefore, they should have the same direction of horizontal displacement. For instance, Menard & Fisher (1958: 249) have stated that "the great transcurrent faults that bound the Caribbean Sea to the north and south lie along extensions of trends of the Clarion and Clipperton fracture zones and appear to be part of the same pattern." The actual relationships, however, are more complex, as it is evidenced by the geological structure of Central America.

The most obvious discrepancy for a simple relationship and similar directions of movement, is presented by the West Indies island arc, formed by an eastward movement of the eastern Caribbean, and the Middle American Trench which resulted from a southwestward shift of Central America. The later stages in the formation of these features were contemporaneous.

One may examine first the possible continuity between the Clarion fracture zone of the Pacific and the Bartlett Trough of the Caribbean (Fig. 3). The possibility of the connection between these two features is suggested by the distribution of earthquake foci (Menard, 1955; Gutenberg & Richter, 1954). However, the geology of Northern Central America

indicates that the fault zones (Polochic, Motagua) that lie along the inland extension of the Bartlett Trough swing, from a general east-west trend, to the northwest, and probably merge with, or are cut off by, the northwest-trending line of faults that parallel the Pacific Coast and that are largely concealed under Quaternary volcanic rocks. As it was pointed out by Menard & Fisher (1958), a problem in relating one fracture zone to another is that the age of faulting is not well known. The Clarion and other Pacific fracture zones have been considered as possible Cretaceous or rejuvenated Precambrian features (Menard, 1955). The Bartlett Trough, on the other hand, according to recent analyses of the regional geological environment, seems to have originated some time during the Paleozoic Era, along an already existing zone of structural weakness, and to have developed its present characteristics during or after the Laramide orogeny (Meyerhoff, 1966; Dengo & Bohnenberger, *In Press*). In spite of the fact that there are difficulties in finding a real continuation between the Bartlett and the Clarion fracture zones, one factor that favors this possibility is that both are of the left-lateral type.

The continuity between the Clipperton fracture zone and the fault zones of northern South America (Fig. 3) is also difficult to explain, even if one considers that their spatial relationships are more apparent than those previously discussed. The age of faulting might be contemporaneous since both could be Cretaceous features (Dengo, 1962a; Rod, 1956; Alberding, 1957). The main problem in this case involves the direction of relative movement, which is sinistral for the Clipperton zone and dextral for the South American faults. East-west faulting, along the trend of the Clipperton zone, in the Santa Elena peninsula of Costa Rica, has been determined to be left-lateral (Dengo, 1962a). These faults cannot be traced across the isthmus because they are cut by the Nicaragua Depression and covered by Quaternary volcanic rocks.

The problem of movements in opposite directions, along fractures on the same trend, has been investigated in the Pacific by Menard (1960) who found that the displacement along the fracture zones is not always the same on the continents. Menard thinks that it is possible that unrelated stresses, at different times, may have produced movement in different directions along the same fracture zone.

The relationships between the Pacific and Caribbean fracture zones are further complicated by other regional features associated with, or resulting from faulting. Of particular importance is the consideration that should be given to the Middle American Trench. The Clarion and Clipperton fracture zones practically limit the trench on both ends, although it actually extends somewhat beyond the intersections with those zones. The trench is a young feature that probably developed during Late Tertiary and Quaternary times, as a result of the continental mass of Mexico and Central America riding over the sea floor. It lies along the continuation of the San Andreas fault of

North America, and probably presents a right-lateral strike-slip component (Williams, McBirney, & Dengo, 1964). The relationships between the trench and the Pacific fracture zones are also complicated by the Tehuantepec Ridge fault zone, a branch of the Clipperton that intersects the trench and divides it in two parts of somewhat different physical characteristics (Menard & Fisher, 1958). The Tehuantepec fault zone seems to be active and presents a horizontal displacement of the dextral type (Fig. 3).

At least two other features should be taken into consideration, namely the Cocos Ridge and the Beata Ridge in the Caribbean. The first, according to Vening Meinesz (1960) is the result of horizontal shear movements in the crust and, at present, is isostatically compensated. The Beata Ridge is also considered by Vening Meinesz (1960) to be located along a shear plane that trends to the northeast. He regards the movement along this shear as left-lateral. The geological information on the possible intersection of this fault with the island of Hispaniola is not very conclusive, however, but it gives a slight indication that the horizontal movement is right-lateral (Bowin, 1966). A northeast-trending fault in eastern Panama (Terry, 1954) may be also an extension of the Beata fault. The arcuate, concave to the south, structural trends of Panama (King, *In Press*) may well be explained by a northward movement of a small wedge-shaped block bounded by divergent faults that strike to the northwest in the western part and to the northeast in the eastern part of that country. If this be the case, the faults along the Beata trend have a right-lateral horizontal component.

From the preceding discussion, it is evident that there is no simple relationship between the Caribbean and Pacific fracture zones. The present tectonic pattern of the region is obviously controlled to a large extent by fracture zones of large dimensions, whose characteristics indicate trans-current movements of different intensities and proportions, as has been suggested by Moody (1963). Moody thinks that this is a very old pattern, but the present author considers that it was basically developed during, or at the end of, the Laramide orogeny. This orogeny produced the rejuvenation of older fracture zones like the Bartlett Trough, and the initiation of new ones like those of Northern South America. Subsequent deformation has probably been controlled by movement of individual blocks relative to each other and did not have either the regional extent nor the intensity of the Laramide orogenic movements. Of prime importance in understanding the present structural framework, therefore, is the unravelling of the paleotectonic conditions from mid-Cretaceous to the end of the Eocene, as well as the interpretation of the stress patterns that were active during the Laramide orogenic episodes. These studies are suggested for future investigations and no attempt is made here to elaborate any further along these lines.

After examining the different directions of movement along some of the

major or fracture zones (Fig. 3) one may arrive at the conclusion that, at present, the region is broken up into crustal blocks that have moved, or are moving, relative to each other. The boundaries between these blocks are prevalingly transcurrent faults. These faults present different characteristics probably related to the nature of the crust in each block. Some faults that separate a block of continental crust from one of oceanic crust, such as the one along the Middle American Trench, also present a large dip-slip component.

It is difficult to establish whether the faults are the result of one major stress pattern. From the description of the geologic history of the region, it seems more likely that they developed at different times under different stress directions, but that the present pattern is the result of one major epoch of deformation, in this case, the Laramide orogeny. Subsequent relative movements of the blocks have produced localized stress patterns within them, which are different in each one. This may account for the different degrees of deformation between Northern Central America and Southern Central America during mid- and late-Tertiary times.

A similar explanation of fragmentation of the region in crustal blocks has been presented by Moody (1963) who has suggested that "wrench-fault tectonics might have been operative on a grand scale, and have provided the basic control for the topography and structure as we see it today." Moody (In Press) has also presented a tectonic map of Central America based on his interpretation of individual blocks bounded by faults. The views presented here differ from those of Moody in that the role assigned to the transcurrent movements is restricted to the present fragmentation of the region and not to a basic control of its structure. Furthermore, the author disagrees with several of the faults that cut across Central America as shown in Moody's map for which there is little or no evidence. The tectonic map recently compiled by King (In Press) presents more accurately the factual data on the structure of the area as it is known today.

Larger displacement of crustal blocks, of continental drift proportions, have been proposed by several authors. A resumé and discussion of some of these interpretations, and a new drift hypothesis, have been presented recently by McBirney & Bass (In Press). It is not possible, with the present knowledge of the area, to support fully any of the drift interpretations involving Central America and its relations to the Caribbean region.

REFERENCES

- ALBERDING, H.
1957. Application of principles of wrench-fault tectonics of Moody and Hill to northern South America. *Bull. geol. Soc. Amer.*, 68: 785-790.
- BENIOFF, HUGO
1954. Orogenesis and deep crustal structure-additional evidence from seismology. *Bull. geol. Soc. Amer.*, 65: 385-400.
- BOWIN, CARL
1966. Geology of Central Dominican Republic. *Mem. geol. Soc. Amer.*, 99: 11-84.

- DENGO, GABRIEL
 1962a. Estudio geológico de la región de Guanacaste, Costa Rica. Inst. Geogr. de Costa Rica, San José, 112 p.
 1962b. Tectonic-igneous sequence in Costa Rica. Geol. Soc. Amer., *Buddington Vol.*, : 133-161.
- DENGO, GABRIEL AND OTTO BOHNENBERGER
 In Press. Structural development of Northern Central America. Amer. Ass. Petrol. Geol.
- EWING, J., J. ANTOINE, AND M. EWING
 1960. Geophysical measurements in the western Caribbean Sea and in the Gulf of Mexico. J. geoph. Res., *65*: 4087-4126.
- FIGUEROA, JESÚS
 1963. Historia sísmica y estadística de temblores de la costa occidental de México. Geof. Oceanogr. Amer. México, Bol. Bibl., : 107-134.
- FISHER, ROBERT L.
 1961. Middle America Trench: topography and structure. Bull. geol. Soc. Amer., *72*: 703-720.
- GUTENBERG, B. AND C. F. RICHTER
 1954. Seismicity of the Earth. Princeton Univ. Press, Princeton, N.J., 310 p.
- GUZMÁN, EDUARDO AND ZOLTAN DE CSERNA
 1963. Tectonic History of Mexico. Mem. Amer. Ass. petrol. Geol., *2*: 113-129.
- HEACOCK, J. G. AND J. L. WORZEL
 1955. Submarine topography west of Mexico and Central America. Bull. geol. Soc. Amer., *66*: 773-776.
- HESS, HARRY H.
 1938. Gravity anomalies and island arc structure with particular reference to the West Indies. Proc. Amer. phil. Soc., *79*: 71-96.
 1955. The oceanic crust. J. Mar. Res., *14*: 423-439.
- HESS, HARRY H. AND J. C. MAXWELL
 1953. Caribbean research project. Bull. geol. Soc. Amer., *64*: 1-6.
- JACOBS, C., H. BÜRGEL, AND D. L. CONLEY
 1963. Backbone of Colombia. Mem. Amer. Ass. Petrol. Geol., *2*: 62-72.
- KING, LESTER
 1962. Morphology of the earth. Oliver and Boyd, Ltd., London, 699 p.
- KING, PHILIP B.
 In Press. Tectonic map of North America, Scale 1:5,000,000. U.S. geol. Surv.
- MCBIRNEY, ALEXANDER R.
 1963. Geology of a part of the Central Guatemalan Cordillera. Univ. Calif. Publ. Geol. Sci., *38*: 177-242.
- MCBIRNEY, ALEXANDER R. AND HOWEL WILLIAMS
 1965. Volcanic History of Nicaragua. Univ. Calif. Pub. Geol. Sci., *55*: 1-65.
- MCBIRNEY, ALEXANDER R. AND MANUEL N. BASS
 In Press. Structural relations of pre-Mesozoic rocks in Central America. Amer. Ass. petrol. Geol.
- MENARD, H. W.
 1955. Deformation of the Northeastern Pacific Basin and the west coast of North America. Bull. geol. Soc. Amer., *66*: 1149-1198.
 1960. The East Pacific Rise. Science, *132*: 1737-1746.

- MENARD, H. W. AND R. L. FISHER
1958. Clipperton fracture zone in the northeastern Equatorial Pacific. *J. Geol.* 66: 239-253.
- MEYERHOFF, ARTHUR A.
1962. Bartlett fault system: age and offset. Paper presented at the Caribbean Geological Congress, Jamaica, April, 1962.
- MILLS, R. A., K. E. HUGH, D. E. FERAY, AND H. C. SWOLFS
(In preparation), *Stratigraphy of Honduras*.
- MONGES CALDERA, J., G. P. WOLLARD, J. A. KOZLOSKY, AND H. DUARTE
1962. Informe sobre trabajos de gravimetría en Centro América y Panamá. *Anales Inst. Geof. Mexico, VIII*: 13-22.
- MOODY, J. D.
1963. Tectonic pattern of Middle America. Paper presented at the A.A.P.G. meeting at Houston, March, 1963.
In Press. *Geology of Central America*.
- NYGREN, V. E.
1950. Bolivar geosyncline of northeastern South America. *Bull. Amer. Ass. petrol. Geol.*, 34: 1998-2006.
- ROD, E.
1956. Strike-slip faults of northern South America. *Bull. Amer. Ass. petrol. Geol.*, 40: 457-476.
- SAPPER, KARL
1937. *Mittelamerika. Handbuch der Regionalen Geologie*. Steinman und Wilckens, Heildelberg, 160 p.
- SCHUCHERT, CHARLES
1935. *Historical geology of the Antillean-Caribbean region*. John Wiley & Sons, Inc., New York, 811 p.
- SCHULZ, RUDOLF
1963. Estudio sobre la sismicidad en la región Centro-Americana. *Geof. Oceanogr. Amer. Mexico, Bol. Bibl.*, : 135-144.
- SCHULZ, RUDOLF Y RICHARD WEYL
1960. Sismos y la estructura de la corteza terrestre en la parte norte de Centro America. *Bol. Sismol. El Salvador, V*: 36-40.
- TERRY, R. A.
1956. A geological reconnaissance of Panama. *Calif. Acad. Sci. Occas. Pap. No. XXIII*: 91 p.
- VAUGHAN, T. W.
1918. Geologic history of Central America and West Indies during Cenozoic time. *Bull. geol. Soc. Amer.*, 29: 615-630.
- VENING MEINESZ, F. A.
1948. Gravity expeditions at sea, 1923-1938. *Neth. geod. Comm. Pub.*, Delft, 4: 233 p.
1960. Interpretation of Caribbean and Pacific Cruises. In Bruins, G. J., Ed., *Gravity Expeditions 1948-1958*. *Neth. Geod. Comm. Pub.*, Delft, 5: 28-34.
- WILLIAMS, HOWELL, A. R. MCBIRNEY, AND G. DENG
1964. Geological reconnaissance of southeastern Guatemala. *Univ. Calif. Publ. Geol. Sci.*, 59: 62 p.
- WOLLARD, G. P.
1959. Crustal structure from gravity and seismic methods. *J. geoph. Res.*, 64: 1521-1544.

WOLLARD, G. P. Y J. MONGES CALDERA

1956. Gravedad, geología regional y estructura cortical de Mexico. *Anales Inst. geof. Mexico, II*: 60-96.

WONZEL, J. LAMAR AND G. LYNN SCHURBET

1955. Gravity interpretations from standard oceanic and continental crustal sections. *In Crust of the Earth. Spec. Pap. geol. Soc. Amer.*, 62: 87-100.

WOODRING, W. P.

1928. Tectonic features of the Caribbean region. 3rd Pan-Pacific Sci. Cong., Tokyo, : 401-431.
1954. Caribbean land and sea through the ages. *Bull. Geol. Soc. Amer.*, 65: 719-732.

SOME PROBLEMS OF ISLAND-ARC TECTONICS, WITH REFERENCE TO THE NORTHEASTERN WEST INDIES

THOMAS W. DONNELLY

Department of Geology, Rice University, Houston, Texas¹

ABSTRACT

Geological evidence (principally based on the physical stratigraphy of volcanic deposits) suggests that the oldest rocks now exposed in the Virgin Islands, the spilites and keratophyres of the Water Island Formation (mid-Cretaceous), represent ocean bottom eruptions during the initial stages of orogenic activity. These eruptions occurred prior to the existence of an island platform or trench and were succeeded by the eruptions of the same magmatic materials in very shallow depths of sea water following the formation of the platform and trench. Later deformation of the area has resulted in continued uplift in response to presumably tangential compressive stresses within the mantle.

Present-day tectonic activity is reflected in post-Pleistocene uplift, seismicity, and regional gravity patterns (the latter for the Greater Antilles only). These show that the entire area continues to be deformed, and that the mode of deformation varies from area to area, according to the relative fractions of the primary deformative stress resolved as strike-slip motion along a hypothetical major fault system south of Puerto Rico, St. Croix, and St. Barts, and that resolved perpendicular to the arc as a compressive stress, which causes crustal thickening, uplift, and magmatic generation. Differences in the Tertiary and Recent tectonic and magmatic activities of the northern Lesser Antilles and the eastern Greater Antilles are explained in this way.

INTRODUCTION

As the symposium convened in Miami in November, 1965, indicates, the West Indies has become an area of extensive geological and geophysical interest. This interest is relatively recent; as recently as a decade ago the East Indies was still generally regarded as the classic island-arc area, largely as the result of the studies of Dutch geologists in the twenties and thirties. More recently, the West Indies has been the site of investigations encompassing a greater variety of disciplines, especially geophysics (seismic refraction, gravity, magnetics) and igneous petrology, in addition to more traditional structural-stratigraphic analysis. This area has not only become "classic" in its own right, but its study is providing important clues as to the origin of the entire middle American area.

Recent papers which have touched upon the problems of this area include Talwani (1964), Hess (1964), Sykes & Ewing (1965), and Donnelly (1964). Shortly after the symposium in Miami a paper by Morgan (1965) discussing aspects of the problem of the Puerto Rico Trench appeared.

¹Present address: Dept. of Geology, State University of New York, Binghamton, N.Y. 13901.

A basic unity among all island-arc systems is evident, and any analysis of one such system must be compatible with observations of the remainder, except where purely local conditions have resulted in purely local phenomena. The problem of the tectonic analyst is to choose which observations are truly analogous and which may be strictly local. The answers to these problems are never simple and every shade of intermediate situation exists.

GEOLOGICAL LIMITATIONS OF THE PROBLEM

Our more important observations are geological; indeed, the only observations we can make which have any projection backwards in time are based on the record of the rocks and of the landscape. To a certain extent, the rocks in all island arcs are basically the same. However, the north-eastern West Indies (more specifically, the eastern Greater Antilles) stands almost alone in the excellence of exposures of the older rock units of the arc platform association (Donnelly, 1964). In relatively few island-arc areas do we find pre-Middle Tertiary rocks exposed, but in Puerto Rico and the Virgin Islands there are excellent exposures of a sequence dating back to the Middle Cretaceous. The inference that similar rocks underlie all island-arc platforms is safe at first glance. However, we cannot be certain that the initiation of orogenic activity in all island arcs was at the same time, and, therefore, the problem of the buried stratigraphy in these other areas must remain one of our most tantalizing unknowns.

The geological evolution of Puerto Rico and the Virgin Islands, as based on the record of the rocks, is reasonably straight forward. The oldest deposits (the Water Island Formation) are submarine volcanic rocks evidently erupted directly on the sea bottom, probably at abyssal depths



FIGURE 1. Index map of northeastern West Indies.

(Donnelly, 1966). These were succeeded by thick and monotonous series of andesitic pyroclastic rocks erupted either subaerially or in relatively shallow water and ultimately deposited, in most cases, as very slightly reworked ash deposits on the shallow sea floor. Interbedded with these are a few biohermal limestones. The later (Upper Cretaceous and Lower Tertiary) rocks reflect increasing uplift and, more important, increasing topographic diversity and ruggedness, with increasing topographic control and restriction of sedimentary facies with time. The rock record shows that the island platform has continually emerged, although local subsidence in dominantly marginal graben has also been a conspicuous feature, especially during the later history.

One aspect of the geological history which might set the eastern Greater Antilles apart from other island-arc areas is the cessation of volcanic activity during the Eocene. I have offered an explanation for this cessation—the development of an extensive strike-slip fault system in the Eocene—which I still believe to be reasonably valid. However, deformation in the Greater Antilles has continued since this volcanic cessation, and rates for post-Eocene uplift can be calculated. The maximum rate that has been suggested is 5 mm/year for the part of the Virgin Bank showing maximum uplift of a surface presumably truncated during Pleistocene time (Donnelly, 1965). A much lower rate of uplift is calculable from the present elevation (450 m maximum) of the middle Tertiary limestones of northern Puerto Rico: assuming an age of approximately 15 million years, we find an average uplift of 1 mm/30 years. The difference between the two rates could indicate that Miocene-Pleistocene uplift proceeded at a different rate than post-Pleistocene uplift. More likely, it shows that the entire island platform is divided into relatively independent fault blocks and that the uplift of those blocks in the center of the island might be expected to be considerably greater than those along the margin. Indeed, the form of the middle Tertiary marginal limestones basins suggests a fault-bounded basin (even though these faults have no surface expression) and evidently the history of these blocks, though generally one of uplift, has included considerable downward movement in the period subsequent to the middle Tertiary.

Although the independence of the individual blocks makes the estimation of an average uplift rate very difficult and the determination of fluctuations of this rate with time all but impossible, stratigraphic evidence suggests that there has been no general subsidence of the island platform subsequent to the formation of this structure. We have no datum planes available which can give us similar information regarding the history of the trench and we do not know if it is very young or very old. I have suggested that it is old, and in fact only slightly younger than the older series of volcanic deposits found on the island platform. The sampling of rock units on the north wall should supply the answer; the youngest terrigenous sediment or sedimen-

tary-volcanic material (excluding, of course, wind-borne ash) found there must represent the maximum age of the trench. To date no material is known that might have originated from the island that is younger than the Albanian-Cenomanian interval, but the extent of sampling is not great. Some of the basaltic andesites from this wall bear a strong resemblance to Albanian-Cenomanian rocks from Puerto Rico and might be transported equivalents of these.² They could, however, be submarine effusions or distinctly older rocks. Many of the fossiliferous samples dredged on the north wall evidently represent planktonic assemblages whose accumulation would not have been affected by the presence or absence of a trench. The stratigraphy of the north wall is still largely unknown and represents one of the most serious gaps in our knowledge of the trench.

No theory of island-arc formation can be advanced which does not take these geological observations into account. Although many gaps remain in the tectonic history as interpreted from the rock record, there is a general evolutionary course which is rather clear. Any hypothesis must provide for emergence of a crustal welt with only limited re-submergence, as well as for the formation of volcanic magmas and the development of a system of dominantly vertical tectonics.

NATURE OF THE DEEP FUNDAMENTAL DEFORMATIVE FORCE

One of the more important problems considered by recent authors concerns the nature of the deep forces responsible for the formation of the arc. Talwani (1964) has presented a mass balance profile derived from an earlier gravity-derived structural cross section (Talwani *et al.*, 1959) of the Puerto Rico trench-platform. According to this mass balance profile, the mass deficiency beneath the trench is not balanced by the mass excess of the platform. Hence, the problem of maintaining a depressed trench is compounded by the possibility that the entire area, and not just the trench, may be out of balance. Morgan (1965) also assumes that the trench is mass-deficient, but that the adjacent island platform is in balance by itself. These two conclusions would contradict Donnelly's (1964) conclusion that the entire system is probably in balance, and that the platform had ridden over the trench and depressed it so that the platform held the trench down and the trench held the platform up. This conclusion is still locally correct.

Talwani's derivation of the mass balance relationship may be criticized on two grounds. The distribution of density with depth of the rock units beneath the trench and island platform is not known, and there are a variety of alternative structure sections which can be made to fit the gravity profile and the seismic refraction sections of the adjacent, relatively undisturbed Atlantic and Caribbean crusts. This objection is probably not serious; if

²A more recent examination of a long series of specimens in the possession of Dr. Richard Chase, Woods Hole Oceanographic Institution, to whom I am indebted for the privilege of examination, casts considerable doubt on a correlation of these volcanic rocks with Puerto Rican examples.

the crustal layers were allowed to vary in density within reasonable limits, the resulting shift of the interfaces derived from the gravity would do little to alter the mass balance solution. Though gravity observations at sea level are not directly convertible into a mass balance expression, they are not a bad approximation.

A second objection to Talwani's mass balance curve is more important. His section crossed the Puerto Rico trench directly north of San Juan where it is abnormally broad. If we consider the entire segment of arc-platform from the western tip of Puerto Rico at the west to Anegada Island at the east end, we note that the average width of the trench (defined here as that portion deeper than 4000 fathoms) is about half of that used by Talwani *et al.* (1959). The platform varies in width also, but averages about 80 per cent as wide (excluding the part around St. Croix) as Talwani's section. Therefore, a three-dimensional mass balance expression would show a much smaller mass deficiency for the trench than Talwani derives, with a slightly smaller mass excess beneath the island platform. However, even if we adjust the mass relationships to take these discrepancies into account the suspicion remains that the entire system will still be out of balance. (This may not be justified fully; the length in an east-west direction of the abnormally wide part of the Puerto Rico trench is about 100 km.) This is by no means certain, but the possibility or even probability of overall imbalance should be considered strongly. Talwani's suggestion that a similar derivation for a section across the East Indies shows an overall mass excess further clouds the question.

Although the conclusion that there exists a net downward force is not completely demonstrated, its existence could be fitted into an overall hypothesis which still emphasizes the dominance of horizontal forces. The observations of vulcanism and the inferences of more or less continual uplift of the arc platform are very basic ones. Because seismic observations tell us that the upper mantle is generally solid throughout, the generation of a magma requires raising the temperature of some part of the mantle. This can be done through the agency of an upwelling convective current, or it might result from the depression and heating of a part of the mantle which is normally solid but which has a melting point less than that of the depth to which it is depressed. An upwelling convective current beneath the arcs is the very antithesis of the gravity observations and inferred subcrustal conditions discussed by Talwani and by Morgan and it must be dismissed. The alternate idea has no such difficulties. The upper mantle is probably more or less stratified in the upper 10 to 20 km, chiefly as the result of isothermal layering which in turn controls degree of hydration. Some of this layering may be recent (base of the 7.2 km/sec layer beneath the Caribbean; [Donnelly, 1964]) and some, "fossil" (Mohorovičić discontinuity [Hess, 1954, 1962]). Visco-elastic failure of layered crustal and upper mantle material in response to deep horizontal forces will be a

thickening through flow, which will in turn produce emergence at the surface (to preserve isostatic balance) and fusion of the base of the root (from heating of hydrated material). There is no mechanism for surficial depression over a long period analogous to emergence; a cessation or momentary relaxation of horizontal forces at depth would simply cause a halt to the uplift and an extension would cause local rifting. Once an arc welt emerges it should remain emerged. Perhaps the strongest evidence supporting the hypothesis of horizontal forces at depth is the stratigraphic evidence that, except for purely local episodes, this is precisely what is observed.

If the inference of a net downward force beneath the arc is accepted, we would have to conclude that it must be a downward deflection of a dominantly horizontal force. The reason for the deflection, in turn, must be found in the nature of the crustal downbulge. The material within the downbulge will be different from that surrounding it and it will have differing physical properties. More important, downbulging should result in downward deflection of isothermal surfaces, both because heating will probably not keep pace with downbulging and because downbulging of any hydrated material will cause dehydration, which is a strongly endothermic process. A likely consequence of downbulging, especially in view of the

21° +
60°

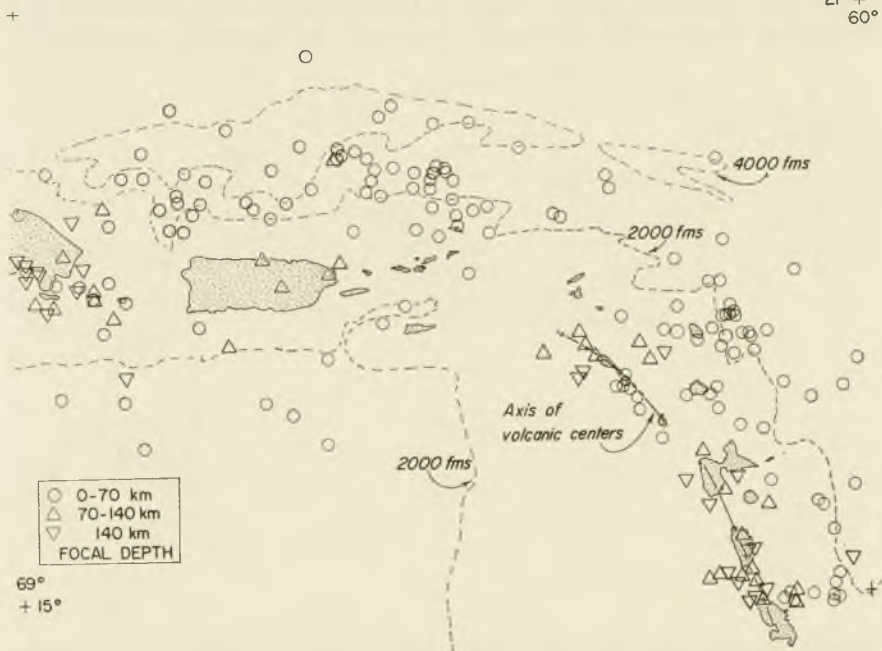


FIGURE 2. Map showing epicenters of recent earthquakes in northeastern West Indies, redrawn from Sykes & Ewing (1965).

possibility of deflection of isotherms, is that the flow of convecting mantle material will be deflected downward beneath the crustal welt. Whether this mantle material will continue to descend behind the arc, or whether it will rise slowly behind the arc, is not known and not really pertinent to the problem. At any rate, a net downward force, at least within the narrow region of the arc itself, can be reconciled to an environment of predominantly horizontal deep forces.

RECENT SEISMICITY OF THE NORTHEASTERN WEST INDIES

One of the most important contributions to our knowledge of the West Indies that has been made in recent years is a summary of slightly more than a decade's seismic activity by Sykes & Ewing (1965). Their epicenters for the region from Puerto Rico to Martinique are plotted on Figure 2, with no distinction made as to magnitude or precision of location. This figure shows that the northeastern West Indies is divided seismically into three regions: two active regions and an intervening apparently aseismic area extending from the Virgin Islands to Saba. This intervening area is only apparently aseismic; in fact, it is not possible to stay in the Virgin Islands more than a few weeks without feeling a small shock. Sykes & Ewing's summary, however, includes few shocks of magnitude lower than 4, and shocks of magnitude 2 are felt with no difficulty if they occur within a few miles and preferably at night. A more accurate interpretation of the distinction between this "aseismic" area and the neighboring seismically

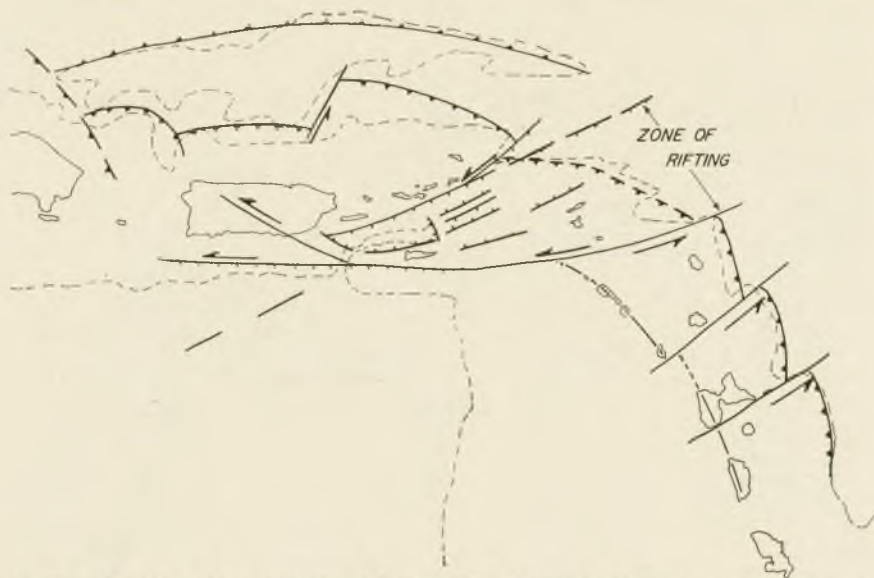


FIGURE 3. Map of northeastern West Indies, showing inferred pattern of deep faults. Note the fault through Puerto Rico is an idealized deep shear whose surface expression is a myriad of small faults.

active areas is that this area responds in a totally different way to the imposed deep horizontal forces that are deforming the entire Antillean area. In my previous summary (1964), I suggested that the cessation of volcanic activity in the Greater Antilles during the Eocene might have been the result of the formation of a major strike-slip fault, located south of Puerto Rico and St. Croix and extending eastward through the islands of the northern Lesser Antilles. I now believe that Sykes & Ewing's seismic map supports this idea and supplies a further interpretation of the tectonics of this corner of the West Indies. The entire area between the northern major bounding fault of the Anegada Trough and the major strike-slip fault to the south is a complex area of rifting (Fig. 3). The zone of rifting — that is, normal faulting accompanied perhaps to a minor extent by strike-slip faulting — now is seen to extend across the entire zone between the Virgin Islands and Saba. Post-Eocene response of the northern block (Puerto Rico and the Virgin Islands) to the subcrustal forces has been largely, though not entirely, strike-slip displacement along a series of fractures, of which no one fracture may be dominant, within this zone of rifting. The entire zone is an area of extension and is hence nearly in isostatic balance. The orientation of the principal undersea scarps within this zone is about 60° east of north; an orientation of the deep forces essentially parallel to this direction would be consistent with extension perpendicular to these scarps and would also be consistent with the major part of mapped structures with both the eastern Greater Antilles and adjacent Lesser Antilles.

The two seismically active areas — better called areas of numerous shocks with magnitudes greater than 4 — show a distribution of hypocenters which reflects the inferred thickening of the crustal welt in response to subcrustal drag. Three plots of the hypocenters in cross-section are given in Figure 4. One of these includes the segment of the arc from western Puerto Rico to the Anegada Island, but excludes the numerous hypocenters beneath easternmost Hispaniola (which evidently belong to a distinct structure). The second plot includes the Lesser Antillean chain from Saba south to Montserrat. The third plot covers the area from the southern tip of Guadeloupe to northern St. Lucia, and is Sykes & Ewing's Figure 2 (top).

The three cross-sections plots represent, first, an area of recent deformation, but lacking any volcanic activity since the Eocene; second, a segment of the Lesser Antilles which has been active throughout the Tertiary but in which there has been no eruptions for at least 300 years; and, third, an area which has had several very impressive historic eruptions, of which the famous Mt. Pelée eruption of 1902 is only one. The distinction between the latter two areas is also reflected in the thickness of Tertiary eruptive centers: the islands to the north of the Lesser Antillean chain appear to have experienced less volcanic activity during the late Tertiary

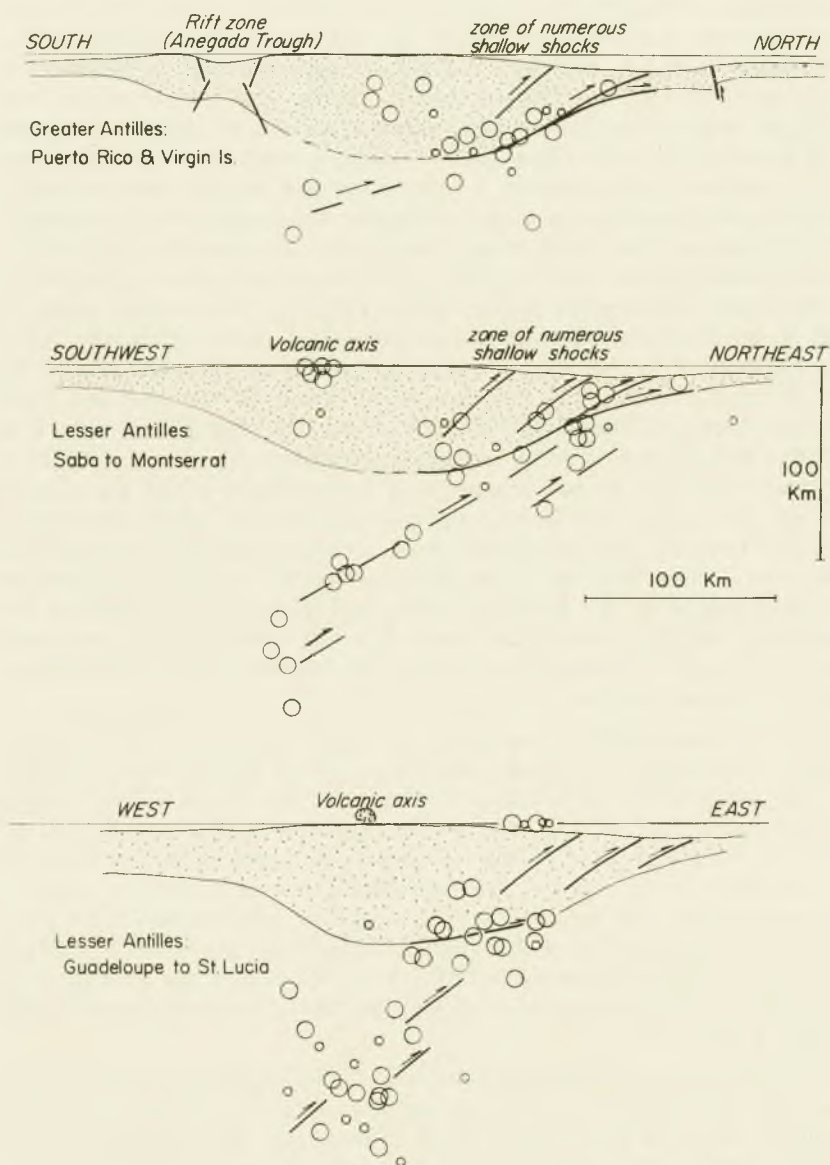


FIGURE 4. Cross sections through the northeastern West Indies, each oriented perpendicular to the arc, showing inferred crustal welt (stippled) and pattern of reverse faults. Upper two drawn from data of Sykes & Ewing (1965), with large circles their computed hypocenters and small circles USC&GS computed hypocenters. Lower figure redrawn from their Fig. 2 (top); "Larger symbols represent more accurate computations."

than their neighbors to the south.

The section underneath Puerto Rico and the Virgin Islands shows a distinct clustering of hypocenters at depths ranging from about 20 to 45 to 50 km beneath the southern slope of the Puerto Rico Trench. Most of these hypocenters can be fitted to a sloping plane which appears to terminate upwards in the trench and downwards at a point beneath the northern boundary of the arc platform. Behind this point the shocks are scattered. The correspondence between these hypocenters and Talwani *et al's* (1959) inferred base of the crustal layer beneath the islands is strong, if we are allowed to depress the base of the crust somewhat. Such a depression might be justified if we could show that there is a density gradient within the crustal layers, with the density increasing downwards. If the materials of the crust were originally stratified in response to isothermal distribution, then their heating through depression, even in the absence of magma formation, should result in metamorphic differentiation, with more extractable components removed upward through the agency of hydrothermal solutions. The residuum would be denser and we should probably expect the base of the crustal welt to be denser than the surface. The hypocenters beneath Puerto Rico and the Virgin Islands, then, might well simply outline the boundary between two different materials. The response of stress (here subcrustal drag, probably caused by convection) on a bipartite system will depend on several variables, including the rate of applied stress and the orientation of the boundary between the two materials. If the stress is applied slowly enough and the boundary oriented nearly parallel to the plane of maximum shear we may expect this plane to resolve the major portion of the stress. A fraction, evidently here a large fraction, of the stresses at depth are released along this plane, though some of this stress is also released along planes which are totally within, or transect the boundary between, the crust and mantle.

The cross section through the northern Lesser Antilles (center of figure 4) shows a somewhat different clustering of hypocenters. In addition to the shallow, obviously volcanic clusters — as, for instance, the seismic episode of Nevis during 1960 and 1961 (Robson *et al.*, 1962) — we can recognize a series of hypocenters analogous to those beneath Puerto Rico and the Virgin Islands. These are slightly more scattered but appear to define a plane extending to a depth perhaps slightly greater than under the Greater Antillean platform. A great many hypocenters, however, do not appear to be related at all to such a plane; some of these extend to great depths beneath the arc while others occur well within the crustal welt. These may represent that portion of the failure which results from a more rapid application of forces — a more purely elastic failure whose locus is completely independent of the boundary between crust and mantle. Carrying our observations one step further we note that the clustering of hypocenters beneath the recently active islands at the center

of the chain (bottom of Figure 4) shows clustering of hypocenters along the 50 to 60 km boundary, and along a vaguely defined plane sloping at about 45° beneath the islands, which is slightly steeper than for the northern Lesser Antilles. We might conclude that the distribution of hypocenters between the two groupings is based on rate of deformation.

Basing our analysis upon inferred rates of recent deformation (vulcanism, post-Pleistocene uplift), we can conclude that the three cross-sectional distributions of hypocenters reflect rate of deformation. At slow rates, much of the stress is dissipated in movements along the boundary between the crust and mantle. At faster rates, a system of fractures not related to this boundary develops. In fact, the generation of magma near the base of the crustal welt in the Lesser Antilles (if that is where it is generated, and much petrologic work still in progress suggests a relatively shallow origin) might, through the generation of a fluid, strengthless phase, prevent the accumulation of stresses sufficient to produce a shock of magnitude 4. A correlation between free-air anomalies (representing crustal downbulging) and seismic activity across the arc in various places would be most interesting.

The division of supposed groups of hypocenters into two categories related to resolution or non-resolution along boundaries and to rates of deformation is probably premature; our understanding of the nature of failure at earthquake foci is very primitive and even our ability to analyze seismic events in terms of strike-slip or dip-slip movement is limited. The groupings suggested here are based more upon the overall present tectonic environment, as evidenced by vulcanism and other manifestations of deformation, than upon any occult knowledge of the orogenic process itself. The seismic activity of the Antillean chain is most easily interpreted as representing the shear created by flow (convecting mantle), resolved in part along the boundary between the crust and the mantle. The absence of large accumulated strains in the "aseismic" zone at the northeastern corner of the chain probably indicates that the chain is pulling apart slowly here and this zone of rifting is incapable of storing large stresses, which are instead dissipated more frequently and at lower energies.

Implicit in this analysis is the view that the primary causative agent is a subcrustal force, which now appears to be the result of convective overturn in the mantle. According to our structural analysis, this flow might have been nearly constant, in orientation and in velocity, since the Middle Cretaceous, though its orientation could well be more easterly now than previously. The force presently exerted by this flow is nearly uniform over the entire area. In the Greater Antilles this force is resolved dominantly into strike-slip movement along the fault system south of Puerto Rico, though in part it is resolved into continued crustal thickening and emergence of the arc platform. South of Saba these conditions are reversed; most of the deformation is taken up by crustal thickening, and as we move

south from Saba the amount taken up by movement along the strike-slip fault system becomes less and less. The curvature of the northern end of the Lesser Antillean arc reflects this balance between relief of forces along the two fault systems very clearly.

THE PROBLEM OF CONTINENTAL DRIFT

In recent years the once moribund theory of continental drift has been resuscitated and, infused with new evidence provided chiefly through geophysical reasoning, has become quite lively and respectable. At the time of World War II there were relatively few geologists who vigorously supported the theory; now there are few who reject it completely. The prime evidence of past drift has been and still is the fit between the continents of South America and Africa, which are thought to have drifted apart during the Mesozoic. These continents are situated so that their drift undoubtedly played a major role in the shaping of the eastern Caribbean. Less clear is the relationship between these two continents and North America; therefore, the history of the northern and western part of the Caribbean prior to and during this episode of drift is entirely uncertain. Perhaps the most striking topographic feature of the Caribbean area is the lineament that stretches from central Guatemala to the eastern end of the Greater Antilles. Though there is little doubt that the late Mesozoic and post-Mesozoic history of this lineament has been diverse, the existence of the lineament cannot be denied, nor can its prominence be avoided. The eastern extension of the lineament beyond the Antilles is poorly defined. Recent seismic refraction studies east of Antigua show that the thickness of oceanic crust here is slightly, though consistently, greater than crust further to the north (H. H. Hess, personal communication). If we extend the lineament, not through the Puerto Rico Trench as most past workers have been tempted to do, but through the island platform and to the east, curving slightly south, it could be extended with little difficulty across the zone of major offset of the mid-Atlantic ridge. This lineament might represent a major Mesozoic line of strike-slip displacement, in fact, a line across which drifting of major proportions took place. The post-drift activity along this zone has been diverse: where diverse and contrasting crustal types have been brought into sharp juxtaposition in a zone of convective forces, island-arc deformation has resulted (Greater Antilles). Where this zone was oriented across a different force environment within the mantle — an environment of extension — a great, complex graben developed (Bartlett Trough). Where this lineament extended towards, and was refracted into, a Pacific-border orogenic zone (a zone of active crustal thickening in response to subcrustal forces from the Pacific) it served as the tear along which much of the ensuing crustal upward and emergence was localized (transverse valleys of Guatemala). Undoubtedly the fate of many such major strike-slip fault systems is to become the loci of entirely different sorts of later deformation, and their

recognition as once-major faults along which drift of continental proportions occurred might be extremely difficult. In the case of the northeastern West Indies, major movements along such a fault probably originated island-arc deformation, independent of their effect on convection currents, by creating a relatively sharp boundary between contrasting crustal types across which orogenic forces were resolved.

CONCLUSION

Unanswered still is the question as to the age of origin of the Lesser Antilles and the difference in topographic form between the Lesser Antilles and Greater Antilles. So little rock is exposed in the Lesser Antilles that the age of inception of volcanic activity is not known. No dates older than Eocene are known for the arc and the possibility of an extensive pre-Cretaceous volcanic history cannot be evaluated. Topographically the Lesser Antilles contrasts strongly with the Greater Antilles: it is broad with relatively ill defined topographic margins, while the eastern Greater Antilles is narrow with sharply defined margins. Because the thickness of volcanic rocks on top of crust for the vast, shallow water-covered parts of the Lesser Antilles (such as the Saba Bank) is not known, there is no way of assessing the possible age of these surficial materials. One possibility is that an open, deep ocean existed between the Virgin Islands and Trinidad prior to the Eocene, and that the Lesser Antilles developed following movements along bounding strike-slip fault systems at both ends of the chain—strike-slip faults whose development allowed a redistribution of the subcrustal forces which had been in existence and still are active in the western Atlantic. The second possibility is that the crustal join along which island-arc deformation was initiated turned a corner, or two joins intersected here, and that the deformation itself turned this "corner." Beneath the Lesser Antilles, then, we might expect to find volcanic rocks equivalent to the entire section so well exposed in the eastern Greater Antilles. The great breadth of the Lesser Antilles and the possible extension of the original crustal join out on to the Atlantic crust both argue against the second possibility, but the question remains one of the most important questions in this area.

Just as our initial understanding of the northeastern West Indies has depended principally on topography (both above water and below water) and upon stratigraphic analysis, so will our future understanding depend most heavily upon geophysical observations. Of prime importance is an accurate delineation of the free-air gravity anomalies over the entire area of the northeastern West Indies. These ultimately will tell us the distribution of isostatic imbalance, and hence of the distribution and orientation of convective currents within the mantle. Heat flow studies cannot fail to be important, especially within the arc itself. A large proportion of the orogenic process may be reflected in endothermic reactions and the mapping of heat flow variations might provide a powerful tool for

assessing the process of deformation.

The continued growth of our understanding, however, will be based neither upon observation nor upon purely deductive reasoning. It will depend on the extent to which we can re-evaluate old concepts and so-called laws, and the extent to which we can escape from the tyranny of assumptions, most of which are very subtle, that have guided our lines of reasoning from the days of our first elementary geology courses. Progress does not result from finding answers but from finding the right questions, and the most important questions are also the best disguised.

ACKNOWLEDGMENTS

My acquaintance with the problems of the West Indies coincides with my acquaintance with Prof. Harry Hess, and I am most grateful for a decade's fascinating and fruitful discussions with him. My work at Rice has been sponsored by three grants from the National Science Foundation and some marine geophysical investigations by the Coast and Geodetic Survey. I also gratefully acknowledge a wealth of discussions with colleagues in numerous institutions, academic and otherwise, whose interest in these problems has been very helpful to me.

REFERENCES

- DONNELLY, T. W.
1964. Evolution of eastern Greater Antillean island arc. *Amer. Ass. petrol. Geol. Bull.*, 48: 680-696.
1965. Sea-bottom morphology suggestive of Post-Pleistocene tectonic activity of the eastern Greater Antilles. *Geol. Soc. Amer., Bull.*, 76: 1291-1294.
1966. The geology of St. Thomas and St. John, Virgin Islands. *In Geol. Soc. Amer., Memoir* 98, pp. 85-176.
- HESS, H. H.
1954. Serpentes, orogeny, and epeirogeny. *In Poldervaart, Arie, Ed., Crust of the Earth. Geol. Soc. Amer., Spec. Pap.* 62: 391-408.
1962. History of ocean basins. *In Hess, Harry, Ed., Petrologic Studies: a volume in honor of A. F. Buddington. Geol. Soc. Amer.*, :599-620.
1964. The oceanic crust, the upper mantle, and the Mayaguez serpentinized peridotite. *In Burk, C. A., Ed., A Study of Serpentinite. Nat. Acad. Sci., Nat. Res. Council, Publ.* 1188: 169-175.
- MORGAN, J.
1965. Gravity anomalies and convection currents, 2, The Puerto Rico Trench and the Mid-Atlantic Rise. *Jour. geophys. Res.*, 70: 6189-6204.
- ROBSON, G. R., K. G. BARR, AND G. W. SMITH
1962. Earthquake series in St. Kitts-Nevis, 1961-62. *Nature*, 195: 972-974.
- SYKES, L. R. AND M. EWING
1965. The seismicity of the Caribbean region. *Jour. geophys. Res.*, 70: 5065-5074.
- TALWANI, M.
1964. A review of marine geophysics. *Mar. Geol.*, 2: 29-80.
- TALWANI, M., G. H. SUTTON, AND J. L. WORZEL
1959. A crustal section across the Puerto Rico Trench. *Jour. geophys. Res.*, 64: 1545-1555.

SEDIMENTS OF THE CARIBBEAN¹

JOHN EWING, MANIK TALWANI, MAURICE EWING, AND
TERENCE EDGAR

Lamont Geological Observatory (Columbia University), Palisades, New York

ABSTRACT

Seismic profiler surveys and sediment coring have indicated that the interior basins of the Caribbean Sea have been stable, deep water areas since middle Mesozoic and possibly earlier. The mapping of a widespread marker of late Mesozoic or earlier Cenozoic age permits certain inferences about the tectonics of the margins of the basins. Vertical, rather than horizontal, forces appear to have been dominant in the deformation. The small variation in the thickness of the Tertiary sediments argues against the concept that convection, producing sea-floor spreading, within the Caribbean Sea is responsible for the marginal deformation.

INTRODUCTION

Several generations of geologists have attempted to explain the origin of the Caribbean Sea, its relationship to the surrounding land and islands, and the nature of the tectonic forces that shaped its intriguing configuration. Earlier hypotheses were based on geographical relationships and the interpretation of the geologic structure described on the adjacent lands. The development of geophysical techniques and their application to marine surveys greatly aided the investigators by supplying a sound structural base on which to develop their theories. Hypotheses have centered around concepts of geosynclines (Meyerhoff, 1954), tectogenes (Hess, 1938; Eardley, 1954), subsiding continents (Eardley, 1954), shifting crustal blocks (Bucher, 1947), and the permanency of ocean basins (Ewing & Worzel, 1954). Most of these concepts were discussed by Butterlin (1956). Special emphasis has been placed on echelon structures, E-W trending structures, and marine trenches. East-West trending strike-slip faults are cited as evidence of major left-lateral strike-slip motion in the Greater Antilles and right-lateral motion along the northern part of South America, implying a relative eastward displacement of the Caribbean.

Since World War II, a number of geophysical surveys have defined the basic structure of the basins, rises, and trenches. Seismic refraction and gravity were extensively used, but gravity does not offer unique solutions and refraction averages conditions over as much as 80 km and is insensitive to subtle variations or detailed sedimentary structure. Since 1960, the continuous reflection profiler (Ewing & Tirey, 1961) has provided detailed sedimentary data to a depth of about 1 km below the sea bottom. The sediment distribution, as determined by the profiler, combined with sedimentary and paleontological data from cores, provides significant tectonic implications that are directly concerned with the development of

¹Lamont Contribution No. 999



FIGURE 1. Chart showing the physiographic features of the Caribbean Sea and section lines of the indicated figure.



FIGURE 2. Chart showing the seismic profiler tracks in the Caribbean Sea made by Lamont's VEMA and ROBERT D. CONRAD.

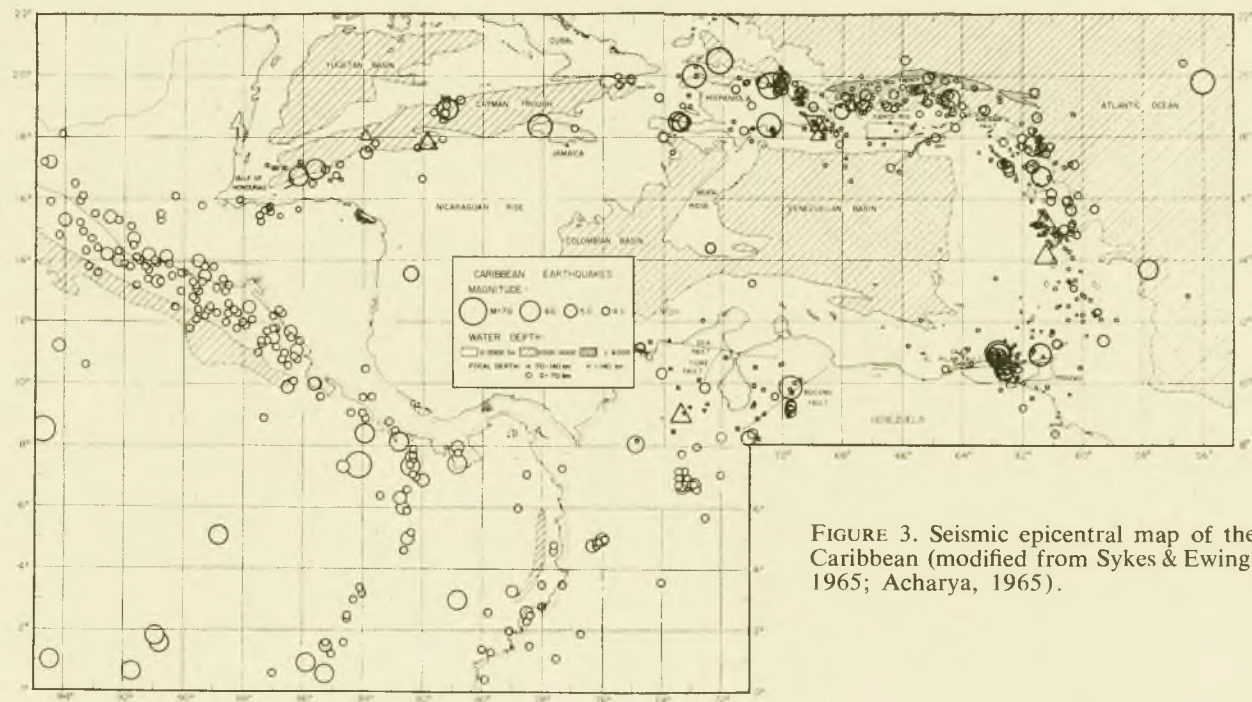


FIGURE 3. Seismic epicentral map of the Caribbean (modified from Sykes & Ewing, 1965; Acharya, 1965).

the Caribbean. It is the intent to demonstrate in this paper the antiquity and stability of the basins and the importance of vertical motion in the formation of the peripheral lands.

The physiographic units of the Caribbean are shown in Figure 1 along with the location of the reflection profiler tracks presented in this paper. Figure 2 shows all the profiler tracks of the research vessels VEMA and ROBERT D. CONRAD in the Caribbean. The small rectangle to the east of the Beata ridge marks an area of fault scarps which was subjected to detailed investigation.

THE BASINS

Figure 3 shows the distribution of earthquake epicenters in the Caribbean (1950-1964) and along the western margin of part of Central and South America (1935-1961, 1964-1965). The most striking observation is the concentration of the epicenters in the marginal areas of the Caribbean and their almost complete absence in the basins, demonstrating that the basins today are tectonically inactive.

Reflection profiling has revealed two prominent horizons that are present throughout the Venezuela and Colombia basins and over both flanks of the Beata ridge, the eastern flank of the Nicaragua rise, and the

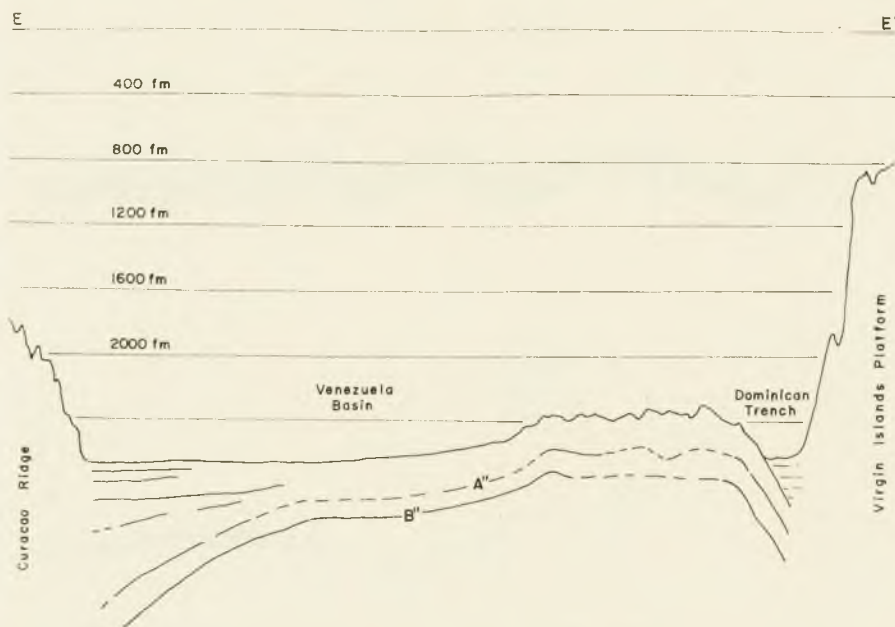


FIGURE 4. Tracing of seismic profiler record from the Curaçao ridge to the Virgin Islands platform. Turbidites cover the Carib beds in the lower marginal areas. Vertical exaggeration is $\times 25$.

western flank of the Aves swell. The presence of these horizons cannot be established with certainty on the western flank of the Nicaragua rise or the eastern flank of the Aves swell. Both the upper horizon, called A", and the lower one, B", have been observed beneath the abyssal plain turbidites of both basins. Figure 4 is a tracing of a reflection profiler track across the Venezuela basin showing the lowest reflecting horizon, B", and two acoustically transparent layers, referred to as the Carib beds, separated by the upper subbottom reflector, A". The horizontal sediments at the base of the Curaçao ridge and in the Dominican trench are turbidites that have been trapped in the marginal areas of the basin. The sediment between A", and B", and above A" (Carib beds), is believed to be fairly homogeneous. This belief is based on the acoustical transparency of the horizons compared with the strongly stratified abyssal plain turbidites that unconformably overlie them in the marginal areas. No reflections have been recorded beneath B", but its smoothness testifies that it is not a typical oceanic basement surface. This assumption is verified by refraction data which show the velocity of this layer is lower than normal basement velocity but apparently has sufficiently high acoustic impedance to restrict penetration by present reflection techniques. The smoothness of this layer suggests that active turbidite deposition that resulted in deposits similar

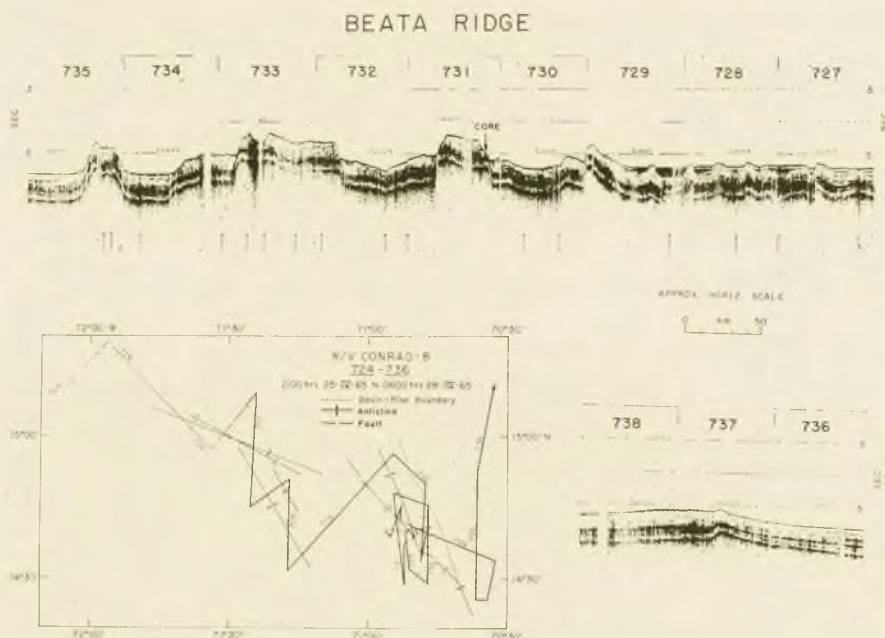


FIGURE 5. Profiler survey of the Beata ridge fault scarp system. Vertical arrows below profile mark changes in course.

to those that form the present abyssal plains, built a level floor on which the Carib beds were later deposited. During this time, pelagic and possibly minor fine grained turbidites dominated the sedimentary section. The break in this depositional pattern, characterized by A'', may represent an interval of coarser turbidite deposition or a change in the type or rate of pelagic sediment accumulation. It is probable that the sea floor remained fairly level throughout most of this depositional interval resulting in conformable deposition with minor changes in thickness. Significant activity in the basins would probably have resulted in less uniform distribution of sediments as evidenced by local ponding of sediment associated with the faulting on the Beata ridge (profiler records 727-729, Fig. 5). During the later depositional intervals, the margins of the Venezuela basin were bowed down relative to the central part and coarse turbidite deposits filled the marginal troughs burying the Carib beds in these areas (Fig. 4). The warping was not so prominent in the Colombia basin and the turbidites leveled practically the whole basin.

On the southeast side of the Beata ridge a system of NW-SE trending faults and folds was thoroughly investigated with the profiler and a number of cores were taken on one of the fault scarps. Figure 5 shows the seismic profiler record of a survey over the fault complex. The fault and fold trends are indicated on the reference map and course changes are shown by the vertical arrows beneath the profiler record. In all but one case the northeast side of the fault is down-thrown relative to the southwest side. The vertical exaggeration of 25:1 gives a misleading indication of the steepness of the scarps. The flatlying sediments filling the small troughs formed by the folding are believed to be isolated pockets of sediment derived from local sources. Subsequent surveys over the same area have shown that topographic barriers would probably have prevented sediments flowing into these pockets from the Colombia abyssal plain. It is unlikely that these barriers developed after the deposition of the undeformed Colombia abyssal plain turbidites which terminate on the flanks of these structures.

One core (indicated by the arrow) was recovered on the fault scarp on this survey and a number of additional cores were taken on a later survey. Several cores recovered lower Eocene radiolarian ooze (Talwani *et al.*, 1966), and since the A'' horizon is barely exposed, the age is believed to represent sediments immediately above this marker. It is therefore reasonable to assume that A'' approximately represents the Mesozoic-Cenozoic boundary. Knowing the approximate age of A'' and thickness of sediment (velocity determined from refraction profiles), the average rate of accumulation for the Caribbean Cenozoic may be calculated (0.7-0.8 cm/1000 years). If extrapolation, by assuming a constant rate of accumulation during the deposition of the Carib beds, is acceptable, then B'' is about $130-140 \times 10^6$ years old (Jurassic-Cretaceous bound-

dary). Considering the uncertainty of extrapolating sediment rates, it is quite possible that B'' is even older; and as it obviously marks a pronounced change in sedimentation, may represent a major geological event such as the transition from the Paleozoic to the Mesozoic Era.

Reflection horizons that appear similar to A'' and B'' have been recorded in the Atlantic (A and B) and in the Pacific Ocean (A' and B'). Horizon A has recently been cored in the Atlantic Ocean and upper Cretaceous sediments were identified (J. Ewing *et al.*, 1966). The sediments in the cores consist of interbedded layers of turbidites and red clay, both of which contain Cretaceous (Maestrichtian) foraminifers (Saito *et al.*, 1966).

The Shatsky rise, which trends NE-SW between the Emperor seamount chain and Japan in the western Pacific, is capped by a thick sequence of sediments. On the flanks of the rise the sediments appear to have been eroded and the interval between two prominent reflectors, A' and B', was cored. The core contained a white foraminiferal chalk that was identified as Lower Cretaceous (M. Ewing *et al.*, 1966).

The age of B and B' in the Atlantic and Pacific areas respectively, is not as easily calculated as B'' of the Caribbean because the thickness of the transparent sediments separating the two reflectors can vary by a factor of 10 (M. Ewing *et al.*, 1966), but assuming an average thickness and extrapolating sediment accumulation rates, the ages appear similar. Despite these apparent correlations, the characteristic uniform thickness of the Carib beds and the smoothness of B'' remain local Caribbean features.

The investigation of the basins has indicated some signs of instability in the later stages of sedimentation. Figure 4 shows a tracing of a reflection profiler record N to S across the Venezuela basin which has a dome-shaped cross section as a result of a relative lowering of the marginal areas. A close study of the profiler records and the Precision Depth Recorder (PDR), which measures depths accurately to about a fathom, shows that the Venezuela abyssal plain is slightly warped and the western part of the Colombian abyssal plain is raised slightly.

The fault scarps described earlier demonstrate late activity in the area of the eastern Beata ridge. Minor fold structures, which became inactive before the deposition of the turbidites, are evident in the Colombia basin and on the flanks of the ridges.

In summary, the basins are considerably older than the Tertiary, and possibly the Mesozoic, and probably have remained relatively stable or tectonically inactive throughout this time. Signs of minor instability developed late in the sedimentary sequence.

THE RIDGES

The method of applying the characteristics of the Carib beds in the investigation of the basins was equally successful in studying the ridges. The identification of these beds on the ridges is not always as easy as in the basins, because sediments are distorted and local ponding tends to

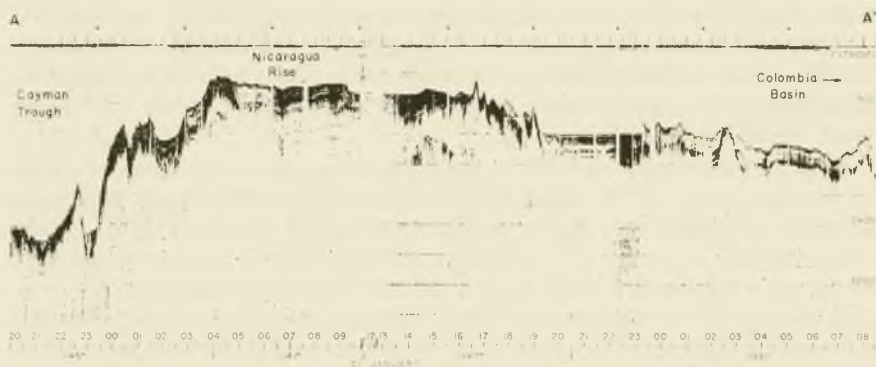


FIGURE 6. Seismic profiler record over the Nicaragua rise. Vertical exaggeration is $\times 25$.

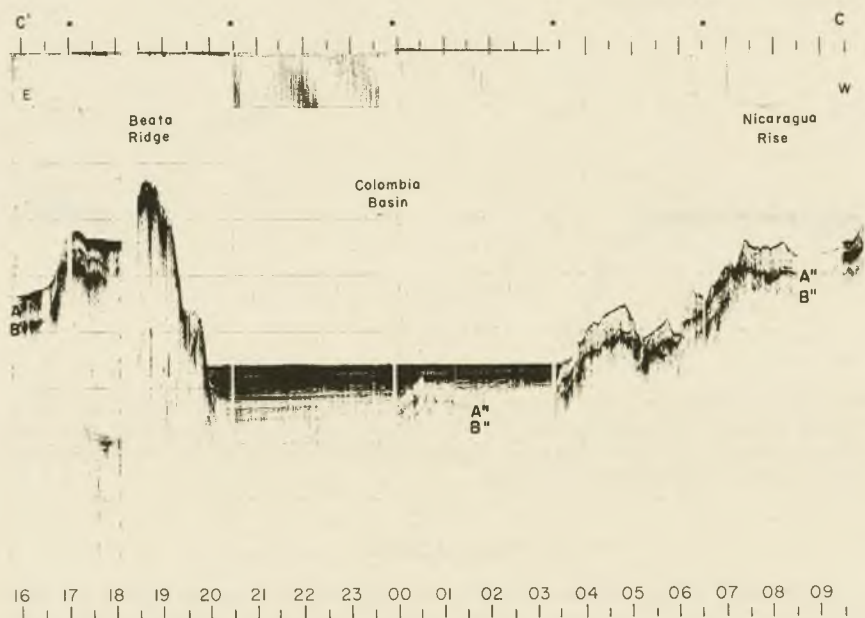


FIGURE 7. Seismic profiler record crossing the northern part of the Beata ridge, Colombia basin and the south flank of the Nicaragua rise. Carib beds can be identified on both ridges and beneath the highly stratified turbidites of the Colombia basin. Vertical exaggeration is $\times 25$.

mask them. However, their distinctive character can usually be identified on the lower flanks (Figs. 6 & 7). Although not well defined, the beds are visible on the western flanks of the Aves swell. The Carib beds cannot be identified on the upper regions of the rises where the sediments tend to be more highly stratified.

On the Nicaragua rise thick accumulations, probably shallow water carbonates, occur on the highest parts of the ridge with thinner sequences trapped or ponded in troughs or fractures on the flanks (Fig. 6). Very little sediment is found in the Cayman trough (Fig. 6). From the geology of Jamaica (Butterlin, 1956), it is evident that the Nicaragua rise was high during the Cretaceous and locally exposed through the lower Eocene. Subsequent deposition of carbonates confirms middle Tertiary subsidence which was terminated by a late Tertiary-Pleistocene uplift resulting in the formation of the island. The difference in the sediment sequence of the crest of the rise, as demonstrated by the reflection profiler, to that of the Carib beds on the lower flanks, may reflect the shallow versus deep water origin. The difference also indicates that the flank areas were raised during a late phase such as the late Tertiary-Pleistocene uplift.

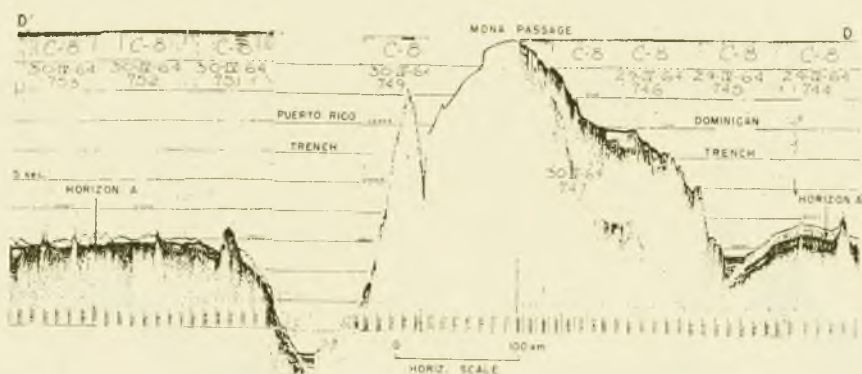


FIGURE 8. Seismic profiler record across the Greater Antilles and Puerto Rico trench between Hispaniola and Puerto Rico. Note the symmetry in structure but the difference in the character of the sediments on each side of the Antilles ridge. Vertical exaggeration is $\times 25$.

THE MARGINS

A crossing of the Greater Antilles through Mona Passage shows obvious symmetry and similarity of structure on each side of the passage (Fig. 8). Atlantic Horizon A and Caribbean Horizon A" show several similarities. Each is overlain by a layer of relatively transparent sediment that can be followed continuously down into the trenches and observed to about the

flank of the Hispaniola-Puerto Rico ridge. In both trenches these transparent sediments are overlain by turbidites that are probably no older than Pleistocene. On both sides of the islands, the sediments below A and A'', respectively, are acoustically more opaque than the upper sediments and bear a strong resemblance, acoustically, to each other and to the upper layer of turbidites in the trenches. There is no evidence of the Carib beds on either flank of the ridge.

The abrupt termination of the basin sediments at the flank of the island ridge also suggests that a seaward migration of the island arc with respect to the basin is highly unlikely and that vertical motion must have played a major role in the arc development. Magnetic trends across the Puerto Rico trench show no offsets, suggesting that strike-slip motion is not a major component (Griscom & Geddes, 1966).

A similar situation is noted at Panama (Fig. 9) where the Carib beds are again observed to dip toward and terminate abruptly at the basin margin with no apparent change in thickness. A late migratory history in the Tertiary, often proposed for the development of Panama, is untenable in view of this evidence. In this area too, vertical motion is apparently dominant.

The profiler records of the Grenada trough, Lesser Antilles, Tobago trough, and Barbados ridge are of inferior quality and only a general pattern can be described. The sediments on the flank of the Lesser Antilles and the west slope of the Barbados ridge are stratified conformably with the bottom topography. They appear continuous beneath the flat, presumably recent turbidite sediments of the Tobago trough associated with the Barbados ridge. Continued to the north, in the zone of the Antilles gravity

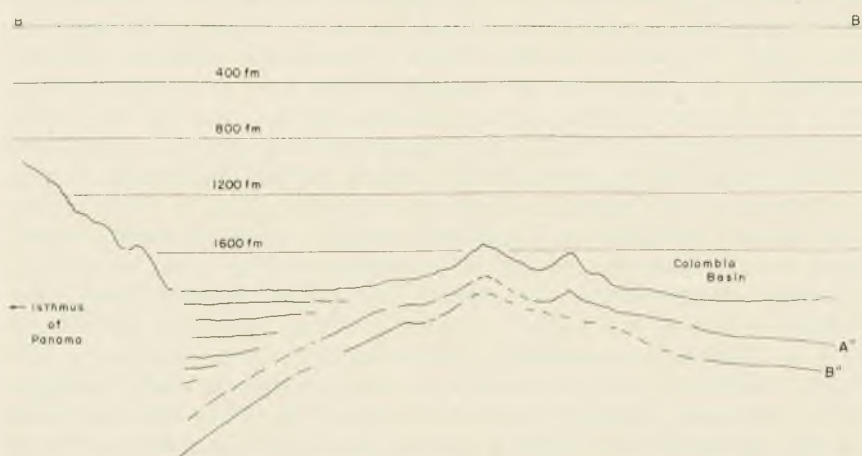


FIGURE 9. Tracing of reflection profiler record in the Colombia basin north of the Isthmus of Panama. Vertical exaggeration is $\times 25$.

minimum, is a characteristic small scale topographic roughness through which no deep subbottom reflectors are recorded. Greater stratification in the upper sediments of the Grenada trough than those at depth suggests a change in the type of sediments deposited.

DISCUSSION

The extremely smooth surface of B" suggests that a levelling process, interpreted as turbidity current deposition, dominated the sedimentary history of the Caribbean sometime prior to the deposition of the Carib beds. After the deposition of B", sedimentary conditions were extremely uniform and contrast markedly with coarse turbidite sedimentation that formed in the marginal depressions presumably in the Holocene. The unique characteristics of the Carib beds, namely uniformity of thickness and acoustical character, are restricted to the Caribbean sea indicating that the land or ridge barriers of the Antilles and Central America have been effective since pre-Tertiary time, probably middle or early Mesozoic.

The presence of the Carib beds in the Yucatan basin has not been established because a very thick blanket of turbidites masks the lower layers. Considering that the Nicaragua rise was in all probability high in the Cretaceous, the presence or absence of these beds in the Yucatan basin would be significant with respect to the nature of the depositional mechanism prior to the turbidite deposition.

The approximate synchronicity of A, A', and A" and probably of B, B', and B" is indicated from cores in three widely separated locations. There is an inference that the layers correspond in time to major geological and paleontological events (defined by geologists on the continents) separating the Mesozoic from the Paleozoic and Cenozoic. The nature of the corresponding events in the oceans has not yet been determined. The cores from Horizon A in the Atlantic demonstrate extensive turbidite deposition near the end of the Mesozoic in this area, inferring an association of oceanic deposition with continental activity, but the application of this discovery to such widely separated parts of the oceans as the western Pacific, South Atlantic, and Caribbean may be invalid. The horizons sharing a common age and depositional mechanism may be related to major activity near the ocean margins that is associated with the major continental events; but it is not necessarily true that all continental activity would be reflected in oceanic sedimentation. For example, the major continental mountain-building events of the Tertiary (Andes, Rockies, Alps, and Himalayas) have no apparent corresponding expression in the ocean sediments. The Pacific reflector A' may be a result of a change in type or rate of accumulation of pelagic sediments that had a universal or almost universal effect on their acoustical properties. It appears likely that an event capable of producing a pronounced change in sedimentation in an area the size of the Pacific Ocean probably was a notable event on the continents. Evidence

for this type of event may be derived from the faunal breaks associated with the Paleozoic-Mesozoic and Mesozoic-Cenozoic boundaries.

There are no means of determining accurately the duration of sedimentation that occurred prior to the deposition of B". The extrapolation of sediment rates, described above, to establish an approximate age of B" was based on the assumption that the acoustical similarity of the layer between A" and B" with the one above A" suggested similar conditions of sedimentation prevailed throughout the deposition of the Carib beds. No such assumption can be made concerning the type of sedimentation that occurred prior to the formation of B". A moderately stable basin would be required for the development of a flat floor despite rapid turbidite deposition.

The Carib beds may have been formed by pelagic accumulation, fine grained turbidite deposition, a combination of these processes or possibly by some other mechanism. The evidence for pelagic accumulation is based on the acoustical transparency, which implies homogeneity of the sediments and the uniformity in thickness, especially in the marginal areas. If the Carib beds are largely a pelagic deposit and their uniform thickness reflects uniform productivity, then they should be present in such places as the flanks of the Greater Antilles ridge, the Curaçao ridge and the Cayman trough, but such is not the case. If pelagic sediments as thick as the Carib beds have slumped off the ridges into the basins, they must have spread themselves evenly over the basin floors, as evidenced by the uniformity of the sediment thickness adjacent to the ridges. In the case of the Dominican trench south of Hispaniola and Puerto Rico, for example, if a layer of sediment as thick as the Carib beds slumped off the southern flank of the island ridge, the trench would have been completely filled. It would be necessary in this case to invoke some mechanism for the assimilation of pelagics into the ridge, destroying the acoustically transparent character of the sediment. A sediment distribution pattern shown in Figure 5, profile No. 737, clearly demonstrates that pelagic sedimentation cannot be the sole process. The total thickness of the layers, as well as individual thicknesses of the lower and upper units separated by A", is greater on the north side of the topographic rise than on the south side. It is probable that the area to the north was slightly depressed and received sediments from the higher surrounding areas.

An alternative suggestion requires the dominance of fine grained turbidites in the basin sediments, restricting these deposits to the lower levels of the basin. Evidence for turbidite deposition may be found in the acoustical character of A" (Fig. 5) which is similar to that of well established turbidite beds. The layer is composed of several conformable reflectors of variable intensity. Turbidite sedimentation would account for the fact that the Carib beds are not found on the flanks of the Curaçao ridge, Cayman trough, nor the Greater Antilles ridge without invoking a con-

venient, but unfamiliar process of sediment assimilation. However, a thickening of the turbidite layer near the sediment source might be anticipated. In addition, there is no strong supporting evidence of turbidites from cores that penetrate the Eocene, Miocene, and Holocene sediments, although the recognition of fine grained turbidites may be extremely difficult.

Recent investigations have demonstrated that a bottom layer of water (several hundred meters thick) with a relatively high content of suspended matter exists in the North Atlantic basin and may play an important role in the sediment distribution (Ewing & Thorndike, 1965). The layer is not present in the Caribbean Sea today but may have been a significant factor during the formation of the Carib beds.

The age determination of the marginal depression of trenches is intricately concerned with the choice of basin sediment process. If pelagic sedimentation is assumed then the trench may be a fairly ancient feature which remained free of clastic sedimentation until the influx of the young turbidites. The youth of the turbidites is demonstrated by the thick section of Carib beds underlying them. If on the other hand turbidites are an important constituent of the Carib beds, then the trench formation must have occurred after the deposition of most of the Carib beds and before the deposition of the young turbidites, requiring a very late trench development. The suggested youth of the marginal trenches and the antiquity of the ridges, as indicated by the Carib beds is remarkable, but not necessarily contradictory.

The faulting that occurred on the eastern side of the Beata ridge (Fig. 5) must be fairly recent regardless of the mechanism of sedimentation.

The Carib beds may be observed on the upper flanks of the Beata ridge, but not on the main peak (Fig. 7). Other profiles suggest that B" is continuous over the peak, but A" terminates against the steep slope. A refraction profile over the ridge supports this observation. It is probable that B" was laid down as a flat surface and at a later time the main peak was raised. During a second phase of uplift, the Carib beds were raised on the flanks possibly at the time Jamaica was uplifted (Late Tertiary-Pleistocene). This may also be the time the Caribbean fault scarps, described earlier, were formed on the southeast flank of the Beata ridge.

The analogy in the apparent tectonic histories of the Aves swell, Beata ridge, and the Nicaragua rise is striking. In each case the Carib beds may be identified on the flanks, but not on the crests, suggesting that each ridge may have had two phases of development, assuming the sediments are not purely pelagic, or assuming the basin sediments are pelagic, the deep deposits of the Caribbean sea have a more homogeneous acoustical character than sediments of equivalent age deposited in shallower water. The profiles offer no indication of lateral movement in any of these features, but substantial vertical motion is evident.

CONCLUSIONS

The lower Eocene cores collected on a scarp of the Caribbean fault system and the continuity of two sub-bottom reflections throughout the basins of the Caribbean offer an extraordinarily rewarding combination in the investigation of the Caribbean basins and ridges. The upper reflector, A", may represent a turbidite deposit or a change in the type or rate of pelagic accumulation at about the end of the Cretaceous, and the lower one, B", apparently concluded a coarser turbidite phase that is probably as old as the early or middle Mesozoic and possibly much older. The smoothness of the lower horizon and the absence of reflectors recorded below it, indicates the presence of earlier turbidites. The antiquity of the Caribbean can now be realized and a Paleozoic or older origin does not appear unreasonable.

The uniformity of sediment layers throughout the basins is impressive evidence of the stability of the central part of the Caribbean through a remarkable length of time, despite intense marginal activity. Late warping of the basins is responsible for depressed marginal areas. The stability of the basins argues against any significant spreading or similar distortion of the crust.

The relationship of the Carib beds to the Greater Antilles and the Isthmus of Panama implies vertical rather than lateral movement played the dominant role in the development of these features.

ACKNOWLEDGMENTS

This work was supported by the U.S. Navy Office of Naval Research Contracts Nonr 266(48), Nonr 266(79), and the National Science Foundation. It is a pleasure to acknowledge the assistance of the officers and crews of the research vessels VEMA and ROBERT D. CONRAD and that of the many members of the scientific staff of Lamont Geological Observatory who helped with the field measurements. We also thank J. L. Worzel and W. J. Ludwig for reviewing the manuscript.

REFERENCES

- ACHARYA, H. K.
1965. Seismicity of the Galapagos Islands and vicinity. *Bull. seis. Soc. Amer.*, 55 (3): 609-617.
- BUCHER, W. H.
1947. Problems of earth deformation illustrated by the Caribbean Sea basin. *Trans. N.Y. Acad. Sci. Ser.*, 2: 98-116.
- BUTTERLIN, J.
1956. La constitution geologique et la structure des Antilles. *Centre National de la Recherche Scientifique*.
- EARDLEY, A. J.
1954. Tectonic relations of North and South America. *Bull. Amer. Assoc. petrol. Geol.*, 38: 707-773.

- EWING, J. AND G. B. TIREY
1961. Seismic profiler. *Jour. geophys. Res.*, 6 (9): 2917-2927.
- EWING, J., J. L. WORZEL, M. EWING, AND C. WINDISCH
1966. Ages of Horizon A and the oldest Atlantic sediments. *Science*, 154 (3753): 1125-1132.
- EWING, M., X. LE PICHON, AND J. EWING
1966. Crustal structure of the mid-ocean ridges, Part 4. Sediment distribution in the south Atlantic Ocean and the Cenozoic history of the mid-Atlantic ridge. *Jour. geophys. Res.*, 71 (6): 1611-1636.
- EWING, M., T. SAITO, J. EWING, AND L. BURCKLE
1966. Lower Cretaceous sediments from the northwestern Pacific Ocean. *Science*, 152 (3727): 751-755.
- EWING, M. AND J. L. WORZEL
1954. Gravity anomalies and structure of the West Indies, Part I, *Geol. Soc. Amer. Bull.*, 65: 165-174.
1954. Gravity anomalies and structure of the West Indies, Part II, *Geol. Soc. Amer. Bull.*, 65: 195-200.
- GRISCOM, A. AND W. GEDDES
1966. Island-arc structure interpreted from aeromagnetic data near Puerto Rico and the Virgin Islands. *Geol. Soc. Amer. Bull.*, 77 (2): 153-162.
- HESS, H. H.
1938. Gravity anomalies and island-arc structure with particular reference to the West Indies. *Proc. Amer. phil. Soc.*, 79: 71-96.
- MEYERHOFF, H. A.
1954. Antillean tectonics. *Trans. N.Y. Acad. Sci.*, ser. 2, 16: 149-155.
- SAITO, T., L. H. BURCKLE, AND M. EWING
1966. Lithology and paleontology of the reflective layer Horizon A. *Science*, 154 (3753): 1173-1176.
- SYKES, L. AND M. EWING
1965. The seismicity of the Caribbean region. *Jour. geophys. Res.*, 70 (20): 5065-5074.
- TALWANI, M., J. EWING, M. EWING, AND T. SAITO
1966. Geological and geophysical studies of the Caribbean submarine escarpment. *Geol. Soc. Amer. Program 1966 Annual Meeting*: 217-218.

TECTONICS OF THE CENTRAL PART OF THE WESTERN CARIBBEAN MOUNTAINS, VENEZUELA

ALFREDO MENÉNDEZ V. DE V.

Ministerio de Minas e Hidrocarburos, Dirección de Geología, Venezuela

ABSTRACT

Four east-trending tectonic belts are recognized in the Western Caribbean mountains (from north to south):

(1) The Cordillera de la Costa tectonic belt to the north contains Jurassic to Lower Cretaceous low-grade metamorphosed sedimentary rocks of the Caracas group. Large open folds trending N 75° E characterize this belt. The northernmost anticline is locally thrust to the north and the southernmost is overturned to the south. Granitic basement is exposed in the core of both these anticlines.

(2) In the Cauagua-El Tinaco tectonic belt there is a discontinuous belt of basement blocks which are overlain by a slightly metamorphosed Cretaceous sedimentary-volcanic sequence. In this belt, open folds, gentle dips, and bedding-plane faults are characteristic. The upper Caracas group is thrust over Upper Cretaceous rocks in the eastern and western parts of the belt. At its southwestern end, large allochthonous blocks composed of Paleocene and Upper Cretaceous rocks (the Tiramuto klippen) are found resting on Upper Eocene beds. In every case the allochthon has been folded together with the autochthon.

(3) The narrow fault-bounded Paracotos belt contains the southward-dipping beds of the Maestrichtian Paracotos formation. The fault bounding this belt to the south (the Agua Fría) is a bedding-plane fault which bounds the northern and western edges of the Villa de Cura block.

(4) The Villa de Cura group, composed of a thick pile of slightly metamorphosed volcanic rocks of unknown age, underlies an elongated area 250 km long and 28 km of maximum width. This block may have slid southward to its present position in Late Maestrichtian time during the early stages of the development of an east-trending deep marine trough.

The main period of folding within the orogenic belt appears to have been in Late Eocene or later. It was preceded by a long period of epeirogenesis and overthrusting which ended with the folding stage. Later movements were of isostatic adjustment. Younger Tertiary-Quaternary basins were formed along the Cauagua-El Tinaco belt and the Cordillera de la Costa was uplifted.

INTRODUCTION

The Caribbean mountains border the north coast of Venezuela, trend N 75°E, and extend from the Barquisimeto depression on the west to the Paria Peninsula on the east, and continue into the northern range of Trinidad. The Barquisimeto depression separates the Caribbean mountains from the Venezuelan Andes. Another depression, determined by Barcelona Bay, divides the mountains into a western and an eastern sector. An axial topographic low extending from the lower Río Tuy embayment on the east through Lake Valencia to the headwaters of the Tinaco River, divides the

Western Caribbean mountains into the Cordillera de la Costa on the north and the Serranía del Interior on the south.

The Caribbean mountains represent an alpine-type mountain system and have been the site of detailed exploration by the Princeton University Caribbean research group under the leadership of H. H. Hess. The main purpose of the Caribbean project has been to determine the evolutionary steps leading to the formation of an alpine-type mountain system (Hess & Maxwell, 1953; Hess, 1960). The present review is based mainly on the published work of the Princeton group (Dengo, 1953; Smith, 1953; MacLachlan *et al.*, 1960; Shagam, 1960; Konigsmark, 1965; Oxburgh, 1965; Menéndez, 1965; Seiders, 1965), in the region between the longitudes of the towns of Cauagua and El Tinaco (see Fig. 1). Aguerrevere & Zuloaga's (1937) regional reconnaissance of the Caribbean mountains guided the exploration carried on by this group. In the light of more recent findings, it has been necessary in the present paper to reinterpret to some extent the data published in earlier papers. This is a natural process in the development of a detailed systematic exploration of a region, particularly if the highly complex nature of the geology of the metamorphic belt is taken into consideration. Needless to say, the account of the geology of the Caribbean mountains presented here may also be subject to some alteration as further detailed work is done. However, the writer is convinced that the broad tectonic picture of the mountains described here will remain unchanged.

THE TECTONIC BELTS

The central part of the Western Caribbean mountains is clearly divisible into four tectonic belts as indicated by the particular structural features encountered across the mountains. Three major east-trending faults of regional extent divide the mountains into the following four tectonic belts, which are from north to south: (1) the Cordillera de la Costa tectonic belt, bounded on the south by the La Victoria fault zone; (2) the Cauagua-El Tinaco tectonic belt, bounded on the south mainly by the Santa Rosa normal fault; (3) the Paracotos belt, bounded on the south by the southward-dipping Agua Fría thrust fault; and (4) the Villa de Cura allochthonous block. The three southern belts may be considered as a single tectonic belt in which overthrusting to the south is the characteristic structural feature. However, owing to the extensive distribution of the Paracotos belt and the Villa de Cura block in the region under consideration, it is better to discuss them separately.

CORDILLERA DE LA COSTA TECTONIC BELT

General.—The Cordillera de la Costa tectonic belt occupies the northern part of the Western Caribbean mountains. This belt is bounded to the south by the La Victoria fault zone. Its structural features are significantly different from those of the tectonic belts to the south.

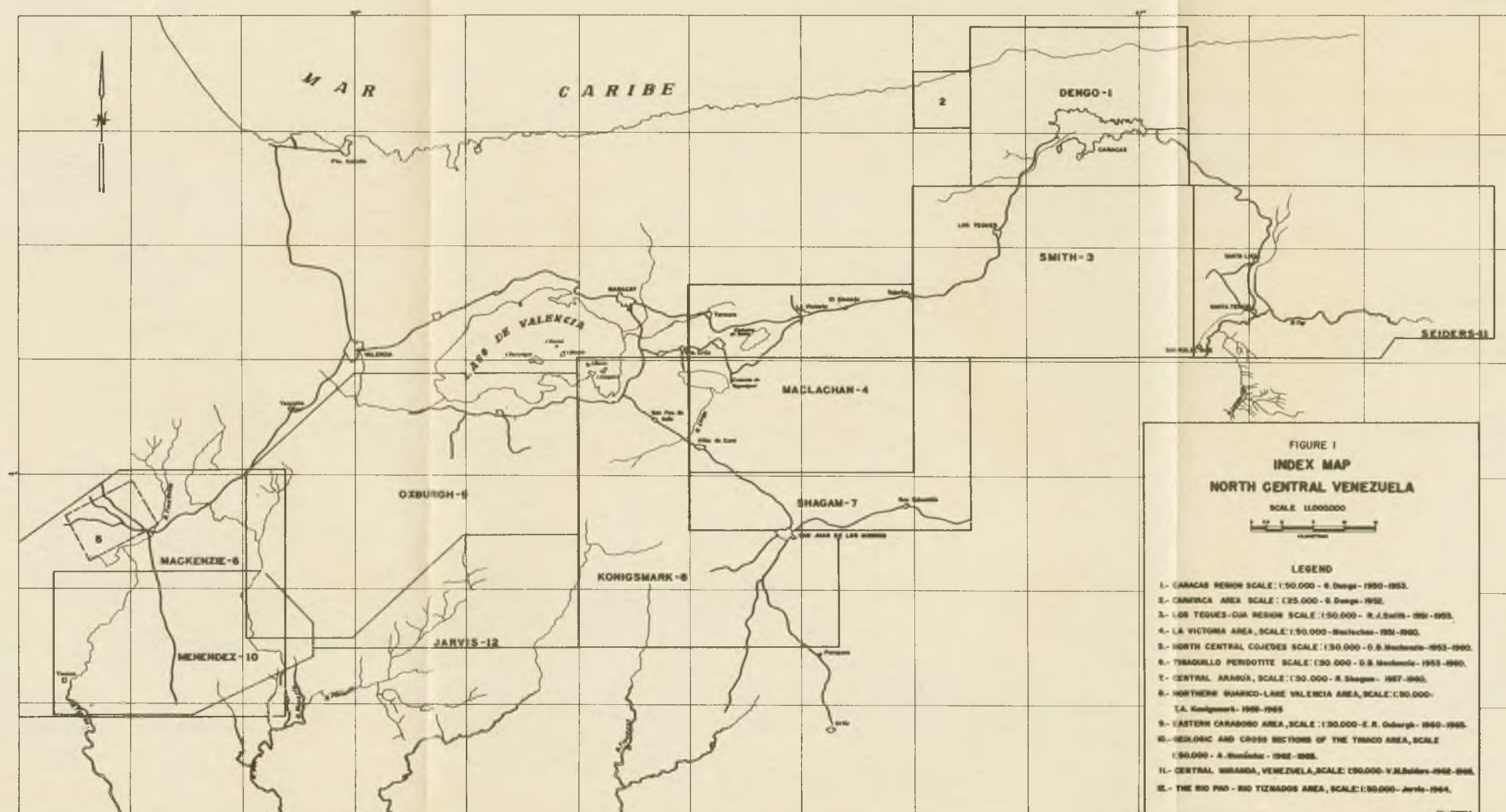
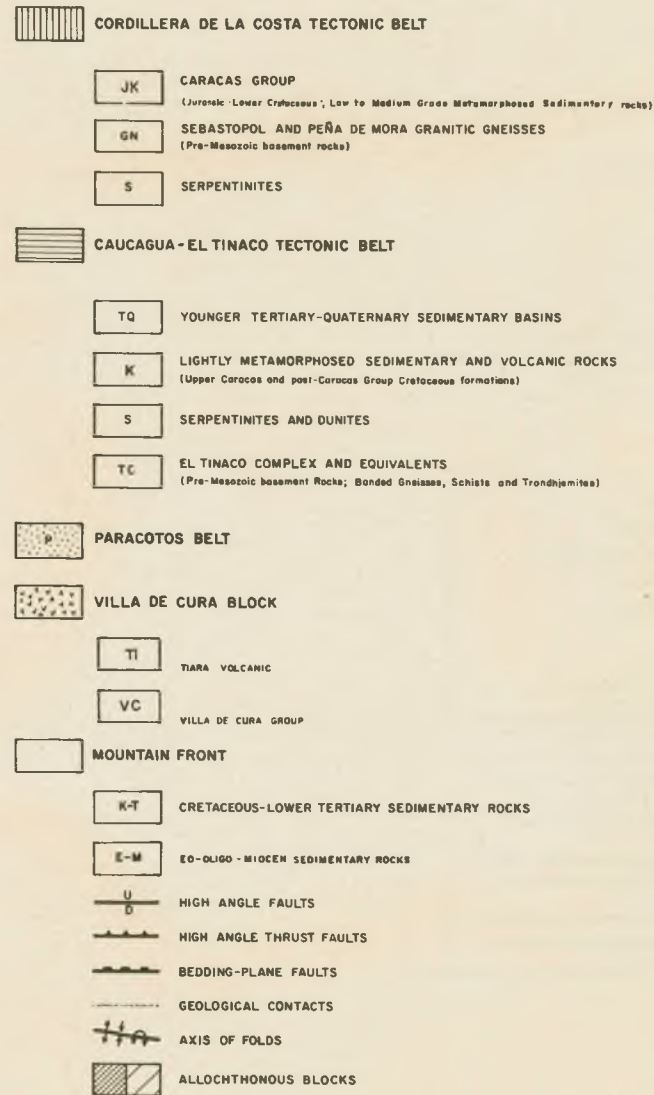


FIGURE 2
GENERALIZED GEOLOGIC-TECTONIC MAP OF THE
CENTRAL PART OF THE WESTERN CARIBBEAN
MOUNTAINS-VENEZUELA

COMPILATION AND MODIFICATIONS BY A. MENENDEZ
SOURCE: CARIBBEAN RESEARCH PROJECT-DEPT. OF GEOLOGY-PRINCETON UNIVERSITY



DIBUJO: DELIA R. DE PEREZ Y MARISABEL CASTILLO
ENERO DE 1966



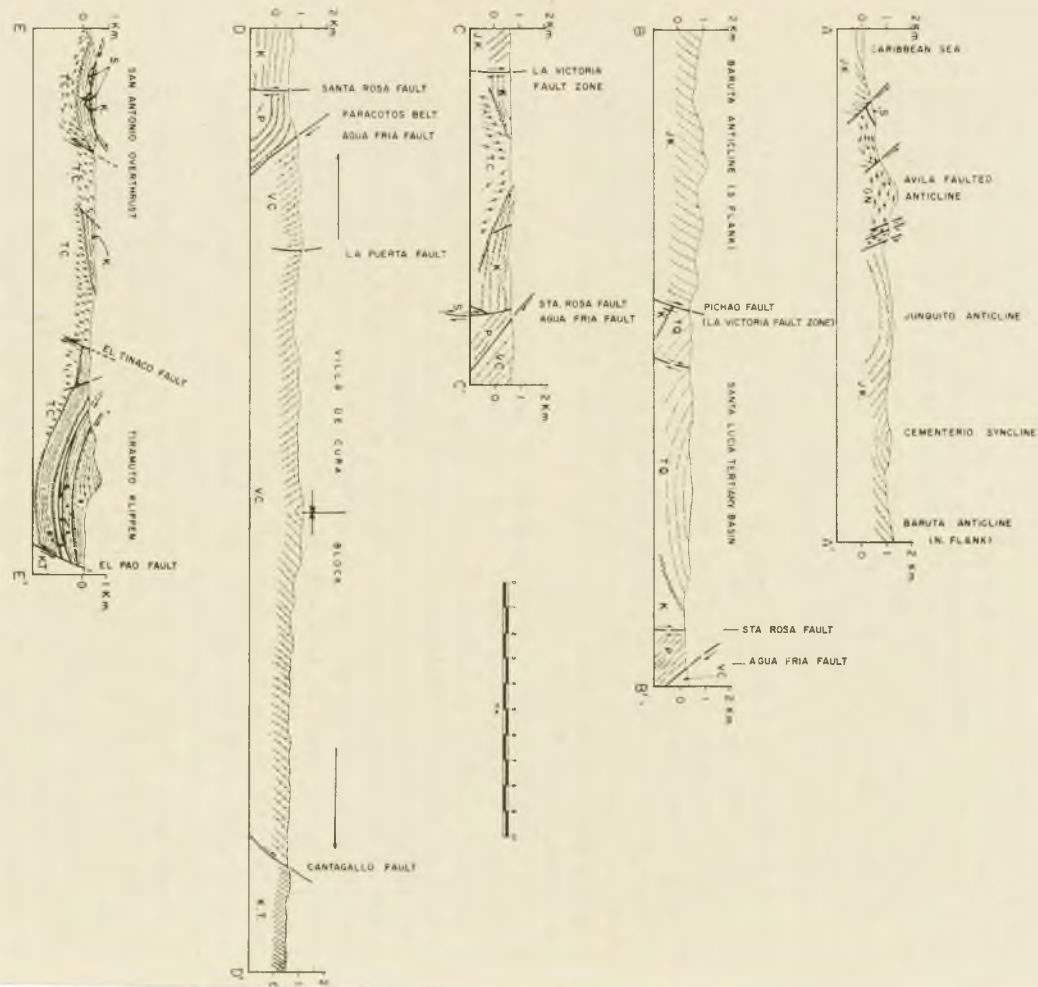
The main lithologic and structural features of the Cordillera de la Costa tectonic belt are known as a result of the detailed work carried out in the Caracas region by Dengo (1953) and in the northern part of the Los Teques-Cúa and central Miranda regions by Smith (1953) and Seiders (1965), respectively. It is considered that the characteristics reported in these regions are common to the entire belt along strike from its western end in the Barquisimeto depression, to its eastern end in Cabo Codera. The structural features encountered in the northern part of the Cordillera de la Costa have been correlated with those of the northward overfolded metamorphics in Margarita by Maxwell & Dengo (1951, p. 266), and those found in the southern part of the belt may be correlated with the structures in the metamorphics, overthrust and overfolded to the south, in Araya-Paria (*cf.*, Maxwell & Dengo, 1951; Smith, 1953, p. 64).

Rock Units.—The Caracas group, of probable Jurassic to Lower Cretaceous age, and the pre-Mesozoic (?) Sebastopol granitic gneiss complex, underlie the Cordillera de la Costa (Aguerrevere & Zuloaga, 1937; Dengo, 1953). The augen-gneiss of Peña de Mora, provisionally included by Dengo in the Las Brisas formation, may well be part of the granitic basement as suggested by the presence, along strike, of similar rocks representing unmistakable basement in the Yaracuy region to the west (A. Bellizzia, personal communication, 1960).

The Caracas group in the Cordillera de la Costa consists of a large proportion of quartz mica schists in its lower part (the Las Brisas formation) and graphitic and calcareous quartz mica schists in its upper part (the Las Mercedes formation). Locally there are thick marble lenses in the middle of the group (the Antimano limestone), and sericite epidote schists (the Tacagua formation) overlying the Las Mercedes formation in the northern part of the belt. Amphibolite layers, representing original basic igneous rocks of probable intrusive nature, are present at several stratigraphic levels in the group and in the Peña de Mora gneiss (Dengo, 1953: p. 23). Serpentinities occur mainly as conformable sheets preferentially intruded along the contact of the Las Brisas and Las Mercedes formation in the northern part of the belt (Dengo, 1953, p. 21).

Rock units similar to the Caracas group are also exposed south of the La Victoria fault zone, but their correlation has been problematic (see pp. 110-115). They have been either correlated with the Caracas group formations (Smith, 1953; MacLachlan *et al.*, 1960; Konigsmark, 1965), exposed north of the fault zone, or included within the group stratigraphically above the Las Mercedes formation (Shagam, 1960; Seiders, 1965). The Tacagua formation may be correlated with the Los Naranjos volcanics and equivalents exposed in the Cauagua-El Tinaco tectonic belt (Seiders, 1965; and see Table 1).

The grade of metamorphism increases from south to north in the Cordillera de la Costa. This feature is better displayed by the rocks of the



STRUCTURAL CROSS-SECTIONS WESTERN CARIBBEAN MOUNTAINS-VENEZUELA

COMPILATION AND MODIFICATIONS BY A. MENENDEZ

SOURCE: CARIBBEAN RESEARCH PROJECT-DEPT. OF GEOLOGY - PRINCETON UNIVERSITY

CORDILLERA DE LA COSTA TECTONIC BELT

- J.K. Caracas Group
- GN Sebastopol and Peña de Mara Granitic Gneisses
- S Serpentinites

CAUCAGUA-EL TINACO TECTONIC BELT

- TQ Younger Tertiary - Quaternary Sedimentary Rocks
- K Cretaceous Lightly Metamorphosed Sedimentary and Volcanic Rocks
- S Serpentinites and Dunites
- TC El Tinaco Complex and equivalents

PARACOTOS BELT

- P Paracotos Formation

VILLA DE CURA BLOCK

- Ti Tiara Volcanics
- V.C. Villa de Cura Group

MOUNTAIN FRONT

- KT Cretaceous-Lower Tertiary Sedimentary Rocks

TIRAMUTO AREA (CROSS SECTION E-E')

Allochthon

- 5 TIRAMUTO FORMATION (= VILLA DE CURA GROUP ? (AGE UNKNOWN))
- 4 PARACOTOS FORMATION (MAESTRICHTIAN)

- 3 GUARICO FORMATION (PALEOCENE)

Autochthon

- 2 ORUPE FORMATION (LATE EOCENE)
- 1 QUEREQUAL FORMATION (CEN-COM)

FIGURE 3. Structural cross-sections of the western Caribbean Mountains.

lower part of the Caracas group. Seiders (1962) reports greenschist mineralogy in the Las Brisas formation close to the La Victoria fault zone and Dengo (1950; 1953, p. 28) finds that rocks of the Las Brisas formation and amphibolites associated with the Antimano limestone in the northern part of the Caracas region belong to the amphibolite facies.

The Caracas group rocks represent an original sedimentary sequence mostly deposited on a stable shelf by a southward transgressing sea (cf. Smith, 1953, p. 51). The source apparently was essentially granitic. Dengo (1953, p. 14) and Smith (1953, p. 51) report some features suggesting a shallow water environment for the deposition of the Caracas group. Seiders (1965, p. 299) observed graded bedding in thin quartzose sandstone layers of the Las Mercedes formation exposed in the northern part of the central Miranda region. This feature mainly indicates deposition in deep water by turbidity currents developed by slumping at the edge of the shelf (Kuenen, 1959). The shelf was probably bordering a deeply eroded terrain which furnished the quartzose sand. However, the paleogeographic significance of Seiders' finding is not yet clear since graded bedding has not been observed elsewhere in the Caracas group. Turbidity currents are usual in elongated deep marine troughs receiving immature detritus and are very rarely developed under normal open sea conditions (Kuenen, 1951, p. 31). Disregarding paleogeographic considerations, the presence of graded bedding in the upper part of the Caracas group may be the first sign of tectonic unrest which prevailed during the accumulation of the post-Caracas group formation (see below).

The age of the Caracas group has not yet been well established. However, lithological correlations of the group with unmetamorphosed sequences exposed in eastern and western Venezuela suggest that it is of Lower Cretaceous age. (See Konigsmark, 1965; Bushman, 1965; and Bucher, 1952 for a detailed discussion on the subject). Furthermore, the presence of dated Late Jurassic beds in the Northern Range of Trinidad (Hutchison, 1939) and of probable Cretaceous-Jurassic fossils in the Las Brisas formation (Wolcott, 1943; Dusenbury & Wolcott, 1950; Bucher, 1952) favor a Late Jurassic age for the base of the Caracas group, at least in the northern part of the Cordillera de la Costa.

Major Structures.—The broad structural picture of the Cordillera de la Costa tectonic belt is simple, but small folding developed in relatively incompetent beds may complicate the structures in detail. The foliation in this belt as well as in the belts to the south is mainly parallel to bedding. Four major folds with an axial trend of about N 75°E have been mapped by Dengo (1953, p. 33) in the Caracas region. Seiders (1965, p. 396), in the northern part of Central Miranda, and Smith (1953) in the northern part of the Los Teques-Cúa region, mapped the southern flank of the southernmost fold.

The complexly faulted Avila anticline lies in the northern part of the

belt. In the core of this fold the granitic basement (the Peña de Mora gneiss) is exposed. The northern flank is cut by several south-dipping thrust faults, the most conspicuous of which is the Curucutí thrust. Along this fault serpentinites are thrust over the overturned Antimano limestone. The northern flank is also crossed by the younger east-trending Macuto fault zone, which may have had some right-lateral sense of movement. The southern flank is cut by several *en echelon* faults with a N 60°W strike (the Avila fault zone). This faulting appears to be younger than the northward thrust faults but older than the Macuto fault zone.

South of the Avila anticline there are two northeast-plunging broad symmetrical open folds: the Junquito anticline and the Cementerio syncline. This syncline is followed southward by the Baruta anticline. In the core of this anticline the Sebastopol gneiss is exposed. The southern flank is steeply dipping and overturned to the south adjacent to the La Victoria fault zone, as indicated by the relative ages of the Las Brisas and Las Mercedes formation (Seiders, 1965, p. 400). Although there is much small folding throughout the belt, particularly in the incompetent Las Mercedes formation, this is more conspicuous to the south. Large isoclinal folding with axes parallel to the major folds, and with northward dipping axial planes appears to be common in the southern part of the belt (Smith, 1953, p. 59; Seiders, 1965, p. 400).

The La Victoria fault zone, which separates the two typically different northern tectonic belts, represents a longitudinal faults system which has been mapped for almost 140 km, from central Miranda on the east up to the east shore of Lake Valencia on the west. It may continue with its N 75°E trend farther westward to die out in the Barquisimeto fault zone (A. Bellizzia, personal communication, 1965). The activity along the La Victoria fault zone probably was long and complex. Along this fault most of the vertical movements of the basement blocks located south of it (see p. 111) may have taken place during the Upper Cretaceous. Seiders (1965, p. 400) finds that axes of small folds plunge about 20° to the west in the belt of exposures of the Las Mercedes formation north of the fault zone. He explains this by suggesting that the rocks north of the fault zone moved upward and westward relative to the block south of the fault. The most recent movement as a normal fault with downthrow to the south can be dated only as post-Miocene, as shown by the offset Miocene beds of the Santa Lucía Tertiary basin. As in the case of the Macuto fault zone, the straightness of the fault zone has suggested to other workers that large strike-slip displacement occurred along this fault zone. Probably there was some strike-slip sense of movement, but the main direction appears to have been vertical. A recent right lateral displacement of only a few kilometers is indicated by the offset of drainage observed by Smith, (1953: 60, Fig. 2) at the La Victoria fault zone.

THE CAUCAGUA-EL TINACO TECTONIC BELT

General.—The northern border of the Caucaja-El Tinaco tectonic belt is defined by the La Victoria fault zone. Its southern limit is the Santa Rosa fault extending from the central Miranda area up to the vicinity of Cerro El Joal on the west. West of this hill the southern border of the El Tinaco massif (the El Tinaco fault) and the limits of the faulted block around Cerro Tiramuto are taken as the southwestern boundary of this tectonic belt. Further to the west this belt may continue with similar characteristics up to the Barquisimeto depression as suggested by the mapping of the area immediately west of the El Tinaco massif by Bushman (1963) and Bellizzia (MS). East of Cerro el Joal, the Caucaja-El Tinaco tectonic belt is followed southwards by the Paracotos belt and west of this hill by the mountain front belt.

Seiders' (1965) detailed mapping in the central Miranda region contributed much to the understanding of the geology along this belt. He pointed out the essential structural and lithologic features differentiating

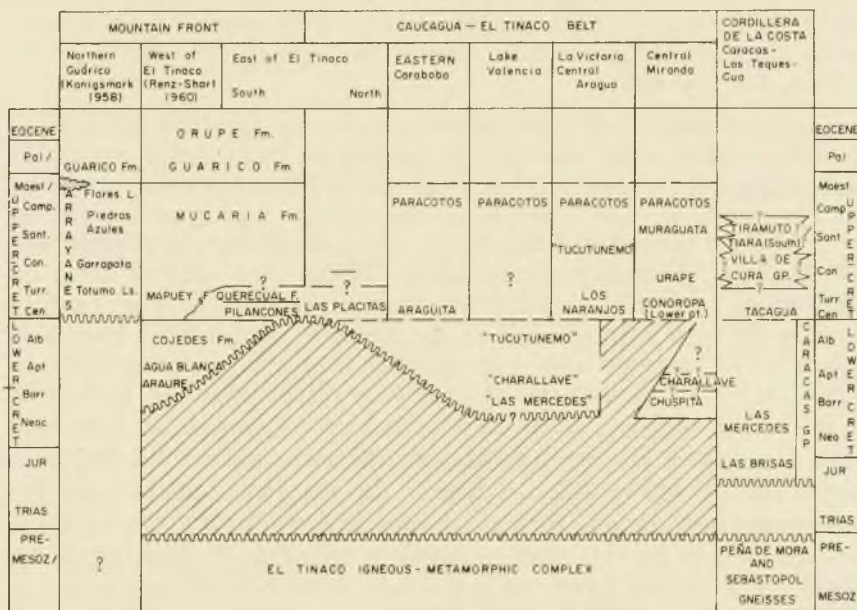


TABLE 1. The following stratigraphic successions as shown in the correlation chart have been modified to fit the interpretation given in the present paper: East of El Tinaco (north); from Menéndez (1965).—Eastern Carabobo; from Oxburgh (1965).—Lake Valencia; from Konigsmark (1965).—La Victoria-Central Aragua; from MacLachlan *et al.* (1960) and Shagam (1960).—Central Miranda; from Seiders (1965).—Cordillera de la Costa; from Smith (1953) and Dengo (1953).

this belt from that north of the La Victoria fault zone. The Lower Cretaceous succession in this belt will be described basically following the findings in the Lake Valencia and El Tinaco areas, and the Upper Cretaceous, as shown by the findings in the Caucagua, La Victoria, and El Tinaco areas.

In the present paper the Lower Cretaceous rocks in the Caucagua-El Tinaco belt are grouped into two conformable units: the older quartzose and the younger carbonate-arkosic units. The quartzose unit includes the "Las Mercedes" and "Charallave" member of MacLachlan *et al.* (1960), Königsmark (1965), and Oxburgh (1965), the Charallave conglomerate of Smith (1953) and Seiders (1965), and the Chuspita formation of Seiders (1965). The carbonate-arkosic unit includes the "Tucutunemo" of Königsmark (1965), Oxburgh (1965), and Menéndez (1965).

ROCK UNITS

The Basement.—The oldest rocks in the Caucagua-El Tinaco belt are represented by the pre-Mesozoic El Tinaco complex (Renz & Short, 1960; Menéndez, 1965) exposed in the southwestern end of the belt. The complex consists of a lower unit (La Aguadita gneiss) made up of hornblende and biotite gneisses, quartz-plagioclase gneisses and minor amphibolites and marbles, and an upper unit composed of muscovite schists, chlorite schists, and conglomeratic schists. In the southern part of the complex the La Aguadita gneiss is intruded by an east-trending belt of trondhjemite plutons which are enveloped by a wide migmatitic zone. Hornblende diorites intrude the Tinapú schist in the northern part of the complex.

The southern border of the complex is overlapped by Albian to Coniacian unmetamorphosed formations (Renz & Short, 1960; Menéndez, 1965). Farther to the east, along the axial zone of the Caucagua-El Tinaco belt, Mackenzie (1953), Seiders (1965, p. 385), and Menéndez (1965, p. 441), correlated some of the units formerly assigned to the Caracas group with the units found in the El Tinaco complex, and reinterpreted them as basement exposures. These correlations seem to be well substantiated on the basis of lithology and mineralogy and on the fact that outcrops are found along the strike. There are hornblende gneisses and quartz-plagioclase gneisses in the basement just east of Santa Lucía, in Quebrada Charallave, and in two isolated localities; one west of Lake Taiguaiguai and the other near Cascabel, west of Lake Valencia. Conglomeratic muscovite schists intruded by hornblende diorites occur in the long basement block south of the town of La Victoria.

The Metamorphosed Cretaceous Sequence.—Two distinct lithologic associations overlie the basement within this belt. The older one, which has been assigned to the upper part of the Caracas group with a Lower Cretaceous age, is characterized by a mature mineralogy with no volcanic influence and was seemingly deposited under stable shelf conditions. The younger se-

quence is of Upper Cretaceous age and is characterized by immature detrital content with much volcanic admixture and associated with basic volcanic rocks (*cf.* Seiders, 1965, p. 312). This lithologic association and the presence of graded-bedding in some of the sandstones indicate deposition under unstable conditions accompanied by volcanic activity. No major break is recognized between the Caracas group and the post-Caracas group formations. They have been found in structural conformity everywhere. The pebbles derived from the Caracas group rocks and contained in younger conglomerates may be explained as the result of local uplift without recurring to a major orogeny (*cf.* Oxburgh, 1965; Seiders, 1965; Menéndez, 1965).

A detailed discussion of the problems of correlation in the metamorphosed Cretaceous sequence is presented by Seiders (1965, p. 382). He suggests a revision of the formations exposed in the Caucagua-El Tinaco belt, and reinterpreted most of the stratigraphic columns given by former workers. Inasmuch as some of Seiders' views are different from those of the writer, an additional review of the stratigraphy in this belt and a new interpretation are presented here. This is particularly necessary because in the Caucagua-El Tinaco belt the tectonic interpretation is related to the stratigraphy in a much greater degree than in any other part of the Caribbean mountains.

Seiders' (1965, p. 384) basic objection, relative to the stratigraphic position of the Charallave conglomerate, is probably invalid since it conflicts with clear-cut structural and stratigraphic relationships well exposed in the Lake Valencia area (Konigsmark, 1965) and in the El Tinaco area (Menéndez, 1965). Seiders (1965, p. 312) describes the younger metamorphic sequence of central Miranda as the post-Caracas group formations, in which he included the Urape, Muraguata, and Paracotos formations. The mainly volcanic lower part of Seiders' Conoropa rocks (see Table 1) will be considered as the basal unit of the post-Caracas group formations in central Miranda.

The Caracas Group in the Caucagua-El Tinaco Belt.—In the Los Teques-Cúa región, Smith (1953) mapped two apparently different rock associations which he described as the older and younger metamorphic complexes. In the older complex he included most of the Caracas group exposed north of the La Victoria fault zone. South of this fault, Smith (1953, p. 50) defined the Charallave conglomerate, essentially composed of lenticular sericitic quartz conglomerates, as the uppermost member of the Las Mercedes formation. He believed that the stratigraphic position of the Charallave conglomerate was definitely established because quartz conglomerates are contained in the upper part of the Las Mercedes formation exposed near Los Colorados north of the La Victoria fault zone. However, the Charallave conglomerate at its type locality, at Quebrada Charallave, overlies a volcanic section equivalent to the probable Upper Cretaceous

Los Naranjos volcanics (Seiders, 1965, p. 386) and is possibly allochthonous (see p. 116).

Konigsmark (1965, p. 219) found a laterally persistent section containing quartz conglomerate lenses in the Lake Valencia area. This section occurs in the upper part of a unit composed of quartzose sericitic schists and quartzites, and grades upwards into an essentially carbonatic-arkosic unit composed of sandy limestones and phyllites and calcareous quartz muscovite schists (Konigsmark, 1965, p. 220). Lenses of thick-bedded limestones are common in the lower part of the carbonate-arkosic unit and appear to be more abundant toward the west. Oxburgh (1965, p. 146) and Menéndez (1965, p. 443) describe calcareous arkoses and feldspathic arenites in association with the lenticular limestones and phyllites of the same unit farther to the west of the Lake Valencia area. Konigsmark (1965) mapped the carbonate-arkosic unit as the Tucutunemo formation of Shagam (1960, p. 254; see p. 114) and the quartzose unit as the Las Mercedes formation. Konigsmark based the correlations on the presence of the quartz conglomerate lenses in the Lake Valencia section, which were correlated with the Charallave conglomerate of Smith (1953). Oxburgh and Menéndez accepted Konigsmark's interpretation and mapped those units accordingly.

The correlation of the quartzose unit with the Las Mercedes formation is probably correct if we consider the quartz conglomerate section as the key horizon, since quartz conglomerates are present in the upper part of the Las Mercedes. The only mistake is related to the nomenclature of these units. Neither the quartzose unit is like the type Las Mercedes nor is the carbonate-arkosic unit like the type Tucutunemo (*cf.* Seiders, 1965, p. 385).

The carbonate-arkosic unit may represent a new formation which has not been formally described as yet. Seiders (1965, p. 303) described the Chuspita formation exposed south of the La Victoria fault zone in central Miranda. This formation is similar and probably equivalent to the quartzose unit of the Lake Valencia area. The main difference is that some of the quartzose beds of the former unit are graded, whereas in the latter this feature has not been reported. Seiders (1965, p. 384) noticed the similarities between the section of the Las Mercedes formation exposed in the northern part of the central Miranda area and the Chuspita formation, and concluded that this formation may be either concordant above the Las Mercedes formation or partially equivalent to it. The latter alternative is probably correct as suggested above in relation to the quartzose unit of the Lake Valencia area. The Chuspita appears to be allochthonous in central Miranda (see p. 116). This may explain the almost abrupt change of facies across the La Victoria fault zone from the calcareous Las Mercedes to the essentially arenaceous Chuspita formation .

The quartzose unit represents the oldest unit that may be assigned to the Caracas group in the Cauagua-El Tinaco belt. It has been correlated with

the arenaceous Araure formation of Lower Cretaceous age exposed west of San Carlos in the mountain front. The younger carbonate-arkosic unit has been correlated with the Agua Blanca and Cojedes formation of Aptian-Albian age, exposed also in the mountain front south and west of the El Tinaco massif (Renz & Short, 1960; Oxburgh, 1965; Menéndez, 1965).

Post-Caracas Group Formations.—In central Miranda, Seiders (1965: 312) describes a lithologic assemblage "... characterized by the presence of clastic rocks with immature detritus and minor mafic metavolcanic rocks ..." as the post-Caracas group formations of Upper Cretaceous age. In this assemblage he included, from older to younger, the Urape, Muraguata, and Paracotos formations. The Urape and Muraguata formations are exposed in the Caucagua-El Tinaco belt and the Paracotos formation in the Paracotos belt (see p. 119). The Urape is composed of phyllites, feldspathic to lithic arenites and wackes, and minor quantities of mafic metavolcanics and dark limestones. The Muraguata formation contains a similar lithology but the phyllites in this formation are more abundant than in the Urape formation.

In central Aragua, Shagam (1960, p. 254) defined the Tucutunemo formation composed of phyllites, limestones, and feldspathic lithic arenites. Shagam was not certain of the stratigraphic position of his Tucutunemo formation and assigned it provisionally to the Caracas group conformably above the Las Mercedes formation. It is more probable, however, that Shagam's Tucutunemo be partially equivalent to the Urape formation since the sandstones of both formations contain chert fragments which are not found in the Caracas group rocks (*cf.* Seiders, 1965, p. 390). Rock units similar to the Urape formation have not been reported west of the La Victoria area in this belt. However it is probable that the transitional zone between the Araguaita formation (Oxburgh, 1965, p. 155) and the Paracotos formation represents the Urape formation in the eastern Carabobo area.

In the La Victoria area, MacLachlan *et al.* (1960, p. 242) found basaltic pillowed lavas and greenstone metatuffs in the lower part of the Tucutunemo of Shagam. These volcanic rocks were named the Los Naranjos member. Similar volcanic rocks have been described by Menéndez (1965, p. 446) in the El Tinaco area as the Las Placitas formation, by Oxburgh (1965, p. 155) in eastern Carabobo as the Araguaita formation and by Seiders (1965, p. 340) in central Miranda as the lower part of the Conoropa rocks. The Las Placitas and the lower Conoropa rocks rest unconformably on the basement. The Las Placitas is probably of Cenomanian to Coniacian in age. In the El Tinaco area the Las Placitas grades laterally into the Cenomanian to Coniacian Querecual formation, and the basaltic lavas of the Las Placitas are chemically and texturally similar to the Pílancones lavas (Menéndez, 1965, p. 457) of probable Cenomanian age. Furthermore, the Querecual and the Pílancones lavas overlie conformably

the Albian Cojedes formation and overlap the southern border of the El Tinaco massif.

Under the present interpretation the Los Naranjos volcanics and equivalents are the basal units of the post-Caracas group formations. All these volcanic units are probably of Cenomanian to Coniacian age as has been indicated for the Las Placitas formation. The basal volcanic unit is followed conformably upwards by a shale-graywacke sequence and minor volcanic rocks, represented by the Urape and Muraguata formations in central Miranda. The Paracotos formation, exposed south of this belt along the Paracotos belt, constitute the uppermost unit of this sequence. The post-Caracas group formations are correlated as a whole with the fossiliferous Arrayanes group (Garrapata and Piedras Azules formations, see Table 1) of Upper Cretaceous age as redefined by Konigsmark (1965, p. 236).

The Tiara volcanics of Smith (1953, p. 58) probably include the Los Naranjos volcanics (MacLachlan *et al.*, 1953, p. 243) and other volcanic rocks of the post-Caracas group formations.

The Tertiary-Quaternary Basins.—Miocene sediments and sedimentary rocks folded into broad synclines are present in the Santa Lucía basin and in the Tuy basin in the eastern part of the Caucagua-El Tinaco belt. These beds unconformably overlie the metamorphosed Cretaceous sequence of this belt. In the western part of the belt there are Quaternary flat-lying lacustrine sediments which are related to Lake Valencia.

MAJOR STRUCTURES

A discontinuous belt of basement exposures is characteristically present along the Caucagua-El Tinaco tectonic belt. The slightly metamorphosed Cretaceous cover is not intensely folded on a great scale, but the structural picture is complicated by the presence of allochthonous sheets and normal faulting. Almost flat-lying beds are described by MacLachlan *et al.* (1960) in the La Victoria area, for example, and in the El Tinaco area gently dipping open folds are present.

The basement blocks appear to have played an active role during the folding stage, because they were at shallow depth at this time. With no apparent deformation in themselves, they effectively transmitted the forces coming from the north and protected the rocks lying directly above them. This behaviour of the basement is well exemplified in the structure found in the El Tinaco area. The upper Cretaceous to Paleocene thick pile of sediments exposed directly south of the massif are steeply dipping, isoclinally folded and overturned to the south. Whereas a thinner and approximately equivalent sedimentary sequence found lying directly on the El Tinaco massif, are gently folded. It is also apparent that the higher degree of deformation and the overturning to the south, present in the southern part of the Cordillera de la Costa tectonic belt, were accentuated

by the presence of the basement blocks at shallow depths in the Cauagua-El Tinaco belt during the deformation stage (cf. Seiders, 1965, p. 408).

The San Antonio Overthrust and the Allochthon in Central Miranda.—In the western part of the Cauagua-El Tinaco belt a carbonate-arkosic sequence ("Tucutunemo" formation of Oxburgh, Menéndez, and Konigsmark) contains Charallave-like quartzose conglomerates in the lower part and conformably overlies the Las Placitas formation which correlates with the Cenomanian-Coniacian Querecual formation. The carbonate-arkosic sequence has been correlated with the Agua Blanca and Cojedes formations of Aptian-Albian age, exposed west and south of the El Tinaco basement complex. Thus, it appears that the contact between the carbonate-arkosic sequence and the Las Placitas formation is a bedding-plane fault (Menéndez, 1965, p. 518). The fault has been folded into an open syncline plunging N 70°E. The trace of the fault has been followed up to the northwest-trending Aragiüta fault on the east, and around the axial zone of the syncline on the west. Small serpentinite bodies sympathetically follow along and near the trace of the bedding-plane fault. Across the Aragiüta fault the trace of the overthrust and the synclinal structure have been displaced for about 5 km to the south. Along this displaced sector of the overthrust, serpentinites are also found. The foliation of the sheared serpentinite conforms with that of both the autochthon and the allochthon.

Seiders (1965, p. 340) finds a similar relationship in the central Miranda area close to the east border of the Santa Lucía basin, and west of this basin in Quebrada Charallave. In these localities he describes the Conoropa rocks made up of metasedimentary and volcanics in the lower part and of the Charallave conglomerate in the upper part. However, he (1965: 387) concludes that the sequence should be a conformable one with no thrust in between, despite the evidence presented in the El Tinaco area. From the relationships in this area it may be deduced that the Charallave conglomerate, equivalent to the upper part of the quartzose unit, should be older than the volcanic part of the Conoropa rocks, equivalent to the Las Placitas (see Rock Units). Seiders' conclusion is based on the impressive lateral continuity of this relationship and on the fact that there is no apparent sign of overthrusting in the well exposed section at Quebrada Charallave. However, subsequent metamorphism may have obliterated any direct evidence of thrusting like shearing or mylonites. The trace of the overthrust may only be evident where serpentinites occur as it is the case in the El Tinaco area.

In the central Miranda area as indicated above (p. 115) the Urape formation should normally overlie the lower volcanic part of the Conoropa rocks. The Charallave conglomerate properly is a part of the quartzose unit, also represented in central Miranda by the Chuspita formation.

The Chuspita formation appears to be also allochthonous. The absence of the thick quartzose Chuspita below the younger Conoropa volcanics

exposed nearby, which directly overlies the basement, is taken as evidence for a relative long distance of transport of the Chuspita (cf. Seiders, 1965, p. 402). The Chuspita probably has been thrust over the Urape formation everywhere as has been found in the northern part of central Miranda (Seiders, 1965, p. 402). The Chuspita probably was deposited in deep water and its partially equivalent coarse conglomerates of the Charallave may represent a near shore deposit. They came to occur close to each other as a result of the overthrusting.

The Tiramuto Klippen.—In the southwestern end of the Cauagua-El Tinaco belt the sedimentary sequence forms an open N 80°E trending synclinal structure which is truncated to the south by a normal fault down-thrown to the south (El Pao fault). The closure of the fold is located to the east in the vicinity of Gamelotal. All layers involved in this structure, excepting those of the Tiramuto formation which occupies the core, dip uniformly towards the axial zone of the syncline. The attitudes of beds in the Tiramuto formation are chaotic except in the basal part where bedding conforms with the underlying Paracotos formation.

In the northern flank of this synclinal structure (see Fig. 5), the following units, structurally from lower to higher, are found:

The *Querecual formation* of probable Cenomanian-Coniacian age (Mackenzie, 1953; Renz & Short, 1960; Menéndez, 1965) is made up of black shales, black limestones, and black chert. It has been intruded by the sill-like *Sabana Larga pyroxene-diorite breccia* of probable Coniacian age (Menéndez, 1965). The Querecual and this unit are disconformably overlain by the *Orupé formation* of Late Eocene age (Renz & Short, 1960) which consists mainly of silty shales and micaceous arenites. This unit is overlain by the shales and lithic wackes of the

Guárico formation which contains Paleocene microfauna (Bermúdez, personal communication, in Menéndez, 1965). The Guárico is in turn overlain by the *Paracotos formation* which does not contain any diagnostic fauna at this locality, but consists of the same lithologic succession as the Lower Maestrichtian Paracotos found all along the Paracotos structural belt. This unit is overlain by the

Tiramuto formation of unknown age, which contains banded tuffs, basic lithic tuff-breccias and basaltic lavas, and is intruded by gabbro sills.

In the closure of the syncline a similar succession is present. The contact between the Orupé formation and the underlying Querecual and diorite breccia is clearly an erosional surface, but the conformable regional distribution of these formations, and the slight difference in attitude of their

beds, indicate that the contact approaches a disconformity. Thus it appears that the folding stage was in the Late Eocene or later.

The contacts between the Orupé Guárico and Paracotos formations are bedding-plane faults as indicated by: (1) the relative ages of these units which are the reverse of what is indicated by their conformable superposition; (2) the sedimentary structures, showing that the layers are right side up, and (3) the trace of the contacts between these units, which are almost parallel to the Querecual-Orupé contact. Therefore, the rocks above the Orupé formation are allochthonous and reached their present position after travelling over flat-lying rocks of the Querecual and Orupé formations.

The writer (Menéndez, 1965, p. 483) pointed out the close lithologic similarity of the Tiramuto formation and the volcanic rocks found in the area of Cerro Copetón, on the northern edge of the Villa de Cura group, proposed their correlation and assumed that a depositional contact existed between the volcanics and the underlying rocks. The volcanics at Copetón also lie conformably on the Paracotos formation and are also intruded by gabbros. If the volcanic rocks at Copetón are part of the Villa de Cura group as mapped by Oxburgh (1965, p. 137) the Tiramuto may also be part of this group. This correlation is supported by the presence of identical pyroxenes (Calcium-rich salites) in the Villa de Cura and in the Tiramuto formation which have not been reported elsewhere in the Caribbean mountains (*cf.* Seiders, 1965, p. 377). The Villa de Cura group is found thrust over the Paracotos formation (see p. 121). Thus it is probable that the contact between the Tiramuto formation and the underlying Paracotos formation be another bedding-plane fault. This interpretation is also supported by the fact that not a single dyke or sill cuts the underlying Paracotos beds, while the Tiramuto is intruded by many gabbro sills.

The Tiramuto allochthonous blocks, or klippen, appear to end in the vicinity of Río Tinaco against a northeast-trending fault. The fault is of small displacement, indicating that the disappearance of the rocks of the klippen to the west is not due to offset, but to the original extent of the blocks. The allochthon has a nearly oval shape with a maximum east-west length of 17.5 km and a maximum width of 6.5 km. The minimum thickness of the allochthon is 1.6 km as deduced by the minimum thickness of the Paracotos and Tiramuto formations. The Guárico allochthon is apparently wedge-shaped.

The Tiramuto klippen appear to represent gravity slide blocks for the following reasons: (1) the allochthon is folded in conformity with regional structures, which implies that their emplacement preceded the folding stage, or in other words, the stage in which lateral forces started to act; (2) the Tiramuto klippen have a present limited geographic distribution; (3) the upper klippen (Tiramuto volcanics) is crossed by many relatively

small rotational faults, which implies tension, and (4) the paleogeography indicates that a southward slope existed during the probable time interval when the allochthon was emplaced (Late Eocene or later).

The minimum distance that the Tiramuto klippen have traveled is 7 km, deduced from the maximum width of the klippen plus the width of the exposures of the Orupé formation. The units making up the allochthon are absent in the autochthon below the Orupé formations. This indicates that strong erosion preceded the emplacement of the klippen and therefore they must have come from a long way off. This is also suggested by the difference in lithology between the allochthonous Paracotos formation and the autochthonous Mucaria formation which is almost exclusively made up of the siliceous shales and is exposed around the allochthon. The Mucaria facies was typically developed south of the Paracotos facies in central Venezuela (Renz, 1955; Menéndez, 1965, p. 473).

THE PARACOTOS BELT AND THE VILLA DE CURA BLOCK

General.—The Paracotos belt is exposed from the central Miranda area to the eastern Carabobo area, between the Santa Rosa fault to the north and the Agua Fría fault to the south, and bounds the northern and western edges of the Villa de Cura block. The belt has been mapped almost continuously for about 200 km with an average width of 2 to 3 km. Eastwards it disappears under the sediments of the Tuy Tertiary basin (Seiders, 1965). The general trend of the Paracotos belt is east-west up to the middle of the eastern Carabobo area where it turns to the southwest.

The Paracotos belt contains the distinctive Upper Cretaceous Paracotos formation as redefined by Shagam (1960). The lithology of this formation persists essentially unchanged throughout the belt. The main rock type of the Paracotos formation is a blue carbonaceous silty phyllitic shale. The presence of gray and pale green aphanitic limestones, however, constitutes the distinguishing lithologic feature of the formation. Particularly distinctive is the persistent close association of gray-green conglomerates and gray aphanitic limestones close to the top of the formation (Shagam, 1960). This lithologic association is always found adjacent to the Agua Fría fault, even where the Paracotos belt curves around to the southern side of the Villa de Cura block in its westernmost occurrence (Oxburgh, 1965). These limestones have yielded fossils indicating an Early Maestrichtian age for the upper part of the Paracotos formation.

The Villa de Cura block is almost exclusively composed of rocks of the Villa Cura group of unknown age as redefined by Shagam (1960). This group essentially consists of an estimated 3 to 6 km-thick pile of slightly metamorphosed water-laid tuffs and lavas, exposed from Cerro El Joval in the west (Oxburgh, 1965) to 250 km east of this locality in the vicinity of El Guapo (Konigsmark, personal communication, 1961). The maximum width of the area, attained in its western part, is 28 km.

Shagam (1960, p. 257) divided the Villa de Cura group into the following four formations, from bottom to top: El Caño, El Chino, El Carmen, and Santa Isabel. He considered the El Caño to be the oldest and the Santa Isabel the youngest owing to their conformable superposition. A similar succession was found by Konigsmark (1965) and Oxburgh (1965) west of the central Aragua map area. Seiders (1965) carried out a detailed mineralogical study of the Villa de Cura rocks exposed in central Miranda, and suggested that the sequence may be the reverse of that originally proposed by Shagam. Seiders found that the Santa Isabel formation contains greenschist mineralogy and that the other three have lower grade pumpellyite-lawsonite bearing assemblages. An additional petrological study is being undertaken by Piburn (Princeton University, Ph. D. Thesis, in progress) who may be able to determine whether this metamorphic inversion is of regional nature.

The Villa de Cura block is bounded on the south by the Cantagallo fault (Konigsmark, 1965; Jarvis, 1964) and by the La Puerta fault (Shagam, 1960) along which it is in contact with the Upper Cretaceous to Lower Tertiary sedimentary rocks of the mountain front. Locally along its southern part the Villa de Cura is overlain by the basic volcanic rocks of the Tiara formation of unknown age (Shagam, 1960; Konigsmark, 1958; Jarvis, 1964). Northwest of the town of San Sebastián the Maestrichtian Escorzonera formation lies on the Tiara formation (Shagam, 1960) and the Escorzonera is in turn overlain with slight unconformity by the Paleocene Guárico formation (Renz, 1965, p. 52). West of San Juan de los Morros, the Guárico formation overlaps onto the Villa de Cura (Shagam, 1960).

From the time that Shagam (1955) reported the presence of the Villa de Cura volcanics and its association with the Paracotos belt, the tectonic setting of these two units and the stratigraphic position of the Villa de Cura have represented the major geologic problems in the Caribbean mountains of Venezuela. Both Shagam and Konigsmark considered the Villa de Cura group to be Lower Cretaceous in age and younger than the Caracas group. Shagam explained the Paracotos belt as the result of downfaulting with the bounding faults later rotated northwards. Konigsmark was impressed by the straightness and continuity of the faults in central Aragua and northern Guárico and believed that the Paracotos belt was restricted to a depressed area between two right-lateral strike-slip faults. Oxburgh (1965) mapped the western end of both the Paracotos belt and the Villa de Cura block and considered the Villa de Cura as pre-Cretaceous basement. However, Oxburgh found great difficulty in explaining the sympathetic distribution of the northern and western borders of the Villa de Cura block and the Paracotos belt. He thought that the faults that bound the Paracotos belt were normal faults surrounding a rising basement block. He also proposed a later northward rotation of the fault planes to account for its present

southward dip. The writer Menéndez (1965) observed the parallel attitudes of the Villa de Cura and Paracotos layers across the Agua Fría fault as mapped by former workers, and pointed out that this fault was a bedding-plane fault, and that the Villa de Cura represented an allochthonous block as previously proposed by Hess (personal communication, *in* Oxburgh, 1965). Seiders (1965) and Jarvis (1964) found further evidence in support of the allochthonous hypothesis.

Tectonic Setting.—Menéndez (1965, p. 523) pointed out the existent structural evidence indicating that the Agua Fría fault is a bedding-plane thrust, and that therefore the sliding of the Villa de Cura over the Paracotos beds should have taken place in Maestrichtian time or later. The structure within the Paracotos belt is complex in detail; disharmonic folds are abundant in phyllites. However, the competent layers of conglomerate and limestone of the upper part have a constant attitude, striking parallel to the Agua Fría fault and dipping toward this fault. In every case these beds and those on the northern side of the Villa de Cura block across the Agua Fría fault, appear to have a similar southward dip (Shagam, 1960; Konigsmark, 1965; Oxburgh, 1965; Seiders, 1965). In the northern Guárico area, the rocks of the Villa de Cura group form an east-trending broad syncline, bounded to the south by the Cantagallo fault (Konigsmark, 1965). Seiders (1965, p. 405) observed that beds equivalent to the Paracotos south of the fault are parallel to the fault and dip northward under the Villa de Cura group at a low angle. Jarvis (1964), who mapped the western sector of this fault in detail, observed a similar attitude. Thus, it appears that the Agua Fría fault, as a gliding plane for the Villa de Cura slide block, crops out again to the south as the Cantagallo fault. East of San Juan de los Morros the nature of the southern bounding fault of the Villa de Cura is somewhat obscured by the presence of the younger east-trending La Puerta fault.

The Santa Rosa fault appears to be a normal fault downthrown to the south. This fault may have formed as result of the depression of the area where the Villa de Cura block came to rest. Several intrusions of serpentinite are closely associated with the Paracotos belt. Hess (personal communication, 1962) has suggested that these serpentinites may have been part of a once probably continuous sheet which supplied the lubricating medium underneath the sliding Villa de Cura block. On the other hand, the localization of the serpentinites may also be the result of deep fractures opened by the sudden loading of the crust with the Villa de Cura slide block (Seiders, 1965).

On the basis of paleogeography, showing that an intra-Senonian regional unconformity was unnecessary, Oxburgh (1965, p. 185) rejected Shagam's (1960, p. 296) proposal of a Cretaceous age for the Villa de Cura group as an autochthonous unit. This is particularly evident because there is no indication of the type of volcanism represented by this group in the Lower

Cretaceous rocks exposed close to the western end of the Villa de Cura block. Oxburgh concluded that the Villa de Cura group may be either an allochthonous block which slid onto its present position during pre-Coniacian time, or that it is part of the pre-Cretaceous basement. He considered that the first alternative was preferable because: (1) nappe-type folding and overthrusting were not characteristic of deformation patterns in northern Venezuela, and (2) the Villa de Cura had to slide southwards in middle Cretaceous time over basins undergoing continuous sedimentation, and there was no record of this event in the middle Cretaceous deposits exposed to the north of the block.

The first objection raised by Oxburgh to the allochthonous hypothesis is no longer tenable after the study of El Tinaco (Menéndez, 1965) and the central Miranda (Seiders, 1965) map areas. The pre-Coniacian age of the sliding of the Villa de Cura was based on the presumed presence of pebbles of the Tiara volcanics in Coniacian conglomerates exposed south of the Villa de Cura block. However, Seiders (1965) has clearly shown that these pebbles may have been derived from other sources.

The basement hypothesis is unlikely because: (1) all basement exposures south of the Villa de Cura block and basement rocks recorded in boreholes are unlike the Villa de Cura rocks types (Shagam, 1960, p. 296); (2) the migmatitic zone of the El Tinaco complex is exposed 2 km along strike from the westernmost outcrop of the Villa de Cura group (Menéndez, 1965). A gradation between these two rock groups, to be expected if the Villa de Cura were equivalent to the El Tinaco complex, is not found. Rocks of the Villa de Cura are not found lying on the El Tinaco complex or on the basement blocks exposed in the Caucagua-El Tinaco belt; (3) the Villa de Cura contains a mineralogical assemblage which is characteristic of the high pressure low temperature metamorphic facies series proposed by Miyashiro (1961), contrasting with the high-temperature low-pressure assemblage of known basement rocks nearby (Seiders, 1965); and (4) the source area of the Caracas group sediments was to the south, in the approximate area of the present exposures on the Villa de Cura block and was essentially of granitic composition (Konigsmark, 1965; Shagam, 1960).

Time of Emplacement of the Villa de Cura Block.—The most appropriate time for the sliding of the Villa de Cura block appears to have been the Late Maestrichtian to Paleocene. During the Late Maestrichtian-Paleocene time there was a suitable southward slope for the sliding to take place and a deep basin to receive the Villa de Cura block. This is indicated by the geographic distribution of the Late Maestrichtian-Paleocene (Renz & Short, 1960) Guárico formation south of the Villa de Cura.

The characteristics displayed by the rocks of the Guárico formation resemble the European flysch facies as described by Dzulynski *et al.* (1959). The accumulation of this type of deposit has been ascribed to turbidity currents at great depth (Kuenen, 1959). The occurrence of

boulder beds in the Guárico formation in close association with turbidites between El Tinaco and El Pao, adds another feature indicative of turbulent depositional conditions during the Late Maestrichtian-Paleocene time (Menéndez, 1965). Allochthonous blocks imbedded in Early Tertiary shales have been described from the State of Lara (Renz *et al.*, 1955; Bushman, 1965; Evanoff *et al.*, 1959). Renz *et al.* (1955) suggested that the allochthonous blocks were transported by submarine sliding and accumulated along the axis of a deep trough, which was called the Barquisimeto trough. Renz & Short (1960, p. 296) reported the presence of boulder beds in the Guárico formation, north of El Pao, and suggested the probable eastward extension of the Barquisimeto trough into the El Tinaco-El Pao area. It is likely that the trough continued even farther to the east with an axis parallel to the southern boundary of the Villa de Cura block. This is suggested by the presence of Paleocene boulder beds in the area north of Ortiz and San Francisco de Cara, State of Guárico (Sellier de Civrieux; *in* Bushman, 1965).

The Cretaceous-Tertiary boundary is within the Guárico formation if the southern part of the El Tinaco area (Renz & Short, 1960) and the Guárico formation transitionally overlies the Mucaria formation (equivalent to the Paracotos). In the area north and northeast of San Juan de los Morros, on the southern part of the Villa de Cura block, on the other hand, the Guárico formation overlaps the Maestrichtian Escorzonera formation (H. H. Renz, 1957, p. 743), which overlaps the Tiara volcanics and the Villa de Cura group (Shagam, 1960; Konigsmark, 1965).

Thus it seems that the pre-Paleocene sequence (the Escorzonera formation and the Tiara volcanics) lying on the Villa de Cura group were transported southwards on top of the Villa de Cura block, and the Paleocene sediments of the Guárico formation were deposited on this block immediately after the sliding. It is also significant that the Guárico deposits lying on the Villa de Cura are represented by reef limestones (the Morro del Faro member).

The sliding of the Villa de Cura in the Late Maestrichtian would explain a pre-Paleocene folding which is not evident except along the Paracotos belt and on the southern side of the Villa de Cura block.

MacLachlan *et al.* (1960, p. 245) found small patches of sedimentary rocks of probable Paleocene age overlying the Paracotos formation unconformably. No diagnostic fossils were found in these rocks, except in a slab of limestone from a hill 4 km east-southeast of the town of Villa de Cura where Paleocene fossils were found. However, the limestone does not seem to be *in situ* as shown by a quarry open in this place recently (H. H. Hess, personal communication, 1965). The age of this limestone was taken by Menéndez (1965, p. 534) as the upper limit for the time of emplacement of the Villa de Cura block. At any rate it is probable that the sliding of this block was immediately after the accumulation of the sediments of the

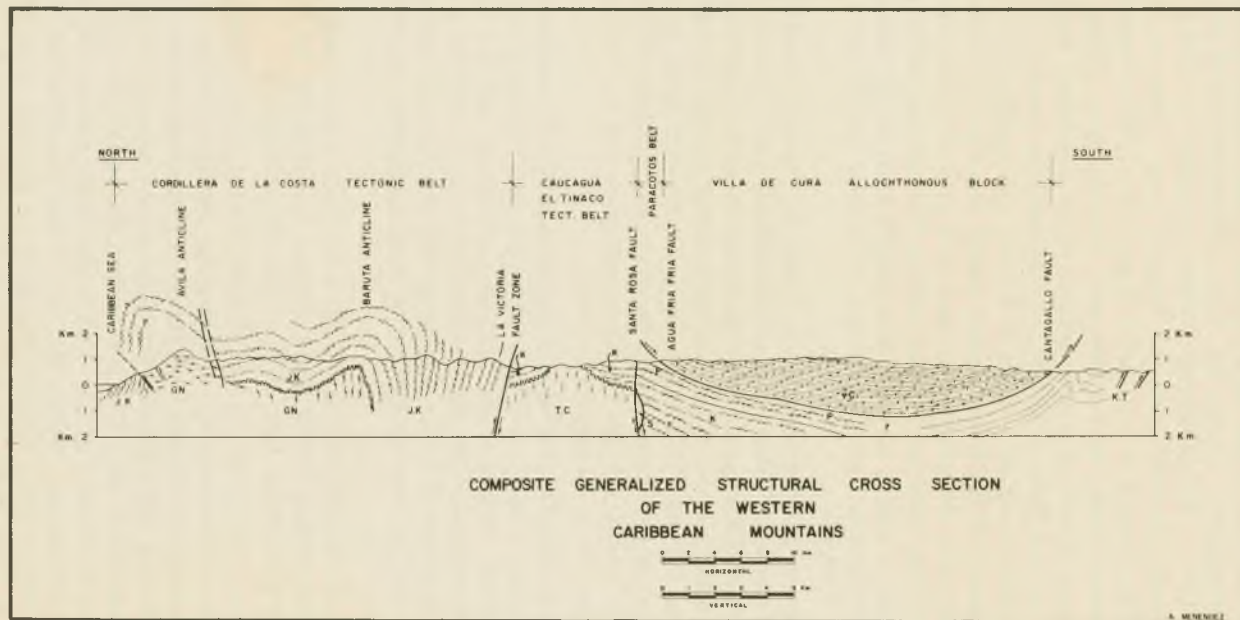


FIGURE 4. Generalized composite north-south structural cross-section of the western Caribbean Mountains.

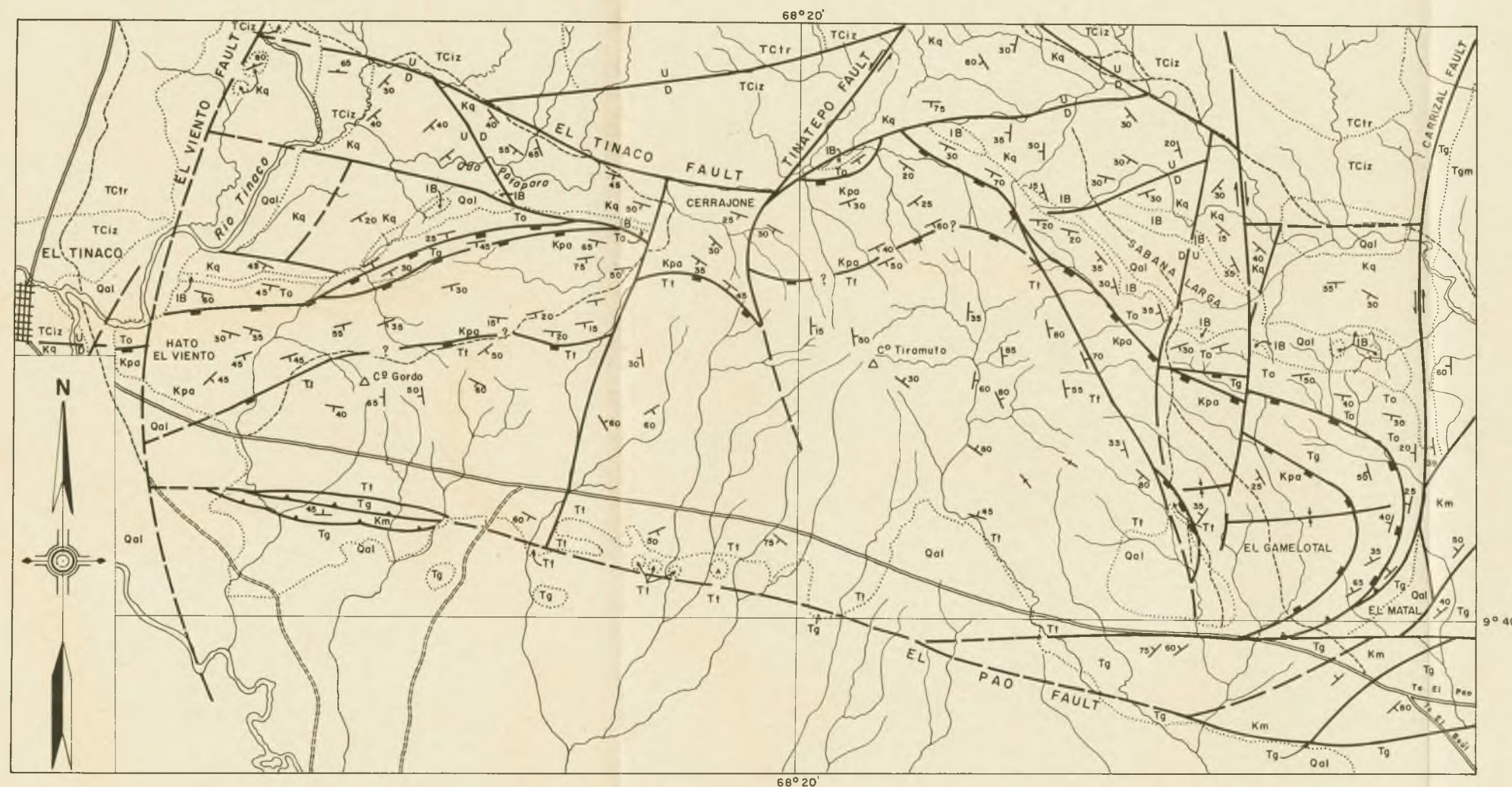


Figure 5
GEOLOGIC MAP OF THE TIRAMUTO AREA, VENEZUELA

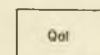


GEOLOGY BY A. MENENDEZ

FIELD WORK SPONSORED BY DIRECCION DE GEOLOGIA, MINISTERIO DE MINAS E HIDROCARBUROS
REPUBLICA DE VENEZUELA
1962

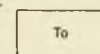
LEGEND

QUATERNARY

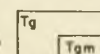


ALLUVIUM

TERTIARY



ORUPÉ formation

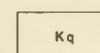


GUARICO formation
MAMONAL member

CRETACEO

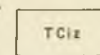


PARACOTOS formation
MUCARIA member

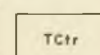


QUEREQUAL formation

EL TINACO BASEMENT
COMPLEX

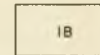


INJECTION ZONE



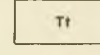
TRONDHEJEMITE

UPPER CRETACEOUS
(CONIACIAN ?)

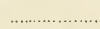


SABANA LARGA igneous breccia.

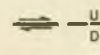
AGE UNKNOWN



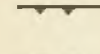
TIRAMUTO formation



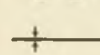
Formation contact



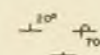
Fault Showing relative movement
(dashed where concealed)



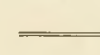
Thrust fault



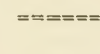
Bedding plane fault



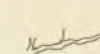
Syncline.



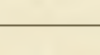
Altitude of bedding



MAIN ROAD



JEEP ROAD



TRAIL



DRAINAGE.

Paracotos formation since no rocks younger than the Paracotos have yet been found underlying the Villa de Cura group.

The complex folding in the incompetent layers of the Paracotos formation along the belt represent drag folds related to the thrusting of the Villa de Cura block. Seiders (1965, p. 405) described drag folds in the southward-dipping beds of the Paracotos formation. The drag folds are overturned in the down-dip direction. He also interpreted this feature as the result of the southward sliding of the Villa de Cura block on top of these beds.

Age and Source of the Villa de Cura Group.—Since the Villa de Cura is an allochthonous block and its roots have not yet been found, the age and original geographic position of the Villa de Cura remain as major problems of the western Caribbean mountain geology. The derivation of the Villa de Cura block from a long east-trending ridge once situated to the north is necessary. If the sliding was due solely to gravity with no intervening lateral pressure, its original position may well be north of the present coast of Venezuela. However, if the sliding was initiated by lateral forces which later folded the mountains, the original position of the Villa de Cura may have been just above the Caracas group, within the area occupied by the Cordillera de la Costa tectonic belt. This is suggested by the asymmetry of the structures which are directed away from an east-trending broad axial zone (see Fig. 4). This zone is located along this belt immediately to the south of the northward thrust Avila Anticline.

From the stratigraphic relationships the age of the Villa de Cura group is pre-Maestrichtian. Assuming a Mesozoic age for the group, the best stratigraphic position of the Villa de Cura is just equivalent to the pre-Paracotos, post-Caracas group formations. This is suggested by the common occurrence of volcanic rocks at that time beginning with the volcanic basal formations of that sequence (the Las Placitas, the Los Naranjos, and equivalents). However, no petrogenetic relationships have been shown as yet between these volcanic rocks and the Villa de Cura to substantiate this inference.

The banded tuff of the El Caño formation are similar to the Los Naranjos tuffs but the associated lavas differ (Shagam, 1960); the El Caño lavas are augite andesites and spilites while those of the Los Naranjos and Las Placitas are normal basalts. The only volcanic rocks outside the Villa de Cura block which have some lithological similarities with the Villa de Cura rocks are those of the Tiramuto formation. However, the Tiramuto formation is also allochthonous and of unknown age.

THE MOUNTAIN FRONT

South of the Serranía del Interior of central Venezuela there is an area of low relief, characterized by low rounding hills with intervening flat alluvial plains up to the Galeras. Within this area, north of the so-called

frontal thrust, sedimentary rocks ranging in age from Lower Cretaceous to Upper Eocene have been described (Evanoff, 1951; Kamen-Kaye, 1942; Renz, 1955; Konigsmark, 1965; Menéndez, 1965; Jarvis, 1965; see also Table 1).

The structure in the mountain front is characterized by the predominance of isoclinal folding and overturning, and high-angle thrusting to the south up to the frontal thrust. This thrust zone has been mapped from south of San Carlos on the west up to the Laguna de Unare on the east (see Peirson, 1963, Fig. 1). Along the frontal thrust zone the Upper Cretaceous to Eocene sequence of the mountain front has been thrust over Eo-Oligo-Miocene sediments (Evanoff, 1951).

TECTONIC EVOLUTION

The structures present in the four tectonic belts of the Western Caribbean mountains were the result of one Upper Cretaceous to Lower Tertiary tectonic cycle.

Sedimentation during the Late Jurassic to Lower Cretaceous took place mainly under stable shelf conditions. The source for the Caracas group sediments was mostly of a granitic composition. The rocks of the Tinaco complex exposed now along the Caucagua-El Tinaco belt represent part of the northern border of the land which supplied detritus to the Caracas group transgressing sea. Probably the sea advanced farther southwards immediately to the east and west of the El Tinaco massif as indicated by dated Lower Cretaceous rocks north of El Pao and west of San Carlos (Renz & Short, 1960; Menéndez, 1965).

Tectonism started with the uplift to an east-trending submarine ridge bounded on the south by a deep fracture zone (La Victoria fault zone) and probably by another deep fracture zone on the north. At the same time, in the area to the south of the ridge, widespread volcanic activity took place at the beginning of the Upper Cretaceous. The deposition of the Villa de Cura volcanics began to the north of the ridge; that of the Tacagua volcanics on the ridge and on the Los Naranjos volcanics and equivalents to the south. At the same time, carbonaceous lime muds (the Querecual formation) were deposited in a basin of restricted circulation to the south.

Renewed uplift along the Cordillera de la Costa submarine ridge was followed by the detachment of the upper part of the Caracas group off the flank of the ridge. This block slid southward over the volcanics and sediments of the lower part of the post-Caracas group succession, which had just been deposited.

The first episode of gravity sliding was followed by the sedimentation of the Urape-Garrapata shale-graywacke still under deep water conditions and in the same broad basin of the Querecual accumulation. Local uplift within the basin may have contributed the coarse clastics for the Urape and Garrapata conglomerate. The accumulation of the Urape was accompanied

by minor volcanism along the southern flank of the Cordillera de la Costa submarine ridge. Along the northern flank of this ridge, the Villa de Cura volcanism may have been continuous up to the Upper Senonian, when the mud and silt of the Paracotos began to be deposited. Probably at this time the Cordillera de la Costa ridge subsided and another east-trending elongated submarine ridge started rising north of the present coast of Venezuela. This uplift may have taken place probably as a result of renewed activity along the northern deep fracture of the older ridge.

Following the deposition of the pelagic limestones and conglomerates of the upper part of the Paracotos, the uplift of the new northern ridge reached a maximum and an east-trending deep trough started forming to the south in the Early Maestrichtian. As a result, the Villa de Cura block slid off the flank of this ridge toward the deep Barquisimeto trough. The part of the Paracotos sediments (the Escorzonera) deposited on the southern flank of the submarine ridge was carried down on top of the Villa de Cura block. Owing to isostatic adjustment, the area where the Villa de Cura came to rest subsided and a deep fracture (the Santa Rosa fault) was formed along the northern edge of the block. The Guárico flysch was deposited in the deep trough to the south of the Villa de Cura block and on top of it to the north.

The area now occupied by the Caucagua-El Tinaco belt was uplifted after the Villa de Cura block slid in, as a result of activity along the La Victoria fault zone and the Santa Rosa fault. This elevated area represented the northern provenance of the Guárico sediments. This is well exemplified in the El Tinaco area, where coarse conglomerates of the Guárico formation (fluxo-turbidites) were deposited close to the upfaulted El Tinaco massif.

The last recorded episode of gravity sliding within the orogenic belt is represented by the Tiramuto klippen, and took place in the Eocene after the deposition of the shallow water sediments of the Orupé. The allochthonous sheets of the Tiramuto may have come from an edge of the Villa de Cura slide block having the Paracotos and the Guárico beds on top. Thus the Guárico sheet slid southward into its present position first, followed by the Paracotos, and then by the Tiramuto volcanics.

After the episode of epeirogenesis and overthrusting, the Caribbean mountains were compressed by NNW-SSE forces. The age of this orogenesis may be bracketed between Late Eocene and Miocene within the Caribbean mountains, as indicated by the angular unconformity below the Miocene deposits of the Santa Lucía basin and the fact that the Late Eocene Orupé beds are folded in conformity with regional structures. Thus, it is quite probable that the main folding stage was in the Late Eocene, since at this time a widespread orogenic episode took place in the rest of northern Venezuela (Kugler, 1953; Hedberg, 1950).

After the folding stage in pre-Miocene time, the Cordillera de la Costa was uplifted. During the Miocene and later, sedimentary basins were

formed along the axial zone of the Western Caribbean mountains. During post-Miocene deformations the entire metamorphic belt acted as one block, as shown by the mild broad folding in the Santa Lucía basin, located in the axial zone of the mountains, and the southward thrusting of the Upper Cretaceous-Eocene sequence over the Eo-Oligo-Miocene beds along the frontal thrust. Tectonism is still going on in northern Venezuela as indicated by periodical earthquakes.

The metamorphism of rocks of the Caribbean mountains appears to have occurred mainly as the result of depth of burial and high thermal gradient. This process may have started with the first tectonic episode at the beginning of the Late Cretaceous and continued up to the final uplift of the Caribbean mountains (*cf.* MacLachlan *et al.*, 1960; and Oxburgh, 1965).

ACKNOWLEDGMENTS

The writer is grateful to Prof. H. H. Hess of Princeton University, who suggested the writing of the present paper, for the lively discussion held with him about problems of the Caribbean mountains geology. Special gratitude is due to Dr. V. Seiders, of the U.S. Geological Survey, for his helpful ideas and critical reading of the original manuscript; to Dr. A. Bellizzia of the Ministerio de Minas e Hidrocarburos, Venezuela, for his criticisms and collaboration; to Dr. Cecilia Petzall for reading the manuscript; to Dr. A. Vivas of the Ministerio de Minas e Hidrocarburos, for permitting the publication of this paper.

BIBLIOGRAPHY

- AGUERREVERE, S. E. AND G. ZULOAGA
1937. Observaciones geológicas en la cordillera de la costa, Venezuela. Bol. Geol. y Min., 1: 3-22.
1938. Nomenclature of the formations of the central part of the cordillera de la costa. Bol. Geol. y Min., 2: 257-260.
- BUCHER, W. H.
1952. Geologic structure and orogenic history of Venezuela. Mem. geol. Soc. Am., 49: 113 p.
- BUSHMAN, J. R.
1965. Geología del área de Barquisimeto. Bol. Geol., Caracas, 6 (11): 3-112.
- DENGO, G.
1950. Eclogitic and glaucophane amphibolites in Venezuela. Trans. Am. geophys. Union, 31: 673-878.
1953. Geology of the Caracas Region, Venezuela. Bull. geol. Soc. Am., 64: 1-39.
- DUSENBURY, A. N. AND P. P. WOLCOTT
1949. Rocas metamórficas cretácicas en la cordillera de la costa de Venezuela. Bol. Ass. Venez. Geol., Min. y Petrol., 1: 17-26.

- DZULYNSKI, S., M. KSIAZKIEWICZ, AND KUENEN, PH. H.
1959. Turbidites in flysch of the Polish Carpathian Mountains. *Bull. geol. Soc. Am.*, 70: 1089-1118.
- EVANOFF, J., J. BUSHMAN, AND E. ARAUJO
1959. Bloque de rocas antiguas incrustados en sedimentos del terciario inferior en la Cuenca de Lara. *Bol. Geol., Caracas*, 5 (10): 67-80.
- HEDBERG, H. D.
1950. Geology of the eastern Venezuela Basin (Anzoategui-Monagas-Sucre-Eastern Guarico portion). *Bull. geol. Soc. Am.*, 61 (11): 1173-1216.
- HESS, H. H.
1960. Caribbean Research Project: Progress Report. *Bull. geol. Soc. Am.*, 71: 235-240.
- HESS, H. H. AND J. C. MAXWELL
1953. Caribbean Research Project. *Bull. geol. Soc. Am.*, 64: 1-6.
- JARVIS, H.
1964. Geology of the Rio Pao-Rio Tiznados area, Cojedes and Guarico, Venezuela. Unpublished Ph. D. Thesis, Rice University.
- KAMEN-KAYE, M.
1942. "Ortiz Sandstone" and Guarumen Sandstone group of northcentral Venezuela. *Bull. Am. Ass. petrol. Geol.*, 26: 126-133.
- KUENEN, PH. H.
1951. Turbidity currents and the transportation of coarse sediments to deep water. *Soc. econ. Pal. Min., Sp. Pub. No. 2*.
1959a. Sand; its origin, transportation abrasion and accumulation. *Annex vol. LXII. A. L. Dutoit. Memorial lectures No. 6*.
1959b. Turbidity Currents—A major factor in flysch deposition. *Ecol. Geol. Helv.*, 51: 1009-1021.
- KUGLER, H. G.
1953. Jurassic to recent sedimentary environments in Trinidad. *Bull. Ass. Suisse Geol. Ing. Petr.*, 20 (59): 27-60.
- MACKENZIE, D. B.
1960. High-temperature alpine-type peridotite from Venezuela. *Bull. geol. Soc. Am.*, 71: 308-318.
- MACLACHLAN, J. C., R. SHAGAM, AND H. H. HESS
1960. Geology of the La Vistoria Area, Aragua, Venezuela. *Bull. geol. Soc. Am.*, 71: 241-248.
- MAXWELL, J. C. AND G. DENG
1951. The Carupano Area and its relation to the tectonics of northeastern Venezuela. *Trans. Am. geophys. Union*, 32: 259-266.
- MENÉNDEZ, A.
1965. Geología del área de El Tinaco, centro-norte del Estado Cojedes, Venezuela. *Bol. Geol., Caracas*, 6 (12): 417-543.
- MIYASHIRO, A.
1961. Evolution of metamorphic belts. *Jour. Petrol.*, 2: 277-311.
- OSBURN, E. R.
1965. Geología de la región oriental del Estado Carabobo, Venezuela. *Bol. Geol., Caracas*, 6: 113-208.

- RENZ, H. H.
 1955. Some upper Cretaceous and lower Tertiary Foraminifera from Aragua and Guarico, Venezuela. *Micropaleontology*, 1: 52-71.
 1957. Stratigraphy and geologic history of eastern Venezuela. *Geol. Rundschau*, 45 (3): 729-759.
- RENZ, O., R. LAKEMAN, AND E. VAN DER MEULEN
 1955. Submarine sliding in western Venezuela. *Bull. Am. Ass. petrol. Geol.*, 39: 2053-2067.
- RENZ, O. AND K. C. SHORT
 1960. Estratigrafía de la región comprendida entre el Pao y Acarigua, Estados Cojedes y Portuguesa. *Mem. Congr. Geol. Venez. III*, (Caracas, 1959), I: 277-316.
- SHAGAM, R.
 1955. Geology of central Aragua, Venezuela. Unpublished Ph. D. Thesis, Dept. Geol., Princeton Univ.
 1960. Geology of central Aragua, Venezuela. *Bull. geol. Soc. Am.*, 71: 249-302.
- SEIDERS, V.
 1965. Geología de Miranda Central. *Bol. Geol. Caracas*, 6 (12): 290-417.
- SMITH, R. J.
 1953. Geology of the Los Teques-Cua Region, Venezuela. *Bull. geol. Soc. Am.*, 64: 41-64.
- WOLCOTT, P. P.
 1943. Fossils from metamorphic rocks of the coast range of Venezuela. *Bull. Am. Ass. petrol. Geol.*, 27: 1632.
- YOUNG, G. A., A. BELLIZZIA, H. H. RENZ, F. W. JOHNSON, R. N. ROBIC, AND J. MASVALL
 1956. Geología de las cuencas sedimentarias de Venezuela y de sus campos petrolíferos. *Bol. Geol., Caracas, Publ. Esp. No. 2*: 140 p.

Carbonate Sedimentation

DONALD L. GRAF

Convener

The following papers were delivered at the Conference but have not been received for publication:

CHARLES L. CHRIST: Inorganic Complexes in Fresh and Marine Waters.

ROBERT N. CLAYTON: Oxygen and Carbon Isotope Effects in the Precipitation, Alteration and Metamorphism of Carbonate Rocks.

ALAN G. WALTON: Heterogeneous Nucleation.

EUGENE D. TRAGANZA: Dynamics of the Carbon Dioxide System on the Great Bahama Bank.*

A. CONRAD NEUMANN: Origin of Harrington Sound, Bermuda and Recent History of Peat and Carbonate Deposition Therein.

ALFRED G. FISCHER AND ROBERT E. GARRISON: Carbonate Lithification on the Sea Floor.

M. GRANT GROSS AND J. I. TRACEY, JR.: Carbon and Oxygen Isotopic Composition of Limestones and Dolomites, Bikini and Eniwetok Atolls.

SEYMOUR O. SCHLANGER: Dolomite-Evaporite Relations on Pacific Islands.

H. G. MULTER AND J. E. HOFFMEISTER: Subaerial Laminated Crusts of the Florida Keys.

*This paper has appeared in *Bull. Mar. Sci.*, 17(2):348-366, June, 1967.

MECHANISMS OF CALCIUM CARBONATE DEPOSITION IN COCCOLITHOPHORIDS AND MOLLUSCS¹

KARL M. WILBUR AND NORIMITSU WATABE

Department of Zoology, Duke University, Durham, North Carolina

INTRODUCTION

Our discussion will concern two groups of organisms which deposit calcium carbonate: coccolithophorids and molluscs. Their pertinence to this symposium on calcium carbonate sedimentation is the possession of mechanisms for converting soluble calcium carbonate into highly complex carbonate structures which contribute to sediments. We shall be speaking of recent experimental studies relating to these mechanisms.

We are grateful to Drs. M. A. Crenshaw, P. E. Hare, V. R. Meenakshi, E. Paasche, R. H. Parker, and E. Degens for permitting us to include unpublished data.

CALCIFICATION IN COCCOLITHINEAE

The Coccolithineae are present in fossil deposits beginning with the Jurassic. They are important constituents of the Cretaceous chalk formations and the calcareous deep sea deposits of the Tertiary as well as occurring in more recent ocean sediments. (Bramlette, 1958; Black & Barnes, 1961; Noël, 1965). Their calcified structures called coccoliths are characteristic of the species and occur in a diverse array of beautifully sculptured forms.

The system of calcification in the coccolithophorids is distinct in two ways from that in molluscs. First, complex structures of calcium carbonate can be produced intracellularly. Secondly, the cells which produce them carry out photosynthesis, and light plays an important role in the deposition of the calcium carbonate. Our attention will be limited principally to two genera, *Coccolithus* and *Hymenomonas* (*Cricosphaera*) on which the major part of recent experimental studies has been carried out. The studies have indicated intracellular processes and environmental conditions which play a part in coccolith growth and form.

Formation of Coccoliths.—Coccoliths have been observed within cells of coccolithophorids (Parke & Adams, 1960; Lavine *et al.*, 1962; Paasche, 1962; and Wilbur & Watabe, 1963); and in certain species at least, their intracellular origin appears certain. Two factors which appear to be important for coccolith formation are a specialized region of nongranular material in which calcium carbonate crystals develop into the completed structure and a contiguous cell component called the reticular body (Wilbur

¹Certain of the studies reported were supported by the National Institute of Dental Research, National Institutes of Health, grant DE 01382 and Office of Naval Research, Biology Branch, grant Nonr 1181 (06) NR 104-016.

& Watabe, 1963). The probable importance of the reticular body in coccolith formation is indicated by two findings. The first concerns two strains of *C. huxleyi*, one of which forms coccoliths (BT-6) and the other which does not (92-A). The non-calcifying strain has no reticular body but another structure termed the X-body. When calcification was induced by culturing the cells in a nitrogen-deficient medium, a reticular body replaced the X-body (Wilbur & Watabe, 1963). The second finding concerns the calcifying strain (BT-6) in which not all of the cells form coccoliths. Watabe & Crenshaw (unpublished) found that cells with coccoliths had a reticular body as expected but that cells which had not formed coccoliths had the X-body which is characteristic of the non-calcifying strain. Perhaps the reticular body is required for organic matrix formation within the cytoplasm and that without the matrix, crystal nucleation and crystal growth do not take place. Further evidence of the role of the reticular body in coccolith formation is provided in the recent study of Isenberg (in this volume). Another cytoplasmic organelle composed of thick-walled tubes within vesicles may be involved in the formation of coccoliths in *Crystallolithus hyalinus* (Manton & Leedale, 1963).

Parke & Adams (1960) observed in *Crystallolithus pelagicus* that with a change in cell phase there was also a change in coccolith type, crystalloliths being produced by the motile phase and placoliths by the non-motile phase. It would be interesting to know whether there are cytoplasmic components related to the differing forms of the calcified structures.

Staining reactions of cells and of decalcified coccoliths of *Hymenomonas* had indicated that mucopolysaccharides are associated with the site of calcification (Isenberg *et al.*, 1963). The organic matrix has now been analyzed for individual amino acids (Isenberg *et al.*, 1965). Hydroxyproline was present; tryptophan and asparagine were absent; and histidine was found in relatively high concentration. The presence of polysaccharide was confirmed.

The sequence of changes in the intracellular development of coccoliths of *Coccolithus huxleyi* was observed with the electron microscope (Wilbur & Watabe, 1963). The completed coccolith consists of an upper and lower disc of radial elements connected by a hollow cylinder (Figs. 1 & 3). Calcification is initiated in several centers in the lower disc from which crystal growth progresses peripherally and centrally, forming the lower disc, and upward and peripherally to form the upper disc. Each upper and lower element with its central connection constitutes a single crystal (Watabe, unpublished). Black (1963) had hypothesized that crystal growth begins centrally and extends peripherally. The completed coccoliths are extruded and form one or more interlocking layers encasing the cell. The manner of the extrusion and positioning of the coccoliths is unknown. While extracellular formation of coccoliths is not excluded, its general occurrence is not to be expected (Wilbur & Watabe, 1963; Paasche, 1965). It is difficult to imagine that on the external surface of the cell there would be mechan-

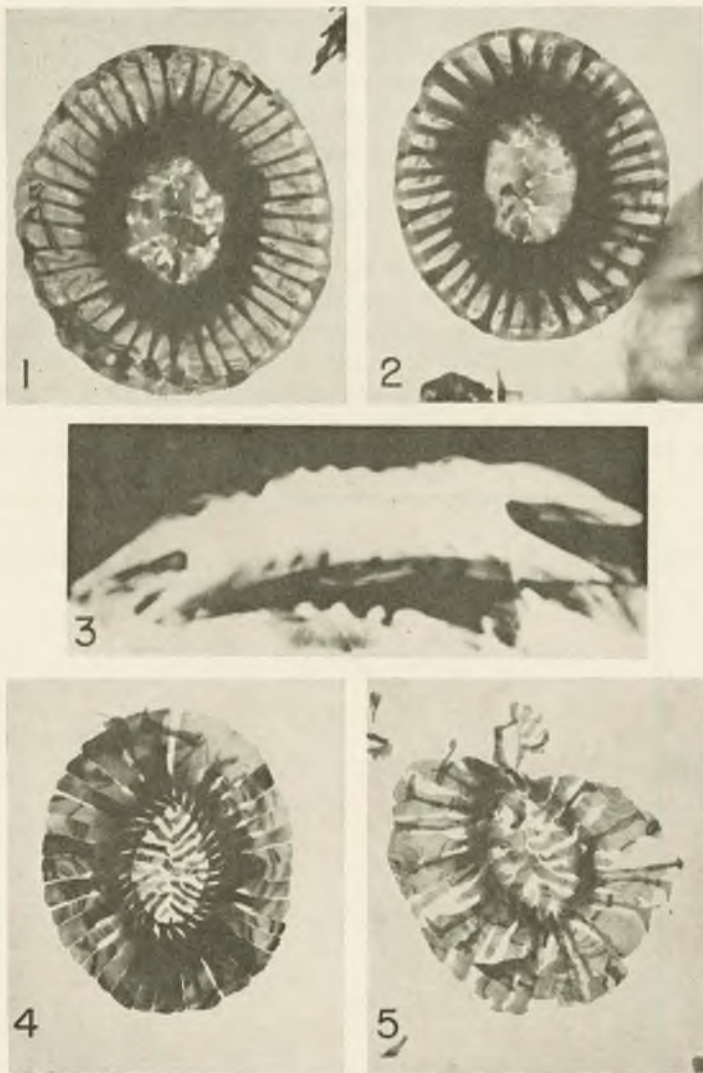


FIGURE 1. A normal coccolith from a cell of *Coccolithus huxleyi* cultured at 18°C. $\times 11,200$.

FIGURE 2. A normal coccolith from a cell of *Coccolithus huxleyi* cultured at 27°C. Note that the overall length and width are less and that the upper elements are wider than in the coccolith shown in Figure 1. at 18°C. $\times 11,200$.

FIGURE 3. Side view of a normal coccolith of *Coccolithus huxleyi*. $\times 19,800$.

FIGURE 4. An abnormal coccolith from a cell of *Coccolithus huxleyi* cultured at 7°C. Note that the coccolith consists almost entirely of a lower disc. $\times 11,200$.

FIGURE 5. An abnormal coccolith from a cell of *Coccolithus huxleyi* cultured at 12°C. Note irregularities of the basal plate and upper elements. $\times 11,200$.

isms to control crystal growth of such complex structures. The same need not apply to such simple structures as the rhombohedral crystalloliths of *Cristallolithus hyalinus* which may be formed within an extracellular space between a skin and the plasmalemma (Manton & Leedale, 1963).

Conditions Affecting Calcium Carbonate Deposition in Coccolithophorids. Studies by Isenberg *et al.* (1963, 1965), Paasche (1964, 1965) and Crenshaw (1964) have provided extensive information on factors governing calcium carbonate deposition.

The degree of calcification will be determined by the calcium concentration of the medium. At very low calcium concentrations (*e.g.*, 1 mM) coccoliths will not be formed and cells with coccoliths will be decalcified (Paasche, 1962, 1964; Crenshaw, 1964). The amount of calcium taken up per cell in *C. huxleyi* was found to increase with the calcium concentration of the medium to a maximum at about 10 mM Ca, which is the calcium concentration of sea water (Fig. 6, Crenshaw, 1964; see also

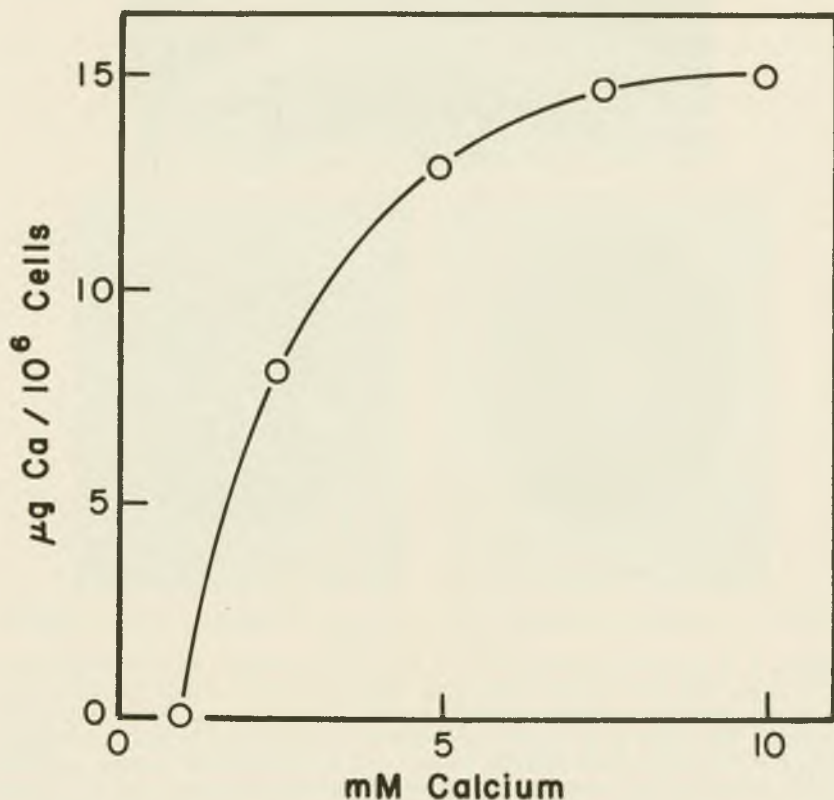


FIGURE 6. The effect of calcium concentration on calcium deposition by decalcified cells of *Coccolithus huxleyi* (Crenshaw, 1964).

Paasche, 1964). Fewer coccoliths were formed per unit time at the lower concentrations (Crenshaw, personal communication).

The rate of accumulation of calcium by decalcified cells is illustrated in Figure 7, upper curve (Crenshaw, 1964) and is seen to require some 70 hours for completion in this instance. Assuming that each cell acquired 15 coccoliths (Paasche, 1964) during this period, a cell would form a coccolith every 4 to 5 hours. From the amount of carbon precipitated per cell, a faster rate of one or two coccoliths per hour has been estimated (Paasche, 1964).

The uptake of both carbon and calcium will be a function of the carbon concentration of the medium. If the carbon is in short supply, growth of *Hymenomonas* and *Coccolithus* will be limited (Isenberg *et al.*, 1963; Crenshaw, 1964), and the cells will be decalcified (Crenshaw, 1964). If now bicarbonate or lactate is added, calcification will take place. Addition of carbonate increases the rate of coccolith formation (Isenberg *et al.*, 1965).

The deposition of cell carbonate in *C. huxleyi* increased with concentration of bicarbonate in the medium and then reached a plateau or continued to increase depending upon pH (Fig. 8, Paasche, 1964). The curves in Figure 8 were taken from experiments in which the pH was varied and the concentration of bicarbonate in the medium calculated. From this and other evidence (Crenshaw, 1964) it appears that the car-

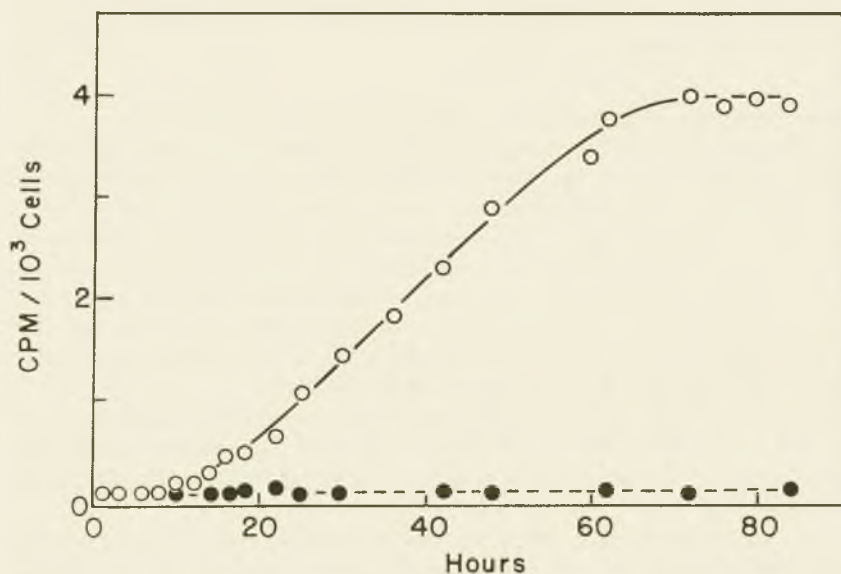


FIGURE 7. The rate of Ca^{45} uptake by decalcified cells of *Coccolithus huxleyi* (Crenshaw, 1964). Open circles—illuminated; filled circles—non-illuminated.

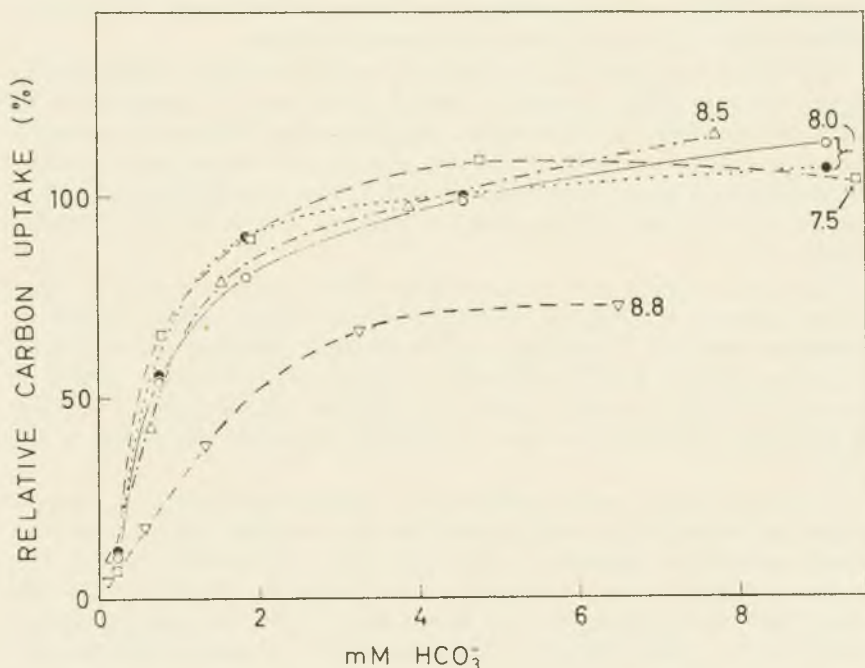


FIGURE 8. Relative carbon uptake in light-dependent coccolith formation in *Coccolithus huxleyi* as a function of bicarbonate ion concentration at pH 7.5 to 8.8 (Paasche, 1964).

bonate deposited in coccoliths is taken up largely as bicarbonate.

Isenberg *et al.* (1965), in studies of the influence of organic non-nitrogenous compounds on the growth and calcification of *Hymenomonas*, have found that cell multiplication is quite independent of mineralization (see also Crenshaw, 1964). The same was true when effects of carbonate were examined. The effect on calcification of adding carbonate to the medium depended upon the particular organic supplement. For example, cultures supplemented with acetate and carbonate grew vigorously but had impaired calcium deposition, whereas the addition of carbonate with propionate depressed growth but increased calcification.

The amino acids proline and hydroxyproline increased the capacity of the cells to deposit calcium (Isenberg *et al.*, 1965), a finding of considerable interest in view of the association of hydroxyproline with vertebrate calcifying systems.

Since coccolithophorids carry out photosynthesis, experimental studies have been directed to an examination of the dependence of calcium carbonate deposition on the photosynthetic process. We shall first summarize some of the findings and then consider proposed explanations.

Coccolith formation is strongly influenced by light. In the absence of light Crenshaw (1964) found essentially no calcification in *C. huxleyi* or in *Hymenomonas* (Fig. 7). Paasche (1962), on the other hand, found calcium uptake reduced but still occurring in *C. huxleyi* in the absence of light (but see Paasche, 1964, p. 24). Microscopic observations also showed that coccoliths could be formed in the dark but at a slower rate (Table 1).

TABLE 1

CALCIFICATION OF *Coccolithus huxleyi* IN LIGHT AND DARKNESS¹. COCCOLITHS WERE FIRST REMOVED FROM CELLS IN CALCIUM-FREE SEA WATER, pH 5.7, AND THEN RETURNED TO CULTURE MEDIUM

Time after Decalcification	Light cells with coccoliths	Dark cells with coccoliths
(hr)	(%)	(%)
1/4	1	1
15	57	25
24	92	47
40	96	65

¹Paasche (personal communication).

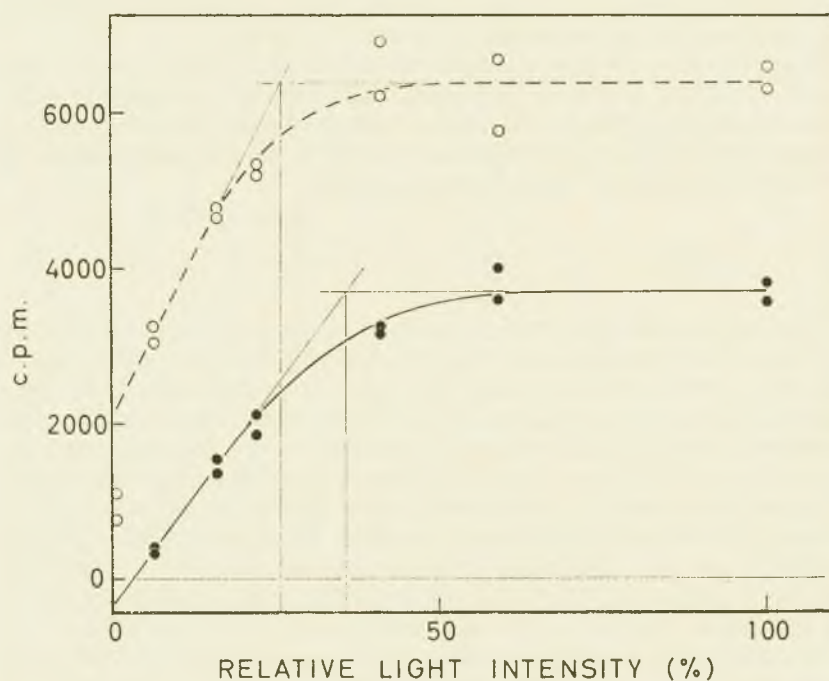


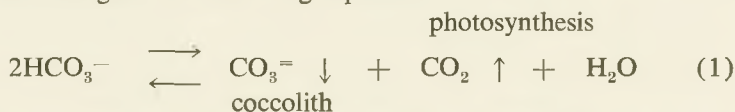
FIGURE 9. C^{14} uptake in photosynthesis (filled circles) and in coccolith formation (open circles) in *Coccolithus huxleyi* as a function of light intensity (Paasche, 1964). Maximum intensity (100 per cent) approximately 15,000 lux.

The difference in the results of the experiments of Crenshaw and Paasche may involve differences in strain.

The uptake of coccolith carbon in *C. huxleyi* increased with light intensities greater than 600 lux and reached a plateau at about 6,000 lux (Fig. 9, Paasche, 1964). The uptake of the carbon of photosynthesis followed a similar course and leveled at a slightly greater light intensity. Below 600 lux the slope of the coccolith carbon uptake curve was approximately twice that at higher intensities (not shown) and was no longer paralleled by the photosynthesis curve.

If assimilation of CO_2 through photosynthesis and carbonate deposition are linked, one might expect that the photosynthesis inhibitors 3-(p-chlorophenyl)-1, 1-dimethylurea (CMU) and (3, 4-dichloro)phenyl-1, 1-dimethylurea (DCMU) would interfere with calcification. CMU, 10^{-6}M , which almost completely inhibited photosynthesis in *C. huxleyi* permitted considerable deposition of C^{14} and Ca^{45} in coccoliths, (Paasche, 1964, 1965). In *Hymenomonas*, Crenshaw (1964) found that the related compound DCMU at 10^{-7}M suppressed both photosynthesis and calcification to about 50 per cent of the control values. At higher concentrations the curves for the two processes were roughly parallel, but at concentrations above 10^{-6}M at which inhibition of photosynthesis was complete, calcification still occurred to the extent of about 15 per cent.

Inorganic carbon is present within the cell as bicarbonate which enters readily (Paasche, 1964), as carbonate which probably enters less readily or not at all (Crenshaw, 1964), and as carbon dioxide. Reduction of CO_2 concentration through photosynthesis would favor the precipitation of carbonate according to the following equation:



Calcium entering the cell from the medium would be precipitated with the carbonate. This hypothesis has been examined by Paasche (1964) and by Crenshaw (1964). On comparing the uptake of carbon utilized in photosynthesis with carbon deposited in coccoliths under various experimental conditions, the data did not always conform to the relations predicted (Paasche, 1964). This was especially true in experiments in which carbon continued to be taken up, presumably in coccolith formation, when photosynthetic carbon assimilation was completely blocked by CMU. Paasche concluded that the experimental evidence did not support the hypothesis that the formation of the CaCO_3 of coccoliths and photosynthesis were closely linked. However, the participation of carbon assimilation by photosynthesis in coccolith formation was not excluded. On the other hand, the finding that DCMU inhibited calcium uptake to the extent of about 85 per cent when photosynthesis was blocked was considered by Crenshaw (1964) as strong support for the hypothesis. One recognizes,

of course, that parallel inhibition can not be taken as conclusive proof of a causal relation.

To explain the importance of light and the failure of CMU to block coccolith formation, Paasche (1964) proposed an alternative hypothesis. In this, light would bring about ATP formation from cyclic photophosphorylation and so supply energy for one or more reactions in coccolith formation. The photophosphorylation would not be inhibited by CMU. The precipitated carbonate would be derived from bicarbonate. On this hypothesis the deficient deposition of CaCO_3 in the absence of light could be due to a lack of high energy phosphate. By supplying substrates which on metabolizing would generate ATP, coccoliths might be formed more readily in the absence of light. However, the addition of metabolic substrates to *C. huxleyi* and *Hymenomonas* in the dark did not induce coccolith formation (Crenshaw, 1964). The substrates may not enter the cell. However, the adequacy of metabolic substrates within the cell for normal metabolism was indicated by a constant respiratory rate over a 5-day period in the dark. Thus, ATP would not be expected to be limiting unless coccolith formation requires more energy than that supplied by respiration. The lack of CaCO_3 deposition in the absence of light could be ascribed to respiratory CO_2 which would favor reaction to the left in equation (1).

Several considerations led us to an examination of temperature effects on coccoliths of *C. huxleyi* (Watabe & Wilbur, 1966). (1) Wada (1957) had observed that crystal size in the shell of the pearl oyster, *Pinctada martensii*, was greater during growth in colder months. (2) *C. huxleyi*, found over wide latitudes (Bernard, 1942), could be presumed to grow over a wide temperature range and to be a suitable organism for studying the influence of temperature on crystal size. (3) If crystal size were altered through temperature influence, the form of the coccolith might then be changed. (4) If it developed that coccolith morphology were especially sensitive to temperature, the form of the coccolith might serve as an indicator of environmental temperature.

Cultures of *C. huxleyi* were maintained at constant temperatures over the range 7° to 27° C. From electron micrographs, dimensions of coccoliths of cells grown at various temperatures have been determined (Fig. 10). For temperatures of 7°, 12°, and 18° C there was no significant difference in overall coccolith length and width, but for the intervals 18° to 24° C and 24° to 27° C both length and width decreased. The differences were not great—all fell between 6 and 8 per cent—but they were statistically significant. The width of the upper radial elements was similar and minimum at 7° and 12° C, increasing progressively and significantly at 18° and 24° C and decreasing slightly but significantly at 27° C (Fig. 10. See also Figs. 1 & 2). The length of the radial elements was affected differently, decreasing progressively at 24° and 27° C (Fig. 10).

From the results of measurements on the radial elements it is evident that coccoliths from cells growing at temperatures differing by 6° in the

range 12° to 24° C could be distinguished. Further, coccoliths developing at 24° C were distinct from those formed at 27° C. One now asks the extent to which the dimensions of *C. huxleyi* can be used as environmental temperature indicators. Certainly, the finding of Bé & McIntyre (1964) that the form of coccoliths from Arctic and tropical waters differs in a manner which parallels the findings on laboratory cultures is strongly suggestive. However, we shall need information on effects of salinity, nutrition, and light before coccolith morphology can be used with confidence as an indicator of environmental temperatures.

In any population of coccoliths, some will be abnormal in form. The percentage of abnormal coccoliths was determined at various temperatures and found to be minimal at 18° and to increase at higher and lower temperatures. The abnormal forms may have a basal plate only, a basal

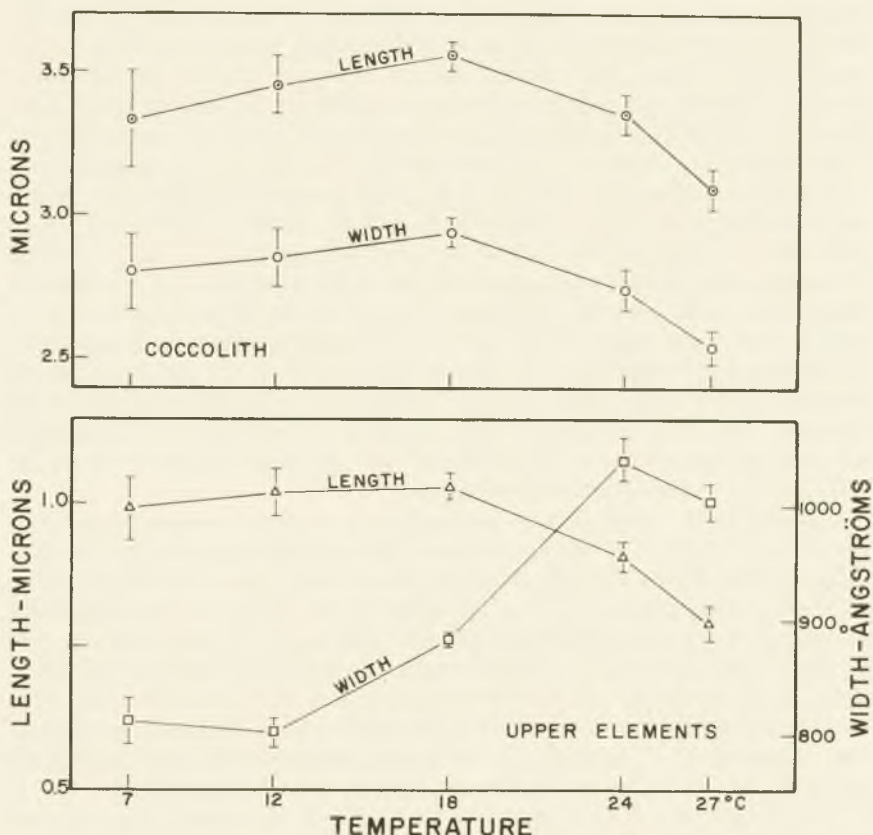


FIGURE 10. The length and width of coccoliths and upper elements of *Coccolithus huxleyi* as a function of temperature. The range indicates 95 per cent confidence interval of the mean value.

plate plus a few upper elements (Fig. 4), or irregularities of upper and lower elements (Fig. 5). No single type of coccolith abnormality was characteristic of a particular temperature.

The effects of temperature on coccolith form and dimensions are to be viewed in terms of crystal growth and of conditions which influence this in the organic matrix within the cytoplasm. Irregular form of the upper plate obviously means unequal crystal growth rates along radii of the plate. Since elements of the plates are parts of single crystals (Watabe, unpublished), changes in the dimensions of the elements produced by temperature reflect differences in growth rate in different crystal axes. Abnormal coccoliths consisting of only a basal plate must come about through premature extrusion from the cell or death of the cell prior to completion of crystal growth.

CALCIUM CARBONATE DEPOSITION IN MOLLUSCS

The mollusc has two major problems in forming its shell. First, it must fashion an organic matrix within cells of the mantle or from the extrapallial fluid produced by the mantle and lying between the mantle and its shell. Secondly, it must provide conditions for nucleation and controlled crystal growth within this matrix, utilizing the calcium carbonate present in the extrapallial fluid. In considering mechanisms of calcium carbonate deposition we will first consider the composition of the extrapallial fluid.

Extrapallial Fluid.—Data on the composition of the extrapallial fluid are limited (Wilbur, 1964). In the two species studied most extensively, *Anodonta cygnea* and *Mercenaria mercenaria*, the inorganic ions of the extrapallial fluid were similar in kind and concentration to those in the blood. They include sodium, potassium, calcium, magnesium, manganese, chloride, sulfate, and phosphate (de Waele, 1930; Potts, 1954; Crenshaw, personal communication). Recent analyses by Crenshaw on *M. mercenaria* and the fresh-water clam *Elliptio complanatus* show that the calcium concentration of the extrapallial fluid is relatively high and is principally in the form of bicarbonate. Data on extrapallial fluids do not permit solubility product calculations.

The proteins of the extrapallial fluid of 14 species of marine and fresh-water molluscs have been studied by paper and cellulose acetate electrophoresis (Kobayashi, 1964a). The results show a relation between proteins and crystal type. In species with a calcitic shell only one protein was found but its migration velocity was not the same in all species. The extrapallial fluid of eight species having aragonitic or both calcitic and aragonitic shells contained three or more proteins.

Acid mucopolysaccharide and PAS-positive material (neutral mucopolysaccharide) of extrapallial fluid were also studied by electrophoretic separation (Kobayashi, 1964b). Here, as with protein, the calcitic shells showed the simpler pattern of one or two bands. The binding of acid muco-

polysaccharide and PAS-positive material with protein was indicated by similar electrophoretic patterns. In the aragonitic and calcitic-aragonitic species, these polysaccharide fractions were more numerous and again associated with protein. Earlier studies had indicated a relation between shell matrix and crystal type (Watabe & Wilbur, 1960; Wilbur & Watabe, 1963) since the extrapallial fluid is in contact with the area of active shell deposition, the findings on extrapallial fluid and crystal type suggest possible interpretations of this relationship.

The relation of shell matrix protein to extrapallial fluid protein, from which the matrix is derived, has also been approached in preliminary studies in collaboration with Dr. P. E. Hare on *Mercenaria mercenaria*. The matrix protein had a low content of basic amino acids and a high content of acidic, neutral, hydroxy, and imino acids, whereas the reverse was true of the extrapallial fluid in which histidine content was 50 to 100 fold that of the shell protein and accounted for 50-60 per cent of the total amino acids (Table 2).

TABLE 2
AMINO ACID COMPOSITION OF THE SHELL AND EXTRAPALLIAL FLUID OF
Mercenaria mercenaria

Amino Acids	Shell	Extrapallial Fluid	
		Insoluble	Soluble
	(%)	(%)	(%)
Basic	8-10	8-10	60-70
Histidine	less than 1	5-6	50-60
Acidic, neutral, hydroxy, imino	70-80	75-80	25
Aromatic	5-7	5	5
Sulphur containing	2-5	5	<5

In all probability the composition of the extrapallial fluid does not remain constant but changes as a result of environmental influences and as organic matrix polymerizes from the soluble phase (see below).

A point of interest was the appearance of an insoluble protein in extrapallial fluid kept in the frozen state. This had a composition different from both extrapallial fluid and shell matrix protein (Table 2). The presence of an insoluble protein raises the interesting possibility of the study of polymerization of extrapallial fluid protein to form the insoluble protein of shell matrix.

Shell Matrix.—Analytical studies have not progressed to the stage of providing a comprehensive view of the shell matrix, but the outlines of the main areas to be examined are beginning to take form. Some of the recent results can be briefly indicated.

On decalcifying shell, a small insoluble fraction, differing in amount according to species, remains. It includes various protein fractions, and

electron micrographs show structure characteristic of the taxonomic group (Grégoire *et al.*, 1955; Grégoire, 1957, 1960). However, until recently it has not been appreciated that the shell of marine, freshwater, and terrestrial gastropods also contain protein soluble in neutral EDTA (Meenakshi & Watabe, unpublished). Surprisingly, in the freshwater gastropods, the entire calcified shell matrix is soluble in EDTA. The solubility of matrix material can be demonstrated in the electron microscope by comparing its appearance in sections decalcified in EDTA for 5 min. and then 30 min.

The amino acid composition of the principal shell layers of a single species differs (Tanaka *et al.*, 1960; Hare, 1963; Beedham & Owen, 1965). A part of the matrix protein may be hardened by tanning; and this is always true in the uncalcified outer layer called the periostracum which has a high tyrosine and phenylalanine content.

Matrix protein of certain molluscs has a predominance of glycine and

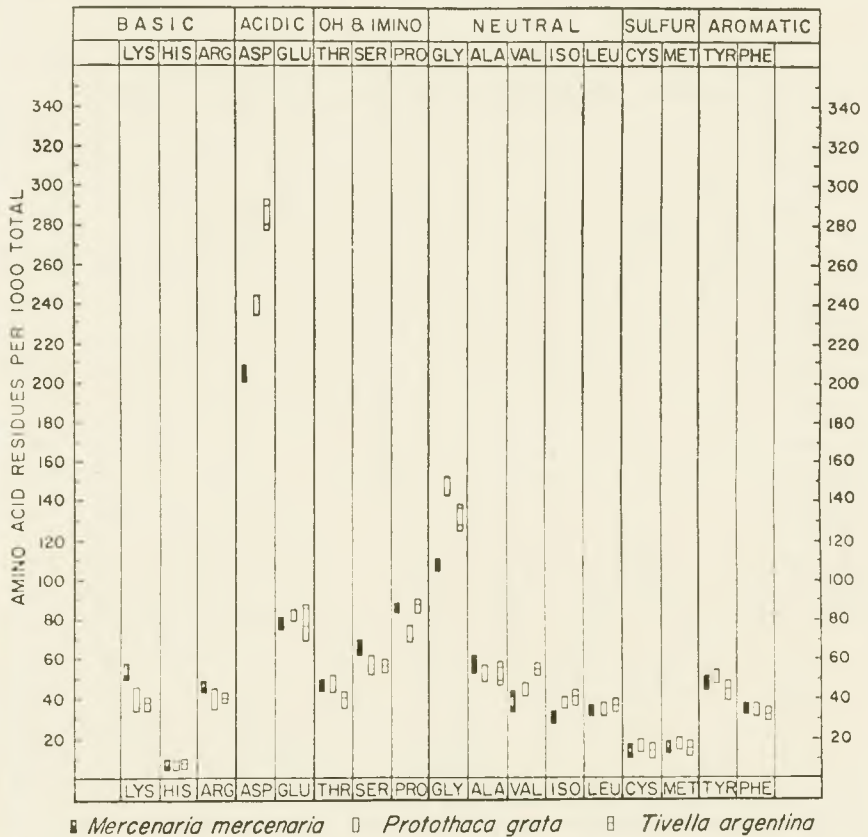


FIGURE 11. Amino acid composition of three related genera within the family Veneridae (Hare & Abelson, personal communication).

alanine and a low proline content. However, *Mercenaria mercenaria* has large amounts of aspartic acid, about the same amount of proline and glycine, and relatively small amounts of alanine (Grégoire *et al.*, 1955; Tanaka *et al.*, 1960; Piez, 1961; Hare, 1963, personal communication; Simkiss, 1965). Hydroxyproline and hydroxylysine are usually absent. However, both are present in the shell of the gastropod *Australorbis* (Piez, 1961) and hydroxylysine has been found in fossil shells of the gastropod *Planorbis* (Degens & Love, 1965).

Mucopolysaccharides, neutral and acidic, lipid, and chitin are present in the organic matrix as shown by histochemical tests and analysis of shell extracts (Meenakshi, personal communication; Beedham & Owen, 1965; Simkiss, 1965). The reactions of individual calcified layers for phenols, polysaccharides, and amino acids may be different (Beedham & Owen, 1965).

The amino acid composition of closely related forms with similar shell

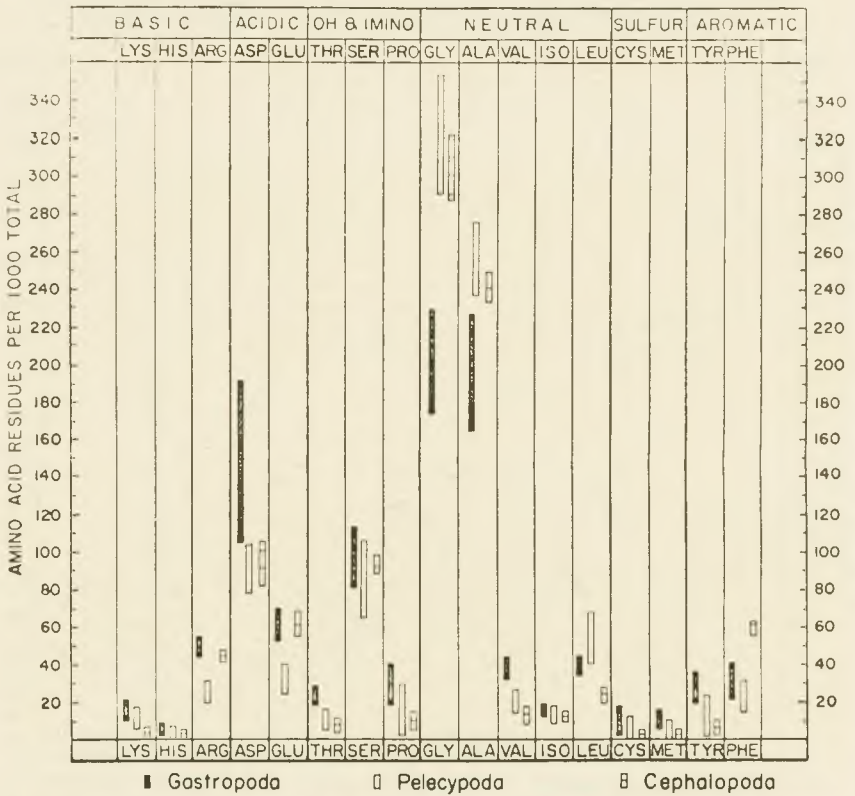


FIGURE 12. Ranges of amino acid composition for nares structures from three classes of molluscs (Hare & Abelson, personal communication).

structure is similar. Figure 11 (Hare & Abelson, personal communication) shows this in remarkable degree for the amino acid pattern in three genera of the family Veneridae. However, there are also differences, particularly in the number of residues of aspartic acid and glycine. For a particular amino acid of a single species the range of values for different individuals is very small indeed and is indicated by the height of the rectangles in Figure 11. By way of comparison, the composition of the nacreous structures of several genera of Gastropoda, Pelecypoda, and Cephalopoda are given in Figure 12. The differences are considerably greater. All groups have low levels of histidine, cystine, and methionine and high values for aspartic acid, glycine, and alanine. Parker & Degens (personal communication) find a stable peptide core diagnostic of Pelecypoda.

Analysis of single species living in wide ranges of temperature, salinity, depth, and redox potential have shown environmental influences on shell matrix protein (Parker & Degens, 1965). Acidic and basic amino acids, ratios of glycine/alanine and phenylalanine/tyrosine reflected environmental changes, whereas a peptide core consisting of a number of neutral amino acids did not. In a study using controlled temperatures of 13° to 25° C, the ratios of vaterite, aragonite, and calcite in the regenerating shell of the snail *Viviparus* changed as a function of temperature (Wilbur & Watabe, 1963). The cause was ascribed to metabolic influences which



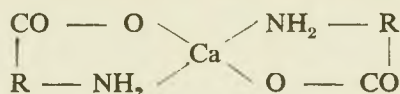
FIGURE 13. Calcite nuclei on the organic matrix (Watabe, unpublished). The nucleation of the matrix was obtained by inserting coated electron microscope grids between the mantle and the shell of *Crassostrea virginica*. $\times 150,000$.

in turn altered the organic and inorganic substances at the nucleation sites. But, in addition, the physical and chemical conditions at the site of crystal growth may be changed to favor the growth of one type of crystal after nucleation.

These findings call attention to the necessity of taking account of the animal's environment in presenting data on shell matrix composition.

Calcification of the Organic Matrix.—We have pointed out that acid mucopolysaccharide-protein complexes are present in the extrapallial fluid of many species of molluscs and that proteins and acid mucopolysaccharides are present in shell matrix where they may also be associated. Both mucopolysaccharides and protein have been suggested as substances necessary for calcification in mollusc shells.

Acid mucopolysaccharides are present in many calcifying systems including bone, calcified cartilage (Sobel, 1955), avian egg shells (Simkiss & Tyler, 1957); coccoliths (Isenberg *et al.*, 1965), crustacean cuticle (Meenakshi & Scheer, 1959), and serpulid tubes (Hedley, 1956). The function of acid mucopolysaccharides in calcification has not been clarified. Nonetheless, their presence in the calcifying system of shell is of considerable interest. As strongly anionic compounds they can bind calcium; and Simkiss (1960) proposed that their acidic groups together with protein amino groups may chelate calcium and so initiate calcification. Carbonate would then be combined with the calcium.



The possible role of mucopolysaccharides in shell mineralization is indicated by Wada's observation (1964) that mineralization of so-called organic crystals deposited on a coverslip inserted between mantle and shell of *Chlamys* begins in localized areas staining for mucopolysaccharide. It has also been suggested that protein acidic and basic groups may bind Ca and CO₃ respectively, and that when these bound ions are sufficiently numerous in a particular area, nucleation may result (Hare, 1963; Degens & Love, 1965).

Nucleation of the shell matrix has not been studied except in a preliminary way. Figure 13 shows nuclei obtained by inserting coated electron microscope grids between the mantle and the shell where crystals normally are formed (Watabe, unpublished). Electron diffraction analysis has demonstrated that the first deposition is calcium carbonate. It had also been thought that the first crystals deposited in shell regeneration were calcium phosphate which later were converted to calcium carbonate (Bevelander & Benzer, 1948).

Matrix-crystal relationships, including crystal growth, have been studied in several species, but this has been discussed in a recent publication (Wilbur, 1964) and will not be reviewed here. However, we wish to

mention two new findings (Watabe, 1965). First, the single crystals of aragonite and calcite shells of three species of bivalves were found to be made up of many small oriented lamellae or blocks. An example is seen in Figure 14 showing crystals of the calcitostracum of the shell of *Crassostrea virginica* which have lamellae 100 to 400 A in width. That the largest units are single crystals was shown by electron diffraction.

A second finding is the presence of matrix within single crystals. On decalcification, the matrix can be seen to envelop the smaller crystal units (Fig. 15). The presence of intracrystalline matrix can be interpreted in terms of crystal growth. The crystals develop by dendritic growth in the matrix, and the individual dendrites probably finally become lamellae. The matrix which is the medium in which the dendrites grow thus comes to surround the internal elements and the crystal as a whole. However, the relative uniformity of the elements, their spacing, and their orientation remain unexplained.

The assumption has been made (Wilbur, 1964) that nucleation and

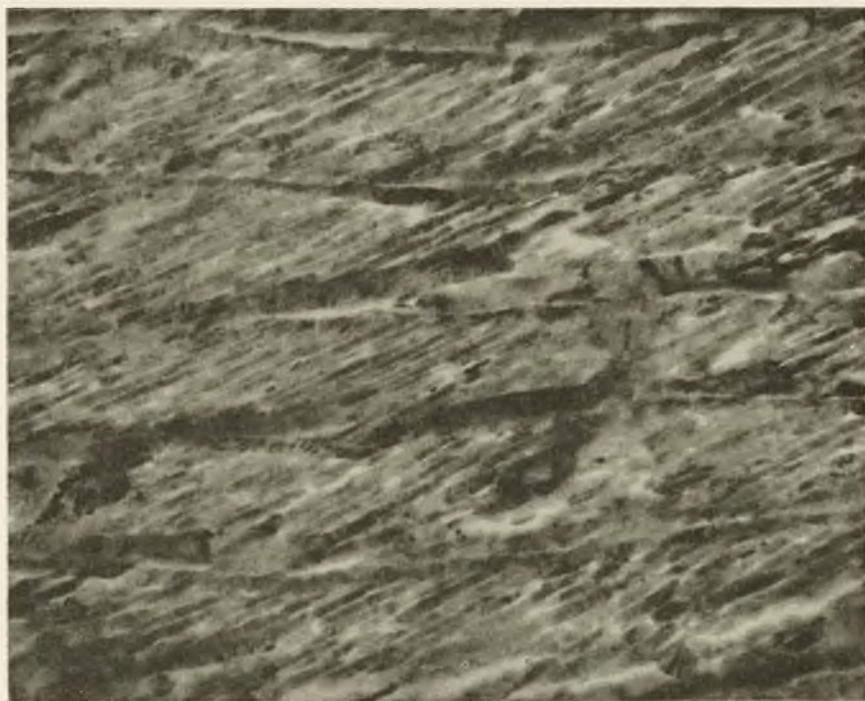


FIGURE 14. Oblique section of undecalcified calcitostracum (*Crassostrea virginica*) showing portions of six single crystal layers of calcite and their component lamellae (Watabe, 1965). The lamellae are oriented obliquely to the crystal surface in the figure and have a width of 100 to 400 A. $\times 58,000$.

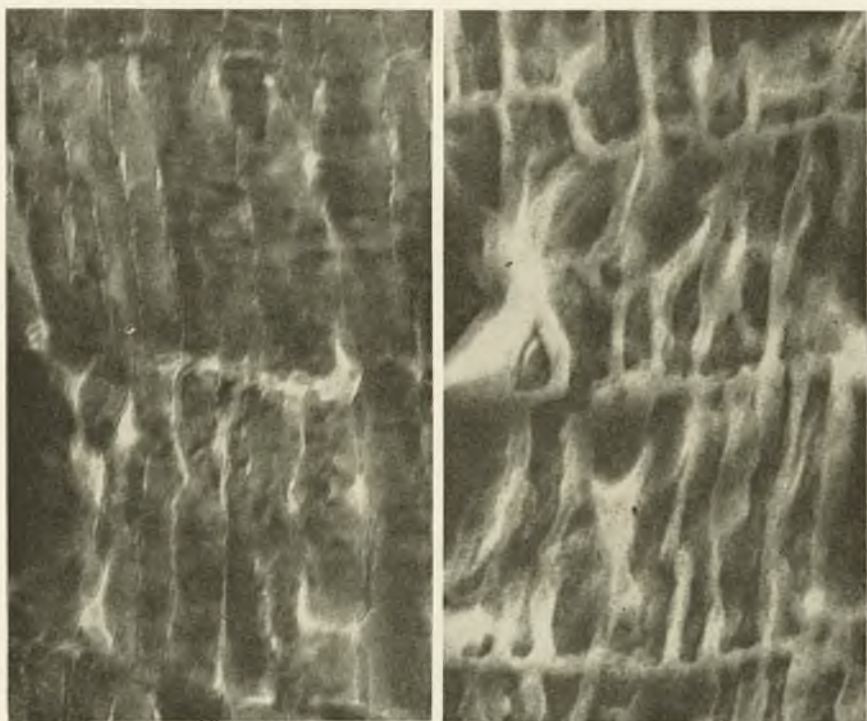


FIGURE 15, left. Vertical section of undecalcified calcitostracum (*Crassostrea virginica*) cut across the width of the calcite crystals (Watabe, 1965). Portions of four superimposed single crystals, the vertical component lamellae, 100-400 Å wide and 150-2,000 Å high are shown. $\times 168,000$.

FIGURE 15, right. Decalcified section of Figure 15, left. The horizontal cords, 120-200 Å thick, are *intercrystalline matrix* surrounding the single crystals (Watabe, 1965). *Intracrystalline matrix* is seen as vertical cords enclosing the lamellar components. $\times 134,000$.

growth of calcium carbonate crystals take place in all molluscs on or in a polymerized protein matrix. If the matrix were soluble, as mentioned above in the case of the freshwater gastropods (Meenakshi & Watabe, unpublished), then the crystals would have as a substratum only the inner surface of the periostracum and the surfaces of other shell crystals. However, there remains the possibility that the *in situ* environment of the matrix is such that it is a gel in which crystals could grow but that under conditions of extraction it disperses.

CONCLUDING REMARKS

Calcium carbonate precipitation by the living organism is under two broad mechanisms of control not found in natural waters. The first

involves the metabolic machinery which governs the environment of the calcification sites. Because of this, the concentration of inorganic ions (including calcium, carbonate, hydrogen), within the living cell, as in the coccolithophorids, or within the compartment formed by the mantle and shell, as in the molluscs, is different from that in the surrounding water. Inhibitory substances such as phosphates (Simkiss, 1964) may be in lower or higher concentration, depending also on cellular metabolism. The overall effect of controlling the environment at the calcification sites may be to increase the rate of calcium carbonate precipitation. But an inhibition of calcification may also result; and in most tissues, including those of the mollusc, there is no precipitation of calcium carbonate, of course.

The second mechanism is that controlling the form of calcified structures. The basis of this control almost certainly rests on the ability of the living system to synthesize organic substances which will partly or wholly influence crystal type, orientation, habit, the extent of crystal growth, and finally the interrelated structure of the crystals and the organic matrix. It seems likely that protein or protein associated with mucopolysaccharide provides a substratum on which crystals nucleate, orient, and grow, and that the organic matrix also provides a three-dimensional medium in which the crystals continue to grow in a pattern characteristic of the specific shell and coccolith. The crystal type and growth pattern in general are under genetic and environmental control in that the calcified structures are characteristic of the species and show changes in structure depending on the environment. This control of form may be exerted, in part at least, through molecular make-up of the matrix in which crystals grow and in the mollusc through the morphology of the mantle. Another mechanism which may influence growth patterns of crystals in the mollusc is concentration gradients of calcium carbonate which could occur in the thin layer of fluid between the mantle and the shell (Watabe & Wilbur, 1961). Trace elements and other impurities which would affect the crystal habit may also be a factor.

Beyond the recognition of these possible mechanisms we can say almost nothing. The manner in which calcium carbonate is fashioned into a particular architectural design in one species of coccolithophorid or mollusc and differently in another lies in the realm of problems to be pursued.

REFERENCES

- BÉ, A. W. H. AND A. MCINTYRE
1964. Recent coccoliths of the Atlantic Ocean. Geol. Soc. Amer. Spec. Pap., 82: 8.
- BEEDHAM, G. E. AND G. OWEN
1965. The mantle and shell of *Solemya parkinsoni* (Protobranchia: Bivalvia). Proc. zool. Soc. Lond., 145: 405-430.
- BERNARD, F.
1942. Essai sur les facteurs de répartition des Flagellés calcaires. Ann. Inst. océanogr. (N. S.), 21: 2.

- BEVELANDER, G. AND P. BENZER
1948. Calcification in marine molluscs. *Biol. Bull.*, 94: 176-183.
- BLACK, M. AND B. BARNES
1961. Coccoliths and discoasters from the floor of the South Atlantic Ocean. *J. roy. micr. Soc.*, 80: 137-147.
- BLACK, M.
1963. The fine structure of the mineral parts of the coccolithophoridae. *Proc. Linn. Soc. (London)*, 174: 41-46.
- BRAMLETTE, M. N.
1958. Significance of coccolithophorids in calcium-carbonate deposition. *Bull. geol. Soc. Amer.*, 69: 121-126.
- CRENSHAW, M. A.
1964. Coccolith formation by two marine coccolithophorids, *Coccolithus huxleyi* and *Hymenomonas* sp. Doctoral thesis. Duke University.
- DEGENS, E. T. AND S. LOVE
1965. Comparative studies of amino acids in shell structures of *Gyraulus trochiformis*, Stahl, from the Tertiary of Steinheim, Germany. *Nature*, 205: 876-878.
- DE WAELE, A.
1930. Le sang d'*Anodonta cygnea* et la formation de la coquille. *Mém. Acad. roy. Belg. Cl. Sci.*, 2 (10): 1-51.
- GRÉGOIRE, C.
1957. Topography of the organic components in mother-of-pearl. *J. biophys. biochem. Cytol.*, 3: 797-808.
1960. Further studies on structure of the organic components in mother-of-pearl, especially in pelecypods. (Part I), *Bull. Inst. roy. Sci. nat. Belg.*, 36, (23): 1-22.
- GRÉGOIRE, C., G. DUCHATEAU, AND M. FLORKIN
1955. La trame protidique des nacres et des perles. *Ann. Inst. océanogr. (Paris) (N. S.)*, 31: 1-36.
- HARE, P. E.
1963. Amino acids in the proteins from aragonite and calcite in the shells of *Mytilus californianus*. *Science*, 139: 216-217.
- HEDLEY, R. H.
1956. Studies on serpulid tube formation I. The secretion of the calcareous and organic components of the tube of *Pomatoceros triqueter*. *Quart. J. microscop. Sci.*, 97: 411-419.
- ISENBERG, H. D., L. S. LAVINE, M. L. MOSS, D. KUPFERSTEIN, AND P. E. LEAR
1963. Calcification in a marine coccolithophorid. *Ann. N. Y. Acad. Sci.*, 109: 49-64.
- ISENBERG, H. D., L. S. LAVINE, C. MANDELL, AND H. WEISSFELLNER
1965. Qualitative chemical composition of the calcifying organic matrix obtained from cell free coccoliths. *Nature*, 206: 1153-1154.
- KOBAYASHI, S.
1964a. Studies on shell formation. X. A study of the proteins of the extrapallial fluid in some molluscan species. *Biol. Bull.*, 126: 414-422.
1964b. Calcification in fish and shell-fish II. A paper electrophoretic study on the acid mucopolysaccharides and PAS-positive materials of the extrapallial fluid in some molluscan species. *Bull. Jap. Soc. sci. Fish.*, 30: 893-907.
- LAVINE, L. S., H. D. ISENBERG, AND M. L. MOSS
1962. Intracellular calcification in a coccolithophorid. *Nature*, 196: 78.

- MANTON, I. AND G. F. LEEDALE
1963. Observations on the micro-anatomy of *Crystallolithus hyalinus* Gaarder and Markali. Arch. Mikrobiol., 47: 115-136.
- MEENAKSHI, V. R. AND B. T. SCHEER
1959. Acid mucopolysaccharides of the crustacean cuticle. Science, 130: 1189-1190.
- NÖEL, D.
1965. Note preliminaire sur des coccolithes jurassiques. Arch. orig. centre Docum. C.N.R.S., 408: 1-12.
- PAASCHE, E.
1962. Coccolith formation. Nature, 193: 1094-1095.
1964. A tracer study of the inorganic carbon uptake during coccolith formation and photosynthesis in the coccolithophorid *Coccolithus huxleyi*. Physiol. Plant. Supp., III: 1-82.
- PARKE, M. AND I. ADAMS
1960. The motile (*Crystallolithus hyalinus* Gaarder and Markali) and non-motile phases in the life history of *Coccolithus pelagicus* (Wallich) Schiller. J. Mar. biol. Ass. U. K., 39: 263-274.
- PARKER, R. H. AND E. T. DEGENS
1965. Study of amino acid components of shell protein, mantle, and periostracum of molluscs and their variation relative to environment and molluscan phylogeny. Contribution 66. Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, 30-31.
- PIEZ, K. A.
1961. Amino acid composition of some calcified proteins. Science, 134: 841-842.
- SIMKISS, K.
1960. Some properties of the organic matrix of the shell of the cockle (*Cardium edule*). Proc. malac. Soc. Lond., 34: 89-95.
1964. Phosphates as crystal poisons of calcification. Biol. Rev., 39: 487-505.
1965. The organic matrix of the oyster shell. Comp. Biochem. Physiol., 16: 427-435.
- SIMKISS, K. AND C. TYLER
1957. A histochemical study of the organic matrix of hen eggshells. Quart. J. microscop. Sci., 98: 19-28.
- SOBEL, A. E.
1955. Local factors in the mechanism of calcification. Ann. New York Acad. Sci., 60: 713-732.
- TANAKA, S., H. HATANO, AND O. ITASAKA
1960. Biochemical studies on pearl. IX. Amino acid composition of conchiolin in pearl and shell. Bull. chem. Soc. Japan, 33: 543-545.
- WADA, K.
1957. Electron-microscopic observations on the shell structures of pearl oyster. (*Pinctada martensii*). II. Observations of the aragonite crystals on the surface of nacreous layers. Bull. natl. Pearl Res. Lab., 2: 74-85.

1964. Studies on the mineralization of the calcified tissue in molluscs. VIII. Behavior of eosinophil granules and of organic crystals in the process of mineralization of secreted organic matrices in glass coverslip preparations. *Bull. Natl. Pearl Res. Lab.*, 9: 1087-1098.
- WATABE, N.
1965. Studies on shell formation. XI. Crystal-matrix relationships in the inner layers of mollusk shells. *J. ultrastruct. Res.*, 12: 351-370.
- WATABE, N. AND K. M. WILBUR
1960. Influence of the organic matrix on crystal type in molluscs. *Nature*, 188: 334.
 1961. Studies on shell formation. IX. An electron microscope study of crystal layer formation in the oyster. *J. biophys. biochem. Cytol.*, 9: 761-773.
 1966. Effects of temperature on growth, calcification and coccolith form in *Coccolithus huxleyi* (Coccolithineae). *Limnol. and Oceanogr.*, 11: 567-575.
- WILBUR, K. M.
1964. Shell formation and regeneration. *In* *Physiology of Mollusca*, I. Edited by K. M. Wilbur and C. M. Yonge. Acad. Press, New York. Chap. 8, 243-282.
- WILBUR, K. M. AND N. WATABE
1963. Experimental studies on calcification in molluscs and the alga *Coccolithus huxleyi*. *Ann. New York Acad. Sci.*, 109: 82-112.

LABORATORY STUDIES WITH COCCOLITHOPHORID CALCIFICATION¹

HENRY D. ISENBERG

The Long Island Jewish Hospital, New Hyde Park, N.Y.

and

State University of New York, Downstate Medical Center, Brooklyn, N.Y.

STEVEN D. DOUGLAS²

National Institute of Arthritis and Metabolic Diseases, Bethesda, Md.

LEROY S. LAVINE AND HENRY WEISSFELLNER

The Long Island Jewish Hospital, New Hyde Park, N.Y.

and

State University of New York, Downstate Medical Center, Brooklyn, N.Y.

ABSTRACT

The test object of these investigations is the supralittoral euryhaline coccolithophorid chrysomonad phytoflagellate *Hymenomonas* Mary Parke 156, growing in axenic culture in chemically defined media. Results obtained suggest that coccolithogenesis is an intracellular process which follows the pathway of biological mineral deposition and in this protist serves to control carbonate pathways in cells which are in the stationary growth phase. The process of mineral deposition may be separated from growth by Sr^{+2} substitution for Ca^{+2} , carbonic anhydrase inhibition, and by environmental organic nutrients among which intermediates of carbohydrate metabolism and amino acids play an especially decisive role. Analyses of supernatant, cellular and coccoliths constituents under various conditions of coccolithogenesis will be presented. It will be shown that this activity is influenced by age and surface: volume ratios.

While attempts to remove the mineral phase chemically without disturbing the organic constituents of coccoliths failed, separation of the coccoliths into an organic, mineralizing fraction and less active remnants has been achieved with distilled water. When compared chemically, this fraction differs only very slightly in terms of chemical composition from the whole coccoliths. It contains only about 25 per cent of protein or peptide found in the intact coccoliths but this Lowry positive moiety and mineralizing fraction harbors an appreciable quantity of hydroxyproline, an aminoacid discernible as barely a trace in the coccoliths proper. The finding of this vertebrate collagen constituent in the mineralizing fraction—which moves as a unit in the ultracentrifuge and electrophoretically—is the first such demonstration in microorganisms. It is of great interest in view of its hypothetical role in vertebrate hydroxyapatite deposition. Coccoliths and the fraction share a qualitatively identical polysaccharide complex consisting of glucose, hexuronic acid, two pentoses, a methylpentose, and an unidentified component possibly a dideoxy sugar. Trace amounts of phosphate are present, but no corroborate histochemical data. The protein or peptide of coccoliths or the fraction is characterized by a paucity of sulfhydryl and aromatic aminoacids. In distilled water organic constituents appear in the dialysate before mineral constituents.

¹This work was supported by Public Health Research Grant No. DE 01662 from National Institute of Dental Research.

²Present address: Mt. Sinai Hospital, New York, N.Y.

INTRODUCTION

It must come as a surprise to many physical scientists that biologists were asked to contribute to a symposium concerned with carbonate sedimentation. However, the incunabula of carbonate deposits were and are almost exclusively biological. Studies of living systems which deposit mineral can be expected, therefore, to provide information salient to the theme of carbonate sedimentation.

The understanding of the intimate chemistry and physics of biological mineral deposition has been hampered by the lack of conversation between the various scientific disciplines engaged in and intrigued by this problem. The theoretical views of this process are, therefore, reminiscent of the descriptions rendered by the proverbial blind Indians on their encounter with the elephant; each view emphasizes the findings which fit the narrow pervue of the modalities and interests of its originators. Yet, paleontology has unveiled a variety of micro-fossils produced by species, the close relatives of which still flourish today (Black, 1965). In view of Kluyver's concept of bio-chemical unity (Kluyver & Donker, 1926) microorganisms, especially those with such an ancient history, should yield useful information for delineating the basic events of mineral deposition. Perhaps the most useful of today's representatives of the fossil record are the coccolithophorids, primitive protista at the juncture of vegeto-animal cleavage. These organisms should be especially suited for such investigations since they liberate their species—specific calcareous coccoliths or microscopic "pearls" into their surroundings. If it can be demonstrated that these organisms follow the general biological pattern of mineralization or calcification, they offer the added advantage of providing their "hard tissue" particles cell free, *i.e.* without the concomitant anabolic and catabolic processes which invariably complicate investigations with higher animals.

DEFINED MEDIUM

The supralittoral, euryhaline coccolithophorid phytoflagellate *Hymenomonas* Mary Parke 156 has served as test object in our investigation of the chemical and physical events which lead to mineral deposition. The organism (Fig. 1), maintained in axenic culture, usually presents as an ovoid to round biflagellate organism measuring 10 to 12 μ in diameter with prominent chloroplasts, an easily discernible nucleus and a peripheral array of coccoliths measuring 1 to 1.5 \times 0.5 μ as previously described (Isenberg *et al.*, 1963a). The protist is cultivated in a chemically-defined medium which always has the following basic composition (mg/100 ml): NaCl, 1800 ($3 \times 10^{-1}M$); KCl, 60 ($8 \times 10^{-3}M$); NaNO₃, 50 ($6 \times 10^{-3}M$), omitted when organic nitrogenous compounds are studied as nitrogen source; sodium- β -glycerophosphate, 31.5 ($1 \times 10^{-3}M$); Na₂CO₃, 0.1 ($1 \times 10^{-6}M$), omitted during studies of organic compound used as carbon source and when studying influence of carbonate on various cell functions;

disodium ethylene-diaminetetraacetate, 10 ($2.7 \times 10^{-4}M$); $CaCl_2$, 111 ($1 \times 10^{-2}M$); $MgSO_4 \cdot 7H_2O$, 246 ($1 \times 10^{-2}M$); $Na_2SiO_3 \cdot 9H_2O$, 20 ($8 \times 10^{-4}M$); Tris (hydroxymethyl) aminomethane, 100 ($8.3 \times 10^{-3}M$); vitamin B_{12} , 0.03; thiamine HCl, 1; Trace metals, 1.0 ml. This trace metal solution has the following composition (mg/100 ml): hydroxyethylethylenediaminetriacetic acid, 300; $FeCl_2$, 20; $MnCl_2$, 10; $ZnCl_2$, 5; $CuCl_2$, 0.1; Na_2MoO_4 , 5; H_3BO_3 , 20; pH 7.5. The pH of the base medium is adjusted to pH 8.0. Difficulty in maintaining the various salts in solution will invariably be encountered unless the sodium silicate is brought to pH 5.0 with HCl before addition to the medium. The maintenance and control medium for the organism usually contains lactic acid 200 mg/100 ml. Under these circumstances, lactic acid is mixed with the silicate, the pH brought to 5 with NaOH before these two constituents are added to the medium. The medium is dispensed in various aliquots into Fernbach flasks which are autoclaved at 15 lbs and $121^\circ C$ for 15 min., cooled prior to inoculation with the organism. Since it is possible to maintain this coccolithophorid for several years on agarized medium (Isenberg *et al.*, 1965a), slants may be prepared by the addition of 1.0 per cent oxoid No. 2 agar. Care must be taken to avoid ordinary, phenol-leaking screw caps. Polypropylene closures are preferable for these

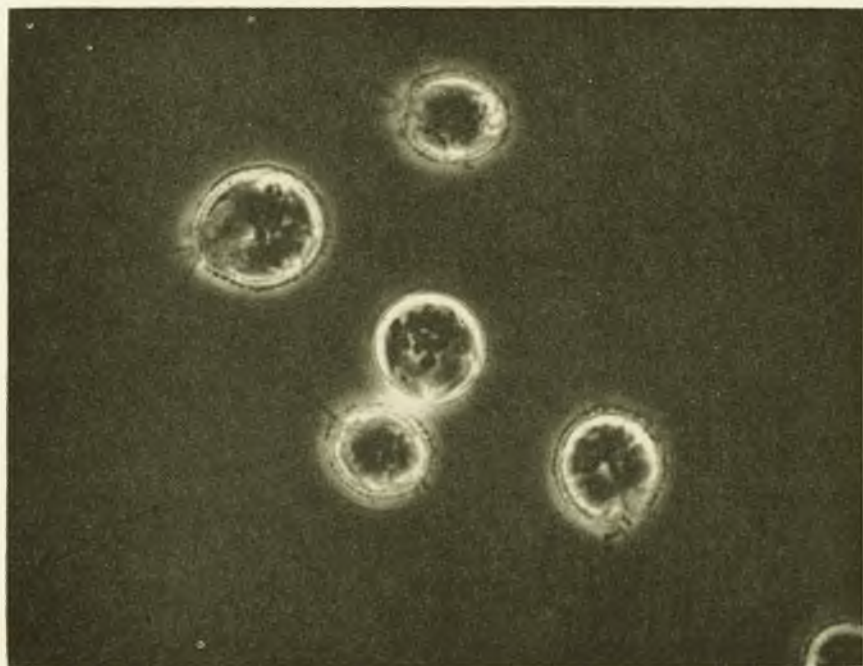


FIGURE 1. *Hymenomonas* Mary Parke 156. Phase contrast. $\times 400$.

preparations. Stainless steel caps are preferred for the liquid culture flasks, but glass wool may serve as well. The phytoflagellate is incubated at 18° C in a cold incubator with inside dimensions of 16 in deep, 26.5 in wide, 62.5 in high, constantly illuminated with eight 40-watt cold white fluorescent bulbs. The various harvesting and analytical and histological procedures have been described.

MINERAL EFFECT ON GROWTH

The first experimental target of this long term study was the evaluation of cations on the growth or cell yields of *Hymenomonas*. When Ca^{+2} was completely omitted from the medium, minimal cell yields amounting to 40 μg nitrogen/20 ml were obtained. This yield may be explained on the basis of inoculum carry-over, since all glassware was and is invariably soaked in 10 per cent ethylenediamine tetraacetate followed by copious Ca^{+2} -free water rinses prior to each use. Increasing amounts of Ca^{+2} resulted in a growth increase (Isenberg *et al.*, 1963a) which was very gradual between 10^{-6} and $10^{-4}M$ Ca^{+2} , precipitously enhanced between 10^{-4} and $10^{-3}M$ and increased by approximately 100 μg nitrogen/20 ml between 10^{-3} and $10^{-2}M$. No growth occurred at $10^{-1}M$ Ca^{+2} but cell survival could be demonstrated by diluting such cultures. Coccolithogenesis was initiated at $10^{-5}M$ Ca^{+2} .

Mg^{+2} could not substitute for Ca^{+2} for growth or coccolith production. In conjunction with Ca^{+2} , this cation exerted a markedly beneficial effect on growth, enhancing cell yields remarkably as concentrations approached $10^{-2}M$ (Isenberg *et al.*, 1963a). In contrast, Mg^{+2} exerted no demonstrable effect on coccolithogenesis.

Ba^{+2} could not substitute for the Ca^{+2} growth requirement and in the presence of Ca^{+2} inhibited growth at $10^{-4}M$. On the other hand, Sr^{+2} partially fulfilled the Ca^{+2} required for cell proliferation. $10^{-5}M$ Sr^{+2} yielded appreciable numbers of *Hymenomonas*, while 10^{-6} and $10^{-4}M$ solutions did so to a lesser degree. Larger concentrations of Sr^{+2} depressed yield to less than 100 μg nitrogen/20 ml. However, no coccoliths were produced by cells in which Sr^{+2} was substituted for Ca^{+2} , an observation now confirmed with the electron microscope. Fine structural studies indicate that Sr^{+2} probably inhibits organic matrix production, since the Sr^{+2} fed organism shows modified WW bodies (Wilbur & Watabe, 1963) and impairment of vesicle formation. This condition of "microbial strontium ricketts" could be prevented by the addition of Ca^{+2} . No Sr^{+2} effect on growth or coccolithogenesis could be detected when both cations were present.

BIPHASIC NATURE OF COCCOLITHOGENESIS

Another fundamental question required experimental proof. Biological mineral deposition in vertebrates, the most frequently studied group, and

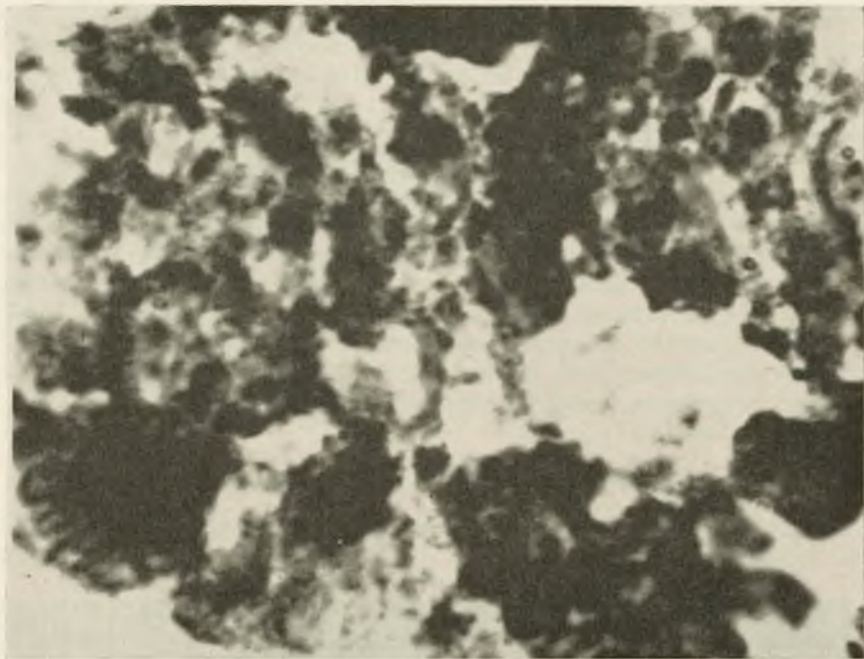


FIGURE 2. *Hymenomonas* Mary Parke 156. Paraffin section of centrifuged cells, von Kossa stain. $\times 400$.

even in some invertebrates such as molluscs and arthropods, indicated that calcification depends on a biphasic mechanism. The deposition of the mineral phase is dependent upon a preformed organic matrix which serves as a nucleation site for the mineral. This organic matrix may be found intracellularly or may be secreted by cells. Its chemical composition is not known but has been the object of much theoretical conjecture (Glimcher, 1960). It is suspected to be composed of collagen-like protein and/or proteins in association with sulfated acid mucopolysaccharides. While the multifarious species-specific coccoliths produced by the coccolithophoridae are excellent indirect proof that a specific organic matrix must be elaborated by the primitive protists, all investigators with the exception of Braarud and his group (Braarud *et al.*, 1952) suspected that coccolithogenesis proceeded as a fortuitous mineral encrustation of cell wall structures. Histological preparations of *Hymenomonas* studied with von Kossa, hematoxylin-eosin, periodic acid Schiff, methylene blue extinction and toluidine-blue stains (Fig. 2) revealed intracellular, ovoid, von Kossa and PAS-positive bodies which were metachromatic and strongly basophilic at pH 2.62. Demineralization obviated the reaction of these bodies with AgNO_3 . This histochemical evidence corroborated phase contrast and light microscopic

findings of intracellular coccoliths and underlines the adherence of *Hymenomonas*' calcification to the general biological pathway of mineral deposition. Further confirmation was achieved by the electron microscope observation of Wilbur & Watabe (1963) with *Coccolithus huxleyi* and with autoradiographs in the authors' laboratory (Isenberg *et al.*, 1964) which demonstrated intracellular as well as peripheral and extracellular deposits of Ca^{45} in structures readily identifiable as coccoliths. Analysis of Ca^{45} enriched cultures growing with carbonate, lactate, and a combination of both indicated that the combination of autotrophic and heterotrophic nutrients resulted in the greatest cell yields but with proportionally less mineral deposition. These findings suggest that the combined mode of nutrition lessens the need for mineral deposition, an observation of possible evolutionary and geological consequence, and ascribe to calcification a regulatory or detoxifying function most probably involving intracellular carbonate.

ACTION OF CARBONIC ANHYDRASE INHIBITOR; LIGHT

Since it had been demonstrated by X-ray diffraction that the mineral of *Hymenomonas* is calcite CaCO_3 , it was logical that the hypothesis of



FIGURE 3. Darkfield photograph of *Hymenomonas* grown 6 months without light; intentionally focused to reveal peripheral coccoliths rather than cellular details. $\times 400$.

carbonate regulation should be investigated with 2-acetyl-1,3,4-thiadiazole-5-sulfonamide-sodium (Diamox), a carbonic anhydrase inhibitor active against animal enzymes but with very minimal effect on the carbonic anhydrase involved in photosynthesis (Isenberg *et al.*, 1963b). Diamox, $10^{-3}M$ abolished coccolithogenesis while growth continued with but minimal inhibition. Lactate and carbonate cell yields were inhibited to the same slight degree by Diamox; interestingly, intracellular Ca^{+2} in the cell fraction of carbonate-grown organisms was no longer detectable at $10^{-4}M$ concentration, while with the lactate-grown cells an increase in cellular Ca^{+2} is noted at this concentration of the inhibitor. These findings considered along with the Sr^{+2} results indicated that coccolithogenesis and cell growth can be separated effectively in contrast to the reports of Paasche (1963, 1964) who claimed a close link between photosynthesis and coccolith production in his short term experiments. Indeed, hitherto unreported findings in our laboratory suggest a connection with light intensity, nutritional milieu and mineral deposition; photosynthesis as part of the cellular mechanisms affecting carbonate is involved but not in the primary fashion suggested by Paasche. Very slow growth by *Hymenomonas* in the complete absence of light has been reported (Isenberg *et al.*, 1965a). Figure 3 shows peripheral coccoliths produced by the organism after 6 months incubation under the most stringent conditions of light exclusion. Diamox inhibition of coccolithogenesis in face of continued cellular proliferation implied that the coccolithophorid elaborated two species of

INDEX OF MINERALIZATION

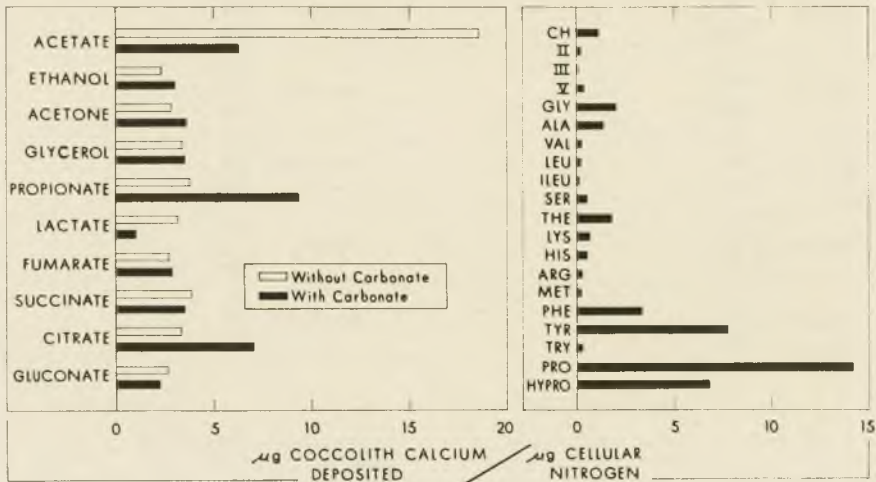


FIGURE 4. Index of mineralization: μg Ca^{+2} deposited in coccolith/ μg cellular nitrogen.

anhydrase; one—Diamox-insensitive—associated with photosynthesis, the other—inhibitor-susceptible—with coccolith production. One might, of course, also postulate a single carbonic anhydrase which displays different degrees of susceptibility toward the inhibitor when associated with different cellular organelles. Electron microscopy of the Diamox treated coccolithophorid shows impairment of WW body completion with some diminution in Golgi vesicle formation in a manner somewhat analogous with the Sr^{+2} fed organism. On the other hand chloroplast fine structure is not discernibly altered by this carbonic anhydrase inhibitor. These studies lend further support to the contention that coccolith elaboration regulates intracellular carbonate.

NUTRITION AND CALCIFICATION

Additional factors greatly influence the rate and quality of coccolith production (Isenberg *et al.*, 1965a). Thus, in a 4-week period, coccolith Ca^{+2} incorporation was increased almost $40 \times$ when the surface to volume ratio was quadrupled. Coccolith production is a process restricted in the laboratory to cells which approach and have reached the stationary growth phase. In environments favoring mineral deposition, nitrogen values remain more or less constant after the initial 2 weeks over a 20-week period. Continuous incorporation of Ca^{+2} into the coccolith fraction persists over the entire period and probably until all of the cation available is deposited as coccoliths.

NITROGEN

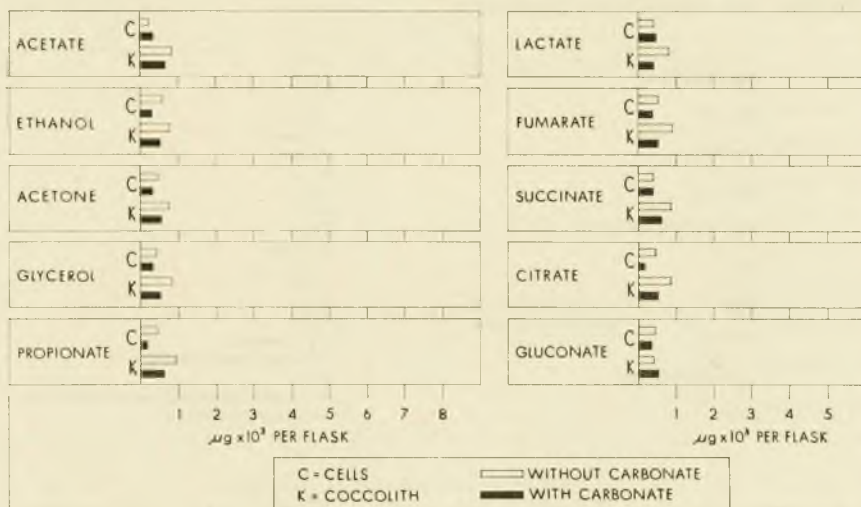


FIGURE 5. Cellular and coccolith nitrogen content of *Hymenomonas* grown on non-nitrogenous organic substrates.

CALCIUM

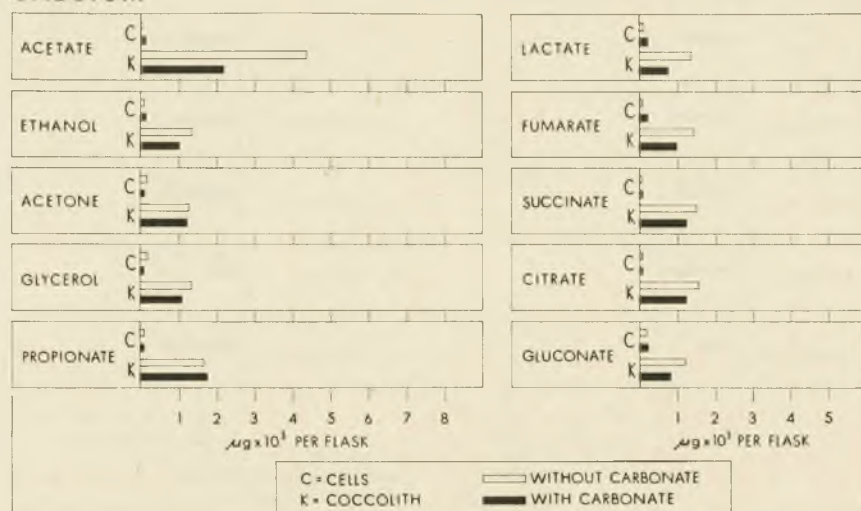


FIGURE 6. Cellular and coccolith calcium content of *Hymenomonas* grown on non-nitrogenous organic substrates.

ANTHRONE REACTING MATERIAL

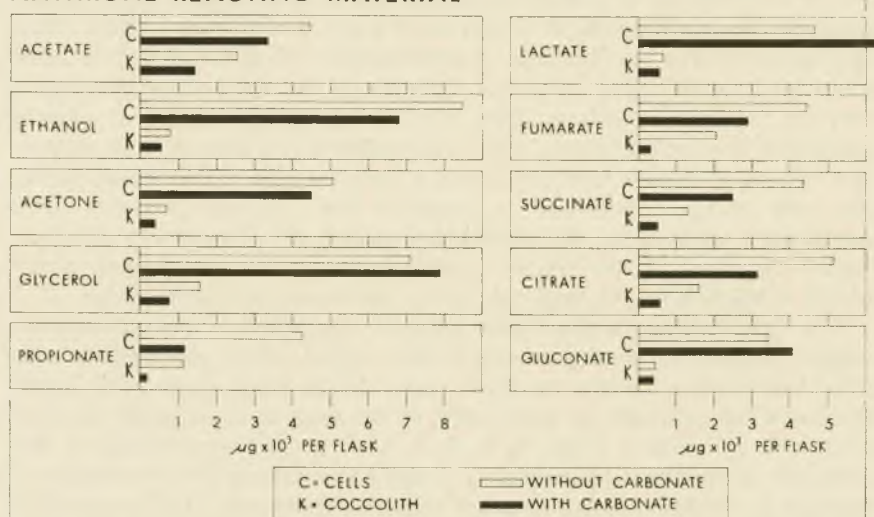


FIGURE 7. Cellular and coccolith anthrone-reacting material of *Hymenomonas* grown on non-nitrogenous organic substrates.

LOWRY REACTING MATERIAL

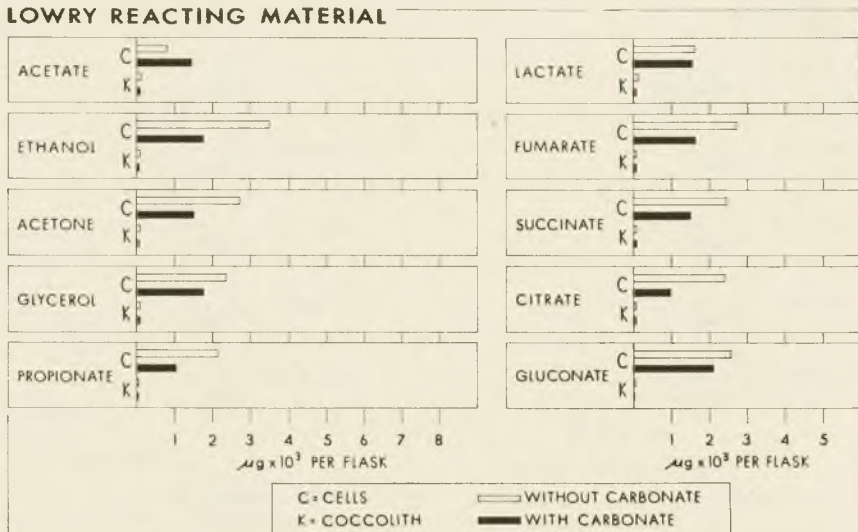


FIGURE 8. Cellular and coccolith Lowry-reacting material of *Hymenomonas* grown on non-nitrogenous organic substrates.

With the Mg^{+2}/Ca^{+2} adjusted to 1, *Hymenomonas* displayed considerable nutritional versatility (Isenberg *et al.*, 1965a). While capable of utilizing all of the organic non-nitrogenous compounds tested as carbon sources and in the presence of carbonate, certain amino acids cannot serve in this capacity. Non-metabolizable amino acids exert an inhibitory effect when they are offered to the organism in combination with as many as four non-toxic amino acids. Most significant, however, is the effect of organic nutrients on mineral deposition. They may be classified roughly as growth enhancing or coccolithogenic, with comparatively few sharing both properties. Figure 4 depicts this classification based on the mineralizing index, the ratio of Ca^{+2} deposited as coccolith Ca^{+2} /cellular nitrogen. This comparison overcomes the impression gained by considering absolute values (Isenberg *et al.*, 1965a) especially with those compounds which hardly supported cell growth but led to significant coccolithogenesis.

The first column of this figure presents the effect of non-nitrogenous organic compounds serving as sole carbon source and in combination with $CO_3^{=}$. Obviously, acetate by itself leads to the most appreciable calcification while certainly the least active of the organic compounds in terms of growth stimulation (Figs. 5, 6, 7, & 8). The striking reversal of this effect by the addition of carbonate is not accompanied by a concomitant increase in cellular nitrogen or other cellular constituents. The explanation for this phenomenon is being sought with intermediary metabolic pathways of *Hymenomonas*. Propionate and citrate addition, on the other hand, lead

NITROGEN

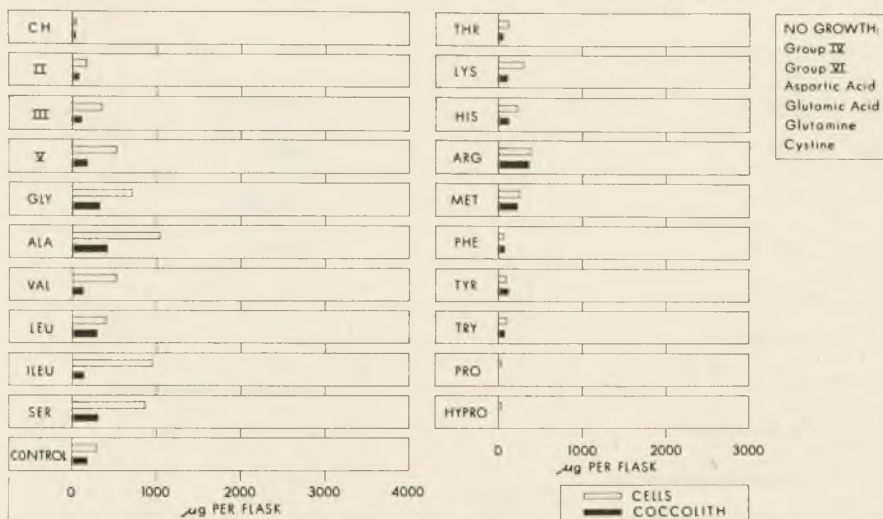


FIGURE 9. Cellular and coccolith nitrogen content of *Hymenomonas* grown on amino acids as sole carbon, nitrogen and energy sources. Artificial combinations of amino acids as well as casein hydrolysate were also included. Group II: alanine, phenylalanine and tryptophan; Group III: cystine, methionine, arginine, histidine; Group IV: aspartate, valine, leucine, and isoleucine; Group V: tyrosine, serine, threonine, and lysine; Group VI: proline, hydroxyproline, glutamate, and glutamine.

CALCIUM

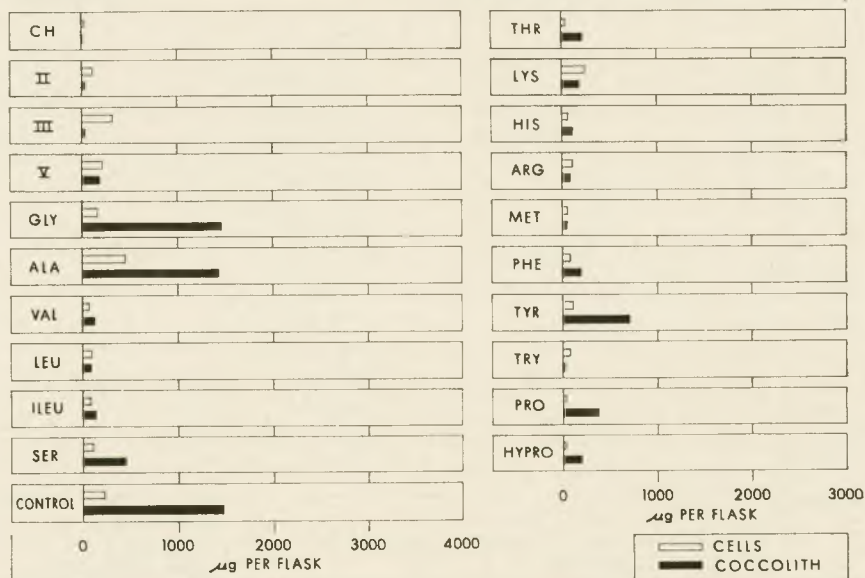


FIGURE 10. Cellular and coccoliths calcium content of amino acid grown *Hymenomonas*. Details in legend of Figure 9 apply.

ANTHRONE REACTING MATERIAL

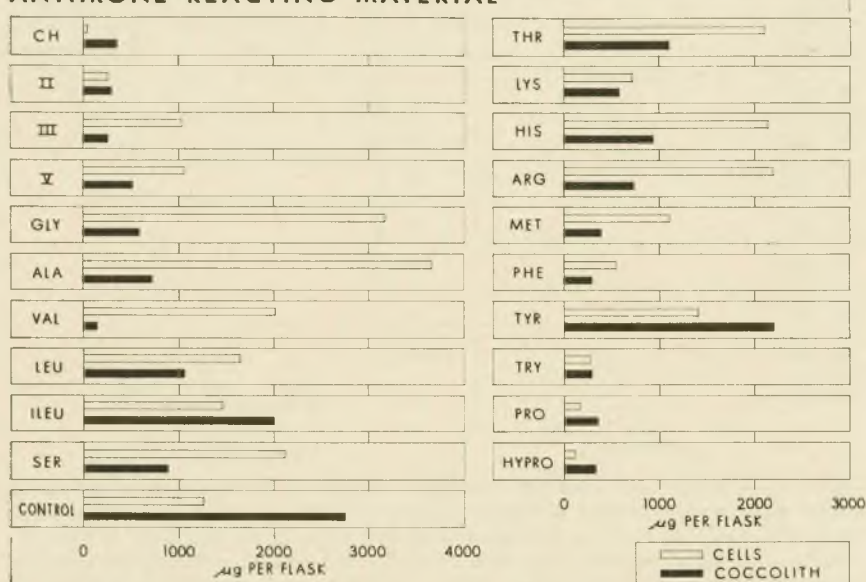


FIGURE 11. Cellular and coccoliths anthrone-reacting material of amino acid grown *Hymenomonas*. Details in legend of Figure 9 apply.

LOWRY REACTING MATERIAL

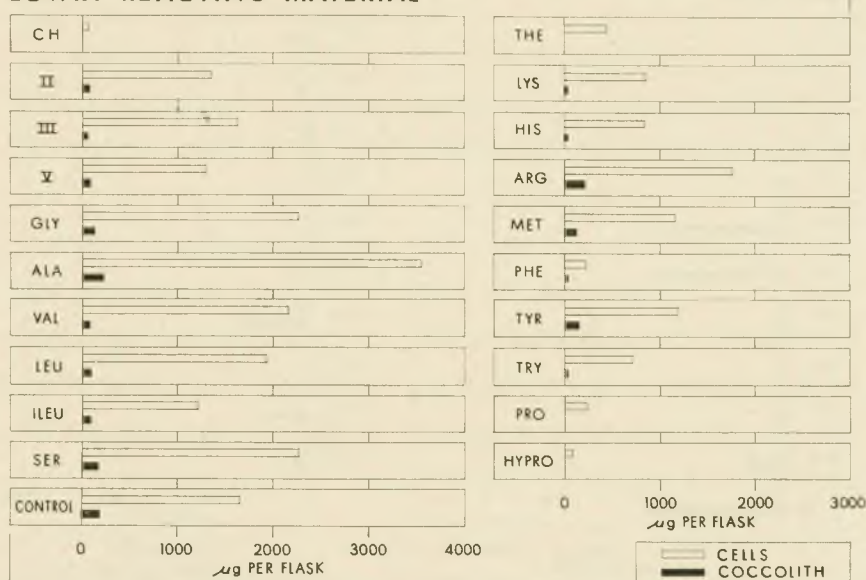


FIGURE 12. Cellular and coccoliths Lowry-reacting material of amino acid grown *Hymenomonas*. Details in legend of Figure 9 apply.

to increased mineral deposition in the presence of carbonate (Fig. 4), accompanied by a depression of growth indicators such as cellular nitrogen (Fig. 5), anthrone reacting material (Fig. 7), and Lowry-reacting constituents (Fig. 8). Despite shifts in various cellular and coccolith fractions, the other organic compounds remain more or less constant with respect to the index of mineralization in face of carbonate addition.

The separation into growth promoting and coccolithogenic compounds becomes more pronounced with the amino acids (Fig. 4). Figures 9, 10, 11, and 12 underline the need to express mineralization as the relationship of coccolith Ca^{+2} to cell yields. Proline, hydroxyproline, tyrosine, and phenylalanine are second only to acetate in promoting coccolithogenesis, while supporting chrysomonad proliferation poorly. The broad categories of

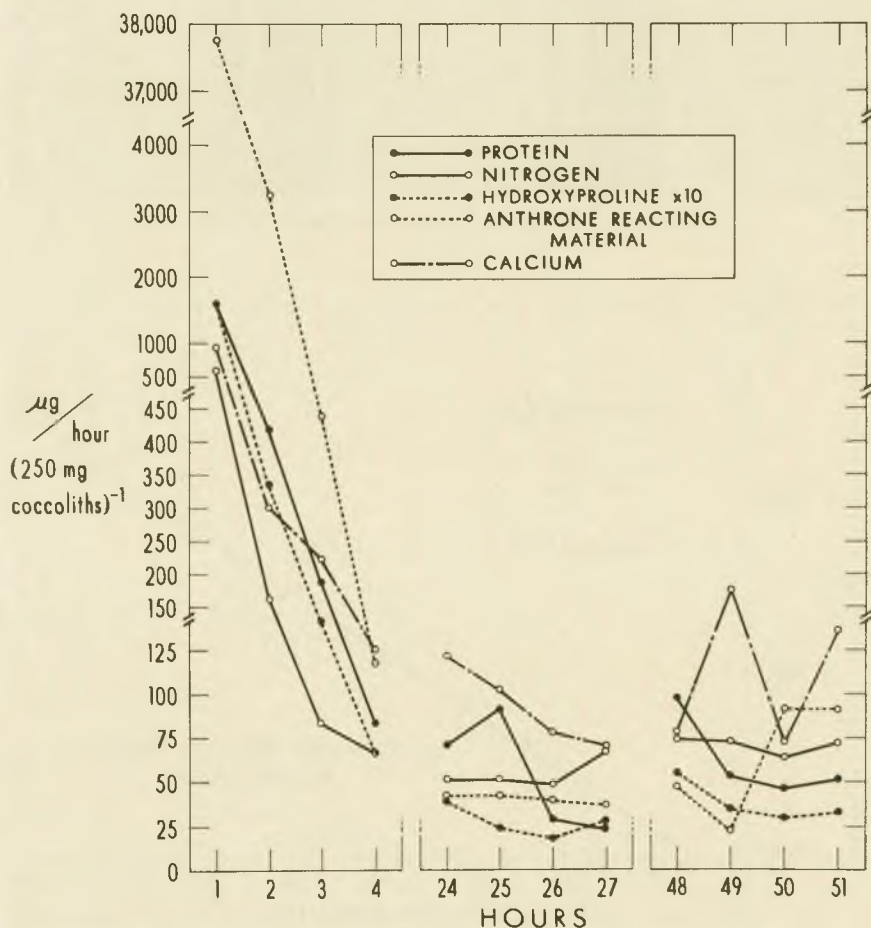


FIGURE 13. The action of distilled water on intact cell-free coccoliths.

chemical analyses used to delineate the constituents of cells and coccoliths did not offer the opportunity to single out a specific material which enhanced mineral deposition, but as shown in an earlier report (Isenberg *et al.*, 1965a), colonial, intercellular and cellular morphology of *Hymenomonas* cultures certainly mirrored the findings in Figure 4.

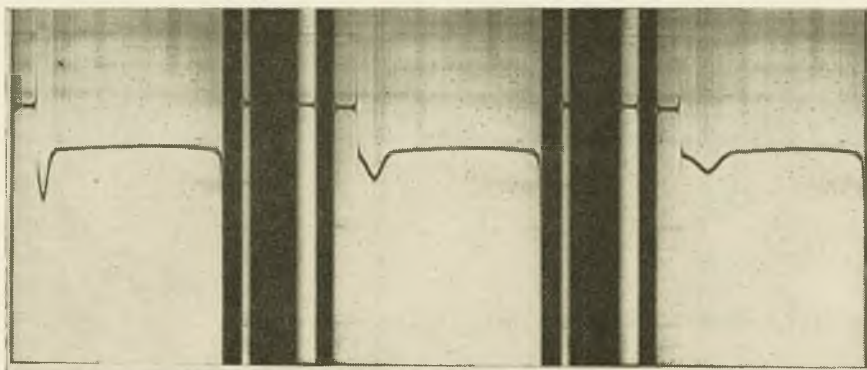


FIGURE 14. Behavior of F_1 in the ultracentrifuge.

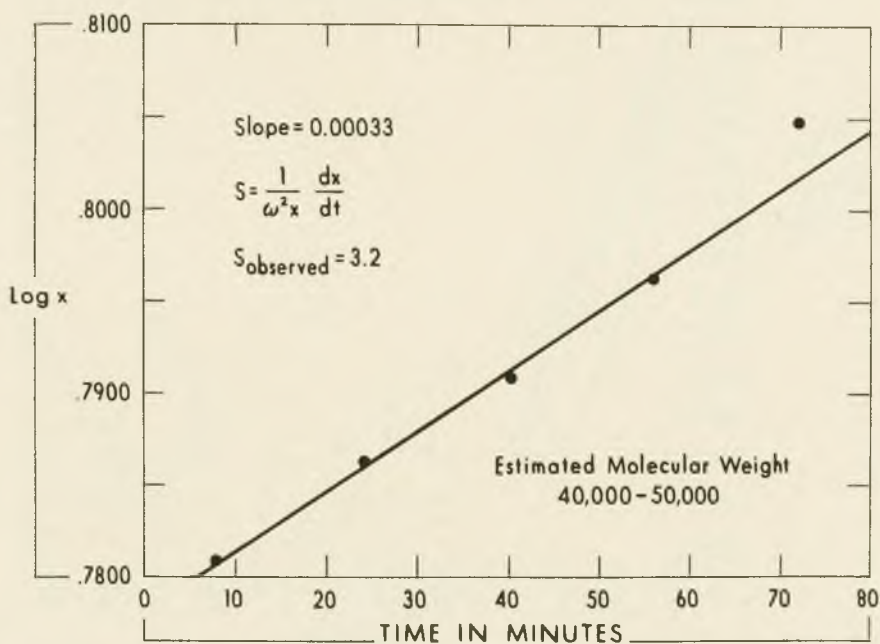


FIGURE 15. Graphic representation of ultracentrifugal behavior of F_1 .

CHEMICAL CONSTITUTION OF COCCOLITHS

While these parameters of mineral deposition were under investigation, repeated attempts, were made to separate cell-free coccoliths into their mineral and organic components. Various established methods of demineralization left 5 to 10 per cent of coccoliths Ca^{+2} associated with the organic fraction (Isenberg *et al.*, 1965b). Rougher treatment of the intact coccoliths with stronger acids or more concentrated chelating agents removed Ca^{+2} successfully but liberated constituents of the organic matrix as well. These constituents could be concentrated by dialysis against running water and lyophilization. They bound Ca^{+2} of tap water but reproducibility of yields was lacking.

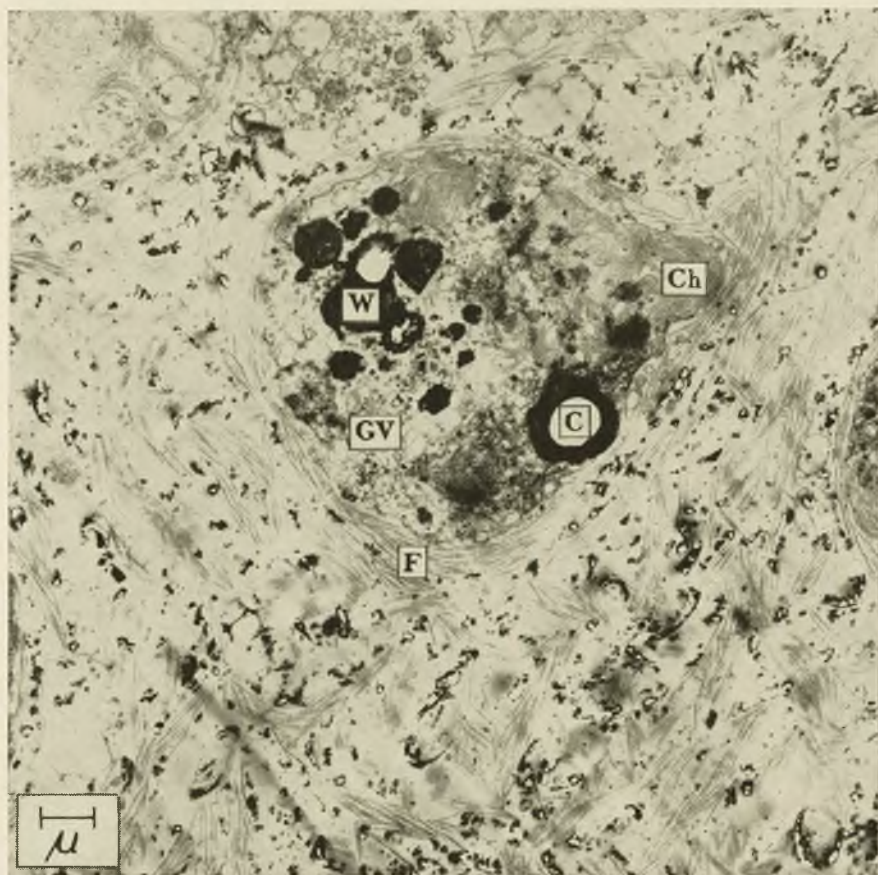


FIGURE 16. *Hymenomonas* grown in mineralizing milieu. Note numerous Golgi vesicles (GV); Wilbur-Watabe bodies (W); chloroplasts (Ch), and intracellular coccoliths (C) in various stages of mineralization. The nucleus cannot be seen in this preparation; F = fibrous structures.

The organic residue of demineralized coccoliths resisted the numerous enzymes applied and only phosphoric and hydriodic acids dissolved the matrix (Isenberg *et al.*, 1965b). Finally, the action of distilled water on intact coccoliths was studied. More than 40 days were required before complete solution could be achieved; however, the fraction liberated during the first 3 days, designated F₁, differed from the remaining products of aqueous action by containing appreciable quantities of hydroxyproline, first noted on two-dimensional chromatograms and confirmed by quantitative analysis (Table 1). The various constituents were released as shown in Figure 13. In addition, F₁ contained 10 $\mu\text{g}/\text{mg}$ phosphorous, the entire



FIGURE 17. Fibrous structures showing periodicity of 190-200 Å associated in profusion only with actively mineralizing organisms. Under conditions of decreased mineral deposition, periodicity of fibers is less discernable and their frequency is decreased.

amount determined for intact coccoliths. This observation was confirmed by infrared spectroscopy. The carbohydrate moieties which make up the bulk of F_1 do not differ from the various carbohydrates determined for the coccolith cores or whole coccoliths comprised as they are of glucose, hexuronic acid, pentose, methylpentose and an unknown moiety. Precipitation of F_1 from the extraction liquor with various combinations of ethanol, ethylether, acetone and HCl does not alter the ultracentrifugal behavior described in Figures 14 and 15. However, the precipitates have a neutral pH while the original is basic. Free ammonia could be determined in the supernatant of the extract. This ammonia could be accounted for as amide-nitrogen for glutamic and aspartic acids and may represent a site of attach-

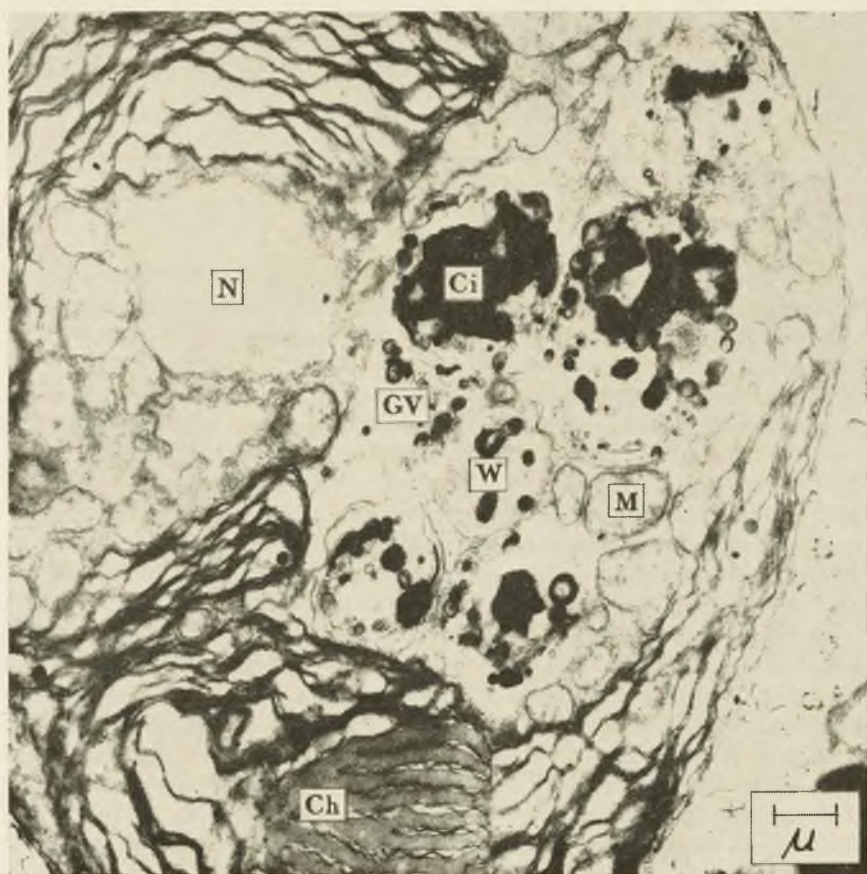


FIGURE 18. Carbonic anhydrase inhibitor effect on mineral deposition. N: nucleus; Ci: incomplete coccolith; Ch: chloroplast; GV: Golgi vesicles; W: Wilbur-Watabe body; M: mitochondrion.

ment for F_1 to the core structures. The precipitated F_1 also contained less Ca^{+2} , but this cation was still in excess of the trace of carbonate associated with F_1 as determined by infrared absorption. This finding suggests that the initial capture of Ca^{+2} may be executed by liganding structures in both the coccolith core and F_1 .

TABLE 1
AMINO ACID COMPOSITION OF COCCOLITHS AND FRACTION¹

AA	μ moles coccoliths $\times 10$	μ moles Fract. 1 $\times 10$	AA	μ moles coccoliths $\times 10$	μ moles Fract. 1 $\times 10$
Asp	3.158	3.510	Met	0.452	0.282
Thr	1.591	1.220	Ileu	1.344	0.682
Ser	1.822	1.928	Leu	2.793	1.200 ²
Glu	3.220	3.890	Tyr	0.576	0.418
Pro	1.631	1.108	Phe	1.288	0.729
Gly	2.925	2.430	Lys	1.293	1.020
Ala	3.400	2.220	His	0.298	0.207
Val	2.093	1.120	Arg	1.305	1.125
Cys	0.158	0.102	Hyp ³	0.300 ³	1.745

¹Protein constitutes 17.8 percent of coccolith weight, 5.6 percent of Fraction 1.

²Estimated value.

³Estimated maximum.

The capacity of F_1 to hold Ca^{45} enriched cation inside Ca^{+2} poor dialysis tubing has been demonstrated. While controls lost activity when exposure to Ca^{45} for 3 days was followed by dialysis against water, F_1 retained 90 per cent of the Ca^{45} bound during the exposure.

The finding of hydroxyproline as part of an actively mineralizing fraction in a microorganism is surprising, since microorganisms generally lack this amino acid. To have found it in appreciable amounts associated with structures which lead to mineral deposition led to a renewed search for sulfated acid mucopolysaccharides. S^{35}O_4 enriched cultures studied autoradiographically and with the special staining procedures developed by Spicer (1964) showed that material with the staining properties of mammalian sulfated acid mucopolysaccharides are present in cultures under conditions which favor mineral deposition. This material has tinctorial properties such as alcianophilia, staining with high iron diamine, and azurophilia which are similar to mammalian sulfated acid mucopolysaccharide. Accordingly, we have tentatively concluded that it is a sulfated protistal carbohydrate. The acid mucopolysaccharide-reacting protistal carbohydrates are associated with intracellular coccoliths. Methylation prevents the staining and autoradiographic reactions of the chrysomonad sulfated acid mucopolysaccharide-like moieties. A detailed report on these histochemical aspects is in preparation.

FINE STRUCTURE STUDIES

Finally, electron microscopic evidence confirmed the microscopic and

the chemical studies reported. Figure 16 presents a view of *Hymenomonas* grown with carbonate and lactate in which the salient features of coccolithophorid mineral deposition are displayed. While the correlation between fine structure and chemical activities will be reported elsewhere, it is obvious from this picture that the artificial conditions of nutrition and illumination resulted in an accentuation of both morphologic and biochemical features involved in mineral deposition. The most striking structures are the numerous fibers which seem to accumulate just within the cell membrane (which is destroyed in processing non-demineralized organisms for electron microscopy), but which can be discerned associated with certain

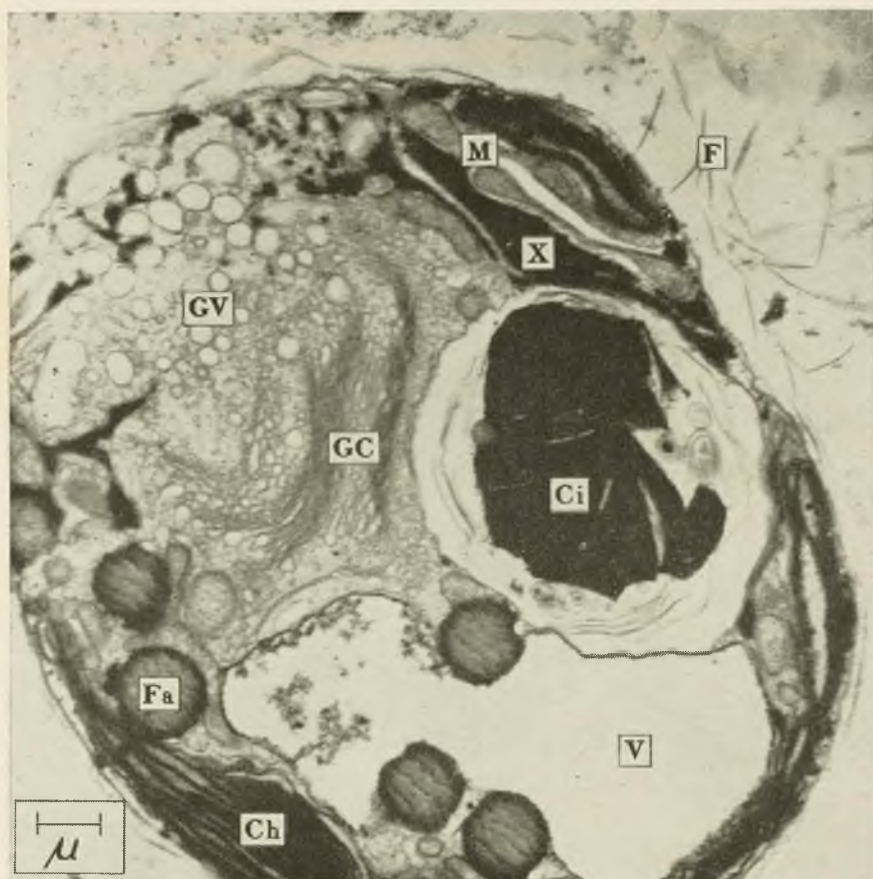


FIGURE 19. Strontium inhibition of mineral deposition. GC: Golgi cysternae; Ci: incomplete coccolith on Wilbur-Watabe body; Ch: chloroplast; X: amorphous electron dense material, possibly mineral; GV: Golgi vesicles; V: vacuole, observed under many conditions of interference with coccolithogenesis; M: mitochondrion; Fa: fat body; F: fibers, note lack of periodicity.

cellular organelles. The greater magnification of these structures shown in Figure 17 underlines their periodicity which measures between 190 and 200 Å and is reminiscent of the electron microscopic appearance of collagen in tissue culture or when ichthyocol is exposed to an increased concentration of NaCl (Gross, 1963). Since this marine chrysomonad must be cultivated in such a saline environment, the spacing may very well reflect the collagenoid nature of material containing appreciable proline and hydroxyproline and most likely corresponding to F_1 . In addition an area reminiscent of the reticular body of Wilbur & Watabe (1963) can be discerned which seems to constitute the core upon which CaCO_3 fibers and Golgi vesicles are deposited according to a pattern which results in the finished coccolith. In the presence of inhibitors such as Diamox or Sr^{+2}

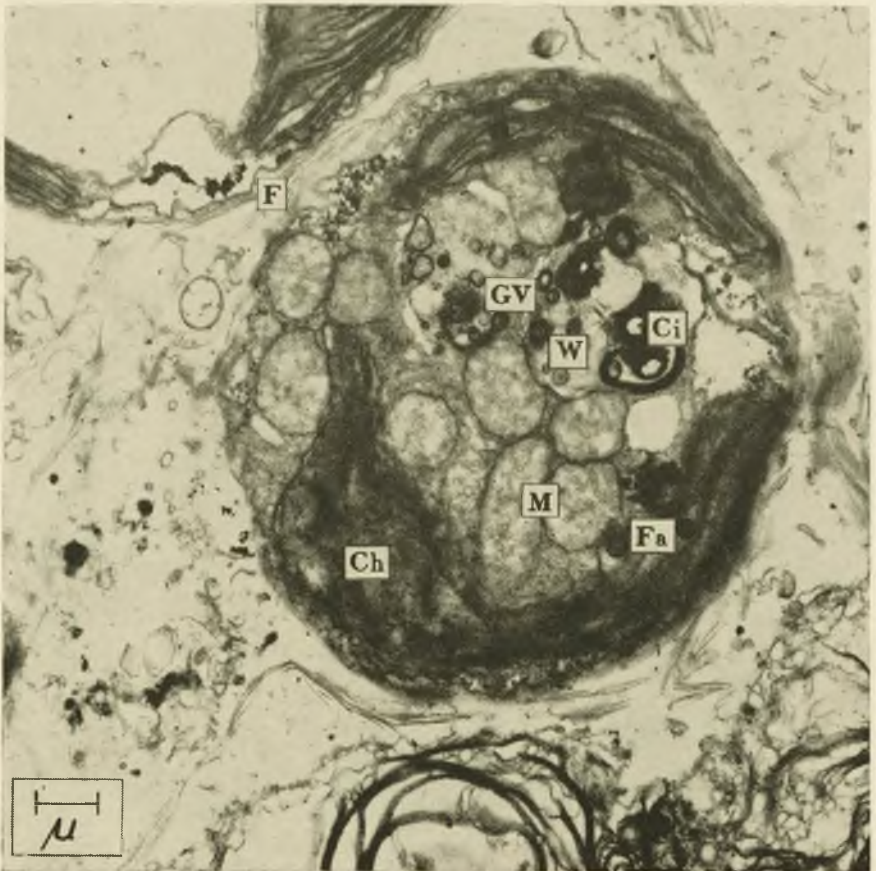


FIGURE 20. Casein hydrolysate nurtured *Hymenomonas*. W. Wilbur-Watabe body; Ci: incomplete coccoliths; ch: chloroplast; GV: Golgi vesicles; M: mitochondrion; Fa: fat body; F: fiber, again lacking periodicity.

Golgi vesicle and fiber formation is impaired as shown in Figures 18 and 19. Complete suppression of coccolith formation is obvious in cells grown with nutrients which do not especially favor calcification (Figs. 21, 22). Here Golgi cysternae and mitochondria can be seen in profusion. Incomplete coccoliths apparently break down into vacuolated structures containing electron dense material in disorganized fashion while WW bodies seem to degenerate; under these conditions there appear typical lipid vacuoles which are abundant and often associated with mitochondria.

The studies with *Hymenomonas* Mary Parke 156 demonstrate that this ancient and primitive coccolithophorid may serve as a protozoan model of hard tissue formation. It fulfills all of the requirements of biological mineral deposition and vindicates again the statements of Kluyver &

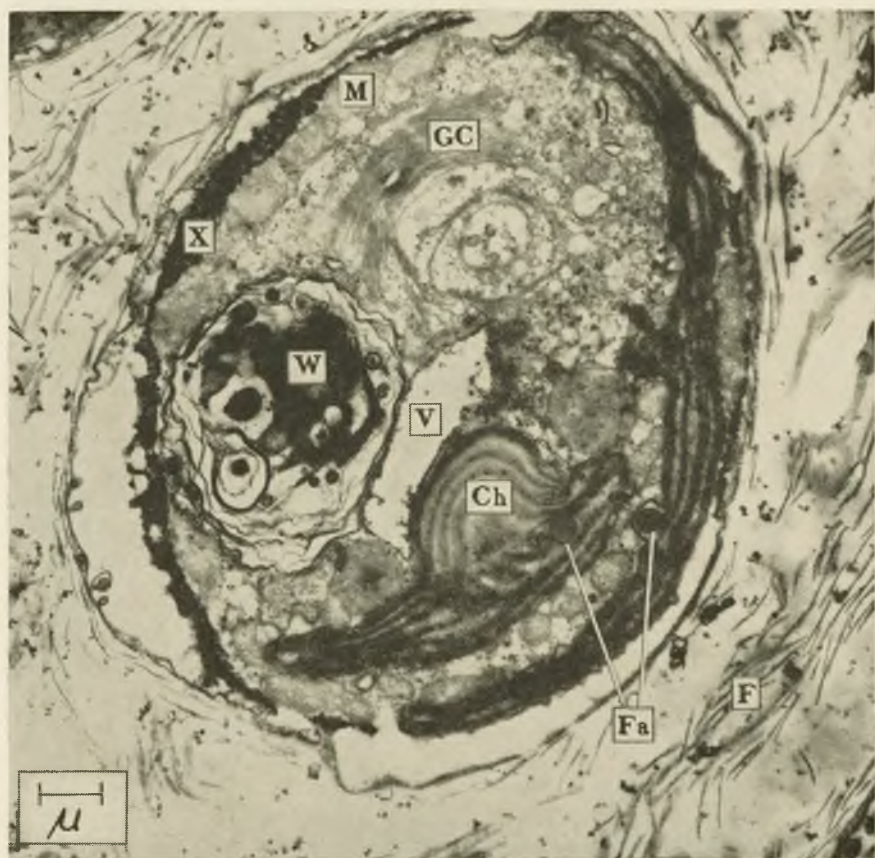


FIGURE 21. Alanine nutrition of *Hymenomonas*. W: Wilbur-Watabe body; Ch: chloroplast; GC: Golgi cysternae; M: mitochondrion; X: amorphous electron dense material, possibly mineral; Fa: fat body; V: vacuole; F: fibers.

Donker (1926) concerning the versatility of nonspecialized acellular protista as physiological and biochemical tools. The fact that this organism permits a total view of calcification from macroscopic morphologic variations to histological and phase contrast detectable changes which find confirmation in the fine structure studies and finally at the level of chemical and physical findings, is to a large degree, a matter of lucky choice of a test object. It certainly makes this and other microorganisms likely candidates for the final explanation of the intimate physics and chemistry which leads to cation and anion capture by the organic matrix. That questions of geological, ecological, and pathological consequence may be asked of this and similar organisms would seem obvious and should

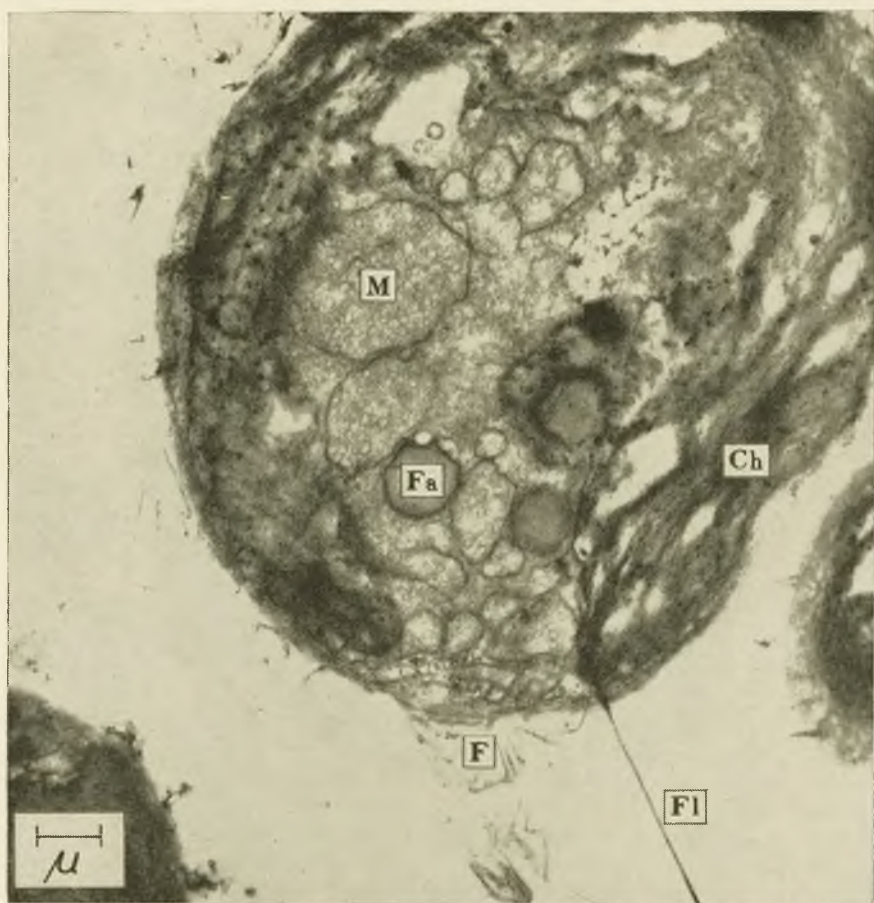


FIGURE 22. Effect of ethanol as sole source of carbon and energy on the fine structure of *Hymenomonas*. Ch: chloroplast; M: mitochondrion; Fa: fat body; F: fiber; Fl: flagellum.

lead to the type of interdisciplinary approach so successful in other areas of scientific endeavor.

REFERENCES

- BLACK, M.
1965. Coccoliths. *Endeavour*, 24: 131.
- BRAARUD, T., K. R. GAARDER, J. MARKALI, AND E. NORALI
1952. Coccolithophorids studied in the electron microscope. *Nytt. Mag. f. Bot.*, 1: 129-138.
- GLIMCHER, M. J.
1960. Specificity of the molecular structure of organic matrices in mineralization. In *Calcification in Biological Systems*, Sognnaes, R. F., Ed., 411 pp. Amer. Ass. Advance. Sci., Washington, D. C.
- GROSS, J.
1963. In *Comparative Biochemistry*, Vol. 5, Florkin, M. & H. S. Mason, Eds., Academic Press, Inc., New York, 307 p.
- ISENBERG, H. D., L. S. LAVINE, M. L. MOSS, D. KUPFERSTEIN, AND P. E. LEAR
1963a. Calcification in a marine coccolithophorid. *Ann. N.Y. Acad. Sci.*, 109: 49-64.
- ISENBERG, H. D., S. L. LAVINE, AND H. WEISSFELLNER
1963b. The suppression of mineralization in a coccolithophorid by an inhibition of carbonic anhydrase. *J. Protozool.*, 10: 477-479.
- ISENBERG, H. D., L. S. LAVINE, M. L. MOSS, M. H. SHAMOS, AND H. WEISSFELLNER
1964. Calcium⁴⁵ turnover in a mineralizing coccolithophorid protozoon. *J. Protozool.*, 11: 531-534.
- ISENBERG, H. D., L. S. LAVINE, H. WEISSFELLNER, AND A. SPOTNITZ
1965a. The influence of age and heterotrophic nutrition on calcium deposition in a marine coccolithophorid protozoon. *Trans. N.Y. Acad. Sci.*, 27: 530-545.
- ISENBERG, H. D., L. S. LAVINE, C. MANDELL, AND H. WEISSFELLNER
1965b. Qualitative chemical composition of the calcifying organic matrix obtained from cell-free coccoliths. *Nature*, 206: 1153-1154.
- KLUYVER, A. J. AND H. J. L. DONKER
1926. Die Einheit in der Biochemie. *Chem. d. Zelle u. Gewebe.*, 13: 134-141.
- PAASCHE, E.
1963. The adaptation of the carbon¹⁴ method for the measurement of coccolith production in *Coccolithus huxleyi*. *Plant. Physiol.*, 16: 186-200.
1964. A tracer study of the inorganic carbon uptake during coccolith formation and photosynthesis in the coccolithophorid *Coccolithus huxleyi*. *Plant. Physiol.*, Suppl. III, pp. 1-82.
- SCHUSSING, B.
1960. *Handbuch der Protophytenkunde*, vol. 2, Gustav Fischer, Jena, Germany, p. 207.
- SPICER, S. S.
1964. Diamine methods for differentiating mocosubstances histochemically. *J. Histochem. Cytochem.*, 13: 211-234.
- WILBUR, K. M. AND N. WATABE
1963. Experimental studies on calcification in molluscs and the alga *Coccolithus huxleyi*. *Ann. N.Y. Acad. Sci.*, 109: 82-104.

THE SOLUTION BEHAVIOR OF CARBONATE MATERIALS IN SEA WATER¹

P. K. WEYL²

Shell Development Company, Houston, Texas

ABSTRACT

A large number of experiments demonstrating that carbonate minerals in sea water do not behave as homogeneous thermodynamic phases are described. The external solution does not come to equilibrium with the mineral phase introduced; rather, the surface layers of the solid adjust themselves to the aqueous environment. This behavior is demonstrated both in laboratory experiments and in field observations. A simple theory of solubility of impure solids is presented in the Appendix. This theory is useful in the interpretation of some of the experimental results.

INTRODUCTION

A new method for determining the state of saturation of carbonate minerals with respect to aqueous solutions, in particular sea water, was reported earlier (Weyl, 1961). This "saturometer" method is rapid, sensitive, and suitable for field work. It seemed at the time of this development that the saturometer would lead to a rapid solution of the problems of carbonate diagenesis. Experimentation with the saturometer, however, soon showed that this was not the case. The solution behavior appeared to depend not only on the compositions of the solution and the solid phase but also on the immediate past history of the solid. This type of behavior was already indicated in Figure 8 of the 1961 paper.

To study the solution behavior of carbonates in more detail, a number of different experiments were carried out. Although the general conclusions drawn from these experiments were suggested earlier (Weyl, 1964), the details of the experiments themselves have not been published previously. In this paper, the various experiments performed are described, the results obtained are interpreted, and finally a simple theory of the solubility of impure substances is presented. This theory has been useful in explaining some of the experimental results.

EXPERIMENTS

Experiment A

The Solution Kinetics of Calcite in Sea Water by the Saturometer Technique

A study of the solution kinetics of calcite in carbonic acid (Weyl, 1958) indicated that the rate of solution depends only on the rate of diffusion

¹EPR Publication 428, Shell Development Company (A Division of Shell Oil Company), Exploration and Production Research Division, Houston, Texas.

²Present address: Department of Earth and Space Sciences, State University of New York at Stony Brook, Stony Brook, New York.

away from the solid-liquid interface, where the solution is always saturated. This conclusion was based on experiments with essentially pure water in which the loss of calcite and the change in conductance of the water were used as a measure of the rate of equilibration. The development of the carbonate saturometer (Weyl, 1961) has provided a very sensitive means for measuring the attainment of equilibrium of carbonates with respect to any solution. The results so far obtained indicate that the previously published simple model of the solution kinetics of calcite is not generally valid.

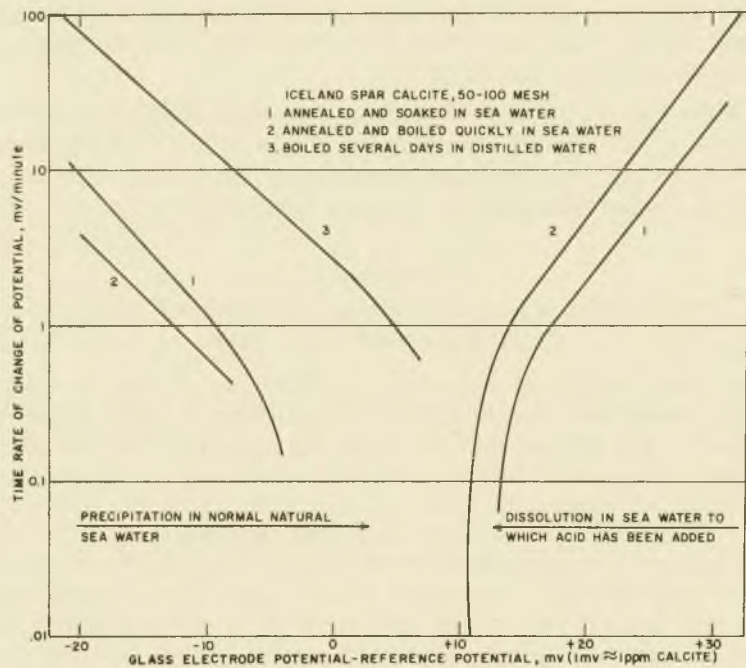


FIGURE 1. Equilibration of sea water with calcite.

Some data on the rate of equilibration of variously treated calcite samples with sea water are shown in Figure 1. In these experiments, the calcite is dropped into the cup of a single-drop glass electrode immersed in the water, and the potential difference between the glass electrode and a standard calomel electrode is recorded. For natural sea water, a change in potential of 1 millivolt corresponds to the precipitation or solution of about 1 ppm of calcite. The natural sea water used, which was surface water from the mid-Gulf of Mexico, is supersaturated with respect to calcite, and when calcite is added, the potential becomes more positive. In order to study the kinetics of dissolution, we added a few drops of 1 N HCl to the water to make it slightly undersaturated.

For a solution or precipitation process dependent only on diffusion, the time rate of change of the potential at each point along the curve should have been at least an order of magnitude higher than was observed for any of the curves shown. During the time of the experiments, approximately $\frac{1}{2}$ hour, equilibrium was not reached. If the rate of equilibration were determined merely by the rate of diffusion in the interstitial water, equilibrium should have been reached in a few minutes. As indicated in Figure 1, experiments were made with samples of the same Iceland spar that had received different treatments. It can be seen that the curves obtained with these different materials gave different results, although the solutions and the gross properties of the materials were the same. The experiments thus raise two questions:

- 1) Why is the rate of equilibration in sea water slower than would be expected if it were limited merely by the rate of diffusion in the solution?
- 2) Why do samples of the same Iceland spar that have received different treatments behave differently in the same solution?

Experiment B

The Solution Kinetics of Calcite in Different Waters by the Saturometer Technique

Experiments similar to experiment A were carried out in waters of different composition. The composition of each water is shown in the insert on Figure 2. It is evident that the series was chosen so that the effect of each major component could be isolated. Iceland spar calcite was boiled briefly in the particular water and was then equilibrated with a fresh portion of the water in the cup of a single-drop glass electrode. Figure 2 is a plot of the time rate of change of the potential as a function of the difference from the final potential. The curves for sea water are also indicated. It can be seen that the only components in the water that materially reduce the rate of equilibration are the divalent cations calcium and magnesium (curves IV and VI). Sodium chloride, the major constituent of sea water, had a much smaller effect on the rate of solution (curve III).

The mechanism by which the calcium and magnesium ions reduce the rate of equilibration of calcite can be either the formation of a barrier layer at the solid-liquid interface or a reaction in the solution itself that has slow kinetics. To check the latter possibility, we have mixed CaCl_2 and MgCl_2 with water containing only NaHCO_3 , without solid carbonates. Because of the formation of carbonate complexes (Garrels & Christ, 1965, p. 98), the pH of the solution changes. The kinetics of this change are extremely rapid; this indicates that the reactions in the solution are rapid and cannot explain the slow kinetics of calcite solution in Ca^{2+} - and Mg^{2+} -bearing waters. We must therefore conclude that the rate-inhibiting mechanism is at the solid-liquid interface.

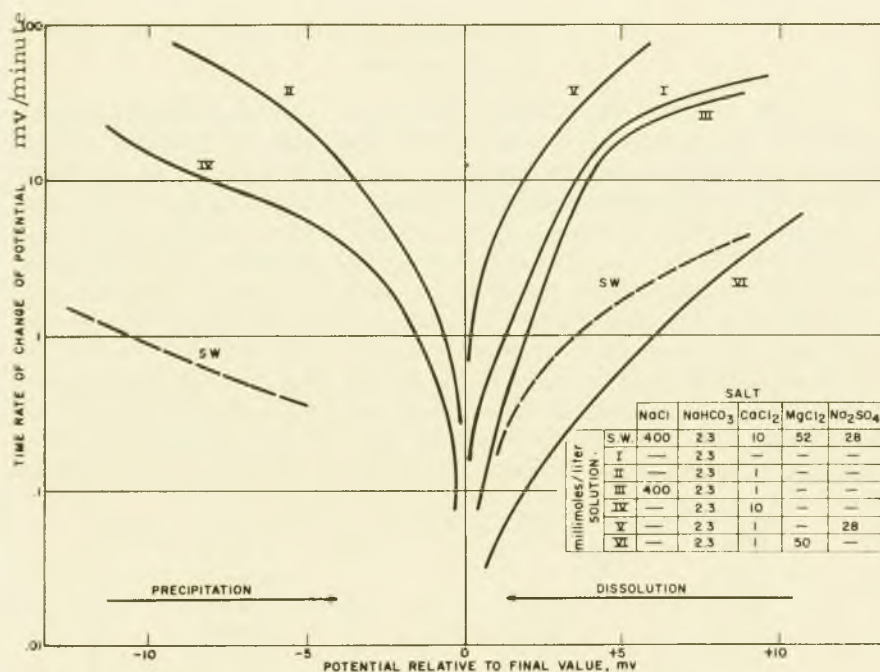


FIGURE 2. Relative rates of solution or precipitation of boiled Iceland spar in various waters.

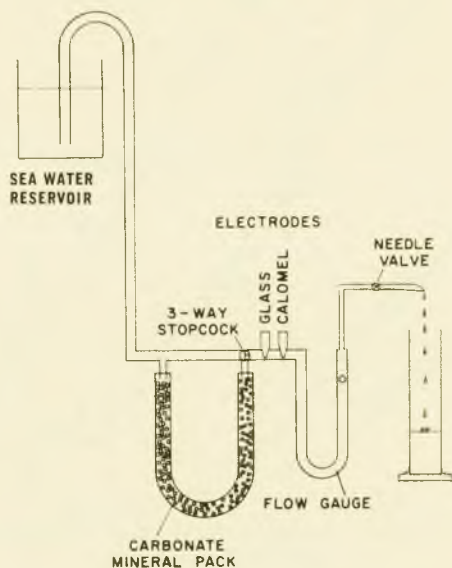


FIGURE 3. Flow experiment.

Experiment C

Flow Experiment

In order to study the solution behavior of carbonate minerals under conditions of continued precipitation from sea water, the following experiment was performed with the apparatus sketched in Figure 3. A carbonate mineral of suitable particle size (40-50 mesh) was placed in a U-tube and restrained there by a permeable disc at the outflow end. Sea water was flowed through the tube. The flow velocity was measured by a flow gauge and could be adjusted by stopcocks. A glass and calomel electrode pair was placed in the flow stream, downstream from the pack. Between the pack and the electrodes, a three-way stopcock was provided, so that the sea water could either be made to bypass the pack and flow directly past the electrodes or be made to flow through the pack first and then past the electrodes. The difference in potential (E_G) of the electrode pair is a measure of the pH of the solution. The difference between E_G measured on

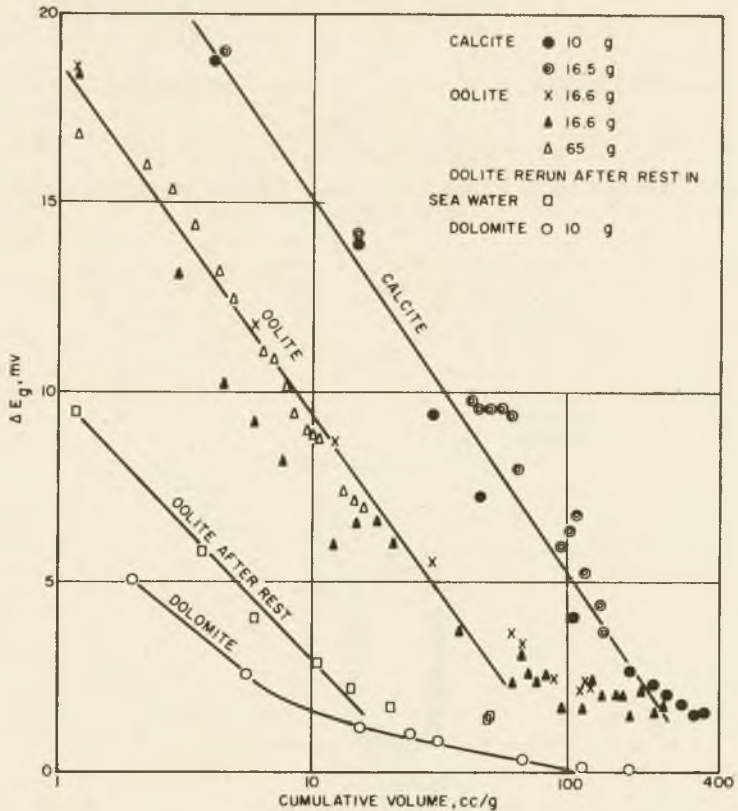


FIGURE 4. Precipitation on carbonates due to continuous flow of sea water.

the inflowing sea water and on the sea water that has passed through the pack (ΔE_G) is due to the interaction of the water with the carbonate minerals in the pack and gives a measure of the amount of carbonate that has precipitated or been dissolved. For sea water, a change of +1 millivolt indicates a precipitation of approximately 1 ppm calcium carbonate.

These U-tube flow experiments have been made for Iceland spar calcite, oolites from the Bahama Banks, and dolomite. The materials used were crushed to 40-50 mesh, except the oolites, for which the size fraction was obtained by sieving natural oolites. The variation in ΔE_G with the log of the cumulative flow through the pack per gram of material is shown in Figure 4. The flow velocity was maintained approximately constant between 0.5 and 1 cc per minute. In interpreting these data, we believe that it can be assumed that the solution can only "see" the surface layer of the carbonate material. Thus, if the properties of the surface layer remain constant during precipitation from sea water, at constant flow velocity the value of ΔE_G must remain constant. (During the course of the experiment the total amount of carbonate precipitated is never more than 1 part in a thousand parts of the original material.) The following conclusions can be drawn from the data:

1) Since ΔE_G changes as precipitation occurs, we conclude that the overgrowth precipitated is different from the original mineral surface and, furthermore, that the properties of the surface change gradually as precipitation proceeds. Figure 5 indicates this change for the oolites as a function of the amount precipitated. In the case of calcite, about four times as much precipitation is required to produce the same change in ΔE_G . For dolomite, the change in ΔE_G is at first rapid and then proceeds more slowly, as is in-

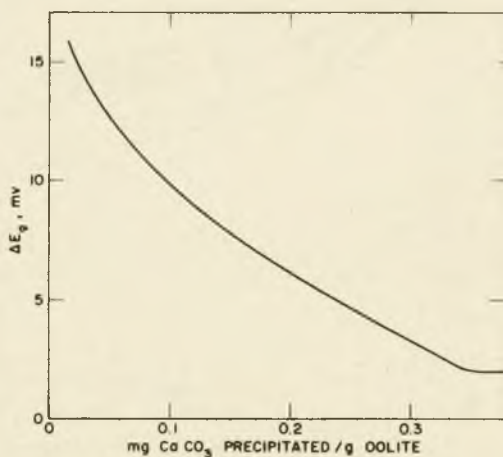


FIGURE 5. Change of precipitation on oolite as function of overgrowth from sea water.

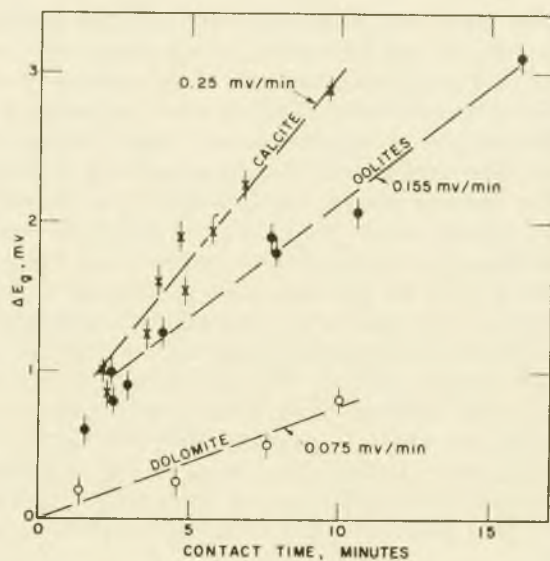


FIGURE 6. Precipitation as function of contact time between minerals and sea water during flow.

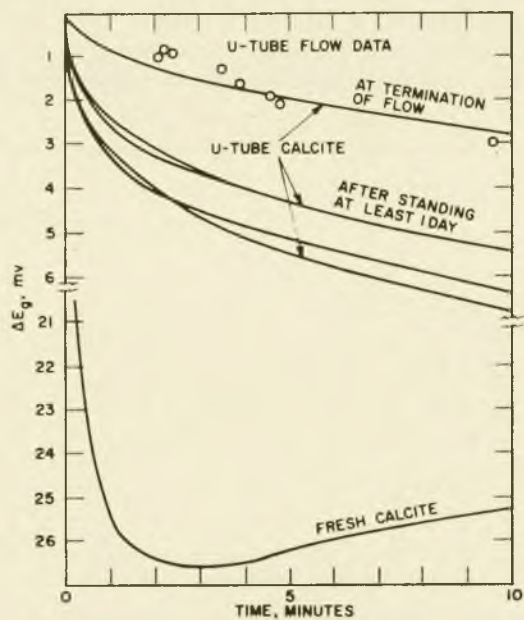


FIGURE 7. Saturometer runs: calcite.

licated by the change in slope of the curve for dolomite shown in Figure 4.

2) When a certain volume has flowed through the U-tube, a steady state is reached, after which ΔE_G remains constant at the same flow velocity. To reach the steady state, the following amount of precipitation is required.

	Oolite	Calcite	Dolomite
Volume (cc/g)	80	300	50
Precipitate (mg/g)	0.33	1.3	0.09
Approx. Overgrowth (Å)	200	800	50

After the steady state was reached, the flow velocity was altered, and ΔE_G was found to be dependent on the flow velocity. Experiment B demonstrated that the rate of equilibration of calcite with solutions was inhibited at the solid-liquid interface when Ca^{2+} or Mg^{2+} was present in solution. The present flow experiments confirm and extend the earlier results. If the rate of equilibration for the size of pack used were only diffusion limited, the time to reduce the difference from saturation to $1/e$ of its initial value would have been about 10 seconds (see Weyl, 1958). As the contact times between the sea water and the minerals ranged from 1 to 10 minutes, we can conclude that the rate of equilibration between the sea water and the steady-state surface is inhibited at the solid-liquid interface. Figure 6 is a plot of the value of ΔE_G versus contact time obtained for the three materials after a steady state had been obtained. After an initial more rapid rate, precipitation appears to proceed at a constant rate. With the assumption that precipitation takes place uniformly over the surface area of the material in our packs, this constant rate gives approximate growth rates of 4.8×10^{-2} , 2.6×10^{-2} , and 1.7×10^{-2} angstrom per minute for calcite, oolite, and dolomite, respectively. The magnitude of this constant

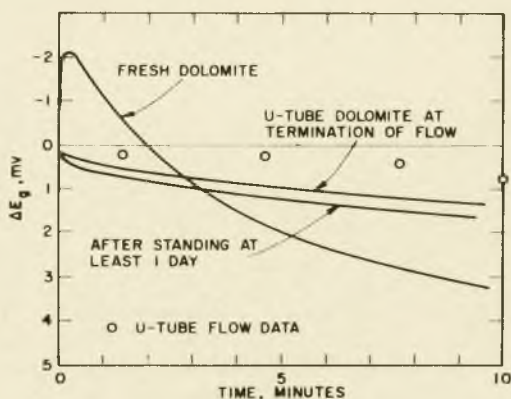


FIGURE 8. Saturometer runs: dolomite.

rate will probably depend on temperature, and, of course, it is directly applicable only to sea water.

After the above-described flow experiments, the water was allowed to remain stationary in the tube for at least 16 hours. When flow was recommenced, the previous steady state was rapidly re-established. In the case of calcite and dolomite, only a few cc per gram had to flow through the pack. In the case of the oolites, about 20 cc per gram was required. The return to steady state for the oolites is indicated in Figure 4.

After the minerals had reached steady state in the U-tube, they were run in the saturometer. A determination was made immediately after the minerals were removed from the U-tube and several days later, after they had been in sea water. Fresh materials were also run for comparison. The data, together with the U-tube flow data (i.e., ΔE_G at various contact times), are shown in Figures 7, 8, and 9 for calcite, dolomite, and the

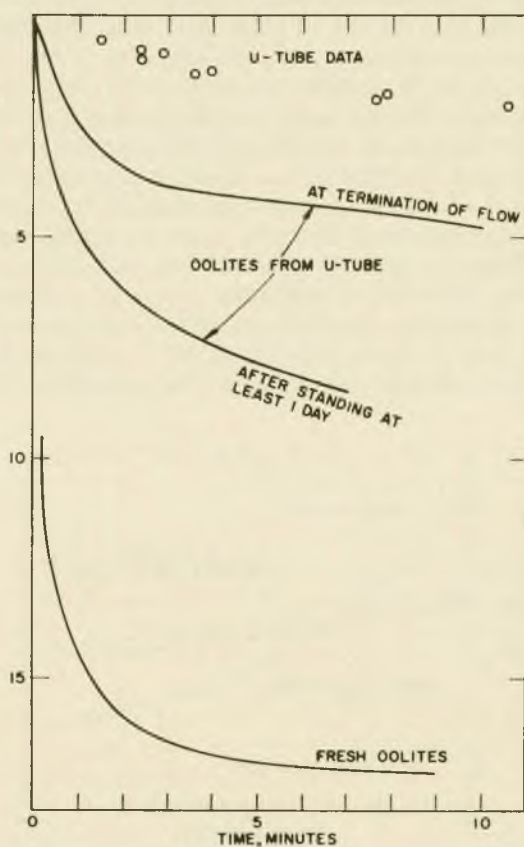


FIGURE 9. Saturometer runs: oolites.

oolites. The saturometer curves for calcite and dolomite are in rough agreement with the U-tube data. The oolite saturometer run indicates a considerably more rapid rate of precipitation than was indicated by ΔE_G values in the flow experiments. This may be due to recrystallization of the surface layer which occurred between the termination of the flow experiment and the beginning of the saturometer run. Such recrystallization is also indicated by the second oolite curve in Figure 4.

Field Experiment D

The results of experiment C indicated that as fresh sea water flows through a pack of carbonate materials, the rate of precipitation is reduced significantly with time. This suggests that the precipitate grown over the carbonate particles gradually becomes less stable and hence more soluble until the solubility of the overgrowth is almost in equilibrium with sea water.

This laboratory observation was verified recently in the field. At Bonaire, Netherlands Antilles (see Deffeyes, Lucia, & Weyl, 1964, 1965) the saturometer response with local sea water of a carbonate sand in the surf zone was compared with that of a carbonate sand higher up on the beach. In 3 minutes, the water precipitated only 3 ppm of calcium carbonate on the sand in the active surf zone, whereas the precipitation on dry sand from the same beach amounted to 13 ppm. For comparison, the precipitation in 3 minutes on dry Bahama oolites amounted to 24 ppm.

A trip to the Bahamas (made possible by the cooperation of R. N. Ginsburg) afforded an opportunity to repeat these observations on the oolite bars off Eleuthera Island. Oolites that had been moving in the tidal current on top of the bar showed a precipitation of about 2 ppm, whereas oolites that were stationary for an unknown period in the bottom of a channel showed a 3-minute precipitation of 19 ppm. For comparison, dry oolites gave readings which averaged about 23 ppm. The recently active oolites were allowed to stand in sea water. After 4 hours the precipitation in fresh sea water had increased to 6 ppm, and after 9 hours it had increased to about 12 ppm.

The field observations thus confirm the laboratory results and indicate that the precipitation of a more soluble overgrowth does take place in nature and is geologically significant. The phenomenon offers a tool for distinguishing carbonate particles that have recently received precipitation from those that have been quiescent for several hours. In view of these observations, oolite growth on a tidal bar appears to take place by the following steps: As the tidal current increases, the previously stationary oolites are brought in contact with fresh sea water. Precipitation takes place rapidly at first and then more slowly as a more and more soluble precipitate is formed. As the current decreases, the oolites come to rest and are buried, and the new overgrowth gradually recrystallizes to a less soluble, more stable form. Then, after one or more tidal cycles, the process is repeated.

AIR THERMOSTAT

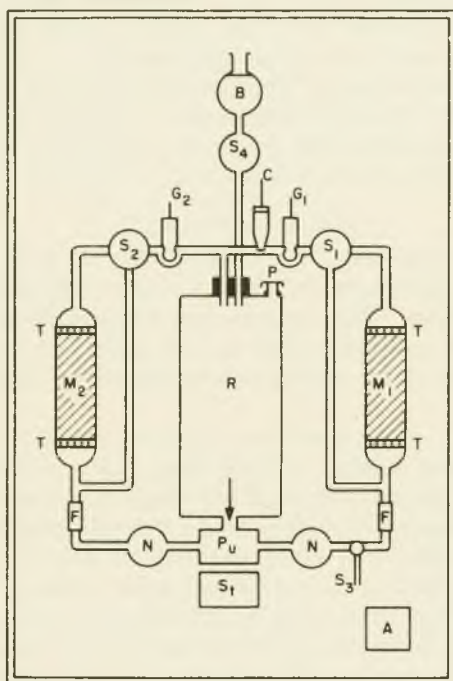


FIGURE 10. Improved flow apparatus: S_1 , magnetic stirrer; P_u , centrifugal pump; R, reservoir 1 liter; $S_{(1,2,3,4)}$, stopcocks; T, perforated teflon disc; B, filling and overflow bulb; P, port sealed with rubber closure; $M_{1,2}$, mineral powder; F, flow gauge; C, calomel electrode; G_1 G_2 , glass electrode; N, needle valves; A, auxiliary electrode assembly.

Apparatus and Procedure for Experiment E

Apparatus.—In order to increase the control and improve the accuracy over that possible by the procedure of experiment C, the flow apparatus shown in Figure 10 was constructed. About 1 liter of sea water or other solution is contained in the reservoir R and isolated from the atmosphere except for a small air interface in the filling bulb B. The system is constructed only from glass or Teflon, and no grease is used. Teflon couplings are used to assemble the apparatus. To circulate the solution through the mineral packs M_1 and M_2 , a centrifugal pump made of glass (Figure 11) is built into the bottom of the reservoir R. Power is provided by a Teflon-coated stirring bar driven by a magnetic stirrer. The flow rate can be adjusted by changing the power to the stirrer and adjusting the needle

valves N. The flow rate is measured by flow gauges F. The apparatus is constructed so that two minerals can be investigated simultaneously in the same solution. Glass electrodes G_1 and G_2 of taper joint construction are placed in each flow loop to measure the pH of the circulating solution.

The reference electrode is a specially constructed calomel electrode (Figure 12). To avoid excessive contamination of the sea water during the long times of the experiment, a special sea water solution containing the major cations of sea water but only chloride as the anion and saturated with calomel is used in the electrode. To maintain a constant liquid junction potential across the capillary leak of the calomel electrode, the electrode solution is made to flow past the leak at a rate of a few drops a minute. To avoid flow potentials, small Teflon tubes are used to conduct the solution from the calomel electrode to the capillary leak and from there to the overflow. The rate of flow of electrode solution can be adjusted by changing the relative levels of the solution reservoir bulb and the overflow. The main part of the calomel electrode is conventional.

Because of unknown liquid junction effects, the "sea water" calomel-glass electrode pair cannot be used to make absolute pH measurements. It is, however, very stable and can be used to measure relative changes in the pH of sea water with high precision without seriously altering the composition of the sea water. To make absolute pH measurements, an auxiliary

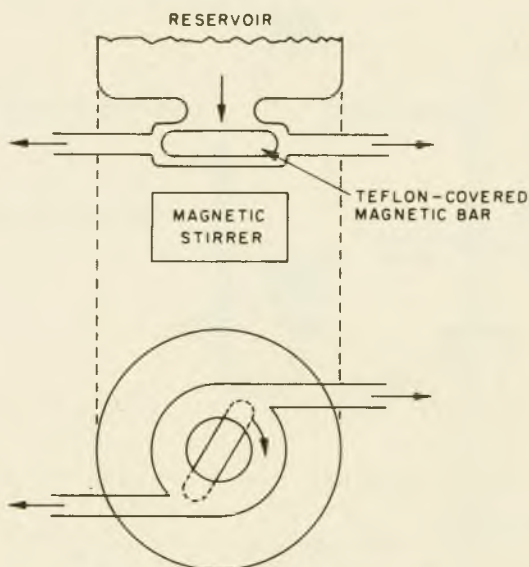


FIGURE 11. The centrifugal pump

electrode assembly A is enclosed in the air thermostat. This consists of a standard glass-saturated KCl calomel electrode pair. This assembly is so constructed that it can be filled with water in the sea water reservoir R by means of stopcock S_3 and can be rinsed and filled with buffers that are stored in the thermostat. Thus, the relative pH measurements of the "sea water" electrodes can be converted to the conventional pH scale, although the accuracy of the relative pH measurement is much higher than that of the absolute pH determination.

In order to change the pH and hence the carbonate concentration of the water in reservoir R, a port P sealed by a medical soft rubber closure is provided. With this, acid or base can be added to the sea water with a syringe having a long fine needle. The centrifugal pump at the bottom of the reservoir also acts as a stirrer to mix the added chemical rapidly.

Procedure.—Experiments with the modified flow apparatus are carried out as follows. The apparatus is cleaned and assembled. It is partially filled

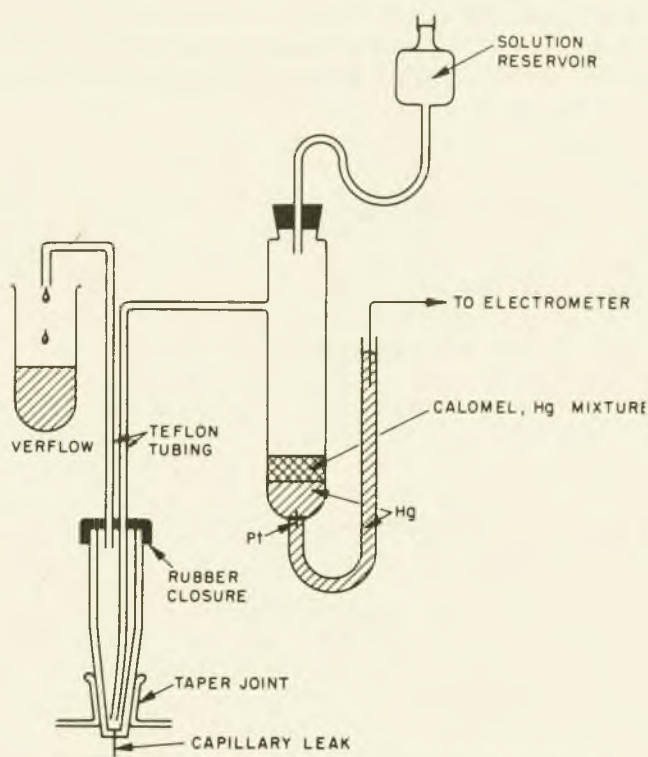


FIGURE 12. The "sea water" calomel electrode.

with the appropriate deaerated solution. The top Teflon pierced discs T in the mineral reservoirs are removed, and the reservoirs are filled with solution. Carefully sieved and washed mineral grains, usually 40-80 mesh, are dropped into the reservoirs through the solution with an auxiliary solution-filled tube extension in order to ensure that no air is trapped in the mineral pack. The top Teflon discs are added, and the rest of the apparatus is assembled and carefully filled with solution. Trapped air can be expelled by lifting out the electrodes, allowing the solution to overflow, and reseating the electrodes. The flow can be controlled by stopcock S₄. Once filled, the air thermostat is closed, and the solution is allowed to come to constant temperature. Meanwhile, the solution is stirred and circulated with the centrifugal pump through the bypass of the mineral packs. Stopcocks S₁ and S₂ direct the solution either through the bypass or through the packs. The pH of the solution is measured with the auxiliary electrode assembly A, and simultaneously the emf of the internal glass electrodes G₁ and G₂ relative to the "sea water" calomel reference electrode is measured. If desired, the pH of the water in the reservoir can now be adjusted by adding dilute acid or base by means of a syringe through port P.

When stopcocks S₁ and S₂ are turned, the water is made to flow through the mineral packs, and the flow velocities are adjusted by means of the needle valves N to the desired rate as read on the flow gauge. As a result of dissolution or precipitation in the mineral pack, the emf of the glass electrode is changed. From the difference in emf between the bypassed water and the water flowing through the pack, the rate of dissolution or precipitation can be determined. To eliminate the effect of electrode drift, the flow is returned to bypass from time to time to get a more accurate measure of the change in pH in going through the pack. After a measurement has been made, the pH and hence the carbonate concentration of the water in the reservoir are adjusted to a new value, and the new rate of dissolution or precipitation is determined. Because of the slow flow rates used and the relatively large size of the reservoir, the pH of the water in the reservoir is not significantly altered by flowing through the packs. If water is withdrawn from the reservoir to measure the pH of the solution or to make other analyses, water is added to bulb B to ensure that no air enters the apparatus.

Experiment E1

Dolomitization, First Experiment

Experiment C has shown that the solution behavior of carbonates depends on their past history. After a considerable amount of solution has flowed through a carbonate material, a steady state is set up. If the pH of the sea water is altered, precipitation or dissolution can be made to take place during this steady state. To compare the steady-state behavior of dolomite with that of calcite for the same water, a double flow experiment was performed. In this experiment a sample of sea water in a rather large

reservoir (approximately 1 liter) is sealed off from the atmosphere and is circulated through packs of calcite and dolomite arranged in parallel (procedure E).³ The change in pH of the water on passing through each pack is determined by the change in potential difference (ΔE_G) of a glass-calomel electrode pair when (1) the water passes through the pack before contacting the electrode pair and (2) the water flows directly from the reservoir over the electrodes by means of a bypass around the pack.

After the apparatus is filled, the water is circulated until a steady state is reached, and ΔE_G values for calcite and dolomite are measured. The pH of the sea water is then changed by the addition of acid or base, and the measurement is repeated. Figure 13 is a plot of the data so obtained. The ΔE_G for Iceland spar calcite is plotted against the ΔE_G for a pure dolomite. The data indicate the existence of a large range of carbonate concentration (created by varying the pH) over which dolomite neither dissolves nor precipitates significantly, whereas calcite changes from dissolution to precipitation. Thus, if sea water passes through a mixture of calcite and

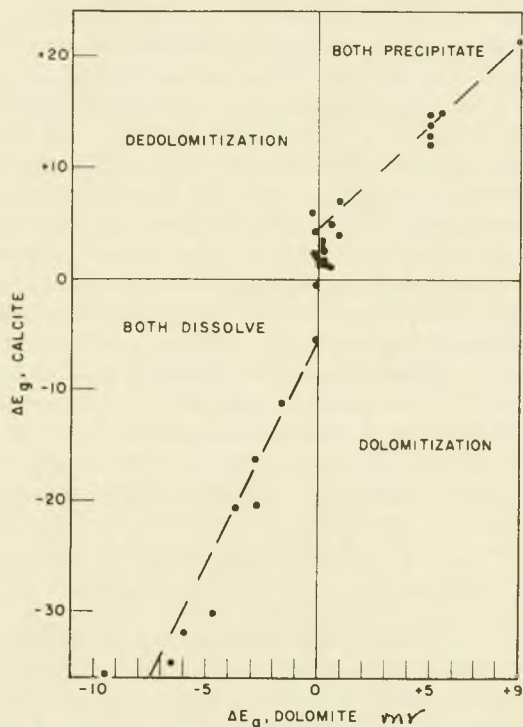


FIGURE 13. Relative solution behavior of calcite and dolomite in sea water of different pH.

³This experiment was carried out at room temperature with a cruder version of apparatus E.

dolomite and comes to equilibrium with calcite, dolomite will neither precipitate nor dissolve rapidly. The sensitivity of the experiment is such that a rate of 0.3 ppm per minute would be detected. This sensitivity is equivalent to an overgrowth rate of 0.25 mm per 100 years.

In a number of runs the concentration of carbonate ion was determined in the altered sea water. The range in carbonate concentration over which dolomite neither dissolves nor precipitates within the sensitivity of the experiment is from 0.02 to 0.2 millimole per kg, whereas the range for calcite extends from 0.03 to 0.1 millimole per kg.

These measurements indicate that the two materials are similar in that they appear to be in equilibrium with sea water over an extended range of carbonate concentration. However, since the carbonate concentration range in which dolomite appears to be in equilibrium with sea water completely brackets that for calcite, only the latter dissolves or precipitates at a significant rate when sea water flows slowly through a mixture of the two. The experiments have shown that sea water neither dolomitizes nor dedolomitizes a sediment of the usual grain size (0.1 to 1 mm) rapidly (i.e., on a 10- to 100-year time scale).

Experiment E2

Dolomitization, Second Experiment

In the study of the solubility of carbonates (experiment C) we found that solubility depends on the previous history of the carbonate mineral. If a precipitate is formed over a material, the solubility behavior of the precipitated layer differs significantly from the solubility behavior of the substrate. This observation prompted a modification of the experimental procedure used in experiment E1. The new experimental setup is essentially the same as that used previously, except that the flow experiment is mounted in an air thermostat at 30°C regulated to 0.1 degree. In the apparatus any two materials can be run simultaneously. At first the pH of the water is made sufficiently acid to dissolve both minerals, and flow is commenced. Dissolution is allowed to continue overnight so that the surfaces of the mineral grains are cleaned up. Next the mineral packs are freed of any CO₂ gas that might have formed as a separate phase.

The solubility determination is then made on the mineral with a freshly exposed surface. The change in pH produced as the water flows through the pack is noted. If necessary, acid is added to the water to ensure that the water starts out by dissolving the minerals. After the degree of undersaturation of the water has been determined by measuring the pH change caused by the dissolution of each mineral (this requires about 20 minutes of flow), the water is made more basic by adding dilute sodium hydroxide. The experiment is continued; each time a small amount of sodium hydroxide is added to increase the concentration of carbonate ion by reacting with HCO₃⁻ until precipitation on both minerals is occurring.

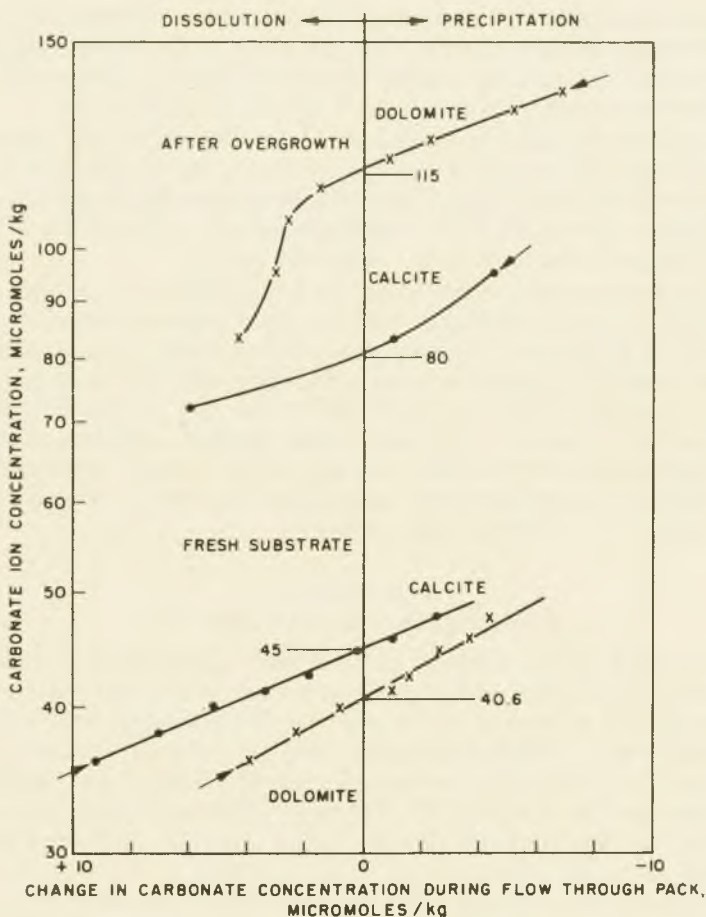


FIGURE 14. Calcite and dolomite solubility in sea water.

After this state is reached, the critical solution composition parameters which may have changed appreciably are determined. The pH of the water is carefully measured in a special cell in the thermostat. A water sample is analyzed for the total CO_2 concentration. In the case of the dilute waters, the magnesium and calcium ion concentrations are determined by versenate titration on another sample. A typical run in sea water is shown in the bottom of Figure 14. The pH change occurring as the water flows through the pack for each case has been converted to the equivalent change in carbonate ion concentration for plotting on the x axis. The y axis shows the actual carbonate ion concentration plotted on a logarithmic scale. It has been calculated by knowing the final analysis and the pH during the

complete run. The minerals neither dissolve nor precipitate if the carbonate concentrations are 40.6 and 45×10^{-6} mole/kg for dolomite and calcite, respectively. Since sea water contains 0.010 and 0.0523 mole of calcium and magnesium ion per kg, respectively, the following concentration products⁴ in filtered sea water at 30°C can be calculated in units of moles/kg solution:

$$\text{Calcite } 4.5 \times 10^{-7} = K'c \text{ (Iceland spar).}$$

$$\text{Dolomite } 0.85 \times 10^{-12} = K'd \text{ (Dolomite marble).}$$

To be in equilibrium with both calcite and dolomite, the magnesium-to-calcium ratio of the sea water would have to be lowered to

$$\frac{\text{Mg}^{2+}}{\text{Ca}^{2+}} = \frac{K'd}{(K'c)^2} = \frac{0.85 \times 10^{-12}}{0.20 \times 10^{-12}} = 4.2$$

compared with a ratio of 5.23 in normal sea water.

After the equilibrium point had been crossed from the dissolution side, the pH of the sea water was raised, and precipitation was allowed to continue overnight. The next morning, the pH of the water was lowered in steps to determine the carbonate concentration at which the overgrowth precipitated would come to equilibrium with the water. As can be seen from the upper curves in Figure 1, the overgrowth has about twice the solubility product of the substrate, and, in particular, the overgrowth on the dolomite is more soluble than that grown on calcite.

The situation with respect to dolomitization by sea water is then as follows. If clean crystals of calcite and dolomite are placed in sea water, at first the dolomite will grow at the expense of the calcite. Soon the overgrowth produced on the dolomite will have the same solubility as the calcite surface. Therefore, the two minerals can coexist, once their surfaces have come to a pseudoequilibrium with the sea water. Dolomite cannot dissolve, since the pure dolomite is less soluble than calcite. Dolomite cannot grow, since the precipitate on the dolomite would become more soluble than calcite or even more soluble than the overgrowth on calcite.

Experiment E3

Solubility of Carbonate Minerals in Sea Water

Using a procedure similar to that in experiment E2, we determined the solubilities of a number of carbonate materials in artificial sea water at 30°C. The results are summarized in Table 1. The change in pH of the water in passing through the pack as a function of the negative logarithm of the concentration product of calcium times carbonate is plotted in

⁴ $K'c = [\text{Ca}^{2+}] [\text{CO}_3^{2-}]$.
 $K'd = [\text{Ca}^{2+}] [\text{Mg}] [\text{CO}_3^{2-}]^2$.

These concentration products measured in sea water are, of course, much greater than the corresponding activity products because of the low values of the activity coefficients in sea water.

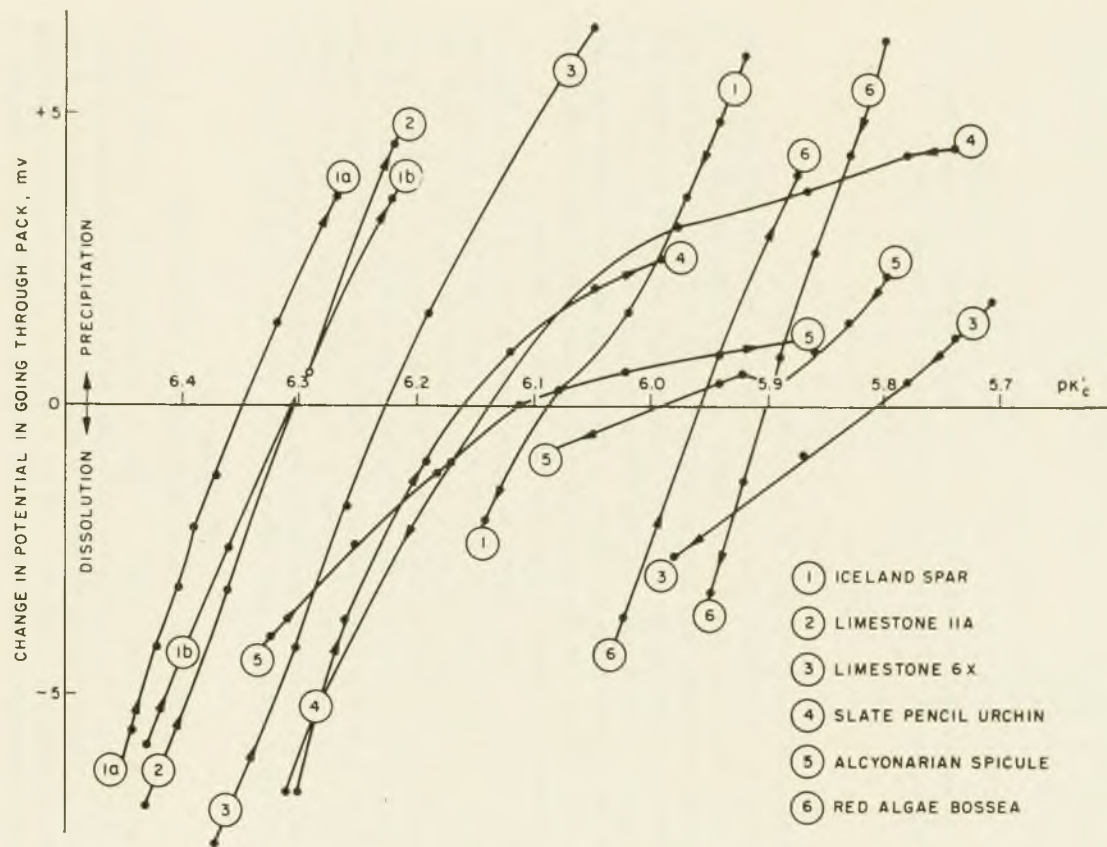


FIGURE 15. Solubility behavior of calcites in artificial sea water at 30°C.

Figures 15 and 16. In each case the apparent solubility after precipitation of an overgrowth is greater than that of the cleaned substrate.

TABLE 1
APPARENT SOLUBILITY OF CARBONATES IN SEA WATER AT 30°C

No.	Material	Mole % Mg	pK'c or ½ pK'd Clean Substrate After Overgrowth	
<i>Calcite</i>				
1	Iceland Spar	0.0	6.35, 6.30	6.09
2	Limestone 11 A	1.7	6.30	
3	Limestone 6x	1.8	6.22	5.81
4	Slate Pencil Urchin	9.4	6.16	6.14
5	Alcyonarian Spicule	12.6	6.11	6.00
6	Bossea	13.5	5.96	5.90
<i>Aragonite</i>				
7	Bahama Oolites		6.03	6.00
8	Mixed Carbonate Sand, Bonaire		6.07	5.83
<i>Dolomite</i> (Expt. E2)			6.03	5.57

$$pK'c = -\text{Log}_{10} [(Ca^{2+}) (CO_3^{2-})],$$

$$pK'd = -\text{Log}_{10} [(Ca^{2+}) (Mg^{2+}) (CO_3^{2-})^2]$$

(concentrations in moles/kg).

Experiment E4

The Solubility of Iceland Spar Calcite in Calcium Bicarbonate Solution

A number of solubility measurements were made with dilute calcium bicarbonate water having a concentration of 1 millimole per liter of calcium chloride and 1 millimole per liter of sodium bicarbonate. This water thus has an ionic strength of 4×10^{-3} mole per liter. The apparent dissociation constants for carbonic acid in this water at 30°C were determined. We found $pK'_1 = 6.30$ and $pK'_2 = 10.07$. The change in emf as this calcium bicarbonate solution flows through packs of Iceland spar was determined as a function of the pH of the water. From this pH and the analyzed content of total CO_2 in the water, the concentration of carbonate and calcium ion was determined for each flow experiment. Figure 17 is a plot of the change in emf produced against the negative logarithm of the concentration product of calcium carbonate $pK'c$. Three separate runs were made. Run Ca 6 is for the calcium water when it was initially made sufficiently acid to dissolve the calcite and its pH was then increased in steps by addition of sodium hydroxide. In run Ca 7 the water, sufficiently basic to precipitate calcium carbonate, was permitted to flow through the pack for a considerable length of time. The pH of the water was then reduced by adding HCl in steps until the water was sufficiently acid to dissolve the calcite. Run Ca 9 is similar to Ca 6, except that deaerated water

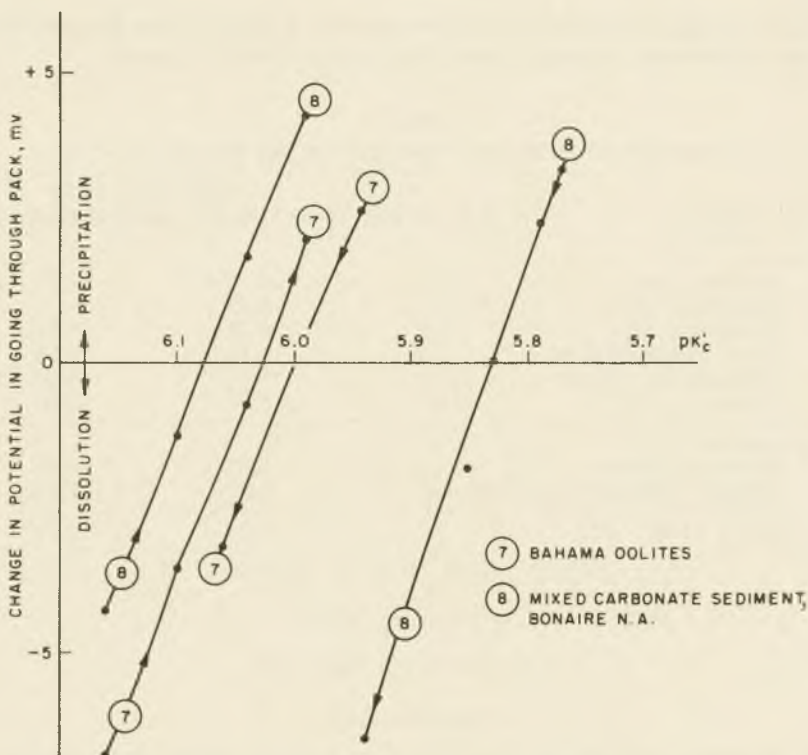


FIGURE 16. Solubility behavior of oolites and aragonitic sediments in artificial sea water at 30°C.

was used. At the calcium-times-carbonate concentration product where the lines cross the $\Delta\text{emf}=\text{zero}$ axis, the calcite is in solution equilibrium with the water. Assuming that the differences between the three experimental lines are due to experimental error, we find a value for the apparent solubility product of calcite in this water of $\text{pK}'_c = 8.07 \pm 0.02$. The error of ± 0.02 in pK'_c corresponds to an error in the absolute pH of approximately ± 0.02 . This uncertainty in the pH measurement is not unreasonable. To convert the apparent solubility product for calcite to the true solubility product, the calcium and carbonate concentrations must be changed to the respective activities. For the dilute solution used, it is assumed that the activities of the ions are functions only of the ionic strength and further that the Debye-Hückel approximate expression for the activity coefficient is applicable:

$$\text{Log } \gamma_1 = \frac{Az^2_1 \sqrt{\mu}}{1 + a^\circ B \sqrt{\mu}} \quad (1)$$

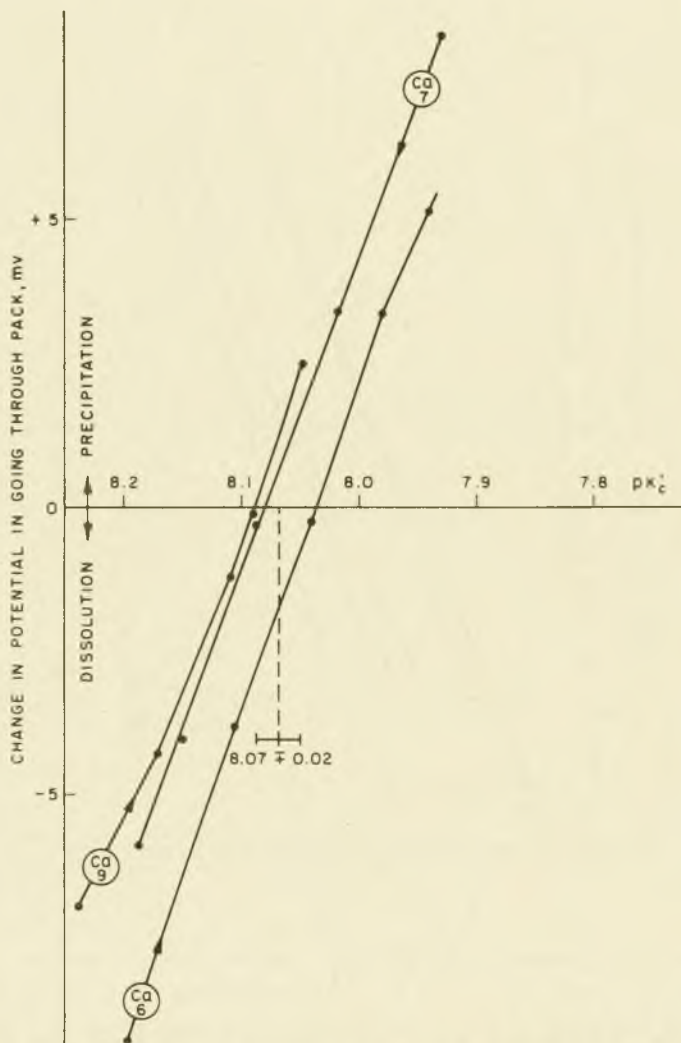


FIGURE 17. Solubility of Iceland spar calcite in dilute solution at 30°C.

At 30°C the coefficients A and B have the following values $A = 0.5130$ and $B = 0.3290 \times 10^8$. The parameter a° is equal to 4.5 and 6.0×10^{-8} for the carbonate and the calcium ions, respectively. To convert the negative log of the apparent solubility product to the negative log of the solubility product, the sum of the logarithms of the calcium and carbonate activity coefficients must be added. From equation (1) this sum at 30°C is given by

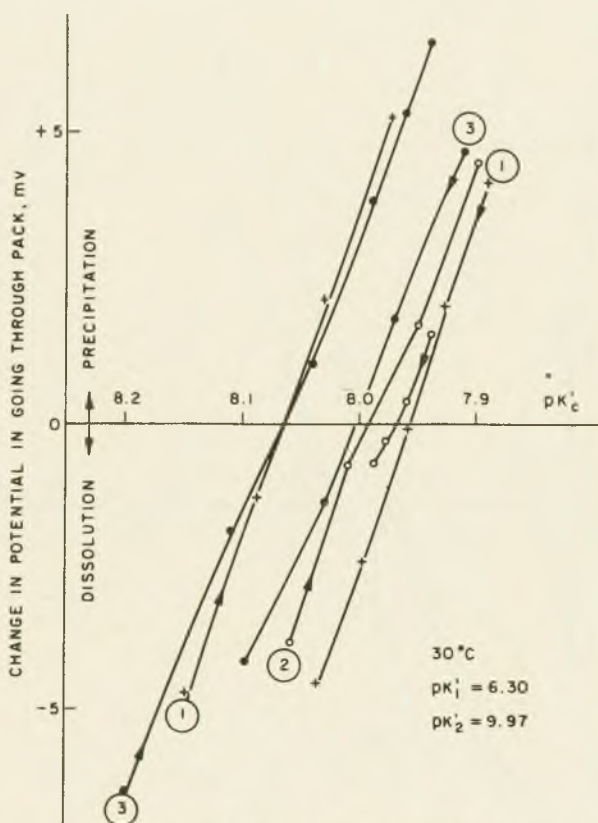


FIGURE 18. The solubility of Iceland spar in cave water.

$$\text{Log } \gamma_{\text{Ca}^{2+}} + \text{Log } \gamma_{\text{CO}_3^{2-}} = 2.052 \sqrt{\mu} \left(\frac{1}{1 + 1.48 \sqrt{\mu}} + \frac{1}{1 + 1.97 \sqrt{\mu}} \right). \quad (2)$$

At an ionic strength of 4×10^{-3} equation (2) gives 0.23; thus the corrected negative logarithm of the solubility product of calcite at 30°C is 8.30 ± 0.02 . This may be compared with a value of 8.40 listed by Garrels & Christ (1965, p. 89).

Experiment E5

Solubility of Iceland Spar Calcite in a Calcium-Magnesium Bicarbonate Solution

A series of solubility determinations were made in "artificial cave water." The cave water contained 1 millimole per liter each of calcium chloride, magnesium chloride, and sodium bicarbonate. At 30°C, the ap-

parent dissociation constants for carbonic acid in this water were determined to be $pK_1' = 6.30$, $pK_2' = 9.97$. The ionic strength of this water is 7×10^{-3} , and the sum of the logarithms of the activity coefficients of calcium and carbonate ions is -0.30 .

Figure 18 shows the solution behavior of Iceland spar calcite in this water. For runs 1 and 3, starting with a clean surface, we find an apparent solubility product for calcium carbonate $pK'c$ of 8.065 ± 0.005 . On the other hand, if equilibrium is approached after an overgrowth has been precipitated, a larger solubility, $pK'c = 7.98 \pm 0.02$, is obtained. In run 2 it appears that the original surface had not been sufficiently cleaned by dissolution. This experiment suggests that even in this dilute calcium-magnesium bicarbonate solution, the overgrowth is significantly more soluble than the substrate. In cave water without magnesium (experiment E4), on the other hand, the solubility behavior appeared reversible within the accuracy of the experiment. Correcting for the activity coefficients of calcium carbonate in this solution, we obtain a solubility product for pure calcite of 8.37 ± 0.2 . This differs by 0.07 from the solubility product obtained in the calcium bicarbonate solution (experiment E4). This difference is probably outside the experimental error and may be due either to the fact that the activity coefficients calculated from the Debye-Hückel approximation are not sufficiently accurate or to the fact that in the three measurements in the calcium bicarbonate solution the surface of the Iceland spar may not have been sufficiently clean. This point should be checked by an independent redetermination of the solubility of Iceland spar in the calcium bicarbonate solution, since the value there obtained depended on only three measurements. If the present results are confirmed by further measurements, they indicate that the presence of 1 millimole per kilogram of magnesium in the water can significantly increase the solubility of calcite precipitated from that water. This increase corresponds to an increase in the solubility product of approximately 12 per cent.

Experiment E6

Solubility of Magnesian Calcites in Calcium-Magnesium Bicarbonate Solution

Using the same water as in experiment E4, we determined the solution behavior of a number of magnesian calcites. The results are shown in Figure 19 and are summarized in Table 2. The results obtained do not show any simple relationship between the magnesium content of the calcite and its solubility behavior. The experiments should be repeated in order to determine the reproducibility of the results. The extremely high apparent solubility of the red alga *Bossea* is particularly interesting. Although it does not contain much more magnesium than the Alcyonarian spicule, its apparent solubility product is twice as large. In attempts to measure the solubility of the red alga *Goniolithon*, it was not possible to make the sea

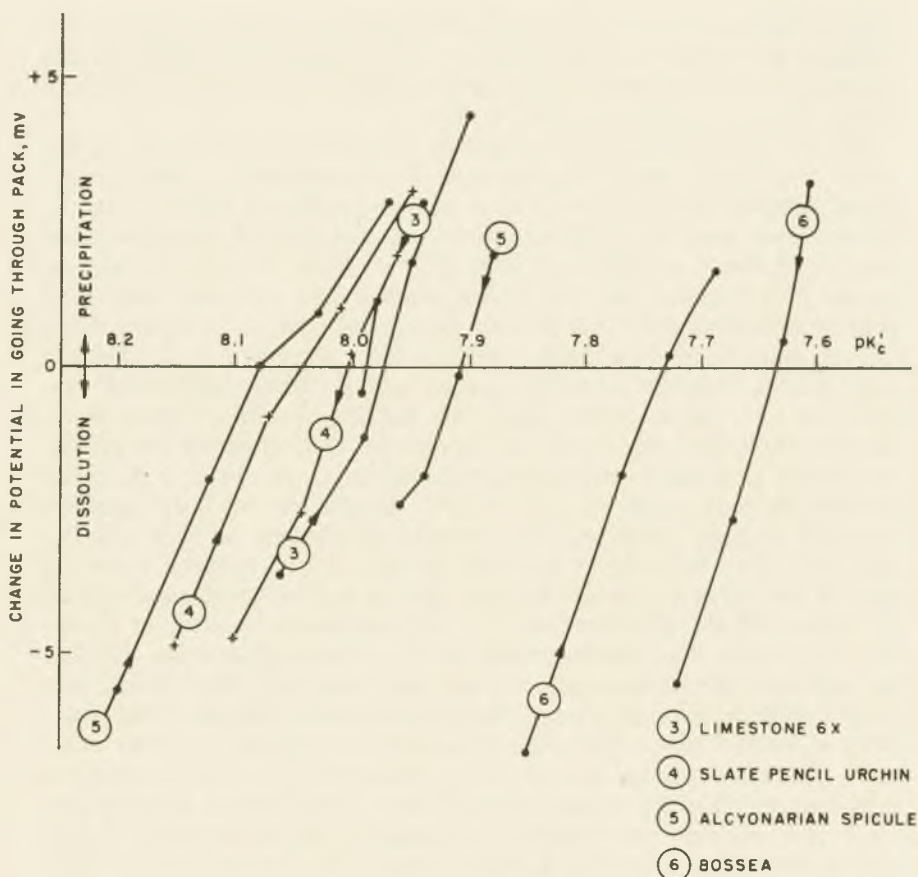


FIGURE 19. The solubility of magnesian calcites in calcium-magnesium bicarbonate solutions at 30°C.

water sufficiently basic to lead to precipitation on this red alga. Before the point of apparent precipitation was reached, spontaneous nucleation in the water led to the precipitation of aragonite throughout the water volume.

Subsequent investigations reported by Schmalz (1965) showed that the red alga *Goniolithon* contains a significant amount of hydroxide ion. Preliminary nuclear magnetic resonance experiments also indicate that hydroxide ion is present in the red alga *Bossea*. It now becomes important to investigate the various carbonate minerals and organically derived carbonates for the presence of hydroxide in the crystal lattice. This investigation is required before the apparent solubility results described above can be relied upon, for in our solubility calculations based on the saturo-

TABLE 2
SOLUBILITY OF CALCITES IN Ca^{2+} , Mg^{2+} - HCO_3^- SOLUTION

No.	Material	Mole % Mg^{2+} *	Fresh pK'_c	Precipitation
1	Iceland Spar (Expt. E5)	0	8.07	7.98
3	Limestone 6x	1.8	7.97	7.985
4	Slate Pencil Sea Urchin	9.4	8.04	8.01
5	Alcyonarian Spicule	12.6	8.07	7.90
6	Bossea	13.5	7.73	7.63

*Determined by X-ray diffraction.

meter flow type experiment, we implicitly assume that all that happens in the pack is either dissolution or precipitation of carbonates. Any recrystallization of hydroxide to a carbonate will lead to erroneous results.

Experiment E7
*Solubility of Aragonite in Calcium-
Magnesium Bicarbonate Solution*

The solubility of three different aragonites was measured in water which contained 1 millimole each of calcium chloride, magnesium chloride, and sodium bicarbonate. The materials used were the aragonite of a ground-up brain coral, large aragonite crystals from Aragon, Spain, and Bahama oolites. The results of the solubility measurements are shown in Figure 20 and are summarized in Table 3.

TABLE 3
SOLUBILITY OF ARAGONITES IN Ca^{2+} , Mg^{2+} - HCO_3^- SOLUTION

No.	Material	Fresh pK'_A	Precipitation
1	A ₁ Brain Coral	7.82	7.79
2	A ₂ Large Crystals (Aragon, Spain)	7.98	7.86
3	Oolites	7.79	7.87

These data confirm that the solubility of the aragonites at 30°C and 1 Atmosphere is greater than that of Iceland spar calcite. (Garrels & Christ, 1965, p. 376.)

Experiment E8
*Solubility of Dolomites in Calcium and
Magnesium Bicarbonate Solutions*

A number of flow saturometer solubility determinations of different dolomites were made. The first experiments were carried out in solutions

containing 1 millimole per liter each of calcium chloride, magnesium chloride, and sodium bicarbonate. Although there were considerable differences between the individual dolomite determinations, the over-all behavior was not too dissimilar from that of calcite. In order to make it easier to compare the measurements on dolomite with those on calcite, the solution behavior of the dolomite was plotted against the negative logarithm of the product of the carbonate concentration multiplied by the square root of the product of the calcium and magnesium concentration. This concentration product thus corresponds to the square root of the concentration product for dolomite. The square root of the dolomite concentration product obtained in these measurements was of the same order of magnitude as the solubility product for calcite.

The flow saturometer measurement indicates only whether carbonate is dissolving or precipitating. There is no direct information about which carbonate phase is actually precipitating. When a particular material is being dissolved, its identity is, of course, known from prior analysis. It has been argued that if the solution's behavior follows a smooth trend from the

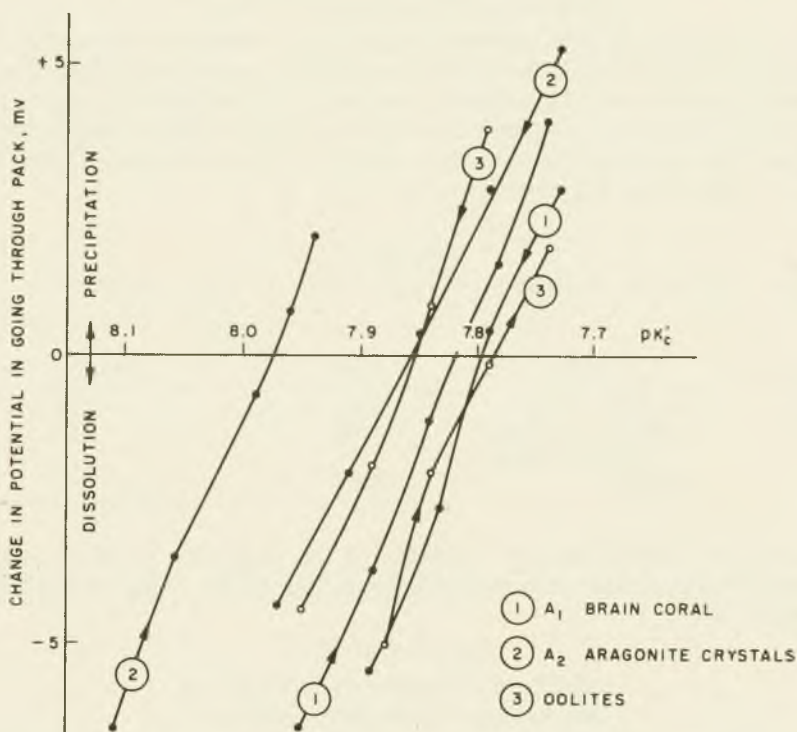


FIGURE 20. The solubility of aragonites in calcium-magnesium bicarbonate solutions at 30°C.

dissolution side through zero toward precipitation, the precipitating phase should be the same as or at least similar to the dissolving phase. This continuity argument was used to suggest that the solubility of dolomite was indeed being measured in the dolomite flow experiments. To confirm this, a number of solubility measurements of dolomite in water containing 1 millimole per liter each of calcium chloride and sodium bicarbonate but no magnesium were made. Obviously, no dolomite could be precipitated from this essentially magnesium-free water. It was expected that the solubility curves for dolomite in this water would be very different from those in water containing both calcium and magnesium. However, the results obtained with this magnesium-free water were quite similar to those obtained in water containing magnesium. Thus, the similarity argument given above was shown to be invalid. In these experiments five different dolomites were utilized. Their properties are given in Table 4.

TABLE 4
PROPERTIES OF DOLOMITES*

Designation	% Calcite	Mole % Mg in Calcite	Mole % Mg in Dolomite
1	≈5	2.7	49.5
2	≈1	0	49.4
5	0	—	50.5
6	Trace	—	44.0
7	Trace	—	45.2

*As determined by X-ray diffraction.

The solubility data for the dolomites in the calcium-magnesium bicarbonate solution are shown in Figure 21 and are summarized in Table 5.

The apparent solubility data for various dolomites in water containing 1 millimole each of calcium chloride and sodium bicarbonate are shown in Figure 22. Since for this water the magnesium concentration is essentially zero, the satrometer response was plotted against the negative logarithm of the product of the calcium and carbonate concentration. The data are summarized in Table 6. For comparison, the negative logarithm of the calcium carbonate concentration product for Iceland spar was 8.07 ± 0.02 . The results of a number of the measurements made with dolomite are very close to this figure.

INTERPRETATION OF THE EXPERIMENTAL RESULTS

The complete implications of the experimental data presented in the preceding sections are not obvious. The usual procedure in measuring solubilities is to contact some solid with a solution and stir the two together until the composition of the solution does not change, i. e., until equilibrium has been reached. The determination of the point at

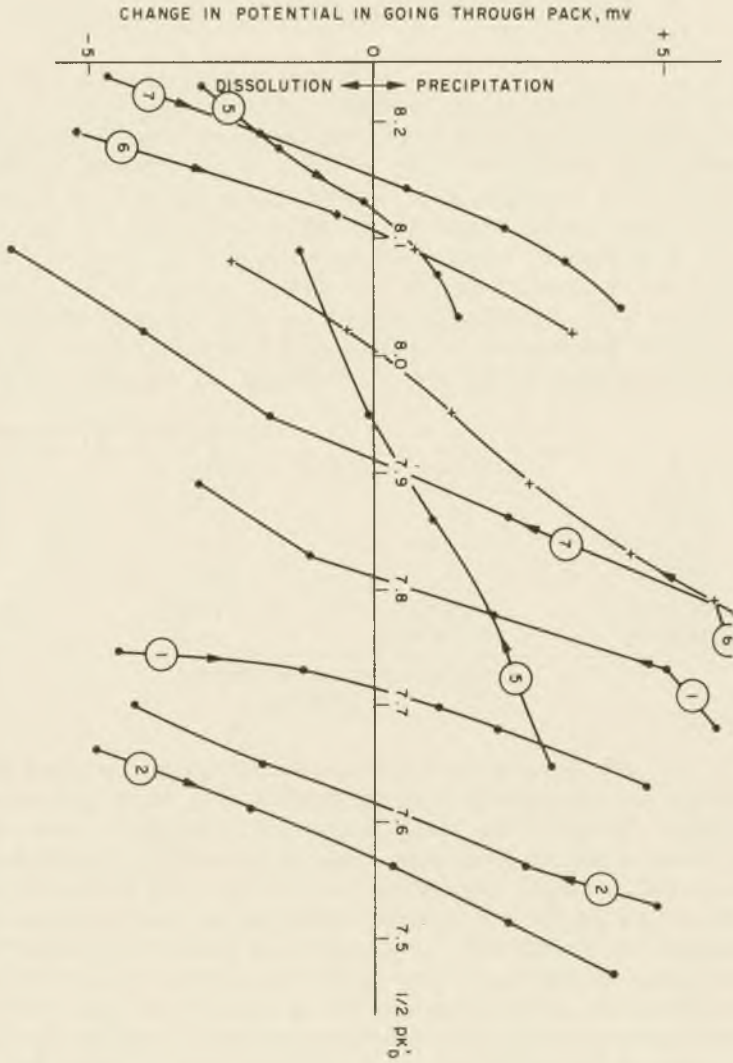


FIGURE 21. The solubility of dolomites in calcium-magnesium bicarbonate solutions at 30°C.

TABLE 5
APPARENT SOLUBILITY OF DOLOMITE IN Ca^{2+} , Mg^{2+} , HCO_3^- SOLUTION

Material	Fresh	$\frac{1}{2} \text{ pK'd}$	Precipitation
1	7.71		7.80
2	7.57		7.62
5	8.12		7.94
6	8.11		8.00
7	8.15		7.90

$$\frac{1}{2} \text{ pK'd} = -\text{Log}_{10} (\text{CO}_3^{2-}) \sqrt{(\text{Ca}^{2+}) (\text{Mg}^{2+})}$$

TABLE 6
APPARENT SOLUBILITY OF DOLOMITE IN Ca^{2+} , HCO_3^- SOLUTION

Material	Fresh	pK'c	Precipitation
1	8.07		8.12
2	7.92		7.96
5	7.96		7.79
6	8.07		8.07
7	8.07		8.09
Iceland Spar (Expt. E4)	8.07 ± 0.02		

$$\text{pK'c} = -\text{Log}_{10} (\text{CO}_3^{2-}) (\text{Ca}^{2+})$$

which the solution does not change depends on the patience of the experimenter and the precision of his chemical analyses. As long as only one measurement is made for each solution under given conditions, a set of consistent solubility data is obtained. Unfortunately, different people have measured the solubility of calcium carbonate in sea water and have obtained different results. The results reported here suggest that the solubility measured in the presence of impurities can have any value within rather wide limits.

The difficulty arises from asking the wrong question of nature. One should not ask "What is the solubility of calcite in sea water?" until it has been established that there exists a unique solubility for the particular solution-solid system. In order that a solution be in thermodynamic equilibrium with a solid phase, the same phase must dissolve and precipitate from the solution. A solid phase is a solid whose composition and properties are uniform throughout. The solution contacts only the outer layer of the solid and is indifferent to its interior. It is the interior that has been characterized by chemical and X-ray diffraction analyses. The experimental results presented above, except possibly for experiment E4, clearly show from the irreversibility of the solution behavior that the precipitate on

the solid differs from the substrate and thus that the outer portion of the solid is not a homogeneous phase.

Solubility studies are handicapped by the fact that no methods are available to investigate the surface "seen" by the solution other than studying the solution behavior itself. If a method were available for examining in detail the outer atomic layer of the solid, it would probably require working in a vacuum so that the soft rays or particles needed for the study could be scattered by the solid surface. Transferring the solid from the solution into the vacuum chamber would destroy the surface of interest. If the adhering solution is permitted to dry on the surface, a new surface will be created, and if the solid is washed in distilled water, the surface layer will be removed.

That the results documented in these experiments are real and not due to poor experimental technique is demonstrated convincingly by the geologic evidence. Almost every handful of carbonate sediments picked up at a beach contains more phases than are permitted by the phase rule. According to this rule, if the system is in equilibrium, there should be only one or at most two carbonate phases, while actually an abundance of different minerals including aragonite, dolomite, and calcites of different magnesium contents is found. The number of phases detected is limited mainly by the care of the analyses. These phases coexist even after deposition. In spite of the fact that they are an intimate mixture of sand size particles whose pore space is filled with interstitial sea water, they show no decrease in the number of phases present over the few thousand years of the Recent record. Only when the sediments become subaerially exposed to the action of fresh water is significant diagenesis evident on a thousand-year time scale.

Magnesium ion has a strong effect on the solution kinetics of calcite (experiment B), and calcite behaves reversibly in a calcium bicarbonate solution (experiment E4), but the addition of magnesium ion, even in small concentrations, leads to irreversibility (experiment E5). This suggests that magnesium ion may be incorporated into the precipitated carbonate, which leads to an increase in solubility. It is therefore of interest to develop a theory of solubility that incorporates the effect of the inclusion on an impurity. Such a theory is presented in the Appendix. The theory is based on the simplest kind of model involving only nearest-neighbor interactions.

The theoretical example shown in Figure 28 (in Appendix) shows how the solubility of the originally pure material increases owing to the precipitation of an impure overgrowth. Adjustment to higher solubility takes place as a few atomic layers are precipitated. Experiment C showed a similar increase in solubility with overgrowth, except that about ten times as many atomic layers are required to adjust the solubility. It is clear that the theory must overestimate the rate of solubility adjustment, since

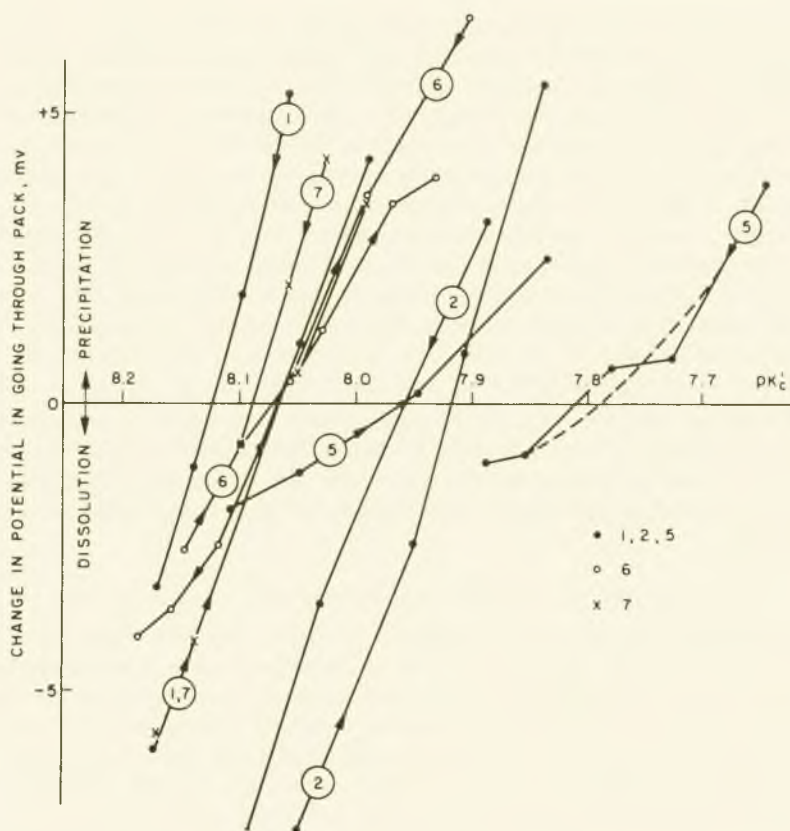


FIGURE 22. Solubility behavior of dolomites in calcium bicarbonate solutions at 30°C.

in an actual crystal, the interionic forces will act over a number of lattice sites.

The theory suggests that the solubility of the precipitate can either increase indefinitely or approach an upper bound, depending on the parameters. The experiments in sea water (experiments E2 and E3) suggest that the solubility product can increase by a factor of about three. These experiments, however, were not designed to determine the upper limit on the solubility increase. Experiment E1, in which calcite and dolomite were exposed to highly supersaturated solutions for a considerable time, suggests that the range over which the solubility product can adjust is about 3 and 10 for calcite and dolomite, respectively.

Magnesium incorporation into the crystal lattice may not be the only factor leading to increased solubility. Other types of lattice defects caused

by a rapid rate of precipitation may also be important. The field and laboratory experiments on the aragonitic oolites (experiments C and D) suggest that when the material is exposed to sea water, precipitation is at first rapid, but soon the overgrowth comes almost to equilibrium with the sea water by becoming more soluble. When allowed to stand in its interstitial solution, the precipitate is apparently cleaned up, possibly by diffusion in the surface layers of the crystal and when it is re-exposed to fresh sea water, the cycle starts over again. Figure 16 shows that the solution behavior of oolites in sea water is more reversible than that of any other carbonate investigated. If the change in solubility is due mainly to an inclusion of magnesium ions, the rapid cleanup of the oolite overgrowth may be due to the fact that the magnesium ion does not fit so well into the aragonite lattice as into the calcite one.

In summarizing the behavior of carbonates in sea water as revealed by the data presented here, it is best to distinguish three environments—the carbonate particle suspended in sea water, the carbonate particle in a marine sediment, and finally the particle at the sediment—sea water interface.

1. THE CARBONATE PARTICLE SUSPENDED IN SEA WATER

If the carbonate particle is suspended in surface sea water, precipitation will occur and will be rapid at first for aragonite or a low-magnesium calcite. As the overgrowth forms, it will gradually become more soluble, and the rate of precipitation will decrease rapidly (experiment C). After between ten and a hundred atomic layers have been deposited, a steady state will be reached. In tropical surface waters this steady state will be one of slow continued precipitation. The data from Figure 6 suggest that for 40- to 50-mesh particles this rate is 40, 27, and 13 milligrams of precipitate per gram of sediment per year for a substrate of calcite, oolites, or dolomite, respectively. For sand size particles, only repeated suspension—for example, on tidal bars—can lead to a visible precipitate. As the particle sinks, it will be exposed to waters of progressively lower carbonate concentration, and the solubility will increase owing to the effect of hydrostatic pressure. The decrease in carbonate concentration is due to the addition of carbon dioxide by respiration below the euphotic zone, which results in a decrease in pH. The effect of hydrostatic pressure on the apparent solubility of oolites has been studied recently by Pytkowicz & Connors (1964).

As the particle sinks into waters of lower supersaturation, the rate of precipitation will decrease and finally stop, once the overgrowth is able to come to equilibrium with the surrounding sea water. Upon further sinking, the overgrowth will readjust itself to remain in equilibrium with the surrounding water. During this readjustment there will be some dissolution, however, because only a few hundred atomic layers may be in-

volved the amount of etching will not in general be apparent under the optical microscope.

Eventually, the carbonate concentration of the surrounding water will fall below the level at which it can be in equilibrium with the least soluble calcium carbonate surface. Further dissolution will now proceed rapidly. Sediment data from the Atlantic Ocean suggest that this condition is reached at a depth of about 4 kilometers. Above this level carbonate tests are preserved in the sediment without evidence of precipitation or dissolution, whereas at greater depth the carbonate content of the sediments drops off rapidly, and the tests preserved show evidence of dissolution.

2. THE CARBONATE PARTICLE IN THE SEDIMENT

Once the particle is incorporated into the sediment, the surface layer of the grain adjusts itself to its environment. In shallow tropical waters, the carbonate concentration of the interstitial water will be reduced below that of the overlying sea water as all the carbonate phases present adjust their surfaces. That the diverse mineral aggregate will persist for times of the order of at least several thousand years is demonstrated by the Recent shallow-water carbonate sediments. For example, the fact that sand size grains of dolomite can survive transport in marine lime sediments without the dolomite being replaced or the other carbonates being dolomitized was documented by Taft (1961) and Deffeyes & Martin (1962). Taft claimed that he had found Recent dolomite formed in the sediments of Florida Bay. Deffeyes and Martin showed that this dolomite was dead to radiocarbon and therefore was older than 35,000 years, although marine sedimentation in Florida Bay started only 3000 to 4000 years ago. Thus, the detrital grains of dolomite of 20- to 70-micron size survived transport in sea water and mixing with other carbonate phases without diagenesis. At the same time the water did not form new dolomite. Although the average time the dolomite rhombs spent in the marine environment is not known, times of the order of a few thousand years are indicated.

Eventually, the mixture of phases in water-filled sediments alters to low-magnesium calcite and dolomite. Exposure to fresh water results in rapid conversion. In the case of sea-water-filled sediments, it is not clear whether diagenesis merely requires times of the order of millions of years or whether a combination of time, elevated temperature due to burial, and hydrostatic pressure is responsible for the recrystallization. Because of the extremely low rates of diagenesis, it is impossible to study these processes realistically in the laboratory. The preservation of unrecrystallized aragonite shells of Pennsylvanian age imbedded in tar, reported by Lowenstam (1964), suggests that in addition to time, temperature, and pressure, exposure to an aqueous phase may be necessary for recrystallization.

3. THE CARBONATE PARTICLE AT THE SEDIMENT—SEA WATER INTERFACE

At the sediment-sea water interface, the carbonate particle is exposed

to the overlying sea water for times which depend on the rate of sedimentation and on the rate of redistribution of the sediment by physical forces and the burrowing action of the bottom fauna. Because of the possible existence of a diffusion layer in contact with the sediment, the rate of alteration will be slower than in environment 1. If there is a hiatus in deposition in shallow tropical waters, the sediment may become cemented, probably by aragonite, into a coherent sheet. Such cementation has been observed on the Bahama Banks (cementation of oolites into grapestones) and in the Persian Gulf. The rates of precipitation observed in experiment C suggest that times between 10 and 100 years are required.

For sediments below 4 kilometers, dissolution of carbonate at the sediment-water interface may become important. In this connection it is interesting to estimate the relative importance of dissolution on the bottom and dissolution which occurs as the particle falls through the sea water column. For a spherical calcite particle of radius r cm having 40 per cent interparticle and 26 per cent intraparticle porosity and a sedimentation rate of 3 cm/thousand years, we obtain the following values:

Time to sink 1 km: $10 r^{-2}$ second.

Number sinking per cm^2 in a 1-kilometer column: $1.4 \times 10^{-10} r^{-5}$ particle.

Total surface area in volume 1 cm^2 by 1 km deep: $1.8 \times 10^{-9} r^{-3} \text{ cm}^2$.

Radius in order that surface area of particles falling in km equals area on bottom: $r = 12$ microns.

Thus, for the above assumptions, particles larger than 12 microns, if they fall through 1 km of undersaturated water, will have more exposure to that water on the bottom, whereas smaller particles will be more likely to dissolve during the fall.

ACKNOWLEDGMENTS

The work described here was carried out over a number of years while the author was at Shell Development Company's Exploration and Production Research Division, Houston, Texas. The help of T. J. Robichaux, D. C. Berkshire, O. L. Jolly, H. Lord, and G. G. Hayes in carrying out the experimental program is gratefully acknowledged. The cooperation of R. N. Ginsburg and his Florida group made the field observations in the Bahamas possible. A cruise on the Texas A. and M. research vessel HIDALGO, under the scientific direction of Dr. D. W. Hood, gave me an early exposure to the complexities of the sea water-carbonate problem. I am grateful to my numerous geological, chemical, and physical colleagues at Shell for many stimulating and sometimes heated discussions. Of particular help were the many suggestions by K. S. Deffeyes, F. J. Lucia, R. C. Murray, and M. H. Waxman. The support and encouragement by J. T. Smith and W. R. Purcell made the research possible.

APPENDIX

A SIMPLE THEORY OF THE SOLUBILITY OF IMPURE SOLIDS

INTRODUCTION

In the body of this report, results of studies of the solution behavior of carbonate minerals were described. As the techniques of measurement improved, and as more data were accumulated, the results became more puzzling. It became apparent that the solubility of calcite and magnesian calcites in water such as sea water depended not only on the temperature and pressure of the water but also on the past solution history of the solid material. The usual physical-chemical solution theory was inadequate as a basis for predicting the behavior of carbonate in laboratory experiments as well as in the Recent geologic environment.

To give direction to the experimental work and to make trial geologic predictions, it became imperative to develop a new theory. In developing such a theory, one must start with as simple a model as possible and then gradually attempt to refine it. Past experimental work has suggested that the magnesium ion plays a very important part in the solution behavior of calcite and that the solubility of calcites is strongly affected by their magnesium content. Furthermore, the solution behavior of calcites appears to be considerably more complex in waters containing magnesium than in waters that do not contain that ion. As the first step, then, we wish to formulate a solution theory of calcite assuming that its solubility is affected exclusively by the magnesium that may be incorporated into the calcite lattice. Although we realize that this assumption is a simplification, our experiments do suggest that, at least in waters such as sea water, the effect of magnesium is dominant. Before proceeding to the solubility model for the impure substance, however, let us first consider the simpler case of the pure substance.

THE SOLUBILITY OF THE PURE CRYSTAL

The solubility model which we shall develop is based on the model for crystal growths proposed by Burton & Cabrera (1949). Let us consider the simplest possible type of crystal lattice—a crystal made up of a simple cubic packing of identical cubes. Each cube represents a molecule of the crystal, and we assume that the process of solution occurs by the removal of single molecules from the crystal surface into the solution. The interaction between the crystal and the solution will be restricted to the surface of the crystal. It thus becomes important to consider the morphology of that surface in some detail. Consider a (100) surface on such a simple cubic crystal. This will consist of a series of steps having (100) surfaces. Because of thermal agitation of the crystal, these steps will not be straight lines but will contain irregularities. These are of three types—kinks, adsorbed molecules, and vacancies.

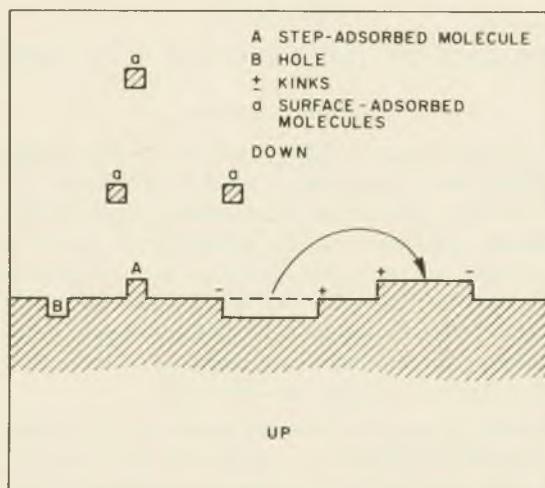


FIGURE 23. Type of defects along step on crystal surface (after Burton and Cabrera, 1949).

The Step on the Crystal Surface.—Let us now consider the step on the crystal surface in more detail. Figure 23 is a plan view of an infinite step on a (100) plane of the crystal surface. The various types of imperfections are indicated. To discuss the energetics of these imperfections, we shall assume the following model for the bonding of our cubic crystal. Assume that each cube is affected only by its nearest neighbors and that per cube face in contact there is a certain binding energy. Assume further that these energies are equal for all faces and that the total binding energy is the sum of the individual binding energies. In order to form one step-adsorbed molecule (A) and a hole (B) (see Figure 23), we must break two bonds. Therefore, the energy per hole or per adsorbed molecule is equal to E . Now let us remove a series of adjoining cubes from one part of the step and attach them to another position along the step. By doing this, we produce four kinks—two negative ones in which the step retreats, and two positive ones in which the step advances. To form these four kinks, we had to break two bonds at the extremity of the row of cubes. The energy per kink is $E/2$; hence, the probability of having a kink at a particular location along the step is $\exp(-E/2 kT)$.

A cube at a kink has three bonds with the crystal. By adding an extra cube to the kink, we add a total of three bonds for the added cube and three for the cubes previously in the crystal. Since the number of bonds for a cube internal to the crystal is six, we can build up the crystal by adding cubes always at the kink edge. Similarly, we can dissolve the crystal by removing cubes at the kink.

Solubility Relations.—Let us now consider an ideal cubic crystal in equilibrium with a solution. The surface of the crystal contains a number of steps along which there is a certain density of kinks determined by the absolute temperature and the bond energy. In addition, there is a concentration of the cubes distributed through the solvent. A number of cubes are adsorbed on the flat crystal surface. Since the surface-adsorbed atoms share one bond with the crystal, the heat of adsorption is E . In addition, there will be a number of holes and step-adsorbed molecules. There is always a flux of cubes from the solution to states on the crystal surface and a flux from the crystal surface back to the solution. At equilibrium these two fluxes must be equal. If the steps on the crystal surface are separated by many lattice sites, then solute cubes going from the solution to the solid surface will generally be intercepted by the flat crystal surface rather than by the steps. At equilibrium the concentration of these surface-adsorbed molecules will be constant. The equilibrium results from the equality of the two fluxes given by the following expressions:

1) The rate of arrival of solute molecules from the solution to the adsorbed solid surface. The number of molecules arriving on the crystal surface from the solution per square centimeter per second is equal to $1/6 c_1 \bar{v}$, where c_1 is the concentration of solute molecules per cubic centimeter of the solution, and \bar{v} is the average velocity of the solute molecule in the solution in centimeters per second.

2) The rate of escape of surface-adsorbed molecules from the solid to the solution. The rate of escape of surface-adsorbed molecules from the solid to the solution per square centimeter per second is equal to $c_2 \nu \exp(-E/kT)$, where c_2 is the density of adsorbed molecules on the crystal surface, ν is a characteristic frequency, and E is the energy per bond.

At equilibrium, then, these two rates must be equal, and we obtain the following expression for the density of adsorbed molecules on the surface:

$$c_2 = \frac{c_1 \bar{v}}{6\nu} \exp\left(\frac{E}{kT}\right). \quad (1)$$

The surface-adsorbed molecules will diffuse over the crystal surface by jumping from lattice site to lattice site. When they are intercepted by a step on the crystal surface, they may become adsorbed by that step and be incorporated into it. Similarly, the molecules at the kink on a step may leave the step for the surface-adsorbed state. Again, at equilibrium these two rates must be equal. For a molecule to leave the kink and move to a surface-adsorbed position, two bonds must be broken, and an energy $2E$ must be expended. At equilibrium the probability of finding an adsorbed molecule at a specific lattice site will therefore be $\exp(-(2E/kT))$. Let a be the lattice spacing. On the surface we then have $1/a^2$ lattice sites per square centimeter. The number of surface-adsorbed molecules per square centimeter c_2 is therefore

$$c_2 = \frac{1}{a^2} \exp \left(- \frac{2E}{kT} \right) \quad (2)$$

By using equation (1), we can now eliminate c_2 from equation (2) and obtain the following relationship for the equilibrium concentration of molecules in the solution:

$$c_1 = \frac{6v}{\bar{v}_a^2} \exp \left(- \frac{3E}{kT} \right) \quad (3)$$

Equation (3) then relates the solubility of the crystal to the heat of solution $3E$ and to the other parameters of the solution and the crystal lattice. We now wish to investigate how the solubility of the crystal will be altered if an impurity is incorporated into the crystal.

THE SOLUBILITY OF THE IMPURE CRYSTAL

So far we have reviewed the theory of Burton & Cabrera (1949) on the solubility of a pure crystal. Now we must investigate how that theory has to be altered if an impurity is incorporated into the crystal. Let the molecules of the pure crystal be of type a . We wish to know what happens if we incorporate molecules of type b into the crystal lattice. The pure crystal has bonds only between molecules a and a . Let the energy of this bond be E_{aa} . When we introduce the impurity b into the crystal, we in addition have bonds between molecules a and b . Let the energy of this bond be E_{ab} . If the crystal should discriminate against the impurity, then the energy E_{ab} will be less than the bonding energy E_a . In addition, we have bonds between impurity molecules b - b . Let the energy of this bond be E_{bb} . Let the concentration of the a molecules in the solution be c_1 . Let the ratio of the impurity molecules to the pure solute molecules be b ; thus, the concentration of type b molecules in the solution is bc_1 . The molecules that happen to be at the kink on the surface step of the crystal can now find themselves in different environments. We can have either a molecule a or a molecule b at the kink, and of its three nearest neighbors, none, one, two, or all three may be of type b . The binding energy for the molecule at the kink will now depend on its molecular environment.

The solubility relation (equation 3) must be generalized to

$$c_1 = \frac{6v}{\bar{v}_a^2} \sum_{i=0}^3 p_{ai} \exp - \frac{E_{ai}}{kT} \quad (4)$$

In this equation \bar{v}_a is the average velocity of molecules of type a in the solution. Let i be the number of nearest neighbors to the molecule at the kink that are of type b . p_{ai} is then the probability that the molecule at the kink is of type a and that it has i nearest neighbors of type b . E_{ai} is the

binding energy of the kink molecule if the molecule at the kink is type a and has i nearest neighbors of type b . To obtain the solubility, one must then sum over the four possibilities.

In a similar way, we obtain an expression for the concentration of b molecules in the solution:

$$bc_1 = \frac{6\nu}{\bar{v}_b a^2} \sum_{i=0}^3 p_{bi} \exp - \frac{E_{bi}}{kT} \quad (5)$$

The symbols used here are similar to the ones in equation (4). For instance, p_{bi} is the probability that the molecule at the kink is of type b and has i nearest neighbors of type b .

We can now combine equations (3), (4), and (5) to obtain new relationships that do not contain the frequency ν and the lattice spacing a .

By dividing equation (4) by equation (3), we obtain the ratio of the solubility of the impure crystal in the impure solution to the solubility of the pure crystal in the pure solution. Let us call this relative concentration c^* . We then obtain

$$\frac{c_1}{c_1(b=0)} = c^* = \frac{\sum_{i=0}^3 p_{ai} \exp - \frac{E_{ai}}{kT}}{\exp - \frac{3E_{aa}}{kT}} = \sum_{i=0}^3 p_{ai} \exp \frac{3E_{aa} - E_{ai}}{kT} \quad (6)$$

Next let us divide equation (5) by equation (4), which gives equation (7):

$$\frac{\bar{v}_b}{\bar{v}_a} = b^* = \frac{\sum_{i=0}^3 p_{bi} \exp - \frac{E_{bi}}{kT}}{\sum_{i=0}^3 p_{ai} \exp - \frac{E_{ai}}{kT}} = \exp \frac{3(E_{aa} - E_{ab})}{kT} \frac{\sum_{i=0}^3 p_{bi} \exp \frac{3E_{ab} - E_{bi}}{kT}}{\sum_{i=0}^3 p_{ai} \exp \frac{3E_{aa} - E_{ai}}{kT}} \quad (7)$$

Here it is convenient to introduce an effective ratio of the concentration of molecules of type b to type a , b^* , which is equal to the actual ratio of the molecules multiplied by the ratio of the average velocity of molecule b to that of molecule a in a solution.

The binding energy of the molecules at the kink for the various configurations is tabulated in Table 7.

It is now convenient to introduce parameters α and β defined by equations (8) and (9), respectively.

TABLE 7
BINDING ENERGY FOR VARIOUS STATES

Neighbors of Type <i>b</i> (<i>i</i>)	Molecule at Kink Is <i>a</i> (E_{ai})	Molecule at Kink Is <i>b</i> (E_{bi})
0	$E_{a0} = 3E_{aa}$	$E_{b0} = 3E_{ab}$
1	$E_{a1} = 2E_{aa} + E_{ab}$	$E_{b1} = 2E_{ab} + E_{bb}$
2	$E_{a2} = E_{aa} + 2E_{ab}$	$E_{b2} = E_{ab} + 2E_{bb}$
3	$E_{a3} = 3E_{ab}$	$E_{b3} = 3E_{bb}$
<i>i</i>	$3E_{aa} - E_{ai} = i(E_{aa} - E_{ab})$	$3E_{ab} - E_{bi} = i(E_{ab} - E_{bb})$

$$\alpha \equiv \exp \frac{(E_{aa} - E_{ab})}{kT} - 1, \quad (8)$$

$$\beta \equiv \exp \frac{(E_{ab} - E_{bb})}{kT} - 1. \quad (9)$$

If the crystal discriminates against the impurity, then the binding energy for an unlike bond will be weaker than the binding energy for like bonds.

If $E_{aa} > E_{ab}$, then $\alpha > 0$.

If $E_{bb} > E_{ab}$, then $0 > \beta > -1$.

Next let us consider the probabilities p_{ai} and p_{bi} . They are products of probabilities that the molecule at the kink is either *a* or *b* multiplied by the probability that the molecule at the kink has 0, 1, 2, or 3 neighbors of type *b*. Let the fraction of molecules along the step on the crystal surface that is of type *b* be *x*. In this case the probability that the molecule at the kink is of type *a* will be equal to $1 - x$. Let p_i be the probability that the molecule at the kink has *i* neighbors of type *b*. Equations (6) and (7) can then be rewritten in the following fashion:

$$c^* = (1 - x) \sum_{i=0}^3 p_i (\alpha + 1)^i, \quad (10)$$

$$b^* = \frac{x}{(1 - x)} (\alpha + 1)^3 \frac{\sum_{i=0}^3 p_i (\beta + 1)^i}{\sum_{i=0}^3 p_i (\alpha + 1)^i}. \quad (11)$$

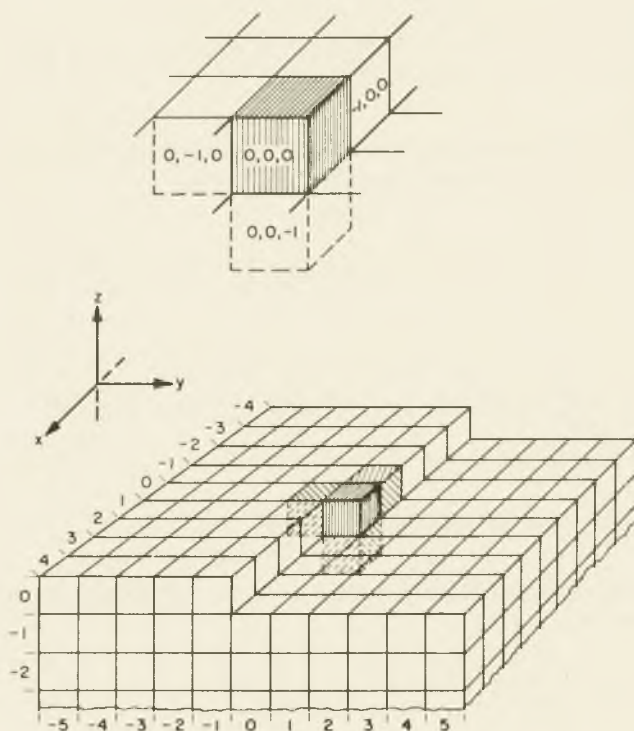


FIGURE 24. The geometry of the kink.

We must now consider the probabilities that the molecule at the kink will have i nearest neighbors of type b (p_i). Before we do this let us examine the geometry of the kink in more detail. Of the three nearest neighbors (see Figure 24), one lies along the step at the crystal surface, and its fraction of molecules of type b is x . If we assign the kink coordinates $0, 0, 0$, then the coordinates of the other molecule along the kink are $-1, 0, 0$. The molecule at position $0, -1, 0$ will lie directly behind the step. It was laid down as the step advanced one lattice position. In general, the fraction of type b molecules in this location may be different from x , since the content of b in the growing step may change with growth. We shall designate the fraction of b molecules in the location step as y . Similarly, the molecule in position $0, 0, -1$ lies in the layer below that of the advancing step. Let us designate the concentration of b type molecules in this layer as z . For a crystal that is completely homogeneous, including the layers at the surface and at the step, $x = y = z$. In the more general case, however, these three concentrations may differ. In terms of the fractional concentration of b type molecules, the probabilities p_i are

$$\begin{aligned}
p_0 &= (1-x)(1-y)(1-z), \\
p_1 &= x(1-y)(1-z) + (1-x)y(1-z) + (1-x)(1-y)z, \\
p_2 &= xy(1-z) + x(1-y)z + (1-x)yz, \\
p_3 &= xyz.
\end{aligned}$$

When these probabilities are multiplied by the appropriate energy factors $\alpha+1$ and $\beta+1$, we obtain the following sums:

$$\sum_{i=0}^3 p_i (\alpha+1)^i = (1+\alpha x)(1+\alpha y)(1+\alpha z),$$

and

$$\sum_{i=0}^3 p_i (\beta+1)^i = (1+\beta x)(1+\beta y)(1+\beta z).$$

Thus, we find that the relative solubility c^* is

$$c^* = (1-x)(1+\alpha x)(1+\alpha y)(1+\alpha z). \quad (12)$$

Similarly, the effective ratio of type b to type a molecules in the solution, b^* , is given by

$$b^* = \frac{x}{(1-x)} (\alpha+1)^3 \frac{(1+\beta x)(1+\beta y)(1+\beta z)}{(1+\alpha x)(1+\alpha y)(1+\alpha z)}. \quad (13)$$

Since equilibration of the solid by diffusion is slow, the variables y and z will depend on the past precipitation or solution history of the crystal. The variable x , on the other hand, is the direct result of the rapid equilibration between the step and the present solution. Thus x is the dependent variable. To find the relative solubility c^* , it is therefore necessary to solve equation (13) for x and substitute the value for x so found in equation (12).

Equation (13) reduces to the following quadratic equation in x :

$$x^2 (\beta\gamma + \alpha) + x[\gamma - (\alpha-1)] - 1 = 0, \quad (14)$$

where

$$\gamma \equiv \frac{(\alpha+1)^3}{b^*} \frac{(1+\beta y)(1+\beta z)}{(1+\alpha y)(1+\alpha z)}.$$

Let

$$A \equiv \beta\gamma + \alpha, \quad B \equiv \gamma - (\alpha-1);$$

then

$$x = \frac{B}{2A} \left(\pm \sqrt{1 + \frac{4A}{B^2}} - 1 \right). \quad (15)$$

As long as $4A/B^2 \ll 1$,

$$x \approx \frac{1}{B}. \quad (16)$$

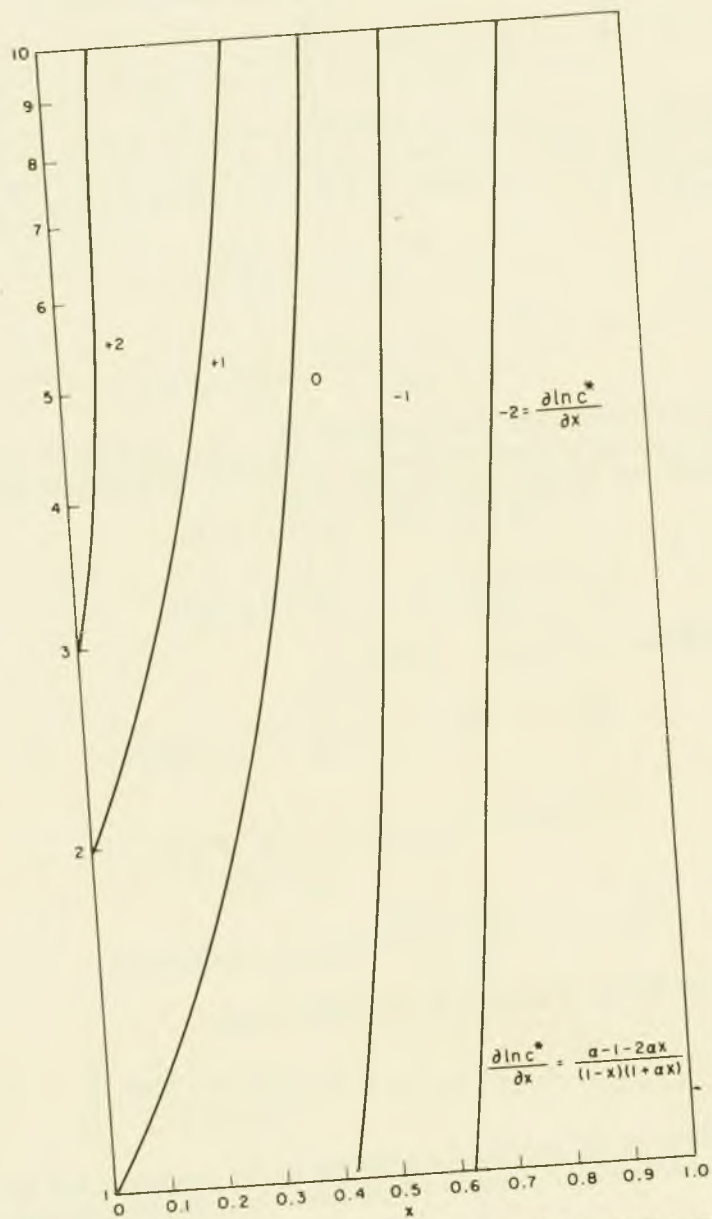


FIGURE 25. The partial logarithmic derivative of c^* with respect to x .

By taking the total logarithmic derivative of c^* , we obtain

$$d \ln c^* = \left[\frac{\alpha - 1 - 2\alpha x}{1 + (\alpha - 1)x - \alpha x^2} \right] dx + \frac{\alpha}{1 + \alpha y} dy + \frac{\alpha}{1 + \alpha z} dz. \quad (17)$$

Thus, if x is constant, the solubility increases as y and z increase. The partial derivative of c^* with respect to x can be positive or negative, depending on x and α . Figure 25 is a plot of $(\partial \ln c^*)/\partial x$ as a function of x and α . If

$$x < \frac{\alpha - 1}{2\alpha}, \quad \frac{\partial \ln c^*}{\partial x} > 0,$$

and if

$$x > \frac{\alpha - 1}{2\alpha}, \quad \frac{\partial \ln c^*}{\partial x} < 0.$$

The exact behavior of the solubility on y , z , α , β , and b^* is complicated. As long as the concentration of impurity molecules is small, the equations can be approximated as follows:

$$\ln c^* = x(\alpha - 1) + (y + z)\alpha, \quad (18)$$

and

$$\gamma = \frac{(\alpha + 1)^3}{b^*} [1 - (y + z)(\alpha - \beta)]. \quad (19)$$

If in addition $(\alpha + 1)^3/b^* > 1$, then

$$\frac{4A}{B^2} < 1, \text{ and } x = + \frac{1}{B} = \frac{1}{\gamma - (\alpha - 1)}.$$

Thus,

$$(\alpha - 1)x = \frac{1}{\frac{(\alpha + 1)^3 [1 - (y + z)\alpha]}{(\alpha - 1)b^*} - 1},$$

$$(\alpha - 1)x \approx \frac{(\alpha - 1)b^*}{(\alpha + 1)^3} [1 + (\alpha - \beta)(y + z)].$$

Substituting this in equation (18), we finally obtain

$$\ln c^* \approx \frac{(\alpha - 1)b^*}{(\alpha + 1)^3} + (y + z) \left[\alpha - \frac{(\alpha - \beta)(\alpha - 1)b^*}{(\alpha + 1)^3} \right]. \quad (20)$$

The logarithm of the ratio of the solubility of the impure crystal to the pure crystal is then approximately a linear function of the impurity content:

$$\log \frac{c^*}{c^*(y=z=0)} \approx (y + z) \left[\alpha - \frac{(\alpha - \beta)(\alpha - 1)b^*}{(\alpha + 1)^3} \right]. \quad (21)$$

THERMODYNAMIC EQUILIBRIUM

For any value of y and z in a solution of a given ratio of effective impurity concentration b^* , the edge can come to equilibrium with the solution if a certain concentration of impurity molecules x is incorporated. In order that the crystal represent a thermodynamic phase, its composition must be homogeneous. To have a thermodynamic equilibrium between the solution and the solid, we thus have the additional constraint

$$x = y = z. \quad (22)$$

We must now investigate the conditions under which a thermodynamic equilibrium can exist. If equation (22) is satisfied, equation (13) becomes

$$\frac{b^*}{(\alpha + 1)^3} = \frac{x}{1 - x} \left(\frac{1 + \beta x}{1 + \alpha x} \right)^3. \quad (23)$$

It is convenient to introduce a new concentration variable q defined by

$$q^3 \equiv \frac{x}{1 - x}.$$

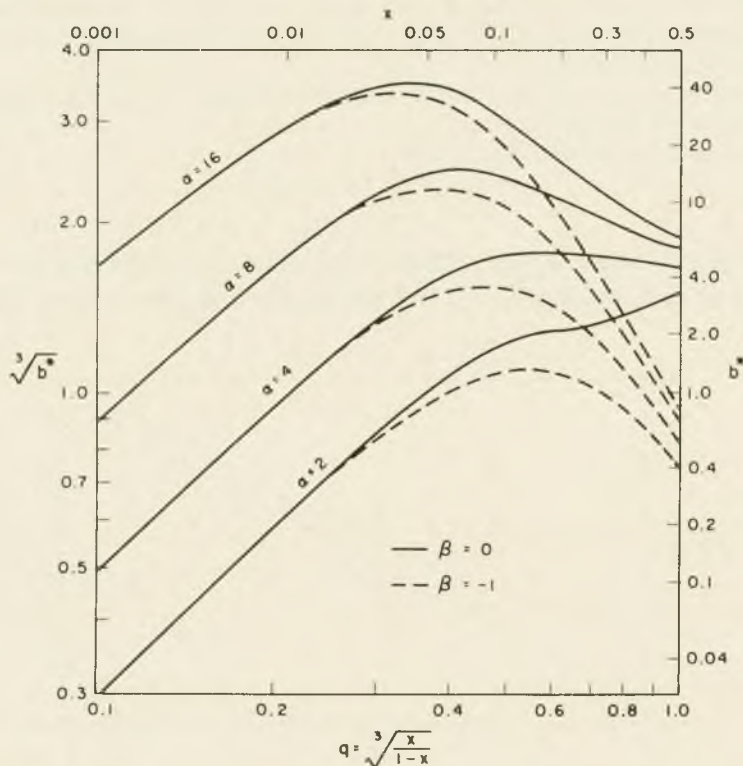


FIGURE 26. Impurity concentration in solid (x) as a function of the effective impurity fraction in the solution (b^*) at thermodynamic equilibrium.

Equation (23) then becomes

$$q \frac{(\alpha + 1)}{\sqrt[3]{b^*}} = \frac{1 + q^3 (\alpha + 1)}{1 + q^3 (\beta + 1)} \quad (24)$$

This leads to the following quartic equation in q :

$$q^4 (\beta + 1) + q = \sqrt[3]{b^*} \left[q^3 + \frac{1}{\alpha + 1} \right] \quad (25)$$

If $b^* = 0$, $q = 0$, and therefore $x = 0$. As b^* increases and as long as $q < 1$,

$$x \approx \frac{b^*}{(\alpha + 1)^3} \quad (26)$$

As q increases, b^* depends on β as well as on α . Figure 26 is a plot of b^* vs q for various values of α and for the extreme values of $\beta = 0$ and -1 .

For each value of α and β there exists an impurity concentration b^* above which no impure solid ($x < 0.5$) can be in thermodynamic equilibrium with the solution.

This maximum value of b^* is plotted in Figure 27 as a function of α for $\beta = 0$ and $\beta = -1$.

The equilibrium solubility c^* is

$$c^* = (1 - x) (1 + \alpha x)^3 \quad (27)$$

THE EQUILIBRATION OF A PURE SOLID WITH AN IMPURE SOLUTION

Let us now investigate what will happen if we immerse a pure solid in

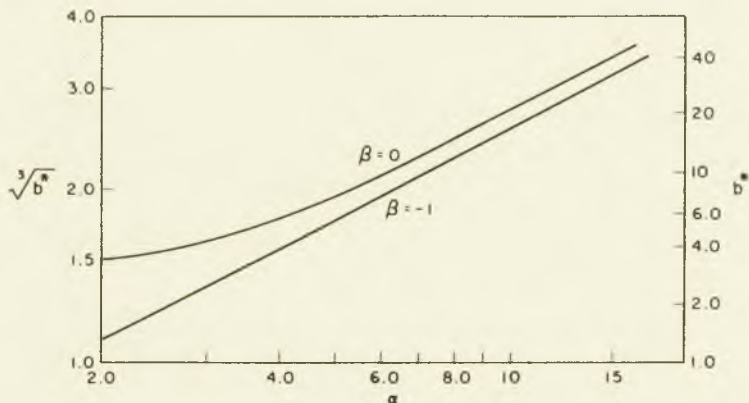


FIGURE 27. Maximum impurity content in solution for which an impure homogeneous phase ($x < 0.5$) can be in equilibrium with that solution.

an impure solution under quasi equilibrium conditions. Let the parameters of the solid be

$$\alpha = 4, \beta = 0.$$

With these parameters, a solid can be in thermodynamic equilibrium with the solution only if b^* is less than 5.4. Let us investigate what will happen if we immerse the solid in solutions with b^* values of 3.0, 5.0, and 10.

At first, the impurity enters the step only on the crystal surface; thus, $y = z = 0$. Solving equation (15) for x , we obtain the following values:

	$y = z = 0$		
$b^* =$	3	5	10
$x =$	0.0258	0.0451	0.1010
$c^* =$	1.074	1.127	1.262

Now we add the next step so that the previous step becomes the layer next to the step. We find

	$z = 0$		
$b^* =$	3	5	10
$y =$	0.0258	0.0451	0.1010
$x =$	0.0287	0.0544	0.1534
$c^* =$	1.194	1.359	1.918

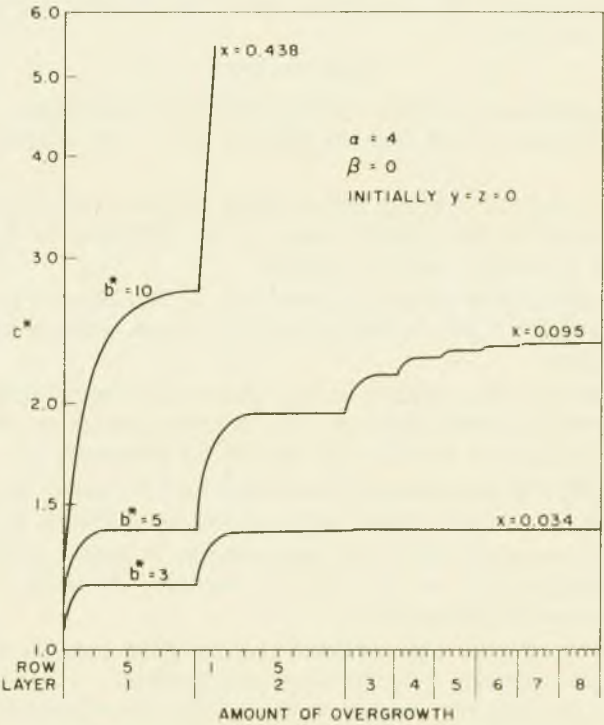


FIGURE 28. Change in solubility of initially pure material with overgrowth.

We continue in this manner until the first layer has been completed. The changes in the relative solubility produced are shown in Figure 28.

At first, the solubility changes as the step advances over the clean surface. Eventually, an asymptotic value of the impurity content is reached, and x is equal to y . Now we are ready to start a new layer. For simplicity we assume that the impurity content in the substrate z now has a constant composition equal to the asymptotic value for the first layer. For the first step on the second layer we obtain the following values:

b^*	3	5	10
z	0.0290	0.0568	0.2202
y	0.0290	0.0568	0.2202
x	0.0327	0.0720	0.4377
c^*	1.363	1.800	5.471

With the help of a computer, we continue this iterative process. The results are shown in Figure 28. For $b^* = 3$, a steady state is reached after a few steps of the second layer have been precipitated. In the case of $b^* = 5$, it takes approximately seven layers before the solubility becomes constant. For $b^* = 10$, no steady state is possible, and the solubility continues to increase. In the second layer the impurity content already exceeds 50 per cent.

CONCLUSIONS

1) An equilibrium solubility theory for a solid containing an impurity has been developed with the assumption that only nearest neighbors interact.

2) The amount of impurity incorporated into the solid depends on the impurity content in the solution and on the difference in bond energy between the pure solid and the impurity.

3) The solubility of the solid depends on its past history. In particular, it depends on how much of the impurity has been incorporated into the last two layers.

4) A solid with any impurity content can be equilibrated with a solution of any impurity content; however, the impurity content of the last step will not necessarily be the same as that of the substrate.

5) In order that the precipitated material have the same composition as the substrate, the solution must have a particular impurity content.

6) If the impurity content of the solution is larger than a specific value, which depends on the binding energies, no solid of constant composition can be precipitated.

7) If an overgrowth is precipitated over the pure material in a solution containing the impurity, two situations are possible:

a) If the impurity content in the solution is sufficiently small, the overgrowth will fairly rapidly reach a steady composition.

b) If, on the other hand, the impurity content of the solution is in excess of a particular value, the precipitated material will continuously increase in impurity content, and as a consequence, the solubility of the solid will monotonously increase.

SYMBOLS

- a lattice spacing, cm.
 $A = \beta\gamma + \alpha$.
 b ratio of concentration of molecules b to molecules a in the solution.
 $b^* = b(\bar{v}_b/\bar{v}_a)$, effective ratio of concentration of type b to type a .
 $B = \gamma - (\alpha - 1)$.
 $c^* = c_1/[c_1 (b=0)]$, ratio of solubility of impure crystal in impure solution to solubility of pure crystal in pure solution.
 c_1 concentration in solution, molecules/cm³.
 c_2 concentration of surface-adsorbed molecules, molecules/cm².
 E energy per bond, ergs/bond.
 E_{aa} energy for an $a \rightarrow a$ bond, ergs/bond.
 E_{ab} energy for an $a \rightarrow b$ bond, ergs/bond.
 E_{ai} binding energy for molecule at kink of type a with i neighbors of type b .
 E_{bb} energy for a $b \rightarrow b$ bond, ergs/bond.
 E_{bi} binding energy for molecule at kink of type b with i neighbors of type b .
 i number of nearest neighbors of type b .
 k Boltzman constant, ergs molecule⁻¹ °K⁻¹.
 p_{ai} probability that molecule at kink is type a and has i neighbors of type b .
 p_{bi} probability that molecule at kink is type b and has i neighbors of type b .
 p_i probability that molecule at kink has i nearest neighbors of type b .
 $q = [x/(1-x)]^{1/3}$.
 T absolute temperature, °K.
 \bar{v} average velocity of solute molecule in solution, cm/sec.
 \bar{v}_a average velocity of solute molecule a in solution, cm/sec.
 \bar{v}_b average velocity of solute molecule b in solution, cm/sec.
 x fraction of molecules on step that are of type b .
 y fraction of molecules of type b behind step (location 0, -1, 0).
 z fraction of molecules of type b below step (location 0, 0, -1).
 $\alpha \equiv \exp \frac{(E_{aa} - E_{ab})}{kT} - 1$ (equation 8).
 $\beta \equiv \exp \frac{(E_{ab} - E_{bb})}{kT} - 1$ (equation 9).
 $\gamma \equiv \frac{(\alpha + 1)^3 (1 + \beta y) (1 + \beta z)}{b^* (1 + \alpha y) (1 + \alpha z)}$.
 ν characteristic frequency, sec⁻¹.

REFERENCES

- BURTON, W. K. AND N. CABRERA
1949. Crystal growths and surface structure, *Disc. Faraday Soc.*, (5): 33-48.
- DEFFEYES, K. S. AND E. L. MARTIN
1962. Absence of Carbon-14 activity in dolomite from Florida Bay. *Science*, 136: 782.
- DEFFEYES, K. S., F. J. LUCIA, AND P. K. WEYL
1964. Dolomitization: observation on the island of Bonaire, Netherlands Antilles. *Science*, 143: 678-679.
1965. Dolomitization and limestone diagenesis. *SEPM, Spec. Publ. No. 13*, Lloyd Pray and R. C. Murray, Eds., pp. 71-88.
- GARRELS, R. M. AND C. L. CHRIST
1965. Solutions, minerals and equilibria. Harper and Row, New York.
- LOWENSTAM, H. A.
1964. Sr/Ca ratio of skeletal aragonites from the Recent marine biota at Palau and from fossil gastropods. *In Isotopic and Cosmic Chemistry*, Craig, Miller and Wasserburg, Eds., North-Holland Publishing Co., Amsterdam, pp. 114-132.
- PYTKOWICZ, R. M. AND D. N. CONNORS
1964. High pressure solubility of calcium carbonate in seawater. *Science*, 144: 840-841.
- SCHMALZ, R. F.
1965. Brucite in cargonate secreted by the red alga *Goniolithon*. *Science*, 149: 993-996.
- TAFT, W. H.
1961. Authigenic dolomite in modern carbonate sediments along the southern coast of Florida. *Science*, 134: 561-562.
- WEYL, P. K.
1958. The solution kinetics of calcite. *J. Geology*, 66: 163-176.
1961. The carbonate saturometer. *J. Geology*, 69: 32-44.
1964. The solution alteration of carbonate sediments and skeletons, *in Approaches to Paleoecology*, J. Imbrie and N. Newell, Eds., John Wiley & Sons, Inc., New York, pp. 345-356.

ELECTROLYTIC REDUCTION OF CARBON DIOXIDE ON LEAD CATHODES

TERRELL N. ANDERSEN, BRYANT A. MINER, (MISS) ELLA
DIBBLE AND HENRY EYRING

*Institute for the Study of Rate Processes
University of Utah
Salt Lake City, Utah*

ABSTRACT

Reduction of alkali chloride and alkali carbonate aqueous solutions containing CO_2 , N_2 and H_2 was carried out on lead cathodes in the acidic and neutral pH range. Steady state polarization curves from the rest potential up to -2.1 volts (vs the N.H.E.) showed five regions with increasing current: (i) a region in which impurities controlled the kinetics; (ii) a region in which reduction of H_3O^+ ions is the rate controlling step, and in which mostly H_2 and a small percentage of formic acid are the products; (iii) a limiting current region for H_3O^+ ions; (iv) a region in which water and carbon dioxide are reduced, and in which the current efficiency for production of HCOOH is greater than 50 per cent; (v) another limiting current region in which OH^- transport away from and CO_2 transport to the electrode influence the kinetics of region (iv). Possible reaction paths and mechanisms are postulated for the cathodic reduction of CO_2 .

INTRODUCTION

The study of reactions of CO_2 is of general interest both because of the relative abundance of the compound, and because of its important role in photosynthesis and metabolism. Several papers (Royer, 1870; Cohen & Jahn, 1904; Ehrenfeld, 1905; Fischer & Prziza, 1914; Rabinowitsch & Maschowitz, 1930) in the early 1900's have shown that formic acid is formed upon electrolytic reduction of CO_2 -containing aqueous solutions. The principal studies were on amalgamated electrodes, since these gave the highest current yields. The latter approached 100 per cent on amalgamated zinc (Cohen, 1904) and on lead amalgam covered with sodium amalgam (Rabinowitsch & Maschowitz, 1930). The solutions in the above studies contained carbonate or bicarbonate salts with CO_2 gas streaming through the solution. Van Rysselberghe and co-workers (1944, 1946, 1946) obtained polarographic waves in solutions with CO_2 present, which they interpreted as being due to CO_2 reduction. Later polarization work by Teeter (1954) and Teeter & Van Rysselberghe (1954, 1955) on large mercury cathodes confirmed the above interpretation and also proved that CO_2 , not HCO_3^- or $\text{CO}_3^{=}$ ions, was the reactive species. The above authors obtained HCOOH in current yields of 100 per cent over a wide voltage range on mercury.

In the present work, electrolytic reduction of aqueous, CO_2 -containing solutions was carried out on lead electrodes. Lead was chosen since it exhibits a high hydrogen overvoltage (a basic criterion for formate—rather

than H_2 —production), and has had little previous attention. Also, the purpose of the present work was to use methods which would lead to an understanding of the reduction mechanism, since the latter was not studied extensively in the previous works.

EXPERIMENTS

A three-electrode system was used; the lead test electrode was the cathode, a platinum foil acted as anode and a saturated calomel electrode served as reference electrode. The cell (see Fig. 1) was of Pyrex glass and was provided with an air-tight polyethylene-coated lid. The anode and cathode compartments were separated by a liquid salt bridge and 3 frits (with interconnecting compartments). Such electrode separation was necessary in order to minimize transfer of the anolyte to the cathode or the reaction product to the anode. The high resistance caused by electrode separation necessitated the use of large (>10 mm) diameter frits in order to prevent excessive heating when currents up to 100 ma were passed. A KCl-agar salt bridge connected the calomel cell and cathode compartment, and was drawn to a capillary tip which was placed very close to the lead cathode.

The cathodes were spirals of lead wires (of .020, .030, and .10 inch diameter) of 99.9⁺ per cent and 99.99⁺ per cent purities. These electrodes were first chemically polished in a solution of 80 per cent glacial acetic acid plus 20 per cent hydrogen peroxide (Tegart, 1959) and then rinsed in

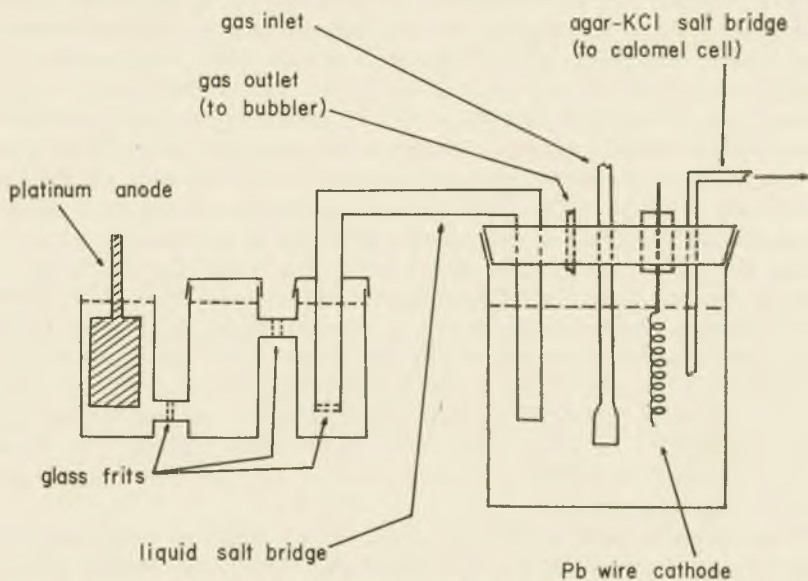


FIGURE 1. Experimental cell assembly.

alcohol, and finally in doubly distilled water. This treatment produced bright, reproducible electrode surfaces, and similar treatment was found to be successful in hydrogen overpotential studies (Srinivasan, 1963). Solutions were prepared from water bidistilled from a basic permanganate solution and from reagent grade chemicals. CO_2 gas was passed through Cu turnings at 400°C to remove oxygen, and N_2 and H_2 , when used, were of 99.99+ per cent purity. The solution was stirred by vigorously streaming the gases through it. When partial pressures of CO_2 less than one atmosphere were required, N_2 and CO_2 were metered together to produce a total pressure of one atmosphere.

Because the multiple frits produced a resistance the order of a thousand ohms, a potential source of several hundred volts was necessary to produce the desired currents. A constant current power supply was constructed following the design of Teeter (1954). The current was measured with a model 260, series 5P Simpson milliammeter, and potential differences between the cathode and reference electrode were measured with a Keithley model 610 A electrometer. At lower overvoltages a Wenking potentiostat could be used for the current source.

Formic acid was tested for qualitatively, by means of the chromotropic acid method (Feigl, 1946), and quantitatively either by direct permanganate titration at 80°C (Kolthoff & Belcher, 1957) or by electrometrically titrating the formate anions with HCl after removing the CO_2 and HCO_3^- by precipitation as BaCO_3 (Van Rysselberghe & Alkire, 1944). The latter method of quantitative analysis was found more satisfactory than MnO_4^- titration due to difficulties in observing the end point with MnO_2 present.

RESULTS

All potentials are given on the normal hydrogen (N.H.) scale using the European sign convention; thus the potential of the saturated calomel electrode is +242mv (vs. N.H.E.) at 25°C . Current densities are calculated using the geometrical area of the cathodes.

Rest potentials.—The rest potentials, V_{rest} in .4 M KCl solutions of varying pH are shown in Fig. 2, both for CO_2 - and N_2 -saturated solutions. It is observed that V_{rest} is independent of pH up to a pH of about 5, above which V_{rest} varies linearly with pH. The latter curve has a slope of from 30 mv to about 50 mv per pH unit indicating that an equilibrium involving H^+ operates at the higher pH's. Figure 2 also shows that the rest potential is essentially independent of CO_2 partial pressure. The potentials in basic solutions with CO_2 present are not stable since the CO_2 reacts with OH^- ions to form HCO_3^- ions.

Formic acid concentrations of the order produced in these experiments (0 to .02M) were shown to have no effect upon the rest potential.

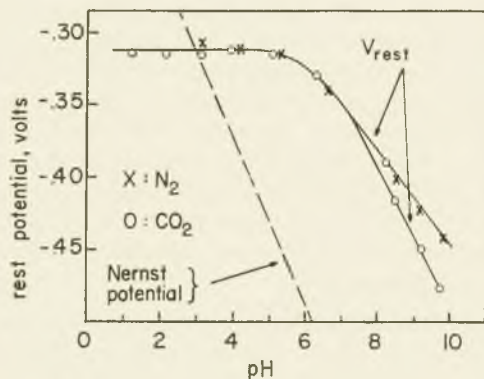


FIGURE 2. Rest potential vs. pH for 0.4M (KCl+HCl); and Nernst potential for $\text{CO}_2 + 2\text{H}^+ + 2\text{e} = \text{HCOOH}$ at $a_{\text{HCOOH}} = 10^{-2}$, $P_{\text{CO}_2} = 1$ atm. $T = 25^\circ\text{C}$.

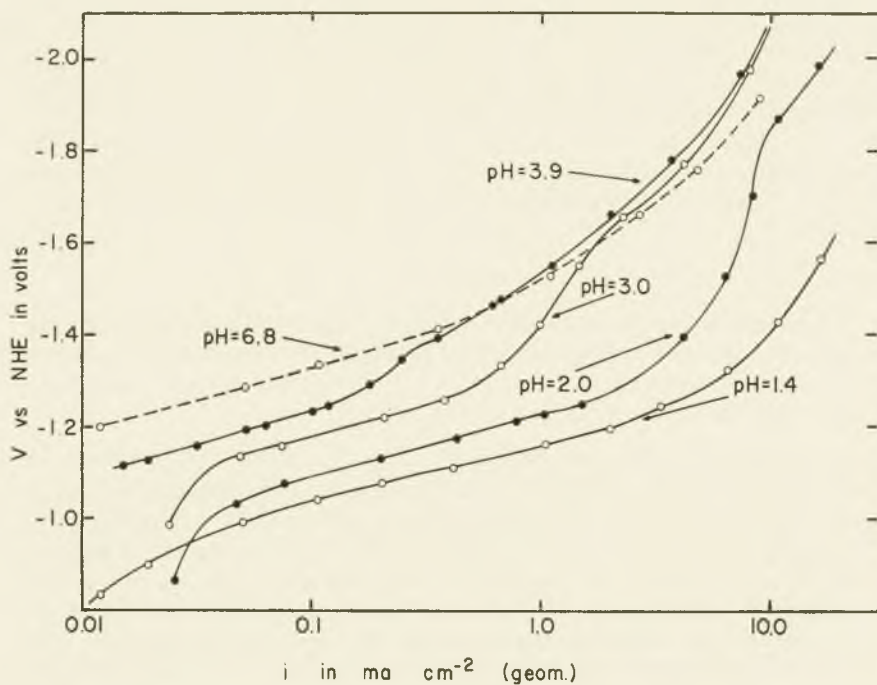


FIGURE 3. Polarization curves as a function of pH. $P_{\text{CO}_2} = 1$ atmosphere; $T = 25^\circ\text{C}$. Solutions: 0.4M (KCl + HCl) for pH = 1.4, 2, 3 and 3.9; 0.2MKHCO₃ + 0.2M KCl for pH = 6.8.

Current-potential relation.—Polarization curves were obtained by applying constant potential (or current) and reading the current (or potential) after the latter reached a steady value. Figure 3 shows the polarization curves in solutions of varying pH with CO_2 bubbling through the solutions. The solutions were 0.4 M Cl^- and .4 M ($\text{K}^+ + \text{H}_3\text{O}^+$) in each case, in order to maintain constant ionic strength. The solution at pH = 6.8 consisted of .2 M $\text{KCl} + .2 \text{ M KHCO}_3$. Figure 4 shows polarization curves in 0.4 M KCl solutions at pH = 3 for varying partial pressures of CO_2 . The total gas pressure was one atmosphere in each case, with N_2 supplementing the CO_2 . Five general regions may be distinguished in the potential vs. log current plots (cf. Fig. 4) although all are not present on all curves:

(i) A potential range at low current density in which voltage at constant current drifted negative with time. The resulting curves (seen in Figures 3 and 4) were concave toward the current axis and very non-reproducible.

(ii) A linear Tafel region with a slope (b) of -120 to -140 mv at 25°C .

(iii) A region where the Tafel line curves upward; this region occurs at higher current densities for higher concentrations of H_3O^+ or CO_2 .

(iv) A second region where the curve begins to level out, and at which it undergoes an inflexion.

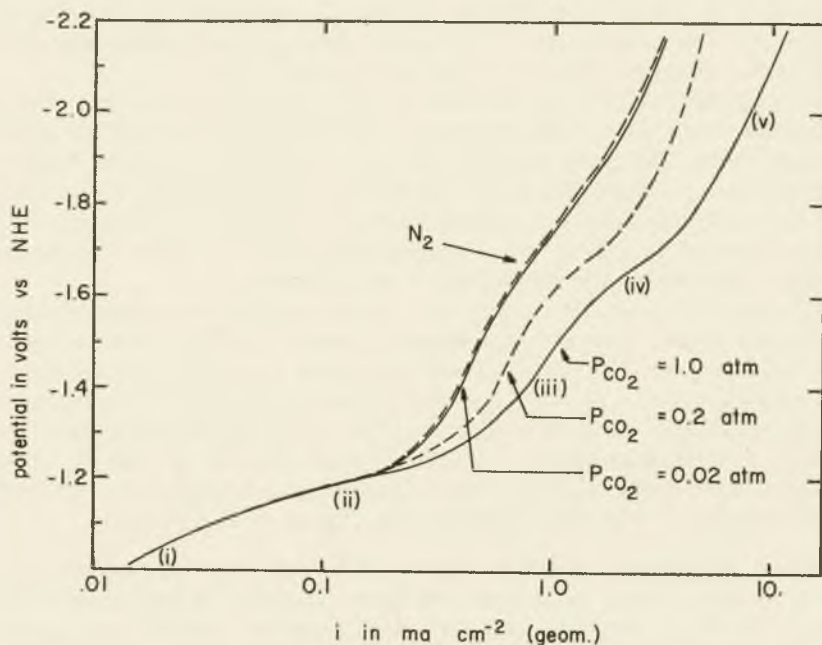


FIGURE 4. Polarization curves as a function of CO_2 partial pressure. Solution: 0.4M KCl , pH = 3, $T = 25^\circ\text{C}$.

(v) The final region shown in Figs. 3 and 4 in which the curve is concave to the potential axis.

The solution of $\text{pH} = 6.8$ has only one region concave to the voltage axis, and this appears to be region (v) since it is very near to the regions (v) for curves of $\text{pH} = 3$ and 3.9 . As will be discussed later, the linear region of the curve for $\text{pH} = 6.8$ appears to be region (iv). Region (v) for $\text{pH} = 1.4$ appeared at higher current densities than were studied. Visible hydrogen evolution began at the higher end of the Tafel regions for $\text{pH} = 1.4$ and 2 , and began in region (v) (at approximately 6 ma cm^{-2} for the 3 solutions of higher pH). Since production of HCOOH began to decrease at this point, a study was not made at very high current densities. It was noted at potentials approaching -2.8 volts, in more basic solutions, that cathodic disintegration of the cathode occurred giving colloidal lead in the solution. This was presumably due to alkali-lead amalgam or lead hydride formation with subsequent decomposition in the solution (Srinivasan, 1963).

Rapid stirring of the solutions (in addition to vigorous bubbling of the gases through them) caused a small increase in current, at a given potential, in regions (iii), (iv), and (v). In the Tafel region stirring had no effect.

Ohmic overpotential was studied by measuring potential vs time decay curves on a cathode ray oscilloscope upon cessation of current. The results indicated no ohmic contribution to the overpotential at polarization potentials more positive than -1.9 volts, and no sizeable contributions in any of the potential range displayed in Figures 3 and 4.

At a given current, the potential at first drifted negative and finally reached a steady value. The amount of drift was greater for smaller values of the current. Therefore, the Tafel slope varied slightly with time between readings. For example, the slope increased by approximately 15 per cent by decreasing the time per reading from 30 minutes to 5 minutes. The Tafel slopes of Figures 3 and 4 approached -120 mv when 10 minutes or more between points on the graph was allowed.

Reproducibility of the current at a given potential, as measured with various electrodes from various batches of lead was ± 50 per cent or better (except in region (i)). In the Tafel region and flatter parts of the curve, the reproducibility was best, and the highest deviations in current were found on steeper parts of the curve. This would be expected since the steeper regions correspond to limiting mass transfer processes; mass transfer varies with relatively small changes in bubbling rate, and with small changes of electrode position with respect to the bubbler.

Products and current efficiency studies.—The only two reaction products detected were formic acid and hydrogen. Tests for formaldehyde and methanol proved negative in each case. Constant current was passed through electrodes of geometrical areas of 3 to 20 cm^2 for times up to 30 hours, in order to determine efficiency of formic acid formation. The

calculated value for the number of moles of formic acid produced, assuming complete reduction according to the equations



or



is given by*

$$N_{\text{HCOOH}} = \# \text{moles formic acid} = \frac{I \quad t}{F \quad (2)} \quad (2)$$

where I is the measured current in amps, t is the time of reduction in seconds and F is Faraday's constant. Dividing the number of moles of HCOOH produced by N_{HCOOH} of equation (2) gives the current efficiency, values for which are given in Tables 1 and 2.

TABLE 1
CURRENT EFFICIENCY (IN PER CENT) FOR PRODUCTION OF HCOOH, AS A
FUNCTION OF CURRENT DENSITY AND pH
Solutions are the same as those of Fig. 3. $P_{\text{CO}_2} = 1$ atm. See Fig. 3
for potentials.

pH/Region (see Fig. 3)	(ii)	(iii)	(iv)	(v)	
1.4	7	5	xx	xx	
2.0	8	40	40	xx	
3.0	14	50	80	70	
				$i(\text{ma/cm}^2)$	efficiency
				5	75
3.9	xx	70	75	9	50
				18	30
6.8	xx	xx	13	9	60

TABLE 2
CURRENT EFFICIENCIES FOR VARIOUS CONDITIONS

Electrolyte	i	Current efficiency
0.2M KCl+0.2M KHCO ₃ +N ₂ (PH=8.2)	2-5 ma cm ⁻²	0-5%
"	0.2-0.5	0-10
0.4MKCl; PH=3.0	$P_{\text{CO}_2}=0.05\text{atm}$	25
"	$P_{\text{CO}_2}=0.2\text{atm}$	50
"	$P_{\text{CO}_2}=1.0\text{atm}$	85

*Equation (2) would be the same whether CO₂ or HCO₃ were the reactant.

Each value recorded is the average of from 3 to 5 experiments since the experimental deviation was large, in some cases being as great as 50 per cent. Factors contributing to this deviation include: (a) a pH change occurred with time of reduction, despite frequent additions of acid; (b) potentials were somewhat unstable over the long electrolysis period, in the limiting current regions; (c) at low current efficiencies and low current densities the small amount of HCOOH present put the analytical procedure in doubt by up to 30 per cent; (d) the electrodes undoubtedly changed catalytic activity over long periods of time, even though they usually remained bright the entire time; this was evidenced by Tafel slopes, on electrodes through which current had been passed for a day, often being higher than those on freshly cleaned electrodes. The blanks in Table 1 represent regions that are not present for the given pH within the current range studied. Region (ii) for pH=3.8 was limited to such a low current density that sufficient amounts of HCOOH could not be produced, in the time allotted, to accurately titrate; this was also the case for region (i), besides the fact that the "known" parameters of the system did not control the kinetics in this latter region. Most regions in Figures 3 and 4 were restricted in current range enough that one current efficiency was indicative of the entire region (within experimental deviation). For the cases in which this was not true (cf. region (v) of pH=3.8), the efficiency as a function of current density is given in the Tables.

Some trends which can be cited from Tables 1 and 2 are: (1) for any given polarization curve, the current efficiency increases as one advances from region (ii) to (iii) to (iv); it reaches a maximum near region (iv), and decreases as i increases in region (v); (2) at a given current density, the current efficiency increases with an increase in pH; (3) within a given potential region, the current efficiency increases as pH increases except when regions of more than one pH overlap; then the efficiencies are essentially the same; (4) CO₂ rather than HCO₃⁻ ion is the principal reactant from which HCOOH is produced; however, HCO₃⁻ appears to reduce to a small extent; (5) current efficiency in high current regions increases with an increase in CO₂ partial pressures; in the Tafel region the experimental deviation prohibits differentiation in the cases of 0.2 and 1 atmosphere.

DISCUSSION

All of the results indicate that the electrolytic CO₂ reduction reaction has a small rate constant, and also takes place irreversibly. The reversible potential for equation (1a) is given by Latimer (1961).

$$V_{\text{rev}} = -.196 - .059\text{pH} + .03 \log \frac{P_{\text{CO}_2}}{a_{\text{HCOOH}}} \quad (3)$$

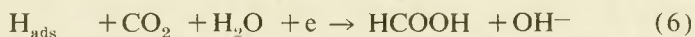
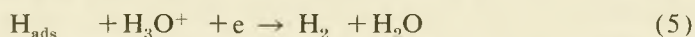
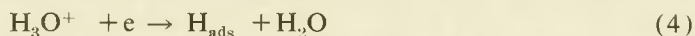
V_{rev} is plotted in Figure 2 as a function of pH for $P_{\text{CO}_2} = 1$ atm and

$a_{\text{HCOOH}} = 10^{-2}$, such conditions being applicable in the V (rest) curve. It is seen that V_{rest} neither follows the Nernst potential with respect to carbon dioxide concentration or pH (except perhaps from pH 5 to 10); also V does not vary with a_{HCOOH} for the concentrations employed (up to .02 M).

From the data we can assess the reactions at each region of the polarization curves as follows:

Region (i): A mixed process here occurs, consisting of the reduction of hydrogen ions and of some impurity depolarizer—probably oxygen. The impurity reduction appears to be limited by mass transfer, based on the steepness of the V vs $\log i$ plot and by instability of the potential values at constant current. That oxygen is the probable depolarizer is shown by the fact that region (i) extends to higher currents when less care is taken to avoid oxygen entrance upon admission of the electrode, and (2) by the fact that cathodizing for long periods of time helps to eliminate region (i). With no depolarizers present and if Pb does not dissolve, region (ii) should extend to more positive potentials and finally curve into the potential axis near the steady state potential. Until region (i) is controlled, it offers little information regarding reduction of CO_2 .

Region (ii): The major product in this region is hydrogen with a small fraction of the current reducing CO_2 , probably as a secondary process. The reaction paths may be written as a hydrogen ion discharge step in series with two parallel processes, an electrochemical desorption leading to H_2 evolution and a process which forms HCOOH . Thus



Reaction (4) is the slow process, and reactions (5) and (6) are both rapid. Evidence supporting such a reaction path sequence includes: (a) the similarity of polarization curves in the presence of CO_2 to those in H_2 or N_2 ; (b) the fact that the limiting current (the i value obtained by extrapolating region (iii) until the curve is vertical), varies approximately linearly with concentration of H_3O^+ ; (c) the displacement of the Tafel curves with pH, and the insensitivity of them to CO_2 pressure; (d) the Tafel slope's ($dV/d \log i$) having the same value as in the case of hydrogen evolution (Srinivasan, 1963). The Tafel slope of -120 mv is consistent with consecutive reactions in which the initial reaction is rate controlling, has a one electron transfer and a transfer coefficient, α , of $1/2$ (i.e., the reaction barrier is symmetrical).

The current vs potential relation is given as follows. Let the forward reactions of equations (4), (5) and (6) have velocities of v_4 , v_5 and v_6 , and the back reactions have velocities of v_{-4} , v_{-5} and v_{-6} , respectively. The velocity of the discharge step, (4), is given by

$$v_4 = K_D (a_{\text{H}_3\text{O}^+}) (1 - \Sigma\theta) \quad (7)$$

where $a_{\text{H}_3\text{O}^+}$ is the activity of hydrogen ions in the pre-electrode layer (the position adjacent to the electrode surface) and $\Sigma\theta$ ($=\theta_{\text{H}} + \theta_{\text{CO}_2} + \theta_{\text{HCOOH}}$) is the fractional coverage of the electrode with H atoms, CO_2 and HCOOH . It is assumed in equation (7) that the adsorption follows a Langmuir isotherm. Justification of this assumption is the fact that neutral organic molecules are usually found to obey Langmuir adsorption and that the fractional coverage of lead with hydrogen, θ_{H} , is extremely small (Frumkin, 1963). K_D is given by

$$K_D = K_4 e^{\frac{-\alpha_4 F \phi / RT}{h}} = \kappa k T e^{\frac{-\Delta G^{0\pm} / RT}{h}} e^{\frac{-\alpha_4 F \phi / RT}{h}} \quad (8)$$

where κ is the transmission coefficient, defined in reaction rate theory (Glasstone, Laidler & Eyring, 1941), $\Delta G^{0\pm}$ is the standard free energy of activation with no electric field present, α is the transfer coefficient (Bockris, 1964) and ϕ is the potential difference (p.d.) between the pre-electrode layer and electrode. The latter approximates the metal solution p.d. if excess neutral salt is present and if a large concentration of specifically adsorbed ions is not present. Both of the latter conditions should apply in the present case. Therefore ϕ is linearly related to the measured potential V , by

$$V = \phi + V_0 \quad (9)$$

where V_0 is the absolute potential of the normal hydrogen electrode. Since V_0 is a constant, we may absorb it into the rate constant and replace ϕ in the exponential by V , the measured potential vs the N.H.E. Thus

$$\text{and} \quad K_4 e^{\frac{-\alpha F \phi / RT}{h}} = K_4 e^{\frac{-\alpha F V / RT}{h}} \quad (10)$$

$$v_4 = k_4 a_{\text{H}_3\text{O}^+} (1 - \Sigma\theta) e^{\frac{-\alpha_4 F V / RT}{h}} \quad (11)$$

The velocity of the reverse step of equation (4) is given, similar to equation (11), by

$$v_{-4} = k_{-4} c' \theta_{\text{H}} e^{\frac{(1 - \alpha_4) F V / RT}{h}} \quad (12)$$

where c' is the concentration of H_{ads} on the electrode when $\theta_{\text{H}} = 1$. Similarly, we have

$$v_5 = k_5 c' \theta_{\text{H}} a_{\text{H}_3\text{O}^+} e^{\frac{-\alpha_5 F V / RT}{h}} \quad (13)$$

$$v_{-5} = k_{-5} P_{H_2} (1 - \Sigma \theta) e^{(1 - \alpha_5) FV/RT} \quad (14)$$

$$v_6 = k_6 \theta_H \theta_{CO_2} c' c'' e^{-\alpha_6 FV/RT} \quad (15)$$

$$v_{-6} = k_{-6} (1 - \Sigma \theta) a_{OH^-} a_{HCOOH} e^{(1 - \alpha_6) FV/RT} \quad (16)$$

c'' converts θ_{CO_2} to concentration. The electrochemical mechanism (equation 5) is considered more probable than H atom combination for metals with small fractional hydrogen coverage (Frumkin, 1961).

Assuming the discharge step (equation 4) to be the slow step, we may solve the equations by assuming a steady state condition for θ_H . Also, assuming $v_5 > v_{-5}$ and $v_6 > v_{-6}$, we have

$$v_4 - v_{-4} - v_5 - v_6 = 0 \quad (17)$$

Since the potential is so far negative of the reversible hydrogen potential, v_{-4} may be neglected in comparison to v_4 , v_5 and v_6 . Therefore solving for θ_H from (11), (13), (15) and (17), with the neglecting of v_{-4} , gives

$$\theta_H = \frac{k_4 (1 - \Sigma \theta_i) a_{H_3O^+} e^{-\alpha_4 FV/RT}}{k_5 c' a_{H_3O^+} e^{-\alpha_5 FV/RT} + k_6 \theta_{CO_2} c' c'' e^{-\alpha_6 FV/RT}} \quad (18)$$

where θ_H in $\Sigma \theta_i$ may be neglected in comparison with θ_{CO_2} and θ_{HCOOH} . The net current is

$$i = 2F (v_5 + v_6) \quad (19)$$

and from (13), (15), (18) and (19)

$$i = 2F a_{H_3O^+} k_4 (1 - \Sigma \theta_i) e^{-\alpha_4 FV/RT} \quad (20)$$

Comparison with experiment:

The Tafel slope is given by

$$dV/d \log i = - \frac{2.3 RT}{\alpha_4 F} = -118 \text{mv (for } \alpha_4 = 1/2) \quad (21)$$

which is seen to agree with the Tafel slope obtained experimentally (see Figs. 3 and 4, region (ii)). Tafel slopes for individual electrochemical steps in the hydrogen evolution reaction have been shown to be one-half (Bockris, 1954).

The total current according to equation (21), is also first order with respect to $a_{H_3O^+}$. Experimentally obtained current vs pH curves are shown

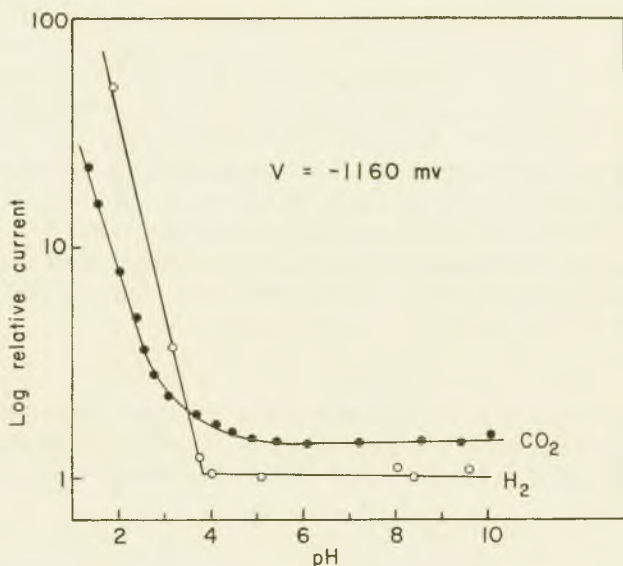


FIGURE 5. Relative current vs pH at constant V . $T = 25^{\circ}\text{C}$; Solution: 0.4M ($\text{KCl} + \text{HCl}$).

in Fig. 5. These were run by potentiostating the electrode, and then adding HCl or KOH . The potential chosen was -1160 mv since this fell in the Tafel region for all pH's studied. It can be seen that i depends on pH to nearly the first power in the region of $\text{pH}=1$ to 3 or 4. For $\text{pH} > 4$ the current is a constant value, which indicates that H_3O^+ is no longer the primary reactant species involved, but rather water.*

Equation (20) predicts the current (at constant potential) to be insensitive to P_{CO_2} (is θ_{CO_2} is small) or to decrease with increasing P_{CO_2} . The present data does not show a variation of i with P_{CO_2} until region (iii) of the polarization curve.

The current efficiency for producing HCOOH is given by

$$\text{current efficiency} = \frac{v_6}{v_5 + v_6} = \frac{k_6 \theta_{\text{CO}_2} c'' e^{-\alpha_6 FV/RT}}{k_6 \theta_{\text{CO}_2} c'' e^{-\alpha_6 FV/RT} + k_3 a_{\text{H}_3\text{O}^+} e^{-\alpha_3 FV/RT}} \quad (22)$$

*The i values of Figure 5 can be found in Figure 4 for $P_{\text{CO}_2}=1$. The exact relationship between i in the case of CO_2 to that in H_2 cannot be ascertained from Figure 5 since there was some deviation in i at a given V in various experiments.

Since α_5 and α_6 are not likely to be very different, the principal factors effecting the efficiency in region (ii) are θ_{CO_2} and $a_{\text{H}_3\text{O}^+}$. The experimental results of Table 1 indicate, at constant current (denominator of equation 22), that efficiency increases with an increase in pH. This is consistent with equation (22). At constant current, the right hand term in the denominator of (22) contributes relatively less to the current as the pH increases. The exponential terms of both the numerator and the denominator increase approximately the same, while $a_{\text{H}_3\text{O}^+}$ in the denominator decreases. Current efficiencies at constant potential were not obtained since the total current for $\text{pH} > 2$ were very low. The efficiency increase with pH shows that equation (6) involves H_2O and not H_3O^+ . The fact that equation (6) is significant in region (ii), while reduction of water to form H_2 is not, means that the former reaction is kinetically faster than the latter. This is further born out by the fact that in regions where water reduction is the main process (i.e. region iv), the main product is HCOOH and not H_2 (see current efficiencies in region iv).

Region (iii): Region 3 is the limiting region for transfer of H_3O^+ to the electrode. Hence, for a given curve, the effective pH near the electrode is higher than in the bulk of the solution. This explains the increase in current efficiencies as well as in (negative) potential at a given current.

Regions (iv) and (v): When the potential has become negative enough, another primary reduction process becomes rate determining. Concentration polarization (of accumulated OH^- ions) interferes with this reaction so extensively that Tafel slopes could not be obtained. Water is involved in this process as evidenced by the following: (1) Fig. 5 shows at -1160 mv that i is independent of pH above a pH of about 4; (2) as the limiting current for H_3O^+ is reached in Fig. 3, the curves for various pH's superimpose; this indicates that the linear part of the curve for $\text{pH}=6.8$ corresponds to region (iv), and a Tafel slope of approximately 120 mv is obtained here; (3) the polarization curve for 0.4 M NaHCO_3 with CO_2 ($\text{pH}=6.8$) and with N_2 ($\text{pH}=8.2$) are seen to show the same essential features (see Fig. 6). Although selection of the proper reaction paths for region (iv) is not possible with the available data, the possible paths chosen must satisfy several criteria: (a) both H_2 and HCOO^- ions must be produced; (b) as V becomes more negative, the ratio of H_2/HCOO^- as product should increase (as seen for region (v)); however both H_2 - and HCOO^- -producing currents continue to increase with a negative potential increase; (c) the net current must increase strongly with an increase in CO_2 partial pressure; (d) for water reduction, the discharge step apparently remains rate determining as shown by hydrogen overvoltage studies on lead in basic solutions (Srinivasan, 1963). A possible mechanism would include two parallel rate-determining initial reactions, the

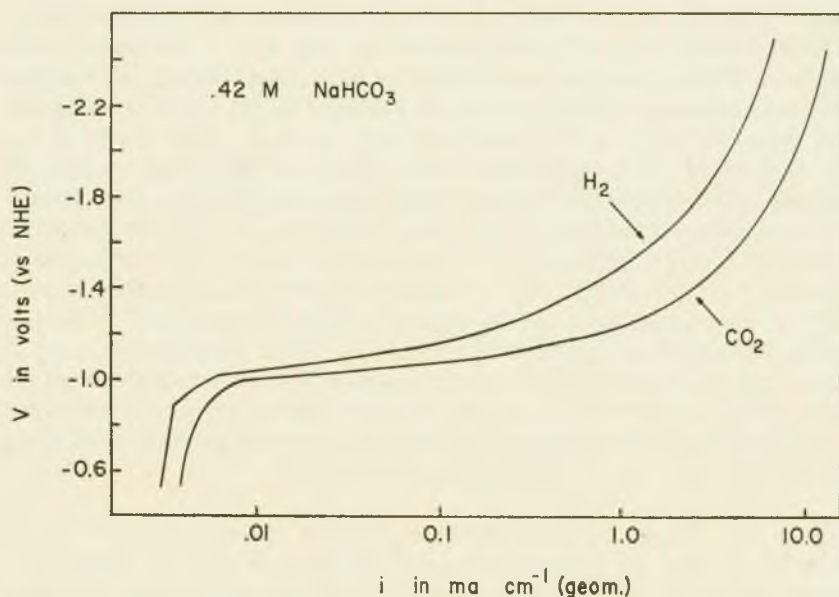
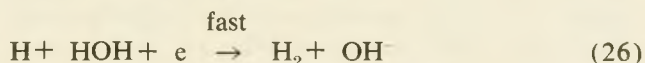
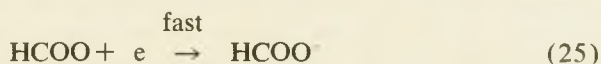
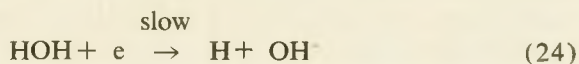


FIGURE 6. Polarization curves for 0.42M NaHCO_3 saturated with H_2 and with CO_2 .

product of one leading to formate ions and the product of the other being H_2 . Thus the paths can be written as



Equations (23) – (26) satisfy criteria (a), (c), and (d) as well as giving a Tafel slope of $2(2.3) \text{ RT/F}$. Criterion (b) is satisfied by the concentration polarization, since OH^- ions react with CO_2 to form HCO_3^- , which is less adsorbed and less reactive than CO_2 . CO_2 , also, would be less adsorbed as the potential becomes more negative in region (v) since organic adsorption decreases as the electrode potential departs drastically ($> \sim 400 \text{ mV}$) from the zero charge potential of the metal

(Bockris, Green & Swinkels, 1964; Bockris & Swinkels, 1964; Blomgren, Bockris & Jesch, 1961). The zero charge potential of lead in solutions such as those used here is approximately 0.7 volts (Bockris & Swinkels, 1964). The limiting current for transport of CO_2 to the electrode is also reached in this region, causing a decrease in yield of formic acid.

ACKNOWLEDGMENT

The authors gratefully acknowledge financial support of this work from the Atomic Energy Commission under contract number AT(11-1) - 1144

REFERENCES

- BLOMGREN, E., J. O'M. BOCKRIS, AND C. JESCH
1961. *J. Phys. Chem.*, **65**: 2000.
- BOCKRIS, J. O'M.
1954. *Modern aspects of electrochemistry*. Vol. I, Chapt. 4, Butterworths, London.
- BOCKRIS, J. O'M., M. GREEN, AND D. A. J. SWINKELS
1964. *J. Electrochem. Soc.*, **111**: 743.
- BOCKRIS, J. O'M. AND D. A. J. SWINKELS
1964. *J. Electrochem. Soc.*, **111**: 736.
- COHEN, A. AND S. JAHN
1904. *Ber.*, **37**: 2836.
- EHRENFELD, R.
1905. *Ber.*, **38**: 4138.
- FEIGL, F.
1946. *Qualitative Analysis by Spot Tests*. Elsevier Publishing Co., New York, pp. 395-397.
- FISCHER, F. AND O. PRZIZA
1914. *Ber.*, **47**: 256.
- FRUMKIN, A. N.
1961. *In Advances in Electrochemistry and Electrochemical Engineering*. Vol. 1, ed. by P. Delahay and C. W. Tobias, Chapt. 2, Interscience, New York.
1963. *In Advances in Electrochemistry and Electrochemical Engineering*. Vol. III, ed. by P. Delahay, Chapt. 5, Interscience, New York.
- GLASSTONE, S., K. J. LAIDLER, AND H. EYRING
1941. *The Theory of Rate Processes*. McGraw-Hill, New York.
- KOLTHOFF, I. M. AND R. BELCHER
1957. *Volumetric analysis*. Vol. III, Interscience, New York, p. 115.
- LATIMER, W. M.
1961. *Oxidation potentials*. 2nd ed., Prentice Hall, Englewood Cliffs, N. J., p. 130.
- RABINOWITSCH, M. AND A. MASCHOWETZ
1930. *Z. Elektrochem.*, **36**: 846.
- ROYER, M. E.
1870. *Compt. Rend.*, **70**: 73.
- SRINIVASAN, S.
1963. Ph.D. Thesis, Univ. of Pennsylvania.

- TEETER, T. E.
1954. Doctoral Thesis, Univ. of Oregon.
- TEETER, T. E. AND P. VAN RYSSELBERGHE
1954. J. Chem. Physics, 22: 759.
1955. Proc. 6th Mtg. Intern. Comm. Electrochem. Thermodynam. and Kinet., p. 538.
- TEGART, W. J. MCG.
1959. The Electrolytic and Chemical Polishing of Metals. Pergamon Press, N. Y. p. 101, 65.
- VAN RYSSELBERGHE, P.
1946. J. Am. Chem. Soc., 68: 2047.
- VAN RYSSELBERGHE, P. AND G. J. ALKIRE
1944. J. Am. Chem. Soc., 66: 1801.
- VAN RYSSELBERGHE, P., G. J. ALKIRE, AND J. M. MCGEE
1946. J. Am. Chem. Soc., 68: 2050.

Nutrient Cycles in Tropical Waters

E. J. FERGUSON WOOD
Convener

The following papers were delivered at the Conference but have not been received for publication:

E. J. FERGUSON WOOD: Thoughts on Vertical Distribution of Phytoplankton in Tropical Waters.

MAX GILLBRICHT: Correlations Between Different Measurements in the Sea.

THE VERTICAL DISTRIBUTION OF MICROBIOMASS IN NORTHERN AND IN TROPICAL SEAS¹

JOHANNES KREY
Institut für Meereskunde, Kiel

ABSTRACT

The microbiomass—here measured as units of albumen-equivalent—gives an idea of the balance between the processes of primary production and those of mineralization. The method allows analyses of quantities down to 2 μg per liter. Average values of the vertical distribution of the biomass in the Arabian Sea were calculated and summarized in diagrams. A comparison between average maxima of the microbiomass values and depth shows that with increasing depth the values become similar. The average maxima of the microbiomass are much higher in northern waters than in tropical waters.

INTRODUCTION

The title of this short paper concerns an old problem which has been partly solved in its general lines. That is, the vertical distribution of zooplankton organisms is known for the surface layer of the ocean in its main principles.

We know today a good deal about the regular distribution of the sum of all small organisms which we try to include here under the general title of microbiomass. Microbiomass is an artificial division of the total plankton and is to be compared with that of nannoplankton, microplankton, etc. The definition is here given as, all living material between 1 and 1000 μ , as well as those of phytoplankton, zooplankton, and bacteria. This microbiomass is the result of different processes which balance against another (Krey, 1961).

The analytical technique is given in Krey, Banse & Hagmeier (1957). It has been shown of great advantage that only filtration and drying must be done aboard ship, the following steps are done in the laboratory. The accuracy can be given for open ocean samples as ± 2 μg albumen/liter.

MATERIALS AND METHODS

The material available for the present considerations has been gained by the same method throughout the past 7 years. Samples have been taken in different parts of the world ocean—a total of about 4500 in the open sea.

The normal *average distribution* (Fig. 1) as found by Hentschel (1936) and others gives a more or less logarithmic decrease of the quantity in the upmost 500 m. This is caused by processes of *primary production* on the one hand and those of *decomposition and accumulation* of the newly

¹Supported by a grant of the Deutsche Forschungsgemeinschaft.

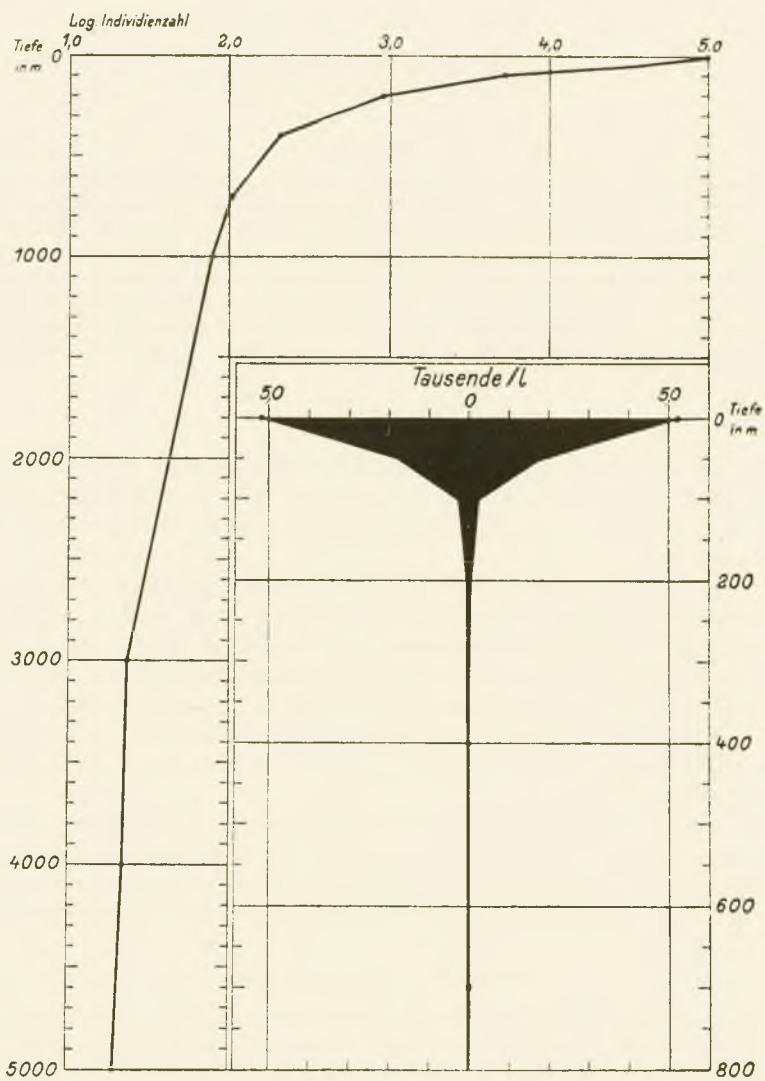


FIGURE 1. Average distribution of the number of total plankton in the South Atlantic (from Hentschel, 1936).

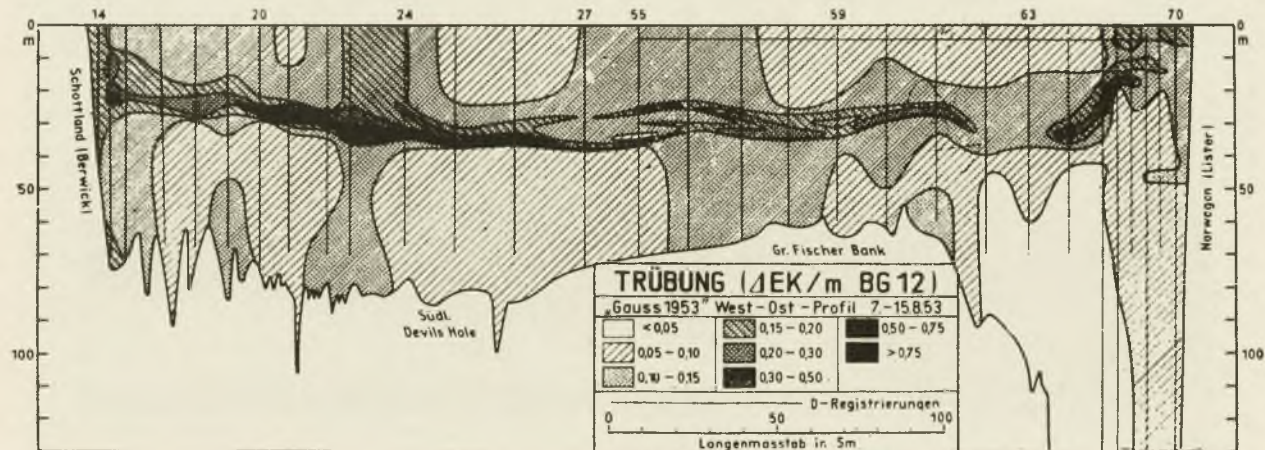
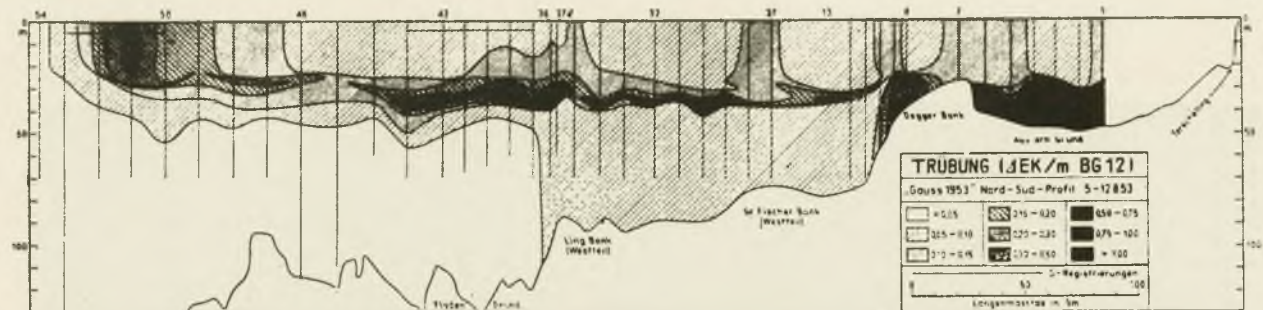


FIGURE 2. Turbidity screen in the North Sea (from Joseph, 1955).

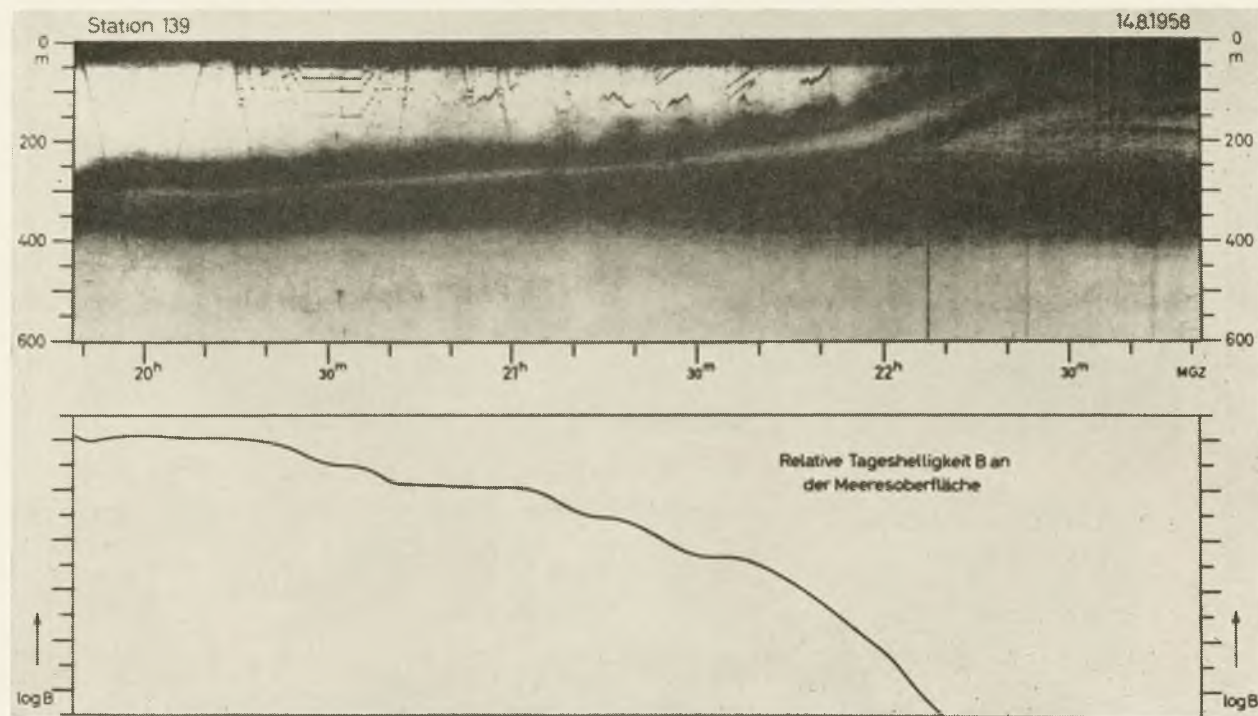


FIGURE 3. Echo-sound scattering layer and light intensity in the North Atlantic (from Joseph, 1959).

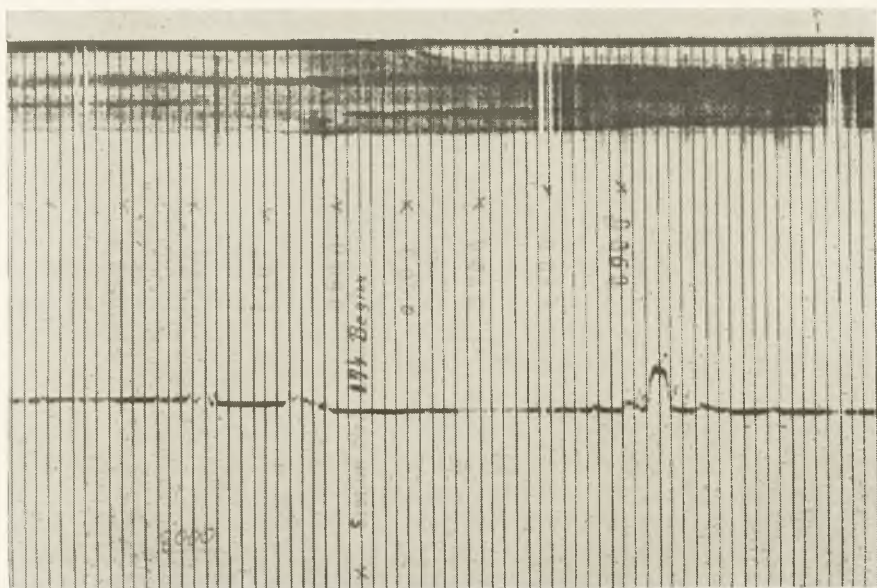


FIGURE 4. Echo-sound scattering layer in the Arabian Sea (as observed by METEOR 1965).

formed organic material on the other. The intermediate products of these processes are: detritus and dissolved organic material, and relatively big crustaceans and fish.

This normal distribution becomes disturbed by: (1) density discontinuity layers which can be the cause of a turbidity screen (Fig. 2) which consists of small living and dead particles (Joseph, 1955); (2) vertical movements of water masses (up- and down-welling); (3) passive sinking of particles; (4) grazing and following vertical migration of these grazing animals (Fig. 3, [Joseph, 1959], & Fig. 4).

This leads to an active vertical transportation (not migration) of the small particles which form the food of so many migrating filter feeders, *e.g.*, Euphausiidae. These feed during the night time in the upmost 50 m and digest during daytime in 200 to 1200 m. If there is much food available, they feed more than they can digest. Digestion products will contain in this case more than 10 per cent (up to 50 per cent) of material, which might serve as food for others.

In consequence of this idea which is partly supported by observations, we shall find besides the *first* maximum of the microbiomass (Fig. 5) which is located in 30 to 50 m, another one in greater depth, where these big organisms stay during the day and give off their digestion products. So we shall have to observe (Fig. 6)—also in average figures—a rather

big *second* maximum which changes in size from one area to the next, according to the vertical migration of the various species and stages of big zooplankton animals.

This second maximum will change in size according to: (a) the quantity of food which is *not* digested, (b) the decomposition of this and, (c) its passive sinking down.

Average figures from the material we gained in the Arabian Sea may support this. But there is an obvious difference between the western and the eastern part (Fig. 6), especially in the near shore eutrophized areas.

These observations which are in good agreement with the echo-sound recordings should be worldwide. At the occasion of the IGY cruises we were able to make similar investigations (Fig. 7).

RESULTS

The *northern waters* show much *higher averages* of standing stock of microbiomass. Because of rather numerous observations we were able to follow this phenomenon in the northern North Atlantic during late winter and late summer, especially when high surface values were observed. Caused by oligotrophic conditions, only a small maximum existed in the northern part during winter time. During Equalant cruises into the

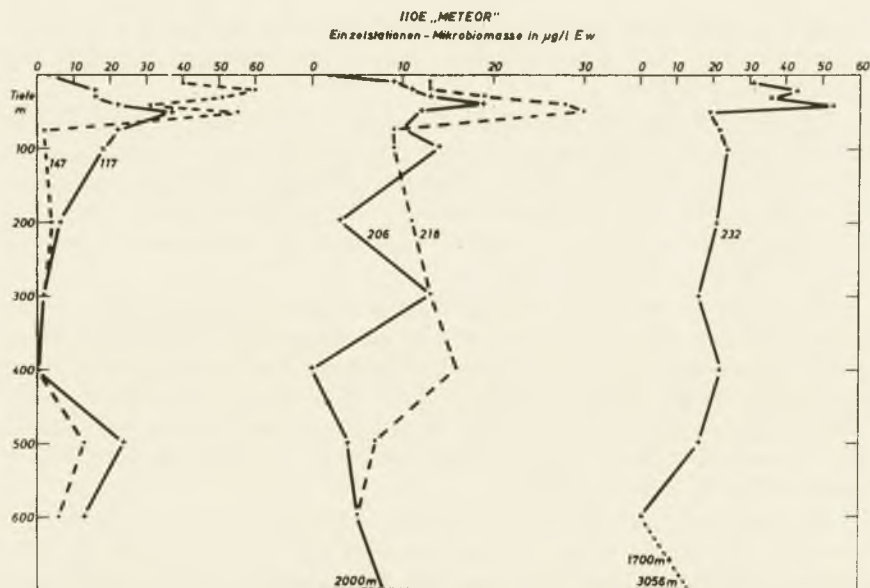


FIGURE 5. Vertical distribution of microbiomass (given as protein in $\mu\text{g}/\text{liter}$) on single stations in the Arabian Sea (as observed by METEOR 1964-65).

II0E „METEOR“

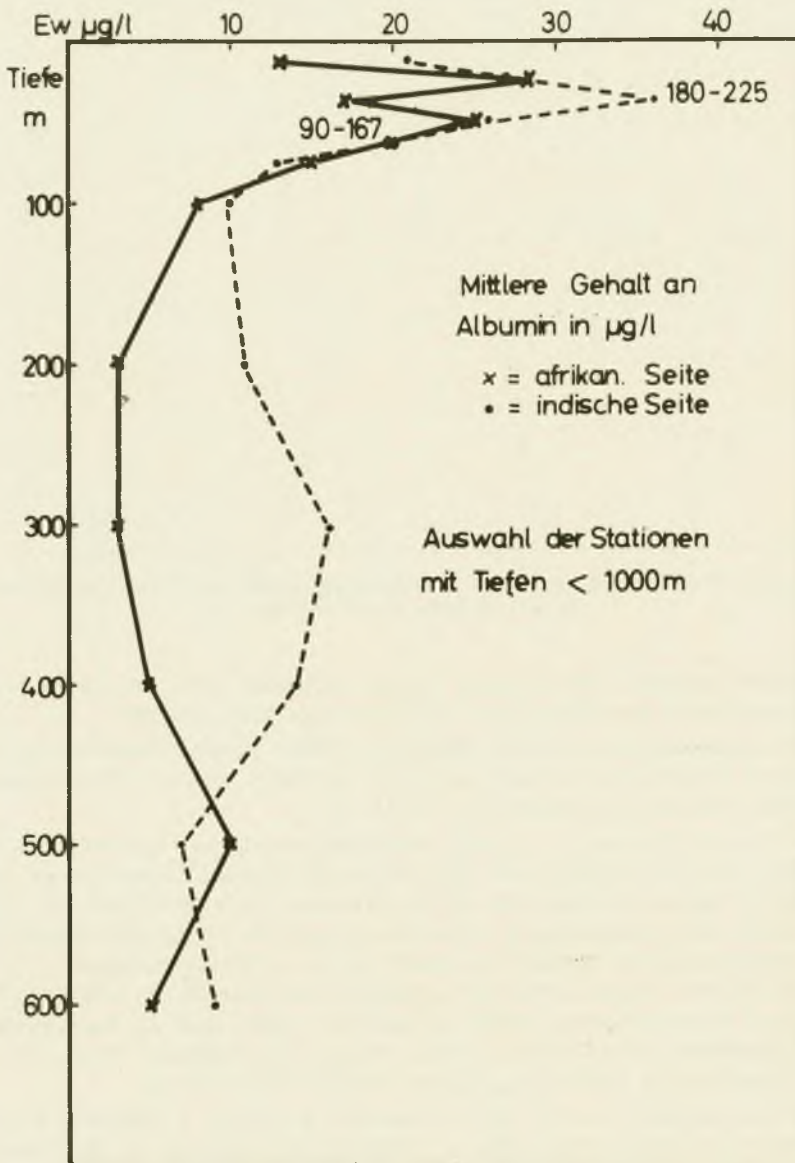


FIGURE 6. Vertical distribution of microbiomass (given as protein in $\mu\text{g/liter}$) averages from the Arabian Sea, West and East part (only stations deeper than 1000 m).

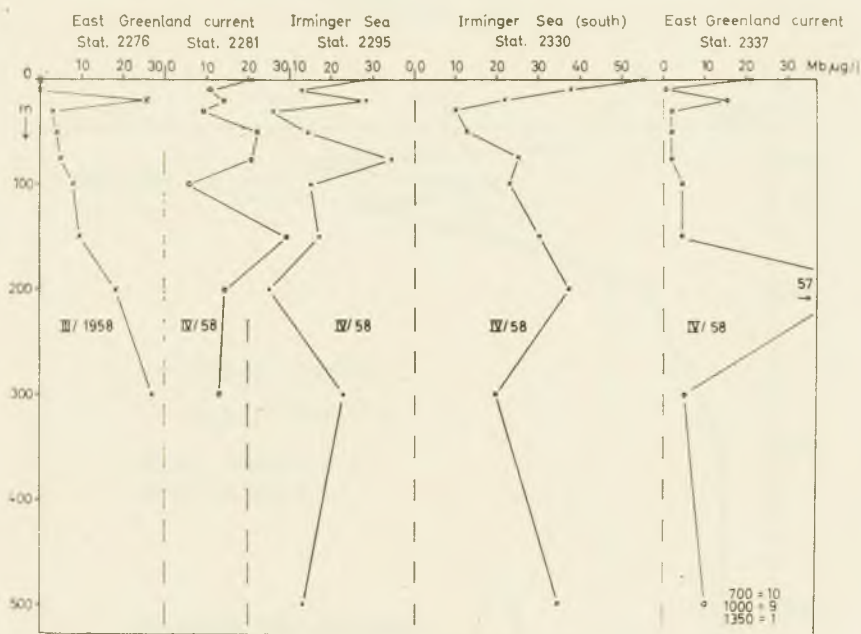


FIGURE 7. Vertical distribution of microbiomass (given as protein in $\mu\text{g/liter}$) in the northern North Atlantic.

Tropical Atlantic, low average figures generally were found and in consequence of that the second maximum is a very low one.

The results of the cruise of Hagmeier (1964) aboard *DIAMANTINA* do not give a sign of the second maximum, probably because of insufficient sampling and an oligotrophic area (Fig. 8).

So we may state as one special result that generally in northern and in tropical seas, especially where high values for surface microbiomass are found, a second maximum in depths between 200 and 600 m are also observed. The comparison between the average size of the first maximum in northern and in tropical seas leads to the following statements: (1) North Atlantic Ocean, about $50 \mu\text{g/liters}$, quite near to the surface; (2) Tropical Atlantic Ocean, about $20 \mu\text{g/liters}$, quite near to the surface; (3) Southwest Indian Ocean, about $35 \mu\text{g/liters}$, between 30 to 50 m; (4) Arabian Sea, about $20 \mu\text{g/liters}$, between 20 to 40 m.

In the Arabian Sea the size of this first maximum is observed to be reverse to the depth layer. This is extremely well observed in the eastern part of the Arabian Sea (Fig. 9), but also in the area of the Somali Current. The second maximum does not follow this general rule so very close, but the trend runs in the same line, especially in the eastern part.

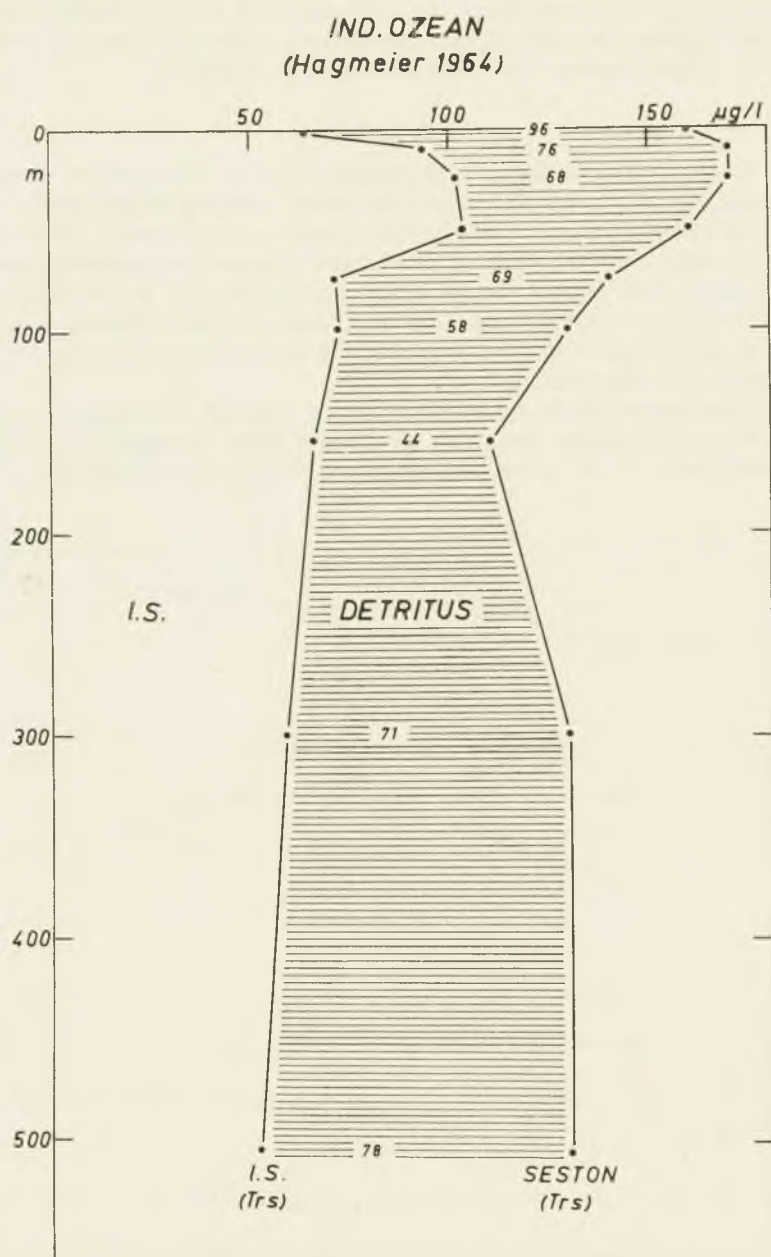


FIGURE 8. Vertical distribution of living substance (given as protein in $\mu\text{g/liter}$) for the southeast Indian Ocean (recalculated from Hagmeier, 1964).

The deepsea values are rather very low and close to the reliability of the method applied. In spite of that the reverse parallelity between average size of microbiomass-values and its depth is evident.

DISCUSSION

It is quite obvious that in the western part of the Arabian Sea, for example, the depth of the second maximum changes rather much (Fig. 10). But there is also a trend in this change to run parallel to the coast and to follow the main lines of the Somali Current. Furthermore there is to be observed a regular change from the layer of 100 to 200 m to that of 400 to 500 m and 200 miles off the coast it is again situated in 100 to 200 m. The reason may be found in the oceanic upwelling on the left border of the big currents.

So, the former observations of Hentschel (1936), Vinogradov (1959) and his collaborators could be confirmed with independent methods. Furthermore: (1) a mechanism of active vertical transportation is made

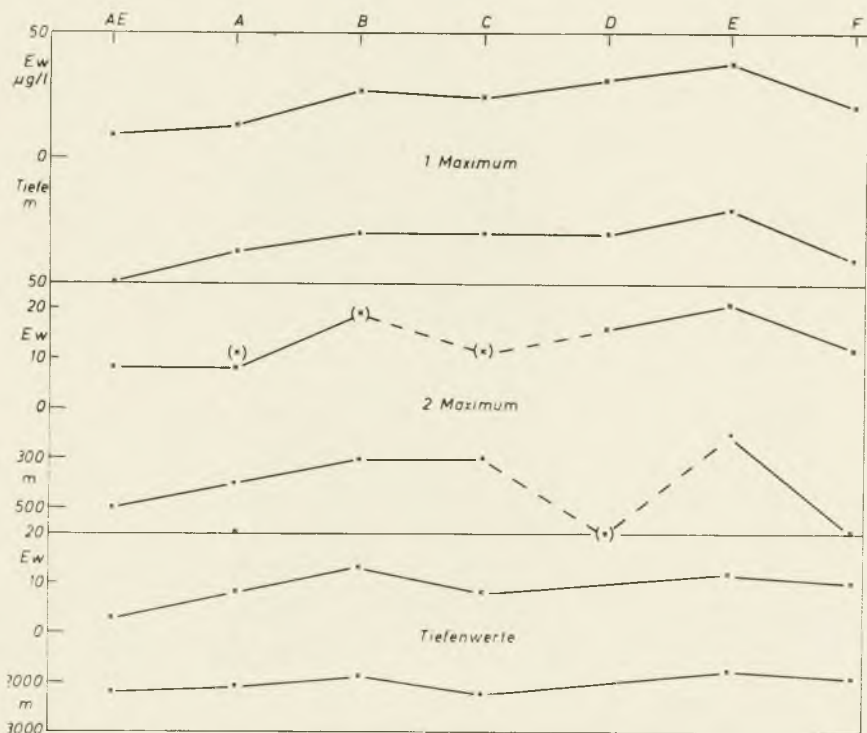


FIGURE 9. Depths layer and average values for microbiomass (given as protein in $\mu\text{g/liter}$) for the first and the second maximum and for the bottom values (observed by METEOR 1964-65).

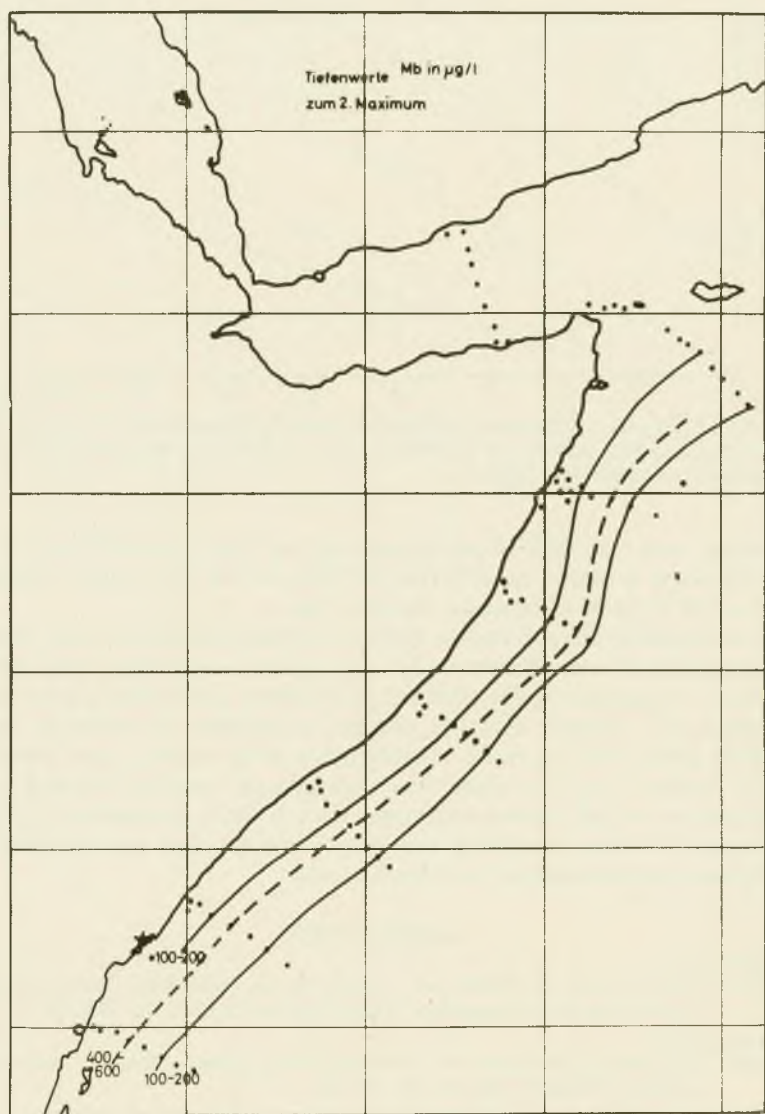


FIGURE 10. Depths layer of the second maximum of microbiomass (given as protein in $\mu\text{g/liter}$) in the area of the Somali Current during northeast monsoon season.

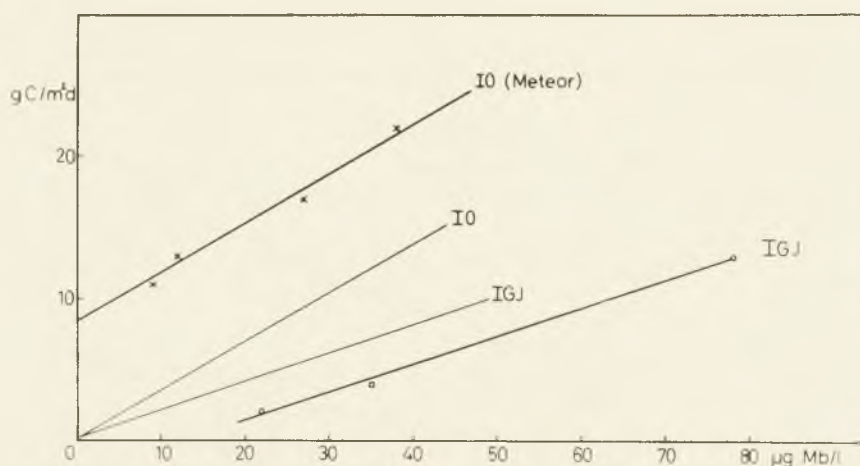


FIGURE 11. Primary production and microbiomass (given as protein in $\mu\text{g/liter}$) in the Arabian Sea and in the northern north Atlantic (crosses and circles are calculated and observed values).

probable, and (2) the depth-dependency of the concentration of the microbiomass is stated as well for the first, as for the second maximum as also for its concentration in the deep sea.

If we consider the correlation between primary production and average standing stock of microbiomass (Fig. 11) (that means: how much microbiomass is supported by the primary production) a diagram can be drawn by which it is evident that the primary production in northern waters supports about twice as much microbiomass as in tropical seas, especially in the Arabian Sea. This raises the very general question, what is made by nature out of this enormous amount of each day's production of organic substance? We hope that time will not be too far that this question can be followed systematically in different areas.

REFERENCES

- HAGMEIER, E.
1964. Zum Gehalt an Seston und Plankton im Indischen Ozean Zwischen Australien und Indonesien Kieler Meeresforsch., Bd. XX, S. 12 ff.
- HENTSCHEL, E.
1936. Allgemeine Biologie des südantlantischen Ozeans. Dtsche. Atlantische Exped. "Meteor", Bd. XI, S. 174 ff.
- JOSEPH, J.
1955. Extinction measurements to indicate distribution and transport of watermasses. Proceedings of the UNESCO Symposium on Physical Oceanography. S. 59 ff.
1959. Vertikale Temperatur-und-Trübungsregistrierung in einer 500 m mächtigen Deckschicht Dtsche. Hydrogr. Zeitschr., Erg. F Heft Reihe B, Nr. 3, S. 48 ff.

KREY, J.

1961. The balance between living and dead matter in the oceans. *In* Sears, Mary, Ed., *Oceanography*, Amer. Ass. Adv. Sci., Washington: 539-548.

KREY, J., K. BANSE, AND E. HAGMEIER

1957. Über die Bestimmung von Eiweiss im Plankton mittels der Biuretreaktion. *Kieler Meeresforsch.*, Bd. XIII, S. 35 ff.

VINOGRADOV, M. A.

1959. Vertikalwanderungen des Tiefseepanktons. *Fortschritte im Studium ozeanischer Tiefen*, herausg. von L. A. Zenkevitch, S. 216 f, [Russ.].

ON SOME CHARACTERISTICS OF THE DISTRIBUTION OF NUTRIENT SALTS IN THE EQUATORIAL AND SOUTH TROPICAL PACIFIC OCEAN¹

H. ROTSCHI

*Office de la Recherche Scientifique et Technique
Outre-Mer, Centre de Noumea, New Caledonia*

ABSTRACT

Studies were made in the equatorial region and some parts of the central tropical south Pacific Ocean to determine the apparent mechanisms of remineralization of the organic matter. Remineralization leads to nutrient rates or oxygen consumption rates which differ according to the water mass and the location. Studies were made of the differences in the observed and the theoretical ratios between the quantities of nitrogen, phosphorous, and carbon that are mineralized. Other differences examined included those that vary with water depth and longitude. Recent evidence indicates that the conditions that are specific to the Coral Sea may also be found in the entire western tropical South Pacific.

INTRODUCTION

The recent cruises of N. O. CORIOLIS, ALIZE from November 1964 to March 1965 along the Equator between the Galapagos islands and the Solomon archipelagos, ATOLL from December 1964 to January 1965 in the central zone of the South Pacific Ocean, have made possible the study of variation of properties of water masses down to a depth of 4000 m in terms of longitude at the Equator and latitude towards 140° W. They have also made possible a comparison between these properties and those of the Coral Sea water masses. Special attention was given to the elements participating in the photosynthesis mechanisms and remineralization of organic matter, and particularly to soluble phosphorus, nitrate and nitrite, total carbon dioxide as well as oxygen.

These studies reveal certain apparent characteristics of the organic matter; to the extent where the distributions reflect the preformed concentrations, they show the liaison between the distribution and the geographic location. In fact, within the limits of certain hypotheses, the studies also emphasize the independence of the rate of mineralization of the various nutrient salts in relation to external factors.

HYDROLOGICAL OUTLINE

The studies were performed in two regions; the zone of equatorial

¹Part of this work was carried out under contract with the Direction des Centres d'Essais Nucléaires (DIRCEN) and Centre d'Expérimentation du Pacifique (CEP).

upwelling in one hand, the central zone of the tropical Pacific Ocean on the other hand.

In the first one, we observe a relative homogeneity of intermediate and deep waters having a sigma-t greater than 26.4 and with a depth greater than 300 m; these waters are located under the Cromwell countercurrent. As for the surface and sub-surface waters of the south equatorial current or of the Cromwell counter-current, the mean temperature and salinity have a tendency to increase regularly towards the west.

The second region, which in view of all the studied properties is extremely differentiated, is diversified as well in latitude as in depth because it forms a transition between the very rich equatorial waters and the oligotrophic waters of the tropical zone.

One can discern in the layer of homogeneous surface water, three regions characterized by waters clearly different; these three regions have a zonal type distribution, their approximate limits being respectively 20° S and 22° S.

Between the surface waters thus clearly defined and the intermediate antarctic waters, the transition layers are a mixture of these two masses; however, their type differs according to the latitude. To the north of 18° S there is a type intermediate between the water of the equatorial Pacific and the water of the southeast Pacific which explains the still very strong influx of the equatorial water. To the south of 18° S the mixture develops towards the water of the central southwest Pacific.

RELATIVE DISTRIBUTION OF THE VARIOUS NUTRIENT SALTS

Oxygen-Soluble Phosphorus.—In the equatorial zone, the apparent ratio $UAO/PO_4\text{-P}$ differs according to the layers and varies with the longitude.

Such also is the case in the surface layer of the south equatorial current where the apparent consumption of oxygen is less than 2 ml/liter, the ratio $UAO/PO_4\text{-P}$ appears to be greater than the theoretical ratio of mineralization of organic matter, as well to the east as to the west of 140° W (Fig. 1); it does not vary with the longitude.

One can regard the south equatorial current, limited toward its lower part by the Cromwell counter-current, as a relatively closed system where the distribution is stationary and which is fertilized essentially by the equatorial water derived from the sub-Antarctic water emerging to the surface west of Peru and then transported towards the west by the south equatorial current. If such is the case, the high under saturation of the oxygen-deficient surface waters in a zone of great primary productivity suggests that mineralization of organic matter is very high. The mineralization of phosphorus being rather fast, a non-negligible fraction of this element can be remineralized in the center of the euphotical layer, with reduced transport, by precipitation in the deeper layers, of phosphorus organic matter produced in the surface. The comparative study of distri-

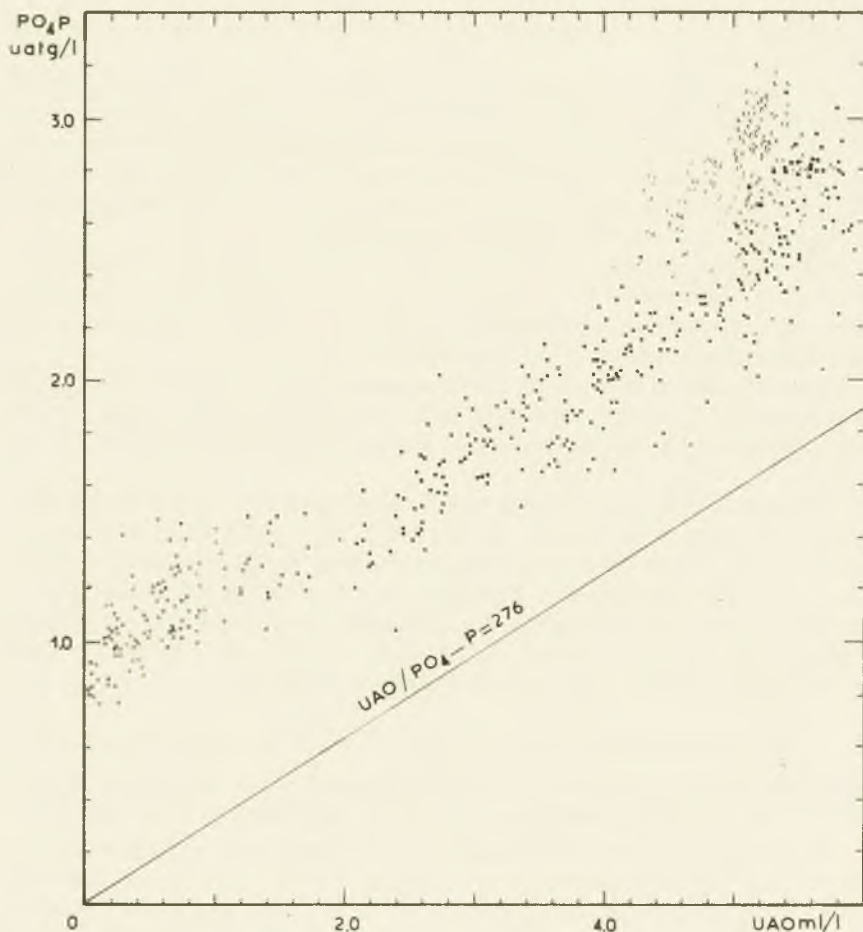


FIGURE 1. Relative distribution of apparent utilization of oxygen and phosphate at the Equator, east of 140° W. Circles: values in the surface waters where UAO is lower than 2 ml/l. Dots: values in the intermediate layer, up to UAO maximum. Cross marks: deep waters.

bution of phosphate and nitrate concentrations with longitude will show later that such is probably the case.

The intermediate zone between the upper part of the Cromwell Current and the maximum of apparent utilization of oxygen is characterized by a mineralization ratio UAO/PO_4-P varying with the longitude; the apparent consumption of oxygen per atom of released phosphorus diminishing toward the West. The significant part of this zone being occupied by Cromwell counter-current (Lemasson *et al.*, 1965), we can also compare

it to a closed system with stationary distribution, in which the exchanges with the adjoining layers are restrained by the considerable stability at the upper and lower limits of the zone. Under these conditions, the balance of mineralization mechanisms are only partially modified by diffusion, and the correlation $UAO/PO_4\text{-P}$ (Fig. 1) could reflect exactly the real mechanisms *in situ*. However, the difference between the mineralization ratios observed, 270 to the east of 140° W and 185 to the west of 140° W, brings certain problems. In fact, if the apparent excess of phosphorus results either from the presence of preformed phosphate in the west or is the consequence of a selective oxidation, the direction of the flow is such

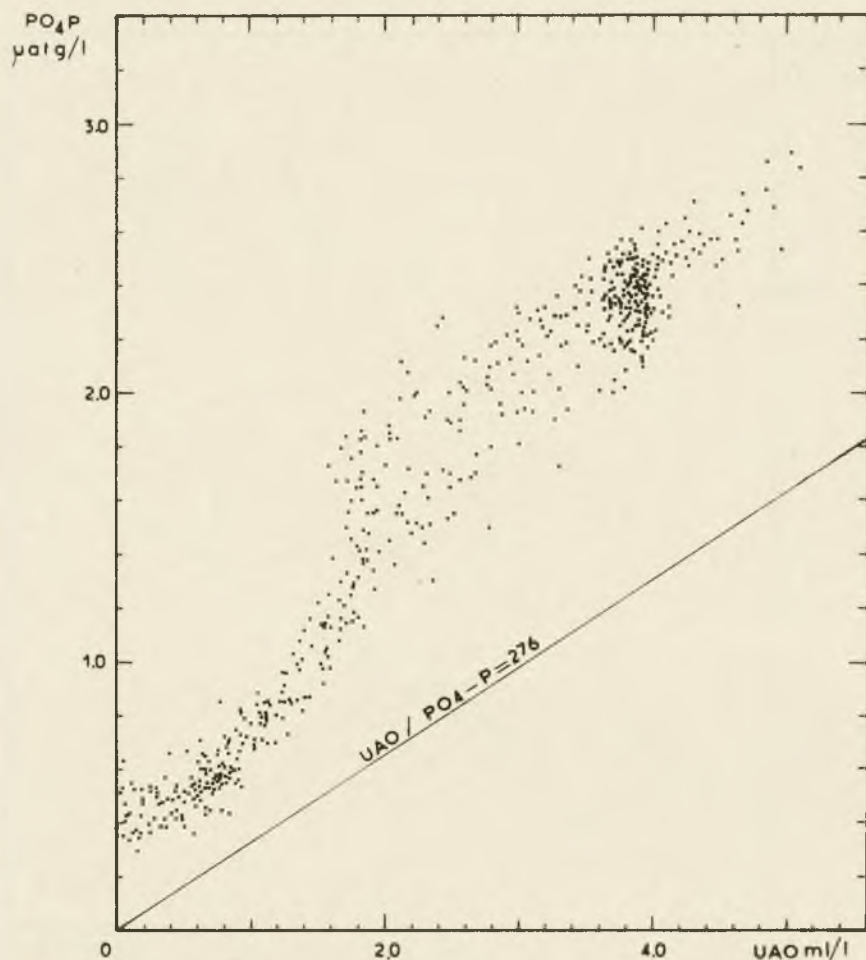


FIGURE 2. Relative distribution of apparent utilization of oxygen and phosphate in the tropical Pacific between 15° S. and 30° S.

that in the eastern part of the Cromwell Current the mineralization according to the normal ratios should lead to a distribution showing the characteristics of the western part. The fact that at the end of the course the regression becomes normal could indicate that the apparent excess of phosphate found in the east was counter-balanced by an ulterior deficiency derived from a mineralization ratio nearing 540, but the mineralization ratios from 185 to 540, although possible, are exceptional.

The preformed phosphate content which derives from the apparent correlations $UAO/PO_4\text{-P}$ is relatively constant along the Equator. In the surface and sub-surface waters, it decreases towards the west starting with

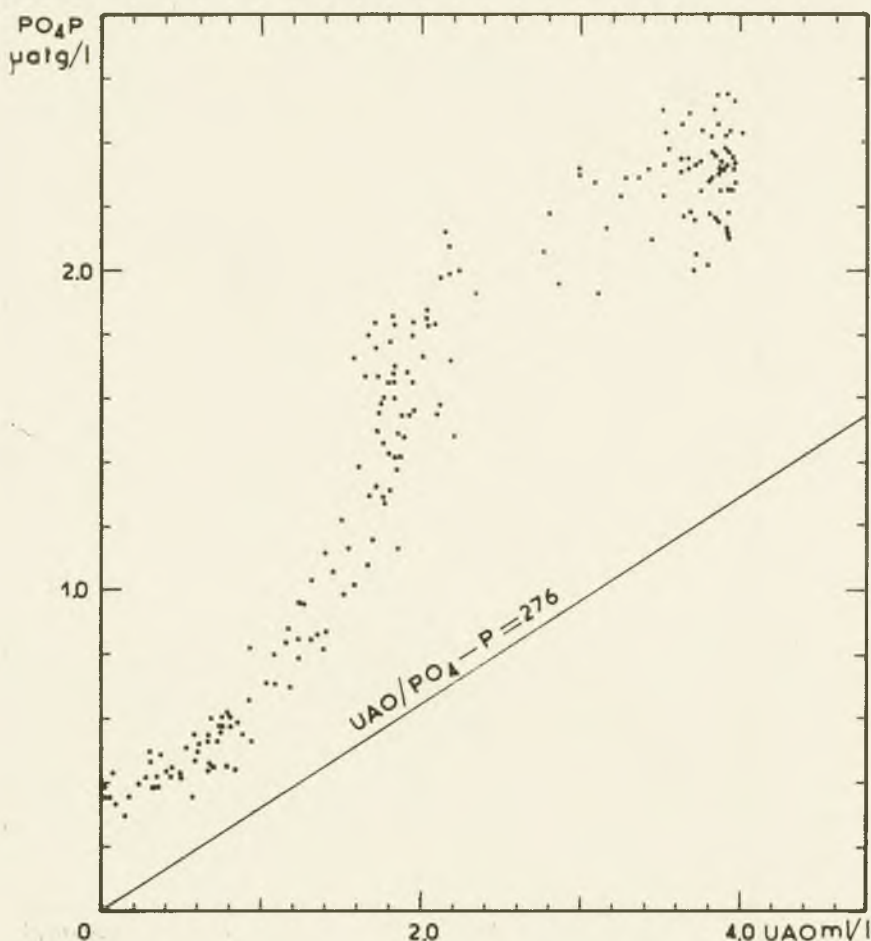


FIGURE 3. Relative distribution of apparent utilization of oxygen and phosphate in the tropical Pacific, south of 22° S.

a value of about 1.0 mg-at/m^3 , which corresponds appreciably to the content found in surface water at the source. To the contrary, in the zone of Cromwell counter-current it decreases towards the east with a value of about 0.8 mg-at/m^3 .

In the tropical zone, the apparent oxygen-phosphate ratio can vary, not only with the depth but also with the latitude. The characteristic diagram of waters between 15° S and 25° S (Fig. 2) is very close to the one found in the Coral Sea (Rotschi, 1962); it shows that there exists two completely different layers. On the one hand the waters with UAO less than 2 ml/liter , which lower limit is the minimum oxygen or the intermediate Antarctic water, give a more or less exponential regression. On the other hand the deep waters with UAO more than 2 ml/liter show a linear regression.

A differentiation appears also in latitude, concerning particularly the intermediate waters, and this differentiation is tied to the zonal fractionation of the surface and sub-surface waters, which was previously described. For example, to the north of 20° S , between the sub-surface waters with a phosphate content between 0.4 and 1.0 mg-at/m^3 , and the deep waters located under the oxygen minimum, both characterized by a ratio $\text{UAO}/\text{-PO}_4\text{-P}$ close to 276 , we have a definite mixing zone indicated also by a linear regression but with a slightly higher slope. However, to the south of 22° S , the same mixing zone indicates an exponential type regression (Fig. 3).

The concentration of preformed phosphate in the deep water is independent from the latitude; it is close to 1.2 mg-at/m^3 , a value which could also be attributed to deep equatorial waters but with less certainty.

The preformed phosphate content in the sub-surface layer varies also with the latitude, with the decrease of phosphate of the surface waters. This content fluctuates about 0.40 gm-at/m^3 to the north of 20° S , and 0.30 gm-at/m^3 to the south of 20° S .

The exponential type regression found in the Coral Sea and in the central tropical Pacific is also characteristic of all the southwest Pacific, as the Australian cruises, between 180° E and 150° E , 30° S and 10° S , have shown (Anonymous, 1962a). Furthermore, the ORSOM III cruises in the southwest Pacific (Rotschi, 1962) also bring into evidence a zonal differentiation. The regression obtained during the only cruise carried out to the south of 20° S coinciding exactly with the one found during the ATOLL cruise at the same latitude, whereas the more northerly cruises in inter-tropical zones, indicate a tendency to become more linear as in the central Pacific.

The Australian cruises in the Indian Ocean, to the north of 20° S and between 110° E and 120° E , reveal some correlations of the same type as the ones found in the corresponding zone of the Pacific Ocean (Anonymous, 1962b).

Oxygen-Nitrate.—The relative distribution of oxygen and nitrate, presents

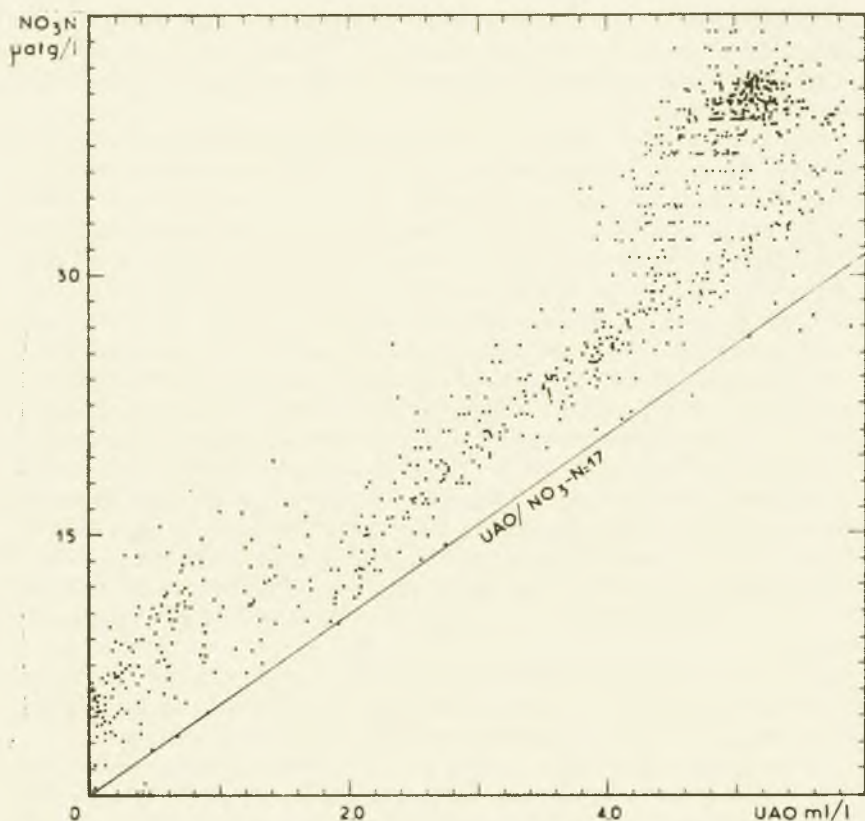


FIGURE 4. Relative distribution of apparent utilization of oxygen and nitrate along the Equator.

all the characteristics previously mentioned. In the equatorial zone, we find three distinct layers distinguished by either a different apparent ratio UAO/NO_3 or a different preformed content.

In the surface layer, the apparent ratio UAO/NO_3 is about 25, which is greater than the theoretical ratio of 17; besides, the preformed nitrate content decreases towards the west, proportional to the increasing rate of utilization of the initial reserve of nitrate contained in the upwelling waters of Peru. The decrease towards the west of the preformed nitrate concentration, with about 10 mg-at/m³ at 100° W, 6 mg-at/m³ at 140° W, and 2 gm-at/m³ at 180° W, indicates that in this upper layer, the rate of remineralization of the nitrogen to nitrate must be very low.

As for the zone of the Cromwell counter-current, limited to one side by the isoline UAO 2 ml/liter and to the other by the UAO maximum, the mineralization ratio of the nitrogen is very close to 17 in the entire

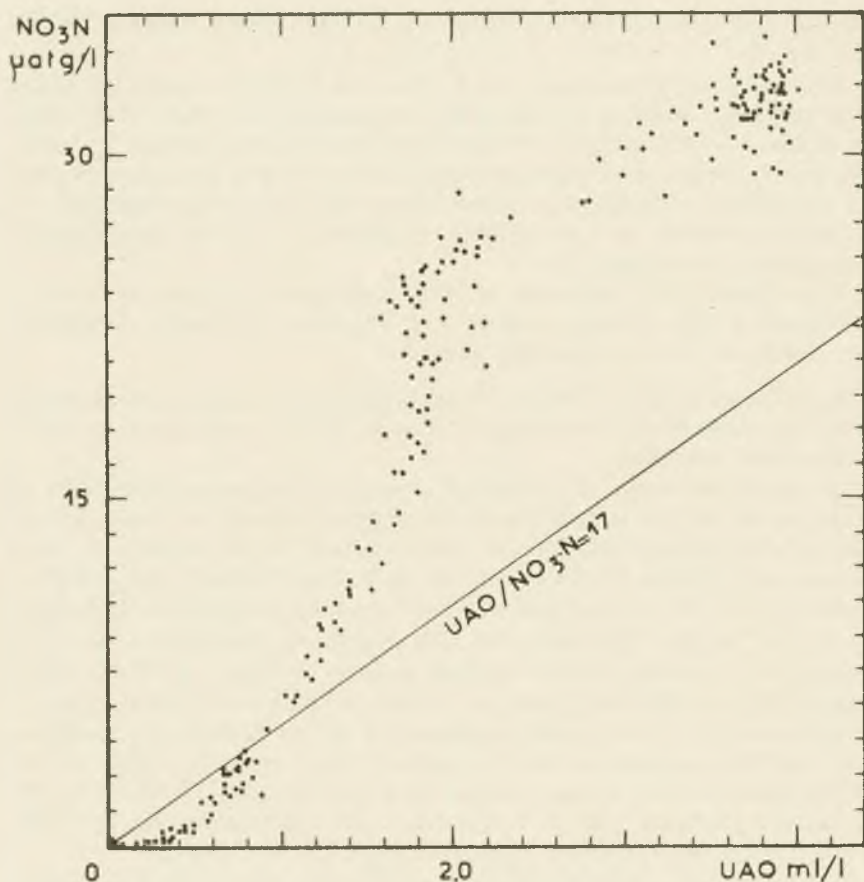


FIGURE 5. Relative distribution of apparent utilization of oxygen and nitrate in the tropical Pacific, south of 22° S.

transpacific section (Fig. 4). However, the calculation shows that some statistically significant differences exist between the regression coefficients at various latitudes; at 110° W we have a ratio of 16, whereas, it is 14 at 140° W and only 12 at 160° W. These differences should be compared with the ones found in phosphate with a correlation UAO/PO_4-P fluctuating with the longitude, and these differences have probably the same origin and the same significance.

The tropical waters present a diagram UAO/NO_3-N of the same type as the diagram UAO/PO_4-P . As for the phosphate, this diagram can be dissociated into an exponential type regression characteristic of sub-tropical waters (Fig. 5), a linear type regression characteristic of inter-tropical

waters, and an intermediate regression for the waters between 20° S and 22° S.

However, the sub-surface waters show an evident nitrate deficiency. This deficiency which is only partially compensated (less than 10 per cent, in general) by the nitrite in solution indicates the slow process by which the mineralization of nitrogen proceeds, compared with the mineralization of phosphorus. Therefore, it corroborates the hypothesis expressed by numerous authors on the relative sluggishness of the mineralization mechanisms of nitrogen.

The characteristic regression of deep tropical-waters indicates that the preformed nitrate content is about 13.0 mg-at/m³, this value could also be significant of deep equatorial-waters.

Oxygen-Total Carbon Dioxide.—The distribution of total carbon dioxide does not indicate any biochemical stratum like the ones found in phosphorus and nitrogen.

In equatorial waters as in tropical waters, the regression UAO/CO_2 is linear up to the proximity of minimum oxygen; however, we must observe that the regression coefficient is, whatever may be the nature of water masses, significantly different from the theoretical oxidation ratio which is equal to 276/106 or 2.6, if we take into account the oxidation of nitrogen.

In fact, in the equatorial zone the regression coefficient UAO/CO_2 equals 2.1, whereas, in the tropical zone it is only 1.8. The oxygen consumption is therefore lower, or rather an excess of carbon exists in comparison with the quantities implicated in the synthesis or the decomposition of the molecule of carbon hydrate; this particular aspect of the distribution of total carbon dioxide had already been observed in the Coral Sea (Rotschi, 1962), as well as in the southeast Pacific (Rotschi, 1965) where the apparent excess of carbon is still greater.

Lastly, if also a significant latitudinal differentiation exists in the above mentioned regression coefficients, there is no longitudinal difference, the entirety of the equatorial zone showing the same ratio UAO/CO_2 .

The mechanisms which intervene in the differentiation of the south equatorial current, the Cromwell counter-current, the sub-surface tropical waters, the intermediate antarctic mass and the deep waters are therefore without effect on the distribution of carbon dioxide.

Essay on Quantitative Interpretation.—From a biochemical view-point, a water stratification which is characterized by certain specific relations between the nutritive elements is present in tropical zones.

The surface and subsurface layers including the south equatorial current with a depth varying between 48 m at 100° W and 140 m at 167° E, is characterized by rates of apparent mineralization leading to a ratio O/C/N/P equal to 400/182/17/1, with an oxygen deficit of 32 atoms. In this layer, in spite of high primary productivity, and although

the phosphate concentration decreases towards the west, the quantity of this compound available for photosynthesis, increases slightly. For example, at 100° W where the equatorial current has a depth of 48 m, the mean phosphate content is 1.48 mg-at/m^3 and the concentration in the entire layer reaches 71.2 mg-at/m^2 ; at 167° E the depth is 141 m, the mean phosphate content is 0.58 mg-at/m^3 and the concentration in the entire layer is 81.4 mg-at/m^2 . Consequently, there is a slight enrichment which is due particularly to the oxidation of organic matter, since the vertical diffusion is limited by a very strong stability.

As far as nitrate is concerned, its concentration runs from 748 gm-at/m^2 at 100° W to 33 gm-at/m^2 at 167° E; there is a loss of 715 gm-at/m^2 representing a fixation by photosynthesis of 42 mg-at/m^2 of phosphate.

Compared with nitrate, the phosphate enrichment of the equatorial zone from east to west is 52 mg-at/m^2 , 42 mg-at/m^2 which can result from the rapid oxidation of the phosphorus fraction of the organic matter originated in the euphotic layer and the complement which can be derived from an excess of the quantity of phosphorus atoms penetrating the zone of the south equatorial current above the one which is swept away to the west of 167° E.

Nevertheless, the surface waters are generally under-saturated in oxygen and there is an oxygen minimum strongly indicated at a depth lower than 500 m, in the vicinity of the lower limit of the Cromwell Current. Therefore, the apparent excess of UAO can be attributed to an excess of the diffusion towards the lower layers upon the transfer of atmospheric oxygen across the surface.

The zone of Cromwell counter-current which draws nearer the surface towards the east is characterized by an apparent ratio of oxidation varying in function of the longitude. In the western part, to the west of 140° W, the oxidation ratio O/C/N/P is 185/84/16/1 with an oxygen deficit of 47 atoms for each phosphorus atom; in the eastern part, it becomes 270/120/16/1 with an apparent deficit of 34 oxygen atoms. In these waters, between 167° E and 100° W, the phosphate content increases from 379 mg-at/m^2 to 512 mg-at/m^2 , with an enrichment of 133 mg-at/m^2 . The nitrate content goes from 3816 mg-at/m^2 to 6560 mg-at/m^2 and augments by 2744 mg-at/m^2 . In relation to phosphate the excess nitrate is close to 500 mg-at/m^2 . This differential enrichment in the direction of the counter-current is an example of the consequences of the estuarial type circulation on the distribution of nutrient salts, as discussed by Redfield, Ketchum & Richards (1963). It clearly indicates that to the extent that the Cromwell Current slows the exchanges with the adjacent layers, there is actually a differential oxidation of the organic matter, the phosphorus being oxidized in the south equatorial current and the nitrogen in the Cromwell Current.

As far as the tropical waters are concerned, one must observe that if in

the sub-surface layer as in the deep layer, the oxidation ratios $\text{UAO}/\text{PO}_4\text{-P}$ and $\text{UAO}/\text{NO}_3\text{-N}$ are close to the theoretical values, there is a nitrate deficiency in the sub-surface layer. This deficiency of about 1.5 mg-at/m^3 can neither be counter-balanced by nitrate which scarcely represents 10 per cent of this deficit nor by particulate nitrogen. However, it is more likely that this deficiency derives from the slow process of nitrogen oxidation compared with the one of phosphorus.

With regard to intermediate layers giving some oxidation ratios slightly different from the theoretical ratios (as the ones of the tropical zone where, according to latitude, the regression is either of a linear or an exponential type) the variation of the composition of mineralized organic matter is not necessarily the best explanation. Pytkowicz (1964) has recalled that, in a standard water, the variation of oxygen content in relation to time is



FIGURE 6. Relative distribution of oxygen and phosphate in the core of the Cromwell Current.

proportional to the variation of phosphate concentration, according to the equation:

$$\Delta O_2 = -a \Delta PO_4 + b$$

In this equation a is the oxidation ratio, and b a parameter representing the preformed concentrations. He emphasizes that the mixture of two types, characterized by two equations having different parameters b , shall be represented by a straight line, except in the instance when the ratio of masses of each of the two types does not vary with depth (which seldom occurs in nature). In another instance, each mixing point can be any point on different straight lines, and the final curve can take a great variety of forms.

In the intermediate layer of the sub-tropical zone where the regression is of an exponential type, we find an example of the mixing of two typical waters characterized by preformed phosphate contents equal to 0.4 mg-at/m³ for the upper water and 1.2 mg-at/m³ for the lower water. The diagram UAO/PO₄P indicates that the upper layers of this intermediate zone are particularly modified according to the biochemical mechanism and that the effect of the diffusion increases with depth. The nature of the final mixture is therefore bound to the variation with depth, of the stability and intensity of vertical turbulences. Such is also the case for the linear regressions observed in inter-tropical waters.

The western part of the Cromwell counter-current, where the apparent oxidation ratios O/P and O/N are lower than the theoretical ratios, presents a particular problem. In the median layer where the mean concentrations of oxygen and phosphorus vary in an inverted direction with longitude, the correlation O/P (Fig. 6) gives an oxidation ratio of 274. During its set towards the east, this median layer keeps the characteristics of a standard water in which the mean composition of organic matter is such that the oxidation ratio is close to the theoretical value. The ordinate, at the origin of the straight line of regression, being 8.0 ml/liter O₂ and the mean content in preformed phosphate 0.9 mg-at/m³, the oxygen content at the point where Cromwell current originates should be about 5 ml/liter. This characteristic could ascertain the theory that the decrease towards the west of the oxidation ratios should be simply the result of a mixing with a lower layer containing a concentration of preformed phosphate increasing towards the west as is generally the case in tropical waters. However, the accumulation of preformed phosphate in the western part should have an effect upon the eastern distribution of phosphate; this does not appear to be the case since the waters of the eastern part seem less abundant in preformed phosphate than the western waters.

In addition, the enrichment greater in nitrogen than in phosphorus in the eastern direction, infers the presence of a selective mineralization of organic matter, proportionally richer in nitrogen than in phosphorus.

Remark.—Part of this work was carried out under contract with the

"Direction des Centres d'Essais Nucleaires" (DIRCEN), "Centre d'Experimentation du Pacifique" (CEP).

REFERENCES

ANONYMOUS

1962a. CSIRO, Australian Oceanogr. Crs. Rep. No. 5: 255 pp.

1962b. CSIRO, Australian Oceanogr. Crs. Rep. No. 1: 134 pp.

LEMASSON, L., Y. MAGNIER, J. NOEL, AND B. PITON

In Press. Sur certaines propriétés physico-chimiques possibles du contre-courant de Cromwell.

MCGILL, D. A.

1964. The distribution of phosphorus and oxygen in the Atlantic Ocean as observed during the IGY, 1957-1958. In Sears, M., Ed., Progress in Oceanography, 2: 127-211, Pergamon Press, Oxford.

PYTKOWITZ, R. M.

1964. Oxygen exchange rates off the Oregon coast. Deep-Sea Res., 11: 381-389.

REDFIELD, A. C., B. H. KETCHUM, AND R. A. RICHARDS

1963. The influence of organisms on the composition of sea water. In Hill, M. N., Ed., The Sea, 2: 26-77, Interscience, N. Y.

ROTSCHI, H.

1962. Oxygène, phosphate et gaz carbonique total en mer de Corail. Deep-Sea Res., 8: 181-195.

1965. Le pH et l'alcalinité des eaux profondes de la fosse des Hébrides et du bassin des Fidji. In Sears, M., Ed., Progress in Oceanography, 3: 301-310, Pergamon Press, Oxford.

In Press. Résultats des observations physio-chimiques de la croisière ATOLL.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING

1942. The Oceans. Prentice-Hall, Inc., N.Y., 1087 p.

NANNOPLANKTON AND THE CARBON CYCLE IN TROPICAL WATERS¹

MARY BELLE ALLEN²

Laboratory of Physical Biology, National Institute of Arthritis and Metabolic Diseases, Bethesda, Maryland

ABSTRACT

An intensive investigation of cultures of two marine chrysomonads, *Coccolithus huxleyii* (an important oceanic primary producer) and *Hymenomonas* sp. (a neritic form), has provided information on their growth and photosynthesis under different light conditions, their pigment composition, the organization of their pigment system, and the relative stability of the pigments. Both organisms contain relatively large amounts of chlorophyll *c*. Active, morphologically intact, chloroplasts have been isolated from these organisms, and studies of the more detailed mechanism of their photosynthesis are proceeding.

INTRODUCTION

The various small algae known collectively as the nannoplankton are important primary producers in the tropical seas. However, although their importance was recognized early in the development of biological ocean-

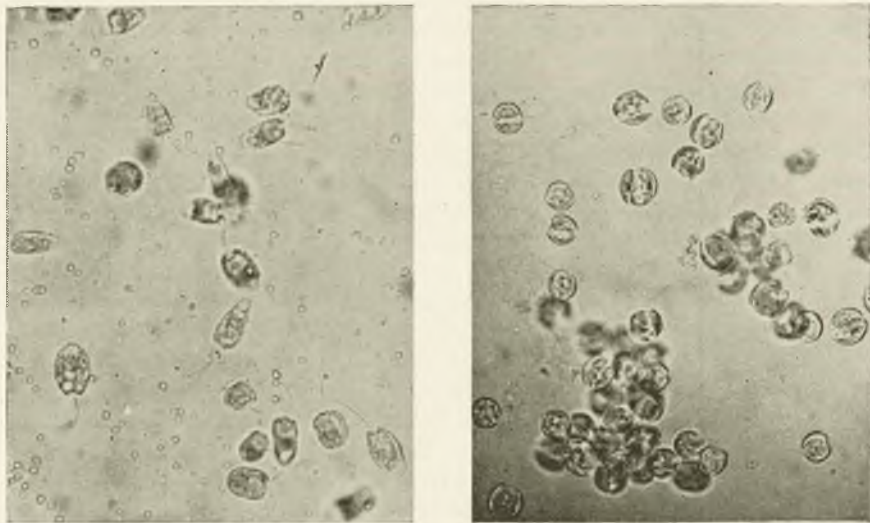


FIGURE 1. Photomicrographs of, (a) a *Tetraselmis* sp., and (b) *Hymenomonas* sp., after 3 months storage in 5 per cent glutaraldehyde solution. 400 \times .

¹Experimental work described in this paper was supported in part by Contract Nonr-3015-00 with the Office of Naval Research and Contract AT-04-3-232 with the Atomic Energy Commission.

²Present address: Department of Tropical Sciences, University of Alaska, College, Alaska.

ography, they have been relatively little studied. This is due partly to the fact that special methods, such as filtering or centrifuging large volumes of water, are necessary for their collection and, possibly more important, to the lack of suitable methods for their preservation. This difficulty with fixation has been a barrier to several types of investigations of these organisms: taxonomic studies, investigations of their distribution, and ecologically oriented cultural studies, since a lack of reference material makes it difficult to compare the material brought into culture with that collected from nature.

Recently, however, a simple technique for preserving nanoplankton, based on the techniques used in electron microscopy, has been developed (Murchio & Allen, In Press). It consists of placing the organisms in 5 per cent neutralized glutaraldehyde (in sea water, for marine plankton), with certain precautions, then keeping them cold and dark. Photographs of nanoplankton organisms preserved in this manner are shown in Figure 1.

The color of the cells is also excellently preserved by this treatment. In fact, it has been found that the pigments are quantitatively preserved, so that samples fixed in glutaraldehyde can be used for future pigment determinations.

MATERIALS AND METHODS

The principal types of organisms in the nanoplankton are chrysomonad and cryptomonad flagellates, small naked dinoflagellates, and small diatoms. Since these organisms are important producers about whose photosynthesis we know little, laboratory studies of growth and photosynthesis of two marine chrysomonads have been carried out (Jeffrey & Allen, 1964).

The chrysomonads, which include the coccolithophores and the golden brown flagellates, are widely distributed in the temperate and tropical oceans. In some areas they are the dominant members of the phytoplankton. (Bernard & Lecal, 1950; Knight-Jones, 1951; McAllister, Parsons & Strickland, 1960) Some chrysomonads, such as the fresh water *Ochromonas*, contain only chlorophyll *a*, but most organisms in this class which have been examined also contain chlorophyll *c* and fucoxanthin as major accessory pigments (Allen, Goodwin, & Phagpolngarm, 1960; Parsons, 1961; Jeffrey, 1964). Although a great deal is now known about the photosynthetic mechanisms of higher plants and green algae which contain chlorophylls *a* and *b* (cf. Vernon & Avron, 1965, for a recent review) and the photosynthetic bacteria (cf. Gest, San Pietro, & Vernon, 1963), little is known of photosynthesis as it occurs in the marine algae which contain chlorophyll *c* and either fucoxanthin (chrysomonads, diatoms, brown algae), peridinin (dinoflagellates), or biliproteins (cryptomonads) as additional accessory pigments. Little is known of the mechanisms of light energy conversion and the products of carbon fixation in these organisms. Action spectra for brown algae and diatoms have suggested a photosynthetic function for chlorophyll *c* and fucoxanthin (Haxo & Blinks, 1950;

Tanada, 1951), but more detailed studies are needed before the precise role of these pigments is known.

The organisms chosen for study were *Coccolithus huxleyii* and a *Hymenomonas* sp. whose nutrition in pure culture was studied by Pintner & Provasoli (1962). These authors found that *C. huxleyii*, which is a widely distributed oceanic organism, is a photolithotrophic organism practically devoid of heterotrophic abilities, whereas the *Hymenomonas*, which inhabits euryhaline inshore environments, can utilize a wide range of organic carbon and nitrogen sources, although they are not necessary for growth.

TABLE 1

PIGMENT COMPOSITION OF *Coccolithus huxleyii* AND *Hymenomonas* SP.
VALUES GIVEN ARE MG PIGMENT/G DRY WT. OF ORGANISMS

	<i>Coccolithus huxleyii</i>	<i>Hymenomonas</i> sp.
Chlorophyll <i>a</i>	7.25	21.4
Chlorophyll <i>c</i>	4.68	3.7
Carotenes	0.09	1.35
Diatoxanthin	0.09	3.20
Diadinoxanthin	0.40	1.13
Unknown xanthophyll ₁	0.17	—
Unknown xanthophyll ₂	0.57	—
Fucoxanthin	2.97	8.94
Neofucoxanthin A and B	0.70	2.10
Total chlorophylls	11.93	25.1
Total carotenoids	4.99	16.72
Ratio chlorophyll <i>a</i> /chlorophyll <i>c</i>	1.55	5.78

(from Jeffrey and Allen, 1964)

The pigments of these two organisms are shown in Table 1. It will be noticed that both of them contain appreciable amounts of chlorophyll *c*. *Coccolithus huxleyii*, in fact, contains almost as much chlorophyll *c* as *a*. There are frequent reports of natural plankton samples that contain much more chlorophyll *c* than *a* (Humphrey, 1960; 1963, for example), although no organisms are known with this proportion of the pigments. Since natural samples may contain appreciable quantities of dead and disintegrating algae, a greater stability of chlorophyll *c* in such cells might account for the results observed. Measurements with broken cell suspensions of *Hymenomonas* and *C. huxleyii* have shown that chlorophyll *c* is indeed more stable than chlorophyll *a* when illuminated in such suspensions (Jeffrey & Allen, 1964). Results of a typical experiment are shown in Figure 2.

RESULTS

The growth, photosynthesis, and chlorophyll content of cultures of *Hymenomonas* and *C. huxleyii* are shown in Figure 3. Both organisms

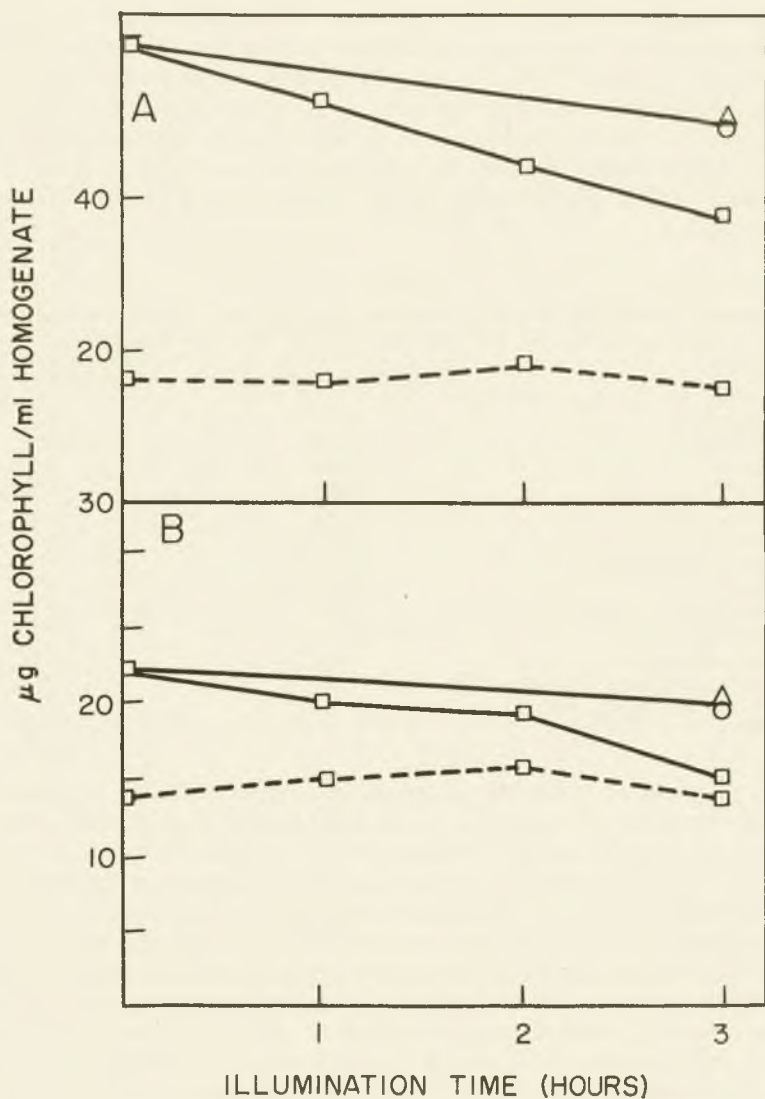


FIGURE 2. Stability of chlorophylls *a* and *c* in broken cell preparations of *C. huxleyii* (bottom) and *Hymenomonas* (top). Dotted lines, chlorophyll *c*; solid lines, chlorophyll *a*; squares, illuminated at 3500 ftc; circles and triangles, dark controls.

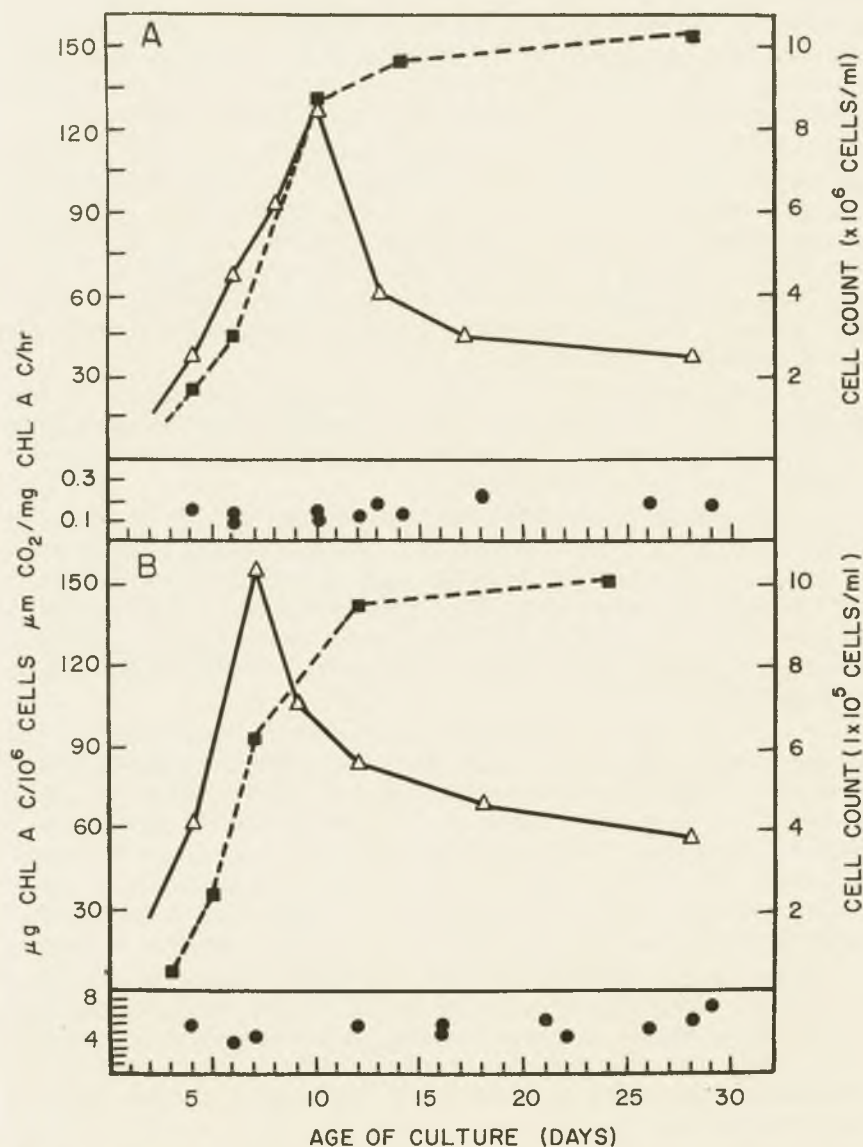


FIGURE 3. Growth, photosynthesis, and chlorophyll content of cultures of *C. huxleyii* (A) and *Hymenomonas* (B). Dotted lines, growth; solid lines, photosynthesis; circles, chlorophyll content per cell (from Jeffrey & Allen, 1964).

reached their maximum population density in about 14 days at 14°C. Since the organisms were grown in stationary culture without added carbon dioxide, the growth rates and population densities observed may not be the maximum obtainable at the temperature and light intensity used. However, Antia & Kalmakoff (1965) have obtained similar growth rates and cell yields in a stirred system with added carbon dioxide.

It will be noted that the chlorophyll content per cell did not vary significantly during growth of the cultures, nor was there any consistent change in the ratio of chlorophyll *a* to *c* as the cultures aged. The rate of photosynthesis, by contrast, varied greatly with the age of the culture, reaching a maximum of 150-200 μ moles CO₂/mg chlorophyll (*a* + *c*)/hr in 10 day cultures, near the end of the period of most rapid growth. After this, although the cultures continued to grow slowly, the carbon-dioxide uptake declined to low values.

Since photosynthesis was measured by radiocarbon uptake, it was possible to show that in these short term experiments all the radiocarbon fixed remained in the cells; soluble photosynthetic products were not "leaked" to the surrounding medium.

Optimal growth of *Hymenomonas* was obtained at light intensities of 800 ft-c or higher, whereas growth of *C. huxleyi* became light saturated at the low intensity of 200 ft-c, and was not affected by further increase in light intensity. Photosynthetic carbon dioxide fixation by both organisms was saturated at 3500 ft-c. This phenomenon of much more light being required to saturate photosynthesis than growth is quite common among the algae (Myers, 1946).

As a preliminary to more detailed studies on the utilization of light energy by these organisms, photosynthetically active chloroplast preparations have been obtained from *Hymenomonas* (Jeffrey, Ulrich, & Allen, 1966). These chloroplasts retain up to 25 per cent of the photosynthetic capacity of the whole cells from which they are derived, and are also active in partial photosynthetic reactions such as the Hill reaction and photophosphorylation. Electron micrographs have shown them to be morphologically intact, possessing their bounding membrane and their pyrenoid.

Carbon dioxide fixation rates and chlorophyll content of sea water samples are widely used to assess the productivity of the planktonic algae in the oceans. Similar, and more detailed, studies applied to organisms in pure culture provide a guide to the interpretation of results with natural populations, particularly in areas where one type of primary producer may predominate.

REFERENCES

- ALLEN, M. B., T. W. GOODWIN, AND S. PHAGPOLNGARM
1960. Carotenoid distribution in certain naturally occurring algae and in some artificially induced mutants of *Chlorella pyrenoidosa*. J. Gen. Microbiol., 23: 93-103.

- ANTIA, N. J. AND J. KALMAKOFF
1965. Growth rates and cell yields from axenic mass culture of fourteen species of marine phytoplankters. Fish. Res. B. Canada, Manuscript Reports Series, No. 203.
- BERNARD, F. AND J. LECAL
1950. Plancton unicellulaire recolte dans l'ocean Indien par le Charcot (1950) et le Norsel (1945-46). Bull. Inst. oceanogr., Monaco, No. 1116.
- GEST, H., A. SAN PIETRO, AND L. P. VERNON, (EDS.)
1963. Bacterial photosynthesis. The Antioch Press, 523 pp.
- HAXO, F. T. AND L. R. BLINKS
1950. Photosynthetic action spectra of marine algae. J. gen. Physiol., 33: 389-422.
- HUMPHREY, G. F.
1960. The concentration of plankton pigments in Australian waters. Div. Fish. Oceanogr., CSIRO, Tech. paper No. 9, 27 pp.
1963. Seasonal variations in plankton pigments in waters off Sydney. Austr. J. Mar. Freshw. Res., 14: 24-36.
- JEFFREY, S. W. AND M. B. ALLEN
1964. Pigments, growth, and photosynthesis in cultures of two chryso-monads, *Coccolithus huxleyii* and a *Hymenomonas* sp. J. gen. Microbiol., 36: 277-288.
- JEFFREY, S. W., J. ULRICH, AND M. B. ALLEN
1966. Some photochemical properties of chloroplast preparations from the chrysoomonad *Hymenomonas* sp. Biochim. Biophys. Acta, 112: 35-44.
- KNIGHT-JONES, E. W.
1951. Preliminary studies of nanoplankton and ultraplankton systematics and abundance by a quantitative culture method. J. du Conseil., 17: 140-155.
- MCALLISTER, C. D., T. R. PARSONS, AND J. D. H. STRICKLAND
1960. Primary productivity at station 'P' in the north-east Pacific Ocean. J. Cons. int. Explor. Mer., 17: 140-150.
- MURCHIO, J. C. AND M. B. ALLEN
In Press. Preservation of nannoplankton. Limnol & Oceanogr.
- MYERS, J.
1946. Culture conditions and the development of the photosynthetic mechanism. VI. Influence of light intensity on photosynthetic characteristics of *Chlorella*. J. gen. Physiol., 29: 429-440.
- PARSONS, T. R.
1961. On the pigment composition of eleven species of marine phytoplankters. J. Fish. Res. B. Canada, 18: 1017-1025.
- PINTNER, I. J. AND L. PROVASOLI
1962. Nutritional characteristics of some chrysoomonads. Symposium on Marine Microbiology in Oppenheimer, C. H., Ed., pp. 114-121.
- TANADA, T.
1951. The photosynthetic efficiency of carotenoid pigments in *Navicula minima*. Amer. J. Bot., 38: 276-284.
- VERNON, L. P. AND M. AVRON
1965. Photosynthesis. Ann. Rev. Biochem., 34: 269-296.

THE NITROGEN NUTRITION OF PHYTOPLANKTON IN THE NORTHEASTERN TROPICAL PACIFIC OCEAN¹

WILLIAM H. THOMAS

Institute of Marine Resources, Scripps Institution of Oceanography

ABSTRACT

Mean surface concentrations of nitrogenous nutrients and phosphate are presented for various areas in the northeastern tropical Pacific Ocean. Except at the Costa Rica Dome and in other areas of upwelling, nitrate concentrations are very low. NO_3/PO_4 ratios are also generally low and phytoplankton might remove all of the nitrate while appreciable concentrations of phosphate were still present. Measurements of nitrate during growth of batch cultures of *Gymnodinium simplex* showed that concentrations below approximately $5\mu\text{g-at/liter}$ probably limited the rate of growth of this dinoflagellate. Since surface nitrate concentrations are generally lower than this value, the rate of growth of *Gymnodinium* would be limited over much of the area. Batch cultures of *Chaetoceros gracilis* were not rate-limited by the lowest nitrate concentrations used ($<1\mu\text{g-at/liter}$), and one would not expect this diatom to be limited by nitrate in this region. In two areas, one slightly northwest of the dome and the other off Baja California, the ammonia concentration is greater than that of nitrate and the N/P ratio is increased if ammonia is included with nitrate. Ammonia (and various amino compounds) supported the growth of three phytoplankton cultures from the region. Ammonia is a relatively important nitrogen source and should be included with nitrate as a measure of the total available nitrogen.

INTRODUCTION

Inorganic phosphate is the phytoplankton nutrient most often measured during oceanographic cruises, and the phosphate concentration is often taken as an index to the total available nutrient level in a given area. Since, in the northeastern tropical Pacific Ocean, phosphate is generally present in concentrations greater than $0.25\mu\text{g-at/liter}$ (Holmes, 1958; Holmes & Blackburn, 1960), a concentration found to limit the growth rate of a common diatom, *Asterionella japonica* (Goldberg *et al.*, 1951), this nutrient is probably not a good index of the *relative fertility*, which might be defined as the ability to support a high rate of phytoplankton growth.

Therefore, we have been measuring the concentrations of other nutrients during routine Scripps Tuna Oceanography Research (STOR) cruises to the eastern tropical Pacific. This paper discusses surface nitrogenous

¹Contribution from the Scripps Institution of Oceanography, University of California, San Diego. This investigation was part of the Scripps Tuna Oceanography Research program and was supported by Contract No. 14-17-0007-221 between the U.S. Bureau of Commercial Fisheries and the Scripps Institution of Oceanography. The author is grateful to Mrs. Anne N. Dodson and Mr. Edward Renger for technical assistance.

nutrient values that we have obtained and compares them with experimental studies of the utilization of nitrogen by cultures of tropical Pacific Ocean phytoplankton.

METHODS

Analytical methods for phytoplankton nutrients were those previously described (Thomas, 1966b). This previous paper also describes the experiment on nitrate uptake by *Gymnodinium* (Fig. 2) and the experi-



FIGURE 1. Map of the northeastern tropical Pacific Ocean showing areas which have been investigated. A, area investigated during cruise TEMPO, 1962; 100 miles south of Acapulco. B, area west of southern Baja California investigated in 1964-65. D, general location of Costa Rica Dome. T, Gulf of Tehuantepec.

ment on utilization of ammonia and other nitrogen sources (Table 3). The latter experiment was carried out with axenic cultures and nitrogen sources were supplied at a concentration of $100 \mu\text{g-at N/liter}$. N sources were sterilized by filtration and were added aseptically to the enriched seawater medium. In this experiment, *Chaetoceros* and *Nannochloris* cultures were incubated for 8 days and *Gymnodinium* cultures were incubated for 9 days.

The experiments on the effects of nitrate concentration on the growth rate of *Chaetoceros gracilis* (Fig. 3) were carried out with an enriched seawater medium, which consisted of 75 per cent seawater enriched with 10 $\mu\text{g-at/liter}$ $\text{PO}_4\text{-P}$, 200 $\mu\text{g-at/liter}$ $\text{SiO}_3\text{-Si}$, 0.25 mg Fe/liter (supplied as citrate), 0.0003 per cent EDTA, 0.2 mg/liter thiamine, 1.0 $\mu\text{g/liter}$ biotin, and 1.0 $\mu\text{g/liter}$ vitamin B_{12} . The inoculum was depleted of nitrate by growing it for 3 days in a portion of this medium without any addition of nitrate. The medium was sterilized by filtration through a membrane filter (pore size 0.22 μ) and 2 liters were then dispensed aseptically into several large Fernbach flasks. Additions of nitrate were made and portions were taken from each flask for nitrate analyses. Depleted cells were inoculated into each flask at low levels of inoculum (300-600 cells/ml initial count). The cultures were then incubated at 27°C and an illuminance of 800-1100 ftc. These incubation conditions were those previously found to be within the optimal range for growth of this diatom (Thomas, 1966a). Cells in each culture were counted at 4 to 8 hour intervals with a Model B Coulter counter. Following the initial lag period (approximately 5 hours) exponential division rates were calculated from logarithmic plots of the increase in cell numbers with time.

Since in this experiment, the lowest nitrate concentration found by actual analysis (1.6 $\mu\text{g-at/liter}$) was above any concentration that limited the growth rate, a second experiment was established using the medium of the first experiment after final growth had occurred. This medium was assumed to be depleted of nitrate. Cells were removed from it by filtration; the medium was reenriched with phosphate and iron; and was resterilized by filtration. It was again dispensed aseptically and the second experiment was carried out (inoculated at low levels) using depleted cells for inoculum and the same incubation conditions.

The experiment on nitrogen limitation off Baja California (Table 5) was performed on the natural phytoplankton population in near-surface water. Seawater was collected from the upper 10 m with a plastic sampler at Sta. 60, cruise TO-65-1 (25°33.3'N lat. 113°24.5'W long). The seawater was dispensed into plastic 20-liter carboys and enriched with nutrients as follows:

TREATMENT	ENRICHMENT
None	None
Complete	All of the single nutrients shown below
+ NO_3	25 $\mu\text{g-at/liter}$ $\text{NO}_3\text{-N}$ as KNO_3
+ PO_4	2.5 $\mu\text{g-at/liter}$ $\text{PO}_4\text{-P}$ as K_2HPO_4
+ SiO_3	5 $\mu\text{g-at/liter}$ $\text{SiO}_3\text{-Si}$ as $\text{Na}_2\text{SiO}_3 \cdot 9\text{H}_2\text{O}$
+ vitamins	0.5 $\mu\text{g/liter}$ vitamin B_{12} ; 100 $\mu\text{g/liter}$ thiamin; 0.5 $\mu\text{g/liter}$ biotin
+ Fe	0.2 $\mu\text{g-at/liter}$ Fe as NaFeEDTA
+ trace metals	10 $\mu\text{g/liter}$ Mn as $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ 1 $\mu\text{g/liter}$ Zn as $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ 0.5 $\mu\text{g/liter}$ Mo as $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$

	0.5 $\mu\text{g/liter}$ Co as $\text{CoCl}_2 \cdot 2\text{H}_2\text{O}$
	0.2 $\mu\text{g/liter}$ Cu as $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$
+ $\text{NO}_3^- + \text{PO}_4^-$	25 $\mu\text{g-at/liter}$ $\text{NO}_3\text{-N} + 2.5 \mu\text{g-at/liter}$ $\text{PO}_4\text{-P}$
+ $\text{NO}_3^- + \text{PO}_4^- + \text{Fe}$	25 $\mu\text{g-at/liter}$ $\text{NO}_3\text{-N} + 2.5 \mu\text{g-at/liter}$ $\text{PO}_4\text{-P}$ + 0.2 $\mu\text{g-at/liter}$ Fe

The 10 enriched carboys were incubated on deck in natural daylight. The plastic reduced the light intensity to 30 per cent of incident irradiance. The carboys were cooled by running surface seawater over them. After 4 days of incubation the chlorophyll in each treatment was measured by *in vivo* fluorescence (Lorenzen, 1966).

RESULTS AND DISCUSSION

Figure 1 shows the areas we have been studying. We have principally made measurements at the Costa Rica Dome (an area of offshore upwelling—Wyrtki, 1964), in the Gulf of Tehuantepec, at a location 100 miles south of Acapulco, and west of the southern half of the Baja California peninsula.

Table 1 gives mean surface concentrations of nitrate, nitrite, and phosphate for several of these areas. Nitrite was always much lower than nitrate, and nitrite would not serve as an appreciable source of nitrogen for phytoplankton. Nitrate was high in the upwelling Costa Rica Dome area, but always low ($< 1.0 \mu\text{g-at/liter}$) elsewhere.

The nitrate/phosphate ratio was high at the Dome but low elsewhere. The usual intracellular nitrogen/phosphorus ratio in phytoplankton is about 15:1, but may vary from 5.5:1 to 17.4:1 in phytoplankton cultures (Parsons *et al.*, 1961). Comparison of such intracellular ratios with the nitrate/phosphate ratios in surface waters suggests that, except at the dome, during nutrient uptake phytoplankton would deplete all of the nitrate before all the phosphate was removed. Nitrate would, therefore, appear to be a more likely limiting nutrient than phosphate.

Since phosphate concentrations were greater than $0.25 \mu\text{g-at/liter}$, it was probable that phosphate would not limit the *rate* of phytoplankton growth. No data were available on the rate-limiting concentration of nitrate for phytoplankton from this region. Therefore, we established batch cultures in which nitrate concentrations could be followed until nitrate had decreased to a level at which the growth rate also decreased. The experimental organism was a dinoflagellate, *Gymnodinium simplex*, which was isolated from the Costa Rica Dome.

Figure 2 shows the results of one such experiment (Thomas, 1966b). The decrease in cell concentration between 96 and 103 hours is probably an experimental error, for growth proceeded at a high rate until 155 hours. At some time between 155 and 170 hours, the growth rate decreased by 40 per cent. The nitrate concentration at 155 hours was $17 \mu\text{g-at/liter}$ and at 170 hours, it was $0.9 \mu\text{g-at/liter}$. The rate-limiting concentration would be some concentration between these values. After 170 hours, the mean

nitrate concentration was 1.5 $\mu\text{g-at/liter}$. Some further growth occurred, but at a low rate.

Addition of nitrate to a separate aliquot of the culture at 200 hours resulted in further growth; another aliquot to which no N was added grew only slightly. This established that the culture was limited by nitrogen and not by some other factor.

In a second experiment, growth decreased at some nitrate concentration between 3.9 and 7.2 $\mu\text{g-at/liter}$, and a rate-limiting concentration appeared to be about 5 $\mu\text{g-at/liter}$. Comparison of this value with surface nitrate concentrations shown in Table 1 suggests that, only in the Costa Rica Dome would one expect *Gymnodinium* to grow at a high rate. The growth rate of this alga would be limited by low nitrate concentrations elsewhere in the northeastern tropical Pacific. Mean nitrate concentrations away from the dome are also less than concentrations remaining in the cultures when growth finally had ceased.

In uptake experiments such as these, it is difficult to sample at just the right time to find exactly the concentration at which the growth rate decreases. To find the rate-limiting nitrate concentration for another Dome organism, *Chaetoceros gracilis*, we changed tactics and measured the rate as a function of initial nitrate concentration (determined by actual analysis) in a series of batch cultures.

TABLE 1
NEAR SURFACE NUTRIENT CONCENTRATIONS AND NO_3/PO_4 RATIOS IN VARIOUS
AREAS OF THE NORTHEASTERN TROPICAL PACIFIC¹
(Numbers in parentheses are numbers of observations taken)

Area	Concentrations ($\mu\text{g-at/liter}$)			Ratio NO_3/PO_4
	$\text{NO}_3\text{-N}$	$\text{NO}_2\text{-N}$	$\text{PO}_4\text{-P}$	
Costa Rica Dome Cruise, November 1959 (Scripps Institution of Oceanography, 1960)				
Costa Rica Dome	6.1(15)	0.10(18)	0.76(16)	8.0
South of Dome to Cocos Island	0.3(9)	0.00(9)	0.37(8)	0.8
Dome northwest to Baja California	0.6(14)	0.01(14)	0.56(25) ²	1.1
Cruise TO-59-2, August 1959 (Blackburn <i>et al.</i> , 1962)				
Offshore waters, southern Baja California	0.5(7)	0.00(6)	0.33(7)	1.5
Cruise TO-61-1, March 1961 (Unpublished data)				
Gulf of Tehuantepec	0.8(20)	0.08(28)	0.41(11) ³	2.0

¹From Thomas (1966b).

²Phosphate values taken from SCOPE data of November, 1956 (Holmes, 1958).

³Phosphate values taken from cruise TO-60-1 (Blackburn *et al.*, 1962).

The results of two such experiments are shown in Figure 3. In an enriched seawater medium the lowest nitrate concentration that we could obtain was $1.6 \mu\text{g-at/liter}$. The growth rate was the same at this concentration as at higher concentrations. When cell numbers no longer increased, we harvested the cells, reenriched the medium with phosphate and iron, and used it over again in an attempt to reach still lower nitrate concentrations. In such nitrogen-depleted medium the lowest nitrate concentration was $0.9 \mu\text{g-at/liter}$ and the rate at this concentration was slightly reduced as compared to rates at higher concentrations. In depleted medium, the maximum rate was about one-third less than that in undepleted medium.

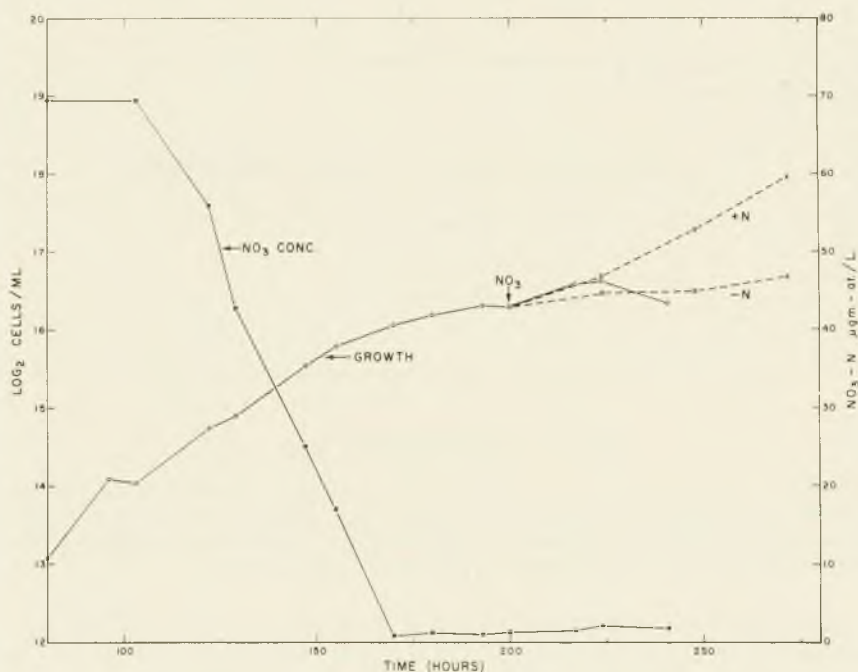


FIGURE 2. Growth and nitrate concentration in a culture of *Gymnodinium simplex*. Nitrate was added to the + N subculture at 200 hours. (From Thomas, 1966b).

In preliminary experiments, we have also used artificial media to obtain still lower nitrate concentrations. Growth rates as a function of concentration were erratic, but a concentration as low as $0.5 \mu\text{g-at/liter}$ has resulted in a high growth rate.

Since nitrate concentrations away from the "Dome" approach this value, it is not so likely that the growth rate of *Chaetoceros gracilis* will be limited by low nitrate concentrations as will *Gymnodinium simplex*. Thus

the lack of nitrate may well limit one organism, a dinoflagellate, but not another, a diatom.

We have also begun to measure the concentration of another nitrogen source—ammonia. Unfortunately, attempts to do this during our earlier

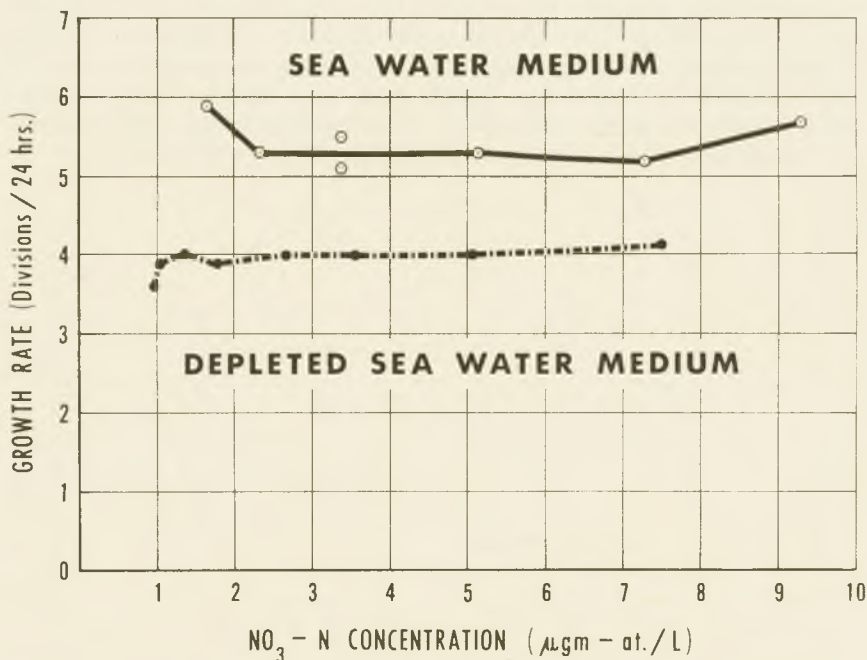


FIGURE 3. The growth rate of *Chaetoceros gracilis* at various initial concentrations of nitrate. Solid line and open circles: growth rates in an enriched seawater medium. Dashed line and solid circles: growth rates in the seawater medium after it had been depleted of nitrate by algal growth.

cruises were unsuccessful, and we have ammonia data for only our later cruises, one to an oligotrophic water mass offshore and north of the Dome (cruise TEMPO) and others off southern Baja California.

During cruise TEMPO in 1962, one surface water mass located 100 miles south of Acapulco (area A, Fig. 1) was sampled for 21 successive

TABLE 2
MEAN SURFACE NUTRIENTS IN A WATER BODY FOLLOWED WITH DROGUES FOR 21 DAYS DURING CRUISE TEMPO, AUGUST 1962¹
(Numbers in parentheses are the numbers of observations taken)

Concentration (μg-at./liter)				Ratios	
NO ₃ -N	NO ₂ -N	NH ₄ -N	PO ₄ -P	NO ₃ /PO ₄	ΣN/PO ₄
0.8(10)	0.05(19)	1.2(10)	0.30(25)	2.8	6.7

¹From Thomas (1966b).

days. Mean surface nutrients during this period are shown in Table 2. The concentration of ammonia was somewhat higher than that of nitrate. Nitrite was again very low. The nitrate/phosphate ratio was low, but was increased if ammonia was included with nitrate as a measure of the total available nitrogen.

TABLE 3
EFFECTS OF VARIOUS NITROGEN SOURCES ON THE GROWTH OF THREE
PHYTOPLANKTON CULTURES FROM THE NORTHEASTERN TROPICAL PACIFIC¹

Source	Growth (Thousands of cells/ml)		
	<i>Gymnodinium simplex</i>	<i>Chaetoceros</i> sp.	<i>Nannochloris</i> sp.
NO ₃	127	982	975
NO ₂	33	60	1,041
NH ₄	68	805	808
Glycine	27	379	2,210
Glutamic acid	4	78	165
Asparagine	4	122	174
Urea	42	695	112
Uric acid	61	133	1,975
None	0.4	50	9

¹From Thomas (1966b).

We then investigated the utilization of ammonia and other nitrogen sources by three phytoplankton cultures from the region. This is shown in Table 3. For the growth of *Chaetoceros gracilis* and *Nannochloris* spp., ammonia was nearly as effective as nitrate in supplying nitrogen. For *Gymnodinium simplex*, ammonia yielded about half the cells that nitrate allowed. Nitrite and organic nitrogen sources varied in their effectiveness depending on the compound and the alga tested.

The ammonia method used to analyze the samples from cruise TEMPO is an oxidation of ammonia to nitrite and it also measures amino nitrogen to a varying degree depending on the amino compound in question. Because amino nitrogen is partially utilized by phytoplankton and partially measured by this method, it appears that ammonia and amino nitrogen, as measured by oxidation and when taken together with nitrate, would provide an adequate measure of the total nitrogen available to phytoplankton.

We have recently been measuring nutrient concentrations in one area (off southern Baja California, area B, Fig 1) in some detail. This area is characterized by inshore upwelling in the spring and early summer, but by September upwelling has ceased.

Mean surface nutrient concentrations are shown in Table 4. In June nitrate/phosphate ratios are fairly high inshore, and neither nutrient would be expected to limit phytoplankton growth. Offshore, nitrogen, even when ammonia is included, was in relatively short supply as indicated by low N/P ratios.

TABLE 4
MEAN SURFACE NUTRIENTS OFF SOUTHERN BAJA CALIFORNIA

	NO ₃ -N	Concentration (μg-at/liter)		PO ₄ -P	Ratios	
		NO ₂ -N	NH ₄ -N		NO ₃ /PO ₄	ΣN/PO ₄
			June 1964			
Inshore	6.32	0.18	1.79	1.10	5.7	7.5
Offshore	0.09	0.00	0.36	0.23	0.4	2.0
			August 1964			
Inshore	22.94	0.03	1.59	0.51	45.0	48.1
Offshore	0.68	0.02	0.66	0.31	2.2	4.4
			September 1965			
Over whole area	0.02	0.02	0.63	0.31	0.1	2.0

Similar conditions were found in August (Table 4). In September nitrate levels were very low throughout the area and ammonia was the more important nitrogenous nutrient. Nevertheless, N/P ratios indicated that, even when ammonia was included, nitrogen was limiting as compared with phosphate.

Further evidence of nitrogen limitation off Baja California was shown by an enrichment experiment performed during the September 1965 cruise. Seawater collected offshore in the upper 10 m was dispensed into plastic carboys. These were enriched with various nutrients and incubated on deck in natural light.

The results of this experiment are shown in Table 5. The greatest increase in chlorophyll occurred in the treatment receiving the complete mixture. Otherwise, of the single treatments, nitrate resulted in the greatest increase (four-fold) in chlorophyll. About a two-fold increase was ob-

TABLE 5
EFFECTS OF NUTRIENT ENRICHMENT ON THE CHLOROPHYLL CONCENTRATION OF A SEAWATER SAMPLE COLLECTED OFF BAJA CALIFORNIA IN SEPTEMBER 1965¹

Enrichment	mg chlorophyll/m ³
None	0.06
Complete nutrient mixture	9.07
+ NO ₃	0.43
+ PO ₄	0.06
+ SiO ₃	0.03
+ vitamins	0.05
+ Fe	0.04
+ trace metals	0.24
+ NO ₃ + PO ₄	0.38
+ NO ₃ + PO ₄ + Fe	0.41

¹Station 60, cruise TO-65-1; initial chlorophyll concentration, 0.11 mg/m³; 4 days incubation in natural daylight.

tained with the addition of a trace-metal mix. This experiment suggests that the major limiting nutrient was nitrogen, but obviously when nitrate is in good supply, other nutrients, such as trace metals, silicate, or vitamins, then become important.

From all these data we can conclude that over the northeastern tropical Pacific as a whole, low nitrate levels may limit phytoplankton growth and control the relative fertility. However, ammonia can moderate the extreme nitrogen deficiency. Off Baja California, there still may be a nitrogen limitation even when ammonia is taken into consideration. Upwelling, both off Baja California and at the Costa Rica Dome, is the principal way in which nitrogen is supplied.

REFERENCES

- BLACKBURN, M., R. C. GRIFFITHS, R. W. HOLMES, AND W. H. THOMAS
1962. Physical, chemical and biological observations in the eastern tropical Pacific Ocean: Three cruises to the Gulf of Tehuantepec, 1958-1959. Spec. Sci. Rept., U.S. Fish Wildl. Serv., No. 420: 1-170.
- GOLDBERG, E. D., T. J. WALKER, AND ALICE WHISENAND
1951. Phosphate utilization by diatoms. Biol. Bull., 101 (3): 274-284.
- HOLMES, R. W. (ED.)
1958. Physical, chemical, and biological observations obtained on Expedition SCOPE in the eastern tropical Pacific, November-December 1956. Spec. Sci. Rept., U.S. Fish. Wildl. Serv., No. 279: 1-117.
- HOLMES, R. W. AND M. BLACKBURN
1960. Physical, chemical, and biological observations in the eastern tropical Pacific Ocean: SCOT Expedition, April-June 1958. Spec. Sci. Rept., U.S. Fish Wildl. Serv., No. 345: 1-106.
- LORENZEN, C. J.
1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res., 13 (2): 223-227.
- PARSONS, T. R., K. STEPHENS, AND J. D. H. STRICKLAND
1961. On the chemical composition of eleven species of phytoplankton. J. Fish. Res. Bd. Canada, 18 (6): 1001-1016.
- THOMAS, W. H.
1966a. Effects of temperature and illuminance on cell division rates of three species of tropical oceanic phytoplankton. J. Phycol., 2 (1): 17-22.
1966b. Surface nitrogenous nutrients and phytoplankton in the northeastern tropical Pacific Ocean. Limnol. Oceanogr., 11 (3): 393-400.
- WYRTKI, K.
1964. Upwelling in the Costa Rica Dome. Fishery Bull. Fish Wildl. Serv. U.S., 63 (2): 355-372.

DISTRIBUTION OF COPPER AND IRON IN TROPICAL SEA WATER¹

E. F. CORCORAN

Institute of Marine Science, University of Miami

ABSTRACT

The distribution of copper and iron is shown in the tropical waters from the northeast coast of Brazil to the Straits of Florida. Iron exists in two principal forms, particulate and a soluble complex in about a 1:1 ratio, while copper is found mainly as a soluble complex. Both iron and copper have slightly greater concentrations near shore and are rather uniformly distributed with depth. Low concentrations of iron in equatorial Atlantic water may be a limiting factor in phytoplankton growth.

INTRODUCTION

In the light of what was written by Richards in 1956 when he described the state of knowledge of the concentrations of trace elements in the sea, the analyses of seawater for trace elements is considered a rather recent innovation. However, in 1822, Marcet showed a similar interest when he presented the conjecture that the sea should contain minute quantities of every substance soluble in water found in nature. However, it was not until 1825 when Pfaff detected iodine in Baltic waters that the first trace element analysis on seawater was performed. Forchhammer's (1865) extensive chemical analyses of seawater constituted the real beginning of modern methods. It was his belief that the cycles of many of the trace elements should be investigated but he lacked the necessary analytical techniques. In recent years, the study of trace elements has been directed towards the investigation of weathered products introduced into the sea by runoff and their subsequent removal by chemical and biological activity.

In the present program concerning the study of primary production, the distribution of several of the biochemically important trace elements in the tropical Atlantic Ocean have been determined. This study was begun several years ago in the Straits of Florida between Miami and Cat Cay. Gradually the investigation has been extended by following the path of the water through the Straits of Yucatan, along the north and northeast coasts of South America and to the west coast of Africa. The first results are concerned with the distribution of two of the trace elements, namely, copper and iron. The importance of the concentration and distribution of these two elements can be realized when it is noted that they are two of the nine elements which are indispensable for the normal growth and function of plant and animal cells.

A full discussion of the biological significance of iron has been presented by Vinogradov (1953). However, some important occurrences are in the

¹Contribution No. 801 from the Institute of Marine Science, University of Miami.

iron-containing prophyryns such as the hemoglobins, catalyses, cytochromes and peroxidases. Using mutants of *Chlorella*, Granick (1953) showed that iron was also necessary in the biosynthesis of chlorophyll.

In much the same manner as iron is necessary in the biosynthesis of chlorophyll, copper is needed in the syntheses of the hemoglobins and is essential to the development of the chlorophyll within the chloroplast. Probably the best known occurrence of copper in the marine environment is in the hemocyanins, the respiratory pigment widely distributed among the phyla Mollusca and Arthropoda. Other areas of biological significance where copper is needed are: (1) in the requirements of oysters and barnacles for settlement and attachment, (2) in the formation of melanin in ink of the octopus, (3) for the hardening of the exoskeleton and egg encasements, (4) in the darkening of blood after injury and (5) in the green coloring of oysters.

Of all the trace elements, the distribution of copper in the sea is the one which has been investigated most extensively. The first study of note was that made by Atkins in 1932; he analyzed one sample of seawater from the English Channel and found a concentration of 10 $\mu\text{g}/\text{Cu}$ per liter. In 1952, Chow & Thompson summarized the work on copper which had been done to that date. They noted in their summary that the amount of copper varied from trace amounts to 90 μg per liter. In all of these studies, however, only ionic copper was measured with no attention given to non-ionic or particulate. Since 1952, the only investigations which have included non-ionic or particulate copper are those of Loveridge and co-workers (1960) at the Plymouth Laboratory, who reported 0.3 μg Cu per liter particulate copper from two English Channel stations, those of Buglio *et al.* (1961) who found 15 μg Cu per liter of ultrafilterable but non-dialyzable copper in a Texas Bay sample. Comprehensive studies on seasonal variations in copper content have been made by Chow & Thompson (1952), who studied the San Juan Channel where they found a summer maximum and a winter minimum, by Atkins (1932) who studied the English Channel and found a summer minimum with a maximum during the winter, and by Alexander & Corcoran (In Press) who found little or no seasonal change in the Straits of Florida. The latter measurements of the soluble ionic copper content in the Straits agree rather well with those of Morita (*in Hood et al.*, 1961) who found from 0.5 to 1.6 μg per liter, and also with the 4.4 to 8.0 $\mu\text{g}/\text{Cu}$ per liter found by Hood *et al.* (1961) in the surface waters in the Gulf of Mexico. In Alexander & Corcoran's studies (1966) it has been found that the soluble non-ionic form of copper predominates, and since most of the procedures for the examination of the copper content preclude the determination of this fraction, it is difficult to compare the results with those of other studies.

In contrast to copper, the distribution of both particulate and soluble forms of iron have been studied. While Cooper (1948) suggested 10 forms

of iron in the sea, Lewis & Goldberg (1954) pointed out that it was practical to measure only two forms, namely, soluble and particulate. In examining the distribution of iron in the Straits of Florida, the maxima and minima for the total soluble iron and particulate iron coincide. This agrees with the findings of Lewis & Goldberg (1954) for the Pacific and with Menzel & Spaeth (1962) for the Bermuda Station. However, the total iron concentrations agree more closely with those of Lewis & Goldberg than those of Menzel & Spaeth. This is probably due to the fact that the former measured the total soluble iron while the latter measured the so-called reactive iron.

METHODS

The methods used in the present study for sampling and for the determination of the individual elements have been described in several publications. A good description of the iron procedures can be found in the doctoral dissertation of James Alexander, and the procedures for copper in an article by Alexander & Corcoran (1967).

In 1948, Cooper, in discussing the presence of iron, mentioned 10 different forms that could occur in sea water. These can be placed in two main groups, namely, particulate and soluble. Before the development of the membrane filter, the particulate was separated from the soluble by use of good quality filter paper. Lewis & Goldberg (1954), in their investigation of iron in the Pacific used the Millipore filter for their separation; in the present study the Whatman GF/C glass filter was utilized since it has

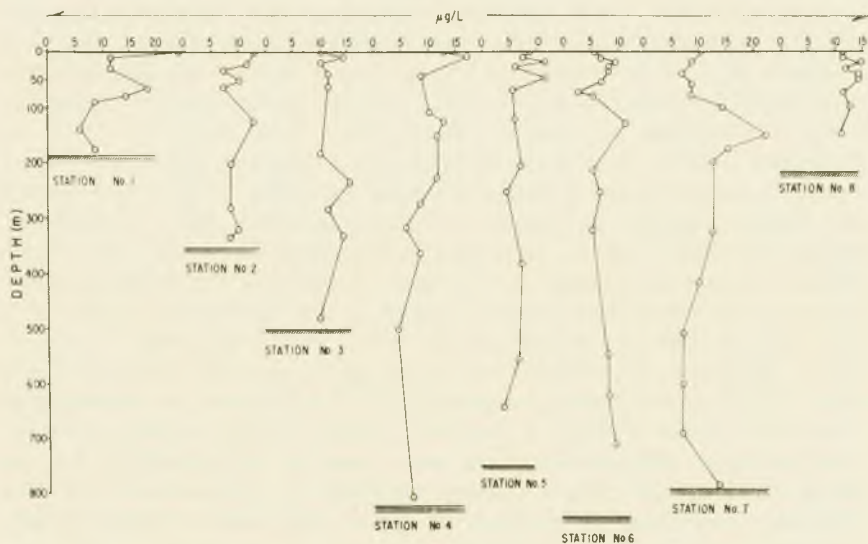


FIGURE 1. The vertical and horizontal distribution of the total soluble copper between Fowey Rocks and Cat Cay during January 1963.

about the same retention characteristics (Corcoran *et al.*, 1964) as the Millipore HA. The retained material was designated "particulate" and the filtrate "soluble." Aliquot samples of the filtrate digested with perchloric acid are termed "total soluble copper and iron" while the results of the analyses on the undigested sea water filtrate are termed "ionic"; these are the designations which have been used in the following figures.

DISCUSSION

In Figures 1 & 2 are seen the distribution of copper found in the Straits of Florida between Fowey Rocks and Cat Cay. Figure 1 shows the total soluble copper in $\mu\text{g}/\text{liter}$. At Sta. 1, just off Fowey Rocks, the copper concentration at the surface and at 75 m is roughly 20 $\mu\text{g}/\text{liter}$; this concentration decreases with the distance from the coast. Stations taken in the Gulf Stream have a maximum concentration of approximately 10 $\mu\text{g}/\text{liter}$; nearing Cat Cay, once again the concentrations exceed 20 $\mu\text{g}/\text{liter}$. Below 300 m the concentrations did not vary much except in the water just above the interfaces. Figure 2 shows the distribution of the particulate copper utilizing the same set of stations from Fowey Rocks to

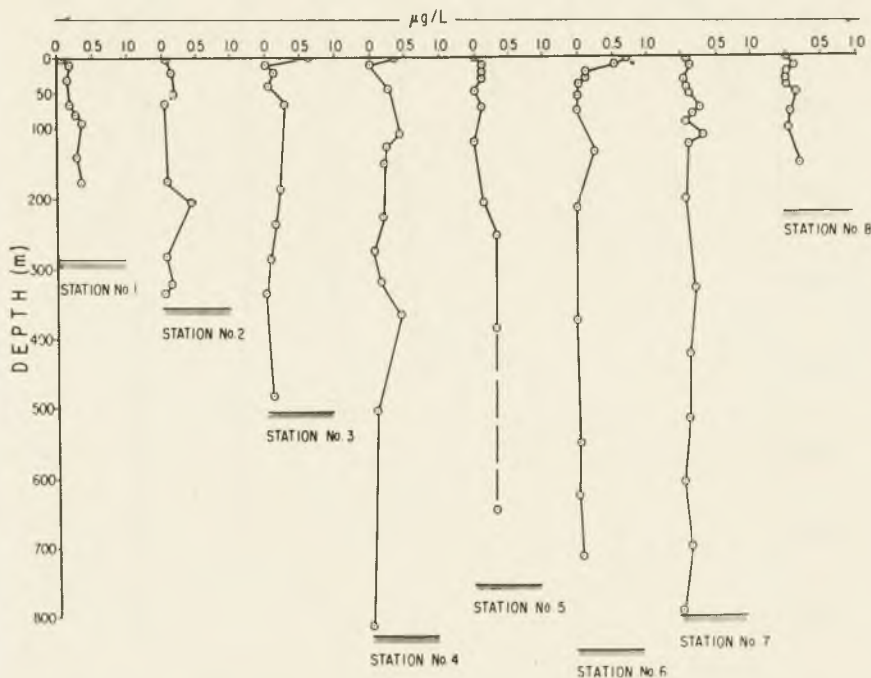
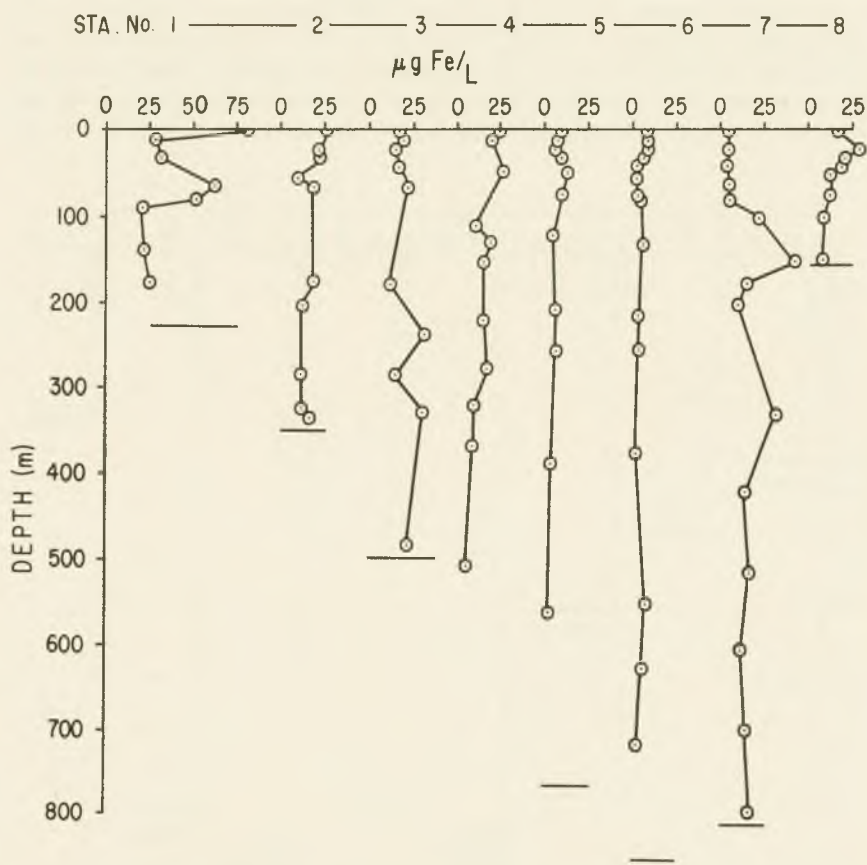


FIGURE 2. The vertical and horizontal distribution of the particulate copper in the Straits of Florida between Fowey Rocks and Cat Cay during January 1963.

Cat Cay. Except for the surface the particulate copper concentration is generally less than $0.2 \mu\text{g/liter}$ and is rather uniform with depth.

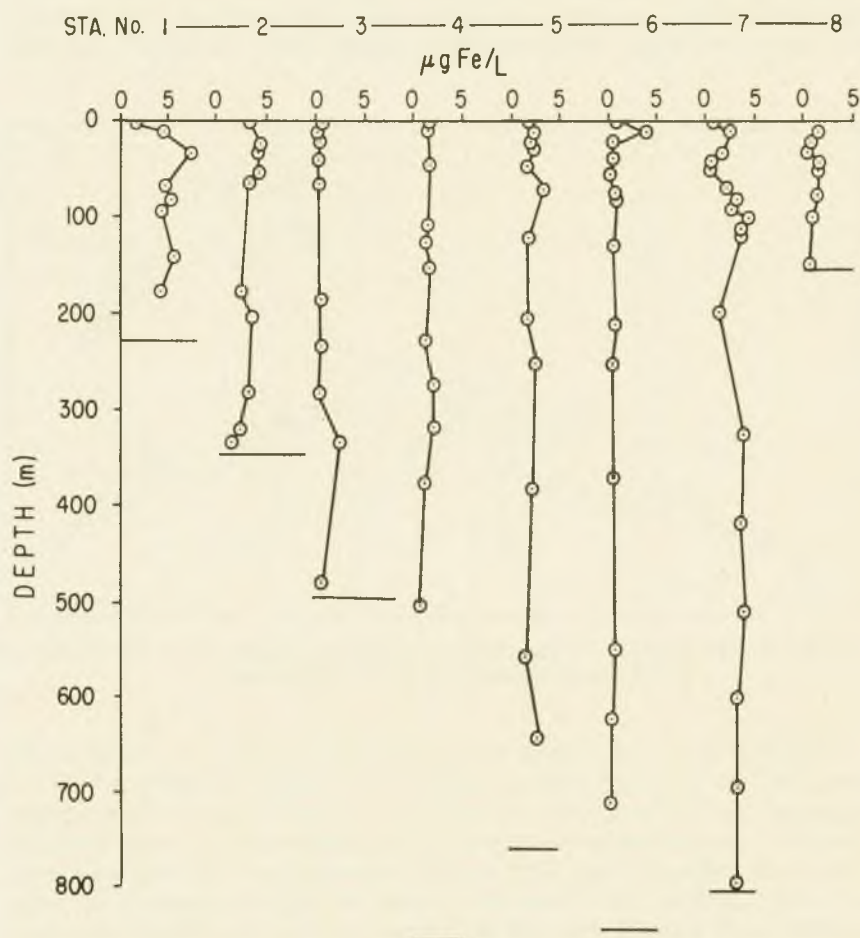
In general, the inshore waters were characterized by a higher iron content than was found in the clear oceanic waters flowing through the center of the Straits. Figure 3 shows the distribution of the soluble iron between Fowey Rocks and Cat Cay. The iron concentrations range from 25 to $50 \mu\text{g/liter}$ with little change in concentration with depth. The station off Cat Cay (Sta. 7) shows a higher concentration below 90 m.

The particulate iron distribution is shown in Figure 4. This pattern is similar to that of soluble iron except that lower concentrations are found. At the Cat Cay station higher concentrations of particulate iron were encountered below 90 m. In order to find the source of the high particulate



iron content at the Cat Cay station, a 24-station cruise was undertaken (Fig. 5) through the Straits of Florida, along the north coast of Cuba and across the Straits of Yucatan. Particulate iron concentrations are shown in Figures 6 & 7.

The distribution of particulate iron in the Straits of Yucatan (Fig. 7) was similar to that found in the water between Miami and Cat Cay. It should be noted that the particulate iron concentration was higher along the western edge rather than on the eastern, which does not account for the higher concentrations at Cat Cay.



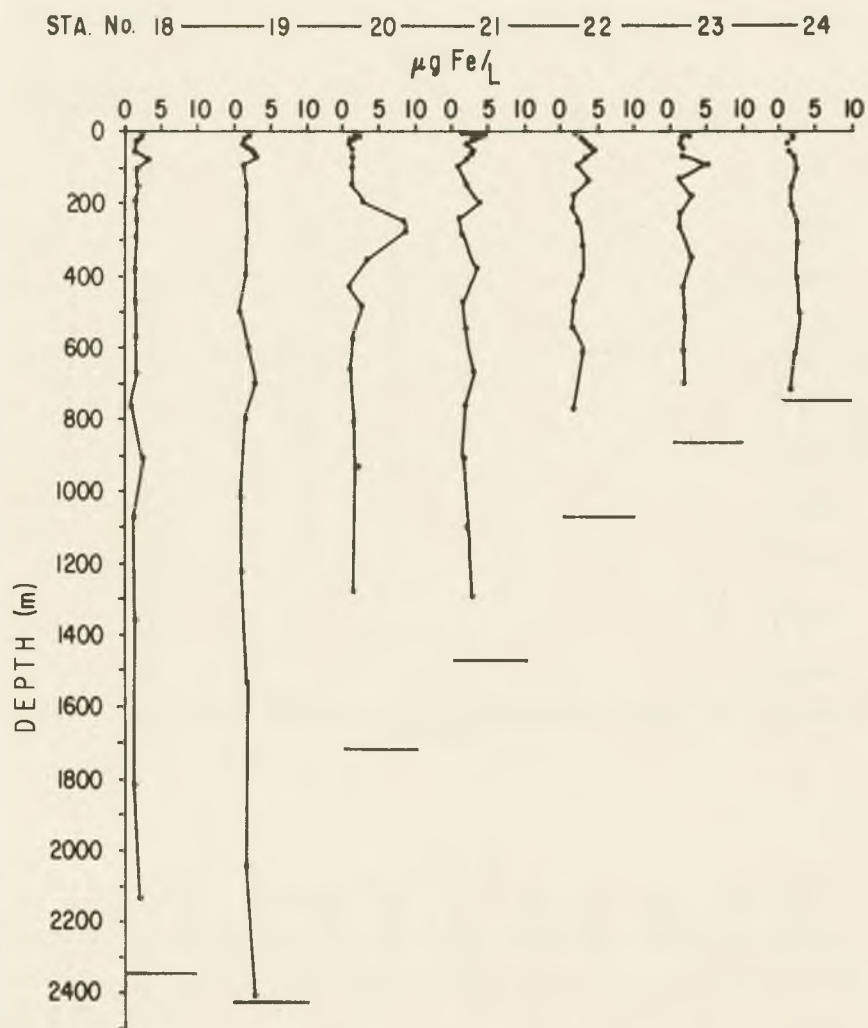


FIGURE 6. The vertical distribution of the particulate iron on the eastern edge of the Florida current between Cuba and Cat Cay.

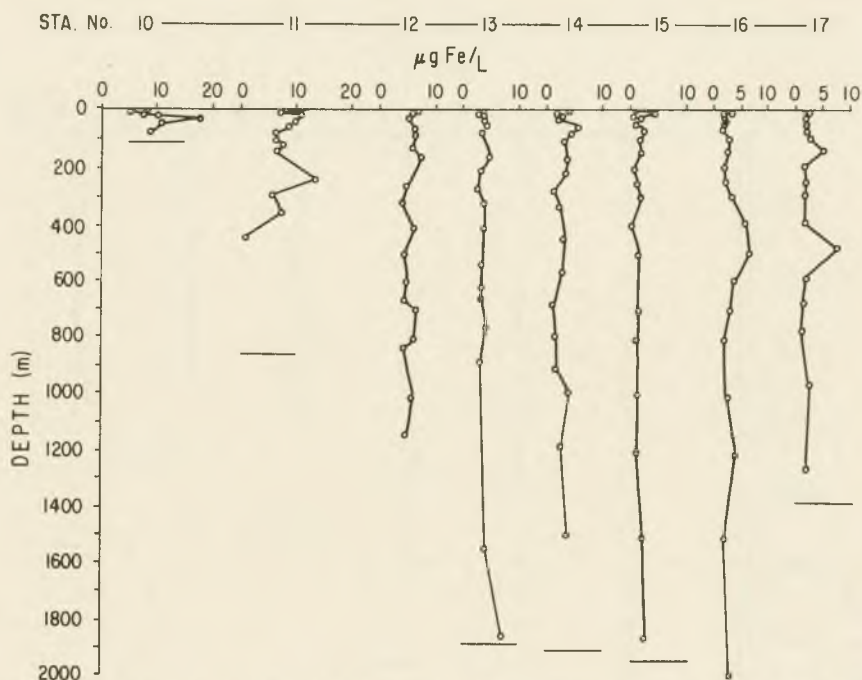


FIGURE 7. The vertical distribution of the particulate iron in the Yucatan Channel.

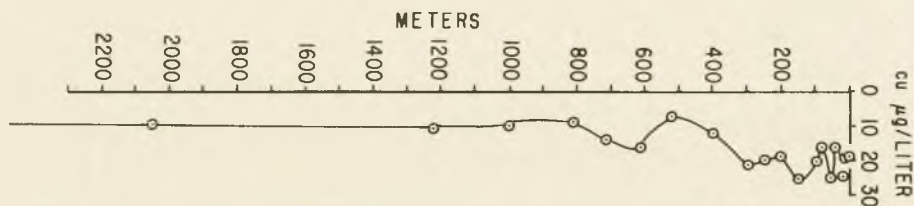


FIGURE 8. The vertical distribution of total soluble copper at a deep water station (6°30'N 46°55'N) off the mouth of the Amazon River.

(Fig. 9) the oxygen minimum was found at 433 m (Sta. H 10), 171 m (Sta. H 11), and 303 m (Sta. H 12), while the phosphate maxima were at 831, 924, and 814 m. Since the salinity was 34.9‰ and sigma-t was 27.8, the mixing with river water could not account for this incongruity.

The biological implications of iron in phytoplankton growth led Alexander to do a diurnal study of the chlorophyll *a* content as an indication of phytoplankton concentration; these samples were also used to determine the particulate iron concentration. The results of this study are shown in Figure 10, where they present somewhat inverse relationship. As a check on this situation, a station from the equatorial Atlantic was randomly selected and chlorophyll *a* concentration was plotted against that of particulate iron (Fig. 11) and here again an inverse relationship exists.

But what about the biological utilization of these two elements by phytoplankton? Based on the pioneering work of Allen & Nelson (1910), and Harvey (1937), and the later work of Goldberg (1952), it was assumed that iron was available only as a particle. However, due to the insolubility of iron in the sea, the amounts of particulate and ionic iron cannot be used to explain the concentration of this element found in phytoplankton.

Copper, on the other hand, is limited only by the solubility of the basic carbonate which is about 180 $\mu\text{g/liter}$ at pH 8.0; if metallic copper is placed in sea water concentrations up to 2000 $\mu\text{g/liter}$ can be temporarily attained. These concentrations are definitely toxic to many organisms. This poses a question, how then is the high concentration of copper that has been found in phytoplankton to be explained? The explanation is not in

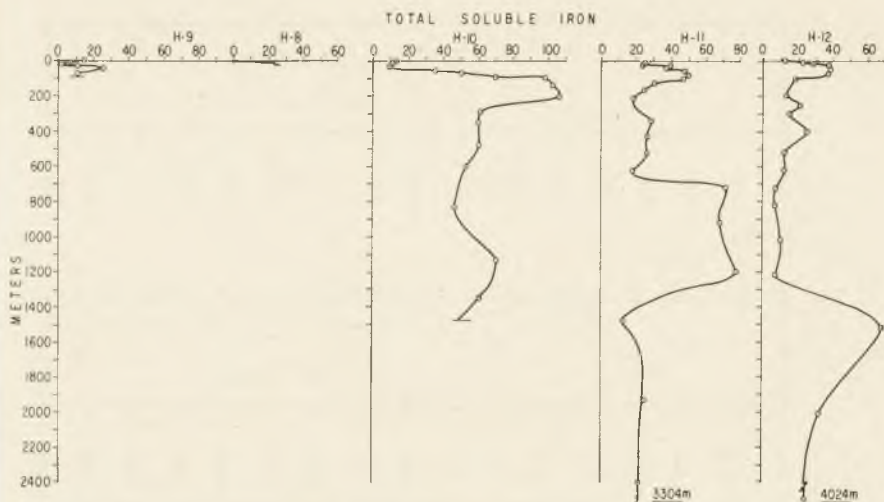


FIGURE 9. The distribution of the total soluble iron off the Amazon River.

the concentrations of ionic and particulate copper but rather that it is known to exist primarily as a soluble organic complex. Fogg (1953) demonstrated the toxicity of $0.5 \mu\text{g/liter}$ of copper in blue-green algae whereas 8 to $16 \mu\text{g/liter}$ of copper could be added without the same toxic effect when a polypeptide was present. *Euglena gracilis* was able to grow in a media colored blue with the high concentrations of copper when sufficient quantities of EDTA were added, and *Aspergillus niger* will grow in saturated copper sulfate solution at pH 0, but not in saturated copper sulfate at pH 8.5 (Jurkowska, 1952).

One of the most striking demonstrations of the biological significance of iron in sea water was done by Alexander (1964) when he showed that the best growth rates for *Amphodinium klebsii* were obtained when 1000 times the normal iron concentration was chelated with EDTA in a defined medium. In 1961, Menzel & Ryther also showed that the lack of iron limits

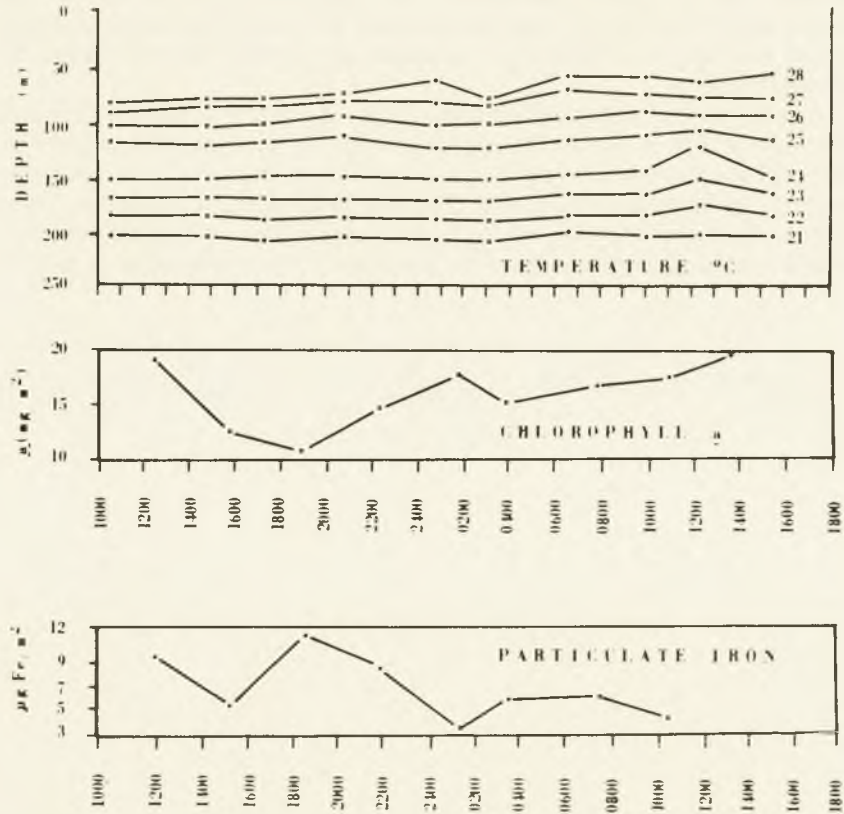


FIGURE 10. The diurnal variations in chlorophyll *a* concentrations and particulate iron content in the upper 200 m in the Tongue of the Ocean.

plant growth in the Sargasso Sea. Figure 12 shows the concentration of iron at a typical equatorial Atlantic station, where it can be seen that iron could be a limiting factor in the growth of phytoplankton.

CONCLUSIONS

Iron exists in two principal chemical forms in the tropical Atlantic, namely, particulate and a soluble organic complex while copper is found mainly as a soluble complex. Except for the waters just off the Amazon River, both iron and copper have greater concentrations near shore and are rather uniformly distributed with depth. As noted, both the copper

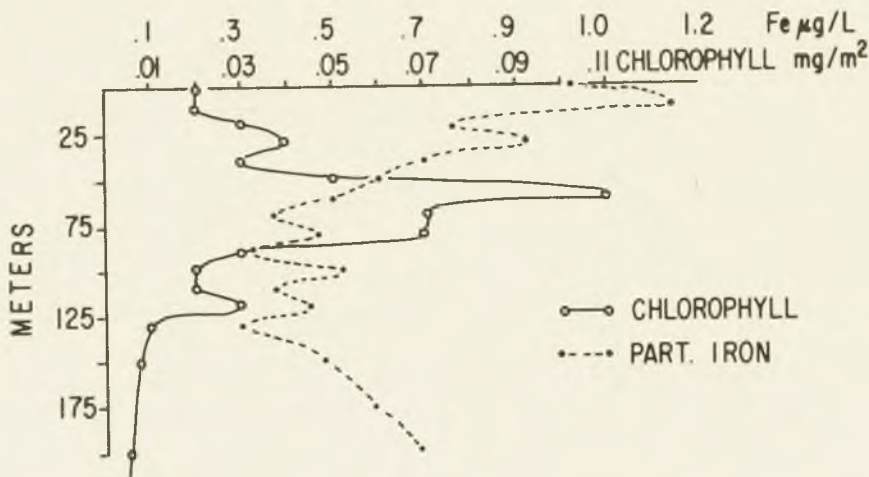


FIGURE 11. The vertical distribution and chlorophyll *a* content at a station in the equatorial Atlantic.

and iron content of seawater was higher near Fowey Rocks off the coast of Florida, near Cat Cay in the Bahamas, near Havana off the coast of Cuba, and near both sides of the Straits of Yucatan. This indicates that both elements enter the sea through runoff. The high iron content found at the station 4 miles west of Cat Cay undoubtedly enters the Florida Current through the Old Bahama Channel or from the Bahama Banks. This bears further investigation, but will be postponed until the international situation will permit it. Studies (Alexander, 1964; Menzel & Ryther, 1961) have shown that the lack of iron limits plant growth in tropical sea water. Low iron concentrations in the equatorial Atlantic waters may be a possible limiting factor in the phytoplankton production of these waters. Also, further investigation is required off the mouth of the Amazon River. Here certainly is a large source of both copper and

iron to the sea, but as yet unexplained are the deep water iron maxima, and the higher ionic copper and iron concentrations found at the deep water station. Answers to these and other questions may become apparent from the cruise to the Amazon River area made in January 1966 by the R/V PILLSBURY. If the average discharge is calculated as 7 million ft³/sec, the supply of iron alone that enters the sea from the Amazon River represents at least 100,000 tons annually. While runoff controls the supply of both copper and iron to the sea, their content within the sea is regulated by water movements, solubility, the ability to form organic complexes, and biological activity.

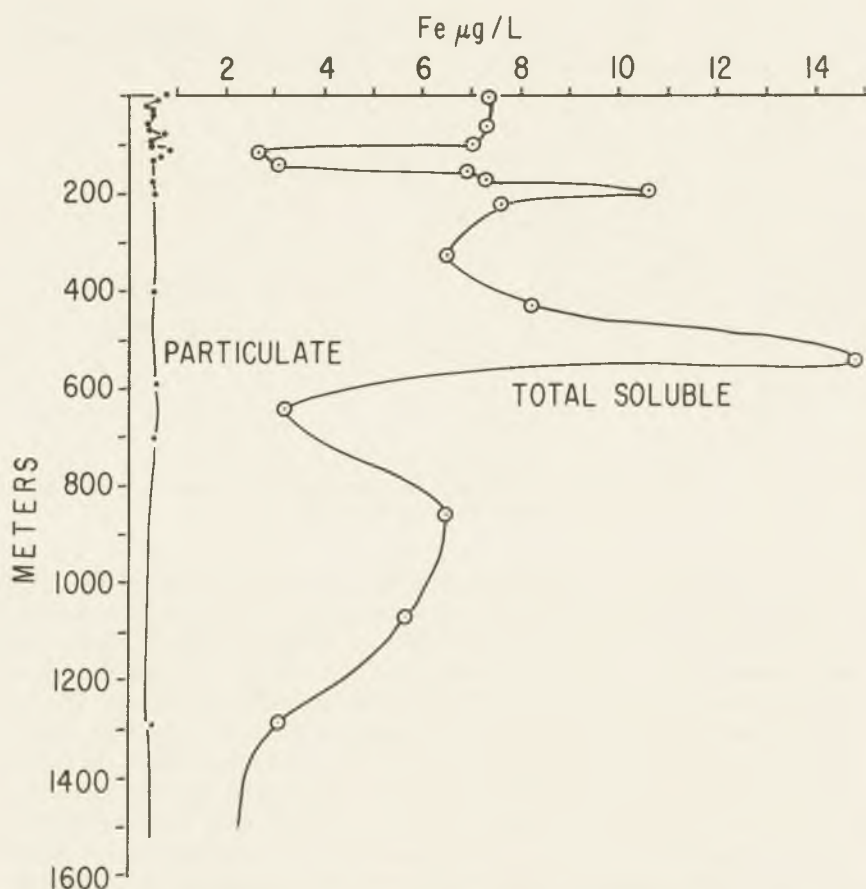


FIGURE 12. The vertical distribution of particulate and soluble iron at an equatorial Atlantic station.

ACKNOWLEDGMENTS

The use of unpublished material from the doctoral dissertation of James E. Alexander, and the financial support from the National Science Foundation, Grant G-16459 and from the Office of Naval Research, Contracts Nonr 840(01) and 4008(02) are gratefully acknowledged. Figures 1 and 2 were redrawn from Alexander & Corcoran (1967) and Figures 3-7 and 10 from Alexander (1964).

REFERENCES

- ALEXANDER, J. E.
1964. Ecology of iron in tropical waters. Doctoral dissertation, University of Miami, 160 p., 29 figs.
- ALEXANDER, J. E. AND E. F. CORCORAN
1967. The distribution of copper in tropical sea water, *Limnol. Oceanogr.*, 12 (2): 236-242.
- ALLEN, E. J. AND E. W. NELSON
1910. On the artificial culture of marine plankton organisms. *J. Mar. biol. Ass. (U. K.)*, 8: 421-425.
- ATKINS, W. R. G.
1932. The copper content of sea water. *J. Mar. biol. Ass. (U. K.)*, 18: 193-197.
- BUGLIO, E., E. RONA, AND D. W. HOOD
1961. U. S. Atomic Energy Comm. Rep. Ref. 61-19A, 5 p.
- CHOW, T. J. AND T. G. THOMPSON
1952. The determination and distribution of copper in seawater. *J. Mar. Res.*, 11 (2): 124-138.
- COOPER, L. H. N.
1948. Some chemical considerations on the distribution of iron in the sea. *J. Mar. biol. Ass. (U. K.)*, 27: 322-325.
- CORCORAN, E. F., J. F. KIMBALL, JR., AND J. E. ALEXANDER
1964. An improved method of filtration for chlorophyll analyses. *Bull. Mar. Sci. Gulf & Carib.*, 14: 545-548.
- FOGG, G. E.
1953. The metabolism of Algae. Methuen, London, New York, 149 p., illus.
- FORCHHAMMER, G.
1865. The complete analysis of sea water. *Phil. Trans.*, 155: 203-207.
- GOLDBERG, E. D.
1952. Iron assimilation by diatoms. *Biol. Bull., Woods Hole*, 102: 243-245.
- GRANICK, S.
1953. Inventions in Iron Metabolism. *American Nat.*, 87: 65-75.
- HARVEY, H. W.
1937. The supply of iron to diatoms. *J. Mar. biol. Ass. (U. K.)*, 22: 221-227.
- HOOD, D. W., E. RONA, L. MUSE, AND B. BUGLIO
1961. Copper, manganese, and zinc analysis of sea water by neutron activation analysis. Preprints, Am. Chem. Soc., Div. Water Waste Chem.: 44-48.

- JURKOWSKA, H.
1952. The adaptation of *Aspergillus niger* to copper. Acta Mikrobiol. Polon., 1: 107-122. [English summary.]
- LEWIS, G. J. AND E. D. GOLDBERG
1954. Iron in marine waters. J. Mar. Res., 13: 183-197.
- LOVERIDGE, B. A., G. W. C. MILNER, G. A. BARNETT, A. THOMAS, AND W. M. HENRY
1960. Atomic Energy Assoc. AERE - R3323, 36 pp.
- MARCET, A. M.
1822. Phil. Trans., 112: 448. In Riley, J. P. and G. Skirrow, Eds., Chemical (1965) Oceanography, Vol. 1, Academic Press, N. Y.: 712 p.
- MENZEL, D. AND J. RYTHER
1961. Nutrients limiting the production of phytoplankton in the Sargasso Sea with special reference to iron. Deep-Sea Res., 7: 276-281.
- MENZEL, D. AND J. SPAETH
1962. Occurrence of Iron in the Sargasso Sea off Bermuda. Limnol. Oceanogr., 7: 155-158.
- PFUFF, C.
1825. Jb. Chem. Phys., 15: 378. In Riley, J. P. and G. Skirrow, Eds., Chemical (1965) Oceanography, Vol. 1, Academic Press, N. Y.: 712 p.
- RICHARDS, F. A.
1956. On the state of our knowledge of trace elements in the ocean. Geochem et Cosmochim Acta, 10: 241-243.
- VINOGRADOV, A. P.
1953. The elementary composition of marine organisms. Mem. L. Sears Found. Mar. Res., New Haven, Conn., 647 p., maps, diagr., tables.

PHYTOPLANKTON PRODUCTION IN RELATION TO NUTRIENTS ALONG THE EGYPTIAN MEDITERRANEAN COAST

A. A. ALEEM AND N. DOWIDAR

Oceanography Department, University of Alexandria, Egypt

ABSTRACT

The hydrographical, hydrochemical, and biological conditions in selected stations along the Delta Coast have been followed for at least 2 successive years and the seasonal variations noted. The Nile River annually discharges about 35×10^9 cubic meters of water into the Mediterranean Sea. The flood water flows in a northeast direction and its effect is felt as far as the coasts of Cyprus and Lebanon. Enormous quantities of nutrients are discharged into the sea making it very fertile along the Delta in the autumn. As a consequence, the sardine fishery prospers. Details of the nutrients and plankton organisms are described.

INTRODUCTION

Since time immemorial, the Nile River has brought fertility to the land of Egypt. This also is true of the marine area adjoining the coast of the delta of this river. Every year, in late summer throughout the autumn, the Nile flood discharges enormous quantities of nutrients into the sea. This brings about a characteristic phytoplankton bloom in the region in question during this period. The flood water not only increases the productivity of our coastal waters, but also imparts productive properties to the brackish water lakes in the north of the Delta.

The phytoplankton bloom in the coastal waters has always been associated with a flourishing pelagic fishery, manifested by the swarming of sardine in these waters, while in the lakes, fishes such as *Tilapia* and *Mugil* find ample food all the year round.

An inquiry into the nature of this periodic bloom and into the factors affecting it was therefore found necessary as a part of a project carried out by the Oceanography Department of the University of Alexandria. The results of such studies are useful not only to throw light on several local fishery problems, but also to forecast hydrobiological and hydrochemical changes expected to take place in our coastal waters after the completion of the High Dam at Aswan.

It is to be noted that the bulk of Nile water after 1967 no longer will reach the Mediterranean Sea but will be utilized to cultivate over 1.5 million acres of desert land. This undoubtedly will bring marked changes in the characteristics of the coastal waters of the delta as well as physical changes in the nature of the coast itself, due to upsetting the balance between forces of deposition and erosion.

The present paper entails mainly the results of work undertaken during

1961, 1962, and partly in 1963, in the area around Alexandria which is in close proximity to the Rosetta Mouth of the River. It comprises the results of seasonal changes in certain physical and chemical characteristics of the coastal waters such as salinity, temperature, transparency, and content of phosphate and silicate, together with data on the distribution and periodicity of the phytoplankton community. Special attention is given to the effect of Nile flood on the fertility of the coastal waters.

Reference also will be made to work done at the Domietta Mouth of the Nile and in the Delta lakes whenever required.

AREA INVESTIGATED

The area investigated lies between lat. $31^{\circ}8'$, $31^{\circ}27'N$ and long. $29^{\circ}46'$, $30^{\circ}3'E$ (Fig. 1). Three offshore stations have been selected and examined periodically. These are designated on Figure 1 as Sta. I, Sta. II and Sta. III. The first of these is the closest to the river mouth at Rosetta, being 30 km to the west of this mouth. Sta. II is situated at 7.5 km off

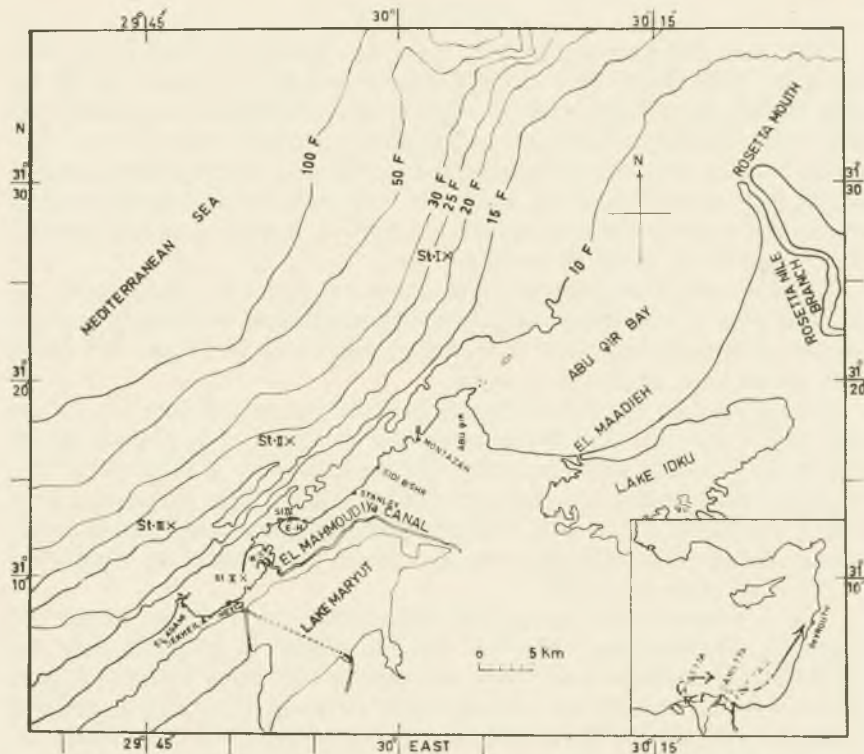


FIGURE 1. The position of stations at Alexandria. (Inset: the Delta and Nile outlets; arrows indicate direction of flood stream in the eastern Mediterranean).

the entrance of the Eastern Harbour, while Sta. III lies at about the same distance off Cape El Agami, to the west of Alexandria. The depth of water at these three stations is about 40 m. The substratum in Abu Qir Bay off Alexandria is predominantly covered with muddy sand with local accumulation of black mud, especially off Abu Qir Bay and in the Eastern and Western Harbours. Planktonic investigations have also been undertaken in these two highly productive harbours, which represent more or less confined inshore polluted habitats. These harbours will be referred to as Sta. IV and Sta. V.

Apart from the Nile flow, the area under consideration receives also fresh or brackish water from other sources. Thus a small navigation canal connects the Western Harbour with the inland water; water from Lake Mariut is pumped into the sea at Mex; while Lake Idku discharges its water into Abu Qir Bay. The average amount of water discharged from these latter lakes combined, during the flood season, is estimated as 180 million m³ per month. This is much less than the average amount of fresh water discharged per day from the Rosetta Mouth alone during the flood peak.

METHODS

Salinity was determined by Knudsen method. Temperatures were recorded at the depths 0, 5, 10, 20, and 30 m respectively in the three main stations.

The transparency of water was determined by a Secchi disc 30 cm in diameter, usually between 11 AM and 3 PM.

Phosphate and silicate were determined after Harvey (1948, 1955) and Armstrong (1951), respectively, adopting the modification of Armstrong & Butler (1962) for silicate, which involves the use of tartaric acid to inactivate excess molybdate and prevent interference by phosphate. Determinations were made colorimetrically using a "Spekker" type absorptiometer. Water samples were kept in polyethylene bottles in the dark.

Quantitative estimations of phytoplankton were made by sedimentation and counting in a 2 ml counting cell. Dense samples obtained during the blooms were further diluted for counting. Results are expressed as numbers of cells per liter. Zooplankton organisms were counted from samples obtained by net, from vertical hauls of known volume of water filtered; these are expressed as numbers of organisms per cubic meter.

CLIMATIC ASPECTS

The monthly averages of maximum and minimum air temperatures recorded¹ during this investigation amount to 32.5° C and 8.2° C. These occur respectively in August and in February. However, higher temperatures (38° - 39° C) are not infrequent during spells of hot weather in

¹Compiled from the Meteorological Office, Cairo.

summer. Relative humidity amounts to an average of 67.4 per cent for the whole year, but higher values (80 - 90 per cent) occur in summer.

Total rainfall averages about 200 mm and is confined to the winter months. Its effect on surface salinity usually does not exceed a few decimal changes.

Northerly winds dominate during most of the year, while northwesterly winds are frequent in winter. Hot and dry southerly winds blowing from the desert and known locally as *Khamasin* blow in spring at a frequency of three to five times between March and June.

Wind force and direction affect mixing processes and also the distribution of plankton. Thus in winter under the influence of strong northwesterly wind, influxes of offshore Mediterranean water, poor in nutrients, may be brought into the coastal area. This water has a high salinity and transparency and is poor in phosphate and silicate. Besides, several oceanic species of *Ceratium* and copepods are met with in coastal waters during this season.

On the other hand, during the *Khamasin* winds in spring, water from the Eastern and Western Harbours may be driven offshore towards Sta. III, thus causing lower salinity and enrichment of the water at this station, beside transportation of several planktonic species usually characteristic of the Eastern Harbour into Sta. III.

Although the flood water is normally deflected to the East under the Coriolis force and hardly reaches Sta. III to the west of the Rosetta Mouth, yet at times when Northeast winds are strong the effect of Nile water could easily be detected at this station. The tides at Alexandria are rather insignificant, fluctuating between 20 to 30 cm throughout the year.

The annual average daily sunshine is 9.6 hr, reaching 11 to 12 hr in summer.

FLOW OF NILE WATER INTO THE MEDITERRANEAN SEA

The flood season usually begins in mid-August, reaches its climax in mid-September and then fades gradually in October and during November until it ceases in December. It has been the tradition in Egypt, since the beginning of the century, to store the excess flood water behind the Aswan Dam so as to be consumed during the period of water shortage between the months of February and July. During this period no Nile water reaches the Mediterranean Sea and the river mouths at Rosetta and Domietta are closed, the former through the Edfina Barrages and the latter through an artificial mud dam at Fareskour.

At the beginning of the flood, when the water level in the river reaches a certain high value, these mouths are opened and the flood water is allowed to flow suddenly into the sea. The magnitude of the flood is usually so high that the Nile water forms a stream in the Mediterranean Sea about 15 km wide and is directed eastwards due to the Coriolis force at a speed of about 8 to 10 km/day, depending on the wind force and

direction. This water has been detected off Cape Carmel on the Palestine Coast (Liebmann, 1935; Oren, 1952) or even to the south of Cyprus (Rouch, 1940; Oren, 1952). Sediments from the Nile also cover the continental shelf off Palestine and Lebanon (Emery & George, 1963).

The water discharged from both the Domietta and Rosetta branches of the Nile during the flood peak in 1961 averaged about 640 million m^3 per day. About 70 per cent of this was discharged from the Rosetta branch alone. The annual average discharge of Nile water into the Mediterranean amounts to 35 billion m^3 , although this figure is subject to fluctuation from year to year.

The flow of Nile water to the west of the Rosetta Mouth is limited by the direction and speed of the prevailing winds as well as by the magnitude of the flood itself. The offshore stations selected off Alexandria are therefore affected by the flood water in different degrees and this is not without effect on the magnitude of the bloom developed in each.

The Nile water spreads in the sea as a dilute surface layer about 5 m thick with a distinct brownish colour, and a sharp demarcation is often

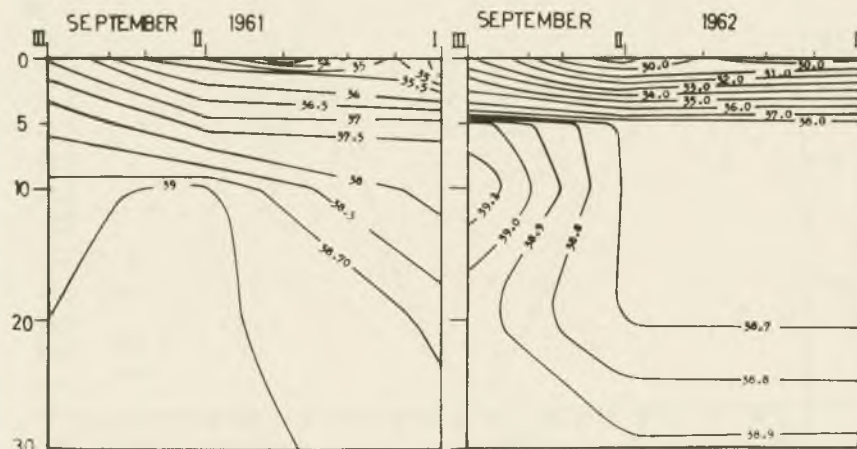


FIGURE 2. Vertical distribution of salinity at the offshore stations during the Nile flood (note compact isohalines in the upper 5 m).

kept between this water and the adjoining sea water near the Nile outlets. The vertical drop of salinity is abrupt and compact stratification of isohalines (Fig. 2) is shown in the upper 5 m.

The flood water is extremely rich in nutrients which are transported to the sea by mixing processes. Halim (1960) estimated the phosphate and silicate in the flood water itself at a station 3 km upstream in the Domietta Mouth during August and found figures as high as $6.38 \mu\text{g}$ at P per liter and $340 \mu\text{g}$ at Si per liter.

A week or so following the discharge of the flood water into the sea,

a dense phytoplankton bloom develops. This bloom becomes most intense in the coastal waters in September. It is composed almost exclusively of diatoms and the water acquires a greenish-brown colour and slimy consistency. The numbers of organisms per liter usually amount to several millions at such times and the bloom is confined to the surface.

SEASONAL CHANGES IN PHYSICAL AND CHEMICAL CHARACTERISTICS OF THE WATER

Owing to the shallowness of the area investigated, the water temperatures usually follow those of the air. The maximum and minimum temperatures of the water column 0 to 30 m in the three offshore stations occur also in August and February respectively (Fig. 3). During periods of settled

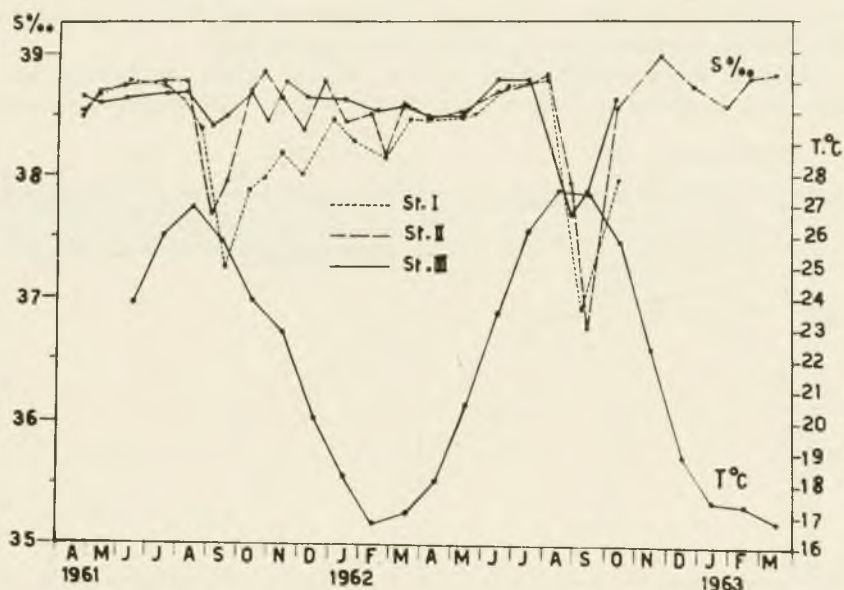


FIGURE 3. Seasonal variations in salinity at the offshore stations, together with mean monthly water temperature at Alexandria.

weather in May or June, a narrow thermocline may be established in the upper few meters, but this is soon destroyed by wind. The highest temperature gradient in the water column 0 to 30 m amounts to 3.0°C in May, while the lowest (0.1°C) is recorded in winter when almost a homothermal water column is formed as a result of mixing.

The seasonal variations of salinity at the three offshore stations as based on the average values for the whole water column (0 - 30 m) are also shown in Figure 3, together with the temperature. Apart from the flood season, salinity variations are rather small and in most cases of a local

nature. The surface salinity gradually increases from April to July, attaining a maximum (38.9 o/oo) just before the discharge of flood water in August. The surface salinity then drops to about 24 o/oo in the Bay of Abu Qir as the flood water reaches this area. The surface water is then diluted in different degrees further west.

The following table shows the vertical distribution of salinity and temperature at Sta. II on August 29, 1962.

Depth (m)	Temperature (°C)	Salinity ‰
0	28.8	33.80
5	28.3	38.78
10	27.9	38.95
20	27.5	38.95
30	27.2	39.13

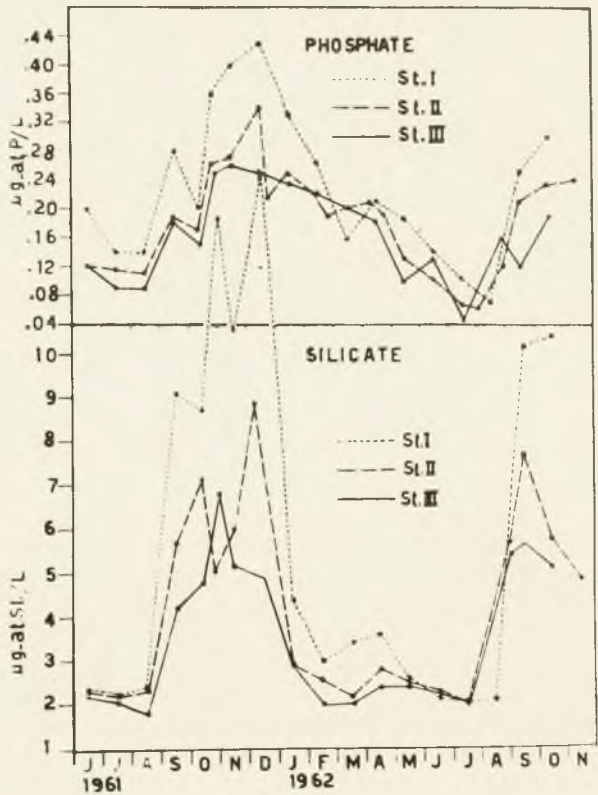


FIGURE 4. Seasonal variations in phosphate and silicate in the offshore stations at Alexandria.

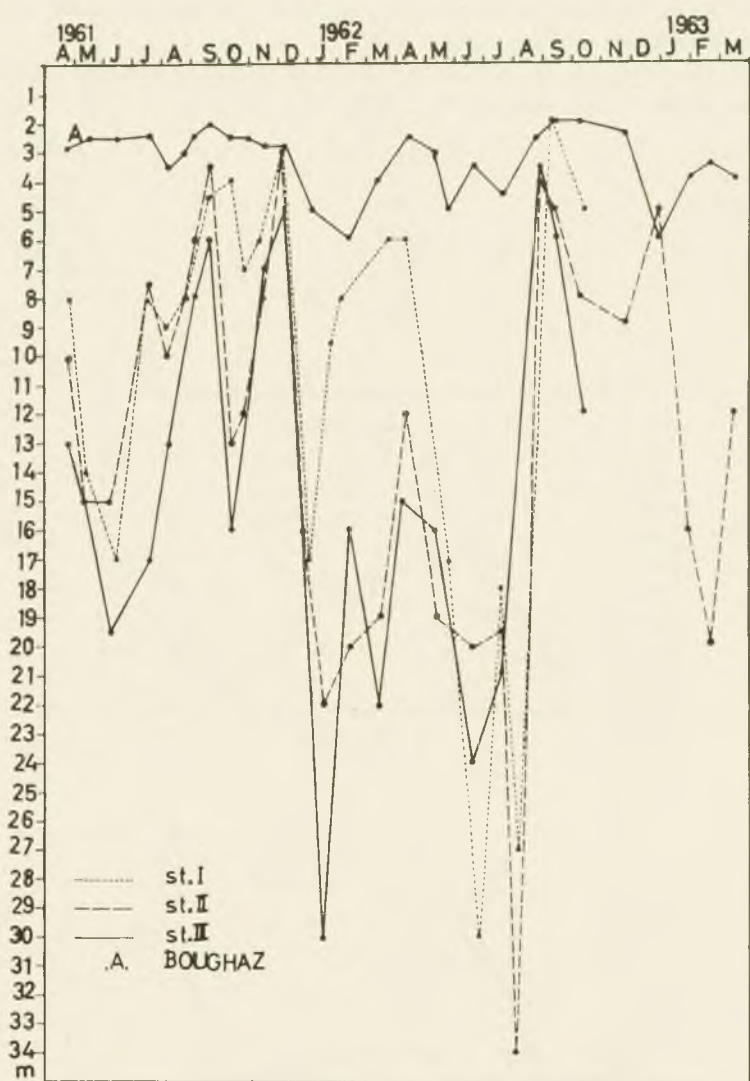


FIGURE 5. Cycle of fluctuations in Secchi disc readings in the off-shore stations and in one inshore station (site A at Sta. IV).

This also shows stratification in the water column during the flood season, and calculations show a high degree of stability of the water column. However, this is not the case in winter.

The water transparency as judged by the Secchi disc readings (Fig. 4) has two maxima, *viz.*, one in winter (30 m at Sta. III) and the other in summer (34 m at Sta. II) before the flood season. However, with the onset of Nile water these readings drop to 2 m in the inshore and to 3 to 4 in the offshore stations.

Phosphate and Silicate.—The monthly variations in the amounts of phosphate and silicate in each of the three offshore stations are shown in Figure 5. This is based on the average values of the whole water column at each station for the period between June 1961 and November 1962.

From this figure it appears that the annual cycle of phosphate in the offshore stations could be divided into four periods.

1. Minimum values are attained in summer before the Nile flood ($0.04 \mu\text{g}$ at P per liter). This usually coincides with the minimal phytoplankton concentration in the water.
2. A sudden rise is noted with the onset of the flood water ($0.2 - 0.3 \mu\text{g}$ at P per liter), which usually coincides with the early phytoplankton bloom.
3. The phosphate concentration drops in the month of October due to rapid uptake by the phytoplankton organisms.
4. The concentration rises again in November and December, reaching a maximum ($>0.4 \mu\text{g}$ at P per liter) due to regeneration and effective mixing in the whole water column in winter, after which time the amounts of phosphate decrease gradually to a minimum in summer.

This cycle is almost repeated every year under normal flood conditions. The silicate variations follow more or less the same pattern. The lowest concentration of phosphate recorded in the offshore water at the surface was $0.025 \mu\text{g}$ at P per liter in July before the flood season, while the maximum value of 0.44 was recorded in December.

The phosphate concentration in the Eastern Harbour (Sta. IV) reaches a minimum also in July ($0.08 \mu\text{g}$ at P per liter), increases at the beginning of the flood to 0.35, and attains the maximum (0.7) in winter.

The silicate concentrations also increase in the surface water of the offshore stations from about $2 \mu\text{g}$ at Si per liter in July and early August to about $30 \mu\text{g}$ at Si per liter in September.

There is no doubt that the major contribution of both the phosphate and silicate in the coastal waters comes from the Nile flood. The concentrations of these nutrients in our area are much higher than in any other area in the Mediterranean (*cf.* Thompson, 1931; Bernard, 1938 & 1958a, etc.).

There is also a strong correlation between low salinity and the concen-

trations of phosphate and silicate in the surface water at the different offshore stations, depending upon the amount of dilution by the flood water as shown from the following table.

TABLE 1
SALINITY, PHOSPHATE AND SILICATE CONCENTRATION OF WATER
DURING THE FLOOD PERIOD

Station	Date	Salinity ‰	μg at P/liter	μg at Si/liter
I	18/9/1961	33.50	0.28	22.50
	9/9/1962	29.80	0.40	38.10
II	20/9/1961	35.15	0.20	17.65
	14/9/1962	28.75	0.32	25.50
III	20/9/1961	37.07	0.16	12.40
	29/8/1962	32.29	0.36	18.90

A similar correlation was found between nutrients and salinity off the Columbia River by Stefansson & Richards (1963).

Nitrate.—Although no nitrate estimations were made during 1961 or 1962, such estimations have been started together with chlorophyll estimations during 1965. The method of nitrate estimation adopted depends upon the reduction of nitrate to nitrite by means of hydrazine in alkaline medium as described by Millin and Riley (1955) (*cf.* also Barnes, 1959).

From the preliminary results obtained, nitrate in offshore surface water reaches lowest concentrations in August before the Nile flood, viz. 0.88 μg at N per liter. This value increases to 3.54 μg at N per liter during September. This does not represent, however, the highest concentrations obtained in surface water during the flood season.

PERIODICITY OF THE PHYTOPLANKTON COMMUNITY

During the flood season the phytoplankton population manifests vigorous growth in both inshore and offshore waters. This bloom is almost ex-

TABLE 2
COMPOSITION OF THE BLOOM DURING SEPT. 1961 IN OFFSHORE WATER

Species	Per cent of total phytoplankton
<i>Chaetoceros socialis</i>	32.3
<i>C. curvisetus</i>	25.5
<i>C. decipiens</i>	7.5
<i>Leptocylicindricus danicus</i>	6.0
<i>Skeletonema costatum</i>	4.8
<i>Chaetoceros densus</i>	4.1
<i>Thalassionema nitzschioides</i>	3.6
<i>Asterionella japonica</i>	3.0
<i>Cerataulina bergonii</i>	2.2
<i>Rhizosolenia fragilissima</i>	2.2

clusively formed of diatoms (99 per cent). Although about 60 species of the latter are involved, only a comparatively small number of species are responsible for the bulk of population. The *Chaetoceros* population ranges between 45 to 85 per cent of the total. The leading species during the September 1961 bloom are shown in Table 2. However, in 1962 the species composition in the bloom was as shown in Table 3.

TABLE 3
COMPOSITION OF THE BLOOM IN LATE AUGUST 1962

Species	Per cent of total phytoplankton
<i>Chaetoceros socialis</i>	29.0
<i>Cerataulina bergonii</i>	23.4
<i>Chaetoceros curvisetus</i>	17.0
<i>Leptocylindricus danicus</i>	7.6
<i>Thalassionema nitzschioides</i>	4.3
<i>Skeletonema costatum</i>	4.1

During the flood bloom the dinoflagellate population is numerically less significant, constituting only about 0.8 per cent of the total phytoplankton with the following species being more or less frequent:

Peridinium steinii
P. trocheideum
Exuviaella compressa
Prorocentrum micans
Dinophysis caudata

However, a small bloom of *Exuviaella cordata* and *Prorocentrum* occurred at Sta. II in September 1962. This bloom was associated with a sharp drop in the percentage abundance of *Chaetoceros curvisetus* from 20.4 per cent in late August to only 0.9 per cent in September. In the meantime, *Thalassionema nitzschioides* increased from 6.8 to 34.7 per cent.

The composition of the bloom off the Domietta Mouth of the Nile was studied by Halim (1960), who observed (Tables 4 & 5) the following composition during August and September:

TABLE 4
COMPOSITION OF THE BLOOM OFF DOMIETTA ON AUGUST 19

Species	Per cent of total phytoplankton
<i>Skeletonema costatum</i>	45.2
<i>Chaetoceros curvisetus</i>	22.0
" <i>costatus</i>	14.8
" <i>affinis</i>	4.2
" <i>decipiens</i>	2.5
<i>Hemiaulus sinensis</i>	1.5
<i>Carataulina bergonii</i>	0.5

TABLE 5
COMPOSITION OF THE BLOOM OFF DOMIETTA ON SEPTEMBER 11

Species	Per cent of total phytoplankton
<i>Cerataulina bergonii</i>	55.7
<i>Chaetoceros curvisetus</i>	20.0
<i>Hemiaulus sinensis</i>	16.6
<i>Rhizosolenia hebatata semispina</i>	2.2
<i>Leptocylindricus danicus</i>	2.2
<i>Skeletonema costatum</i>	0.2

This shows that the population of *Skeletonema costatum* decreased considerably during a 3 week period, while *Cerataulina bergonii* increased vigorously during the same period, so as to form over half the total population of the phytoplankton bloom.

During the month of October, the phytoplankton population in offshore waters at Alexandria dropped to almost half the total numbers recorded in September. The *Chaetoceros* population was still leading during October, but *Chaetoceros curvisetus* became most abundant (24.2 per cent), while *Chaetoceros socialis* occupied the second position. *Asterionella japonica* and *Thalassionema nitzschioides* progressively increased in numbers, being 10.5 and 7.7 per cent of the total respectively; while *Skeletonema costatum* was still common (8.6 per cent). The dinoflagellate population during October was still insignificant in the bloom.

Several of the diatom species exhibit a secondary maximum at Alexandria in late October or in November. This maximum is due to populations of *Thalassionema nitzschioides* (16.3 per cent), *Asterionella japonica* (14.6 per cent) and *Nitzschia* spp. (13 per cent) (*N. seriata* and *N. delicatissima*) in the order of abundance mentioned. During this period, too, *Chaetoceros* spp declined in numbers, while other diatoms such as *Dactyliosolon mediterraneus* and *Thalassiothrix mediterranea*, reached their maximum abundance, contributing 6.5 per cent and 5.1 per cent to the whole phytoplankton population respectively. The dinoflagellate population decreased considerably in numbers during this month.

During the month of December the Nile bloom came to a minimum. There was a marked drop in all diatom species with the exception of *Thalassionema nitzschioides*, which attained its maximum concentration in this month, constituting 36.2 per cent of the total phytoplankton population. However, the dinoflagellate population flourished in December, forming a population of about 11.5 per cent of the total phytoplankton. This was due particularly to *Prorocentrum* and *Exuviaella* spp.

During the months of January and February, the standing crop of the phytoplankton community attained its winter maximum. *Chaetoceros* spp. dominated the population once more, constituting between 70 to 80 per cent of the whole winter community. Both *Thalassionema nitzschioides*

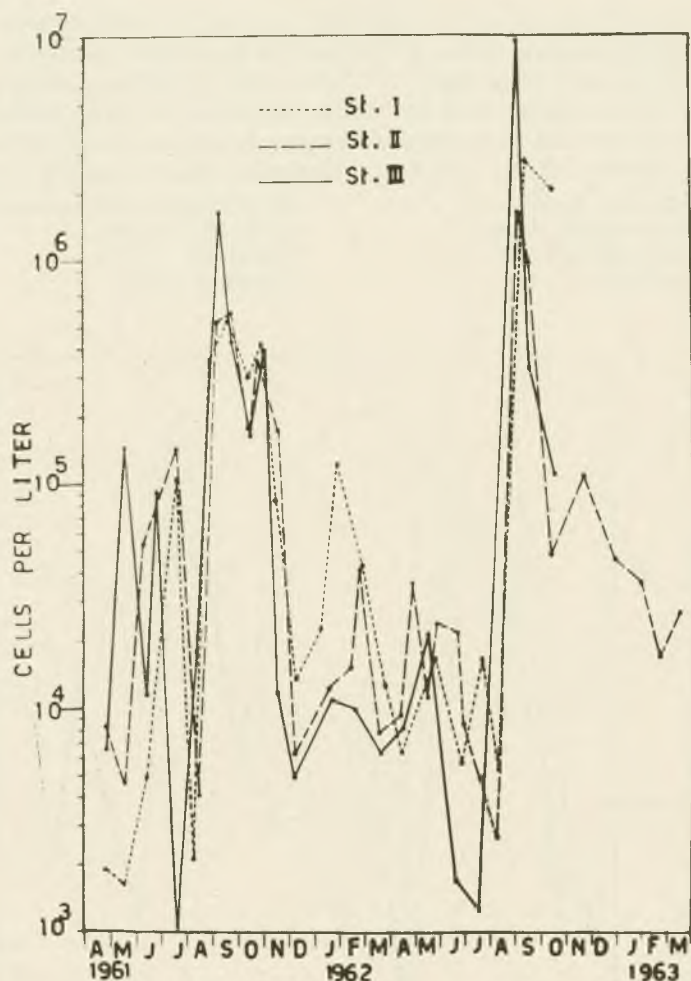


FIGURE 6. Seasonal variations in the numbers of diatoms at the surface in offshore stations.

and *Asterionella japonica* decreased considerably in numbers during this period.

Several oceanic species of dinoflagellates occur in the area in winter. These are rather poor in numbers of individuals, and in many instances are found in subsurface layers. The bulk of these consists of *Ceratium* spp such as *C. coarctatum*, *C. declinatum*, *C. digitatum*, *C. incisum*, *C. gravidum*, *C. ranipes*, as well as *Dinophysis hastata* and *Phalacroma* spp. It is suggested that such species owe their presence in coastal waters to

influxes of offshore waters brought into the area by the westerly winds.

The spring increase in the phytoplankton population occurs in April-May. This is more pronounced in inshore than in offshore stations and, although slightly higher than the winter population, is still considered as much lower than the population developed during the flood bloom.

The following diatoms may be considered as leading species in spring:

Skeletonema costatum
Leptocylindricus danicus
Rhizosolenia hebatata
R. fragilissima

Dactyliosolon mediterraneus
Hemiaulus sinensis
H. hauckii
Chaetoceros spp

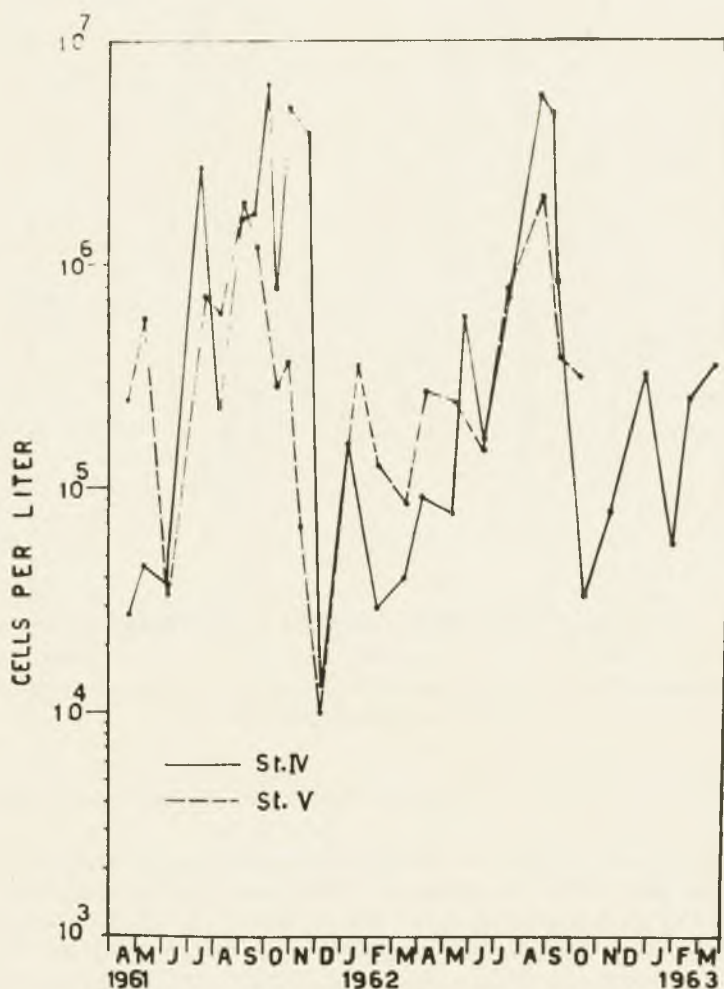


FIGURE 7. Seasonal variations in total phytoplankton numbers at Stas. IV and V.

On the other hand, the dinoflagellates show another peak in spring, particularly in May and in early June. *Prorocentrum*, *Ceratium* and *Peridinium* spp become numerous both in inshore and in offshore stations.

The summer population is made up of the least number of species, of which *Skeletonema costatum*, *Rhizosolenia hebatata*, *Leptocylindricus danicus*, and *Ditylum brightwellii* are the more important diatoms.

Dinoflagellates may at times dominate the phytoplankton community locally in summer for longer or shorter periods. Among the leading species, mention may be made of *Prorocentrum*, *Exuviaella*, *Peridinium*, and *Goniaulax* spp.

The summer condition is characterized also by the lowest concentration of nutrients in the water, high temperature, salinity, illumination and transparency of the water, as well as by relatively high zooplankton production.

Figure 6 shows the seasonal variations of diatoms at the surface in the three offshore stations from April 1961 to March 1963. This shows that the cycle of phytoplankton production is almost repeated from year to year, although the magnitude of production may differ from one station to another. The highest production is developed at the surface, particularly during the Nile bloom.

The seasonal phytoplankton production in the two inshore stations is also shown in Figure 7. This figure manifests higher total production in the inshore than in offshore stations throughout the whole year.

Comparing these changes, on the whole, with the physical and chemical variations pertaining in the water in the different seasons, one could find a strong correlation between the degree of dilution of water by the Nile flood, hence high nutrient content, and the total biological production.

Biological succession.—There is also evidence of biological succession among individual species of phytoplankton which does not seem to be due to the temperature effect. This is also manifested throughout the several weeks during which the Nile bloom flourishes in the sea. For example, in 1962, the late August population dominated by *Chaetoceros socialis* and *Cerataulina bergonii* in offshore stations at Alexandria was succeeded in September by a population dominated by *Thalassionema nitzschioides*, while at Domietta (Halim, 1960) the August population dominated by *Skeletonema costatum*, *Chaetoceros curvisetus*, and *C. costatus* gave way to a population dominated by *Cerataulina bergonii* in September. It already has been mentioned that the blooming of *Exuviaella* and *Prorocentrum* at Sta. II in September 1962 had been associated with a sharp decline in the percentage abundance of *Chaetoceros curvisetus* at this station. This was followed by a marked increase in the abundance of *Thalassionema nitzschioides* from 6.8 to 34.7 per cent of the total population. In this respect, the blooming of one or more species may alter the biological level of the surrounding water, making it either favourable or unfavourable for

the successful propagation of other species as have been advocated by several workers (*cf.* Ryther, 1954; Lucas, 1956, etc.). The grazing selectivity of animals also should not be excluded as a possible factor determining the succession of diatom species, especially during the phytoplankton bloom.

During the period of massive phytoplankton production in autumn, the zooplankton community also is maximal (Fig. 8). The bulk of the latter (*ca* 75 per cent by numbers) is composed of copepods (*e.g.*, *Paracalanus parvus*, *Euterpina*, *Oithona*, *Centropages*, *Acartia* spp, etc.) which graze intensively on diatoms. However, the high reproduction rate of the diatoms during this time seems to compensate for the loss.

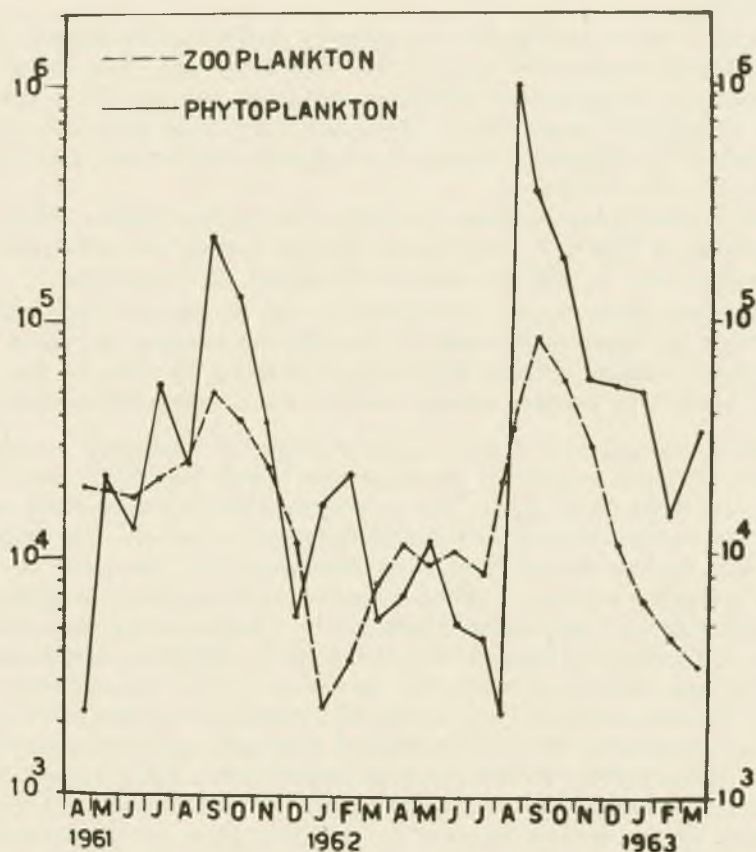


FIGURE 8. Periodicity of zooplankton organisms in relation to the phytoplankton in offshore stations (phytoplankton expressed as cells/liter, zooplankton expressed as numbers of organisms/m³).

MAGNITUDE OF THE PHYTOPLANKTON PRODUCTION DURING THE NILE FLOOD

Massive outbursts of diatoms in the coastal waters immediately follow the discharge of the Nile flood into the sea and the bloom is maintained high for some weeks after. However, the magnitude of this bloom may differ from year to year and even from one station to another along the same coast, depending upon the degree of dilution by Nile flood, atmospheric condition, etc. Nutrient concentrations seem, however, to be the decisive factor. The following table shows maximum numbers of the phytoplankton population obtained in different localities and at different dates from the Delta Coast during the flood period.

TABLE 6
PHYTOPLANKTON PRODUCTION (cells/liter) DURING THE NILE BLOOM
ALONG THE DELTA COAST

Locality	Date	Cells/liter
Sta. III (Alexandria)	Aug. 1962	9,362,600
1 km offshore (Alexandria)	Aug. 29, 1962	5,950,000
1 km offshore (Alexandria)	Sept. 9, 1962	9,812,000
Sta. I (Alexandria)	Aug. 1962	2,000,000
Domietta (Halim, 1960)	Oct. 14, 1959	2,347,000
Domietta (Halim, 1960)	Sept. 11, 1956	2,400,000

Such a production is without a parallel in tropical or subtropical waters. It is considered as much higher than the maximum number of phytoplankton organisms recorded in any other locality in the Mediterranean Sea. The latter numbers, ranging between 109,000 to 759,000 cells/liter (Bernard, 1938, 1958*b*), amount only to less than 0.1 of the production along the Egyptian coast during the Nile bloom.

The Nile flood fertilizes also the North Delta lakes which normally receive water drained from cultivated land containing high concentrations of phosphate and nitrate. Besides, the level of water in such lakes rises during the flood season.

Primary production studies are being undertaken at present in Lake Maruit near Alexandria using C^{14} technique. This lake has a net primary production ranging between 7.7 and 3.4 gm C/m² per day, which is considered the highest known production in such lakes. The water in this lake contains about 25 μ g at NO₃-N per liter and 3 to 5 μ g at PO₄-P per liter in winter. However, phosphate uptake and release is rapid in this lake.

Such lakes with a very high production provide the country with about 50 per cent of the total annual fish yield, nearly 50,000 tons (chiefly *Telapia nilotica*, *Mugil cephalo*, and *M. capito*).

It already has been mentioned that the stream of Nile flood in the Mediterranean Sea is responsible for a flourishing sardine fishery (*Sardi-*

nella aurita and *S. maderensis*) during the autumn every year for feeding on both the phyto- and zooplankton developed. The annual yield of this fish from the Delta Coast averages about 10,000 tons.

In conclusion one can safely state that the fishing industry in Egypt has been depending to a great extent upon the annual flood of the Nile. The latter fertilizes both the inland and coastal waters with nutrients, which in return result in a high primary production. The magnitude of this production is unusual for tropical or subtropical zones.

LITERATURE CITED

ARMSTRONG, F. A. J.

1951. The determination of silicate in sea water. J. ar. biol. Ass. (U.K.), 30: 149-160.

ARMSTRONG, F. A. J. AND I. E. BUTLER

1962. Chemical changes in sea water off Plymouth during 1960. J. Mar. biol. Ass. (U.K.), 42: 253-258.

BARNES, H.

1959. Apparatus and methods of Oceanography, Part I - Chemical. G. Allen & Unwin, London.

BERNARD, F.

1938. Cycle annuel du nanoplankton à Monaco et Banyuls. Ann. Inst. Oceanogr. 17: 349-405.
1958a. Le problème biologique de la fertilité marine élémentaire. Bull. Soc. Hist. Nat. de l'Afrique du Nord. 49: 44-73 (Alger).
1958b. Données récentes sur la fertilité élémentaire en Méditerranée. Rapp. Cons. perm. int. Explor. Mer, 144: 103-108.

EMERY, K. O. AND C. J. GEORGE

1963. The shores of Lebanon. Publ. Amer. Univ. Beirut, Misc. pap. No. 1: 1-90.

HALIM, Y.

1960. Observations on the Nile bloom of phytoplankton in the Mediterranean. J. Cons. perm. int. Explor. Mer, 26: 57-67.

HARVEY, H. W.

1948. The estimation of phosphate and total phosphorus in sea water. J. Mar. biol. Ass. (U.K.), 27: 337-359.
1955. The chemistry and fertility of sea water. Cambridge Univ. Press. viii + 224 p., illus.

LIEBMANN, E.

1935. Some oceanographical observations on the Palestine Coast. Comm. Inter. Exp. Scie. Mer Medit. 9

LUCAS, C. E.

1957. External metabolites and productivity. Rapp. et Proc. Verb. (C.I.E.M.M.), 144.

MULLIN, J. B. AND J. P. RILEY

1955. The spectrophotometric determination of nitrate in natural waters with particular reference to sea water. Analyt. Chem. Acta, 12: 464-480.

OREN, O. H.

1952. Some hydrographical features observed off the coast of Israel. *Bull. Inst. Oceanogr. Monaco*. No. 1017.

ROUCH, J.

1940. Observations superficielles en Méditerranée et l'Atlantique. *Ann. Inst. Oceanogr. Monaco*, 20: 51-74.

RYTHER, J. H.

1954. Ecology of plankton blooms in Moriches Bay and Great South Bay, Long Island. *N.Y. Biol. Bull.*, 106: 198-209.

STEFANSSON, U. AND F. A. RICHARDS

1963. Processes of contributing to the nutrient distributions of the Columbia River and Strait of Juan de Fuca. *Limnol. Oceanogr.* 8: 394-410.

THOMPSEN, H.

1931. Nitrate and phosphate content of Mediterranean water. *Dana Oceanogr. Expdn.* (1908-1910) 3, No. 6, 14 p.

ORGANIC PRODUCTION AND PHOSPHATE IN AN ARID COASTAL LAGOON^{1,2}

MAYNARD M. NICHOLS
Virginia Institute of Marine Science

INTRODUCTION

Shallow water systems along ocean margins are more productive than the ocean itself. High productivity is developed by the favorable action of tidal mixing, abundant nutrient supply or rapid nutrient turnover (Schelske & Odum, 1962). Systems on humid coasts, fertilized by river inflow, are generally regarded to have greater production than systems along arid coasts that receive little land drainage and derive their water from the phosphorus-poor upper layer of the sea (Emery & Stevenson, 1957). However, data from arid tropical lagoon systems are few.

This paper describes the distribution of phosphate and the rates of production in an arid coastal lagoon. An attempt is made to identify processes active in the circulation of phosphate that may influence production.

DESCRIPTION OF AREA

The study was concentrated at Estero Tastiota, a shallow lagoon that lies behind a barrier spit on the seaward edge of the Sonoran coastal plain (Fig. 1). The coast is backed by a terrain of basic volcanic rocks which are a potential source of phosphorus in soils of the region.

Water in the lagoon is mainly of gulf origin. The tide, which ranges about 0.6 m, alternately floods and drains the lagoon. This action mixes lagoon water with gulf water and is a means of transporting particulate materials in or out of the lagoon. Superimposed on the oscillatory movement of the tide there is a small inward net or residual flow from the gulf to renew lagoon water lost by evaporation. Circulation of lagoon water and the chief physiographic elements are diagrammatically shown in Figure 2E.

Lagoon waters are hypersaline most of the time owing to excess evaporation. Salinity at Estero Tastiota increases with distance inward from the entrance, reaching about 41 o/oo at the head (Fig. 2A). Farther inward, beneath exposed pans and high mud flats bordering the lagoons dissolved salt concentrations of interstitial "ground" water exceed an estimated 200 o/oo. These salts are drawn upward by capillary action and precipitated in nearsurface sediments as the water evaporates, a process

¹Contribution No. 246 from the Virginia Institute of Marine Science. A complete paper on this study is published in *Pub. Inst. Mar. Sci., Univ. Texas*, 11: 159-167.

²While this volume was in press, a slightly different version of the present article was submitted for publication elsewhere (Nichols, 1966). As the paper was presented in this form at the Conference, and had been set in type before its publication was called to our notice, it has been retained in the volume. We regret the duplication.—*The Editors*.

reported by Oppenheimer and Ward (1963) in Texas Bay. Sediments of the high flats are oxidized (+95 to +590 mv Eh) but in the central lagoon they are reduced (0 to -195 mv Eh) and anaerobic beneath a thin oxidation layer.

Desert winds that sweep surface waters generate local waves capable of stirring up bottom muds including benthic algae and detritus. Visibilities measured by Secchi disk decrease inward, ranging from about 400 cm off the lagoon entrance to 6 cm in the inner reaches. The depth of light penetration may be expected to show a corresponding inward diminishment. Material that is churned up in the central lagoon tends to settle out and accumulate in quiet-water embayments at the head.

Organic material is synthesized by three types of producers; each occupies different but interrelated sub-environments of the lagoon system. Benthic algae flourish on the high flats and pans when flooded during summer spring tides; whereas, phytoplankton is important in the near-

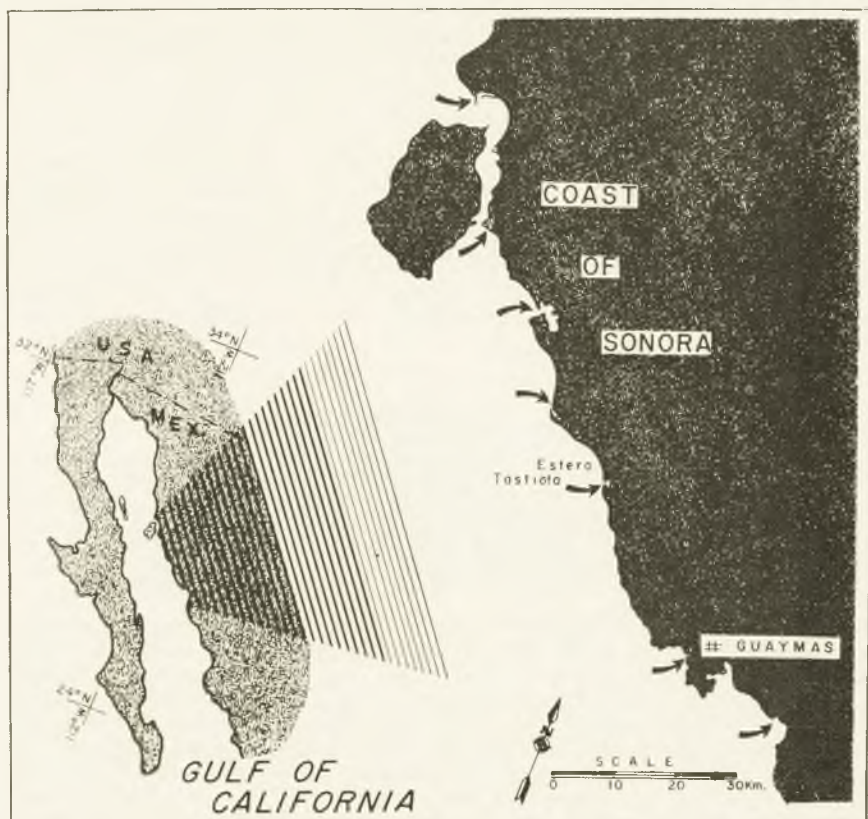


FIGURE 1. Location of lagoon systems on the arid Sonoran coast of Mexico.

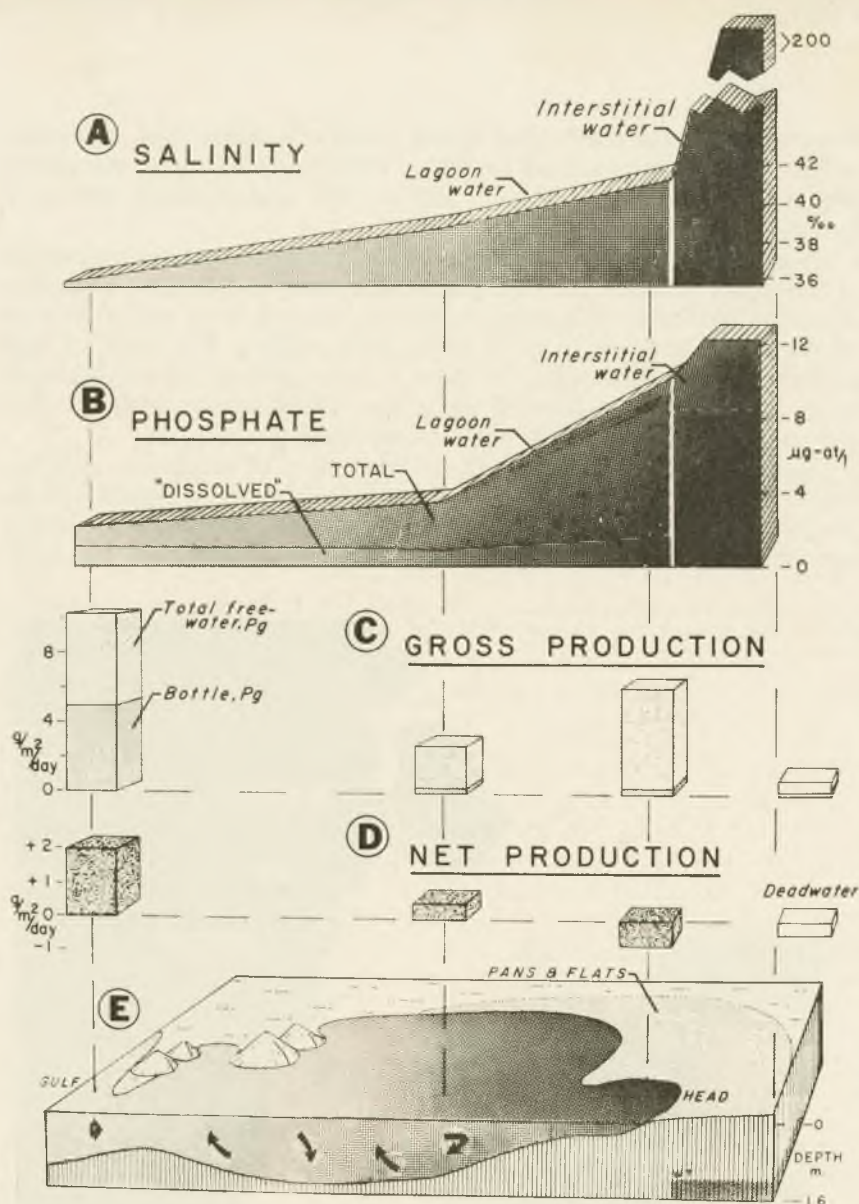


FIGURE 2. Horizontal distribution of chemical properties and organic production in a schematic lagoon system. (A) Average concentration of salinity in lagoon and interstitial water at Estero Tastiota, April, 1961.—(B) Average concentration of phosphate fractions with distance headward at Estero Tastiota, April, 1961.—(C) Average rates of total free water gross production including the "bottle" increment, in different areas of Estero Tastiota. Averages are based on data of Table 1.—(D) Average rates of free water net production in different areas of Estero Tastiota. Averages based on data of Table 1.—(E) Schematic diagram of Estero Tastiota showing circulation (arrows), and major physiographic elements; WT = water table.

shore gulf. *Zostera*, a benthic grass, is the chief producer of the central lagoon; in winter it is partly replaced by abundant growths of *Enteromorpha*.

PROCEDURES

Phosphate concentrations of water and sediment samples were determined by the method of Robinson & Thompson (1948). For total phosphate the samples were digested with perchloric acid prior to stannous chloride-ammonium molybdate colorimetry. Inorganic phosphate was determined after a 3-minute reaction with acid molybdate and the "dissolved" phosphate was determined after removal of particulate material on a membrane filter. Estimates of total organic production were accomplished by the free water diurnal oxygen curve method of Odum & Hoskins (1958). Dissolved oxygen concentrations were determined by the Winkler method on samples collected at two to three depth intervals and at several stations for a 24-hour period. Rates of gross production and respiration were calculated graphically after correction for diffusion between air and water was outlined by Odum. Metabolism of suspended material, chiefly phytoplankton, was estimated concurrently with ordinary light and dark bottles.

RESULTS OF OBSERVATIONS

Concentrations of total phosphate at Estero Tastiota increased inward ranging from about $1.3 \mu\text{g-at/l}$ at the lagoon entrance to $10.1 \mu\text{g-at/l}$ at the head, an eight-fold increase (Fig. 2B). Variations of total phosphate, both with time and from place to place, paralleled variations of turbidity except at the shallow lagoon head. Most of the phosphate was present in the particulate form, either organically combined or possibly inorganically adsorbed on suspended detritus. Its distribution, therefore, mainly depends on the total amount of material in suspension.

The diurnal change of phosphate concentrations during a short period of wind-induced turbidity, generated by an afternoon sea breeze in the central lagoon, is shown by selected curves in Figure 3. A rise in turbidity during the early afternoon was accompanied by an increase of total phosphate and by a slight increase of inorganic phosphate. Corresponding concentrations of dissolved oxygen dropped, a time when oxygen normally reaches a photosynthetic peak.

Concentrations of "dissolved" phosphate also increased with distance headward but they varied within relatively narrow limits: $1.0\text{--}1.4 \mu\text{g-at/l}$. Farther landward, in interstitial water about 1.2 m beneath the high flat surface, dissolved concentrations reached $8.2 \mu\text{g-at/l}$. Phosphorus also increased upward in the nearsurface sediments from 0.08 per cent near the water table to 0.12 per cent at the surface.

Data for production and respiration from varied environments are summarized in Table 1. Average rates of total free water gross production,

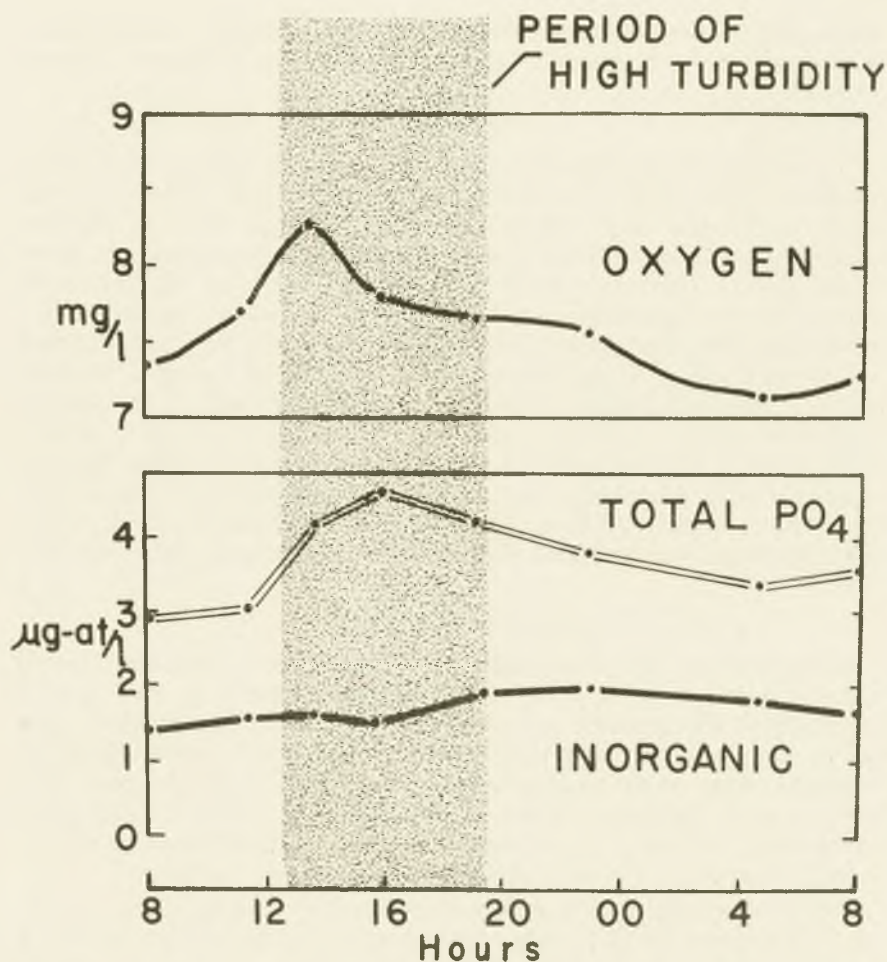


FIGURE 3. Diurnal variations of phosphate fractions showing effect of short-term wind-induced turbidity; central lagoon, Estero Tastiota, April, 1961.

including the production of phytoplankton, reached $10.3 \text{ g/m}^2/\text{day}$ in clear water off the tidal entrance, whereas in the turbid central lagoon rates were $2.6 \text{ g/m}^2/\text{day}$ (Fig. 2C). Gross production in bottles emplaced off the entrance reached more than 50 per cent of the total gross production, whereas in the central lagoon this fraction contributed less than 15 per cent of the total.

Average rates of free water net production reached $1.9 \text{ g/m}^2/\text{day}$ off the tidal entrance (Fig. 2D). The lowest rate, $-0.9 \text{ g/m}^2/\text{day}$, was measured in an embayment at the head. The negative value indicates that

community respiration exceeds photosynthesis. In Tastiota Deadwater, a turbid brackish pond cut off from tidal influence, net production was $-0.3 \text{ g/m}^2/\text{day}$. In the central lagoon, community respiration nearly balanced gross production and there was a substantial average net production of $+0.4 \text{ g/m}^2/\text{day}$. The rates of production at any single station generally were lower in winter than in summer but the trend of relatively high values off the entrance and relatively low values in the central lagoon persisted from season to season.

TABLE 1
VALUES FOR GROSS PRODUCTION (P_G), COMMUNITY RESPIRATION (R), AND
NET PRODUCTION (P_N), $\text{G/M}^2/\text{DAY}$, FROM VARIED ENVIRONMENTS AT
ESTERO TASTIOTA, MEXICO.

Location	Date	Light-Dark Bottle Method			Free Water Curve Method			Water Depth (m)
		P_G	R	P_N	P_G	R	P_N	
Nearshore gulf	Apr. 12-13, 1961	3.2	0.4	+2.8	9.5	7.8	+1.7	4.0
	July 16-17, 1960	6.2	0.2	+6.0	12.2	10.2	+2.0	
Central lagoon	Jan. 8-9, 1961	0.1	0.1	0.0	1.7	1.4	+0.3	0.9
	May 24-25, 1961	0.6	0.3	+0.3	3.9	3.4	+0.5	
	July 16-17, 1960	0.3	0.2	+0.1	2.2	1.8	+0.4	
Inner embayment	Dec. 26-27, 1960	0.7	0.5	+0.2	4.6	5.2	-0.6	0.2
	Apr. 12-13, 1961	0.6	0.3	+0.3	5.2	6.0	-0.8	
	July 16-17, 1960	0.9	0.2	+0.7	8.5	9.4	-0.9	
Deadwater	Mar. 22-23, 1961	0.3	0.4	-0.1	0.7	1.0	-0.3	0.2

DISCUSSION

Phosphate.—The supply and distribution of phosphate in lagoon water is regulated by processes of sedimentation inasmuch as this nutrient occurs chiefly in the particulate form. Phosphate is ultimately derived from the land and from the gulf. The terrigenous-borne fraction consists of complex polyphosphates combined with clay minerals in calcareous soils of the region. A land source is shown by the relatively high content of phosphate in sediments at the entrance of dry rivers. Mineralogic analyses of these river-mouth sediments, as well as sediments on the lagoon floor, indicate that both types are derived from the land. Although imports of sediment into the lagoons are spasmodic and of short duration in the arid climate, nutrient-bearing sediments tend to deposit in the lagoons and remain there. Hutchinson (1957) reports high phosphate levels in inland saline lakes and enclosed basins of semi-arid regions. By contrast, in some humid coastal lagoons, floods of low-nutrient fresh water tend to dilute, as well as flush-out, previously accumulated nutrients (Odum & Wilson, 1962).

Phosphate supplied to the lagoons from the gulf chiefly consists of particulate organic phosphate present in plankton and detritus. This increment is carried into the lagoons by flood flow, or by the net inward flow of density currents, and eventually settles out in relatively quiet areas of the lagoon. A small amount may accumulate near the head by the scour and lag mechanism described by Postma (1961). Inward transport of gulf-derived organic materials is traced by the occurrence in the central lagoon of empty foraminiferal tests believed to be indigenous to the nearshore gulf.

The high inward gradient of total phosphate is attributed to a combination of processes that are intermittently active in the lagoon. Diurnal measurements of total phosphate showed that wave stirring of the lagoon floor produced dense suspensions of bottom materials and corresponding high levels of phosphate. Inasmuch as the lagoons widen and shoal inward, agitation of the bottom is most effective in the broad inner reaches. Near the entrance wind-induced concentrations are reduced by mixing and exchange of lagoon water with relatively dilute gulf water. Near the head, settling in quiet embayments tends to reduce suspended concentrations, especially during calm periods; whereas transport by the scour and lag mechanism favors headward accumulation against the gradient. The small headward increase of dissolved phosphate is attributed to evaporitic concentration in the inner lagoon.

It is supposed that phosphate is rapidly recycled between water, sediments, and plants. The variable character of the environment permits a wide variety of liberation and exchange phenomena to take place. Rapid turnover rates were observed by Bruce & Hood (1959) in a study of diurnal variations in Texas bays. Liberation from the sediment may be effected by bacterial decomposition of entrapped organic matter. It is possible that release is aided by wave agitation which exposes anaerobic sediments beneath the thin oxidation-reduction layer. Part of the liberated phosphate may be adsorbed on sediment particles in overlying water and redistributed by sedimentary processes. Benthic plants, such as *Zostera*, rooted in anaerobic sediments, may directly take up phosphate. Baas Becking & Mackay (1956) called attention to the ability of *Enteromorpha* to accumulate and solubilize phosphate.

Organic Production.—The broad range of values for production show that organic matter is produced at different rates in different but interrelated environments of the lagoon system. Varied production rates are partly attributed to the different types of producers that inhabit the various environments and utilize available light and nutrients. Phytoplankton production is important off the entrance, whereas benthic plant production dominates the lagoon proper. High rates of gross production in relatively clear water off the lagoon entrance, in contrast to low rates in the turbid central lagoon, also reflect differences in incident light reaching the producers. The influence of turbidity in depressing oxygen production is

evident in diurnal variations of dissolved oxygen concentrations and corresponding turbidity (e.g., Fig. 3). In a study of lagoons on the Texas coast, Odum & Wilson (1962) demonstrated that the amount of adsorption and scattering by turbid materials controlled the photosynthetic output. Clear lagoons contained much greater production than turbid lagoons at the same light intensity. In Sonora, shading of suspended materials may be partly compensated by relatively high annual illumination which permits year-around production with successive crops.

Superimposed on light-quenching influence of turbid materials, imbalances in lagoon metabolism arise from exchange of water and deposition of suspended detritus. At the lagoon head in very shallow water, where turbid materials rapidly settle out, respiration was high and exceeded photosynthesis. This imbalance was probably due to the oxidation of organic detritus redistributed from the central lagoon where it was churned up by wave agitation. Whereas, at the mouth, it is possible that gross production is stimulated by the alternate discharge of nutrient-rich lagoon water into the nearshore gulf. Most of the organic material produced in the lagoon is decomposed prior to permanent burial.

SUMMARY

Phosphate, present chiefly in the particulate form, is derived from land drainage and partly from the sea. In the lagoon, suspended phosphate concentrations are redistributed by a variety of processes that lead to a high headward gradient paralleling turbidity. Phosphate-enriched suspensions, produced largely by wave-agitation of the lagoon floor, may accumulate toward the head by inward transport of tidal flow. Settling of suspended materials and mixing with dilute gulf water tend to level the gradient.

Variations of production from place to place reflect variations of turbidity and the activity of different types of producers. Phytoplankters are important producers off the entrance and benthic grasses are significant in the lagoon proper. Wind-induced turbidity of the central lagoon retards rapid photosynthesis and leads to a balance between community respiration and gross production; whereas, off the lagoon entrance, better light penetration results in excess photosynthesis and substantial net production.

REFERENCES

- BAAS BECKING, L. G. M. AND M. MACKAY
1956. Biological processes in the estuarine environment. Va. The influence of *Enteromorpha* upon its environment. Proc. K. Ned. Akad. van Wetenschappen, B, 59: 109-123.
- BRUCE, H. E. AND D. W. HOOD
1959. Diurnal inorganic phosphate variations in Texas bays. Pub. Inst. Mar. Sci., Univ. Texas, 6: 133-145.
- EMERY, K. O. AND R. E. STEVENSON
1957. Estuaries and lagoons. In Treatise on Marine Ecology and Paleoecology (J. Hedgpeth, Ed.) Geol. Soc. Amer. Mem., 67, 1: 673-749.

- HUTCHINSON, G. E.
1957. A treatise on limnology. Vol. 1. John Wiley and Sons, Inc., New York, 1015 pp.
- NICHOLS, MAYNARD M.
1966. A study of production and phosphate in a Sonoran lagoon. *Publ. Inst. mar. Sci., Texas*, 11: 159-167, figs. 1-2.
- ODUM, H. T. AND C. M. HOSKINS
1958. Comparative studies on the metabolism of marine waters. *Pub. Inst. Mar. Sci., Univ. Texas*, 5: 16-46.
- ODUM, H. T. AND R. F. WILSON
1962. Further studies on reaeration and metabolism of Texas bays, 1958-1960. *Pub. Inst. Mar. Sci., Univ. Texas*, 8: 23-55.
- OPPENHEIMER, C. H. AND R. A. WARD
1963. Release and capillary movement of phosphorus in exposed tidal sediments. *In* Symposium on Marine Microbiology (C. Oppenheimer, Ed.) C. C. Thomas, Springfield, Illinois, pp. 664-673.
- POSTMA, H.
1961. Transport and accumulation of suspended matter in the Dutch Wadden Sea. *Neth. J. Sea Res.*, 1: 148-190.
- ROBINSON, R. J. AND T. G. THOMPSON
1948. The determination of phosphate in sea water. *J. Mar. Res.*, 7: 33-41.
- SCHELSKE, C. L. AND E. P. ODUM
1962. Mechanisms maintaining high productivity in Georgia estuaries. *Proc. Gulf Carib. Fish. Inst.*, 14: 75-80.

Economics of Tropical Fisheries

JAMES A. CRUTCHFIELD
Convener

FISHERIES DEVELOPMENT AND NATIONAL ECONOMIC DEVELOPMENT

ANTHONY D. SCOTT

University of British Columbia, Vancouver

ABSTRACT

Fisheries can make a contribution to national economic development in any of three ways. First, it may contribute to the national food supply so that industrialization and the urbanization of the population can progress without having to divert resources to import food from abroad. Second, countries with fertile fisheries can obtain needed supplies for economic development through the export of fish products. Third, an emerging fishing industry may have important indirect effects on other parts of the economy, e.g., textiles, ship-building. Fisheries are likely to provide a useful contribution to food supplies and to exports but are unlikely to provide the foundation for national economic development.

INTRODUCTION

It is commonly said that fisheries provide a great untapped food resource, especially in the tropical high seas. It is also said that national economic growth of the tropical underdeveloped countries depends upon the rapid discovery of larger supplies of food, so that men can be freed from food production in order to get on with the jobs of industrialization and urbanization.

The purpose of this paper is to see whether there is a bridge between these two statements. In what sense can it be said that fishing, like farming, is an essential stage in national economic growth? What contribution can fisheries make to national growth? Below we present an inquiry into these questions. While the conclusion is a skeptical one, reflecting the view that fisheries do not in fact play an important role, it should not be misinterpreted. We are not asking whether fisheries should be abolished as a wasteful appendage to the national economy. That question has its own answer, differing probably in each country. But the question here is about *growth*: Do fisheries correctly claim to have contributed to the economic *growth* of their countries?

Finally the inquiry briefly examines some "common property" characteristics of the fishery. The question here is: Are there special institutional characteristics in the fishery unlike those of land-based industries that prevent it from playing an important role in economic development? The suggested answer is in the affirmative, and some routes for improvement are indicated.

ECONOMIC DEVELOPMENT

The contribution of the primary industries to the process of national development has long been a subject for research by economists. But much

of the early work is now subject to suspicion, not only because its logic and method left much to be desired, but also because it assumed that what must be true of one type of primary production, agriculture, must be true of other types as well.

For the most part the method adopted in these studies was of a simple, straightforward *post hoc ergo propter hoc* type. Because farming had preceded the economic development of the U.K., France, Germany, Russia, Japan, and the United States, it must have been a necessary precondition for their respective types of development. This train of thought led to two types of analyses. One has been dubbed "historicism." The historicists may be briefly described as a group of writers in Germany and France who studied the economic and social histories of the European countries in order to distil a series of "stages of history" through which every country must pass. Every schoolboy is now vaguely aware of their conclusions: each and every civilization must begin as hewers of wood and catchers of fish and game; later domesticating animals and adopting a nomadic pastoral life; then beginning to plant crops and breed plants; then after a short, sharp Industrial Revolution becoming urban and factory oriented, and experiencing a rapid gain in per capita income.

This view has definite drawbacks. It does not explain those countries that have flourished without proceeding beyond one or two of these stages. It does not explain the industrialization of some countries that have never been agricultural at all. And it does not explain the reverse progress of certain nations like Spain that appear to have gone "backwards" through these stages in the last couple of centuries.

Thus those of us who are interested in the application to fisheries of theories about agriculture's contribution to national development are left with the feeling that the "stages" (or historicist) approach is of no help at all, even to the understanding of agriculture's role.

The other approach has been more analytical. Its users have asked a question rather like the following:

Given that a series of countries appear to have reached high levels of income by industrializing; and given that they had little to draw upon during this process except the existing farm community; what had the farm community to offer the nation during the process that was a *necessary* precondition for industrialization?

In the following few pages I intend to review some of their answers, hoping that they will provide clues to the contribution that fishing industries may also make. But it should be said in advance that of the possible list of contributions, some are entirely implausible when applied to fisheries. I will deal with the implausible list first (Johnston & Mellor, 1961).

A Source of Capital.—Industrialization involves the use of machines, buildings, and other durable fruits of previous savings. Some countries of

new settlement, like Canada and Australia, got their start by borrowing savings from already mature nations. But many others have had to start from a stationary peasant economy, either because there was nowhere else to borrow from or because like India today, they were simply too big to lean on the comparatively thin flows of savings available from the already advanced nations.

Economic analysts have traced how in the past such economies have been able to draw on rural saving. Sometimes, in dictatorial states, the funds have been simply extorted from unwilling lenders who have had to tighten their belts and stay at work to stay alive. Sometimes a wealthy feudal class has owned much of the land; if so, a sudden improvement in demand or a drop in production costs has raised their rents so they have been able to lend to the new industries. Europe provides examples of both these processes.

But we find few analogies for these processes in fisheries. England, Holland, Japan, and the United States all had important fishing industries during their growing stages. Yet there is no record of the profits or rents of the fishing industry having provided an important reservoir of savings for the growth of other industries. If anything, the opposite has been the case.

A Source of Labor.—History shows that in pre-industrial eras it was necessary for everyone to work on the land, or close to it. There was not enough surplus production in farming to free men to work at other things. The towns were small and the villages and manors were numerous.

Investigation of industrial histories has shown that the growth of factories and towns depended on agricultural labor becoming more productive. This was accomplished in a multitude of ways: the introduction of farm machines, fertilizers, improved stock and species, drainage, irrigation, and roads. With these improvements, every farm worker could feed his own family and others too. Then labor could be spared — indeed it was driven off the land in many places — to migrate to the towns and cities and form a pool of labor available to build an industrialized economy.

In my opinion, this process has been of negligible importance in the fisheries. The obvious reason is that the fisheries were never tremendous users of labor, so that their modernization could not free many workers.

The matter deserves closer examination. Without, however, going deeply into the subject, two assertions can be made. On the one hand, most fisheries that have released labor to the national economy have not done so because fishermen could now produce more, but because fishermen could now produce less. In short, they have left the fishery because their resource was depleted and total catches were declining in their capacity to sustain the former fleet.

On the other hand, we have fisheries that have continually expanded their yield, as new methods and demands have made it possible to tap

larger and larger fish populations. In these cases, I suggest that the fisheries have absorbed more and more labor. Indeed, it is a hypothesis of economists that a rise in demand leads to more fisheries employment, *even if the total catch does not increase.*

Both these observations suggest that whatever else the contribution of the fishing industry to industrial growth, it is not through its releasing of labor. At least one study of this matter has been made, by Dr. S. Comitini at the University of Washington. Examining the Japanese fishery, he attempted to discover the impact of its rapid development around the turn of the century upon the overall Japanese expansion. Although he grappled ingeniously with the data on manpower, he was unable to show convincingly that fishery development was other than a neutral influence on the growth of the labor force available for industrialization.

A Source of Food.—It would appear that the above comments, though implying some criticism of the performance of the fishing industry in the past, are fairly widely accepted. The evidence of their acceptance is contained in the objectives of those whose business it is to promote fisheries development. Unlike farm specialists attempting to speed the modernization of tropical agriculture, they are not concerned with the reform of tenure, taxes or rents, rural depopulation or overpopulation, or the adjustment of production to new demands. All these topics relate ultimately to releasing land, labor, or capital to other uses.

But most fisheries' development officers one meets rarely speak of anything except (a) maintaining fishermen's incomes, and (b) expanding the size and product of the fishery. In new fisheries, especially in tropical waters, the expansion of the catch is the chief objective.

Here at least one can agree. There is no doubt that in certain parts of the tropics, fish can make a valuable contribution to local nutrition, not only in providing protein for otherwise sub-standard diets, but also in helping the other sources of food to keep pace with human population growth.

In this respect the role of the fishing industry is similar to that of agriculture, a similarity symbolized by the fact that national food industries and international organizations like the FAO take responsibility for both agriculture and fishing industries.

Without developing the matter thoroughly, we may briefly inquire how this supply of food does actually assist economic development. Improved nutrition makes it possible for men to work harder longer, and for diseases of malnutrition to be checked. Cheaper food makes it possible for people to buy other products or to save, thus indirectly encouraging industrialization processes and investment. No one would deny these effects which are, of course, the reason most economic development plans of maritime nations include a chapter or two on fisheries' improvement.

But it is not yet clear that increased availability of fish-food has *in fact*

played an important role in raising the output of backward countries. My impression is that most fisheries' development has been passive, responsive to increased demands for food from rapidly increasing inland populations. We have yet to hear of situations where a fairly sudden access to new fish supplies has made the difference to national diets or food prices so that rapid economic development has become possible. To repeat, it is not necessary that fisheries' officers justify their employment by showing that the production of fish is indispensable for national development. But it is interesting that, even in those nations where fishing is an important part of the national economy, it is difficult to show that fishing has played a role similar to agriculture in providing necessary food during the national development process.

A Source of Export Income.—We come now to a noteworthy contribution that fishing has been able to make. When we examine the world's great fisheries of the past — cod, whales, herring, haddock, and so forth — we realize at once that these have been for the local economy "cash crops" rather than a source of food. They have yielded an export commodity, or staple, that has made it possible for certain communities to flourish on the basis of the fishing industry alone. In our own time, the most important example would be the role of the anchovy industry in Peru.

But on examination even the production of important exports fails to convince the skeptic that the fishery is an important engine of economic growth. No doubt it has been from time to time, and may be here and there. But good economic historians have subjected several fisheries and whaling to intense scrutiny, and their conclusions have not been enthusiastic.

The reason seems to be that in the terminology of Harold Innis, the export fishery has tended to be "commercial," based on trade with other countries and unrelated to other activities inland. Innis has suggested that when the Atlantic fisheries attempted to become "continental," supplying the home, inland market, they fared less well and certainly were less capable of providing a basis for national development.¹

In more recent terminology, Innis may be said to have been hinting at the idea that export fisheries are often "enclaves" of the outside world rather than frontiers of their own domestic economies. Thus, their success

¹Harold A. Innis was an important Canadian economic historian who devoted much of his early scholarly career to the study of the American Atlantic fisheries. An examination of his book, *The Cod Fisheries, the Spanish fishery in the North Atlantic in the 17th century*, and his specialized essays on development themes leads one to the conclusion that Innis regarded the fisheries as interesting in themselves, important in the early history of New England, Newfoundland and Nova Scotia, and Quebec, and an essential element in our understanding of the grand strategy of the developing Atlantic powers: Britain, Holland, Spain, France, and Portugal. But rarely does he give any suggestion that the early development of the fishing industry was in any way essential for what was to follow in North America's massive development. One of the few suggestions he does make is that the Atlantic fishery made it possible for Britain to acquire Spanish gold in the fish trade to Catholic Spain. This gold was of course important for Britain's subsequent imperial growth. But the connection of that trade with North American development is very indirect.

contributes more to their markets abroad than to their neighbors inland.

Much of this disappointing performance of fishery exports in economic growth has a very simple explanation. Like other raw materials, fisheries' products can move in international trade fairly easily; but the higher the degree of processing, packing, or transformation that they have been given, the more exclusive are the trade barriers they must surmount. Sometimes there is an absolute prohibition of their importation. More usually, tariffs are very high. These barriers are intended to protect the processing industries in the importing countries; thus Peru is able to export meal easily, but not poultry or animals fed on such meal, and even less can she export cooked meat products based ultimately on her fish meal production.

As a consequence of these typical import tariff structures, the size of the industry that can be based locally on the export fishery is extremely small, relative to the number of dependent industries that will be started in other regions. This brings us to the topic of "linkages."

Linkage.—Like most other industries, fishing is "linked," in the exchange of partly-finished goods, with other industries. Farming, for example, has a "backward linkage" with the fertilizer industry, creating a demand for chemicals and thus leading to the development of a chemical industry in an otherwise rural economy. Similarly, in producing raw materials it has a "forward linkage" in creating opportunities for profitable investment in manufacturing industries that process foods and turn fibres into textiles and clothing. Thus, a newly productive farming industry may have the result of inspiring and supporting industrialization both behind and ahead of it; and this industrialization has often in its turn provided the sources of further industrial and income growth.

What can we say of the fishery in this respect? It undoubtedly has such linkages. In a few countries it has provided an important market for an indigenous textile and tackle industry — but probably this linkage is weak in countries where nets, line, and tackle are cheaply imported. More important is the support it gives to a shipbuilding industry which, in turn, may by its demands and by-products lead to the creation of other industries. I would suggest, however, that this linkage is not, in terms of the development of most countries, an important source of industrialization. It is more often an extension of the fishing industry itself than an industry which, once born, is capable of taking on an independent existence.

What about forward linkage? Fish must be iced, cured, canned, or reduced. In tropical countries one of these types of processing is highly necessary, and absorbs more labor and capital than in the temperate-zone fisheries. Here it seems to me is a definite influence that the fishery is likely to make. As Albert Hirschman (1958) has said, processing industries that already depend upon imported raw material are usually chary of making new investments that can utilize new sources of domestic materials, such as fish. But if the domestic raw material appears first, the

incentive to invest appears immediately; potential processing establishments have the opportunity to take the raw fish and create a local demand for it in some processed form, without worry about comparison with a previously-imported product. This is true whether the final product is meal, fertilizer or food.

A great deal more should be said on this subject, for the existing literature (based on fisheries' linkages in the temperate countries) ignores the different situation of some types of fish processing in the tropical countries. It does appear that new fisheries in tropical climates are bound to create incentives for investment at levels that are urbanized, closer to the final market, provide new skills for backward working forces, and have by-products in the demand for other materials.

This is particularly true of the new availability of fish-based fertilizers. In the temperate countries, a new fishery may at the best inspire some new sea-food restaurants, leading to the development of new cooking and serving skills. But in tropical agriculture, the availability of new and cheap fertilizers may be the basis of a revolution in food production.²

These observations on the possible role of the fishery in economic development are too scattered and speculative to deserve summary. They do, however, illustrate two related points. First, the development of tropical fisheries is often regarded as a salvage operation for an industry that is backward even by the standards of underdeveloped countries. This is shown by the fact that most national development plans and programs that one sees deal with fisheries as just one of a list of industries that have to be expanded, brought up to date, or rationalized.

Second, it must be said that there is hardly an analytical work in the field of general economic development that even refers to the fishery, except when statistics of fisheries and farming are grouped together in tables. One can think of exceptions (some semi-historical works on Soviet and on Japanese development do make minor references to fishery development, and the anthropologist Raymond Firth has written an excellent study of Malay fishermen as an example of economic change). But if the reader were to draw the name of a well-known development economist, at random, from a hat, and to ask that economist where fisheries fit into his schemata and models of economic growth, he would probably be faced with a shrug and an admission that they have not been fitted in at all.

²It is interesting that Innis (1956) could find few examples of linkage between the North Atlantic fisheries and the neighboring settlements. His pages are filled with accounts of the *conflicts* between settlers and fishermen for land, creeks, and beaches. The fishermen seem not to have been a good market for farm products. His most interesting remarks are on the size of the early vessels: when coming empty to Newfoundland from Europe, they were too small to provide cheap transportation of imports or capital goods for the new settlements. Interesting in itself, this observation implies also that Innis could conceive of no other way in which the fishery could possibly contribute to the development of the new settlements.

NEEDED CONDITIONS IN FISHERIES

This omission of fisheries from any appointed role in development models is perhaps understandable purely on the basis of size: the fertility of the seas is nowhere concentrated enough to make it the raw-material basis of a considerable fraction of the local population. Yet this cannot be the whole story; something is wrong in the fishing industry when we find that even in Iceland, even in Japan, and even in Peru the fishery is not regarded as an important source of growth.

The following points deal briefly with conditions that must exist *within* the fishing industry before we may be hopeful that it will make a useful contribution to national economic development.

Adoption of New Techniques.—Obviously, if the fishing industries now existing are to release labor or capital, yield more fish, or provide a basis for linked industries, something new is going to have to occur. Fisheries' researchers everywhere are looking for the "something new," including the finding of previously unknown fish populations; new ways of attracting and catching the fish; methods of impounding and growing fish; techniques for the preservation of fish while at sea, thus making possible longer trips and a better product; greater speed and weather-fastness; the discovery of new uses for old fisheries; and means of preventing fisheries' depletion.

Compared to research in other industries, fisheries' innovations are hard to come by. The nature of the catching process seems capable of remarkably little variation compared to the wide variety of ways in which mankind can benefit from terrestrial animals. This paper does not pretend to have views on the profitable direction of research, but offers only two comments.

First, the fragmentation of research in national laboratories and local laboratories is so great, and such a small part of the research is devoted to the improvement of fisheries technology, that it is surprising to an outsider that any technological progress is made at all. It does appear that a grouping of national and local establishments, coupled with a close economic scrutiny of the direction of research, might produce more results.

Second, and more important, the search for new catching and preservation techniques is inhibited (or killed off entirely) by regulations that forbid the use of any but the most primitive techniques. There are "conservation" reasons for this, of course, but one suspects that the regulatory authorities could find other ways of managing fisheries than forcing a large number of fishermen to use gear and methods that would be recognizable to an observer transported from a century ago.

Such at least is the view of economists experienced in the temperate-zone fisheries. Because there is no source of information on the extent to which the world's catches are taken under regulated conditions, it may turn out that in many of the newer tropical fisheries no government exerts an

influence on the permitted methods. We simply don't know what the quantitative importance of regulation is today. So the above remarks may be unjustified when applied to tropical fisheries. If so, we may hope that governments and industry will use their freedom to promote the most efficient possible methods, freeing capital and labor for use elsewhere in the growing economy.

Prevention of Congestion and Over-Entry.—One of the few lines of progress made by the handful of fisheries' economists has been in connection with the subject of entry into the fisheries. The accepted view today is that in most ocean fisheries new discoveries and techniques create new profit opportunities for fishermen; that entry being free, fishermen and vessels crowd in to an extent that would not be allowed on private property on land; that this crowding not only creates congestion and conflict but also represents a sheer waste of men and capital useful elsewhere in the developing economy; that this overcrowding poses a threat to the existence of the fish population and is usually met by inefficient regulations of seasons, or catching methods; and that the answer to the waste, congestion and depletion lies in restricting the number of fishermen allowed to enter a given fishery.

I have already referred to this view in connection with the observed tendency of more fishermen to enter a fishery when the price of fish rises, even when the total catch does not and cannot increase at all. Such an increase in the size of a fleet obviously cannot be efficient; it is accomplishing nothing more than was previously achieved with a smaller fleet. The same is true of the more normal case where a small increase in the catch is possible (Crutchfield, 1961; Crutchfield & Zellner, 1962; Gordon, 1954).

This tendency is surely one of the explanations of the failure of fisheries to make significant contributions to national development. Consider the following sequence. A country grows in population and income. Hence its demands for food, capital, and labor increase. The increased demand for food raises the price of fish in its known fisheries. This increase in fish price draws *more* people into fishing. Further, it makes it possible to profitably borrow large sums of money to build larger and faster vessels. Thus labor and capital are drawn *into* the fishery as the country grows, even if no larger amount of fish can be taken.

This sequence represents a real loss of growth-encouraging resources. It may be modified by technical progress, by the discovery of new fisheries, and by the appearance of new opportunities for fishermen's employment elsewhere. But to the extent it exists it suggests that one of the first items on the agenda of anyone concerned with fisheries' development should be the drafting of new regulations that (1) permit or encourage the adoption of new techniques, and (2) prevent the wasteful growth of the fleet and the labor force.

Prevention of Wasteful International Competition.—A third pre-condition for the increase in fisheries' performance is the rationalization of fish-catching activities on the high seas (Christy & Scott, 1965). This condition does not require that fishing nations prevent competition in the sale of fish or fisheries' products; far from it. What is implied is that countries should cooperate in (a) the finding of the fish; (b) the decision on the amount of each competing species of fish to be harvested; (c) the assignment of vessels and gear to their catching. The proposal therefore is similar to suggesting that it is proper, in rounding-up range cattle, for the various ranches to work together in finding all the animals, rather than starting a range war or racing each other to see who will find each animal first. Ranchers worked their procedures out years ago. Yet countries sink more and more labor and capital into the task of trying to anticipate each other on the best fishing grounds. Further, their unrestrained efforts lead to overfishing and expensive reductions in the annual yield.

This is not the place to review the various fishing treaties and systems of international law that can prevent this wasteful racing for fish, and the congestion, conflict, and depletion that go with it. All that needs to be said is that while many of the world's fishing authorities are already attempting to work in this direction, many underdeveloped countries are inhibiting their own economic growth by insisting on the continuation of what amounts to battles over the division of an essentially fixed catch. The battles do not produce more fish; but they do soak up national resources.

CONCLUSIONS

An attempt has been made to summarize a few of the main connections between fishery development and the impact on the national economy. They all suggest that while the fishery may be, especially for the tropical countries, a largely untapped source of food and income, holding some significance for the growth of national economies, the fishery is afflicted by serious institutional barriers to its efficient, and expanding, use. These institutional, "common property" characteristics were formerly usual also in land-based industries, but have largely disappeared even in underdeveloped countries. The conclusion seems clear that each tropical country developing new fisheries must:

- (a) establish regulations that restrict the wasteful over-use of labor and capital, and the depletion of the yield;
- (b) frame the regulations so that rapid technical change can be accommodated; and
- (c) make the regulations and restrictions on entry complementary to similar regulations in other countries using the same high seas fisheries.

REFERENCES

- CHRISTY, F. T., JR. AND A. D. SCOTT
1965. The common wealth in ocean fisheries. Baltimore, Johns Hopkins University Press.
- CRUTCHFIELD, J. A.
1961. The role of the fisheries in the Canadian economy. *In* Resources for Tomorrow, vol. II, Ottawa, Queen's Printer: 739-758.
- CRUTCHFIELD, J. A. AND A. ZELLNER
1962. Economic aspects of the Pacific Halibut Fishery. *Fish. Industr. Res.*, 1 (1): 1-173.
- GORDON, H. SCOTT
1954. The economic theory of a common property resource: the fishery. *J. Political Econ.*, 62: 124-142.
- JOHNSTON, B. F. AND J. W. MELLOR
1961. Agriculture in economic development. *Am. Econ. Rev.*, 51 (4): 566-593.
- HIRSCHMAN, A. O.
1958. The strategy of economic development. Yale Univ. Press, New Haven.
- INNIS, H. A.
1956. Unused capacity as a factor in Canadian economic history. *In* Essays in Canadian Economic History, Toronto: 141-143.

DEVELOPMENT OF TRADITIONAL AND LARGE-SCALE INDUSTRIAL FISHERIES IN THE TROPICAL WATERS OF AFRICA

JOHN L. DIBBS

F.A.O. Regional Fishery Field Service Officer for Africa

ABSTRACT

The paper is based on fishery development in the Gulf of Guinea area of West Africa, and the West Indian Ocean from the north of Madagascar to the border of the Somali Republic. The Gulf of Guinea in particular has seen rapid development as a major fishery during the last ten years. First by overseas interests, but of late there has been increasing participation by African countries with a seaboard. By comparison, the countries of East Africa are only now beginning to realize the potential of the Indian Ocean which until recently, has been the undisputed domain of the Japanese Indian Ocean tuna fleet.

Various kinds of aid programs to individual countries as well as regional surveys of marine resources are now being made to plan the national exploitation of the resources.

The role played by research in development is briefly discussed, and recommendations for continued work in this field are described.

INTRODUCTION

The tropical waters of the earth remain the least developed as fisheries. This can be attributed to a number of causes; many of the inshore waters are coral covered with a vast number of demersal species but few in commercially exploitable quantities; also remoteness from world markets and high population centres; while possibly the principal reason for late development and exploitation is the stage of development of the countries and fishermen which border the vast tropical sections of the major oceans and seas.

This paper deals with the Gulf of Guinea area of the eastern tropical Atlantic, tracing the development of the traditional fisheries of Ghana and nearby countries and the recent introduction of industrial fisheries. By comparison, the countries on the east coast of Africa are even farther behind and although tropical marine research is continuing, locally, as yet the exploitation of the western Indian Ocean is the undisputed domain of the Japanese Indian Ocean tuna fleet.

GHANA

To understand the stages of development necessary to convert a traditional peasant fishery into a modern mechanized fishery and simultaneous introduction of large scale fishing units with appropriate shore facilities, it is necessary to describe something of the coastal geography and the background and structure of the indigenous fishing communities.

There are few natural harbors or sheltered moorings along the Guinea coast from Nigeria to Sierra Leone. The greatest section of the 350-mile coastline of Ghana is open sandy beaches constantly pounded by heavy surf with a few rocky outcrops and the occasional low wooded headland. The Volta River enters the sea across a treacherous bar navigable only to those with local knowledge. Two large artificial harbors have now been built to handle commercial shipping, but up to 1961 much of the cargo for the capital, Accra, was unloaded into open surf boats which landed through the surf onto a partially sheltered beach.

There are three major coastal tribes with a fishing tradition. East of the Volta River are the Ewe people who are the beach seiners using large seine nets up to a mile in length. This group seasonally migrate along the coast in their dugout canoes to work beaches as far away as Sierra Leone and Guinea. The middle group are the Ga-Adagbe tribe, centered around Accra, who were the traditional line fishermen, while in the West, the Fanti people specialized on the sardinella fishery known locally as "herrings" and various forms of inshore gill netting.

Over the years the various groups have adopted the fishing techniques of the others and there has been a general intermingling. The craft used were all dugout canoes ranging from the large "ali" canoe with a crew of 8-10 men to the small, single-man gill-net canoe. Most landings took place through open surf onto the beach closest to the village, and up to 1958 the sole propulsion for canoes was paddle and sail.

A count of canoes and fishermen in 1959 showed 8,956 operational canoes with 67,000 fishermen.

There are three main fishing seasons; "herrings" are caught between June and October over the section of the coast from the Volta River to the Ivory Coast border.

Corresponding with this is the best line-fishing season when the canoes venture well out to sea to the edge of the continental shelf, catching a number of species of sea breams, tuna, snapper, sea perch or groupers, and several species of shark.

From September to December, a specialized beach-seine fishery operates east of the Volta for *Caranx hippos*, while beach seining has a general 6-month season from October until April.

This is the background upon which development was based when a Fisheries Department was formed in the then Gold Coast in 1948.

First Development.—With little detailed knowledge of the marine fishery, the first effort was directed at improvement of fishing craft for the "herring" fishery. This consisted of importing of small mechanized vessels to work from open beaches. This proved unsatisfactory as even the smallest vessel with inboard engine was unsuitable for landing through surf and could be severely damaged.

At this stage, work was progressing on a major extension to Takoradi harbor, the first artificial harbor built for commercial shipping in the west of the country. Although no part of the harbor was allotted to fishing boats, one breakwater provided a sheltered anchorage outside the harbor area.

It was soon realized that vessels imported from Europe were much too expensive for local fishermen, and new fishing methods would have to be introduced to provide a continuous income for the higher expenses incurred with mechanical power.

In 1952, the Government sponsored a boat-building yard with an expatriate master shipwright to commence building vessels using local timbers and training African boat-builders. This yard has since developed into an operational commercial yard building wooden vessels up to 56 ft. (17 m).

Inshore otter trawling was introduced using the 31-ft (9.4 m) locally built vessels and in the first years showed very promising results. As more vessels joined the fleet, based at Takoradi, operating within a range of 20 miles, catches began to decline severely, indicating that the resources in this particular area were limited and other harbors would be necessary to accommodate the expanding fleet.

Harbors.—Early in the 1950's at the time the country was granted internal self-government as the first step towards independence, the Government decided to build a major artificial harbor at Tema to serve the needs of the expanding capital of Accra 18 miles away. The Fisheries Department, realizing the urgent need for dispersion of motorized fishing vessels along the coast, successfully negotiated the building of a small fishing harbor as an adjunct to the main harbor scheme. This was scheduled for completion in 1959 and would include berthing quays for motorized vessels as well as a sheltered beach for canoes. A third small harbor was also planned for Elmina, a town 46 miles east of Takoradi, where the entrance and a lagoon provided the basis for a harbor.

Impact of Catch of Mechanized Vessels on Traditional Canoe Fishery.—In 1954, the newly developed mechanized fleet began to have the first impact on the traditional canoe fleet at Takoradi. In 1959 there were 147 mechanized vessels working between 27 ft. (8.2 m) and 31 ft. (9.4 m) in length, with six vessels over 40 ft. (12 m). The owners and crews of these vessels were the more progressive canoe fishermen who had converted across to the new and more efficient equipment. However, it would be only about six of the total number of new boats which could be considered to be reasonably efficient by developed standards. These fished different methods with the seasons, trebling the catch of an "ali" canoe during the "herring" season by more mobility, longer range and following schools of fish along the coast. The balance of the fleet was content to continue trawling all the year round for decreasing returns.

Research and Experimental Fishing.—From the immediate post war years until 1957, fisheries research for the English speaking colonies was conducted by the West African Fisheries Research Institute based in Sierra Leone. After this institute was disbanded, research became the responsibility of the individual countries, but with few research scientists in the late 1950's there was no impact on development.

Experimental fishing by small Government vessels indicated new grounds and the possibility of extending fishing operations to grounds farther out towards the edge of the continental shelf and other areas inaccessible for non-mechanized craft.

Government Decision to Encourage Mechanization of Canoes.—In 1958, after considerable time experimenting, a means of using an outboard motor on the traditional canoes without altering the structure was perfected, and experimental fishing proved the economic feasibility of mechanization.

Loans were made available to canoe owners for purchase of outboard motors and bracket attachments, and schools operated to train in operation and maintenance of outboard engines. In two years, between 1959 and 1961, over 2,000 outboard engines were ordered. It is estimated that the sardinella catch by canoes in 1959 of approximately 24,000 tons increased by at least a third by 1961 due to the mechanization program.

No major problems were encountered in absorbing the catches of small mechanized vessels and canoes in local markets which expanded through the traditional marketing channels, namely the famous West African Fish Mammies.

It is important to note that in 1959/60, three Ghanaian fishermen who had been amongst the first fishermen to purchase small 27-ft (8.2-m) mechanized fishing boats with Government-assisted finance, introduced vessels of over 50 ft (15 m), one of which was imported from the United Kingdom.

First Landings in Ghana of Fish Caught by Large Foreign Vessels Fishing in the Gulf of Guinea.—In early 1959, a Russian factory ship landed 50 tons of frozen fish, mainly *Sardinella* sp., at Takoradi Harbor. This immediately had an impact on the local market, being an out-of-season landing of "herrings," and the fact that cold storage facilities were not available at Takoradi for holding, the fish had to be distributed quickly, affecting sales of local fish.

This trade quickly developed after initial difficulties with customs and overcoming license problems under the Fisheries Act. At this time the first major cold store opened in Accra and regular landings of frozen fish were then stored for distribution.

The next stage of development was the chartering of foreign vessels by Ghanaian registered companies to fish in the Gulf of Guinea. Fishing methods used were principally midwater and off-bottom trawling tech-

niques, thus exploiting the sardinella stocks all the year round instead of the seasonal fishing between June and October when the shoals appear close off shore.

Government Initiative in Commencing Commercial Feasibility Surveys of Pelagic Stocks (Tuna).—Sufficient information had become available to warrant investigation of large shoaling schools of fish seasonally reported in the Gulf of Guinea and known to comprise tuna.

The Ghana Government approached the Star Kist Foods Inc., of California, to undertake a joint survey with the Government of the tuna resources and an agreement was duly signed. The first Star Kist tuna clipper arrived to commence the survey in the second half of 1959.

This may be said to be the forerunner of widespread overseas interest in the tuna resources of the Gulf of Guinea which are now being exploited by numerous foreign vessels.

As a direct result of this survey, the Ghana Government decided to commence a large scale industrial fishery based at the new port of Tema. A total of 6 vessels, 4 purse seiners and 2 distant water trawlers, were ordered from the United Kingdom and the enterprise was to be a state-owned corporation.

Expatriate management was recruited on a managing-agency basis for the early years of operation, and specialized personnel from overseas were used for the fishing operations pending the training of Ghanaians. The first vessel arrived in Ghana in August 1961.

Shore Facilities.—The provision of cold storage in Tema, at first a 700-ton store followed by a 4,500-ton store, was carried out by a joint government and commercial enterprise. The first plan was to export frozen tuna to foreign processors, while frozen trawled fish would be sold on the home market.

This large-scale fishing enterprise is still in the stages of development. Many early difficulties are being encountered, principally the complete reliance on foreign "know how" both in fishing and in management. The government has invested heavily in vessels, equipment and shore facilities, and has had to spend over \$3,000,000 in increasing the size of the original fishing harbor, which was designed for a small inshore fishing fleet.

Private Sector.—In the private sector, similar development is taking place using both local and foreign invested capital. At least three companies have entered the large-scale industrialized fishery, for increasing supplies of fish to the home market. These companies provide their own cold-storage facilities and, if necessary, utilize the commercial cold stores in Accra and Tema for overflows.

Production Increases.—The statistical increase in fish production for Ghana rose from 36,000 metric tons in 1959 to 57,000 metric tons in 1963, and from available figures, to over 65,000 metric tons in 1964.

By far the biggest increase will have come from the operations of the larger industrial units, which, when firmly established, will equal or exceed the traditional type fishing unit catch, the scope of which will always be limited, as will also be the small mechanized units of 27 ft (8.2 m) to 30 ft (9.1 m).

This is likely to cause a socio-economic problem, for although the immediate estimate of fish requirements for the country are over 130,000 tons calling for double the present production, the greatest number of fishermen will remain in the canoe fishery with very little chance of increasing their earning power. A survey carried out in 1959/60 showed the average earning per canoe fisherman during the "herring" season as £24 or \$67; earnings during the balance of the year would be considerably lower. The Government is conscious of this problem and has developed a bigger boat, 38 ft (11.4 m) to 40 ft (12 m), capable of using a ring net for herring, much more efficient gear than the traditional "ali" net, which resembles a herring drift net, as well as other gear for the off season, such as trawling and long lines. These vessels, if used efficiently, should raise the earning power of fishermen that use them, but this will only be a small percentage of the total number.

In the long term, the traditional canoe fisherman will have to give way to the more efficient mechanized and industrial-type fishing operation and seek other employment in more remunerative fields.

Summary.—Ghana was chosen as the first country for detailed description as Ghanaians are traditional fishermen and form the largest single fishing community of any country in Africa. The influence of groups of fishermen from Ghana is evident from the Congo right up the coast to Sénégal. The Ghanaian canoe is the most seaworthy of all dugout canoes on the coast and are acquired by many fishermen in countries bordering the Gulf of Guinea.

NIGERIA

Compared with Ghana, the fishery carried out by Africans in Nigeria is very small. In two of the three maritime regions covering a distance of 250 miles of coast, 1500 canoes of all types have been recorded. Total estimated production of marine fisheries for the early years of the 1960's is given as 30,000 long tons of which 3,500 tons are caught by trawlers.

From scientific data available, the inshore waters of Nigeria are not rich in fish resources. At the present time, 10 small trawlers operate from Lagos and Port Harcourt; and although an average catch rate of 350 tons is being maintained, the size of several of the important species is declining and proving difficult to market.

In 1962, Nigeria imported a total wet fish weight of 265,000 long tons and it is difficult to see how local production can be increased to anything like this figure. A distant-water trawl fleet such as proposed for Ghana

may bridge some of the gap, but this will require heavy investment by private or government interests, and will be dependent on expatriate skills for a number of years. Meanwhile the fish requirements of the country are increasing steadily with population increase and rising living standards.

There are possibilities of a shrimp or prawn fishery being developed off the Delta area of the Niger River and the Bight of Biafra, but the full extent of the resource has not yet been determined. In all probability, if this is developed, the shrimps would be exported as a foreign exchange earner.

Nigeria is within the range of the tuna resource in the Gulf, the present catch of which is estimated at over 100,000 tons exploited by Japanese, American, Spanish, and Portuguese interests. Once again this must be considered as a long-term project due to heavy capital costs and the years of training for Nigerians to fully participate in all skills.

The bonga-shad fishery (*Ethmalosa* spp.) is perhaps the most important traditional fishery which takes place in the sheltered bays and delta area. Mechanization, improved vessels and gear will improve the efficiency of the fishery, but the extent of the resource is limited and it is unlikely to develop into an industrial fishery, but will remain an important domestic fishery for inshore fishermen.

OTHER ENGLISH-SPEAKING COUNTRIES OF WEST AFRICA

The pattern of existing fisheries in Sierra Leone, Liberia, and Gambia is very similar to Nigeria. There are small domestic fisheries using rudimentary vessels and equipment. Small trawl fisheries operate with European skippers and other skilled hands. Tuna is being fished by foreign vessels and shore facilities have been established to handle the bulk of the catch for export and processing. There is little national participation in this fishery. The Governments of these countries are interested in development of the Gulf resources and are participating in surveys of resources.

FRENCH-SPEAKING COUNTRIES OF WEST AFRICA

The Ivory Coast.—The Ivory Coast is taken as the example of marine fishery development in French-speaking countries of West Africa. Although the coastline is slightly longer than that of Ghana, nearly 400 miles, the coastal strip is sparsely populated, with very few indigenous fisheries from the country. The Ghanaian fishermen have dominated coastal fishing with full crews of 50 to 60 men operating beach seines and the Fanti "herring" fishermen moving across seasonally to extend the inshore herring season which moves from east to west.

In 1951, the opening of the port of Abidjan, which linked the Ebrie Lagoon with the sea by a canal, offering a safe sheltered harbor for all vessels and port facilities, marked the start of a non-African fishing industry.

The first ships to operate were European small trawlers which fished the relatively close inshore grounds. These vessels have European skippers and

African crews. By the end of 1959, there were 32 trawlers operating from Abidjan but no African skippers had taken over. A number of these vessels are owned by French companies and the others operated individually by French nationals. Between the start of this fishery in 1951 and 1960, there was a marked decline in catches in close grounds and vessels started traveling east and west up to 500 miles to work new grounds. This decline has continued and at least 12 of the trawlers now carry ring nets for herring besides trawl gear.

The year 1957 saw the commencement of the ring-net fishery for the three species of *Sardinella* (*S. aurita*, *S. eba*, *S. cameronensis*), once again by French interests, using European skippers with African crews. The short season from June through September was greatly extended by the use of mechanized vessels which travel farther afield. By 1959, of the total catch from Abidjan of 18,393 metric tons, 15,000 tons was herring and 15 fully equipped vessels were operating besides the 12 trawlers carrying ring nets mentioned above. All herrings caught are sold to the African market, while trawled fish and crustaceans go to the European-type market and shops in Abidjan.

The rapid increase in the mechanized fleet over-crowded the existing public wharf facilities, and private firms could not handle extra ice and cold storage requirements. This has led the government to extend the fish terminal to be able to handle all the requirements of a mechanized industrial fishery including a base area for a tuna fleet.

Control of the fisheries of the Ivory Coast is vested in the Section Technique de Pechez Maritime, a Division of the Ministere de l'Elevage et de la Production Animale. The Section has a research vessel equipped for experimental fishing with trawl, ring net and live bait tanks for tuna. A research team works in the Centre de Recherches Oceanographique and carries out biological and scientific research. This is a branch of the Office de la Recherche Scientifique et Techniques Outre Mer (ORSTOM), France.

Every effort is being made by the Section Technique de Pech Maritime to improve the small traditional fishery, such as mechanizing canoes and testing new fishing methods. A comprehensive marine training school is also operated by the Section for training African fishermen to take a more important role in the developing fishery.

Sénégal.—In Sénégal, development has been to the same pattern based on private enterprise, but the mechanized industrial fishery has been established for a much longer period. The Port of Dakar is close to highly productive fishing grounds for trawl and other demersal species, and a small-scale tuna fishery has operated for a number of years. Shore facilities have long been established, such as ice-making plants, freezing and cold storage, and several small-scale canneries are operating.

The traditional fishery by Africans is carried out from planked canoes of a unique design typical of that section of the coast. Mechanization with

outboards is well established. Marketing and processing of the canoe catch from beaches outside Dakar is primitive and, as is the case of most West African countries, it is a deterrent to large-scale development of the traditional fishery.

REGIONAL SURVEYS AND RESEARCH

The accelerated development of the principal fishery resources of the Gulf of Guinea, namely trawl fisheries, *Sardinella* stocks and tuna resources, has aroused the keen national interest of the countries with access to the waters as each country has development plans for exploiting these shared resources. As explained earlier, research (biological and oceanographic) is on an individual-country basis, and no single country has the resources to carry out a full assessment survey of the Gulf. This has led to a regional approach either on a multi-country participation basis or through international organizations.

One of the first of such regional approaches to survey resources was undertaken by the then CCTA/CSA (Commissione Co-operative Techniques African/Commissione Scientific African) which is known as the Guinean Year, or the Guinea Trawling Survey. This survey commenced in July 1963 with finance from the United Kingdom, American A.I.D., and France. Early reports from the survey of trawl fish stocks confirm the views already expressed by local scientists that the resources are limited and could easily be over-exploited.

At the same time, the International Oceanographic Commission of UNESCO had undertaken oceanographic research in the area in close association with the Guinean Year Project.

Three other surveys are in operation or have reached an advanced stage of planning. The tuna-resources surveys are being undertaken by the EQUALANT Expedition of the International Co-operative Investigations of the Tropical Atlantic (ICTA) under the auspices of the Inter-Governmental Oceanographic Commission. A survey of the *Sardinella* stocks from Sierra Leone to Pointe Noire is being planned through a Regional Project of the United Nations Special Fund, and a shrimp-resources survey of Nigerian waters is being initiated by a biologist assigned to the U.N. Special Fund Fishery Survey Project in western and mid-western Nigeria.

An FAO/EPTA marine biologist has conducted experimental light-fishing for *Sardinella* from Ghana for the first time with satisfactory results, which is leading to commencement of this new method of fishing.

COMPARATIVE AUSTRALIAN DEVELOPMENT

At the end of World War II, the Australian fishing industry was barely operational. Many small vessels had been commandeered for war purposes and the whole structure needed complete rehabilitation.

As far back as 1924, the State Government of New South Wales had undertaken a Government State Fisheries Enterprise for trawling off the East Australian coast and had acquired steam trawlers from Britain. This enterprise failed within two years and the ships and assets were sold to private enterprise. From then until the end of the war, the fishery was in the hands of private enterprise with no government assistance or participation other than administration of fishery laws.

The state of affairs in 1946 was two industrial type fishing companies, steam trawling with obsolete vessels on the coast (east) and individual vessels up to 60 ft (17.5 m) carrying out Danish seining operations and a small-boat inshore fishery.

The commonwealth Government undertook certain rehabilitation for fishermen from war service by setting up a fisheries training scheme, which admitted fishermen with previous experience as well as young ex-service-men wishing to start as fishermen. This scheme was supported by rehabilitation grants and loans.

A progressive approach to fishery development emerged with the entry of young men into the industry with higher educational standards and broader vision from overseas observations. The Fisheries Division of the Commonwealth Council for Scientific and Industrial Research Organization began more extensive studies of the resources of Australian waters.

Import restrictions on canned fish and scarcities of accepted processed fish products then led to investigation of the availability of such species as tuna which had been reported in an early survey in 1937. The first survey of tuna resources off southeastern Australia was undertaken at Government expense by a Samoan-based American tuna clipper in 1949. During the survey cruises, selected fishermen were given training in fishing techniques using live bait. The results of this survey almost immediately attracted private investment in suitable vessels to carry out tuna fishing. Also, individual boat owners adapted vessels for tuna fishing during the then established season from August through to December.

In further government-sponsored surveys and individual exploratory fishing trips round the coast, the tuna season has now been extended to eight months of the year. Over 15 years, that is from 1959 to 1964, the catch of tuna has risen from 1,000 tons caught by troll lines, to approximately 10,000 tons. This is not spectacular compared with West African production increases from the small canoe catches of tuna in 1958 to an estimated 100,000 tons in 1964, but the Australian development represents private investment from within the country with much of the capital coming from the industry, and the establishment of a new fishery for Australian fishermen, while in the Gulf of Guinea the catch is almost all from foreign vessels landing catches for transshipment overseas. Tuna surveys are continuing in Australian waters financed either by the Commonwealth Government from a fund established in 1957 known as the Fisheries

Development Trust Fund, or jointly by the Commonwealth Government and individual State Governments.

The Western and South Australian crayfish industry over the same period has been developed by fishermen themselves with little help from government sources. The principal incentive has come from the high price realized by frozen tails on world markets, especially in the U.S.A. This export trade will reach almost £A5,000,000 or \$11,000,000 for the current year.

The ocean shrimp or prawn industry has had a spectacular increase in production since the first discovery of ocean shrimps on the east coast in Stockton Bight during 1947. New grounds are constantly being discovered by enterprising fishermen and the Commonwealth Government in association with State Governments has carried out further extensive surveys looking for new grounds. The discovery of any new shrimp fishing ground is immediately followed by commercial exploitation with no assistance from the government. Currently the shrimp resources of the Gulf of Carpentaria, a remote and sparsely populated section of the north of Australia, is being surveyed with joint funds from the Commonwealth and Queensland Governments and in cooperation with the C.S.I.R.O.

Much of the Australian coastline is similar to that of tropical Africa. The continental shelf is narrow, which limits demersal stocks in areas where conventional trawl gear can be operated. Also, long lengths of coast are coral fringed, a handicap to large-scale commercial fishing operations.

Although prior to the second World War the Australian fishing industry could be considered as undeveloped, since the War the skills and capital are available for rapid development if the resources warrant it. At the present time Australia imports two-thirds of its fish requirements but the Government has shown its willingness to protect development of any section of the industry by tariff restrictions if it will lead to increased production and investment.

THE WESTERN INDIAN OCEAN AND EAST AFRICAN COAST FROM THE SOMALI-KENYA BORDER TO MOZAMBIQUE

This section of the East African coastline of approximately 700 miles has a number of natural harbors, such as Lamu and Mombasa in Kenya, and Tanga, Dar es Salaam, Kilwa, Lindi, and Mtwara in Tanzania, besides several large river estuaries, Tana River, Pangani River, Ruvu and Eufigi Rivers. Except for Lamu, none of these ports have developed a major fisheries, and Lamu is primarily a collection point for onward markets.

The continental shelf is very narrow along this section of the coast. There are three wider areas, the North Kenya Banks off Lamu where there is an area of approximately 1140 sq nautical miles between the coast and the 100-fathom line, the Zanzibar Channel and the Mafia Island Channel both with a maximum width of 40 miles. The Pemba Channel between

Pemba Island and the mainland is not part of the shelf as the depth drops to 500 fathoms.

The North Kenya Banks comprise rock, coral formations and some clear areas, while the rest of the shelf area is predominantly coral covered.

The ocean waters are strongly influenced by two currents, the East African Coastal Current which is a northerly branch of the South Equatorial Current dividing off the northern tip of Madagascar and the Arabia Sea water which seasonally penetrates south as far as Tanzanian waters. Newell (1957: "A preliminary survey of the hydrography of East African Coastal Waters") states "the tropical East African waters have a deficiency in nutrients which limits the quantities of plankton growth and therefore affects the 'chain' of marine foods."

These conditions may account for the fact that only a small peasant-type coastal fishery has developed, even though this coast has had Arabian, Indian and early Chinese influence for centuries.

Most of the coast has a fringing coral reef permitting safe landings on most beaches, and therefore the limited fishery is very much on village basis, each small village having its own fishing craft.

Traditional Craft.—The principal local craft is a very narrow planked-up dugout canoe with two outriggers known as an *ngalawa*. Its range and fishing capacity is very limited. There are two larger vessels, the *mashua* and the *dhow*, which in design follow the Arab pattern. These vessels, although reasonably seaworthy, are mainly used for a type of seining in shallow water over coral and rely on sail and paddle. There has been little attempt at mechanization although the *ngalawa* performs well with a low powered outboard motor; the *mashua* and *dhow* are hard to mechanize, being too heavy and large for outboards, and because of crude planked construction they are unsuitable for installation of inboard engines.

The Resource.—Apart from the North Kenya Banks which have been partially surveyed by scientists from the East African Marine Fisheries Organization, principally with line fishing the yield from which is given as 10.8 lbs per line hour (EAMFRO Report 1961) in experimental fishing operations, the demersal stocks on the coast seem to be very limited.

Methods of catch in order of importance used by local fishermen are, inshore gill nets, traps (both moveable basket traps and permanent barricade traps) and line fishing including trolling. *Sardinella* fishing using light-attraction and Mediterranean-type ring net has been carried out on a small scale since 1961, at first with European skippers based in Zanzibar, but in the last year African skippers have taken over, with only moderate success. The resource from fishing operations appears to be limited, not comparing with the Gulf of Guinea *Sardinella* stocks.

Large shoals of pelagic fish seasonally are seen close inshore but the composition of the schools is not known as the fish cannot be taken with

troll lines and encircling gear or a suitable vessel is not available to sample the schools.

Prawns or shrimps are caught in and near all river deltas by beach seines and traps but the extent of the resource is not known.

Investigations of particular fisheries have been severely hampered by lack of suitable vessels along the coast. The one research vessel was not originally designed as an experimental fishing vessel and, until recently when modifications and a general refit were carried out, lacked equipment and gear to carry out fishing operations successfully.

Since late 1964, Japan has been co-operating with the Tanzanian Government and has supplied suitable vessels up to 100 tons to carry out a commercial survey for shrimps, sardines and other inshore species.

Government Assistance for Coastal Fisheries. — Although government fisheries officers have been employed since 1948 in both Kenya and Tanzania, little impact has been made in improving the coastal fishery. With limited personnel and finance, government assistance has mainly been in extension work, but short visits to coastal villages has had little effect on fishing methods and catch. It is as well to point out at this stage that the major fish production in East Africa comes from the great lakes and inland waters of the countries. In Tanzania in 1962, the total production of fish was 63,000 short tons of which only 9,000 tons came from coastal waters.

Although both from research and practical knowledge of the inshore waters, it is known that a major fishery will not be possible, it is still vitally important that coastal fishermen increase their incomes to keep pace with improving living standards in other sections of the population. The number of part- or full-time fishermen does not compare with that in a country such as Ghana, the estimated total number being 12,000. These people cannot be excluded from development planning as it is unlikely that they could be absorbed into other occupations in their present location.

Even with the limited inshore resource it has been proved experimentally that catches can be substantially increased by using vessels with a greater range, greater lengths of gill netting, more efficient traps and, with mechanization, more efficient trolling seasonally for pelagic species.

The governments are now fully conscious of the needs of the coastal fishermen and plan to step up development by providing funds together with fully trained staff to concentrate on selected villages. These teams will move into a village teaching gear technology, handling and maintenance of mechanized vessels, fish handling, processing and marketing and fully training the local fishermen. After a period of 18 to 24 months, the village should become a much more efficient fishing unit. The scheme will eventually cover all major coastal villages.

Research in East Africa.—Marine research for Kenya and Tanzania is carried out by the East African Marine Fisheries Organization (EAMFRO) a branch of the East African Common Services Organization.

In major fisheries of the world, research officers have the benefit of statistics, and the catch-records of the industrial fisheries on which to base stock assessments, as well as liberal samples of catch to study the biology of the various species. Where research precedes development, few if any statistics are available and the research organization has to carry out its own experimental fishing operations in order to study species and estimate resources as a guide to future development.

A number of valuable studies have been carried out by EAMFRO, among them "The Fishery Banks of Lamu," and "The Fisheries of the North Kenya Coast," by J. F. C. Morgan (1959, 1961), and "Preliminary Survey of the Pelagic Fishes of East Africa," by F. Williams (1956). These studies are not conclusive as the authors have had insufficient material available on which to base firm conclusions on which development can be planned.

It has been known to the governments that a pelagic resource exists wide of the continental shelf which has been exploited by the Japanese Indian Ocean tuna fleet. Vessels of this fleet periodically call at East African ports for bunkering and transshipping catches for delivery to Japan. With independence, the governments are keen that their countries should enter such a fishery, which is within comparatively easy reach of the local ports. With this aim in mind, EAMFRO has been instructed to carry out experimental long line fishing in the area from 20 to 100 miles to sea. The Research Organization is being assisted in this study by two international experts attached to the Kenya Government, one a marine biologist and the other a master fisherman with long experience in Japanese fishing techniques. At the same time, the Kenya Government is carrying out long line fishing experiments in the 10 to 20 mile belt and all available information on Japanese catches in the Western Indian Ocean is being assembled.

It is hoped that with the results of this a concentrated study (1 year), to attract foreign capital to establish a deep sea tuna industry in East Africa, the catch of which would be principally exported to earn foreign exchange.

The Japanese Indian Ocean tuna fleet comprises 200 catching vessels with an annual stated catch of approximately 124,000 tons. Long lines are the method of catch and bait for the lines is transported frozen from Japan.

The economics of the Japanese industry are unknown to the East African governments and it is possible that the economic structure is not fitted for a national industry in any of the countries of East Africa. This means that should any of the governments attract foreign capital to establish a tuna

fleet based in East Africa, it is almost certain to be Japanese or Far Eastern interests who know the fishing techniques and have established overseas outlets for the catch. It is unlikely that a state-owned company could be successful as it would be wholly dependent on recruiting foreign skippers and fishermen and it would be many years before competent local people could be trained to run such a venture.

The most likely method for establishing such an enterprise is a foreign owned company to establish a local East African branch registered locally, and the transfer of ships to work from local ports, besides providing necessary shore installations.

This would be a matter for a government policy decision. Governments may wish to participate in such a scheme either by a direct share such as a 51 percent - 49 percent share or less, with a direct voice in the management policy. This is an established method of setting up an industry where private local capital is not available for participation, and has already been successful with the meat canning industry in both Kenya and Tanzania.

The International Indian Ocean Expedition will contribute substantially to the knowledge of the Indian Ocean which in the long term will benefit the countries of East Africa in their development planning for greater exploitation of available marine resources.

THE FUTURE NEEDS OF AFRICAN COUNTRIES FOR DEVELOPMENT OF TRADITIONAL AND LARGE- SCALE INDUSTRIAL FISHERIES

There must be a continued flow of capital into the developing countries of Africa if governmental aims to modernize the traditional fisheries are to be accomplished. The first need is a sound fisheries administration, with sufficient trained staff and finance to develop all branches of a fishery service. It is not enough for government officers to lay down a policy, there must be an active extension program to demonstrate the use of new vessels and equipment to replace dugout canoes which are limited in their catching capacity.

Any extension program must be supported by a loan scheme. Training and demonstration in new methods are of no use if fishermen cannot acquire the new equipment. Few fishermen have the capital required for even an outboard engine let alone a small conventional fishing vessel. Fishermen, especially African, are conservative and the transformation from a peasant fishery, little above subsistence level, to a commercially paying operation can only be accomplished over an extended period of time. Loan repayments must be spread over sufficient time to permit the fishermen to perfect the new skills. In this regard a moratorium of at least a year should be allowed when the loan is a substantial amount, such as when a new vessel and engine is acquired.

It is inevitable that the backward and less efficient fishermen will be bypassed in development. As a general rule, the numbers of fishermen involved are far too many for the industry to support and the use of more efficient gear with larger bulk landings by the progressive men will mean a general lowering of price, which will either leave a larger number on bare subsistence or put them out of the industry altogether.

The large industrial fishery with vessels capable of staying at sea for long periods with refrigeration to preserve the catch can only be warranted if the country has access to known large fish resources. The capital for such an enterprise must come from government sources or overseas investment in the country. There are few private African firms which could raise even a small portion of the capital needed, not only for vessels but the supporting shore facilities. The skilled personnel would for a number of years need to be experienced expatriates.

Trained Personnel.—The fisheries service must be staffed with qualified and experienced personnel. Academic qualifications alone do not make a fisheries officer, and Africans graduating from universities and colleges need experience in the field under expert guidance to teach them the practical application of their newly acquired knowledge. Lack of experienced management is one of the greatest handicaps to development in the newly independent countries. Many fishery enterprises have failed in the initial stages by trying to do things "on the cheap" by employing inexperienced people in top positions. The investment necessary to modernize tropical marine fisheries warrants the highest skills in all sections.

Training.—Training is the key to development. There are few available facilities for training in fisheries in Africa, and for that matter throughout the world.

Most governments in recent years have become aware of this and many national training schemes are commencing. This in itself taxes the resources of government as there are insufficient teachers to man the training institutes.

Training must be undertaken in three fields. In the first place, traditional fishermen must be trained in the use of modern vessels and equipment. This itself is a major undertaking when the intricacies of modern engines and gear must be understood and fishermen are often illiterate and have had no background experience.

The skills necessary for handling and operating large ocean going fishing vessels require a formal training besides considerable sea experience. It is often said that fishermen are born, not made, so it will remain to be seen whether Africans, new to modern fishing techniques, will be able to acquire the skills and judgement needed for successful fishing operations.

A modern fishery requires numerous shore facilities and many specialized skills are necessary. Besides management and business experience to control operations and undertake marketing, refrigeration and many

forms of processing form an integral part of a large scale industrial fishery. The men to operate such facilities need technical training through specialized technical colleges which are not always available locally.

Training of Personnel for Fisheries Services.—A Fisheries Service which has to guide the industry through all stages of development needs many qualified men.

Top administrators must understand sound administration, research, technology and economics and be capable of sound phased development planning.

Research in all its forms needs graduated from Universities. The science faculties of African universities are now producing a steady flow of graduates who, with guidance and possible overseas post graduate experience, can fill the necessary research posts.

The technologists and extension officers are more difficult to train. Most governments have plans for national training schools for the lower cadre of field personnel where comparatively large numbers of men are necessary to operate expanding fisheries departments.

The major difficulty arises in training the important field officer of diploma level who comes between the graduate and the artisan grade. Although the present rapid expansion may call for ten or more of such officers per country, the future needs to replace normal wastage in the service may only be one or two per year.

This training is then uneconomical at national level, and there are moves to establish a regional training course attached to an established institute to train the future field officers for groups of countries with similar fishery development plans.

CONCLUSION

The last decade has seen rapid development and a great awareness of the potential of the tropical seas. The developing countries need to utilize all available resources, and with fish, which is a high protein food of which there is deficiency in many countries in the tropics, this is a means to improve national diet as well as boosting the national economics by exploitation of a natural available resource.

ASPECTS OF FISHERIES IN THE DEVELOPING PHILIPPINES ECONOMY¹

JAMES A. STORER²

Division of Economics, U.S. Bureau of Commercial Fisheries, Washington, D.C.

ABSTRACT

Fisheries in the Philippines have undergone changes in the last decade with the construction of large trawlers equipped with refrigeration, and the establishment of canneries. The developments have been instituted by American and Japanese entrepreneurs. A result has been an increased total catch at significantly improved rates of productivity compared to the primitive techniques that mark the major part of the country's fishing efforts.

Problems in the industry include too easy entry, unproductive capital equipment and techniques, and inadequate and outdated shoreside facilities. Government aid efforts have been less than satisfactory although they have been assisted by the FAO and the United States.

INTRODUCTION

There is some concern on my part that a paper about Philippine fisheries may be stretching too much the concept of a shrinking world. However, I note that I am not alone in this international conference in directing attention to another part of the world. Furthermore, the problems of underdeveloped regions have much in common. This is particularly so in comparing the Philippines to some of the Caribbean areas where the general climate, geographical environment, and even the Hispanic culture provide a striking similarity.

The Philippines is a country of 7,000 islands, of which about 800 are inhabited. This basic geographic condition has had a tremendous impact on its political, social, and economic development. Indeed, one of the amazing aspects of the Philippines has been its ability to achieve a reasonably cohesive and integrated structure in the face of this physical fragmentation.

ECONOMIC DEVELOPMENT

The country has traditionally relied on agriculture with the emphasis placed upon a few crops such as sugar, copra, and rice. After the end of World War II, and the simultaneous achievement of independence, the young Republic embarked upon a program of economic development which was focused upon achieving a significant design of industrialization. The concentration upon industrialization as the panacea and the lack of interest in agriculture, as well as fishing, are not unique to the Philippines. The recent industrial development of the country has been startling; manufacturing has been the most rapidly growing sector of

¹The views expressed in this paper represent the personal ones of the author and do not necessarily reflect those of the Bureau of Commercial Fisheries.

²Present address: Bowdoin College, Brunswick, Maine.

the economy and in recent years has accounted for at least a fifth of the national income whereas immediately after the war it represented only one-twelfth.

This industrial growth has been assisted by substantial U.S. grants and technical assistance programs. It has received the attention and investment of a number of American and other foreign private investors who have seen in the Philippines opportunities for growth and profits notwithstanding the many manifestations of Filipino nationalism. A rather surprising aspect of this development has been the concomitant emergence of a Filipino entrepreneurial class which has sprung up from a number of sources within the pluralistic society. An amazing feature of this development has been the extent to which western (or U.S.) business practices and associated social customs have pervaded Manila and its suburbs. It should, of course, be clearly kept in mind that these manifestations are rarely to be found in the rest of the Philippine Islands where the traditional rural pattern is dominant.

In this brief overview of the Philippines, it is essential to point out one or two other features. One is the fact that the process of development has been carried out within the framework of a clear decision to rely essentially on private enterprise. This reliance is a part of the heritage of the 50 years of American occupation and there is little evidence in the post-war period to suggest a change in this viewpoint.

This is not to say that there has not been an active role by Government. There has been, and it has taken a number of forms including, at times, an extensive array of controls over the foreign trade and international payments sector in which preferential treatment has been accorded to desired industries and interests. There has also been a flirtation with economic planning. Though the techniques of planning have become more refined and sophisticated, it has never become a very substantive part of the development process. This is partly because of the basic tendency to rely on free enterprise, which has been so handsomely profitable for some, but it is also due in part to the political structure. More often than not, the executive and legislative branches have not been in harness together and party discipline has been hard to enforce in a country where personal power has transcended party loyalty. Furthermore, administrative limitations as well as the prevalence of "anomalies" have presented a block to the effective prosecution of any government program.

POPULATION GROWTH

Finally, a word must be said about the population of the Philippines. The most recent estimates would indicate that it is growing at a rate of 3.3 per cent a year, one of the highest rates in the world. The population now is above 30 million and by 1970 it will probably be 38 million or more. Birth control measures are hard to implement in the Philippines

for the usual number of reasons that apply to underdeveloped regions including, in this case, the dominance of the Roman Catholic religion among the Malay population.

Despite the population growth, there have been gains in the per capita income even when taking into account the rising price level and it now amounts to more than \$130 yearly. Such a per capita figure, however, does not reflect the very unequal distribution of income that pertains in the Philippines. It is therefore to be questioned if the bulk of the rural population has made any real gains.

PHILIPPINE FISHERIES

Let me now turn to the fisheries of the Philippines. They are important to the country and bear promise of becoming even more so. (The statistic that fisheries represent only about 4 per cent of the Philippine gross national product (GNP) is an understatement and does not adequately reflect the extensive subsistence fishery activity.) It has been indicated in a recent survey that 75 per cent of the population ate fish daily. Fish, together with rice, constitute the basic items in the diet. In 1963, the fish consumption of the Filipinos, locally produced as well as imported, amounted to 18.7 kilos per capita while meat and dairy consumption was less than 14 kilos (31 lb). Though this consumption seems like a great deal when compared to fish consumption in the U.S. (about 5 kilos; 11 lb), in the Philippines it is considered inadequate in view of other nutritional shortages. One of the frequently used measures in the Philippines of this inadequacy is an estimate by the National Research Council of the Philippines that the nutritional standard in the Philippines called for an annual consumption per capita of fish of 26.97 kilos. Consumption in 1963 was 8.25 kilos short of this standard. Production, of course, was even more deficient since the Philippines import significant amounts of fish products. Domestic production in 1963 amounted to an estimated 547 million kilos, or about two-thirds of the total desired amount of 831 million kilos.

Collection of Fishery Statistics.—At this point it is wise to insert a note of caution about the statistics concerning fishing in the Philippines. Fishing statistics are never what one would desire or even need, including in the United States. In the Philippines, as in other underdeveloped regions, they are particularly inadequate and inaccurate. Concern with this problem has been manifested by every foreign expert who has investigated any facet of Philippine fisheries. Filipino fishery officials have also been aware of the problems.

One of the obvious problems lies in the inadequate support given to the statistical arm of the fishery service. Until a few years ago the office in Manila consisted of nine people, one typewriter, one adding machine, and a hand-cranked calculator. Recently the staff has been augmented by

both statisticians and equipment. However, financial support is still inadequate. The annual salary, for instance, of the chief economist and statistician is less than 7,000 pesos a year which amounts to less than (U.S.) \$2,000 and is also below the salary level for economists in other units of the Philippine government.

Formidable difficulties also arise from the fact that most of the data are collected as an adjunct to the taxation system. All commercial fishery vessels are supposed to land their catch at one of the official landings. The boats all tend, however, to arrive at about the same time, between 0300 and 0400 hours, in order to take advantage of the early morning retail market. The great number of vessels, most of them small, and the rapidity with which the catch is disposed of, make checking by the few wardens a haphazard affair.

Operators of such vessels are also required to provide a monthly tally of the catch and to pay on the basis of this 2 pesos per ton to the Fisheries Commission. In addition, on the basis of the same catch data, they are supposed to pay the Bureau of Internal Revenue a tax of 7 per cent of the value of the catch (ex-vessel price). The pressure of these two tax measures tends to distort the reporting of data; the under-reporting of the volume of the catch and a downgrading of the species of fish caught in order to provide, for the record, a lower value of fish landed. The estimates of the extent of this downward bias vary but they have run as high as 50 per cent on the volume and even higher on the value.

A further problem in obtaining reliable statistics is that the jurisdiction of the fisheries is divided between the federal government and the municipalities. (The provincial governments have no authority in this instance.) The federal government licenses all boats of over 3 gross tons and it is these boats that constitute the commercial fishing activity, one of the three statistical categories of fishing in the Philippines. On the other hand, the largest portion of the total volume of catch is ascribed to the category of municipal or sustenance fishing. Over this fishery there is no effective control or statistical reporting. A tremendous degree of "guesstimating" enters into the statistical development of this component.

A third category of fishponds is the smallest, but probably the most reliably estimated with respect to output, since registration of fishponds giving their area is quite complete. Though there are rather wide differences in productivity the catch can in the aggregate be reasonably well estimated.

All of these limitations to the statistical data place great limitations in turn upon the uses to which the data can be put. One cannot avoid, however, making some application of the statistics and one hopes that the inferences drawn, at least in their general direction and emphasis, are not incorrect.

Characteristics of the Fisheries.—The threefold division of Philippine fisheries into commercial, municipal or sustenance, and fish ponds is useful for reasons other than governmental convenience. These divisions can be followed in describing the nature and characteristics of the fishing activity for there is, in effect, not one fishing industry but rather several distinct ones.

As I have indicated, the Fisheries Commission estimates that municipal or sustenance fishing is the largest component, in 1963 accounting for some 277 kilos or 51 per cent of the total catch of 547 kilos. It represented a somewhat smaller share of value, 43 per cent, reflecting the fact that the species and their size were somewhat less favored in the market than those of the commercial catch, or, more particularly, that of the fish ponds where the *bangoes* (milkfish) are raised.

The municipal or sustenance fishery absorbs at least 65 per cent of those directly or indirectly engaged in the industry. This amounts to some 260,000 persons of a total number of about 400,000 persons to be found in Philippine fisheries. Fisheries represent, incidentally, about 3 per cent of the Philippine labor force.

These thousands of fishermen in the municipal fishery carry on for the most part a pitifully ineffective effort to obtain some yield from the over-fished waters near the coast and on the inland lakes and rivers. An infinite variety of rigs and gear are employed including a wide range of nets, traps, weirs, corrals, baskets, and other devices. When boats are employed they are customarily *bancas*, or *vintas* among the Moros in the south, usually equipped with outriggers and increasingly with some kind of an outboard motor. Some of this effort when viewed by the tourist is most picturesque, but it is never in its individual or mass effect an efficient way of exploiting the resource or of providing a livelihood for its practitioners.

About 100,000 of these fishermen crowd the shores of Laguna de Bay, the largest fresh water body of water in the Philippines, located just south of Manila. Here with incredibly small meshed gear they try to catch fish measuring only 6 to 15 cm long, shrimp and clams 3 to 5 cm long, and what they catch is sold by the gallon. On Manila Bay and elsewhere along the coast, they have resorted to dynamiting for fish in lieu of any other alternative. Indeed, the effort to stop such illegal as well as ineffective practices has occupied a disproportionate amount of time and personnel of both municipal and federal officials. Such efforts are, of course, largely futile. There is no incentive to prosecute; the offender cannot pay a fine and if committed to jail, the burden of supporting his wife and many children is merely shifted to the government. Furthermore, such efforts to control the problem are easily thwarted.

The pressures upon these people to fish are tremendous and essentially add up to a complete lack of alternatives, some of which are a mani-

festation of their own limited personal development. A few years ago, a sampling of 125 fishermen operating small boats in Manila Bay was undertaken. It revealed that the men enter the fishery at the average age of 18 with less than 1 per cent of them having finished high school. Only 23 per cent have finished the fourth grade and over 6 per cent have had no formal education at all. Yet over half of them had dependents and even a majority of the single men had one or more dependents. Over 80 per cent had no radios, which one is inclined to feel are ubiquitous in the Philippines, and over half of them had no electricity. Their employment was exceedingly irregular, but when they did work, those on a wage system received 18 pesos a week while those on a share system received but 7 pesos a week.

Let me return, however, to a consideration of the output of the municipal or sustenance sector. Its total output of 283 million kilos in 1963 is an understatement. Nonetheless, it has grown since 1959 by only 6 per cent. I have no statistics about the certain growth of manpower in this activity but one is not encouraged about the gains in total production or productivity of this sector. In view of the annual increase in population of about 3.3 per cent, it would be difficult indeed if Filipinos had to rely on this sector of the fishery for increased protein supplies.

Some notion of the differences in productivity of the sustenance segment of the fishing industry as compared to other more productive sectors is provided by the 1961 Census of Fishing that has just been released. In that year, fish corral operators, who are certainly not the poorest of all fishermen, were reported to have had gross receipts averaging 530 pesos a year, or a "value added" of only 290 pesos. On Laguna de Bay "baklad" or corral operators exceed 1,000 in number and in 1962 it was estimated that they were averaging gross receipts of about 2.50 pesos a day which would amount to about (U.S.) 80 cents at the then prevailing rate of exchange.

Measures to improve the lot of these fishermen and to improve the pattern of exploiting the resource are hard to come by. With an absence of other alternatives and the existence of widespread unemployment, it is impossible to think of fewer fishermen, at least for the foreseeable future. Neither is cooperative effort among the fishermen a very likely alternative. Cooperatives of various sorts in the fisheries have been tried without any great success. The independence of the men themselves together with their isolation, provide an unlikely climate at best. The lack of a sustained and adequate cooperative program by the government also has been a factor. Nor can a program be recommended that would, through the use of trawls, for instance, be efficient in the harvesting but would have completely devastating effects upon the bulk of the fishermen who were left out of the enterprise.

It would not be proper to assume that nothing is being done to help

this sector of the fishery. Research efforts are being carried out at Laguna de Bay, having originally and painstakingly been set in motion by a number of experts sent out by the FAO. Technical assistance is also being directed not only toward the lake fisheries but the inshore fisheries of the coast. Some beginning efforts at the badly needed control of the environment through pollution and sedimentation abatement are also being made but these are hard to effect in the political and economic climate of the Philippines. All of these programs are long range in their impact and one cannot be very sanguine about this sector of fishing in terms of its own improvement or its role in the rest of the economy. This is not a "lead" sector of the economy; rather, it awaits progress in overall development in the Philippines which will provide more freedom for movement within and from out these backward sectors.

FISHING VESSELS

Let me now turn to what is termed the commercial fishing in the Philippines. This, as has been indicated, concerns the vessels of over 3 gross tons. In 1963, these vessels landed 209 million kilos, or 38 per cent of the total catch. Five years previous, in 1959, commercial fishing had accounted for only 27 per cent of the domestic catch. The volume of catch of this sector has increased by 77 per cent since 1959 while municipal or sustenance fishing has increased by only 6 per cent and fishpond production, from which much more had been expected, increased by 7 per cent. Even with a large degree of inaccuracy in the data, the commercial fisheries give clear evidence of being the dynamic segment of the Philippine fishing industry.

The total number of vessels registered has increased from 1,477 to 1,929 in 5 years, most of the increase occurring since 1961. There has been a significant change, also, in the type of vessel, the gear employed, as well as in the size. The use of bagnet gear is still the dominant type, accounting for over half of the total number of vessels. There are now, however, a large number of purse seiners as well as otter trawlers. The utilization and development of the former, including mechanization and power blocks, have been due in part to the efforts of FAO technical assistance and aid together with training programs of the Philippine government. In an FAO analysis of the project it was reported that the purse seiners were able to land between 35 and 100 tons from each trip while the earlier basignan rigs were able to catch only about 3-½ tons on a comparable run.

With respect to the increased size of vessels, it should be noted that in 1959 there were only five boats of 100 gross tons or more. By 1963 there were 63 such vessels. These larger boats were usually rigged for either bagnet fishing or otter trawling and they have made possible the exploitation of the fishing resources in the waters surrounding Palawan,

and this area together with the Visayan Sea now accounts for over 60 per cent of the commercial fish landed.

FISHING ESTABLISHMENTS

Some further notion of the dualism that exists in the Philippines fisheries can be found in an analysis of the 1961 Census of Fishing which has been mentioned earlier. According to the census, large fishing establishments, meaning those with 10 or more persons engaged in them, and most of these establishments are boats operating in offshore ocean waters, had gross receipts of 2,469 pesos per person, compared to 531 pesos for the small in-shore corral operator. Value added per person was 1,845 and 292 pesos, respectively. A further useful insight into the very different nature of the larger fishing establishments compared to the smaller efforts is provided by looking at the number and kind of people engaged in these two categories. In the 1,300 large establishments covered by the census some 31,000 persons were engaged, of whom only 2,000 were owners or unpaid family helpers. The rest, 29,000 persons, were paid employees. However, among the 15,000 small establishments, 25,000 of the 34,000 persons engaged were owners or family helpers and only 9,000 were paid employees. In the larger establishments wages to the employees averaged 755 pesos a year while wages for those associated with the smaller establishments averaged only 390 pesos.

GOVERNMENT AID

There are several factors which help to explain the relatively rapid and encouraging rate of growth of the commercial category of fishing. Naturally, the growing population and its customary reliance upon fish provides a large and expanding market. There has been the incentive, too, of acquiring the share of the market now occupied by imported fish products, chiefly canned sardines and mackerel. Imports in 1963 amounted to 50 million kilos with South Africa and Japan being the most important sources. The role of the United States as a major supplier of sardines has declined in recent years partly because of the reduction in the California catch. Maine sardines with their use of soya and cottonseed oils have not been very acceptable to the Filipino taste. In an effort to encourage production, the government has recently tended to remove the imported canned fish from preferential treatment and instead to allow tax free importation of tomato paste and tin plate. Such a policy, of course, is based upon the existence not only of a fishing industry but a canning industry as well.

The government has made other gestures to help the fishing industry including the availability of credit from government development agencies. However, over three-quarters of the credit extended by the Philippines National Bank devoted to fisheries has been concentrated upon fish ponds and only about 20 per cent has been devoted to marine fisheries. The same

sort of situation holds true for commercial bank activity. And the very small fishing operator is, naturally, outside the credit range of either the government or the commercial system. To the extent that credit is available from such institutions as the Development Bank of the Philippines, there have been complaints, notably from the Inter-island Deep Sea Fishing Association, that the interest rates, stated and actual (after the payment of "tong"), are prohibitively high. A basic rate of 8 per cent is charged to which is added a mandatory insurance fee of 6 per cent, making a total official rate of 14 per cent.

The government has recently put somewhat greater emphasis upon fishing in its various development programs. Macapagal was elected in 1961 on a platform of improving economic and social conditions and fisheries received explicit attention. As a matter of fact, the only bill included in Macapagal's development program that got through the first session of the congress was the one reorganizing the fisheries effort and creating a Fisheries Commission out of what had been the Bureau of Fisheries. While the reorganization by itself did not accomplish much, it did considerably increase the funds and staff available to the Commission. It also provided in its organizational structure for a greater emphasis upon marine fisheries and the accompanying necessary research.

In 1962, a new program entitled the Emergency Employment Administration was set up to get at the rising problem of unemployment. As a part of this effort, 15 million pesos were to be devoted to fisheries for the construction of fishing ports, piers, refrigeration facilities, as well as for fishponds and stocking. Unfortunately, like most other programs boldly announced by the government, there has been little sign of follow-through from the original conception of the plan. Furthermore, such programs tend to be associated with the particular administration inaugurating them. As in the past, it can now be expected that a new plan, perhaps embracing fisheries, will be announced by President Marcos.

INVESTMENT IN FISHERIES

While the profit opportunities have prompted a large number of Filipino businessmen to expand the fishing industry, there is generally felt to be a reluctance on the part of those not already associated with the industry to put their money into it. Philippine entrepreneurs, it is true, have demonstrated a preference for the processing of branded consumer items for which acceptance has already been established in the country and for which they can receive a franchise from the parent foreign company as well as preferential exchange and tax arrangements from the government. Profits in many of these consumer oriented industries as well as in trading ventures have been very high. In some the capital has been turned over very frequently and there has been little risk. There are also other sociological and cultural influences that have tended to establish a preference

for investment in sectors other than fishing.

Actually, a significant segment of the present expansion of the fishing industry, especially, the larger and more integrated ventures, has been triggered or financed by foreign entrepreneurs. Such integrated structures have been concerned with the exploitation of the resources in the Sulu and Visayan seas and have been related to efforts to establish cannery operations. In these ventures, United States, Australian, and Japanese interests have been evident. Quite the most extensive of these efforts is that of a concern with American backing and executive personnel. This company is now in the process of completing a cannery in Batangas. The firm will rely on landings from its own vessels. Four of an eventual fleet of 13 vessels have already been received by the company. They have been built in Japan and are financed through the reparations agreement between the Philippines and Japan. These particular ships are approximately 22 m (72 ft) long, and are refrigerated purse seiners arranged for conversion to trawlers. They are to be captained by U.S. personnel though the crew will be Filipino. The vessels are planned for sardine operations during the season in which they are available, while in the remainder of the year it is assumed that they will fish for shrimp and tuna. In the case of the tuna, it is expected that the frozen fish will be in large part exported into the United States. While there has been some rather widespread concern about the adequacy of stocks for such an operation, the company obviously believes there is ample supply. It should be noted also that the company has received from the United States, Cooley loans to assist it in the construction of its cannery. These loans are made in the local currency from counterpart funds and are also repaid in the local currency.

This enterprise, therefore, is heavily subsidized by various international governmental programs and the situation is not unique to this firm. A large part, as a matter of fact, of the fleet expansion has been possible by utilization of the Japanese reparations agreement. This also applies to the acquisition of fishing gear and has been in part brought about by the familiarization with Japanese fishing techniques and gear through the services of Japanese fishery experts made available by FAO. The technical assistance programs of FAO have been quite successful, particularly so in the introduction of mechanized purse seining, the productivity of which has been mentioned earlier. There is also now under way a \$1.3 million Special Fund project of the United Nations directed toward deep sea fishing as well as marketing. These aspects make it abundantly clear that in several dimensions the role of foreign capital (private and government), technical assistance, and entrepreneurial talent have been a vital part of the recent development of commercial fisheries in the Philippines.

SHORESIDE FACILITIES

The parallel development of other integrated fishing operations such as that previously discussed will depend upon the outcome of this effort,

especially since there has been a rather general record of failure in previous attempts. Most of these, however, have either been of inadequate scale or have had inadequate sources of supply to maintain an economical operation. And to a certain extent the present effort can circumvent the very real limitations that exist with respect to the marketing and distribution of fish products. It will use its own piers and landing facilities and will be marketing, at least in the Philippines for the time being, canned items. The wider distribution of either fresh or frozen fish products, however, does require a more adequate system of distribution.

The main fish exchange from which the landings are transferred from the boat to the shore is at Navotas, north of Manila. This market accounts for almost half of the fish sold in the country. Yet, the exchange essentially consists of nothing but a series of open-ended shacks fronting a beach about 90 m long. Army surplus barges, *hancas*, or even men wading in the water, are used to transfer the fish from the boat to the shore. The general lack of facilities and the expense of ice, have an obvious and direct effect upon the quality and handling of the fish. Beyond this fish exchange, there is almost a total lack of proper transportation facilities or retail outlets. The tiled, clean market at Zamboanga with its adequate water supply as well as ice is a happy exception in the country. Obviously, little can be done to expand the marketing of fresh fish into the hinterland until these inadequacies are dealt with, and this does require the initiative and financing of the government. It should also be noted that such improvements would benefit the small as well as the large fisherman, not to mention the consumer.

CONCLUSION

What emerges then is a picture, not unique to Philippines fisheries; it is to be found in other sectors of the economy; nor is it unique to the country. A sector in this case commercial fishing, has "taken off" (if I may use this somewhat suspect terminology). It is still too early to see if it will be self-sustaining. To do so will require that the fishery resource prove sufficient. Research activity as well as training of a sufficient level and extent will have to be sustained. The broadening of the base through marketing and distribution improvements will have to take place. It is also possible that the pressure of firms upon the supply may call for some unified approach and control which will not be easy to establish or maintain in the context of the Philippine political, economic, and social structure, though the off-shore operations may conflict less with inshore operations. Even so, commercial fishing and fishpond operations (which I have barely mentioned) will remain islands of development within the vast expanse of marginal sustenance fishermen whose salvation lies in another range of solutions and time.

REFERENCES

HEGDEM, OLE

1959. Observations on Philippine fisheries. U. S. Intl. Coop. Admin., Oper. Miss. to Philippines, Manila.

ONGCHANGCO, B. J.

1955. Fish marketing in the Philippines. *In* Report of the First FAO-ETAP International Fish Marketing Training Centre. Food and Agriculture Organization of the United Nations, Rome.

PARSONS, JOHN W.

1962. Report to the government of the Philippines on freshwater fisheries investigations. Food and Agriculture Organization of the United Nations, Manila.

REPUBLIC OF THE PHILIPPINES

1964. Philippine fisheries yearbook 1962. Dept. Agr. and nat. Res., Bur. Fish., Quezon City.
1964. Annual report 1963. Central Bank of the Philippines, Manila.
1965. Economic census of the Philippines, 1961, forestry, logging, and fishing. Dept. Comm. Ind., Bur. Census Statist., 1 (B).
1965. Fisheries statistics of the Philippines 1963. Philippine Fish. Comm., Quezon City.

TIEWS, K. F. W.

1957. Interim report to the government of the Philippines on research on marine fishery resources. Food and Agriculture Organization of the United Nations, Rome.

U. S. DEPARTMENT OF COMMERCE

1965. A market for U. S. products in the Philippines. Bur. Intl. Comm.

MARKETING AS A CONSTRAINT ON FISHERY DEVELOPMENT IN TROPICAL COUNTRIES

JAMES A. CRUTCHFIELD
University of Washington, Seattle

ABSTRACT

Inadequacy of local, regional and national marketing networks may constitute a very real constraint on fishery development programs, particularly in underdeveloped countries in tropical latitudes. It is argued that this is no less true of other bottlenecks: inadequate biological knowledge of the size and composition of the yield that can be obtained from available fish stocks; inadequate development of gear and of trained personnel to use it; or lack of proper processing facilities. Any fishery development program aimed at increasing the output of protein foods and the incomes of those engaged in the fisheries must be balanced with respect to all of these associated elements

INTRODUCTION

Since one theme of this paper is that the role of marketing in fishery development programs has suffered from overstatement and improper definition, it is probably appropriate at the outset to define a few of my own terms. Production of fish (or of any other useful good or service) involves a set of processes running from primary producer to final user, each of which adds to the satisfaction derived from the product by changing its form or the time and place at which it is made available. Fishery development simply means an increase in the market value of output less associated costs of labor and capital, and reflects either of two types of change: (1) increased output and/or reduced costs resulting from technological improvements in fishing, processing, or marketing methods; and (2) identification and exploitation of previously under-utilized resources.

CONSTRAINTS IN FISHERY DEVELOPMENT

In the broadest sense, fishery development is limited by three sets of constraints, all of which can be altered by man only at some cost: the pattern of consumer preferences; the physical factors determining the availability of fish; and the technological knowledge that enables us to convert fish into more useful forms and to make it available at the time and place required.

The implications of these definitions for my topic are obvious. Though bottlenecks in the marketing process, arising out of inadequate size or technical organization of marketing facilities, can obstruct the development of a particular fishery, precisely the same may be said of any other element in the process: biological knowledge of the yield capabilities of the exploited stocks; fishing or processing capacity; or the supply of trained personnel to perform each of these tasks. The emphasis on marketing as

the weak link in the fishing industries of underdeveloped tropical countries appears to be much too great, reflecting either of two factors: (1) fishery experts are generally unfamiliar with its role in a balanced development program; and (2) marketing surveys, even when included in a development program, frequently generate too little information of the type needed. Development programs frequently fail to specify appropriate standards of performance of the marketing sector and thus attribute to it weaknesses that actually originate elsewhere in the economy.

MARKETING SURVEY

Any plan for economic expansion of fishing activity calls for a careful survey of existing marketing arrangements prior to or contemporaneously with implementation of the development plan. Properly designed, a survey of this type is not a particularly formidable job. To overcome barriers imposed by space and time—the essence of marketing perishables—requires assembly, transportation and storage, and subsequent dispersion of the end products involved. The nodal points in the distribution system can be located without major difficulties; and at such points relatively simple survey techniques will suffice, even in underdeveloped countries with poorly organized markets, to indicate major sources of supply, seasonal variations in demand and supply, and market outreach of the subsequent reselling operations. Given sufficient time and cooperation from the marketers involved, it is usually possible to develop a reasonably accurate “marketing map” and to provide some quantitative estimates of product flows.

A reconnaissance survey of this type will often suffice to point up obvious weaknesses in the existing marketing structure and potential bottlenecks that might arise with rapid expansion of fish landings.

Assuming that such a study has been undertaken, how can we assess the effectiveness of the existing system and formulate recommendations for additional investment and/or technical assistance where modification or expansion is required? The following are suggested as generally inclusive standards of performance:

- (1) The marketing sector should register accurately and conform to the preferences of fish consumers, providing fish of the desired quality, variety, and preparation. In practical terms, this means that returns to the industry could not be increased by further changes in the mix of the various end-products available.

- (2) All products should be so allocated among different geographic markets (including export markets) that returns could not be increased by selling more in one market and less in another.

- (3) Processing and marketing costs should be as low as possible given existing technical knowledge, transportation and communication

facilities, and the costs of capital and labor.

(4) The marketing mechanism should be flexible enough and deep enough to prevent extreme short run price fluctuations, through its ability to move fish rapidly from areas of temporary surplus to areas of temporary deficit and by providing adequate storage. It is particularly desirable that seasonal fluctuations in demand and supply be anticipated to prevent unnecessary instability in prices and incomes to fishermen.

The key phrases in these criteria are consumer preferences and minimum costs. With regard to the former, it can be argued that many of the so-called obstacles to fishery development originating in the marketing sector reflect a conscious or unconscious tendency to associate quality requirements with European and North American rather than local tastes. Most open markets in underdeveloped countries operate under sanitary conditions that would be unacceptable in more developed countries, and the quality and appearance of the fish offered in these markets would arouse little enthusiasm in the local supermarket. But in economies with very low per capita incomes, both sanitary conditions and product quality may reflect quite accurately the preferences of individual consumers. Where knowledge of the techniques required to produce a superior product and to market it under better physical conditions is available but is not used, there is at least some presumption that the marketing system is providing an acceptable mix of quality, quantity, and price. The generally dismal record of government efforts to improve product quality and sanitation conditions at all levels of fish marketing in the tropics may reflect, at least in part, a perfectly rational resistance on the part of both buyer and seller to unwanted change.

Similarly, a great deal of time, technical assistance, and money has been wasted on marketing facilities in underdeveloped countries through failure to distinguish technical and economic concepts of efficiency. Virtually all technical assistance work by United Nations representatives in Africa, for example, has emphasized the surprising degree of sophistication in the organization and operation of indigenous marketing systems (and the clear economic advantage, at least in the short run, of using a bicycle-based transportation system that runs on starch rather than gasoline). The ability of East and West African traders to move dried fish over very long distances is a case in point. The hodge-podge of river canoes, old cotton lorries, bus tops, and bicycles that make up the major elements of the transportation network may appear hopelessly inefficient in a technical sense; but their use of otherwise under-utilized facilities and their adaptability to the rigorous physical conditions of African water and road conditions make them quite efficient in an economic sense. Obviously, there is much room for improvement, but most African or Asian fish marketing systems have a remarkable degree of flexibility, and deliver acceptable products on very low margins. Moreover, they are usually

systems; and there are real dangers in partial changes without full analysis of repercussions along the full chain of distributors.

COMMUNICATION AND TRANSPORTATION

The real obstacles to balanced development of fisheries seem to lie in other directions. The most common, in both Africa and Asia, are weaknesses in communications and transportation networks that affect the entire economy, but bear particularly hard on the marketing of perishables. For example, the generally poor and expensive telephone and telegraphic services in such countries, coupled with the absence of recognized grades and standards, makes it virtually impossible to buy and sell fish without detailed examination of each lot. Inadequate communication facilities may also account for the common failure to shuttle temporary surpluses from area to area to balance local supplies and demands. Throughout Africa, for example, price differentials far in excess of even public transportation costs are common even in markets separated by as little as twenty or thirty miles. Such insulation of markets is much greater than required by transfer costs *per se*, and produces persistent short-run misallocation of supplies and an unnecessary deterrent to development of the fisheries affected.

The common resistance in underdeveloped areas to pricing by weight and to the use of even rudimentary grades and standards is part of a more general problem. Marketers accustomed to dealing in scattered open markets (which are as much a way of life as a means of carrying on retail trade) do not grasp easily the basic requirements of wholesaling. The interrelationships that link bulk transportation, the assembly function, the provision of storage facilities, and the ability to buy without the necessity of physical inspection are relatively sophisticated concepts. The fact that Westerners grow up with them makes it even more difficult for them to understand the reluctance of traders in less developed economies to adopt what seem to be completely obvious methods of reducing costs and extending market outreach.

Technical assistance that takes the form of demonstration and instruction of these principles is likely to produce uniformly good (and in some cases, spectacular) results in expanding the coverage and efficiency of inherently viable but restricted indigenous marketing structures.

TECHNICAL ADVANCES

The limiting effect of inadequate communication and transportation facilities on the development of fishing industries is in turn part of a still more general problem affecting underdeveloped economies and—all too frequently—the thinking of technical assistants dispatched to aid them. It is extraordinarily difficult to get a highway engineer, for example, to think in incremental rather than average terms: if agriculture provides 90 per cent of the geographic income of an area it is very likely to get

90 per cent of the available funds and technical skills for road construction. Yet the relevant point is clearly the incremental return that can be obtained from small reallocations among competing demands for transportation services. Fisheries are usually in a particularly unfortunate situation in this respect. Despite the exceptional "rates of return" that can be earned by relatively minor government investments required to tie fisheries more closely to regional and national economies, the dominant concern with agriculture and trade tends to choke them off. The number of underdeveloped areas, even within my own experience, in which failure to extend feeder roads to landings inhibits growth of the fisheries is too large for comfort.

Much the same type of problem underlies the limited success of investment in freezing and refrigeration equipment in tropical countries. Doubtless the freezer chain has an increasingly important role to play in fishery development, but few underdeveloped countries are yet within hailing distance of the "preconditions" for large scale processing and marketing of fish in frozen form. Even in the developed economies fish alone can rarely bear the overhead costs associated with a frozen storage and transportation sequence. Only when all elements in the chain could be utilized by marketers of meat, dairy products, vegetables and other frozen foods has the unit cost of frozen fish dropped to levels at which it becomes attractive to middle income buyers.

In low income tropical countries frozen fish remains a luxury item, with one notable exception. A spectacular growth in the marketing of frozen whole fish has occurred in West Africa, based on bulk landings from long range European and Japanese trawlers. Even in this case, however, the emphasis is on price. Refrigerated storage at major wholesale points represents the only specialized capital employed; local transportation and retailing are handled entirely by the long-established "mammy" system.

MONOPOLISTIC MARKETS

Perhaps the most common—and certainly the most pernicious—of the true marketing impediments to balanced fishery development in tropical countries is the existence of monopolistic practices on both selling and buying sides (particularly the latter). The physical conformation of the fishing industry in underdeveloped areas makes it particularly vulnerable to this type of structural defect. Landings are scattered over such a wide area that the number of alternative buyers available at any given landing is frequently limited. And since the cost of providing gear and supplies and of moving fish from scattered and isolated landings is likely to be quite high, the dominant position of a well-financed middleman, once achieved, is hard to shake.

This situation is, of course, far from universal; anyone who has ever witnessed the clamorous battle for fish among dealers at canoe landings on

the coast of West Africa or on the Rift Valley Lakes of East Africa can vouch for the vigor of competition in areas where markets and fishing villages are reasonably close together. On the other hand, the influence of non-competitive practices in fish buying is so extensive in some areas, the Indian Ocean perimeter in particular, that it permeates the entire social structure of the fishing communities. The subordinate position of the fisherman vis-a-vis the middleman tends to slip very easily into a kind of debtor peonage in which the fish buyer assumes more and more financial responsibility, not only for fishing operations but for the whole family expenditure pattern. Quite apart from the devastating effects of such arrangements on the economic position of the fishermen, the "tajiri system" militates against progress and development in general. The dominant middleman is likely to resist stubbornly any technological or institutional change that would threaten his position regardless of its favorable effects on costs and productivity. It is not surprising that areas dominated by this type of organization are among the least progressive in any part of the world fishing community.

FISHERY COOPERATIVES

There are a number of alternative methods of dealing with the problem — none of them completely satisfactory, but all capable of providing the necessary latitude for expansion where physical supplies of fish and strong consumer demand warrant it. Perhaps the most effective is the organization of cooperatives, with the aid of or under direct sponsorship by government, which integrate fishing, supply, and marketing functions. In the more developed economies, the cooperative has proved an effective antidote to monopsony or oligopsony where technical factors restrict competition on the buying side. In underdeveloped countries, however, the road is likely to be more thorny, particularly where the entire marketing sequence is in the hands of racially or culturally specialized groups. In such cases the cooperative may find it impossibly difficult to obtain supplies, to make the necessary contacts with retail outlets, or to compete successfully with established fish dealers who are part of the "in" group.

In addition, the fishery cooperative in the emerging tropical countries suffers from an overdose of hope as to what it can accomplish. There is a ubiquitous tendency to expect miracles of cooperative organization, including the most miraculous accomplishment of all — good management at salaries no higher than the earnings of fishermen themselves. Fishery cooperatives have also shown a pronounced tendency to absorb too many functions without full understanding of the complexity of the physical and economic risks involved in handling a perishable product over long distances under tropical conditions.

Quite apart from the usefulness and limitations of the cooperative as a device for breaking down monopolistic restrictions in fish marketing, there

has been a tendency in underdeveloped areas to view the cooperative as a means of solving all sorts of problems, including some that are quite independent of the organizational form of marketing ventures. Experience in the developed countries demonstrates strikingly that the cooperative is the most difficult of all forms of business organization in which to generate managerial flexibility, efficiency, and adaptability. The assumption that the cooperative will somehow provide effective management where small scale entrepreneurship is lacking misses the point entirely; lacking a well-developed entrepreneurial or managerial group, the cooperative form is likely to prove even less efficient than other types of enterprise.

From the standpoint of organization, the emphasis in marketing development must be on the development of personnel fully aware of the heavy demands on management of the day-to-day problems that characterize the marketing of perishable products in economies with serious deficiencies in basic government services and transportation and communication facilities. In a few countries (Tanzania, for example) where the tribal structure of certain major groups is closely akin to the cooperative table of organization, the cooperative may provide an ideal vehicle, but this is the exception rather than the rule.

CONCLUSION

There are doubtless impediments to fishery development in marketing in virtually all underdeveloped areas and they are likely to be particularly acute in the tropics. But most of them appear less troublesome than they have been painted, and most of the really difficult ones stem from a fundamental misunderstanding of the relationship of fishery development plans to national and regional economies or from failure to deal adequately with the influence of monopoly. The fish marketing specialist, like the biologist and technologist, has a role to play in accelerating the development of tropical resources, but only if all are viewed in a broader perspective as part of the overall process of economic growth.

DECISION PROBLEMS IN FISHERIES¹

WILLIAM F. ROYCE

*Fisheries Research Institute, College of Fisheries
University of Washington, Seattle*

ABSTRACT

Current fishery decisions are examined and discussed from the standpoint of research strategy. All maritime European countries, Japan and the USSR have provided various kinds of government assistance to modernize their fleets, their processing and their distribution systems. Their emphasis has been much greater on modernization than in the United States and Canada where a major concern has been to protect the resources.

It is suggested that research strategy should be developed from the decision frameworks and that more emphasis should be placed on the study of the fishery systems.

INTRODUCTION

My discussion of decision problems in fisheries concerns fundamentally questions of research strategy. How can we plan and execute research on our fishery resources more effectively?

If we are to use any of our knowledge and skills about fish or their environment, we must help make decisions—decisions by governments about aiding or regulating fishermen—decisions by industry about investment or operating procedures—decisions by fishermen about equipment or where to fish. It is fruitless to expect that information gathered at random and stored in scientific journals will be used effectively by the decision makers. We, as fishery scientists, must understand how the decision makers function and the decision makers must ask the scientists more questions and we must expect to participate in the decisions. I think the collaboration should be much more effective than it has been in the past.

We have a rapidly developing body of theory about the decision process, decision frameworks, and systems analysis (Churchman, 1961; Ackoff, 1962; Cowan, 1963; and others), and I believe it is to our benefit to use this decision theory as much as we can.

My purpose in this article is to outline the broad framework of fishery decisions that are now being made and consider how to apply some decision theory. I start with a brief but broad review of fundamental policy and development factors in fisheries.

FISHERY POLICIES

All countries possessing fisheries make a continuing series of decisions regarding their control or regulation. The structure of the recent decisions indicates the policies of each country, whether these are specifically stated

¹Contribution No. 229, College of Fisheries, University of Washington.

or not. A comprehensive summary of the fishery policies in western Europe and North America to 1960 has been prepared by the Organization for European Economic Co-operation (OEEC, 1960). The authors have reviewed for each country the general state of production, processing, consumption, and trade. They have then stated the policy objectives as they *seem to be*. This provides an entirely unofficial and a somewhat subjective summary of policies, but if we assume that the authors looked at all countries in a similar fashion, then their summary is probably a better judgment about which policies receive the most emphasis than an attempt to unravel the enormously complicated laws and policy-making activities of the several countries.

An analysis of the fishery policies of 18 European countries (North-west Europe plus Greece and Turkey) provides some interesting generalizations, as follows:

1. All of the policies are intensely nationalistic and are designed to aid the domestic fishing and fishing industry while protecting them from foreign competition.

2. All countries have placed strong emphasis on modernizing the fishing fleets and employ substantial and varied kinds of subsidies to stimulate shipbuilding.

3. Most countries are trying to convey better fish to the consumer more rapidly and are taking steps to facilitate marketing, to improve processing, and to improve distribution facilities. Many offer subsidies or special credits to the processing industry or distribution trade.

4. Almost all countries are much concerned about the social problems of fishermen and provide special protection for inshore fishermen, special vocational training, price stabilization schemes, etc.

5. Many countries view the fisheries as highly important to their national security and economy. They strive for self-sufficiency in fish production, consider the fishing fleets as good training ground for the merchant marine or the military, and are anxious to encourage exports and their earnings of foreign exchange. Iceland has obtained more than 90 per cent of its commodity exports in the form of fish and fish products. Norway and Portugal have made the export of fish a significant part of their total economy. In most other countries, even though the fisheries occupy a comparatively small sector of the national economy, fishing is a major industry in coastal areas.

6. All countries are concerned about the condition of the fish stocks and the failure of expanded fishing to yield a proportionate increase in catch. Yet, wide differences of opinion exist as to the best method of managing the resources and little progress has been made on the problems of overinvestment or of obtaining maximum sustained yield from the fish stocks.

Across the Atlantic in Canada and the United States, the fisheries are

mainly short-range operations seeking relatively abundant fish stocks. Both countries have segments of the industry with relatively low productivity and have given some social and financial assistance, but the primary emphasis in the fishery policies is on the maintenance of the fishery resources. Canada is a major fish-exporting country and the United States is the world's leading importer of fish. Both countries have relatively low per capita consumption of fish.

The policy of the United States and Canada is unofficially indicated by the fisheries scientists in the "North American Fish Policy," which was adopted by the American Fisheries Society in 1938, revised in 1954, and further amended in 1964 (American Fisheries Society, 1965). The society adopted the policy "to aid in the protection and scientific development of the fishery resources for the greatest possible use and enjoyment by the people of this continent." The policy's articles embrace the jurisdiction of fisheries, administration, fish culture, management (meaning largely regulation and population manipulation), multiple use of waters, education, and publicity. No specific mention is made of any concern about the welfare of commercial fishermen. Rather, the policy is almost completely oriented toward the maintenance and protection of the resources.

The recent policies of Japan and the USSR were not discussed by the OEEC and I must judge their policies from the limited material available. Each country has expanded greatly its long-range fishing operations and each now fishes extensively in all of the world's seas. The USSR has had the target of increasing annual per capita consumption from 21 to 30 pounds (10-14 kg) and intends to produce the quantity needed by larger and better fleets (Ishkov, 1961; Nikolskii, 1962; Moiseev, 1964). The Japanese have provided long-range and better fleets and, in addition, have entered into agreements about fishing bases, sales, or processing with dozens of countries around the world. These two fishing countries with the largest fishing fleets in the world appear to be battling for domination of the world's fisheries.

FISHERY DEVELOPMENT

One of the most striking phenomena in the production of the world's food is the recent rate of increase in fisheries production from the ocean: approximately 8 per cent per year (Olcott & Schaefer, 1963). This is much higher than the rate of increase of agricultural products in general. It is unquestionably leading to serious dislocations of people and governments—in biological terms, to changes in the human ecosystem.

One kind of dislocation is occurring because the men equipped with modern vessels are able to catch from 10 to 1,000 times as many fish per person per year as the primitive fishermen in the same areas. This leads immediately to price dislocation, to unemployment, to substantial shifts of people from one occupation to another.

Next, much of the modern equipment is being sent far from its home

ports to fish on stocks off foreign shores in direct competition with inshore fishermen who have competed only among themselves in the past. Examples of this are to be found in the North Pacific with the trawling, crabbing, and whaling activities of the USSR and Japan. Similar intense competition is developing in the Gulf of Guinea with trawling for bottom fish and line fishing for tuna. Such competition in both the sea and the market reduces the income of the inshore fishermen from countries which do not possess the modern equipment.

FISHERY DECISIONS

I have undertaken this examination of the trends in fishery policy and fishery development in order to establish the importance of the decisions that are being made. Obviously, a large proportion of the world's population is being affected and a great many of the decisions are being made by heads of governments. At the other end of the decision spectrum in terms of number of people and relative importance, are the day-to-day problems faced by fishermen about when and where to fish or the decisions by government fishery managers about changing fishing seasons, fishing areas, etc. Between these extremes lie a host of intermediate decisions, many of which are interrelated, many of which become consequences of other decisions, and many of which must be made sequentially. Some decisions await technical information to be gathered, but others, especially those being made by politicians, evolve from the political scene.

Practically all of these decisions will be made better if they are based on better information. Each will be better if it is technically practical and in accord with the behavior of fish, the requirements of the fishermen, the behavior of the ocean, our engineering competence, economical feasibility, political acceptability, and the appropriate laws. Practically none of the decisions can be made on the basis of the technical information in the absence of the social, and decisions based on social considerations without regard to the technical realities will frequently be absurd.

All of these decisions share the fundamental problems and procedures of decision making as they have been outlined by Ackoff (1962) and others. Practically all will involve the following factors:

1. who are the decision makers;
2. what are the motives, ostensible and real, of the parties concerned;
3. who will be affected;
4. what are the restrictions on possible action;
5. what are the possible counteractions?

RESEARCH STRATEGY

If the fishery scientist is to advise effectively on the major decisions or, in other words, if he is to apply his findings to some kind of a mission, he must plan and execute his research with the decision-making problems in

mind. Let us take a hypothetical example which is typical of many of the present problems of harvesting oceanic fisheries, and consider some of the decisions which must be made.

Let us assume that we have a newly discovered population of fish, partly in international waters immediately off the coast of one country. Word has gotten around that fish can be caught and that money can be made. Hence, fishermen and processors are considering how to find, catch, process, and market the fish. They will start making decisions immediately about investing money in boats, plant sites, machinery, handling methods, etc.

While in some countries the industry is becoming interested and perhaps deciding that this stock of fish is beyond its means to harvest, numerous decisions will face each government whose fishermen might have a hand in harvesting this new population of fish. The governments of nearby countries will be concerned with how much of the stock it can claim for its own fishermen. Every government will be deciding the extent of its country's interest in this new resource and how much it should strengthen its industry in order to take part in the harvest. The decisions about strengthening the industry will involve consideration of subsidies, exclusive licensing, tax concessions, low interest loans, permission for the industry to integrate vertically in order to reduce costs, together with exploration to find the fish, to trace their migrations, to forecast their abundance, etc.

Next, let us assume that exploitation of this fishery has continued for a few years, that catch rates have fallen, that some fishermen are losing money and others operating with little profit. The fishermen and industry are apprehensive about being able to pay off their loans and they are blaming fishermen from other countries with lower operating costs for ruining the fishery. Each government will now want to know the expected maximum sustained yield from the population of fish and how its fishermen can get the maximum proportion. Each might also be farsighted enough to join with other governments to decide how to maximize the sustainable profits from the fishery.

Such decisions should be based on the results of major fishery investigations which in turn should be planned according to our understanding the basic food-producing systems of the ocean. Obtaining such an understanding requires continuing broad programs of discipline-oriented research into the animals and the ocean which sustains them. Clearly such research needs to be correlated with the fishery investigations and I suggest that the research directors face another decision—that of an appropriate balance between the basic and applied aspects of their programs.

CONCLUSION

My main argument to the fishery scientist, therefore, is: let us consider the ways in which we can help make better decisions. Let us study the

decision makers, their problems, their successes, their failures, their requirements. Let us recognize the fundamental differences between governmental, intergovernmental, and industrial decisions. Let us recognize that technical information on the fish stocks or the environment must always be used in the context of economic, political, legal, and other social considerations. Let us expect to work as a team and let us not just study fish or the ocean but study fishery systems, which involve people.

REFERENCES

- ACKOFF, RUSSELL L.
1962. Scientific method optimizing applied research decisions. John Wiley and Sons, Inc., New York and London, 464 pp.
- AMERICAN FISHERIES SOCIETY
1965. North American fish policy. *Trans. Am. Fish. Soc.*, 94: 117-118.
- CHURCHMAN, C. WEST
1961. Prediction and optimal decision. Prentice Hall, Inc. Englewood Cliffs, N. J., 394 pp.
- COWAN, THOMAS A.
1963. Decision theory in law, science, and technology. *Science*, 140: 1065-1075.
- ISHKOV, A. A.
1961. The general direction of progress in fisheries. [In Russian.] *Rybnoe Khozaistvo*, (5): 3-21.
- MOISEEV, P. A.
1964. The present state and perspectives for the development of the world fisheries. Seminar in Fishery Biology and Oceanography, Aug., Sept., 1964, Fishery Division FAO.
- NIKOLSKII, G. V.
1962. The new party program and the tasks of fisheries science. [In Russian.] *Rybnoe Khozaistvo*, (9): 3-6.
- ORGANIZATION FOR EUROPEAN ECONOMIC CO-OPERATION (OEEC)
1960. Fishery policies in western Europe and North America. Paris. 302 pp.
- OLCOTT, H. E. AND M. B. SCHAEFER
1963. The sea as a source of organic chemicals. Symposium on economic importance of chemicals from the sea. *Am. Chem. Soc.*, Los Angeles, Calif., pp. 132-137.

High Seas Fisheries

JOHN L. KASK AND WILBERT M. CHAPMAN
Co-Conveners

The following papers were delivered at the Conference but have not been received for publication:

WILBERT M. CHAPMAN: High Seas Fisheries of the Eastern Pacific.

SAUL B. SAILA AND J. M. FLOWERS: A Simulation Model Study of Sex Ratios and Regulation Effects with the American Lobster.

K. TIEWS: The Development of Trawl Fisheries in South East Asian Countries as a Means to Increasing the Marine Fisheries Production.

THOMAS S. AUSTIN AND P. A. MAZEIKA: Seasonal Differences of Zonal Temperature. Anomalies in the Upper Layers of the Eastern Tropical Atlantic Ocean.

JORGE SANCHEZ R.: General Aspects on the Ecology and Biology of the Anchovy (*Engraulis ringens*).

FISHERY DEVELOPMENT IN PERU

ALFREDO FREYRE

Director General del Instituto del Mar del Perú

ABSTRACT

The fishery in Peru is reviewed historically from the time of the Incas until June 1965. The sensational growth of the fishing industry began in 1954.

The paper analyzes the development of the fishing fleet and the association of fishermen, the growth of the fish meal factories, the development of the industry of naval architecture, and the investigations of the Instituto del Mar del Peru to determine the population dynamics of the different species from the anchovy to those used in human consumption. It presents statistical tables comparing the growth of the fleet, fish landings, the manufacture of fish meal, factories, and the different species which are captured. The economic and social problems which were encountered with the growth of the fishery are analyzed and legislation is reviewed as it existed, as well as changes which were made.

This contribution describes the industrial development which brought about the growth of the fishery and points out the need of the industry for better technically trained personnel. It comments on the recommendations which the Instituto del Mar presented to the government, for the purpose of establishing better conservation of the anchovy.

1. INTRODUCTION

The sea is the largest of the geographical spaces and has production capacity and biological resources necessary for the well being of man. Exploitation of these natural resources has not been the same in both hemispheres; and only after the II World War, the Southern Hemisphere gained certain importance, in which Perú holds an outstanding position.

My intention is to make a brief description of the sea fishery development in Perú, stressing its impact over the industries, human consumption, exports, researching and training, trying to focus the future prospects.

To achieve this purpose, I will make a short exposition on the guano, whaling, and fishing industries, especially of the anchovy and auxiliary industries, in order to point out the prospects open to the fishery exploitation in Perú.

2. BACKGROUND INFORMATION

People of the Peruvian coast have been dedicated to fishing since some

centuries ago, using hooks and lines and homemade nets. This has been proved through several archeological findings that can be seen in museums and books. Fish shapes and fishing crafts of old times can be seen in the pottery and weavings of ancient civilizations such as Paracas, Chimú, and Mochica.

Highly esteemed data on domestic fishing and barter trade with sea fish can be found in the Narrations of the "Inca Garcilaso de la Vega" J. and A. Ulloa among others. It is said that the Inca in Cuzco used to get every day fresh fish sent from the coast by mail delivery ("Chasquis" system). During the 19th Century, the activity of foreign ships was intensive off the Peruvian and Chilean coasts, and it was in this way that ships coming from North America and England were occupied in the catching of whales and seals. For this reason, the government issued a series of regulations regarding the activity of these ships. Among them, Law No. 1236 given in February 1858, extended certain concessions accorded to the United States whaling ships to be applied also to whaling vessels from England. In January 1889, the Congress exempted the whaling ships from anchorage duties in Peruvian ports.

In the second half of the 19th Century, began also the guano industry, which developed rapidly due to its exceptional fertilizing properties. The Government took part in the first decades of the present century protecting birds and issuing norms for the exploitation of the guano and creating the *Compañía Administradora del Guano* (Supreme Resolution of March 1st, 1909) and Law No. 3069 of January 27, 1919.

The sea fishery in Perú left its industrial domestic stage just in 1923, when an authorization was granted through Engineer Nakashima to make studies on the industrial exploitation of the Peruvian sea and to install a fish canning plant. His activity led to the planning of the possibility to produce fish meal and also obtain fish oil for industrial purposes.

In 1924, the *Compañía Nacional de Pesca* was created, but failed one year after it started, because of having operated with trawling nets in zones where they were not convenient.

Another *Compañía Pesquera Nacional* was created in 1936 which supplied the local market and exported frozen fish (tuna). The attempt failed because of technical deficiencies.

The Second World War created a great demand for fish and vitamins A and D. This encouraged in Perú the development of the selachian fishery (sharks and rays), processing of bonito and tuna livers, as well as a fish canning industry.

In October 1941, a government decree entrusted to the *Compañía Administradora del Guano* the installation of a fish meal plant. However, even though the necessary equipment was purchased, the company did not install it nor was it put into operation.

In 1954, the *Sociedad Nacional de Pesquería* was created and began

to encourage the development of the fish canning and freezing plants. Also, it was dedicated to the safeguard of the interests in other fishing industries, especially the anchovy industry, the sudden boom of which began in 1955.

The fish meal and oil industry, based principally in the use of the anchovy as raw material, was explosive and brought with it new problems and of great magnitude. Likewise, the unilateral development of the Peruvian fishing industry, with 90 per cent of the production based in only one species (the anchovy), constituted a stimulus for the initiation of fishing for domestic consumption.

The unforeseen development of the fishing industry had influence upon: (1) the Peruvian commercial and industrial development; (2) the training in marine sciences and its application; and (3) the investigation of marine problems. It is in this way that the interest of the country has been aroused regarding oceanography and fisheries around the world, and that our participation in this Conference, taking place here in Miami, is justified.

The development of the sea fishery in Peru has attracted attention everywhere and there are several publications presenting our problems, such as, in the first place, the reports and bulletins issued by the Marine Resources Research Institute, and continued by the Instituto del Mar del Perú; the magazine Pesca, published in Lima, which yearbooks contain data regarding all the companies of the country; the publications of the Compañía Administradora del Guano, and of the Servicio de Pesquería y Caza, besides some others dealing with fishery.

Moreover, we can mention the Symposium on the Peruvian Fisheries Development prepared by the Universidad Agraria La Molina de Lima in collaboration with the Marine Resources Research Institute from November 5 to November 10, the results of which were published under the same title.

3. SEA INDUSTRIES IN PERÚ

Sea industries have gained principal importance in Perú; these are: 1) the guano industry, 2) the whaling industry, and 3) the fishing industry; especially the anchovy fishery which was developed in the last decade (1955-1964) and the results will be briefly exposed in this same order.

3.1.—*The guano industry* has been in Perú during more than a century the principal activity based in the use of an indirect sea product. The annual production obtained from 1909 to 1964 inclusive, can be seen in Table 1.

Three species are the most important birds that contributed to the guano production in Perú: the "guanay," the "piquero" and the "alcatraz;" from these, the "guanay" has contributed with 80 per cent of the total production.

The guano industry in this century has had some ups and downs: a serious crisis in the gathering of guano came up two years after the invasion of oceanic waters (*El Niño*) in the coldest habitat of the Peruvian

TABLE 1

Year	Total Guano Production in Metric Tons	Remarks
1909	24122	—
1910	32267	Mortality year
1917	80866	"
1920	64110	—
1925	125995	Mortality year
1930	132974	—
1932	133741	Mortality year
1939	152778	"
1940	126545	—
1941	119642	Mortality year
1950	218456	"
1953	260797	"
1957	285406	"
1958	167009	"
1960	157914	—
1961	159246	—
1962	206108	—
1963	191842	Mortality year
1964	205092	—

Source: Bulletins from "Cía. Administradora del Guano" and "Corporación Nacional de Fertilizantes".

TABLE 2

NUMBER OF ANIMALS CAUGHT, BY SPECIES					
Years	Sperm Whale	Blue Whale	Fin Whale	Humpback Whale	Grand Total
1951	15	4	21	22	62
1952	37	7	14	20	78
1953	1260	10	28	6	1304
1954	1505	8	30	1	1544
1955	1869	8	7	2	1886
1956	2019	—	1	7	2027
1957	2381	—	—	—	2381
1958	2554	—	—	—	2554
1959	3406	—	—	—	3406
1960	3423	—	—	1	3424
1961	3438	2	2	41	3483
1962	3301	—	—	—	3301
1963	3269	—	—	—	3269
1964	1973	2	3	37	2015
1965	233	29	100	17	379

Source: Instituto del Mar del Perú.

current. The greatest was in 1959 when production diminished from 336,000 tons in 1956 to 105,000 tons as consequence of the decrease in the "guano" birds population that from an estimated total of 27,000,000 of birds in 1956 only remained 12 million in 1958 due to the sudden increase of the mortality index and migration. In Table 1, it has been emphasized the year in which occurred the bird mortalities.

Studies realized on the fluctuation observed in the "guano" birds population and production have given the opportunity to establish that there are factors beyond human control that give rise to great changes in the behaviour and density of these birds. Among these factors can be mentioned: changes in the atmospheric and oceanic circulation especially the presence of very warm tropical waters with little food in the coastal zone of Perú that drive away the birds. From here comes the concern in Perú for all that is related with the probable presence of the phenomenon called "*El Niño*."

3.2.—*The whaling industry* in Perú is based principally in the catching and use of spermwhales the stock of which is actually decreasing, in accordance with informations given by Saetersdal, Ramírez and Mejía. In 1916, and confirmed in 1962 and 1964, it also caught isolated specimens of blue whales, finwhales, and humpback whales.

The number of animals caught during 1951-1964 and the first 6 months of 1965 can be seen in Table 2.

According to values shown in this table, the largest quantity of spermwhales (3,438) was captured in 1961, in which year began the reduction or the decrease that was worst in 1964. The following contributed to this situation:

- (1) Diminishing of the spermwhale stock that used to come to the waters in front of the Peruvian coast.
- (2) Condition of the catching fleet that should be renewed.
- (3) The slowness in the reproduction of the specie.

Now, in Perú there is only functioning one whaling plant, located in Tierra Colorada, Paita; the other two are temporarily closed and yet, the analysis shows that the index is decreasing.

3.3.—*The sea fishery*. Table 3 shows separately the landing values of anchovy, other species and prawns, as well as the total during 10 years (1955-1964), including also the values corresponding to the first 6 months of 1965.

In the figures shown, it can be seen which has been the development of the anchovy fishery in comparison with other sea species of the country. It can be observed that the anchovy catching increased during these last 10 years from 58,707 metric tons in 1955 to 8,863,367 metric tons in 1964, i.e. more than one hundred fifty times, while catching of other species increased only 1.47 times during the same period, that is from

124,379 metric tons in 1957 to 183,208 metric tons in 1964, reaching the maximum of 202,129 tons in 1961.

The table shows a unilateral development, similar to the monoculture in agriculture that exhibits great disadvantages during the seasons in which appear adverse conditions, in the sea or in the world market of fish meal and oil (See Popovici 1960).

The unilateral development can also be seen in the performance of the fish meal plants and fishing fleet, as can be appreciated below.

(1) *Fishmeal Plants.* The great increase in demand for fish meal in the world market, because of its exceptional properties for the feeding of swine and poultry, had favorable effect on the industrial development of Perú. It constituted a strong incentive for important investments in fish meal plants, equipped with centrifugal machines to separate oil from fish.

Table 4 shows the number of fish meal plants functioning in Perú during the period 1955-1964. The same table also shows the hourly capacity of reduction of raw material into fish meal, expressed in metric tons; the respective values were only established from 1950 on, when the statistical work was organized based in the regular visit to the reduction plants.

In 1946 there were in Perú two fish meal plants that used fish waste as raw material, while the number of plants in 1954 was 17. Our table shows the numerical development of these plants from 1955 on, indicating also that in 1965 there were 178 plants with an hourly capacity of reduction of 8,152 metric tons and at present all of them use the anchovy as raw material.

In 1960, when there was an intense activity in the fish meal plants, a serious problem existed in Lima and surroundings, caused by the bad odors which bothered the people and which brought with it some cases of allergy giving rise to frequent complaints. This obliged the Government to issue strict regulations, namely the factories should install deodorizing equipment, should limit the entry temperature to a maximum of 500°C, install automatic recorders and send them twice a month to the appropriate

TABLE 3

Year	Anchovy	Other Species	Prawns	Annual Total
1955	58,707	124,379	251	183,337
1956	118,726	148,360	199	267,285
1957	325,624	127,167	344	453,135
1958	737,019	162,917	231	900,167
1959	1,942,386	179,977	121	2,122,363
1960	3,310,157	191,279	176	3,501,436
1961	5,010,930	202,129	245	5,213,059
1962	6,691,521	190,362	205	6,881,883
1963	6,634,836	186,195	315	6,821,346
1964	8,863,367	183,208	200	9,046,775

Source: Instituto del Mar del Perú.

TABLE 4
FISH MEAL PLANTS WORKING IN PERU DURING 1955-1964

Fish Meal Plants			
Year	No.	Hourly Capacity in Metric Tons	Remarks
1955	19	—	
1956	27	—	
1957	39	—	
1958	53	—	
1959	68	873	This year began the applying of the Statistical Programme of the Consejo de Investig. Hidrobiológico.
1960	89	1,565	
1961	102	2,279	
1962	118	4,126	
1963	154	6,329	
1964	169	7,166	
1965	178	8,152	
6/month.			

Source: Instituto del Mar del Perú.

office, install close circulation in the fish pumps in Callao in order to avoid the decomposition of water and blowing of gases, stop work in the plants at 4 and 8 in the morning, change location, and others. The non-compliance of any of these regulations was strongly fined and, in other cases, the plant was closed. One time, 29 plants were closed because they failed to install adequate equipment. This severe measure duly permitted control of the problem and people from Lima and surroundings were able to breathe pure air without bad odors. However, Chimbote is suffering from the same problem, and the bad odors coming from the factories contaminate the air.

In the light of the anchovy industry development, it is interesting to know what occurred in the same period of 10 years in the fish-canning and freezing industry.

(2) *Fish-canning and freezing plants by ports.* Table 5 shows the number of fish-canning and freezing plants functioning in the Peruvian ports during 1958-1964. As far as the canning plants are concerned, we are facing a situation that has hardly progressed since 1959, and also a decreasing situation regarding the number of freezing plants. All this has certain relation with catching of species for human consumption, which increase was very low during the last 10 years.

(3) *The fishing fleet* increased considerably during the last 10 years and experienced serious changes because of the addition of bigger ships, better built and better equipped. Table No. 6 shows in figures this development for 4 types of ships, namely: trawlers, whalers, purse seiners and tuna clippers.

TABLE 5
NUMBER OF CANNING AND FREEZING PLANTS IN PERÚ, BY HARBORS,
DURING 1958-1964
(C = Canning; F = Freezing)
Numbers of Plants, By Years

Harbors	1958		1959		1960		1961		1962		1963		1964	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Caleta Cruz	—	1	—	1	—	1	—	1	—	1	—	1	—	1
Máncora	—	4	—	3	—	3	—	3	—	3	—	2	—	2
Paita	1	2	1	—	1	—	1	—	1	—	1	3	1	3
Chimbote	13	1	11	1	11	1	12	1	12	1	12	1	12	1
Samanco	1	—	1	—	1	—	1	—	1	—	1	—	1	—
Casma	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Huarmey	2	1	3	—	3	—	3	1	3	1	3	—	2	—
Supe	1	—	1	—	1	—	1	—	1	—	1	—	1	—
Huacho	4	—	2	—	3	—	3	—	3	—	2	—	2	—
Chancay	2	1	1	—	1	—	1	—	1	—	1	—	1	—
Callao	22	—	10	—	11	—	11	—	11	—	11	—	11	—
Pucusana	1	—	1	—	1	—	1	—	1	—	1	—	1	—
Atico	—	—	—	—	—	—	—	—	—	—	1	—	—	1
Mollendo	1	—	1	—	1	—	1	—	1	—	1	—	1	—
Ilo	2	1	2	1	2	1	2	1	2	1	2	1	2	1
TOTALS:	51	11	34	6	36	6	37	7	37	7	36	9	35	9

Source: Instituto del Mar del Perú.

TABLE 6
DEVELOPMENT OF THE FOUR MAIN TYPES OF FISHING VESSELS USED IN
PERÚ DURING 1955-1964
(RGT = Register Gross Tons)

Years	Number of Vessels and Tonnage by Types							
	Trawlers		Whales		Purse Seiners		Tuna Clippers	
	No.	RGT	No.	RGT	No.	RGT	No.	RGT
1955	2	46	4	1041	175	3599	11	1866
1956	2	46	4	1041	220	5075	12	2146
1957	3	77	7	2007	272	7167	14	2731
1958	7	133	8	2264	321	9963	18	4092
1959	9	299	8	2264	426	15130	19	4846
1960	10	321	8	2264	731	33354	20	5173
1961	11	361	10	2993	846	40923	23	5960
1962	10	330	10	2993	1070	58713	29	7003
1963	10	330	10	2993	1523	98460	28	6971
1964	10	330	10	2993	2082	147120	16	3200

Source: Instituto del Mar del Perú.

It can be appreciated that the number of trawling ships was small and without changes since 1962; similar was the case of the whaling ships; however, the number of tuna clippers decreased from 29 in 1962 to 16 in 1964. The purse seiners, used in the anchovy fishery, had a sudden increase in number since 1959, changing the features of the Peruvian fishing fleet. The increase of this type of ship from 175 units with a capacity of 3,599 G.T. in 1955 to 2,082 units with a capacity of 147,120 G.T. in 1964, shows, really, what happened in all the other activities, after the blossoming forth of the anchovy fishery in Perú.

3.4.—*Auxiliary industries.* The sudden boom in the development of the sea fishery had influence on the coastal trade and some auxiliary industries, such as boatbuilding, boat equipment and accessory manufacturing and net manufacturing.

(1) *Boatbuilding.* In the field of naval manufacturing, many small boat builders were created, exclusively for the purse seiner construction. At a given time, there were 47 of these boat builders and some of them used the port streets for this work. At the beginning, wood was used; later, some of them associated together for the building of iron ships, more powerful and with greater stowage capacity, due to the request made by the insurance companies.

At present, the boat builders are able to build around 500 vessels a year. In 1961, there were 1,474 wooden boats and 608 made of iron; in 1964 only 26 wooden boats were built and 102 of iron, some of them have a stowage capacity of 180 tons.

Many of these boat builders that were prosperous some years ago, have had to stop working. The decrease in the building rhythm affected especially those who were located far away from the shore and did not have facilities for boat repairing.

(2) *Boat equipment and accessory manufacturing.* The increasing of the fleet that was being built in our boat builders encouraged the development of small accessory industries; however, it had a more effective influence in those of mechanical type, such as the ones that manufactured pumps, crankshafts, rowlocks, and everything connected with engineering and electricity. Likewise, it brought with it the increase in the import of equipment which could not be built in our country and were necessary for the boats.

(3) *Net manufacturing.* The sudden increase of the Peruvian fishing fleet brought with it a great demand for nets in the country. At the beginning, a great quantity of nets were imported from Japan, Norway and Canada. The demand for anchovy nets reached, in 1963, to 1,561,947 kilos in the amount of 258,651,103 Peruvian soles. This local demand was the incentive for the installation of 5 net factories in the country. The productive capacity of 4 of these plants are shown in Table 7. This

activity was also the reason to make enlargements in the rope factory which was already functioning.

There is also the project of installing two more factories due to the fact that there exists in the country a good market for the use of the nylon nets as well as custom protection for these articles.

TABLE 7
PRODUCTION CAPACITY OF FOUR NET FACTORIES IN PERÚ

Name of Factory	Annual production capacity in lbs.	
	Nets with knots	Nets without knots
Textil Marítima S.A.	650,000	—
Retex Peruana S.A.	—	1,500,000
Rayón Celanese Peruana S.A.	540,000	350,000
Pabilos S.A.	120,000	—

4. COMPARISON OF FISH LANDINGS IN PERÚ AND JAPAN

Japan was the leading country among the sea nations, regarding the fish quantity landed until 1962 inclusive. Perú took the leadership in 1963. This competition for the first place is shown below in Table No. 8.

TABLE 8
FISH LANDINGS IN PERÚ AND JAPAN DURING 1957-1964
(in thousand of metric tons)

Year	Perú	Japan
1957	453.1	5,399.0
1958	900.1	5,505.0
1959	2,122.3	5,884.6
1960	3,501.4	6,192.5
1961	5,213.0	6,700.0
1962	6,881.8	7,000.0*
1963	6,821.3	6,697.7
1964	9,046.7*	5,870.0

* = maximum.

Source: Instituto del Mar del Perú and FAO.

5. PERUVIAN EXPORTS OF FISHERY PRODUCTS DURING 1955-1964

Among fish products exported by Perú, fish meal became the leading export product. It can be seen in Table No. 9, which covers period 1955-1964.

The crisis that encountered the international fish meal market in 1960 was the reason for the creation of the Fish Meal Export Organization (F.E.O.), based on an agreement signed in Paris in October 18 of same

year. The principal task of this organization is to order sale of fish meal in the international markets, establishing annual export quotas for each signing country; promote investigation and regulation of market in order to contribute to stabilization of prices.

TABLE 9
EXPORTS OF FISHERY PRODUCTS IN 1955-1964
(in metric tons)

Year	Fish Meal	Fish Oil	Frozen Fish	Canned Fish	Salt Fish	Total Exports	Total Value in Thous. of Soles
1955	18,717	92	11,848	16,706	50	47,416	226,114
1956	27,792	1,721	12,894	18,502	134	61,043	284,015
1957	61,645	4,338	12,738	19,271	92	98,084	356,678
1958	105,777	1,643	16,437	13,321	148	137,326	452,447
1959	278,056	17,165	26,118	17,475	133	338,947	1,172,839
1960	507,042	35,008	18,129	15,423	345	575,947	1,365,778
1961	708,366	102,306	19,932	19,186	331	850,121	1,874,352
1962	1,055,883	127,969	20,141	15,131	556	1,219,680	3,215,595
1963	1,038,270	125,477	22,973	12,875	274	1,119,869	3,228,740
1964	1,426,359	110,550	13,353	15,104	486	1,574,980	4,472,995

Source: Customs General Statistics.

The "Sociedad Nacional de Pesquería" obtained in Perú the support of the Government in order to assign quotas for the fish meal exports. Later, the "Consorcio Pesquero del Perú" was created, having as members 40 per cent of the fish meal producers, so as to centralize exports and to maintain the quality of the export product. This organization obtained more stability in prices and encouraged the building of new plants. However, a powerful group remained outside and did not associate to the "Consorcio."

TABLE 10
FISH OIL PRODUCTION
(in metric tons)

Year	Total	Remarks
1957	7,669.1	
1958	10,271.2	
1959	23,696.3	
1960	48,210.9	
1961	118,885.7	1st port in the world as producer
1962	142,691.7	
1963	154,870.8	
1964	140,000.0	

Source: Servicio de Pesquería.

TABLE 11
PRINCIPAL FISH AND SHELLFISH SPECIES CAUGHT ON THE PERUVIAN COAST

Native Name	Scientific Name	Fishing Season
Anchovy	<i>Engraulis ringens</i>	October/ May
White seabass	<i>Sciaena deliciosa</i>	All year round
Snake eel	<i>Ophichthus pacifici</i>	"
Angelfish	<i>Squatina armata</i>	"
Yellowfin tuna	<i>Thunnus macropterus</i>	November/ June
Skipjack	<i>Katsuwonnus pelamis</i>	All year round
Catfish	—	"
Bereche (bereche)	<i>Larimus</i>	
Bonito	<i>Sarda chilensis</i>	December/ July
Pacific mackerel	<i>Pneumatophorus peruanus</i>	July/ Nov. & January-April
Grunt	<i>Isacia conceptionis</i>	All year round
Seabass	<i>Paralabrax humeralis y calaensis</i>	"
Weak fish	<i>Paralanchurus peruanus</i>	"
Cojinoba	<i>Neptomenus crassus</i>	June/ September
Cusk eel	<i>Genypterus chilensis</i>	All year round
Drum	<i>Sciaena gilberti</i>	"
Sea bream	<i>Anisotermus scapularis</i>	November/ Mar.
Guitarfish	<i>Rhinobatos planiceps</i>	All year round
Horse mackerel or scad	<i>Trachurus murphyi</i>	April
Flatfish	<i>Paralichthys adspersus</i>	All year round
Mullet	<i>Mugil</i>	"
Shad	<i>Ethmidium chilcae</i>	January/ October
Rock bass	<i>Alphestes fasciatus</i>	January/ May
Croaker	<i>Stellifer minor</i>	All year round
Moray	<i>Gymnothorax wieneri</i>	"
Seabass	<i>Hemilutjanus macrophthalmus</i>	"
Pompano	<i>Trachinotus peitensis</i>	"
Whitefish	<i>Caulolatilus princeps</i>	"
Swordfish	<i>Xiphias gladius</i>	"
Silverside	<i>Austromeniia regia</i>	August/ October
Pintadilla	<i>Cheilodactylus variegatus</i>	All year round
Rays	<i>Pteroplatea afuerae</i>	"
Drums	<i>Sciaena starksi</i>	"
Sardine	<i>Sardinops sagax</i>	January/ October
Spanish mackerel	<i>Scomberomorus maculatis</i>	All year round
Blenny	<i>Labrisomus</i>	"
Dogfish	<i>Mustelus spec.</i>	"
Wrasse	<i>Bodianus y Pimelometopon</i>	"
Crabs	—	"
Squids	—	"
Scallops	<i>Pecten purpuratus</i>	April/ December
Mussels	—	All year round
Sea urchins	—	"
Prawns or shrimps	—	"
Oysters	—	"

The development of the fish meal export contributed to the increasing of the fish oil production and to its exportation. The increasing of the fish oil production can be seen in Table 10.

This product is absorbed in more than 90 per cent by Holland, Denmark and Western Germany.

6. FISHERY CONTRIBUTION TO HUMAN CONSUMPTION

The Peruvian sea fishery has developed with private investments and is looking forward to obtaining benefits; this is why it has been orientated more to export than to supplying the domestic market with sea products. The contribution to human consumption has been relatively small, although we must mention that some fishing enterprises have tried to place fresh and frozen fish, as well as canned products, at fair prices.

In the Peruvian coast, there is a great variety of species; some of them could be caught all year round, or during most part of it. The "Instituto del Mar del Perú" investigates the biology and conditions of the physical environment in which these species live. Table 11 shows the native and scientific names of those species, indicating as well, the seasons in which they can be caught.

Although the number of species caught is large enough, it is necessary to mention that the annual volume of these species caught for the domestic market hardly represents 2 per cent of the total annual catch. This shows that Perú has yet a large field for the development of fisheries.

In spite of the great volume of annual catches, Perú is considered among the South American countries suffering the effects of undernourishment. In this connection, some data could be mentioned regarding the world fish consumption.

6.1.—*Fish Consumption.* The animal protein is one of the principal components of the human diet; the minimum amount required is 70 g. per capita. Fish is one of the most important sources of rich animal protein, notwithstanding its consumption is very deficient in many countries as can be seen in Table 12.

Therefore, Perú is considered among the countries with low fish consumption. The Peruvian inland people are not used to include fish in their diet; this is due to the fact that fish is not always found in the market at fair prices. On the other hand, they do not have the necessary education as to the adequate way to prepare the sea products.

The exploratory fishing recently done by the Instituto del Mar del Perú in collaboration with the Sociedad Nacional de Pesquería and the Dirección de Pesquería (Ministry of Agriculture) with a trawling boat, disclosed large hake schools in the northern zone of Perú, reaching as far southward as Callao. These raise the possibility of using hake in greater scale as a food source for human consumption.

Since times of the Spanish control and afterwards during the Republic,

there have been isolated regulations on fishery that refer more to jurisdiction and authority matters than to technical rules or encouragement for its development. In August 1947 the Government issued "The Peruvian Right Doctrine of the Territorial Sea," declaring domain and jurisdiction out to 200 miles, in order to reserve, preserve, and utilize the sea sources, without interfering with free navigation. In 1952, the tripartite agreement under the title of "Santiago Statement" was signed by Perú, Chile and Ecuador, referring to the 200-mile jurisdictional waters.

TABLE 12
ANNUAL FISH CONSUMPTION IN THE WORLD, PER CAPITA

<i>Very low</i> under 5 kgs.	Countries with Fish Consumption		
	<i>Low</i> from 5 to 10 kgs.	<i>Regular</i> from 10 to 20 kgs.	<i>High</i> more than 20 kgs.
Argentina	Australia	Ceylon	Denmark
Austria	Belgium	Chile	Great Britain
Brazil	China	Finland	Iceland
Bulgary	France	Germany	Japan
Czechoslovakia	Greece	Holland	Norway
Eastern Germany	Indonesia	Philippines	Portugal
India	Perú	Siam	
Italy	U.S.S.R.	Sweden	
Pakistan		United States	
Polony		Venezuela	
Rumany			
Switzerland			
Turkey			
Uruguay			

Source: Anuario Estadístico de FAO.

At the opening of so many fish meal plants and because of the air contamination, as already described, a series of technical and sanitary regulations were issued. Furthermore, the zones where plants could be installed and the necessary requisites that should be met, were duly delineated. Sanitary rules were issued for transportation of raw material to fish meal plants and even fixing the operating hours both for transportation as well as for plants.

6.2.—*Legislation.* This year the Congress approved a law to promote fishery production for the domestic market. This law considers of social interest and national necessity the promotion of fishery for human consumption in the country. It establishes that people dedicated to the catching, transport and preservation will be granted a ten-year exoneration from the commercial and industrial income tax up to 10 per cent of the net sales and a 75 per cent exoneration of the patent tax. They will also be exonerated from the company constitution tax as well as the corresponding to opening and functioning of commercial plants and establishments. Like-

wise, they will not have to pay the fiscal tax on sales for domestic consumption and on ice use. The law also establishes that fishery products will be marketed and sold by the weight metric system and that the Executive Power will indicate the coastal ports and coves that will exclusively be dedicated to fishery for human consumption.

It is hoped that this law will contribute to the quick promotion in the trade of sea products supplied to the domestic market in order to raise the nutrition level of the people.

Furthermore, just now the Congress has approved another project which establishes a private bank for development of the fishery industry, with a minimum investment of 100 million soles; 60 per cent of this investment should be in the hands of Peruvian, legal or native persons, with nominative shares. This bank, besides taking care of the common credit requests, will have to promote and encourage the fishery industry.

7. FISHERY CONTRIBUTION TO THE INDUSTRIAL DEVELOPMENT OF THE COUNTRY

The increasing of the fishing activities in the sea, contributed to strengthen the trade along the Peruvian coast and the industrial development of the country.

The large anchovy catches obtained by the purse seiners gave rise to a two-fold problem, namely: (1) the quick carrying of fish from net to the storeroom, and (2) unloading of fish in the port. The Swiss engineer Martín Stahle built for Hidrostral in 1957 a type of pump that permitted pumping the anchovies from boats to dock or directly to the reduction plants. In the port of Huacho, the new pumps permitted transport of the anchovies, without water, through pipes for a distance of 600 meters and at a speed of 3,000 tons per hour.

At present, landings in all coastal ports are made by fish pumps with a capacity of 100-200 tons per hour. These pumps are installed in the docks or in small flat-bottomed boats.

There are more than 500 purse seiners that have their own 8 to 12 inches pumps, with a capacity of 120 tons per hour which permitted them to carry fish from the net to the store room and leave the boat ready for an immediate net lowering.

There are in Callao 7 fish-pump installations that unload the purse seiners into 5-ton trucks, which transport the anchovies from the port to the reduction plants located in the Argentine Avenue.

The use of these pumps has been spread out in many countries, and the Hidrostral del Perú, exports them to Germany, Canada, Iceland, South Africa, Chile and Norway.

The impact of the anchovy fishery was also felt in other branches of the national industry. One of these is the manufacturing of equipment for reduction fish meal plants. An equipment for a complete plant in the

amount of 200,000 dollars was built in Perú and sent to Panamá.

Another industry that has been developed in the country, is the construction of iron boats.

In summary, we can state that development of the Peruvian anchovy industry brought with it a favorable encouragement for the evolution of several industries in the country.

8. RESEARCH AND TRAINING ON OCEANOGRAPHY AND FISHING

The Peruvian Government created a Consejo de Investigaciones Hidrobiológicas on November 24, 1954, to fulfill the function of coordinating and promoting hydrobiological research in the country, looking forward to the best use and control of the native resources. In 1957, it was granted legal attorneyship. This Council began in February 1958 a systematic research of the sea, using the B.A.P. "Bondy." In June 1958, a whaling program began and at the same time a statistical program was initiated, assigning inspectors to the principal fishing ports of the country. In the near future, this program will be the principal mean as to changes in the amount of catching by boats.

In April 1959, the Council began negotiations with the Technical Assistance Board of the United Nations and FAO in order to get technical and financial aid, and speed up the research programs as well as solve the bigger problems that came out during the sudden development of sea fisheries. In accordance with the Agreement signed with the Special Fund of the United Nations, in July 1960 the Marine Resources Research Institute was created with headquarters in La Punta-Callao. This Institute had the following Departments: Oceanography, Biology, Economics and Technology, intensifying the research programs initiated in 1958 and sponsoring them regarding development in fisheries on basis of rational exploitation. The Institute stopped functioning in June 1964, at which time the actual Instituto del Mar del Perú, created in July 1964, began operations.

The budget for this new Institute is covered by funds given by the Ministry of the Navy, Sociedad Nacional de Pesquería and the whaling industry. It carries on programs of Oceanography, Biology, Technology and Economics, and has four FAO experts as advisers; one for each of the programs mentioned.

As far as Oceanography and Fisheries are concerned, training is given to college students and supervisors as well as to laborers.

This training for laborers and fishermen created some problems. There were some attempts to create fishery schools. In 1920, a law was issued creating the Fishing and Salting School in Callao; in 1961 was created the Technical School "José Olaya" for fishing shipmasters. Although this school planned its program of studies, it never functioned. In 1963, the Industrial and Fishery Institute was created by a supreme decree and began

operation in Callao, giving training onshore in carpentry, Diesel engines, net manufacturing and techniques in fishing and radio.

As many of the laborers of the fishery and by-product plants, as well as many of the fishermen that belong to the boat crew, entered their actual occupation, attracted by the possibility of higher incomes, the need to increase their knowledge sprang up with the purpose of reducing accidents in the sea and increasing the amount of catching as well as fish quality during its transportation to ports. They needed the technical and social training in order to improve their level of living and organize their work in the sea and ashore under the best benefit and safety conditions.

The actual fishery industry has understood the unpostponed need to train its personnel. For this reason, the Sociedad Nacional de Pesquería, the International Petroleum Co., and the Servicio Nacional de Aprendizaje y Trabajo Industrial (SENATI) agreed to have programs to train and qualify laborers and supervisors, including the following courses.

Courses for laborers

Workshop mathematics
Basic lessons for reading of designs and drawings
Care and handling of tools
Autogenous and electric welding
Material technology
Mechanical and electrical maintenance
Operation and maintenance of diesel engines
Operation and maintenance of boilers
Plant protection and first aid

Courses for Supervisors

Human relations
Leading of meetings
Improvements of working methods
Continuation techniques

Around 150 plants follow this plan and benefit some 9,000 laborers and 370 supervisors in different ports along the Peruvian coast.

Therefore, we can say that training to improve the professional knowledge of the Peruvian fishmeal industry laborers and fishermen is in full development. The fishery industry has contributed in a large measure to this, having had the best government support.

As far as training in fishery oceanography at a college level is concerned, the following can be said:

- (1) Oceanography is taught in several universities of the country and one of the newly created universities has a Faculty of Oceanography and Fishery.
- (2) There are not enough faculty personnel having sufficient experience in all that relates to marine sciences who could teach in the interested universities.
- (3) The universities have initiated an intensified program of oceanography based on the collaboration of the visiting professors coming to this country under the assistance of UNESCO.
- (4) The Instituto del Mar del Perú, in collaboration with FAO, maintains

a fellowship program in order to increase the knowledge of its personnel, part of them acting as teachers in universities and fishery schools.

9. SOCIAL AND LABOR LEGISLATION

The practice of fishing is free in Perú. However, anyone who wishes to engage it should have a fisherman's card and should be registered in the port where he will work.

Fishermen or any other persons who wish to work in the fish trade, are obliged to request a fishing license extended, free of charge, by the Control Department (Servicio de Pesquería). This regulation binds everybody, wholesalers, retailers, exporters and even those engaged in the sport fishery.

The processing of fishery products is subject to many other regulations. Laborers in fish meal plants and auxiliary industries, are included in the social and labor legislation of the country.

Fishermen and personnel working in boats going to sea are subject to social laws regarding social aid which include life insurance as an obligation.

Ministerial Resolution No. DC-867 of 1960, establishes a provision fund with the contribution of 1 per cent of the income resulting from fishing, but only when the fisherman is working under a location contract. For this fund, Sociedad Nacional de Pesquería contributed 500,000 soles.

Later, a Social Aid Fund was created with the contribution of 2.50 soles per anchovy ton from which 1.50 soles corresponds to shipowners and 1.00 sol to fishermen. This fund was not regulated and only functioned as an Assistance fund, that extended limited medical assistance to the fishermen but only in case that they would have worked at least three weeks in a month.

In March 1963, was issued the accident insurance table for fishermen, shipmasters, and crew men through collective policies; in April of the same year, the government approved by Supreme Resolution No. 163 the agreement between fishermen and shipowners as well as the "fisherman fund" established with the contribution of 3.00 soles per ton of landed anchovy and which should be paid by the shipowners.

Due to economical troubles encountered by the Peruvian fishing industry in 1963, the government issued Law No. 15048/1963 that frees the fishing industry of duties for a period of three years; in order to relieve some of its problems, granting a moderate period of time to consolidate as well as to renew equipment and machinery.

The government also helped the shipowners, granting them a credit of 180,000,000 soles.

10. FUTURE PROSPECTS

After having reviewed the condition of the Peruvian sea fishery, based in its explosive development during 1955-1964, we should mention some ideas regarding the future prospects.

In the whaling industry field, the prospects are not very good due to the slow process for the recovery of the decreased stock of sperm whales. On the other hand, the catching fleet will require greater investments to be modernized.

In the fishing production field, there are good prospects due to the fact that during the first six months of 1965, 5,043,202 metric tons of anchovy and 71,270 metric tons of other species were obtained. On the other hand, the regulation in August over the anchovy exploitation for the first time in this year influenced the fish meal prices in the international market, during the second half of 1965, as they were increased from US\$105 per metric ton to more than US\$160 (F.O.B. Callao). The prospects for the future international trade of fish meal seems to be very good.

However, everything was not so easy, as in the first half of 1965, an anomaly was registered in the oceanographical conditions, characterized by the presence of very warm waters with temperature of 25° to 27°C in front of the central coast of Perú. Under these conditions of its physical environment, the anchovy was beyond reach of the guano birds and fishing boats in certain areas. Birds in the mass emigrated to Chile and Ecuador, a phenomenon which is repeated at irregular intervals, following drastic changes in the conditions of the Peruvian sea. It remains to be seen the effects on the anchovy fishery during the second half of 1965, which up to the first part of October were rather gloomy.

In the guano industry field, there is still much to be done. It is estimated that the irregularities observed in the sea conditions off Perú during the first half of 1965 will have negative effects on the total amount of guano in 1967, because the crisis in the exploitation of this product usually comes two years after the disturbances occurred in the sea. Meanwhile, the guano bird population will be subject to an intense research by the Instituto del Mar del Perú in collaboration with Yale University and also the cooperation of the Corporación Nacional de Fertilizantes. It can also be stated that there are many advanced studies to obtain superior guano products, and acquisition of the necessary equipment is also considered.

In the research field, the Instituto del Mar del Perú hopes that its new building, at present under construction in Chucuito (Callao) will be concluded in October 1966. It is also hoped to intensify its research activity in the Eastern Pacific with its own vessels and in collaboration with oceanographic vessels from other American countries, in the continuation of studies of mutual interest. Likewise, it is to be initiated a joint activity with the national universities in Pisco and Ilo. Moreover, it is hoped that a new Interamerican cooperation will result from this conference.

In the Legislation field, there is the need to legislate with scientific criterion the way of exploiting the biological sources of the sea in order to ensure a prudential annual yield, however, in a lasting way instead of having a high income but in a short period.

It will be necessary to adopt measures towards the ensuring of the preservation of the exploited aquatic species, and, on the other hand, towards the normal development of the industry based in the utilization of raw material obtained from the sea.

As far as whales is concerned, it is in force the Regulation for the whaling catch in the South Pacific, which establishes that the new whaling plants ashore could be installed within a distance not less than 250 miles in between.

Regarding the anchovy, much remains to investigate concerning its biology until the obtention of the most suitable knowledge towards the granting of a fair legislation of its exploitation.

The most important matter in the immediate future will be the problem of the existing biological resources that could be used to improve people nourishment and contribute, in this way, to the raising of its living level.

BIBLIOGRAPHY

ANONYMOUS

1957- Anuario de Comercio Exterior; Anuario Estadístico de Pesca (FAO), 1958. Vol. 7.

BEDOYA, L. E.

1964. Pesca Peruana en 1963.

BELAUNDE G., CÉSAR

1963. La Legislación Pesquera en el Perú.

BRAVO B., JORGE

1963. El desarrollo de la pesquería. Symposium 5-10 Nov. 1962. Bases para el desarrollo 107-120.

COMPAÑIA ADMINISTRADORA DEL GUANO, LIMA

———. Informe del Ingeniero Luís Gamarra Dulanto. Volume XVII, No. 3.

DE LA VEGA, INCA GARCILASO

———. Relatos.

DOUCET, W.

1965. Mercado de peces marinos de Consumo en el Perú. (Inf. No. 5).

ESTADÍSTICA DE SUPERINTENDENCIA GRAL. DE ADUANAS, 1964.

GARCIA CALDERON, J.

———. Diccionario de Legislación Peruana.

GRZYWACZEWSKI, Z., Z. HUELLE, S. SZMID, AND J. SWIECICKI

1964. Modern Fishing Vessels.

HEDGES, JOHN K.

———. Ocean Fisheries. Vol. I, No. 3.

IPARRAGUIRRE C., JAVIER

1959. Estadística económica de la Industria Pesquera.

1963. Política económica de la Pesquería en el Perú.

IPARRAGUIRRE C., JAVIER, J. GARCIA AND A. ELEJALDE Z.

1963. Diagnóstico económico social de la Pesquería.

IREMAR

1960. Ligera Reseña de la Creación.

LORA, J.

1965. Crecimiento de la flota pesquera industrial al 31.12.63 (Informe No. 2, IMARPE).
1965. La pesquería de la anchoveta. (Informe No. 1, IMARPE).

LECCA, ROBERTO P.

1963. El desarrollo de la pesquería. Symposium 5-10 Nov. 1962. Desarrollo industria . . . 1-6.

MEJIA J. C.

1965. Notas sobre ballenas (Informe Interno).

PESCA, LIMA

1965. Surge Industria . . . 10 (3): 10-15.
1965. Armadores deben . . . 10 (4): 12-15.
1965. Vuelven las . . . 11 (1): 12-17.
1965. Capacitación . . . 11 (2): 18-20.

POPOVICI, Z.

1960. Aspectos contradictorios de la industria pesquera del Perú. Consejo de Investigaciones Hicrobiológicas. Informe (Mimeo, 28 págs.) Lima.
1962. El desarrollo de la Pesca Marítima e Investigación de los Recursos Marítimos en el Perú. Conferencia de las Naciones Unidas sobre la aplicación de la Ciencia y Tecnología. Ginebra E/Conf. 39C/413.
1962. Corrientes oceánicas y la pesca peruana. Anuario de Pesca 1961/62: 162-172 Lima.
1963. La Oceanografía al Servicio de la Pesca en el Perú. Anales del Symposium sobre "El Desarrollo de la Pesquería en el Perú" Publ. por la Univ. Agraria La Molina: 7-37 Lima.
1963. Horizontes oceánicos de Sudamérica. Anuario de Pesca 1962/63.

REGLAMENTO GENERAL DE CAPITANÍAS Y MARINA MERCANTE, 1962.

TOVAR, AGUSTÍN

- . Historia de la Pesca en el Perú.

DEVELOPMENT OF JAPANESE HIGH-SEA FISHERIES

T. KAMENAGA

Production Division, Fisheries Agency, Tokyo

ABSTRACT

Japanese tuna fisheries, though having a long history of operation, have developed to the present scale since the end of World War II. Fishing techniques have changed from pole-and-line fishing for skipjack and bonito to longlining for tunas including skipjack.

Factors affecting the growth of the Japanese tuna fishery are: (1) exploitation of new fishing grounds, (2) technical improvements in refrigeration equipment and navigational instruments, and (3) the expansion of markets in Europe and the United States.

The size of the tuna fleet and its catch data are described. The industry is presently faced with a declining catch rate, sharply increased labor costs, reduced labor force, and price fluctuations for tuna. For the future it is desired to accelerate research activities, achieve a balance between fishing effort and international cooperation, adopt labor saving devices on board vessels, and expand domestic and foreign markets.

GENERAL ASPECTS

Japanese fisheries have developed remarkably after World War II and made a great contribution to the revival and development of the national economy. The contribution can be divided into the following three main categories. The first is to have helped the nation cope with its food problems; two-thirds of the animal protein for the Japanese people are now from fishery products. In 1963, the gross landing value was 1,342-million dollars accounting for 2.1 per cent of the Gross National Income. The second is to have earned dollars from foreign markets, and they accounted for 5.2 per cent of the total export value in 1963. The third is to have afforded employment to people, and persons engaged in fisheries numbered 626 thousand in 1963.

Those developments which have driven Japanese fisheries forward in the last 10 years, are offshore and pelagic fisheries, especially tuna long-line, trawl, and salmon gill net fisheries. In 1963, the production of offshore and pelagic waters amounted to 4.2 million metric tons, namely 63 per cent of the total catch (Fig. 1).

Main pelagic fisheries are factory-ship fisheries for salmon, bottom fish, and king crab in the North Pacific, trawl fisheries in the Eastern China Sea, South China Sea, and the sea off the coast of Africa, and whaling. There are many offshore fisheries operated in the high seas adjacent to the coastal waters by boats over 10 gross tons. Most of these are medium-size trawlers, purse seiners, saury dipnet boats, salmon drift net vessels, pole-and-line boats for tunas, skipjack, and mackerel, and angling for squids.

As for coastal fisheries, they have not made any conspicuous development because fishing grounds are limited and fishery resources have been exploited from olden times. One of the most important aspects in coastal fisheries in recent years is a remarkable development of fish culture in shallow waters. Fish culture tries to utilize coastal fishing grounds to the utmost possible, and to increase the productivity per unit area by the artificial management of fish, shellfish, seaweed, etc. In 1963, coastal fisheries produced about 2.6 million metric tons, including the products of fish culture and inland waters, for about 37 per cent of the total catch. The average income of a household of coastal fishermen in the same year was a little less than that of a city worker's household.

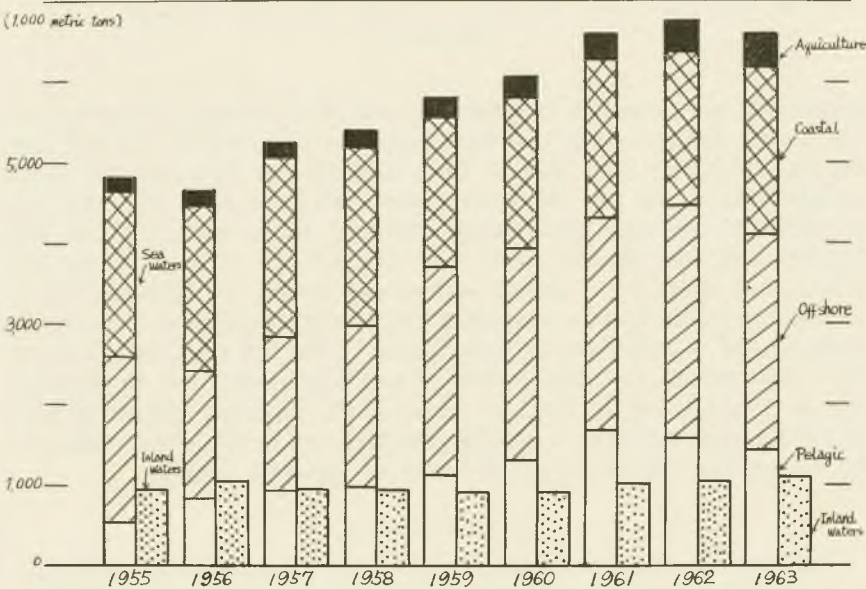
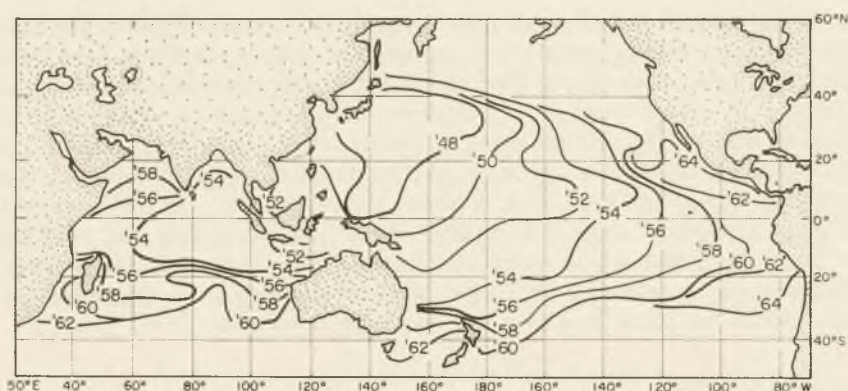


FIGURE 1. Total catch by type of fisheries.

As Japanese people have been familiar with the seas from olden times and are fond of fish, they eat over 20 kg of fish and fishery products per head in a year. Since the domestic demands tend to increase, and some high-priced fishes have come to fail in meeting the demand, the imports of fish have come to increase year after year. What has made Japanese fisheries so large? My opinion on this point is, first, that there is and has been strong economic impetus to engage in fisheries and invest capital in them. In other words, fisheries are among the profitable industries in Japan. In the case of high-sea fisheries, long-term government loans were made only for ship construction by the management which has less



than 1,000 gross tonnage in ownership and 300 persons in employment. The yearly interest of the long-term loans has been usually 7.5 per cent, supposedly higher than that of other nations. So it is not too much exaggeration if we say that government aid has played a major role in Japanese fisheries development. Second, Japan had its own ship builders and well trained crews who would serve at lower costs, and third, entry check by a license system was usually so administrated as to make the fishermen's management reasonable, to avoid excessive competition, and to contribute to conservation of the fish resources. Through these observations, the main impetus of past development was an economic one as I had stated at first. In recent years, however, industrialization of the Japanese economy is rapidly promoted and it will give a considerable change for the situation and future of Japanese fisheries.

TUNA FISHERIES

Although the origin of Japanese tuna fishery dates far back into history, it is only since the end of World War II that it has shown the prospect of growth to its present scale. In the course of its development, less efficient skipjack angling has come to be gradually replaced by tuna long-lining. (In 1963, the ratio of the former to the latter shifted from 70:30 in pre-war days to 23:77.)

The contribution of Japanese tuna fishery in 1962 amounted to as much as 10 per cent of the total Japanese catch or 64 per cent of the world tuna landings. Their catches are being used both for domestic consumption and export purposes. Very large amounts of frozen and canned tunas are shipped annually not only to the United States but also to Italy and other European countries, thus playing an important role in keeping Japanese foreign trade in balance.

Such outstanding growth of the Japanese tuna industry is accounted

for by a number of economic and technological factors as follows:

Development of New Fishing Grounds and Vessels.—In 1952, the restrictions on fishing grounds were lifted and further, in the following year, the average tonnage of tuna boats was increased with the amendment of tuna fishery regulations. In 1954, expansion of the Japanese tuna fishing grounds had reached to the whole waters of the eastern Pacific and some parts of the Indian Ocean (Fig. 2).

During these several years, many larger boats were launched mostly by the owners of small boats less than 100 tons or those who gave up their long-experienced dragnet and seine fishing. Thus, the total tonnage of the tuna fleet increased from 103,000 metric tons (1130 boats) in 1952 to 197,000 metric tons (1380 boats) in 1956 (Fig. 3). As a result, the fishing grounds of the tuna fleet have expanded farther into the Indian Ocean since around 1954, and into the Southwest Atlantic Ocean since around 1957, when Las Palmas was made available as their base port (Fig. 4).

Since 1956, increase in the number of tuna boats has been barred by the Government with the exception of the addition of 150 boats made at the expense of so many salmon gillnetters. At present, construction of larger boats is limited only to those who meet strict qualifications, or on the condition that the tonnage of new boats shall be less than that of the boat or boats to be replaced. The government policy is designed to

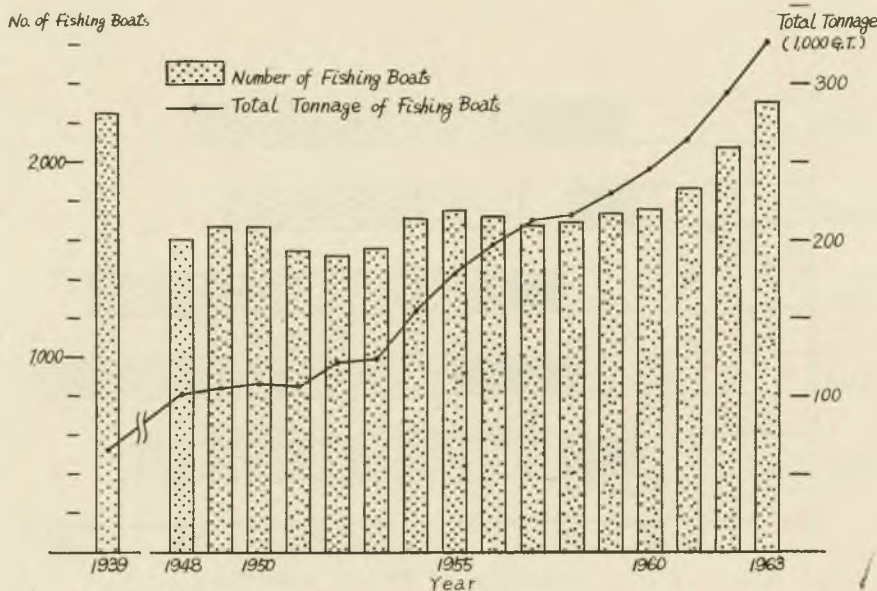


FIGURE 3.

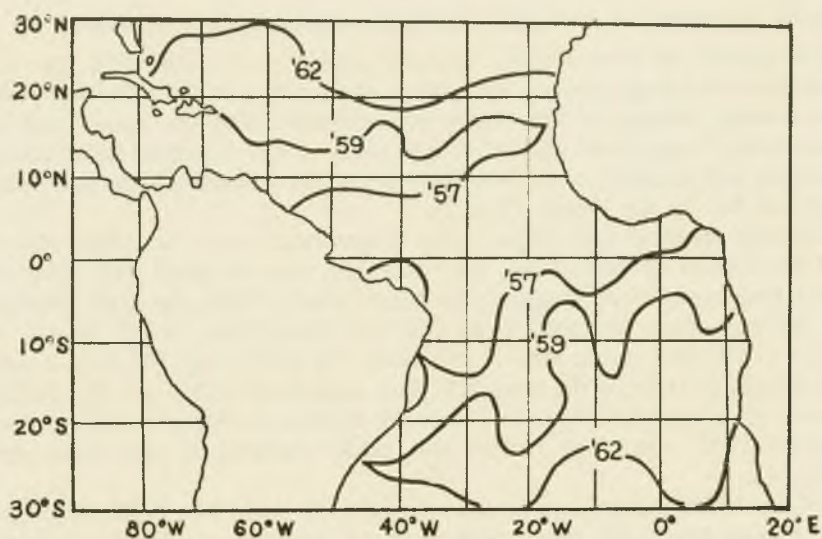


FIGURE 4.

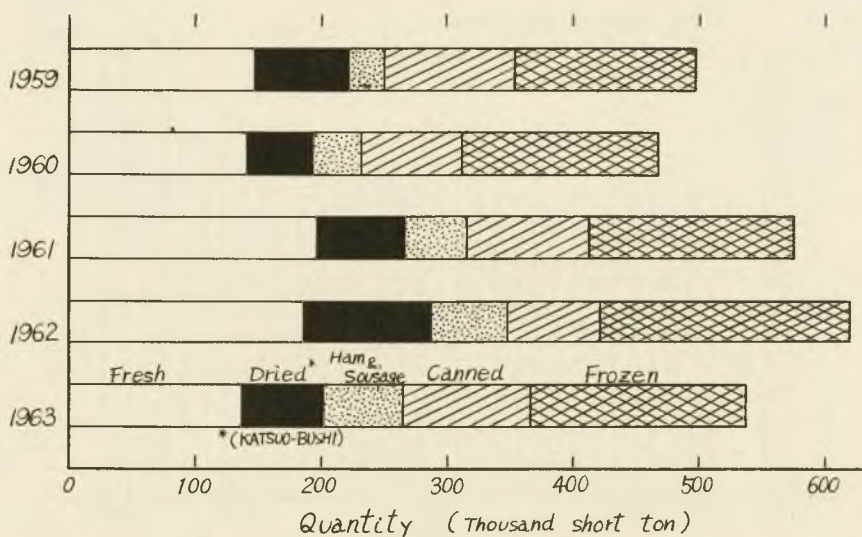


FIGURE 5.

offset the effect of the increase of the total tonnage at the cost of the decrease in number. Most of the tuna boat owners in Japan are not big enterprises but are rather small ones; those who have engaged in this fishery for many generations. For the purpose of stabilizing these small managements, long-term and low investment loans are given for the construction of new tuna boats. Such long-term government loans, though not necessarily low in interest from the view of the world standard, have served substantially to free these small enterprises from the high interest rates of commercial loans.

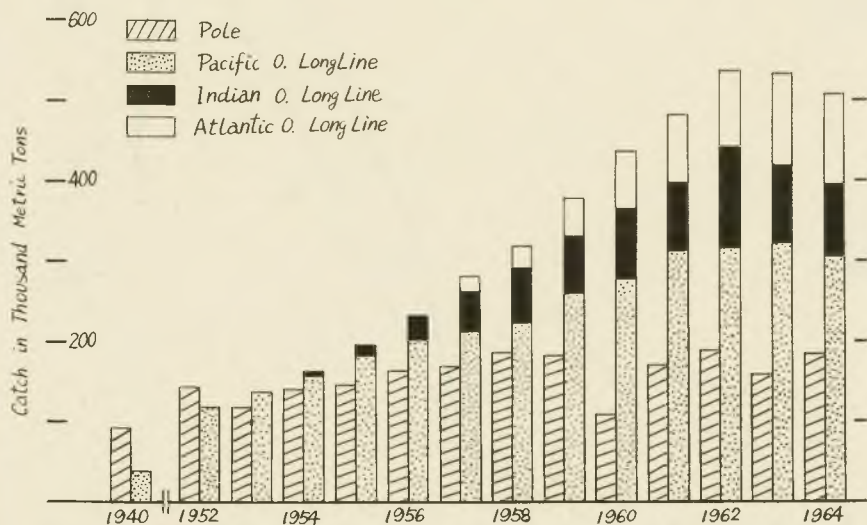


FIGURE 6. Yearly catch by tuna long-line and skipjack pole and line fisheries.

Modernization of Freezing Techniques and Navigation Instruments.—In the past, the catches were brought home stored in ice and this method of preservation was long believed to work to the satisfaction of the public who generally favor fresh tuna. However, in order to meet the expansion of the overseas market and of the fishing ground far out into the distant oceans, the industry has endeavoured to improve their freezing techniques and facilities. Modern, large boats built since around 1952 are all equipped with modern quick-freezing facilities. Introduction of many modern navigation instruments, such as loran, radar, etc., has contributed a great deal to the safety of navigation.

Expansion of Consumption Market.—Tuna has been since olden times prepared as sliced raw meat, and dried stick for soup. In pre-war days

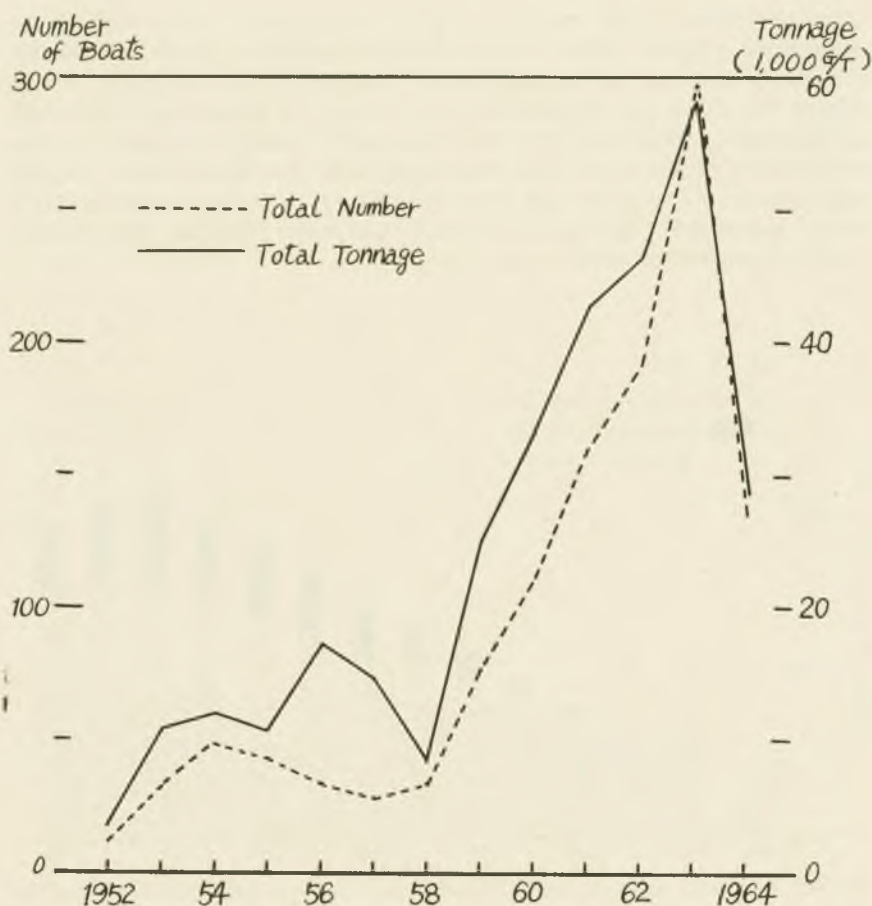


FIGURE 7.

and shortly after the war, the consumption depended upon the domestic market except for a small amount of canned tuna for export (Fig. 5). However, development of modern freezing techniques has enabled the industry to produce superquality frozen tuna meat, and meet the growing demand from the United States and European markets, which in turn contributed to the improvement of the profitability of the industry.

THE PRESENT SITUATION AND PROBLEMS INVOLVED

The Stagnation of Catches.—The catch amount, number of vessels, and their tonnage, are as shown in the attached figures (Figs. 6 & 7). Total catch of tuna increased from year to year, at a rate of 40 or 50 thousand

tons a year before 1958, but the rate of increase has slackened in recent years. This slackening was deemed due to the poor catch record in the pole-and-line fisheries. The total catch was not raised in spite of a substantial increase in fishing efforts (Figs. 8 & 9). The rate of profit per invested capital has also shown a downward trend, due to such factors as decrease in catch per day, increase in operational cost and longer days per voyage. Thus, the tuna fishing industry now requests that the government should strengthen research on the resources and refrain from authorizing the replacement of licensed vessels and the building of larger vessels.

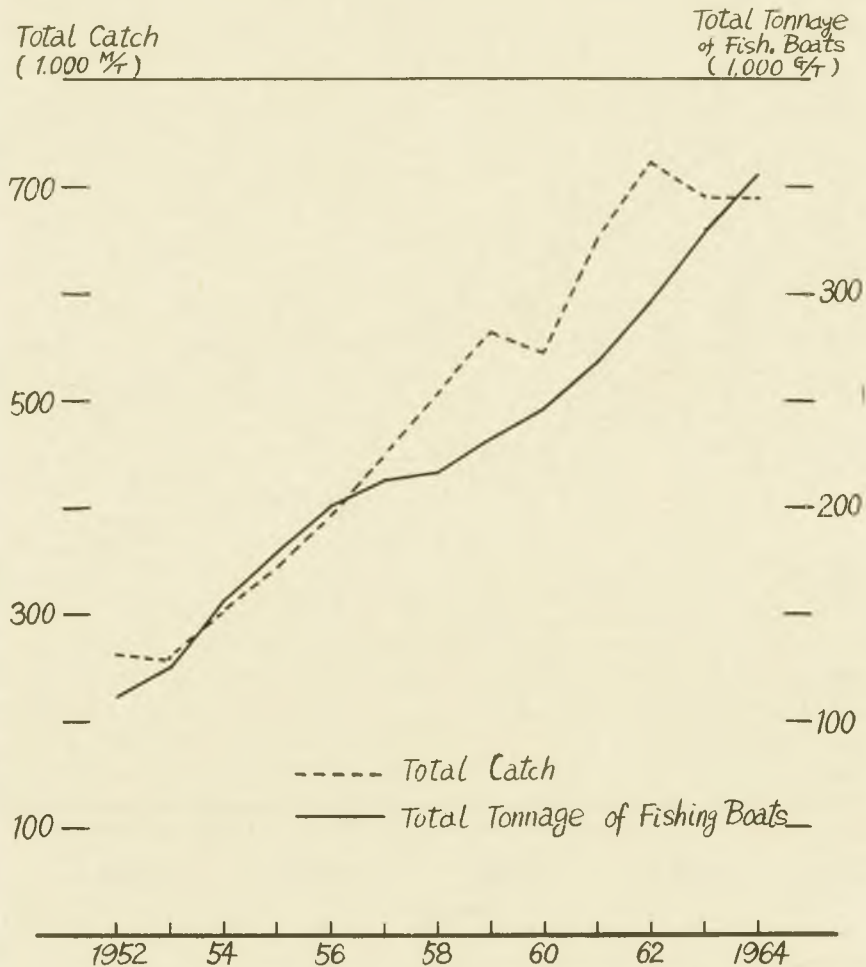


FIGURE 8.

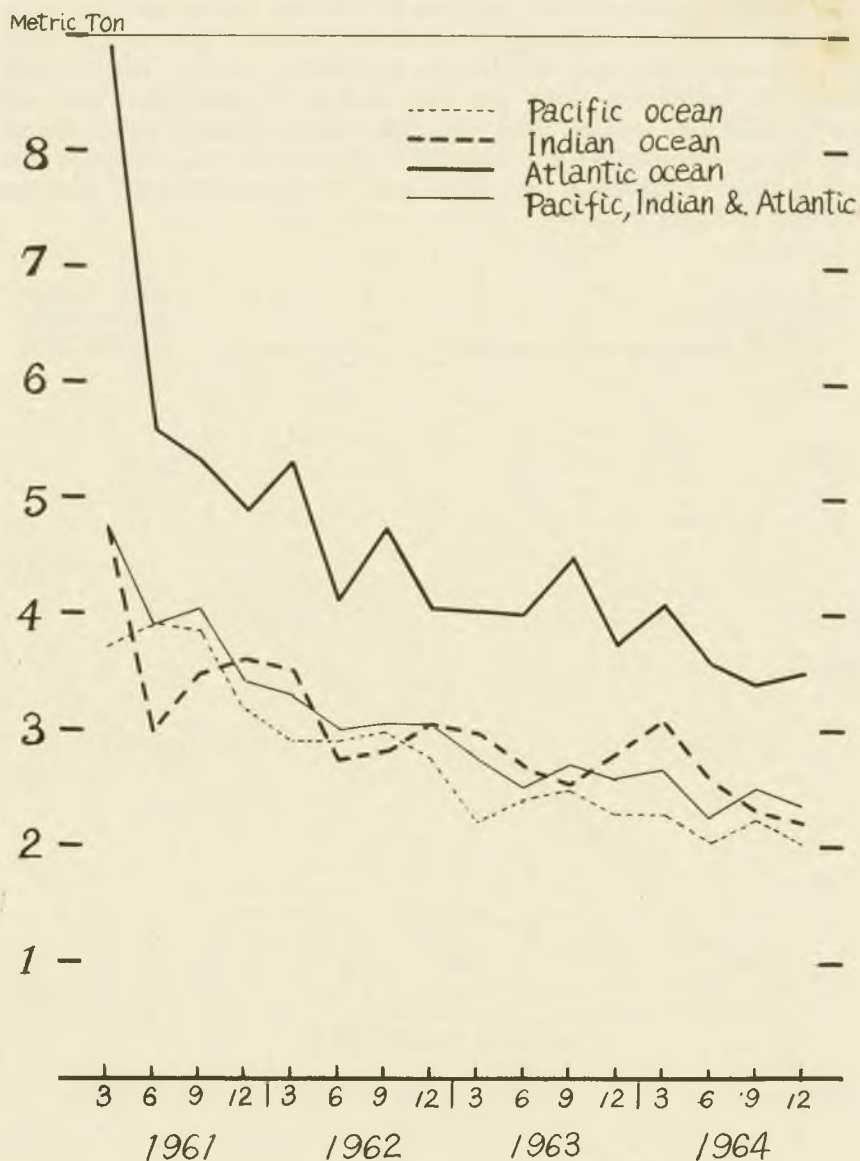


FIGURE 9.

Labor Problems.—The recent growth of the Japanese economy has caused a considerable rise in wages and tightening of labor supply (Fig. 10). This tendency was particularly apparent in such primary industries as agriculture and fisheries, and the number of people engaged in fisheries is decreasing. In order to secure the necessary number of crews and fishermen, the industry has been obliged to increase labor payments to the maximum which fishery management allows. The cost for maintaining skilled fishermen and for providing them with satisfactory living facilities has continued to increase with the result that labor cost now accounts for 35 or 40 per cent of the total sale of the catch.

Market and Price.—So far, a higher price due to an expanded overseas market and increasing demand in domestic market has compensated for

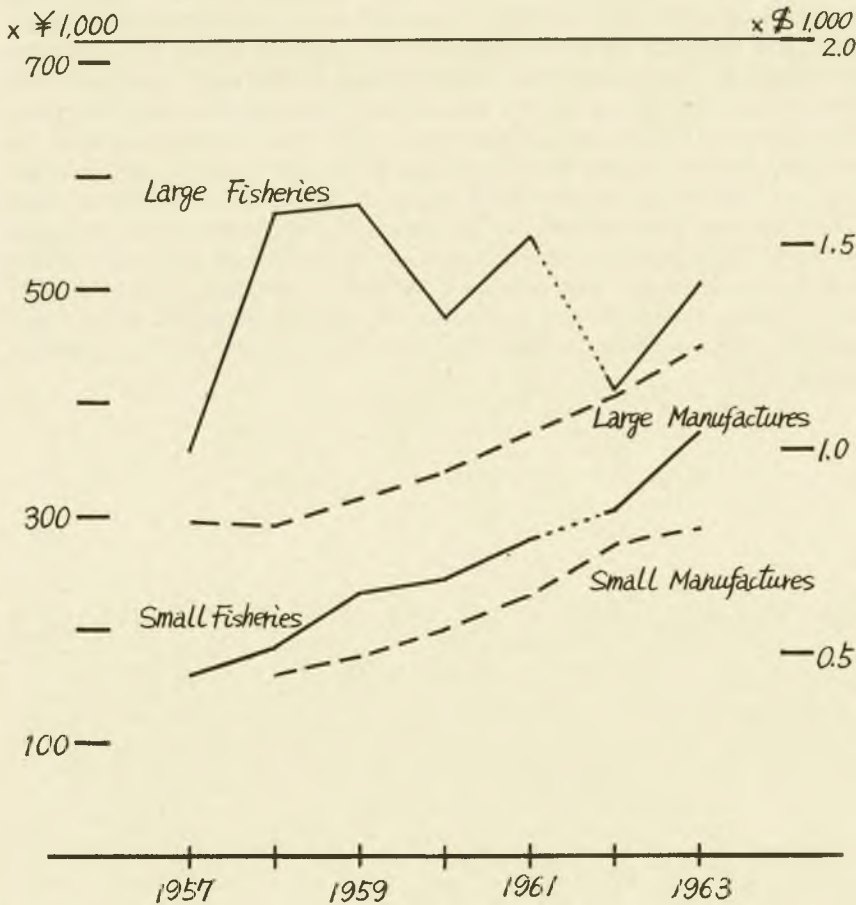


FIGURE 10.

higher production cost and lower productivity. In recent years, however, stagnation or decline in the price of tuna has been shown, although it cannot be ascertained whether this tendency is temporary or not. There are differences in marketing the species. Albacore are mainly exported to the United States and domestic consumption is rather negligible. As the catch of yellowfin continues to decline, more fishing efforts are directed to albacore fishing, thus causing the weakening of the price of albacore.

FUTURE PROSPECT OF THESE PROBLEMS

It is keenly felt that research on tunas should be expanded and especially be carried out on an international basis because of its extending to broader areas. Among the Japanese tuna industry there is an opinion that the number of tuna boats should be reduced provisionally before the completion of such research. This will serve to decrease the fishing effort and maintain the stable price because research on the tuna resource is thought to need more time. Labor-saving devices and techniques are required to avoid a rise in cost due to labor shortage and wage increase. Although great efforts are now exerted to solve this technical problem, for so called less-man-power technique both by the Government and industry, they are still in the experimental stage. It will take a few more years before any concrete methods can be obtained. For improvements of price problems, maintenance and expansion of domestic and overseas markets is required. However, not only is it difficult to develop a home market for albacore, but there are a number of difficult problems in overseas markets such as trade barriers and other restrictions such as different eating habits.

FISHERY DEVELOPMENT ON THE WEST COAST OF AFRICA

H. KASAHARA

*United Nations Special Fund, New York*¹

ABSTRACT

Abundant fishery resources are found in West African waters, particularly in areas of upwelling. With the exception of some of the tuna stocks and a few demersal species, resources are still largely under-exploited. Production will continue to increase rapidly as fishing becomes more intensive and new stocks come under commercial exploitation.

The development of fisheries is reviewed for the region from Senegal to Nigeria. Due to strong local demand, most of the countries have been successful in expanding their fishing and related activities. The actual pattern of development differs from country to country, particularly with regard to the degree and form of foreign participation and government assistance. Full advantage is taken of the capacity and effectiveness of the traditional marketing system.

The phenomenal expansion of foreign fishing activities in West Africa has in general had favorable effects on local development.

INTRODUCTION

It is a difficult task to review the status and prospects of fishery development in West Africa. There are some 20 different countries, including sovereign and non-sovereign, along the coastline stretching from about 36°N to 34°S. Extensive canoe fishing co-exists with highly industrialized fisheries, and traditional marketing systems with modern methods of fish handling. Large numbers of vessels from such foreign countries as Russia, Japan, Poland, Spain, France, Portugal, Italy, Greece, Israel, etc., are not only fishing in African waters but also landing large portions of their catches to be sold locally or for trans-shipment to the United States, Europe, and Japan. Statistics are very incomplete in many of the countries concerned. Furthermore, the situation changes so rapidly that what we know at the moment may become out of date within several months.

RESOURCES

Among the various known processes by which the lighted surface layers are replenished with nutrients, vertical mixing by cooling of the surface waters is most important practically in all areas of higher latitudes. The waters off the west coast of Africa, however, are almost entirely outside the regions in which this mechanism plays an overridingly important role in the productive cycle of the ocean.

In the tropics and subtropics, the most important process of enriching

¹The views expressed in this paper are those of the author and do not necessarily reflect the views of the United Nations.

the surface waters is upwelling caused directly or indirectly by winds. The areas of strong upwelling are normally restricted to narrow coastal bands, but their productivity can be enormous. For example, from a small area of permanent upwelling off Peru, roughly 50 nautical miles (92 km) wide and 800 miles (1470 km) long, a total of 8.8 million tons of one species of fish (*Engraulis ringens*) was landed in 1964. This amount exceeds the total landings of Japanese fisheries from the world ocean, which include catches of hundreds of different species. The effects of upwelling in waters off southern and Baja California, as well as seasonal upwelling in limited areas of Central America, are well known. The situation on the west coast of Africa will later be described in some detail.

It is also believed that the Gulf of Aden and adjacent areas constitute one of the rich potential fishing grounds due to a strong upwelling, which appears to be seasonal except in a small area off northern Somalia and Socotra. The Indian coast of the Arabian Sea is also characterized by seasonal upwelling. There is a very limited but apparently productive area of seasonal upwelling in eastern Venezuela, with its centre in the vicinity of Margarita Island and the Gulf of Cariaco. In the Gulf, which is about 56 km long with a maximum width of 14 km narrowing to 3 km at the entrance, some 30 thousand metric tons of *Sardinella* are caught by beach-seines during an upwelling season of approximately 6 months. I also believe that localized upwelling is a major factor contributing to the fairly high production of *Sardinella* in Philippine waters. There are a number of other examples, all of which indicate the overriding importance of this ocean phenomenon to fish production in tropical waters.

There are two zones of permanent upwelling in the coastal waters of West Africa: one ranging from southern Morocco to northern Senegal and the other southward from Angola. Water enriched within these zones is carried, by the prevailing currents, to the south and north, respectively, as well as offshore. The influence of such water from the northern zone is noticeable, at least seasonally, as far south as Sierra Leone. In addition, marked seasonal upwelling, presumably related to the Equatorial Counter Current, is observed in waters off Ivory Coast and Ghana. Waters in the northern and southern upwelling zones are very abundant in both demersal and pelagic species. Fairly large quantities of various pelagic species are also present in the central upwelling zone. Due to the under-exploited status of many of the important species and the lack of reliable statistics, it is not possible, however, to make even a rough estimation of the magnitude of potential resources exploitable in waters off the west coast of Africa. The following short summary is admittedly incomplete and perhaps somewhat erroneous.

Pilchards (Sardina/Sardinops).—Approximately 130 thousand metric tons of pilchard are landed in Morocco, mainly for fish meal and canned sardines, but the production is controlled by economic rather than natural

factors. The magnitude of pilchard stocks in waters off Spanish Sahara is unknown.² In the southern region, pilchard is abundant in waters off the coast from Angola to South Africa. The present annual catch in Angola is in the order of only 100 thousand metric tons, but the rate of exploitation must be very low. The pilchard industry of South West Africa and South Africa, which produces a little less than 1 million metric tons a year for fish meal manufacturing and canning, has been under strict regulations, including a quota system, which are basically for the purpose of maintaining the high profitability of the industry. Thus, the potential production of pilchards from West African waters cannot be estimated until more intensive exploitation takes place in all major areas of concentration. I believe this will come fairly soon in view of the rapidly increasing demand for fish meal.

Anchovies (Engraulis).—Until recently, anchovies in West African waters were almost untouched. Since fishing for anchovies (for fish meal) in South West and South Africa, which began only in 1963, has been expanding rapidly, we may have some indication of the magnitude of anchovy stocks in this region in the near future. Little is known about their abundance in the northern region.

Tropical Sardines (Sardinella).—The biological distribution of *Sardinella* extends from southern Morocco to South West Africa. They are apparently the most abundant pelagic fish in the coastal waters along the Gulf of Guinea. They do not occur in high concentrations, however, in waters between the western border of Nigeria and Cape Lopez. Among the two known species of *Sardinella*, *S. aurita* predominates along the coast from Senegal to Ghana, although *S. eba* (syn., *cameronensis*) is almost equally important in the Ivory Coast. Their occurrence in the uppermost layer normally coincides with the period of strong upwelling, particularly in the central upwelling zone off the Ivory Coast and Ghana. Their presence, however, in deeper layers during the period of hydrographic stability has been demonstrated by the results of experimental fishing with lights as well as trawl fishing (Russian trawling expeditions and the Guinean Trawling Survey). The present commercial catch of *Sardinella* on the west coast is roughly in the order of 100 thousand metric tons a year, but this amount appears to be only a fraction of the potential production which could be made from these resources.

Other Coastal Pelagic Species (Trachurus, Decapterus, Caranx, Scomber, Ethmalosa, etc.).—Large stocks of rough scad (*Trachurus*) seem to occur in wide areas along the coast of West Africa. It is a dominant species in the catches of large foreign trawlers operating in the northwest African grounds (ranging roughly from 30°N to 10°N and centered in waters off

²There is a sizeable fish meal industry in the Canary Islands, but I have no information on the species involved.

Mauritania). The results of the Guinean Trawling Survey also seem to indicate the presence of concentrations of *Trachurus* (and *Decapterus*) in some shelf areas of the Gulf of Guinea. No pelagic fishing has been developed for this species along the west coast except in Angola and South Africa. Bonga (*Ethmalosa*) is extremely important for inshore and estuarine fishing by local canoes, particularly along the coast from Senegal to Nigeria. Bonga feeds mainly on phytoplankton in waters more or less under the influence of freshwater. Little is known about the abundance and potential production of other coastal pelagic species, some of which apparently occur in good quantities.

Tunas (Thunnus spp., Euthynnus pelamis, etc.).—Practically all tuna species of commercial importance are present in waters off West Africa. In discussing the tuna situation, we cannot consider waters off West Africa separately from the rest of the middle and south Atlantic, since the distribution of many species is continuous from the African coast to the American coast. Furthermore, the Japanese longliners operating from African ports visit all areas of the middle and south Atlantic where good quantities of tuna can be found. From a practical point of view, however, tuna stocks presently under exploitation can be considered under two main categories: deep-swimming, relatively old yellowfin, albacore, and bigeye tunas, as well as some bluefin tuna, which are found in wide offshore areas; skipjack and surface-swimming, young yellowfin tuna, which are present in waters relatively close to the shore, sometimes in large concentrations. The former stocks are fished almost exclusively by longliners, while the latter are caught mainly by live-bait fishing and partly by a combination of live-bait and purse-seine. There is also a small bluefin tuna fishery by traps in Morocco, but its production is insignificant. The exploitation of yellowfin and albacore, particularly the former, by Japanese longliners in the Atlantic is apparently very intensive, and a further expansion seems unfeasible due to natural as well as economic limitations.³ There is also a small Japanese-type longline fishery in South Africa. The exploitation of tunas under the second category, which has also expanded rapidly in the past decade, is likely to grow further.

Demersal Species.—Unlike the west coast of South America, there does not seem to be serious oxygen deficiency in the waters in any part of the shelf and slope area along the coast of West Africa. The greatest concentrations of demersal species apparently occur in the northern and southern permanent upwelling zones and in areas under the strong influence of water therefrom. The shelf area of the central upwelling zone is also inhabited by considerable quantities of demersal fishes. The shelf areas off

³A fleet of some 130 Japanese longliners (not including the number of deck-loaded catchers used) produced roughly 110 thousand metric tons of tuna and tuna-like fishes from Atlantic waters during 1963, of which more than one-half was landed at African ports for trans-shipment and the remainder landed in various countries of South America and Europe.

the coast from the western border of Nigeria to Cape Lopez, and, to a lesser extent, off southern Liberia and the western Ivory Coast appear to be characterized by lack of large stocks of demersal fishes. The Japanese catches from the northern trawl grounds are dominated by cuttlefish (particularly *Sepia filliouxii*), octopus, and fishes of the families Sparidae, Sciaenidae, and Carangidae (*Trachurus*), but this does not reflect the true composition of the stocks since fishing by large Japanese trawlers is highly selective for porgies, cuttlefish, and octopus. The results of the Guinean Trawling Survey will reveal the details of the composition of demersal species in waters off the coast of the Gulf of Guinea (from Senegal to the Congo River mouth). Data on the trawl grounds off Angola and South West Africa are scanty, although the Japanese catches indicate the presence of good stocks of porgies in these areas. Hake is predominant in the catches from the trawl grounds off South Africa. There is no way of estimating the total production of demersal species from West Africa, since the greatest portions of catches are made by foreign vessels of many different nationalities. I would guess that it is in the neighbourhood of 700 thousand metric tons, but I might be grossly wrong.⁴ I believe, however, that the stocks on the major trawl grounds are still far from a state of maximum utilization, with the possible exception of some species of Sparidae. More intensive fishing on the present trawl grounds and the exploitation of deeper waters (some trawlers are already fishing to a depth of 600 m) will result in a much greater total production.

Shrimp.—Commercial quantities of penaeid shrimp, particularly *Penaeus duorarum*, occur in waters off Nigeria, and a shrimp fishery is developing there rapidly. Although apparently there are other shrimp grounds in scattered areas, the potential production of penaeid shrimp in tropical waters of West Africa seems to be rather limited. The results of the Guinean Trawling Survey will shed more light on this question.

In short, with the exception of some of the tuna stocks and possibly a few demersal species, the fishery resources along the west coast of Africa are generally under-exploited or not exploited at all. Production will continue to increase rapidly as fishing becomes more intensive and new resources come under commercial exploitation.

DEVELOPMENT OF FISHERIES

In reviewing the status and prospects of fishery development in West Africa, I would like to limit my discussion more or less to the coast from Senegal to Nigeria. I have no first-hand information on the situation in the countries north and south of this region. It is also difficult to discuss, in this short paper, the fishing industries of all West African countries. The development of fisheries in South and South West Africa, for example,

⁴In 1964 a total of 49 Japanese trawlers, mainly large stern trawlers, operated in West African waters; their combined catch might have been as high as 150,000 metric tons.

is a unique topic, which should be dealt with by someone who has experience in that region. There is another reason for my taking up the situation along this particular stretch of coast.

The following table (Table 1) indicates, in a general way, the population distribution along the west coast of Africa. Morocco and South Africa are listed separately since they have coastal areas on the Mediterranean and the Indian Ocean sides, respectively.

Not considering Morocco and South Africa, it is noted that population concentrations occur mainly along the coast from Senegal to Cameroon, with a great centre in Nigeria. This region of high population densities generally falls in the western part of the Middle Africa belt, in which protein malnutrition caused by an insufficient intake of animal proteins is very common. The production of livestock in the belt is limited due to endemic animal diseases, the worst of which is the tsetse-fly-borne trypanosomiasis. Fish has long played an important role in supplying the populations of these West African nations with animal proteins. In addition to fishing by coastal canoe fishermen, particularly those from Ghana and Senegal, there are two inland areas which have been major sources of fish supply, the upper Niger basin in Mali and the Lake Chad

TABLE 1
POPULATION ALONG WEST COAST OF AFRICA, 1963

Country	Estimated Population (millions)	Density per Square kilometres
Spanish Sahara	0.3	0
Mauritania	0.8	1
Senegal	3.4	17
Portuguese Guinea	0.5	15
Guinea	3.4	14
Sierra Leone	2.2	31
Liberia	1.0	9
Ivory Coast	3.7	12
Ghana	7.3	31
Togo	1.6	28
Dahomey	2.3	20
Nigeria	55.6	60
Cameroon	4.6	10
Rio Muni (Spanish)	0.2	7
Gabon	0.5	2
Congo Brazzaville	0.8	2
Angola	5.0	4
South West Africa	0.6	1
Morocco	12.7	28
South Africa	17.1	14

basin. Fish from these inland production centers as well as from the coast has been distributed mainly as smoked fish.

Demand for fish in this region as a whole, however, has never been satisfied and large amounts of fish products have been imported not only from the neighbouring African nations but also from Europe. In fact, Nigeria has been the world's greatest consumer of Norwegian stockfish. This is one of the most important factors contributing to the recent development of fisheries on the central west coast of Africa, the other factor being the effectiveness of the traditional marketing system. Rather than try to generalize the main features of fishery development in the region, however, I will first review the situation in some of the countries I have visited, namely, Nigeria, Ghana, the Ivory Coast, Sierra Leone, Guinea, and Senegal. In so doing, I shall touch upon some of the international fishing activities which have had great effects on the local situation.

Nigeria.—With an estimated population of 56 million (in an area of 924 thousand square kilometers), most of whom eat fish, the country is consuming unknown but apparently great amounts of fish products. Smoked fish from the Chad and Upper Niger (Mali) basins are carried into the country by water and road transportation. Large quantities of smoked fish from the traditional inshore fisheries of different West African countries are also consumed in Nigeria. As mentioned previously, Nigeria has been the greatest importer of Norwegian stockfish. Rapidly increasing landings by large foreign trawlers are being absorbed without creating any marketing problems. The country could consume much greater amounts of fresh and processed fish with little social and economic repercussions. From the foregoing review of the available resources, however, it is obvious that the marine fishery resources in waters off Nigeria are quite limited, except for the stocks of bonga found in inshore and estuary waters and some shrimp stocks.

The marine fishing industry of Nigeria consists of three sectors. First, an unknown but vast number of canoe fishermen are landing very substantial quantities of fish, mostly bonga, from lagoons and estuaries. Their production in the Western Region may be in the order of 20 thousand - 25 thousand metric tons a year. The catches are largely smoked for local consumption as well as for transport by vessels to outside areas. Second, there are a few small trawlers (mostly Spanish), which land (mainly in Lagos) an estimated annual total of 3,500 tons from coastal grounds. Most of them make only day trips; fish landed are immediately sold to woman fish-dealers (mammies) with great competition among them and practically no marketing overheads on the side of the Spanish operators. A shrimp fishery has been developed in waters off Nigeria (to a depth of 35-40 fathoms [65-74 m]) mainly by American shrimp trawlers; some of the Spanish trawlers and perhaps one Nigerian trawler are also shrimping now. The third and most rapidly expanding sector of the industry consists

of landings by large foreign trawlers, mainly Japanese, Russian, and Polish. These trawlers fish in the major trawling areas of northwest and southwest Africa. Their annual landings in Nigeria have increased from 500 tons in 1962 to 7000 tons in 1963 and 15 thousand in 1964, and will perhaps exceed 30 thousand tons in 1965.

There are two interesting features with regard to this phase of development: the participation of Nigerians and the capacity and effectiveness of the traditional marketing system. One of the two companies dealing with foreign trawl landings (under so-called "charter contracts" to avoid import duties) is a Nigerian firm. The company not only handles landings from foreign vessels but also owns two trawlers (500 GT each) purchased from a Japanese fishing company. These two vessels are manned mainly by Japanese fishermen provided by the Japanese firm and partly by Nigerians. The company plans to increase the proportion of Nigerian crew members gradually and hopes to run large trawlers with Nigerians alone within 15 years' time. The process is slow, but progressing without affecting the profitability of the scheme. As of early this year, the company was constructing one large trawler in Japan and planning to buy one from Russia; two shrimp trawlers were also on order from Japan. Some of these vessels might have been delivered by now.

Another feature of this trawl fishery is the way in which fish are marketed. Fish are landed in the form of frozen fish packed in boxes of 30 kg (Russian catches) or 20 kg (Japanese catches) each. They are shipped unrefrigerated, for up to 8-10 hours, to be sold as fresh fish on retail markets. They are in acceptable condition when sold and the leftovers are smoked by the mammies to be carried farther into the interior. The economic efficiency of this system is surprisingly high. Fish landed in Lagos are sold on the retail market of Ibadan with a markup of only 100 per cent (relative to the ex-vessel price). I do not think any modern system of fish marketing could beat this. Because of an undetermined but obviously enormous capacity of the country to absorb fish and fish products and of the economic efficiency of the traditional marketing system, the operations of the two companies dealing with trawl landings are very profitable and are expanding rapidly. Overhead costs are exceedingly low. Fish move so fast that cold storage requirements are also relatively small. The present total capacity of cold storage facilities for fish, including a brand new plant in Sapele, the Mid-West Region, is perhaps in the neighbourhood of 6,000 tons.

In view of the fact that there have been little social and economic repercussions from rapidly increasing trawl landings, except for some adverse effects on the stockfish markets, the Nigerian markets for fresh and smoked fish are still far from a state of saturation. So far there has been practically no government intervention at any stage of fishery development in this country. As long as the present liberal policies concerning foreign

participation are maintained, the industrial fisheries of Nigeria do not need much assistance from the government, although the construction of a well designed fishing harbour in Lagos would be of great help. Participation by the Nigerians in the long-distance trawl operations will undoubtedly become more and more active, but it would be unwise at this stage to try to speed up the process of nationalization by changing the present pattern of international business arrangements which seem to be working quite well.

Ghana.—Although her population is much smaller than Nigeria's, Ghana is another important fish-consuming country in Africa. Due to the presence of seasonal upwelling, fishery resources are somewhat more abundant along the Ghanaian coast. The pattern of fishery development in Ghana is also different from Nigeria in that intervention by the government has had impact on many aspects of development.

In 1964, approximately 10 thousand canoes, of which over 3,000 are motorized, landed a total of 43 thousand tons of fish, 60 per cent of which was *Sardinella*. This type of fishing seems to be approaching its limit of expansion. With the financial assistance of the Government, however, fishing operations by small motor vessels, including a fleet of little trawlers (only 9 m in length) operating from Takoradi as well as trawlers and seiners (up to 18 m in length) based in Tema, have developed successfully and, in 1964, landed roughly 20 thousand tons. Taking advantage of strong domestic demand for fish, the marketing of frozen fish landed by foreign trawlers (mainly Russian, Japanese, and Polish vessels under so-called "contract") was started by the private sector and expanded rapidly. The government, however, has established a state corporation to take over the marketing of foreign vessel landings through a large cold storage plant in Tema and a newly established chain of small cold stores throughout the southern part of the country. There are still private companies actively engaged in fishing operations of various types, but they can no longer hold licenses for contracting foreign vessels. Furthermore, the government has decided to directly undertake long-distance trawling operations through the same corporation.

As of June 1965, the state corporation was operating ten large trawlers, ranging from 900 to 1850 GT, imported from the USSR, Norway and Japan. The main officers of these vessels are foreigners, with Ghanaian fishermen working on deck. Twenty-five to 33 Ghanians are aboard each vessel, together with 14 to 25 foreigners. A number of Ghanaian fishing technicians are being trained abroad, and a Ghana-Norway training scheme will start soon. The corporation plans to expand its fishing activities by importing a number of additional vessels. The import contracts already signed (delivery by 1967) include 23 large trawlers, 2 carriers and 12 small (75 ft [23 m]) combination boats (trawl/purse-seine). Both the foreign vessels and the corporation trawlers are fishing on the main trawl-

ing grounds of northwest and southwest Africa, and not in waters adjacent to Ghana.

In spite of initial mistakes and some shortcomings still to be overcome with regard to the operations of the state corporation, the general trend of development is encouraging. During the period 1961-64, the marine landings of the Ghanaian fisheries increased from 30 thousand to 67 thousand tons, with a substantial decrease in the importation of fish products. The total landings in Ghana, including those by foreign vessels, increased from 45 thousand (rough estimate) to 92 thousand tons during the same period. Both the coastal fisheries and the long distance trawl fishery will continue to expand until the total landings will have increased to satisfy the domestic demand. Financial difficulties presently faced by the country might temporarily slow down the expansion of fishing operations by the government but will not greatly affect the development of the other sectors of the industry. The production of the corporation vessels is still a relatively small portion of the total landings.

Although there is a chain of small cold stores, a vast number of woman fish-dealers are still playing an overridingly important role in fish marketing. Even frozen fish landed by large trawlers are directly sold to the mummies at Tema or other points of the cold storage chain. They naturally maintain full control of fish landed by canoes. Since the whole system is working satisfactorily, there is no need for introducing radical changes. Smoking is the most common method of processing, although two modern fish-processing plants are under construction in Tema. An American company trans-ships roughly 5 thousand - 6 thousand tons of frozen tuna landed mostly by Japanese boats. Attempts to establish a Ghanaian tuna fishery have not been successful.

Ivory Coast.—The country has a population of 3.7 million in an area of 322 thousand square kilometres. This is another progressive fishing nation. Industrial fisheries of various types, based in Abidjan and operated by both foreigners and Africans, are in the process of rapid expansion. Most of these ventures apparently involve substantial foreign investment, particularly French, but I have no detailed information on the capital structure of the fishing industry. The total annual landings in Abidjan by the Ivory Coast fleet, which was only 5 thousand tons in 1955, reached 38 thousand tons in 1964. The present fleet consists of 31 trawlers (12-42 metres in length), 35 sardine (*Sardinella*) fishing boats (15-32 metres) and 4 tuna boats. In addition, a number of foreign tuna vessels (French, Spanish, and Japanese) regularly use Abidjan for the trans-shipment of their catches. The artesanal fisheries land roughly 15 thousand tons a year from inshore and lagoon waters, making the total landings in the Ivory Coast approximately 53 thousand tons a year (not including foreign tuna landings for trans-shipment). Some of the trawlers and purse seiners based in Abidjan regularly fish in waters off the coasts of other African countries.

Except for the trans-shipment of frozen tuna, most of the landings are consumed domestically and demand still exceeds supply. The traditional system of marketing and processing seems to work well in this country also. The government, however, has been making efforts to provide sufficient infrastructure for the development of fisheries. An excellent new fishing port in Abidjan, with supporting facilities, is now half complete. The government is also building a fish smoking centre in the Abidjan area to provide the mammals with modernized smoking ovens and other facilities. One can see in this country a happy combination of private initiatives and government assistance in the field of fishery development, which does not happen very often.

With respect to the resources, fishing for local consumption depends greatly on *Sardinella* and other pelagic species. Out of the total landings of 38 thousand tons by the local industrial fisheries in 1964, 26 thousand tons consisted of pelagic species, mostly *Sardinella*. Both *S. aurita* and *S. eba* are important in Ivory Coast waters. To overcome the seasonality of pelagic fishing associated with a seasonal nature of local upwelling, some of the larger seiners are going as far north as Senegal for *Sardinella* fishing. Both in Ghana and Ivory Coast, surveys and research are needed to extend fishing seasons for coastal pelagic fishes.

Sierra Leone.—With a population of 2.2 million persons inhabiting a small area of 72 thousand square kilometres, Sierra Leone is also an important fish-consuming country. Landings by a large number of canoe fishermen from estuaries and inshore areas still constitute the main source of fish supply; their total catch might be 15 thousand - 20 thousand metric tons a year. Bonga makes up an overwhelming majority and is marketed as smoked fish. A fleet of small trawlers, mostly owned by Spaniards, catches approximately 3,000 tons a year. An American tuna company in Freetown collects 5,000 to 8,000 tons of tuna, mainly from Japanese and Spanish boats, for trans-shipment to the United States and Europe. Increasing amounts of fish are landed in Freetown by foreign trawlers and carriers for local consumption, their total landings reaching some 5,000 tons in 1964. Demand for fish is increasing steadily and the fish distribution system is improving.

It is difficult to forecast the future development of fisheries in Sierra Leone. Considering the apparent abundance of pelagic fish resources in coastal waters (*Sardinella*, bonga, carangids, mackerels, etc.), the long-term development of the industry seems to depend on the better utilization of these stocks. On the other hand, the business people might find it more profitable, for the time being, to buy frozen fish from foreign trawlers and, as in the case of Nigeria, to even own a few vessels for long distance trawling operations.

Guinea.—Large quantities of *Sardinella* and other pelagic fishes are present

in waters off Guinea, as well as considerable stocks of demersal species (the continental shelf broadens off Guinea). There is a good demand for fish in the country, which has a population of 3.4 million. Fish production in Guinea, however, has declined to a lowest level, as a result of a sudden withdrawal of the French administrators and business interest and also because most of the Senegalese canoe fishermen have left the country. The government has tried to rebuild the industry by importing a few trawlers and establishing a state corporation for fish marketing; the result has been a failure. What will happen in the future seems to depend on so many political and economic factors that no prediction is possible at this stage.

Senegal.—The country has a population of 3.4 million in an area of 200 thousand square kilometres. Conditions very favourable for fishery development exist. Its coast, between 16°N and 12° 30'N, is under the strong influence of northwest African upwelling waters and is quite abundant in both demersal and pelagic species. The coastal climate is more suitable for fish-handling than in the other countries along the coast of the Gulf of Guinea. Fishing being a traditional occupation, there is a good supply of industrious and progressive local fishermen. Domestic markets are considerable, and there are also good markets in other West African countries and in Europe for many of the species found in Senegalese waters. The total marine landings, which were only 29 thousand tons in 1953, exceeded 100 thousand tons in 1963 (not including tuna landings for trans-shipment). Of this amount, roughly 80 per cent were landed by local canoes, most of which were motorized. These canoes are quite efficient for line-fishing (mainly for catching sparids). Large quantities of tuna (small yellowfin and skipjack) are caught by French vessels operating from Dakar. Although the bulk of the catch is trans-shipped to France and the United States as frozen tuna, some 11 thousand tons are packed annually. French seiners and trawlers also operate from Dakar, along with a few Senegalese line-fishing vessels. Shore facilities in Dakar are excellent.

The government seems to be anxious to build up industrial fisheries operated by the Senegalese. With financial support from the government, 11 line-fishing vessels (13 m in length, built in Senegal) have been put in operation successfully. The first purse-seiner (16 m in length) is now under construction as part of a government programme to develop a Senegalese purse-seine fishery as well as a small boat-building industry. The government also plans to establish a Senegalese tuna fishing and processing industry with foreign assistance.

Available information indicates the presence of large concentrations of *Sardinella* and other coastal pelagic species, but the present combined catch of *Sardinella* and bonga is only 36 thousand tons, which would perhaps be a fraction of what might be caught under full exploitation. In addition to consumption as food, *Sardinella* is used extensively as livebait for tuna

fishing. Even some of the Japanese tuna long-liners are using it as bait.

Since the potential fishery production in Senegal appears to be much greater than the potential domestic demand for fish, the long term development of the Senegalese fisheries will depend, to a considerable degree, on the expansion of the export of fish and fishery products to the neighbouring African countries as well as to Europe.

In summary, taking the region (Senegal to Nigeria) as a whole, the demand-supply relationship is very favourable for a rapid development of fisheries, and a number of countries are taking advantage of the situation. Through more intensive exploitation of coastal pelagic fish resources available in the region and the continuous expansion of long distance operations to fish in waters outside the region, a high rate of growth will be maintained for years to come. The actual pattern of development differs from country to country, particularly with regard to the degree and form of participation by foreign enterprises and assistance given by the government. Under such generally favourable conditions as existing in West Africa, some of the different approaches may equally be successful. Full advantage is taken of the enormous capacity and effectiveness of the traditional marketing system.

FOREIGN ACTIVITIES AND THEIR EFFECTS

It is only in the late 1950's that the USSR began exploratory fishing in West African waters. Japanese trawlers had not been seen in this part of the world until 1959. Expansion of trawl fishing activities by foreign vessels in West Africa has been truly phenomenal during the past six years. At least 400⁵ foreign trawlers of various nationalities, including a number of stern trawlers of over 2,500 GT, now operate in waters off the coasts of northwest and southwest Africa. Considerable numbers of small local trawlers owned by foreigners also fish in coastal areas close to their bases, although their total production is relatively small. The development of tuna fishing by foreign vessels has also been impressive. In addition to a fleet of Japanese longliners fishing in the offshore areas of the Atlantic, large numbers of French and Spanish livebait tuna fishing boats, along with a few seiners, operate in waters relatively close to the shore. Tuna transshipping facilities (and some canneries) have been established at Las Palmas, Cape Verde Islands, Dakar, Freetown, Monrovia, Abidjan, Accra (Tema), Pointe Noire, etc.

Most of these foreign operations are of a very complex nature. For example, different portions of Japanese trawl catches are either delivered directly or shipped, via Las Palmas, by carriers to various countries of West Africa and Europe as well as to Japan. Sparids caught by Japanese vessels find good markets in Greece, while considerable quantities of

⁵This number includes Spanish trawlers operating from the Canary Islands.

cuttlefish caught by Greek vessels are shipped to Japan via Las Palmas. Tuna catches by a group of longliners belonging to a Japanese co-operative are landed at Cape Verde Islands (Portuguese) under the management of a Japanese trade company, kept in a Portuguese cold storage plant, and shipped to Puerto Rico by boats of various nationalities to be packed in an American cannery. There are many other examples of similarly complicated arrangements. A complete review of all these foreign activities is clearly beyond the scope of the present paper. Only a brief appraisal of the role played by the foreign fisheries in the fishery development of the region is made here.

Generally speaking, fishing and related activities by foreign enterprises have had more favorable than adverse effects on the economic development of West African countries. Large landings of frozen fish by foreign trawlers at relatively low prices have directly contributed to the amelioration of the chronic shortage of animal protein food in the areas of high population concentrations along the coast of the Gulf of Guinea. New landing and storage facilities have been established at main points of delivery, as well as a chain of small cold stores in Ghana, to handle large amounts of frozen fish. Frozen fish, or rather thawed fish, has become acceptable to consumers. Perhaps the most important aspect is that these foreign activities have stimulated the interest of the peoples of the countries concerned in developing their own fisheries and have also given them opportunities to come into contact with the technical and managerial phases of industrial fisheries. The Africans, on the one hand, now realize that these fishing ventures are not as easy as they look. They are convinced, on the other hand, that by taking proper steps they will be in a position to carry out modern fishing and processing operations within a reasonably short period of time.

With one or two exceptions, none of the governments concerned have made a serious attempt to shut out foreign vessels. The rapid expansion of foreign activities has inevitably caused some resentment among the Africans, but in most of the countries concerned it has not developed into any political action or campaign against such activities. It is generally recognized that the only long term solution is the development of their own fisheries on a competitive basis and that for the time being they should take advantage of the favorable effects of foreign activities rather than try to force out the foreigners. Also, it will soon become obvious that most of the countries along the coast of the Gulf of Guinea would gain nothing by extending their territorial limit, since the long-term development of their own offshore fisheries will depend, to a large degree, on fishing in waters far from their coasts, particularly in areas off northwest and southwest Africa.

TRENDS IN WORLD HIGH SEAS FISHERIES AND POTENTIAL EXPLOITATION OF LIVING RESOURCES OF THE SEA¹

MARIO RUIVO AND ADAM BEN-TUVIA
FAO Marine Biology and Environment Branch, Rome

ABSTRACT

A world catch of 60 million tons is predicted by 1970 and 70 million tons by 1975 on the basis of trends in the period 1948-64. Main characteristics of the fisheries in the tropics and subtropics are compared with those of temperate and cold zones. Some economic and technical developments in high sea fisheries, as well as problems of international cooperation, management and research, are discussed.

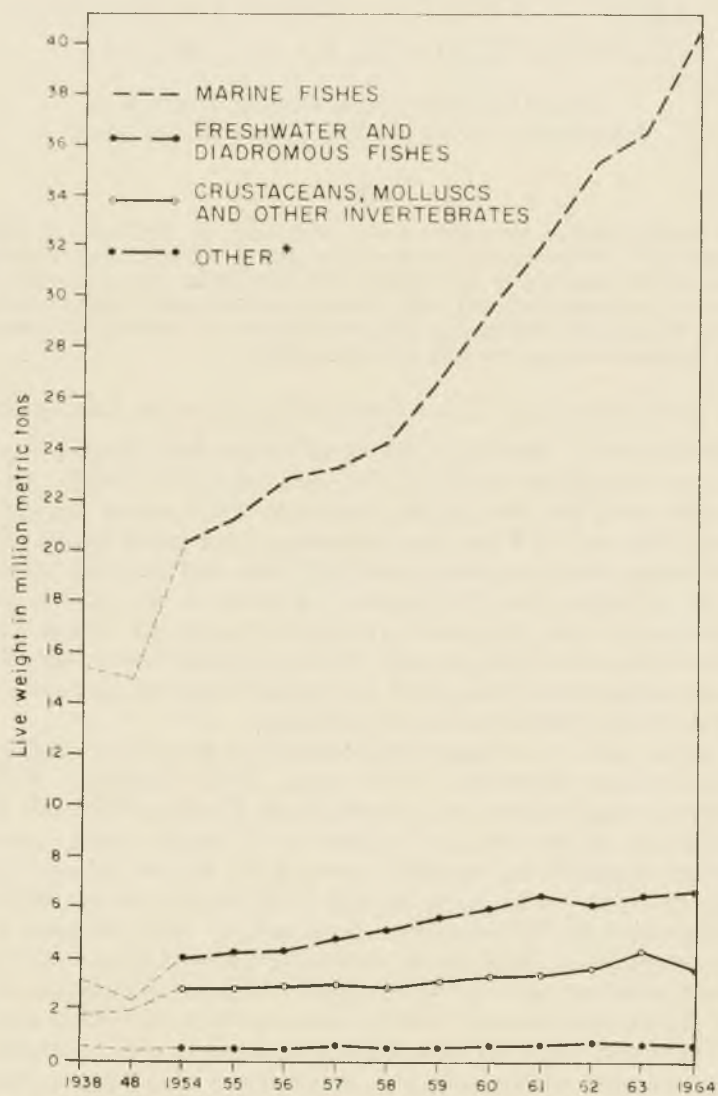
CATCH, POTENTIAL CATCH, AND DISTRIBUTION OF RESOURCES

Over the period 1948-1964, the world fishery catch increased continuously from 19.5 million tons to 51.6 million tons (FAO, 1965). According to the data for 1964, most of the catch came from marine sources (87.2 per cent), the rest (12.8 per cent) originating from inland waters (Fig. 1). On the average each year, the annual catch increased by about 6.5 per cent over the preceding year. Particularly impressive is the rise in catch of clupeoid fishes which has almost quadrupled during this period. Fisheries for other species also show increases although at much lower rates (Fig. 2). The constant growth of the catch and fishing industries gives rise to the question whether this trend can be sustained.

In recent years, there have been renewed attempts at evaluating living aquatic resources (Kesteven, 1962; Lucas, 1964; Chapman, 1965) and at predicting world catches on a scientific basis. Graham & Edwards (1962) concluded that no more than 60 million tons of marine fishes of the kinds at present exploited are available annually for harvest. Meseck (1962) thought the total catch (including that from inland waters) might reach 55 million tons by 1970 and 70 million tons by 1980. Schaefer (1964) was more optimistic. Based on our knowledge (incomplete as it is) of under-exploited resources and on the dynamics of marine ecosystems, he concluded that the annual catch could be raised to 70 or 80 million tons in the fairly near future. How do these predictions relate to what is actually happening, and what are the long-term consequences of ceilings of this order of magnitude?

Most countries are now interested in developing their fisheries, and many are investing considerable sums in building new fishing vessels to complement their existing fleet or to replace the old and less efficient vessels by

¹This paper is an edited version of one read at the International Conference on Tropical Oceanography (Miami, 1965). It reflects the authors' views and not necessarily those of FAO.



* "Seals and miscellaneous aquatic mammals"
 "Miscellaneous aquatic animals and residues"
 "Aquatic plants"

FIGURE 1. Aquatic animals and plants. World catch by divisions (FAO, 1965).

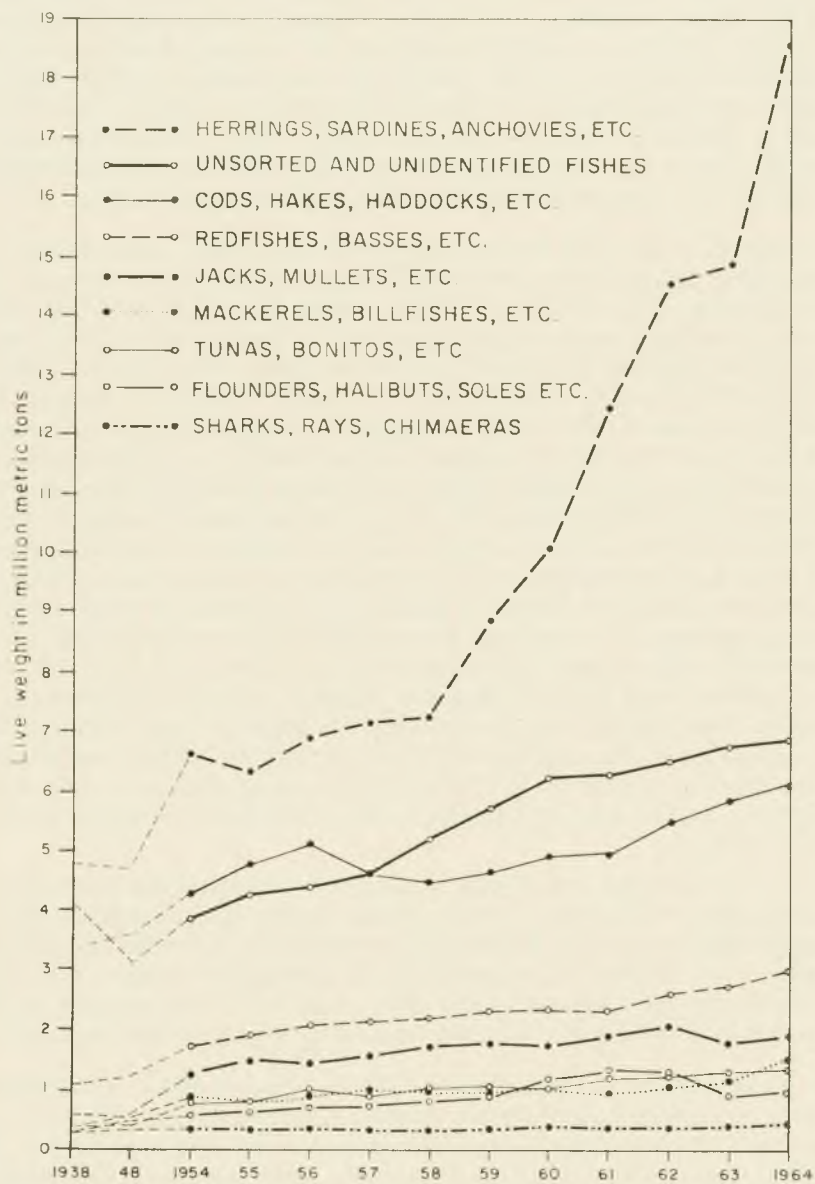


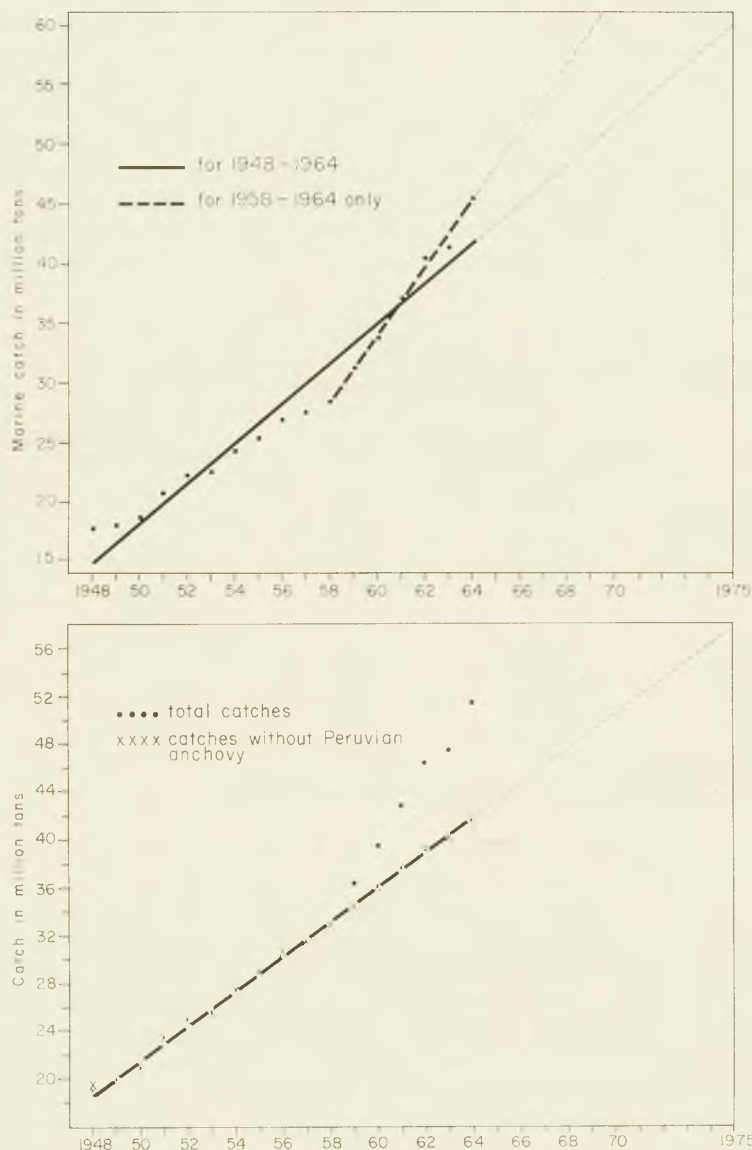
FIGURE 2. Marine fishes. Catch by groups of species (FAO, 1965).

new and more powerful ones. The present economic situation in the socialist (and some of the developing) countries encourages investments in the fishing industry. The United Nations Development Programme (UNDP) and other forms of international or bilateral aid help in creating favourable conditions for this. Interested governments in effect subsidise fishing enterprises not only by direct investments but also by developing a widely applicable fisheries research program. Keen competition among the fleets spurs the search for under-exploited resources and the development of more efficient fishing techniques and processing methods.

Increasing Catches and the Peruvian Fisheries.—There is no evidence of impending change in the policies of fishing countries that will limit the development of world fisheries in the coming years. The post-war trend shows continuous increase in catches (Fig. 3). Extrapolation of the linear regression based on the data for the period 1948-1964 predicts a marine catch of over 50 million tons in 1970. The yearly increase in catch for the past seven years (1958-1964) was higher and the linear regression based on the data for this period predicts a marine catch of over 60 million tons. However, these recent high catches were mostly due to the unprecedented growth of the anchovy (*Engraulis ringens*) fishing industry along the coast of Peru and Chile. This is a unique case in the history of the development of world fisheries and there is no expectation that similar cases will occur in the future, since we have no evidence of the existence of other stocks of such magnitude. It seems that the Peruvian anchovy fishery has nearly reached its point of maximum sustainable yield (Boerema *et al.*, 1965) and the anchovy catch for the future will probably remain in the order of 9 million tons. Thus a more accurate estimate might be given by fitting the regression line to the data for 1948-1964 without the anchovy catch. After extrapolation, an addition of 9 million tons for the potential anchovy catch predicts a marine catch of 60 million tons by 1970 and 70 million tons by 1975 (Fig. 4).

We are using the linear regression only to obtain an indication of the possible future catch, but of course we are aware of the inadequacy of this method since so many variable factors (biological, economic and technological) are involved. It is inadvisable to extrapolate further than 1975 since in the more remote future there may be drastic changes in the conditions governing the economy and technology of fishing industries.

Increasing Catches in Other Areas.—Now let us cast a glance at predictions on an ocean-wide basis—say the Atlantic. Laevastu (1961) predicted, on the basis of comparative fishing and environmental data, a ceiling of 21 million tons, mainly from the Patagonian shelf and from the Atlantic Boreal. However, he under-estimated the yield from the coasts of West and South West Africa which has contributed considerably to recent increases in catches. The Atlantic catch in 1964 was already 18 million tons, and it



FIGURES 3 & 4. Trends in development of world fisheries. 3 (top), marine only; 4 (bottom), marine and inland. The regression line is fitted to values of annual catches (Peruvian anchovy excluded in Fig. 4).

seems that, with the growing interest in exploitation of the South American and West African coasts, it may soon exceed 21 million tons.

Of course, the different ocean areas vary greatly in their production. The North Atlantic yields a third of the world catch but its surface is only 13 per cent of the total. The North Pacific (23 per cent of total area) yields another third. The South Pacific produces 23 per cent from an area of 23 per cent, however, almost all this is the anchovy of Peru and northern Chile. Without the anchovy the total catch from that vast region is only 0.1 per cent of the world catch. The South Atlantic Ocean (10 per cent of the surface) yields 6 per cent of the world catch. The Indian Ocean lags with only 4 per cent of the total catch from 18 per cent of the total sea surface.

TABLE 1
DISTRIBUTION OF THE 1964 MARINE CATCHES IN RELATION TO THE
SURFACE OF THE OCEANS¹

Ocean	Sea surface Millions of sq. km.	%	Marine catch Millions of tons	%
Arctic	14,090	3.9	— ²	—
North Atlantic	46,740	12.9	15.4	33.8
South Atlantic	37,360	10.4	2.7	5.9
North Pacific	81,600	22.6	15.2	33.4
South Pacific	83,460	23.1	10.4	22.9
			(0.6) ³	(0.1)
Indian	65,520	18.2	1.8	4.0
Antarctic	32,250	8.9	—	—
Atlantic	106,463	29.5	25.6	40.0
Pacific	179,679	49.8	18.1	56.0
Indian	74,917	20.7	1.8	4.0

¹including adjacent seas

²included in the catches for North Atlantic and North Pacific

³without the catch of Peruvian anchovy

It has been generally acknowledged that the cold ocean regions, especially those of the northern hemisphere, are very productive. Less attention was given in the past to the fact that tropical and subtropical zones, between latitudes of about 35° North and South, contain some large fisheries and areas of relatively high production. The marine catches from these zones give 62 per cent of the world catch as compared with 38 per cent from the temperate and cold zones. Furthermore, the increases of world catches during the post-war years are mainly attributable to rapid developments in the tropical and subtropical zones. These zones contributed 37 per cent of the total catch in 1948, 50 per cent by 1957, and 62 per cent by 1964 (Fig. 4).

Demersal catches by trawl are a small part of the tropical and subtropical production; 14 per cent as compared with 50 per cent of clupeoids and 10 per cent of scombroids (mostly tuna and mackerel). The increases in recent years are chiefly due to increased catches of pelagic species. On the

other hand the temperate and cold seas produce almost as much demersal as pelagic fish, and the recent developments in these areas are in the direction of more intensive exploitation of trawling grounds in the North West Atlantic and North East Pacific.

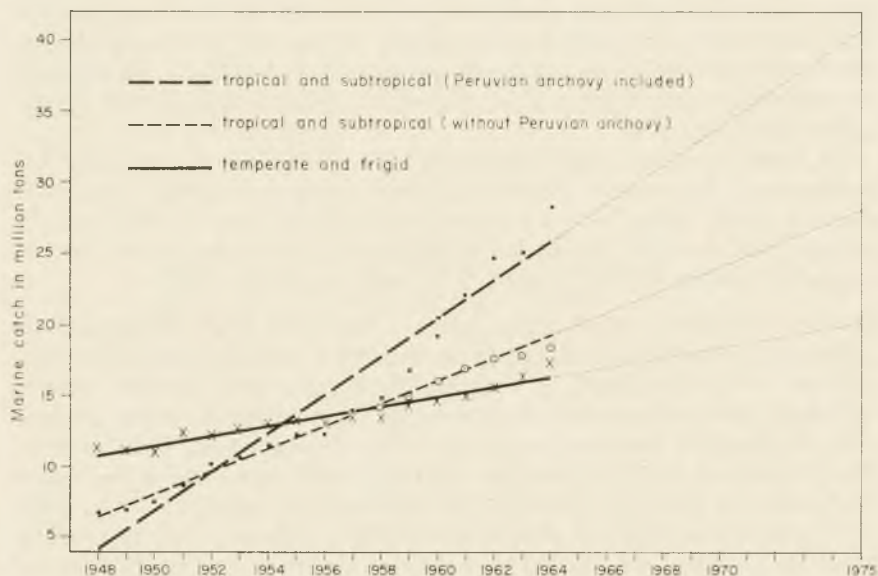


FIGURE 5. Trends in development of world catches in the two main regions (marine only).

Increased Exploitation of Tropical Waters.—There are still many virgin areas in the tropics at some distance from the shore, and beyond the reach of the indigenous fishing fleets. Their exploitation requires better equipment than commonly used by the nearby countries. By introducing new types of boats, mechanizing the existing fleets, and improving fishing gear, new resources could be exploited, but consequent increases are not expected to be spectacular. These fishing grounds are usually of much lower grade than the classical fishing banks. They are characterized by having a large number of species requiring additional labour for sorting and processing and a high proportion of fishes of small size and of low value on international markets. Nevertheless, these resources could be exploited by the nearby coastal countries with comparatively small investments, and they may prove to be of considerable importance in supplying cheap protein food to the populations of adjacent regions. Such developments, each small in itself, could together give one more sizeable increase in total catch. The recent development of trawl fisheries off some parts of India and the Gulf of Thailand (Tiews, 1965) is particularly instructive in this regard.

It is characteristic of the tropical and subtropical fisheries that they are mostly based on species with a short life cycle, but often a very fast growth rate. The largest single species fishery in the world, the Peruvian-Chilean anchovy fishery, is based almost entirely on zero and one-year age groups. Tunas, such as yellowfin (*Thunnus albacares*) and bluefin (*T. thynnus*), grow very rapidly and may attain lengths of about 60 cm by the end of their first year. The yearly increment of weight for the first few years of their life is about 25 to 30 kg. *Sardinella aurita* and *S. longiceps*, the typically warmwater species of the tropics, grow to a length of about 14 cm by the end of their first year.

In terms of value, tunas constitute one of the most important fish resources of the tropics. Their fishery has developed rapidly during the past 16 years, rising from a catch of 0.39 million tons in 1948 to 1.31 million tons in 1964. A similar development took place in the case of mackerel catches which reached 1.34 million tons in 1964.

Growth of Fisheries off Western Africa.—The West coast of Africa is of increasing importance, particularly its southwest region. Large fleets now operate along the coasts of Senegal, Mauritania, and Spanish Sahara, although opinions have been expressed that some of the resources, particularly of demersal species, are already being over-exploited. The resources off the coasts of Brazil, Venezuela, and Chile, and some parts of the Indian Ocean such as the Gulf of Bengal, the Gulf of Aden, and the Persian Gulf, are clearly under-exploited. Richardson (1963) estimated that the landings from the Brazilian coast could be increased 10 times. The introduction of purse-seining with lights increased the Philippine catches in the past two years by 35 per cent.

A considerable part of the large Japanese, USSR and other fleets is now operating in the tropics. Spain is active along the whole coast of West Africa, as also are Portugal, France, Belgium, Poland, Italy, Greece, Taiwan, Israel and others. More countries are entering this kind of fishery every year; Rumania, Cuba, Ghana, even Hungary.

Particularly spectacular has been the growth of the fishery off South and South West Africa (Hjul, 1965; FAO, 1965). The South African catches increased more than three-fold from 1948 to 1962, reaching 700,000 tons, mostly pilchards (*Sardinops ocellata*). However, from 1962 onwards, as a consequence of a sharp decline in the availability of pilchard, the total catch by 1963 amounted to 614 thousand tons and by 1964 to 586 thousand tons only. The South West African fishery amounting to only 13,000 tons in 1948, rose to 450,000 tons by 1962 and 700,000 tons by 1965. Because of the scarcity of pilchard in the South African waters during 1963 and 1964, the South West African anchovy (*Engraulis japonica*) was introduced as an industrial fish for the reduction plants. By 1964, anchovy landings reached 100,000 tons—an excellent illustration that there are still many latent resources. It seems likely that in the next decade or two, these

resources will have been explored, and most of them exploited, and the total catch will be of the order of magnitude predicted by extrapolation in Figure 2.

Ghana presents an example of a developing country forcefully building up its fishing industry. Its goal is to supply most of the country's need of proteins from the sea. In an attempt to fulfill this requirement Ghana aims at an annual catch of at least 200,000 to 250,000 tons per year, while the present catch is less than 80,000 tons. Besides a number of improvements introduced in the inshore fishery, bold programmes have been drawn up for a rapid development of the high sea fisheries. Thirty-six large, modern trawlers are being built for Ghana in the USSR, Norway, and Japan. Smaller ones are being built in other countries as well as in Ghana. With some of these new boats fully operating, a catch of at least 100,000 tons has been predicted for the year 1966.

Greater Utilization of Fishery Resources.—By presenting examples of rapidly developing fisheries we do not attempt to imply that this is an overall picture. On the contrary, we are well aware of the fact that in several areas stocks are being exploited close to their maximum sustainable yield. In such cases of course there is no justification for adding fishing effort which will lead inevitably to overfishing. However, on some of the international fishing grounds it is possible for a country to augment its fleet and obtain a larger total catch in spite of the decreasing catch per unit of effort. Thus it creates situations such that the level of catches may be too low to make the fishing enterprise economically sound for some countries whereas for others, with different types of economy or subsidized fishing industry, even the decreasing catches are still adequate to justify the expansion of their fleets.

The highly competitive character of high seas fisheries leads to a search for new fishing grounds and for new resources, even in the most remote regions of the ocean. Powerful engines and efficient equipment make it possible to fish commercially in depths which were unthinkable a short time ago. During exploratory fishing in the Gulf of Alaska, for example, rich resources of bottom fishes were found in depths of 600 to 1,000 fathoms (Alverson, 1964). Following discoveries of numerous deep demersal stocks the USSR fleet is preparing to fish at depths of 1,000 m or even more. Fishing nations have recently given a great deal of attention to the possibility of developing an effective midwater trawl which, in conjunction with improved acoustic techniques for fish detection, could prove to be a completely revolutionary means of exploiting hitherto untouched resources.

The exploitation of the ocean by fish-hungry nations such as Japan and the USSR, which are prepared to use a great variety of aquatic animals either directly for human consumption or for fish meal, is a progressive factor towards fuller utilization of marine resources. On the other hand, however, it often happens that, for the purpose of fish meal production,

the factory ship does not discriminate between shoals composed of undersized individuals of commercial species and real trash, and this jeopardises the efforts made towards the rational exploitation of some stocks.

RESEARCH TRENDS ASSOCIATED WITH HIGH SEA FISHERIES EXPANSION

An important trend in high sea fisheries is the use of fleets consisting of large vessels which are expensive to build and costly to operate, and therefore usefully employable only in areas with a high concentration of fishes. The fishing grounds of such fleets are normally far from shore bases and the number of non-working days, with expenses that must be covered by the income from catches, is generally large. The operation of these fleets is becoming more expensive and difficult largely because of high labour costs attributable to rising standards of living and to competition offered by other industries. For example, in Japan the number of fishermen declined continuously during the past 10 years, resulting in a recent labour shortage in the fishing industries, especially in the high sea fishery. A partial solution is to reduce the labour element by the extensive use of more efficient fishing methods, and, where possible, semi-automatic processing equipment, as in the case of the modern factory trawlers. This creates a need for a highly qualified crew (especially captains, engineers, and technicians) with specialized training and education.

For more primitive fishing methods, based chiefly on manual work, for example longlining and shrimping, some large fishing companies of developed countries are often searching for opportunities to employ semi-skilled and cheaper labour from other countries. Thus the Japanese longliners operating from Brazilian bases employ local workers on their fishing vessels. The Canadian and German cod trawlers try to hire Portuguese and Spanish fishermen in increasing numbers.

Finding Productive Fishing Grounds.—The search for suitable fishing grounds, a routine operation for the old type of fleet, calls for careful planning with the advent of the big factory ships. The stocks on some fishing grounds have their own peculiarities which require special adjustments of fishing equipment, filleting machines, processing units, etc.

To minimize the risk of moving to unproductive or unsuitable fishing grounds, an elaborate intelligence service and scouting has been developed in some countries. The starting point in the identification of suitable areas for prospective fishing activities is the analysis of the information scattered through scientific and technical reports of various countries, expeditions and institutions. Large fishing companies, *e.g.*, some of the Japanese longline companies, supplement the information provided by national institutions with information from the records of their own ships. A further development, as in the case of the USSR, through VNIRO and PINRO, consists of producing long-term fishing forecasts which are periodically

revised during the fishing season, on the basis of catch and biological information broadcast by fishing and scouting vessels. Such revised forecasts are broadcast back to fishing fleets to guide their activities. This requires an integrated fleet and a considerable degree of standardization of data, particularly of fishery statistics.

Sophisticated techniques are required for scouting new fishing grounds, and may include the use of aerial and underwater surveys and of a complex set of scientific instruments, the acoustic methods of fish detection being among the most important. The recent introduction of narrow beam, high resolution equipment, and the developments of target counting associated with the use of direct underwater optical methods, such as photography and television, will become more extensively used, particularly in new or relatively unexplored areas.

Environmental Data.—For the correct use of echo-sounding equipment, the interpretation of results, and the adjustment of fishing methods to fish behaviour, environmental data are required on the spot, and the tendency is to provide such data by automatic recording instruments. The need for environmental data for some selected physical and chemical features of the sea was a matter for speculation some years ago, even in areas covered by active international organizations, such as the International Council for the Exploration of the Sea (ICES) or the International Commission for the Northwest Atlantic Fisheries (ICNAF) whose research programs were very complex and elaborate. Now that support for research in fisheries oceanography on a large scale, is accepted as necessary, we are in the era of international cooperative investigations. These offer a framework for the collection of environmental data, the analysis of which will contribute to a better understanding of the factors governing fluctuations in fish abundance and distribution, and also to improve the forecasts so badly needed for the rational and economic operation of industrialized highsea fleets. Following a pattern similar to that in forecasting fish abundance and distribution mentioned earlier, the pooling and analysis of environmental data is passing beyond the pilot stage to an operational phase. In this connection, there are now about 30 facsimile broadcast stations throughout the world, some of which include in their regular broadcast schedules oceanographic and environmental data. An increasing need for improved biological data, fish catch and effort statistics, their standardization for rapid pooling, the use of a world-wide system for recording, centralization and rapid diffusion to the fishing industry, is a common feature of this age, and for full effectiveness requires constant contact with distant fleets.

International Commissions.—Such large amounts of data on economic, biological, environmental parameters call for new methods of rapid compilation, analysis, and interpretation. Operational research, on large company or governmental scale, is becoming the best way of providing the

guidance required for fleets operating on a world-wide basis. The shifting of fleets from one fishing ground to a more productive area may cause excessive concentration in a particular zone, unless carefully coordinated with other fleets, by appropriate international agreements.

We are approaching a period when almost all stocks will be accessible, not only to the coastal countries, but to all countries operating distant fishing fleets. The present intensive fishing is already causing in certain areas a decline of stocks (resulting in a lower catch per unit fishing effort, and therefore higher costs per unit catch), and in some cases even reduction of total yield with increased fishing.

This situation can be controlled by international agreements leading to management and conservation measures. In many areas attempts are being made to achieve agreement through regional or specialized fisheries commissions. The discussions in such bodies and the agreements reached in them, must be based on extensive research; such research is expensive and requires careful organization and a large degree of international coordination.

Mobility and heterogeneity of fishing fleets are making it more difficult to consider the management of a particular stock or area in isolation from the total world fishing economy. Furthermore in many areas, especially in the areas in which new or relatively unexplored stocks are located, there do not yet exist responsible regulatory bodies, nor adequate research bases.

We can foresee some of the trends which, in the relatively near future, will shape the characteristics and the work of such commissions. The tendency is, as can be observed in the North Atlantic, for coalescence of ICNAF and the North East Atlantic Fisheries Commission (NEAFC), and the extensive use of ICES as the advisory body for research problems concerned with the whole North Atlantic and therefore serving both commissions.

Conservation of Marine Resources.—Research and regulatory bodies with geographic limits are likely to become obsolete. In the immediate future, the spirit of the Geneva Convention on the Conservation of Living Resources of the Sea (which came into force on March 20, 1966) establishing the principle that the responsibility for research and conservation is that of the countries exploiting certain stocks, will dominate the shaping of the terms of reference of international fishing regulatory bodies. The part to be played by UN Agencies, such as FAO, in directly stimulating the establishment of appropriate international machinery, as in the case of the proposed Atlantic Tuna Commission, is likely to increase in significance. The responsibilities to be thrust on FAO, as a neutral body in peaceful settlement of disputes, or as an international watching body—as demonstrated recently in the crisis of the International Whaling Commission—will change its present pattern of work and make it more operational in the field of resources management and conservation.

Important readjustments in the internal structure and in the methods of work of FAO would be necessary to cope with these increasing duties. The Advisory Committee on Marine Resources Research (ACMRR) which provides general guidance in research programs, and the newly established FAO Committee on Fisheries, have important roles to play, as tools for developing appropriate policy and scientific advice on these global management needs. Important steps towards the same goal, in specialized fields, are the establishment of a Fish Stock Evaluation Branch and a Fishery Data Centre, which are already assisting FAO regional bodies and some developing Member Nations in their research, fisheries development, and management programs. In some areas the maintenance of wild fish stocks and the future development of sea farming requires control of marine pollution, as well as control of exploitation, and FAO is initiating an active program to cope with this increasingly acute problem.

Fisheries Economics.—Discussions on the economics of fisheries, hitherto more or less taboo in regional fisheries commissions and regulatory bodies, are now beginning in these circles in the discreet form of discussion in symposia or exchange of views for mutual information. In fact, in view of the present crisis in the application of classic conservation measures (minimum mesh size, minimum legal size of fish, closed season, etc.) attention is oriented to measures typically of an economic nature, such as the establishment of quotas, limitation of fishing power or effort, shares in stock property, and others.

Arriving at this stage, the competition of the distant fleets, operated by industrialized countries (fleets that are expensive to run and require the support of very costly research to keep productivity high and to ensure economic stability), with the fleets of the developing coastal countries, could lead to the advantage of the latter.

CONCLUSIONS

The trend in total catch, considered in conjunction with evidence on catching techniques and other matters, indicates that world fisheries are approaching a limit of production from wild stocks. According to the state of exploitation, stocks fall into three broad classes: (1) at or near (either just approaching, or just surpassed) the maximum sustainable yield; (2) some distance below this maximum; (3) neglected. As a result of recent developments in the organization of fishing operations and fishing equipment, most of the resources are technically accessible. A relatively large proportion of stocks belong to class (1) and a relatively small proportion to class (3). Important in the latter class are the resources of the midwaters of the oceans, and those of the Antarctic. It seems probable that in one or two decades, virtually all stocks will have been discovered and some estimates made of their size.

Current trends in fish production are: to increase fish-finding efficiency; to increase fishing power and efficiency; to bring all resources under exploitation; to increase mobility in deployment of fishing effort.

These trends are apparent in the activities of the developed fishing nations. At the same time countries which hitherto engaged only in moderate fishing are increasing their activities, and a reallocation of fishing opportunity is taking place. Bilateral and international forms of aid are playing a major part in this.

These trends are steadily raising the level of fish production, but the results of innovations are becoming more and more marginal.

The conclusions to be drawn from this situation are:

1. The existence of a limit to production already demonstrated for particular species and in some instances for particular localities, must be accepted for world marine fishery resources as a ceiling which may be of the order of 80 to 100 million tons.

2. This ceiling may be achieved, and perhaps raised a little, by the management of fishing operations on the basis of stock assessment studies; (a "perfect" system of management of all fishing operations, bringing each stock to condition of full use of its food supply, might give a 10 to 30 per cent increase of production over present levels); this management could lead to reduction in costs.

3. This ceiling might be raised still further by substantial changes in the exploitation pattern, making greater use of organisms standing low in the food chain (for example the krill on which the great baleen whale stocks depend).

4. The most promising approach to greater production is by way of intervention in the resources themselves, to increase their size (as standing crop) and/or to increase the rate of their turnover. This is demonstrably practicable for freshwater fisheries, although the possibilities have by no means yet been fully realized or even evaluated. For marine fisheries (in which we include those of brackish-waters) the most practicable possibilities at present are offered by inshore stocks.

5. It is likely that for many decades fish production will be obtained from a combination of wild-stock harvest and fish farming.

To be able to make the best use of fishery resources (in the broadest sense) we need a detailed survey of fish populations (not only as separate stocks but also as components of ecosystems), and a comprehensive study of the ecology and physiology of each species and community.

To sum up, it is foreseeable that countries will advance from the hunting stage to the stage of husbandry where research results, those already existing and those to be obtained in the near future, are fully applied for estuarine and coastal cultivation of marine organisms.

REFERENCES

- ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT
1964. A study of demersal fishes and fisheries of the north-eastern Pacific Ocean. H. R. McMillan lectures in fisheries. Univ. British Columbia Press, Vancouver, B.C., 190 pp.
- BOEREMA, L. K., G. SAETERSDAL, I. TSUKAYAMA, J. E. VALDIVIA, AND B. ALEGRE
1965. Report on the effects of fishing on the Peruvian stock of anchovy. FAO Fish. tech. Pap., (55): 44 pp.
- CHAPMAN, W. L.
1965. Potential resources of the ocean. Van Camp Sea Food Company, San Diego, Calif., 43 pp.
- FOOD AND AGRICULTURE ORGANIZATION
1965. Yearbook of fishery statistics—catches and landings 1964. FAO, 1/8: [No total pagination]
- GRAHAM, H. W. AND R. L. EDWARDS
1962. The world biomass of marine fishes. pp. 3-8 *in* Heen, E. and R. Kreuzer, Eds., *Fish in Nutrition*. Fishing News (Books) Ltd., London, xxiii + 447 p., illus.
- HJUL, P.
1965. S. Africa's quest for anchovy. *Fish. News Int.*, 4 (3): 273-278.
- KESTEVEN, G. L.
1962. World aquatic biomass—its future abundance. pp. 9-21 *in* Heen, E. and R. Kreuzer, Eds., *Fish in Nutrition*. Fishing News (Books) Ltd., xxiii + 447 p., illus.
- LAEVASTU, T.
1961. Natural bases of fisheries in the Atlantic Ocean, their past and present characteristics and possibilities for future expansion. pp. 18-39 *in* Borgstrom, G. and A. J. Heighway, Eds., *Atlantic Ocean Fisheries*. Fishing News (Books) Ltd., London, viii + 336 p., illus.
- LUCAS, C. E.
1964. Aspects of marine fisheries research. *Advmt. Sci., Lond.*, XXI, 1964-65, 11 pp.
- MESECK, G.
1962. Importance of fisheries production and utilization in the food economy. pp. 23-37 *in* Heen, E. and R. Kreuzer, Eds., *Fishing News (Books) Ltd.*, London, xiii + 447 p., illus.
- RICHARDSON, I. D.
1963. Estimation of marine resources off the Atlantic coast of South America. pp. 119-133 *in* *The Better Use of the World's Fauna for Food*. The Institute of Biology, London.
- SCHAEFER, M. B.
1964. The potential harvest of the sea. ASLO Symposium, June 1964, 17 pp.
- TIEWS, K.
1965. The German fisheries mission to Thailand (2nd project phase 1962-1964). *Veröff. Inst. Küst. -u. Binnenfish.*, (36): 32 pp.

ANOMALIES IN THE WATERS OFF THE PERUVIAN COAST DURING MARCH AND APRIL 1965

OSCAR GUILLÉN

Instituto Del Mar Del Perú, Lima, Perú

ABSTRACT

The data for the present work were obtained during the cruise of the B.A.P. UNANUE which took place from March 29 to April 22, 1965. Eleven profiles were obtained, which extended to 110 miles offshore, except the profile from Callao, which was 170 miles. Hydrological observations were made to a depth of 150 m. At the extreme seaward station observations were made to 1,200 m.

In March-April 1965, the waters off the Peruvian coast presented abnormal conditions with the presence of a warm tongue of equatorial waters which had its extreme southern front off Huarmey (10° S).

The equatorial superficial waters dominated the central and northern regions. The waters of the Peruvian Coastal Current and the subtropical waters dominated the southern region.

In general the area studied showed a higher temperature than normal with an average increase of 3° C on the surface of the sea.

The coastal upwellings were reduced to small areas and were above 75 m. The outstanding areas were Supe, Pisco, and Atico, with lower temperatures, high values for phosphate and low values for dissolved oxygen. Offshore from Pisco and Atico an average velocity of 1.4 m/day was estimated.

A strongly developed thermocline was present off Punta Aguja, with 9 isotherms (25° - 17° C); another in front of Supe, with 10 isotherms (25° - 16° C); and the third one in front of Pisco, with 9 isotherms (23° - 15° C). The first one was deepest, between 20-60 meters, and the other two appeared between 0-60 meters.

INTRODUCTION

The anomalies in the waters off the Peruvian coast producing catastrophic effects on the guano bird populations, the distribution of pelagic fish and the climate along the coast, are known as the El Niño phenomenon.

During November 1964 the oceanographic vessel UNANUE confirmed that a flow of tropical water south of Talara (Latitude 5° S) had occurred northwest of the waters off the Peruvian coast.

On March 1965, the EXPLORER obtained some data concerning changes in the distribution of the sea temperature, due to the presence of warm surface waters, which seemingly affected all the maritime region between Punta Aguja in the north, and Callao in the south.

The EXPLORER only investigated a narrow strip of 40 to 50 miles width along the central region of Peru, which was not enough to establish the magnitude of the change which had occurred, or its causes. For this reason, the UNANUE had conducted cruise No. 6504 with the principal objective of making a reconnaissance of all the sea between latitudes 4° S and 18° 30'S.

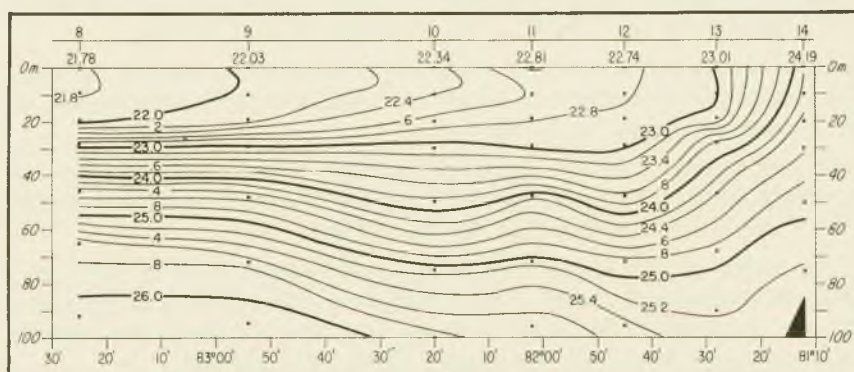
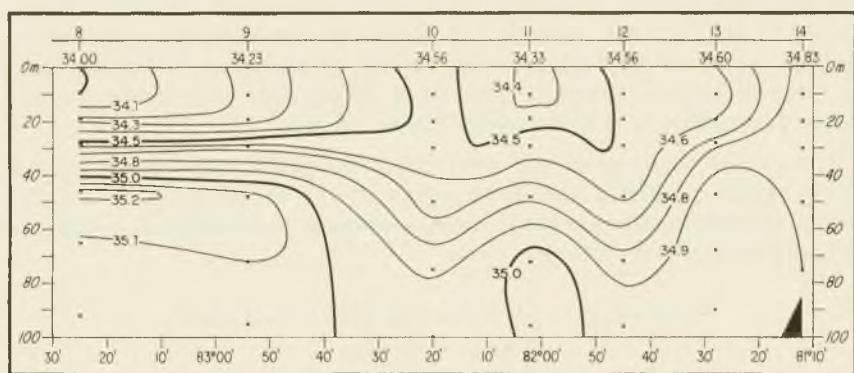
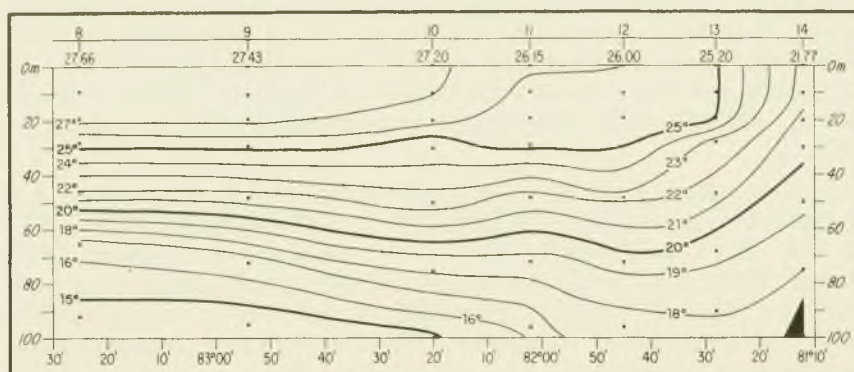


FIGURE 1. Vertical distribution of temperature (*top*), salinity (*center*), and density (*bottom*), Profile VIII. April 13-14, 1965.

The cruise was conducted from March 29th to April 22nd, 1965 with a total of 11 profiles, which extended as far as 110 miles from the coast, except the Callao profile which was 170 miles long (Fig. 1).

Hydrological observations were made to a depth of 150 m except at extreme stations where observations were extended only to a depth of 1200 m.

Studies regarding the El Niño phenomenon have been described and recorded for the year 1891 (Schott, 1931); 1925 (Murphy, 1926); 1941 (Lobell, 1942; Schweigger, 1942); 1953 (Wooster & Jennings, 1955; Posner, 1957); and 1957-58 (Wooster, 1960). Other studies have been made by Bjerknes (1961); Schweigger (1961-1964); Wyrski (1963, 1965); Gunter (1936). Gilmartin (1964) prepared an extensive bibliography.

Although there have been several approaches, the El Niño phenomenon has not been totally described, because the anomalies recorded in the waters off the Peruvian coast lacked complete oceanographic and meteorological observations. Future studies on the phenomenon El Niño should be made with more complete data, both atmospheric and oceanographic, before proceeding to give a comprehensive theory.

The present study gives the most important preliminary results of this cruise, which permitted the investigation of the actual position and the extent of changes taking place in the hydrological and biological conditions of the waters off the Peruvian coast.

DESCRIPTION OF HYDROGRAPHIC CONDITIONS

Northern Region

(Plate 1; Plate 2 a; Figs. 1-2)

Equatorial surface waters prevailed in a large part of the northern region with temperatures of 27°-24°C and salinities of 34.8-33.8‰.

These waters extended to the southeast in the 0-20 m layer in the form of a tongue, the extremities of which were found in the central region, as can be seen in Figures 2, 3 and 4.

At the boundary of the equatorial surface waters, concentrations of phosphate between 1.0-0.3 $\mu\text{g-at/L}$ and of dissolved oxygen between 5.0-4.0 ml/L were recorded at the sea surface.

The waters present in the 0-10 m layer with temperatures of 28°C and 26°C and salinities of 34.0-33.7‰, which were observed west of Mancora, near the longitude 83°W, seem to be the remainder of the tropical waters which possibly dominated the region during the summer.

The subtropical waters were below the thermocline, principally off Mancora.

The Peruvian coastal current waters were present near the coast, between Talara and Punta Aguja, with temperatures of 22°-18°C and salinities of 35.0-34.8‰. These waters caused a marked weakening of the thermocline, below 40 m, near the coast.

Near the coast, at Punta Aguja, a strong horizontal gradient appeared with four isotherms (25°-22°C) occurring in 16 miles (2.10°C for each 10 miles).

Near the coast, the iso-oxygens, as well as the isophosphates were closer to the surface. In general, the phosphate content was less than the regularly found in previous cruises (Guillén, 1962; 1964a, b, c; In Press), especially in the surface layer just off the coast.

The maximum phosphate concentration in the 0-100 m layer was 2.50 µg-at/L (Station No. 8), while the minimum dissolved oxygen content was 0.41 ml/L (Station No. 9).

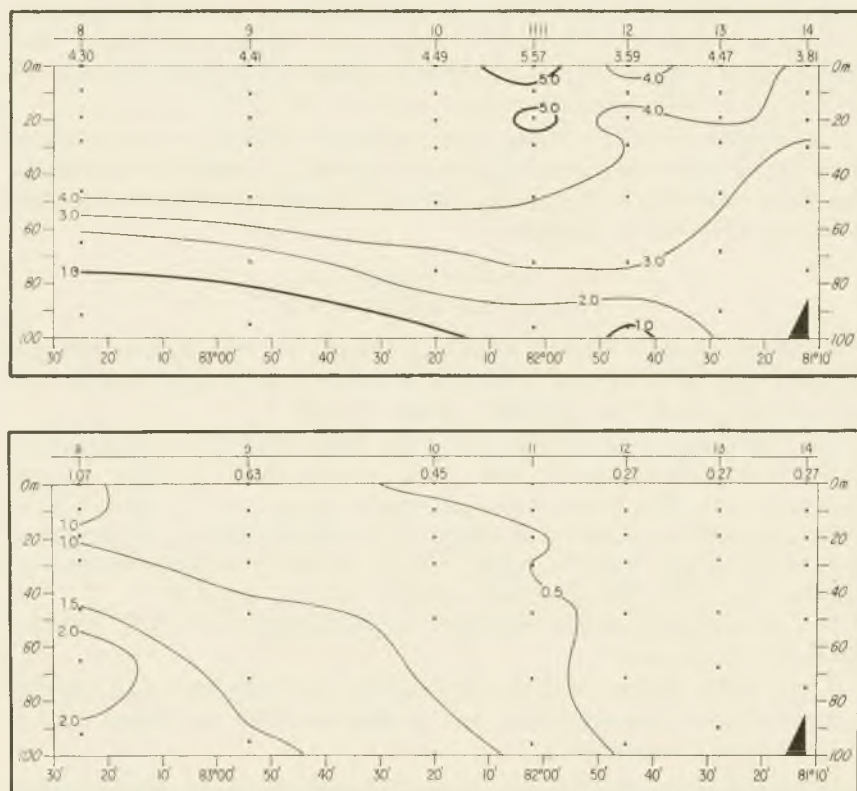


FIGURE 2. Vertical distribution of oxygen (*top*) and phosphate (*bottom*), Profile VIII. April 13-14, 1965.

Central Region

(Plate 1; Plate 2 a; Figs. 1-4)

Equatorial surface waters extended in the form of a tongue whose southern end reached as far as Huarney. If we compare this with the conditions encountered in cruise 6503 (EXPLORER), it can be confirmed that these waters were receding to the north, although their effects were predominant in a great part of the region.

The Peruvian coastal current was near the coast, with a width of approximately 30 miles and was more intense between Chimbote and Callao.

The subtropical surface waters, with temperatures above 24°C and salinities above 35.1‰, were observed off shore west of longitude 79°W at about 12°S latitude. Near the coast, one horizontal thermal gradient of 2.6° C/10 miles was found with 6 isotherms (25°-20°C) in 21 miles which was stronger than in the north.

Between Pimentel and Chimbote, concentrations of 0.6-0.2 $\mu\text{g-at/L}$ for phosphate and 6.0-5.0 ml/L for dissolved oxygen were found. The coastal zone between Callao-Chimbote showed phosphate contents of 1.6-0.6 $\mu\text{g/L}$ and dissolved oxygen contents of 5.0-4.0 ml/L.

The distribution of the oxygen and phosphate isolines in the 0-100 m layer was similar to the one found in the northern region. The maximum phosphate value was 2.68 $\mu\text{g-at/L}$ (Station 40) while the minimum oxygen value was 0.14 ml/L (Station 37).

Southern Region

(Plate 1; Plate 2 a; Figs. 3-4)

Equatorial surface waters were not present in this region. All the southern coast of Peru was under the influence of subtropical waters and those coming from the Peruvian coastal current.

The subtropical waters had temperatures higher than 22°C and salinities above 35.1‰. Furthermore, they were characterized by high oxygen content (>5.0 ml/L) and a low phosphate content (<0.7 $\mu\text{g-at/L}$).

The Peruvian coastal current waters were characterized by low temperatures of 22°C and salinities under 35.1‰, dissolved oxygen contents of less than 5.0 ml/L and phosphate greater than 0.7 $\mu\text{g-at/L}$.

The subantarctic waters extended approximately to 15°S latitude, below the thermocline.

A big water pocket of high temperatures and salinities, and slightly higher phosphate concentrations was produced off Ilo and Arica due to an anticyclonic movement.

The distribution patterns of iso-oxygens and isotherms were similar. Comparing these with the distribution of isophosphates, they generally maintained an inverse relation.

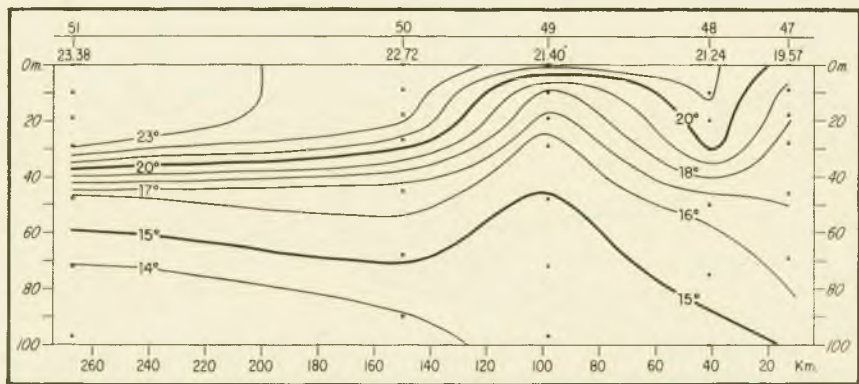
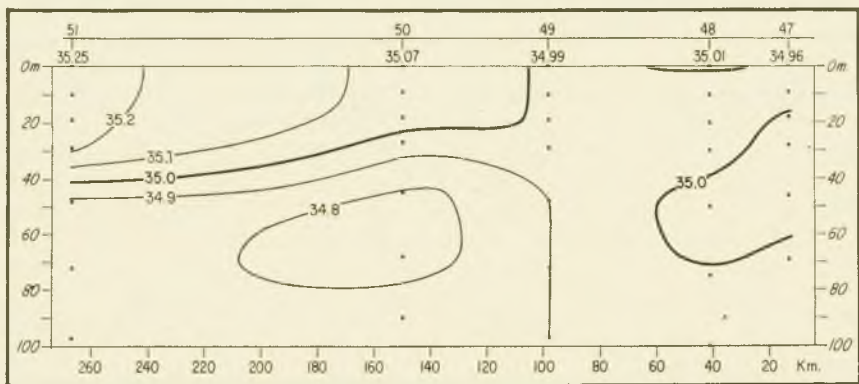
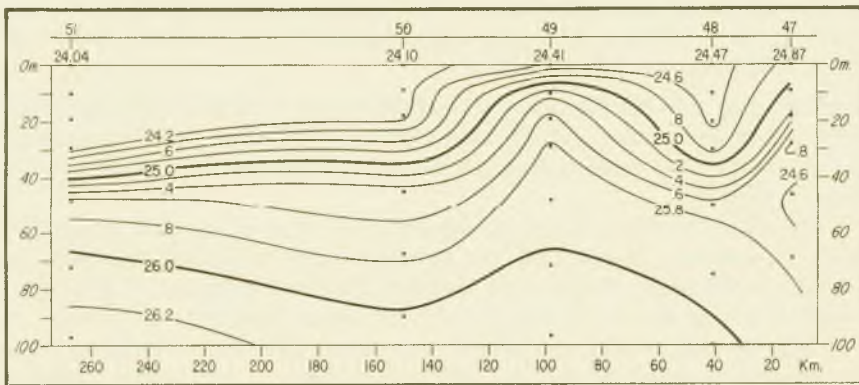


FIGURE 3. Vertical distribution of temperature (*top*), salinity (*center*), and density (*bottom*), Profile II, April 3-4, 1965.

The maximum concentration of phosphate in the 0-100 m layer was 3.10 $\mu\text{g-at/L}$ (Station 60), and the minimum oxygen content was 0.16 ml/L (Stations 42, 53, and 56).

Variations of the Oceanographic Conditions in the Surface.—The following table shows the extreme values found at the sea surface. The numbers in brackets show the corresponding stations, the positions of which can be seen in Figure 1.

Both the minimum and the maximum temperature decreased in relation with the latitude. In contrast, the maximum and minimum salinities increased to the south, revealing in this way the great influence of the equatorial waters in the north and of the subtropical waters in the south.

The maximum oxygen and phosphate contents followed in the same trend of salinities, but not the minima which were lower in the central region.

On the other hand, taking as a comparison the average temperature for April of the years 1939-1956, published in the monthly charts of the Peru-

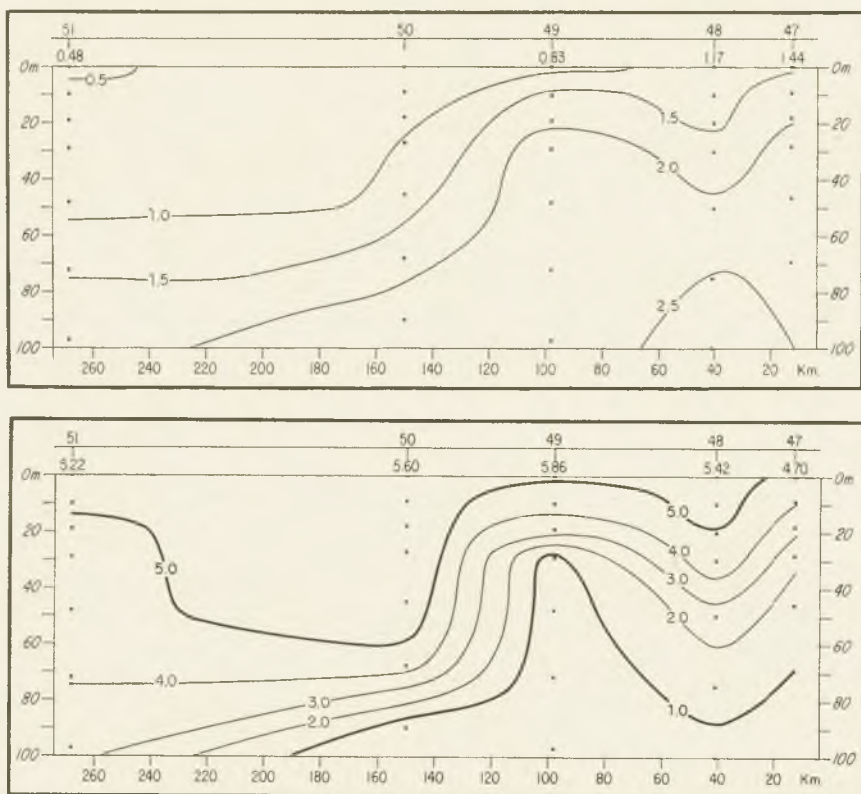


FIGURE 4. Vertical distribution of temperature (*top*), salinity (*center*), and II. April 3-4, 1965.

vian littoral (Cia. Adm. del Guano, 1956), we found that the studied zone had a temperature increase, being greater than the average of 3°C at the sea surface.

	Maximum		
	Northern Region	Central Region	Southern Region
Temperature °C	27.66(8)	27.03(27)	23.93(42)
Salinity ‰	34.83(14)	35.26(40)	35.46(59)
Dissolved Oxygen ml/L	5.57(11)	6.20(21)	7.08(57)
Phosphates µg-at/L	1.07(8)	1.65(33)	1.84(56)
	Minimum		
Temperature °C	21.77(14)	19.58(33)	18.03(56)
Salinity ‰	33.66(7)	34.40(16)	34.87(64)
Dissolved Oxygen ml/L	3.59(12)	3.12(33)	3.22(45)
Phosphates µg-at/L	0.27(12-14)	0.19(20)	0.43(42)

Thermocline.—The thermocline was strongly developed in three places: one in the northern region off Punta Aguja, with 9 isotherms (25°-17°C) another off Supe with 10 isotherms, (25°-16°C); and the third off Pisco, with 9 isotherms (23°-15°C). The first one was deeper, lying between 20-60 m, and the other two between 0-60 m.

In general, the thermocline was deeper farther from the coast. The surface mixed layer was found above the thermocline with an average thickness of 20 m in all three regions. Off Supe this layer was 50 m thick in the part corresponding to the cyclonic movement.

Upwelling.—The upwelling areas along the coast were poorly developed being observed off Supe, Pisco, and Atico; the more southern places the weaker, as we can see in the following table:

	Supe	Pisco	Atico
Temperature °C	19.58	18.33	18.03
Salinity ‰	34.96	34.82	35.01
Dissolved Oxygen ml/L	3.12	3.22	5.16
Phosphates µg-at/L	1.68	1.60	1.84

The upwelling was restricted to depths above 75 m. With the repetition of the stations off Pisco and Atico, we estimated the average velocity of the upwelling to be 1.4 m/day.

COMPARISON OF NORMAL AND ABNORMAL CONDITIONS ON PERUVIAN SEA

Unfortunately, it is not easy to discuss the Peruvian El Niño in quantitative terms. The lack of a long record of systematic observations throughout the year makes it difficult to determine satisfactory averages with which to compare observations believed to be abnormal.

Charts of sea surface temperatures during March, May, 1936-1938 and 1939 (Pl. 2 b,c) have been reproduced from Bjerknes data, as representative of a normal and abnormal year, respectively. The most sharp difference observed is that in the average period 1936-1938, the warm mass

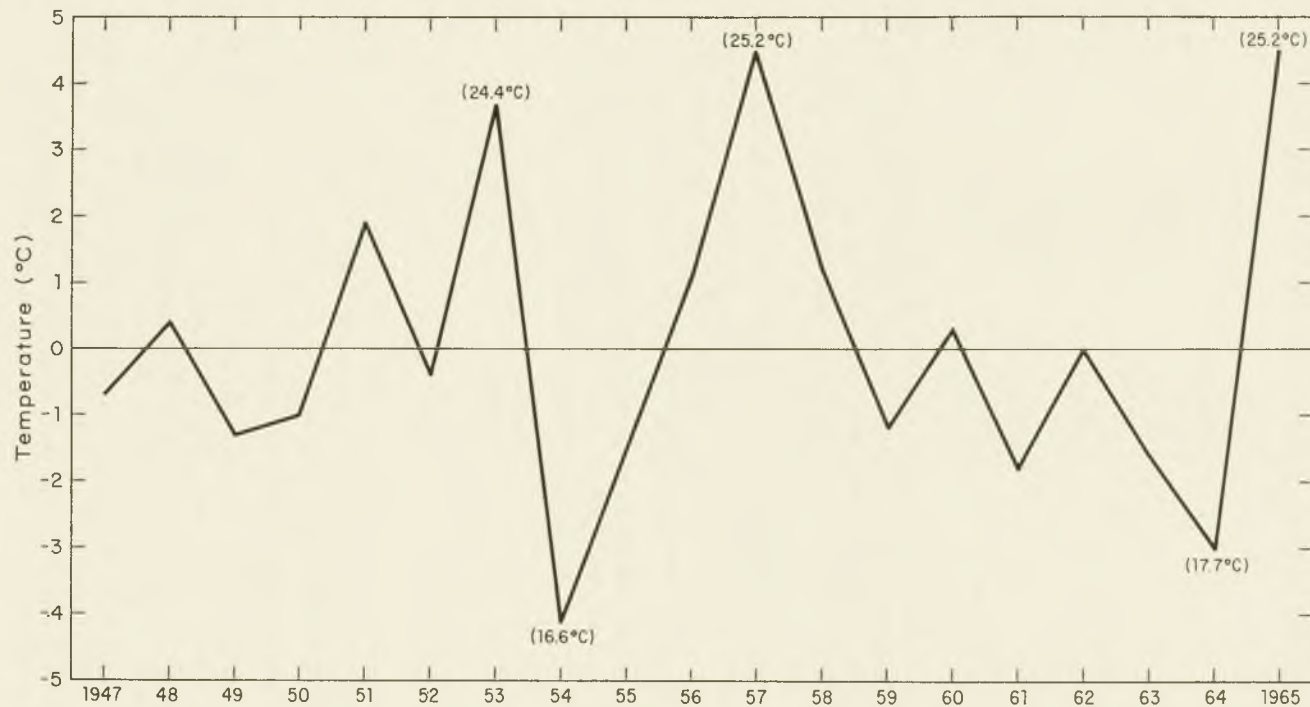


FIGURE 5. Surface temperature anomaly (°C) for April, 1947-1965, in the areas between 10°-12° South and 78°-80° West.

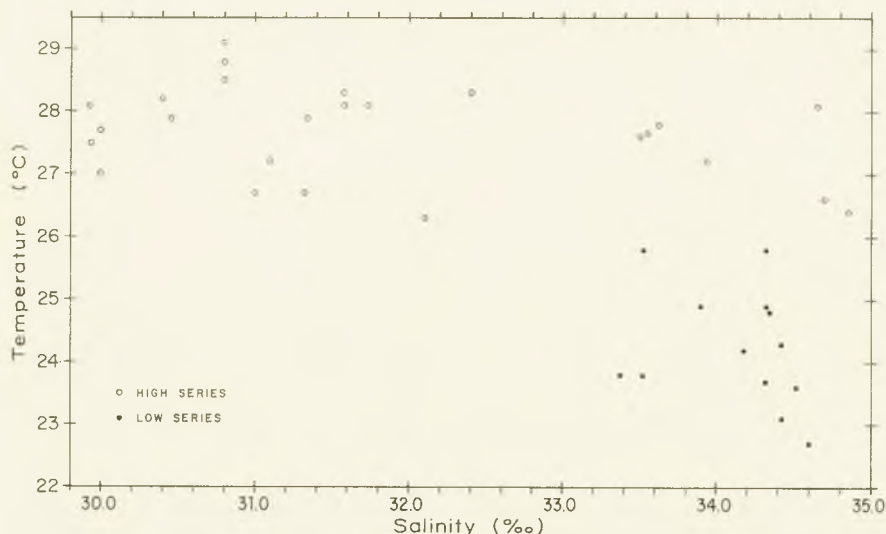


FIGURE 6a. Surface temperature-salinity diagram for the Yale South American Expedition of March-May 1953. Data in the Cabo Blanco-Talara region (from Posner, 1957).

coming from the tongue of warm waters, goes west, while during 1939 it lay near the coast. The anomalies observed during April 1965 are similar to those encountered in 1939.

Furthermore, the temperature anomalies variation in the sea surface during April 1947-1965 (data Renner [1963], and from the Instituto del Mar del Perú) have been shown graphically for the zone between 10° - 12° S at 78° - 80° W (Fig. 5). We could observe in this zone, that the average temperature reached during April 1965 (25.2°C) was equal to the one encountered during 1957 and was 0.8°C above the average recorded in 1953.

Schott (1931) found during the El Niño of 1891 that the Callao temperature was 26.6°C .

Diagrams of T-S in the surface waters have been made to study the origin of the waters encountered during April 1965 (Figure 6), and for its comparison with other abnormal years, diagrams of T-S for the years 1953 (Posner, 1957), and 1958 (Wooster, 1960) have been reproduced. We could observe in these diagrams that the sea surface anomalies encountered during April 1965 were caused by the surface equatorial waters going southeast, and that these anomalies were similar to those of 1953. However, these waters were cooler, more saline, and quite different from the ones encountered in 1957, characterized by their high temperature and salinity.

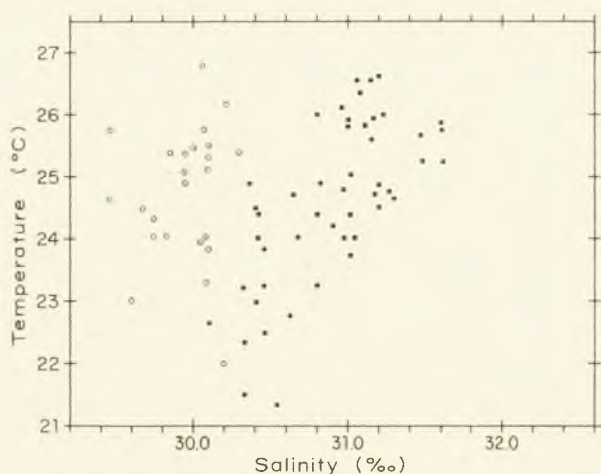


FIGURE 6b. Surface temperature-salinity diagram for Bondy cruise of February-March 1958. Observations north of 7°S shown by open circles, south of 7°S by solid dots (from Wooster, 1960).

Plate 2d shows the sea surface pressure and wind distribution respectively. Comparing these figures with those of Bjerknes (1961) for March, and the monthly charts published by the Cia. Administradora del Guano for April 1939-1955, we can observe a low atmospheric pressure, favoring the surface equatorial waters advance to the Peruvian coast.

CONCLUSIONS

The conditions continued to be abnormal during April 1965, with the presence of a warm tongue of equatorial waters with its southern end extending to Huarmey (10°S). Comparing these with the March conditions we can confirm that this tongue was receding to the north, which can be considered as "returning" to normality.

The anomalies encountered during April 1965 were caused by the southeast surface equatorial waters advance, favored by the low atmospheric pressure.

The equatorial surface waters dominated the northern and central regions. The Peruvian coastal current waters and the subtropical waters dominated the southern region. Generally speaking, there was a warming up higher than normal in all areas studied, with an average increase of 3°C at the sea surface.

The average temperature found in the area between 10° - 12°S at 78° - 80°W during April 1965 was 25.2°C . This is similar to the 1957 average and is 0.8°C higher than the average recorded during 1953.

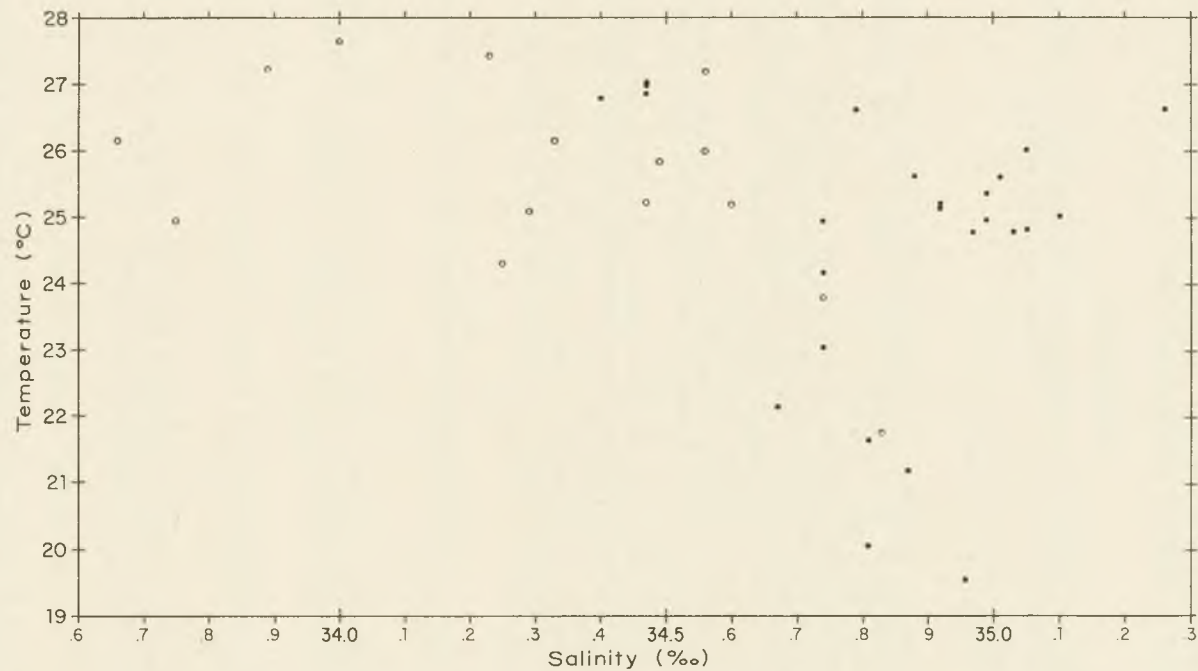


FIGURE 6c. Surface temperature-salinity diagram for Unánue cruise of March-April 1965. Observations north of 7°S shown by open circles, south of 7°S by solid dots.

The coastal upwellings were restricted to small areas, above 75 m. The most important areas were Pisco, Supe, and Atico, with low temperatures, maximum phosphate and minimum dissolved oxygen content. A velocity of 1.4m/day was observed off Pisco and Atico.

REFERENCES

- BJERKNES, J.
1961. "El Niño" study based on analysis of ocean temperatures 1935-1937. Bull. Inter-Amer. trop. tuna Comm., 5 (3): 219-303.
- CIA. ADMINISTRADORA DEL GUANO
1956. Mapas mensuales del litoral Peruano.
- GUILLÉN, O.
1962. Distribución de fosfatos y oxígeno disuelto en la región de la Corriente Peruana en el otoño y primavera de 1960. Inf. Inst. de Inv. de los Rec. Mar., No. 7: 1-13 p.
1964a. Distribución del contenido de fosfatos en la región de la Corriente Peruana. Inf. Inst. de Inv. de los Rec. Mar., No. 28: 20.
1964b. Distribución y variación anual de fosfatos y oxígeno disuelto en la región marítima del Callao (Febrero 1961-Enero 1962). Inf. Inst. de Inv. de los Rec. Mar., No. 28: 28.
1964c. Distribución y variación anual de fosfatos y oxígeno disuelto en la región marítima del Callao durante al año 1962. Inf. Inst. de Inv. de los Rec. Mar., No. 28: 20.
In Press. Distribución y variación del oxígeno disuelto y de los fosfatos en la región Callao-Chimbote. Primer Seminario Latino Americano sobre el Océano Pacífico Oriental.
In Press. Variación de fosfatos en la región marítima del Callao como medida de la producción primaria. Primer Seminario Latino Americano sobre el Océano Pacífico Oriental.
- GUNTHER, E. R.
1936. A report on oceanographic investigations in the Peru Coastal Current. Discovery Rep., 13: 107-276.
- GILMARTIN, M.
1964. Compilación bibliográfica sobre la oceanografía de las aguas litorales de Colombia, Ecuador y Perú con especial referencia al fenómeno El Niño. Inst. Nac. de Pesca del Ecuador, 1 (1): 15.
- LOBELL, M. J.
1942. Some observations on the Peruvian coastal current. Trans. Amer. geophys. Union, 2: 332-336.
- MURPHY, R. C.
1926. Oceanic and climatic phenomena along the west coast of south America during 1925. Geogr. Rev., 16: 26-54.
- POSNER, G. S.
1957. The Peru Current. Bull. Bingham oceanogr. Coll., 16 (2): 106-155.
- RENNER, J. A.
1963. Sea surface temperature monthly average and anomaly charts, eastern tropical Pacific Ocean. Spec. sci. Rep. U. S. Fish Wildl. Serv. Fish. 442.

SCHOTT, G.

1931. Der Peru Strom und seine nordlichen Nachbargebiete in normaler Ausbildung. *Ann. Hydrog. Mar. Meteorol.*, 59: 161-169, 200-213, 240-252.

SCHWEIGER, E. H.

1942. Las irregularidades de la Corriente de Humboldt en los años 1925 a 1941, una tentativa explicación. *Bol. Soc. admin. Guano*, 18: 27-42.
1961. Anomalías térmicas en el océano Pacífico Oriental y su pronóstico. *Bol. Soc. geogr. Lima*, 58: 1-50.
1964. El litoral Peruano. *Unv. Nac. Federico Villarreal*: 414 pp.

WOOSTER, W. S.

1960. El Niño. *Calif. Coop. Ocean. Fish. Invest. Rept.* 7: 43-45.

WOOSTER, W. S. AND F. JENNINGS

1955. Exploratory oceanographic observations in the eastern tropical Pacific January to March 1953. *Calif. Fish Game*, 41 (1): 79-90.

WYRTKI, K.

1963. The horizontal and vertical field of motion in the Peru Current. *Bull. Scripps Inst. oceanogr.*, 8 (4): 313-346.
- 1965a. Oceanography of the Eastern Equatorial Pacific Ocean. *Univ. of Hawaii*, pp. 1-43.
- 1965b. Surface currents of the eastern tropical Pacific Ocean. *Bull. Inter-Amer. trop. tuna Comm.*, 5: 271-304.

ZUTA, S. AND O. GUILLÉN

- In Press. Condiciones Oceanográficas en el Pacífico Peruano durante el año 1964. *Inf. Inst. del Mar del Perú*.

RECENT DEVELOPMENTS IN THE FISHERIES OF CALIFORNIA

PHILIP M. ROEDEL

California Department of Fish and Game, Terminal Island

ABSTRACT

Marine fisheries research in California has made great strides since World War II. A major factor precipitating this work was the establishment of the California Marine Research Committee in 1948. This body, acting with a coordinating committee of scientists, has been able to instigate a highly successful program among state and federal agencies and universities. Research results demonstrate a large population of anchovies off California and Baja California plus sizeable stocks of other species, particularly hake. California plans to start an augmented research program in 1966 to delineate the magnitude and distribution of the latent resources off its coast, and to study food habits of major species.

INTRODUCTION

The last two years have seen great activity among scientific, administrative and political bodies concerned with the marine fisheries of California, for nearly 20 years of scientific study on the California Current System culminated during these recent months. The findings have led to a new interest by California-based industry, long oriented toward distant-waters and the high-seas tuna fishery, for they have disclosed resources of considerable magnitude lying virtually latent off our coast.

The program which brought this about was organized originally to determine what happened to the Pacific sardine (*Sardinops caeruleus*). The story of the rise and fall of that once-great fishery has been told many times; the cause of its collapse and the effects of this collapse on the ecosystem have only in recent years become evident.

It took considerable managerial and scientific effort to mount the augmented program which produced this knowledge.

THE RESEARCH PROGRAM

Studies made between the two world wars by the California Department of Fish and Game had provided much basic data on sardine biology and on the fishery, but these could not be conducted on a broad enough scale to answer the question to everyone's satisfaction.

In 1948 the California Legislature established within the Department a body known as the Marine Research Committee (MRC), charged with "... financing research in the development of commercial fisheries of the Pacific Ocean and of marine products susceptible to being made available to the people of California." The landing tax supporting the Committee produces relatively little income (\$60,000—\$180,000 per year) but MRC has generated expenditures of far greater sums by sponsoring

and providing modest financial support to a coordinated research effort. The major partners are the U.S. Bureau of Commercial Fisheries (BCF), University of California (Scripps), and the California Department of Fish and Game, with Stanford University and California Academy of Sciences filling important but lesser roles. Among them, they spend perhaps a million dollars a year on research pertinent to problems of the California Current System.

Over the years BCF has concerned itself chiefly with egg and larval surveys, Scripps with obtaining oceanographic data, and the Department of Fish and Game with studies of juvenile and adult fish and the fishery itself.

Since 1959, a full time Coordinator has chaired a committee consisting of the working heads of the appropriate research activities of the three agencies. This body is California Cooperative Oceanic Fisheries Investigations Committee, and it is CalCOFI that has led the recent advances.

Studying the ecosystem rather than sardines *in vacuo* was apparently a rather unique idea in 1948, at least in our area where research was traditionally species oriented. The dividends have been great.

RESULTS

The most significant single result has stemmed largely from the systematic egg and larval surveys. These have shown that over the years, as the sardine population was driven to lower and lower levels, the northern anchovy (*Engraulis mordax*) population increased tremendously. Some of the scientists theorize that the anchovy was an active mechanism in driving the sardine down. Others believe that it simply filled the gap left by the sardine. Regardless, the anchovy population is now at a very high level, with the biomass off Mexico and California between 2½ million tons, (by the most conservative estimate), and 5 million tons.

The department's initial sea survey work dealt with estimating sardine abundance, and sampling with a blanket net proved extremely effective and permitted preseason catch predictions which proved gratifyingly accurate. This net does not sample all other species adequately and we have turned to a midwater trawl dragged fairly near the surface. This appears to be an excellent sampling tool for anchovies, as well as other inhabitants of the upper layers. The program will be augmented substantially in 1966 better to delineate the magnitude and distribution of the resources off the coast.

The CalCOFI surveys have also demonstrated a huge population of hake (*Merluccius productus*) off California and Mexico (perhaps 3 million tons) as well as a large and very widespread population of jack mackerel (*Trachurus symmetricus*). Interestingly, six of the dozen most common eggs and larvae are those of bathypelagic fishes.

These results have poured out at a tremendous rate recently and much

of the data remains to be published. However, Murphy (1965) touches on many of these matters and most importantly concludes that overfishing played a prominent role in the collapse of the sardine fishery (long the department's contention) — this combined with a series of years of poor spawning success. Thus, some 18 years later, he has answered the initial question.

Based upon the tremendous increase in the anchovy population, CalCOFI recommended in 1964 that a carefully controlled scientifically planned experimental harvest be instituted (Murphy *et al.*, 1964). Theoretically, a selective fishery for anchovies might permit the sardine to resurge. Further, one might manage the combined resource at any ratio of anchovies to sardines desired, from a virtually pure anchovy fishery to a virtually pure sardine fishery.

This stimulated public interest not only in anchovies but hake as well. People saw fisheries aggregating hundreds of thousands of tons a year lying unused at their doorstep. Using the most conservative figures, the potential annual anchovy harvest off California is on the order of a quarter of a million tons. Estimates of the maximum sustainable yield range from at least half a million to perhaps as much as a million tons a year for California and Baja California combined. Hake data indicate a potential of perhaps 300 thousand tons.

DISCUSSION

It now becomes necessary to consider the interaction of politics and fish on the California scene as well as to consider the economics of exploiting these resources. California, like every state, manages its own living marine resources and exercises some control in international waters through laws governing landings. There is nothing, of course, to prevent fishermen from another state or from a foreign nation operating in the adjacent high seas and delivering their catches elsewhere. The fact that these resources extend off Mexico cannot be ignored, nor can the apparently growing interest of the USSR and Japan in the waters off our coast. But, for better or worse, California can, for the moment, control its destiny and manage fisheries for hake and anchovies with reasonable effectiveness.

Control mechanisms are awkward, for the state Legislature has delegated partial authority over commercial fisheries to the California Fish and Game Commission (such as controlling the use of whole fish in a reduction process) but has retained the balance to itself. The result is divided authority, and a very complex group of institutional problems.

California's recreational fishermen play an exceedingly important and effective part politically. Ocean sport fishing is very popular and its followers fear that the anchovy may go the way of the sardine. Their concern with anchovies is twofold. First, and most importantly, the anchovy forms the greater portion of the live bait used by ocean fishermen. Sec-

ondly, it plays a major but undetermined role as a forage organism for the primary game fish. It is most important that this question be resolved, and the department is instituting a food habit study under PL 88-309 (Bartlett Act).

Feelings on hake are less pronounced. If anything, the recreationalist might favor a hake fishery as the hake is believed to be a rather heavy predator on anchovies. But fundamentally the sport-commercial conflict is a most serious impediment to rational exploitation of California's marine resources and one which many of us are actively attempting to resolve.

The state is presently engaged in a major planning effort and the Department of Fish and Game has made a policy recommendation which, if adopted, should have a profound effect in this area. This policy says that first priority shall go toward satisfying the reasonable and legitimate demands of sport fishermen, and that commercial fishermen shall be encouraged to harvest any surplus consistent with the principle of maximum sustainable yield.

What as to economics? The only feasible use of anchovies and hake at this time is as fish meal, though clearance of fish protein concentrate by the Food and Drug Administration is a hoped-for possibility which would open a new avenue.

Interest in hake is low at present though there has been limited processing on a pilot basis and future prospects are encouraging.

The anchovy situation is quite different. The rising price of fish meal on the world market and the situation in the Peruvian anchovy fishery coupled with aggressive pro-anchovy fishery action by boat owners and by smaller processors in central California have changed the major producer's attitudes from one of indifference to varying degrees of enthusiasm. A bill authorizing a reduction fishery of 115 thousand tons per year passed the state Legislature this year. It was pocket-vetoed by the Governor because of possible constitutional defects (the bill called for a limited entry fishery) and because he felt this was a proper area for commission action.

Within the past week, the commission has authorized a closely regulated 75 thousand ton reduction fishery for 1965-1966. Whether this will be sufficient to bring about detectable permutations in the population remains to be determined, but the department has a scientific monitoring program, including a tagging experiment, ready to be put into effect in co-operation with CalCOFI.

CONCLUSIONS

We know of no other instance in which so much has been known about a fish in advance of a fishery or where there had been so much opportunity for advanced planning prior to commencement of a fishery. The scientific input for management will be available here if it ever is to be available, and given some resolution of managerial problems it should be possible

to test the theory that fishing for the anchovy will permit the sardine to resurge. Even if this does not happen, or if economically an anchovy fishery seems best — the state will still have a fishery where none existed before and one which we would hope to sustain indefinitely.

REFERENCES

MURPHY, GARTH I.

1965. Population dynamics of the Pacific sardine (*Sardinops caerulea*). Univ. Calif., San Diego, Doctoral Thesis, 169 p.

MURPHY, G. I., J. D. ISAACS, J. L. BAXTER, AND E. H. AHLSTROM

1964. Requirements for understanding the impact of a new fishery in the California Current System. *In* Mar. Res. Comm., Minutes, 6 March 1964, doc. 12, 5 p. Terminal Island, Calif., Dept. Fish and Game.

Deep Sea Biology

JORGEN KNUDSEN
Convener

The following paper was delivered at the Conference but has not
been received for publication:

HOWARD L. SANDERS: Density, Diversity, Structure, and Zonation of the Deep-
Sea Benthic Fauna.

THE ORGANIZATION OF DEEP-SEA FISHES

N. B. MARSHALL

British Museum (Natural History) London

ABSTRACT

Living organisms display certain ascending levels of organization—from molecules to ecosystems. Here we consider aspects of the organization of individuals and populations of deep-sea fishes.

Concerning their organ systems, bathypelagic teleosts (*ca.* 1000-4000 m) contrast strikingly with mesopelagic (*ca.* 200-1000 m), benthopelagic, and benthic species. Bathypelagic forms have not only lost the swimbladder, which is well developed in many mesopelagic and virtually all benthopelagic fishes, but there has been a marked down-grading of all their organ systems. These stringent economies are seen as evolutionary responses to the most barren major living space in the ocean. In the horizontal plane there are certain less pronounced contrasts between mesopelagic fishes of the central water masses and those inhabiting richer peripheral water masses.

At a higher level, populations of deep-sea fishes cohere by certain forms of communication. Light signals must play a leading role in the lives of mesopelagic species, but sounds, as shown by a wide development of drumming swimbladders in macrourids and brotulids, are much more important than lights to benthopelagic species.

Populations also cohere through reproductive adaptability. In particular, the recruitment of new lives would seem to be most critical in slope-dwelling fishes. To counter too great a dispersal of larvae from a relatively narrow dropping zone, the earliest stages live below the seasonal thermocline and assume deeper levels as they grow. But more careful exploration is needed to reveal such special life history patterns.

Biologists are well aware of certain ascending levels of organization in plants and animals. Molecules and macromolecules interplay to produce organelles. Organelles make cells. Cells are integrated in tissues, which in turn form the organs and functional systems of individuals. Individuals of a species live in populations, some of which may eventually evolve into new species. Species cohere in communities and ecosystems. But as Mather (1955) wrote: "... all levels of organization are interlocked and interdependent, so that a true understanding of one is impossible in isolation from the rest." In the space available, though, I must restrict this paper to certain aspects of the organization involving individuals and populations of deep-sea fishes.

Deep-sea fishes fit well in a conference on tropical oceanography. Some four out of five species have their reproductive living space within the bounds of the subtropical convergences. If the entire fauna is divided into these ecological groups: mesopelagic (*ca.* 100 to 1,000 m); bathypelagic (*ca.* 1,000 to 4,000 m); benthopelagic (species habitually swimming or hovering close to the bottom), and benthic (species habitually resting *on* the bottom), we see that members of the first three groups are predomi-

nantly tropical in the sense outlined above. But well over half the deep-sea benthic fishes belong to the families Zoarcidae and Liparidae, which are almost entirely confined to polar and temperate waters.¹ The Chlorophthalmidae and Bathypteroidae form the main groups of benthic fishes in tropical and deep-sea regions.

Deep-sea fishes live in rather uniform but demanding environments. Even in the clearest waters sunlight virtually disappears at depths close to 1,300 m. In the twilight above this level many fishes have risen above their surroundings by evolving highly sensitive eyes and elaborate systems of light organs. There is also a striking fall in the quantities of suitable food with depth. The biomass of plankton in the surface layers is generally 10 to 100 times greater than that at levels below 1,000 m. Such scarcity of food must have posed problems special to fishes, which have large and expensive propulsion systems. But, as we shall see, there is quite a diverse fauna of bathypelagic fishes.

The steady increase of pressure with depth (1 atmosphere per 10 m) poses less stress on fishes than has often been supposed. In the deep ocean the swimbladder functions just as well as a hydrostatic organ as it does in coastal seas. It is present in three-quarters or more of the individuals and in about half the species of mesopelagic fishes. Nearly all of the benthopelagic species (halosaurs, notacanth, *Synaphobranchus*, morids, macrourids, and brotulids) have a swimbladder, and it is not lost in the abyssal forms. As Kuhn and his colleagues (1963) have shown theoretically, a swimbladder with a rete mirabile system 10 mm in length should produce, by counter-current multiplication, gas pressures up to 1,000 atmospheres. Abyssal benthopelagic fishes have retia up to 25 mm in length: in fact, there is a direct linkage between the retial length and the depth of the living space in deep-sea fishes, (Marshall, 1960; 1965).

But bathypelagic and benthic deep-sea fishes have no swimbladder. This is understandable in members of the latter group, which spend most of their lives resting on the deep-sea floor. Such fishes, like their counterparts in coastal seas, have no need for a hydrostatic organ. The loss or regression of the swimbladder in bathypelagic fishes, many of which live at lesser depths than do some benthopelagic forms, is another question. As I have argued elsewhere (Marshall, 1960), the loss of this float is the key to great economies in the organ systems of bathypelagic fishes — economies that are evidently needed in their food-poor surroundings (see above). The regression of the swimbladder, which in well-endowed fishes carries well developed organs at neutral buoyancy, must have been followed closely by the paring down of all kinds of tissue systems. To take but one aspect, this down-grading of organization is reflected clearly in the sensory and central nervous systems. If we compare mesopelagic and

¹Even so, twelve zoarcid species were taken by the BLAKE in deep waters from the Galapagos Islands towards Central America and Mexico. (Garman, 1899.)

bathypelagic fishes, it soon becomes evident that the only element of these systems that is not markedly reduced in the second ecological group is the acoustico-lateralis complex. Moreover, the cerebellum and Mauthner's apparatus are particularly good indicators of the overall elaboration of fishes. Both are poorly developed in bathypelagic species (Figs. 1 and 2).

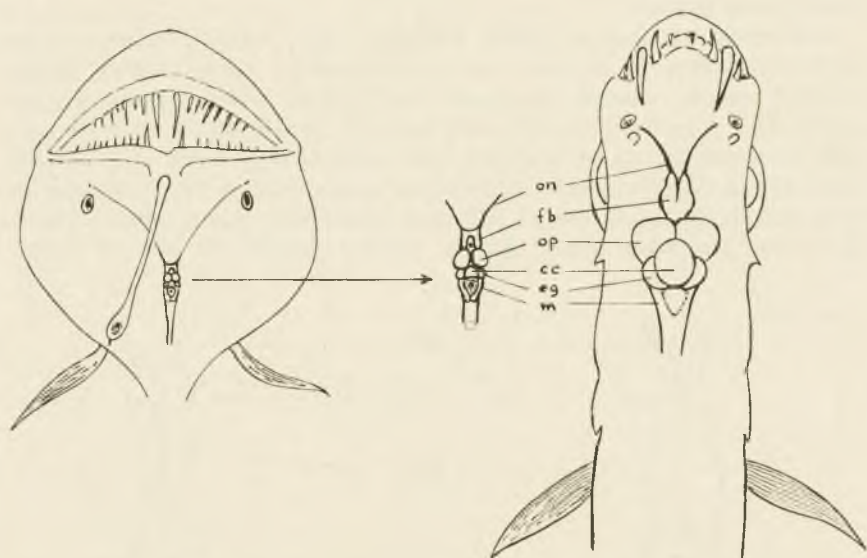


FIGURE 1. Two common predatory deep-sea fishes, on the left a female ceratioid angler-fish, *Melanocetus johnsoni*, a bathypelagic form ($\times 4$); and on the right a stomiatoid, *Astronesthes niger*, a mesopelagic form ($\times 8$). Though the angler-fish is about $1\frac{1}{2}$ times the volume of the stomiatoid, note its very reduced brain, which is shown again on the same scale as that of *Astronesthes*. cc, corpus cerebelli; eg, eminentia granularis cerebelli; fb, forebrain; m, medulla; on, olfactory nerve; op, optic lobe.

Even so, by reducing their organ systems, more particularly the muscles and skeleton, bathypelagic fishes gained neutral buoyancy and thus an ever present means of saving energy. It is surely significant that the bathypelagic fauna is dominated by ceratioid angler-fishes, the males of which are dwarfs and the females patient floating traps, baited with a luminous lure.

These striking changes in the organization of deep-sea fishes are thus in the vertical plane of deep-sea space. Lesser, but quite appreciable changes may be detected in the horizontal plane. I am thinking of certain biological contrasts between the central water masses and those on their periphery. The central water masses, formed by sinking processes at the subtropical convergences in winter, overly the permanent thermocline (centered at ca.

500-800 m). They underly the deepest blue waters of the open ocean, which are appreciably less productive than are the peripheral waters. Compared to the equatorial systems, for instance, where upwelling is more lively, the central water masses contain smaller standing crops of plankton and fewer fishes, (e.g., white-tipped sharks, silky sharks, yellow-fin tuna, skipjacks, wahoo, dolphin-fish, etc.). Sea birds are less common over the central water masses.

Concerning mesopelagic fishes, Ebeling (1962) found that four dwarf species (one inch [25 mm] or less) of *Melamphaes* live exclusively in the relatively sterile western equatorial and central water masses. Larger species (4 - 6 inches [100-152 mm]) inhabit peripheral water masses or parts of water masses of relatively high productivity. There is a parallel in the North Atlantic, where *Chauliodus danae* lives in the central water mass and grows to a length of 133 mm. *Chauliodus sloani*, which lives in the richer, peripheral water masses, reaches double the size of *danae*.

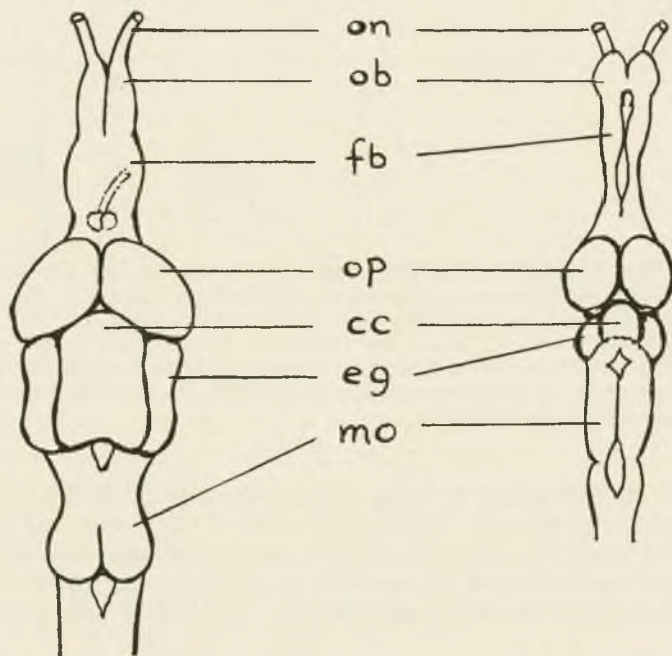


FIGURE 2. Left, the brain of *Gonostoma denudatum*, a mesopelagic species, and right, the brain of its bathypelagic relative, *G. bathyphilum* (both $\times 10$). Though both brains came from individuals of the same standard length (130 mm), note the smaller brain of the bathypelagic species, and, in particular, the very reduced cerebellum. cc, corpus cerebelli; eg, eminentia granularis cerebelli; fb, forebrain; mo, medulla oblongata; ob, olfactory bulb; on, olfactory nerve; op, optic lobe.

Moreover, *sloani* has a better developed gill system. Some such differences are seen in the melamphaid genus, *Scopelogadus* (Ebeling & Weed, 1963). In brief, some mesopelagic fishes have become adapted for life in the food-poor central water masses by a drastic reduction in size and even by some regression in their organ systems. With such ideas in mind, further exploration of the central water masses should be rewarding.

Turning now to a higher level of organization, the most thorough investigations of deep-sea fishes are gradually indicating that each species is composed of populations. Each population occupies a particular living space and some may be found there year after year. The coherence of a population is due partly to communication between its members. In the mesopelagic twilight zone we immediately think of the evolution of a remarkable diversity of light-organ systems. Lights used as signs by schooling species and those involved in sexual activities must do much to keep populations in being. But there is no evidence that sounds play a part in the communications of mesopelagic fishes. Though many individuals and species have a swimbladder, this is not provided with drumming muscles, nor is there any sign of stridulatory mechanisms. The absence of a swimbladder or of likely stridulatory structures in bathypelagic fishes also suggests that this is a silent fauna. But near the deep-sea floor there is a remarkable change. Nearly all macrourids and brotulids, which make up well over half of the benthopelagic fauna, have drumming muscles on the swimbladder. In the macrourids and oviparous brotulids the males alone have these means of sound production. Most probably sounds are a short-range way of communication in slope-dwelling species during the breeding season. At all events, abyssal macrourids, which are spread more thinly over the ground, have no drumming muscles (Marshall, 1965).

In contrast to this sonic profusion, there is no great elaboration of light organ systems, such as is typical of the mesopelagic fauna. Certain morids and a number of macrourids have a tubular or globular light gland on the abdomen, which may well play a part in mating activities.

Lastly, populations maintain their organization — they cohere and endure — through reproductive adaptability. In particular the life history pattern must be such that there is adequate recruitment of new individuals. Nearly all mesopelagic and bathypelagic fishes produce floating eggs and the larval life is passed in the lively, plankton-rich surface waters. Now the populations of these fishes are deployed over great areas of the ocean, so there is room enough for considerable dispersal of the eggs and larvae from spawning areas. Most benthic and benthopelagic deep-sea fishes do not enjoy this latitude. They are bound narrowly to the continental slopes, where food is more plentiful than in the abyssal reaches. Thus, the addition of new lives to slope dwelling populations calls for a precision in recruitment that is not needed by mesopelagic and bathypelagic fishes. Many slope-dwelling species, for instance macrourids, and probably oviparous

brotulids, reproduce by means of mid-water larvae, and for such young, as they grow, metamorphose and descend, entry to an adult existence is a settling on a narrow dropping zone.

Concerning the macrourids, there is some inkling of how their life history pattern is adapted to these rather critical circumstances. The eggs, which seem to be shed and fertilized near the deep-sea floor, are presumed to develop and hatch as they float upwards. The youngest larvae are most common around depths of 200 m; older stages live at deeper mid-water levels (Marshall, 1965). Most likely, the nursery grounds are close below the seasonal thermocline, where the circulation is presumably slower than that in the surface mixed layer. If so, there is less chance of the larvae being dispersed away from narrow slope waters. This kind of history pattern is evident in Pacific hake, *Merluccius productus* and in the bathylagids, *Leuroglossus stilbius* and *Bathylagus wesethi*; for Ahlstrom (1959) found that the eggs and larvae of these three species — in contrast to other pelagic fish eggs and larvae off California and Baja California — were most abundant within and below the thermocline. But hake, which are alternately mid-water and benthopelagic fishes, are even more narrowly tied to the slopes than are most of the macrourids. *Leuroglossus stilbius*, though a mesopelagic species, is seemingly distributed along a narrow band off the western coasts of North and Middle America. In these species, a near-thermocline early life-history may well, as postulated for macrourids, counter the dispersion of larvae away from restricted adult living spaces.

But our knowledge of life-history patterns in slope-dwelling fishes is well behind that amassed for mesopelagic and bathypelagic species. Even so, the above considerations should help to indicate the lines of future explorations, which will need to be more precise than is usual.

REFERENCES

- AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull. U.S., 60 (161): 107-146.
- EBELING, A. W.
1962. Melamphaidae I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Gunther. Dana Rep., 58: 1-164.
- EBELING, A. W. AND W. H. WEED
1963. Melamphaidae III. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. Dana Rep., 60: 1-58.
- GARMAN, S.
1899. Reports on an exploration off the west coast of Mexico, Central and South America and off the Galapagos Islands in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer 'Albatross' XXVI—The Fishes. Mem. Harv. Mus. comp. Zool., 24: 1-431.
- KUHN, W., A. RAMEL, H. J. KUHN, AND E. MARTI
1963. The filling mechanism of the swimbladder. Experientia, 19 (10): 457-511.

MARSHALL, N. B.

1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. *Discovery Rep.*, 31: 1-122.

1965. Systematic and biological studies of the macrourid fishes. *Deep-Sea Res.*, 12: 299-322.

MATHER, K.

1955. Biological organization. Presidential Address, Brit. Assoc. Adv. Sci. 1955. *Advancement of Sci.*, XII: 250-257.

THE TAXONOMY AND ZOOGEOGRAPHY OF THE DEEP-SEA HOLOTHURIANS IN THEIR EVOLUTIONARY ASPECTS

BENT HANSEN
Zoological Museum, Copenhagen

ABSTRACT

Problems regarding the distribution and derivation of the deep-sea fauna are discussed in the light of a taxonomic revision in progress of the deep-sea holothurians. The revision is based on work with the collection from the GALATHEA Expedition 1950-52 combined with re-examination of collections from previous expeditions.

INTRODUCTION

The deep sea presents to its inhabitants a remarkably uniform environment compared to the land and the littoral zone of the sea. Differences in the temperature and composition of the water and in the nature of the bottom deposits are small, and it is difficult to demonstrate environmental factors which may limit the distribution of a species or break it up into isolated populations.

This uniformity of the environment raises questions regarding species-formation and evolution in the deep sea. While speciation by geographical segregation is known to be of paramount importance on land and in the shallow sea (Mayr, 1963), very little is known about the mode of speciation in the deep sea or about the origin and evolution of the higher taxa of the deep-sea fauna.

The present contribution to the study of these questions is based on work in progress on the material of holothurians (especially of the order Elaspoda) collected by the Danish GALATHEA Expedition 1950-52, combined with a re-examination of the materials from most previous deep-sea expeditions. The study of these materials adds to our knowledge mainly in regard to the taxonomy, the vertical range, and the geographical distribution of the species. We shall now try to combine some of the knowledge gained in these three fields of study in an attempt to throw light upon the nature of a possible species-formation in the deep sea.

VARIATION IN TAXONOMIC CHARACTERS

It is now generally recognized that a thorough taxonomic knowledge of a group is essential for an understanding of many other aspects of its biology. This may be especially true when we are dealing with zoogeography. Of course, the limits of distribution of a species can only be demonstrated if we are able to decide upon the synonymy within the genus. But this dependence of zoogeography upon taxonomy becomes

even more pronounced when we try to analyze the distribution at the intraspecific level — to demonstrate a possible geographical pattern in the variation of the taxonomic characters. It is not surprising that very little is known about this type of variation in deep-sea animals. By far most of the deep-sea species are known from too few specimens and too few localities to make possible the demonstration of such a variation.

Apart from the scarcity of material available for study, the demonstration of a geographical variation in the species is made difficult by the existence of an often pronounced individual and local variation. In fact, differences between populations from two distant stations are not necessarily indicative of a geographical variation; they may represent purely local features.

Despite these difficulties and sources of error it seems worthwhile to attempt to demonstrate a possible geographical pattern in the variation of the better known species. Firstly, we cannot avoid making our decision as to whether specimens found at a definite locality are to be regarded as a separate species, or as a geographical form of another species. Secondly, the variation suggested by our present scattered findings may form the basis for future work with the species. Through a detailed knowledge of the geographical variation we may hope to get an insight into the evolutionary forces which act upon the species of the deep sea.

BATHYMETRICAL DISTRIBUTION

As a material for the study of speciation and evolution in the deep sea, the holothurians have the advantage that almost no admixture with species from shallower depths has taken place. The deep-sea groups of holothurians are only distantly related to the littoral groups, and even within the deep sea itself a remarkable correlation exists between taxonomic groupings and bathymetrical distribution. Apparently, species formation as well as evolution of higher taxa has taken place within the bathymetrical zones which the groups inhabit today. The following examples serve to illustrate the point.

The order Elasipoda, one of the five orders of the class Holothurioidea, is confined to the deep sea; it comprises one half of the about 180 known species of deep-sea holothurians.

A mapping of the bathymetrical distribution of the species of two of the families of the Elasipoda, the Deimatidae and Laetmogonidae (Fig. 1), combined with a taxonomic revision of the families indicates that the relationships are closest between species from the same bathymetrical zone. The features upon which the taxonomy of the family Deimatidae was based were found to be less reliable than thought before. Thus, the spicules of the species *Oneirophanta mutabilis* comprise in their variation the type regarded as characteristic of the genera *Orphnurgus* and *Scotodeima*. Instead, the shape of the tentacle-discs may form a better

basis for a subdivision of the family. The discs seem to belong to two distinct types in the family; in the species *Deima validum*, *Scotodeima setigerum*, and *Oneirophanta mutabilis* the discs are shield-shaped, whereas in the species *Orphnurgus glaber*, *O. protectum*, and *O. asper* they possess dendritic ramifications (which may, however, be completely retracted). The shape of the tentacle-discs is unknown in the species *Oneirophanta conservata*, which therefore must be omitted from our considerations.

A division of the family according to type of tentacle would largely separate the bathyal species from the abyssal, although the species *Deima validum* to some degree blurs the distinction, being one of the few species of holothurians which range over the greater part of both the bathyal and abyssal zones.

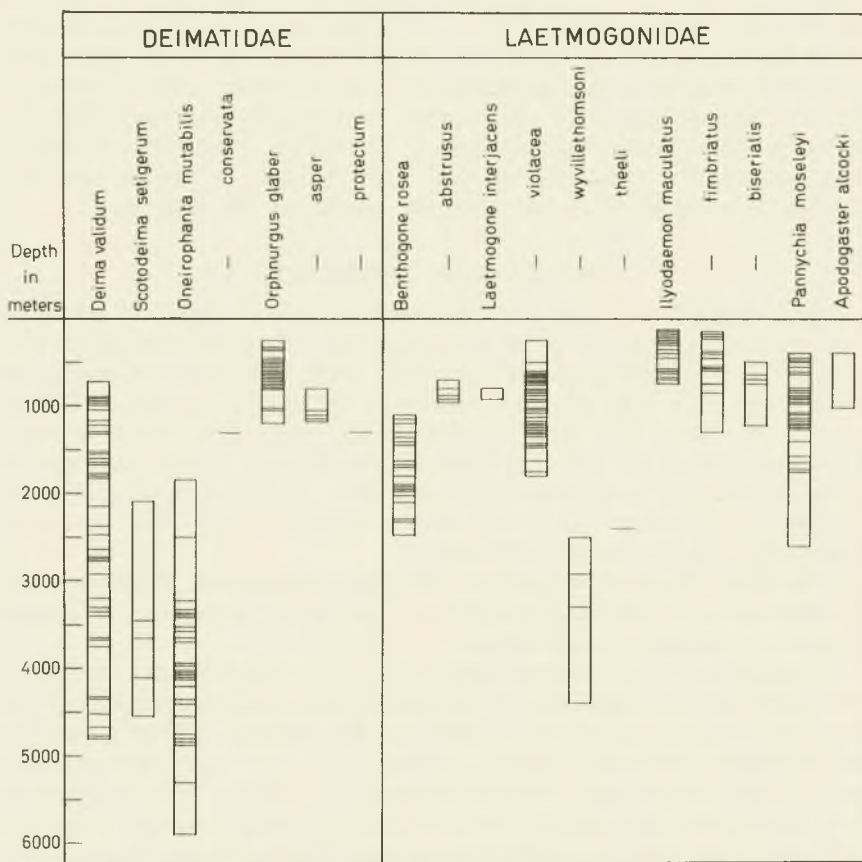


FIGURE 1. Bathymetrical distribution of the species of the families Deimatidae and Laetmogonidae. Each find is indicated by a line.

The family Laetmogonidae is characteristic of the bathyal zone. The only two abyssal species, *Laetmogone wyvillethomsoni* and *L. theeli*, are closely related.

The family Psychropotidae is abyssal. A few species range over the upper abyssal and the deeper bathyal zone, but none are exclusively bathyal.

The family Elpidiidae is abyssal, with a few species penetrating into the bathyal zone.

Similar features of bathymetrical distribution are found in the other four orders of the Holothurioidea. Of the three families of the order Aspidochirota, the Synallactidae is confined to the deep sea; the family contains one-fourth of the known species of deep-sea holothurians. The family Stichopodidae is littoral, with only the species *Stichopus tremulus* descending to about 1200 m depth. The family Holothuriidae is found in shallow water, especially in the Tropics. One genus, *Gastrothuria*, with the single species *G. limbata*, was known from a depth of 564 m. Examination of a number of specimens taken at a station of the Danish ATLANTIDE Expedition (depth 206-650 m) proved that the genus is a typical member of the Synallactidae, except in the fact that tentacle-ampullae are present. This feature, per definition, would exclude the referring of the genus to the family Synallactidae. However, the combination of features found in the genus *Gastrothuria* shows that a strict adherence to the presence or absence of tentacle-ampullae as a defining character of the two families leads to an unnatural classification.

The transferring of the genus *Gastrothuria* to the family Synallactidae, which is more in accordance with its natural affinities, gives to the two families an entirely different depth range.

The correlation between taxonomic groupings and bathymetrical distributions is also present at the species level in the Aspidochirota. Thus, in the genus *Synallactes* the abyssal species are more closely related to each other than any of them are to the bathyal species of the genus.

Examples of a similar kind could be cited from the other orders of holothurians, the correlation between taxonomy and bathymetrical distribution being found throughout the class.

The environmental factors responsible for the restriction of the taxa to certain depths are not easy to point out. Temperature is apparently the decisive factor in the bathymetrical distribution of the species which ascend into shallower depths in colder regions (*Elpidia glacialis* in the Arctic, *Scotoplanes globosa* off northern Japan).

However, by far most of the deep-sea species stick to their depths even in regions where the temperature would permit them to live in shallower water. For most of the deep-sea species the temperature is apparently not the crucial limiting factor.

This non-dependence of temperature in the bathymetrical distribution of

the species supports the idea that the deep-sea groups of holothurians are old inhabitants of the bathymetrical zones which they inhabit today. There is no reason to assume that the deep-sea groups of holothurians occurred in shallower water during colder climatic periods.

A factor other than the temperature which might limit the species to certain depths throughout the distributional area would be found in the increasing pressure of the water. Indeed, with the omission of the temperature factor, it seems difficult to avoid the conclusion that the deep-sea groups are physiologically adapted to the high pressures under which they live.

GEOGRAPHICAL DISTRIBUTION AND VARIATION

Work with the GALATHEA material shows that the deep-sea holothurians are as a rule more widely distributed than known before. In abyssal species a worldwide distribution may even prove to be the rule, although at the present time most species are known from too few finds to allow this conclusion.

In the following, the distribution and variation of a few of the better

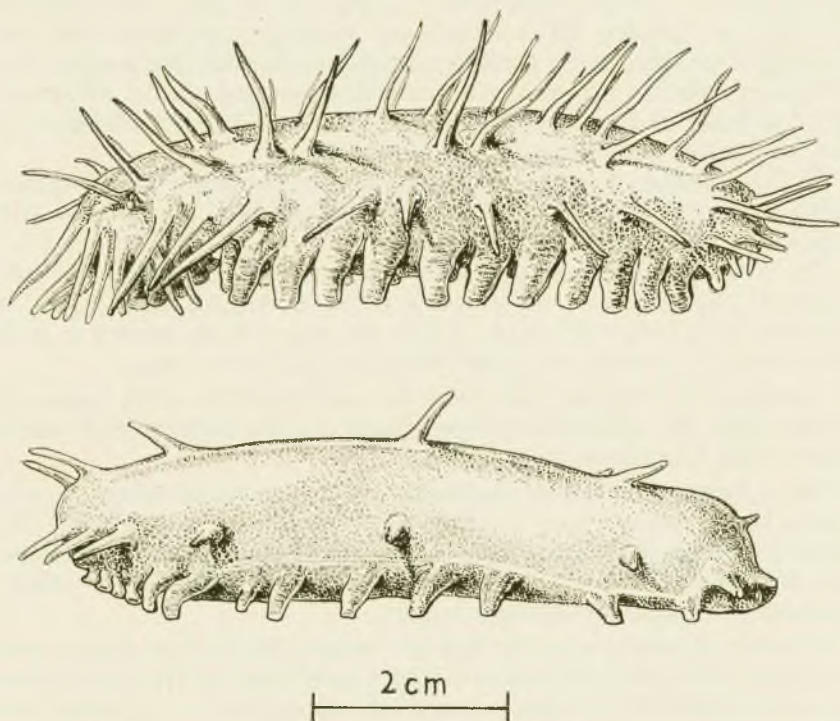


FIGURE 2. *Oneirophanta mutabilis affinis*. Two specimens from the GALATHEA st. 716 ($9^{\circ} 23'N$, $89^{\circ} 32'W$; depth 3570 m). (Julie Tesch del.).

known species are examined with a view to finding evidence for the existence of geographical speciation in the deep sea.

Oneirophanta mutabilis (Figs. 2-3) was known from the CHALLENGER Expedition to be a cosmopolitan, abyssal species. Two species subsequently described from the same genus, the North Atlantic *O. alternata* and the Eastern Pacific *O. affinis*, are here regarded as synonyms of *O. mutabilis*. Both species were taken within the distributional area of *O. mutabilis* and are reminiscent of specimens of this species taken in the same area.

A geographical variation is shown by the number of dorsal papillae. In the Eastern Pacific the variation in number is 5-35 pairs. However, in the greater part of the distributional area of the species 4-14 pairs are present, although at no single locality is the whole variation represented.

A similar geographical variation is shown by the shape of the tentacle-discs. Outside the Eastern Pacific the discs bear 6-10 rounded knobs on the margin. In the Eastern Pacific this type of tentacle occurs simultaneously with tentacles with a smooth, or even slightly incised, margin of the discs.

The spicules of the skin (Fig. 4) in this species consist of large, reticulated plates. In some Eastern Pacific specimens the spicules do not differ from the usual type; but in most specimens the spicules are more sturdy and slightly smaller. Besides, a peculiar type of spicule with an irregular meshwork surrounding a long, median rod occurs in many specimens.



FIGURE 3. Distribution of the two subspecies of *Oneirophanta mutabilis*.

This type of spicule has not been found in specimens from other localities.

Based on the differences in number of papillae, shape of tentacle-discs, and shape of spicules, the species *O. mutabilis* may be divided into two geographical subspecies, *O. m. mutabilis* and *O. mutabilis affinis*. The subspecies *affinis* comprises the specimens hitherto referred to the species *O. affinis* Ludwig and the specimens of the species *O. mutabilis* reported from the Eastern Pacific (Ludwig, 1894; Clark, 1920). The subspecies *mutabilis* comprises all the other specimens hitherto referred to the species

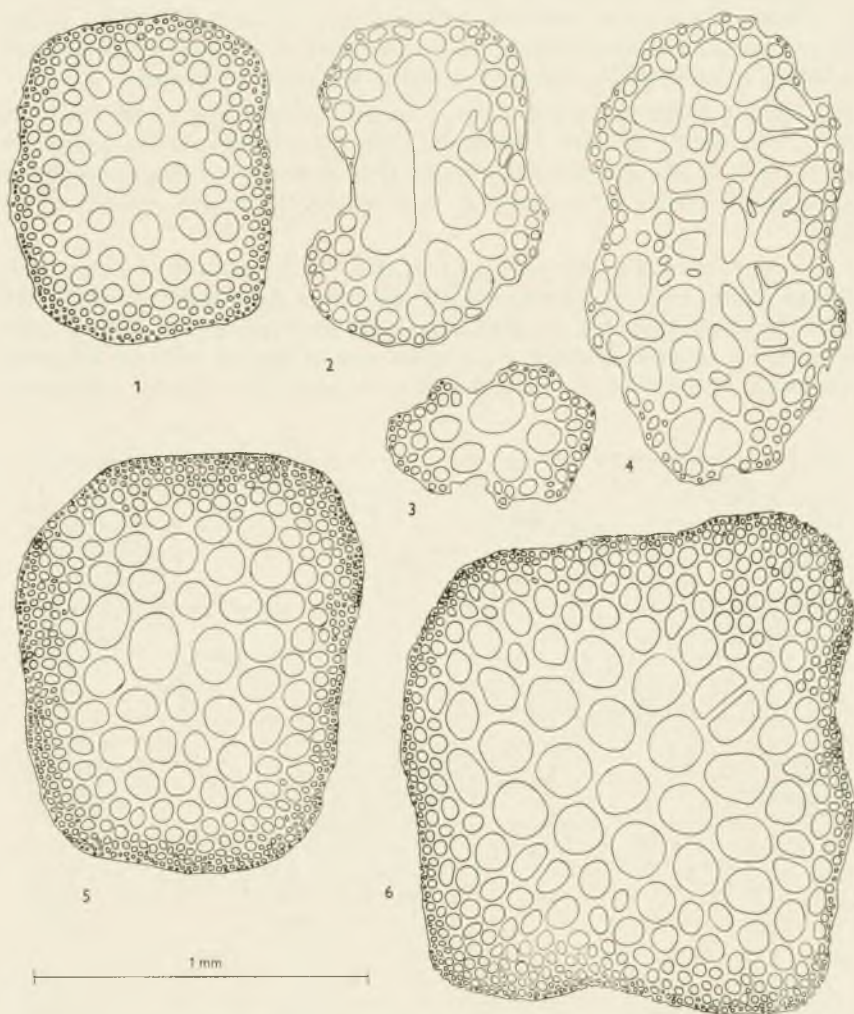


FIGURE 4. *Oneirophanta mutabilis*. Spicules. 1-5, subspecies *affinis*; 6, subspecies *mutabilis*.

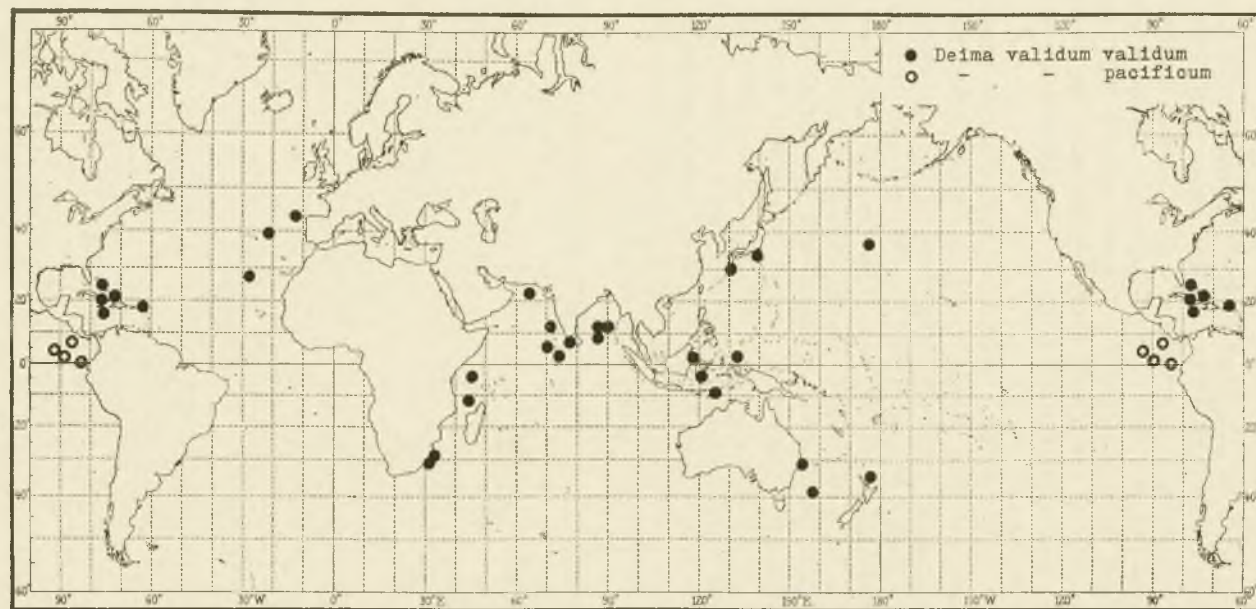


FIGURE 5. Distribution of the two subspecies of *Deima validum*.

O. mutabilis Théel, as well as the species *O. alternata* Perrier (Théel, 1882; Perrier, 1902).

A better knowledge of the variation in the species might reveal the presence of characteristic populations also from other areas. Thus, a high number of dorsal papillae was present in a CHALLENGER specimen from the North Pacific (17 left and 19 right papillae) and in a GALATHEA specimen from off South East Africa (17 left and 18 right papillae). However, as the range of variation in number is unknown, we do not know whether the high number of dorsal papillae in these specimens is indicative of geographical variation.

Deima validum (Fig. 5) differs in details of its distribution in many ways from *Oneirophanta mutabilis*. However, also in *Deima validum* the Eastern Pacific specimens differ markedly from those of the remaining part of the distributional area. The species *Deima validum* is here taken to include all the six described species of the genus. The species *D. pacificum* Ludwig 1894 is retained as a subspecies, *Deima validum pacificum*, while the species *D. validum* Théel 1882 together with four other species (*D. fastosum*, *D. blakei*, *D. atlanticum*, and *D. mosaicum*) forms the subspecies, *Deima v. validum*. The two subspecies differ especially in the number of dorsal papillae (4-10 pairs in subspecies *validum*, 11-16 pairs in subspecies *pacificum*). The variation in West Indian specimens of *D.v. validum* comprises the whole variation found in that subspecies, but at all other localities the variation seems to be more narrow.



FIGURE 6. Distribution of the two species of the genus *Scotoplanes*.

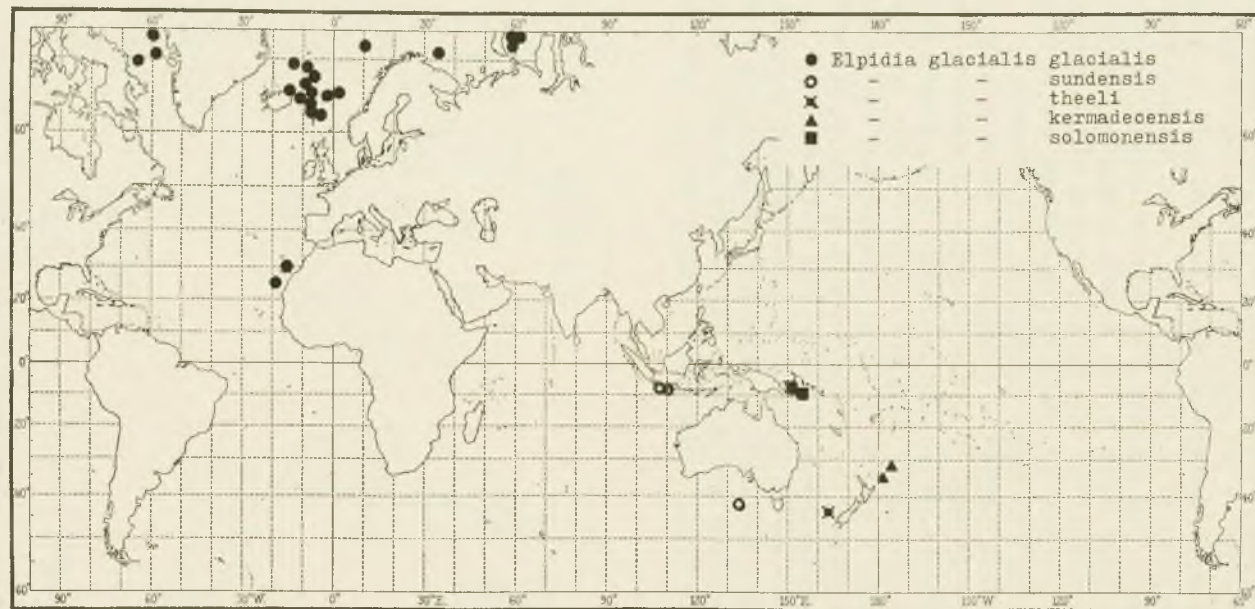


FIGURE 7. Distribution of the five subspecies of *Elpidia glacialis*.

Some geographical variation is also present in the shape and size of the reticulated plates of the skin. In the subspecies *validum* the plates usually reach a size of 4-7 mm across and have one or more layers of calcareous network superimposed upon the basal plate. In the subspecies *pacificum* the plates do not exceed 2 mm across and they possess no additional networks. The differences between the spicules, however, are not as distinct as those shown by the number of papillae. Spicules as small as those of *pacificum* and with feebly-developed additional layers of network may be prevalent also within the distributional area of the subspecies *validum* (off the West Indies, Tasman Sea, and Indonesia).

A geographical variation of a similar kind, but at a higher taxonomic level, is shown by pairs of species, of which one member of the pair is widely distributed while the other is restricted to the Eastern Pacific.

The genus *Scotoplanes* comprises two species (Fig. 6). The smooth-skinned species *S. globosa* is almost cosmopolitan, but in the Eastern Pacific it is replaced by a closely related species, characterized among other things by the skin being covered with vesicular warts.

The only two abyssal species of the genus *Molpadia* represent a similar case, the widely distributed *Molpadia blakei* being replaced in the Eastern Pacific by the closely related species *M. granulata*. Possibly, the two abyssal species of the family Laetmogonidae should also be cited. The species

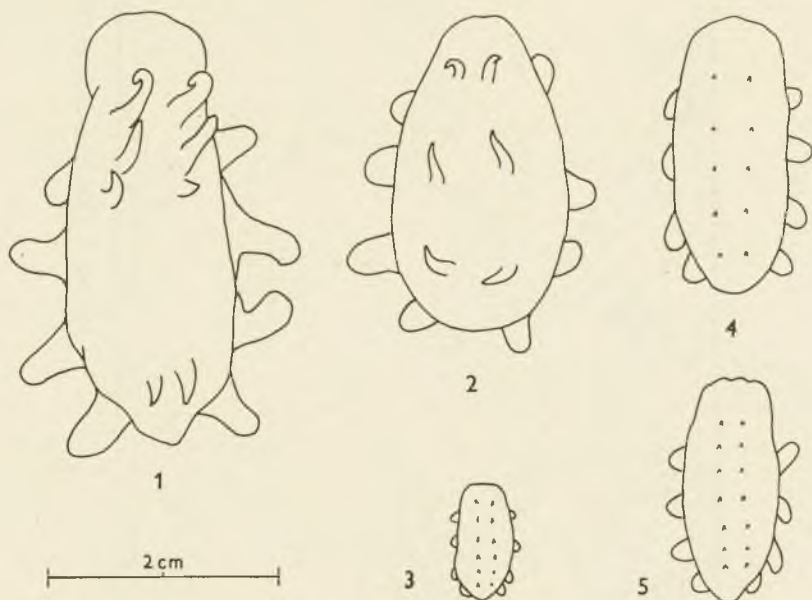


FIGURE 8. The five subspecies of *Elpidia glacialis*. 1, *glacialis*; 2, *sundensis*; 3, *theeli*; 4, *kermadecensis*; 5, *solomonensis*.

Laetmogone wyvillethomsoni is widely distributed while the closely related species *L. theeli* is known from the Eastern Pacific (so far, however, only from a single station).

These species-pairs represent a further step in the evolution compared to the conditions found in *Oneirophanta mutabilis* and *Deima validum*. A geographical subspeciation has here lead to the separation of two distinct species.

The species *Elpidia glacialis* (Fig. 7) represents a different case of geographical variation in abyssal holothurians. Based on differences in the number, size, and arrangement of the dorsal papillae (Fig. 8), and to some degree in the shape and size of the spicules, the species has been divided into five geographical subspecies (Hansen, 1956). The species occurs in abundance in the North Polar Basin with its negative temperatures and in the hadal parts of a number of trenches, but it has also been found in smaller numbers outside these regions. As yet, we have finds from too few localities to demonstrate the limits of distribution of the subspecies, or to point out the ecological factors or distributional barriers which may have been responsible for the separation of the species into subspecies. It is remarkable, however, that the specimens taken off the coast of Morocco are similar to those from the North Polar Basin, despite the fact that this basin is separated from the Atlantic Ocean by what might be supposed to be an effective zoogeographical barrier — the North Atlantic Ridge. Furthermore, it is interesting that the specimens taken in the Sunda Trench by the GALATHEA are similar to the specimen taken south of Australia by the CHALLENGER.

Also, in the bathyal holothurians we find the allover pattern of widely distributed species with a geographical variation. Different types of distribution are represented, but in contrast to the abyssal species, none of the bathyal species seem to be cosmopolitan.

As an example of geographical variation in a bathyal species we may take the deimatid, *Orphnurgus glaber* (Fig. 9). This species is here taken to include six previously described species. A geographical variation can be demonstrated in the number of papillae and tubefeet (Table 1) and in the shape of the spicules (Fig. 10), although an extensive individual variation in all three features tends to obscure the geographical variation.

In general, the dorsal papillae decrease in number from the Bay of Bengal to the Hawaiian Islands. The tubefeet, on the other hand, are fairly constant in number over the whole distributional area; only the specimens taken off the Kei and Jolo islands fall outside the variation found at other localities.

The spicules may vary extremely in shape, even within a single specimen. Nevertheless, a geographical pattern seems to be present in the distribution of the various types of spicule. Rods with spatulated ends (or with open ramifications at the ends) occur over the whole area of distribution.



However, in the Bay of Bengal and the Bali Sea these spicules are possibly the only ones present. Transformed rods in the form of irregular, ellipsoid and spherical bodies prevail in the remaining part of the area of distribution. In Hawaiian and Japanese specimens these bodies are partially covered with small spines (Fisher, 1907; Ohshima, 1915).

A closely related bathyal species, *Orphnurgus asper*, is known from off the West Indian Islands. The spicules of this species are small, spinous rods, a type which is not known from the species *O. glaber*.

TABLE 1

Orphnurgus glaber. NUMBER OF TUBEFEET AND DORSAL PAPILLAE IN SPECIMENS FROM DIFFERENT LOCALITIES.

Locality	Pairs of tube feet	Pairs of papillae	Number of specimens
Bay of Bengal	15-25	60-100	3
Bali Sea	18	125	3
Kei and Jolo islands	30-60	30-75	7
Japan	16-25	15-46	18
Hawaii	17-22 ¹	12-36 ¹	123

¹One specimen had 30 pairs of tube feet; another had forty-odd papillae.

THE HADAL FAUNA

The hadal fauna occupies the greatest depths of the oceans, from 6000 to 11,000 m. Being confined to geographically isolated deep-sea trenches, the hadal fauna is of interest in a discussion of the factors involved in geographical speciation in the deep sea.

Of the five deep-sea trenches investigated by the GALATHEA, the Kermadec Trench was especially well studied, with stations covering not only the hadal, but also the abyssal zone. The three prevailing species of holothurians in the hadal part of the Kermadec Trench were *Elpidia glacialis*, *Scotoplanes globosa*, and *Peniagone willemoesi* (syn. *P. vedeli* Hansen, 1956). All three species have a remarkably wide bathymetrical distribution, quite apart from their occurring at hadal depths. *Elpidia glacialis* is the shallowest recorded member of the Elasipoda, being found at a depth of only 70 m in the Arctic. *Scotoplanes globosa* has been taken at 545 m off northern Japan, an unusually shallow record for the family Elpidiidae. Even the finding of the species *Peniagone willemoesi* (under the name *P. azorica*) at 1385 m depth in the North Atlantic is exceptional in this pronouncedly abyssal genus.

Two other of the common abyssal species in the trench, *Oneirophanta mutabilis* and *Psychropotes longicauda*, were absent from the hadal stations. Both species are cosmopolitan and characteristic of the deeper part of the abyssal zone, with almost no records shallower than 3000 m. Apparently,

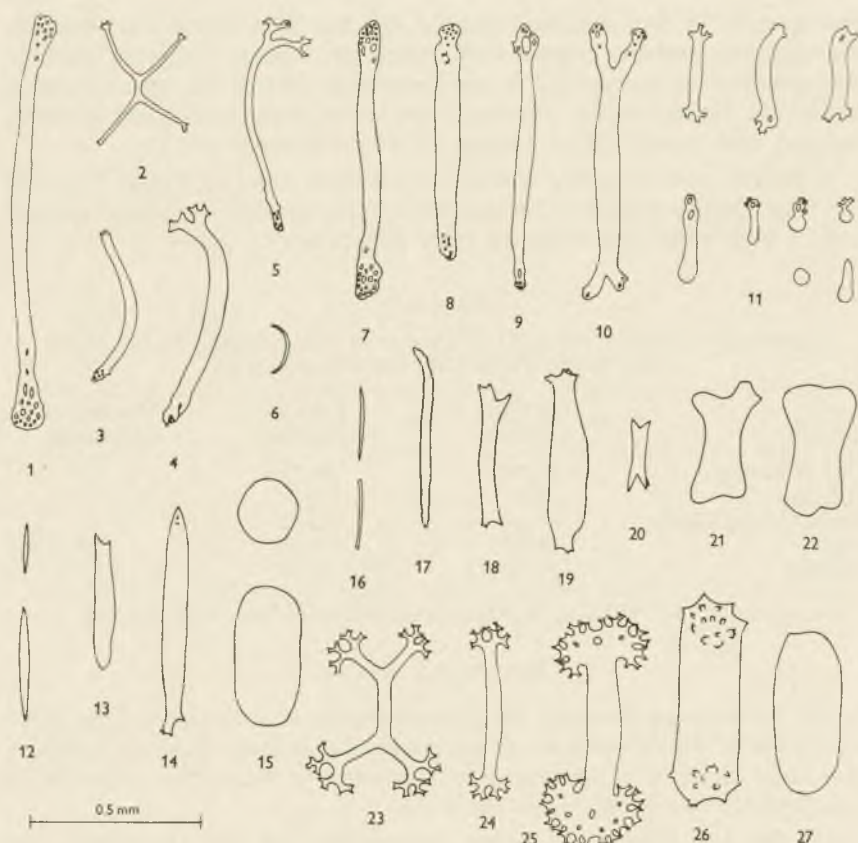


FIGURE 10. *Orphnurgus glaber*. Spicules. 1-6, Bali Sea; 7-15, off the Kei Islands; 16-22, off the Jolo Islands; 23-27, off the Hawaiian Islands.

the hadal zone has been populated by eurybathic rather than by deep abyssal species.

Of the three abysso-hadal species of the Kermadec Trench, two (*Elpidia glacialis* and *Scotoplanes globosa*) are known to occur also in other trenches. (Deep-sea photographs, taken by the American PROA Expedition and placed at my disposal, show the occurrence of *Scotoplanes globosa* in the New Britain [7665-7710 m] and the New Hebrides trenches [6740-6760 m].)

In view of this apparent tendency of the abysso-hadal species to penetrate into more than one trench it is surprising that only 3 out of 109 exclusively hadal species are common to two or more trenches (Wolff, 1966). If it is true that many of these hadal species are derived from abysso-hadal species once common to several trenches, this high degree of

endemism is due either to an extinction of the species in the other trenches, or to a divergent evolution in the different trenches subsequent to the restriction of the species to hadal depths. The role played by a possible diverging evolution in the trenches might be tested by a careful taxonomic study of the hadal fauna. Possibly, a number of trench-species could be arranged into superspecies, which have originated by splitting up of a species into isolated trench-populations.

Although superspecies are not known among the hadal holothurians, a study of this group gives some indication of the evolutionary forces which act upon the species of the trenches.

The two subspecies of *Elpidia glacialis* taken in the New Britain and Kermadec trenches may have evolved in isolation in the hadal parts of these trenches. At any rate, we have fairly good evidence of the absence of the species from abyssal depths in the Kermadec Trench. On the other hand, the fact that the specimens from the Sunda Trench are similar to the specimen taken by the CHALLENGER south of Australia calls for circumspection in the demonstration of subspecies-formation in the trenches.

Another indication of the existence of evolutionary forces in the trenches is shown by a peculiar correlation between taxonomic features and depth in the two abysso-hadal species of the Kermadec Trench.

TABLE 2
Scotoplanes globosa. NUMBER OF TUBEFEET IN SPECIMENS FROM THE
KERMADEC TRENCH

Tubefeet- pairs Depth (m)	5	6	7
2640	1	15	25
4410		1	2
5850-5900	5		
6620-6730	12	14	
6660-6770	2	12	

In the species *Scotoplanes globosa* the hadal specimens differ from the abyssal ones by the number of tubefeet (Table 2) and by the calcareous rods of the skin being more spinous (Fig. 11). Apparently, there is more communication between the specimens from the two hadal stations than between the hadal and abyssal specimens, despite the fact that the hadal stations are separated by a greater distance.

A similar variation with depth is shown by the other abysso-hadal species of the Kermadec Trench, *Peniagone willemoesi*. Here, the apophyses on the dorsal spicules are higher in the abyssal than in the hadal specimens (Fig. 12).

These variations with depth are not easy to interpret. The apparently limited communication between hadal and abyssal specimens might be due

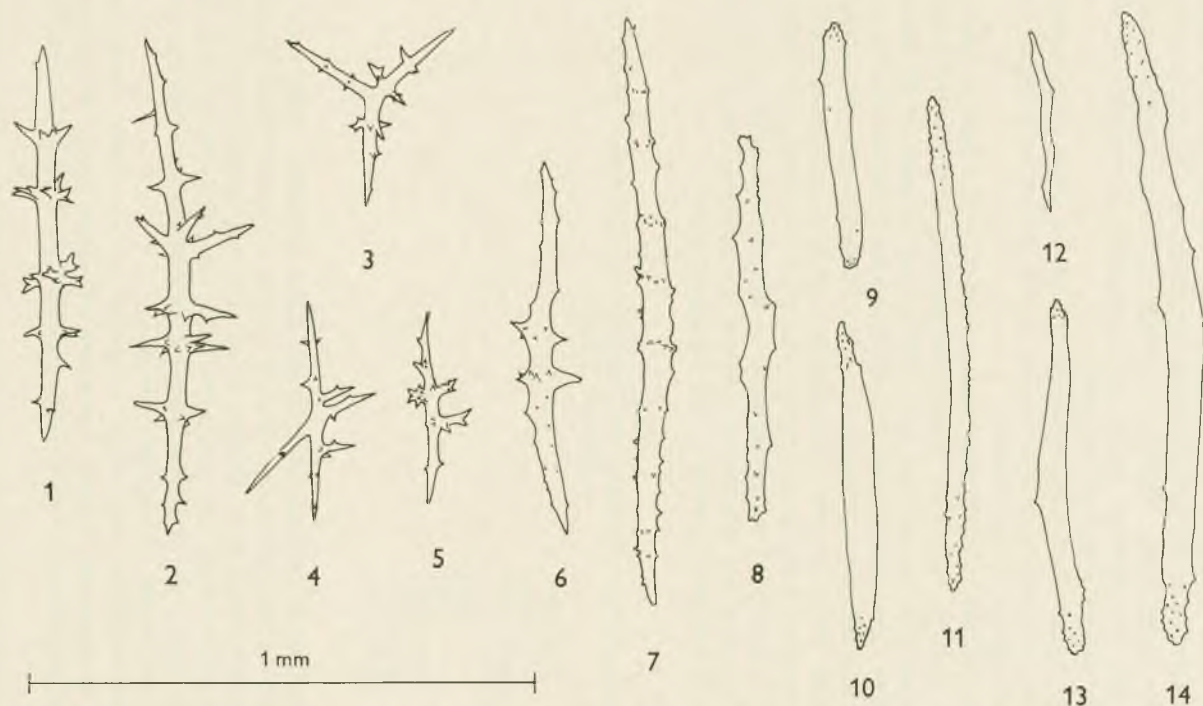


FIGURE 11. *Scotoplanes globosa*. Spicules of GALATHEA specimens from the Kermadec Trench. 1, st. 658 (6660-6770 m); 2-5, st. 650 (6620-6730 m); 6-9, st. 663 (4410 m); 10, st. 665 (2470 m); 11-14, st. 668 (2640 m).

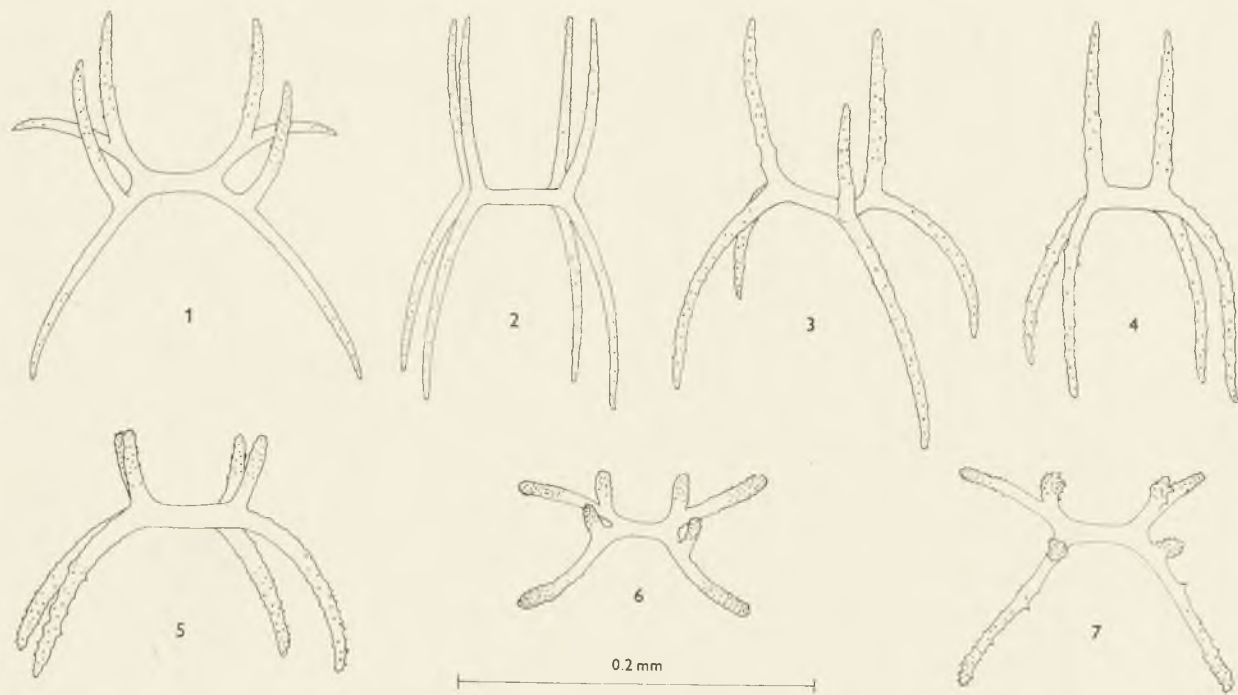


FIGURE 12. *Peniagone willemoesi*. Dorsal (1-6) and ventral (7) spicules of *GALATHEA* specimens from the Kermadec Trench. 1, st. 668 (2640 m); 2-4, st. 663 (4410 m); 5, st. 661 (5230-5340 m); 6, st. 649 (8210-8300 m); 7, ventral spicule, the type prevailing at all depths in the trench.

to topographical features of the trench, that is, to a partial isolation of the specimens living at different depths. Besides, a physiological adaptation to life at high pressures possibly plays a role in minimizing the gene-flow in vertical direction, thus speeding up a segregation which has been started by topographical isolation.

ON THE EVOLUTION OF THE HIGHER TAXA

The fact that the different groups of holothurians are to such a high degree restricted to definite depths suggests that not only species but also higher taxa evolved wholly within the deep sea. Due in part to a lack of paleontological evidence we have very little information on the relationships and antiquity of the different holothurian groups. In the present connection we shall only deal with one aspect of macro-evolution in the holothurians, the possible paedomorphic origin of some of the families.

The family Elpidiidae exhibits a number of features which may be regarded as retained larval or juvenile characters: the short and ovoid body form of many species, the few and large tubefeet, the presence of ten tentacles, and the occurrence in several species of scattered wheel-shaped spicules. Wheel-shaped spicules occur outside the order Elasipoda in the Auricularia-larvae of the order Apoda, and are here retained in the adult stage in the families Chiridotidae and Myriotrochidae. Although the elasipod wheels are not quite similar to those of the Apoda, their scattered

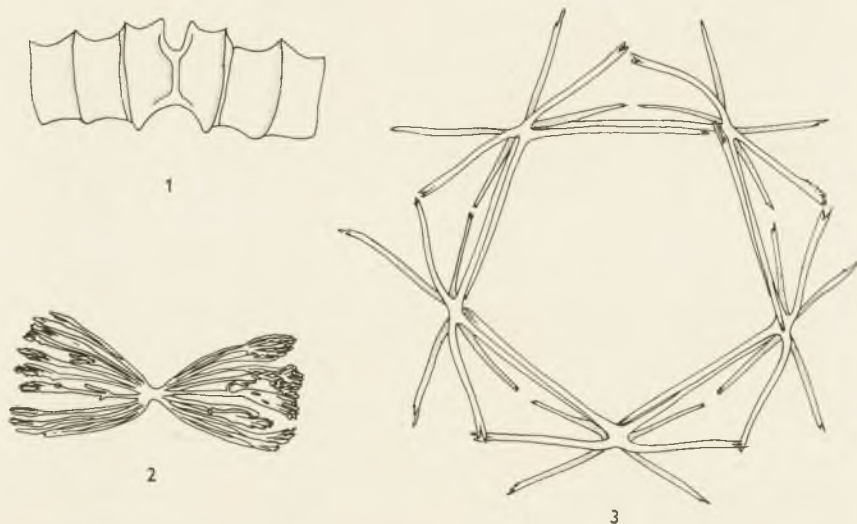


FIGURE 13. Types of calcareous ring. 1, *Paroriza prouhoi* (a radial and two interradiar segments); 2, *Peniagone willemoesi* (a single segment, greatly magnified); 3, *Elpidia glacialis*. (1. after Hansen 1956; 2. after Théel 1882; 3. after Théel 1877).

occurrence in the Elpidiidae suggests that here also they represent a spicule-type belonging to an earlier stage of ontogeny. (Unfortunately, since larval stages are not known from the order Elaspoda this mode of origin of the wheels has not been checked.)

However, the features which are most indicative of a paedomorphic origin of the Elpidiidae are found in the structure of the calcareous ring (Fig. 13). In holothurians other than the Elpidiidae the ring consists of ten firmly joined segments, together forming a massive structure surrounding the pharynx. The five radial pieces of the ring form the points of attachment of the five longitudinal muscles of the body wall. The degree of calcification of the ring may vary a great deal, but the ring is essentially of the same structure in all groups with the exception of the family Elpidiidae. Here, the ring consists of only the five radial segments, each formed as a number of rods radiating from a common centre.

In the genera *Peniagone* and *Achlyonice* the segments are very small, and each segment possesses a large and varying number of rods. This type of ring is reminiscent of the embryonic stage of the ring in other holothurians. In the species *Elpidia glacialis*, *Irpa abyssicola*, and *I. ludwigi* we find a peculiar type of ring; here, the segments are large and each consists of four pairs of rods, two pairs of which are firmly joined to the corresponding pairs of the neighbouring segments. This firm and continuous ring apparently has the same function as the massive ring in other holothurians, although it is quite different in structure. To attain the type of ring found in the genera *Elpidia* and *Irpa* we have to start afresh from the embryonic stage, as represented by the ring of the genera *Peniagone* and *Achlyonice*. An intermediate stage in this evolution is possibly represented by the ring of *Kolga hyalina*, where the segments touch each other although they are not joined firmly together.

In the three closely related genera *Ammaperi*, *Ellipinion*, and *Scotoplanes* the ring-segments are as small as in *Peniagone* and *Achlyonice*. But similar to the ring in *Elpidia* and *Irpa* each segment has a constant number of four pairs of rods. This ring-type may represent a secondary reduction of the *Elpidia-Irpa* type. The acquisition of a low and constant number of rods in the segments probably happened as a consequence of the ring having reached a firm structure. In such a ring a large and fluctuating number of rods would apparently be a disadvantage.

The family Elpidiidae is closely related to the family Psychropotidae and seems to represent a paedomorphic trend of evolution from this family. This evolution probably took place within the abyssal zone. The families Psychropotidae and Elpidiidae are the most strictly abyssal among the Holothurioidea. Moreover, it may also be significant that *Peniagone*, the genus which represents the starting point for the evolution within the Elpidiidae both with regard to the calcareous ring and the spicules, is the most strictly abyssal genus within the family.

The family Laetmogonidae, the most strictly bathyal among the families of the Holothurioidea, may similarly represent a case of paedomorphic evolution from the Deimatidae. The small wheel-shaped spicules which are characteristic of laetmogonids are similar to those found scattered in various species of the Elpidiidae.

CONCLUSION

The fact that the different groups of holothurians are to a high degree confined to definite depths suggests that evolution of species as well as higher taxa has taken place within the bathymetrical zones which the groups inhabit today, rather than by immigration from other zones. A study of the geographical variation within the species combined with the finding that closely related species sometimes replace each other geographically, indicates that speciation by geographical segregation plays a major role also in the deep sea, although barriers which may promote geographical speciation are as yet difficult to visualize. A distributional barrier seems to be present in the Eastern Pacific, separating the Eastern Pacific fauna from that of the remaining part of the oceans.

The deep-sea trenches have probably been populated by eurybathic rather than by deep-abyssal species. While these eurybathic species tend to penetrate into more than one trench, the exclusively hadal species are with almost no exceptions confined to one trench each. This indicates that once an abyssal-hadal species has become restricted to hadal depths the populations isolated in the different trenches each develop into their own species.

A variation in taxonomic characters with depth in the two common abyssal species of the Kermadec Trench suggests that forces which may promote a subspeciation are already at work in the trenches before the hadal populations are isolated. The apparently limited communication between the hadal and abyssal populations may be due to topographical features of the trench, possibly supported by an adaptation to life under high pressures.

The family Elpidiidae probably represents a paedomorphic trend of evolution from the Psychropotidae. The same may apply to the derivation of the Laetmogonidae from the Deimatidae, and to the evolution of the families Myriotrochidae and Chiridotidae of the order Apoda.

A detailed account of these investigations will be published in the GALATHEA Report.

I wish to thank Mrs. Mary Petersen for correcting the language.

REFERENCES

- CLARK, H. L.
1920. Tropical Pacific Holothurioidea. Mem. Mus. comp. Zool. Harv., 39: 115-154.
- FISHER, W. K.
1907. The holothurians of the Hawaiian Islands. Proc. U.S. natn. Mus., 32: 635-744.

- HANSEN, B.
1956. Holothurioidea from depths exceeding 6000 meters. *Galathea Rep.*, 2: 33-45.
- LUDWIG, H.
1894. The Holothurioidea. Rep. Explor. west coast Mexico etc. by the ALBATROSS. *Mem. Mus. comp. Zool. Harv.*, 17: 1-183.
- MAYR, E.
1963. Animal species and evolution. Belknap Press, Cambridge, Mass.
- OHSHIMA, H.
1915. Holothurians collected by the Albatross in the northwestern Pacific. *Proc. U.S. natn. Mus.*, 48: 213-291. [A Japanese version, with more numerous illustrations, appeared 1916-19 in *Zool. Mag.*, Tokyo: 28-31.]
- PERRIER, R.
1902. Holothuries. Expéd. scient. TRAVAILLEUR TALISMAN. Paris.
- THÉEL, H.
1882. Report on the Holothurioidea. Part 1. Rep. scient. Results Voyage CHALLENGER, *Zoology*, 4: 176 p.
- WOLFF, T.
1966. Hadal Zone. In R. W. Fairbridge, Ed., *The Encyclopedia of Oceanography*. Reinhold Publishing Corp., New York.

THE EVOLUTION OF THE DEEP-SEA CORAL FAMILY MICRABACIIDAE

DONALD F. SQUIRES

Museum of Natural History, Smithsonian Institution

ABSTRACT

Corals of the Family Micrabaciidae first appear in the lower Cretaceous of Europe. Paleocological data suggest that these corals inhabited the inner neritic region. Subsequent evolution of the family Micrabaciidae has been toward life in deeper waters accompanied by increasing size of the animal and reduction of skeletal material.

From a structural viewpoint, this genus converges towards *Fungiacythus*, the deepest occurring coral (to 6000 m), in formation of the base, septa and septal strengthening mechanisms. In many Micrabaciids a critical point is apparently reached at a depth of about 500 m, below which reduction of skeletal structures is most marked.

INTRODUCTION

Corals are not a characteristic part of the true deep-sea fauna for they are seldom found in the greater depths of the ocean. The great majority of ahermatypic corals live within the confines of the continental shelves: 48 per cent of the living genera are found in depths of less than 500 m; 71 per cent in less than 1,000 m; 97 per cent in less than 4,000 m. Only three genera, *Fungiacythus*, *Deltocythus*, and *Leptopenus*, characteristically inhabit the abyssal zone, and, of these, only *Fungiacythus* is found in depths exceeding 5,000 m (Vaughan & Wells, 1943). The ahermatypic scleractinian corals are, then, a group having limited representation in the deep ocean and are, perhaps, incorrectly called deep-sea corals.

At a generic level ahermatypic corals are eurythermic: 89 per cent occur in waters of 18° or warmer (Vaughan & Wells, 1943). Even those species found in cold waters of constant temperature have a broad range of temperature tolerance (Squires, unpublished data).

Because of their simple bodily organization and their ability to form a skeleton of calcium carbonate, corals are faced with interesting problems of organization and conservation in deep sea conditions. It is this aspect of their study which makes the group of particular interest. Adaptation of the coral family Micrabaciidae (of which *Leptopenus* is a member) illustrates the kinds of adjustments required by the movement from shallow waters to the deeper ocean.

This paper, which is a slightly enlarged version of an address given at the Deep Sea Biology session of the International Conference on Tropical Oceanography, sponsored by the Institute of Marine Science, University of Miami, is only a general summary of a larger study which is in the stages of final manuscript. Because adequate systematic details and gener-

al documentation on the distribution of the micrabaciid corals cannot be given in a short paper, only a general survey of the study is presented here.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. Gilbert Voss, Institute of Marine Science, University of Miami, and Dr. Jorgen Knudsen, Zoological Museum, Copenhagen, for the opportunity to present this paper at the Conference on Tropical Oceanography. A number of research assistants have been associated with this study and will be more fully acknowledged in the final report. I should, however, like to express my thanks to Miss Carolyn Waldman, Mr. Ian Keyes, and Mrs. Drina Byer for their assistance. Portions of this research have been supported by a grant from the National Science Foundation, GB-353.

SYSTEMATIC SUMMARY

Micrabaciid corals are known as fossils from the early Cretaceous through the latest Tertiary and by species living in modern seas. At present they are found in waters as shallow as 15 and possibly as deep as 4,000 m. Within this depth range the family shows remarkable structural modification for life in increasing depths of water, and, because their skeletal characteristics reflect this adaptation, species preserved as fossils permit us to trace their evolution.

The systematics and zoogeographic history of the group will first be summarized and then the morphological adaptations for life in the deep sea will be discussed.

Micrabaciid corals are small, solitary, free-living corals of the suborder Fungiina. The polyps (polyps of only a few species are known) are small and highly compact and completely invest the corallum. They are generally a dark red with green or orange stripes radially disposed on the oral surface. Heavy muscular pleats in the mesenteries of these corals suggest that the polyps are very active, but there are no recorded observations on the living animal. The tentacles are short and knobbed. Experience with other living solitary corals suggests, however, that the polyps may, in fact, be capable of great expansion, so that the volume of polyp may far exceed that of the skeleton. The usual concept of a polyp sitting in a cup must be abandoned. Rather, I have observed (unpublished) that the skeleton may be an "insignificant" disc-like structure in the base of a large upright polyp. The usual functions attributed to coral skeletons, those of support and of protection, must also be disregarded for neither would apply in the case of the micrabaciids.

The corallum of micrabaciid corals is not usually cup-shaped, but rather the cone of the corallum has been broadened until the wall is nearly horizontal and forms a "basal plate". The septa arch upward from the wall and form a cupoloid corallum. Characteristically, the wall is reduced to simple linear structures, costae alternating in position with the septa, and

attached to the septa by cross bars of synapticalae. Septa are perforate and are joined at various places by an intricate arrangement of synapticalae; they become wavy, thus forming a highly compartmented structure of great complexity. The character of the highly dentate septa places the micrabaciids with the fungiid corals, while the peculiar structure of the wall separates them from others of that group and from the structurally similar deep-water coral *Fungiacyathus*.

The Micrabaciidae are first known from Lower Cretaceous strata in France where small, button-like, structurally compact, coralla are found. In younger sediments, ranging from Cenomanian to Campanian, nine nominal species are known, many species being represented by only a few specimens. *Micrabacia* occurs in England, Central Europe, and as far east as Siberia. During the Campanian time, a sudden evolutionary burst in the region of the Gulf states and interior United States resulted in five abundantly represented species. This was succeeded during the Maestrichtian by eight additional species, represented by numerous small coralla seldom exceeding a centimeter in diameter, which extend the range of the genus to include the Atlantic Coast of the United States (Stephenson, 1916; Wells, 1933). These ancestral species differ from their modern counterparts in having a dense, stout, heavily constructed corallum remarkable for the diversity of its structural ornamentation. All occurrences of fossil coralla are associated with shallow-water faunas and sediments, suggesting that none lived at depths exceeding 100 m. European species, distributed from Neocomian to Campanian, show no sudden evolutionary bursts although half of the species appear first during the Senonian. These species, like the American, appear to be common (although less numerous than the American) in shallow water sediments.

At the end of the Cretaceous there was a sudden and drastic reduction in numbers of individuals and species of micrabaciid corals. Throughout the Tertiary the record of the family is very sparse, an observation which is in itself significant. Early Tertiary species of the micrabaciid corals are placed in the genus *Stephanopsammia* which quite possibly had its origins in a poorly known species from sediments of Santorian or Campanian age in the Malagasy Republic. Also included in this genus are rare specimens of *S. discoides* (Milne-Edwards & Haine) from the lower Eocene of England, and *S. implexa* (Dennant) from the Eocene of Australia and two Paleocene species: *S. schweinfurthi* (Oppenheim) from Egypt, and *S. regularis* (Traub) from Austria. Fragmentary materials from the Eocene of California indicate the presence there of two additional species, *S. californica* (Nomland) and *S. vacavillensis* (Palmer). This array suggests that the family had achieved a circum-Pacific distribution by the Lower Tertiary, but there is little record of its further development. No micrabaciids have been recorded from the Oligocene. However, during the Miocene and Lower Pliocene, a complex association of what is probably a single species of

Stephanophyllia is known from northern Europe and the Mediterranean (*S. elegans*, *S. imperialis*, *S. nysti*). Another species, *Stephanophyllia fungulus*, apparently arose during the Upper Tertiary in Japan and is abundant in the modern Japan and China seas, about the Philippine Islands and into the Indian Ocean as far as Ceylon. Two other closely related extant species occurring only in the Indo-Pacific are *Stephanophyllia complicata* from the Indian Ocean and Coral Sea, and *Stephanophyllia neglecta* of the Philippine Islands and Coral Sea regions. These latter are small and compact, seldom over a centimeter in diameter, and are not known from depths in excess of 450 m. *Letepsammia* may well have arisen during the Tertiary, but its history is fragmentary. Probably the best known of all the micrabaciid corals is *Letepsammia formosissima*, which is widely distributed in the Celebes, Banda, and Coral Seas and around the Philippine Islands between 100 and 600 m in depth. This species was thoroughly described by Moseley (1881) in the CHALLENGER reports. Six species of *Letepsammia* occur around the Hawaiian Islands, Australia, and New Zealand, the East African Coast of the Indian Ocean and in the Japanese Seas. In this last area an undescribed species occurs in slightly over 75 m depth. A single specimen from the ALBATROSS collections from a depth of 960 m off the Philippine Islands shows interesting structural alterations and is, I believe, the most highly modified member of this group.

An unnamed, undescribed genus occurs first as a fossil in the Pliocene of Italy and two other undescribed species are from modern seas. One of these ranges in depths from 500 to 850 m while the other rarer species is found from 900 to 950 m depth.

The most structurally modified member of the family Micrabaciidae is the genus *Leptopenus*, represented by three living species and known from a total of seven specimens, all but two of which were collected by the CHALLENGER Expedition. *Leptopenus* has two described species: *L. hydrocaelus* is known from a single specimen taken off Valparaíso, Chile from 3,950 m, and *L. discus* is represented by four specimens collected by the CHALLENGER Expedition from the Crozet Islands, the southern Indian Ocean, and east of Rio LaPlata at depths of 2,900 to 3,500 m (Moseley, 1881). A single specimen collected by the GALATHEA Expedition from 2,000 m in the Makassar Strait is believed to represent the central portion of the corallum of *L. discus* (Squires, 1966). Another specimen (Agassiz, 1888) from the North Atlantic, still deeply imbedded in the dried integument of a salp upon which it became impaled during dredging, was captured by the BLAKE Expedition from a depth of 2,800 m.

The family is anomalous, for although it presents a very complete record of its early evolutionary history and is rather diverse at the present time, the middle portion of its history is only sparsely recorded in the geological record. The reasons for this may become apparent in the following discussion of the adaptation of the group.

ADAPTATIONS OF THE MICRABACIIDAE

As early as 1908, Steinmann had suggested that the micrabaciid corals demonstrated an evolutionary adaptation for life in the deep sea as demonstrated by the decreasing amounts of skeletal material deposited by the polyp. The example was not further amplified although there is clear implication of unspecified problems of bio-extraction and bio-deposition of skeletal material at great depths and under unfavorable conditions. The "difficulty" of forming a skeleton, by implication, is the requirement for modification and reduction of skeletal material. In my own studies I have found four morphological modifications among living micrabaciids which approximately correlate with increasing depths of occurrence. These same trends may be found among the fossils, and therefore are taken to represent evolution for life in the deep sea. None of the morphological adaptations is orthogenetic and the family appears to be polygenetic in origin. With increasing depth of occurrence, living species show:

1. Increasing size of animal (and therefore corallum).
2. Decreasing weight of skeleton.
3. Reduction of the number of septal trabeculae.
4. Reduction in the thickness and the massiveness of the basal plate.

It would be desirable to study these morphological trends as much as possible from an objective standpoint. For example, if sampling of populations were perfect, one might expect to find some general correlation between the mean diameter of the corallum and the depth of its occurrence. This has not been the case, because micrabaciids are not common corals, and samples are small at best. It has been possible therefore to quantify only in certain instances, and in other instances it has been necessary to extrapolate from information derived from other kinds of corals.

In the absence of a more conclusive measurement of total size the greatest diameter of corallum of specimens known to me are cited here. In the shallow water genus *Stephanophyllia*, *S. fungulus* (15 to 400 m) has a maximum diameter of about 1.5 cm; *S. complicata* (100 to 400 m) 1.75 cm; and *S. neglecta* (90 to 140 m) 1.0 cm. The complex of *Letepsammia* species occurring in depths from 100 to 500 m, and more commonly the deeper portions of that range has a maximum diameter of 3.6 cm. The undescribed genus, occurring between 500 and 1,000 m and again more typically associated with the 700 to 900 m range, is up to 3.5 cm in diameter. The largest of the five known complete specimens of *Leptopenus* (3400 m) has a diameter of 2.5 cm, but the polyp is reported as being 3.8 cm in diameter. This is a demonstrable increase in size with increase in depth but the trend is not linear. A parallel to the modern situation is found among the fossils. Species of *Micrabacia* (Cretaceous) are seldom 1 cm in diameter, while the Miocene species *Stephanophyllia imperialis* may be up to 3 cm in maximum diameter.

Because the polyp invests the corallum it need not have a direct relationship to the size of the corallum. The trend described above could be better stated as one of increasing size of polyp, rather than as increasing size of corallum. There is ample evidence, not only from measurements of corallum diameter, but also from observations reported below, that the total amount of calcium carbonate in the skeleton decreases with increasing depth of occurrence of the representatives of the family. The relationship is therefore complex; both polyp and corallum increase in size with depth, but the former increases more rapidly. The corallum may, in fact, show a reversal, and become lighter.

The relationship alluded to between weight of skeleton and depth of occurrence has been as yet only partially studied. Perhaps one of the most significant measurements which could be made of that relationship would be mass of the skeleton relative to the actual volume of polyp, and perhaps that of the density of the skeleton material itself. Although not applicable for all solitary corals, the usual cubic relationship between weight of skeleton and any linear dimension has been found among the micrabaciids. The ratio of these two parameters remain relatively constant within populations and may with refinement of measurement be a species characteristic. The data which follow are only approximate values and are given in order of increasing depth of occurrence. Species of *Stephanophyllia* range from 0.15 to 0.35 in the weight:greater-diameter ratio. *S. fungulus* has the greatest range in both this function and in depth of occurrence. The index values for species of *Letepsammia* range from 0.043 to 0.095 and within the genus approximate a correlation of decreasing index with increasing depth of occurrence. Species of the new genus, found at somewhat greater depths than *Letepsammia*, have indices of 0.060 to 0.086. Unfortunately, ratios for *Leptopenus* have not been obtained but it is clearly apparent that they would be lower than those of any of the genera mentioned. The trend suggested is present, but is as yet only highly generalized. It is expected that with further refinement a very specific relationship between weight and depth will be found.

The third trend, that of the reduction of number of septal trabeculae is apparent on a generic level, although species have not yet been studied to demonstrate the correlation with depth of occurrence. Each species has a characteristic value for number of septal trabeculae which is constant throughout the depth range of that species, suggesting that this character is genetic. Among the modern species we find that the shallow species of *Stephanophyllia* have 15 to 25 septal trabeculae per septum. Species of *Letepsammia* have 10 to 21 trabeculae while *Leptopenus* has only 4 to 5. The new genus has no externally visible septal trabeculae. These generalizations based on comparisons at the generic level, show decreasing numbers of trabeculae, but may obscure some of the finer relationships occurring at the species level.

A fourth trend is one which I have not been able to approach quantitatively. Reduction in skeletal material can be observed in the two primary structures of the micrabaciid corals, the basal plate and the septa. Both of these structures become more fragile in the deeper water species, and the mechanisms for maintaining skeletal strength becomes more intricate as the corallum is lightened. This easily observed trend is most marked below about 1000 m, and is shown dramatically in *Letepsammia*.

EVOLUTION OF THE MICRABACIIDAE

How do the trends which have been observed in the modern species of Micrabaciidae correspond to the evolutionary history as demonstrated in the fossil record? All of the Cretaceous forms of *Micrabacia* are small, averaging a centimeter or less in diameter, and are compact, massively constructed coralla. The number of trabeculae forming the septa is high, ranging from 20 to 30. All of these species lived in environments which appear to have been shallow, probably less than 100 m in depth. The few species known from the lower Tertiary are also small, although they show the beginnings of structural differentiation and there is some lightening of corallum structure, evidenced by the increasing fenestration of septal structures and basal plate. These forms were small, however, and again probably lived in relatively shallow waters. After a considerable gap in record through the Oligocene, micrabaciid corals reappear in the Miocene in the form of *Stephanophyllia elegans*. This complex species usually has a small- to medium-size compact corallum, although some tall forms having high, elegantly pointed septa become quite large. The latter are associated with the deeper water facies of Miocene sedimentation in the European region but do not necessarily have a "deepwater" origin. More probably the environment of deposition was that of the margins of the shelves. *Stephanophyllia elegans* ranges on into the Pliocene. The new genus also occurs in the Pliocene of Italy as does *Stephanophyllia fungulus* in Pliocene sediments of Japan. None of these appear to have been collected from deeper water facies, quite possibly not exceeding 200 to 300 m.

Does the fossil evidence indicate that the micrabaciid corals have only recently evolved and migrated into the deep sea? It seems more likely that the fossil record of the group is incomplete and is evidence for evolution in shallow waters during the Tertiary. Those fossil species which we know have a diversity of structural modification suggesting that they are shallow water lineages or are convergent upon those lineages. Thus the gross similarities between shallow water *Stephanophyllia* of modern seas and *Micrabacia* of the Cretaceous are perhaps not an indication of direct ancestry but rather demonstrate evolutionary convergence, both forms being adapted for life in shallow water. What a small, compact, heavy skeleton represents in an adaptive sense I have not deduced. Perhaps it represents a response to physiological requirements for the deposition of

calcium carbonate which may be stronger in shallower waters. Smaller, more active polyps, possibly reflecting greater predation in shallow waters, may require stronger skeletal structures for muscular support.

If there is significance in the coincidence of the several structural changes occurring at a depth of about 1000 m, is it possible that this depth (or pressure-temperature combination) represents some sort of threshold over which it is difficult for the Scleractinia to pass? If this is so, then one might have an explanation for the fragmentary fossil record. At the conclusion of the Cretaceous the broad inland seas were drained. Perhaps this geological event caused a movement of the micrabaciids into deeper water, particularly on the outer shelf and slope. These environments are poorly recorded in the fossil record and it is only when these corals invaded the shallower waters and were preserved that they became a part of the known fossil record. The poor record of the micrabaciids during upper Tertiary time is not so easily explained. One would not, however, expect to find an abundant record of the deep water species in any event for those facies are seldom found at the surface or margins of the continents.

SUMMARY

It appears that the micrabaciid corals have undergone an evolution of at least some 60 million years, during which they migrated into deeper waters of the ocean and in the course of this migration became adapted to life in an environment which is progressively more alien to the presence of calcium carbonate skeletons. The development of an "internal" skeleton greatly reduced quantity of calcium carbonate "required," while ingenious construction maintained maximum structural strength and supportive features.

LITERATURE CITED

- AGASSIZ, A.
1888. Three Cruises of the United States Coast and Geodetic Survey Steamer BLAKE . . . Vol. 2. Riverside Press, Cambridge, 220 pp.
- MOSELEY, H. N.
1881. Report on certain hydroid, alcyonarian and madreporarian corals procured during the voyage of H.M.S. CHALLENGER. *In*. Report on the scientific results of the voyage of H.M.S. CHALLENGER during the years 1873-76. Zoology, vol. 2, London, pp. 1-248, pls. 1-16.
- SQUIRES, D. F.
1966. A new record for *Leptopenus*, a rare deep-water coral. *Nature*, 207 (4999): 878-879.
- STEINMANN, G.
1908. Die Geologischen Grundlagen der Abstammungslehre. Wilhelm Engelmann, Leipzig, 284 pp.
- STEPHENSON, W.
1916. North American Upper Cretaceous corals of the genus *Micrabacia*. Prof. Pap. U.S. Geol. Surv., 98-J: 115-131, pls. 20-23.

VAUGHAN, T. W. AND J. W. WELLS

1943. Revision of the suborders, families and genera of the scleractinia.
Geol. Soc. Amer. Spec. Pap., 44: 1-363, 51 pls.

WELLS, J. W.

1933. Corals of the Cretaceous of the Atlantic and Gulf coastal plains and
the western interior of the United States. Bull. Amer. Paleont., 18
(67): 85-288, pls. 1-16.

THE BIOLOGY AND BATHYMETRIC DISTRIBUTION OF DEEP-SEA CEPHALOPODS¹

GILBERT L. VOSS

Institute of Marine Science, University of Miami

ABSTRACT

The decapod cephalopods are clearly divisible into three oceanic groups; epipelagic, mesopelagic, and bathypelagic. Similarly, the octopods may be divided into three oceanic groups; epipelagic, bathypelagic, and abyssopelagic. Benthic octopods are divisible into littoral benthic, mesobenthic, and bathybenthic. There are characteristic families and subfamilies of decapods and octopods for each depth zone.

The squids of the upper layers are strong active swimmers with well muscled mantles. The octopods are similarly well muscled. With increasing depth, the mantles of all the groups become increasingly modified by the decrease in musculature and the appearance of a gelatinous material which forms the bulk of the mantle.

Variation and changes with depth of pigmentation, light organs, feeding, and reproduction are described. The probable functions of light organs are discussed.

INTRODUCTION

It has been known for many years that there are cephalopods which live in the depths of the oceans. Among the first to mention this was Alcide d'Orbigny (1841) who drew attention to the occurrence of cephalopods at the surface of the sea primarily at night, disappearing during the day, and came to the conclusion that they inhabit the depths at or below the zone of light penetration. This, he felt, was confirmed by the fact that they were fed upon by dolphins and sperm whales which he believed lived at depths of around 160 to 180 m or more.

The first cephalopods to be mentioned in the literature, which belong to what is now commonly recognized as the deep-sea fauna, were *Cranchia scabra*, described by Leach in 1817 from the Tuckey Expedition and captured in the Gulf of Guinea, and *Taonius pavo* and *Leachia cyclura* described by Lesueur in 1821, both from specimens taken at or near the surface. In the following 50 years a considerable number of forms now known to inhabit the depths were recorded in the literature. Many of these were from the surface waters of the Arctic and from the beaches of the Mediterranean Sea, specially from the Straits of Messina, collected under conditions somewhat obscuring the evidence concerning their original habitat.

Two events occurred in the 1870's which drew the attention of biologists

¹Contribution No. 803 from the Institute of Marine Science, University of Miami. This research has been supported by a grant from the National Geographic Society and grant GB 1090 from the National Science Foundation Systematic Program and GA 103 from the Office of Antarctic Programs, National Science Foundation.

to the possibilities of a deep-sea cephalopod fauna; these were the voyage of HMS CHALLENGER and the trawling investigations undertaken by A. E. Verrill and the U.S. Fish Commission in Canadian and New England waters. The rich cephalopod collections of the CHALLENGER were first sent to Huxley for study but were later turned over to Hoyle. This delay prevented the full report from coming out until 1886. In the meantime, Prof. Verrill began the publication of his results, drawing attention for the first time to the unusual deep-sea cephalopod fauna living in the deeper parts of the sea. If one were to name the Father of Deep-sea Teuthology, the title would certainly go to A. E. Verrill.

The greatly increased investigations of the deep-sea fauna since then have, unfortunately, been little felt in cephalopodan circles; this is probably due to the small numbers of these animals taken in conventional nets. As a result, there are few works which have dealt in any detail on the subject of the deep-sea cephalopods. Hoyle (1886) in the CHALLENGER Report devoted a special section to bathymetric distribution. Chun (1910) dismissed it in his lengthy treatment of the VALDIVIA cephalopods and devoted less than a page to the subject when dealing with the MICHAEL SARS collections (1914). Pfeffer briefly discussed the depth distribution of the Oegopsida in the Plankton-Expedition report (1912) but drew no particular conclusions.

The first detailed study of the deep-sea cephalopods was undertaken by Guy Robson (1925) and dealt with the morphology and biology of the deep-sea Octopoda. His statements concerning the problems of studying these animals are very pertinent even today and will be treated later on in the present account.

Little of a general nature has been added since, although the treatment of the octopods of the DANA expeditions by Thore (1949) and of the Vampyromorpha by Pickford (1946) have made solid contributions to the field. Rees & Maul (1956) made particular mention of the deep-sea cephalopods of Madeira. Finally, Arthur Clarke (1962), in his list of the abyssal mollusks of the world, included a list of the cephalopods reportedly occurring in depths below 1830 m (1000 fathoms).

With the vastly greater number of cephalopods being collected today because of increased oceanographic research and new and improved high speed nets, the time seems appropriate for a resurvey of the field. In the writing of this paper I have been assisted in general information, in details of various phases of deep-sea research, and in listening to my arguments, by a number of my colleagues at the Institute of Marine Science. On the subject of the deep-sea cephalopods, their anatomical features, adaptations and mode of life, I am deeply appreciative of the assistance of my wife, especially in reference to the histioteuthids, and of my senior assistants and collaborators, Mr. Clyde Roper and Mr. Richard Young. All of these have not hesitated to argue vehemently when the occasion arose and I

owe much to their friendly criticisms and suggestions.

The data presented here are based upon researches in cephalopods and deep-sea biology undertaken by me over the past 15 years and supported by funds from the National Science Foundation and the National Geographic Society. To both of these organizations I express my grateful appreciation.

THE DEEP SEA

For the purposes of this discussion, the term deep sea is used in its familiar connotation; it is that part of the oceans lying beyond the edge of the continental shelf and below about 200-400 m or beyond the lower limit of daytime illumination. Within this region I will use the terminology presented by Anton Bruun (1957) and refer to the following zones: *mesopelagic* (ca. 200-700 m), *bathypelagic* (ca. 700-2000 m), *abyssopelagic* (ca. 2000 m to near the bottom), and *benthic* (*mesobenthic*, *bathybenthic*, and *abyssobenthic*). The use of meters of depth to define the regions is adhered to here mainly because of lack of temperature data at the sites of capture but I realize temperatures are more meaningful.

In deciding what zone a particular species inhabits emphasis has been placed upon the temperatures likely to be found at the depth of capture. What effect pressure may have upon the deep-sea cephalopods is unknown. Cephalopods of the deep sea possess no air or gas spaces so that direct damage does not occur when they are brought to the surface. However, there is a considerable amount of evidence being accumulated (Menzies, 1965) which indicates that pressure has a direct effect upon the physiology and biochemistry of marine animals. No work to date along these lines has been carried out on cephalopods.

The study of the bathymetric distribution of the cephalopods with the exception of the benthic Octopoda is fraught with difficulties and every investigator has at some time or other complained of the lack of reliability of his depth data. The most detailed comments are those of Robson (1925). The major problem is the method of sampling and the type of nets used. Although this has often been discussed, a brief review seems useful.

Most cephalopods are active swift swimmers, adept at avoiding all types of nets. Thus it is not remarkable that the numbers of cephalopods available for study are most numerous in the planktonic stages and decrease rapidly with increasing size due to their greater ability to dodge the net; the adults of many species are rare in collections and in a number of species completely unknown. The depth distribution of the planktonic larvae of identifiable species is fairly easily attainable (*cf.* Thore, 1949) through the use of closing nets. It is well known that DISCOVERY type closing nets fish little or not at all on descent and are closed after fishing at depth, nonetheless there is still a margin of uncertainty. The new Bé closing plankton net does not have this objectionable feature and accurate and reliable depth data can be obtained by its use. With any of a number of telemetering

devices or *in situ* depth recorders, accurate depth records can be obtained.

However, most of our plankton data unfortunately were obtained in the past with open nets and even worse by means of oblique or vertical tows which are almost useless for depth determinations.

The capture of juvenile and adult cephalopods has mainly been accomplished by six methods: collected dead while floating at the surface or washed ashore (all *Architeuthis* records except from whale stomachs); collected from the stomachs of marine mammals or fishes; caught with a dip net and night light; jigged; seined; or trawled with large open nets.

Floating at Surface or Washed Ashore.—No depth data can be obtained. A number of oegopsids are known only from these conditions and all seven known specimens of *Histioteuthis elongata* were found floating at the surface although they are obviously deep-sea animals.

Mammal or Fish Stomachs.—As in the above case, many species are known only from the stomachs of predators. Depth data has about the same reliability as open nets except in the case of predators known to have a limited vertical range. The fresh appearance of stomach contents, for example from *Alepisaurus*, is no evidence that it was only recently swallowed by the fish.

Dip Net and Night Light.—As d'Orbigny (1841) has pointed out, the fact that many cephalopods are caught on the surface at night only indicates that they are probably scotophylic and during the day live in the mesopelagic zone. This may be considered valid when trawling in the upper surfaces (0-200 m) during the day fails to reveal their presence in the photic zone.

Jigging.—Jigging depth is easily determined but very few squid, specially oceanic species, have been obtained by this method except commercial species.

Seining.—This method is only possible in shallow surface waters.

Open trawls.—The majority of deep-sea cephalopods are taken with open trawls or net dredges. In the case of obviously bottom dwelling species there is no problem. For the others various difficulties present themselves.

In the last few years, several types of midwater nets with closing devices have been developed, all using a basic Isaacs-Kidd Midwater Trawl net. The Foxton net (Foxton, 1963) is equipped with a double canister, one of which fishes down and up, the other at a predetermined depth. The Aron net (Aron, *et al*, 1964) consists of a compartmented canister electrically operated from a console on deck through a conductor cable, and the Percy-Hubbard closing net (Percy & Hubbard, 1964) uses a Bé Multiple Plankton Sampler (Bé, 1962) in the cod end. All of these systems are subject to erroneous depth data since the trawl webbing does not flush itself between each level collected and contamination from level to level occurs. It often occurs that there are more cephalopods clinging to the inside of the

net, even with knotless webbing, than are in the canister, and often squids are brought on deck holding to the *outside* of the trawl. Until a system is developed whereby the entire net is closed and opened, the data from these nets will be subject to doubt. By careful analysis of the hauls, however, valid data can sometimes be obtained.

The most useful methods for such analysis are:

a. By collecting all data from the tows, it is usually possible to determine the upper limits of capture of a species by simple examination. The exceptional record or two from shallower tows need not be a complicating factor. By analyzing all tows by small depth increments it is possible to arrive at two other pieces of data, the depth of greatest abundance, and the lower level indicated by a rather sharp drop in abundance of capture. No data can be obtained from vertical and oblique tows except by this method and the bottom of the range can never be determined.

b. When duration of the time at fishing depth is very long in relation to the time utilized in setting and hauling in, it is possible statistically with reasonable certainty to determine the depth of capture if enough tows are made.

c. Depth of capture is fairly certain when the species is found repeatedly only in association with animal communities whose level is already known (Bruun, 1955, 1957).

In order that data from open nets can be utilized by other workers, the depth of fishing should be given as accurately as possible. The tendency to report depth by meters of wire out leaves the reader at a loss as how to interpret it. In the case of the Isaacs-Kidd trawl, the depth fished is maintained at about a 3:1 ratio, but this changes slightly with greater depth. In almost all nets the actual depth of the gear will depend upon its type, the length of wire out, the speed of the ship, and wind and sea conditions.

Despite all of these considerations, it is still very difficult to arrive at definite conclusions concerning the depth inhabited by many species, either because they are very rare, or because there is no conclusive capture data available. Our only recourse is to fall back upon consideration of the morphology of the specimens and correlate this with the morphology of groups of known epipelagic and deepsea forms. For this purpose it is necessary to consider the vertical distribution of the cephalopods as a whole.

BATHYMETRIC DISTRIBUTION AND GENERAL HABITAT

In the following section the cephalopods will be dealt with systematically. The depth ranges are biased since all drastically non-verifiable depth records are disregarded.

Figures 1 to 3 show the depth distribution by family and smaller groups based upon literature records supplemented by unpublished data at the Institute of Marine Science. The groups are arranged systematically. Undoubtedly amplification of the ranges will be necessary as more data

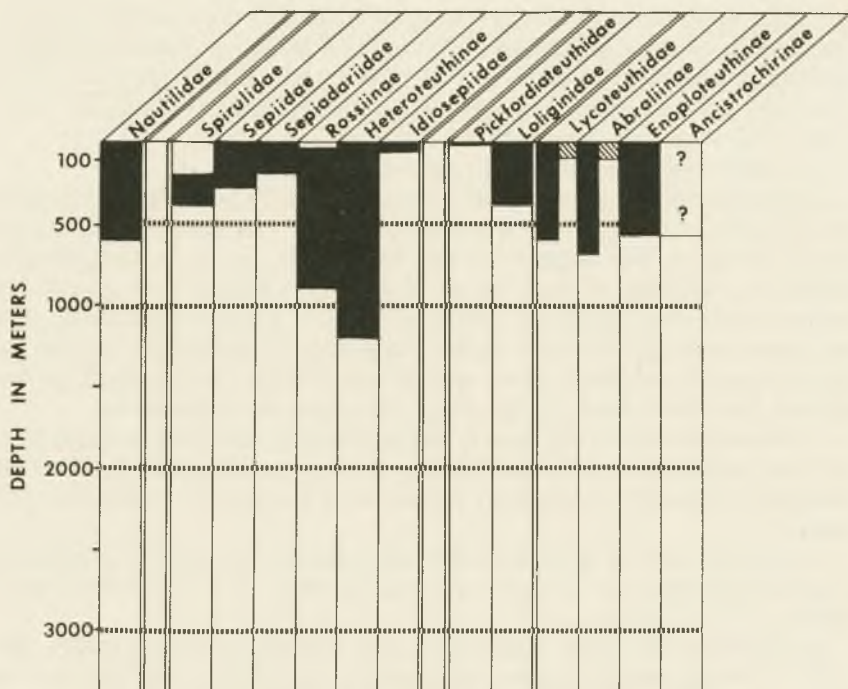


FIGURE 1. Bathymetric distribution of the cephalopods. Diagonal shading indicates larvae and juveniles.

TABLE 1
EPIPELAGIC ZONE

Characters	Examples
Squids	
1. Large, active swimmers, mantle thick, muscular	<i>Loligo</i>
2. Coloration normal	<i>Ommastrephes</i>
3. Light organs lacking or undifferentiated	<i>Onykia</i>
4. Active predators	<i>Onychoteuthis</i>
5. Larvae in surface waters	
Octopods	
1. Large, active swimmers; mantle thick, muscular	<i>Argonauta</i>
2. Coloration normal	<i>Tremoctopus</i>
3. Plankton feeders	<i>Ocythoe</i>
4. Incubate eggs	
5. Autotomizing hectocotylus	
6. Larvae at surface	

are made available but the writer believes that the records are essentially correct at the present time.

Based partly upon these graphs the following pages discuss the fauna occupying the various zones in the sea.

THE EPIPELAGIC FAUNA

Decapods.—The squids of the epipelagic zone (Table 1), in common with littoral species, are active swimmers. They possess in general large dorsal axons, muscular fleshy bodies of the typical torpedo shape with large, strong fins and well developed and prominent swimming keels on the third arms and the tentacular clubs. The funnels are stout, the funnel valve usually a free crescentric flap, and the funnel organ simple and unadorned. The carpal fixing apparatus of the tentacular stalk is usually discrete and covers a small area.

The coloration of these animals is controlled by discrete chromatophores of the typical construction and full control seems characteristic.

Bioluminescence is found in the epipelagic squids of almost all taxonomic groups. However, the organs in general display a tendency towards undifferentiation, consisting of long streak- or band-like organs (*Ornithoteuthis*) or collections of luminescent spherules such as the dorsal mantle organs of

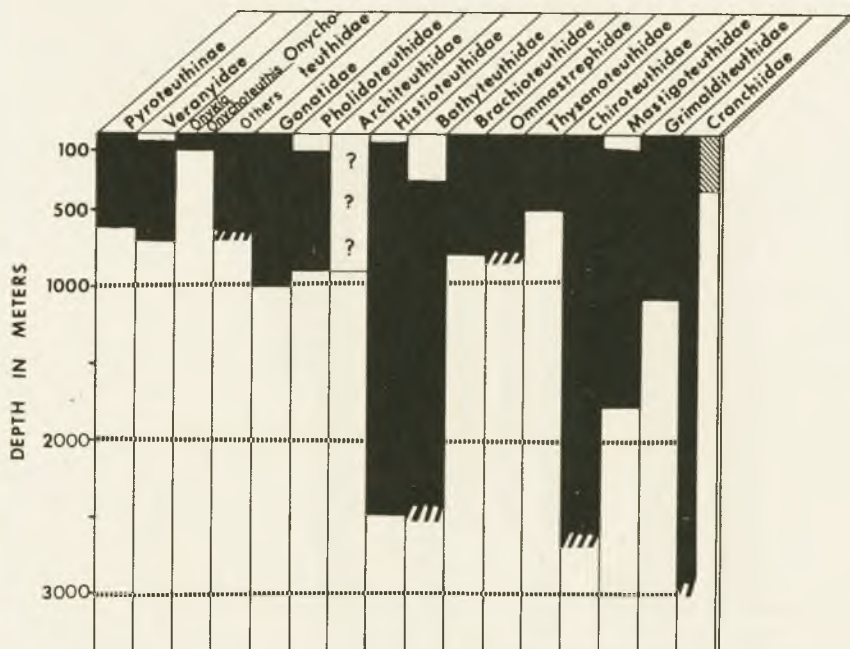


FIGURE 2. Bathymetric distribution of the cephalopods. Diagonal shading indicates larvae and juveniles.

Ommastrephes pteropus or single undifferentiated granules in the ventral surface of the same species. The ventral internal organs of *Onychoteuthis banksi* seem to fall midway between the striplike organs and the more discrete organs of the mesopelagic species.

The method of feeding seems similar in most species. It has been commonly described as a direct onslaught at full speed, but, in shipboard observations, this has not been confirmed. The feeding is more deliberate, the general approach slow and unspecified, often a distinctly side approach occurring, with only a last second swift dart. This has been observed many times in *Ommastrephes pteropus*. The light organs do not seem to enter into the action although they may have some attractive function with flyingfish, a common prey.

Mating has been reported in detail for several species of epipelagic squid. Recently it has been observed in *Ommastrephes pteropus* and found similar to Drew's (1911) observations on *Loligo*.

The eggs of very few epipelagic squid are known although various species have been reported to lay them in long gelatinous tubes, attached to floating objects, fastened to the bottom in moderate depths, or free floating. The larvae in all species known are found in the surface layers. In some there is no true larval stage and development is direct.

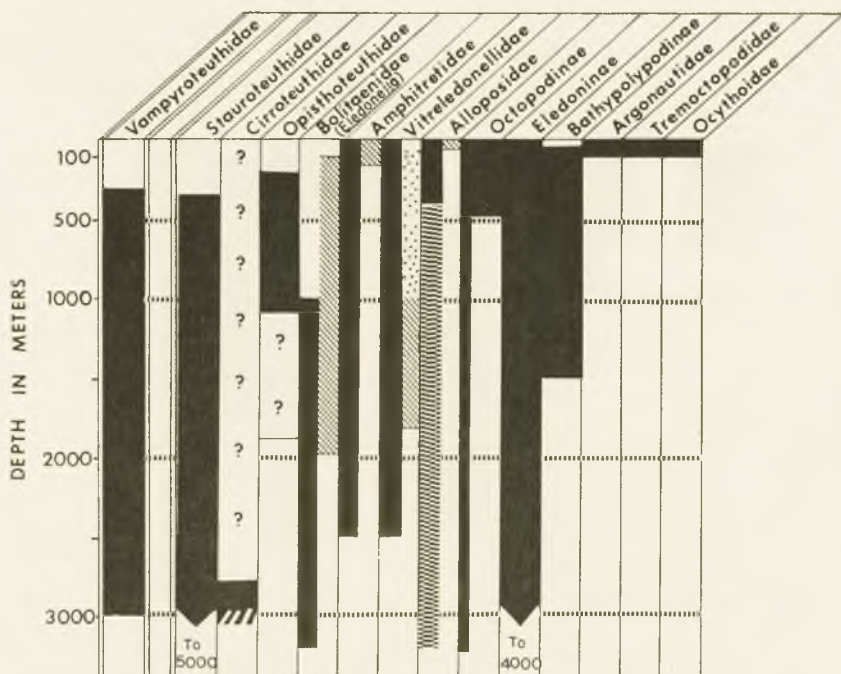


FIGURE 3. Bathymetric distribution of the cephalopods. Diagonal shading indicates larvae and juveniles.

Octopods.—The epipelagic octopods are restricted to the larvae of the small-egg species of *Octopus* and its allies and *Argonauta*, *Tremoctopus*, and *Ocythoe*. Little is known about *Ocythoe*, although it has a wide distribution in the sea.

Argonauta is well known and needs no discussion here. It lives near the surface, feeds upon plankton which it locates by the sensory mechanism of the shell flaps of the dorsal arms (Young, 1960) and undoubtedly uses its shell as a hydrostatic organ probably over only a very limited vertical range. It incubates its young within the shell from which they escape as well developed late larvae.

Mating has not been observed in *Argonauta* but the most marked difference in size of the sexes in the animal kingdom occurs in this genus.

Tremoctopus presents another problem for apparently at least two forms exist, one is a moderately large, firm, muscular bodied, deeply pigmented form of the *violaceus* type, obviously a surface dweller with purple back and silvery ventral surface, and the other is a deep water form presently un-named, of larger size, with few chromatophores, very gelatinous and fragile, and almost completely transparent. Mating has not been observed in either form but both possess autotomizing arms in the male and very small eggs in the females indicative of prolonged larval stages.

The littoral octopods need not be discussed here. Their features are well known and will be compared with the deeper forms in the following sections.

MESOPELAGIC FAUNA

Decapods.—The mesopelagic squids form a fairly characteristic group sharing a number of features in common (Table 2). They are in general small squids rarely exceeding 30 cm in overall length excluding the tentacles and averaging only about 15 cm with large numbers of adult at 4 to 5 cm. They are active, swift swimmers daily migrating from depths of 500 m or more to the surface and return. In general morphology they are like their epipelagic relatives in the feature previously mentioned. However, although

TABLE 2
MESOPELAGIC ZONE

Characters	Examples
Squids	
1. Small, active swimmers; mantle thin, muscular	<i>Lycoteuthis</i>
2. Coloration normal	<i>Abralia</i>
3. Numerous light organs of complicated structure	<i>Abraliopsis</i>
4. Active predators	<i>Pyroteuthis</i>
5. Larvae near surface	
Octopods	
1. Body gelatinous	Young of <i>Japetella</i>
2. Reduced pigmentation	and perhaps some adults of <i>Alloposus</i>

the mantle wall is strong and muscular, it is relatively much thinner in cross-section.

The most prominent character is the possession of numerous small to large light organs or photophores distributed chiefly upon the ventral surface of the mantle, funnel, head, arms and the ventral periphery of the eyeball. Perhaps nowhere in nature are photophores more highly developed and complex as in the mesopelagic and bathypelagic squids. Their function is not known with certainty but has been suggested as: a protection against predators by giving a general glow to the ventrum which does not contrast with the faint illumination from above (W. Clarke, 1963), a means of species recognition, sexual recognition, dymanitic display to predators, and a means of capture of prey.

Almost nothing is known about reproduction in these squids except that the larvae of most species seem concentrated in the upper levels within 50 m of the surface. Gravid females of a number of species have been taken at the surface. Ripe females of at least two species of enoploteuthids have been taken within harbors at night leading the writers to believe that they had come ashore to spawn; since the localities were small oceanic islands this hypothesis seems to be mainly guess work.

The coloration of the mesopelagic species is similar to that of the epipelagic and little tendency towards red or black is seen.

Octopods.—The only octopods known to be mesopelagic are the young of *Japetella diaphana* and perhaps the adults of *Alloposus mollis* (Thore, 1949). These forms have the characteristic body consistency of their bathypelagic adults and relatives and will be discussed below.

THE BATHYPELAGIC FAUNA

Decapods.—The squids living between about 700-2000 m share a number of features in common (Table 3). In general they are not strong swimmers. Evidence for this is the small size of the fins (an exception is *Mastigoteuthis*) in relation to body size, poorly developed swimming keels, small not so mobile funnel and poorly developed funnel valve. The funnel organ in these species is often complex, equipped with ridges, papillae, flaps, and pits.

The mantle wall is often thick but it is not very muscular. Instead it is composed of a more or less loose network of muscle fibers with the bulk of the material formed of a jelly-like material; the animal has a soft, gelatinous consistency. This type of construction is found in all groups of cephalopods found below 700 m with the major exception of the cranchiids.

The general coloration is various shades of red from light orange to deep vinous red bordering on purple.

Light organs are present in most species but are not numerous except in the Histiotteuthidae and in certain *Mastigoteuthis*. They are almost certainly used here for species recognition and for attracting prey.

TABLE 3
BATHYPELAGIC ZONE

Characters	Examples
Squids	
1. Mantle thick but gelatinous with degenerate musculature	<i>Histioteuthis</i>
2. Poor swimmers with small fins and poorly developed swimming keels	<i>Mastigoteuthis</i>
3. Color reddish to reddish purple	<i>Bathyteuthis</i>
4. Reproduction unknown, larvae in upper 100 meters	
5. Highly modified for predation, sight, etc.	
Octopods	
1. Body gelatinous	<i>Eledonella</i>
2. Few or no chromatophores	<i>Japetella</i>
3. Plankton feeders	<i>Vitreledonella</i>
4. Larvae concentrated at deep discontinuity layer	<i>Alloposus</i>
5. Reproduction unknown but <i>Vitreledonella</i> reportedly viviparous	<i>Amphitretus</i>

Reproduction in the bathypelagic squids is unknown. In the Histioteuthidae the larvae are found in the upper 50 m, based on the DANA material from the Atlantic (N. Voss, In Press), so it must be presumed that the eggs are spawned in the upper regions and these may be found in the vicinity of the subsurface discontinuity layer. Many of the bathypelagic species have highly modified planktonic stages such as the *Doratopsis* stage of *Chiroteuthis*, etc.

The general morphology of the squids undergoes its greatest modifications in the bathypelagic species; this is probably a result of the more passive mode of life in the mid-depths. In the Histioteuthidae, for example, the left eye is greatly enlarged in comparison with its fellow. It is possible (Voss in Lane, 1957) that the enlarged eye is functional at the level of bioluminescent illumination while the normal eye functions in the surface waters. Some support to this theory has been given by microscopic examination of the retina. In the mastigoteuthids and especially the chiroteuthids, the tentacles are greatly elongate and very slender; in the latter the clubs are equipped with long pedicelled hooks arranged near a large terminal light organ. This suggests its use as a fishing apparatus which might be compared with the luminescent lures of the ceratioid fishes.

An inexplicable feature found in the bathypelagic squids is a well developed ink sac like that found in epipelagic species. As the ink sac in the oegopsids, except for a few species of cranchiids, has no light organs associated with it (and in the chanchiids it does not appear to harbor symbiotic luminescent bacteria) it would seem to be of little value to its owner.

Octopods.—The bathypelagic octopods are uniformly gelatinous in con-

struction, with few to no chromatophores (*Vitreledonella*) and seem to be very poor swimmers; this is supported by their common occurrence in plankton tows. Knowledge of the biology of these forms is mainly due to Thore (1949) who studied the DANA material. In general these octopods (Bolitaenidae, Amphitretidae, Vitreledonellidae, and Alloposidae) live below the deep discontinuity layer (1000 m) to depths of about 2,000 to 3,000 m. The young are concentrated just below the discontinuity layer but the larger specimens are in the greater depths, adult forms living near 2000 m. Joubin (1929) has reported that *Vitreledonella* is viviparous. The bathypelagic octopods feed upon small planktonic organisms.

THE ABYSSOPELAGIC FAUNA

The only cephalopods positively known to inhabit this region are the finned octopods and *Vampyroteuthis* (Table 4). They have a delicate,

TABLE 4
ABYSSOPELAGIC ZONE

Characters	Examples
Squids	
None known from this zone	
Octopods	
1. Body very gelatinous	<i>Cirrothauma</i>
2. Large fins supported by cartilaginous shell	<i>Stauroteuthis</i>
3. Suckers greatly reduced and supplemented by cirri	<i>Grimpoteuthis</i>
4. Color deep red or black, some colorless	<i>Cirroteuthis</i>
5. Deep interbranchial web	
6. Eyes reduced or absent in <i>Cirrothauma</i>	
7. Plankton feeders	
Vampyromorpha	
1. Body very gelatinous	<i>Vampyroteuthis</i>
2. Fins present	
3. Suckers reduced, supplemented by cirri	
4. Color black	
5. Light organs numerous	
6. Plankton feeder	

very gelatinous consistency with very delicate black pigmented skin which is easily torn loose or rubbed off; *Cirrothauma* is colorless and transparent. If preserved in 70 per cent alcohol these animals shrink severely, losing up to 50 per cent of their size. Only *Vampyroteuthis* possesses photophores.

The finned octopods are poor swimmers and probably catch their prey with the aid of the well developed interbranchial web. They seem to feed upon small crustaceans and other minute life. Swimming is probably accomplished by a medusoid type of movement with the web and the assistance of the feeble funnel and poorly developed but often large fins. *Cirrothauma* is blind and some of the others have reduced eyes.

THE LITTORAL BENTHIC FAUNA

Decapods.—The benthic squids of the Continental Shelf (Table 5) are in the main small animals and are confined to the Sepioidea and the Myopsida, or those squids having the eye closed except by a minute anterior pore. They possess thick muscular mantles and, with the major exception of the genus *Sepia* (which are large active animals), have small fins and are rather inactive. *Idiosepius* lives clinging to bottom grasses while the others burrow slightly in the mud and sand but swarm at the surface around the night light. The general coloration is similar to the pelagic forms. Their eggs are large, capsulated, and attached to the bottom. Development is direct. Mating in *Rossia* has been described by Racovitza (1894). Food is obtained by darting out the tentacles, which are retractable.

TABLE 5
LITTORAL BENTHIC ZONE

	Characters	Examples
Squids		
1.	Poor swimmers, small fins, mantle muscular	<i>Idiosepius</i>
2.	Color normal	<i>Rossia</i>
3.	Eggs attached to bottom, larvae at surface	<i>Sepiadarium</i>
4.	Eyelids closed	
Octopods		
1.	Sedentary, heavy, muscular body	<i>Octopus</i>
2.	Crawling forms	<i>Scaevargus</i>
3.	Color normal	
4.	Eggs small to large, development direct or with larvae stage	<i>Pteroctopus</i>
5.	Ink sac present	

Octopods.—The shallow water octopods are stout, muscular animals living either in caves or burrows. They are predators living mainly on crustaceans and bivalve mollusks. Their coloration is normal but they are usually only slightly sculptured, much due to the action of the preservative. Mating and reproduction has been described by various writers and the eggs are usually laid in festoons (small eggs) or in single layers (large eggs). In the small egg species the young hatch out as larvae spending considerable time in the plankton. The large eggs yield large young which immediately adopt the adult habitat (Voss in Lane, 1957). Representative genera are *Octopus*, *Scaevargus*, and *Pteroctopus*, the latter occupying the deeper part of the zone. All of these species have a characteristically high gill lamellae count.

THE MESOBENTHIC FAUNA

Decapods.—The squids of this region (Table 6) are almost universally small with muscular but soft bodies. Characteristic genera are *Rossia*, *Sepiola*, and *Stoloteuthis*. The coloration is usually light red or reddish.

TABLE 6
MESOBENTHIC ZONE

	Characters	Examples
Squids		
	1. Body short, squat, muscular but soft	<i>Rossia</i>
	2. Color tending towards red	<i>Sepiola</i>
	3. Eggs large, attached to bottom, larvae unknown	<i>Stoloteuthis</i>
	4. Light organs usually involved with ink sac	<i>Heteroteuthis</i>
Octopods		
	1. Muscular to gelatinous	<i>Octopus</i>
	2. Crawling forms	<i>Benthoctopus</i>
	3. Color tending towards red	<i>Bathypolypus</i>
	4. Eggs large, young unknown	
	5. Decrease in size of ink sac	
	6. Decrease in size and complexity of ink sac	

Reproduction is probably the same as in the littoral benthic forms but has not been observed. The eggs are usually heavily capsulated, either in bunches or in a single fused sheet. Development apparently is direct with the young living on the bottom.

Most mesobenthic squids belong to the Sepiolidae and possess a large well developed ink sac in association with a large simple or compound light organ containing luminescent bacteria. When the ink is discharged the bacterial culture is also expelled so that the ink glows in the darkness. This has been well described for *Heteroteuthis dispar* and is undoubtedly the same in the others possessing the combined organs. It is doubtful if *Heteroteuthis* is entirely a bottom dweller; it may be mesopelagic living close to the continental slope.

Octopods.—The mesobenthic octopods, like the squids of this zone, are muscular but soft and slightly gelatinous. They are pinkish or light red. Most of them have rather stout arms; none possesses the long arms found in some littoral species. The web is also deeper. The deep water species of *Octopus* have ink sacs of normal size; in *Pteroctopus* it is somewhat reduced. In *Bathypolypus* and *Benthoctopus*, which are only occasionally found in this zone, the ink sac is absent. The eggs are very large and the spermatophores few and large. The gill lamellae are slightly fewer and the gill in general is reduced. *Benthoctopus* and *Bathypolypus* are only found in this zone in high latitude waters.

THE BATHYBENTHIC FAUNA

Decapods.—The bathybenthic squids (Table 7) are probably restricted to the *Rossia mastigophora* complex, *Heteroteuthis*, and the rare little squids belonging to the genus *Nectoteuthis*. The body is soft to gelatinous, the fins large but soft and flabby, and the color is reddish to purple. Reproduction is unknown. They are presumed to be detrital and discriminate

TABLE 7
BATHYBENTHIC ZONE

Characters	Examples
Squids	
1. Body gelatinous to soft	<i>Rossia</i>
2. Color red to reddish purple	<i>Nectoteuthis</i>
3. Reproduction unknown	
4. Light organs involved with ink sac	
Octopods	
1. Body muscular to gelatinous	<i>Opisthoteuthis</i>
2. Color reddish to white	<i>Bathypolypus</i>
3. Gills greatly reduced	<i>Pareledone</i>
4. Ink sac absent or reduced	<i>Thaumeledone</i>
5. Crop reduced or absent	
6. Radula, normal, reduced, or absent	

plankton feeders. Most have a light organ associated with the large, well developed ink sac.

Octopods.—The bathybenthic octopods are mostly small animals with the exception of Taki's (1961) new genus *Megaleledone* from Antarctic waters. The body is soft and gelatinous but is often heavily sculptured with simple or branched papillae, peripheral ridges, etc. The color in fresh specimens is pinkish due to the reduced number of red chromatophores, or is a dull to livid purple. The color in preserved specimens is untrustworthy. *Opisthoteuthis* alive is bright red. Preserved, *Pareledone* and *Thaumeledone* are often colorless to flesh color or even white. In *Benthoctopus*, *Pareledone*, and *Thaumeledone* the gills are greatly reduced in size and there are only four or five gill lamellae per demibranch although a few have an exceptionally high number (10-17 in *P. polymorpha*)¹. The ink sac is small, buried deeply in the liver or more often absent. In *Bathypolypus* and some others the crop is reduced or absent and in some, such as *Thaumeledone*, the radula is reduced to only a single row of rhachidian teeth. The spermatophores in almost all genera are very large and few in number and the eggs are exceptionally large.

THE ABYSSOBENTHIC FAUNA

Decapods.—There are no known benthic squids in this zone (Table 8). Even doubtful records are extremely rare.

Octopods.—The records of abyssobenthic octopods are limited to a few specimens of *Graneledone* from the northwestern Atlantic and records of a few specimens of *Benthoctopus* and *Bentheledone*. The characters of these forms are generally the same as in the bathybenthic zone. These are the deepest known records for the benthic cephalopods which seem valid

¹Investigations by the writer have shown that Robson was in error. The gill count for this species is 7-8-9.

TABLE 8
ABYSSOBENTHIC ZONE

Characters	Examples
Squids	
None known below 1200 meters	
Octopods	
1. Body soft to gelatinous	<i>Benthoctopus</i>
2. Color reddish to white	<i>Graneledone</i>
3. Gills greatly reduced	<i>Bentheledone</i>
4. Ink sac reduced or absent	
5. Eggs large, spermatophores large and few	

and are given as follows: *Benthoctopus piscatorum*, 2500 m; *Graneledone verrucosa*, 2300 m; *Bentheledone rotunda*, 3565 m; and *Bentheledone* sp., 4120 m (Robson, 1932).

ADAPTATIONS TO LIFE IN THE DEEP SEA

The immigration of cephalopods into the deep sea has required a number of morphological changes (Fig. 4) certainly accompanied by physiological changes of which we at present have no knowledge. Before discussing morphological changes, it is necessary to consider first the effect of pressure, *per se*. Great pressure occurs in the depths of the sea. It is the one absolute factor which can be precisely measured for any depth of capture, yet it can be said flatly that there is no evidence at present that a stenobathic species exists among the cephalopods. The picture concerning adaptive modifications should not be muddled by considering pressure until something is known of its affect upon biological systems.

The most important factors other than pressure found in the deep-sea environment are the almost complete lack of light, extreme cold, somewhat lowered dissolved oxygen, and scarcity of food. These factors must be examined in order to explain certain features found in the deep-sea cephalopods.

Light.—It is interesting that the greatest development of luminescence in the sea occurs just at the depth at which visible light nears extinction. It is pleasant to conjecture that photophores evolved in mesopelagic animals which, being derived from shallow photic zone relatives, survived better if equipped with supplementary lighting. How it is used is not germane to the present discussion. True abyssal forms in many animal groups have degenerate eyes or have lost them altogether but they survive well without any apparent lighting.

To utilize the low illumination levels available from photophores, eyes grew larger and larger, or became thrust completely outside of the head on long stalks. No one has worked out the eye mantle length ratios of the

decapods from the surface to the sunless depths. However, *Histioteuthis* has one gigantic eye and even the normal one is larger in relation to mantle length than in the surface forms. The same can be said for *Bathyteuthis* and *Mastigoteuthis*, all true deep-sea forms. Robson (1925) showed that there is from the surface to abyssal depths a distinct increase in the size of the eye in octopods. Only *Cirrothauma* has no functional eyes and it lives in abyssal depths throughout its life far below the bioluminescent zone of the middepths and above the secondary luminescent zone on the sea floor¹.

Related to the light problem is the presence or absence of an ink sac. In lighted surface waters its use is self evident and well known. Some species living in the mesopelagic or mesobenthic zone still use their ink secreting abilities as a means of survival but mix the ink with luminescent bacteria; they shoot out luminescent clouds to confuse their enemies.

Below this zone this last attempt to use the ink sac for defense disappears; the deep-sea cephalopods still equipped with an ink sac must find it about as useful as man does his vermiform appendix. The squids, being recently derived from the surface have retained the ink sac. Numerous groups of octopods have already rid themselves of this drain on their systems.

Dissolved Oxygen.—Oxygen in the open sea, with the exception of a few

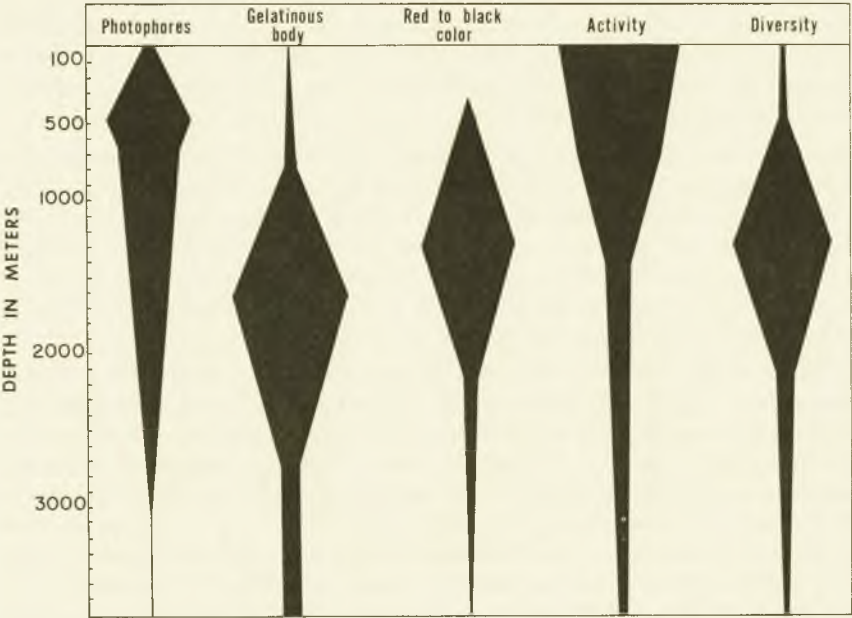


FIGURE 4. Correlation of certain characters with depth.

¹Since this was written the writer has received a specimen of *Cirrothauma* dipped from an ice hole in the Arctic Ocean by Mr. Ronald H. McPeak of the University of Southern California. Apparently its only limitation is temperature.

rather unusual areas, never decreases to such an extent as to inhibit life. The oxygen minimum layer in the open ocean seems not to be a detriment to the number of cephalopods found in it. According to Harvey (1957) the amount of dissolved oxygen is roughly 5.0 cc/liter at the surface in low latitudes decreasing to about 3.0 cc/liter at the oxygen minimum layer and then rising to about 6.0 cc/liter below to then diminish slowly in the greatest depths. In Antarctic waters it may rise to above 8.0 cc/liter.

Robson (1925) in his study of the deep-sea octopods showed that in general the number of gill lamellae decreased with increasing depth until in the deep-sea octopods the lamellae of the inner demibranch were lost entirely in some groups (*Vitreledonella*). In the surface forms the usual number of gill lamellae is about 20 counting both demibranchs. In some of the deep-sea forms the total lamella count is only four to six. Although there is a slight increase in the size of the individual lamellae in these reduced forms the total area of the gills is greatly reduced. Robson has considered the question of adaptive significance of this trend but did not reach a clearcut decision. If Boyle's law holds true under extreme pressures and temperatures then the only interpretation for the marked decrease in gill size is to reduce the total metabolic requirements of the animal in a habitat of low metabolic activity and low availability of food. Robson's apparent anomaly of shallow-water octopods sharing this feature is understandable when it is seen that he was concerned with shallow water forms in the Antarctic where conditions quite near the surface are similar to those in the depths in the equatorial region. *Opisthoteuthis*, a special case, will be examined later.

Metabolic Requirements and Availability of Food.—It is fortunate for deep-sea animals that as the available food decreases, the ambient temperature decreases also, for this lowers the rate of the metabolic processes and thus cuts down on food requirements. Feeding activities also diminish since this is wasteful of the low energy available. Also in general in the depths of the sea it is not particularly useful to go dashing off in search of food when the chances of finding it are rather slim.

There seems to be two ways in which an animal can survive on a limited food supply: (1) It can cut down its activities to the barest minimum, (2) It can cut down its demand by being much smaller or (3) It can achieve this last end in another fashion, by decreasing the amount of the body which is metabolically active while maintaining its size. There seems to be a certain limit in most groups beyond which it is not useful to become much smaller and it is worth noting that the smallest cephalopod known is a surface form, *Idiosepius*, and the largest known are *Architeuthis* and *Galiteuthis* both of which live at considerable depths. Probably also in the deep sea it is not an advantage for a cephalopod to be too small as it would then fall prey to the rather large number of active fish predators; it would also be at some disadvantage in capturing its own prey.

Apparently the deep-sea cephalopods have adapted by following the line of 1) and 3).

REDUCED ACTIVITIES: In strict contrast to the epipelagic and mesopelagic squids there seem to be few active predators in the deep sea. *Architeuthis*, the giant of the class, is considered by Robson (1933) and Voss (1956) on the basis of its morphology to be a sluggish animal living as a scavenger along the middle part of the continental slope. The next largest squid, a giant cranchiid of a type closely resembling *Galiteuthis* has an arm spread of about 24 feet, the arms equipped with a battery of giant curved claws, but the mantle is ridiculously small and thin walled. It is presumed that this animal lives with the arms out spread and hanging downward in the mid-depths waiting for its prey to venture near its arms.

Spirula maintains itself in this fashion by means of its gas-filled shell. Recently Roper (personal communication) has shown that *Bathyteuthis* has the posterior end of its body filled with an oily fluid which in the aquarium maintains the animal in a similar fashion. The numerous instances of fatty material in the posterior end of the mantle cavity in various deep-sea forms suggests that this is a fairly common attitude in deep-sea squid. The writer has previously suggested that sedentary fishing occurs in the genus *Chroteuthis* whose long hook-covered tentacular club with its terminal light organ is directly comparable to the fishing lures of the ceratioid fishes.

All of the finned abyssopelagic octopods and *Vampyroteuthis* have extensive webbing between their arms, a decrease in the size and numbers of suckers, and the development of cirri on the arms; all probably are adaptations for feeding on plankton. On the evidence of stomach contents, the deep benthic forms have changed from feeding on active crustaceans and other shellfish to eating small benthic forms and detrital material; this is also indicated by the loss of the radula in many of the species. Swimming is carried out in these animals by the slow beating of the fins but mostly by a medusoid type of swimming utilizing the interbrachial web.

REDUCED METABOLIC AREA: In 1925, Robson pointed out that there were two lines of change in the construction of the mantles of cephalopods (octopods): (1) an invasion of the connective tissue of the mantle by a gelatinous material which appears to be non-living since it is not cellular in structure, and (2) a continuing decrease in the thickness of the otherwise normal tissue.

By gelatinous material is meant a material which in the living animal is gelatinous and results in the mantle being very soft and almost transparent. A similar softening of the mantle which at first sight appears to be of a similar nature is often found in poorly fixed material or material from fish stomachs resulting from the action of digestive juices, both being cases of histolysis.

In the cephalopods this change may take place by the development of a subcutaneous gelatinous layer in otherwise normal tissue, or by the direct invasion of the muscle by the gelatinous material with the amount of muscle remaining about normal, or by the reduction of the muscle fibers to only a scattered fine network. This latter is the case in *Vampyroteuthis* according to R. Young (personal communication); this species also has large fatty cells in the gelatinous material.

The nature of this gelatinous material, unfortunately, has not been investigated and there is no information available about its chemistry or density.

It is possible, however, that this material may function in several ways: (1) being non-cellular, it is more or less metabolically inactive. In this way it permits the animal to retain its bulk without having to maintain it, a possibility with great advantage to a deep-sea animal; (2) there is the possibility that it is less dense than seawater, in which case it may assist in flotation; and (3) it may possibly be a food storage mechanism to tide the animal over the long periods between capture of prey. It may well act in all three capacities.

Robson considered that the gelatinous material was purely an adaptation for withstanding the extreme pressures found in great depths. Such a function seems very remote. If it were so it would pose the same exasperating problems which confronted Robson, since this same type of tissue is found in certain forms living near the surface but exhibiting a very sedentary type of existence.

Apparently this same problem has been solved by another group of cephalopods, the cranchiid squids, in quite a different fashion. These animals have mantles which are formed of very thin but muscular walls, so thin that the giant mentioned previously had a mantle wall of not more than 2 mm thick. This however, is much denser than the surrounding water and the animal compensates for this by the development of a closed body cavity, designated a coelom by Denton *et al.* (1958), within which are concentrated the light ions of NH_4^+ and Cl^- . In this way flotation is accomplished without the gelatinous matrix of the other groups.

Marshall (1954) has given a discussion of the occurrence of gelatinous material in various groups of marine animals from salps to fish larvae and has pointed out that whatever other value it may have, it must help reduce the specific gravity of the animals, thus in essence acting as a flotation mechanism. If it is metabolically inert as well, the advantage to the deep ocean dweller is obvious.

It is the writer's opinion that the gelatinous construction of the body tissue of most deep-sea forms and the extremely thin construction of the mantle wall in the cranchiids are two of the most obvious and important adaptations to the deep-sea habitat found in the cephalopods.

THE DERIVATION OF THE DEEP-SEA FAUNA

The general picture of the derivation of the deep-sea cephalopod fauna seems fairly clear. With only a few exceptions the deep-sea fauna is derived from the surface fauna. One of the most telling arguments is the possession of an ink sac in various species of almost all groups, clearly only of real value in the upper sunlit areas of the oceans, and the presence of large enervated chromatophores. However, there are a few groups in which this general pattern differs.

The Nautiloidea is an ancient assemblage of which only about five or six species survive in modern seas. They are equipped with an external shell, which, in the class, must be considered as quite heavy and cumbersome. The ancient nautiloids occurred most commonly in the shallow seas and the modern descendants have probably survived through adapting to the mesobenthic zone where conditions have probably remained stable over long periods of time. Nautiloids do not possess an ink sac.

The Sepioidea are in the main benthic forms and the vast majority of the recent species are found in the upper regions of the oceans with only two groups, the Rossiinae and the Heteroteuthiinae having examples which deserve the term "deep-sea." In all of these however the deep-sea forms are in the minority and show a distinct relationship to the shallow-water forms.

The Myopsidea are all shallow water dwellers.

The Oegopsida is a large and diverse group with four families, the Chiroteuthidae, the Mastigoteuthidae, the Grimalditeuthidae, and the Cranchiidae, showing rather marked differences from the main stem, especially the latter family which at present still defies satisfactory classification. With the exception of these last four families, the Oegopsida seem easily derived from surface ancestors with only moderate modifications for deep-sea life. Indeed, the depth to which some of these groups penetrate seems mainly related to their size, speed and predatory habits. With no gaseous spaces to effect their movements from one level to another there seems little reason why such swift moving and excitable creatures as the Ommastrephidae and the Thysanoteuthidae should not roam at will over the depths, limited primarily only by the availability of food. The Histioteuthidae among all of this assemblage is the most abyssal; it might be regarded as a peculiarly deep-sea group if it were not for the visible lines of change from a long, rather slender bodied, symmetrical form (*H. elongata*) to a partially asymmetrical, short, cone-shaped mantle form (*H. reversa*) with grossly differentiated eyes.

The Cranchiidae, which many specialists regard as a separate group from the other Oegopsids, is peculiar in its different method of adapting to deep-sea life, its great diversity of form, and its strange larval life histories. Whence it originated and whether from a deep-water or shallow-water ancestor is not certain, but the occurrence in abundance of the larvae of almost all species in the surface waters of the oceans seems to indicate a

shallow-water origin. The depth range of the adults, of which almost none are known, is still a major problem. Evidence points towards near gigantic size.

The Octopodidae, within certain circumscribed limits, is also a very diversified group. Robson (1925, 1932) has discussed their affinities and adaptations in considerable breadth and detail. The gelatinous mantles, absence of ink sac, degenerate radula, closure of the mantle aperture, reduced gills, etc., are all, in the main, adaptations to the deep-sea life; however, they occur over and over again in various groups whose other members are quite typical octopods of the shallow seas. There seems no recourse but to consider them all as derived from a common shallow-water ancestor, with the Eledoninae evolving into a specialized deep-water offshoot of which the genus *Eledone* remains the sole shallow water representative. If they are considered in this fashion, Robson's (1932) arguments for separation of *Eledone* from the rest of the group lose much of their former force.

The Argonautidae, Tremoctopodidae, and Ocythoidae seem obvious epipelagic families.

The Bolitaenidae, Amphitretidae, Vitreledonellidae, and Alloposidae pose more of a problem. However, the possession of an ink sac in all members indicates a surface origin although the group as a whole seems evolving into a deep-sea branch.

The Vampyromorpha and the cirromorph octopods remain for final consideration. The Vampyromorpha is represented only by *Vampyroteuthis*, an archaic cephalopod whose relationship to the rest of the class is still undetermined. There seems no doubt that it is a true deep-sea form. It is a highly modified form but whether the order evolved in the deep-sea or in the shallow seas is as yet an unsolved problem.

The Cirromorpha alone form a fairly large and homogeneous group of deep-sea or abyssal cephalopods. They possess no ink sac in any of the investigated forms, they are gelatinous, either colorless or deep red or black, the crop is missing, the radula is atrophied, fins are present, and other modifications are found. It seems probable that this group is evolved from a deep-water ancestral form in which these adaptations had already taken place, hence the lack of exceptions in any members of the group. *Opisthoteuthis* has apparently evolved into a benthic form and, in areas favorable to it, has ascended into somewhat shallow depths. The problem raised by Robson concerning the depths occupied by members of this genus need give no concern in the light of the modifications discussed in the preceding section.

Robson and others have been perturbed in reasoning out their theories concerning the deep-sea fauna due to their insistence that the gelatinous structure found so commonly in deep-sea cephalopods is a modification due to adaptation to pressure and the fact that in polar waters a number

of gelatinous species are found in shallow water. Since, however, most of the deep-sea adaptations seem to be due to absence of light and presence of low temperatures, characters found both in the deep-sea and polar regions, no real difficulties are encountered.

LITERATURE CITED

- ARON, WILLIAM, NEWELL RAXTER, ROY NOEL AND WILLIAM ANDREWS
1964. A description of a discrete depth plankton sampler with some notes on the towing behavior of a 6-foot Isacss-Kidd mid-water trawl and a one-meter ring net. *Limnol. Oceanogr.*, 9 (3): 324-333.
- BÉ, ALLAN
1962. Quantitative multiple opening and closing plankton samplers. *Deep-Sea Res.*, 9: 144-151.
- BRUNN, ANTON FR.
1955. New light on the biology of *Spirula*, a mesopelagic cephalopod. Essays in the Natural Sciences in Honor of Captain Allen Hancock; 61-72, 2 pls.
1957. Deep Sea and Abyssal Depths. *Geol. Soc. Amer. Mem.*, 67: 641-672.
- CHUN, CARL
1910. Die Cephalopoden. 1. Teil: Oegopsida. *Wiss. Ergebn. Deutschen Tiefsee-Exped. Valdivia 1898-1899*, 18 (1): 1-402, 32 figs., 61 pls.
1914. Cephalopoda. *Rep. Sci. Res. Michael Sars N. Atl. Deep Sea Exped.* 1910, 3 (1): 1-28, 2 pls.
- CLARKE, ARTHUR H., JR.
1962. Annotated list and bibliography of the abyssal molluscs of the world. *Bull. Nat. Mus. Canada*, 181: i-v, 1-114.
- CLARKE, W. D.
1963. Function of bioluminescence in mesopelagic organisms. *Nature*, 198 (4887): 1244-1246.
- DENTON, E. J., T. L. SHAW AND J. B. GILPIN-BROWN
1958. Bathyscaphoid squid. *Nature, London*, 182: 1810-1811.
- DREW, G. A.
1911. Sexual activities of squid *Loligo pealii* (Les.) 1. Copulation, egg-laying and fertilization. *J. Morph.*, 23: 327-359.
- FOXTON, P.
1963. An automatic opening-closing device for large plankton nets and mid-water trawls. *J. Mar. biol. Ass., U.K.*, 43: 295-308.
- HARVEY, E. NEWTON
1952. Bioluminescence. Academic Press, New York. xvi + 649 p., illus.
- HARVEY, H. W.
1957. The chemistry and fertility of sea waters. Cambridge Univ. Press. viii + 224 p., illus.
- HOYLE, WILLIAM E.
1886. Report on the cephalopods collected by H.M.S. Challenger during the years 1873-76. *Challenger Exped., Zool.*, 16 (44): 1-246, 33 pls.

- JOUBIN, L.
1929. Notes préliminaires sur les céphalopodes des croisières du "Dana" (1921-1922). Octopodes 2c partie. Ann. Inst. oceanogr. (N.S.), 7 (1): 1-24, 42 figs.
- LANE, FRANK
1957. The kingdom of the Octopus. Jarrold's, London. xx, 287 pp., 13 text figs., 48 pls.
- LEACH, W. E.
1817. Synopsis of the orders, families and genera of the class Cephalopoda. Zool. Miscell., 3: 137-141.
- LESUEUR, C. A.
1821. Description of several new species of cuttlefish. J. Acad. nat. Sci. Philad., 2: 86-101, 6 pls.
- MARSHALL, N. B.
1954. Aspects of deep sea biology. Hutchinson, London.
- MENZIES, ROBERT
1965. Conditions for the existence of life on the abyssal sea floor. Oceanogr. Mar. Biol. Ann. Rev., 1965, 3: 195-210.
- D'ORBIGNY, ALCIDE
1841. Histoire naturelle générale et particulière des céphalopodes. Paris.
- PEARCY, WILLIAM G. AND LYLE HUBBARD
1964. A modification of the Isaacs-Kidd mid-water trawl for sampling at different depth intervals. Deep-Sea Res., 11: 263-264.
- PFEFFER, GEORG
1912. Die Cephalopoden der Plankton-Expedition. Ergebn. Plankton-Exped. Humboldt-Stift., 2: 1-815, atlas, 48 pls.
- PICKFORD, GRACE
1946. *Vampyroteuthis infernalis* Chun, an archaic dibranchiate cephalopod. I. Natural history and distribution. Dana-Rep., 29: 1-40, 8 text figs.
- RACOVITZA, E. G.
1894. Notes de biologie. II. Moeurs et reproduction de la *Rossia macrosoma* (D. Ch.) Arch. Zool. exp. gen., 2 (3): 491-539, 6 figs. 3 pls.
- REES, W. J. AND G. E. MAUL
1956. The Cephalopoda of Maderia. Bull. Brit. Mus. (Nat. Hist.), 3 (6): 259-281.
- ROBSON, G. C.
1925. The deep sea Octopoda. Proc. zool. Soc. Lond., 1925: 1323-1356.
1932. A monograph of the recent Cephalopoda based on the collections in the British Museum (Natural History). Part II. The Octopoda (excluding the octopodinae). Brit. Mus. London. 359 pp., 79 figs., 6 pls.
1933. On *Architeuthis clarkei*, a new species of giant squid, with observations on the genus. Proc. zool. Soc. Lond., 1933: 681-697.
- TAKI, IWAO
1961. On two new eledonid octopods from the Antarctic Sea. J. Faculty Fish. animal Husb. Hiroshima, 3 (2): 297-316, 16 text-figs, 3 pls.

THORE, SVEN

1949. Investigations on the "Dana" Octopoda. Part 1. Bolitaenidae, Amphitretidae, Vitreledonellidae and Alloposidae. Dana-Rep., 33: 1-85, 69 text-figs.

VOSS, GILBERT L.

1956. A review of the cephalopods of the Gulf of Mexico. Bull. Mar. Sci. Gulf and Carib., 6 (2): 85-178, 18 text-figs.

VOSS, NANCY A.

- In Press. A monograph of the cephalopods of the North Atlantic. 2. The family Histoteuthidae. Bull. Mar. Sci.

YOUNG, J. Z.

1960. Observations on *Argonauta* and especially its method of feeding. Proc. zool. Soc. Lond., 133 (3): 471-479.

Behavior Patterns in Tropical Waters

ECKHARD HESS
Convener

The following paper was delivered at the Conference but has not
been received for publication:

THEODORE J. WALKER: Behavior of the California Gray Whale in Scammon's
Lagoon, Baja California.

SPECIALIZATION OF ORGANS HAVING A SIGNAL FUNCTION IN SOME MARINE FISH

WOLFGANG WICKLER

Max-Planck-Institut für Verhaltensphysiologie, Seewiesen über Starnberg (OBB.), Germany

ABSTRACT

This report deals with a few signal characters to show how they are linked with the special ecological situation of particular marine fishes. Behavioural studies by various authors strongly indicate that behaviour changes precede evolutionary changes in morphology. A few examples from such studies are discussed.

Some of the groups considered are the triggerfishes, puffers, porcupine fishes, damselfishes, blennies, and blenny-like fishes, wrasses, frogfishes, and batfishes.

(A number of films were presented at the conference to illustrate various points stressed in the presentation.)

INTRODUCTION

When looking at tropical marine fish, especially those from coral reefs, one is immediately impressed by their highly conspicuous and vivid colouration, and sometimes by bizarre forms of the whole body or of its appendages. Both features, the strangeness and the beauty of these creatures, have been attributed to an overflow of Nature's creative forces, being so to speak beautiful nonsense. This shirking hypothesis would conveniently allow an immediate stop to further research on this subject. However, up to now in the natural sciences we have preferred working-hypotheses; so we suggest that these colours and structures are biologically valid characters, that they have a special significance and, moreover, that some or even the majority of them are signal characters. If this is correct, then it is necessary to determine the receiver and the exact meaning of these signals. Some function as camouflage, but others do not (as is clearly indicated by the behaviour of fish which often display these colours in a conspicuous manner). Behavioural studies are the only means to find out more about these phenomena, but after working for several years in this field I must say that this kind of study is rather painstaking. To begin with, one does not know how many discrete signals the general colouration of the given animal comprises. We still do not know this even for one given species. We do, however, know some of these signals and their special significance. I should like to give you a few examples, to show how these signals are linked with the special ecological situation of each particular species.

There is one other point of view to which I should like to direct attention. Darlington (1938) postulated that "form overlaps function at both ends," that is to say, morphological changes occur before they are of any use, and persist afterwards. Behaviour studies of various authors

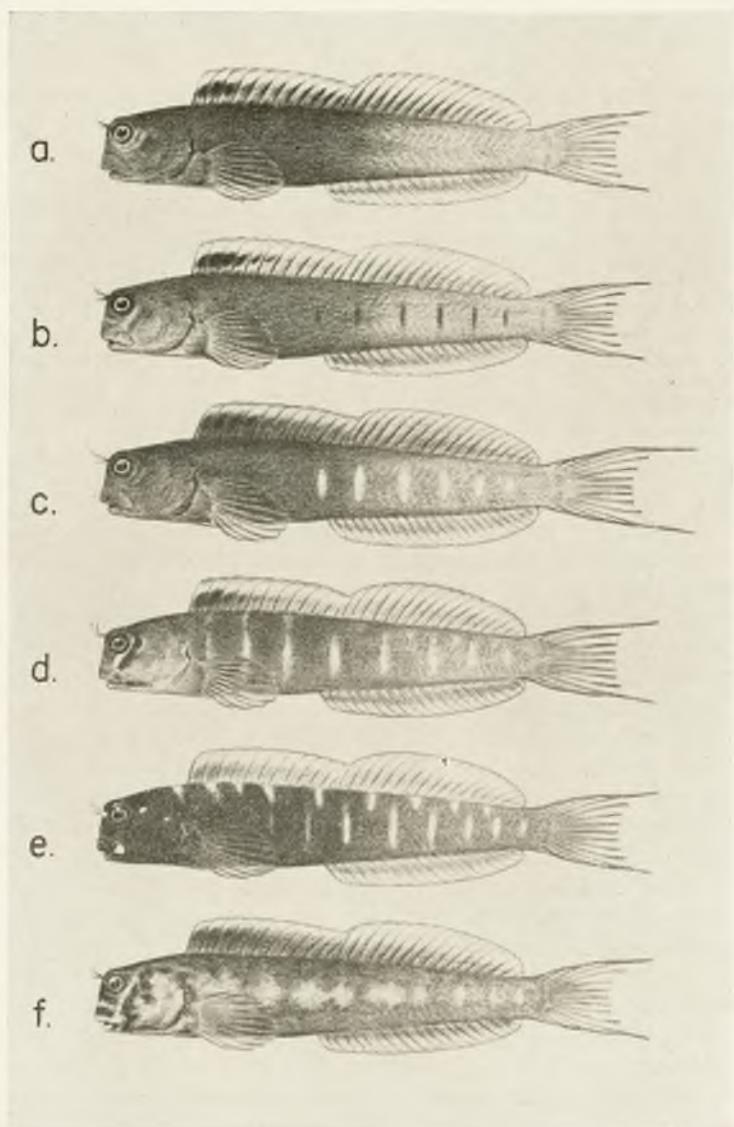


FIGURE 1. Colour patterns of *Ecsenius bicolor*: a, Neutral—b, Aggressive and courting within its living hole—c, Same as B but outside the living hole—d, Frightened and swimming—e, Frightened and resting on the bottom—f, Defending eggs (from Wickler, 1965).

strongly indicate the opposite, however, that behaviour changes precede evolutionary changes in morphology.

To stick to tropical waters: during their phylogeny, fast swimming pelagic fish have reduced the original (in both the phylogenetic and ontogenetic sense) rhythmic, pectoral fin movements to non-rhythmic movements; the pectorals are held almost motionless like wings, and in two subspecies of marlins (*Makaira marlina marlina* and *M. m. tahitiensis*) have finally come to be supported by a rigid three-point suspension, which prevents the fins from being folded (Morrow, 1957). The position of the fin was originally designed for locomotion, that is towards a behavioural character, but in these latter forms has developed into a purely anatomical structure (Wickler, 1960).

In the Tetraodontiformes, a number of species are able to inflate themselves tremendously with water or air, as is known in "globe-fishes" for "puffers") and in porcupine fishes (Diodontids). In young specimens of *Diodon*, during inflation the median fins disappear in definite pouches of the skin. This reversible inflated globe-like stage has become an irreversible character in *Hyosphaera* among the Diodontidae, and in *Kanduka michiei* among the Tetraodontidae. The latter species, as an adaption to this pouched stage, has even lost the dorsal fin and the anal fin is only vestigial (Hora, 1924). Behaviour as the "pacemaker" of evolution will also become visible in the following examples. These examples are illustrated by films which I have shown.

The morphological character which changes most easily in evolution is that of colouration. In fish with a pronounced "mood"-dependent colour change, one can determine the different signal patterns from which the general colouration is composed without tedious dummy-experiments for correlating colour patterns with specific situations and reactions of an opponent (Figs. 1 and 2). By the way, where these colour changes have not been taken into consideration, even species definitions have been erroneously based on different colour phases of the same species or even of the same individual, as, for example, in the genus *Ecsenius* among the blennies. Two behavioural elements are mainly concerned with the display of special colour patterns in blennies:

1. Nodding with the head
2. Doing this whilst swimming, which results in a sort of "swaying dance."

Nodding in blennies can be either a courtship or a threat movement, depending on the particular species. Since these fishes usually lie within a hole, with only the head and sometimes the forepart of the body visible, colour patterns underlining the nodding movements are mainly confined to these parts of the body. Head and face colourations are, therefore, characteristic for the species and/or sex or motivational state of the fish. The motivation of nodding, as arising from a rather generalized conflict of



a



b



c

FIGURE 2. *Sufflamen albicaudatus*: a, Young animal—b, Adult while defending its territory—c, Adult tail-flicking for territory demarcation.

tendencies to approach an object and to withdraw from it, has been dealt with elsewhere (Wickler, 1963).

The swaying dance is well-marked in some species which have a peculiar colouration of the tail-region; in *Ecsenius bicolor* this region is bright orange to red, whilst the forepart of the body is black. Traces of the swaying dance can be found in nearly all species irrespective of their colouration, so the original movement is older than the conspicuous colouration underlining it. Normally, this dance is directed towards conspecifics; in *Ecsenius bicolor* it is the courtship dance of the male. The special conflict-nodding, while swimming, has, however, also given rise to the dance of the fin-eating blenny, *Aspidontus taeniatus*. Thus it mimics the dance of the cleaner, *Labroides dimidiatus*, and deceives fish inviting cleaning, which approach the mimic as well as the true cleaner (Wickler, 1963). In this case, the signal is clearly directed towards fish of another species. This is the first time that it has been possible to reconstruct the phylogeny of a mimetic behaviour pattern.

Together with, or instead of, the head-nodding there occurs in some species a rapid spreading and folding of the anterior dorsal fin. This part of the fin may bear special colour markings—black and white stripes or large red and blue ocelli. But in *Emblemaria pandionis* (a species from the

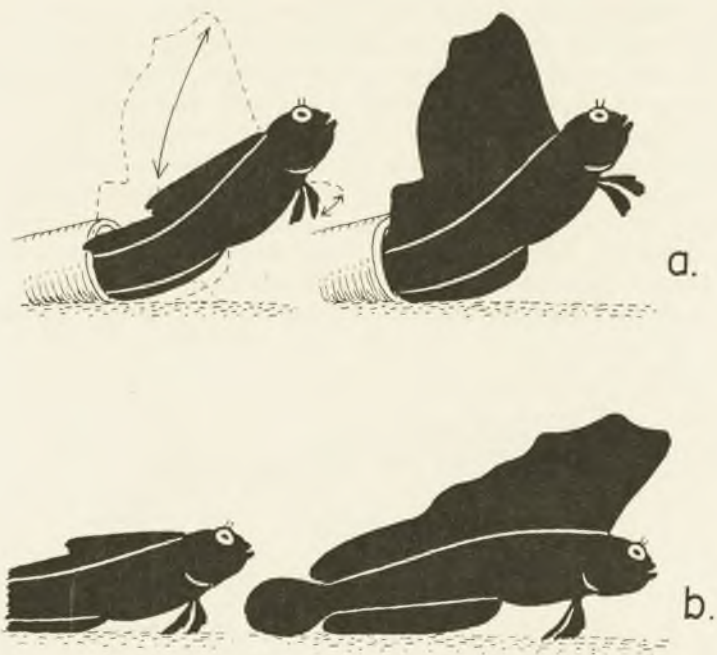


FIGURE 3. *Emblemaria pandionis*: a, Flickering the dorsal and ventral fins—
b, Spreading the dorsal fin during threat.

Florida shore area), the dorsal fin is structurally adapted to this flicker-movement (it is very much enlarged into a sail-fin, which is of no use in swimming, and in fact remains folded during normal locomotion). But it is very conspicuously displayed by fighting and courting males (Fig. 3) as the film shows.

Emblemaria has no scales and so the body surface is virtually unprotected. Nevertheless, no damage is done to combatants, since fighting in this species is "highly ritualized;" it follows certain rules:

1. Each single attack is preceded by a head-waving from side to side with the mouth open, which may be translated into a rule: "Do not attack without careful threatening beforehand."

2. Biting attacks always come from in front of the opponent and so cannot commence unnoticed by him: "Do not attack other than face-to-face."

3. Biting is directed towards the mouth of the opponent or towards an annulate spot on the operculum. This "false eye" is more conspicuous than the real eye of the fish. We know from a number of fish that in biting they aim preferably at eyes and that supernormal eye dummies are placed on the bony operculum to deflect the bites into this area: "Do not attack parts other than the allowed areas of the opponent."

Biting the mouth of the opponent results in jaw-locking (Fig. 4) and mouth-pulling; aiming at each other's false eye results in "carousselling." Both phases of the fight are demonstrated in the film, in which it can be seen that the eye-spot on the operculum becomes visually emphasized by rapid colour change at the beginning of the fight. False eyes may be inter-specific signals, too, though we still have only scanty evidence of this. *Runula*, a small blenny, eats skin particles and mucus from other fishes and preferably bites on the eye of its prey. Experiments have shown (Wickler, 1960; 1961) that dark bands through the eye as well as eye-spots in the dorsal fin, both of which are often met with in Chaetodontids and other fish, distract the attacks of the *Runula* from the real eye.

We have presented *Runula* with 24 different fish species, among them

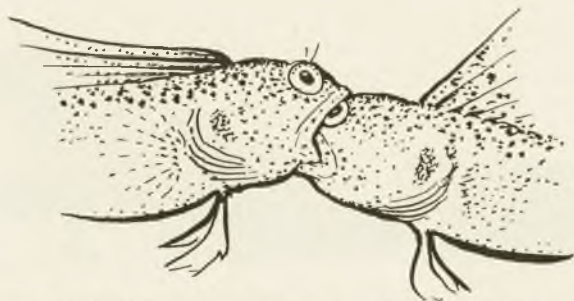


FIGURE 4. *Emblemaria pandionis*: Jaw-locking while fighting.

Amphiprion, and the latter was never bitten. *Amphiprion* lives among the tentacles of large sea anemones, which may become dangerous for a pursuer. In fact, in order to sneak up on its prey unnoticed, *Runula* even took cover behind the harmless *Amphiprion*. I would suggest that the conspicuous orange (or black) and white banded colouration of the *Amphiprion* is more likely a warning than a disruptive pattern. Whether this has to be learnt by other animals is still unknown.

On the other hand, from comparative studies I am almost convinced that the peculiar colour pattern of the cleaner fishes has to be learned by the other fish, and that its conspicuousness has evolved under the selection pressure of rapid learning by the fish to be cleaned. Finally a learning process occurring in the cleaning-customer is responsible for the very exact mimicry between the fin-eating *Aspidontus* and the cleaner-wrasse *Labroides dimidiatus*. The deceived fish try to find differences between model and mimic according to different experiences with them, and so selection in the mimic will extinguish all externally visible differences from the model.

This example may show the complicated network of interspecific relations which do exist and which have to be taken into account to understand the signal pattern of a single species.

Another peculiar colour-pattern has very probably been erroneously considered as a case of mimicry; that is the orange-brown and pure white coloured tail fin in *Hemibalistes albicaudatus* from the Red Sea. Tortonese (1956) suggested this might be an imitation of the similarly coloured tail fin of *Acanthurus xanthopterus*. But there seems to be no reason for the *Hemibalistes* to mimic the *Acanthurus*, and during life the resemblance is barely convincing. We have reared both species in our tanks and I would suggest another function for the *Hemibalistes*' tail. This species hides in empty mollusc shells and similar crevices; it has a special digging behaviour by which it empties these places of sand and debris. It then establishes a territory around this hiding place. Within the territory, the fish will swim around in the normal balistid manner, using the rapidly waving dorsal and anal fins and keeping the tail motionless. But every now and then, when passing the entrance of its hole, it starts a series of diving movements. It turns the head down, spreads the tail fin and beats it once or twice from side to side, thereby moving towards the entrance; then turning away. It swims upwards with folded tail fin, dives with spread and flicking tail again, etc., (Fig. 2c). This behaviour serves as territory-marking and it nicely displays the species-specific green and black, blue and yellow, bright red, etc., tail fins of otherwise rather inconspicuously coloured fishes. We have seen the same behaviour pattern in other plectognaths, too, even in trunkfishes (*Ostracion*) without special tail fin colouration. So once again, the motor pattern seems to be older than the colour markings.

Aspidontus, mimicking the cleaner, needs a rather complete imitation of its model, because it is necessary repeatedly to deceive other fish which

might succeed in finding out differences between it and the model. There are other fish, however, which deceive every prey-animal but once—because the latter is eaten by them. This is the case, for example, in the angler-fishes, the Antennariids. Their first dorsal fin spine, the so-called illicium, is situated on the border of the upper lip and is freely moveable in all directions. On its tip it bears an appendage which acts as a lure and may be jerked over wide arcs in different directions and which, since the rod is almost invisible, simulates some tiny creature darting about. Other fish are attracted by this bait, which is skillfully flicked out of their way just in time. Instead of catching the “prey,” the fish, which finally comes to stand with its head just in front of the angler’s jaws, is suddenly sucked into the angler’s mouth. By means of experiments, we were able to show that the angler (*Antennarius nummifer*) snaps at the fish only if it can be caught head-on, and that he uses the eye of the prey as an indicator of its front-end.

So far we have observed and filmed two ogocephalid species, two species of *Antennarius*, one species of *Phrynelox*, and *Histrio histrio*. The latter is sedentary pelagic in Sargassum weed and will follow its prey much more often than other anglers. In doing so, it carefully avoids fin movements, swimming instead with the aid of a respiratory water current, forcibly expelled through the spout-like gill slits. Immediately after catching the prey, the angler returns to normal swimming, with noticeable movements of the tail and pectoral fins. This suppression of fin movements

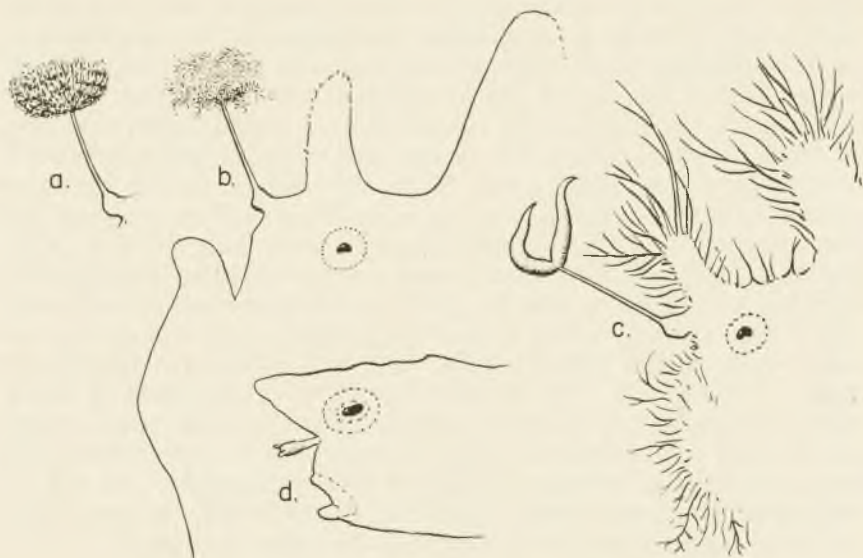


FIGURE 5. Lures of different Antennariids: a, *Antennarius nummifer*—b, *Antennarius nummifer*—c, *Phrynelox scaber*—d, *Ogocephalus* sp.

when sneaking up on a prey, whereby the angler simulates a clump of drifting weed, is the opposite of the elaboration of a signal; the signal-communication is reduced as much as possible. Inhibition of movements within view of the prey is to be seen in all anglers, but without the additional specialization of jet-propulsion.

Signalling with the bait, however, is made as conspicuous as possible by developing a nearly unbelievable mobility of the fin-ray. This is further specialized by peculiar differentiation of the tags of skin on its tip. These baits are dummies based on a model that elicits positive reactions in other fish (Fig. 5). In some cases, as in *Phrynelox*, it clearly resembles a worm; the appendage is thick and fleshy and does show active curling movements. In *Antennarius* I have only seen the bait passively moved by the rod-movements. The form of the bait is quite different in the various angler-species; they are dummies of different objects and elicit the attention of different animals. This is very clearly shown by a comparison of *Antennarius* and *Ogcocephalus*. The frog-fish's lure is directed downwards and attracts crustaceans. But the same is true for different *Antennarius*-species which, as far as our observations show, inhabit different ecological niches, preying upon different animals (probably different fish-species), to which their respective lures are specially adapted. Therefore, it is still almost impossible to offer these fish their correct food in captivity; some individuals learn quickly that under these circumstances their angling remains ineffective and learn, instead, to corner the prey and catch it in this way.

Further, the angling with the bait is used in intraspecific situations as well, for example, in threatening a rival. We have, however, only very few observations on this and do not know how this behaviour may affect a conspecific.

Our main interest in studying these deceptive signals lies in the fact that here Nature herself has made dummy-experiments, indicating to us what signal parameters of the model are important to the receiver; moreover, we can find out and then determine the model as the final stage towards which the "dummy" will evolve, which gives us an indication of an evolutionary trend that is still operating and will probably further elaborate the mimetic signals. So, to a certain degree, we may be able to predict the course of evolution in specific cases.

Finally, studying the specialization of movements and organs with signal function is another way towards understanding animal communities, which to a large degree are based upon mutual communication.

APPENDIX

The behaviour patterns mentioned are documented in the following films of the Encyclopedia Cinematographica, published by the Institut für den Wissenschaftlichen Film, Göttingen and now available in the United States from the Pennsylvania State University, University Park, Pa.

Film No. E 66/1962—*Histrio histrio*, Feeding and Locomotion

- Film No. E 127/1962—*Labroides dimidiatus*, Cleaning activity in aquaria
 Film No. E 754/1965—*Labroides dimidiatus*, Cleaning activity in the ocean
 Film No. E 139/1962—*Runula rhinorhynchus*, Feeding on other fish
 Film No. E 140/1962—*Aspidontus taeniatus*, Feeding behaviour
 Film No. E 141/1962—*Antennarius nummifer*, Feeding and Locomotion
 Film No. E 513/1963—*Sufflamen albicaudatus*, Digging behaviour
 Film No. E 517/1963—*Emblemaria pandionis*, Ritual fighting
 Film No. E 521/1963—*Ecsenius bicolor*, Courtship activities
 Film No. E 522/1963—*Ecsenius bicolor*, Fighting activities
 Film No. E 1039/1964—*Phrynelox scaber*, Alluring prey and Feeding

REFERENCES

DARLINGTON, C. D.

1938. The evolution of genetic systems. Cambridge.

HORA, S. L.

1924. Notes on fishes in the Indian Museum. On a new genus of globe-fishes, *Tetraodontidae*. Rec. Ind. Mus., 26: 579-582.

MORROW, J. E.

1957. On the morphology of the pectoral girdle in the genus *Makaira*. Bull. Bingham oceanogr. Coll., 16: 88-105.

TORTONESE, E.

1956. Mimetismo mulleriano e rapporti filogenetici. Boll. Zool., 23: 721-725.

WICKLER, W.

1960. Die Stammesgeschichte typischer Bewegungsformen der Fisch-Brustflosse. Z. Tierpsychol., 17: 31-66.
 1960a. Aquarienbeobachtungen an *Aspidontus*, einem ektoparasitischen Fisch. Z. Tierpsychol., 17: 277-292.
 1961. Über das Verhalten der Blenniiden *Runula* und *Aspidontus* (Pisces, Blenniidae). Z. Tierpsychol., 18: 421-440.
 1963. Zum Problem der Signalbildung, am Beispiel der Verhaltensmimikry zwischen *Aspidontus* und *Labroides* (Pisces, Acanthopterygii). Z. Tierpsychol., 20: 657-679.
 1965. Zur Biologie und Ethologie von *Ecsenius bicolor* (Pisces, Teleostei, Blenniidae). Z. Tierpsychol., 22: 36-49.

TRENDS IN THE EVOLUTION OF REPRODUCTIVE BEHAVIOR IN KILLIFISHES

NEAL R. FOSTER

*Department of Limnology,
Academy of Natural Sciences of Philadelphia, Pennsylvania*

ABSTRACT

The sexually dimorphic oviparous cyprinodonts, or killifishes, number more than 300 species and are widespread in shallow fresh, brackish, and marine waters, especially in the tropics and subtropics. For comparative ethological studies on reproductive and other behavior patterns, killifishes and their close relatives the medakas (*Oryziatidae*) are virtually unsurpassed. This report integrates some of the ecological, ethological and morphological information obtained for more than 40 species and 20 genera in the context of the phylogeny of killifishes and other atheriniform fishes.

For purposes of analysis, the reproductive behavior of a given species is divided into separate components according to the probable sensory modalities by which they are perceived. An acousticolateralis component, for example, is *headflicking*, a violent lateral shuddering movement performed during courtship by males of many species of killifishes and some atherinoids. A tactile component of reproductive behavior is *contacting* (any species-typical behavior by which the male consistently comes in physical contact with the female during courtship or spawning). Fundamentally different types of contacting behavior characterize different evolutionary lines among killifishes. *Visual displays* play a very important role in the behavior of killifishes, and in some extremely sexually dichromatic and dimorphic species, the tactile and acousticolateralis components of the courtship behavior seem to have disappeared altogether. Species in which schooling behavior is well-developed tend to exhibit a lesser degree of permanent sexual dimorphism and dichromatism.

The most important single advance in the behavioral evolution of killifishes was the shift from expelling and fertilizing all of the ovulated eggs at the climax of a single clasp to expelling and fertilizing them singly, a change which greatly increased the amount of courtship behavior per fertilized egg and thereby the impact of sexual selection in the evolution of these fishes.

Three main factors are responsible for the great evolutionary diversity in species-typical behavior patterns: (1) genetic background; (2) adaptation to existing niche parameters; and (3) reinforcement of isolating mechanisms.

INTRODUCTION

Although the subject of this paper, a group of fishes of which the majority are strictly freshwater forms, may at first seem inappropriate for the International Conference on Tropical Oceanography, I think it is high time that someone reemphasized the important role which studies on freshwater fishes, because of their greater opportunity for endemism, can play as a source of information on the principles of evolution in

aquatic environments. Indeed, the great wave of current studies in marine ichthyology not only threatens to engulf the research interests and future commitments of beginning students but also shows signs of becoming something of a scientific bandwagon.

Despite the great shift which seems to be taking place in current ichthyological research, there is clearly a greater immediate need for studies on freshwater fishes than on marine ones simply because a considerable number of the freshwater species are threatened with extinction. The biological impact of mankind's alteration of his environment on marine fishes is slight indeed when compared with the plight of many freshwater forms. Impoundments, pollution, introductions of various species of bait, aquarium, or voracious predatory sport fishes, and the careless use of pesticides and herbicides cannot help but interfere in some way with the ecological requirements of the native forms which had been endemic to the altered habitats.

Even within the fish group which I have studied, the killifishes, there are several examples of endangered or extinct species. Within the United States, the native populations of at least two species of *Cyprinodon* and one species of *Empetrichthys* are in danger, and two additional species, *Cyprinodon bovinus* and *Empetrichthys merriami*, appear to have already become extinct (Miller, 1961, 1964). In South America, a large predaceous endemic species, *Orestias cuvieri* of Lake Titicaca, apparently became extinct soon after the successful introduction of several species of salmonids there (Villwock, 1963:615). The widespread use of a very aggressive species of American poeciliid, *Gambusia affinis*, for the purposes of mosquito control in various parts of the world has definitely been injurious to populations of many of the indigenous larvivorous killifishes which were previously native to those areas. Myers (1965) gives several examples of the results of the introduction of *Gambusia* upon the native fish faunas in various Old World localities. It seems as though the attributes of *Gambusia* for mosquito control have been considerably overrated.

In view of the many inevitable changes which threaten the future existence of many freshwater fishes, it is very probable that certain additional species will also become extinct in due time, except for those individuals which may happen to survive in captivity.

EVOLUTION OF KILLIFISHES

The present study began a little over 6 years ago as an attempt to deduce the phylogenetic relationships among the killifishes through detailed comparative studies on the reproductive behavior patterns which are characteristic of the various taxa. However, such a static approach to the dynamic process of evolution within this large and diverse group of fishes was doomed to failure from the very start, as long as no provision had been made to fully integrate the behavioral information with the ecological

and morphological data for each species. There is a tendency nowadays to put ethology on a pedestal, as if it should be a science wholly unto itself. But this practice ignores the intimate functional relationships which exist among the morphological, ethological, and ecological traits of any given organism. Evolutionary change in any one trait requires a concomitant change in the other two traits. Indeed, it was not until the ecological data for the killifishes were analyzed and collateral morphological studies were made that the phylogenetic relationships among the killifishes and their allies finally became apparent.

As ichthyologists, we are very much in need of at least one fairly large group of fishes for which the phylogenetic relationships have been worked out in detail. Then we could apply the generalizations obtained from a knowledge of the evolutionary trends in that one group in helping us to understand the origins of the diversity in other groups of fishes. Virtually all of the classical generalizations regarding vertebrate evolution above the species level have been concerned with *terrestrial* animals. However, since many of the selective forces which operate in freshwater or marine environments appear to be significantly different in kind from those operating on dry land, the famous examples of Darwin's finches, the Hawaiian honey creepers, proboscidean mammals, horses, or the Australian marsupials are not apt to be of much help to us in the task of understanding the evolution of fishes.

Therefore, before considering the evolution of reproductive behavior patterns of killifishes, I must first consider the origin and evolution of the killifishes themselves. Then we can begin to distinguish between the older, less-modified traits from the newer, more-modified ones within the group.

Now to do this I cannot avoid a somewhat controversial area of current ichthyological activity, beset with theoretical difficulties which have their origins in an assumption that has been made for a very long time, namely that the presence of a spinous first dorsal fin in a fish is indicative of a "higher evolutionary level," and the absence of a spinous dorsal is indicative of a "lower, more primitive evolutionary level." Semantic difficulties (especially "level") aside, it appears that fish groups of either category can be intimately related, and Rosen's (1964) new assemblage, the order Atheriniformes, seems to represent such a natural group. It contains three suborders, of which only one, the Atherinoidei, includes fishes which still retain a spinous dorsal.

Except for those forms which have secondarily evolved viviparity, the order Atheriniformes unites for the first time a host of mostly pelagic, surface-swimming forms which produce eggs with long filamentous chorionic appendages. Rosen (1964) demonstrates that the many fundamental morphological characters which are shared by the sauries (scomberesocids), the needle fishes (belonids), the halfbeaks (hemiramphids), the flying

fishes (exocoetids), the silversides (atherinids), the peculiar rainbow fishes of Australia and New Guinea (melanotaeniids), the phallostethids, and the killifishes and other cyprinodonts (several families) can not be due simply to convergence, that overused crutch for explaining away fundamental similarities.

The suborder Exocoetoidei appears to be more specialized than either the Atherinoidei or the Cyprinodontoidei in that (1) exocoetoids have secondarily lost the conspicuous oil globules which are present in the eggs of members of the other two suborders (Orton, 1955); (2) exocoetoids have a peculiarly reduced olfactory apparatus which lacks incurrent and excurrent openings communicating with a concealed nasal sac. Instead, there is just a single open pit on each side of the snout, with a small hillock of exposed olfactory tissue in its center (Burne, 1909); (3) they have the lower pharyngeal bones well fused; and (4) they have a well-developed lateral line canal (lacking or poorly developed in the other two suborders), which has secondarily moved to a position very low on the sides of the body as Rosen (1964) points out.

The phylogenetic relationships within the suborder Cyprinodontoidei, which contains the killifishes or oviparous cyprinodonts as well as various

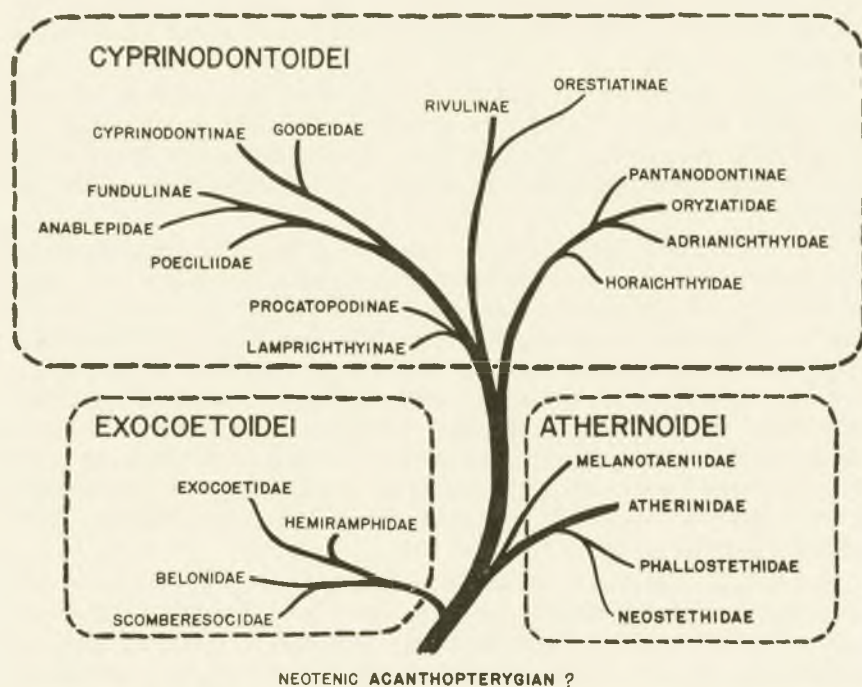


FIGURE 1. A schematic representation of the evolution of killifishes and other atheriniform fishes.

other groups of viviparous and ovoviviparous cyprinodonts, can be ascertained if we consider as many morphological characters as possible. I have used a minimum of about 16, which are as follows: presence or absence of epiotic processes, the metapterygoid, free pseudobranchiae, and vomerine teeth; the number of ossified basibranchials; the size and shape of the first vertebra; the shapes and functional arrangement of the maxillary and premaxillary; the caudal skeleton (especially the number of epurals); the frontal scalation pattern; the number of oil globules in the egg; the relative positions of the dorsal and anal fin fold origins in the prolarva and whether or not a preanal fin fold occurs; the pattern formed by the vitelline circulation in the wall of the yolk sac; the relative position of pectoral fin placement; the shape and number of cusps of the jaw teeth; and the shape and arrangement of the pharyngeal teeth with respect to the pharyngeal bones.

Many of these morphological characters have been studied by previous workers, notably Myers (1931), Rosen & Bailey (1963: 24-29), Rosen (1964), Sethi (1960), Hoedeman (1958), and Whitehead (1962).

There is no more elegant and direct way to set forth my conception of the phylogenetic relationships, or relative recency of common ancestry, among the different taxa than to present these hypotheses in the form of a phylogenetic tree. I have drawn such a diagram for the killifishes and other atheriniform fishes in Figure 1. The cyprinodontid subfamily names (*-inae*), with the exception of the Oryziatinae, which Rosen (1964) recently elevated to familial rank, are taken from Myers (1955). The suborder (*-oidei*) and family names in Figure 1 follow Rosen's (1964: 260-261) new arrangement.

The term "killifish" is used herein to refer to those oviparous cyprinodonts which are members of the families Oryziatidae and Cyprinodontidae.

BEHAVIOR OF KILLIFISHES

There are about 45 genera and between 300 and 400 species of killifishes, which occur in shallow freshwater, brackish, and marine environments throughout the tropical and subtropical parts of all the continents except Australia. If any generalization could be made about the ecology of killifishes, it is that they exploit niches mostly in ephemeral waters, places which are temporarily submerged by tides, floods from heavy rains, or similar causes. However, several species normally occur in shallow areas of larger, more permanent bodies of water also.

The brain of killifishes has relatively poorly developed chemosensory centers, but the acousticolateralis centers are quite well developed (Bhimachar, 1937). This fact, coupled with the existence of well developed eyes and cephalic lateral line systems in killifishes, helps us to anticipate which sensory modalities will be most important in the behavior. For the purposes of analysis, I divide the reproductive behavior into separate visual,

acousticolateralis, or tactile components, according to the probable types of sense organs by which they are perceived. The olfactory organs do not appear to play an important role in the behavior of killifishes except for purposes of food object discrimination.

Most species of killifishes are sexually dimorphic and dichromatic to some degree, and these differences become especially pronounced during that time of the day when the fish are spawning (Fig. 2). However, there



FIGURE 2. *Fundulus similis* (Baird & Girard), female above, male below. These freshly collected members of a spawning aggregation show the sexual dichromatism.

is a definite relationship, which Parr (1931) first pointed out, between schooling and the relative amount of permanent sexual dichromatism and dimorphism in fishes. Species in which schooling behavior is highly developed, such as the medakas (*Oryziatidae*) and the lampeyes (*Procato-podinae*), tend to display a relatively slight degree of sexual differences except when actually breeding, and forms in which schooling behavior is poorly developed, mostly bottom-feeding forms, tend to be extremely dimorphic and dichromatic (Table 1). Visual displays are well developed in the courtship behavior of killifishes, especially in those species in which the permanent adult sex differences are most pronounced. The often spectacularly gaudy color patterns displayed by the males of many species are in part responsible for the great popularity of these fishes among aquarists.

An example of an acousticolateralis component of male courtship behavior, which is heard and/or felt by the female (see Harris & Bergeijk, 1962), is headflicking. I think that this behavior should be regarded as a

TABLE 1

RELATIONSHIP BETWEEN DEGREE OF SEXUAL DICHROMATISM AND DIMORPHISM
AND THE RELATIVE AMOUNT OF SCHOOLING BEHAVIOR EXHIBITED BY ONE
ATHERINOID AND SEVEN CYPRINODONTOID SPECIES OF FISHES

Example	Degree of permanent sexual dimorphism and dichromatism	Relative development of adult schooling during breeding season
Melanotaeniidae		
<i>Melanotaenia maccullochi</i>	slight	well developed
Oryziatidae		
<i>Oryzias latipes</i>	slight	well developed
Cyprinodontidae		
Procatopodinae		
<i>Micropanchax</i> sp.	slight	well developed
Rivulinae		
<i>Aplocheilichthys panchax</i>	slight	well developed
<i>Rachovia brevis</i>	great	poorly developed
Fundulinae		
<i>Fundulus notti</i>	great	poorly developed
<i>Fundulus similis</i>	slight, until spawning (Fig. 2)	well developed until spawning time
Cyprinodontinae		
<i>Jordanella floridae</i>	great	poorly developed

form of low frequency vocalization. It is performed by the males of many species of New and Old World killifishes and I have also observed it in four species of atherinoids (three species of *Melanotaenia* and a species of *Pseudomugil*). Headflicking consists of a rapid lateral movement of the head, resembling a violent shuddering, a behavior pattern which appears to have evolved as an exaggeration of the amplitude, especially at the anterior end of the body, of the lateral undulatory movements normally associated with fast swimming. The forward component of motion has been lost, however.

The tactile component of the reproductive behavior is represented by contacting, a broad term which I use to refer to any species-typical behavior pattern by which the male consistently comes in contact with the female. If developed, this contacting behavior usually occurs after the preliminary phases of the courtship behavior but shortly before the spawning act (clasping).

Almost invariably present, in the males of those species of killifishes in which some form of contacting behavior is developed, are minute osseous spinelike processes which project outward from the margins of certain scales and/or certain fin rays, which are called *contact organs* (Newman, 1907, 1909). Evidence that the contact organs are tactile in function comes from both morphological and behavioral studies. For example, Egami & Nambu (1961: 271) found that vital staining with

methylen blue demonstrated that the innervation in the anal fin of the male medaka (*Oryzias latipes*) was better developed along those fin rays possessing contact organs than along the corresponding fin rays of the female, in which contact organs are lacking. Also, when the fins of preserved specimens of adult males of the African rivuline (*Nothobranchius guentheri*) are prepared by a special staining technique which brings out nerve fibers, one can see that each of the contact organs in the anal fin receives a lateral branch from the threadlike nerve running down the length of that particular fin ray (W. Michael Kaill, personal communication). Contact organs are usually also present on those parts of the male's body or fins which come in contact with the female during the spawning act, in addition to being present on those parts used in contacting.

I think that the best analogy that could be used to explain contact organs is that they are like the curb-finders in use on some automobiles, "telling" the male how his body and fins are positioned with respect to the female. They essentially act as flexible lateral extensions of the surface of the body and fins of the male.

To some extent we can say that killifishes are better adapted for comparative ethological studies than virtually any other group of fishes. They are all relatively small forms, fairly easy to breed and rear to sexual maturity in the laboratory. Their most valuable attribute for comparative studies is the fact that most species breed essentially daily. The females ovulate sometime during the night, and each day the spawnings and associated behavior patterns may be observed, often within a short time after the fish have been fed. There is no pair bond (such as is developed in many species of cichlid fishes) between male and female killifishes. Neither is there any parental care, with a few dubious exceptions. In general, the reproductive behavioral repertoire is fairly simple and can be observed in its entirety in the space of a few minutes. In the course of the present study, the reproductive behavior patterns of more than 40 species in 20 genera were studied, several of the American forms being observed by me in the field as well as in the laboratory. One species in each of the following genera was studied: *Oryzias*, *Micropanchax*, *Epiplatys*, *Pachypanchax*, *Pterolebias*, *Rachovia*, *Austrofundulus*, *Rivulus*, *Leptolucania*, *Adinia*, *Aphanius*, *Cyprinodon*, *Jordanella*, and *Floridichthys*. Two species of each of the genera *Aplocheilichthys*, *Aphyosemion*, and *Nothobranchius*, five species of *Cynolebias*, three species of *Lucania*, and 12 species of *Fundulus* were also studied.

One of the most peculiar groups of killifishes, the medakas, family Oryziatidae, exhibit a host of primitive morphological characters which are shared with the atherinoids but not with other cyprinodontoids. These characters are thoroughly discussed by Rosen (1964). The medakas are pelagic, surface-swimming, plankton-eating forms which exhibit a strong

tendency to school. Sexual dichromatism and visual displays are neither very well developed. Most of the courtship behavior consists simply of the male pursuing the female, swimming along a short distance below and behind her. If the female is receptive to the courtship activities of the male she performs a peculiar "head-up" behavior which has been described and figured by Ono & Uematsu (1957). The male stays ventral to the female throughout the preliminaries of the courtship behavior. The spawning act or clasp is similar to that observed in other species of killifishes, in that the dorsal and anal fins of the male are inclined toward and closely appressed against the corresponding fins of the female, while the bodies of both fish are bent into parallel sigmoid curves.

However, I wish to point out that the spawning of the medaka differs in two significant ways from that of most of the other killifishes which have been studied by me or described in the literature: (1) the spawning clasp of the medaka is "pelagic," *i.e.*, consistently performed in open water, not in contact with any substrate; and (2) all of the eggs are extruded by the female and fertilized by the male at the culmination of a single clasp, which may last 30 seconds or more.

This pelagic type of spawning, *i.e.*, the extrusion and fertilization of many eggs in the open water, is also characteristic of the spawning behavior of many atherinoids, such as *Melanotaenia*. In *Melanotaenia maccullochi*, for example, about 30 or more eggs are shed at the climax of a single clasp in open water, and these shower downwards to become attached by their long chorionic filaments to various fibrous substrata on the bottom. In *Oryzias latipes*, however, the extruded, fertilized eggs are held in a cluster by the female, who carries them about for approximately an hour or so before finally (deliberately) rubbing them off, usually singly but sometimes in two's or three's, onto leaves or roots of vegetation near the surface. Thus actual oviposition does not come until some time after spawning in *Oryzias*.

In all the other species of killifishes which have been observed by me or discussed in the literature (with the possible exception of some species of the African rivuline genus *Epiplatys*), we do not observe this pelagic type of spawning, with a large number of eggs being expelled all at once in open water. In most species of killifishes, only one egg is expelled and fertilized per clasp, and the spawning fish always clasp against some substrate. Since courtship behavior must usually precede every clasp, it follows that the total daily amount of courtship behavior performed by the male must be much higher in the killifishes proper (Cyprinodontidae) than in the medakas (Oryziatidae). Hence the significance of sexual selection has probably been much greater in the evolution of the former group, because the ratio of the amount of courtship per expelled egg tends to be higher, even though females in either family produce comparable total numbers of eggs each day.

The behavioral diversity displayed among the 200 or more species which are members of the subfamily Rivulinae (having moved to the family Cyprinodontidae now in our discussion) seems to exceed in some ways the morphological diversity among these forms. Several species are "annuals," that is, fishes which exploit niches in temporary bodies of water which exist only during the tropical wet seasons and dry up a short time after the rains end. Annual killifishes do not live more than 8 months, as a rule, in nature. Their eggs, however, survive for months, sometimes years, buried in the bottoms of the former pools.

Among the South American rivuline annuals, I distinguish two groups, probably representing two distinct phyletic lines, by means of the reproductive behavior. One group is exemplified by *Pterolebias longipinnis* (see Sterba, 1962: Plates 122-123, for excellent photos of the spawning behavior taken by Foersch). In this group, the large and brightly-colored male, after much headflicking and preliminary visual advertisement displays, induces the smaller female, if she is receptive, to begin burrowing downwards into the soft bottom substrate. After she has gone a little way into the substrate, the male starts to also burrow down alongside her, and soon the fish more or less completely disappear from view, for the clasp occurs beneath the substrate, where the eggs are individually buried. Likewise in some other South American annuals, such as *Rachovia brevis* and *Austrofundulus myersi*, after the preliminary displays and headflicking by the male, the receptive female precedes the male in burrowing down into the substrate.

Now in the other group of South American annuals the situation is reversed. In this assemblage, exemplified by fishes of the genus *Cynolebias*, after the preliminary headflicking and visual displays (headflicking appears to have become secondarily lost in *C. melanotaenia*), during which the male assumes a head-down posture just slightly ahead of the female, she indicates her physiological readiness to spawn by nudging against the male with her snout just in back of, or in some species such as *C. whitei* (see Carvalho, 1957) on the inside face of, his pectoral fin, and then both fish burrow downwards into the substrate, with the *male preceding* the female. As in the above species, spawning occurs deep within the substrate (aquarists generally use waterlogged peat moss for the breeding tanks), where the eggs are laid singly. The place where the female *Cynolebias* nudges against the male is abundantly supplied with contact organs. For excellent photos by Foersch of some of these behavior sequences, see Sterba (1962: Plates 114-115, *C. bellottii*; Plate 121, *C. nigripinnis*) and for photos of *C. whitei*, known in some older literature as *Pterolebias elegans*, see the photos on pages 113-114, 116-117 in the recent book by the skilled fish photographer, Nieuwenhuizen (1964).

Inasmuch as there are many morphological characters which are shared by species of *Cynolebias* and some species of the sole oreostietine genus

Orestias, in addition to the fact that contact organs may occur on the pectoral fin in some species in both genera, I think that the female in many species of *Orestias* probably exhibits the *Cynolebias*-like trait of nudging against the side of the displaying male to "trigger" the spawning clasp. However, nothing whatever has yet been published about the reproductive behavior of any species of *Orestias*.

If we consider the African rivulines, a very common pattern in the courtship behavior, which occurs after the preliminary advertisement displays of the male, is what I call ventrolateral contacting, in which the male assumes a position just dorsal and slightly to one side of the female and proceeds to follow her as she swims slowly along. The female will posture in a spawning attitude when she comes to a suitable substrate, and since the male is usually right beside her when she does this, he can immediately slip alongside to clasp the female against the substrate. The ventrolateral contacting which occurs in the behavior of *Aphyosemion nigerianum* (see photo on page 128 in Nieuwenhuizen, 1964, where name *A. cailiurum* used) appears to be homologous to a similar prespawning behavior pattern in *Nothobranchius guentheri* (Nieuwenhuizen, 1964: photo in middle of page 120), an annual African rivuline.

One consistent difference which I have noted between the prespawning behavior of female rivuline killifishes and that of the females of the funduline and cyprinodontine killifishes is that while it seems to be characteristic for the receptive females of the Rivulinae to display their physiological readiness to spawn by darkening the melanophores in specific patterns of longitudinal stripes, lateral bands, or vertical bars, just the reverse generalization seems to hold for most of the funduline and cyprinodontine females, which become extremely pale-colored or washed-out in appearance when they are ready to spawn. However, this generalization as to the differences in female prespawning behavior in different phyletic lines may turn out to be invalid, for we still need to study more species in both lines to be sure that the apparent difference is not just an artifact.

The last two subfamilies to be discussed both occur in North America. In the Fundulinae, there is a small species which dwells amid the brackish weedy areas near the shores of the Gulf of Mexico, *Adinia xenica*. The male of this species exhibits a peculiar courtship behavior trait which I call jaw-nudging. After the preliminary visual advertisement displays (in which there is no head-flicking), the male assumes a position just dorsal to the female and protrudes his premaxillaries and lowers his mandible so that he nudges the top of the female's head and snout with his extremely protrusible mouth. The female, if she is receptive to these courtship activities, will nip a suitable crevice in the aquarium (presumably in nature also), and the pair will promptly clasp there and deposit a single egg. Now the interesting thing about this behavior, which I have observed in at least one other species of North American funduline, *Fundulus kansae*, is

that it may also occur in the courtship behavior of a Spanish killifish, *Valencia hispanica*. *Valencia* is one of the very few living species of Old World fundulines, a species which had at one time been placed in the genus *Fundulus*. However, I have not yet been able to personally study the behavior of *Valencia* and have had to rely upon a brief description published some years ago by Mayer (1948). Mayer speaks of the male *Valencia*, moving its mouth in a "chewing, gulping manner," while he "balances himself perfectly in front" of the female, perhaps referring to jaw-nudging.

There is some evidence that at least one group of species within the genus *Fundulus* displays a lunar periodicity in their reproductive activities, burying their eggs in sand beaches high in the intertidal zone, during the highest tide of the daylight hours, on the same day as, or up to 4 days after, a new or a full moon. This pattern is displayed by *Fundulus similis* (Fig. 2), a killifish of the beaches along the shores of the Gulf of Mexico and southeastern Florida. Similar patterns of reproductive activity may also occur in *F. parvipinnis* (Dr. G. W. Barlow, personal communication) and *F. majalis*.

In southern Georgia and northern Florida in the vicinity of the Okefinokee Swamp, I have found three sympatric species of killifishes, each with its own distinctive ecological preferences and reproductive behavior. In the open areas of the sluggish streams occurs *Fundulus notti lineolatus*, essentially a pelagic, surface-swimming insectivore which seems to rely heavily upon vision and is very alert to movements above the water or near the shore, and is also very difficult to collect. The *F. notti* cruise up and down in the open areas of the stream, but in the backwaters we find a bottom feeding form, *Fundulus cingulatus*. In very weedy areas, usually in backwaters or along the shore, a third but very small form, *Leptolucania ommata*, occurs.

The reproductive behavior of *Fundulus notti* relies almost exclusively upon visual displays for information exchange between potential spawning partners. Headflicking was never observed in this species, either in the field or in the laboratory. The sexes in *F. notti* are extremely dichromatic, the female being marked with horizontal black stripes and a reddish head while the male displays vertical black bars and a greenish head. In *F. cingulatus*, on the other hand, headflicking is well developed. The plain-colored female becomes very pale and her eye becomes quite dark. Spawning takes place after much vigorous headflicking and visual displays by the male. In *Leptolucania ommata*, headflicking and visual displays are well developed. The female, if receptive to the male's courtship, performs a peculiar lateral undulatory movement ("wriggling") and swims upward toward the surface, where spawning subsequently takes place.

A courtship behavior pattern which does not occur in any of the species of South American, African, or Indian rivulines which have been studied

by me, yet appears in each of two closely related oviparous subfamilies, the Fundulinae and the Cyprinodontinae, and in one viviparous family, the Poeciliidae, is contacting with the top of the head by the males in certain species. Correlated with the occurrence of this behavior pattern is the presence of contact organs on top of the head in most of the forms which display the behavior. In its simplest form, I observed this behavior in many species of *Fundulus* and in three species of *Lucania* (all Fundulinae). Nieuwenhuizen (1961: 194, middle photo) has depicted this behavior in *Lucania goodei*. A similar behavior occurs in the Cyprinodontinae in *Cyprinodon macularius*, in which it has been called "nuzzling" by Barlow (1961: 342, Fig. 1D). In poeciliids, a similar behavior of the courting males occurs in several species in the genera *Poecilia* and *Poeciliopsis*, and is called "mouth-contacting" (Rosen & Tucker, 1961: 204-205).

In at least one population which I have studied of the Atlantic Coast cyprinodontine killifish, *Cyprinodon variegatus*, the contact organs still occur on the tops of the heads of the breeding males, but the associated contacting behavior is absent, apparently having been secondarily lost.

The last species which I will consider in any detail is *Jordanella floridae*, the flagfish, a cyprinodontine killifish which is endemic to the Florida peninsula. This species has developed what could be loosely referred to as a form of parental care.

Jordanella is mainly a bottom-feeding herbivore. The males "stake out" and defend territories associated with specific areas of bottom substrate during the breeding season, usually amid piles of plant debris or mats of filamentous algae. These forms are very sexually dimorphic and dichromatic, and the male defends his territory very vigorously against all other fishes, including the females of *Jordanella*. The females have a large black lateral spot conspicuously placed on each side of their bodies, a marking which I believe may act as a releaser ("bullseye") for the vigorous chasing of the female by the males. When a female is ready to spawn, her body coloration and lateral spot fade and she approaches the territorial male tailfirst, always keeping her head pointed away from his body. The male meanwhile performs a lateral display, with all his median fins spread, oriented toward the female, and slowly swims in ever-narrowing circles around her. By this tactic the male finally slides alongside of the female and the two fish clasp and settle to the bottom substrate to spawn.

After spawning, the male (who occupies one specific territory, at least in captivity, for several weeks at a time) intermittently fans with his pectoral fins the places within his territory where the fish were previously observed spawning. This behavior has usually been regarded as a form of egg care. However, since (1) fanning is performed by juvenile flagfishes in a feeding context, to uncover tubificid worms buried in loose detritus; (2) males will fan completely eggless substrata as vigorously as those with eggs; and (3) fanning males often terminate a fanning "run" across the

substrate with a nip-like behavior resembling feeding, I believe that males fan because they have learned that this will disclose eggs in the substrate, which they promptly eat. It is unlikely that a male could find and eat all of the eggs which he has fertilized in his territory, and since each day several females will spawn with a given male, the thinning of the eggs in the substrate would not only provide food for the male, but also help to maintain selection for this peculiar behavior by providing extra food reserves for the male's vigorous defense of the egg-filled territory against all other fishes, which are potential egg robbers.

DISCUSSION

I think that the multitude of factors which are responsible for the great evolutionary diversity in species-typical and other behavior patterns in fishes and other animals can be reduced to three main categories: (1) genetic background; (2) adaptation to existing niche parameters; and (3) reinforcement of isolating mechanisms.

The first category, "genetic background," includes the coded morphogenetic instructions contained in the genes, and not only represents the preexisting structural and neurophysiological mechanisms upon which selection acts, but also would involve changes in populations which had nothing to do with the agency of natural selection, such as those due to genetic drift. Hinde & Tinbergen (1958) discuss some of the ways in which preexisting innate behavior patterns may be evolutionarily modified into new behaviors.

The second category, which until recently has been almost wholly ignored by ethologists, is also one of the most difficult aspects of the current problems in animal behavior because it usually requires detailed field studies in order to ascertain the adaptive significance of a given behavior pattern. Inspection of Table 2 demonstrates some of the correlations which I have found to exist between the places where killifishes most often seek food and where they spawn and hold territories. Tinbergen (1965) discusses some of the problems associated with this category. Learning, which is any behavioral modification resulting from experience, may be regarded as a combination of the first and second categories.

The third category of factors, which I ignored for a long time during the present study, appears to be one of the most important reasons for the especially sharp differences which we observe in the behavior and color patterns between the members of sympatric species pairs such as *Fundulus grandis*-*Fundulus similis* and *Fundulus cingulatus*-*Fundulus notti*. This is one aspect of species-typical behavior which cannot be studied or appreciated except by the methods of *comparative* ethology. Spieth (1958) reviews the significance of isolating mechanisms in behavioral studies on various groups of animals.

TABLE 2
RELATIONSHIP BETWEEN ECOLOGY, TERRITORIAL BEHAVIOR, AND SPAWNING ACT
IN ONE ATHERINOID AND EIGHT CYPRINODONTOID SPECIES OF FISHES

Example	Ecological notes	Territorial behavior of breeding male centered around:	Number of eggs shed and where
Melanotaeniidae <i>Melanotaenia maccullochi</i>	pelagic omnivore	female	many per clasp, in open water - eggs drop to bottom
Oryziatidae <i>Oryzias latipes</i>	pelagic, surface plankton-feeder	female	many per clasp, in open water - eggs retained by female, later rubbed off
Cyprinodontidae Procatopodinae <i>Micropanchax</i> sp.	pelagic, surface plankton-feeder	female	one egg per clasp, against leafy substrate near surface
Rivulinae <i>Epiplatys "chaperi"</i>	surface-swimming insectivore	female	one per clasp, against leafy substrate
<i>Rachovia brevis</i>	bottom-feeding omnivore (annual)	female, if near bottom	one per clasp - eggs buried in bottom substrate
Fundulinae <i>Fundulus notti</i>	surface-swimming insectivore	shallow shore area, especially if female near	one per clasp, in fibrous substrate on bottom
<i>Fundulus similis</i>	bottom-feeding in very shallow water—moves with tides	shallow shore area, especially if female near	several per clasp - eggs buried in sand high in intertidal zone at high tide
Cyprinodontinae <i>Aphanius cypris</i>	midwater omnivore	specific area near surface, regardless of female's presence	one per clasp, against fibrous substrate near surface
<i>Jordanella floridae</i>	bottom-feeding herbivore	specific bottom area regardless of female's presence	several eggs laid per "spawning run" of clasping pair across fibrous bottom substrate

In originally trying to deduce the phylogenetic relationships among killifishes solely on the basis of the similarities and differences in reproductive behavior patterns among the various forms, I was misguided for several years by the following assumption:

Inasmuch as even slight changes in the reproductive structures or behavior patterns of a species will probably drastically affect the reproductive success of the genotypes having the altered structures or behaviors, evolutionary change in these traits will tend to proceed more slowly than changes in structures or behaviors which are more directly related to the exploitation of a particular ecological niche by those genotypes. That is to say, we would expect not only a greater diversity, but also a higher probability of convergence, in body form, dentition, types of food eaten, and color pattern than we would ever expect to find in the reproductive structures, physiology and behavior, especially courtship behavior, within a group of closely related species. Especially where fertilization is external, the stereotyped, reciprocal courtship interactions of the male and female must communicate unambiguously to each individual the information as to whether or not the other individual is physiologically ready to spawn. Also, this behavior precisely synchronizes the process of gamete release so that the maximum number of eggs are fertilized and gamete wastage is kept to a minimum. Always selected against would be the genotypes which made mistakes, resulting in the missynchronization of gamete release, hybridization, or any other form of gamete wastage. In a sense, then, we can regard the reproductive behavior of a given species as its four-dimensional genitalia, a structure in the time dimension. The evolutionary conservatism of reproductive characters is reflected by their great utility in plant and animal systematics.

The naivete of too literal an application of this assumption to the solution of phylogenetic problems becomes clear when we recall the very important evolutionary mechanism by which differences in reproductive phenomena such as courtship behavior tend to become accentuated between closely-related sympatric species. For each species that is sympatric with a closely related form tends to be ecologically distinct, *i.e.*, physiologically, ethologically and morphologically adapted to exploit a different niche from that which is exploited by the other form. Any similarities that might once have existed between the reproductive behavior patterns of closely-related sympatric species which breed concurrently would tend to disappear through the agency of selection against hybrids. Hybrid inviability, sterility, or conditions of morphological and physiological intermediacy in the hybrids would preclude the possibility of any effective competition between the hybrids and either parent species, and thus the hybrids would also constitute a form of gamete wastage.

The assumption that any evolutionary change in the reproductive biology is always going to be extremely conservative probably can not be meaningfully applied to any group of living organisms except the hypothetical case in which every one of the species is allopatric.

ACKNOWLEDGEMENTS

Most of the studies which led to the conclusions which are presented in this paper were made while the author was a research assistant at Cornell University, when these studies were supported by grants (G-9773, G-23395) awarded to Dr. Edward C. Raney by the National Science Foundation. Since my joining the staff of the Academy of Natural Sciences, additional studies on killifishes have been supported by funds from an anonymous donor and by United States Public Health Service Grant EF-00266-03.

LITERATURE CITED

- BARLOW, G. W.
1961. Social behavior of the desert pupfish, *Cyprinodon macularius*, in the field and in the aquarium. *Am. Midl. Nat.*, 65 (2): 339-359.
- BHIMACHAR, B. S.
1937. A study of the medulla oblongata of cyprinodont fishes with special reference to their feeding habits. *Proc. roy. Soc. London, B*, 123: 59-68.
- BURNE, R. H.
1909. The anatomy of the olfactory organ of teleost fishes. *Proc. zool. Soc. London*, 1909: 610-663.
- CARVALHO, A. L. DE
1957. Notas para o conhecimento da biologia dos peixes anuais. *Rev. Brasil. Biol.*, 17 (4): 459-466. [Transl. by H. Schultz in *Trop. Fish Hobbyist*, 1958, 7 (1): 16-26.]
- EGAMI, N. AND M. NAMBU
1961. Factors initiating mating behavior and oviposition in the fish *Oryzias latipes*. *J. Fac. Sci., Univ. Tokyo, Ser. 4*, 9 (2): 263-278.
- HARRIS, G. G. AND W. A. VAN BERGELJK
1962. Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. *J. acoust. Soc. Am.*, 34 (12): 1831-1841.
- HINDE, R. A. AND N. TINBERGEN
1958. The comparative study of species-specific behavior. In Roe, A. and G. G. Simpson, Eds., *Behavior and Evolution*, Yale Univ. Press, New Haven: 251-268.
- HOEDEMAN, J. J.
1958. The frontal scalation pattern in some groups of toothcarps (Pisces—Cyprinodontiformes). *Bull. aquat. Biol.*, 1 (3): 23-28.
- MAYER, F.
1948. *Valencia hispanica*. *The Aquarium*, 17 (6): 134-135.
- MILLER, R. R.
1961. Man and the changing fish fauna of the American Southwest. *Pap. Mich. Acad. Sci., Arts Letters*, 46: 365-404.
1964. Extinct, rare and endangered American freshwater fishes. *Proc. 16th Int. Congr. Zool.*, 8: 4-16.
- MYERS, G. S.
1931. The primary groups of oviparous cyprinodont fishes. *Stanford Univ. Publ., Biol. Sci.*, 6 (3): 241-254.
1955. Notes on the classification and names of cyprinodont fishes. *Trop. Fish Mag.*, 4 (7): 7.
1965. *Gambusia*, the fish destroyer. *Trop. Fish Hobbyist*, 13 (5): 31-32, 53-54.

- NEWMAN, H. H.
 1907. Spawning behavior and sexual dimorphism in *Fundulus heteroclitus* and allied fish. Biol. Bull., 12 (5): 314-345, 2 pls.
 1909. Contact organs in the killifishes of Woods Hole. Biol. Bull., 17 (2): 170-180.
- NIEUWENHUIZEN, A. VAN DEN
 1961. *Chriopeops goodei*, der Rotschwanzhechtling. Aquar. u. Terrar. Z., 14 (7): 193-196.
 1964. Tropical aquarium fish, their habits and breeding behavior. Van Nostrand, Princeton, N. J., 200 p.
- ONO, Y. AND T. UEMATSU
 1957. Mating ethogram in *Oryzias latipes*. J. Fac. Sci., Hokkaido Univ., Ser. 6, Zool., 13: 197-202.
- ORTON, G. L.
 1955. Separation of eggs of syngnath and allotriognath fishes in early embryonic stages. Calif. Fish Game, 41 (1): 103-105.
- PARR, A. E.
 1931. Sex dimorphism and schooling behavior among fishes. Am. Nat., 65: 173-180.
- ROSEN, D. E.
 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Bull. Am. Mus. nat. Hist., 127 (5): 217-268, 2 pls.
- ROSEN, D. E. AND A. TUCKER
 1961. Evolution of secondary sexual characters and sexual behavior patterns in a family of viviparous fishes (Cyprinodontiformes: Poeciliidae). Copeia, 1961 (2): 201-212.
- ROSEN, D. E. AND R. M. BAILEY
 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography, and systematics. Bull. Am. Mus. nat. Hist., 126 (1): 1-176, 2 pls.
- SETHI, R. P.
 1960. Osteology and phylogeny of oviparous cyprinodont fishes (order Cyprinodontiformes). Ph.D. Thesis, Univ. Florida, xiii + 275 p.
- SPIETH, H. T.
 1958. Behavior and isolating mechanisms. In Roe, A. and G. G. Simpson. Eds., Behavior and Evolution, Yale Univ. Press, New Haven: 363-389.
- STERBA, G.
 1962. Freshwater fishes of the world. [Transl. & revised by D. W. Tucker.] Longacre Press, London, 878 p.
- TINBERGEN, N.
 1965. Behavior and natural selection. In Moore, J. A., Ed., Ideas in Modern Biology. Proc. 16th Int. Congr. Zool., 6: 519-542. Natural History Press, Garden City, N.Y.
- VILLWOCK, W.
 1963. Die Gattung *Orestias* (Pisces, Microcyprini) und die Frage der intra-lakustrischen Speziation im Titicaca-Seengebiet. Verh. Dtsch. Zool. Ges. Wien (1962). Zool. Anz. Suppl., 26: 610-624.
- WHITEHEAD, P. J. P.
 1962. The Pantanodontinae, edentulous toothcarps from East Africa. Bull. Brit. Mus. (Nat. Hist.), Zool., 9 (3): 103-137.

Varied Approaches in Marine
Zoogeography

GEORGE MYERS

Convener

The following papers were delivered at the Conference but have not been received for publication:

JOHN P. WISE: The Western Tropical Atlantic: Fulcrum of Two Mirror-Image Oceanographic and Ecological Systems.

ROBERT L. CORY AND E. LOWE PIERCE: On the Distribution and Ecology of Lancelets (Order Amphioxii) over the South Eastern Continental Shelf of the United States.

GEORGE A. SEIGLIE: Distribution of Foraminifers in the Sediments of the Continental Shelf from Araya to Los Testigos, Venezuela.

RELATIONSHIP OF THE TROPICAL SHELF REGIONS

JOHN C. BRIGGS

The University of South Florida, Tampa

ABSTRACT

Four highly efficient zoogeographic barriers separate the tropical shore faunas of the world. The most effective is the New World land barrier having been, except for certain euryhaline forms, completely closed to traffic since the latest Pliocene-earliest Pleistocene times. The next most efficient is the Old World land barrier which permits only a limited migration around the Cape of Good Hope and through the Suez Canal. Third is the East Pacific barrier, and last is the mid-Atlantic barrier.

Circumstantial evidence indicates that successful migration across the East Pacific and Old World land barriers is entirely, or almost entirely, unidirectional—proceeding outward from the Indo-West Pacific. The Western Atlantic tropics may be considered a secondary center of evolutionary radiation. The differential behavior of species in crossing the major barriers provides a good demonstration of the importance of competition in zoogeography.

INTRODUCTION

In the sea, as on land, the richest fauna is found in the tropics. Furthermore, it can be said that the marine fauna of the shelf is far richer than that of the pelagic or deep-water habitats. Zoogeographically, four great tropical regions may be identified, the Indo-West Pacific, the Eastern Pacific, the Western Atlantic, and the Eastern Atlantic. At the species level, each region possesses a high degree of endemism. The existence of so many autochthonous species may be attributed to the relatively great effectiveness of the barriers that separate the regions from one another.

EAST PACIFIC BARRIER

The East Pacific barrier is the formidable stretch of deep-water that lies between Polynesia and America. Its efficiency in regard to the migration of shore fishes has been investigated recently (Briggs, 1961, 1964). The distributional patterns and evolutionary relationships of the 62 trans-Pacific species may be summarized as follows:

1. In the eastern Pacific, the ranges of many of the trans-Pacific species were found to be quite restricted. In fact, the majority (35 out of the total of 62) are apparently confined to, or are most typical of, the offshore islands (principally the Galapagos, Cocos, Clipperton, or Revillagigedos).
2. On the western side of the barrier, in contrast, almost all of the trans-Pacific species are widespread with the great majority (47 of 62) extending from Polynesia through the Indian Ocean and reaching the East African coast or its vicinity.
3. Aside from the few monotypic genera represented and the parrotfish

genus *Scarops*, all of the genera to which the trans-Pacific species belong are better developed in the Indo-West Pacific.

4. There is not a single example of a species belonging to a typical New World genus gaining a foothold on the western side of the barrier, even at its outermost fringes.

In view of the foregoing information, it has been concluded that there is good circumstantial evidence of a western origin for the great majority of the trans-Pacific species. It can be said, therefore, that there is a recent (or current) invasion of the Eastern Pacific tropics from the west. This has been referred to as an "eastward colonization movement" (Briggs, 1964: 708).

For fishes, a rough estimate of the degree of effectiveness of the East Pacific barrier can be made by taking into consideration the total number of shore species that are theoretically available for transport across the Pacific and comparing it to the number that apparently have successfully made the journey.

The Line Islands are the easternmost Polynesian group that lie along the course of the Equatorial Countercurrent. Unfortunately, the fauna of this archipelago is very poorly known. However, one might expect to find at least as many shore fishes as have recently been reported from Hawaii by Gosline & Brock (1960)—387. There is probably a total of about 650 species inhabiting the coastal waters between southern Mexico and Peru. Since 62 (the shore fishes that are apparently trans-Pacific in range) is about 6 per cent of 1,037, the efficiency of the Barrier can be approximated at 94 per cent.

Such information as is available indicates that the shore invertebrates may have more difficulty crossing the East Pacific barrier than the fishes. Ekman (1946: 38) calculated that only 2 per cent of the echinoderms ranged across the barrier, Hertlein (1937) listed but 18 trans-Pacific mollusks, and Deichmann (1963) referred to only five such holothurians. As Thorson (1961: 469) has pointed out, under average conditions even the most long-distance invertebrate larvae have much too short a pelagic life to survive the critical distance across the eastern Pacific. At least some fish larvae are apparently better suited for such transport by ocean currents.

NEW WORLD LAND BARRIER

With the exception of a few euryhaline species that can negotiate the Panama Canal or migrate by means of freshwater streams, the New World land barrier is a complete block to the movement of tropical species between the Eastern Pacific and Western Atlantic. This state of affairs has existed long enough (since the latest Pliocene or earliest Pleistocene when, according to the evidence presented by Simpson [1950: 381], the Isthmus of Panama made its latest emergence) so that, at the species level, the faunas are well separated.

Despite the obvious physical effect of the isthmus in separating the marine populations of the American tropics, its evolutionary effects have not been fully investigated. The need for research along this line has become most urgent in view of the plans that are now being made for a new sea-level canal.

As more work is done on the fishes, the species which can be recognized as common to both the Eastern Pacific and Western Atlantic become fewer. Recently, it was estimated that, aside from the circumtropical species and a few euryhaline forms, there are probably less than a dozen shore species that are found on both sides of the Barrier (Briggs, 1961: 550).

Considering the total number of fish species that probably exist on both sides of Central America (about 1,000), the fact that about 12 can still be considered identical indicates that the New World land barrier is approximately 99 per cent effective. Apparently, evolutionary change has proceeded so slowly in a few species, such as the serranids *Paranthias furcifer* and *Epinephelus itajara*, that specific differences have not yet developed. However, for the great majority, it is interesting to see that distinct morphological change has occurred during the separation interval of about 1½ million years.

The New World land barrier is also important for the marine invertebrates although, in some groups, it does not seem to be quite as effective as it is with the fishes. Haig (1956, 1960) studied the crab family Porcellanidae in both the Western Atlantic and Eastern Pacific and found that 7 out of a total of 107 species (about 7 per cent) are amphi-American, de Laubenfels (1936) found a similar distribution in about 11 per cent of the sponges he studied, and Ekman (1946) gave 2.3 per cent and (1953) 2.5 per cent for the echinoderms (Asteroidea, Ophiuroidea, and Echinoidea). In discussing speciation in tropical echinoids, however, Mayr (1954: 13) noted that not a single species is identical on both sides of the isthmus.

MID-ATLANTIC BARRIER

The Mid-Atlantic barrier is the broad, deep-water region that separates the Western Atlantic tropics from those of the West African coast. In regard to the fishes, it has been recognized for many years, particularly since the writings of the Portuguese zoologist Balthazar Osorio (a series from 1890 to 1911), that the tropical fauna of West Africa has many species in common with the American side of the Atlantic. Many additional trans-Atlantic species have been noted in the more recent literature so that now an uncritical compilation of records would give a much greater total than is actually warranted.

The task of putting together a reasonably dependable list of trans-Atlantic shore fishes has been lengthy and complicated. Many of the earlier records consisted of names only or else were accompanied by descriptions so brief that confirmation of the identification was difficult.

Fortunately, it was possible to study Osorio's material in the Museu Bocage in Lisbon and to examine many important specimens in the British Museum of Natural History. As a result, a list of 118 species has been compiled (Briggs, 1967) that gives, I believe, a fairly dependable indication of the degree of relationship between the two sides of the tropical Atlantic.

Perhaps more important than an attempt to discover the degree of faunal relationship, is the determination of the direction of migration. Aside from a group of about 24 shore fishes that apparently make their way around the Cape of Good Hope and then westward across the Atlantic, the predominant migratory movement across the mid-Atlantic barrier seems to be from west to east. Many of the trans-Atlantic species range broadly along the Western Atlantic shelf but have attained only limited purchase in the east. Others that have achieved broad distributions in the east are clearly representatives of American genera (such as *Mycteroperca*, *Rypticus*, *Eucinostomus*, *Sparisoma*, *Labrisomus*, etc.). None of the trans-Atlantic species belong to genera that are typically Eastern Atlantic. Further, it is of interest to note that trans-Atlantic species comprise about 30 per cent of the shore fish fauna of tropical West Africa.

Approximately 900 species of tropical shore fishes may be found in the Western Atlantic and about 380 species in the Eastern Atlantic giving a total of 1280. At present, 118 trans-Atlantic species are recognized. Since 118 is 9.2 per cent of 1280, the efficiency of the mid-Atlantic barrier may be calculated at about 91 per cent.

Recent works on West African invertebrate groups also show that an appreciable percentage of the species are trans-Atlantic. Dekeyser (1961) found that about 25 per cent of the ascidians were trans-Atlantic, Forest (1959:21) noted the same distribution for four out of the six species of madreporan corals, Burton (1956) for 18 per cent of the sponges, Monod (1956) for 16 per cent of the anomuran and brachyuran crabs, Knudsen (1956) for 6 per cent of the prosobranch mollusks, Kramp (1955) for 50 per cent of the neritic medusae, and Ekman (1953:59) for 16 per cent of the starfishes, brittlestars, and sea urchins. Although no evidence has been offered, it may be predicted that the great majority of these trans-Atlantic species also represent successful eastward migrations across the mid-Atlantic barrier.

OLD WORLD LAND BARRIER

The linked continental masses of Eurasia and Africa have provided an effective block to the migration of tropical marine organisms between the Atlantic and the Pacific probably since the beginning of the Pleistocene (Gohar, 1954:5). The construction of the Suez Canal has had interesting distributional repercussions but its effects are relatively recent. Currents of tropical water have extended around the Cape of Good Hope often

enough to provide passage for some Indo-West Pacific shore species that have pelagic larvae or adults that can safely enter the pelagic environment.

THE SUEZ CANAL

Although water-borne traffic between the Red Sea and the Mediterranean was possible in the days of the Pharaohs, it was accomplished by means of canals supplied with freshwater from the Nile so there was little or no effect on the distribution of marine animals. However, since the opening of the modern Suez Canal in 1869, some interesting changes have taken place.

Gohar (1954:27) suggested that the greatest exchange of faunas occurred during the first few years after the opening of the Canal since there was comparatively little deposition of mud and accompanying turbidity. Other environmental factors that have certainly tended to minimize migration through the Canal are the unusually high temperatures and salinity, particularly in the Bitter Lakes region.

The movement of fishes through the Suez Canal has been studied more closely than that of the other animal groups. The works of Ben-Tuvia (1953, 1955, 1962), Fowler & Steinitz (1956), and Gohar (1954) indicate that about 20 species have penetrated into the Mediterranean from the Red Sea, some of them quite extensively. Movement in the opposite direction has been very limited, if it has occurred at all. Recent collecting activity at the head of the Red Sea has been quite extensive, yet no Mediterranean species have been taken.

As far as invertebrates are concerned, Ekman (1953:89) noted that 18 species of Red Sea decapods were established in the Mediterranean but made no mention of any reciprocal migration in this group. Also, Gohar (1954) in his more detailed discussion of faunal migration through the canal, gave no evidence of a north to south movement of invertebrates.

THE CAPE OF GOOD HOPE

Considering that the New World land barrier has been impassable to tropical marine animals, with the exception of a few euryhaline species, since about the Pliocene-Pleistocene boundary, it is assumed that the circumtropical shore species have been able to preserve their genetic homogeneity by means of migration around the Cape of Good Hope (in addition to crossing the open ocean barriers in the Pacific and Atlantic). Talbot & Penrith (1962:559) remarked that surface temperatures of 21°C are often present 'round the cape outside a cold upwelling area and under certain conditions there is evidence of mixing of Agulhas Current water and South Atlantic subtropical water.

In addition to the circumtropical species, there are a number of others that are common to the tropical Atlantic and the Indo-West Pacific also indicating the existence of gene flow around the Cape of Good Hope.

Among the fishes, eight such species are found on both sides of the Atlantic, four are confined to the West African fauna, and three have been taken only at the Island of St. Helena. These 15 species plus the 16 known circumtropical shore fishes, (Briggs, 1961) give a total of 31 that apparently transgress the Old World land barrier.

Of the total of 31 fish species, eight are monotypic but all the rest represent genera that are best developed in the Indo-West Pacific. There is, therefore, apparently a similar situation to that seen in the case of the East Pacific barrier. That is, a movement of species has taken place from the Indo-West Pacific across a major barrier into an area where a suitable habitat is found. However, in this instance, the colonization movement is to the west instead of the east.

The efficiency of the Old World land barrier may be roughly calculated as follows: mainly from the information given in the recent lists of Blache (1962) and Postel (1959-60), the total shore fish fauna of tropical West Africa can be estimated at about 380 species. The fish fauna of tropical southeast Africa is a good deal richer with probably close to 1,000 species in the area between Mozambique and Algoa Bay. If it can be assumed that some 1,380 are immediately separated by the barrier in question and that only 31 have successfully crossed it, then it can be considered as about 98 per cent effective.

Apparently, only a few tropical invertebrate species have been able to migrate around the Cape. Monod (1956) in his monographic study of West African decapods (Hippidea and Brachyura) showed that 10 out of 176 shore species were also found in the Indo-West Pacific. Ekman (1953: 60) noted that only 2 per cent of the tropical Atlantic echinoderms (Asteroidea, Ophiuroidea, and Echinoidea) extended around the Cape. As yet, the evidence is sparse but it looks as though the Old World land barrier can be just as effective for the invertebrates as it is for fishes.

DISCUSSION

Information presented here indicates that, for tropical shore fish species, the New World land barrier is the most efficient (separating about 99 per cent), followed by the Old World land barrier (98 per cent), the East Pacific barrier (94 per cent), and the Mid-Atlantic barrier (91 per cent). For at least some of the groups of shore invertebrates, the East Pacific barrier seems to be a more effective block to migration than it is for the fishes. This is probably attributable to a generally shorter life for the invertebrate pelagic larval stages. On the other hand, the New World land barrier seems to be less effective for certain invertebrate groups probably due to slower evolutionary rates in the populations separated by the Isthmus of Panama. Examples are the sea stars, brittlestars, sponges, and porcellanid crabs.

Except for the neritic medusae and madreporan corals, the West African

invertebrate groups that have recently been investigated include fewer trans-Atlantic species than do the fishes. This indicates that the mid-Atlantic barrier is probably more effective for groups such as the ascidians, sponges, crabs, mollusks, and echinoderms. For the Old World land barrier, the evidence is very sparse but it looks as though it can be just as effective for the invertebrates as it is for fishes.

There is no doubt that the Indo-West Pacific Region has served as *the* evolutionary and distributional center for the entire marine tropics. Its fauna is almost unbelievably rich with, for example, more than 3,000 species of shore fishes. It seems clear that the unusually stable ecosystems and high level of competition provide the proper environment for the evolution of dominant species than can successfully invade the other regions.

From the Indo-West Pacific, dominant species migrate eastward across the open ocean to America, westward around the Cape of Good Hope into the Atlantic, and northward through the Suez Canal into the Mediterranean. Successful reciprocal migrations are, at least, very rare and may be completely lacking. Furthermore, judging from the general indications of relationship among the four great tropical faunas, this process has been going on for many millions of years. Some of the dominant species are so successful that they have been able to establish and maintain circumtropical distributions (indicating more or less regular migrations across the East Pacific, Old World land, and mid-Atlantic barriers).

The Western Atlantic tropics may be considered a secondary center of evolutionary radiation. Many species produced in this area have proved capable of migrating eastward to colonize the Eastern Atlantic region. However, species originating in the Eastern Atlantic are apparently incapable of successfully invading the western side. Again, the advantage seems to lie with the area that possesses the richer fauna and higher level of competition.

The modern trend in marine zoogeography is to place more and more emphasis on the physical and chemical characteristics of the environment such as temperature, salinity, and currents with usually no mention of the effects of competition. The differential behavior of species in crossing these major zoogeographic barriers provides a good demonstration of the importance of competition.

SUMMARY

Four, highly efficient zoogeographic barriers separate the tropical shore faunas of the world. The most effective is the New World land barrier having been, except for certain euryhaline forms, completely closed to traffic since latest Pliocene-earliest Pleistocene times. The next most efficient is the Old World land barrier which permits only a limited migration around the Cape of Good Hope and through the Suez Canal.

Third is the East Pacific barrier, and last is the mid-Atlantic barrier.

Circumstantial evidence indicates that successful migration across the East Pacific and Old World land barriers is entirely, or almost entirely unidirectional — proceeding outward from the Indo-West Pacific. This interesting migration pattern is apparently attributable to the evolution of dominant, successful species in the Indo-West Pacific. Unusually stable ecosystems and the high level of competition seem to provide the proper environment for the production of such dominant species. Some of them have even been able to establish and maintain circumtropical distributions.

The Western Atlantic tropics may be considered a secondary center of evolutionary radiation. Many species produced in this area have proved capable of migrating eastward to colonize the Eastern Atlantic region. But, species originating in the Eastern Atlantic are apparently incapable of invading the western side.

The differential behavior of species in crossing the major barriers provides a good demonstration of the importance of competition in zoogeography.

ACKNOWLEDGMENTS

I thank Dr. P. H. Greenwood and Mr. G. Palmer of the British Museum of Natural History and Mr. C. Almaca of the Museu Bocage in Lisbon for their kindness in allowing me to examine specimens under their care.

The research for this paper was accomplished with the aid of National Science Foundation grant number GB-2836.

REFERENCES

BEN-TUVIA, ADAM

- 1953. Mediterranean fishes of Israel. Bull. Sea. Fish. Res. Sta. Israel, (8): 1-40, 20 figs.
- 1955. Two Indo-Pacific fishes, *Dasyatis narnak* and *Upeneus moluccensis*, in the eastern Mediterranean. Nature, 176: 1177-1178.
- 1962. Collection of fishes from Cyprus. Bull. Res. Council, Israel, 11 (3): 132-145.

BLACHE, J.

- 1962. Liste de poissons signalés dans l'Atlantique tropico-oriental Sud. Trav. Cent. oceanogr. Pointe-Noire, (2): 13-102, 2 maps.

BRIGGS, JOHN C.

- 1961. The East Pacific Barrier and the distribution of marine shore fishes. Evolution, 15 (4): 545-554, 3 figs.
- 1964. Additional transpacific shore fishes. Copeia, 1964, (4): 706-708.
- 1967. Marine zoogeography. A manuscript in progress. To be published by McGraw-Hill.

BURTON, MAURICE

- 1956. The sponges of West Africa. Atlantide Rept., (4): 111-147, 4 figs.

DEICHMANN, ELISABETH

- 1963. The holothurians of Clipperton Island in the Eastern Tropical Pacific. Breviora, (179): 1-5.

- DEKEYSER, P. L.
1961. Liste provisoire des urocordés de la côte occidentale d'Afrique. Bull. Inst. Française d'Afr. Noire, Sér. A., 23 (1): 217-230.
- EKMAN, SVEN
1946. Zur verbreitungsgeschichte der warmwasserechinodermen in stillen ozean (Asteroidea, Ophiuroidea, Echinoidea). Nova Acta Regiae Sci. Upsaliensis, 14 (2): 1-42, 1 map.
1953. Zoogeography of the sea. Sidgwick and Jackson, London, xiv + 417 pp., 121 figs.
- FOREST, J.
1959. Campagne de la "Calypso" dans le golfe de Guinée et aux îles Principe, São Tomé, Annobon (1956). Ann. Inst. Oceanogr. Monaco, 37 (4): 1-36, 3 pls.
- FOWLER, H. W. AND H. STEINITZ
1956. Fishes from Cyprus, Iran, Iraq, Israel and Oman. Bull. Res. Council Israel, 5B (3-4): 260-292, 33 figs.
- GOHAR, H. A. F.
1954. The place of the Red Sea between the Indian Ocean and the Mediterranean. Pub. Hydrobiol. Res. Inst., Univ. Istanbul, Ser. B., 2 (2-3): 1-38, map.
- GOSLINE, W. A. AND V. E. BROCK
1960. Handbook of Hawaiian fishes. Univ. Hawaii Press, Honolulu. ix + 372 pp., 277 figs., 2 pls.
- HAIG, JANET
1956. The Galatheidea (Crustacea Anomura) of the Allan Hancock Atlantic Expedition with a review of the Porcellanidae of the western North Atlantic. Allan Hancock Atl. Exped., (8): 1-44, 1 pl.
1960. The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. Allan Hancock Exped., 24: viii + 440, 12 figs., 42 pls.
- HERTLEIN, L. G.
1937. A note on some species of marine mollusks occurring in both Polynesia and the western Americas. Proc. Am. Philos. Soc., 78 (2): 303-312, 1 pl.
- KNUDSEN, J.
1956. Marine prosobranchs of tropical West Africa (Stenoglossa). Atlantide Rept., (4): 8-110, 2 figs., 4 pls.
- KRAMP, P. L.
1955. The Medusae of the tropical west coast of Africa. Atlantide Rept., (3): 239-324, 14 figs., 3 pls.
- DE LAUBENFELS, M. W.
1936. A comparison of the shallow-water sponges near the Pacific end of the Panama Canal with those at the Caribbean end. Proc. U. S. Nat. Mus., 83 (2993): 441-466, 6 figs.
- MAYR, E.
1954. Geographic speciation in tropical echinoids. Evolution, 8 (1): 1-18, 7 figs.
- MONOD, T.
1956. Hippidea et brachyura ouest-africains. Mém. Inst. Français d'Afr. Noire, (45): 1-674, 884 figs., 1 map.

POSTEL, E.

- 1959-60 Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du Cap Spartel au Cap Roxo, suivie d'un bref aperçu sur leur répartition bathymétrique et géographique. *Bull. Soc. Sci. Bretagne*, 34 (1-4): 130-170, 241-281, 3 figs.

SIMPSON, G. G.

1950. History of the fauna of Latin America. *Am. Scientist*, 38 (3): 361-389, 10 figs.

TALBOT, F. H. AND M. J. PENRITH

1962. Tunnies and marlins of South Africa. *Nature*, 193 (4815): 558-559.

THORSON, GUNNAR

- 1961 Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. *In Oceanography. Pub. Amer. Assoc. Adv. Sci.*, (67): 455-474, 3 figs.

THE ZOOGEOGRAPHIC RELATIONSHIPS OF THE MARINE SHORE FISHES OF TROPICAL AMERICA¹

RICHARD H. ROSENBLATT

Scripps Institution of Oceanography, La Jolla, California

ABSTRACT

Despite the differences in habitat and the presence of a complete barrier to marine fishes between the Atlantic and Pacific, the shore fish faunas of the two sides of the Americas exhibit profound similarities. This is true on familial, subfamilial and generic level. However, few species (except for those that are circumtropical) occur on both coasts of the Americas. Instead there are a number of pairs of sibling species. These pairs are by no means equally distributed among the family-groups. Also the numbers of species and genera represented in the eastern Pacific and western Atlantic is markedly unequal in several groups.

The similarities and differences revealed by an analysis of the fish faunas of Tropical America can be understood only in relation to the past geological and climatological history of the region.

The most recent review of the ichthyofauna of the American tropics is that of Ekman (1953). Ekman's treatment was of necessity brief, and much has been learned since his synthesis, so that a good deal can now be said that was impossible at that time.

The marine environments on the two sides of the American continents differ profoundly, both physically and biotically. Perhaps the most important physical factor is the great restriction of the tropics along the west coast of the Americas. The California Current in the northern hemisphere and the Peru Current in the southern, transport cold water equatorward. This cooling effect is less pronounced in the north, where the tropical fauna extends to the level of Magdalena Bay on the Pacific Coast of Baja California (25°N). The effect of the California Current may be estimated by comparing the northern limit of the tropical fauna along the open Pacific, with the limit inside the Gulf of California. Here the tropical fauna extends a full 5° farther north, although with some diminution in number of species (Walker 1962).

This pinching in effect is much more accentuated in the southern hemisphere. Here the tropical fauna extends south only to Cabo Blanco, Peru, some five degrees south of the equator. Indeed, as a result of the influence of the Peru Current, a number of temperate types are found at the Galapagos Islands, on the equator.

In the Atlantic the situation is quite different, especially to the south. The northern boundary of the tropical fauna is usually placed at or about

¹Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

Cape Kennedy, and many tropical types extend to Cape Hatteras and beyond. To the south a fully tropical fauna extends to Rio de Janeiro. The deficit in extent of the tropics in the eastern Pacific with respect to the western Atlantic thus amounts to some 30 degrees of latitude.

This disparity in living space is more marked if certain other factors are taken into consideration. The Continental Shelf along the western side of the Americas is exceedingly narrow, and there are but few offshore islands. This stands in great contrast to the western Atlantic with its broad continental shelf and island-rich Antillean Arc. All in all the available amount of living space for shore and shelf fishes is very much greater in the Atlantic, and this may be partially responsible for the greater diversity of types in some groups.

Other factors may be of even greater importance. Perhaps the most important of these is the virtual absence of coral reefs and the rarity of reef-corals in the eastern Pacific. There is but one true coral reef in the eastern Pacific, and that is at the isolated and oceanic Clipperton Island. Elsewhere there may be considerable development of coral in certain localized areas (Squires [1959] has described reef suites in the Gulf of California) but nowhere is there anything comparable to the well developed coral reefs of the Indo-West Pacific or the western Atlantic.

There are indications that this relative lack of coral may be a recent phenomenon. Squires (1959) has discussed the Pliocene and Pleistocene corals of the Gulf of California region in relation to the northern extension of the ranges of several genera during parts of these periods. Jordan & Hertlein (1926) and Hanna (1926) have reported extensive Pliocene fossil reef deposits at María Madre Island, Tres Mariás Islands. To the north a Pleistocene coral reef has been discovered at Guadalupe Island, Mexico and dated at 140,000 years B.P. (C. L. Hubbs, personal communication). Squires (1959) has reported a fossil coral of the genus *Pocillopora* from Guadalupe Island (presumably from the above mentioned reef). This record from almost 30°N Lat, is 8° of latitude north of the present northern limit of the genus, and at a point where present surface water temperatures are below 20°C for ten months of the year (Anonymous, 1963).

Despite the aforementioned differences in the physical and biological environment, the most striking feature of the fish fauna of the tropical Americas is its essential unity. In a negative sense it can be defined by the absence of a number of characteristic Indo-West Pacific families. Some of the more prominent are the Chirocentridae, Gonorhynchidae, Plotosidae, Solenostomidae, Centriscidae, Maenidae, Plesiopidae, Plectorhynchidae, Theraponidae, Sillaginidae, Monodactylidae, Platacidae, Scatophagidae, and Siganidae. This list indicates that, as pointed out by Myers (1942), tropical fish faunas may be defined by the Indo-West Pacific family groups that they lack. However, in the case of the new world fish fauna, there are

certain positive features which may be used in framing a definition. There are not many endemic family-groups. Probably the only one consistently recognized is the Dactyloscopidae. Other Amphi-American families that have been recognized by some are the Achiridae (sometimes treated as a subfamily of the Soleidae), and the recently defined Chaenopsidae.

There are, in addition, several subfamilies which constitute an important element in the American fauna which are more or less restricted to it. The atherinid subfamily Atherinopsinae is restricted to the new world. The speciose subfamily Labrisominae of the family Clinidae is restricted to the Americas, except for the two West African species which almost certainly represent recent invasions from the western Atlantic. The largest and most diverse subfamily of the clingfishes, the Gobiesocinae, is likewise restricted to the New World, with the possible exception of a single South African genus. It is significant that not only are the subfamilies Labrisominae and Gobiesocinae essentially restricted to the American tropics, they are the only representatives of their respective families in the region.

TABLE 1
DISTRIBUTION OF THE NEOTROPICAL MARINE SHORE AND SHELF FISH GENERA
BY OCEAN

	East Pacific	West Atlantic
	(per cent)	(per cent)
Endemic	14	18
New World Endemic	35	30
Indo-West Pacific	9	9
East Atlantic	0.002	2
Circumtropical	42	41
Total No. of Genera	362	423

This pattern of resemblances extends to the generic level. In an attempt to assess the relationships of the ichthyofauna of the American tropics on the generic level, a list of the genera of tropical American shore and shelf fishes was compiled. High-seas pelagic genera were excluded, but coastal-pelagic types (as exemplified by the bulk of the Carangidae) were included. Genera with numerous American species and with but one or a few types in the eastern Atlantic were tabulated as "American." In this category would fall genera such as *Mycteroperca* and *Larimus*.

It is recognized that such a list is bound to contain errors, both of omission and commission. It is hoped however, that it is sufficiently correct and complete that subsequent additions and corrections will not substantially alter the conclusions to be drawn from it. In order that this assumption may be checked, the list on which the following discussion is based is appended to the main body of the paper.

A total of 479 genera of shore and shelf fishes were counted from the

tropical waters of the Western Hemisphere. Of these, slightly more than half occur in both the western Atlantic and the eastern Pacific. Most of these are circumtropical genera but an important fraction, 46 per cent, of these common genera are new world endemics. This is, about 25 per cent of the total number of new world genera occur on both sides of the Americas, but nowhere else. Many of these Amphi-American endemic genera are important elements in the fauna. Included are genera such as *Anchoa*, *Achirus*, *Mycteroperca*, *Stellifer* and *Haemulon*, which are important both in number of species and in biomass.

Not all families exhibit this pattern. For example the blennioid fish family Tripterygiidae is represented in the New World by four endemic genera. Of these, only one is Amphi-American, the other three being restricted to the eastern Pacific. Moreover, these genera belong to two subfamilies and each is most closely related to an Old World genus (Rosenblatt, 1959). Similarly, of the three eastern Pacific genera of the Chaetodontidae, only one is found in the western Atlantic.

Exceptions of this sort need to be accounted for, and the puzzles may be fascinating to unravel, but they do not invalidate the generality that the fish faunas of the western tropical Atlantic and the eastern tropical Pacific are closely related on the generic level.

It is instructive to take a more detailed look at the distribution on genera among the faunas taken one at a time. The data are summarized in Table 1. In numbers they are remarkably similar. There are 423 genera in the Atlantic and 362 in the Pacific. Looking first at the Atlantic fauna we see that, as expected, the largest single component is the group of circumtropical genera, with 42 per cent of the total. The next largest group, 30 per cent of the total, is composed of Neotropical endemic genera. The remaining large fraction, 18 per cent, is made up of western Atlantic endemic genera. There are some 38 genera in the Western Atlantic which also are found in the Indo-West Pacific, but not the eastern tropical Pacific. In contrast to the large and important group of Amphi-American endemic genera, there are very few Amphi-Atlantic endemic genera. There are only about ten genera common to and limited to the tropical Atlantic. This amounts to but 2 per cent of the total for the western Atlantic. Underlying the independence of the two sides of the Atlantic is the presence in the eastern Atlantic of several characteristic Indo-West Pacific groups. Prominent among these are the families Plectorhynchidae, Platycephalidae, Lethrinidae and Monodactylidae, and the genera *Arnoglossus*, *Cynoglossus*, *Psettodes* and *Citharus* among the flatfishes and *Cepola*, *Coris*, *Periophthalmus*, *Drepane*, *Cirrhitus* and *Girella* among the perciforms.

This set of data leads to the inference that the journey across the Atlantic from east to west is not an easy one, nor has it been for some time.

The generic composition of the eastern tropical Pacific fish fauna parallels that of the western Atlantic quite closely. Again, the single largest

group is that of the circumtropical genera, which make up 42 per cent of the total, followed by the Neotropical endemic genera at 35 per cent. Endemic east-Pacific genera make up 14 per cent of the total. Genera in common with the Indo-Pacific, but which are absent in the western Atlantic, number 34, or 9 per cent of the total. It is of interest that this is less than the number of Atlantic-Indo-West Pacific genera. This seeming paradox is lessened by the circumstance that most of the Indo-East Pacific genera are represented in the east Pacific by species that also occur in the Indo-West Pacific, but almost all of the Atlantic genera in this category are represented in the western Atlantic by endemic species.

One anomaly is the pearlfish genus *Echiodon* which contains three species, one in the Mediterranean, one in the eastern Atlantic and one in the Gulf of California. This single genus comprises but three-thousandths of one per cent of the total, but it seems quite out of place. When the eastern Pacific species was described it was predicted that a species of *Echiodon* would be found in the western Atlantic (Rosenblatt, 1961), but it has not been forthcoming to date.

As might be predicted from the existence of a complete land barrier, the Atlantic and Pacific faunas have few species in common. And there are differences in patterns of distribution in the two faunas. Perhaps the most striking is that the eastern Pacific fauna is much more parochial in character. Although a majority of the species range from the Gulf of California to northern Peru, there is evidence that there has been much independent speciation in certain areas, and that local subfaunas have evolved. The most clear-cut of these subregions, the Gulf of California, has recently been reviewed (Walker, 1960). Of the 530 species of shore and shelf fishes known from the Gulf of California, two-thirds are wide ranging eastern Pacific forms. However, there are over 90 endemic species in the Gulf, mostly concentrated in groups characteristic of rocky shores. It is evident that the long area of depositional coastline between Guaymas and Mazatlan has acted as a barrier to the distribution of rocky shore fishes, as has the relatively short open water stretch between Cape San Lucas and the mainland. Other factors must have been in operation as well, since there has been differentiation in certain fishes characteristic of sandy and muddy bottoms as well. In addition to the endemics, there is another important element. In the northern Gulf there is a group of species which also occur on the Pacific side of northern Baja California and in southern California. These forms are but weakly differentiated if at all from the outer coast populations, and it is likely that they are relicts of a former continuous population allowed by Pleistocene cooling.

South of Mazatlan the fauna is considerably more uniform. However, an area of depositional shoreline between Salina Cruz, Mexico, and the Gulf of Fonseca, Nicaragua has apparently acted as a barrier to the distribution of small rocky shore fishes, and a number of species and

subspecies find the limits of their distribution on one or the other side of it (Springer, 1959). This area has been termed The Pacific American Faunal Gap, although its effects are not as marked as are those of the area between Guaymas and Mazatlan, and it is a barrier to rocky shore fishes only.

The oceanic islands of the eastern Pacific add considerably to its faunal heterogeneity. These islands and Island groups, consisting of the Revillagigedos, about 250 miles off the tip of Baja California, Clipperton Island, about 800 miles south west of Acapulco, Cocos Island about 300 miles off Costa Rica, and the Galapagos Islands some 650 miles west of Ecuador, are characterized by a relatively high degree of endemism. This is especially true of the Galapagos Islands. The Galapagos fish fauna is large, consisting of slightly over 260 species. Of these fully one-quarter are endemic forms. In addition the Galapagos has a number of warm temperate types, derived from the coast of Peru (Rosenblatt & Walker, 1962).

On the oceanic islands is another conspicuous element, the Indo-West Pacific species. A number of species have been able to cross the three thousand mile stretch of open ocean, termed by Ekman the Eastern Pacific Barrier, that separates the Central Pacific Islands and the New World land mass. A considerable body of evidence, which will not be reviewed here, indicates that these are recent migrants and that the equatorial counter-current has been the route into the eastern Pacific (Hubbs & Rosenblatt, 1961; Briggs, 1961). However, these species form but a small part of the eastern Pacific fauna, and represent but an infinitesimal fraction of the total Indo-West Pacific fish fauna.

My first hand experience with tropical western Atlantic fishes is small but it seems safe to say that this area is considerably more homogeneous than the eastern Tropical Pacific. The Gulf of Mexico is depauperate in many groups and characterized by a small number of northern types of disjunct distribution, and there are differences between the Antilles and the mainland, but it does not seem possible on the basis of presently available data on fish distribution to divide the western Atlantic into discrete subunits. There appears to have been some transgression of the Atlantic, mostly from west to east, although a few Mediterranean types have infrequently been reported from the tropical western Atlantic. One important feature of the Atlantic is that certain groups are much richer in species than in the eastern Pacific. This disparity is particularly great in the Pomacentridae, Labridae, and Scaridae. This is no doubt because of the lack of the ecologically diverse coral reefs in the Pacific. It should be pointed out, however, that the rocky shores of the eastern Pacific harbor very many more species of clingfish than does the coralliferous Atlantic. It also appears that the eastern Pacific may be somewhat richer in certain characteristic sandy and muddy bottoms types such as anchovies, catfishes, and croakers. This may be more apparent than real however, as the fishes of

Panama Bay have been more intensively collected than those of Venezuela and Brazil. It is difficult to account for some peculiar gaps in the eastern Pacific fauna. A number of Indo-West Pacific families which are found in the Atlantic, such as the Dactylopteridae, Pempheridae, Parapercidae, and Moringuidae are absent, as are some 38 genera. It has been hypothesized that late Pleistocene cooling may have extirpated much of the eastern Pacific fauna (Hubbs, 1960). This would account nicely for what is missing, but how are we to explain what is there? It is not conceivable for example that the strongly endemic Gulf of California fauna has developed in a few thousand years. The degree of cooling which could account for the missing genera would thus leave us in dire straits in trying to account for the 344 genera still there.

There are but few species in common to the two sides of the Americas, if the circumtropical forms are eliminated. There are, however, a large number of species pairs. These were termed geminate or twin species by Jordan. All degrees of morphological differentiation can be found. Members of pairs such as *Anisotremus interruptus* and *A. surinamensis*, and *Epinephelus niveatus* and *E. niphobles* are true cryptic species separable with difficulty on the basis of rather minor morphological characters. Others such as *Pomadasys corvinaeformis* and *P. leuciscus*, and *Haemulon bonariense* and *H. scudderi*, although obviously closely related, can be separated with ease. I have elsewhere (Rosenblatt, 1963) pointed out that these geminates are by no means evenly distributed among the fish families. Instead they form a much higher fraction of the total among large fishes and those characteristic of depositional bottoms, and are much less frequent in small rocky shore fishes.

The relationships of the present day fish fauna of tropical America makes little sense in relation to present-day geography. The western Atlantic has a strong faunal connection with the Indo-West Pacific, from which it is completely cut off, and the fishes of the two sides of the Americas are closely related, although separated by an absolute barrier. The answer of course is to be sought in the past configuration of land and sea. From the Cretaceous through the Miocene the Tethys Sea served to connect the Indian and Atlantic Oceans, and the Bolivar Trough in northern South America and various Central American seaways have connected the Atlantic and the Pacific. The final destruction of the Tethyan geosyncline was accomplished in the Miocene and the uplift of the last Central American connection probably took place in the early Pliocene. It is not likely that there was a completely common fauna at any time. At least it would be difficult to account for the observed degree of endemism at the generic level in the length of time available. However, the communality of faunas must have been considerable.

When the last seaway connecting the tropical Atlantic and Pacific was uplifted, a natural experiment of tremendous scope was initiated. Two

faunas which must have been very similar in species composition were cut off by an absolute barrier. We are just beginning to examine the evolutionary consequences of this experiment. After some million years, however, it is about to be terminated by the activities of man. The sea-level canal which is now planned to replace the Panama Canal, will once again mix the waters and the faunas of the tropical Atlantic and Pacific. The possibilities are admittedly exciting. A number of fundamental theories will be testable. For example what will happen when two very similar species with similar ecologies are brought together? Will there be rapid differentiation through character displacement, will one eliminate the other, or will both persist side by side?

It is an axiom of taxonomy that morphological differences reflect genetic differences. However, differentiated allopatric populations of marine fishes have always been difficult to handle under the biological species concept. It should be of prime interest to study hybridization and intergradation among the geminate species. It may well prove to be the case that morphological differentiation will not be closely correlated with genetic isolation.

However, if a sea level canal were to be completed today, or this year, it would be an unmitigated disaster. Even for fishes we simply do not know enough about the existing species and their ecology. I could not today characterize the populations of any rocky shore fish between Acapulco and the Bay of Panama, and the situation is not much better for sand and mud bottom species. The material is simply not available to study. And afterwards it will be too late.

It will be expensive to mount major expeditions and house the material in museums. The cost is negligible, however, compared to the money to be spent digging the canal. And the possible economic effects of mixing the two faunas should also be taken into consideration. The job is immense, time is short, and the task must be undertaken soon.

REFERENCES

ANONYMOUS

1963. CALCOFI Atlas of 10-meter temperatures and salinities 1949 through 1959. California Cooperative Fisheries Investigations, Atlas No. 1.

BRIGGS, J. C.

1961. The east Pacific barrier and the distribution of marine shore fishes. *Evolution*, 15(4): 545-554.

EKMAN, S.

1953. *The zoogeography of the sea*. London, Sidgwick and Jackson, 417 p.

HANNA, G. D.

1926. Expedition to the Revillagigedo Islands, Mexico, in 1925, Pt. I, General Account. *Proc. California Acad. Sci.* (4) 15(1): 113.

HUBBS, C. L.

1960. Quaternary paleoclimatology of the Pacific coast of North America. *Rept. California Coop. Ocean. Fish. Invest.* 7: 105-112.

HUBBS, C. L. AND R. H. ROSENBLATT

1961. Effects of the equatorial currents of the Pacific on the distribution of fishes and other marine animals. Tenth Pacific Sci. Congress, Abstracts of Symposium Papers: 340-341.

JORDAN, E. K. AND L. G. HERTLEIN

1926. Expedition to the Revillagigedo Islands, Mexico in 1925. Pt. 7, Contribution to the geology and paleontology of the Tertiary of Cedros Island and adjacent parts of Lower California. Proc. California Acad. Sci. (4) 15 (14): 409-466.

MEYERS, G. S.

1942. The fish fauna of the Pacific Ocean with especial reference to zoogeographical regions and distribution as they affect the international aspect of the fisheries. Proc. Sixth Pac. Sci. Congr., 3 (1939): 201-210.

ROSENBLATT, R. H.

1961. A new pearlfish (family Carapidae) from the Gulf of California. Proc. Biol. Soc. Washington, 74: 207-212.
1963. Some aspects of speciation in marine shore fishes. Systematics Assoc. Publ. No. 5: 171-180.

ROSENBLATT, R. H. AND B. W. WALKER

1962. The marine shore fishes of the Galapagos Islands. Occ. Papers California Acad. Sci., 44: 97-106.

SPRINGER, V.

1959. Systematics and zoogeography of the clinid fishes of the subtribe Labrisomini Hubbs. Publ. Inst. Mar. Sci. Univ. Texas, 5: 417-492.

SQUIRES, D. F.

1959. Corals and coral reefs in the Gulf of California. Bull. Am. Mus. nat. Hist., 118 (7): 371-431.

WALKER, B. W.

1960. The distribution and affinities of the marine fish fauna of the Gulf of California. Systematic Zool., 9 (3-4): 123-133.

APPENDIX

LIST OF SHORE AND SHELF FISH GENERA OF THE NEW WORLD TROPICS. A = WESTERN ATLANTIC; EA = ATLANTIC AND/OR MEDITERRANEAN; IP = INDO-WEST PACIFIC; P = EASTERN PACIFIC; W = CIRCUMTROPICAL.

BRANCHIOSTOMIDAE

Branchiostoma W

EPIGONICHTHYIDAE

Asymmetron A, IP

MYXINIDAE

Eptatretus P, IP

Myxine W

HETERODONTIDAE

Heterodontus P, IP

SCYLIORHINIDAE

¹*Scyliorhinus* A, EA

ORECTOLOBIDAE

Ginglymostoma W

TRIAKIDAE

Mustelus W

Triakis W

Triaenodon, P, IP

RHINCODONTIDAE

Rhincodon W

CARCHARHINIDAE

Aprionodon A, IP

²*Carcharhinus* W

Galeocerdo W

Hypoprion A, IP

Negaprion W

Prionace W

Rhizoprionodon W

ISURIDAE

Carcharodon W

Isurus W

CARCHARIIDAE

Carcharias W

ALOPIIDAE

Alopias W

SPHYRNIDAE

Sphyrna W

PRISTIOPHORIDAE

Pristiophorus A, IP

SQUATINIDAE

Squatina W

RHINOBATIDAE

Zapteryx A, P

Rhinobatos W

PRESTIDAE

Pristis W

TORPEDINIDAE

Diplobatis A, P

Narcine W

DASYATIDAE

Dasyatis W

Himantura W

GYMNURIDAE

Gymnura W

UROLOPHIDAE

Urolophus W

Urotrygon A, P

MYLIOBATIDAE

Aetobatus W

Myliobatis W

Pteromylaeus W

Rhinoptera W

MOBULIDAE

Ceratobatis A

Manta W

Mobula W

ELOPIDAE

Elops W

MEGALOPIDAE

Megalops, A, IP

ALBULIDAE

Abula W

Dixonina A, P

CHANIDAE

Chanos P, IP

CLUPEIDAE

Chirocentron A

Etrumeus W

Harengula A, P

Ilisha W

Jenkinsia A

Lile A, P

Neopisthopterus A, P

Odontognathus A, P

Opisthonema A, P

Opisthopterus P, IP

Pellona A

Pliosteostoma P

Pristigaster A

Rhinosardinia A

Sardinella A, EA, IP

ENGRAULIDAE

Anchoa A, P

ENGRAULIDAE (cont.)

Anchovia A, P

Anchoviella A, P

Cetengraulis A, P

Engraulis W

Lycengraulis A, P

Pterengraulis A

CONGRIDAE

Conger A, IP, EA

Gnathophis W

Gorgasia P, IP

Neoconger A, P

Nystactichthys A

Paraconger A, P

Taenioconger P, IP

Uroconger W

MURAENESOCIDAE

³*Hoplunnis* A, P, EA

Muraenesox W

NETTASTOMIDAE

Facciolella A, P, EA

Saurenhelys P, IP

OPHICHTHIDAE

Ahlia A

Aplatophis A

Bascanichthys A, P

Caecula W

Callechelys W

Caralophia A

Gordiichthys A

Leptenchelys P

Letharchus A, P

Myrichthys W

Mystriophis W

Ophichthus W

Phaenomonas P

Pisodonopis P, IP

Pogonopis P

Pseudomyrophis A, P

Quassiremus P

Verma A

XENOCONGRIDAE

Chilorhinus A, IP

Chlopsis A, P, EA

Kaupichthys A, IP

HETERENCHELIDAE

Heterenchelys A, EA

Panturichthys A, EA

APPENDIX (Cont.)

LIST OF SHORE AND SHELF FISH GENERA OF THE NEW WORLD TROPICS. A = WESTERN ATLANTIC; EA = ATLANTIC AND/OR MEDITERRANEAN; IP = INDO-WEST PACIFIC; P = EASTERN PACIFIC; W = CIRCUMTROPICAL.

MORINGUIDAE
Aphthalmichthys A, IP
Stilbiscus A

MURAENIDAE
Anarchias W
Channomuraena A
Echidna W
⁴*Enchelycore* W
⁵*Enchelynassa* P, IP
Gymnothorax W
Muraena W
Pythonichthys A
Rabula W
Uropterygius W

⁶ARIIDAE
Arius W
Bagre W
Cathorops A, P
Galeichthys W
Netuma P, IP
Sciadeichthys W

SYNODIDAE
Saurida A, IP
Synodus W
Trachinocephalus A, IP

BELONIDAE
Ablennes W
Platybelone W
Strongylura W
Tylosurus W

HEMIRHAMPHIDAE
Chriodorus A
Euleptorhamphus W
Hemirhamphus W

BOTHIDAE
Ancyclopsetta A, P
Bothus W
Chascanopsetta A, IP
Citharichthys A, P, EA
Cyclopsetta A, P
Engyophrys A, P
Etropus A, P
Gastropsetta A
Hippoglossina P
Monolene A, P, EA
⁷*Paralichthys* A, P
Perissias P
Syacium A, P, EA

BOTHIDAE (cont.)
Trichopsetta A
Xystreurus A, P

SOLEIDAE
Achirus A, P
Apionichthys A
Aseraggodes P, IP
Gymnachirus A
Solea A, EA
Trinectes A, P

CYNOGLOSSIDAE
Symphurus W

HOLOCENTRIDAE
Corniger A
Holocentrus W
Holotrachys W
Myripristis W
Ostichthys A, IP
Plectrypops A

SYNGNATHIDAE
Bryx P
Doryichthys A, IP
Doryrhamphus P, IP
Hippocampus W
Nannocampus W
Syngnathus W

AULOSTOMATIDAE
Aulostomus W

FISTULARIIDAE
Fistularia W

MACRORHAMPHOSIDAE
Macrorhamphosus W

ATHERINIDAE
Atherina A, EA, IP
Atherinella P
Colpichthys P
Eurystole P
Hepsetia A, IP
Hubbesia P
Kirtlandia A
Leuresthes P
Menidia A, R
Melanorhinus A, P
Nectarges P
Thyrinops P

MUGILIDAE
Chaenomugil P

MUGILIDAE (cont.)
Mugil W
Xenomugil P

SPHYRAENIDAE
Sphyraena W

CAPROIDAE
Antigonia A, IP

POLYNEMIDAE
Pentanemus A, EA
Polydactylus W

APOGONIDAE
Apogon W
Cheilodipterus A, IP

KUHLIIDAE
Kuhlia P, IP

CENTROPOMIDAE
Centropomus A, P, EA

SERRANIDAE
Acanthistius A, P
Alphestes A, P
Anthias W
Anthiascus A
Centropristes A
Cephalopholis W
Dermatolepis W
Diplectrum A, P
Dules A
Epinephelus W
Gonioplectrus A
Hemanthias A, P
Hemilutjanus P
Holanthias W
Hypoplectrus A
⁸*Liopropoma* W
Mycteroperca A, P, EA
Paralabrax P
Paranthias A, P
Petrometopon W
Plectranthias A, IP
Polyprion A, IP
Schultzea A
Serraniculus A
Serranus A, P, EA

PRIACANTHIDAE
Priacanthus W
Pseudopriacanthus W
LOBOTIDAE
Lobotes W

APPENDIX (Cont.)

LIST OF SHORE AND SHELF FISH GENERA OF THE NEW WORLD TROPICS. A = WESTERN ATLANTIC; EA = ATLANTIC AND/OR MEDITERRANEAN; IP = INDO-WEST PACIFIC; P = EASTERN PACIFIC; W = CIRCUMTROPICAL.

GRAMMIDAE

Gramma A

Lipogramma A

GRAMMISTIDAE

Pseudogramma W

Rypticus A, P, EA

POMADASYIDAE

Anisotremus A, P

Bathystoma A

Boridia A

Brachygenys A

Conodon A, P

⁹*Haemulon* A, P

¹⁰*Orthopristis* A, P

XENICHTHYIDAE

Xenichthys P

¹¹*Xenistius* P

LUTJANIDAE

Aphareus P, IP

Etelis A, IP

Hoplopogrus P

Lutjanus W

Ocyurus A

Pristipomoides A, IP

Rabirubia P

Rhomboplites A

Verilus A

EMMELICHTHYIDAE

Emmelichthys A

Inermia A

SPARIDAE

Archosargus A, P

Calamus A, P

Diplodus A, IP

Lagodon A

¹²*Pagrus* A, EA

SCIAENIDAE

Bairdiella A, P

Corvula A, P

Cynoscion A, P, EA

Elattarchus P

Equetus A

Isopisthus A, P

Larimus A, P, EA

Lonchurus A

Macrodon A, P

Menticirrhus A, P

Micropogon A, P

SCIAENIDAE (cont.)

Nebris A, P

Odontoscion A, P

Ophioscion A, P

Paralanchurus A, P

Pareques A, P

Pogonias A

Stellifer A, P

Umbrina A, P, EA

MALACANTHIDAE

Malacanthus A, IP

BRANCHIOSTEGIDAE

Caulolatilus A, P

CIRRITIDAE

Amblycirrhitus A, IP

Cirrihitichthys P, IP

Cirrhitus P, IP

Oxycirrhites P, IP

SCOMBRIDAE

Sarda W

Scomber W

TRICHIURIDAE

Trichiurus W

CARANGIDAE

Alectis W

Carangoides P, IP

Caranx W

Chloroscombrus A, P

Citula W

Decapterus W

Elegatis W

Gnathanodon P, IP

Hemicaranx W

Nematistius P

Oligoplites A, P, EA

Selar W

Selene W

Seriola W

Trachinotus W

Trachurus W

Uraspis W

Vomer W

Zalocys P

POMATOMIDAE

Pomatomus A, IP

RACHYCENTRIDAE

Rachycentron A, IP

STROMATEIDAE

Palometa P

Poronotus A

ECHENEIDAE

Echeneis A, EA, IP

Remora W

GERRIDAE

Diapterus A, P

Eucinostomus A, P, EA

Eugerres A, P

Gerres W

Gen. nov. A

Moharra A

Ulaema A

MULLIDAE

Mulloidichthys P, IP

Mullus A, EA

Pseudupeneus A, P

CHAETODIPTERIDAE

Chaetodipterus A, P, EA

Parapsettus P

CHAETODONTIDAE

Centropyge A, IP

Chaetodon W

Forcipiger P, IP

Heniochus P, IP

Holacanthus W

Pomacanthus W

Prognathodes A

ZANCLIDAE

Zanclus P, IP

ACANTHURIDAE

Acanthurus W

Ctaenochaetus P, IP

Prionurus P, IP

Zebrasoma P, IP

POMACENTRIDAE

Abudefduf W

Azurina P

Chromis W

Eupomacentrus A, P

Microspathodon A, P

Nexilarius A, P

Nexilosus P

LABRIDAE

Bodianus W

Decodon A

APPENDIX (Cont.)

LIST OF SHORE AND SHELF FISH GENERA OF THE NEW WORLD TROPICS. A = WESTERN ATLANTIC; EA = ATLANTIC AND/OR MEDITERRANEAN; IP = INDO-WEST PACIFIC; P = EASTERN PACIFIC; W = CIRCUMTROPICAL.

LABRIDAE (cont.)

Doratonotus A
Halichoeres W
Hemipteronotus W
Lachnolaimus A
Pseudojulis W
Stethojulis P, IP
Thalassoma W

SCARIDAE

Cryptotomus A, EA
Leptoscarus P, IP
Nicholsina A, P
¹³*Scarus* W
Sparisoma A, EA

ELEOTRIDAE

Chriolepis A, P
Eleotrica P
Erotelis A, P
Eviota W
Gymneleotris P
¹⁴*Ioglossus* A, P

GOBIIDAE

Aboma A, P
Awous A, P
Barbulifer A, P
Bathygobius W
Bollmannia A, P
Coryphopterus A, P
Evermannia A, P
Evorthodus A, P
Garmannia A, P
Gillichthys P
Gnatholepis A, IP
Gobioides A, P
Gobionellus A, P, EA
Gobiosoma A, P
Gobulus A, P
Ilypnus P
Lophogobius A, P
Lythrypnus A, P
Microgobius A, P
Parrella A, P
Psilotris A
Quisquilius A
Tyntilastes P

MICRODESMIDAE

Clarkichthys P
Microdesmus W

CALLIONYMIDAE

Callionymus W

OPISTOGNATHIDAE

¹⁵*Lonchopisthus* A, P
Opistognathus W

PARAPERCIDAE

Mugiloides A
Pinguipes A

PERCOPHIDAE

Percophis A, IP

BEMBROPIDAE

Bembrops A, IP

URANOSCOPIDAE

Astroscopus W
Execestides A
Gnathagnus A, IP
Kathetostoma A, P

DACTYLOSCOPIDAE

Dactylagnus A, P
Dactyloscopus A, P
Gillellus A, P
Heteristius P
Myxodagnus A, P

CLINIDAE

Auchenistius A
Cryptotrema P
Dialommus P
Exerpes P
Labrisomus A, P, EA
Malacoctenus A, P, EA
Paraclinus A, P
Starksia A, P
Stathmonotus A, P

CHAENOPSIDAE

Acanthemblemaria A, P
Chaenopsis A, P
Coralliozetus A, P
Ekemblemaria A, P
Emblemaria A, P
Emblemariopsis A
Hemiemblemaria A
Lucayablennius A

¹⁶TRIPTERYGIIDAE

Axoclinus P
Enneanectes A, P

BLENNIIDAE

Blenniulus P

BLENNIIDAE (cont.)

Blennius A, EA, IP
Chasmodes A
Entomacrodus W
Homesthes P
Hypleurochilus A
Hypsoblennius A, P
Ophioblennius A, P, EA
Runula P, IP

BROTULIDAE

Ogilbia W
Oligopus W
Petrotyx A, P

OPHIDIIDAE

Brotuloides P
Chilara P
Lepophidium A, P
Ophidion A, P, EA
Otophidium A, IP
Rissola A

CARAPIDAE

Carapus W
Echiodon P, EA
Encheliophis P, IP

SCORPAENIDAE

Phenacoscorpius A, IP
Pontinus W
Scorpaena W
Scorpaenodes W

TRIGLIDAE

Bellator A
Prionotus A, P

DACTYLOPTERIDAE

Dactylopterus A, IP, EA

BATRACHOIDIDAE

Amphichthys A
Aphos P
Batrachoides A, P, IP
Halophryne A, IP
Opsanus A
Porichthys A, P
Thalassophryne A, P

GOBIESOCIDAE

Acyrtops A
Acyrtus A
Arcos A, P
Gobiesox A, P

APPENDIX (Cont.)

LIST OF SHORE AND SHELF FISH GENERA OF THE NEW WORLD TROPICS. A = WESTERN ATLANTIC; EA = ATLANTIC AND/OR MEDITERRANEAN; IP = INDO-WEST PACIFIC; P = EASTERN PACIFIC; W = CIRCUMTROPICAL.

<p>GOBIESOCIDAE (cont.)</p> <p><i>Pherallodiscus</i> P</p> <p><i>Tomicodon</i> A, P</p> <p>TRIACANTHODIDAE</p> <p><i>Hollardia</i> A</p> <p><i>Parahollardia</i> A</p> <p>MONACANTHIDAE</p> <p><i>Alutera</i> W</p> <p><i>Cantherines</i> W</p> <p><i>Monacanthus</i> A, IP</p> <p><i>Stephanolepis</i> A</p> <p>BALISTIDAE</p> <p><i>Balistes</i> W</p> <p><i>Canthidermis</i> W</p>	<p>BALISTIDAE (cont.)</p> <p><i>Melichthys</i> W</p> <p><i>Xanthichthys</i> W</p> <p>TETRAODONTIDAE</p> <p><i>Arothron</i> W</p> <p><i>Guentheridia</i> P</p> <p><i>Lagocephalus</i> W</p> <p><i>Sphoeroides</i> W</p> <p>CANTHIGASTERIDAE</p> <p><i>Canthigaster</i> W</p> <p>DIODONTIDAE</p> <p><i>Chilomycterus</i> W</p> <p><i>Diodon</i> W</p> <p>ANTENNARIIDAE</p> <p><i>Antennarius</i> W</p>	<p>ANTENNARIIDAE (cont.)</p> <p><i>Antennatus</i> P, IP</p> <p><i>Histrio</i> W</p> <p>OGCOCEPHALIDAE</p> <p><i>Halieuthichthys</i> A</p> <p><i>Ogcocephalus</i> A, P</p> <p><i>Zalieutes</i> A, P</p> <p>LOPHIIDAE</p> <p><i>Lophiodes</i> W</p> <p><i>Lophius</i> A, IP</p> <p>OSTRACIONTIDAE</p> <p><i>Acanthostracion</i> A, EA</p> <p><i>Lactophrys</i> A</p> <p><i>Lactoria</i> W</p> <p><i>Ostracion</i> P, IP</p>
---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------

¹Also S. Africa and temperate Asia.

²Including the nominal *Eulamia* and *Pterolamiops*.

³Represented in the eastern Pacific by an undescribed species.

⁴*Gymnothorax octavianus* Myers and Wade of the eastern Pacific and the central Pacific *G. bikiniensis* Schultz and *G. bayeri* Schultz are referred to the genus *Enchelycore*.

⁵*Enchelynassa canina* has been taken at Clipperton Island (record based on specimens in UCLA fish collection).

⁶The classification of marine catfishes is chaotic; the names and distributions given here may not bear much resemblance to reality.

⁷Also represented in the western north Pacific.

⁸Including the nominal *Chorististium* and *Pikea*.

⁹Including the nominal *Lythrulon* and *Orthostoechus*.

¹⁰Including the nominal *Microlepidotus*.

¹¹Including the nominal *Xenocys*, wrongly supposed to have 9 first dorsal spines rather than 11.

¹²Also temperate Asia, Australia and New Zealand.

¹³Including the nominal *Scarops* Schultz.

¹⁴Represented in the eastern Pacific by an undescribed species.

¹⁵Represented in the eastern Pacific by an undescribed species.

¹⁶Two undescribed eastern Pacific endemic genera are included in the count, but not listed.

ZOOGEOGRAPHY OF TROPICAL DEEP-SEA ANIMALS

ALFRED W. EBELING
University of California, Santa Barbara

ABSTRACT

Tropical distributions of pelagic deep-sea animals generally follow two main geographical patterns: 1) that of the equatorial water masses, which are enriched by upwelling in their eastern portions, and 2) that of the less productive central water masses, which overlies and merge with deeper intermediate masses formed in higher latitudes. Meridionally in all tropical oceans, abrupt faunal changes are usually observed about the Equator and Subtropical Convergences. Productivity and standing crop show concordant changes in these regions, where upwelling and advective mixing enrich the euphotic surface waters.

Within broad distributional patterns there occur vertically, temporally, and microgeographically oriented ecological animal groupings. These, which can be identified by computer cluster analysis, are often difficult to define precisely because of their vertical contamination during sampling. The large proportion of their variability that is not due to the multiple regression may result from the interplay of complex factors, such as general water-mass structure and the distribution of productivity and standing crop.

INTRODUCTION

The mid-depths of the deep-sea comprise a vast three-dimensional environment, spatially delimited by coordinates of latitude (x), longitude (y), and depth (z). The " x " and " y " describe two-dimensional or geographical space, subdivided by continents and the major currents, convergences, and divergences that bound the oceanic water masses. Along the depth coordinate, vertical boundaries are constituted by sunlight penetration, thermocline depth, the stratification of deep water masses, oxygen concentration, and the like. Near the surface, the epipelagic or euphotic zone of wind-mixed water supports photosynthesis. Below this, the aphotsynthetic mesopelagic zone in the thermocline is characterized by dim light and steep vertical environmental gradients. Next, at depths greater than 500-1000 m overlying the oceanic abyss, the cold bathypelagic realm of darkness, uniformity, and low food supply supports a fauna adapted for metabolic economy (e.g., Bruun, 1956; Hedgpeth, 1957; Marshall, 1960; Carter, 1961). Considering, in turn, each of the three broad dimensions of the tropical oceanic mid-depths, I shall briefly exemplify pertinent aspects of the constitution and distribution of deep-sea faunal assemblages.

METHOD

My first investigations of the taxonomy and zoogeography of deep-sea fishes mainly concerned the bathypelagic family Melamphaidae. For this

study, a nucleus of specimens and oceanographic data provided by the Danish Carlsberg Foundation was supplemented by materials from the Pacific and Indian Oceans collected during extensive oceanographic surveys by the U.S.A. and U.S.S.R. Captures were simply recorded on maps showing geographic boundaries of physicochemically-defined water masses and high surface biomass as measured by productivity and standing crop. To further demonstrate the general inclusion of particular species within various water masses, regressions of temperature on salinity, which define a family of curves that indicate the water mass or masses of occurrence, were plotted for the presumed maximum depth range of each capture, from hydrographic data obtained at most trawling stations (cf. Fig. 2).

Currently, ichthyologists at the University of Southern California, my students at Santa Barbara, and I are analyzing the composition of vertically and microgeographically associated ecological groups of deep-sea fishes and invertebrates trawled off southern California. Such analyses of local distributions are complex. Not only are several parameters, such as the precise depth of trawl, time of day, season, temperature, etc. involved in their delimitation, but it is necessary to resolve the statistical "error term" introduced into their numerical analysis by non-random and contaminated sampling with open nets and by the lack of sufficient measurements of their environment at trawl depth. This error is especially large for mesopelagic samples, which are necessarily contaminated both above and below their target populations. To resolve this error, we, in cooperation with oceanographers at the General Motors Defense Research Laboratories near Santa Barbara, are now trawling locally with a 6-foot Isaacs-Kidd Midwater Trawl equipped with electronically operated discrete-depth codend samplers and continuous on-deck monitors of depth, light, and temperature at the trawl while it is in tow (cf. Aron *et al.*, 1964).

These studies were supported entirely or in part by grants from the National Science Foundation, Washington D.C.: G-17937 and GB-1654 for systematic and distributional studies of the Melamphaidae, G-23467 to the University of Southern California for midwater trawling operations from the R/V VELERO off southern California, and GB-2867 for facilities and one year's monthly charter of the General Motors R/V SWAN for discrete-depth sampling in deep basins off Santa Barbara, California. Also, considerable information concerning the Indian Ocean fauna was provided by hydrobiological studies made during Cruise III of the International Indian Ocean Expedition, U.S. Program in Biology.

ZONAL COMPONENT OF DISTRIBUTIONS

The Atlantic, Pacific, and Indian oceans each contain equatorial, central, and boreal water masses that extend zonally between the continents (Fig. 1). The central water masses, however, are generally restricted at their eastern margins by meridional intrusions of cooler boreal and equa-

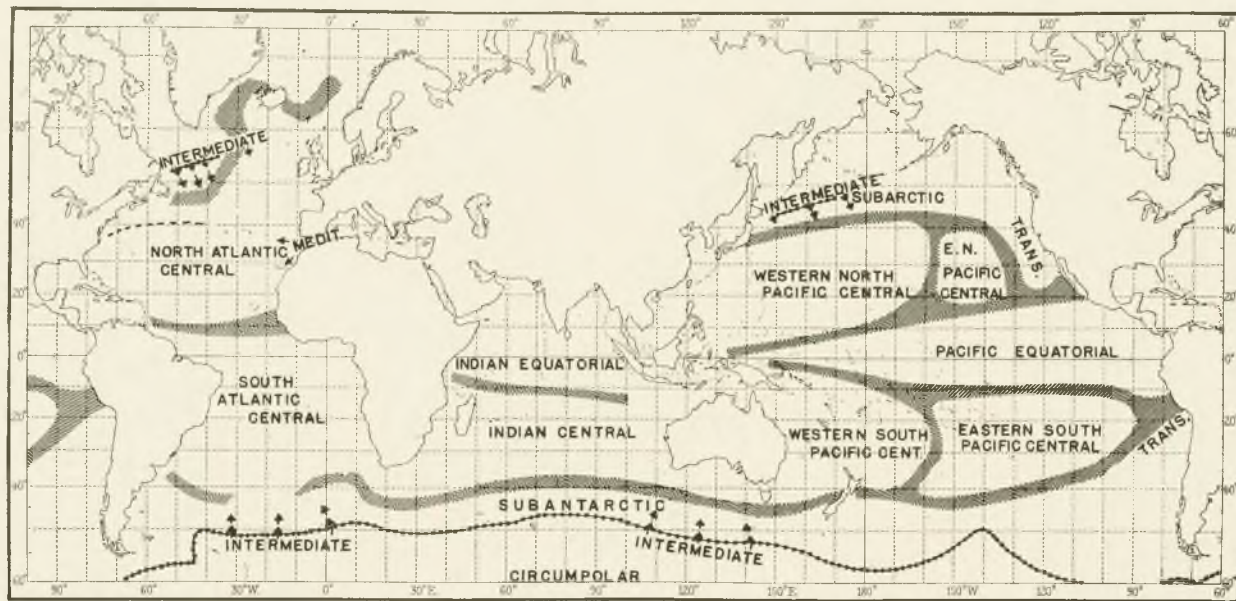


FIGURE 1. Water masses of the oceans, adapted from Sverdrup *et al.*, 1942. Hatched bands delimit the major water masses; dotted lines indicate convergences where intermediate waters are formed. The dashed line in the north Atlantic approximates the southern boundary of "Gulf Stream water." (This and all succeeding figures from Ebeling, 1962.)

torial waters. Underlying the central waters below 500-1000 m, intrusions of intermediate and deep waters flow generally equatorward to blend as the deep components of the equatorial masses (Sverdrup *et al.*, 1942). In contrast with the closed zonal circulation of the Pacific, where the extensive central water masses are uniformly stable and warm almost amphioceanically, is the open meridional circulation of the Atlantic, where cooling occurs equatorward and poleward across most latitudes (e.g., Backus *et al.*, 1965). In the Indian Ocean, the curtailment of the circulation to the north by the Indian subcontinent and the seasonal reversal of equatorial flow

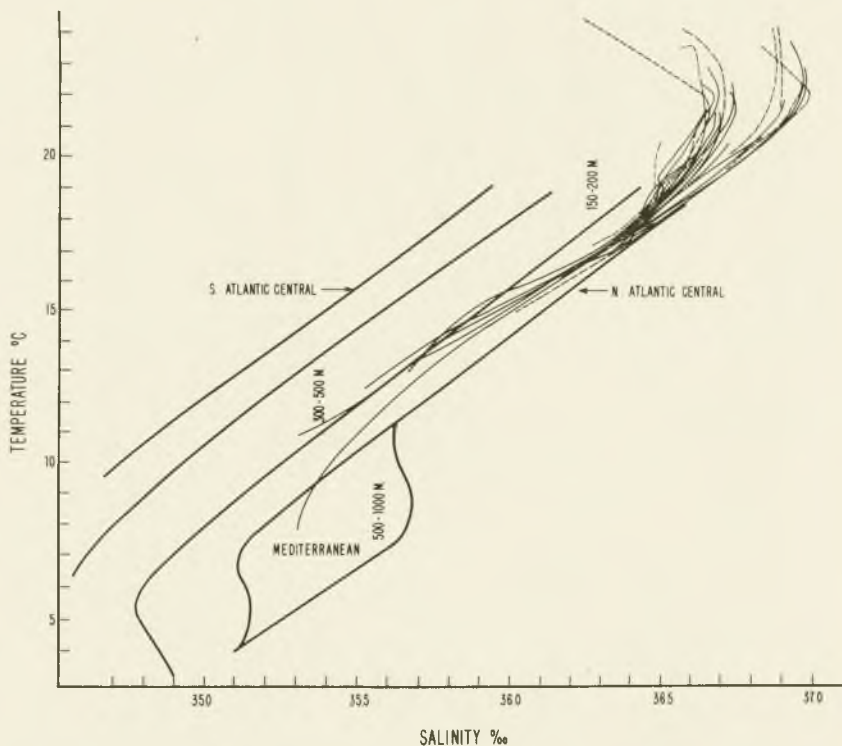


FIGURE 2. Temperature-salinity capture diagram for *Melamphaes pumilus*. The broad lines enclose water-mass envelopes (i.e., limits of the nested family of curves of temperature plotted against salinity with depth that defines the oceanic water mass). The thin lines are temperature-salinity segments through the maximum possible depth range for each capture (from the presumed upper depth limit of the species to the maximum depth attained by each net haul); dashed lines are for young, solid lines for adults. Note that most segments originate within the envelope defining North Atlantic central water and extend into areas representing shallower masses of overlying warm water in the upper part of the thermocline within the central gyre.

caused by the monsoons leaves only the southern part with a typical gyre of stable central water (Sverdrup *et al.*, 1942; Wooster, 1965). Although Bieri (1959) and Brinton (1962) implied that the shallower plankters are more restricted by the surface boundaries of these water masses than are the deep species, Ebeling (1962) showed that geographical distributions of many bathypelagic fishes generally follow these boundaries.

Throughout the tropics, zonal distributions of mid-depth animals generally follow two main geographical patterns. Many species are "central-tropical" in that they inhabit the relatively sterile central water masses that stretch from the tropical Atlantic to the Pacific Ocean. Ekman (1953) remarked on the similarity of such areas throughout the major oceans. These vertically stable water masses are warm, saline, and have relatively deep thermoclines (Sverdrup *et al.*, 1942). Because relatively little vertical mixing occurs between the nutrient-rich deep water and the euphotic surface water, their primary production of plants is low (e.g., Nielsen & Jensen, 1957; Bogorov, 1958).

Ranging throughout most central waters are, for example, the tiny bristlemouth fishes *Cyclothone pallida*, *C. obscura*, and *C. braueri* (cf. Mukhacheva, 1964), the melamphaid *Melamphaes simus* (cf. Ebeling, 1962), and the krill shrimp *Euphausia paragibba* (cf. Brinton, 1962; Baker, 1965). Within this vast region, however, the insular area of the

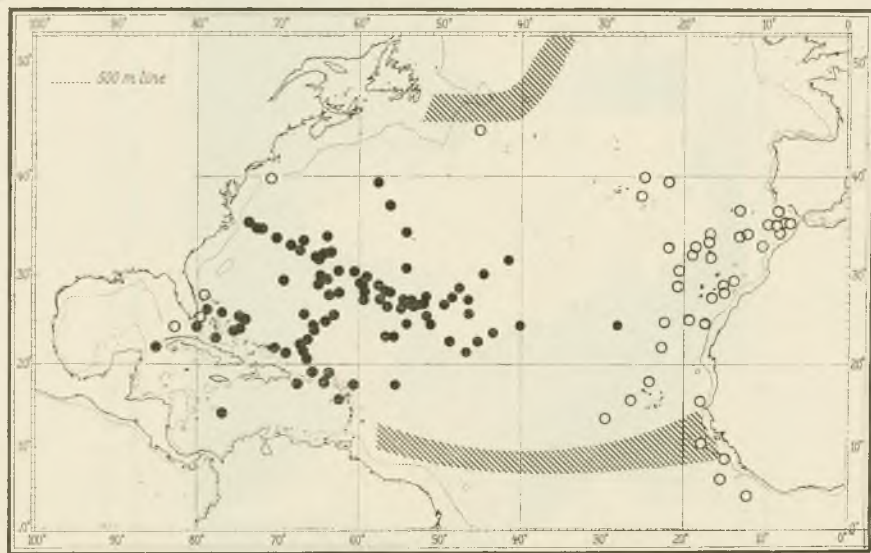


FIGURE 3. Distributions in the North Atlantic of *Melamphaes pumilus* (solid circles) and its sibling *M. simus* (open circles). The hatched bands delimit North Atlantic central water. Note that the distribution of *M. simus* circumscribes the western central gyre (Sargasso Sea).

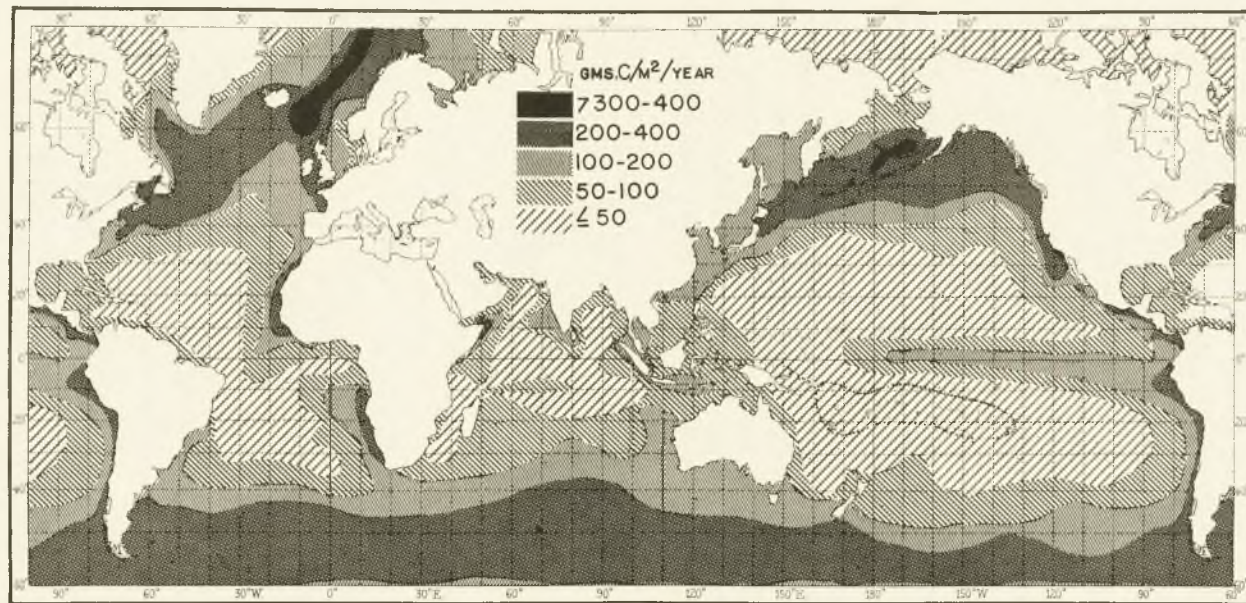


FIGURE 4. Estimation of the organic production in the oceans, adapted from Fleming & Laevastu (1956). The contours are in grams of carbon biologically fixed under each square meter of sea surface per year.

Indo-western Pacific shows considerable endemism. The lanternfish *Centrobranchus andrae* (cf. Becker, 1964), melamphaid *Scopelogadus unispinis* (cf. Ebeling & Weed, 1963), and four species of krill shrimp (Brinton, 1962; Baker, 1965) are generally restricted to this area. The large central current gyres appear to integrate certain endemic faunal elements (Ebeling, 1962). The mesopelagic fish *Melamphaes pumilus* inhabits only the gyre of North Atlantic central water (Fig. 2) and is peripherally replaced by a sibling, *M. simus* (Fig. 3). Brinton (1962) described the krill shrimp *Stylocherion affine* as comprising a series of morphologically distinguishable geographical races (Rassenkreis) distributed about the central gyre in the North Pacific, with the overlapping terminal populations in the eastern Pacific showing little or no morphological intergradation in the varying characters. Fager & McGowan (1963) showed that certain planktonic associations of chaetognath worms, pteropod molluscs, and euphausiid crustaceans are generally confined to North Pacific central water.

The central-tropical representatives of some groups are "dwarfed" compared with their large relatives that inhabit the richer peripheral boreal and equatorial water masses (Figs. 4, 5). The fish genus *Melamphaes* contains a natural group of four dwarf species (Fig. 6) that inhabit only central waters (Ebeling, 1962). Among other wide-ranging melamphaid species, intraspecific variants restricted to central gyres tend to be smaller than their peripheral relatives: e.g. a population of *Scopelogadus m. mizolepis* in N. Atlantic central water (cf. Ebeling & Weed, 1963) and central populations of *Scopeloberyx robustus*. Carl L. Hubbs and Robert L. Wisner (personal communication) described the mainly central distribution of the dwarf, surface-pelagic saury fish *Cololabis adocetus*, and Brinton (personal communication) noted that some central euphausiid species comprise relatively small individuals. Many central representatives of other groups (e.g., some bathylagid and stomiatoid fishes), however, are as large or larger than their peripheral congeners.

The equatorial water masses, which are best developed in the eastern Pacific, are formed *in situ* by subsurface mixing of central and underlying intermediate waters (Sverdrup *et al.*, 1942). Such mixing is facilitated by the relatively great depth of the equatorial currents (cf. Knauss & King, 1958). Upwelling and resulting high productivity and biomass characterize the equatorial Atlantic, Pacific, and Indian oceans (e.g., Nielsen & Jensen, 1957; Fleming & Laevastu, 1956; Holmes *et al.*, 1957; Holmes, 1958; Reid, 1962; Raymont, 1963). Brandhorst (1958) demonstrated the inverse relationship between depth of thermocline and size of standing crop of plankton in the eastern tropical Pacific. Therefore, due to the subsurface oxidation of sinking organic matter, equatorial waters contain a well-developed oxygen minimum zone below the wind-mixed surface layers, which extends northward and southward in upwelled waters (Wooster & Cromwell, 1958; Austin, 1960; Hart & Currie, 1960; Weyl,

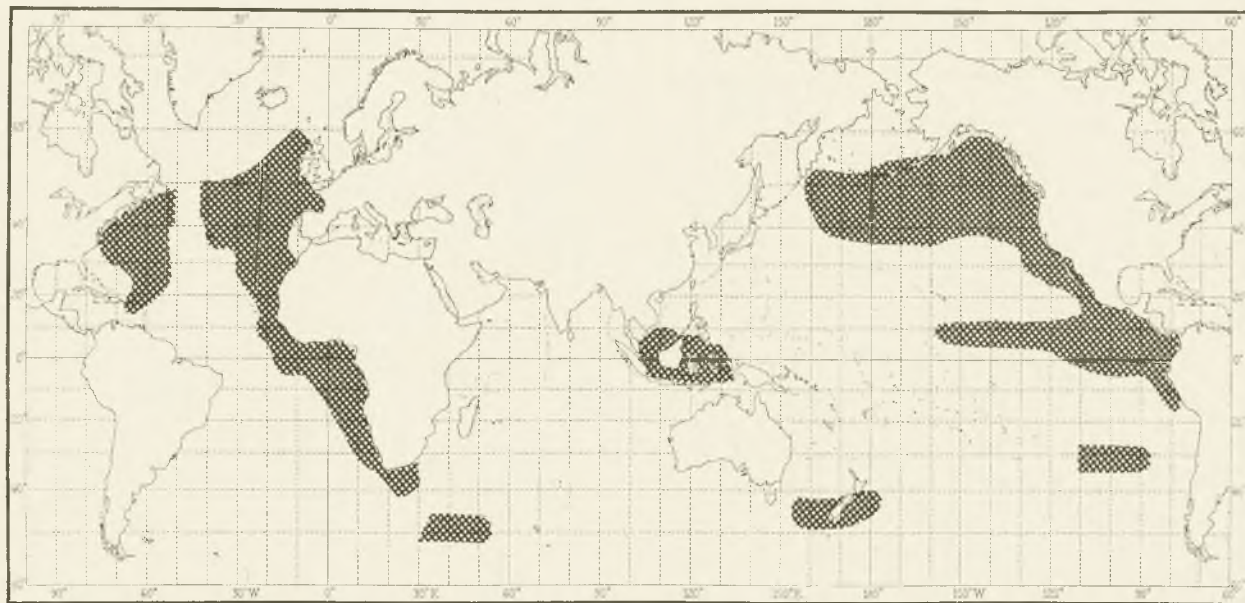


FIGURE 5. Composite of the distributions of the seven species of *Melamphaes* that include the largest adult individuals in the genus, often exceeding 80-100 mm in standard length. Note their exclusion from most of the relatively sterile central water masses.

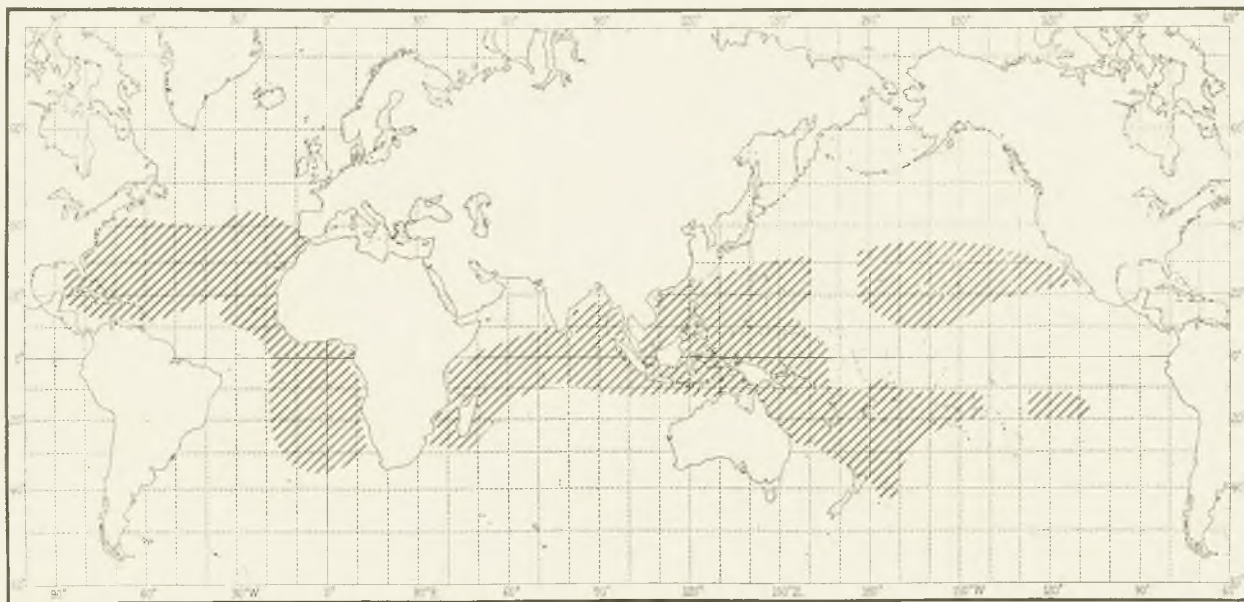


FIGURE 6. Composite of the distributions of the four species of *Melamphaes* comprising a group of "dwarf" individuals that measure less than 28 mm in standard length.

1965). In the eastern equatorial Pacific, the bathypelagic mysid shrimp *Gnathophausia gracilis* is excluded from this mid-depth oxygen minimum (Dr. William D. Clarke, personal communication), whose oxygen concentration is less than 0.5 ml/l over broad areas (Weyl, 1965). Here, the endemic subspecies of the bathypelagic fish *Scopelogadus m. bispinosus* and geographical variant of *Poromitra megalops* have relatively large gills (Ebeling & Weed, 1963).

The complex, productive oceanographic regime of integrating current eddies and upwellings in the relatively large eastern part of the Pacific equatorial water mass probably maintains its endemic fauna. A complex of three species in the *Lampanyctus omostigma* group of lanternfishes (Wisner, 1963), three species and one subspecies of melamphoids (Ebeling, 1962; Ebeling & Weed, 1963), the stomiatoid *Chauliodus barbatus* (cf. Morrow, 1961), several krill shrimps (Brinton, 1962), and chaetognath worms (Bieri, 1959), among many others, are confined to this area. Fager & McGowan (1963) depicted a numerically-determined, recurrent ecological group of two euphausiids and one chaetognath worm as Pacific equatorial. This considerable endemism caused Ebeling (1962) to classify this region as a "primary faunal region," having less than 17 per cent of its reported deep-sea fish fauna occurring throughout adjacent central and transitional waters and showing surprisingly little faunal overlap with the vast circumcentral-tropical region, which comprises most of the remaining tropical deep-sea environment (Fig. 7). Many Pacific equatorial species, such as the alepocephalid fish *Talismania bifurcata*, melamphaid *Melamphaes acanthomus*, and eel pout *Melanostigma pammelas*, however, range poleward in deep intrusions of equatorial water along the western continental shelf (Lavenberg, 1964; Bussing, 1965).

The zonal distributions of many species are interrupted by local oceanographic regimes in semi-isolated deep-sea basins. The deep-sea fish faunas of the Mediterranean and Red Seas are depauperate, probably due to the restrictive influence of their shallow sills and relatively warm deep waters (Tortonese, 1960; Marshall & Bourne, 1964). To a lesser extent, localized conditions limit the diversity of midwater faunas in semi-isolated oceanic basins such as the Sea of Japan, although basins with relatively free interchange with the adjacent ocean such as the Sulu Sea and Gulf of Mexico have diversified mid-water faunas (Marshall & Bourne, 1964). Mead (1963) noted that only non-migrating midwater fishes were trawled over the Cariaco Trench off Venezuela, whose isolated depths are anoxic below 300 m.

MERIDIONAL COMPONENT OF DISTRIBUTIONS

Water masses that constitute zoogeographical regions are delimited meridionally by converging and diverging oceanic currents, which cause vertical mixing or upwelling manifest as oceanic fronts between biologically and physicochemically discrete water masses (Sverdrup *et al.*, 1942;

PERCENT OVERLAP OF SPP. AT BOUNDARY BETWEEN	REGIONS OF WATER MASSES	ZOOGEOGRAPHICAL REGIONS			
		PRIMARY	SECONDARY	TERTIARY	QUATERNARY
	(CARIBBEAN)				
35	GULF OF MEXICAN				
			GULF OF MEXICAN ?		
16	MEDITERRANEAN SEA	MEDITERRANEAN			
16	ATLANTIC SUBARCTIC (N. OF SEC. POLAR FR-40° N)	ATLANTIC SUBARCTIC			
63	W.N. ATL. CENTRAL GYRE (INC. CARIBBEAN)	CIRCUM-CENTRAL = TROPICAL	ATLANTIC CENTRAL	W.N. ATL. CENTRAL	
58	E.N. ATL. CENTRAL (EAST OF 40° W)			E.N. ATL. CENTRAL	
58	ATLANTIC TROPICAL (OFF WEST AFRICA)			ATLANTIC TROPICAL	
45	SOUTH ATLANTIC CENTRAL		INDO = PACIFIC		
75	INDIAN CENTRAL & EQUATORIAL				INDIAN ?
68	INDONESIAN				INDONESIAN
40	SOUTH PACIFIC CENTRAL		?		S. PACIFIC CENTRAL ?
62	NORTH PACIFIC CENTRAL			N. PACIFIC CENTRAL	
0	W. PACIFIC EQUATORIAL				
5	E. PACIFIC EQUATORIAL	E. PACIFIC EQUATORIAL			
36	NORTH PACIFIC TRANSITIONAL	N. PACIFIC SUBARCTIC = TRANSITIONAL			
	PACIFIC SUBARCTIC		PACIFIC SUBARCTIC		
2	SUBANTARCTIC	SUBANTARCTIC			
	(CIRCUMCENTRAL = TROPICAL)				

FIGURE 7. Faunal boundaries, regions, and subregions associated with water masses and based on distributions of 135 species of mesopelagic and bathypelagic fishes representing 18 genera. The percentages of overlap across faunal boundaries are found by extending the horizontal lines to the percentage values on the left margin. The eastern Pacific equatorial region is here listed under "primary zoogeographical regions."

Bogorov, 1958, 1959, 1960; Beklemishev & Parin, 1960; Baker, 1965). Abrupt changes in both hydrography and plankton composition occur over relatively small distances; generally, meridional transects cross steep gradients in temperature and other environmental parameters (Baker, 1965). The tropical convergences about the equator and subtropical convergences between the central and boreal water masses constitute important meridional zoogeographical boundaries (e.g., Sverdrup *et al.*, 1942; Tebble, 1960). At the edge of the oceans, these faunal boundaries converge over a relatively small area, so that especially in the eastern oceans, equatorial, central, and boreal elements co-occur in a region of transition (ecotone) between water masses. In the eastern Pacific, Griffiths (1965) described such a convergence off Baja California, Mexico. Lavenberg (1964) and Paxton (1965) analyzed the temporal and depth composition of the heterogeneous transitional midwater fish fauna off southern California. In the Atlantic, Backus *et al.* (1965) described the abrupt discontinuity in mesopelagic fish faunas associated with the tropical convergence north of the equator.

Between the tropical convergences, asymmetrically about the equator, upwelling enriches the zone between the diverging equatorial currents (e.g., Wooster & Cromwell, 1958; Sette, 1958; Knauss & King, 1958). Although the Indian Ocean, like the other oceans, has a subsurface undercurrent, its equatorial circulation is uniquely reversed by the seasonal monsoons (Wooster, 1965). In the Pacific and Atlantic, however, the large north and south equatorial currents continuously transport water westward. To maintain a stable distribution of mass, extensive deep countercurrents and jet-like undercurrents forming between the diverging equatorial currents establish an eastward transport of water, balancing the westward. This complex current structure causes vertical enrichment of surface waters and a concomitant increase in the equatorial biomass (Sette, 1958; Reid, 1962). The resulting discontinuity of central masses between the tropical convergences has perhaps created antiequatorial distributions, that is, disjunct central distributions of, for example, lanternfishes (Rass, 1960; Becker, 1964) and euphausiid shrimps (Brinton, 1962) across the equatorial water masses.

At about 40° latitude, at the polar edge of the central water masses, the subtropical convergences constitute ecotones between the central and peripheral boreal masses in the Pacific, Atlantic, and southern Indian oceans. In the eastern Pacific and, to some extent, the eastern Atlantic, central and boreal waters mix in the equatorward nearshore components of the central gyre to form heterogeneous transitional water (Fig. 1, "Trans."), which often overlies northward intrusions of equatorial water (Sverdrup *et al.*, 1942; Reid *et al.*, 1958; Wooster & Gilmartin, 1961). Here, as explained previously, the various faunas mix, especially in the northeastern Pacific, where transitional water is widespread and supports

endemic transitional faunal elements. The melamphaid fish *Melamphaes parvus* (cf. Ebeling, 1962) and a few euphausiid crustaceans (Brinton, 1962) exemplify such transitional species.

The meridional distributions across the convergences of various biological parameters of the midwater and surface pelagic zones show considerable concordance. Raymont (1963), in citing the work of Hentschel and Wattenberg, recalled the remarkable concordance of high plankton with inorganic phosphate distributions in the surface waters of the central and south Atlantic. In the Pacific Ocean, contours of surface phosphate concentrations coincide with those of zooplankton volumes from oblique tows. The statistical analysis of King & Iversen (1962) demonstrated significant correlations among the distributions of phosphates, zooplankton volumes, and occasionally C_{14} productivity in meridional transects across the tropical and subtropical convergences in the North Pacific. Correlated with these parameters of productivity and standing crop of plankton are distributions of micro- and macronekton. King (1954) first suggested the causal relationships that associate equatorial divergences and upwelling with high concentrations of surface nutrients, organic productivity, high zooplankton volumes, and tuna fisheries across the equatorial Pacific.

A transect including 17 hydrobiological stations from 12°N to 44°S along the 60°E meridian in the Indian Ocean revealed associations of high productivity (C_{14} and chlorophyll *a*) with relatively large standing crops of surface plankton, mesopelagic animals, and bathypelagic animals. These stations, which were spaced at intervals of about 3°, were occupied during Cruise III of the International Indian Ocean Expedition, U. S. Program in Biology, August-September, 1963. The fishes and invertebrates were captured with a 10-foot Isaacs-Kidd Midwater Trawl in paired shallow and deep hauls to an average depth of either 500 or 1900 meters. At 26-35°S, just north of the Subtropical Convergence, a sharp increase in productivity and in surface and deep volumes of plankton and trawled animals coincided with a similar increase in the proportion of boreal specimens in the catch of melamphaid fishes: between 23 and 29°S, all of 21 specimens were tropical species, but between 32-38°S, 11 of 23 were boreal, as were 20 of 29 at the convergence, 41-44°S. Baker (1965) noted similar meridional discontinuities in abundance and distributions of 16 species of the krill shrimp genus *Euphausia*. Citing Brinton's (1962) observations, he further showed that analogous distributions occur among the same or similar species in the Pacific.

Beklemishev & Pasternak (1960) and Parin (1962) indicated that surface accumulations of flying fishes mark convergences and deeper faunal discontinuities. Beklemishev & Parin (1960) believe that the relatively shallow planktonic existence of young bathypelagic fishes may account for the concordance of distributions of all growth stages with surface phenomena. Bogorov (1958) constructed meridionally oriented

biogeographical regions delimited by a host of physicochemical and biological parameters, rather than simply temperature alone.

The diversity of the midwater fauna increases from the boreal waters equatorward across the subtropical convergences. In the northeastern Pacific, for example, more species inhabit central and intermediate waters south of the convergence at 40°N than the subarctic water to the north, even though the standing crop of animals decreases by an order of magnitude to the southward (Aron, 1959, 1962). King & Iversen (1962) noted that in the eastern tropical Pacific, the variety of organisms in the South Equatorial Current and Equatorial Countercurrent exceeds that of the North Equatorial Current (10-20°N) and Aleutian Current (40-45°N).

Adult populations of deep-sea animals often form meridionally allochthonous expatriate distributions, reproductively lost to the whole species (Ekman, 1953; Bullock, 1958). In the eastern tropical Pacific, all ontogenetic stages of the melamphaid fish *Melamphaes acanthomus* occur in equatorial water off Panama, although only large sterile adults inhabit the basins and troughs off the Californias and Peru-Chile in deep poleward intrusions of equatorial water (Ebeling, 1962; Bussing, 1965). Conversely, expatriation equatorward is exemplified by the planktonic worm *Poeobius meseres*, which breeds relatively near the surface in Pacific subarctic water, but submerges as anatomically degenerate adults in equatorial waters along the tropical coast of western America (McGowan, 1960). In the Atlantic, the deep-sea anglerfish *Ceratias holbolli* breeds as small adults in the tropics but has been taken as very large adults as far north as Greenland (Clarke, 1950). Large adults of the melamphaid fish *Scopelogadus beanii* inhabit waters associated with the Gulf Stream far to the north of its major breeding grounds in the northwestern part of the large central gyre (Ebeling & Weed, 1963; Mead *et al.*, 1964). Possibly the ontogenetic and breeding stages of many midwater species are integrated by current gyres and eddies in the tropical water masses. Here they may be dependent on a particular food supply or temperature regime and may comprise a "relict" distribution at the evolutionary center of origin of the species.

VERTICAL, TEMPORAL, AND MICROGEOGRAPHICAL COMPONENTS OF DISTRIBUTIONS

Within a limited geographical area, ecological associations are constituted by a complex array of environmental parameters. In space, the distributions may be correlated with depth, contagious clumping, water-mass structure, and food supply; in time, distributions may vary diurnally and seasonally. Also, the diversity of the midwater fauna increases offshore with the expanding vertical range of the deep-sea habitat. Superimposed on these factors are the large-scale geographical faunal restrictions mentioned before. Further complicating the analysis of the many causes of ecological assemblage is the fact that most previous samples of deep-water micronekton were made without trawl-closing devices or *in situ* environ-

mental monitors. The resulting vertical contamination of samples and lack of information as regards the target environment accounts for the large "error term" in the statistical analysis of the constitution of recurrent ecological groups.

Therefore, I suggest that the problem of defining such ecological groups that exhibit considerable horizontal, vertical, and temporal overlap might best be resolved using high-speed computers. Glover (1961), in citing the work of Kontkanen (1957) and Colebrook & Robinson, suggested the use of multivariate techniques to analyze seasonal and spatial fluctuations in numbers and species of plankton. Fager & McGowan (1963) employed a computerized cluster and multiple regression analysis to define and analyze the distributions of recurrent ecological groups of zooplankters in the North Pacific Ocean. Similarly, the "Taxometric Method," whereby a matrix of species-pair correlations can be clustered into a dendrogram of taxonomic or spatial relations, is applicable to ecological as well as taxonomic studies, for which it was originally devised (cf. Sokal & Sneath, 1963; modified by Dr. F. J. Rohlf, personal communication). The resulting dendrogram of product-moment correlations among species provides degrees of spatial association, which contrast with the all-or-none interspecies relations defined by the "index of affinity" used by Fager & McGowan.

The calculated ecological clusters of midwater species are usually associated with geographical, bathymetric, and temporal features of the environment. Vertically, the resulting recurrent groups can be generally classified as either mesopelagic or bathypelagic, but within these categories considerable overlap among groups often obscures the cause of their association. Fager & McGowan (1963) showed statistically that the taxonomic diversity of their computed zooplankton groups is significantly greater than would be expected by chance. This, of course, suggests a "competitive exclusion" within groups of closely related species or members of "congeneric pairs." In the present studies, groups of fishes usually comprise members of different families, or even orders: e.g., one such bathypelagic group off southern California contains the following six fishes, which represent six genera in five families among four orders: *Bathylagus milleri* (Clupeiformes, Bathylagidae) *Cyclothone acclinidens* (Clupeiformes, Gonostomatidae); *Anoplogaster cornuta* (Beryciformes, Anoplogasteridae); *Melamphaes acanthomus* (Stephanoberyciformes, Melamphaidae); *Poromitra crassiceps* (do.); and *Melanostigma pammelas* (Perciformes, Zoarcidae). However, some mesopelagic groups may contain two to three congeneric lanternfishes. Interestingly, some of the shallower mesopelagic fishes and crustaceans may be spatially (vertically) separated. Dr. William D. Clarke (personal communication) has shown that closed mesopelagic samples trawled in particular rising or falling isolumines of sunlight may contain mostly shrimps or fishes, but seldom an equal mixture of both.

In a multiple regression analysis that computes partial correlations, the numerical "success" of each group can be compared among all samples with measured parameters of the environment. The calculation of partial regressions between pairs of variables, holding all others constant, presumes causal relations, in that all variables are simultaneously taken into account. For example, preliminary analyses of deep-sea animals from off the Californias indicate that factors such as depth, length of haul, and season may influence the distribution of bathypelagic groups, but for mesopelagic groups, time of day and an inverse correlation with depth are significant factors in their numerical variability among samples. Several investigators have emphasized the important interrelationships of light and thermocline depth on the diurnal distributions of vertically migrating species (e.g., Aron, 1962; Percy, 1964; Lavenberg, 1964; Paxton, 1965). Fager & McGowan (1963) concluded that within the scope of their multiple regression analysis, only the constitution of the entire water mass (as indexed by temperature-salinity relations) was significantly correlated with the distributions of an ecological group of zooplankters (three euphausiids, one chaetognath, one pteropod mollusc) associated with Pacific subarctic water. However, they also noted possible correlations with depth of thermocline, time from midnight, depth of the oxygen minimum layer, temperature maxima and minima, and salinity distributions.

In the present investigation, the effect of geographical locality (as expressed by latitude, longitude, and depth to bottom) between the southern Californian borderlands and offshore or southern regions is much greater than the other parameters (e.g., depth of trawl, time of day, season, and length of haul) included in the multiple regression. Between the two localities, the water masses become progressively more tropical (central) to the south and west. Also, the diversity of the midwater fauna increases with bottom depth and distance offshore (Percy, 1964; R. L. Lavenberg, personal communication). Percy observed that off Oregon the average number of mesopelagic fishes taken per haul increased from less than 5 to more than 20 as bottom depth increased from 200 to more than 1000 m.

CONCLUSIONS

For each of the three broad dimensions of the deep-sea midwater environment, a different set of problems besets the analysis of the distribution of tropical midwater animals.

Zonally, the distributions follow two main geographical patterns; central and equatorial. Ranges in the relatively sterile central water masses extend from the Atlantic to the central Pacific Ocean. The Indo-Australian Archipelago, however, enriched by land runoff and upwelling, supports a diverse and abundant fauna. The more productive equatorial waters support a significantly different fauna and larger biomass. The relatively few

pantropic species exhibit patterns of geographical variation correlated with water-mass boundaries.

Meridionally, faunal discontinuities are more abrupt and occur over shorter distances. The tropical convergences about the equator and subtropical convergences at 40° latitudes constitute important barriers to dispersal for deep sea animals. Not only physicochemical, but also biological parameters of the environment, such as productivity and standing crop, account for the discontinuities in geographical distributions.

Vertically, the ecological relationships within the broad geographical patterns are difficult to analyze because of the complexity of factors controlling the cohesion of recurrent ecological groups and their transgression of the deep-water masses. This suggests the benefit of computer analyses of these many variables, the monitoring of more environmental parameters, and the use of discrete depth samplers.

LITERATURE CITED

ARON, W.

- 1959. Midwater trawling studies in the North Pacific. *Limnol. Oceanogr.*, 4: 409-418.
- 1962. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. *J. Fish. Res. Bd. Canada*, 19: 271-314.

ARON, W., N. BAXTER, R. NOEL, AND W. ANDREWS

- 1964. A description of a discrete depth plankton sampler with some notes on the towing behavior of a 6-foot Isaacs-Kidd Midwater Trawl and a one-meter ring net. *Limnol. Oceanogr.*, 9: 324-333.

AUSTIN, T. S.

- 1960. Oceanography of the east central equatorial Pacific as observed during Expedition Eastropic. *Fish. Bull., U.S.*, 60: 257-282.

BACKUS, R. H., G. W. MEAD, R. L. HAEDRICH, AND A. W. EBELING

- 1965. The mesopelagic fishes collected during Cruise 17 of the R/V CHAIN, with a method for analyzing faunal transects. *Bull. Mus. comp. Zool. Harvard*, 134: 139-158.

BAKER, A. C.

- 1965. The latitudinal distribution of *Euphausia* species in the surface waters of the Indian Ocean. *Discovery Rep.*, 33: 309-334.

BECKER, V. E.

- 1964. (Slendertailed myctophids, genera *Loweina*, *Tarletonbeania*, *Gonichthys*, and *Centrobranchus*, of the Pacific and Indian oceans. Systematics and distribution.) *Trudy Inst. Okeanol.*, 73: 11-75. [In Russian.]

BEKLEMISHEV, C. W. AND N. V. PARIN

- 1960. (Pelagic biogeographical boundaries in the North Pacific in winter 1958-59.) *Trudy Inst. Okeanol.*, 41: 257-265. [In Russian.]

BEKLEMISHEV, C. W. AND F. A. PASTERNAK

- 1960. (Census taking of flying fishes in the Atlantic and the problem of evaluation of the productivity of tropical waters.) *Vopr. Ichthyol.*, 14: 72-77. [In Russian.]

- BIERI, R.
1959. The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. *Limnol. Oceanogr.*, 4: 1-28.
- BOGOROV, B. G.
1958. Biogeographical regions of the plankton of the northwestern Pacific Ocean and their influence on the deep sea. *Deep-Sea Res.*, 5: 149-161.
1959. (The biological structure of the ocean.) *Doklady Akad. Nauk S.S.S.R.*, 128: 819-822. [In Russian.]
1960. (Differentiation of geographical zones of the central Pacific.) *Biol. Mor., Trudy Okeanogr. Kom. Akad. Nauk S.S.S.R.*, 10: 3-7. [In Russian.]
- BRANDHORST, W.
1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. *J. Cons. perm. int. Explor. Mer.*, 24: 16-31.
- BRINTON, E.
1962. The distribution of Pacific euphausiids. *Bull. Scripps Inst. Oceanogr.*, 8: 51-270.
- BRUUN, A. F.
1956. The abyssal fauna: its ecology, distribution and origin. *Nature*, 177: 1105-1108.
- BULLOCK, T. H.
1958. Homeostatic mechanisms in marine organisms. In Buzzati-Traverso, A. A., Ed., *Perspectives in marine biology*, University of California Press, Berkeley: 199-210.
- BUSSING, W. A.
1965. Studies of the midwater fishes of the Peru-Chile Trench. *Antarctic Res. Serv. (American Geophysical Union)*, 5: 185-227.
- CARTER, G. S.
1961. Evolution in the deep seas. In M. Sears, Ed., *Oceanography*, Washington, D.C., Amer. Assoc. Adv. Sci.: 229-237.
- CLARKE, R.
1950. The bathypelagic angler fish *Ceratias holbolli* Kröyer. *Discovery Rep.*, 26: 1-32.
- EBELING, A. W.
1962. *Melamphaidae* I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. *Dana-Rep.*, (58): 1-164.
- EBELING, A. W. AND W. H. WEED
1963. *Melamphaidae* III. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. *Dana-Rep.*, (60): 1-58.
- EKMAN, S.
1953. *Zoogeography of the sea*. London, Sidgwick and Jackson. 417 pp.
- FAGER, E. W. AND J. MCGOWAN
1963. Zooplankton species groups in the North Pacific. *Science*, 140: 453-460.
- FLEMING, R. H. AND T. LAEVASTU
1956. The influence of hydrographic conditions on the behavior of fish. *F. A. O. Fish. Bull.*, 9: 181-196.

- GLOVER, R. S.
1961. Biogeographical boundaries: the shapes of distributions. In M. Sears, Ed., Oceanography, Washington, D. C., Amer. Assoc. Adv. Sci.: 201-228.
- GRIFFITHS, R. C.
1965. A study of ocean fronts off Cape San Lucas, Lower California. Spec. scient. Rep. U. S. Fish Wildl. Serv., No. 499: 1-54.
- HART, J. I. AND R. I. CURRIE
1960. The Benguela Current. Discovery Rep., 31: 123-298.
- HEDGPETH, J. W.
1957. Classification of marine environments. Mem. geol. Soc. America, (67): 93-100.
- HOLMES, R. W.
1958. Physical, chemical, and biological oceanographic data obtained on Expedition SCOPE in the eastern tropical Pacific, November-December 1956. Spec. scient. Rep. U. S. Fish. Wildl. Serv., No. 279: 1-117.
- HOLMES, R. W., B. SCHAEFER, AND B. M. SHIMADA
1957. Primary production, chlorophyll, and zooplankton volumes in the tropical eastern Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm., 2: 129-169.
- KING J. E.
1954. Variations in zooplankton abundance in the central equatorial Pacific, 1950-52. Symp. mar. freshw. Plankton Indo-Pacific. Bangkok, F.A.O.: 10-17.
- KING, J. E. AND R. T. B. IVERSEN
1962. Midwater trawling for forage organisms in the central Pacific 1951-1956. Fish. Bull. U.S., 62: 271-321.
- KNAUSS, J. A. AND J. E. KING
1958. Observations on the Pacific Equatorial Undercurrent. Nature, 182: 601-602.
- KONTKANEN, P.
1957. On the delimitation of communities in research on animal bio-coenotics. Cold Spring Harbor Symp. quant. Biol., 22: 373-378.
- LAVENBERG, R. J.
1964. An ecologic analysis of the midwater fishes of the San Pedro Basin. M. A. Thesis (unpublished), University of Southern California.
- MARSHALL, N. B.
1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Rep., 31: 1-122.
- MARSHALL, N. B. AND D. W. BOURNE
1964. A photographic survey of benthic fishes in the Red Sea and Gulf of Aden, with observations on their population density, diversity, and habits. Bull. Mus. comp. Zool. Harvard, 132: 223-244.
- MCGOWAN, J. A.
1960. The relationship of the distribution of the planktonic worm, *Poeobius meseres* Heath to the water masses of the North Pacific. Deep-Sea Res., 6: 125-139.

- MEAD, G. W.
1963. Observations on fishes caught over the anoxic waters of the Cariaco Trench, Venezuela. *Deep-Sea Res.*, 10: 251-257.
- MEAD, G. W., E. BERTELSEN, AND D. M. COHEN
1964. Reproduction among deep-sea fishes. *Deep-Sea Res.*, 11: 569-596.
- MORROW, J. E., JR.
1961. Taxonomy of the deep-sea fishes of the genus *Chauliodus*. *Bull. Mus. comp. Zool. Harvard*, 125: 249-294.
- MUKHACHEVA, V. A.
1964. (The composition of species of the genus *Cyclothone* (Pisces, Gonostomidae) in the Pacific Ocean.) *Trudy Inst. Okeanol.*, 73: 93-138. [In Russian.]
- NIELSEN, E. S. AND A. JENSEN
1957. Primary oceanic production, the autotrophic production of organic matter in the oceans. *Galathea Rep.*, 1: 49-136.
- PARIN, N. V.
1962. (Some features of the distribution of massing pelagic fishes in the zone of equatorial currents in the Pacific Ocean, according to materials of the 34th cruise of the E/S VITJAZ.) *Okeanologiya*, 2: 1075-1082.
- PAXTON, J. R.
1965. An ecological analysis of distribution for the lanternfishes (Family Myctophidae) of the San Pedro Basin, California. M.A. Thesis (unpublished), University of Southern California.
- PEARCY, W. G.
1964. Some distributional features of mesopelagic fishes off Oregon. *J. Mar. Res.*, 22: 83-102.
- RASS, T. S.
1960. (Geographical distribution of bathypelagic fishes of the family Myctophidae in the Pacific Ocean.) *Trudy Inst. Okeanol.*, 41: 146-151. [In Russian.]
- RAYMONT, J. E. G.
1963. Plankton and productivity in the oceans. New York, Macmillan. 660 pp.
- REID, J. L., JR.
1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. *Limnol. Oceanogr.*, 7: 287-306.
- REID, J. L., JR., G. I. RODEN, AND J. G. WYLLIE
1958. Studies of the California Current system. In California Cooperative Oceanic Fisheries Investigations Progress Report 1 July 1956 to 1 July 1958. California Dept. Fish and Game mar. Res. Comm., Calif. State Printing Office: 27-56.
- SETTE, O. E.
1958. Nourishment of central Pacific stocks of tuna by the equatorial circulation system. In Proceedings of the Eighth Pacific Science Congress of the Pacific Science Association 1953. Volume III, Oceanography. Quezon City, National Research Council of the Philippines: 131-148.

- SOKAL, R. R. AND P. H. A. SNEATH
1963. Principles of numerical taxonomy. London, W. H. Freeman. 359 pp.
- SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING
1942. The oceans, their physics, chemistry, and general biology. New York, Prentice-Hall. 1087 pp.
- TEBBLE, N.
1960. The distribution of pelagic polychaetes in the South Atlantic Ocean. Discovery Rep., 30: 161-300.
- TORTONESE, E.
1960. General remarks on the Mediterranean deep-sea fishes. Bull. Inst. Oceanogr. Monaco, (1167): 1-14.
- WEYL, P. K.
1965. On the oxygen supply of the deep Pacific Ocean. Limnol. Oceanogr., 10: 215-219.
- WISNER, R. L.
1963. *Lampanyctus hubbsi*, a new myctophid fish from the east-central tropical Pacific Ocean, with notes on the related, sympatric eastern Pacific species, *L. omostigma* and *L. parvicauda*. Copeia, 1963: 16-28.
- WOOSTER, W. S.
1965. Indian Ocean expedition. Science, 150: 290.
- WOOSTER, W. S. AND T. CROMWELL
1958. An oceanographic description of the eastern tropical Pacific. Bull. Scripps Inst. Oceanogr., 7: 169-282.
- WOOSTER, W. S. AND M. GILMARTIN
1961. The Peru-Chile Undercurrent. J. Mar. Res., 19: 97-122.

ZOOGEOGRAPHICAL EVIDENCE OF THE AGE OF THE SOUTH ATLANTIC OCEAN

GEORGE SPRAGUE MYERS
Stanford University, Stanford, California

ABSTRACT

The evidence of terrestrial and fresh-water continental faunas during the Cenozoic and Mesozoic is brought to bear upon continental and ocean basin genesis involving Africa, South America, and the intervening South Atlantic Ocean. Mammalian fossil evidence is decisive for the Cenozoic, but not for the Mesozoic. Mammals demonstrate that South America can have had no dry land connection with Africa during the entire Cenozoic. South America was likewise isolated from Central America by a sea gap from some indeterminate time in the Mesozoic until Late Cenozoic (probably Late Pliocene) time, although the southern termination of Central America was evidently close enough so that occasional overwater mammalian exchange could take place.

Recent studies of teleostean fish evolution demonstrate; (1) that cypriniform ostariophysan fishes must have evolved in fresh water and retained their intolerance of salt water since their Mesozoic origin, (2) that these fishes (especially Characoidea) are more archaic, hence older, than previously assumed, and (3) that their origin probably occurred in the Middle or Early Mesozoic. No other assumptions fit both morphological findings and the general picture of teleostean evolution now emerging from recent research. Characoid and some other ostariophysan fishes almost certainly pre-date mammals of all but the earliest types.

Recent studies of freshwater fish-faunal assemblages in Central America give evidence that no cypriniform-ostariophysan fishes had ever been present in Central America previous to the very late Cenozoic. This negates derivation of ancestral South American cypriniform ostariophysans from North America. Strong similarities shown by the characoids and other freshwater fishes of South America and Africa therefore point with the utmost insistence towards South Atlantic continental union.

Mammalian evidence negates Cenozoic union and almost certainly Late Cretaceous as well. The nature of the African-South American fish relationship would permit a postulated union at almost any time in the Mesozoic, but it is most probable that characoids evolved in a Jurassic or even a Triassic southern continent, which soon thereafter split to form the beginnings of the South Atlantic Ocean.

The fish evidence is favorable to a final parting of Africa and South America, and the origin of the South Atlantic Ocean, at some time during the earlier half of Mesozoic time.

INTRODUCTION

The present paper is an outgrowth of several lines of investigation. In a series of studies beginning nearly 30 years ago (Myers, 1938, 1940, 1949, 1951), I have investigated the distribution and history of various fish faunas and fish groups. Secondly, a brief period of field work in Nicaragua has produced certain critical ecological observations bearing upon the comparative times at which different fresh-water fish groups entered the

area (Myers, 1966). Thirdly, in a study of teleostean fishes as a whole, four of us have recently come to some new and far-reaching conclusions about the evolution and probable age of a number of the major phyletic lines of modern fishes (Greenwood *et al.*, 1966). In addition, I have drawn heavily upon the geological history of reptiles and mammals so ably presented by Simpson and Darlington.

A synthesis of this research leads to a new evaluation of the historical zoogeography of continental faunas during both the Cenozoic and the Mesozoic. A fuller account will be presented elsewhere. However, because the nature and age of continents and ocean basins is involved in my results, and because the type of zoogeography represented by this work needs to be represented in a symposium exhibiting the varied types of zoogeographical approaches, it seems desirable to present a summary here.

STABILITY VERSUS CONTINENTAL DRIFT

As I indicated as long ago as 1938, a majority of the most eminent students of historical zoogeography, among them Alfred Russel Wallace (1876, 1880) and William Diller Matthew (1915), have insisted upon the comparative stability of continents and ocean basins through geological time. Matthew, in particular, adduced a very large body of sound paleontological evidence in favor of his view. More recently, G. G. Simpson, in a variety of studies (1940, 1943a, 1943b, 1947, 1950, 1953) has demonstrated beyond reasonable doubt that the extensive and constantly mounting evidence derived from fossil mammals not only does not need drifting continents to explain it, but also demonstrates with crushing effectiveness that continental union of the type envisioned by Wegener could not have existed during the evolution and deployment of the main mammalian lines. The same view is inherent in Darlington's major work (1957) on the zoogeography of vertebrate animals as a whole.

On the other hand—again as I pointed out in 1938—the evidence of continental freshwater fishes strongly favors some southern continental connections. My ideas on some of these things have suffered certain evolutionary changes. In an investigation of fish and amphibian distribution in the East Indies (1951, 1953) I found that the fish evidence needed no great extension of the classical ideas of paleogeography presented by Wallace, but I did point out that the evidence of freshwater fishes is far more conservative, and presents a much sharper picture of East Indian paleogeography, than the bird and mammal evidence upon which Wallace, and later, Ernst Mayr (1944), chiefly depended. More recently, it has become clear that the main question of whether fish distribution favors stability or drift cannot be decided upon the basis of the East Indian fish evidence. The really critical areas are Africa and South America, and the ocean between them.

OLD AND NEW EVIDENCE ON FISH DISPERSAL

Much of the fish evidence for some sort of former union of Africa and South America was presented a long time ago by Eigenmann (1909) and Regan (1922). My own contribution (1938) re-emphasized the soundness of the evidence, if not the conclusions, presented by Eigenmann and Regan. Especially, I pointed out that what had been ecologically segregated as true freshwater fishes by Günther (1880) and succeeding workers are, in fact, composed of two ecological groups differing profoundly in their tolerance of salt sea water. Primary (*i.e.*, obligatory) freshwater fishes cross sea barriers with even less facility than amphibians or mammals, and their osmoregulatory aversion to salt appears to have existed for a long geological period. But those apparently obligatory freshwater fishes, which I called secondary freshwater fishes, demonstrate, not only by experiment but also by their distribution, that they can and have dispersed partly by sea. Raft-dispersal over salt water, which has obviously helped to disperse terrestrial animals, is closed to fishes, and freshwater fishes disperse more slowly across land areas than do terrestrial animals. Their dispersal patterns are thus far more conservative than those of other vertebrates.

The similarities shown by certain elements of the African primary freshwater fish fauna to those of South America, therefore, are of much greater importance than had previously been assumed. Darlington (1957) assumed a derivation of both African and South American primary freshwater fishes from northern sources, by way of trans-Tethys dispersal into Africa and a southward dispersal through Central America.

My recent observation of the Central American fish fauna (Myers, 1966) has cast the gravest sort of doubt upon the existence of any primary freshwater fishes in middle Central America prior to the latest Cenozoic (Pliocene or Pleistocene). Moreover, the absence in North America and Eurasia of any possible ancestors, Recent or Fossil, of a large part of the primary fishes of Africa and South America also casts the strongest doubts upon a northerly derivation of the southern fish faunas.

The problem presented is obvious. To paraphrase Regan (1922), the view that the principal groups of primary freshwater fishes held in common by Africa and South America originated in the north and spread southwards, involves so many improbabilities as to be unbelievable. On the other hand, the mammalian evidence presented by Simpson and his predecessors permits no paleogeographic conclusion other than dispersal of successively evolved mammalian orders in the absence of direct southern continental connections.

NEW EVIDENCE ON FISH EVOLUTION

Our new evaluation of the evolution of teleostean fishes (Greenwood *et al.*, 1966) indicates that many teleostean lineages must be considerably older than the Late Cretaceous origins hitherto usually assumed. Moreover,

there is indirect but mounting evidence that the Mesozoic origin of many teleostean groups occurred in fresh water. This is especially true of the great superorder Ostariophysi, to which the majority of the primary freshwater fishes of the world belong, and particularly true of the included order Cypriniformes—the characoids, cyprinoids, and their very close relatives. The most primitive of the cypriniform fishes are the characoids, and it is precisely this large suborder of characoid fishes that provides the most striking and meaningful similarity between African and South American fishes.

The characoids, comprising 16 families and probably over 1100 species of Neotropical and Ethiopian primary freshwater fishes, present a number of primitive morphological and developmental characteristics indicating not only closeness to holosteans but also an age comparable to that which has been assumed for herringlike forms. They undoubtedly originated in fresh water and have retained a general osmoregulatory nature which has (unlike most other groups) prevented their entrance into the sea throughout their history. Except for their obviously post-Pliocene invasion of Central America and Mexico, with one species reaching northern Mexico and Texas, there is no evidence that the characoids were ever present in North America or Eurasia (see Greenwood *et al.*, 1966).

AFRICA AND SOUTH AMERICA

The only reasonable explanation is that the characoids evolved in one southern land mass which must have included some parts of both South America and Africa. That we have found no Mesozoic fossil characoids or other cypriniform ostariophysans is not surprising. Unlike marine deposits, fluvial and lake deposits are rarely of wide geographical extent and are highly subject to quick subsequent erosion by the same streams which laid them down. Moreover, if my conclusions as to the origin of ostariophysans are correct geographically, the center of origin of these fishes—in a Mesozoic southern continent—is in an area where there has been comparatively little search for freshwater fish-bearing deposits, and small interest in study of what has been or may be found.

That “Africa” or “South America,” or both, were fragmented into islands separated by epeiric seas during some parts of the Mesozoic is highly probable. It seems certain that holosteans, and palaeoniscoids as well, were present in the continent, or fragments of it, at the time ostariophysans appeared. Thus, the existence of archaic freshwater assemblages of the same age as early ostariophysan assemblages would be expected, although the two might not occur together if the same factors of freshwater fish faunal isolation that we find today were then operative.

The ostariophysans, especially the Cypriniformes, almost certainly soon became the dominant freshwater fish type in any land mass to which they gained access—a distinction which they have probably never shared with

other teleostean groups. The shift from a purely holostean (or holostean-paleoniscoid) assemblage to one dominated by ostariophysans would, in all probability, have been a fairly rapid one, although accompanied by the continued survival of certain specialized holostean or other archaic types, such as lungfishes. However, the evolution of many insectivorous and phytophagous types, especially very small species, would almost surely have awaited the main evolutionary flowering of the angiosperms and insects during the Cretaceous.

AGE

In regard to the age of characoids in a southern land mass, we have no direct information. However, they give evidence of an age comparable to that of the Salmoniformes, which began to enter the sea during the Cretaceous, and of which we therefore have some Mesozoic fossil evidence. The first fishes of recognizably teleostean nature now known are certain Triassic Leptolepidae. These must have had a much earlier origin because they were already rather specialized. It would thus cause no great surprise to find holosteans which had begun to assume teleostean characteristics in the Early Triassic or perhaps even in the latest Paleozoic.

Once it is accepted that the most primitive ostariophysans (characoids) evolved in the fresh waters of a southern land mass, some attempt at a very general dating of the Atlantic split of such a land mass becomes possible. Mammalian evidence indicates clearly that any African-South American split must already have been of long standing at the dawn of the Cenozoic. It further indicates very clearly that South America was separated by a sea-gap from Central America from some undetermined time in the Mesozoic (perhaps the Jurassic), until the end of the Tertiary—in Late Pliocene or earliest Pleistocene time (Patterson and Pascual, 1963). Perhaps no previous connection ever existed. This Panama gap must at times have permitted some Mesozoic and Cenozoic mammalian exchange via an overseas "sweepstakes route," but it must have been a complete barrier to primary freshwater fishes. In fact, except for animals to which overseas methods of transport are available, the South American continental fauna appears to have been evolving in complete isolation during the whole of the immensely long period from the Jurassic or earliest Cretaceous to the Pleistocene, when the Panama gap was finally closed (Patterson & Pascual, 1963). Previous to the end of the Tertiary, all mammals which reached South America from other regions appear to have done so via overseas routes. What this means to primary freshwater fishes, to which sea gaps are far greater obstacles than to mammals, is obvious.

We are thus forced to push the southern origin of ostariophysan fishes much farther back than had previously been thought, but it will be recalled that the fishes themselves lead us to suspect a pre-Cretaceous origin for at least the characoids. Very little is known of Jurassic freshwater fishes anywhere in the world, and, except for one or two small African assemb-

lages, almost nothing is known of freshwater Triassic fishes in Africa or South America. Beyond placing probable characoid origin in a southern land mass during the Triassic or Jurassic, we cannot reasonably go.

There has been much published of late on continental drift (*e.g.*, Runcorn, 1962) but a great deal of it is concerned with geophysics rather than dating. Caster (in Mayr, 1952), du Toit (1937) and others are inclined to place the split between Africa and South America in the Triassic. A Late Triassic or Jurassic split would not only suit my concept of teleostean evolution, but it would place the beginnings of South Atlantic drift at a time which is permissible in view of the mammalian evidence.

The conceptual model which seems best to suit the evidence can be briefly sketched as follows:

Once the teleostean level was reached by the protacanthopterygian fishes, their early evolution was probably rapid, and if ostariophysans arose from the same stem as the salmoniform fishes (as Greenwood *et al.*, [1966] believe), the ostariophysans were probably one of the earliest offshoots of that stem. There can be no serious doubt that the earlier protacanthopterygian lines were already well established by Lower Cretaceous times. The characoids comprised one of these lines, and they or their immediate ancestors gave rise very early to the siluriform fishes.

Ostariophysans originated in a southern land mass comprising parts of what are now Africa and South America. The definitive form of the family Characidae, and of the siluriform branch, was established in that land mass, probably very shortly before its fragmentation, which, from the fish evidence, could have occurred either during the Jurassic or, more probably, in Late Triassic time. The South Atlantic appeared and has since broadened.

South America had no further dry-land connections until the Pliocene. Africa (or its fragments) was isolated from both Madagascar and Eurasia from pre-ostariophysan times until some so far undated bridgings of the declining Tethys Sea permitted primary freshwater fish exchange with Eurasia. However, post-Triassic Africa was apparently always more subject to mammalian invasions than to primary freshwater fish invasions, as would be expected.

Cyprinoid fishes evolved in Asia from some toothless protocyprinid characoid which got across the Tethys from Africa. In Eurasia, the cyprinids blossomed into the largest familial group of the Ostariophysi, and in the Tertiary invaded both Africa (across the greatly shrunken Tethys) and North America (via a Bering land bridge).

Siluriform fishes, or certain groups of them, have never shown quite such a sharp restriction to fresh water as their cypriniform relatives, and have not only accompanied cypriniform fishes in their dispersal, but have also, in part, had sea-routes available to them.

CONCLUSIONS

Recent studies demonstrate the extreme improbability that the ancestors of the present primary freshwater fishes of South America either had a marine origin or entered that continent from the north via Central America. Close similarity of the generalized and obviously ancient characoid ostariophysans of Africa and South America necessitates the assumption of common origin in a southern land mass comprising the whole or parts of what now constitutes Africa and South America. The evidence of the fishes, when set against the background of fossil mammalian evidence, strongly favors continental drift, with the South Atlantic split beginning during the first half of the Mesozoic, probably in Late Triassic or Jurassic times.

[Note: After this paper was completed, Darlington (1965) has cautiously favored continental drift in a new book on the biogeography of southern continental areas.]

LITERATURE CITED

DARLINGTON, P. J.

1957. *Zoogeography: The geographical distribution of animals*. New York, John Wiley: xiv + 675 pp.

1965. *Biogeography of the southern end of the world*. Cambridge, Mass., Harvard Press: xii + 236 pp.

DU TOIT, A. L.

1937. *Our wandering continents, an hypothesis of continental drifting*. Edinburgh and London, Oliver & Boyd: xiv + 366 pp.

EIGENMANN, C. H.

1909. The fresh-water fishes of Patagonia and an examination of the Archiplata-Archhelenis theory. *Reports Princeton Univ. Expeds. to Patagonia, Zool.*, 3 (3): 225-374, 1 map, pls. 30-37.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS

1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Amer. Mus. nat. Hist.*, 131 (4): 339-456, pls. 21-23.

GÜNTHER, A.

1880. *An introduction to the study of fishes*. Edinburgh: xvi + 720 pp.

MATTHEW, W. D.

1915. *Climate and evolution*. *Ann. New York Acad. Sci.*, 24: 171-318. (Reprinted 1939 as: *Spec. Publ. N.Y. Acad. Sci.*, no. 1.)

MAYR, E.

1944. Wallace's Line in the light of recent zoogeographic studies. *Quart. Rev. Biol.*, 19: 1-14.

1952. The problem of land connections across the South Atlantic, with special reference to the Mesozoic. (A symposium.) *Bull. Amer. Mus. nat. Hist.*, 99 (3): 81-258.

MYERS, G. S.

1938. Fresh-water fishes and West Indian zoogeography. *Ann. Report Smithsonian Inst. for 1937*: 339-364, 3 pls.

1940. The fish-fauna of the Pacific Ocean, with especial reference to zoogeographical regions and distribution as they affect the international aspects of the fisheries. *Proc. 6th Pacific Sci. Congr.*, 3: 201-210.
 1949. Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. *Bijdragen tot de Dierkunde*, 28: 315-322.
 1951. Fresh-water fishes and East Indian zoogeography. *Stanford Ichth. Bull.*, 4: 11-21.
 1953. Ability of amphibians to cross sea barriers, with especial reference to Pacific zoogeography. *Proc. 7th Pacific Sci. Congr.*, 4: 19-27.
 1966. Derivation of the freshwater fish fauna of Central America. *Copeia*, 1966 (4): 766-772.
- PATTERSON, B. AND R. PASCUAL
1963. The extinct land mammals of South America. 16th Internat. Congr. Zool., Program: 138-148. (Published in the Program, not the Proceedings.)
- REGAN, C. T.
1922. The distribution of the fishes of the order Ostariophysi. *Bijdragen tot de Dierkunde*, 22: 203-208.
- RUNCORN, S. K.
1962. Continental drift. (A symposium.) New York and London: xii + 338 pp.
- SIMPSON, G. G.
1940. Mammals and land bridges. *J. Washington Acad. Sci.*, 30: 137-163.
 - 1943a. Mammals and the nature of continents. *Amer. J. Sci.*, 241: 1-31.
 - 1943b. Turtles and the origin of the fauna of Latin America. *Amer. J. Sci.*, 241: 413-429.
 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. *Bull. geol. Soc. America*, 58: 613-688.
 1950. History of the fauna of Latin America. *Amer. Scient.*, 38: 361-389.
 1953. Evolution and geography, an essay on historical biogeography with special reference to mammals. *Condon Lectures, Oregon State Syst. of Higher Education*: 64 pp.
- WALLACE, A. R.
1876. The geographical distribution of animals. London: 2 vols., xxiv + 503 pp., and + 607 pp.
 1880. Island life. London: xx + 563 pp.

BIOLOGICAL CLUES IN INTERPRETING THE BIOGEOGRAPHY OF THE FORAMINIFER *NUBECULARIA LUCIFUGA* DEFRANCE

ZACH M. ARNOLD

Department and Museum of Paleontology, University of California, Berkeley

ABSTRACT

Distributional data for both Recent and fossil representatives of this warm-water, calcareous imperforate foraminifer must be reevaluated. A demonstration of environmental correlates for variations in several taxonomically significant features of the test (shell) seems to invalidate several specific and possibly some generic designations within the nubeculariid complex.

On broad intact blades of *Posidonia oceanica*, *Nubecularia lucifuga* generally assumes a planispiral form, but on the decaying shreds of dead blades that flank the central viable ones in the tuft, the foraminifer is acervuline, agglomerate, or otherwise irregular. Among planispiral forms, the degree of test agglutination is correlated with the length of and the foraminifer's position on the blade to which it is attached and is probably correlated with wind-induced turbulence, these, in turn, having seasonal correlates.

Laboratory cultures of asexually-produced siblings revealed an impressive spectrum of infraspecific variability that lacks obvious environmental correlates. In developing a taxonomic concept upon which biogeographical conclusions for the nubeculariid complex rest, cognizance should also be taken of such an inherent variation potential.

INTRODUCTION

The resources of paleontological interpretation in the study of foraminiferan biostratigraphic, paleoecological, and biogeographical problems are being severely strained today by the snowballing revelation of an unbelievably rich, an embarrassingly complete, and an increasingly perplexing spectrum of fossil and Recent species that has, at one and the same time, resulted from and been significantly contributory to the successful exploitation of one of nature's most highly valued resources—oil. Without continual guidance and disciplinary jolts from biologists working with living foraminifera, the paleontologist must remain an empiricist in many of those classificatory interpretations that are so fundamental to the use of foraminifera in recognizing and correlating sedimentary strata and in developing relevant paleoecological and biogeographical conclusions. Boltovskoy (1965) recently portrayed the alarming taxonomic confusion that has resulted from the failure of many students of the group to recognize the natural variation potential of the foraminifera, which, admittedly, by geological or inorganic standards must oftentimes appear almost incomprehensibly lavish. With equal candor, McLean (1965) has focused attention on the disastrous professional consequences of such inadequacies.

A century ago, students of the foraminifera tended to be biological rather than geological in training and orientation, but with the application of foraminiferology to the correlation of sedimentary strata, and particularly with the practical application of such data to problems related to petroleum exploration, large numbers of geologists began the study of foraminifera, both fossil and Recent. Their concept of variation was naturally and understandably narrower. The resulting excesses in splitting species, however, have produced the chaotic taxonomic scene which Boltovskoy has so vividly described. The need for a broader and deeper understanding of the general biology of living species of foraminifera, based on the study of both natural and laboratory populations, is becoming so obvious to paleontologists generally that several of them are now themselves undertaking the necessary biological investigations.

Anachronistically enough, one of the most important areas in which the biologist can contribute significantly to paleontology is rather remote from the assiduous esotericism of modern computerized biology. Requiring neither biochemical sorcery, mathematical wizardry, nor electronic necromancy, the mere definition of ranges of infraspecific variation potentials, as determined through the study of controlled lineages of laboratory populations, is what many paleontologists seem fervently to desire from the biologist.

The taxonomic history and the current status of *Nubecularia lucifuga*, a calcareous perforate species having a fairly widespread distribution in present-day seas and a respectably long geological history, is a case in point that illustrates well what simple biological observation can contribute to the solution of paleontological problems involving functional-morphological relationships and taxonomic decisions.

Originally described as a fossil from the Eocene of France (Defrance, 1825), the Recent form and much of its test's truly protean nature were ably described in great detail by Carpenter *et al.* (1862), who believed that similar fossil forms of still greater age [then called Triassic, now Lower Jurassic, (Adams, 1962)] from the English Midlands actually belonged to the same species, this on the basis of sheer morphological similarity between fossil and empty Recent tests. With the 20th Century ascendancy of geological thought and discipline in the study of foraminifera, however, has come the division of the single species, *lucifuga*, into many. Ten Dam (1950) designated as a new species, *N. triloculina*, forms from the Lower Cretaceous of the Netherlands that he believed were the same as those earlier called *N. lucifuga* by Jones & Parker (1860) from the Lias of England. Barnard (1950), shortly thereafter, applied the name *Calcitonella woodi* to specimens from another Lias locality in England which Adams (1962), in a well-documented and comprehensive study of adherent calcareous species, synonymized with *N. triloculina*. It was at this point that I, in hopes of contributing to the solution of the problem,

undertook the biological study of large numbers of specimens of *N. lucifuga* obtained from the Mediterranean in the vicinity of the University of Paris' marine biological laboratory (Laboratoire Arago) at Banyuls-sur-Mer, Pyrénées-Orientales, France.

MATERIALS AND METHODS

Specimens of *N. lucifuga* were collected from the viable blades and from the threads of shredded and decaying blades of the marine grass, *Posidonia oceanica*, dredged from a depth of 6 to 8 m by a large construction crane during the course of excavations being made for the foundations of a new breakwater in the bay just adjacent to the laboratory. Individual foraminifera responded well to simple culture techniques whether removed from the blade or left on small fragments of it. Kept in closed plastic boxes (5 cm diameter, 2.5 cm depth) they rapidly constructed new chambers and many of them eventually reproduced. A convenient device for maintaining large numbers of mass or isolation cultures, the latter particularly useful in the study of controlled lineages of known ancestry, was developed at the Banyuls laboratory and has been described elsewhere (Arnold, 1966). Consisting essentially of a 5-liter reservoir from which sea water is carried by air lift to a small distributor above for passage, drop-by-drop, down through intervening stacks of shallow, 5 cm, porous-bottomed culture dishes, the apparatus provided an excellent environment for bacterial growth as well, but by adding 2-3 mg each of chloramphenicol and streptomycin to each liter of sea water (on the advice of Dr. E. Lagarde, Chef du Service Microbiologique, Laboratoire Arago, Banyuls) this growth was kept under control without noticeably inhibiting that of the foraminifera. Heat-killed naviculoid diatoms were a satisfactory food for this species.

Following the completion of the culture studies, which extended over a six-month period, I compared specimens from Banyuls with collections at the British Museum of Natural History, with Recent materials from Monterey Bay, California, and Biscayne and Florida bays in Florida, and with Jurassic specimens kindly collected for me by Professor T. Barnard (University College, London) from Byfield, Northamptonshire.

The generous assistance of Professor Barnard in obtaining the Jurassic specimens from England, of Professor G. Petit (Director, now retired, of the Banyuls laboratory) for permission to conduct research at Laboratoire Arago, of Dr. E. Lagarde for advice on the use of antibiotics in the culture effort, of Dr. C. G. Adams for valuable discussions of the taxonomic status of the nubeculariids, and of Dr. Ronald Hedley for permission to use the magnificent collections of the British Museum of Natural History is most gratefully acknowledged.

OBSERVATIONS

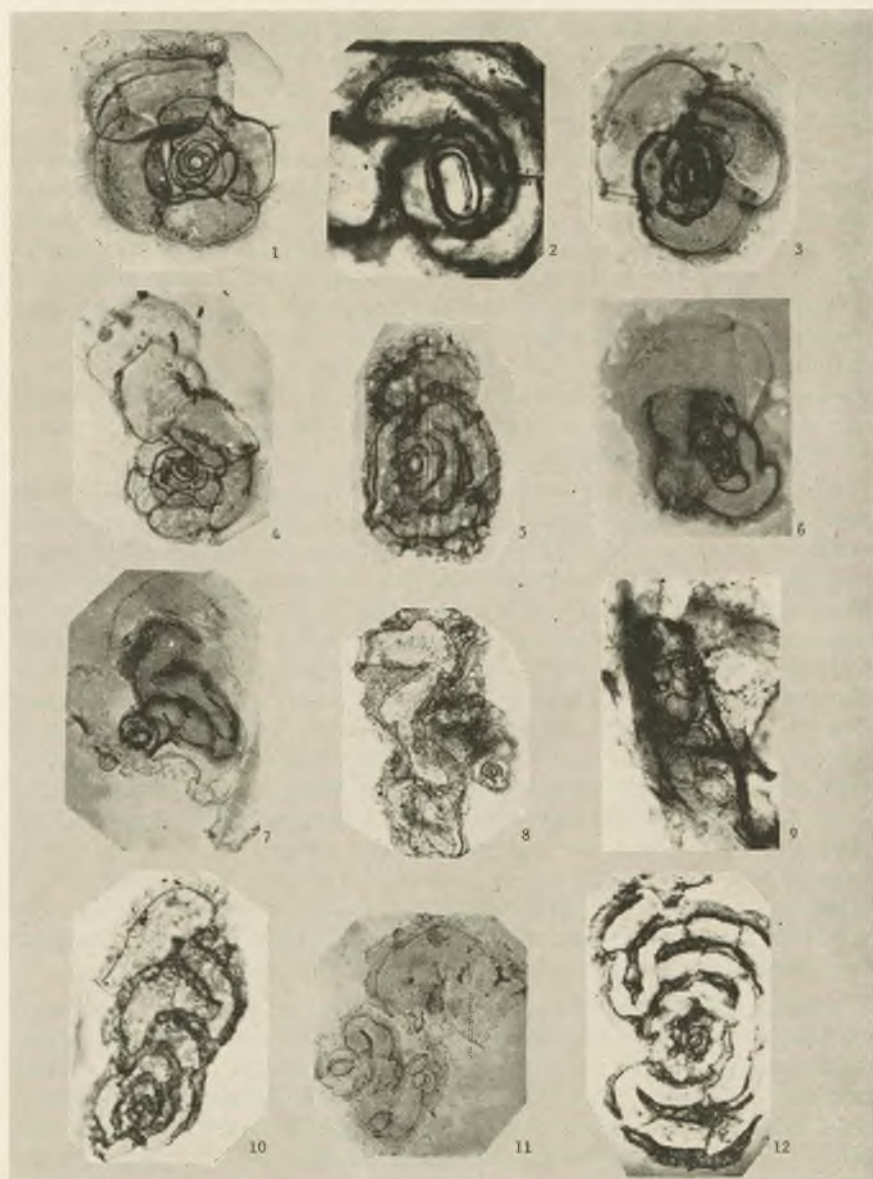
During the relatively short period of culture observations, numerous cases of asexual (multiple fission) and a few of sexual reproduction were

observed. In some of the latter, flagellated gametes were cast directly into the water, while in others they were enclosed in sturdy membranous sacs in which they remained active for many hours or even a few days, a mechanism that might well facilitate dispersal through wave and current action or even by rafting on extirpated blades of grass. Fertilization was not observed in the laboratory, inasmuch as no two parents produced gametes simultaneously during the course of this study.

The alternation of generations which occurs in the life cycle is associated with test dimorphism, but is by no means obligatory, since, in cultures asexually-produced adults (megalospheric) often themselves reproduced new megalospheric forms (Fig. 9) by asexual means, rather than microspheric forms by sexual means as one would expect if alternation were obligatory and the correlation between prolocular size and reproduction mode strict. Judging from the growth rate in cultures, it seems likely that whereas the asexual phase alone may be completed in only a few to several weeks, the entire cycle, involving two or more asexual phases and a sexual one as well, might require a full year, if one makes allowance for slower growth during the colder winter months.

The protoplasmic body of an asexually-reproducing individual divides completely into small masses that secrete embryonic tests, these almost certainly deriving their calcareous material from the wall of the parental test, often so intensely excavated that the outermost chambers are mere diaphanous remnants. Moreover, the entire floor of the parental test is dissolved at this time, with the result that the test may easily be dislodged from the substratum to which it was attached. In cultures, one often finds that the parental test has been torn loose and even displaced some distance from the incubation area by the ebullient egress of the new generation of young. It is frequently so dissolved and fragmented that it is difficult or even impossible to determine whether it was microspheric or megalospheric, so such a determination should always be attempted *before* reproduction. Since dissolution does not take place during sexual reproduction, one is tempted to predict that the test of sexually-reproducing forms will be found relatively intact in the death assemblage or as a fossil and that heavily excavated tests, of the type so frequently encountered in both Recent and fossil assemblages, represent individuals that reproduced asexually.

Like all miliolideans, the young of this species start life as a small mass of protoplasm filling a test that consists of a central sphere or oval around which is tightly wrapped a tubular extension. In cultures, it is easy to notice that the young animal having only a few additional chambers is as active as those belonging to miliolidean species that remain vagile throughout life, but that as the animal settles down and attaches to the substratum the disposition of the chambers which form subsequently is related to the position the prolocular apparatus itself assumes at this critical time. Thus, if the prolocular apparatus becomes attached with the axis of coiling of its



FIGURES 1-12. Variation in *Nubecularia Lucifuga*.

1. Microspheric test with axis of coiling unchanged throughout development of the individual. Ventral view, showing floor of chambers and highly irregular marginal extensions of test. Maximum diameter: 348 μ ; prolocular diameter: 33 μ .
2. Prolocular apparatus and early chamber of megalospheric test. Maximum length of oval proloculus: 154 μ .
3. Microspheric test having form characteristic of and indistinguishable from that of Jurassic and Cretaceous tests assigned by some workers to *N. trilocolina*. Maximum test diameter: 298 μ .
4. Microspheric tests similar to that illustrated in Figure 1, but uncoiling in later stage of growth. Diameter of closely coiled stage: 330 μ ; maximum overall length of test: 664 μ .
5. Heavily agglutinated test having meandroloculine form. Ventral view showing impressions left on test floor by *Posidonia oceanica* cells following separation of test from grass blade by use of NaOH; test rendered transparent by treatment with HF. Axis of coiling of prolocular tube lies at 90° to that of subsequent chambers, in contrast to the pattern seen in Figures 1, 2, & 4. Maximum test length: 460 μ ; maximum prolocular length: 55 μ .
6. Microspheric test of type encountered in same asexually-produced brood as ones containing tests of the type illustrated in Figures 1 & 2. The axis of coiling of the prolocular apparatus remained unchanged as the juvenile chambers were added, but rotation occurred as later ones developed, producing the typical milioline appearance. Maximum test length: 352 μ .
- 7, 8, 11, 12. Meandroloculine growth in microspheric (Fig. 8) and megalospheric (Figs. 7, 11, 12) tests. The test in Figure 8 is heavily agglutinated, unlike the other three. Maximum length: Figure 7, 1232 μ ; Figure 8, 1265 μ ; Figure 12, 1875 μ .
9. Fragment of adult megalospheric test containing seven megalospheric prolocular apparatuses from young that had not escaped from parental test when sample was collected. Maximum prolocular length: 110 μ . Compare with Figure 11, a megalospheric test containing the prolocular apparatuses of three asexually-produced young that had not escaped from parental test. The parental proloculus lies in the upper left part of the test.
10. Heavily agglutinated microspheric test showing "textulariform" chamber arrangement strikingly suggestive of that described for *Calcitornella textulariiformis*. Maximum test length: 1265 μ .

tubular element perpendicular to the substratum, the coiling axis of the entire test will be so (Fig. 1), because once attachment has occurred the coiling axis of subsequent chambers is essentially restricted to the perpendicular. If, by contrast, however, the prolocular apparatus remains upright rather than falling on its side (i.e., if the mouth of the young remains flat against the substratum during attachment), its axis of coiling will be

horizontal and thus significantly out of phase with that of subsequent chambers (Fig. 6). These conclusions are based on the assumption that attachment occurs at the prolocular stage, but oftentimes in cultures an animal remains vagile while a few chambers are formed and then attaches to the substratum, in which case other factors—still unknown—undoubtedly play an important role in determining the pattern of chamber arrangement.

With continued growth, the effect of the size, form and texture of the substratum upon this chameleonic species becomes more pronounced. If the developing animal happens to lie on a flat surface larger than the area it requires for full growth, the test it produces tends to lie in a single plane and, at least in its early stages, to be essentially planispirally coiled. By contrast, if it grows on a surface narrower than its normal test or than individual chambers of the test, the entire test or the affected chambers will conform closely to the more restricted area and mirror faithfully the shape of the attachment surface. Thus, those animals that grow on the broad, flat, viable blades of grass are themselves flat and essentially planispiral in their coiling (with the exception of the prolocular apparatus, as mentioned previously), whereas those that attach to and grow upon threads of the finely shredded dead blades that flank the base of the living plant tend to ensheath the thread if the thread or mass of threads is smaller in diameter than the width of a normal test; in the latter case, the resulting test, frequently a jumbled mass of chambers, tends to be elongated, often grotesquely so. Such conformity between organism and substratum was obvious to Carpenter *et al.* (1862) from their study of collections of empty tests of this species, but in the laboratory the extreme sensitivity of the developing test to external forces becomes more strikingly obvious and readily demonstrable. If, for example, one dislodges a young animal from its attachment after it has formed a few chambers and then permits it to re-attach and proceed with development, it is easy to observe that the shape of the young test itself, the size and shape of the clumps of food material which the animal has accumulated or with which it otherwise comes into contact as it begins attachment, and the proximity to other actively feeding foraminifera all exert some influence upon the growing test's ultimate form. Conversely, it is also easy to observe that much variation in growth patterns and test form occur, even among siblings, in the absence of obvious differences in the substratum. In other words, internal factors, probably genic ones, play their expected role in much of the variability one encounters in this protean species.

An intriguing correlation exists within the distributional pattern of microspheric and megalospheric adults of this species. The predominant form on the broad, viable blades of grass—particularly on the distal ends—is the megalospheric. Microspheric forms appear farther down the blade towards its base, and on the shredded threads that flank the base both types are easily found. This pattern suggests that the reproductive

cycle has distinct seasonal aspects and that these are possibly correlated, in turn, with the seasonal aspects of growth and death in *Posidonia oceanica*, the foraminifer's substratum in this particular niche in the bay at Banyuls.

Another impressively variable feature having environmental correlates—this one possibly also with seasonal overtones—is that of agglutination. The shells of some individuals are devoid of sand grains, while those of others are richly endowed with them. Among the flat members of the Banyuls population, the most heavily agglutinated forms are found on the shortest blades of grass or toward the base of the blade; frequently the amount of agglutination can be observed to decrease as one moves out toward the free end of the blade, particularly in the case of the longer blades. Moreover, whereas the flattened forms from the broad, viable blades may at times be moderately heavily agglutinated, the ensheathing forms are characteristically riddled with them. This is not surprising in view of the fact that the decaying threads are seldom more than a few inches in length, that the bottom is sandy, and that frequent storms keep the water turbid—heavily laden with sand—for protracted periods. The shells of individuals born and raised to reproductive maturity in laboratory cultures devoid of sand grains are, of course, themselves devoid of sand grains, without obvious deleterious effect to the living animal, although from a mechanical viewpoint, and of importance in geological interpretation, the postmortem disadvantage to them as potential fossils might well be analogized with the relative weakness of concrete from which the aggregate of sand and gravel has been eliminated.

An examination of collections of this species from various parts of the world has revealed both agglutinated and nonagglutinated shells, the one sometimes to the exclusion of the other, but frequently both types together, corroboratory evidence that the ability to agglutinate is probably inherent in the species throughout its known geographical (and geological) range, but that the potential is realized only when, and to the extent that, the environment provides the necessary raw materials. At Banyuls, the violent protracted winds that sweep the coast from December to April—the ignominious mistral and tramontane—keep such shallow bays in almost continual turmoil, the turbid water a rich source of the fine sand essential to agglutination; hence, most of the forms one encounters there are agglutinated. The next inference to be drawn is that the degree of agglutination can be a clue to the nature of the environment (including turbulence-inducing storms) in which this species lived.

Passing from biological to geological considerations derived from the comparative study of laboratory and natural populations, it is obvious that several factors may contribute to the differential elimination as potential fossils of certain elements of a *N. lucifuga* population. Mention has already been made of the dissolution that weakens the test of asexually-reproducing

adults: those megalospheric parents that have a sexual reproductive destiny are favored over those with an asexual one. The natural wrinkling and contraction that befalls any blade of *Posidonia* which happens to be washed ashore and allowed to dry out destroys or badly fragments any attached *Nubecularia*; the larger the foraminifer, the greater the hazard. Those blades that remain in the sea eventually decay, during which process the natural bond between foraminifer and blade is broken, the fragile test left to the abrasive mercy of the grinding, shifting sands of the sea floor or beach. Few tests, particularly the larger, flat ones, survive unless the water is spectacularly calm, the sediment too fine for effective abrasion. In a rigorous environment the ensheathing types, being structurally sturdier, stand the better chance of preservation. In such a case, however, the premium is less on size than it was in the preceding ones. In an active environment, containing sand-size sediments, an advantage accrues to agglutinated tests, tests that can withstand the abrasion that would destroy nonagglutinated ones, but in quieter environments, where silt and clay predominate, agglutination would seem to be of no consequence, because nonagglutinated forms are found in good numbers both in Recent and in fossil deposits.

The study of living and culture populations, including sibs, has stimulated the re-evaluation of the broad variation potential for which this species was notorious in 19th century biological circles. The complete spectrum from ensheathing to planispiral types can be found living on *Posidonia oceanica* at Banyuls, and in the laboratory one can easily obtain individuals (Fig. 3) which are indistinguishable from specimens of *Nubecularia triloculina*, the Jurassic "species" from the Netherlands and Great Britain. Several of the Lias samples from England sent by Professor Barnard contain a rich assortment of types that resemble specimens from culture so strikingly that I should certainly be unable to distinguish fossil from Recent were they to be maliciously mixed and presented for sorting. In the light of this study of variability in natural and culture populations, careful examination of original descriptions of the thirty-odd species of living and fossil *Nubecularia* (and a not insignificant number of species assigned to other genera as well!) suggests quite strongly that almost half of them should more properly be assigned to *N. lucifuga*.

The types of variation one encounters in living populations parallel in many respects those encountered in the miliolid *Spiroloculina hyalina* (Arnold, 1964). The degree of rotation of prolocular apparatus and early chambers in relation to older ones varies as greatly as in the miliolid and can be observed to do so in members of the same asexually-produced generation, just as in the miliolid. A comparison of specimens from the Mediterranean, the English Channel, Florida Bay (Florida), and Monterey Bay (California) indicates that while the mean values for such characters as ontogenetic rotation in the axis of coiling, number of chambers per

whorl, chamber inflation, or ratio of microspheric to megalospheric individuals may differ noticeably—as they did for Florida and California populations of the miliolid—the ranges overlap to such a confusing degree that any more drastic classificatory designation than that of geographical subspecies or variety would be not only biologically unwarranted but seriously misleading.

The problem of determining present and past distributional patterns for this species is vastly complicated by the taxonomic chaos its protean form has sired. A laboratory study of controlled lineages has delineated some of the variations that are more obviously responsive to environmental than hereditary factors, but much additional study will be required before the more complex interactions of the two can be sufficiently well exposed to permit the comprehensive taxonomic revision from which alone a sound biogeographical, biostratigraphical or paleoecological interpretation of the species can be launched.

This study has shown this species, a paleontological patriarch, to be a promising neophyte in the experimental biological laboratory where fundamental studies on variation ranges must be conducted before a sensible taxonomic basis can be developed for zoogeographical studies and the solution of paleoecological and biostratigraphical problems.

REFERENCES

- ADAMS, C. G.
1962. Calcareous adherent Foraminifera from the British Jurassic and Cretaceous and the French Eocene. *Palaeontology*, 5 (2): 149-170.
- ARNOLD, Z. M.
1964. Biological observations on the Foraminifera *Spiroloculina hyalina* Schulze. Univ. of Calif. Publ. Zool., 72: 1-80.
1966. A laboratory system for maintaining small-volume cultures of Foraminifera and other organisms. *Micropaleontology*, 12 (1): 109-118.
- BARNARD, T.
1950. Foraminifera from the Upper Lias of Byfield, Northamptonshire. *Quart. Journ. geol. Soc. London*, 105: 1-36.
- BOLTOVSKOY, E.
1965. Twilight of Foraminiferology. *J. Paleo.*, 39 (3): 383-390.
- CARPENTER, W. B., W. K. PARKER, AND T. R. JONES
1862. Introduction to the Study of the Foraminifera. Roy. Soc., London, 319 pp.
- DAM, A. TEN
1950. Les Foraminifères de l'Albien des Pays-Bas. *Mem. Soc. geol. France*, 29: 1-66.
- DEFRANCE, M. J. L.
1825. Mineralogie et Geologie. In *Dictionnaire des Sciences Naturelles*. Paris, p. 534.
- JONES, T. R. AND W. K. PARKER
1860. On some fossil Foraminifera from Chellaston near Derby. *Quart. Journ. geol. Soc. London*, 16: 452-456.
- MCLEAN, J. D., JR.
1965. Why certify a dying profession? *Bull. Amer. Assoc. petrol. geol.*, 49 (10): 1704-1707.

Ecology of Tropical Organisms

GUNNAR THORSON
Convener

The following papers were delivered at the Conference but have not been received for publication:

THOMAS F. GOREAU, N. I. GOREAU, AND C. M. YONGE: Evidence for a Soluble Algal Factor Produced by the Zooxanthellae of *Tridacna elongata* (Bivalvia, Tridacnidae).

RUDOLF S. SCHELTEMA: Transport of Pelagic Long-Distance Larvae from Tropical Seas by Means of Ocean Currents.

JAN KOHLMAYER: Ecology of Marine Fungi in Mangrove Habitats.

W. D. NESTEROFF: Development of Madreporarian Corals from the Red Sea, Atlantic and Pacific Ocean.

JOHN H. DAY: A Comparison of Tropical and South African Estuaries and the Distribution of the Polychaete Fauna.

IVAN GOODBODY: Survivorship in a Tropical Ascidian.

JOHN B. LEWIS: A Preliminary Account of Some Tropical Marine Benthic Communities from Barbados.

ECOLOGICAL AND ETHOLOGICAL STUDIES AND EXPERIMENTS ON THE ECHINODERMS OF THE RED SEA

DIETRICH B. E. MAGNUS

Department of Zoology. Technical University of Darmstadt, Germany

ABSTRACT

Field observations, experiments, and measurements were conducted in order to investigate the relations between ecological factors and behavior patterns on the ophiuroid *Ophiocoma scolopendrina*, on the crinoid *Heterometra savignyi*, and on some "partners" of the echinoid *Diadema setosa*. *O. scolopendrina* lives in crevices in the tidal zone. In quiet waters it collects food from the substratum, in running waters it filters, and while the tide is coming in, it brushes (only during the day as a special form of collecting from the substratum) the dry particles from the water surface. It must be suggested, that other ophiuroids also are suspension feeders obtaining their food exclusively by filtration of the particles driving parallel to the bottom surface with the currents and not by collecting sinking particles as often assumed. Sedimenting material will only be collected after its sedimentation.

Heterometra savignyi lives in shallow water areas having weak currents and feeds by filtration of fine suspended material. It arranges its 20 arms in a shallow filtration-fan. There is not, as supposed till now, a sedimenting "rainfall of food" into an upward directed collecting funnel formed by the oral sides of the arms, but in exact contrary the aboral arm surfaces are held toward the current. For crinoids there is the same fact as for the ophiuroids, that downward sinking organic material would never suffice for the feeding of these animals. Each *H. savignyi* filtrates 40,000 liters of water as a minimum quantum at a current speed of 2 cm/sec per night!

Ten species of fishes, two decapods, and one *Sepia* have been observed in "partnership" with *Diadema*. Symbiotic associations are never found. *Diadema* is seen by its partners only as an element of the bottom-structure which offers optical resp. mechanical protection to them. By field experiments with dummies in the coral-reefs an exact analysis of the relations was possible and it was found that "super-normal" dummies can be more attractive than living *Diademas*.

INTRODUCTION

These researches were carried out during four visits (1959, '61, '62, '64) in different seasons (spring, summer, autumn) for 3 to 4 months at different areas in the Red Sea, especially in the environs of Al Ghardaqa and Kosseir (Egypt) as well as Dongonab Bay, Mohammed Gul, Port Sudan, and Suakin (Sudan). Ecologically these areas differ in their climate but also mainly in their tidal phenomena. On the Egyptian coasts there are regular daily double-tides with a sea-level difference of up to 90 cm, whereas on the Sudan coast (middle of the Red Sea) we can only find irregular high- and low-waters with small level differences, caused by

wind-pressure and therefore often lasting for several days. These differences are especially important for the inhabitants of the tidal zone.

Researches, except in the tidal zone, have mostly been made by snorkeling and diving. Great value has been set on the fact that the measurements, experiments, and observations lasted for a continuous period of at least 24 hours without any interruption. Thus the night time was included for the animals active during the day and the daytime for those active in the night. The results were obtained by direct and long-term observation under different conditions at the study sites and in different seasons and at different day-times, but always of the same species. The results show obviously the locally and temporally caused special states and occasional happenings. Therefore, they are indispensable for the understanding of ethological-ecological relations. In addition, as long as it could be technically accomplished, controlled experiments were made in aquaria with captured animals.

For documentation, an underwater still camera with flash and a 16-mm movie camera in an underwater housing were used. During the night, light was furnished by underwater hand-lamps powered by batteries.

The special objectives of the research were the following: (1) Ecology and ethology of the brittlestar *Ophiocoma scolopendrina* living in the tidal zone, and the featherstar *Heterometra savignyi* living in shallow water. From the results of the study of those easily observable animals, it was hoped to draw general conclusions about the behavior patterns (especially the feeding) of the other species of this class of echinoderms. Until now extraordinarily little was known about these animals, because most of them live in greater depths and cannot, except with difficulty, be studied in their biotope by direct observations. (2) Experimental and observational researches about the problem how many animals, especially fishes, live in partnerships with the sea urchin of the genus *Diadema*.

I. *Ophiocoma scolopendrina* (Lamarck)

Habitats and Periods of Activity.—This brittlestar is very common and numerous in some places in the tidal zone of the Red Sea. There are often 50 specimens to be found in 1 m². The habitats are between a little under the mid-water and the mid-low-water lines of rocky areas of the coast, protected from the surf. The animals live on creviced grounds, no matter if there is a thin sediment-layer. Mostly the habitats are always covered by water, small or greater tide pools on abrasion terraces or on reef flats. But also the higher places, occasionally or regularly dry at low-tide, are occupied by the same number of individuals as the other places. Special ecological conditions such as the changes of tides, the level of water and the local structure of the ground of the habitat induce the periods of activity of *O. scolopendrina*.

The method, the time, and the duration of feeding depends on the available food and the moving condition of the water at the stand. This is why there are great local differences. Also the number of the engaged arms is different. Brittlestars are very sensitive to the movements of the waves. Because of this sensitivity, *O. scolopendrina* cannot be outside of its hole when there is high tide. Usually even in the habitats protected against heavy breakers there is a chopping going down to the bottom also at the spring high tide.

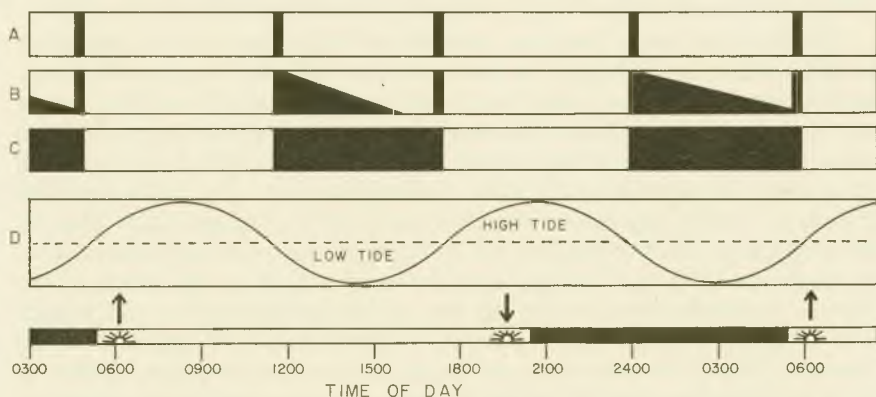


FIGURE 1. Periods of activity (shown as dark zones) of an *Ophiocoma scolopendrina* population in relation to the changing ecological conditions at different levels of the tidal zone.—A, highest habitats, without water at low tide;—B, medium habitats, drying out at low tide;—C, lowest habitats, water covered at low tide;—D, tides. 18, 19 July 1964, Ghardaqa.

Most of the time during high tide the animals are inactive and retreat as far as possible into their hiding places. The entrance of the hole is mostly filled with sand at this time. Activity is possible at high tide only when there is no wind and there are no waves. For all the brittlestars living at a stand without water at low tide, feeding is only possible in the brief periods at the beginning or the end of high tide when the level of the water is just so low that there are no heavy waves (Fig. 1).

The high tide interrupts every activity of the whole *O. scolopendrina* population. While these animals, whose stands are almost dry at low tide, have only the short periods of the beginning and the end of high tide for the feeding, all the others, whose habitats are covered during low tide, can also feed during low tide in the smooth water of pools.

For the special analysis of the ecology and the ethology of *O. scolopendrina*, I chose a tide-terrace, 80 m in length and up to 25 m broad, near Al Ghardaqa. It was a very different structured abrasion terrace having almost all of the typical conditions of *O. scolopendrina* habitats on a very

small place, which usually are to be found only on much more extensive areas. Each individual of this species of brittlestar occupies its own home, that is a rock-crevice, a cavity in the bottom, or even a breach between the roots of seagrass. The inhabitant will not change this stand for weeks. The hole is defended violently against occupancy, by other brittlestars and other small animals of this biotope, *i.e.*, hermit-crabs, by characteristic movements, pushing and turning aside with the aboral sides of the arms. Feeding is near the hole. At night, the distance is about double the length of the arm and at least the end of one arm will be inside of the hole. At daytime indeed there is usually one arm and the body-disk inside of the hole.

This strict territorial behavior, unusual for echinoderms, is an important predisposition for settlement in these extreme habitats, for it protects the animals from drying out when their stands get dry at ebb tide. They retreat into rock-crevices and other breaches of the ground where there is enough water for them to endure the ebb tide. On the other hand they are protected there from the movements of water during flood tide. The holes get filled with sand during high water and afterwards will be cleaned each time by the brittlestars. Each sediment particle is picked up by the ambulacral feet, is passed on from foot to foot, and so transported from the inside of the crevice outwards; then it is dropped at the tip of the arm or just before. The transport occurs rather constant, at the rate of 6.9 cm/min on an average. This is the same rate at which, in the other direction, pieces of food are transported to the mouth. In most cases only one or two arms are engaged in this occupation. From time to time the extended transporting

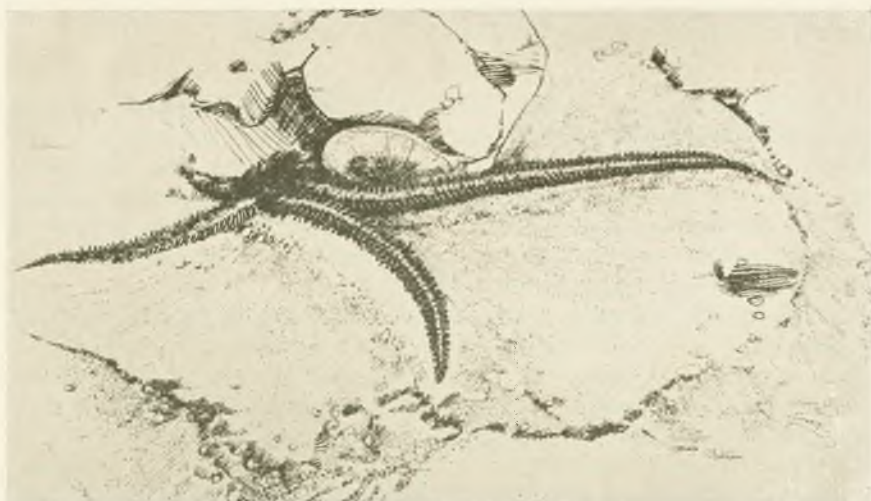


FIGURE 2. *Ophiocoma scolopendrina* forms a semicircle-like slope by cleaning the crevice and dropping sand before the entrance. Drawing from a photograph.

arms move a bit sideways and thus wave to and fro in a semicircle before the hole. In the course of an ebb-tide period, semicircular mounds of sediment arise before the entrances to the holes (Fig. 2). After the rest, caused by a flood, the animals transport their excrement outwards in the same way.

Feeding.—*O. scolopendrina* feeds on any living or dead animal and vegetable organisms, particularly particles, but normally vegetable food predominates in the natural biotope. On taste stimuli distributed in the smooth water of tide pools or carried along with the current (in the experiment, snail or seaweed extracts were used) the brittlestars react with winding movements of the arms, the tips of which are slightly erected. The conditions of water movements control as mechanical stimuli the specific type of feeding. Later on a taste-examination by the ambulacral feed decides if the collected material will be transported into the stomach or if it will be dropped again.

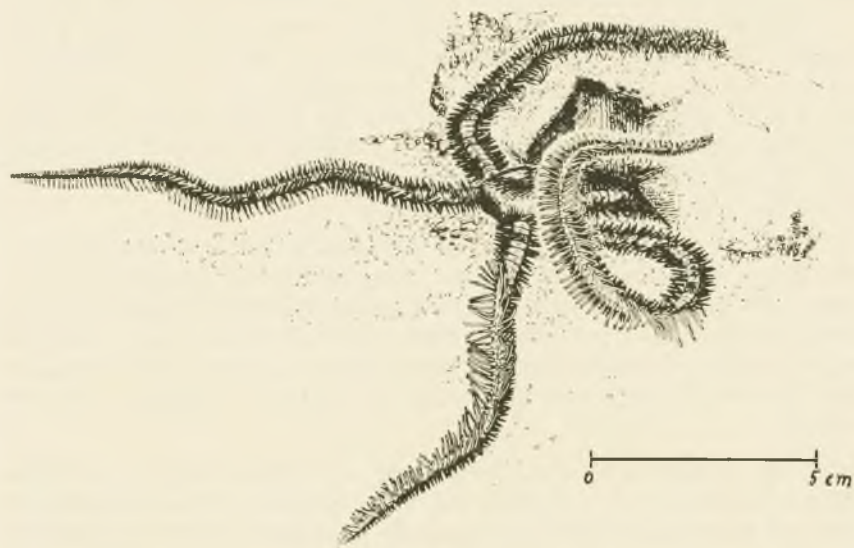


FIGURE 3. *Ophiocoma scolopendrina* feeding. Arm-positions in water current. One arm staying into the crevice, one arm gathering from the bottom surface, three arms filtering. The current comes from left. Drawing combined from photographs.

Gathering or Plucking off From the Bottom Surface.—In smooth water without current, during ebb tide in the tide pools, the winding arms touch the ground in the neighborhood of the hole until they make contact with food particles (Fig. 3). The feet pick up the particles, cover them with

glandular secretions, and transport them in the oralside of the arms by passing over from foot to foot with a rate of 6.9 cm/min on an average. Accidentally collected unedible particles are separated and dropped during the transport towards the mouth. Stationary fixed food, *i.e.*, seaweed, is held by the feet by means of their glandular secretions and torn off by a quick rearing back of the whole arm.

Filtering.—In currents the arms are held up from the bottom for their entire length or just with their ends and directed against the current. Thereby the feet will be stiffly outstretched and work like lime-twigs [ed. note: reference is to bird lime spread on tree twigs to trap birds]. The two rows of feet of each arm form in this position two rough filter combs standing opposite at an angle of about 90°. The movements of these filtering arms are never coordinated. Each arm acts independently (Fig. 3). A more or less constant and not too strong laminar current causes a more or less obvious crossing to the current of the oral arm side. Turbulences of the current caused a "screwed" holding of the arms. But the feet are always stiffly stretched. Particles carried to the filter combs by the current are held by glandular secretions and, after being examined, are either dropped or passed to the mouth. It depends on the local conditions of current and structure of the bottom, how many arms of an animal are filtering. Usually there are not more than two. In the night when there is a slight current, *O. scolopendrina* often climbs on seaweed or seagrass near by, and filters. However, they never go so far but that at least the tip of one arm will stay inside of the hole.

The filter apparatus consisting of ambulacral feet is very rough; the filtration is only efficient if it lasts a long time or if there is plenty of suspended food. The animals capture greater quantities of food if they hold their arms flat above the bottom surface. Thus they are able to filter the larger particles of detritus, floating just above the ground. Larger particles like bunches of *Sargassum* are caught in this way and taken into the stomach.

Sweeping Together the Dust Film From the Water Surface.—Another form of feeding of *O. scolopendrina*, until now not correctly understood although very remarkable, is especially connected with the ecological conditions in this extreme habitat (Clark, 1921; Murakami, 1938). This is the collecting of the dust film obviously containing plenty of nutritive material (diatoms and other algae). This film is lifted from the tidal zone by the swelling water after an ebb tide, while it has been dried by the sun, and is carried along with the flood. This feeding behavior is only to be seen during the daytime and first of all in animals whose stand has fallen dry at ebb tide. In the night, such a dust film cannot be formed.

The brittlestars, quickly creeping out of their crevices at the moment of overflowing, touch the dust film at the surface of the still very flat water

with the tips of their arms. Released by this stimulus the arms turn around, so that their light unpigmented oral side is directed towards the water surface they are breaking through. They perform quick, winding, perpendicular movements, and two neighboring arms operate in the contrary direction. The tips of two arms swinging towards each other always make the first contact. That is why the dust film, encircled between the arms, cannot escape (Fig. 4). The film is pressed together and towards the sides



FIGURE 4. *Ophiocoma scolopendrina* feeding. Typical arm-movements sweeping together the dust film from the water surface. Time difference between the pictured phases, $1/4$ sec. After $2 1/4$ sec. the arms are in the same position again. Drawings from a movie-film taken at 16 frames/sec.

of the arms by the following winding movements of the approaching arms. The ambulacral-feet, which meanwhile, uninterruptedly, are rhythmically swinging on the oral arm side, lift it from the water surface up to the arms, cover it with glandular secretions, press it together into a solid food-roll, and slide it on to the mouth (Fig. 5).

This form of food collecting, in contrast with the other two, gathering or plucking off and filtering, is very fast and well coordinated. A single act of capture, i.e., one sequence of swinging together and separating of two arms lasts only 2.25 sec on an average (Fig. 4). The contact of the arm tips is the releaser for the coordination and synchronization of the arm movements. As a rule, the animals use three arms for this act. The middle one synchronizes the movements of the two outer ones, as it imparts its own winding and perpendicular rhythm to them at each contact with the tips of their arms. The velocity of this act seems to be useful because the dust film of the flood border is washed off after a short while.

Normally in the biotope there is no selection of useful and useless particles during the collection of the dust film from the surface of the calm water; the complete dust film is taken by the arms and transported to the stomach. Probably the positive taste-stimuli always predominate in the natural dust film. Experimentally the proportion of stimuli in an artificial

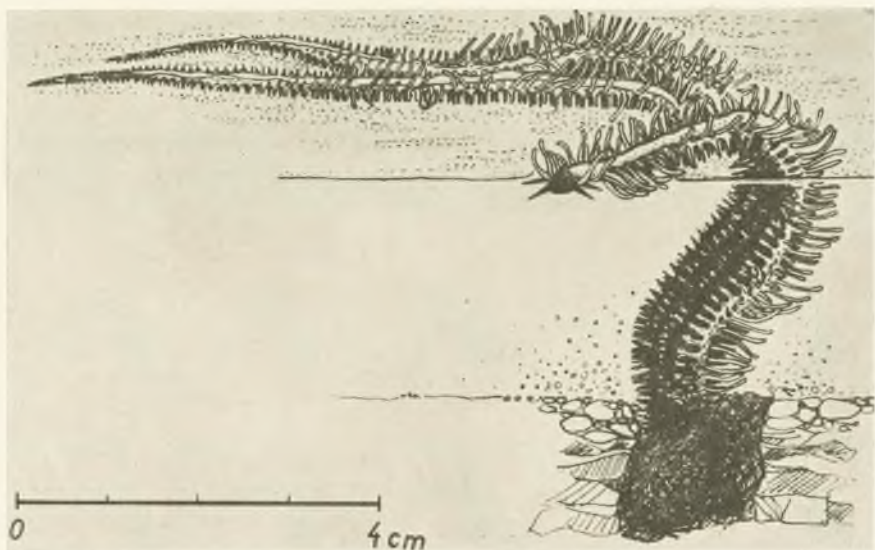


FIGURE 5. *Ophiocoma scolopendrina* sweeping together the dust film from the water surface. Drawing half-schematic from photographs.

dust film can be changed as desired, by mixing powdered sawdust with an addition of attractive powdered food, for example fish. In this way a proportion can be achieved in which the animals begin to collect the film and to take it up on their arms but drop it before it reaches the mouth.

In the biotope the sweeping reaction can be caused at any time (even in the night); this happens not only in rising water, but also in the calm water of small tide pools, by an artificial dust film consisting of pure powdered fish. The results of these researches show that this form of food collecting at the water surface is probably the same form of movement and behavior as in collecting from the bottom surface although at first glance it seems to be different from the others. With a smooth water surface and in a completely positive field of food stimuli, the form of collecting is unrestrained and, therefore, the movements are extremely fast.

It is this extraordinary form of feeding which catches a lot of food in a very short time, together with the characteristic territorial behavior and a great toleration to light, sun radiation, and differences of temperature, that enables *O. scolopendrina* to occupy ecological extremes in the tide zone even without water at ebb tide. It is interesting that this species, adapted to the changing tides, is not to be found at those localities where there is no daily change of tides such as along the complete coastline of the Sudan.

Discussion.—Feeding by filtration of the water current is only one of the two or three possible ways by which *O. scolopendrina* gets its food. As

with grazing at the water surface, it can usually only be done for a relatively short time. It should be more important only for those individuals which live in habitats that dry out, whilst most of the species will collect their food from the surface of the bottom. On the other hand, filtration seems to be much more important for some other species of brittlestars especially those in which it is the only type of feeding. Pictures taken by automatic cameras of very crowded populations of *Ophiothrix fragilis* (Abildgaard) in the English channel 55 m deep (Vevers, 1952) or of *Ophiothrix 5-maculata* (Della Chiaje) in the Northern Adria 32 m deep (Czihak, 1959) show that many of these animals turn the dorsal side to the bottom. The animals lying on their backside, as well as all the others, lift one or more arms from the bottom and hold them stretched out. No doubt in this position they filter out the suspended material in the current. In some of the pictures published by Vevers (1952) the arms of *O. fragilis* are arranged in several layers and held in a definite position in relation to the direction of the current. One can conclude the presence of a constant strong current which supports many organic particles just above the bottom because this mass of brittlestars can filter enough food even though the filter apparatus is rather incomplete. Unfortunately almost nothing is known about the special "climate of current" in these habitats.

Roushdy & Hansen (1960) showed that in the aquarium the two species of brittlestars *Ophiothrix fragilis* and *Ophiopholis aculeata* (L.) filtered phytoplankton and ate it, whereas *Ophiocomina nigra* (Abildgaard) did not do so under the same conditions. The cause of this different behavior is as yet unknown. It could depend on the inability of the food glands of *O. nigra* to hold suspended particles from the current, as well as on the fact that this species is not a phytoplankton eater.

New experimental researches on feeding behavior by Buchanan (1964) in *Amphiura filiformis* (O. F. Müller) and *Amphiura chiajei* Forbes showed obviously that the first one is a rheotactic filterer, while the second one is not but without exception collects sedimented particles from the bottom. There are obvious differences in the behavior and morphology between the species.

The gorgonocephalids, for example *Astrophyton muricatum* (Lamarck), seem to feed only by filtration; the branched arms are extended to form a very large filter fan (Schroeder, 1964).

Nevertheless, it seems as if there are only two alternatives for catching food in the brittlestars: 1. collecting from the surface of the bottom, and/or 2. filtering suspended material from the current. The oft made statement that brittlestars can subsist on a falling rain of detritus certainly must be generally refuted. Regardless of the fact that nowhere on the sea floor is so much organic material settling and that the brittlestars could catch enough food by just holding their arms erected, these animals do not have the ability to react to the stimulus of falling material by turning their arms

around and lifting them towards the rain. Such a reaction can only be released by a current of water.

My experiments with *O. scolopendrina* in aquariums and in tide pools showed that if there is an attractive rain of food offered in water free of currents, the animals do not turn over and direct their oral armsides towards the "rainfall." They collected the food falling down in the usual way that it is done in still water, only after it has settled. It can be concluded, that other brittlestars on the sea floor in quiet water act in the same way. In the still water there is obviously no stimulus for erecting the arms, and the small velocity of the food particles striking the arms can not compensate for it.

II. *Heterometra savignyi* (J. Müller)

Biotope.—The adults of this featherstar have 20 arms with a length up to 25 cm. The species lives in the seagrass meadows and on rocky bottom in protected lagoons such as shallow waters with slight currents between shore reefs or in harbours or bays such as is found in Suakin. Sandy bottom can be occupied if there are pieces of coral rocks or such for settlement. The number of individuals in the populations is varying: in the seagrass there were up to 10 animals per m², but mostly less than that. The upper limit of the habitats near the tidal zone varies in depth in different localities and is as deep as the bottom of the zone where no ripple marks can be produced by waves. In the bay which forms the harbor of the ruins of Suakin, parts of the population of featherstars are located just below the limit of low water. In the vicinity of the Marine Biological Station of Al Ghardaqa they are to be found on seagrass meadows 1.5 m below mid tide and downwards.

Periods of Activity.—The animals are nightactive. During the day they arrange their arms in narrow spirals above the body and stay in the shade of holes or in the clefts of pier walls. On the bottom they are hidden in between the seagrass or more rarely are found completely free when there is no possibility of hiding (Fig. 6). Their period of activity does not always depend only on darkness, but it can also be during the evening and morning hours, in, for example, open and lighted places in seagrass meadows. Certainly the animals in these places are more adapted to the light.

Feeding.—Feeding obviously takes place only by filtration from the current. To catch food the animals try to climb to higher places such as the tips of seagrass leaves or rock ledges, and at first unroll only few of their arms but later unroll all of them. Each arm takes a position in which the aboral side faces the current. The pinnulae, pressed against the oral arm side when inactive, become erect and bend towards the aboral side so that all of them form a grating on each arm, opened against the current. The tentacles situated on the edge of the skin bordering the pinnula food grooves are



FIGURE 6. *Heterometra savignyi*. Inactivity position at daytime, 2.5 m deep. Drawing from an underwater photograph.

erected so far that they contact the neighbor pinnulae. In this position they form a fine network (Fig. 7a, b). With the arms extended against the current, they orient themselves in a single plane to form a filtration fan across the axis of the current (Fig. 8a, b and c). In order to do this the arms on the side of the body that is not facing the current have to turn up to 180° around their length axis (Fig. 9). If two animals are found side by side, they together form one unique fan with 40 arms, because each arm tries to get into a position with undisturbed current (Fig. 8c).

The filtration fan is usually held vertically. It can be pressed down and finally be resolved by a stemming pressure of the current. Generally, however, the animals seem to settle down at those places where there is a more or less constant and slight current. The current speed at the study sites was generally between 2 to 5 cm/sec. In this current strength the fans could remain such. They could not withstand stronger currents of even brief duration. In the areas of my studies near Al Ghardaqa the direction of the water current is dependent upon wind direction. It maintains the same direction even when the tide is running in or out and only changes with a change of wind direction. When the direction is changing, the fans are first untied and then the arms are held randomly upward or to the side, but they never form a cup or funnel. As soon as the water flows in the new direction, the arms turn against the current and form a new uniform filtration fan.



FIGURE 7a. *Heterometra savignyi*. Pinnulae in filtration position. Aboral side of a white-spotted arm.

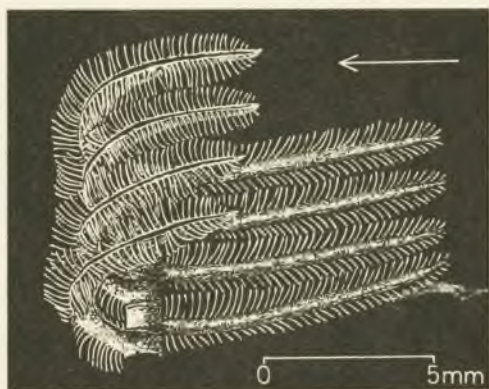


FIGURE 7b. *Heterometra savignyi*. Pinnulae with opened food grooves in typical position bent towards the aboral side forming a grooved grating. The current comes from right. Drawing from a photograph.

The water is so shallow in the areas inhabited by the featherstars that if the water is choppy the fans oscillate to and fro from the surge. Thus the filtration fans oscillate while the same water passes the fan several times.

The nutrient plankton particles in the current are caught by the tentacles by means of their glandular secretions when they strike them, and delivered to the pinnula food grooves, which are opened for this process. The food contains mainly small to minute living planktonic organisms: diatoms, foraminifera, radiolaria, and copepoda. Larger, unsuitable particles are released from the filter net by turning aside the pinnulae. An adult *H. savignyi* with 20 arms has a filtration plane of at least 500 cm² (Fig. 8). Thus, if 60 liters of water/min are passing the fan at a current speed of 2cm/sec, about 40,000 liters are filtered in one night. If the water current is oscillating the filtration is more successful because the same water will pass to and fro several times.

Discussion.—Some of the results of my researches on *H. savignyi* are contrary to the opinions held up to now concerning the feeding of crinoids. One assumes because of aquarium studies that the radial arrangement and position of the arms during periods of inactivity when they form a sort of funnel around the mouth is a typical feeding position, and that this funnel is either directed towards a slight current or erected vertical in unmoved water towards a "rainfall" of food falling downwards. In any case one assumes that the oral sides of the arms where the food grooves are situated (called catching grooves by some authors) catch the food from the water. The pictures in almost every text book and the plastic models in the museums are made to show the crinoids represented in this misleading position. The very fine suspension of organic material which forms the food

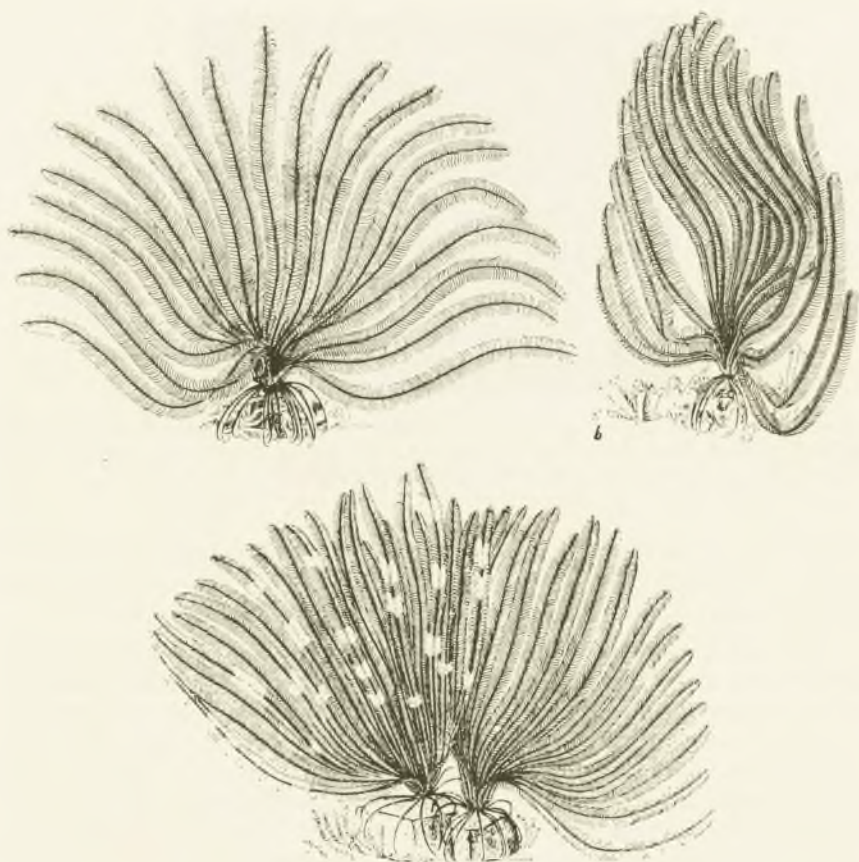


FIGURE 8. *Heterometra savignyi* at night, 2.5 m deep in slight current, about 3 cm/sec. Drawings from underwater colour photographs.—a, typical filtration fan, lee-sided oral sides of the arms;—b, the same, side-view, current from right;—c, unique fan of two animals, lee-side.

of the featherstars usually does not settle, at least as long as it is living. That is why a "sediment-rain" could never be sufficient for the animals. As a result of my studies on the shallow water species *H. savignyi*, it certainly must be concluded that the other species of crinoids also catch their food only by filtration from currents in such a position that the aboral arm-sides are presented to the current. Perhaps this form of feeding is the key to understanding the histological structure of the arm muscles of crinoids, a question which is still unsolved today. The muscles of the aboral sides of the arms look like ligaments so that even their muscle function was denied.

I have also observed in the Red Sea *Lamprometra klunzingeri* (Hartlaub), which has 40 arms and is very common in the coral reefs, filtering in the same manner as *H. savignyi*. This featherstar forms an almost complete flat filtration disk. It uses its tentacles which have extraordinary viscous glandular secretions, not only for catching food but also for climbing; it can also withstand stronger currents.

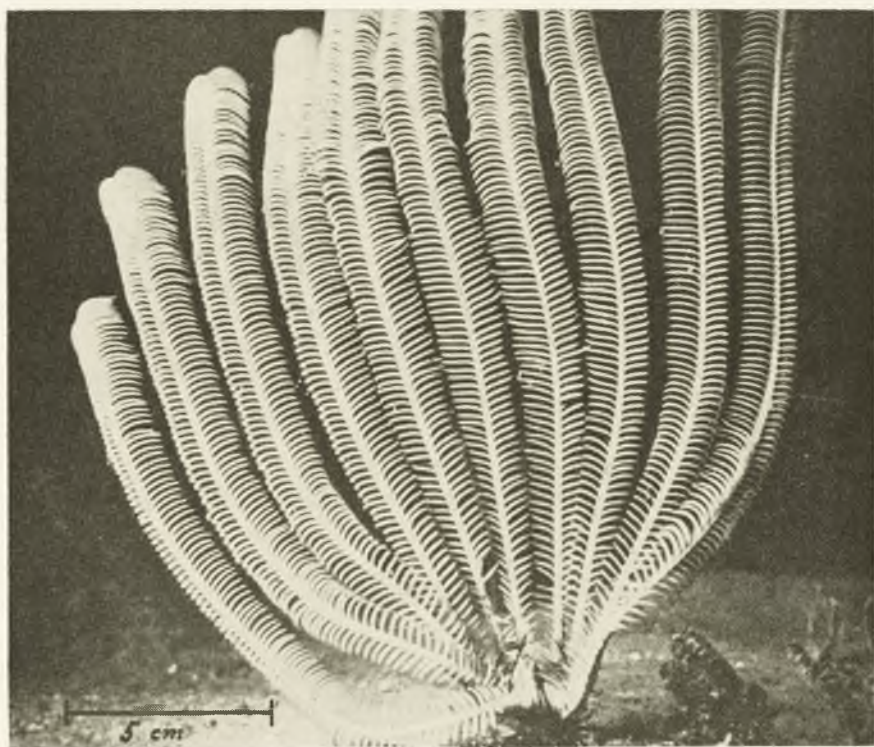


FIGURE 9. *Heterometra savignyi* juv. at night, 2 m deep, oral sides of the arms in lee. The lateral arms of the fan are turned around their length axis up to 180°. From an underwater colour photograph.

The few published pictures of other crinoids in their natural habitats which I have seen, for example a comatulid with 10 arms, 1327 m deep (Emery, 1952), or a sealily from the deep sea with 10 arms (Menzies, 1963) all show a more or less obvious filtration fan formed by the arms of the animals. Nevertheless these pictures don't show the direction of current. Thus, it must be a widespread behavior of this class of echinoderms, and certainly the formation of a flat filtration fan presenting the aboral side to

the current flow is the general feeding position. Comparative studies in the future may yield more information concerning these interesting new problems.

III. PARTNERSHIPS WITH *Diadema setosa* (Leske)

For a long time, it has been known that a number of fishes and crustaceans can live in partnership with sea urchins. The communication about a sea urchin-fish partnership made by Sarasin (1886) seems to be the oldest one. Since then new contributions on this phenomenon have been contributed from almost all oceans, specially since many zoologists are diving themselves in the habitats of these animals. Thus, it must be a widespread phenomenon. It is very astonishing that there still is a great lack of clearness about the essence of these partnerships and it seems that complete systematic study or experimental analysis has not as yet been made. It is agreed only that at least some gobiesocids living together with sea urchins behave like ectoparasites. The other types of this partnership are usually thought to be symbiotic associations or commensalisms.

Over the last few years I have studied specifically those species that live in the Red Sea in association with *Diadema setosa*, and I have tried to analyze the conditions for these phenomena by experiments and long duration observations over a 24-hour period. Until now all observations seem limited to the daytime only. Altogether I have studied 13 species: 10 fishes, two decapod crustaceans, and one cephalopod (*Sepia*).

The first task was to observe as exactly as possible the ecology and the behavior of *D. setosa* and its partners. In many places *Diadema* lives without its partners and in other places at least some of its partners live without urchins. It seems that at certain places no associations can take place, perhaps this is because the ecological demands of the partners do not coincide.

On the Ecology and Ethology of Diadema setosa.—During the day, the preferred resting places of the sea urchins which are active at night are in the shade or half-shade of niches at the bases of the coral reefs or of other rocky bottom structures in shallow water. On account of the competition for these places between individuals often a great part of the population is forced to rest relatively free. Obviously they avoid having contact with the upper parts of the living coral reefs. Also bottom formed of soft sediments without pieces of solid material, and seagrass meadows, are avoided. On coasts protected from the surf, or in the tide pools of reef flats, the highest habitats are often situated at the limit of low tide; this occurs about 50 cm below the mid tide level in the northern Red Sea. Depending upon local conditions, the main habitats extend from there to a depth of 6 m. On a surf coast no *Diadema* are to be found, although they can tolerate a slight chop and strong tidal currents. They are less sensitive to turbidity. In the harbour of Suakin their spines sometimes look lightly spotted because

algae and mudflakes are hanging on them. The animals clean themselves again and again by crossing neighboring spines, sweeping them against each other from the base to the tip. Because of this action I did not succeed in marking individuals by fixing glass beads, threads or colour markings in the spines. The spines are so extraordinarily movable that they could quickly wipe off all marks and even threads fastened tightly around the body.

During the day *Diadema* is inactive. In the evening, during the first minutes after sunset, they suddenly leave their resting places all at the same time (Fig. 10). At night they crawl around in the immediate vicinity of

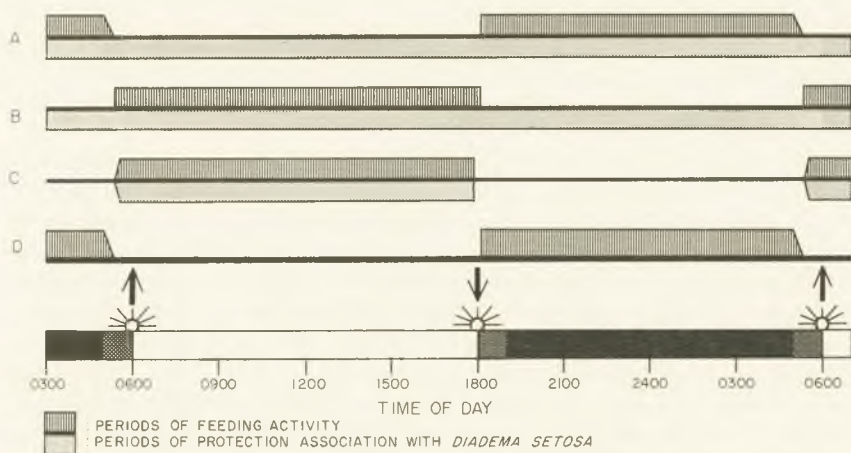


FIGURE 10. Periods of feeding activities and of protection associations of some species with *Diadema savignyi*.—A, *Saron marmoratus* and *Schizophrys aspera*.—B, *Siphamia permutata* and *Doryrhamphus excisus*;—C, *Paramia bipunctata*, *Archamia lineolata*, and *Apogon chrysotaenia*;—D, *Diadema setosa*.

their homes moving only some meters away and graze the algae from the substrate. At this time they also go to the soft bottom which they avoid during the day. But seagrass meadows are even avoided at night. They also try even at night as far as possible to avoid touching live coral polyps. They often climb up to the water surface on rocks, walls, and posts of piers.

They do not return to their resting places in the morning in such a mass movement as they depart in the evening. It starts at the break of dawn in the morning and is finished about 20 min later (Fig. 10). The discovery of the places is undoubtedly activated by optical stimuli. Dark contrasting structures on the horizon are preferred. The fastest crawling speed of the urchin on solid ground is 0.80 m/min at a water temperature of 29° C. On flat less irregular substrate, such as on wide reef plains,

very remarkable mass meetings are found because the animals perceive the "resting place stimuli" of each other and run together in the early twilight.

Associations of fish-shoals with Diadema setosa.—The apogonid fishes *Paramia bipunctata* Lachner, *Apogon chrysotaenia* Bleeker and *Archamia lineolata* (Cuvier & Valenciennes) are undoubtedly the most remarkable and abundant partners of *Diadema*. In general small to large schools of these fishes stay beside or above the urchins and take refuge between the long spines in case of danger, for example when a diver comes near by. All three species are found in association with the urchins only during the day. After sunset they leave them.

The species *Paramia bipunctata* is obviously identical with the one observed by Abel (1960 a,b) and called *Cheilodipterus novemfasciatus* Rüppell). The fishes form loose groups averaging 40 to 60 animals near small groups of *Diadema*.

The number in the groups varies and changes continually because some fishes of one group swim over to a neighboring group and vice versa. It is not the urchin that is responsible for this change but changes in the habitats. For instance the changing of shade or current. At noon, the fishes prefer the urchins which are in the shade, while before and later on they prefer other groups of urchins. The members of such a fish school are normally always directed into the current and swim against it, so that they are actually remaining in the same place (Fig. 11a). Nevertheless they change their places often in order to catch zooplankton which seem to be their only food. They never take nonmoving food from the surface of the substrate, or the spines of sea urchins.

When a larger fish or a diver comes near them, they draw together towards the spines of the urchin and finally swim in between them (Fig. 11b). The following flight behavior depends on the locality of the urchin. When the urchin is sitting relatively free, the fishes usually leave it as soon as the aggressor, for example, the hand of the observer, comes between the longest spines. They then flee to another sea urchin or above the bottom and the group disbands. But if the urchin is protected by a cleft or a hole, the fishes stay and squeeze themselves between the bases of spines, the heads directed to the body of the *Diadema*. In this position parallel to the spines, their black longitudinal stripes become of morpholytic importance, because the stripes are as broad as the spines.

Just before sunset, that means before the sea urchins become active, the schools of *P. bipunctata* quickly disband. Then the fishes swim away singly and inconspicuously in different directions from the urchins toward the open sediment areas. Their back stripes turn pale. During the whole night they remain a few centimeters above the bottom, and swim around singly or in small groups, or they stay at the same place maintaining their positions head towards the current. Twenty to 30 minutes after daybreak,

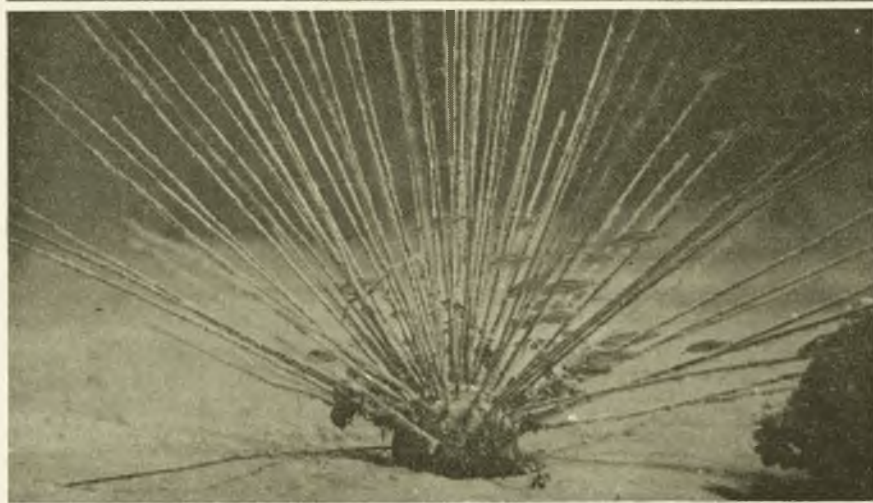
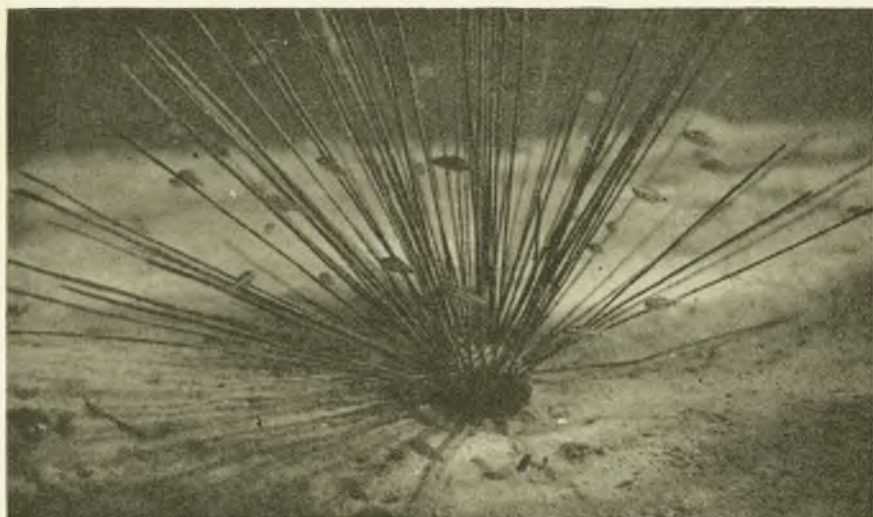


FIGURE 11. *Paramia bipunctata* shoal directed towards the current among the wire spines of a dummy (length of spines 25 cm). Underwater photographs, 2 m deep. (top) Fishes less alarmed by the photographer. (bottom) Fishes more alarmed.

not later, they assemble 1 m above the sand patches in groups, and each group searches for a place for the day near the unmoved urchins, which returned to their daily resting places just before (Fig. 10).

Probably during their nightly period of inactivity the fishes avoid such places in shallow water because they can not escape from the strong chop which reaches from the surface to the bottom. At places with a strong chop sea urchins are found but they are never joined by fishes. On the other hand there are frequently places found where there are schools of *P. bipunctata* which take no notice of the urchins, or where there are no urchins. I observed a number of groups of these fishes on the reef at Shab Abu Sadaf near Ghardaqa in a depth of 1.5 m staying in and in front of a spacious hole in a dead coral, *Acropora*, with many lateral openings. These observations showed that probably the long spined urchins compensate for lack of protection structures in the bottom for the fishes, and experiments with dummies established this hypothesis.

Experiments With Dummies on Paramia bipunctata.—I used two different types of dummies which simulated long-spined sea urchins. The body was a wooden ball with a diameter of 4 cm weighted on the underside with a leaden disk. Each dummy of one type had 100 wire spines 1 mm thick and 25 cm long (Fig. 11). Each of the others had 50 wooden spines 3 mm thick and 18 cm long. All wire dummies were coloured black, while the wooden dummies were coloured black, red, or white. The experiments were carried out at an isolated miniature reef of the coral *Galaxea fascicularis* near the Marine Biological Station at Ghardaqa. The reef lies 3 m deep, is 6 m \times 8 m broad, and rises 1 m above the surrounding sediment floor. On this reef there was about 300 sea urchins and at least 2000 *P. bipunctata*.

The dummies were placed in isolated small groups of *Diadema* accompanied by an average size school of fishes. When the dummies were set in place, the fishes sought protection between the spines of their urchin and almost dispersed from above the dummy. When I displaced the urchins one by one, the fishes stayed at the dummy which was left and treated it like a sea urchin; that means that in case of danger the complete school or at least most of it escaped between the dummy spines (Fig. 11a, b). The experiments succeeded with all dummies of both types, the coloured too, but best with the stronger structured wire-spine dummies.

Some dummies were placed in favourable spots beside the miniature reef for 8 weeks. They soon were covered with algae, *Spirorbis* tubes, and sponges, and during all the time they were joined by *P. bipunctata* groups each morning and treated like sea urchins as protecting structures of the bottom (Fig. 11b).

For choosing-experiments, all of the types of *Diadema* dummies were placed around an old rusty iron tun, which stood isolated on a sediment plain. Its lower part was perforated with big openings. Fifteen *Diadema*

stayed in and around the tun, accompanied every day by a large number of *P. bipunctata*.

The fishes were easily chased out of the tun with a stick and they distributed themselves in small groups both with the dummies and living urchins round about. The results of these experiments showed that the stronger structured wire-spine dummies were sought more frequently and by bigger groups of fishes than the wood-spine dummies or than the natural *Diadema*. Plate (1908) already had discovered in the Gulf of Suez that a society of *Diadema*-fishes can be caught by sliding the *Diadema* in a bucket and lifting the bucket out of the water. I repeated this experiment successfully in many cases using a wire-spine dummy in the bucket, and caught fishes for experiments in aquaria and as living proof



FIGURE 12. *Paramia bipunctata* shoal nearby and among the wire spines of a dummy in a bucket. Underwater photograph. *Galaxea* miniature reef at Ghardaqa, 2.5 m deep.

(Fig. 12). In the aquarium the fishes reacted just the same towards the dummies as in nature and obviously preferred the larger spine forest of wire dummies instead of the living *Diadema*.

The two apogonid fishes *Archamia lineolata* (Cuvier & Valenciennes) and *Apogon chrysotaenia* Bleeker also remain near *Diadema* in small to large schools during the day and leave the urchins during the night. Their behavior with *Diadema* and dummies is generally the same as the one of

P. bipunctata, but in particular there were some differences (Fig. 10). *A. lineolata* is not nearly so abundant as *P. bipunctata*. For several years during frequent stays in Ghardaqa, I could observe these fishes at any given time for several months. Year after year, they remained exactly in the same place, the above mentioned *Galaxea* miniature reef, and were found nowhere else in the surrounding area. It seems that this species is more sensitive to distinct, narrow ecological conditions although the connection with the sea urchins is nearly the same as in *P. bipunctata* although *A. lineolata* leaves the sea urchins about 5 to 10 min later in the evening. Schools of these two species are always separate but when they occur side by side, almost always some single animals will swim for a short time with the groups of the other species.

A. chrysotaenia appears to be more tolerant of the demands of ecological conditions than are the two other species. This species is more abundant than *A. lineolata* and seems to prefer stronger moving water or at least to endure it better. Its connection with *Diadema* is not so strong. Certainly they often live over or beside *Diadema* for a longer time but they are often seen far from the urchins near dead coral rocks or similar kinds of hiding places. Generally in case of danger not all members of such a school near *Diadema* will escape to the refuge of the spines, but only some, while the others dissipate around. They do not appear to be associated with finer structures of the bottom like the two other species.

Associations of Single Fishes With Diadema setosa.—Certainly numerous fish species escape as single individuals between the long spines of *Diadema* such as *Heniochus*, *Chaetodon*, *Ostracion*, *Syngnathus*, and other species, but in such cases they often seek out other hiding places. Now I will only specify such species as stay singly or only in a few individuals exceptionally or mostly with *Diadema* and prefer its spines instead of other structures on the surrounding bottom.

(1). The apogonids *Paramia 5-lineata* (Cuvier & Valenciennes), *Cheilodipterus lachneri* Klausewitz, and *Apogon annularis* Rüppell live mostly separate but near *Diadema* as well during the day as during the night. It is a matter of territorial behavior because the individuals stay at these places for a longer time, so that one can observe the same animals for weeks. Only during the day do they escape to the urchin in case of danger, the head inward, and of course larger individuals up to a body length of 15 cm. They prefer such places where the urchins are half hidden in rock caves or between dead coral stacks. At night they retire mostly for sleeping in bottom crevices or stay nearby. I often observed at Ghardaqa singles or few young individuals of *Cheilodipterus lachneri* in between schools of *Paramia bipunctata*. They are so much like them in size, colouring, and pattern that they could be mistaken for another. Undoubtedly they share such cover as a crowd can give its members.

(2). A second group of *Diadema* partners living singly is represented

by other fish species. They too stay during the day as well as the night with the urchins; however they live already without exception in the interspaces between their spines. Therefore they are to be found with the walking sea urchins. The following species are represented: *Siphamia permutata* Klausowitz (1966) (Apogonidae), *Dorprhamphus excisus* (Kaup) (Syn-gnathidae), *Plectorhynchus* spec. (Plectorhynchidae) and *Litores vulgare* (Klunzinger) (Eleotridae).

Siphamia permutata stays with *Diadema* either singly or rarely in pairs. The fishes prefer to stay above the sea urchins between the spines. They seem hardly to leave this protective region. The fishes are excellently masked by their dark brown colouring. They only change place voluntarily if several sea urchins stay so close together, that the fishes do not need to swim through free spaces when they pass from one urchin to the other. In addition, they behave very calmly and stay in the same place without



FIGURE 13. *Siphamia permutata* squeezed between the upper spines of *Diadema setosa*.

moving for a long time, the head directed slightly downwards to the body of the sea urchin (Fig. 13).

In case of danger they retire deeper and deeper between the spines and close to the body of the sea urchin. They catch their food, zooplankton, only inside the forest of spines. Experiments with dummies showed that this species only looks for the sea urchins as a fine underground structure. The releasing stimuli are optical and mechanical ones. Experiments of

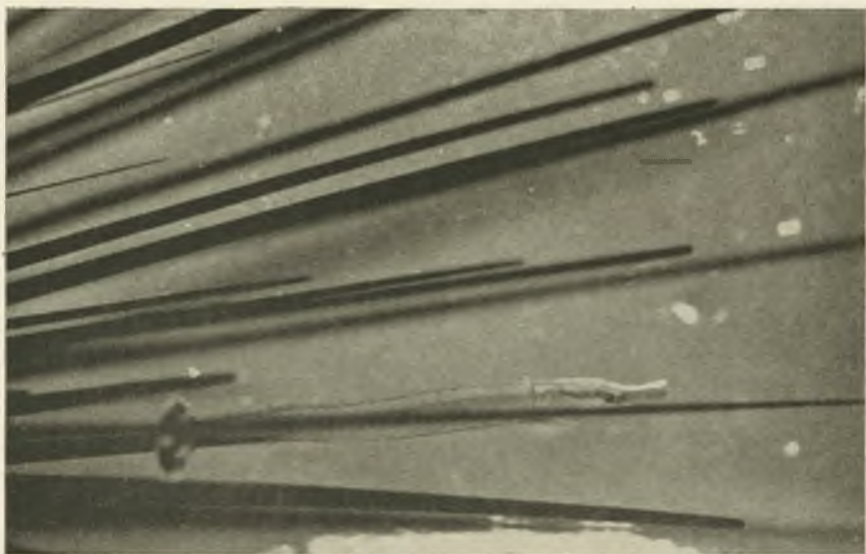


FIGURE 14. *Doryrhamphus excisus* typical lying in wait for prey between the lower spines of *Diadema setosa*.

choice, when normal sea water and water taken from an aquarium containing many *Diadema* were offered, ended absolutely without results. It appeared that chemical stimuli are not important as far as this community is concerned. When these fishes were transported to the aquarium, they spontaneously changed colouring. Then they became light silvery, and broad black stripes appeared along the sides, which could not be seen before. Such a change of colouring never appeared as long as the fishes were together with sea urchins.

A similar close connection with the sea urchins was identified in the syngnathid *D. excisus*. I saw these shining orange and blue-tinged fishes only singly and very rarely between the spines of *Diadema*. They prefer to stay between the long lateral spines arranging themselves parallel to the spines where they lurk for food their heads directed outwards (Fig. 14). They behaved in the same manner between the wire spine of the dummies.

In the juvenile stage a *Plectorhynchus* species stays between the lowest spines of *Diadema* and the surface of substratum, catching living food out of it. It too does not set out from the region of spines.

Litores vulgare, which I found very often associated with *Diadema* in the harbour of Suakin living directly on the surface of the substratum always stays, however, in the protection of the spines of the sea urchins. Mostly it stays under the midst of the urchins near to its mouth. During the night it moves around with the urchin, and during this time it presumably mainly feeds in the small organisms stirred up by the urchin.

Associations of Crustaceans with Diadema setosa.—The sexually dimorphic shrimp *Saron marmoratus* (Olivier) (Hippolytidae) and the crab *Schizophrys aspera* (H. Milne-Edwards) (Majidae) were associated with *Diadema* only in those places where during the day the sea urchins rested in rock clefts and caves which would be fit as daylight resting places for these nightactive crabs. Most frequently I found them at the old and ruined wall at the quay in Suakin. Often two to five shrimps of different sexes and age and one to three crabs live together with one sea urchin. During the day they share one cave, where the shrimps and crabs stay lateral to the entrance under the ceiling, the head directed outwards (Fig. 15). When

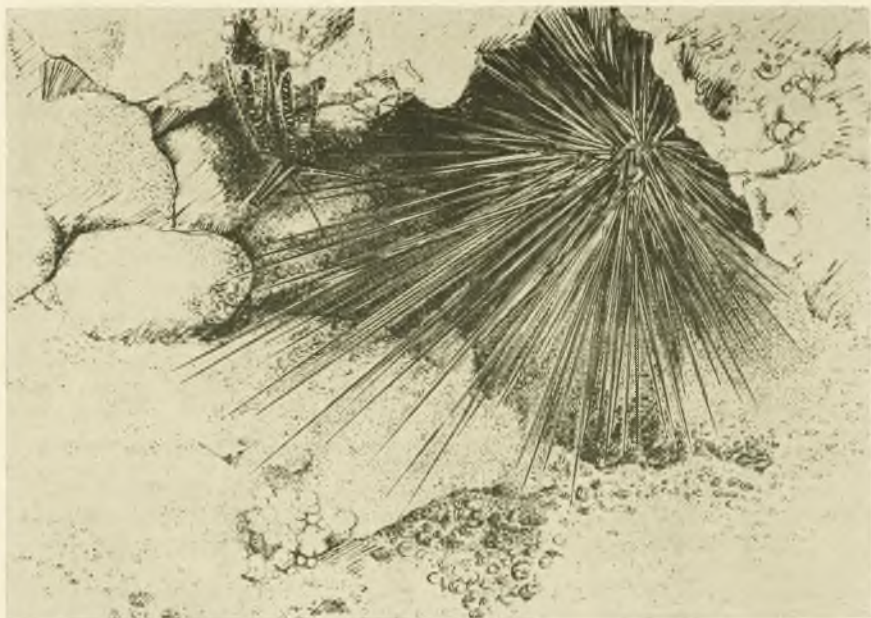


FIGURE 15. *Diadema setosa* and *Saron marmoratus* (♂) side by side in inactivity position at day time, 1 m deep. Drawing from an underwater photograph.

the sea urchins leave their hiding places after sunset, they are accompanied by the shrimps and crabs, which thereby always stay in the area of the spines.

Both the crustaceans and the *Diadema* graze jointly on the algae in stones and return jointly to the caves at sunrise. Neither the shrimps nor the crabs were alone at night without meeting a sea urchin outside the crevices on the bottom. If one takes the urchin away from the animals during the grazing, they all escape into the next crevices. But if one pulls the sea urchin only a bit faster over the bottom, the crabs and shrimps run after it and try to stay under its spines. It seems as if the urchins compensate the stimulus for the animals which a cave offers to them. By walking around under the cover of a sea urchin as a equivalent of a crevice they win an extension of their food habitats.

Assembling of Sepia gibba Ehrenberg With Diadema setosa.—In the harbour basin of Suakin I also observed regularly single individuals of *Sepia gibba* (5 cm long) on their way together with *Diadema* at night. While the feeding urchin walks around slowly, the *Sepia* is floating with the same speed, mostly beside it but also in the region of the longest lateral spines just above the bottom and also frequently sits down on the bottom for a short time. Then its skin forms small papillae. Similar to *S. marmoratus* and *Sch. aspera*, *Sepia gibba* never was to be found at night without a sea urchin.

ACKNOWLEDGMENTS

Travel was granted by the Deutsche Forschungsgemeinschaft, the Technical University of Darmstadt, the University of Cairo, and the Oceanographic and Fisheries Research Center of the U.A.R. In addition I have to thank Prof. Dr. H. A. F. Gohar for help in the researches; Prof. Dr. A. A. Al Kholy, Prof. Dr. W. Adam, Bruxelles, Prof. Dr. L. B. Holthuis, Leiden, Dr. W. Klausewitz, Frankfurt, and G. Cherbonnier, Paris, for determination of the animals; Miss E. Althaus, Darmstadt, for the drawings (Fig. 2, 3, 4, 5, 6, 8, and 15); and Prof. Dr. G. L. Voss, Miami, for correcting the English manuscript.

REFERENCES

- ABEL, E. F.
1959. Zur Kenntnis der Beziehungen der Fische zu Höhlen im Mittelmeer. Publ. Staz. Napoli., Suppl., 30: 519-528.
1960a. Fische zwischen Seeigel-Stacheln. Natur u. Volk., 90: 33-37.
1960b. Zur Kenntnis des Verhaltens und der Ökologie von Fischen an Korallenriffen bei Ghardaqa (Rotes Meer). Z. Morph. Ökol. Tiere., 49: 430-503.
1961. Über die Beziehungen mariner Fische zu Hartbodenstrukturen. SB. Österr. Ak. Wiss. Wien, Mathem.-naturw. Kl., Abt. I., 170: 223-263.
1962. Freiwasserbeobachtungen an Fischen im Golf von Neapel als Beitrag zur Kenntnis ihrer Ökologie und ihres Verhaltens. Int. Rev. ges. Hyrobiol., 47: 219-290.

- BUCHANAN, J. B.
 1962. A re-examination of the glandular elements in the tube feet of some common British Ophiuroids. *Proc. zool. Soc. Lond.*, 138: 645-650.
 1963. Mucous secretion within the spines of Ophiuroid Echinoderms. *Proc. zool. Soc. Lond.*, 141: 251-259.
 1964. A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution. *J. Mar. biol. Ass. U. K.*, 44: 565-576.
- CLARK, H. L.
 1921. The Echinoderm Fauna of Torres Strait: its composition and its origin. *Carnegie Inst. Wash.*, Dpt. Mar. Biol. Publ. 214, 10: 125-126.
- COUTIÈRE, M. H.
 1898. Observations sur quelques animaux des recifs madreporiques de Djibouti. *Bull. Mus. Hist. nat. Paris*, 4: 238-240.
 1910. Les crevettes à males dimorphes du genre *Saron*. *Bull. Soc. philom. Paris, Sér. 10*, 2 (2-3): 71-87.
- CROSSLAND, C.
 1938. The Coral Reefs at Ghardaqa, Red Sea. *Proc. zool. Soc. London. Ser. A.*, 108: 513-523.
- CZIHAK, G.
 1959. Vorkommen und Lebensweise der Ophiothrix quinquemaculata in der nördlichen Adria bei Rovinj. *Thalassia Jugoslavica*, 1: (6-10) 19-27.
- CZIHAK, G. AND M. ZEI
 1960. Photography, television and the use of the bottom-sampler, compared as methods for quantitative analyses of benthic populations. *Extr. Rapp. Proc. - verb. Réunion C.I.E.S. M. M.*, 15 (2): 81-83.
- DAVENPORT, D.
 1955. Specificity and behavior in symbioses. *Quart. Rev. Biol.*, 30: 29-46.
- DECARY, R.
 1921. Observations sur les Echinoderms de Madagascar. *Bull. Mus. Hist. nat. Paris*, 28: 243-244.
- EIBL-EISBESFELD, I.
 1961. Eine Symbiose zwischen Fischen (*Siphamia versicolor*) und Seeigeln. *Z. Tierpsychol.*, 18: 56-59.
- EMERY, K. O.
 1952. Submarine photography with the Benthograph. *Sci. Monthl. N. Y.*, 75: 3-11.
- FONTAINE, A. R.
 1955. Secretion of a Highly Sulphated Acid Mucopolysaccharide by the Brittle-star, *Ophiocomina nigra*. *Nature (Lond.)*, 176: 606-607.
 1962. Neurosecretion in the Ophiuroid *Ophiopholis aculeata*. *Science*, 138 (3543): 908-909.
 1963. A Comparative Study of the Integumentary Mucous Cells of Ophiuroids. *Proc. XVI Int. Congr. Zool., Wash., D. C.*, 1963, 1: 87.
 1964. The integumentary Mucous Secretions of the Ophiuroid *Ophiocomina nigra*. *J. Mar. biol. Ass. U. K.*, 44: 145-162.
- GERLACH, S.
 1960. Über das tropische Korallenriff als Lebensraum. *Verh. Dtsch. Zool. Ges. Münster/Westf. 1959 (Zool. Anz.)*, Suppl., 23: 356-363.

- GOHAR, H. A. AND A. M. EISAWY
 1961. The Biology of *Cassiopeia Andromeda* (From the Red Sea) (With a note on the species Problem). Publ. Mar. biol. Stat. Al-Ghardaqa (Red Sea), 11: 3-42.
- GUDGER, E. W.
 1927. Inquilinism between the Cheilodipterid fish, *Apogonichthys puncticulatus*, and the univalve mollusk, *Strombus bituberculatus*. Zoologica (N. Y.), 9: 193-200.
- HERALD, E. S.
 1961. Living fishes of the world. Doubleday, Garden City, N.Y., 303 pp., illus.
- HIATT, R. AND D. STRASBURG
 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr., 30: 65-127.
- HYMAN, L. H.
 1955. The Invertebrates: Echinodermata. McGraw-Hill, New York, vii + 763 pp.
- JORDAN, D. S. AND B. W. EVERMANN
 1898. The fishes of North and Middle America. Bull. U. S. nat. Mus., 47 (part 3): 2183-3136.
- KAESTNER, A.
 1963. Lehrbuch der Speziellen Zoologie. Teil I, Wirbellose, 2. G. Fischer, Stuttgart, 1181-1212, 1341-1367.
- KLAUSEWITZ, W.
 1959a. Biologische Bedeutung der Färbung der Korallenfische. Verh. dtsh. zool. Ges. Frankfurt a.M. 1958 (Zool. Anz.), Suppl., 22: 329-333.
 1959b. Fische aus dem Roten Meer. II. Knochenfische der Familie Apogonidae (Pisces, Percomorphi). Senck. Biol., 40: 251-262.
 1963. Wie schwimmt der Schnepfensch. Natur u. Museum, 93: 69-73.
 1964. Fische aus dem Roten Meer. VI. Taxionomische und ökologische Untersuchungen an einigen Fischarten der Küstenzone. Senck. Biol. 45: 123-144.
 1966. Fische aus dem Roten Meer. VII. *Siphamia permutata* n. sp. (Pisces, Perciformes, Apogonidae). Senck. Biol., 47: 217-222.
- LACHNER, E. A.
 1955. Inquilinism and a new record for *Paramia bipunctata*, a cardinal fish from the Red Sea. Copeia, 1955: 53-54.
- MAGNUS, D. B. E.
 1963a. Über das "Abweiden" der Flutwasseroberfläche durch den Schlangensterne *Ophiocoma scolopendrina* (LAMARCK). Verh. dtsh. zool. Ges. Wien 1962. Zool. Anz. Suppl., 26: 471-481.
 1963b. Der Federstern *Heterometra savignyi* im Roten Meer. Natur u. Museum, 93: 355-368.
 1964a. Zum Problem der Partnerschaften mit Diadem - Seeigeln. Verh. dtsh. zool. Ges. München 1963. Zool. Anz. Suppl., 27: 404-417.
 1964b. Gezeitenströmung und Nahrungsfiltration bei Ophiuren und Crinoiden Helgol. Wiss. Meeresunters., 10: 104-117.
 1965a. *Ophiocoma scolopendrina* (Ophiuroidea). "Abweiden" des Staubfilms von der Flutwasser-Oberfläche. Begleitveröffentlichung zu Film E 490/1963 (Farbfilm, 28m) der Encyclopaedia Cinematographica (Göttingen): 3-8.

- 1965b. *Ophiocoma scolopendrina* (Ophiuroidea). Nahrungserwerb. Begleitveröffentlichung zu Film E 554/1963 (Farbfilm, 109m) der Encyclopaedia Cinematographica (Göttingen): 3-10.
- 1965c. Wasserströmung und Nahrungserwerb bei Stachelhäutern des Roten Meeres. (Untersuchungen an Schlangensterne und Federsterne). Ber. Phys.-Med. Ges. Würzburg, N. F., 71: 128-141, 1962-1964.
- MENZIES, R. J.
1963. General results of biological investigations on the deep sea fauna made on the U.S.N.S. ELTAININ (U.S.A.R.P.) during cruise I between Panama and Valparaiso, Chile in 1962. Int. Revue ges. Hydrobiol., 48: 185-200.
- MILLOT, N. AND M. YOSHIDA
1959. The photosensitivity of the sea urchin *Diadema antillarum* Philippi: responses to increases in light intensity. Proc. zool. Soc., London, 133: 67-71.
- MORTENSEN, TH.
1950. A monograph of the Echinoidea, III. C. A. Reitzel, Kobenhavn, pp. 250-251.
- MURAKAMI, S.
1938. A curious habit of *Ophiocoma scolopendrina* (Lamarck). Kagaku Nanyo (Sci. of S. Sea), 1 (2): 40-41.
- NICHOLS, D.
1960. The histology and activities of the tube-feet of *Antedon bifida*. Quart. J. micr. Sci., 101: 105-117.
- NOBILL, G.
1906. Diagnoses préliminaires de Crustacés, Décapodes et Isopodes nouveaux recueillis par M. le Dr. G. Seurat aux îles Touamotou. Bull. Mus. Hist. nat. Paris, 12: 256-270.
- PFaff, J. R.
1942. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-1916. LXXI. On a new genus and species of the family Gobiesocidae from the Indian Ocean, with observations on sexual dimorphism in the Gobiesocidae, and in the connection of certain Gobiesocids with Echinids. Vidensk. Medd. fra Dansk. nat. Foren., 105: 413-422.
- PLATE, L.
1908. *Apogonichthys strombi* n. sp., ein symbiotisch lebender Fisch von den Bahamas. Zool. Anz., 33: 393-399.
1916. Fauna Ceylanica. Untersuchung zur Fauna Ceylons nach den Sammlungen von L. Plate. II. Übersicht über biologische Studien auf Ceylon. Jen. Zeitschr. Naturwiss., 54: 11.
- RANDALL, J. E.
1964. Notes on the biology of the echinoid *Diadema antillarum*. Carib. J. Sci., 4: 421-433.
- RIEDL, R.
1956. Automatische Photographie von Meeresböden für ökologisch-faunistische Zwecke. Österr. Zool. Zschr., 6: 532-541.
1963. Probleme und Methoden der Erforschung des litoralen Benthos. Verh. dtsch. zool. Ges. Wien 1962. Zool. Anz. Suppl., 26: 505-567.

1964. Die Erscheinungen der Wasserbewegung und ihre Wirkung auf Sedentarien im mediterranen Felslitoral. Helgol. Wiss. Meeresunters, 10: 155-186.
- ROUSHDY, H. M. AND V. K. HANSEN
1960. Opiuroids feeding on Phytoplankton. Nature (Lond.), 188: 517-518.
- SARASIN, C. F. AND P. B. SARASIN
1886. Über einen Lederigel aus dem Hafen von Trincomalie (Ceylon) und seinen Giftapparat. Zool. Anz., 9: 80-82.
- SCHROEDER, R. E.
1964. Photographing the night creatures of Aligator Reef. Nat. Geogr., 125: 128-154.
- SEMON, R.
1903. Im australischen Busch und an den Küsten des Korallenmeeres. 2. Aufl., Verl. Engelmann, Leipzig, pp. 505-506.
- SMITH, J. E.
1937. The structure and function of the tube feet in certain echinoderms. J. Mar. biol. Ass. U. K., 22: 345-357.
- THORNTON, I. W. B.
1956. Diurnal migrations of the echinoid *Diadema setosum* (Leske). British J. anim. Behav., 4: 143-146.
- VEVERS, H. G.
1952. A photographic survey of certain areas of sea floor near Plymouth. J. Mar. biol. Ass. U. K., 31 (2): 215-222.
1956. Observations on the feeding mechanisms in some echinoderms. Proc. zool. Soc. Lond., 126: 484-485.
- WHITLEY, G. P.
1959. More ichthyological snippets. Proc. roy. zool. Soc. New South Wales, 1957-1958, pp. 11-26.

FOOD HABITS OF REEF FISHES OF THE WEST INDIES¹

JOHN E. RANDALL

Hawaii Institute of Marine Biology

University of Hawaii, Honolulu

and

Bernice P. Bishop Museum, Honolulu

ABSTRACT

The stomach contents of 5,526 specimens of 212 species of reef and inshore fishes representing 60 families were analyzed. Most of these fishes were collected by spearfishing in Puerto Rico and the Virgin Islands. The principal plant and animal groups eaten by the fishes are listed by percentage volume of the stomach contents under fish family and species headings. When practicable, the food organisms were identified. Following the species accounts, the major groups of food organisms are discussed.

In the following summary, the various families, genera, and species of fishes are grouped into major feeding categories, based on their principal food habits as determined from the data of this report.

Plant and detritus feeders (food 50 per cent or more plant material): The mullet *Mugil curema*; the porgies *Archosargus rhomboidalis* and *Diplodus caudimaculatus*; the sea chubs (Kyphosidae); the damselfishes *Abudefduf taurus*, *Microspathodon chrysurus*, *Pomacentrus fuscus*, and *P. variabilis*; the parrotfishes (Scaridae); the gobies *Coryphopterus glaucofraenum* and *Gnatholepis thompsoni* (and probably the other gobiids as well); the angelfish *Centropyge argi*; the surgeonfishes (Acanthuridae); the blennies *Blennius cristatus*, *B. marmoreus*, *Entomacrodus nigricans*, and *Ophioblennius atlanticus*; the triggerfish *Melichthys niger*; and the filefish *Alutera schoepfi*. In addition, the following omnivorous fishes feed heavily on marine plants: the halfbeak *Hemiramphus brasiliensis*; the damselfishes *Pomacentrus leucostictus* and *P. planifrons*; the angelfishes *Pomacentrus arcuatus* and *P. paru*; the filefishes *Alutera scripta*, *Cantherhines pullus*, and *Monacanthus ciliatus*, and the sharpnose puffer *Canthigaster rostrata*.

Zooplankton feeders: The herrings (Clupeidae); the round herrings (Dussumieridae); the garden eel *Taenioconger halis*; the halfbeak *Hemiramphus balao*; the soldierfish *Myripristis jacobus*; the silversides (Atherinidae); the creole fish *Paranthias furcifer*; the sea bass *Serranus tortugarum*; the fairy basslets (Grammidae); the hawkfish *Amblycirrhitus pinos*; the cardinalfishes (Apogonidae); the big-eyes (Priacanthidae); the sweeper *Pempheris schomburgki*; the boga *Inermia vittata*; the snapper *Ocyurus chrysurus* (except large adults); the drum *Equetus acuminatus*; the scads *Decapterus macarellus*, *D. punctatus*, and *Selar crumenophthalmus*; the damselfishes *Chromis cyanea* and *C. multilineata*; the razorfish *Hemipteronotus splendens*; and the jawfish *Opisthognathus aurifrons*. The following fishes also feed in part on animals of the plankton: the croaker *Odontoscia dentex*; the remoras (Echeneidae); the damselfish *Abudefduf saxatilis*; the wrasse *Thalassoma bifasciatum*; the triggerfishes *Canthidermis sufflamen* and *Melichthys niger*; and the filefishes *Monacanthus ciliatus* and *M. tuckeri*. In addition, the juveniles of many fishes such as the

¹Contribution from the Institute of Marine Biology, University of Puerto Rico, Mayagüez, P. R.

pomadasyids and carangids feed primarily on zooplankton.

Sessile animal feeders: *Abudefduf saxatilis* and to a lesser extent several other damselfishes; the spadefish *Chaetodipterus faber*; the butterflyfishes and angelfishes (Chaetodontidae) (except *C. argi*); the filefishes *Alutera scripta*, *Cantherhines macrocerus*, and *C. pullus*; and the trunkfishes *Acanthostracion polygonius*, *A. quadricornis*, and *Lactophrys bicaudalis*. The angelfishes and *C. macrocerus* feed primarily on sponges; the sharp-nose puffer *Canthigaster rostrata* and some of the trunkfishes also feed in part on sponges. *Abudefduf saxatilis* feeds on a wide variety of organisms, but the largest percentage of its stomach contents proved to be *Zoanthus*. The butterflyfishes consume mainly anthozoans (especially *Zoanthus*) and the tentacular crowns of tube-dwelling polychaetes. *Alutero scripta* is unusual in feeding heavily on stinging coral (*Millepora*) and gorgonians. The three trunkfishes appear to show a preference for tunicates. Many of these fishes also feed in part on plants.

"Shelled"-invertebrate feeders: The eagle ray *Aetobatis narinari*; the grunts *Anisotremus surinamensis*, *Haemulon carbonarium*, *H. macrostomum*, and to a lesser extent *H. plumieri* and *H. sciurus*; the porgy *Calamus bajonado*, and to a lesser degree other species of *Calamus*; the permit *Trachinotus falcatus*; the wrasses *Bodianus rufus*, *Halichoeres* spp. (except *maculipinna*), *Hemipteronotus novacula*, and *Lachnolaimus maximus*; the triggerfish *Balistes vetula*; the trunkfish *Lactophrys trigonus*; the puffer *Sphaeroides spengleri*; and the porcupinefishes (Diodontidae). All of these fishes are able to crush their prey of gastropods, pelecypods, echinoderms, crabs, and hermit crabs with their jaws or pharyngeal teeth.

Generalized carnivores (on a variety of mobile benthic animals such as crustaceans, worms, and small fishes): The stingray *Dasyatis americana*; the moray *Echidna catenata* (all crustaceans, mostly crabs); the snake eels *Myrichthys acuminatus* and *M. oculatus*; the squirrelfishes *Holocentrus* spp.; the groupers *Alphesites afer*, *Cephalopholis fulva*, *Epinephelus* spp., *Hypoplectrus* spp., *Petrometopon cruentatum*, and *Serranus tigrinus*; the soapfish *Rypticus saponaceus*, the snappers *Lutjanus* spp. (except *L. cyanopterus* which feeds on fishes, as to a lesser extent do *L. apodus*, *L. jocu*, and *L. mahogoni*); the grunts *Anisotremus virginicus*, *Haemulon album*, *H. aurolineatum*, *H. chrysargyreum*, *H. flavolineatum*, and *H. parra*; the mojarras (Gerreidae); the drums *Equetus lanceolatus* and *E. punctatus*; the goatfishes (Mullidae); the tilefish *Malacanthus plumieri*; the palometa *Trachinotus glaucus*; the wrasse *Halichoeres maculipinna*; the flounder *Bothus ocellatus*; the clinids *Labrisomus* spp.; the jawfishes *Opisthognathus* spp. (except *O. aurifrons*); the scorpionfishes (Scorpaenidae); the flying gurnard *Dactylopterus volitans*; the trunkfish *Lactophrys triqueter*; and the batfish *Ogcocephalus nasutus*.

Ectoparasite feeders: Juvenile porkfish *Anisotremus virginicus*; the shark suckers *Echeneis naucrates* and *Remora remora*; the wrasses *Bodianus rufus* and *Thalassoma bifasciatum* (the former as juveniles, the latter as juveniles and adults except the terminal male phase); the goby *Elacatinus* sp.; and juvenile angelfishes of the genera *Holacanthus* and *Pomacanthus*. In addition, the fairy basslet *Grama loreto* and the young of the damselfish *Microspathodon chrysurus* occasionally feed in part on the crustacean ectoparasites of fishes. Probably none of these fishes are facultative "cleaners." The shark suckers, *Thalassoma bifasciatum*, and the young angelfishes appear to feed more on other organisms than on fish parasites.

Fish feeders: Sharks of the families Orectolobidae (reported to feed heavily on various invertebrates as well) and Carcharhinidae; the tarpon

Megalops atlanticus (also known to feed on crustaceans and other invertebrates); the lizardfishes (Synodontidae); moray eels of the genus *Gymnothorax*; the snake eel *Ophichthus ophis*; the needlefishes (Belonidae); the cornetfish *Fistularia tabacaria*; the trumpetfish *Aulostomus maculatus* (about 1/4 of the diet was shrimps); the barracudas (Sphyraenidae); groupers of the genus *Mycteroperca*; the sea bass *Serranus tabacarius* (one specimen); the snapper *Lutjanus cyanopterus*; the cobia *Rachycentron canadum* (one specimen); jacks of the genera *Caranx*, *Oligoplites*, and *Seriola*; the little tuna *Euthynnus alletteratus* and mackerels of the genus *Scomberomorus*; the flounder *Bothus lunatus*; and the frogfishes *Antennarius multiocellatus* (about 1/5 of the food was crustaceans) and *A. scaber*. A number of the above piscivorous fishes fed in part on cephalopods, but in all cases except *Ophichthus ophis* (half of the stomach contents of four of these eels consisted of octopuses) and *Euthynnus alletteratus* (36.6 per cent squids), the cephalopods were less than 18 per cent by volume of the stomach contents.

INTRODUCTION

In November, 1958, the Institute of Marine Science of the University of Miami commenced a marine biological and fisheries survey of the Virgin Islands National Park from a small field station at Lameshur Bay, St. John. The program terminated in June, 1961. Some phases of the survey, including that of the present paper, were continued in Puerto Rico from July, 1961, to October, 1965, while the author was a member of the Biology Department and the Institute of Marine Biology of the University of Puerto Rico at Mayaguez.

Among the projects undertaken during the survey was a study of the food habits of fishes from inshore reefs and adjacent habitats. Emphasis was placed on fishes of sportfishing value because of partial support from the Dingell-Johnson program. The data presented for few of the fishes, however, may be regarded a definitive expression of their food habits. Analysis of the stomach contents of more specimens is needed, as well as additional underwater observation of their actual feeding. Since so little is known of the habits of West Indian reef fishes, in general, a decision was made to carry out research on many species rather than confine the study to just a few. For many of the fishes the data presented herein constitute the first published information on their food habits. It was realized that the information for some would be fragmentary. More field work, particularly on the smaller species, was planned; however, a move from the Caribbean precluded further collection of fishes. The present report is based on the examination of the stomach contents of a total of 5,526 specimens of 212 species.

A number of publications have appeared as a result of the marine biological survey in the Virgin Islands, most of which complement the research on food habits. In addition to systematic papers, there has been a report on the fisheries potential of St. John (Idyll & J. Randall, 1959), a study of mimicry and protective resemblance of tropical marine fishes

(Randall & Randall, 1960), tagging studies of reef fishes (J. Randall, 1960, 1962a, 1963a), a chart of the marine environments of St. John (Kumpf & H. Randall, 1961), studies on the grazing effects of herbivorous fishes on marine plants (J. Randall, 1961a, 1965a), analysis of fish populations of natural and artificial reefs of St. John (J. Randall, 1963b), observations on the spawning of scarid and labrid fishes (Randall & Randall, 1963), biology of the West Indian topshell (*Cittarium pica*) (H. Randall, 1964), biology of the queen conch (*Strombus gigas*) (J. Randall, 1964a), biology of the echinoid *Diadema antillarum* (J. Randall, Schroeder, and Starck, 1964), and food habits of the hogfish (*Lachnolaimus maximus*) (J. Randall & Warmke, in press). Three additional papers are in progress which are pertinent to the present study. One by J. Randall and Willard D. Hartman will discuss sponge-feeding reef fishes. Another by J. Randall, Luis R. Almodóvar, and Francisco Pagán is concerned with the algae eaten by parrotfishes and the role of these fishes in the production of sediment. Jorge Rivera will report on the food habits and other aspects of the biology of sharks caught inshore off southwestern Puerto Rico. This study, which was initiated by the author, is supported by the Office of Naval Research.

The importance of obtaining the correct names of organisms in ecological studies cannot be overemphasized. Considerable effort was made in this report to correctly identify the fishes and food organisms. Determinations of identifiable plant and invertebrate animal remains from fish stomachs were made largely by systematists who specialize in the various groups or from reference collection material prepared by them. For data on classification of the fishes, the reader is referred to a forthcoming guidebook on West Indian fishes in preparation by the author.

The two most significant publications on the food habits of West Indian reef fishes are Beebe & Tee-Van's "Fishes of Port-au-Prince Bay, Haiti" (1928) and Longley & Hildebrand's "Systematic Catalogue of the Fishes of Tortugas, Florida" (1941). Information on the food habits of fishes from these works and other papers will be summarized in the Remarks section of individual species accounts.

The food-habit data are presented in approximate phylogenetic sequence by family. Within each family the individual fish accounts are given alphabetically by genus and species. When more than one species is discussed in a family, a short family discussion is included, primarily for remarks that apply to all of the species.

ACKNOWLEDGMENTS

The survey in the Virgin Islands was supported by Federal Aid in Fish Restoration (Dingell-Johnson project of the Virgin Islands), the National Science Foundation (Grant No. 5941), and the National Park Service.

Many ichthyologists helped in the identification of fishes. They will

be acknowledged in the guidebook mentioned above. Noteworthy among them are James E. Böhlke and C. Richard Robins.

The following persons have assisted the author in collecting fishes for the present study: Luis R. Almodóvar, Loredon Boynes, James R. Chess, Donald S. Erdman, Peter W. Glynn, Nicholas H. Hylton, Herman E. Kumpf, Gladston Matthias, Luis Morera, Francisco Pagán, Jorge Rivera, Daniel Rosado, Pedro Rosado, Victor Rosado, and Robert E. Schroeder.

Marine plants from fish stomachs were identified by Luis R. Almodóvar and Harold J. Humm. Invertebrates were determined primarily by J. Laurens Barnard, Frederick M. Bayer, Thomas E. Bowman, Charles E. and Bertha M. Cutress, Peter W. Glynn, J. Gerardo Gonzalez, Ivan M. Goodbody, Willard D. Hartman, Raymond B. Manning, William A. Newman, Marian H. Pettibone, Anthony J. Provenzano, Jr., Helen A. Randall, Joseph Rosewater, A. C. Stephen, Lowell P. Thomas, Gilbert L. Voss, and Germaine L. Warmke. Walter A. Starck, II, has reviewed the manuscript. The author is very grateful to all of these persons for their unstinting aid.

METHODS

The majority of the fishes taken for this food-habit study were collected in the Virgin Islands and Puerto Rico (a few were taken at other West Indian islands). Most were collected with a Hawaiian sling spear or a multi-prong spear. Although spearfishing is a time-consuming method of collecting fishes, it is free of certain problems associated with some of the other methods. Anything found in the stomach of a fish taken with a spear can be confidently regarded as having been normally ingested by the fish. Fishes captured in traps usually have empty stomachs. The trap-caught piscivorous fishes, on the other hand, may have full stomachs due to the opportunity to prey upon smaller fishes in the same trap. These small fishes might ordinarily elude the predators in the natural environment.

Studies of the stomach contents of carnivorous fishes taken with rotenone or other poisons may also be unreliable. The smaller fishes and certain invertebrates are usually killed by the poison first, and the larger fishes often feed freely upon them before they, in turn, succumb. Rotenone was used, however, to collect some of the smaller herbivorous fishes or fishes that feed primarily on sessile invertebrates.

Fishes taken on hook and line often have empty stomachs or contain only the bait or chum. Presumably, a fish with an empty stomach is more apt to take the hook. Also, during the struggle on the line, some fishes tend to regurgitate. This is particularly true of fishes caught in water deeper than about 50 feet. The gas bladder expands as a fish is brought rapidly to the surface and tends to force the stomach toward the mouth. Physoclistic fishes from deep water may be expected to have the stomach fully everted into the mouth. Regurgitation was often observed during the transport of

spearred fishes to the surface from depths of about 50 to 200 feet, but it was usually possible for the diver to recover this material. In spite of the higher percentage of empty stomachs among fishes taken by hook and line, this method of capture was used for several species such as king mackerel (*Scomberomorus cavalla*) and porgies of the genus *Calamus*, which are difficult to approach underwater.

A few fishes were taken for the study by seines, throw nets, and explosives.

Everything found in the stomach of a fish does not always represent what is specifically sought as food. Not infrequently sand, stones, or pieces of algae or seagrass were encountered in the stomachs of carnivores. These items were probably taken in accidentally with the prey or in the attempt to capture prey. Bottom-dwelling fishes often ingest inorganic sediment incidentally during feeding. Some of this material may be of organic origin. Examples are fragments of calcareous algae, foraminifera, sponge spicules, small pelecypod and gastropod shells or fragments of larger shells, chiton plates, spines and pieces of the test of echinoids, and ophiuroid fragments. Usually it was possible to identify such fragments as sediment by their eroded appearance, and in the light of the remaining material in the fish stomachs. It might be added that some sedimentary material in the alimentary tracts of fish may be present as a result of the digestion of sipunculids, holothurians, and certain polychaetes which had either ingested the sand themselves or utilized it to form tubes in which they lived. Inorganic material in the stomachs of fishes was not included in the analyses of the stomach contents; nor was plant material in the stomachs of carnivorous fishes. Mention is made, however, of significant amounts of indigestible stomach-content material in the Remarks section of individual species accounts.

Occasional small animals, especially crustaceans and mollusks, were noted among the algae or seagrass in the stomachs of herbivorous fishes. It was evident from their small size that these animals were not selected by the grazing fishes.

The stomachs of some carnivorous fishes were at times found with tiny copepods and other small planktonic organisms that seem too small to be normal prey. Although some large fishes may eat surprisingly small organisms, their stomachs may contain even smaller animals as a result of the liberation of the contents of the alimentary tracts of their prey. If an animal such as a salp or small fish is sufficiently crushed or digested to expose its food organisms, these could be erroneously attributed to the large predator.

When nocturnal habits become apparent for certain fishes by the consistent finding of empty stomachs during late morning and afternoon hours, further collecting was concentrated very early in the morning.

Data on the food habits of fishes were obtained throughout the period

of study, thus tending to eliminate any possible bias due to seasonal variation in food habits. Although tropical marine fishes would not be expected to show significant differences in their diet with season, some variation might be expected from local fluctuations in the abundance of food organisms. This would seem particularly true of larval stages or of adults aggregating for reproductive purposes.

Marked changes in food habits may be expected for most fishes as they grow from juveniles to adults. Most data for the present study were obtained from adult fishes. The adults, in general, have more impact on the reef community through their feeding than juveniles. Determination of the varying food habits of the different stages of the life histories of the reef fishes must await detailed autecological studies.

Many species of reef fishes occur in diverse reef habitats, and their food habits may differ profoundly from area to area. This was aptly demonstrated for the gray snapper (*Lutjanus griseus*) by Longley, Schmitt, & Taylor (1925) who stated that it would be possible from an average sample of 10 fish to determine from which of seven different sites at Dry Tortugas, Florida, that the snappers had been collected. For this reason an effort was made in the present study to collect in all environments in the Virgin Islands and Puerto Rico in which the fishes were encountered. The analysis of stomach contents of a few specimens from several different areas is usually more indicative of the full spectrum of the diet than the examination of many fish from a single area.

One source of error in food-habit studies of fishes which prey upon a variety of organisms is the result of the varying rate of digestion of the different food organisms. Soft-bodied animals such as ctenophores, salps, and certain worms are digested rapidly and may be difficult to identify even to major group after a relatively short sojourn in a fish stomach. On the other hand, organisms with hard parts are digested slowly, and the skeletal material may not be digested at all. The inevitable result is a bias in the data toward the less digestible organisms. Such a bias is greater if working with intestinal contents than with stomach contents; for this reason, only stomach-content analyses were made except for a few fishes such as the diodontids and *Lachnolaimus maximus* which feed almost exclusively on invertebrates with shells or exoskeletons.

Within a group of organisms certain ones with a distinctive morphological feature which is not readily digested may permit a relatively high percentage of identification to the lower taxonomic categories. It should be pointed out, therefore, that large numbers of such distinctive animals listed from the stomachs is not necessarily an indication of their abundance relative to other forms. Examples of distinctive animals are the parrotfishes with their unmistakable beak-like fused teeth and characteristic pharyngeal mill, and the alpheid shrimps with their unique snapping chela.

Not infrequently only the chela of an alpheid was found in the stomach

of a fish, indicating that the shrimp had escaped by way of autotomy of its claw. Detached crab chelae were also often detected in fish stomachs with no remains of the rest of the crabs.

In the stomach content analyses the term "shrimp," in general, refers to decapod shrimps. When identified, the mysid shrimps (Mysidacea) and euphausiids (Euphausiacea) were considered as separate categories. In the grouping "crabs," however, the anomurans were not distinguished from the brachyurans except for the hermit crabs. The great majority of crabs from fish stomachs were brachyurans.

A reference collection of the common fishes and invertebrates was assembled at St. John. This and a comparable collection at the Institute of Marine Biology of the University of Puerto Rico were most useful in identifying the broken and digested remains of animals in fish stomachs. Still there was a considerable amount of material from the stomachs of many fishes that could not be identified to class or phylum.

The dentition of the fishes and the morphology of their digestive tracts are often indicative of the food habits. Information on the structure of teeth and digestive system may be found in certain systematic works such as Jordan & Evermann (1896-1900), and in Suyehiro (1942), and Hiatt & Strasburg (1960). Although the latter two studies concern species of fishes from Japan and the Marshall Islands, respectively, the remarks on morphology usually apply equally well to species of the same genera in the Atlantic. Information on the food habits of fishes in these two papers provides interesting comparison with that of the present work.

The lengths were recorded for all of the fishes that were examined. Usually the standard length (tip of snout to base of caudal fin) was tabulated. This is abbreviated in the species accounts as SL. Total length (TL) was used for sharks and eels, and fork length (FL) for most of the carangids and scombrids. Numbers in parentheses following the names of food organisms indicate the number of stations at which fishes were taken that fed upon these organisms. The abbreviation "juv." designates the food organisms as small juveniles, and "larv." as larvae or postlarvae.

The results of the stomach-content analyses are given in terms of the percentage volume of the different major groups of food organisms. The percentages were visually estimated for individual fish, and the totals computed from all of the stations combined.

Identifications of organisms from fish stomachs are given at the specific, generic, family, or higher category depending on the condition of the organism and the status of the knowledge of the classification of the group. The same species of shrimp, for example, might be labelled *Brachycarpus biunguiculatus*, *Brachycarpus* sp., palaemonid, caridean, shrimp, or simply as crustacean, depending on how thoroughly it was crushed when eaten or how extensively it had been digested. Most of the stomach-content data are grouped under the higher categories.

FOOD HABITS
ORECTOLOBIDAE (Nurse Sharks)

Ginglymostoma cirratum (Bonnaterre) NURSE SHARK
19 stations; 24 specimens: 605 to 2338 mm TL; 15 empty.

FOOD	VOLUME (%)
Fishes	89.0
<i>Acanthurus</i> sp.	
<i>Cantherhines pullus</i>	
clupeid	
<i>Jenkinsia</i> sp.	
scarid	
Cephalopods	11.0

Remarks.—Bigelow & Schroeder (1948) described *G. cirratum* as “proverbially sluggish” and stated that it feeds chiefly on invertebrates such as squids, shrimps, crabs, spiny lobsters, sea urchins, and also on small fishes. Only nine of the 24 specimens examined by the author contained food. Eight of these had eaten fishes, and the ninth had a cephalopod beak in its stomach. Beebe & Tee-Van (1928) reported two parrotfish in the stomach of one specimen. Admittedly the species seems sluggish; much of its diurnal time appears to be spent resting on the bottom. Its mouth and teeth are small; the teeth occur in from 7 to 12 functional bands in the jaws. Possibly its success in feeding on fishes is related to nocturnal habits. The nurse shark is observed more frequently on West Indian reefs than any other shark. It is disliked by fishermen because it often damages fish traps. It is popularly regarded as harmless to man; actually it is prone to bite when provoked (Randall, 1961b).

CARCHARHINIDAE (Requiem Sharks)

This is the largest family of sharks. Species of the largest genus, *Carcharhinus*, may be difficult to identify. J. A. F. Garrick kindly assisted the author in the identification of some sharks of this genus. A few specimens of *C. limbatus* and *C. acronotus*, which were caught inshore, had empty stomachs or contained only bait. Limited data for offshore species are not included. The carcharhinids, in general, are nocturnal. Were this not the case, the number of shark attacks on man would probably be much greater. Some species such as the tiger shark (*Galeocerdo*) are rarely encountered inshore during the day but are often caught on set lines in shallow water at night. The teeth of sharks often provide clues to their feeding habits. Sharks that have slender, smooth-edged teeth tend to feed on fishes of relatively small size; those with broad, coarsely-serrate teeth are better equipped to tear pieces from large prey. Bigelow & Schroeder (1948) should be consulted for details on the morphology and habits of western Atlantic species.

Carcharhinus springeri (Bigelow & Schroeder) SPRINGER'S SHARK
5 stations; 5 specimens: 935 to 1660 mm TL; 2 empty.

FOOD	VOLUME (%)
Fishes	100.0

Priacanthus arenatus

Remarks.—*C. springeri* appears to be the most common inshore shark of the genus in the Virgin Islands. It is capable of lying motionless on the bottom like the nurse and lemon sharks. The 1660-mm specimen was speared when it was discovered lying on the bottom in a cave. Its stomach contained one bigeye (*P. arenatus*), which measured 245 mm SL.

Galeocerdo cuvier (Peron & LeSueur) TIGER SHARK
2 stations; 2 specimens: 2223 and 2340 mm TL.

FOOD	VOLUME (%)
Fishes	50.0

Diodon hystrix

Monacanthus sp.

Sea turtles	50.0
-------------	------

Caretta caretta

Remarks.—The tiger shark is well known for the great variety of food organisms, as well as indigestible objects, that have been found in its stomach. Recent food-habit data from Puerto Rican specimens will be reported by Rivera (MS). The powerful jaws and coarsely serrate teeth enable this species to cut pieces from large prey including such durable animals as sea turtles. The loggerhead turtle cited above was taken from the stomach of a specimen collected in the Bahamas.

Negaprion brevirostris (Poey) LEMON SHARK
2 stations; 2 specimens: 632 and 1605 mm TL; 1 empty.

FOOD	VOLUME (%)
Fishes	100.0

Remarks.—Clark & von Schmidt (1965) listed five different species of fishes fed upon by lemon sharks from West Florida; also they reported octopods from the stomachs.

Rhizoprionodon porosus (Poey) SHARP-NOSE SHARK
4 stations; 5 specimens: 585 to 895 mm TL; 4 empty.

FOOD	VOLUME (%)
Fishes	100.0

Halichoeres sp.

Remarks.—Prior to the review of the genus *Rhizoprionodon* by V. Springer (1964), the name *Scoliodon terraenovae* was used most often for this small species in the West Indies.

DASYATIDAE (Stingrays)

Dasyatis americana Hildebrand & Schroeder SOUTHERN STINGRAY
23 stations; 25 specimens: 320 to 1360 mm disc length; 2 empty.

FOOD	VOLUME (%)
Fishes	21.8
<i>Acanthurus</i> sp. (juv.)	
engraulids	
<i>Opisthognathus</i> sp. (2)	
<i>Scorpaena plumieri</i>	
Sipunculids	20.6
<i>Aspidosiphon</i> sp.	
Crabs	17.6
calappid	
hippid	
majid	
portunids (3)	
<i>Portunus</i> sp.	
xanthid	
Polychaetes	17.3
Pelecypods	10.8
<i>Asaphis deflorata</i>	
Shrimps	7.6
alpheid	
penaeids (2)	
<i>Solenocera</i> sp.	
Hemichordates	2.3
Stomatopods	2.0

Remarks.—Although not a resident of reefs, this ray is often seen cruising over reefs or lying at rest in small sand patches among reefs. It may make broad excavations in the sand when feeding. Bigelow & Schroeder (1953) listed the stomach contents of specimens from Florida, North Carolina, and the Bahamas as clams, crabs, shrimps, stomatopods, worms, and small bony fishes. Very few fragments of pelecypod shells were found in the stomachs. Clams are apparently crushed in the plate-like jaws of the rays, and only the soft parts selected. One 300-mm ray had 52 penaeid shrimps (*Solenocera* sp.) and 12 crabs (*Portunus* sp.) in its stomach.

MYLIOBATIDAE (Eagle Rays)

Aetobatis narinari (Euphrasen) SPOTTED EAGLE RAY
4 stations; 4 specimens: 600 to 1040 mm disc length; 1 empty.

FOOD	VOLUME (%)
Gastropods	53.4
<i>Astraea tuber</i>	

Strombus gallus
Strombus gigas
 Pelecypods

46.6

Remarks.—In contrast to species of *Dasyatis* which are often encountered during the day at rest on the bottom, the spotted eagle ray is usually in motion, swimming gracefully over sand, grass, and mud flats and reefs. Bigelow & Schroeder (1953) reviewed its food habits. They stated that it feeds chiefly on bivalve mollusks; in some areas the rays are very destructive to commercially important clams and oysters. Randall (1964a) has discussed the depredations by this ray on the most valuable West Indian mollusk resource, the queen conch (*Strombus gigas*). The mollusks are crushed by the dental plates of the rays during feeding. Shell fragments are rarely encountered in the stomachs, however. Bigelow & Schroeder postulated that the rays separate out the shells by means of their buccal papillae. It seems more likely that an entire crushed mollusk is ejected from the mouth and only the fleshy part picked up. Randall noted that the horny opercula were missing from the *Strombus* which had been eaten. The operculum adheres strongly to the foot of a conch and would seem to require a separate wrenching action by a ray to remove it.

ELOPIDAE (Ladyfishes and Tarpons)

Megalops atlantica Cuvier & Valenciennes TARPON
 4 stations; 4 specimens: 395 to 1100 mm SL; 2 empty.

FOOD	VOLUME (%)
Fishes	100.0
<i>Allanetta harringtonensis</i>	
<i>Atherinomorus stipes</i>	

Remarks.—Data on the food habits of the tarpon have been reported by Knapp (1949), Babcock (1951), Moffett & Randall (1957), Harrington & Harrington (1960), and Hildebrand in Bigelow *et al* (1963). The adults prey upon a wide variety of fishes, crabs, and shrimps. Several tarpon from west Florida were noted by the author to regurgitate ctenophores when boated. The juveniles feed principally on copepods, aquatic insects, and small fishes. *M. atlantica* is a fish of diverse habitats. In the Virgin Islands adult are most commonly seen off promontories, but they often range into shallow bays to feed on small schooling fishes. At times two or three were observed to attack simultaneously side by side; such a maneuver probably increases the efficiency of feeding.

CLUPEIDAE (Herrings)

The three clupeids for which food-habit data are presented are all schooling fishes which are often seen in shallow water. They may be found near the surface, in mid-water, or near the bottom. When they swim

over reefs they are often preyed upon by the resident carnivorous fishes. They feed primarily on zooplankton.

Harengula clupeola (Cuvier) FALSE PILCHARD
2 stations; 21 specimens: 70 to 107 mm SL; 9 empty.

FOOD	VOLUME (%)
Copepods	55.0
<i>Candacia pachydactyla</i>	
<i>Undinula vulgaris</i>	
Crab larvae	25.0
Shrimp larvae	8.0
Polychaetes	5.0
Pteropods	5.0
<i>Creseis</i> sp.	
Fish eggs	2.0

Harengula humeralis Cuvier & Valenciennes RED-EAR SARDINE
2 stations; 24 specimens: 60 to 93 mm SL.

FOOD	VOLUME (%)
Fishes	60.5
Polychaetes	29.0
Shrimp larvae	5.0
Plants	2.5
<i>Enteromorpha</i> sp.	
<i>Thalassia</i> and <i>Cymodocea</i>	
Unidentified animal material	2.0
Crab larvae	1.0

Remarks.—The fish material in the stomachs consisted primarily of small fish scales. Entire larval fishes were also present. The plants were mostly small fragments of seagrass and green algae; these fragments may have been ingested accidentally during feeding on the zooplankton. This species is probably not as different in its food habits from *clupeola* as the above data would suggest. The component organisms of the plankton may vary greatly from one area to another, and the stomach contents of plankton-feeding fishes vary accordingly. More samples of these two fishes would probably show a greater similarity in the diet.

Opisthonema oglinum (LeSueur) THREAD HERRING
5 stations; 23 specimens: 127 to 177 mm SL; 6 empty.

FOOD	VOLUME (%)
Copepods	26.6
<i>Candacia pachydactyla</i>	
<i>Oithona</i> sp.	
<i>Temora stylifera</i>	
Polychaetes	22.4

SYNODONTIDAE (Lizardfishes)

The lizardfishes generally occur on sand or mud bottoms and are able to partially bury themselves in the sediment. They are carnivorous, as would be expected from their numerous sharp teeth which are inwardly depressible. Characteristically they feed by swimming very rapidly upward to seize their prey which usually consists of small fishes.

Synodus intermedius (Spix)

SAND DIVER

30 stations; 38 specimens: 65 to 325 mm SL; 20 empty.

FOOD	VOLUME (%)
Fishes	94.5
atherinid	
carangid	
<i>Jenkinsia</i> sp.	
<i>Haemulon</i> sp.	
<i>Harengula</i> sp.	
<i>Serranus</i> sp.	
Squids	5.0
Shrimps	0.5

Remarks.—Of this species, Beebe & Tee-Van (1928) stated, "Our food records mention fish, especially engraulids and atherinids, and shrimps." *S. intermedius* is the largest and most common inshore lizardfish in the West Indies. It is a clear-water species usually found on a sand bottom, but it may also come to rest on a rock substratum. Not infrequently it is caught by fishermen trolling lures over shallows.

Synodus foetens (Linnaeus)

INSHORE LIZARDFISH

4 stations; 9 specimens: 102 to 270 mm SL; 6 empty.

FOOD	VOLUME (%)
Fishes	100.0
<i>Anchoa</i> sp.	

Remarks.—*S. foetens* lives on both sand and mud bottoms in shallow water; it is rarely encountered on or near reefs. Linton (1905) recorded fishes, shrimps, small crabs, annelids, and a spatangoid sea urchin from 21 specimens from North Carolina with recognizable food in their digestive tracts. H. Smith (1907) reported small fish as the principal food of specimens from the same state; he added that crabs, shrimps, worms and other animals are also eaten. Reid (1954) examined 11 stomachs with food from West Florida; 10 contained fishes, including *Alutera schoepfi* and *Anchoa mitchilli*, and two contained penaeid shrimps. Reid (1955) found digested fish in three stomachs of *S. foetens* from Texas. Springer & Woodburn (1960) examined 20 stomachs from West Florida; 13 were filled with fishes (among them *Gobiosoma robustum*, *Anchoa mitchilli*, and *Menidia beryllina*); five contained crustaceans (two of these mixed with fish), and the remaining four were empty.

Synodus synodus (Linnaeus)

RED LIZARDFISH

2 stations; 4 specimens: 50 to 106 mm SL; 2 empty.

FOOD	VOLUME (%)
Fishes	100.0

MURAENIDAE (Moray Eels)

Proverbially voracious carnivores, most morays are equipped with numerous long depressible canine teeth and powerful jaws. Although they may be lured from their holes by day to feed on animal matter that strongly stimulates their olfactory sense, they normally seek food only at night. Their feeding, however, seems to consist more of waiting for their prey to come within striking range of their holes than actively hunting for it. Night diving usually reveals more morays than do observations on reefs during daylight hours, but poison stations with rotenone invariably produce many more of these eels than an observer would notice by night or day.

Echidna catenata (Bloch)

CHAIN MORAY

9 stations; 11 specimens: 250 to 450 mm TL; 3 empty.

FOOD	VOLUME (%)
Crabs	96.3

Acanthonyx petiverii

Cronius tumidulus

majid

Mithrax sp.

Shrimps	3.7
---------	-----

Lysmata moorei

Remarks.—The chain moray occurs in very shallow water in reefs or along rocky shores. Unlike most morays, its teeth are short and blunt, hence adapted to feeding on crustaceans. An eel with needle-sharp teeth would have more difficulty rendering a crustacean into pieces than one with rounded teeth.

Gymnothorax funebris Ranzani

GREEN MORAY

3 stations; 5 specimens: 340 to 1120 mm TL; 5 empty.

Remarks.—*G. funebris* is the largest western Atlantic moray. Although the stomachs of all five specimens were empty, the intestine of a 900-mm individual speared among rocks near a sandy beach in the early morning contained the remains of a xanthid crab and a ghost crab (*Ocypode albicans*). Gudger (1929) reported fish in the stomachs of three specimens from Dry Tortugas.

Gymnothorax moringa (Cuvier)

SPOTTED MORAY

12 stations; 26 specimens: 255 to 1090 mm TL; 20 empty.

FOOD	VOLUME (%)
Fishes	100.0

Haemulon aurolineatum

Lutjanus griseus

Remarks.—*G. moringa* is the most common moray of West Indian reefs. The stomach of the 1090-mm specimen contained a 200-mm gray snapper (*L. griseus*); however, the eel was caught in a trap. Gudger (1929) briefly discussed the mode of feeding on fishes, and Winn & Bardach (1959) and Bardach, Winn, & Menzel (1959) studied the role of the senses in feeding, and the nocturnal behavior.

Gymnothorax vicinus (Castelnau) PURPLEMOUTH MORAY
6 stations; 11 specimens: 260 to 770 mm TL; 7 empty.

FOOD	VOLUME (%)
Fishes	62.5
<i>Scarus</i> sp.	
Crabs	25.0
Octopuses	12.5

Remarks.—Additional data on the food habits of this species would probably reveal a higher percentage of fish in the diet than the 62.5 per cent indicated above. Bardach, Winn, & Menzel (1959) noted that this species, like the preceding, is nocturnal. They determined that the olfactory sense is used to detect distant food. Actual contact of the food with the snout stimulates taste receptors and elicits a grasping response.

OPICHTHIDAE (Snake Eels)

The snake eels are primarily burrowing forms in mud or sand. They apparently do not live in permanent burrows but move freely in the sediment. Their sharp-pointed snouts and tails represent an adaptation for such existence. Little is known of their habits. The two species of *Myrichthys* discussed below may be seen on reefs occasionally by day, generally in motion from one part to another.

Myrichthys acuminatus (Gronow) SHARPTAIL EEL
5 stations; 8 specimens: 420 to 890 mm TL; 1 empty.

FOOD	VOLUME (%)
Crabs	86.0
<i>Mithrax sculptus</i>	
Stomatopods	7.0
<i>Gonodactylus curacaoensis</i>	
Echinoids	7.0

Remarks.—Most of the specimens of *M. acuminatus* and those of the following species were collected with rotenone. Since they emerged from the sand nearly dead from the effect of the rotenone, it may be presumed that all of the stomach content material was normally consumed prior to the dispersal of the poison. A few of both species were taken with spears. These eels may have freshly-ingested material in their stomachs in the afternoon, so they feed at least in part during daylight hours.

Myrichthys ocellatus (Kaup)

OCELLATED EEL

7 stations; 22 specimens: 309 to 700 mm TL; 6 empty.

Food	VOLUME (%)
Crabs	61.2
xanthid	
portunid	
majid	
Unidentified crustaceans	18.7
Stomatopods	12.5
Shrimps	3.2
Fishes	3.2
Polychaetes	1.2

Remarks.—See *M. acuminatus*.

Ophichthus ophis (Linnaeus)

SPOTTED SNAKE EEL

4 stations; 5 specimens: 552 to 1220 mm TL; 1 empty.

Food	VOLUME (%)
Fishes	50.0
<i>Haemulon aurolineatum</i>	
Octopuses	50.0

Remarks.—The head of this eel is occasionally seen protruding diagonally from sand by day, thus affording a target for a spear. The largest specimen weighed 1400 grams, and its stomach contained an octopus weighing 197 grams. An 843-mm eel ate a 122-mm *Haemulon aurolineatum*, and a 552-mm specimen an 82-mm grunt of the same species. *O. ophis* has sharp teeth of moderate size, and it is feared by fishermen as much as morays.

CONGRIDAE (Conger Eels)

Taenioconger halis (Böhlke)

ATLANTIC GARDEN EEL

3 stations; 12 specimens: 187 to 450 mm TL; 1 empty.

Food	VOLUME (%)
Copepods	66.3
calanoids	
harpacticoids	
Tunicates	18.6
appendicularians	
Pteropods	4.5
Ostracods	3.8
Shrimp larvae	2.5
Unidentified eggs	2.4
Gastropod larvae	1.9

Remarks.—Garden eels live in groups in permanent burrows in the sand. Beds of these eels occur in a region of current and are often encountered

near reefs. The eels are very slender (the depth of the body is contained about 60 times in the length). Approximately the anterior three-fourths of the body emerges for feeding (the posterior fourth which remains in the burrow is distinctly paler than the rest of the body); the anterior end is bent forward facing the oncoming current. Small planktonic organisms are picked one by one from the passing water mass. The feeding movements made by a group of these eels is a fascinating sight. As many as 600 copepods varying in length from 0.4 to 2.1 mm were found in the stomach of a single adult garden eel.

BELONIDAE (Needlefishes)

The belonids are surface-dwelling fishes. They often swim over reefs, but they are not an integral part of the reef community. Their jaws are armed with an impressive array of needle-sharp teeth. The fulcrum arrangement and muscle attachment of the jaws is unique, providing for their opening and closing simultaneously with rapidity (Nelson, MS). The needlefishes feed voraciously on small fishes, especially clupeoids that school near the surface. They have been reported to drift slowly into range of their prey before making a quick rush. They are also capable of long skipping leaps on the surface, although such runs are probably associated more often with escaping predation than securing prey.

Platybelone argalus (LeSueur) KEELED NEEDLEFISH
6 stations; 15 specimens: 230 to 330 mm SL; 2 empty.

FOOD	VOLUME (%)
Fishes	97.0
<i>Jenkinsia</i> sp. (10)	
Insects	3.0
carpenter ants	

Strongylura timucu (Walbaum) TIMUCU
8 stations; 20 specimens: 159 to 378 mm SL; 5 empty.

FOOD	VOLUME (%)
Fishes	96.0
<i>Anchoa parva</i>	
<i>Jenkinsia</i> sp. (5)	
Shrimps	4.0

Remarks.—This needlefish is primarily an inshore species; it is often seen in mangrove sloughs and freely enters freshwater. It is closely related to and easily confused with *S. marina*. According to B. Collette (personal communication), only *timucu* occurs in the West Indies. The two species are found together in Florida and Central America to Brazil. Only *marina* ranges north of Florida. Linton (1905), H. Smith (1907), Hildebrand & Schroeder (1928), McClane (1965), Darnell (1959), and Springer &

Woodburn (1960) reported on the food habits of *marina*. As with *timucu* of the present study, fishes predominated in the diet, but copepods, other crustaceans, annelids, and insects were also listed from the stomachs.

Tylosurus acus (Lacépède)

AGUJON

9 stations; 13 specimens: 234 to 732 mm SL; 6 empty.

FOOD	VOLUME (%)
Fishes	96.3
carangid	
<i>Tylosurus</i> sp.	
Hermit crab larvae	1.4
Insects	1.4
wasp	
beetle	
Stomatopod larvae	0.9

Remarks.—Linton (1905) recorded small crustaceans and fragments of insects from a specimen from North Carolina.

Tylosurus crocodilus (Peron & LeSueur)

HOUND FISH

14 stations; 19 specimens: 250 to 1320 mm SL; 8 empty.

FOOD	VOLUME (%)
Fishes	90.9
<i>Acanthurus</i> sp. (larv.)	
<i>Anchoa</i> sp.	
<i>Cetengraulis edentulus</i>	
<i>Harengula humeralis</i>	
<i>Mugil</i> sp.	
Shrimps	9.1

Remarks.—*T. crocodilus* is the largest of the needlefishes; it occurs more inshore, in general, than the preceding species. Linton (1905) recorded menhaden and a few small crustaceans from the stomach of a specimen about 3 feet long from North Carolina. Jordan & Thompson (1905) observed individuals of this species prey upon sardines at Tortugas. They wrote, "After catching one they manipulate it very ingeniously with their jaws until it is pointed 'head on' toward the throat before any endeavor is made to swallow it."

HEMIRAMPHIDAE (Halfbeaks)

The hemiramphids are primarily surface-dwelling fishes; some species are characteristic of coastal waters, and others completely pelagic. The inshore species often range over shallow reefs. On one occasion a half-beak was observed to swim down to the bottom where a "cleaning" fish picked over its body, ostensibly in search of ectoparasites. Jordan & Evermann (1896) ascribed herbivorous habits to the halfbeaks, adding

that they feed chiefly on green algae. Uchida (1930) (reference from Suyehiro, 1942), however, reported a species of *Hemiramphus* as a zooplankton-feeder, and Hiatt & Strasburg (1960) found small fishes, planktonic crustaceans and other planktonic animals in the stomachs of two species of *Hyporhamphus*. The study by the author of the food habits of two West Indian *Hemiramphus* indicates that the food habits can vary markedly with the species. The family is more properly termed omnivorous than herbivorous. It is doubtful that they feed on green algae (see Remarks of *H. brasiliensis* below). Opinions differ on the possible use of the long lower jaw of the hemiramphids. Uchida concluded that it is not only useless in feeding but is actually a hindrance. J. Randall (MS) has suggested that it might serve as a cutwater.

Hemiramphus balao LeSueur

BALAO

6 stations; 16 specimens: 130 to 196 mm SL; 7 empty.

FOOD	VOLUME (%)
Fishes	39.1
<i>Jenkinsia</i> sp. (larv. and juv.) (4)	
Pteropods	31.4
cavolinids	
Unidentified animal material	11.8
Polychaetes	8.9
Crab larvae	4.7
Shrimp larvae	2.9
Copepods	1.2

Remarks.—This species occurs more offshore, in general, than the following. No plant material was found in its stomachs.

Hemiramphus brasiliensis (Linnaeus)

BALLYHOO

8 stations; 39 specimens: 164 to 246 mm SL.

FOOD	VOLUME (%)
Seagrasses (and epiphytes)	81.0
<i>Cymodocea manatorum</i>	
<i>Thalassia testudinum</i>	
Fishes	19.0
<i>Jenkinsia</i> sp. (3)	

Remarks.—Beebe & Tee-Van (1928) reported that three specimens of *H. brasiliensis* from Haiti had eaten *Thalassia*, algae, land plants, a spider, and insects, including a hymenopteran. Burkholder, Burkholder & Rivero (1959) stated that *Thalassia* is the principal food of the species. Randall (1965a) wrote that the stomach contents of ballyhoo in St. John consisted of manatee grass (*Cymodocea*) and *Jenkinsia* and noted that the halfbeaks fed upon the seagrasses as floating fragments. The pieces of seagrass are grasped at one end and drawn into the mouth apparently by the action of the pharyngeal mill which grinds the plant material to a fine pulp. *Thalassia*

is also eaten as fragments on the surface. In a mixed flotsam of *Thalassia* and *Cymodocea*, the fish usually took the latter. They readily ate green, straw-colored, or brownish strands of seagrass, whether covered with epiphytic algae or not, but they avoided dark brown or black fragments. When pieces of land plants (several coarse grasses and the needles of Australian pine) were allowed to drift toward a school of feeding ballyhoo off the dock of the Institute of Marine Science of the University of Miami, these plants were not consumed. At times the fish took the land-plant fragments in their mouths but always rejected them.

FISTULARIIDAE (Cornetfishes)

Fistularia tabacaria Linnaeus

CORNETFISH

3 stations; 4 specimens: 357 to 1000 mm SL; 2 empty.

FOOD	VOLUME (%)
Fishes	100.0
<i>Monacanthus setifer</i>	
<i>Pseudupeneus maculatus</i>	

Remarks.—The cornetfish appears to be a rare species in the West Indies. It was more often seen over beds of seagrass than reefs. The specimen containing the identified fishes measured 810 mm in standard length. The filefish in its stomach measured 38 mm SL, and the two goatfish about 60 mm. This cornetfish was itself taken from the stomach of a black grouper (*Mycteroperca bonaci*) 920 mm in SL which was speared in 60 feet off the Dominican Republic. Hiatt & Strasburg (1960) found only fish in the stomachs of nine specimens of the Indo-Pacific *Fistularia petimba*. These authors do not agree with Suyehiro (1942) (after Marukawa) that this fish takes only minute, floating creatures by utilizing its snout as a pipette.

AULOSTOMIDAE (Trumpetfishes)

Aulostomus maculatus Valenciennes

TRUMPETFISH

32 stations; 80 specimens: 290 to 650 mm SL; 11 empty.

FOOD	VOLUME (%)
Fishes	73.5
<i>Acanthurus</i> sp. (larv.)	
<i>Acanthurus bahianus</i> (larv.)	
<i>Anchoa</i> sp.	
apogonid	
blenniid	
clinids (2)	
<i>Chromis cyanea</i>	
<i>Haemulon aurolineatum</i>	
<i>Haemulon flavolineatum</i>	

Holocentrus coruscus
Holocentrus rufus
Labrisomus kalisherae
Malacoctenus gilli
Myripristis jacobus
Ophioblennius atlanticus (3)
Pomacentrus sp.
Pomacentrus pictus
Pseudupeneus maculatus
Quisquilius hipoliti
Thalassoma bifasciatum

Shrimps

26.5

carideans (3)

Remarks.—Beebe & Tee-Van (1928) reported fish, including an engraulid and *Pomacentrus* sp., in the stomachs of three specimens of *Aulostomus* from Haiti. Trumpetfish were often observed on reefs in the Virgin Islands and Puerto Rico hovering vertically in the water over small bottom-dwelling fishes, and on several occasions they were seen darting down on them. Hiatt & Strasburg (1960) have suggested that the Indo-Pacific species *A. chinensis* might utilize its long tubular snout to probe into holes or interstices. Some of the fish taken from the stomachs of *A. maculatus* were surprisingly large. A 590-mm individual, for example, contained a fully intact, 128-mm squirrelfish (*Holocentrus rufus*). Prey of this size seemed too large for the narrow snout of the trumpetfish until the distensible membranous floor of the buccal region was noted. Since the trumpetfish mouth is small and the teeth minute, it may be assumed that the prey is sucked in by the expansion of the floor of the snout and of the gill membranes. The same mode of feeding probably takes place in *Fistularia*. The acanthurids from the stomachs of trumpetfish were the transforming late postlarval stage known as the acronurus. Trumpetfish were found in the stomachs of the snappers *Lutjanus apodus* and *L. jocu* and the groupers *Mycteroperca venenosa*, *Cephalopholis fulva*, and *Epinephelus guttatus*. The elongate bodies of all of the trumpetfish were folded once in the predators' stomachs.

HOLOCENTRIDAE (Squirrelfishes)

The squirrelfishes are nocturnal, as their large eyes would suggest. Although they may occasionally be taken on hook and line by day, their stomachs are almost invariably empty except during night and early morning hours. They tend to hide in holes and cracks in reefs during the day but forage actively at night. Stomachs sometimes contain fragments of seagrass along with the prey, thus indicating that the fish had been seeking food in grass beds away from their home reef. Crustaceans constitute the most important group of food organisms. Fish forms an insignificant part

of the diet, as might be predicted from the small size of the teeth in the jaws.

Holocentrus ascensionis Osbeck

SQUIRRELFISH

9 stations; 31 specimens: 125 to 235 mm SL; 11 empty.

FOOD	VOLUME (%)
Crabs	73.3
<i>Actaea rufopunctata</i>	
<i>Chlorodiella longimana</i>	
<i>Macrocoeloma trispinosum</i>	
majids	
<i>Mithrax forceps</i>	
<i>Mithrax sculptus</i> (3)	
<i>Pitho</i> sp.	
<i>Platypodia spectabilis</i>	
portunid	
<i>Portunus</i> sp.	
Shrimps	10.6
alpheids (2)	
penaeids	
Unidentified crustaceans	10.6
Polychaetes	3.9
Gastropods	1.0
<i>Tricolia adamsi</i>	
Isopods	0.6

Remarks.—This species appears to be more inclined to forage over grass flats than the remaining holocentrids listed herein.

Holocentrus coruscus (Poey)

REEF SQUIRRELFISH

8 stations; 24 specimens: 45 to 102 mm SL; 5 empty.

FOOD	VOLUME (%)
Shrimps	70.0
alpheid	
carideans	
penaeids (2)	
Crabs	27.3
<i>Ebalia stimpsonii</i>	
<i>Mithrax</i> sp.	
<i>Portunus</i> sp.	
<i>Sicyonia</i> sp.	
Unidentified crustaceans	2.7

Remarks.—Beebe & Tee-Van (1928) reported a shrimp in the stomach of one specimen of this species.

Holocentrus marianus Cuvier & Valenciennes LONGJAW SQUIRRELFISH
8 stations; 13 specimens: 82 to 113 mm SL; 4 empty.

FOOD	VOLUME (%)
Shrimps	51.7
Crabs	30.6
Unidentified crustaceans	13.3
Stomatopod larvae	3.3
Copepods	1.1

Remarks.—*H. marianus* occurs in deeper water, on the average, than the other squirrelfishes considered herein; it is rarely seen in less than 40 feet.

Holocentrus rufus (Walbaum) LONGSPINE SQUIRRELFISH
16 stations; 55 specimens: 132 to 250 mm SL; 13 empty.

FOOD	VOLUME (%)
Crabs	56.9
<i>Domecia hispida</i>	
<i>Euryplax nitida</i>	
majids (2)	
<i>Mithrax</i> sp.	
<i>Mithrax coryphe</i>	
<i>Mithrax forceps</i>	
<i>Mithrax sculptus</i> (2)	
<i>Pitho lherminieri</i>	
porcellanids	
xanthids (3)	
<i>Xanthodius denticulatus</i>	
Shrimps	15.0
alpheids (3)	
gnathophyllids (2)	
penaeids	
Gastropods	7.8
<i>Acmaea</i> sp.	
<i>Acmaea pustulata</i>	
acmaeid	
<i>Emarginula pumila</i>	
<i>Hyalina</i> sp.	
<i>Hyalina albolineata</i>	
<i>Hyalina avena</i>	
<i>Mitrella lunata</i>	
<i>Pseudostomatella coccinea</i>	
<i>Pseudostomatella erythrocoma</i> (2)	
<i>Purpura patula</i>	
Ophiuroids	7.1
<i>Ophionereis</i> sp. (2)	

<i>Ophiothrix</i> sp.	
Polychaetes	4.5
Unidentified crustaceans	2.4
Isopods	1.5
<i>Exocorallina antillensis</i>	
Mysids	1.4
Ostracods	1.2
Fishes	1.2
Chitons	0.6
<i>Acanthochitona pygmaea</i>	
Stomatopods	0.4
<i>Holocentrus vexillarius</i> (Poey)	DUSKY SQUIRRELFISH
14 stations; 55 specimens: 45 to 118 mm SL; 13 empty.	
FOOD	VOLUME (%)
Crabs and crab larvae	26.9
<i>Domecia hispida</i>	
<i>Mithrax</i> sp.	
<i>Petrolisthes galathinus</i> (2)	
Gastropods	25.1
<i>Acmaea</i> sp. (2)	
<i>Acmaea antillarum</i>	
<i>Acmaea pustulata</i>	
acmaeids (2)	
<i>Diodora viridula</i>	
<i>Fissurella</i> sp.	
<i>Fissurella barbadensis</i>	
<i>Hyalina albolineata</i>	
<i>Nitidella nitida</i>	
<i>Persicula lavalleeana</i>	
<i>Pseudostomatella coccinea</i>	
<i>Synaptocochlea picta</i>	
Shrimps and shrimp larvae	20.8
alpheids (3)	
gnathophyllid	
<i>Gnathophylloides mineri</i>	
palaemonids	
Chitons	10.3
<i>Choneplax lata</i>	
Isopods	5.7
Fishes and fish larvae	5.2
<i>Acanthurus</i> sp. (larv.)	
Polychaetes	4.0
Unidentified crustaceans	1.6
Copepods	0.4

Remarks.—*H. vexillarius* is the most common inshore squirrelfish in the West Indies. It is abundant in holes and beneath ledges along protected rocky shores. McKenney (1959) reported the stomach-content material of a series of *vexillarius* from young to adults to consist of copepods, ostracods, mysids, alpheid shrimps, crabs, isopods, barnacle appendages, gastropods and gastropod larvae, pelecypod larvae, chitons, octopuses, and brittle stars.

Myripristis jacobus Cuvier & Valenciennes BLACKBAR SOLDIERFISH
14 stations; 46 specimens: 69 to 180 mm SL; 12 empty.

FOOD	VOLUME (%)
Shrimps and shrimp larvae	30.3
alpheids (3)	
carideans	
gnathophyllids	
penaeids	
Stomatopod larvae	17.4
<i>Gonodactylus</i> sp.	
<i>Nannosquilla</i> sp.	
<i>Squilla</i> sp.	
Crabs and crab larvae	14.9
Mysids	11.2
Polychaetes	7.0
Fish larvae	5.4
chaetodontid	
Amphipods	3.2
hyperiids	
Unidentified crustaceans	2.7
Copepods	2.4
Isopods	1.8
Cephalopod larvae	1.5
Hermit crab larvae	0.9
Scyllarid larvae	0.9
Ostracods	0.3
Unidentified animal material	0.1

Remarks.—In contrast to the species of *Holocentrus*, *Myripristis jacobus* feeds predominantly on planktonic organisms. Nearly all of the shrimps and crabs from the stomachs, for example, were larval forms.

Plectrypops retrospinis (Guichenot) CARDINAL SOLDIERFISH
8 stations; 10 specimens: 45 to 98 mm SL; 8 empty.

FOOD	VOLUME (%)
Crab	50.0
xanthid	
Polychaete	50.0

MUGILIDAE (Mulletts)

Mulletts are characteristic of mud or sand bottoms. Most feed on fine detrital and bottom algal material. They usually ingest a large amount of fine sediment. Except for *Agonostomus* and two other small genera, they have thick-walled stomachs. This gizzard-like organ probably makes use of the sedimentary material to triturate the plant food. Thomson (1954) has written a review of the feeding of six mugilid species, including discussions of mouth structure.

Mugil curema Cuvier & Valenciennes

WHITE MULLET

5 stations; 17 specimens: 200 to 290 mm SL; 4 empty.

FOOD	VOLUME (%)
Plant material	100.0
diatoms	
<i>Lyngbya majuscula</i>	
<i>Rhizoclonium riparium</i>	
<i>Thalassia testudinum</i>	
<i>Vaucheria</i> sp.	

Remarks.—The majority of the material in the stomachs of these mullet consisted of mud and fine silt. *Mugil curema* is the most common species of mullet in the West Indies. It occurs along sandy shores, in brackish mangrove sloughs, and in freshwater. Linton (1905) found mud, vegetable debris, and diatoms in one specimen from North Carolina. Hildebrand & Schroeder (1928) described the food as almost wholly minute organisms, mixed with quantities of mud and vegetable debris. Beebe & Tee-Van (1928) reported the stomach contents of freshwater specimens as mud, decayed vegetation, and bottom debris. Ebeling (1957) noted that the young may feed directly on attached algae; their stomachs contained primarily diatoms and algal filaments.

SPHYRAENIDAE (Barracudas)

The barracudas are open-water predaceous fishes with notably long, sharp-edged teeth in the jaws and on the palate. They feed primarily on fishes. De Sylva (1963) noted from aquarium observations that *Sphyræna barracuda* may feed by taking its prey entire, either head-first or tail-first, fold it in mid-section before swallowing, or slice it into two or more pieces. The author observed the feeding by a large individual on the cero mackerel (*Scomberomorus regalis*) in the Virgin Islands. A very swift attack was made on the mackerel, resulting in its being cut into two approximately equal halves. The barracuda then circled slowly to pick up the halves. Another large barracuda was observed trying unsuccessfully to bite through a speared member of the same species slightly more than half its length. Barracudas, in general, are diurnal, although there are some reports of certain species feeding at night, particularly during periods of full moon.

Two of the three West Indian species enter the reef community in the sense that they may feed on reef fishes.

Sphyraena barracuda (Walbaum)

GREAT BARRACUDA

78 stations; 104 specimens: 70 to 1070 mm SL; 46 empty.

Food	VOLUME (%)
Fishes	95.5
<i>Ablennes hians</i>	
<i>Acanthurus bahianus</i>	
<i>Allanetta harringtonensis</i>	
atherinids	
<i>Canthigaster rostrata</i>	
carangids (3)	
<i>Caranx fusus</i>	
clupeid	
<i>Decapterus</i> sp.	
<i>Diodon</i> sp.	
<i>Echidna catenata</i>	
<i>Haemulon</i> sp. (2)	
<i>Harengula clupeiola</i>	
<i>Jenkinsia</i> sp. (2)	
<i>Ocyurus chrysurus</i> (2)	
scarid	
<i>Sphyraena picudilla</i> (2)	
<i>Trachinocephalus myops</i>	
Octopuses	2.6
Scyllarid lobster (larv.)	1.9

Remarks.—*S. barracuda* is common in the West Indies; it is usually solitary. Nine of the specimens examined ranged from 70 to 125 mm SL; the remaining fish all exceeded 232 mm. The smaller barracuda fed upon schooling clupeoid and atherinid fishes. One 595-mm fish was caught while trolling on a bright moonlight night; the rest were collected by day, about half by hook and line and half by spearing. De Sylva (1963) reported on the examination of the stomachs of 901 barracudas, mostly taken by hook and line off Florida and the Bahamas. Fishes predominated in the diet. He noted that the size of prey is highly variable. This was substantiated by the author's analyses. A 1040-mm barracuda ate six *Diodon* sp. that ranged from 55 to 60 mm in standard length; an 840-mm fish contained only a 30-mm scyllarid. On the other hand, a 910-mm individual had eaten a 700-mm moray (*Echidna catenata*); it was folded in the stomach. Other prey fishes such as *Acanthurus bahianus*, *Aulostomus maculatus*, *Caranx fusus*, *Ocyurus chrysurus*, and *Sphyraena picudilla* were cut into two or three pieces. In the case of the former two, only the posterior halves were found in the barracuda stomachs. Most of the larger barracuda contained only a single fish. An exception was the largest

specimen collected (1070 mm SL) which had eaten 18 false pilchards (*Harengula clupeola*) from 84 to 100 mm in standard length. No squids were found by the author in barracuda stomachs, but probably they are eaten now and then. A large barracuda was observed to chase a small school of *Sepiateuthis sepioides* into very shallow water, but it failed to catch any. Randall (1960) discussed the problem of barracuda which fed upon tagged reef fishes before they could reach the shelter of the reef after release from a boat. The following tagged fish were taken from the stomachs of two such marauding barracudas: *Acanthurus bahianus*, *A. coeruleus*, *Mulloidichthys martinicus*, *Pseudupeneus maculatus*, and *Sparisoma* sp.

Sphyræna picudilla Poey SOUTHERN SENNET
5 stations; 13 specimens: 265 to 395 mm SL; 6 empty.

FOOD	VOLUME (%)
Fishes	82.1
Squids	17.9

Remarks.—*S. picudilla* is a small schooling species of barracuda. Schools are occasionally seen over reefs, but more often encountered over seagrass beds. The species was not observed to be common in any region, however.

ATHERINIDAE (Silversides)

The silversides are small schooling fishes. They are represented by two species which occur inshore throughout the West Indies. *Atherinomorus stipes* is the most common. These fishes feed primarily on zooplankton, and they, in turn, are fed upon heavily by jacks, barracudas, certain scombrids, and various piscivorous reef fishes.

Allanetta harringtonensis (Goode) REEF SILVERSIDES
4 stations; 23 specimens: 39 to 60 mm SL; 9 empty.

FOOD	VOLUME (%)
Copepods	89.2
<i>Corycaeus</i> sp.	
<i>Labidocera scotti</i>	
<i>Paracalanus crassirostris</i>	
Fish larvae	8.1
Polychaete larvae	2.7

Atherinomorus stipes (Müller & Troschel) HARDHEAD SILVERSIDES
4 stations; 20 specimens: 35 to 69 mm SL; 11 empty.

FOOD	VOLUME (%)
Shrimp larvae	35.6
Copepods	30.0
<i>Calocalanus</i> sp.	
<i>Farranula gracilis</i>	

<i>Oncaea</i> sp. (2)	
<i>Paracalanus aculeatus</i>	
<i>Pontella</i> sp.	
Fish scales	20.0
Barnacle appendages and larvae	10.0
Fish eggs	2.2
Foraminifera	2.2

SERRANIDAE (Groupers and Sea Basses)

The serranids are among the most important carnivorous fishes of coral reefs. They are characteristically robust of build, with large mouths, numerous depressible inner teeth, and usually a few stout fixed outer canines in the jaws. Typically they are demersal. As C. Smith (1961) has noted, they eat primarily fishes and crustaceans. With the exception of the jewfish (*Epinephelus itajara*), the larger groupers tend to feed more on fishes than crustaceans. They feed both by night and day but are most active at dawn and dusk. The smaller serranids, in general, are primarily diurnal.

Alphestes afer (Bloch) MUTTON HAMLET
5 stations; 36 specimens: 127 to 195 mm SL; 6 empty.

FOOD	VOLUME (%)
Crabs	77.0
<i>Chorinus heros</i>	
<i>Mithrax</i> sp. (2)	
<i>Pitho</i> sp.	
portunids (2)	
<i>Portunus</i> sp.	
Fishes	7.0
<i>Acanthurus</i> sp. (juv.)	
eels (2)	
Shrimps	6.8
alpheids	
Unidentified crustaceans	6.7
Octopuses	2.5

Remarks.—*Alphestes afer* is a small grouper that is most often found in seagrass beds; only occasionally is it seen in natural reefs. When an artificial reef was built in a seagrass bed in the Virgin Islands, however, this species became the principal serranid fish which colonized it (Randall, 1963b); the individual mutton hamlets moved in as adults from the adjacent seagrass bed. The occurrence of bits of *Thalassia* or *Cymodocea* in the stomachs with the prey indicated that feeding took place, at least in part, in the grass bed.

Cephalopholis fulva (Linnaeus)

CONEY

36 stations; 58 specimens: 146 to 240 mm SL; 29 empty.

FOOD	VOLUME (%)
Fishes	46.0
<i>Acanthurus</i> sp. (juv.) (2)	
<i>Aulostomus maculatus</i>	
<i>Cantherhines pullus</i>	
<i>Monacanthus tuckeri</i>	
scarid	
<i>Sphaeroides</i> sp.	
<i>Starksia</i> sp.	
Shrimps	20.7
stenopodid	
<i>Stenopus hispidus</i> (2)	
Crabs	17.2
<i>Percnon gibbesi</i>	
porcellanid	
Stomatopods	12.4
<i>Gonodactylus</i> sp.	
<i>Gonodactylus oerstedii</i>	
Unidentified crustaceans	3.7

Remarks.—The coney is relatively wary for a grouper, and it was difficult to obtain many specimens by spearfishing. It is one of the most common of the reef-dwelling serranids. Beebe & Tee-Van (1928) stated that most of their specimens from Haiti contained crustaceans, especially shrimps.

Epinephelus adscensionis (Osbeck)

ROCK HIND

40 stations; 56 specimens: 122 to 395 mm SL; 25 empty.

FOOD	VOLUME (%)
Crabs	66.7
<i>Domecia hispida</i>	
<i>Leptodius floridanus</i>	
<i>Mithrax</i> sp.	
<i>Mithrax sculptus</i> (2)	
<i>Percnon gibbesi</i>	
<i>Petrolisthes galathinus</i> (2)	
<i>Portunus sebae</i> (2)	
portunid	
<i>Stenorynchus seticornis</i>	
xanthid	
Fishes	20.1
<i>Cantherhines pullus</i>	
<i>Sparisoma</i> sp.	
Shrimps	4.4
Unidentified crustaceans	4.0

Gastropods	3.2
<i>Cittarium pica</i>	
Chitons	1.6
<i>Acanthochiton hemphilli</i>	

Remarks.—Although it may be taken in more than 100 feet of water, the rock hind is most typically seen in shallow water on a rock bottom with some surf action. It is more difficult to approach than the closely related red hind. The gastropod remains in the stomach of one 390-mm fish consisted of two individuals of *Cittarium pica* without shell; they were identified from the characteristic opercula. As indicated by H. Randall (1964), it is highly unlikely that the rock hind crushed the shell of this stout gastropod. It probably obtained the meal after some other predator exposed the soft parts.

Epinephelus guttatus (Linnaeus) RED HIND
83 stations; 110 specimens: 82 to 450 mm SL; 60 empty.

FOOD	VOLUME (%)
Crabs	39.5
<i>Calappa gallus</i>	
<i>Cronius ruber</i>	
majid	
<i>Panopeus</i> sp.	
<i>Portunus sebae</i> (2)	
<i>Stenorynchus seticornis</i> (2)	
Fishes	21.1
<i>Aulostomus maculatus</i>	
<i>Cantherhines pullus</i>	
<i>Gymnothorax</i> sp. (3)	
<i>Inermia vittata</i>	
<i>Mulloidichthys martinicus</i>	
scarid	
Stomatopods	16.6
<i>Gonodactylus oerstedii</i>	
Shrimps	10.5
<i>Stenopus hispidus</i>	
<i>Synalpheus</i> sp.	
<i>Trachypenaeus</i> sp.	
Octopuses	7.0
<i>Octopus briareus</i>	
Unidentified crustaceans	3.3
Echiuroids	2.0

Remarks.—The red hind is the most abundant grouper in Puerto Rico and the Virgin Islands. It is more easily approached than any other West Indian grouper, hence highly vulnerable to spearfishing. Bardach &

Menzel (1957) reported it as one of the most prevalent small groupers of the shallow reefs of Bermuda and the tamest in captivity. They conducted growth studies from the rearing of captive fish and tagging on Bermuda reefs. Randall (1962a) also studied the growth from tagging. Beebe & Tee-Van (1928) reported on the stomach contents of two individuals from Haiti, one of which had eaten a small parrotfish and shrimps. Menzel (1960) listed the principal food at Bermuda as crustaceans, especially crabs of the genus *Calappa* and alpheid shrimps; some fishes were eaten, especially the wrasse *Thalassoma bifasciatum*.

Epinephelus itajara (Lichtenstein)

JEWFISH

9 stations; 9 specimens: 1250 to 1650 mm SL.

FOOD	VOLUME (%)
Spiny lobsters	45.6
<i>Panulirus argus</i> (5)	
Scyllarid lobsters	23.3
<i>Scyllarides aequinoctialis</i> (2)	
Fishes	13.3
<i>Dasyatis americana</i>	
<i>Diodon</i> sp.	
Crabs	12.2
Sea turtles	5.6
<i>Eretmochelys imbricata</i>	

Remarks.—Beebe & Tee-Van (1928) reported the remains of a parrotfish from the stomach of a 367-mm jewfish. Erdman (1956) listed three spiny lobsters (*Panulirus argus*) from an 187-pound specimen from Puerto Rico. C. Smith (1961) stated that *E. itajara* feeds chiefly on crustaceans. It is the largest reef fish in the Atlantic, attaining a weight of at least 680 pounds. It is not common in the West Indies, which is fortunate for fishermen seeking the valuable spiny lobster. As many as five adult lobsters have been taken from the stomach of a single jewfish. One fish of 150 pounds speared by the author in St. John contained two lobsters that weighed 6.75 and 3.5 pounds. The stomach of another from St. John of 340 pounds taken with spears contained the scutes of the carapace of a small hawksbill turtle, a spiny lobster, a slipper lobster, and fish remains.

Epinephelus morio (Cuvier & Valenciennes)

RED GROUPER

5 stations; 5 specimens: 228 to 340 mm SL; 3 empty.

FOOD	VOLUME (%)
Unidentified crustaceans	50.0
Crabs	33.3
Fishes	16.7

Remarks.—Although a common species in Florida and the Gulf of Mexico, the red grouper is rare in the West Indies. Gudger (1929) reported fish, including a lutjanid and two sparids, from the stomachs of three specimens

from Dry Tortugas, Florida. Longley & Hildebrand (1941) stated that this species at Dry Tortugas feeds indifferently by day or night; they listed fishes, octopuses, and crustaceans such as shrimps, stomatopods, and spiny lobsters as the food.

Epinephelus striatus (Bloch)

NASSAU GROUPER

166 stations; 255 specimens: 170 to 686 mm SL; 102 empty.

Food

VOLUME (%)

Fishes

54.0

Acanthurus sp.
Anchoa lamprotaenia
 atherinids
Cantherhines pullus
Cephalopholis fulva
Chromis cyanea
Chromis multilineata
Clepticus parrae (3)
Enchelycore nigricans
 engraulids
Gymnothorax moringa
Haemulon aurolineatum (2)
Haemulon flavolineatum
Halichoeres bivittatus (2)
Halichoeres garnoti
Harengula clupeola
Holocentrus, sp.
Holocentrus rufus (2)
Hypoplectrus puella
Jenkinsia lamprotaenia (2)
Lactophrys sp.
Lutjanus sp.
Microspathodon chrysurus
Muraena miliaris
 muraenid
Myripristis jacobus
Ocyurus chrysurus (3)
 pomacentrid
Pomacentrus fuscus
Priacanthus cruentatus
Pseudupeneus maculatus (2)
 scarids (11)
Scarus sp.
Scarus vetula
Sparisoma aurofrenatum
 synodontid

<i>Synodus intermedius</i>	
Crabs	22.5
<i>Calappa</i> sp.	
<i>Calappa flammea</i>	
calappids (2)	
<i>Cronius ruber</i>	
<i>Macrocoelema</i> sp.	
majids (4)	
<i>Mithrax</i> sp.	
<i>Mithrax cinctimanus</i>	
<i>Mithrax verrucosus</i>	
<i>Petrolisthes galathinus</i>	
porcellanids	
portunids (4)	
<i>Portunus sebae</i> (3)	
<i>Stenorynchus seticornis</i> (3)	
xanthids (3)	
Stomatopods	5.5
<i>Gonodactylus oerstedii</i> (4)	
<i>Pseudosquilla ciliata</i>	
Cephalopods	5.2
Shrimps	5.0
alpheids (2)	
carideans	
penaeids	
Spiny lobsters	3.5
<i>Panulirus argus</i> (3)	
<i>Panulirus guttatus</i>	
Gastropods	1.6
<i>Strombus gigas</i> (3)	
Hermit crabs	1.2
<i>Paguristes depressus</i>	
<i>Petrochirus diogenes</i>	
Pelecypods	0.7
<i>Barbatia cancellaria</i>	
Unidentified crustaceans	0.6
Isopods	0.2

Remarks.—Randall (1965b) reported on the analysis of the stomach contents of 250 Nassau groupers. A summary of this study is presented above, with the addition of data from five more specimens (two empty, three with fishes in their stomachs). The larger Nassau groupers fed more upon fishes and less on crustaceans than the smaller individuals. The mollusks and hermit crabs from the grouper stomachs contained no shells or shell fragments. Cephalopod remains included both octopuses and squids.

Hypoplectrus aberrans (Poey)

YELLOW-BELLIED HAMLET

17 stations; 25 specimens: 67 to 97 mm SL; 9 empty.

FOOD	VOLUME (%)
Shrimps	43.8
Crabs	18.7
Unidentified crustaceans	18.7
Fishes	11.9
Stomatopods	6.3
Mysids	0.6

Remarks.—This and the other species of *Hypoplectrus* are small compressed serranid fishes that live as adults on reefs. Unlike species of *Epinephelus* which frequently come in contact with the substratum, the hamlets usually swim a few inches off the bottom. They are slow-swimming, seemingly inquisitive, and easily approached. Beebe & Tee-Van (1928) described the food of hamlets, in general, as crustaceans and fishes. Randall & Randall (1960) stated that they feed mostly on benthic crustaceans of moderate size such as crabs, shrimps, and stomatopods, and occasionally on small fishes and polychaetes.

Hypoplectrus chlorurus (Cuvier & Valenciennes)

YELLOWTAIL HAMLET

16 stations; 20 specimens: 65 to 110 mm SL; 5 empty.

FOOD	VOLUME (%)
Shrimps	51.2
carideans	
<i>Periclimenes</i> sp.	
Fishes	25.0
blenniid	
Crabs	17.1
<i>Domecia hispida</i>	
<i>Pilumnus</i> sp.	
Unidentified crustaceans	6.7

Hypoplectrus nigricans (Poey)

DARK HAMLET

24 stations; 35 specimens: 67 to 123 mm SL; 18 empty.

FOOD	VOLUME (%)
Fishes	44.2
Shrimps	29.4
Crabs	17.6
Mysids	5.9
Stomatopods	2.9

Hypoplectrus puella (Cuvier & Valenciennes)

BARRED HAMLET

21 stations; 38 specimens: 54 to 98 mm SL; 19 empty.

FOOD	VOLUME (%)
Shrimps	51.0
alpheids	

<i>Brachycarpus biunguiculatus</i>	
<i>Periclimenes</i> sp.	
Crabs	21.1
<i>Petrolisthes</i> sp.	
Fishes	10.0
Mysids	8.9
Stomatopods	5.3
Isopods	3.7

Remarks.—The most common of the species of *Hypoplectrus* in the West Indies.

<i>Mycteroperca bonaci</i> (Poey)	BLACK GROUPER
5 stations; 6 specimens: 307 to 920 mm SL; 2 empty.	
FOOD	VOLUME (%)
Fishes	100.0
<i>Fistularia tabacaria</i>	
<i>Haemulon flavolineatum</i>	

Remarks.—The black grouper, the largest of the Atlantic *Mycteroperca*, is a common fish in Florida and the Bahamas, but rare in Puerto Rico and the Virgin Islands. The stomach of the 920-mm fish contained a cornetfish (*Fistularia*) 810 mm in standard length; it was folded once in the stomach, and the snout projected from the grouper's gullet into the mouth. See Remarks under *Mycteroperca venenosa* for some general statements on the genus.

<i>Mycteroperca interstitialis</i> (Poey)	YELLOWMOUTH GROUPER
8 stations; 8 specimens: 168 to 420 mm SL; 3 empty.	
FOOD	VOLUME (%)
Fishes	100.00
atherinids	
<i>Chromis multilineata</i>	
<i>Scarus croicensis</i>	

Remarks.—*M. interstitialis* is not a common species of grouper in the West Indies. The 420-mm specimen contained two individuals of *Chromis multilineata*, 78 and 100 mm in standard length.

<i>Mycteroperca tigris</i> (Cuvier & Valenciennes)	TIGER GROUPER
52 stations; 59 specimens: 153 to 572 mm SL; 25 empty.	
FOOD	VOLUME (%)
Fishes	100.0
<i>Acanthurus</i> sp.	
<i>Acanthurus bahianus</i>	
<i>Acanthurus coeruleus</i> (2) (juv.)	
atherinids	
<i>Cantherhines pullus</i> (juv.)	

Haemulon sp.
Haemulon flavolineatum (2)
Jenkinsia sp. (2)
Odontoscion dentex
Ophioblennius atlanticus (2)
Pomacentrus fuscus (2)
Pomacentrus planifrons
 scarid
Sparisoma sp.

Remarks.—The tiger grouper is the most easily approached of the species of *Mycteroperca* discussed herein; therefore, more specimens were speared per unit of effort than the other species of the genus. The two juvenile blue tangs and the one filefish from the grouper stomachs were all transforming from the late postlarval stage. The one specimen of *Acanthurus* sp., which measured 110-mm in standard length, was taken from the stomach of a 380-mm *M. tigris*.

Mycteroperca venenosa (Linnaeus) YELLOWFIN GROUPER
 109 stations; 127 specimens: 175 to 745 mm SL; 76 empty.

FOOD	VOLUME (%)
Fishes	95.3
<i>Abudefduf saxatilis</i>	
<i>Acanthurus bahianus</i>	
atherinids	
<i>Aulostomus maculatus</i> (3)	
<i>Caranx ruber</i> (2)	
<i>Chromis cyanea</i> (2)	
<i>Chromis multilineata</i>	
<i>Haemulon flavolineatum</i>	
holocentrid	
<i>Holocentrus</i> sp.	
monacanthid	
<i>Pomacentrus</i> sp.	
<i>Pomacentrus fuscus</i> (3)	
<i>Pomacentrus planifrons</i>	
scarids (5)	
<i>Scarus croicensis</i>	
<i>Scarus vetula</i>	
serranid	
<i>Synodus intermedius</i>	
<i>Thalassoma bifasciatum</i>	
Squids	3.9
<i>Sepioteuthis sepioidea</i> (2)	
Shrimps	0.8
<i>Tozeuma</i> sp.	

Remarks.—The yellowfin grouper is the most common species of *Mycteroperca* in the West Indies. The species of this genus are less intimately associated with the bottom than those of *Epinephelus*. Also, in contrast to *Epinephelus* and other West Indian serranid genera, they feed almost exclusively on fishes. They are more slender-bodied (hence probably more rapid in their feeding rushes) and have better developed canine teeth; both of these characteristics would be expected of a predominantly piscivorous group of serranid fishes. That the yellowfin grouper can capture such swift-swimming fishes as the bar jack (*Caranx ruber*) would seem to indicate that it is more active than the more robust groupers such as species of *Epinephelus*. The bar jacks measured 150 and 160 mm in fork length and were taken from groupers that measured 450 and 485 mm, respectively, in standard length. The one lizardfish, which measured 182 mm SL, was found folded in the stomach of a 380-mm *M. venenosa*. Two of the groupers had fed on *Sepiateuthis sepioidea*, a squid which is often seen in small aggregations in shallow water in the West Indies. Two small hippolytid shrimps (*Tozeuma*) were found in the stomach of one 404-mm fish, along with a 35-mm damselfish (*Chromis cyanea*).

Paranthias furcifer (Cuvier & Valenciennes)
7 stations; 13 specimens: 162 to 198 mm SL.

CREOLE FISH

FOOD	VOLUME (%)
Copepods	61.7
<i>Candacia pachydactyla</i>	
<i>Coryaceus</i> sp.	
<i>Eucalanus attenuatus</i>	
<i>Eucalanus monachus</i>	
<i>Euchaeta marina</i>	
<i>Paracalanus</i> sp.	
<i>Temora stylifera</i>	
<i>Undinula vulgaris</i> (3)	
Tunicates	12.2
salps	
Shrimps and shrimp larvae	11.9
<i>Lucifer faxani</i>	
Unidentified animals	7.7
Amphipods	3.1
hyperiid	
Mysids	2.3
Fish larvae	0.6
Gastropod larvae	0.2
Unidentified crustaceans	0.2
Unidentified eggs	0.1

Remarks.—*Paranthias furcifer* is a schooling serranid that feeds on zoo-

plankton. Typically, it rises well above reefs for its feeding, but descends for shelter with the approach of danger. The individual planktonic organisms are picked one by one from the passing water mass. This fish has a small mouth, small teeth, numerous gill rakers, fusiform body, and a deeply forked caudal fin — all representing departures from the typical grouper morphology, and all specializations for feeding in mid-water on zooplankton.

Petrometopon cruentatum (Lacépède)

GRAYSBY

44 stations; 75 specimens: 124 to 260 mm SL; 49 empty.

FOOD	VOLUME (%)
Fishes	66.2
<i>Abudefduf saxatilis</i>	
<i>Apogon pigmentarius</i>	
chaetodontid (juv.)	
<i>Coryphopterus</i> sp.	
<i>Coryphopterus personatus</i>	
<i>Haemulon</i> sp.	
<i>Holocentrus coruscus</i>	
Shrimps	17.3
alpheids	
Stomatopods	8.9
<i>Gonodactylus oerstedii</i>	
Crabs	3.8
Gastropods	3.8
<i>Strombus gigas</i>	

Remarks.—A bold little grouper, the graysby will approach a diver closely and may even take food from his hand. It is frequently observed in caves on reefs.

Serranus tabacarius (Cuvier & Valenciennes)

TOBACCO FISH

4 stations; 4 specimens: 92 to 135 mm SL; 3 empty.

FOOD	VOLUME (%)
Fish	100.0

Remarks.—*S. tabacarius*, like other species of *Serranus*, is usually encountered swimming a few inches off the bottom. Beebe & Tee-Van (1928) listed an engraulid fish as the sole contents of the stomach of one fish. Robins & Starck (1961) reported the stomach contents of three specimens to consist equally of fish and shrimp remains.

Serranus tigrinus (Bloch)

HARLEQUIN BASS

13 stations; 26 specimens: 32 to 85 mm SL; 7 empty.

FOOD	VOLUME (%)
Shrimps	71.9
carideans	

Fishes	9.7
Stomatopods	8.9
Crabs	7.8
Unidentified crustaceans	1.7

Remarks.—*S. tigrinus* is the most common West Indian species of *Serranus*, and it is more characteristic of shallow-water reefs than other species of the genus. Beebe & Tee-Van (1928) stated that most of their specimens of this species from Haiti had fed upon shrimps and other small crustaceans. Robins & Starck (1961) reported 99 per cent of the stomach contents of 22 specimens that contained food to consist of crustaceans (primarily shrimps), and only 1 per cent fish.

Serranus tortugarum Longley

CHALK BASS

2 stations; 2 specimens: 21 and 45 mm SL.

FOOD	VOLUME (%)
Copepods	92.0
<i>Coryaceus amazonicus</i>	
<i>Euterpina acutifrons</i>	
<i>Farranula gracilis</i>	
<i>Paracalanus aculeatus</i>	
<i>Paracalanus parvus</i>	
Fish eggs	8.0

Remarks.—Robins & Starck (1961) examined the stomach contents of 14 specimens of *S. tortugarum* which contained food. The material in half of these stomachs was too digested to permit identification, but the remaining seven contained crustaceans, especially amphipods. These authors noted that *S. tortugarum* has numerous gill rakers and swims above the bottom. The copepods from the two stomachs examined for the present report consisted of calanoids, cyclopoids, and harpacticoids.

GRAMMISTIDAE (Soapfishes)

Rypticus saponaceus (Bloch & Schneider)

SOAPFISH

15 stations; 27 specimens: 98 to 224 mm SL; 15 empty.

FOOD	VOLUME (%)
Fishes	47.9
<i>Halichoeres poeyi</i>	
<i>Quisquilius hipoliti</i>	
<i>Thalassoma bifasciatum</i>	
Shrimps	34.2
Crabs	9.6
<i>Percnon gibbesi</i>	
<i>Petrolisthes polita</i>	
Stomatopods	8.3
<i>Pseudosquilla ciliata</i>	

Remarks.—Beebe & Tee-Van (1928) recorded eight specimens from Haiti (as *R. coriaceus*). Of these specimens they wrote, "All fishes of this species examined had been feeding upon shrimps." The soapfish is named for the copious quantity of slime that it secretes, particularly when disturbed. The author inadvertently discovered, after spearing a specimen in the Florida Keys and placing it inside his swimming trunks, that the slime is strongly irritating. Marezki & del Castillo (1967) have determined that the mucus contains a protein toxin. The author has not found any soapfishes in the stomachs of predatory fishes. Feeding experiments might demonstrate that the toxic slime of *Rypticus* is repelling to predators.

GRAMMIDAE (Fairy Basslets)

In the western Atlantic, this family consists of two species of *Gramma* and three of *Lipogramma*. These are very colorful reef fishes of small size that usually live in caves or beneath ledges; they retreat to holes in the reef when frightened. Beebe & Tee-Van (1928) described the food of *G. loreto* Poey merely as small crustaceans. Eibl-Eibesfeldt (1955) reported this species among those he observed picking at the bodies of other fishes at Bonaire, ostensibly to feed on ectoparasites. Böhlke & Randall (1963: Table 4) recorded the stomach contents of 56 specimens of *G. loreto*. The fish had fed primarily on small free-living crustaceans such as copepods, mysids, and shrimp larvae. A few parasitic crustaceans (one calagoid copepod and six larval gnathiid isopods) were found in the stomachs. The stomach contents of five specimens of *G. melacara* Böhlke & Randall were examined by the same authors. All of this material consisted of free-living planktonic crustaceans. The two species of *Gramma* normally do not move more than a few inches from the rock or coral substratum during feeding. No new data on the food habits of grammids are reported here.

CIRRHITIDAE (Hawkfishes)

Amblycirrhitus pinos (Mowbray)

HAWKFISH

10 stations; 16 specimens: 29 to 74 mm SL; 4 empty.

Food	VOLUME (%)
Copepods	45.8
<i>Candacia pachydactyla</i>	
<i>Centropages hamatus</i>	
<i>Euchaeta marina</i>	
<i>Scolecithrix danae</i>	
<i>Undinula vulgaris</i>	
Shrimps and shrimp larvae	21.1
alpheids (2)	
carideans	

gnathophyllids	
palaemonids	
Crabs and crab larvae	14.2
Polychaetes	12.1
Isopods	2.5
flabelliferan	
<i>Stenetrium</i> sp.	
Amphipods	2.1
Tanaids	1.4
Unidentified animals	0.8

Remarks.—*A. pinos*, the only western Atlantic hawkfish, is a small species which rests upon a hard substratum. Most of its prey consists of zooplanktonic organisms.

APOGONIDAE (Cardinalfishes)

Food-habit data were obtained for only two of the 19 species of shallow-water western Atlantic cardinalfishes, *Apogon conklini* and *A. maculatus*. It seems likely from underwater observations, however, that the other species will be found to feed in a similar manner. These little fishes hide deep in the recesses of the reef by day; at night they come out to feed. Often they are several feet above the bottom where they appear to be feeding mainly on small crustaceans in the plankton. *Astrapogon stellatus* (Cope) is a commensal in the mantle cavity of the queen conch (*Strombus gigas*). Plate (1908) concluded that this fish leaves the conch only at night to feed. He described its food as shrimps, sea lice, and other crustaceans.

Apogon conklini (Silvester) FRECKLED CARDINALFISH
4 stations; 29 specimens: 33 to 47 mm SL; 12 empty.

FOOD	VOLUME (%)
Shrimp larvae	24.1
alpheids	
Amphipods	18.8
hyperiid	
Unidentified crustaceans	18.2
Crab larvae	10.0
Tunicates	7.3
appendicularians	
Polychaetes	5.9
Copepods	5.9
Isopods	5.3
Tanaids	2.7
Fish eggs	1.8

Apogon maculatus (Poey)

FLAMEFISH

5 stations; 22 specimens: 43 to 68 mm SL; 11 empty.

Food	VOLUME (%)
Shrimps and shrimp larvae	49.0
carideans	
Crabs	23.7
Unidentified crustaceans	12.7
Copepods	9.1
Polychaetes	3.7
opheliid	
Isopods	1.1
Amphipods	0.7

Remarks.—*Apogon maculatus* is the largest and probably the most common of inshore cardinalfishes in the West Indies. Beebe & Tee-Van (1928) and Longley & Hildebrand (1941) reported a shrimp from the stomach of a single specimen from Haiti and Dry Tortugas, respectively.

PRIACANTHIDAE (Bigeyes)

Two species of *Priacanthus* occur with moderate frequency on West Indian reefs. Their large eyes are suggestive of nocturnal activity, and this has been confirmed by Longley & Hildebrand (1941) who wrote of *P. cruentatus*, "Feeding occurs chiefly at night." That they can feed by day as well is evident from the fresh food material in stomachs during various diurnal hours.

Priacanthus arenatus Cuvier & Valenciennes

BIGEYE

18 stations; 29 specimens: 125 to 273 mm SL; 11 empty.

Food	VOLUME (%)
Fishes and fish larvae	37.5
atherinids	
<i>Dactylopterus volitans</i> (larv.)	
<i>Lactophrys</i> sp. (larv.)	
Shrimps	34.7
carideans	
penaeids	
<i>Trachypenaeus</i> sp.	
Polychaetes	11.1
eunicids	
Crabs and crab larvae	9.8
<i>Cronius tumidulus</i>	
portunid	
Cephalopods	2.2
Stomatopod larvae	1.7
Isopods	1.6
Scyllarid larvae	1.4

Remarks.—*Priacanthus arenatus* is most often seen at depths of about 50 feet or more. It is usually encountered in schools and is less inclined to hide in holes or crevices in the reef by day than *P. cruentatus*. Most of the fishes and crustaceans on which it feeds are larval forms, thus indicating a tendency to feed more on zooplanktonic than benthic organisms.

Priacanthus cruentatus (Lacépède)

GLASSEYE

19 stations; 32 specimens: 116 to 215 mm SL; 7 empty.

FOOD	VOLUME (%)
Fishes	28.7
<i>Dactylopterus volitans</i> (larv.)	
<i>Jenkinsia</i> sp.	
<i>Lactophrys</i> sp. (larv.)	
tetraodontid (larv.)	
Polychaetes	16.8
Crabs and crab larvae	14.4
oxystome	
Shrimps and shrimp larvae	10.0
alpheids	
Cephalopods and cephalopod larvae	8.9
Mysids	7.8
Stomatopod larvae	5.4
Isopods	4.9
Unidentified animals	1.2
Gastropods	1.2
Amphipods	0.7

Remarks.—*Priacanthus cruentatus* is a shallow-water solitary species. Most of the food organisms consist of the larger animals of the plankton.

PEMPHERIDAE (Sweepers)

Pempheris schomburgki Müller & Troschel

GLASSY SWEEPER

5 stations; 19 specimens: 93 to 111 mm SL; 1 empty.

FOOD	VOLUME (%)
Polychaetes	27.3
Crab larvae	24.5
Shrimp larvae	18.9
Stomatopod larvae	16.7
<i>Gonodactylus</i> sp.	
<i>Squilla hyalina</i>	
Hermit crab larvae	5.4
Octopus larvae	3.3
Unidentified crustaceans	2.8
Amphipods	1.1

Remarks.—*P. schomburgki* is nocturnal. It appears to feed almost entirely on zooplankton.

EMMELICHTHYIDAE (Bogas)

Inermia vittata Poey

BOGA

2 stations; 3 specimens: 130 to 184 mm SL.

FOOD	VOLUME (%)
Copepods	76.7
<i>Candacia pachydactyla</i>	
<i>Farranula gracilis</i>	
<i>Miracia efferata</i>	
<i>Nannocalanus minor</i>	
<i>Oncaea</i> sp.	
<i>Rhyncalanus cornutus</i>	
<i>Undinula vulgaris</i> (2)	
Siphonophores	16.7
Fish scales	3.3
Crab larvae	2.0
Polychaetes	1.3

Remarks.—*Inermia vittata* is a slender schooling fish that is generally seen in deep outer-reef areas where the water is clear and blue. It feeds on mid-water zooplankton, for which its highly protrusible mouth is probably very effective.

LUTJANIDAE (Snappers)

The snappers are a large family of carnivorous fishes. In general, they are nocturnal. Although they are regarded as reef fishes, some of the species feed primarily on the animals that live on the sand and seagrass flats. Night diving revealed individual snappers foraging over these flats. By day they retire to reefs for cover, often in small aggregations. The larger the canine teeth of the lutjanid species, in general, the higher the percentage of fish in the diet. Within a species, the larger individuals feed proportionately more on fishes.

Lutjanus analis (Cuvier & Valenciennes)

MUTTON SNAPPER

55 stations; 66 specimens: 204 to 620 mm SL; 13 empty.

FOOD	VOLUME (%)
Crabs	44.4
<i>Calappa gallus</i>	
calappids (3)	
<i>Cronius ruber</i>	
majid	
<i>Parthenope serrata</i>	
<i>Petrolisthes</i> sp.	
portunids (7)	

<i>Portunus</i> sp.	
<i>Portunus sebae</i> (2)	
<i>Ranilia muricata</i>	
Fishes	29.8
<i>Acanthurus bahianus</i>	
<i>Diodon</i> sp. (2)	
<i>Fistularia tabacaria</i>	
gobiid	
<i>Haemulon</i> sp.	
<i>Haemulon aurolineatum</i>	
<i>Halichoeres garnoti</i>	
<i>Holocentrus ascensionis</i>	
<i>Malacanthus plumieri</i>	
<i>Monacanthus</i> sp.	
<i>Monacanthus setifer</i>	
<i>Pseudupeneus maculatus</i> (2)	
scarid	
<i>Scorpaena plumieri</i>	
<i>Sphaeroides spengleri</i>	
Gastropods	13.0
<i>Fasciolaria tulipa</i>	
<i>Murex pomum</i>	
<i>Strombus</i> sp. (2)	
<i>Strombus gigas</i> (5)	
Octopuses	3.1
Hermit crabs	2.8
<i>Petrochirus diogenes</i> (2)	
Shrimps	2.3
penaeid	
Unidentified animal material	1.9
Spiny lobsters	1.9
<i>Panulirus argus</i>	
Stomatopods	0.8
<i>Lysiosquilla glabriuscula</i>	

Remarks.—The mutton snapper is a highly esteemed food fish which is more of a roving species than the snappers of the genus *Lutjanus* discussed in the accounts which follow. It swims above the bottom over reefs but is more frequently encountered over sand, seagrass, or coral rubble (although often near reefs). It feeds both by day and by night. Beebe & Tee-Van (1928) reported the species as strictly carnivorous, specializing in small fishes, crustaceans such as shrimps and crabs, and mollusks. Longley & Hildebrand (1941) state that fishes (largely small grunts) predominated in the food taken from 29 stomachs at Dry Tortugas. They added that the only other food of importance consisted of shrimps. In

contrast to Longley & Hildebrand, the author found that crabs were the most important item of food in the 66 specimens examined from the West Indies. Gastropods represented 13 per cent by volume of the food material. Of particular importance were species of *Strombus*, especially *S. gigas*. These were found in the stomachs mostly as large adults, but without shell or shell fragments. *Lutjanus analis* does not have the jaw strength and dentition to crush an adult *Strombus gigas*, the shell of which is massive. Randall (1964a) postulated that the fish obtained the soft parts of these large gastropods only after they have been made available by other predators such as octopuses. The large hermit crabs (*Petrochirus diogenes*) were also found in the mutton snapper stomachs without their protective gastropod shells. One 572-mm individual contained a fully adult *P. diogenes*, a 191-mm *Pseudupeneus maculatus*, and a 76-mm *Halichoeres garnoti*. Seven mutton snappers in the range of 484 to 528 mm in standard length contained the following fishes (standard lengths given in parentheses): *Acanthurus bahianus* (137 mm), *Diodon* sp. (74 mm), *Fistularia tabacaria* (110 mm), *Haemulon aurolineatum* (130 mm), *Holocentrus ascensionis* (130 mm), *Malacanthus plumieri* (320 mm), *Monacanthus* sp. (50 mm), *Monacanthus setifer* (78 mm), and *Sphaeroides spengleri* (75 and 77 mm).

Lutjanus apodus (Walbaum)

SCHOOLMASTER

90 stations; 117 specimens: 125 to 445 mm SL; 59 empty.

FOOD	VOLUME (%)
Fishes	60.7
atherinids	
<i>Aulostomus maculatus</i> (2)	
<i>Bodianus rufus</i>	
<i>Cantherhines pullus</i> (juv.)	
<i>Chromis multilineata</i>	
<i>Gymnothorax moringa</i>	
<i>Haemulon</i> sp.	
<i>Jenkinsia</i> sp.	
<i>Pomacentrus fuscus</i>	
scarids (3)	
<i>Scorpaena plumieri</i>	
scorpaenid	
serranids (2)	
<i>Sparisoma</i> sp.	
<i>Sparisoma aurofrenatum</i>	
Crabs	22.2
<i>Actaea acantha</i>	
calappid	
majid	
<i>Mithrax sculptus</i>	
<i>Pernon gibbesi</i>	

<i>Portunus sebae</i> (2)	
portunids (3)	
Unidentified crustaceans	6.0
Stomatopods	3.7
Shrimps	3.45
Octopuses	3.45
Gastropods	0.5

Remarks.—*L. apodus* appears to be more confined to reefs than other snappers. It is often seen among stands of *Acropora palmata* during the day. Beebe & Tee-Van (1928) examined the stomach contents of 25 specimens from Haiti. They found crabs, shrimps, and numerous fishes, especially *Anchoviella* sp., *Opisthonema oglinum*, and *Diodon hystrix*, in the stomachs. The porcupinefish were taken from 15 stomachs. Longley & Hildebrand (1941) reported on the examination of 241 stomachs from Dry Tortugas, Florida. Crabs were the most numerous; they included spider crabs (*Mithrax*) and porcelain crabs (*Porcellana* and *Petrolisthes*). Shrimps, such as the snapping shrimps *Alpheus* and *Crangon*, were next in importance. Fishes were notably less numerous than crabs and shrimps; among them were scarids and labrids. Other food items were polychaetes, octopuses (six stomachs), clam (one stomach), isopod (one stomach), and an amphipod (one stomach). These authors stated that feeding occurs at night. This fish also feeds heavily during daylight hours, however. The author often noted fresh food material in the stomachs of fish taken during various hours of the day. The high percentage of fish in the stomachs stands in contrast to the data of Longley & Hildebrand. Possibly this difference is due to smaller size of the Tortugas specimens that were examined by these authors. In general, the smaller snappers feed mostly on crustaceans and the larger ones more on fishes. Unfortunately Longley & Hildebrand did not give the size of their specimens. Fifty-two of those examined by the author ranged from 200 to 300 mm in standard length, and 34 exceeded 300 mm. The stomach of a 400-mm schoolmaster contained a scarid fish (*Sparisoma aurofrenatum*) 189 mm in length. A 340-mm snapper had eaten a 165-mm *Bodianus rufus*. A 288-mm one contained a 300-mm *Aulostomus maculatus* and a 255-mm one a 230-mm *Gymnothorax moringa*. The latter was well digested at 8:30 a.m., so was probably eaten during the night. The two specimens of *Portunus sebae* from schoolmaster stomachs measured 23 and 30 mm across the carapace; they were taken from fish which were 295 and 223 mm in standard length, respectively. The latter also had eaten a 105-mm stomatopod.

Lutjanus cyanopterus (Cuvier & Valenciennes) CUBERA SNAPPER
11 stations; 11 specimens: 410 to 990 mm SL.

FOOD	VOLUME (%)
Fishes	100.0
clupeid	
<i>Diodon</i> sp. (2)	

Haemulon aurolineatum

Haemulon sciurus

scarids (2)

Scarus coeruleus

Remarks.—*Lutjanus cyanopterus* is the largest snapper in the western Atlantic. It is the least common of the shallow-water species in the West Indies and the most wary, hence the small number of specimens procured. The large canine teeth in the jaws are indicative of its piscivorous habits.

Lutjanus griseus (Linnaeus)

GRAY SNAPPER

64 stations; 90 specimens: 120 to 400 mm SL; 62 empty.

FOOD	VOLUME (%)
Crabs	40.0
<i>Callinectes</i> sp.	
goneplacid (<i>Speocarcinus</i>)	
portunids (3)	
xanthid	
Fishes	39.1
<i>Jenkinsia</i> sp.	
Shrimps	13.2
penaeids (3)	
Gastropods	6.8
<i>Strombus gigas</i>	
Scyllarid lobsters	0.9

Remarks.—Longley (1923) noted that *L. griseus* is primarily a nocturnal bottom fish. It feeds individually over sand and seagrass flats by night and aggregates in reefs or other areas of cover by day. The large number of empty gray snappers recorded above reflects the nocturnal habits. Occasional fish, however, did have fresh food material in their stomachs during late morning or afternoon hours. Longley & Hildebrand (1941), Reid (1954), Springer & Woodburn (1960), Tabb & Manning (1961), Croker (1962), and especially Starck (in press) have all studied the food habits of the gray snapper. Juveniles in the seagrass beds feed by day mainly on amphipods, shrimps, and copepods. Larger individuals continue to eat shrimps but add crabs and fishes as major items to the diet. The largest snappers eat more fish than crustaceans. Other invertebrates such as annelid worms may be eaten when locally abundant.

Lutjanus jocu (Bloch & Schneider)

DOG SNAPPER

65 stations; 92 specimens: 190 to 630 mm SL; 36 empty.

FOOD	VOLUME (%)
Fishes	60.7
atherinids	
<i>Aulostomus maculatus</i>	
<i>Clepticus parrae</i>	

<i>Gymnothorax moringa</i>	
<i>Haemulon</i> sp.	
<i>Haemulon aurolineatum</i>	
<i>Haemulon plumieri</i>	
<i>Holacanthus tricolor</i>	
<i>Holocentrus</i> sp. (2)	
<i>Holocentrus rufus</i>	
<i>Jenkinsia</i> sp.	
<i>Myrichthys</i> sp.	
<i>ophichthid</i>	
<i>Opisthonema oglinum</i>	
<i>Pseudupeneus maculatus</i> (2)	
scarids (4)	
<i>Scarus</i> sp.	
serranid (<i>Cephalopholis</i> ?)	
<i>Sparisoma</i> sp. (2)	
<i>Sparisoma viride</i>	
<i>Xanthichthys ringens</i>	
Crabs	15.4
<i>Carpilius corallinus</i>	
<i>Cronius ruber</i> (2)	
<i>Pitho lherminieri</i>	
portunids (2)	
<i>Portunus</i> sp.	
Octopuses	7.0
<i>Octopus vulgaris</i>	
Spiny lobsters	6.6
<i>Panulirus argus</i>	
<i>Panulirus guttatus</i> (3)	
Gastropods	3.6
<i>Strombus gigas</i> (2)	
Squids	2.2
Fish eggs (belonid)	1.8
Scyllarid lobsters	1.8
Unidentified crustaceans	0.9

Remarks.—The dog snapper attains moderately large size. Sixty of the 92 specimens examined were 400 mm or more in standard length. The larger fish usually take relatively large prey. Eight dog snappers from 538 to 630 mm SL had eaten a 150-mm *Opisthonema oglinum*, four scarids (140 to 230 mm), *Holocentrus rufus* (150 mm), *Aulostomus maculatus* (250 mm), *Gymnothorax moringa* (450 mm), and *Myrichthys* sp. (600 mm). Four other snappers in the size range 368 to 418 mm ate *Holocentrus* sp., *Haemulon aurolineatum*, *H. plumieri*, and *Holacanthus tricolor* ranging from 100 to 145 mm in standard length. On the other hand, one 510-mm snapper contained 11 atherinid fish from 49 to 58 mm and a

crab 21 mm across the carapace. The dog snapper is both diurnal and nocturnal.

Lutjanus mahogoni (Cuvier & Valenciennes) MAHOGANY SNAPPER
16 stations; 27 specimens: 135 to 295 mm SL; 19 empty.

FOOD	VOLUME (%)
Fishes	75.0
atherinid	
<i>Holocentrus</i> sp.	
<i>Saurida</i> sp.	
Shrimps	12.5
penaeid	
Octopuses	9.4
Crabs	3.1
portunid	

Remarks.—The mahogany snapper appears to be strictly nocturnal. Stomachs of fish taken during afternoon hours were invariably empty. It is not a very common fish in the West Indies but is more frequently seen than the relatively few specimens cited above would indicate. It is moderately wary and hence difficult to collect with a spear.

Lutjanus synagris (Linnaeus) LANE SNAPPER
5 stations; 6 specimens: 148 to 280 mm SL; 4 empty.

FOOD	VOLUME (%)
Crabs	50.0
goneplacid	
<i>Leiolanus nitidus</i>	
portunid	
Stomatopods	50.0
<i>Lysiosquilla glabriuscula</i>	

Remarks.—The lane snapper is a species of many habitats. It is known from the shore to depths of at least 220 fathoms, from coral reefs in clear water to murky brackish water over a mud bottom. Beebe & Tee-Van (1928) reported it as the most abundant species of the genus in Port-au-Prince Bay, Haiti. They examined 78 stomachs and found that fishes and crustaceans dominated the food material. In the following list the number in parentheses denotes the frequency with which they encountered the food item: eels (2), silversides (5), anchovies (5), porcupinefish (10), unidentified fish (8), stomatopods (2), crabs (15), shrimps (15), other crustaceans (3), mollusks (1), polychaete worms (3), purple holothurians (1), sponge spicules (1), and seaweed (2). Longley & Hildebrand (1941) found *Jenkinsia lamprotaenia* in one specimen from Dry Tortugas. Reid (1954) stated that crustaceans represented the main constituent of the diet of young lane snappers off West Florida. Of nine with food, eight contained shrimps, one had mysids, two had copepods, and two contained fish. Springer & Woodburn (1960) listed copepods, gammarid amphipods,

shrimps, crustaceans, a fish and a gastropod in the stomachs of four juveniles. Lowe (1962) reported crustaceans and some fishes as the food of specimens from British Guiana. She specifically cited a batfish (*Ogcocephalus*) and *Squilla* from one lane snapper. Rodriguez Pino (1962) examined the stomach contents of 207 individuals from Cuba. Her results were summarized as follows: fishes (32 per cent), crustaceans (27 per cent), annelids (12 per cent), mollusks (1 per cent), algae (2 per cent), and unidentified (26 per cent).

Ocyurus chrysurus (Bloch)

YELLOWTAIL SNAPPER

29 stations; 52 specimens: 114 to 440 mm SL; 10 empty.

FOOD	VOLUME (%)
Crabs and larvae (15 % larv.)	23.3
<i>Calappa ocellata</i>	
<i>Mithrax</i> sp.	
<i>Mithrax sculptus</i>	
<i>Pitho aculeata</i>	
Shrimps and larvae (60% larv.)	16.2
carideans	
penaeids	
<i>Sicyonia laevigata</i>	
<i>Trachycaris restrictus</i>	
Fishes and fish larvae	15.1
<i>Jenkinsia</i> sp.	
Siphonophores	7.1
Pteropods	6.1
<i>Cavolina</i> sp.	
Copepods	5.1
Cephalopods and larvae	3.8
Mysids	2.9
Tunicates	2.7
appendicularians	
salps	
Ctenophores	2.7
Unidentified animal material	2.5
Gastropods (except pteropods)	2.4
<i>Strombus gigas</i>	
Stomatopods	2.4
<i>Gonodactylus oerstedii</i>	
<i>Pseudosquilla ciliata</i>	
Scyllarid larvae	1.9
Heteropods	1.2
Pelecypods	1.2
Fish eggs	0.9
Euphausiids	0.8
Gastropod larvae	0.7

Amphipods	0.5
hyperiids	
Hymenopteran insect	0.5

Remarks.—The yellowtail snapper is one of the most common reef fishes in the tropical Western Atlantic and one of the most highly esteemed as food. The young are abundant in seagrass areas. Both young and adults are active fishes which usually swim well above the bottom. Their somewhat slender bodies and deeply forked tails (compared with *Lutjanus*) are indicative of such a mode of life. The adults are difficult to approach underwater. Beebe & Tee-Van (1928) reported copepods and a pteropod in the stomach of a 40-mm specimen; 15 larger fishes had eaten bottom detritus, including coral fragments and sand grains, mud, algae, sponges, polychaete worms, crustaceans such as shrimps and crabs, and small fishes, notably anchovies. Longley & Hildebrand (1941) observed that *Ocyurus* is not as restricted in its feeding to night hours as other members of the family. They noted that the species will take food at the surface over the deeper part of the lagoon at Dry Tortugas. They listed the food organisms as *Jenkinsia lamprotaenia* and other small fishes, shrimps, crabs, stomatopods, and annelids. The smaller individuals among the 42 reported herein with food in their stomachs had fed mostly on zooplankton. Large adults were primarily responsible for the benthic animals from the stomachs, but they also fed on pelagic animals, including some of small size. A 253-mm yellowtail, for example, contained numerous slender pteropods 3 to 6 mm in length. One fish speared in 60 feet off southwestern Puerto Rico had eaten a wasp. Curiously, this insect represented a species not yet recorded from the island. The 2.4 per cent by volume of stomach-content material attributed above to gastropods consisted of the soft parts of one adult conch (*Strombus gigas*) (see discussion under *Lutjanus analis*).

POMADASYIDAE (Grunts)

Like the snappers, the grunts are carnivorous (although rarely piscivorous) and primarily nocturnal. They are among the most abundant of reef fishes in the West Indies. From a trophic standpoint, however, they would more properly be classified as seagrass-bed and sand-flat feeders. Along with the lutjanids, they use the reefs primarily for protection from open-water predaceous fishes during daylight hours. Longley often made reference to the pomadasyids and lutjanids idling the day away among the corals. Some of the species such as *Haemulon chrysargyreum* tend to form schools in and about reefs. The prey animals of grunts, in general, vary from moderate to very small in size. Juvenile pomadasyids appear to feed primarily on zooplankton.

<i>Anisotremus surinamensis</i> (Bloch)	BLACK MARGATE
45 stations; 62 specimens: 180 to 478 mm; 22 empty.	
FOOD	VOLUME (%)
Echinoids	53.5

<i>Diadema antillarum</i> (21)	
<i>Echinometra</i> sp. (3)	
<i>Echinometra lacunter</i>	
<i>Echinometra viridis</i>	
<i>Eucidaris tribuloides</i> (2)	
spatangoid	
Gastropods	16.0
acmaeids (2)	
<i>Acmaea antillarum</i> (2)	
<i>Acmaea pustulata</i> (2)	
<i>Alvania auberiana</i>	
<i>Anachis</i> sp. (2)	
columbellid	
<i>Diodora cayenensis</i>	
<i>Diodora listeri</i>	
<i>Fissurella barbadensis</i> (3)	
<i>Hemitoma octoradiata</i>	
<i>Hyalina</i> sp.	
<i>Mangelia</i> sp.	
<i>Mitrella lunata</i>	
<i>Nassarius albus</i>	
<i>Nitidella ocellata</i>	
<i>Olivella</i> sp. (2)	
<i>Persicula lavalleeana</i>	
<i>Pyrgocythara</i> sp.	
turrid	
Crabs	9.9
majids (2)	
xanthids (3)	
Ophiuroids	5.3
<i>Ophiocoma</i> sp.	
<i>Ophiocoma echinata</i>	
<i>Ophiothrix</i> sp.	
Hermit crabs	2.9
Stomatopods	2.3
Shrimps	2.3
alpheids (4)	
Asteroids	1.75
<i>Linckia guildingii</i>	
Fishes	1.5
Pelecypods	1.3
<i>Laevicardium</i> sp.	
<i>Papyridea soleniformis</i>	
<i>Tellina</i> sp.	
Unidentified crustaceans	1.1

Anthozoans	0.75
Scyllarid lobsters	0.5
Polychaetes	0.4
serpulid	
Ostracods	0.25
Unidentified animal matter	0.12
Sponge	0.08
Isopods	0.05

Remarks.—The black margate, one of the largest of the grunts, is often seen during the day in caves near shore where the surf is not strong. It is nocturnal, at least as an adult. It feeds almost exclusively on invertebrates with hard parts. Intestinal contents of some of the specimens were analyzed along with stomach material. Echinoids strongly dominate the food of large adults, particularly *Diadema antillarum*. The spines and test of this formidable echinoid were found crushed into small pieces, along with soft parts, in the alimentary tracts of the fish. Randall, Schroeder, & Starck (1964) noted that the pale fleshy lips of the black margate often display purple dots as a result of penetration by the spines of this urchin, and the bones of the roof of the mouth may be stained purple, apparently from the tattooing effect of the pigment from countless spine wounds. The smaller fish feed more heavily on gastropods, particularly limpets. Three fish contained small amounts of algae; this was probably consumed accidentally.

Anisotremus virginicus (Linnaeus)

PORKFISH

12 stations; 16 specimens: 112 to 264 mm SL; 3 empty.

FOOD	VOLUME (%)
Ophiuroids	16.5
<i>Ophiothrix</i> (3)	
Crabs	16.2
Shrimps	14.7
alpheids (5)	
carideans	
Polychaetes	14.0
<i>Eunice</i> sp.	
Isopods	8.2
anthurids	
<i>Asellote</i> sp.	
<i>Cymodoce</i> sp.	
excorallanid	
sphaeromid	
Pelecypods	5.5
<i>Americardia guppyi</i>	
<i>Americardia media</i>	
<i>Chione</i> sp.	
<i>Chione cancellata</i>	
<i>Cumingia antillarum</i>	

<i>Papyridea semisulcata</i> (2)	
<i>Pecten</i> sp.	
Unidentified crustaceans	5.1
Stomatopods	4.7
Gastropods	3.8
<i>Columbella mercatoria</i>	
<i>Hyalina</i> sp.	
<i>Mitra</i> sp.	
<i>Modulus modulus</i>	
<i>Olivella</i> sp.	
<i>Zebina browniana</i>	
Amphipods	3.0
caprellids	
gammarid	
lysianassid	
metopid	
Copepods	1.8
harpacticoids	
Tunicates	1.5
<i>Tridemnum savignii</i>	
Tanaids	1.1
apseudid	
Ostracods	0.9
<i>Bairdoppilata carinata</i>	
cypridinine	
Chitons	0.8
Hermit crabs	0.6
Foraminifera	0.5
Nebaliaceans	0.5
<i>Nebalia</i> sp.	
Sipunculids	0.4
<i>Aspidosiphon</i> sp.	
Scaphopods	0.2
<i>Dentalium</i> sp.	

Remarks.—The porkfish is not common in Puerto Rico or the Virgin Islands, in contrast to the Florida Keys where it is abundant on coral reefs. Beebe & Tee-Van (1928) stated that the stomach contents of their two specimens from Haiti were dominated by minute crustaceans, other comminuted animal remains, including many small elongate spines (which may have been spines from *Ophiothrix*), and small mollusks. Longley & Hildebrand (1941) reported the stomach contents of six individuals taken at daybreak to consist of ophiurans, mollusk shells, annelids, and fragments of crustaceans. They noted that small porkfish (which are colored differently than adults; they have two lengthwise black bands instead of a black bar through the eye and another anteriorly on the body) nibble and peck at the

surfaces of larger fishes, presumably to remove ectoparasites. The author has often observed the same behavior at West Indian localities. The young porkfish restrict themselves to small sectors of reef, and the other fishes in the vicinity come to these stations for "cleaning." No stomach contents of juvenile fishes were examined, but the observations strongly suggest that fish ectoparasites will be found in their stomachs. The food animals from adult porkfish stomachs were noteworthy for their small size. For example, none of the many and varied crustaceans and mollusks in the stomach of a 200-mm individual exceeded 5 mm in greatest dimension of the body or shell.

Haemulon album (Cuvier & Valenciennes) MARGATE

48 stations; 57 specimens: 278 to 535 mm SL; 18 empty.

FOOD	VOLUME (%)
Sipunculids	25.2
<i>Aspidosiphon</i> sp.	
<i>Aspidosiphon speciosus</i>	
<i>Siphonosoma cumanensis</i>	
Echinoids	19.9
<i>Brissus brissus</i>	
<i>Clypeaster</i> sp. (4)	
<i>Lytechinus variegatus</i>	
<i>Moiria atropus</i>	
spatangoids (4)	
Polychaetes	14.0
arabellids	
Crabs	7.6
<i>Albunea gibbesii</i>	
hippids (2)	
<i>Sesarma</i> sp.	
Pelecypods	5.4
<i>Laevicardium</i> sp.	
pinnid	
Ophiuroids	5.2
<i>Amphiura fibulata</i>	
<i>Ophiothrix</i> sp.	
Shrimps	3.9
alpheids (3)	
axiid	
Hemichordates	3.5
Unidentified crustaceans	3.3
Gastropods	2.7
<i>Oliva</i> sp.	
Fishes	2.0
monacanthid	
Unidentified animals (mostly worms)	1.9

Stomatopods	1.4
<i>Squilla tricarinata</i>	
Echiuroids	1.0
Chitons	0.8
Priapuloids	0.8
Amphipods	0.5
caprellids	
Hermit crabs	0.5
Scaphopods	0.2
<i>Dentalium</i> sp.	
<i>Dentalium semistriolatum</i>	
Sponges	0.1
Bryozoans	0.1

Remarks.—The margate, a highly regarded food fish, is the largest grunt of the genus *Haemulon*. Although active by night, it also feeds heavily by day. It is most often seen over sand and seagrass near reefs. It has been observed to nose into the sand, and the large number of sand-dwelling animals in its diet is indicative of such a mode of feeding. The stomachs of five specimens contained fragments of *Cymodocea*, and one fish had ingested *Thalassia*. Probably these seagrasses were taken in incidentally while feeding. The same is true of some sand and bottom detritus. Cummings, Brahy, & Spires (1966) studied the feeding of *H. album* at Bimini. The stomach contents of 32 night-caught fish and 23 day-caught fish from 160 to 480 mm standard length were analyzed. The average food volume was greater for the night-caught fish; however it is possible that floodlights used in the study area at night and the plankton attracted by these lights promoted heavier-than-normal night feeding. These authors reported crabs to be eaten by the highest percentage of margates, with polychaetes, stomatopods, pelecypods, and fishes also of importance in the diet.

Haemulon aurolineatum Cuvier & Valenciennes TOMTATE
12 stations; 28 specimens: 97 to 170 mm SL; 12 empty.

FOOD	VOLUME (%)
Shrimps and shrimp larvae	33.6
Polychaetes	31.0
<i>Chloeia</i> sp.	
Unidentified crustaceans	8.8
Unidentified eggs	6.2
Hermit crabs and larvae	4.4
Crabs and crab larvae	3.7
Amphipods	3.4
<i>Ampelisca</i> sp.	
<i>Elasmopus</i> sp.	
<i>Eurystheus</i> sp.	
<i>Megamphopus</i> sp.	

photid	
<i>Photis</i> sp.	
Copepods	2.5
<i>Undinula vulgaris</i>	
Gastropods	2.1
<i>Alvania auberiana</i>	
<i>Caecum pulchellum</i>	
<i>Retusa</i> sp.	
Pelecypods	1.6
<i>Solemya occidentalis</i>	
Barnacle larvae	1.2
Tanaids	0.9
Scaphopods	0.4
<i>Cadulus acus</i>	
<i>Dentalium</i> sp.	
Isopods	0.2

Remarks.—*Haemulon aurolineatum*, sometimes classified in the genus *Bathystoma*, is one of the smallest and most common of the grunts in the West Indies. Beebe & Tee-Van (1928) stated that it is omnivorous and listed the principal items of food as follows: sand, mud, and bottom detritus, algae sometimes in very large amounts, worms of various kinds, mollusk shells, broken and entire, and crustaceans such as copepods, isopods, shrimps, and small crabs. Longley & Hildebrand (1941) noted that the species is less intimately associated with coral than some of the other Pomadasysidae, and indicated that copepods provide much of the food. They mentioned that an estimated 1000 were taken from the stomach of a 50-mm fish. The author would hesitate to regard this fish as an omnivore because large amounts of algae were found in the stomachs of some specimens by Beebe & Tee-Van. Since the family, in general, is carnivorous, it would seem more likely that the algae were consumed incidentally while feeding on invertebrates.

Haemulon carbonarium Poey CAESAR GRUNT
18 stations; 30 specimens: 156 to 273 mm SL; 9 empty.

FOOD	VOLUME (%)
Crabs	38.3
majids (2)	
<i>Pisosoma</i> sp.	
Gastropods	15.2
<i>Acmaea pustulata</i>	
acmaeids (2)	
<i>Columbella mercatoria</i> (2)	
<i>Diodora</i> sp.	
<i>Emarginula pumila</i>	
<i>Fissurella</i> sp.	
<i>Fissurella barbadensis</i>	

<i>Hyalina</i> sp.	
<i>Nitidella</i> sp.	
Echinoids	10.9
<i>Diadema antillarum</i> (4)	
<i>Echinometra</i> sp.	
<i>Echinometra viridis</i>	
Chitons	9.8
<i>Ischnochiton papillosus</i>	
Polychaetes	8.0
Ophiuroids	6.0
<i>Ophiocoma echinata</i>	
<i>Ophiothrix</i>	
Sipunculids	4.85
Shrimps	4.1
alpheids (3)	
Barnacle appendages	1.9
Fish	0.7
blennioid	
Amphipods	0.2
Ostracods	0.05

Remarks.—Longley & Hildebrand (1941) wrote that *Haemulon carbonarium* feeds at night like the other grunts. The stomach contents of two Tortugas specimens consisted of small crabs, gastropods, starfish, and annelid worms. The author found echinoids only in the large adults.

Haemulon chrysargyreum Günther SMALLMOUTH GRUNT
8 stations; 30 specimens: 97 to 180 mm SL; 13 empty.

FOOD	VOLUME (%)
Crabs and crab larvae	19.4
<i>Herbstia</i> sp.	
majid	
<i>Mithrax</i> sp.	
xanthid	
Polychaetes	19.1
<i>Cariboa</i> sp.	
<i>Eunice</i> sp.	
flabelligerid	
<i>Semiodera</i> sp.	
Shrimps and shrimp larvae	15.9
alpheids	
<i>Alpheus</i> sp.	
penaeid	
Pelecypods	14.7
<i>Laevicardium</i> sp.	
Stomatopods	5.9
<i>Gonodactylus</i> sp.	

<i>Squilla</i> sp.	
Unidentified crustaceans	5.7
Amphipods	5.7
caprellids	
Isopods	4.7
Unidentified eggs	3.5
Hermit crabs	1.8
Gastropods	1.8
<i>Haminoea elegans</i>	
Sipunculids	1.2
<i>Aspidosiphon</i> sp.	
Fishes	0.4
Cephalopods	0.2

Remarks.—As noted by Courtenay (1961), *Haemulon chrysargyreum* is a small shallow-water species which may be found in sizeable schools. Longley & Hildebrand (1941) observed that it remains close to corals, particularly *Acropora*, by day. Some were seen to be feeding high in the water, and one such fish contained 21 copepods, an amphipod, an ostracod, and a crab zoea. These authors added, however, that the species usually feeds at night and may be found hundreds of yards from its nearest daytime schooling places. Stomachs of these fishes contained shrimps.

Haemulon flavolineatum (Desmarest) FRENCH GRUNT
19 stations; 47 specimens: 113 to 228 mm SL; 17 empty.

FOOD	VOLUME (%)
Polychaetes	39.6
capitellids	
<i>Eunice</i> sp.	
maldanids	
terebellids	
Crabs	15.5
Sipunculids	10.2
<i>Aspidosiphon</i> sp.	
Chitons	5.7
<i>Acanthochitona pygmaea</i>	
Holothurians	5.0
Isopods	3.8
Shrimps	3.3
Octopuses	3.3
Pelecypods	3.2
<i>Pitar</i> sp.	
<i>Tellina</i> sp.	
Ophiuroids	3.1
<i>Ophiothrix</i> sp.	
Unidentified crustaceans	2.2
Echinoids	1.5

<i>Diadema antillarum</i> (juv).	
spatangoid	
Scaphopods	0.8
<i>Cadulus</i> sp.	
<i>Dentalium</i> sp.	
Hermit crabs	0.8
Stomatopods	0.7
Amphipods	0.6
Gastropods	0.5
<i>Arene</i> sp.	
Unidentified animal material	0.2

Remarks.—*H. flavolineatum* is the most common grunt on West Indian reefs. Beebe & Tee-Van (1928) cited food material only as echinoderms and crustacean remains. Longley & Hildebrand (1941) stated that this species will feed by day, but they believe most feeding takes place at night.

Haemulon macrostomum Günther SPANISH GRUNT
24 stations; 28 specimens: 147 to 360 mm SL; 9 empty.

FOOD	VOLUME (%)
Echinoids	86.8
<i>Diadema antillarum</i> (15)	
spatangoid	
Crabs	7.9
Unidentified crustaceans	5.3

Remarks.—*H. macrostomum* is nocturnal. The adults from the West Indies had fed primarily on echinoids, particularly *Diadema*. Longley & Hildebrand (1941) listed the recognizable food of four Tortugas examples as small crabs, fish, gastropods, sea urchins, starfish, amphipods, and an isopod.

Haemulon parra (Desmarest) SAILORS CHOICE
10 stations; 33 specimens: 115 to 280 mm SL; 12 empty.

FOOD	VOLUME (%)
Shrimps	37.6
alpheids (3)	
carideans	
penaeids	
Crabs	33.3
majids	
portunids	
Amphipods	7.1
Gastropods	5.1
<i>Olivella</i> sp.	
Anemones	3.4
<i>Phyllactis flosculifera</i>	
Holothurians	3.3

Polychaetes	2.9
Pelecypods	2.8
<i>Gouldia cerina</i>	
<i>Pecten</i> sp.	
<i>Pitar</i> sp.	
<i>Solemya occidentalis</i>	
<i>Tellina</i> sp.	
Ophiuroids	2.4
Unidentified crustaceans	0.9
Isopods	0.5
Stomatopods	0.5
Scaphopods	0.2
<i>Cadulus</i> sp.	

Remarks.—Longley & Hildebrand (1941) reported this species as feeding almost wholly at night. They found stomachs of specimens taken in the early morning to contain much sand, with algae, mollusks, and annelids. The stomachs of the 21 West Indian specimens reported herein with food material contained more sand, algae, and bottom detritus than most other pomadaspid species. The anemone which accounted for 3.4 per cent by volume of the food material was found in the stomach of one adult.

Haemulon plumieri (Lacépède)

WHITE GRUNT

13 stations; 22 specimens: 130 to 279 mm SL; 7 empty.

FOOD	VOLUME (%)
Crabs	26.0
<i>Mithrax</i> sp.	
Polychaetes	14.5
Echinoids	12.4
<i>Diadema antillarum</i> (2)	
<i>Eucidaris tribuloides</i>	
spatangoid	
Sipunculids	8.3
<i>Aspidosiphon</i> sp.	
Gastropods	6.9
<i>Acmaea antillarum</i>	
<i>Strombus gigas</i>	
Shrimps	5.8
alpheids (2)	
Ophiuroids	5.7
<i>Ophiothrix</i> sp.	
Unidentified crustaceans	5.3
Fishes	3.3
Hemichordates	3.3
Unidentified animal material	3.0
Holothurians	2.7
<i>Thyone pseudofusus</i>	

Pelecypods	1.3
<i>Cumingia antillarum</i>	
Chitons	0.7
<i>Ischnochiton papillosus</i>	
Amphipods	0.5
Tanaids	0.3

Remarks.—Beebe & Tee-Van (1928) listed the food of *H. plumieri* as echinoderms, polychaetes, mollusk shells, shrimps, crabs, fishes (including *Diodon hystrix*) and bottom debris. Breder (1929) stated that the species is omnivorous. Plant material is probably ingested occasionally, but in view of our existing knowledge of the food habits of this fish and that of related pomadasyids, it would seem doubtful that it actively selects plants *per se* as food. Longley & Hildebrand (1941) designated the species as nocturnal and reported the food of Tortugas examples as worms, gastropods, lamellibranchs, and crustaceans. Reid (1954) found crustaceans such as copepods and mysids in six stomachs from West Florida. Crushed *Diadema* formed most of the stomach and gut contents of two adults from St. John, Virgin Islands. The conch (*Strombus gigas*) was found in the stomach of a 204-mm fish; there was no shell or fragments thereof (had there been a shell it would have been about 80-mm long).

Haemulon sciurus (Shaw)

BLUESTRIPED GRUNT

28 stations; 60 specimens: 105 to 312 mm SL; 26 empty.

FOOD	VOLUME (%)
Crabs	26.9
portunids (2)	
xanthids (2)	
Pelecypods	15.0
<i>Macoma cerina</i>	
<i>Pitar fulminata</i>	
<i>Tellina caribaea</i>	
Shrimps	10.0
alpheids (2)	
axiid	
Echinoids	8.7
<i>Diadema antillarum</i>	
Ophiuroids	5.6
<i>Ophiothrix</i> sp.	
Unidentified animal material	5.2
Polychaetes	5.0
Gastropods	4.5
<i>Acmaea</i> sp.	
<i>Anachis</i> sp.	
<i>Arene</i> sp.	
<i>Bittium varium</i>	
<i>Cyclostremiscus ornatus</i>	

<i>Diodora</i> sp.	
<i>Hyalina</i> sp.	
<i>Hyalina albolineata</i>	
<i>Mangelia</i> sp.	
<i>Melampus coffeus</i>	
<i>Mitra barbadensis</i>	
<i>Modulus modiolus</i>	
<i>Nitidella</i> sp.	
<i>Olivella</i> sp.	
<i>Persicula lavalleana</i>	
<i>Rissoina</i> sp.	
<i>Strombus gigas</i>	
<i>Zebina browniana</i>	
Stomatopods	4.4
<i>Pseudosquilla ciliata</i>	
Sipunculids	3.0
Fishes	2.9
Amphipods	1.9
Unidentified crustaceans	1.8
Octopuses	1.5
Isopods	1.4
Tunicates	1.0
Ostracods	0.6
Bryozoans	0.3
Scaphopods	0.2
<i>Cadulus</i> sp.	
Tanaids	0.07
Hermit crabs	0.03

Remarks.—Longley & Hildebrand (1941) noted that the bluestriped grunt is nocturnal. It schools around large coral stacks by day, and at night the schools break up for feeding. These authors listed the food material as mostly crustaceans, mollusks, and annelids, with some small ophiuroids. Five of the 34 specimens with full stomachs reported above contained small amounts of seagrass or algae.

SPARIDAE (Porgies)

Three genera of porgies occur in the West Indies: *Archosargus*, *Diplodus*, and *Calamus*. The former two are omnivorous, and *Calamus* appears to be carnivorous. The teeth at the front of the jaws of sparids are conical or incisiform; those along the sides are molariform. The hard parts of invertebrates are crushed with the molariform teeth. Beebe & Tee-Van (1928) reported on the food habits of four species of *Calamus* from Haiti. According to Randall & Caldwell (1966), who reviewed this difficult genus, two of the four names used by Beebe & Tee-Van do not apply to known species in the West Indies. Also, one cannot be certain of the

taxonomic entities from their descriptive information. Their data, therefore, should be regarded as applying to the genus, in general. The species of *Calamus* swim above but close to the bottom. They are diurnal. Although often seen over or near reefs, they are not tied to reefs for shelter. These fishes are very alert; characteristically they maintain a considerable distance between themselves and a potential source of danger, such as a spearfisherman. For this reason they are best collected by hook and line.

Archosargus rhomboidalis (Linnaeus)

SEA BREAM

6 stations; 23 specimens: 105 to 220 mm SL.

FOOD	VOLUME (%)
Seagrasses	44.6
<i>Cymodocea manatorum</i>	
<i>Thalassia testudinum</i>	
Algae	38.8
<i>Ceramium nitens</i>	
<i>Enteromorpha</i> sp.	
<i>Enteromorpha flexuosa</i>	
<i>Lyngbya majuscula</i>	
<i>Rhizoclonium riparium</i>	
Crabs	4.8
Gastropods	4.3
Unidentified invertebrate eggs	3.5
Pelecypods	3.4
<i>Pinctada radiata</i>	
Polychaetes	0.4
Amphipods	0.2

Remarks.—*Archosargus rhomboidalis* is usually seen in mangrove sloughs. Only rarely may it be found near coral reefs. It feeds primarily on plants. Most of the seagrass material from its stomachs consisted of *Thalassia*.

Calamus bajonado (Bloch & Schneider)

JOLTHEAD PORGY

9 stations; 10 specimens: 137 to 500 mm SL; 1 empty.

FOOD	VOLUME (%)
Echinoids	45.2
<i>Diadema antillarum</i> (5)	
<i>Lytechinus variegatus</i>	
Crabs	22.2
Pelecypods	13.4
arcid	
<i>Musculus lateralis</i>	
<i>Ostrea</i> sp.	
Gastropods	11.1
<i>Turbo castanea</i>	
Polychaetes	6.7

Hermit crabs	1.1
--------------	-----

Clibanarius tricolor

Paguristes sp.

Paguristes anomalus

Unidentified animal material	0.3
------------------------------	-----

Remarks.—*Calamus bajonado* is the largest species of the genus. The three largest fish listed above (338 to 455 mm SL) and one of 247 mm had eaten only *Diadema*.

<i>Calamus calamus</i> (Cuvier & Valenciennes)	SAUCEREYE PORGY
------------------------------------------------	-----------------

10 stations; 15 specimens: 190 to 250 mm SL; 3 empty.

FOOD	VOLUME (%)
Polychaetes	19.2
Ophiuroids	15.5
<i>Ophioderma</i> sp.	
<i>Ophiothrix</i> sp. (2)	
Pelecypods	15.0
<i>Codakia orbicularis</i>	
<i>Gouldia cerina</i>	
<i>Pinna carnea</i>	
Hermit crabs	13.4
Crabs	12.8
majids	
Echinoids	8.9
<i>Diadema antillarum</i>	
Gastropods	8.3
<i>Nassarius albus</i>	
<i>Tegula</i> sp.	
<i>Tegula fasciata</i>	
Unidentified crustaceans	3.6
Chitons	1.8
Unidentified animal material	0.9
Sipunculids	0.6
<i>Aspidosiphon</i> sp.	

<i>Calamus penna</i> (Cuvier & Valenciennes)	SHEEPSHEAD PORGY
----------------------------------------------	------------------

3 stations; 3 specimens: 190 to 283 mm SL; 2 empty.

FOOD	VOLUME (%)
Crabs	50.0
portunid	
Gastropods	50.0

<i>Calamus pennatula</i> Guichenot	PLUMA
------------------------------------	-------

13 stations; 15 specimens: 127 to 270 mm SL; 5 empty.

FOOD	VOLUME (%)
Crabs	21.5
calappid	

leucosid	
Ophiuroids	14.2
<i>Ophiothrix</i> sp.	
Polychaetes	14.0
Pelecypods	12.3
<i>Laevicardium</i> sp.	
<i>Trachycardium</i> sp.	
Gastropods	8.2
Hermit crabs	8.0
Shrimps	5.8
Sipunculids	5.0
Echinoids	4.0
<i>Diadema antillarum</i>	
Holothurians	4.0
Stomatopods	3.0

Remarks.—*C. pennatula* is the most common species of the genus in the West Indies.

Diplodus caudimacula (Poey) ROUNDSPOT PORGY
3 stations; 5 specimens: 110 to 217 mm SL.

FOOD	VOLUME (%)
Algae	80.0
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp.	
<i>Dictyota dentata</i>	
<i>Ectocarpus</i> sp.	
<i>Udotea flabellum</i>	
Gastropods	16.0
acmaeids	
Chitons	2.0
Crabs	2.0

Remarks.—*Diplodus caudimacula* is not common in the West Indies. Most individuals have been observed along steep rocky shores exposed to wave action, but they may also occur in a shallow, calm, rock-sand habitat. The stomachs of three of the specimens that were examined consisted of two-thirds algae and one-third sand.

KYPHOSIDAE (Sea chubs)

The sea chubs are active diurnal fishes usually associated with rocky bottom. Although often seen near shore, they range to depths of at least 100 feet. Although they may occasionally be taken on hook and line with animal material as bait, they are characteristically herbivorous, at least as adults. Their incisiform teeth are well adapted for cropping algae. In addition to browsing on benthic algae, they feed on floating *Sargassum* and

occasional fragments of seagrass. Very little sedimentary material was found in the stomachs.

Kyphosus incisor (Cuvier & Valenciennes)
5 stations; 6 specimens: 192 to 552 mm SL.

YELLOW CHUB

FOOD	VOLUME (%)
Algae	100.0
<i>Dictyopteris delicatula</i>	
<i>Dictyota divaricata</i> (2)	
<i>Pocockiella variegata</i>	
<i>Sargassum fluitans</i>	
<i>Sargassum hystrix</i> (2)	
<i>Sargassum natans</i>	
<i>Turbinaria turbinata</i>	

Remarks.—Longley & Hildebrand (1941) reported that this species at Dry Tortugas, Florida feeds chiefly on algae, including much *Sargassum*.

Kyphosus sectatrix (Linnaeus)
18 stations; 19 specimens: 130 to 590 mm SL.

BERMUDA CHUB

FOOD	VOLUME (%)
Algae	99.5
<i>Botryocladia occidentalis</i>	
<i>Bryothamnion triquetrum</i> (2)	
<i>Ceramium</i> sp.	
<i>Ceramium nitens</i>	
<i>Chondria littoralis</i>	
<i>Dictyopteris delicatula</i> (3)	
<i>Dictyopteris plagiogramma</i>	
<i>Dictyopteris justii</i>	
<i>Dictyota</i> sp.	
<i>Dictyota bartayresii</i> (2)	
<i>Dictyota ciliata</i>	
<i>Dictyota divaricata</i> (3)	
<i>Dictyota linearis</i>	
<i>Digenia simplex</i>	
<i>Eucheuma acanthocladum</i>	
<i>Gelidiella acerosa</i>	
<i>Gelidium corneum</i> (3)	
<i>Gracilaria mammillaris</i>	
<i>Hypnea musciformis</i> (2)	
<i>Jania capillacea</i>	
<i>Laurencia papillosa</i> (2)	
<i>Laurencia corallopsis</i>	
<i>Padina</i> sp.	
<i>Padina gymnospora</i>	
<i>Padina sanctae-crucis</i>	

Pocockiella variegata (3)
Polysiphonia sp. (2)
Sargassum sp.
Sargassum fluitans
Sargassum hystrix (3)
Sargassum natans (4)
Sargassum platycarpum (2)
Sargassum polyceratum (3)
Sargassum rigidulum
Sphacelaria tribuloides
Spyridia filamentosa
Turbinaria turbinata

Seagrasses

0.5

Cymodocea manatorum (2)

Remarks.—H. Smith (1907) reported that Linton examined four specimens from North Carolina that contained crabs, small bivalve shells, vegetable debris and sand. Beebe & Tee-Van (1928) found small crustaceans in the stomach of a 78-mm specimen. Gudger (1929) referred to the species as a herbivore and commented on the dentition and visceral anatomy. He pointed out that its specific name and one of its common names (rudderfish) are derived from its habit of following in the wake of vessels probably to feed on wastes. The author has not observed this, but has seen an Indo-Pacific species of *Kyphosus* feed on offal released from an anchored ship in the Marshall Islands. In reference to Tortugas fish, Longley & Hildebrand (1941) described *K. sectatrix* as chiefly if not wholly herbivorous, feeding on the bottom and on floating *Sargassum*. *Sargassum* was found in the stomachs of 12 of the 19 West Indian specimens that were examined by the author. In eight of these it comprised from 25 to 100 per cent of the stomach-content material. The browns *Dictyota* and *Dictyopteris* were also prominent in the stomachs. Only one fish had eaten the very coarse *Turbinaria*, but this constituted 75 per cent of its stomach contents. The delicate red *Ceramium nitens*, on the other hand, represented 97 per cent of the stomach contents of one 264-mm specimen.

GERREIDAE (Mojarras)

The mojarras are silvery fishes that usually occur over sand or mud bottoms. They feed at least in part by day. During feeding they may thrust their highly protrusible mouths into the sediment for subsurface invertebrates. Considerable amounts of sand may be expelled through the gill openings during the feeding process.

Eucinostomus argenteus Baird & Girard
 5 stations; 19 specimens: 75 to 152 mm SL.

SANDFLAT MOJARRA

Food
 Amphipods
 gammarids

VOLUME (%)
 41.8

<i>Hyale</i> sp.	
Polychaetes	19.5
eunicids	
Crabs	10.9
calappids	
majid	
raninids	
Shrimps	7.6
alpheids	
<i>Callinassa</i> sp.	
Tanaids	5.9
Pelecypods	3.4
<i>Tellina</i> sp.	
Sipunculids	2.6
Unidentified crustaceans	2.6
Unidentified animal material	2.1
Copepods	2.0
harpacticoids	
Gastropods	1.6

Remarks.—This mojarra is a solitary fish that occurs in shallow, clear-water areas over sand bottoms. It does not often swim over reefs but is frequently seen near them. Beebe & Tee-Van (1928) reported detritus of both animal and vegetable origin in specimens from Haiti; they identified their fish as *E. californiensis*. According to C. L. Hubbs and C. R. Robins (personal communication) *E. pseudogula* is also a probable synonym of *argenteus*.

Gerres cinereus (Walbaum) YELLOWFIN MOJARRA
34 stations; 51 specimens: 95 to 280 mm SL; 24 empty.

Food	VOLUME (%)
Crabs	27.0
hippids (2)	
majids	
portunid	
Pelecypods	23.0
<i>Laevicardium</i> sp.	
<i>Macoma cerina</i>	
<i>Solemya occidentalis</i>	
<i>Tellina</i> sp. (2)	
<i>Yoldia perprotracta</i>	
Gastropods	14.5
<i>Acmaea antillarum</i> (2)	
<i>Fissurella barbadensis</i>	
<i>Hemitoma octoradiata</i>	
<i>Olivella</i> sp.	
<i>Tricolia tessellata</i>	

Polychaetes	12.7
Sipunculids	6.0
<i>Aspidosiphon</i> sp.	
Unidentified crustaceans	4.4
Shrimps	4.3
alpheids	
<i>Callianassa</i> sp.	
Stomatopods	2.8
<i>Gonodactylus oerstedii</i>	
Hemichordates	1.9
Ophiuroids	1.9
<i>Ophiothrix</i> sp.	
Unidentified animal material	1.1
Amphipods	0.4

Remarks.—This mojarra, a larger species than the preceding, is often found over reefs or rocky areas and on sand flats. It may be observed feeding freely on a hard substratum (as indicated by the limpets and *Ophiothrix* in its stomach contents) and in sand patches among reefs. Beebe & Tee-Van (1928) reported it to be a general feeder and listed the food as an assortment of worms, mollusks, crustaceans, and parts of small fish. Longley & Hildebrand (1941) found the remains of a large worm and much sand and debris in the stomach of one fish from Tortugas.

SCIAENIDAE (Croakers)

Most sciaenids are found on open sand or mud bottoms. Four West Indian species, however, are characteristic of reefs: *Odontoscion dentex* and three *Equetus*. They appear to be primarily nocturnal.

Equetus acuminatus (Bloch & Schneider) STRIPED DRUM
12 stations; 35 specimens: 68 to 152 mm SL; 16 empty.

FOOD	VOLUME (%)
Shrimps and shrimp larvae	73.2
alpheids (2)	
palaemonid	
<i>Periclimenes</i> sp.	
<i>Processa</i> sp.	
penaeids (2)	
Unidentified crustaceans	10.5
Crabs	5.3
<i>Petrolisthes galathinus</i>	
Fishes and fish larvae	3.7
Isopods	3.1
Stomatopod larvae	2.3
Copepods	1.6
Amphipods	0.3

Remarks.—*E. acuminatus* hides, often in the company of several others of the same species, in crevices or beneath rock ledges by day and emerges to feed at night. Most of the food organisms of the specimens listed above were planktonic.

Equetus lanceolatus (Linnaeus) JACKKNIFE FISH

4 stations; 5 specimens: 116 to 145 mm SL; 1 empty.

FOOD	VOLUME (%)
Shrimps	62.5
alpheid	
palaemonid	
Polychaetes	31.3
Crabs	6.2

Remarks.—Lowe (1962) reported tiny *Triton*-like gastropods from the stomachs of specimens from British Guiana.

Equetus punctatus (Bloch & Schneider) SPOTTED DRUM

20 stations; 28 specimens: 76 to 216 mm SL; 12 empty.

FOOD	VOLUME (%)
Crabs	34.4
<i>Cronius ruber</i>	
grapsoid	
<i>Mithrax</i> sp.	
Unidentified crustaceans	22.5
Shrimps and shrimp larvae	20.6
alpheids (2)	
hippolytids	
Hermit crabs	11.3
Polychaetes	5.4
Gastropods	3.2
<i>Hipponix subrufus</i>	
Isopods	1.0
Pelecypods	0.6
Fishes	0.4
Ostracods	0.3
Stomatopods	0.3

Remarks.—*E. punctatus*, the largest of West Indian *Equetus*, was usually encountered as solitary individuals hiding beneath ledges in coral reefs by day. The stomachs of fish taken in late morning or afternoon hours were usually empty, but some individuals contained freshly ingested food material, thus indicating some daytime feeding.

Odontoscion dentex (Cuvier & Valenciennes) REEF CROAKER

6 stations; 75 specimens: 79 to 137 mm SL; 50 empty.

FOOD	VOLUME (%)
Shrimps and shrimp larvae	38.0
alpheid	

carideans	
penaeids	
Fishes and fish larvae	37.8
Isopods	17.8
<i>Excorallana antillensis</i>	
Crabs	5.2
Stomatopod larvae	1.2

Remarks.—*O. dentex* is a small fish which forms aggregations in caves in reefs by day. In contrast to the preceding three sciaenids, it has moderately well developed canine teeth in the jaws; thus the large amount of fish in the diet was not unexpected. The shrimps in the stomachs ranged from 2 to 13 mm in length.

MULLIDAE (Goatfishes)

The goatfishes are most commonly found on sand or mud bottoms. They feed primarily on benthic invertebrates from the surface or beneath the surface of the sediments. They have a pair of long chin barbels which are well supplied with chemosensory organs (judging from the work of Sato, 1937, on *Upeneus bensasi*). During feeding, these barbels are rapidly moved over the substratum in front of the mouth or are thrust into the sediment. Often the entire snout is shoved deeply into the sand in search of subsurface prey. Such feeding is generally followed by the expulsion of considerable inorganic material. The mullids lack a crushing dentition. The larger food items from their stomachs are usually soft-bodied animals, such as worms. The hard-shelled invertebrates which are eaten are invariably very small. The adults of two West Indian species, *Mulloidichthys martinicus* and *Pseudupeneus maculatus*, are often seen on reefs, and the young are abundant in seagrass beds. The feeding by adults takes place primarily on sand bottoms adjacent to the reefs.

Mulloidichthys martinicus (Cuvier & Valenciennes) YELLOW GOATFISH
21 stations; 23 specimens: 148 to 280 mm SL; 9 empty.

FOOD	VOLUME (%)
Polychaetes	18.6
Crabs and crab larvae	15.9
portunid	
Pelecypods	13.1
<i>Cumingia antillarum</i>	
<i>Laevicardium</i> sp.	
<i>Tellina</i> sp. (3)	
Shrimps and shrimp larvae	11.9
alpheid	
carideans	
penaeids	
Ophiuroids	8.9

<i>Amphipholis gracillima</i>	
<i>Ophiothrix</i> sp.	
Chitons	7.9
<i>Acanthochiton pygmaea</i>	
Sipunculids	6.8
<i>Aspidosiphon</i> sp.	
<i>Siphonosoma cumanense</i>	
Isopods	5.7
Amphipods	4.3
<i>Neomicrodentopus</i> sp.	
<i>Paraphoxus</i> sp.	
Ostracods	1.6
Unidentified animal material	1.5
Tanaids	0.9
Stomatopods	0.8
Gastropods	0.7
Scaphopods	0.4
Echinoids	0.4
Copepods	0.3
Unidentified crustaceans	0.3

Remarks.—Longley & Hildebrand (1941) listed annelids, crabs, small ophiurans, and an occasional small fish from the stomachs of specimens from Dry Tortugas, Florida. Longley believed this species to be primarily nocturnal. It certainly feeds by day as well; all of the collections reported on above were made during daylight hours. Sand was present in most of the stomachs of the West Indian specimens; in one fish it constituted 25 per cent of the stomach contents. Most of the crustaceans and mollusks from the stomachs were extremely small. An exception was a 20-mm chiton from a 240-mm fish. The same fish also contained a crab 12 mm in carapace width.

Pseudupeneus maculatus (Bloch) SPOTTED GOATFISH
22 stations; 27 specimens: 128 to 218 mm SL; 1 empty.

FOOD	VOLUME (%)
Crabs	30.2
calappids (2)	
grapsoid	
majids (3)	
portunids (2)	
xanthids (2)	
Shrimps	21.8
alpheids (3)	
carideans	
palaemonid	
penaeids	
<i>Tozeuma</i> sp.	

Polychaetes	13.3
Unidentified crustaceans	7.3
Pelecypods	6.7
<i>Pecten</i> sp.	
<i>Tellina</i> sp.	
Sipunculids	4.4
<i>Aspidosiphon cumingi</i>	
Fishes	4.3
<i>Coryphopterus personatus</i>	
syngnathids (2)	
Stomatopods	3.2
<i>Pseudosquilla ciliata</i>	
Unidentified animal material	2.7
Isopods	1.9
Amphipods	1.8
Ophiuroids	0.8
Gastropods	0.8
<i>Turbonilla</i> sp.	
Ostracods	0.4
Tanaids	0.2
Unidentified eggs	0.2

Remarks.—Beebe & Tee-Van (1928) reported the food of Haitian examples as "bottom debris, organic and inorganic, animal and vegetable." Longley & Hildebrand (1941) stated that the species is diurnal and feeds almost exclusively on small animals. Some of the above specimens from Puerto Rico and the Virgin Islands had liberal amounts of sand mixed with their food (up to 10 per cent or more), but none contained any significant amount of plant material. Most of the polychaetes were sub-surface species, and many were tube-dwelling. Some of the polychaetes or pieces thereof were as long as 90 mm. Most of the prey animals, however, were small. The calappid crab from the stomach of a 185-mm fish measured only 10 mm across the carapace. Seven crabs from the stomach of a 186-mm fish ranged from 7 to 15 mm in greatest carapace measurement.

BRANCHIOSTEGIDAE (Tilefishes)

Malacanthus plumieri (Bloch) SAND TILEFISH
6 stations; 8 specimens: 285 to 417 mm SL; 1 empty.

FOOD	VOLUME (%)
Ophiuroids	21.9
<i>Ophiocoma echinata</i>	
<i>Ophionereis</i> sp.	
Crabs	18.5
Stomatopods	15.0
<i>Gonodactylus</i> sp.	

Fishes	12.4
eel	
<i>Halichoeres</i> sp.	
Polychaetes	7.2
Sipunculids	7.2
Unidentified worms	6.4
Chitons	5.7
<i>Choneplax lata</i>	
Echinoids	2.7
spatangoids	
Amphipods	1.6
Shrimps	1.4

Remarks.—*M. plumieri* is the only shallow-water representative of the family Branchiostegidae in the western Atlantic. It makes a burrow in a sand bottom. Often a patch of coral rubble and eroded shells lies near the entrance, apparently the result of excavation by the fish. It ranges over the open bottom a considerable distance from its burrow, but with the approach of danger it rapidly swims to the entrance and hovers over it nervously, entering head-first with further provocation.

RACHYCENTRIDAE (Cobias)

Rachycentron canadum (Linnaeus)

COBIA

1 station; 1 specimen: 840 mm SL.

FOOD	VOLUME (%)
Fishes	100.0

Lactophrys sp.

Lactophrys triqueter

Remarks.—The cobia is a rare species in the West Indies (only the single specimen listed above was collected), but it is not uncommon in continental waters of the tropical western Atlantic. H. Smith (1907) stated that it feeds primarily on crabs but also eats shrimps and small fishes. One of its local names in the eastern United States is crab-eater. Breder (1948) noted that it feeds on fishes and crabs. Knapp (1949) reported the following food organisms by percentage of occurrence in the stomachs of 22 cobias from the coast of Texas: fishes (95.5 per cent), crabs (50 per cent), shrimps (50 per cent), squids (13.7 per cent), and other invertebrates (59.1 per cent). Reid (1954) found a cowfish (*Acanthostracion tricornis*) and three catfish in the stomach of one of two specimens examined from Florida.

ECHENEIDAE (Sharksuckers)

The echeneids are well known for their ability to attach to sharks, the larger bony fishes, and sea turtles with the sucking disc on the top of their head. It has long been presumed that they feed on scraps from their hosts' meals. Strasburg (1959), however, has shown that they may also feed on

zooplankton and the smaller nekton or on their hosts' ectoparasites. Although no species seems to fit exclusively into one of the three feeding categories, there is a tendency for some to concentrate in one or another.

Echeneis naucrates Linnaeus

SHARKSUCKER

10 stations; 12 specimens: 100 to 680 mm SL; 7 empty.

FOOD	VOLUME (%)
Fishes	40.0
<i>Cantherhines pullus</i> (larv.)	
Unidentified animal material	35.0
Isopods	20.0
Unidentified crustaceans	5.0

Remarks.—*E. naucrates* was observed both free-swimming and attached to sea turtles, sharks, rays, and many different bony fishes including the larger reef fishes. Once the author watched a small individual with its head inserted in the gill chamber of a large parrotfish. The unidentified animal material which comprised 35 per cent of the stomach contents seemed to be mostly vertebrate muscle tissue.

Remora remora (Linnaeus)

REMORA

5 stations; 7 specimens: 58 to 175 mm SL; 2 empty.

FOOD	VOLUME (%)
Copepods	22.0
calagoid	
<i>Candacia pachydactyla</i>	
<i>Scolecithrix danae</i>	
Isopods	20.0
Vertebrate muscle tissue	20.0
Crab larvae	10.0
Fish remains	10.0
Unidentified crustaceans	10.0
Amphipods	8.0
hyperiid	

Remarks.—The most common host of the remora is a shark, and frequently an offshore species. Szidat & Nani (1951) found caligid copepods in the stomachs of *R. remora*; Maul (1956) reported caligids and oxycephalid amphipods. Strasburg (1959) found a variety of fishes and planktonic crustaceans in the stomachs of seven Pacific specimens, but no parasitic forms. Only a single parasitic copepod was taken from the stomach of the West Indian specimens reported above; this was found in the smallest specimen, along with a free-living copepod and a hyperiid amphipod.

CARANGIDAE (Jacks)

The jacks are swift-swimming, carnivorous fishes which sometimes run in small schools. They are not residents of reefs, but many enter the reef community by virtue of their preying upon reef animals. They appear to be

primarily diurnal, but it is possible to catch some species on moonlight nights with hook and line. The family is divisible by food habits into three major groups: fish-feeders such as *Caranx* and *Seriola*, plankton-feeders such as *Decapterus* and *Selar*, and mollusk-feeders such as *Trachinotus*. The various species do not all fit perfectly into such categories, and some transcend the boundaries as they grow from young to adults. The following carangids were only occasionally seen over reef areas at West Indian localities, and the few specimens obtained all had empty stomachs or contained only bait or chum: *Alectis crinitus*, *Caranx hippos*, *Elagatis bipinnulatus*, and *Seriola rivoliana*. *Caranx hippos* was observed in clear-water regions only as solitary large adults. This species is more characteristic of turbid inshore waters, including regions of low salinity. Data on its food habits have been presented by Linton (1905), Hildebrand & Schroeder (1928), Knapp (1949), Reid (1954), Darnell (1959), and Tabb & Manning (1961). *Elagatis bipinnulatus* was described by Hiatt & Strasburg (1960) as more-or-less pelagic, and its food as "probably pelagic fish although it certainly will take swimming crustaceans or squid." *Chloroscombrus chrysurus*, *Selene vomer*, and *Vomer setapinnis* are all common in the tropical western Atlantic, but they were not observed in association with coral reefs.

Caranx bartholomaei (Cuvier & Valenciennes) YELLOW JACK
6 stations; 7 specimens: 310 to 478 mm FL; 1 empty.

FOOD	VOLUME (%)
Fishes	100.0
<i>Chaenopsis ocellata</i>	
<i>Halichoeres maculipinna</i>	
<i>Ocyurus chrysurus</i>	
<i>Sparisoma</i> sp.	
syngnathid	

Remarks.—Longley & Hildebrand (1941) stated that the yellow jack swims near the bottom in its foraging. This is demonstrated by the fishes listed above from the stomachs of Virgin Islands specimens. The pike blenny and most pipefishes are strictly benthic, and the parrotfish and wrasse are usually found close to the bottom.

Caranx fusus Geoffroy BLUE RUNNER
18 stations; 44 specimens: 190 to 520 mm FL; 27 empty.

FOOD	VOLUME (%)
Fishes	87.0
atherinids	
engraulids	
<i>Jenkinsia</i> sp.	
<i>Pseudupeneus maculatus</i>	
Crabs	5.9
Stomatopods	3.5

Pteropods	1.2
<i>Cavolina</i> sp.	
Unidentified animal material	1.1
Siphonophores	0.7
Copepods	0.6
<i>Candacia pachydactyla</i>	

Remarks.—The author follows Tortonese (1961) in regarding *Caranx crysos* a synonym of *fuscus*. The blue runner is usually encountered as rapidly moving schools over open bottom. Only occasionally does it make excursions over reefs. McKenney, Alexander, & Voss (1958) examined the stomach contents of 128 larvae, postlarvae, and juveniles from 2.6 to 95.0 mm standard length. The young fish proved to be plankton-feeders, with cyclopoid and calanoid copepods strongly dominating the stomach contents. In reference to larger fish these authors stated, “. . . blue runners are normally caught trolling with small Japanese feathers or a piece of white cloth tied to the shank of the hook, indicating a predilection for somewhat larger food, and they are often taken with shrimp in their stomachs.” The stomach contents of two of the West Indian specimens analyzed above consisted of 40 per cent planktonic organisms and the rest was fish remains. These two jacks measured 222 and 250 mm in fork length. With the exception of one 295-mm individual which had eaten a crab, all of the others contained only fishes. Most of the prey fishes were small silvery schooling species.

Caranx latus Agassiz HORSE-EYE JACK
22 stations; 22 specimens: 145 to 640 mm FL; 10 empty.

FOOD	VOLUME (%)
Fishes	87.1
atherinids	
<i>Harengula</i> sp.	
<i>Myripristis jacobus</i> (juv.)	
Pteropods	8.4
<i>Cavolina longirostris</i>	
Shrimps	3.8
penaeids	
Isopods	0.7

Remarks.—Beebe & Tee-Van (1928) reported on the stomach contents of specimens from Haiti in the size range of 72 to 280 mm which were observed to be feeding on the animals that accumulated around a night light. Although worms were as abundant as small fishes at the light, only fishes were eaten by the jacks. Ten of the specimens of the present study had eaten only fishes. Another had 46 per cent fish by volume, and the last, a 12-pound horse-eye, was filled with pteropods (*Cavolina longirostris*) 3 to 4 mm in length.

Caranx lugubris Poey

BLACK JACK

6 stations; 6 specimens: 400 to 680 mm FL; 4 empty.

FOOD

VOLUME (%)

Fishes

100.0

Remarks.—The black jack is rarely encountered in shoal areas. The specimens above were speared in the depth range of 70 to 190 feet, and all from water of high clarity.

Caranx ruber (Bloch)

BAR JACK

80 stations; 96 specimens: 160 to 547 mm FL; 26 empty.

FOOD

VOLUME (%)

Fishes

91.5

Acanthurus sp. (larv.) (3)

Acanthurus coeruleus (juv.) (2)

Anchoa hepsetus

atherinids (3)

engraulids

Entomacrodus nigricans

Harengula clupeiola

Jenkinsia sp.

Monacanthus sp.

mullid

Ophioblennius atlanticus (2)

Pomacentrus planifrons

Pseudupeneus maculatus (3)

scarids (3)

Scarus croicensis

Sparisoma aurofrenatum (2)

Sparisoma viride

syngnathid

Shrimps

3.4

penaeids

Tozeuma sp.

Mysids

2.2

Squids

1.4

Stomatopods

0.6

Gastropods

0.4

Crabs

0.4

hippid

Unidentified crustaceans

0.1

Remarks.—*Caranx ruber* is the most abundant jack in clear, shallow-water areas of the West Indies. It is often seen over reefs. Not only does it prey in part upon fishes and other animals there, but it also receives the attention of reef-dwelling "cleaning" fishes. Longley & Hildebrand (1941) noted that it is groomed by *Thalassoma* and *Anisotremus*. The author has also observed it enter into this symbiotic relationship with *Bodianus rufus*.

When its ectoparasites are being removed, the bar jack may alter its hue from silvery white to deep bronze. It, in turn, has been observed to pick at the body of the great barracuda. The jacks were about 4 inches long and the barracuda about 3 feet. Fishes predominated in the stomach contents of *C. ruber*. Small silvery schooling forms such as clupeids, dussumierids, engraulids, and atherinids were found in the stomachs of 21 of the bar jacks. Because these small delicate fishes are digested rapidly, it was usually not possible to place them to family by gross external examination. The largest fish in a bar jack stomach relative to the size of the predator was a 130-mm (SL) spotted goatfish (*Pseudupeneus maculatus*); the jack containing it measured 380-mm in fork length. Also noteworthy for prey size was a 158-mm *Sparisoma aurofrenatum* from the stomach of a bar jack 475-mm in fork length. Only one of the jacks had eaten cephalopods; this was a 415-mm adult which contained three squids up to 60 mm in length. Mysids were found in the stomachs of two of the jacks, one of 165 mm and the other of 180 mm fork length. A few stomachs contained small amounts of sand, indicating that the jacks may at times take their prey directly from the bottom. Feeding rushes were observed on occasions in which the sand was disturbed.

Decapterus macarellus (Cuvier & Valenciennes) MACKEREL SCAD
2 stations; 2 specimens; 236 and 257 mm FL.

FOOD	VOLUME (%)
Pteropods	96.5
Copepods	1.2
Unidentified crustaceans	0.8
Mysids	0.5
Shrimp larvae	0.5
Crab larvae	0.5

Decapterus punctatus (Agassiz) ROUND SCAD
4 stations; 10 specimens; 131 to 171 mm FL.

FOOD	VOLUME (%)
Copepods	60.0
<i>Candacia pachydactyla</i> (2)	
<i>Farranula gracilis</i>	
<i>Miracia efferata</i>	
<i>Oncaea</i> sp.	
<i>Scolecithrix danae</i>	
Gastropod larvae	18.5
Ostracods	8.5
Pteropods	6.0
Unidentified animal material	6.0
Shrimp larvae	1.0

Remarks.—The two West Indian species of *Decapterus* are schooling, mid-water forms that feed on zooplankton. Beebe & Tee-Van (1928)

reported copepods, zoea, and ostracods from the stomach of one 95-mm specimen of *D. punctatus* from Haiti, and Longley & Hildebrand (1941) found copepods in Tortugas examples. The unidentified material that represented 6 per cent by volume of the stomach contents of the 10 specimens listed above was soft and gelatinous; possibly it was the remains of ctenophores or salps.

Oligoplites saurus (Bloch & Schneider) LEATHERJACKET
3 stations; 11 specimens: 149 to 234 mm FL; 4 empty.

FOOD	VOLUME (%)
Fishes	98.7
<i>Jenkinsia</i> sp.	
Shrimp larvae	1.3

Remarks.—The leatherjacket is a small, swift, predaceous fish that usually runs in small groups near the surface. It is more frequently found where the water is turbid rather than clear. Its finlets make it suggestive of scombrids, and its feeding is probably similar to small *Scomberomorus*. At times it leaps free of the surface, as indicated by occasional strandings inside small boats. Hildebrand & Schroeder (1928) found fish remains and plant tissue in the stomachs of two specimens from Chesapeake Bay, and Beebe & Tee-Van (1928) reported small anchovies in the stomachs of Haitian examples. Breder (1948) wrote that it feeds mainly on fishes. Tabb & Manning (1961) stated that it is a common fish of the muddy waters of northern Florida Bay where it feeds heavily on the snapping shrimp *Alpheus heterochaelis*, small pink shrimp, larval anchovies, and ladyfish.

Selar crumenophthalmus (Bloch) BIGEYE SCAD
4 stations; 26 specimens: 115 to 192 mm FL; 14 empty.

FOOD	VOLUME (%)
Fish scales	50.0
Shrimp larvae	25.0
Crab larvae	12.5
Fishes and fish larvae	9.6
engraulids	
Copepods	2.1
<i>Candacia pachydactyla</i>	
<i>Nannocalanus minor</i>	
<i>Scolecithrix danae</i>	
<i>Undinula vulgaris</i>	
Gastropod larvae	0.8

Remarks.—This circumtropical fish, sometimes classified in the genus *Trachurops*, is a schooling species which may occur in such shallow water that it can be taken with a throw net. Beebe & Tee-Van (1928) found a variety of small fishes and polychaete worms in the stomachs of two specimens from Haiti. Longley & Hildebrand (1941) reported that the

stomach of one from Dry Tortugas contained a large shrimp and a partly digested fish, probably *Harengula*. Hiatt & Strasburg (1960) examined the stomach contents of 27 specimens from the Marshall Islands. They found foraminifera in 60 per cent of the fish, followed in the order of importance by gastropods, fishes, and crustaceans. The scads had fed primarily on the benthonic fauna of the reef shallows. The fish scales which represented 50 per cent of the stomach content material of West Indian specimens (the only item in the stomachs of six fish) appeared to have been recently detached from small clupeoid fishes. Probably the scads ate the scales after an attack on a school of clupeoids by large predaceous fish.

Seriola dumerili (Risso)

GREATER AMBERJACK

6 stations; 8 specimens: 890 to 1180 mm FL; 2 empty.

FOOD	VOLUME (%)
Fishes	100.0
balistid	
<i>Calamus</i> sp.	
<i>Caranx ruber</i>	
<i>Haemulon aurolineatum</i>	
<i>Priacanthus arenatus</i>	

Remarks.—The amberjack is a large roving predator that often makes excursions over reefs in quest of fishes (of which it is capable of eating sizeable quantities). The stomach of a 27-pound individual contained seven bigeyes (*Priacanthus arenatus*) 110 to 120 mm in standard length. A 30-pound fish had eaten a 220-mm *Caranx ruber*, two 150-mm individuals of *Haemulon aurolineatum*, and two other 100-mm fish. The balistid which was found in the stomach of an amberjack 1100 mm in fork length measured 200 mm in standard length; with it was a 40-mm piece of coral rubble.

Trachinotus falcatus (Linnaeus)

PERMIT

8 stations; 8 specimens: 500 to 810 mm SL; 1 empty.

FOOD	VOLUME (%)
Gastropods	47.8
<i>Astraea longispina</i>	
<i>Cerithium</i> sp.	
<i>Columbella mercatoria</i>	
<i>Oliva</i> sp.	
<i>Strombus gigas</i>	
<i>Tegula lividomaculata</i>	
<i>Turbo castanea</i>	
Echinoids	25.0
<i>Diadema antillarum</i>	
<i>Echinometra</i> sp.	
Pelecypods	17.2
<i>Arca zebra</i>	

<i>Glycymeris decussata</i>	
<i>Trachycardium magnum</i>	
Hermit crabs	6.1
<i>Paguristes grayi</i>	
Crabs	3.9
<i>Albunea gibbesii</i>	
porcellanid	

Remarks.—*Trachinotus falcatus* is not a common fish in the West Indies, but it may be found in diverse habitats. It has been observed on sand flats and reefs from depths of a few to at least 100 feet. It has also been taken from mud-bottom areas (*T. carolinus*, however, is more apt to occur in the latter). Hildebrand & Schroeder (1928) found worms, crustaceans, mollusks, and fish in the stomachs of small permit from Chesapeake Bay. Longley & Hildebrand (1941) reported *Strombus bituberculatus* (= *rarinus*), the large hermit crab *Petrochirus bahamensis* (= *diogenes*), echinoid spines and test, and fragments of the majid crab *Piitho* and other crustaceans in the guts of two adults from Dry Tortugas. Springer & Woodburn (1960) listed *Hippa* and *Donax* as the food of young individuals from the Tampa Bay area of Florida. One of the specimens collected by the author in the Virgin Islands (500 mm SL, 8 pounds), contained an assortment of crushed gastropods and pelecypods in its alimentary tract, including nine individuals of *Turbo castanea* with opercula 9 to 11 mm in diameter. Another permit was observed feeding on turbinids. These were picked up individually and crushed. Shell fragments were then seen passing out of the gill openings. Usually a number of shell fragments are swallowed with the soft parts, however. An 810-mm, 33-pound permit contained enough of the shell of a queen conch (*Strombus gigas*) to determine that the shell length was about 70 mm. Another individual had eaten *Strombus gigas*, but only the mantle and viscera which had been discarded from a dock where conchs had been cleaned. Randall, Schroeder, & Starck (1964) reported *T. falcatus* among the 15 species of West Indian reef fishes that feed upon *Diadema antillarum*; however, they pointed out that the one 610-mm individual which contained this echinoid was observed, before it was speared, to feed upon urchins that had been killed by the fish poison Pro-Noxfish on the previous day.

Trachinotus goodei Jordan & Evermann PALOMETA
 11 stations; 28 specimens: 87 to 250 mm SL; 5 empty.

Food	VOLUME (%)
Fishes	85.2
engraulids	
<i>Jenkinsia</i> sp. (3)	
Gastropods	8.3
<i>Littorina meleagris</i>	
<i>Tricolia tessellata</i>	
Pelecypods	3.9

Isopods	1.7
cymothoid	
Hermit crabs	0.9

Remarks.—The palometa was most often encountered in very shallow clear water along sandy beaches. It seemed to be attracted to bathers, for small groups of fish would circle fearlessly around the feet of persons wading in the shallows. The attraction may have been small invertebrates exposed as the feet disturbed the sand. The large percentage of fish in the diet of *T. glaucus* was not expected. All but one of 14 specimens taken in a shallow bay in St. John where small schooling fishes were in great abundance had fed heavily on the small fishes. The results of this one station may have raised the percentage of fish higher than normal for the species as a whole. The invertebrates from the stomachs were much smaller than the fishes that were consumed. None of the gastropods and pelecypods from the stomach of a 202-mm palometa, for example, exceeded 4 mm in greatest measurement. About two-thirds of the shells from this fish were in pieces. The stomach contents of two other fish, which had eaten primarily gastropods, consisted of about 50 per cent green algae. Presumably this was ingested incidentally with the gastropods.

SCOMBRIDAE (Mackerels and Tunas)

Most of the tunas and their allies are pelagic fishes that are rarely, if ever, associated with reefs except through feeding on the larval stages of reef animals that are carried offshore by currents. Two species of *Scomberomorus* and the little tuna (*Euthynnus alletteratus*), however, often range over reefs and feed in part on resident fishes.

Euthynnus alletteratus (Rafinesque) LITTLE TUNA
22 stations; 29 specimens: 240 to 690 mm FL; 14 empty.

FOOD	VOLUME (%)
Fishes	56.7
<i>Allanetta harringtonensis</i>	
atherinids (2)	
clupeoids (larv.)	
engraulids	
<i>Jenkinsia</i> sp. (2)	
<i>Mulloidichthys martinicus</i>	
Squids	36.6
<i>Doryteuthis</i> sp.	
<i>Doryteuthis plei</i> (3)	
Polychaetes	6.7

Remarks.—More than any other Atlantic tuna, *E. alletteratus* is characteristic of the green inshore water over continental or insular shelves. It swims rapidly in compact schools. When feeding, the schools become more diffuse as individuals dart this way and that in pursuit of their prey.

The presence of a feeding school of little tuna is often made known by a flock of diving birds overhead. The author once ran a small boat into the center of a feeding school in the Virgin Islands and dived into it with a face mask to observe the fish. It was noted that the dorsal fins were erected from their folded position in the groove on the back as the tuna made a rapid rush at the small prey fish at the surface. Longley & Hildebrand (1941) reported four halfbeaks (*Hemiramphus*) and one needlefish (*Strongylura raphidoma*) (= *Tylosurus crocodilus*) in the stomach of a little tuna from Dry Tortugas. Postel (1950, 1954) found a variety of fishes including clupeids, scombrids, carangids, hemiramphids, and exocoetids, in the stomachs of individuals from West Africa, along with cephalopods, shrimps, copepods, and mysids. Carlson (1952) recorded 33 per cent squids, 46 per cent round herring (*Etrumeus teres*), and the rest other fishes from specimens off the eastern coast of the United States. Anderson, Gehringer, & Cohen (1956a, 1956b) found fishes, squids and a few crustaceans in the stomachs of little tuna taken off the South Atlantic coast of the United States. De Sylva & Rathjen (1961) examined food from the stomachs of three specimens from Florida. One fish had eaten a round herring, another a shrimp (*Penaeus duorarum*), and the third a jack (*Caranx* sp.).

Scomberomorus cavalla (Cuvier) KING MACKEREL
19 stations; 22 specimens: 350 to 1022 mm FL; 9 empty.

Food	VOLUME (%)
Fishes	92.3
carangid	
<i>Caranx ruber</i>	
engraulids (2)	
<i>Harengula humeralis</i>	
<i>Ocyurus chrysurus</i>	
<i>Opisthonema oglinum</i>	
<i>Parexocoetus brachypterus</i>	
Squids	7.7

Remarks.—The kingfish or king mackerel is the largest species of the genus in the Atlantic. It may be observed as a solitary fish or in small groups, swimming in mid-water, but often nearer the bottom than the surface. It is not easily approached by a diver, and all of the specimens reported above were taken on hook and line. One was caught while trolling a halfbeak for bait on a moonlight night. The specimen of *Caranx ruber* was taken from the stomach of a 28-pound king mackerel. Only the caudal half of the jack was present, suggesting that this species may feed at times in the same manner as the great barracuda—*i.e.* cut the larger prey in two and circle back for the pieces. The 28-pound fish had also eaten a 250-mm yellowtail snapper. Knapp (1949) reported the following food animals by percentage of occurrence in the stomachs of 327 specimens

from the coast of Texas: menhaden (7.9 per cent), other fishes (42.7 per cent), shrimps (43.5 per cent), squids (25.1 per cent), crabs (0.6 per cent), and other invertebrates (0.9 per cent).

Scomberomorus regalis (Bloch)

CERO

87 stations; 116 specimens: 269 to 703 mm FL; 31 empty.

FOOD	VOLUME (%)
Fishes	96.1
<i>Allanetta harringtonensis</i> (4)	
atherinids (4)	
belonid	
<i>Caranx ruber</i>	
<i>Chromis cyanea</i>	
<i>Chromis multilineata</i> (2)	
<i>Clepticus parrae</i>	
engraulids	
<i>Harengula</i> sp. (2)	
<i>Harengula clupeola</i> (2)	
<i>Hemiramphus brasiliensis</i>	
<i>Jenkinsia</i> sp. (3)	
labrid	
<i>Opisthonema oglinum</i>	
<i>Selar crumenophthalmus</i>	
Squids	2.3
Unidentified crustaceans	1.2
Shrimps	0.4

Remarks.—The cero, sometimes called the painted mackerel, is usually a solitary fish, but occasionally several appear to be travelling together. They are always on the move. They occur primarily in clear water inshore from a few feet above the bottom to just below the surface. They feed primarily on small schooling clupeoid and atherinid fishes. Their feeding rushes toward such small fishes are extremely rapid. Often they make a long low leap into the air and re-enter the water with little splash. Small fishes may at times scatter into the air at the site of re-entry. Robert E. Schroeder (personal communication) suggested that the cero leaps are executed in order to drop suddenly from the air into a group of small fishes for the purpose of feeding on them. Only the anterior or posterior halves were found of four of the larger fishes from cero stomachs (*Clepticus parrae*, *Hemiramphus brasiliensis*, and two individuals of *Chromis multilineata*). A bar jack 150 mm in fork length was the largest intact fish taken from a stomach; the cero which had eaten it measured 590 mm in fork length.

POMACENTRIDAE (Damsel-fishes)

The damselfishes are small reef fishes which are often highly territorial and pugnacious. Most are omnivorous, feeding on a great variety of benthic

and occasional planktonic organisms. Two species of *Chromis*, on the other hand, appear to be obligate zooplankton-feeders.

Abudefduf saxatilis (Linnaeus)

SERGEANT MAJOR

13 stations; 35 specimens: 101 to 135 mm SL; 2 empty.

FOOD	VOLUME (%)
Anthozoans	43.2
<i>Zoanthus sociatus</i>	
Copepods	13.6
<i>Candacia pachydactyla</i>	
<i>Coryaceus subulatus</i>	
<i>Euchaeta marina</i> (2)	
<i>Euterpina acutifrons</i>	
<i>Microstella norvegica</i>	
<i>Miracia minor</i>	
<i>Nannocalanus minor</i> (3)	
<i>Oncaea</i> sp.	
<i>Scolecithrix danae</i>	
Algae	8.8
<i>Bryopsis pennata</i>	
<i>Ceramium</i> sp.	
<i>Champia parvula</i>	
<i>Cladophora delicatula</i>	
<i>Dictyopteris delicatula</i>	
<i>Dictyopteris plagiogramma</i>	
<i>Dictyota dentata</i>	
<i>Dictyota divaricata</i>	
<i>Hypnea spinella</i>	
<i>Jania rubens</i>	
<i>Laurencia papillosa</i>	
<i>Lyngbya majuscula</i>	
<i>Polysiphonia</i> sp.	
Tunicates	7.1
appendicularians	
Opisthobranchs	5.3
<i>Tridachia crispata</i>	
Fish eggs	4.7
Fishes	4.5
<i>Jenkinsia</i> sp.	
Unidentified animal material	3.7
Shrimp larvae	3.2
Barnacle appendages	3.0
Ants (winged)	1.2
Polychaetes	0.9
Siphonophores	0.8

Remarks.—Longley & Hildebrand (1941) examined the contents of three

sergeant major stomachs. They found mostly algae mixed with some copepods; one fish had eaten a pelagic fish egg. Their data and the above indicate that this species is one of the most diversified of all fishes in its food habits. It may be observed well above reefs feeding on individual zooplankters (at which time it often occurs in small aggregations) or grazing on benthic algae or sessile animal life on the bottom. The food habits may vary markedly with the environment from which the fish are collected. Fish from a reef with a high cover of algae can be expected to have as much as 100 per cent algae in their stomachs. The high percentage of *Zoanthus sociatus* was the result of the analysis of 16 stomachs from fish taken in two stations from shallow reefs in southwestern Puerto Rico where this anthozoan is abundant. Many of these fish had eaten only *Zoanthus*. Sergeant majors beneath piers at Crashboat Basin, Aguadilla, Puerto Rico are in a zone of changing current rich in planktonic life. They feed mostly on zooplankton, but their stomachs contained an average of about 20 per cent barnacle appendages by volume. Nudibranchs, a rare item of fish diet, comprised the majority of the stomach contents of two fish. Fish eggs were taken from the stomachs of fishes from four different stations. Those from three of the stations were pomacentrid eggs (demersal, and elliptical in shape).

Abudefduf taurus (Müller & Troschel)

NIGHT SERGEANT

9 stations; 17 specimens; 104 to 152 mm SL.

FOOD

VOLUME (%)

94.0

Algae

Amphiroa fragilissima (3)

Bryopsis sp.

Calothrix crustacea

Caulerpa sertularioides

Centroceras clavulatum

Ceramium sp. (2)

Ceramium byssoideum

Chaetomorpha sp.

Champia parvula

Chondria sp.

Coelothrix irregularis (2)

diatoms

Dictyopteris delicatula

Dictyota divaricata

Ectocarpus breviarticulatus

Enteromorpha sp.

Enteromorpha flexuosa

Gelidium corneum

Gelidium pusillum

Gelidium rigidulum

Gracilaria sp.

<i>Grateloupia cuneifolia</i>	
<i>Herposiphonia secunda</i>	
<i>Heterosiphonia wurdemanni</i>	
<i>Hypnea musciformis</i>	
<i>Jania</i> sp.	
<i>Jania capillacea</i>	
<i>Jania rubens</i>	
<i>Laurencia obtusa</i> (2)	
<i>Lyngbya</i> sp.	
<i>Polysiphonia</i> sp. (2)	
<i>Polysiphonia ferulacea</i>	
<i>Spyridia filamentosa</i>	
Anthozoans	5.3
<i>Zoanthus sociatus</i>	
Crabs	0.3
porcellanid	
Gastropods	0.2
Chitons	0.1
Hydroids	0.1

Remarks.—*Abudefduf taurus* is the largest West Indian damselfish. It is characteristic of inshore, somewhat turbulent water and rocky bottom. Longley & Hildebrand (1941) wrote that this species hugs the bottom closely, in contrast to *A. saxatilis*. Longley observed it at Dry Tortugas "browsing greedily" on the bottom where algae such as *Laurencia* predominated. The gastropods and chitons found in the stomachs of the West Indian specimens were very small and could have been ingested incidentally with the algal food. The *Zoanthus*, on the other hand, formed nearly the entire stomach and intestinal contents of one 134-mm individual. A few individuals contained small amounts of sand mixed with the algae, but the stomachs of most were surprisingly free of sediment.

Chromis cyanea (Poey) BLUE CHROMIS
5 stations; 17 specimens: 43 to 83 mm SL.

FOOD	VOLUME (%)
Copepods	52.4
<i>Calanopia americana</i>	
<i>Coryaceus</i> sp.	
<i>Miracia efferata</i>	
<i>Nannocalanus minor</i>	
<i>Paracalanus aculeatus</i>	
<i>Paracalanus parvus</i>	
<i>Oncaea</i> sp.	
<i>Temora turbinata</i>	
<i>Undinula vulgaris</i>	
Tunicates	33.9
appendicularians	

<i>Oikopleura</i> sp.	
Shrimp larvae	8.4
Siphonophores	2.9
Fish eggs	2.1
Ostracods	0.3

Remarks.—This species and the following appear to feed only on the smaller zooplankton. They rise well above the reefs in loose aggregations, face the oncoming current, and pick the tiny copepods and other planktonic animals individually from the passing water mass. Analysis of motion pictures of blue chromis taken by the author revealed the jaws snapping rapidly outward during feeding. With the approach of danger, these damselfishes moved downward to the refuge of the reefs. They are more elongate and have more deeply forked caudal fins than other Atlantic pomacentrids. These morphological differences probably represent adaptations for the mid-water habitat. The bright iridescent blue color of *cyanea* appears to have some camouflage value when the fish are seen in offshore localities where the water is deep blue. Once a descending individual was observed to alter the brilliant blue to a dull grayish blue as it reached the shelter of the reef. As with other plankton feeders, the organisms comprising the food may vary greatly with their availability. Appendicularian tunicates, for example, comprised 90 per cent of the stomach contents at one station, 2 per cent at another, and 0 per cent at a third. Copepods ranged from 0 to 94 per cent by volume.

Chromis multilineata (Guichenot) BROWN CHROMIS
5 stations; 68 specimens: 58 to 109 mm SL; 5 empty.

FOOD	VOLUME (%)
Copepods	87.8
<i>Candacia pachydactyla</i>	
<i>Corycaeus</i> sp.	
<i>Corycaeus amazonicus</i>	
<i>Farranula gracilis</i>	
<i>Miracia efferata</i>	
<i>Nannocalanus minor</i>	
<i>Oncaea</i> sp.	
<i>Paracalanus aculeatus</i>	
<i>Temora turbinata</i>	
<i>Undinula vulgaris</i> (3)	
Tunicates	3.2
Shrimp larvae	2.1
Siphonophores	1.8
Pteropods	1.6
Unidentified crustaceans	1.3
Unidentified animal material	1.2

Crab larvae	0.8
Ostracods	0.2

Remarks.—See *Chromis cyanea*.

Microspathodon chrysurus (Cuvier & Valenciennes)

YELLOWTAIL DAMSELFISH

10 stations; 45 specimens: 78 to 125 mm SL; 3 empty.

FOOD	VOLUME (%)
Algae and organic detritus	89.3
<i>Anacystis</i> sp.	
<i>Ceramium byssoideum</i> (3)	
<i>Centroceras clavulatum</i>	
<i>Coelothrix irregularis</i> (2)	
diatoms	
<i>Enteromorpha</i> sp.	
<i>Gelidium rigidulum</i>	
<i>Herposiphonia</i> sp.	
<i>Herposiphonia secunda</i>	
<i>Lyngbya</i> sp. (3)	
<i>Lyngbya majuscula</i> (3)	
<i>Microcoleus</i> sp.	
<i>Oscillatoria</i> sp.	
<i>Polysiphonia</i> sp. (3)	
<i>Polysiphonia ferulacea</i> (2)	
<i>Plectonema nostocorum</i>	
<i>Wrangelia argus</i> (2)	
Unidentified animal material	3.8
Corals	2.2
Unidentified crustaceans	1.8
Shrimps	1.2
Ophiuroids	1.0
Sponges	0.2
Ostracods	0.2
Amphipods	0.1
Gastropods	0.1
Fish scales	0.1

Remarks.—*Microspathodon chrysurus* is one of the most common fishes of coral reefs in the West Indies, and second only to *Abudefduf taurus* in size. It is strictly a bottom fish and is often associated, especially when young, with *Millepora*. It was never observed feeding on planktonic organisms. Beebe & Tee-Van (1928) stated that the stomach contents of a number of fish from Haiti consisted mostly of large quantities of chewed algae and bottom debris, with an occasional entomostracan. Longley & Hildebrand (1941) wrote that it browses on the delicate algae covering dead coral surfaces. That the algae on which it feeds is delicate is verified

by the stomach-content algae listed above. Most are finely filamentous blue-greens and reds. Considerable amounts (from 10 to nearly 50 per cent) of very fine calcareous silt were usually present with the algae in the stomachs. Along with the silt were sponge and gorgonian spicules and fragments of shelled invertebrates; these appeared to be primarily sedimentary in origin. Small fragments of live coral were found in one fish. A. Ciardelli (MS) has also found corals in the stomachs of this species. Randall (1958) reported observing a juvenile *M. chrysurus* picking over the body and fins of an angelfish (*Pomacanthus arcuatus*) in Florida, thus indicating apparent feeding on ectoparasites.

Pomacentrus fuscus Cuvier & Valenciennes DUSKY DAMSELFISH
10 stations; 51 specimens: 50 to 98 mm SL; 8 empty.

FOOD	VOLUME (%)
Algae and organic detritus	56.2
<i>Acanthophora spicifera</i>	
<i>Amphiroa fragilissima</i>	
<i>Anacystis marina</i>	
<i>Asterocystis ramosa</i>	
<i>Avrainvillea nigricans</i>	
<i>Bryopsis pennata</i>	
<i>Caulerpa racemosa</i>	
<i>Caulerpa sertularioides</i>	
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp. (2)	
<i>Ceramium nitens</i> (2)	
<i>Cladophora</i> sp.	
<i>Codium intertextum</i>	
<i>Coelothrix irregularis</i>	
diatoms (3)	
<i>Dictyota</i> sp.	
<i>Enteromorpha</i> sp.	
<i>Halimeda</i> sp.	
<i>Heterosiphonia wurdemanni</i>	
<i>Lyngbya</i> sp. (2)	
<i>Polysiphonia</i> sp.	
<i>Polysiphonia ferulacea</i>	
<i>Spirulina</i> sp.	
<i>Wrangelia argus</i>	
Unidentified animal material	8.6
Polychaetes	5.6
Copepods	5.2
Fishes	4.9
Gastropods	3.3
<i>Columbella mercatoria</i>	
<i>Rissoina fischeri</i>	

turrid	
vermetid	
Anthozoans	3.0
<i>Zoanthus</i> sp.	
Crabs	2.1
Seagrasses	1.9
<i>Cymodocea manatorum</i>	
Isopods	1.6
Amphipods	1.2
Unidentified eggs	1.2
Scyphozoans	1.1
Mysids	1.1
Shrimps	0.9
Unidentified crustaceans	0.9
Pelecypods	0.5
Hermit crabs	0.3
Tunicates	0.2
Hydroids	0.2

Remarks.—*Pomacentrus fuscus* is a drab shallow-water species of coral reefs and reef-sand areas. It is the species listed as *Eupomacentrus dorso-punicans* by Bailey, *et al* (1960). In many such areas it is the most common damselfish and one of the most abundant of all reef fishes. It feeds primarily on sessile organisms, especially algae. A few stomachs contained as much as 25 per cent inorganic sediment. Although this was usually fine-grained sand, some pieces of gravel were as large as 3 mm in diameter. The teeth of this and other species of *Pomacentrus* are incisiform and occur in a close-set, rigid band; thus they are well adapted for grazing.

Pomacentrus leucostictus (Müller & Troschel)

BEAU GREGORY

5 stations; 41 specimens: 38 to 73 mm SL.

Food	VOLUME (%)
Algae and organic detritus	22.6
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp. (2)	
diatoms (2)	
<i>Halimeda opuntia</i> (small fragments)	
<i>Hypnea spinella</i>	
<i>Lyngbya</i> sp.	
<i>Lyngbya majuscula</i>	
<i>Polysiphonia</i> sp. (2)	
Eggs	21.2
mollusk	
pomacentrid	
Unidentified animal material	18.2
Polychaetes	12.6

Fish remains	7.1
Coelenterate polyps	5.1
Tunicates	2.9
Crabs	2.9
Amphipods	1.6
Corals	1.5
Foraminifera	1.5
Hermit crabs	1.0
Shrimps	1.0
Copepods	0.5
Gastropods	0.3

Arene tricarinata

Crassispira nigrescens

Remarks.—The beau gregory is a very common small fish of calm, shallow, coral and sand areas. Sand was often present in the stomachs. In one fish it represented 42 per cent of the stomach contents.

Pomacentrus planifrons Cuvier & Valenciennes THREESpot DAMSELFISH
4 stations; 18 specimens: 65 to 88 mm SL.

FOOD	VOLUME (%)
Unidentified animal material	25.9
Algae and detritus	24.4
<i>Centroceras clavulatum</i>	
<i>Ceramium byssoideum</i>	
diatoms	
<i>Lyngbya</i> sp.	
<i>Lyngbya majuscula</i>	
<i>Microcoleus chthonoplastes</i>	
Anthozoans (except corals)	19.4
<i>Zoanthus</i> sp.	
Crustacean remains	11.1
Polychaetes	5.6
Seagrasses	3.9
<i>Thalassia testudinum</i> (small fragments)	
Echinoderm remains	3.3
Copepods	2.8
<i>Oncaea</i> sp.	
Unidentified eggs	2.4
Tunicates	0.6
appendicularians	
Corals	0.6

Remarks.—On reefs off southwestern Puerto Rico this species is found in somewhat deeper water on the average than *Pomacentrus fuscus*, whereas the following species, *P. variabilis*, is usually taken in still deeper water. All three species are abundant.

Pomacentrus variabilis (Castelnau)
3 stations; 7 specimens: 70 to 80 mm SL.

COCOA DAMSELFISH

FOOD	VOLUME (%)
Algae and organic detritus	51.5
<i>Amphiroa fragilissima</i>	
<i>Avrainvillea</i> sp.	
<i>Enteromorpha</i> sp.	
<i>Herposiphonia</i> sp.	
Polychaetes	15.7
sabellids	
Isopods	10.0
<i>Excorallana</i> sp.	
excorallanid	
sphaeromid	
Unidentified animal material	9.3
Hydroids	2.8
Unidentified crustaceans	2.6
Sponges	1.7
Corals	1.7
Gastropods	1.1
<i>Diodora variegata</i>	
Shrimps	0.85
alpheid	
Ophiuroids	0.85
Amphipods	0.7
Pelecypods	0.6
Tanaids	0.6

Remarks.—Algae varied from 0 to 65 per cent in the stomachs of this damselfish. Most of the polychaete material consisted of the tentacular crowns of sabellids.

LABRIDAE (Wrasses)

With the exception of the plankton-feeding *Clepticus*, all of the tropical western Atlantic wrasses swim near the bottom. They tend to feed on invertebrates with hard parts such as mollusks and crustaceans. They crush these with their well-developed pharyngeal teeth. Since a large percentage of the fragments of the crushed animals is usually present, they apparently do not make much effort to eject the hard parts. Characteristically, the anterior canine teeth of labrids protrude prominently. Such teeth are probably useful for detaching gastropods and other adhering forms from rocks. The wrasses are diurnal. Most bury themselves in sand at night.

Bodianus rufus (Linnaeus)

SPANISH HOGFISH

20 stations; 31 specimens: 125 to 275 mm SL; 1 empty.

FOOD	VOLUME (%)
Crabs	32.4
majid	
<i>Mithrax</i> sp. (2)	
<i>Petrolisthes</i> sp.	
<i>Petrolisthes galathinus</i>	
<i>Porcellana sayana</i>	
xanthid	
Ophiuroids	19.5
<i>Ophiocoma riisei</i>	
<i>Ophioderma rubicundum</i>	
<i>Ophioderma squamosissimum</i>	
<i>Ophiothrix</i> sp. (11)	
Echinoids	14.4
<i>Diadema antillarum</i> (5)	
<i>Echinometra</i> sp. (3)	
<i>Echinometra viridis</i>	
Gastropods	10.4
<i>Anachis</i> sp.	
<i>Calliostoma javanicum</i>	
<i>Cerithiopsis emersoni</i>	
<i>Diodora listeri</i>	
<i>Nassarius</i> sp.	
<i>Nitidella ocellata</i>	
<i>Planaxis lineatus</i>	
turbinid	
turrids	
Pelecypods	8.0
<i>Arca</i> sp.	
<i>Arcopsis adamsi</i>	
<i>Barbatia cancellaria</i> (2)	
<i>Brachidontes exustus</i>	
<i>Chlamys</i> sp. (2)	
<i>Isognomon radiatus</i>	
<i>Lima pellucida</i>	
<i>Lyropecten antillarum</i>	
<i>Microcardium</i> sp.	
<i>Pecten</i> sp.	
Shrimps	6.0
palaemonid	
Hermit crabs	3.7
<i>Clibanarius</i> sp.	
Unidentified crustaceans	2.2

Stomatopods	1.2
Isopods	0.7
<i>Paracerceis caudata</i>	
Chitons	0.7
<i>Calloplax janeirensis</i>	
Unidentified animal material	0.6
Polychaetes	0.2

Remarks.—*Bodianus rufus* is a moderately large reef fish which lives at depths of about 10 to approximately 100 feet. In deeper water it tends to be replaced by *Bodianus pulchellus*. The latter species, however, is rare in the West Indies. Eibl-Eibesfeldt (1955), Limbaugh (1961), and Randall (1962b) have discussed the "cleaning" behavior of the young of the Spanish hogfish. Randall, Schroeder, & Starck (1964) noted that adults may feed on *Diadema*. One was observed in St. Croix feeding on several long spines after consuming the test to which they were attached.

Clepticus parrae (Bloch & Schneider) CREOLE WRASSE
7 stations; 15 specimens: 150 to 197 mm SL.

FOOD	VOLUME (%)
Copepods	43.6
<i>Candacia pachydactyla</i>	
<i>Euchaeta marina</i>	
<i>Temora turbinata</i> (2)	
<i>Undinula vulgaris</i> (3)	
Siphonophores	20.0
Pteropods	19.2
Shrimp larvae	5.0
Tunicates	4.7
salps	
Crab larvae	2.3
Unidentified eggs	1.7
Ostracods	1.5
Gastropod larvae	1.4
Stomatopod larvae	0.3
Unidentified animal material	0.3

Remarks.—*Clepticus parrae* exhibits a mode of life similar to that described for *Paranthias furcifer*, *Inermia vittata*, young *Ocyurus chrysurus*, *Chromis cyanea*, and *C. multilineata*. It is a reef fish only in the sense that it uses reefs for shelter from predators. Most of its time during daylight hours is spent in aggregations well above the bottom feeding on zooplankton. It does not strain numerous planktonic animals from the water but picks them up one by one. Its mouth and teeth are very small.

Halichoeres bivittatus (Bloch)

SLIPPERY DICK

17 stations; 46 specimens: 67 to 153 mm SL.

FOOD	VOLUME (%)
Crabs	22.3
majids (3)	
<i>Mithrax</i> sp.	
<i>Mithrax sculptus</i> (2)	
<i>Platypodia spectabilis</i>	
portunid	
xanthid	
Echinoids	17.9
<i>Diadema antillarum</i>	
<i>Lytechinus variegatus</i> (5)	
Polychaetes	17.4
ampharetid	
Gastropods	12.4
<i>Acmaea</i> sp.	
<i>Acmaea pustulata</i>	
acteonid	
<i>Arene</i> sp.	
<i>Arene tricarinata</i>	
<i>Bittium varium</i>	
<i>Bulla striata</i> (2)	
<i>Bullata ovuliformis</i>	
<i>Cerithium</i> sp.	
<i>Modulus modulus</i> (2)	
<i>Nassarius</i> sp.	
<i>Olivella</i> sp.	
<i>Planaxis lineatus</i>	
<i>Pseudostomatella coccinea</i>	
<i>Seila adamsi</i>	
<i>Smaragdia viridis</i>	
<i>Synaptocochlea picta</i>	
<i>Tegula lividomaculata</i>	
<i>Tricolia bella</i>	
<i>Tricolia tessellata</i> (3)	
turrid	
Ophiuroids	7.3
<i>Ophioderma</i> sp.	
<i>Ophiothrix</i> (3)	
Unidentified animal material	4.0
Pelecypods	3.7
<i>Aequipecten gibbus</i>	
<i>Americardia guppyi</i>	
<i>Brachidontes exustus</i>	

<i>Crassinella</i> sp.	
<i>Cumingia antillarum</i>	
<i>Ervilia nitens</i>	
<i>Isognomon</i> sp.	
<i>Laevicardium</i> sp.	
<i>Nuculana</i> sp.	
<i>Papyridea semisulcata</i>	
<i>Tellina listeri</i>	
<i>Trachycardium</i> sp.	
Shrimps	3.5
alpheid	
Chitons	3.3
<i>Acanthochiton pygmaea</i>	
<i>Ischnochiton</i> sp.	
Fish remains	3.2
Stomatopods	3.0
Unidentified crustaceans	1.0
Hermit crabs	0.9
diogenid	
pagurid	
Foraminifera	0.1

Remarks.—*Halichoeres bivittatus* is the most common wrasse of the genus in the West Indies. It is a shallow-water species that is most abundant on sand bottoms with scattered small coral patches. It also ranges into sea-grass beds. One series of five specimens which had eaten principally *Lytechinus variegatus* contained fragments of *Thalassia* that represented about 5 per cent by volume of the stomach contents. Germaine L. Warmke, who made the identifications of many of the mollusks of the present report, noticed that this fish tends to select the more brightly colored gastropods. Longley & Hildebrand (1941) wrote, "This species, according to the few stomach contents examined, seems to feed chiefly on fish. One individual had attempted to eat a pipefish, of which fully a sixth of the length projected from its mouth."

Halichoeres garnoti (Cuvier & Valenciennes) YELLOWHEAD WRASSE
13 stations; 14 specimens: 64 to 159 mm SL; 4 empty.

FOOD	VOLUME (%)
Crabs	20.5
Ophiuroids	15.5
amphiurid	
<i>Ophiothrix</i> sp. (2)	
Unidentified crustaceans	14.0
Gastropods	13.5
<i>Caecum pulchellum</i>	
<i>Epitonium</i> sp.	

<i>Rissoina cancellata</i>	
vermetids	
<i>Zebina browniana</i>	
Unidentified animal material	7.5
Pelecypods	7.0
<i>Arcopsis adamsi</i>	
Polychaetes	5.5
Shrimps	5.0
Hermit crabs	3.0
Fish remains	3.0
Echinoids	3.0
<i>Echinometra</i> sp.	
Chitons	2.0
Sipunculids	0.5

Remarks.—*H. garnoti* is not uncommon on reefs and reef-sand areas from shallow water to depths of at least 160 feet. Beebe & Tee-Van (1928) stated that the species is omnivorous, but listed the food as small crustaceans, sea urchins (spines and all), and mollusks and their shells. No plant material was found in the stomachs of the specimens reported upon in the present report.

Halichoeres maculipinna (Müller & Troschel) CLOWN WRASSE
11 stations; 24 specimens: 45 to 110 mm SL; 1 empty.

FOOD	VOLUME (%)
Polychaetes	47.1
lumbrinerids	
neroids	
Copepods	10.2
<i>Euterpina acutifrons</i>	
harpacticoids (3)	
Shrimps	6.5
alpheids (2)	
Ostracods	5.9
Gastropods	5.3
<i>Caecum nitidum</i>	
<i>Caecum pulchellum</i>	
<i>Petalconchus</i> sp.	
<i>Tricolia adamsi</i>	
vermetid	
Amphipods	5.1
gammarids	
hyperiids (2)	
Octopuses	4.3
Crabs	3.1
Pelecypods	2.4

Unidentified crustaceans	1.9
Isopods	1.7
Unidentified eggs	1.6
mollusk?	
Chitons	1.5
Tanaids	1.5
Sipunculids	0.9
Unidentified animal material	0.8
Scaphopods	0.2

Remarks.—The clown wrasse is a moderately common reef fish. The analyses of the stomach contents above seem to indicate a preference for polychaetes. The stomachs of five individuals contained up to 50 per cent copepods. These were the five smallest specimens (45 to 50 mm SL). The remaining fish ranged from 71 to 110 mm SL, and few of these had eaten copepods (and then in small amounts). One 79-mm fish contained only a small octopus.

Halichoeres poeyi (Steindachner) BLACK-EAR WRASSE
12 stations; 34 specimens: 50 to 140 mm SL; 3 empty.

FOOD	VOLUME (%)
Crabs	24.5
Gastropods	21.3
<i>Bittium varium</i>	
<i>Hemitoma octoradiata</i>	
<i>Modulus modulus</i>	
<i>Schismope</i> sp.	
Ophiuroids	10.2
<i>Ophiocoma echinata</i>	
<i>Ophiothrix</i> sp.	
Unidentified crustaceans	7.4
Echinoids	6.8
<i>Diadema antillarum</i>	
<i>Lytechinus variegatus</i>	
Sipunculids	5.2
Hermit crabs	5.1
Fish remains	5.0
Chitons	4.4
<i>Ischnochiton papillosus</i>	
Unidentified animal material	3.9
Pelecypods	2.2
ostreid	
<i>Tellina</i> sp.	
Polychaetes	1.9
Holothurians	1.6
Isopods	0.3

Stomatopods

0.2

Gonodactylus sp.

Remarks.—Although *H. poeyi* may occur on inshore reefs, it is more characteristic of seagrass beds. The remains of adult *Diadema* in the stomach of this species and *H. bivittatus* seem to be from larger-sized urchins than could be crushed by these wrasses. Probably the fish fed upon the *Diadema* after the latter were made available by a larger predator such as the queen triggerfish.

Halichoeres radiatus (Linnaeus)

PUDDINGWIFE

22 stations; 32 specimens: 127 to 355 mm SL; 5 empty.

FOOD	VOLUME (%)
Pelecypods	25.1
<i>Arca imbricata</i>	
<i>Arca umbonata</i> (2)	
<i>Barbatia cancellaria</i> (2)	
<i>Barbatia domingensis</i>	
<i>Brachidontes exustus</i>	
<i>Glycymeris</i> sp.	
<i>Isognomon</i> sp.	
<i>Isognomon alatus</i>	
<i>Isognomon radiatus</i> (3)	
<i>Musculus lateralis</i>	
<i>Pteria colymbus</i>	
Gastropods	21.3
<i>Acmaea leucopleura</i> (2)	
<i>Acmaea pustulata</i> (2)	
<i>Bittium varium</i>	
buccinid	
<i>Cittarium pica</i>	
<i>Columbella mercatoria</i>	
<i>Coralliophila caribaea</i>	
<i>Cymatium labiosum</i>	
<i>Daphnella lymneiformis</i>	
<i>Diodora</i> sp.	
<i>Diodora listeri</i>	
<i>Fissurella</i> sp.	
<i>Fissurella angusta</i>	
<i>Fissurella barbadensis</i> (4)	
<i>Hemitoma octoradiata</i> (2)	
<i>Hyalina</i> sp.	
<i>Nerita peloronta</i>	
<i>Olivella</i> sp.	
<i>Risomurex roseus</i>	
<i>Tegula excavata</i>	

<i>Tegula fasciata</i>	
<i>Turbo castanea</i>	
Echinoids	19.9
<i>Diadema antillarum</i> (6)	
<i>Echinometra viridis</i>	
<i>Eucidaris tribuloides</i> (2)	
<i>Lytechinus variegatus</i> (2)	
spatangoid	
Crabs	18.8
majid	
<i>Percnon gibbesi</i>	
Ophiuroids	6.8
<i>Ophiocoma echinata</i> (2)	
<i>Ophiothrix</i> sp. (2)	
Hermit crabs	4.5
Polychaetes	1.4
Unidentified crustaceans	1.1
Stomatopods	0.9
<i>Gonodactylus curacaoensis</i>	
Chitons	0.2
<i>Ischnochiton papillosus</i>	

Remarks.—The puddingwife is the largest species of Atlantic *Halichoeres*; it is exceeded in maximum size among West Indian wrasses only by the hogfish. It is found on reefs and adjacent bottom habitats. Except during courtship and spawning, it was never seen much above the bottom. Beebe & Tee-Van (1928) reported the young of this species in Haiti to feed on floating bits of dead food, small crustaceans, etc. while the older individuals are browsers, taking sponge, coral, or other organic debris. These remarks certainly do not correspond closely with the food habit data collected by the author.

Hemipteronotus novacula (Linnaeus) PEARLY RAZORFISH
5 stations; 9 specimens: 85 to 150 mm SL; 1 empty.

FOOD	VOLUME (%)
Gastropods	38.5
<i>Batillaria</i> sp.	
<i>Caecum</i> sp.	
<i>Drillia</i> sp.	
<i>Litiopa melanostoma</i>	
<i>Natica</i> sp. (juv.)	
Pelecypods	27.9
<i>Ervilia nitens</i>	
<i>Pitar</i> sp.	
Polychaetes	7.5
Shrimps	6.3
Unidentified animal material	6.3

Scaphopods	5.6
<i>Dentalium</i> sp.	
Unidentified crustaceans	4.2
Isopods	3.1
Amphipods	0.6

Remarks.—This species, most frequently known in the western Atlantic literature as *Xyrichthys psittacus*, and the other Atlantic razorfishes live over sand bottoms. With the approach of danger they rapidly thrust their bodies headfirst into the sand. If one is not successful in spearing them, they can still be collected by forcing liquid rotenone into the sand where they have sought refuge. Longley & Hildebrand (1941) reported several stomachs of Tortugas specimens to contain crabs and fragments of mollusk shells. Oliver & Massuti (1952) examined the stomach contents of 50 examples from the Balearic Islands. Their analysis from a histogram is approximately as follows: organic material (26 per cent), crustaceans (24 per cent), sand (16.4 per cent), gastropods (11.5 per cent), pelecypods (7.7 per cent), fishes (4.8 per cent), echinoderms (4.8 per cent), brachio-pods (1.4 per cent), coelenterates (1.4 per cent), foraminifera (1 per cent), and bryozoans (1 per cent). In their discussion they indicated that mollusks seemed to have contributed primarily to the category "organic material." They noted that the gastropods and pelecypods were of small size, and several of both groups were identified. The echinoderm category consisted mostly of echinoids (believed to be either *Echinocardium flavescens* or *Echinocyamus pusillus*). There was a small ophiuroid in one stomach. Sand was present more-or-less abundantly in all stomachs. The author also noted that the animals eaten by West Indian specimens were all very small and that sand was present in most stomachs.

Hemipteronotus splendens (Castelnau) GREEN RAZORFISH
8 stations; 14 specimens: 57 to 108 mm SL; 2 empty.

FOOD	VOLUME (%)
Copepods	60.8
<i>Candacia pachydactyla</i>	
<i>Euchaeta marina</i>	
<i>Nannocalanus minor</i> (2)	
<i>Oncaea</i> sp.	
<i>Sapphirina</i> sp.	
<i>Scolecithrix danae</i>	
<i>Undinula vulgaris</i>	
Amphipods	12.5
<i>Cymadusa</i> sp.	
Shrimp larvae	11.2
Gastropods	5.0
Pelecypods	3.3
Unidentified crustaceans	3.3

Unidentified animal material	1.7
Fish eggs	1.4
Isopods	0.8

Remarks.—This is a smaller species than the preceding. Curiously, it appears to feed primarily on zooplankton. Even the largest example, 108 mm in standard length, had eaten copepods (especially *Candacia pachydactyla*) almost exclusively.

Lachnolaimus maximus (Walbaum)

HOGFISH

49 stations; 80 specimens: 175 to 600 mm SL.

FOOD	VOLUME (%)
Pelecypods	42.6
Gastropods	39.7
Crabs	6.1
Hermit crabs	4.9
Echinoids	4.6
Amphipods	1.0
Scaphopods	0.6
Barnacles	0.5

Remarks.—The hogfish is the largest tropical Atlantic wrasse. It is usually found over open areas of sea bottom near reefs, especially where gorgonians are abundant. Evermann & Marsh (1902) wrote that it feeds chiefly upon small fishes and on bottom mollusks and crustaceans. The above results do not substantiate their statement with respect to fish in the diet. Longley & Hildebrand (1941) reported that the hogfish feeds freely by day on univalve and bivalve mollusks and *Echinometra*. Reid (1954) collected five specimens of the species from Cedar Key, Florida. The food of these fish consisted of crustaceans, pelecypods, and the gastropod *Mitrella*. The analysis of the stomach contents of the 80 West Indian specimens listed above was made by J. Randall & Germaine L. Warmke (in press, *Carib. Jour. Sci.*). Fifty-three gastropods and 42 pelecypods were identified to genus or species from hogfish stomachs by these authors.

Thalassoma bifasciatum (Bloch)

BLUEHEAD

11 stations; 60 specimens: 36 to 105 mm SL; 8 empty.

FOOD	VOLUME (%)
Copepods	18.8
calagoids	
calanoids	
<i>Undinula vulgaris</i>	
Crabs and crab larvae	13.0
majid	
Gastropods and gastropod larvae	11.4
<i>Acmaea pustulata</i>	
acmaeids	

Fishes	8.7
Unidentified crustaceans	7.9
Unidentified animal material	7.7
Ophiuroids	7.5
<i>Ophiothrix</i> sp. (4)	
Shrimps and shrimp larvae	6.5
alpheid	
Isopods	6.0
gnathiids (larv.)	
Polychaetes	5.1
onuphid	
polynoid	
Pycnogonids	1.9
Tanaids	1.9
Echinoids	1.5
<i>Diadema antillarum</i>	
Mollusk eggs	1.3
Stomatopods	0.8

Remarks.—*Thalassoma bifasciatum* is one of the most abundant of West Indian reef fishes. It feeds on small benthic animals, zooplankton, and ectoparasitic crustaceans of fishes. Beebe & Tee-Van (1928) reported polychaete worms and crustaceans from specimens from Haiti. Longley & Hildebrand (1941) stated that small crustaceans seem to provide the greater part of the food of the species in Dry Tortugas. They were the first to record its habit of removal of ectoparasites from fishes, although were unable to demonstrate any parasitic forms from the stomach contents. They also reported feeding on the demersal eggs of *Abudefduf saxatilis*. Randall & Randall (1960) found a few crustacean ectoparasites of fishes, primarily small isopods, among 27 stomachs examined from the Virgin Islands and five from Florida. Most of the stomach-content material consisted of free-living pelagic crustaceans, especially copepods. The analyses of the 27 Virgin Islands specimens are included in the present report. Feddern (1965) reviewed the literature on the food and feeding of *T. bifasciatum*. He observed that juveniles most often form schools and roam close to the bottom picking at rocks, algae, and gorgonians, apparently searching for small benthic organisms. He stated that adults are most often in loose aggregations feeding on particulate plankton. Yellow-phase individuals of both sexes occasionally pick parasites off other fishes, but those of the bluehead phase were not observed to do this. Twelve of the 60 fishes examined by the author were in the bluehead phase. They ranged from 85 to 105 mm in standard length. No copepods or small planktonic crustaceans were found in any of these specimens. Their stomach contents by percentage volume were as follows: ophiuroids (30.8 per cent), crabs (20.4 per cent), fishes (19.2 per cent), polychaetes (12.0 per cent), pycnogonids

(8.4 per cent), unidentified (4.2 per cent), shrimps (3.3 per cent), and isopods (1.7 per cent). Oddly, there were no mollusks. A larger sample of this color form might well reveal gastropods in the stomachs, however. Although most of the gastropods eaten by yellowphase fish were small, one 67-mm specimen contained an intact limpet (*Acmaea pustulata*) which measured 4 by 5 mm. The remains of *Diadema antillarum* from yellow-phase fish consisted primarily of soft tissue. Probably the fish stole scraps of this echinoid while it was being fed upon by a larger predator.

SCARIDAE (Parrotfishes)

The parrotfishes are among the most abundant of West Indian reef fishes. Randall (1963b) found them the dominant family on a weight basis in two large poison stations on fringing reefs in the Virgin Islands. They are diurnal and are frequently cited as herbivores. Bardach (1959) classified the adults as omnivores and the young as herbivores, but he gave no qualifying data. Hiatt & Strasburg (1960) reported all of the specimens that they examined from the Marshall Islands to have scraped coral polyps from living heads of coral, as well as algae from reef rock. The author and associates have failed to observe any scraping of live coral by West Indian species; nor have significant amounts of coral been found in any of the stomachs. The small amounts of coral that were detected in two species could have been ingested accidentally while the fishes were grazing algae. The fused teeth of scarids are well adapted for such scraping. More important in terms of nutrition is their distinctive pharyngeal mill. With this they grind the soft coral rock or sand together with the algae. The rock is rendered to a fine sediment, and the algae is well trituated and thus made much more digestible. The parrotfishes are also able to utilize the filamentous algae growing interstitially in the upper part of dead coral rock (this algae is sometimes referred to as boring algae or skeletal algae—see Odum & Odum, 1955). Longley (in Longley & Hildebrand, 1941) observed the direct feeding by *Scarus coeruleus* and *S. guacamaia* on sand. He wrote, "I have seen them feeding actively on what seemed a perfectly bare sand patch, taking up mouthful after mouthful of fine sand, grinding it to powder in their pharyngeal apparatus, and treating the whole with their digestive juices, presumably for the microscopic food in it." In the opinion of the author, this ingestion of sand may serve primarily the purpose of providing hard material to grind plant food in the pharyngeal mill. Parrotfishes feeding on high stands of algae or seagrass would not get much sedimentary material with which to grind the plant tissues. They might, therefore, take in mouthfuls of bare sand. When the available substratum for algal growth is limited (as on a well-developed reef with numerous live corals), the parrotfishes are probably superior competitors to other herbivorous fishes. If the algae has been reduced to a low stubble, little is left for the browser. The parrotfishes, by contrast, may still have an ample food supply. They

are at times, however, responsible, along with other herbivores such as the surgeonfishes, for the overgrazing of algae (Stephenson & Searles, 1960 and Randall, 1961a) and of seagrasses (Randall, 1965a). They also play a major role in the production of sediment, as discussed by Emery (1956), Cloud (1959), Bardach (1961), and Randall (1964b). Randall, Almodóvar, & Pagán (MS) have made determinations of the percentage of inorganic material in the alimentary tracts of eight species of West Indian scarids. These data are repeated here for the individual species.

Scarus coelestinus Cuvier & Valenciennes MIDNIGHT PARROTFISH
8 stations; 14 specimens: 240 to 587 mm SL; 2 empty.

FOOD	VOLUME (%)
Algae	97.3
<i>Acanthophora spicifera</i>	
<i>Amphiroa fragilissima</i> (3)	
<i>Bryothamnion triquetrum</i>	
<i>Centroceras</i> sp.	
<i>Coelothrix irregularis</i>	
<i>Corallina cubensis</i>	
diatoms	
<i>Dictyopteris delicatula</i> (2)	
<i>Enteromorpha</i> sp. (2)	
<i>Gelidium pusillum</i> (2)	
<i>Herposiphonia</i> sp. (2)	
<i>Jania rubens</i> (2)	
<i>Laurencia obtusa</i>	
<i>Laurencia papillosa</i>	
<i>Lithothamnion</i> sp.	
<i>Lyngbya</i> sp.	
<i>Polysiphonia</i> sp. (2)	
<i>Rhizoclonium</i> sp.	
<i>Spermothamnion investiens</i>	
<i>Ulva lactuca</i>	
<i>Vidalia obtusiloba</i>	
Seagrasses	1.3
<i>Thalassia testudinum</i>	
Mollusk shells	0.4
Crustacean fragments	0.4
Foraminifera	0.2
Coral fragments	0.2
Echinoid fragments	0.1
Sponge spicules	0.1

Remarks.—The midnight parrotfish is second only to *Scarus guacamaia* in size attained. It is moderately common on West Indian reefs. The invertebrates consumed were all small and fragmented. Probably they were

ingested incidentally with the algae and soft coral rock. Inorganic sediment represented more than 50 per cent of most gut material. The dominant alga in the stomachs of three fish from northwestern Puerto Rico was *Amphiroa fragilissima*. Longley & Hildebrand (1941) reported that a bit of material found in the pharyngeal grinding apparatus of this species consisted of sand far coarser than that taken from the intestine, along with fragments of perhaps a half-dozen genera of algae. The only animal remains listed by them was one small amphipod.

Scarus croicensis (Bloch)

STRIPED PARROTFISH

2 stations; 9 specimens: 111 to 227 mm SL.

FOOD

VOLUME (%)

Algae

100.0

Calothrix crustacea

Centroceras sp.

Centroceras clavulatum

Coelothrix irregularis (2)

Enteromorpha sp.

Gelidium sp.

Herposiphonia sp. (2)

Lyngbya sp.

Polysiphonia sp. (2)

Remarks.—*Scarus croicensis* is the smallest Atlantic species of the genus and perhaps the most abundant on West Indian reefs. The terminal male phase was named *S. punctulatus* (taxomic discussion in Randall, 1963c). Beebe & Tee-Van (1928) recorded the food of *croicensis* as algae, small crustaceans, etc. The inorganic residue from the guts of nine specimens from Puerto Rico ranged from 15.7 to 96.5 per cent of the dried contents (mean 75.4 per cent).

Scarus guacamaia Cuvier

RAINBOW PARROTFISH

6 stations; 15 specimens: 276 to 516 mm SL.

FOOD

VOLUME (%)

Algae

92.0

Amphiroa fragilissima

Centroceras clavulatum (2)

Cladophora sp.

Coelothrix irregularis (4)

Enteromorpha sp. (2)

Gelidium sp. (2)

Gelidium corneum

Herposiphonia sp. (4)

Jania rubens

Laurencia sp. (2)

Laurencia obtusa

Lyngbya majuscula

Seagrasses	8.0
<i>Cymodocea manatorum</i>	
<i>Thalassia testudinum</i>	

Scarus taeniopterus Desmarest PAINTED-TAIL PARROTFISH
4 stations; 8 specimens: 127 to 191 mm SL.

FOOD	VOLUME (%)
Algae	81.2
<i>Centroceras</i> sp. (2)	
<i>Enteromorpha</i> sp. (2)	
<i>Gelidium</i> sp. (2)	
<i>Lyngbya</i> sp.	
<i>Microcoleus</i> sp.	
<i>Oscillatoria</i> sp.	
<i>Polysiphonia</i> sp. (2)	
<i>Polysiphonia ferulacea</i>	
<i>Rhizoclonium riparium</i>	
Seagrasses	17.3
<i>Thalassia testudinum</i>	
Sponges	1.5

778

Scarus vetula Bloch & Schneider
6 stations; 14 specimens: 210 to 330 mm SL.

QUEEN PARROTFISH

FOOD	VOLUME (%)
Algae	94.0
<i>Acanthophora spicifera</i>	
<i>Centroceras</i> sp. (2)	
<i>Ceramium byssoideum</i>	
<i>Cladophora</i> sp.	
<i>Coelothrix irregularis</i>	
<i>Enteromorpha</i> sp.	
<i>Gelidium</i> sp. (3)	
<i>Gelidium corneum</i>	
<i>Herposiphonia</i> sp. (2)	
<i>Laurencia</i> sp.	
<i>Lyngbya</i> sp.	
<i>Polysiphonia</i> sp. (4)	
<i>Polysiphonia ferulacea</i> (3)	
<i>Rhizoclonium</i> sp.	
Seagrasses	3.2
<i>Thalassia testudinum</i>	
Gorgonians	1.8
Sponges	1.0

Remarks.—The queen parrotfish is one of the most common of West Indian parrotfishes and seems to be closely restricted to the reef habitat. The percentage of sediment in the dried material from the alimentary tracts of 13 fish from Puerto Rico varied from 53.6 to 94.7 per cent (mean 76.9 per cent). The gorgonian and sponge material was in small quantity in the digestive tracts and was probably ingested incidentally with the algal food and inorganic material.

Sparisoma aurofrenatum (Cuvier & Valenciennes) REDBAND PARROTFISH
3 stations; 11 specimens: 120 to 175 mm SL.

FOOD	VOLUME (%)
Algae	97.8
<i>Centroceras</i> sp.	
<i>Coelothrix irregularis</i>	
<i>Gelidium</i> sp. (2)	
<i>Herposiphonia</i> sp.	
<i>Lyngbya</i> sp.	
<i>Microcoleus</i> sp.	
<i>Microcoleus chthonoplastes</i>	
<i>Polysiphonia</i> sp. (3)	
Seagrasses	1.3
<i>Cymodocea manatorum</i>	
Gorgonians	0.7
Corals	0.2

Remarks.—*Sparisoma aurofrenatum* is a moderately common, reef-dwelling species. The inorganic residue following the removal of organic matter from the dried contents of the alimentary tracts of ten fish constituted 8.0 to 93.8 per cent of the total contents (mean 75.5 per cent).

Sparisoma chrysopterum (Bloch & Schneider) REDTAIL PARROTFISH
2 stations; 6 specimens: 125 to 292 mm SL.

FOOD	VOLUME (%)
Algae	83.2
<i>Enteromorpha</i> sp.	
<i>Gelidium</i> sp.	
<i>Herposiphonia</i> sp.	
<i>Laurencia</i> sp.	
Seagrasses	16.8
<i>Thalassia testudinum</i> (2)	

Remarks.—*Sparisoma chrysopterum* occurs both on reefs and seagrass beds. It is second only to *S. radians* in abundance in the latter habitat in the West Indies. Beebe & Tee-Van (1928) reported the food of Haitian examples merely as vegetable matter. Inorganic sediment from the alimentary tracts of six specimens from Puerto Rico varied from 38.9 to 92.5 per cent of the total (mean value 69.5 per cent). Two had eaten large amounts of *Thalassia*.

Sparisoma rubripinne (Cuvier & Valenciennes) REDFIN PARROTFISH
5 stations; 18 specimens: 153 to 350 mm SL.

FOOD	VOLUME (%)
Algae	92.6
<i>Acrochaetium</i> sp.	
<i>Anacystis marina</i>	
<i>Calothrix</i> sp.	
<i>Centroceras</i> sp. (2)	
<i>Ceramium</i> sp. (3)	
<i>Ceramium byssoideum</i>	
<i>Coelothrix irregularis</i>	
<i>Dictyota</i> sp.	
<i>Enteromorpha</i> sp. (3)	
<i>Gelidium</i> sp.	
<i>Gelidium corneum</i>	
<i>Halimeda</i> sp.	
<i>Herposiphonia</i> sp.	
<i>Laurencia obtusa</i>	
<i>Lomentaria uncinata</i>	
<i>Lyngbya</i> sp. (2)	
<i>Polysiphonia</i> sp.	
<i>Polysiphonia binneyi</i>	
<i>Polysiphonia ferulacea</i>	

Rhizoclonium sp.
Rhizoclonium riparium
Sphacelaria sp.

Seagrasses 7.0

Thalassia testudinum (5)

Sponges 0.4

Remarks.—*Sparisoma rubripinne* is the most common member of the genus in the inshore portions of West Indian reefs. Randall & Randall (1963) noted that this species ordinarily spends much of the day grazing on benthic plant life (except during periods of reproductive activity). The specimens listed above varied greatly in the amount of sediment in their digestive tracts. Two of 16 fish analyzed had only 0.6 and 0.8 per cent by volume of inorganic material in their guts. The highest percentage was 98.6, and the mean was 68.6 per cent.

Sparisoma radians (Cuvier & Valenciennes) BUCKTOOTH PARROTFISH
 2 stations; 5 specimens: 57 to 110 mm SL.

FOOD VOLUME (%)

Seagrasses 88.0

Thalassia testudinum

Algae 12.0

Acanthophora spicifera

Dictyota sp.

Remarks.—*S. radians* is the smallest species of the genus. It lives primarily in shallow beds of seagrass. There was almost no inorganic material mixed with the *Thalassia* and algae of the gut contents of the five specimens that were examined.

Sparisoma viride (Bonnaterre) STOPLIGHT PARROTFISH
 5 stations; 20 specimens: 132 to 369 mm SL.

FOOD VOLUME (%)

Algae 97.3

Centroceras sp.

Ceramium sp.

Enteromorpha sp. (3)

Enteromorpha flexuosa

Gelidium sp. (5)

Herposiphonia sp.

Laurencia papillosa

Lyngbya sp. (2)

Microcoleus chthonoplastes (2)

Polysiphonia sp. (5)

Polysiphonia ferulacea

Rhizoclonium sp.

Seagrasses 2.5

Thalassia testudinum

Sponges	0.1
Gorgonians	0.1

Remarks.—Beebe & Tee-Van (1928) listed the food of this species as unrecognizable detritus. Longley & Hildebrand (1941) stated that the fish nip algae from dead coral, and on gravel bottom take bits of the weedy "stone" in their mouths and mumble them over. One may see them drop many of these, though some of the smaller ones are perhaps milled by the pharyngeal teeth. The percentage of inorganic sediment of the dried digestive tract material of 19 specimens from Puerto Rico varied from 45.1 per cent to 95.8 per cent with a mean of 72.9 per cent.

BOTHIDAE (Lefteye Flounders)

Flatfishes of the family Bothidae are represented in the West Indies by two species that may be found on the sand patches in and around coral reefs. Like other flatfishes, they are able to alter their color to match that of the bottom. They also agitate the sand so that it settles on and partially obscures their form. They are believed to take their prey of small fishes and crustaceans from such a position of concealment.

Bothus lunatus (Linnaeus) PEACOCK FLOUNDER
9 stations; 11 specimens: 99 to 300 mm SL; 4 empty.

FOOD	VOLUME (%)
Fishes	85.7
engraulids	
<i>Jenkinsia</i> sp.	
<i>Selar crumenophthalmus</i>	
Stomatopods	11.4
Octopuses	2.9

Remarks.—The largest peacock flounder taken, a specimen from the Virgin Islands 300 mm in standard length, had two bigeye scads in its stomach which measured 84 and 90 mm in fork length. A 290-mm flounder contained two individuals of *Jenkinsia* about 52 mm SL and six engraulids about 40 mm in length. These small schooling fishes were at the surface 25 feet above the bottom when the flatfish was speared. It seems more likely that the small clupeoids had previously ventured closer to the bottom rather than postulate that the flounder had made a feeding rush from the bottom to the surface.

Bothus ocellatus (Agassiz) EYED FLOUNDER
8 stations; 9 specimens: 68 to 130 mm SL.

FOOD	VOLUME (%)
Fishes	28.3
<i>Coryphopterus</i> sp.	
Crabs	25.0

<i>Calappa ocellata</i>	
majid	
Shrimps	17.8
Amphipods	15.0
isaeid	
Unidentified crustaceans	11.1
Stomatopods	2.8
<i>Pseudosquilla ciliata</i>	

Remarks.—Among the amphipods taken from a 77-mm *B. ocellatus* from Curaçao is an undescribed genus and species of Isaeidae (determined by Barnard).

GOBIIDAE (Gobies)

The gobies are the largest family of fishes in the West Indies. They are small, some only about an inch in length at maturity. Most are found on sand or mud bottoms, often in burrows, but many occur on coral reefs. Nearly all of the species rest upon the bottom, and most have the pelvic fins fused medially to form a sucking disc. The stomach contents of only a few specimens of four species were examined. Limited data on three are reported below. The food habits of the fourth, an undescribed species of *loglossus*, will be discussed by Randall (MS).

Coryphopterus glaucofraenum Gill

BRIDLED GOBY

1 station; 4 specimens: 28 to 37 mm SL.

FOOD	VOLUME (%)
Algae and detritus	50.0
Ostracods	12.0
Ophiuroids	10.0
Unidentified eggs	10.0
Pelecypods	10.0
Copepods	8.0

Remarks.—*C. glaucofraenum* is perhaps the most common goby living on a sand or silty bottom in and around shallow reefs and seagrass beds in the West Indies. Large amounts of fine sand were present with food material in the stomachs.

Gobiosoma sp.

WEST INDIAN CLEANING GOBY

1 station; 4 specimens: 21 to 26 mm SL; 3 empty.

FOOD	VOLUME (%)
Isopods	100.0
gnathiids (larv.)	

Remarks.—James E. Böhlke will describe this goby. It is a light bluish gray with a black stripe along the side of the head and body, and yellow above the stripe on the head and anteriorly on the body. It often occurs in pairs on West Indian reefs. It is restricted to a small section of reef, often

a prominent brain coral. Reef fishes in the vicinity are aware of its location and come to it for removal of ectoparasites. This goby is frequently encountered lying directly on live coral. With the approach of a host fish, it leaves the coral, swims to the fish, and moves leisurely over the surface of the body and fins; it may even enter the gill chamber and mouth of some fishes. It appears to make use of its ventral sucking disc to attach directly to the surface of the host fish. The larval gnathiid isopods from the stomach of one specimen appear to be fish parasites. More data on the food habits of this species would be of interest. It is expected that it will prove to be an obligate "cleaner." Longley & Hildebrand (1941) have described the parasite-picking activity of the related neon goby, *Gobiosoma oceanops* (*Elacatinus oceanops* of most authors) from Dry Tortugas, Florida (which is not known from the West Indies), and Eibl-Eibesfeldt (1955) and Randall (1958, 1962b) have made observations on the West Indian species.

Gnatholepis thompsoni Jordan

GOLDSPOT GOBY

2 stations; 10 specimens: 30 to 43 mm SL.

FOOD	VOLUME (%)
Algae and detritus	74.0
Copepods	18.0
Amphipods	4.0
Ostracods	2.0
Unidentified crustaceans	2.0

Remarks.—The stomachs of some of the specimens of *G. thompsoni* contained as much as 50 per cent fine sand.

BLENNIIDAE (Blennies)

The blennies are small, strictly benthic, diurnal fishes which are characteristic of hard bottoms. The four species discussed below appear to feed primarily on algae and detritus. Limited data presented by Randall (1966) suggest that the blenniid genus *Hypoleurochilus*, represented by two species in the West Indies (a third is known only from Cay Sal, Bahamas), is principally carnivorous.

Blennius cristatus Linnaeus

MOLLY MILLER

4 stations; 22 specimens: 52 to 87 mm SL; 1 empty.

FOOD	VOLUME (%)
Algae and organic detritus	99.2
<i>Acanthophora spicifera</i>	
<i>Amphiroa fragilissima</i>	
<i>Bryopsis</i> sp.	
<i>Caulerpa</i> sp.	
<i>Ceramium</i> sp.	
<i>Ceramium byssoideum</i>	

Dictyota sp.
Dictyota divaricata
Hypnea musciformis
Laurencia gemnifera
Laurencia obtusa
Laurencia papillosa (2)
Lyngbya sp.

Gastropods 0.8
 acmaeid

Remarks.—*B. cristatus* lives along rocky shores. Sand, echinoid spine fragments, etc. were present in almost all of the stomachs, but in relatively small amounts (less than 10 per cent by volume). The algae seem to have been ingested in fairly large mouthfuls. The few gastropods that were detected in the stomach contents were very small and were probably not selected by the fish when feeding.

Blennius marmoreus Poey SEAWEED BLENNY

3 stations; 12 specimens: 33 to 76 mm SL.

FOOD	VOLUME (%)
Algae and organic detritus	79.2
<i>Asterocystis ramosa</i>	
<i>Ceramium</i> sp. (2)	
diatoms	
<i>Dichothrix</i> sp.	
<i>Polysiphonia</i> sp.	
Ophiuroids	9.2
Polychaetes	9.2
Hydroids	2.4

Remarks.—Longley & Hildebrand (1941) reported that this blenny feeds largely on filamentous algae, and to a lesser extent on a variety of animals including small tunicates, clams, amphipods, bryozoans, bits of sponge, etc. More sand was present in the stomachs of this species (up to 50 per cent) than the preceding.

Entomacrodus nigricans Gill PEARL BLENNY

3 stations; 16 specimens: 35 to 56 mm SL; 2 empty.

FOOD	VOLUME (%)
Algae and organic detritus	96.4
diatoms	
<i>Herposiphonia secunda</i>	
<i>Lyngbya majuscula</i>	
<i>Microcoleus</i> sp.	
<i>Polysiphonia</i> sp.	
<i>Polysiphonia ferulacea</i>	
Polychaetes	3.6

Remarks.—Like *B. cristatus*, *E. nigricans* is an inshore species. Fine sand and calcareous debris were present in the stomachs in moderate amounts. In five specimens from one station they represented 50 per cent by volume of the stomach-content material.

Ophioblennius atlanticus (Cuvier & Valenciennes)
8 stations; 50 specimens: 35 to 89 mm SL.

REDLIP BLENNY

FOOD	VOLUME (%)
Algae and organic detritus	99.5
<i>Acanthophora spicifera</i>	
<i>Amphiroa fragilissima</i>	
<i>Anacystis marina</i> (2)	
<i>Callithamnion</i> sp.	
<i>Ceramium</i> sp.	
<i>Ceramium byssoideum</i>	
<i>Ceramium nitens</i>	
diatoms (3)	
<i>Enteromorpha</i> sp.	
<i>Herposiphonia</i> sp.	
<i>Herposiphonia tenella</i>	
<i>Lyngbya</i> sp.	
<i>Lyngbya majuscula</i>	
<i>Phormidium penicellatum</i>	
<i>Plectonema nostocorum</i>	
<i>Polysiphonia</i> sp. (2)	
<i>Polysiphonia ferulacea</i>	
Fish eggs	0.5

Remarks.—*Ophioblennius atlanticus*, often classified in the genus *Rupis-cartes*, is one of the most abundant fishes on shallow reefs in the West Indian region. Randall (1963b) found it the most numerous fish in a large poison station on a fringing reef at St. John, Virgin Islands, and the third in number in a second large collecting station at the same island. Beebe & Tee-Van (1928) stated that the food of their specimens from Haiti consisted only of organic detritus, apparently of both animal and vegetable origin. Diatoms and various bluegreen algae dominated the plant material in the stomachs of specimens from the Virgin Islands and Puerto Rico. Fine sand was often present, but in small quantities (no more than 15 per cent of the volume of the stomach contents). This species does not bite off large amounts of algae like *Blennius cristatus* but scrapes detrital material and fine filamentous algae from rock surfaces. *B. cristatus* is primarily an intertidal fish and feeds on the luxuriant algal flora there, whereas *O. atlanticus* lives in deeper (though still shallow) water and must compete for a meager algal supply with larger herbivores such as the acanthurids and scarids.

CLINIDAE (Clinids)

The clinids are small blennioid fishes that usually live inshore on a rock substratum, but they may occur on sand or coral rubble. Information on their feeding is limited but suggestive of carnivorous habits. Robins & Randall (1965) analyzed the stomach contents of 19 specimens of *Chaenopsis limbaughi*, a species of the subfamily Chaenopsinae. Small crustaceans were the dominant food organisms.

Labrisomus guppyi (Norman) SHADOW BLENNY
3 stations; 6 specimens: 56 to 75 mm SL; 2 empty.

FOOD	VOLUME (%)
Crabs	72.5
<i>Mithrax</i> sp.	
<i>Petrolisthes</i> sp.	
Chitons	20.0
Gastropods	5.0
<i>Acmaea</i> sp.	
Isopods	2.5

Labrisomus kalisherae (Jordan) DOWNY BLENNY
1 station; 1 specimen: 62 mm SL.

FOOD	VOLUME (%)
Ophiuroid	100.0
<i>Ophiocoma echinata</i>	

Labrisomus nuchipinnis (Quoy & Gaimard) HAIRY BLENNY
8 stations; 22 specimens: 59 to 131 mm SL; 3 empty.

FOOD	VOLUME (%)
Crabs	27.2
majid	
<i>Microphrys bicornutus</i>	
<i>Percnon</i> sp.	
<i>Petrolisthes galathinus</i>	
Gastropods	16.5
<i>Acmaea pustulata</i>	
<i>Cerithium eburneum</i>	
<i>Modulus modiolus</i>	
<i>Olivella petiolita</i>	
<i>Tricolia adamsi</i>	
Ophiuroids	12.3
<i>Ophiocoma</i> sp.	
<i>Ophiocoma echinata</i>	
Echinoids	10.5
<i>Echinometra lacunter</i>	
Fishes	10.5
Polychaetes	10.0

Shrimps	7.7
Amphipods	5.3

Remarks.—*Labrisomus nuchipinnis* is the largest and most common West Indian clinid. Some of the animals on which it feeds are of considerable size in comparison to its size. All of the gastropods in the stomachs were intact. A 95-mm fish contained an unbroken limpet (*Acmaea pustulata*), the shell of which measured 8 by 10 mm. *Modulus modulus* from a 117-mm individual was 9.5 mm in length. Two fish, 128 and 131 mm SL, each contained intact *Echinometra*; the tests of these echinoids, however, were only about 6 mm in diameter.

OPISTHOGNATHIDAE (Jawfishes)

Jawfishes live in burrows in sediment which they line with stones or bits of shell or coral. Often small groups of burrows are encountered in the vicinity of reefs. The individual fish make short excursions for feeding or hover above the burrow to eat zooplankton. They back into their burrows tail first for shelter. They are diurnal, and at least one species (*Opisthognathus aurifrons*) covers the entrance to its burrow for the night by backing in with a large stone in its jaws.

Opisthognathus aurifrons (Jordan & Thompson) YELLOWHEAD JAWFISH
4 stations; 16 specimens: 46 to 68 mm SL.

FOOD	VOLUME (%)
Copepods	85.0
<i>Acartia negligens</i>	
<i>Calanopia americana</i>	
<i>Candacia pachydactyla</i>	
<i>Coryaceus subulatus</i>	
<i>Oncaea</i> sp.	
<i>Temora turbinata</i>	
<i>Undinula vulgaris</i>	
Shrimp larvae	9.4
Unidentified animal material	1.9
Fish eggs	1.5
Siphonophores	1.3
Barnacle larvae	0.6
Polychaetes	0.3

Remarks.—Longley & Hildebrand (1941) described the burrow of *O. aurifrons* and its construction and repair. They stated that the jawfish are usually seen "floating" a foot or more above their burrows. With the approach of danger they settle in tail first but in an emergency they dart in head foremost. These authors stated that the fish feed on drifting plankton. In a small amount of material from the gut of one, W. L. Schmitt recognized a shrimp zoea, small hermit crab, two barnacle larvae, several ostracods, a tanaid, an amphipod, a dozen copepods representing several

species, and several recently hatched snails. Böhlke & Thomas (1961) have postulated that the peculiar tear-drop shaped pupil of the eye, with its anteroventral-posterodorsal alignment, seems to be an adaptation to this hovering plankton-feeding existence. The antero-ventral lobe is oriented so that the fish probably has binocular vision along a plane parallel to the horizontal while maintaining a near-vertical position.

Opisthognathus macrogathus Poey

SPOTFIN JAWFISH

1 station; 1 specimen: 100 mm SL.

FOOD	VOLUME (%)
Shrimps	100.0

Opisthognathus maxillosus Poey

MOTTLED JAWFISH

9 stations; 14 specimens: 53 to 110 mm SL; 7 empty.

FOOD	VOLUME (%)
Shrimps	28.6
Isopods	28.6
Fishes	22.7
Polychaetes	14.3
Mysids	5.4
Copepods	0.4

Remarks.—This species, the preceding, and the following, were not observed hovering above their burrows to feed on plankton, at least as adults. Their stomach contents indicate that they feed primarily on benthic forms or free-swimming animals such as mysids which live near the bottom.

Opisthognathus whitehurstii (Longley)

DUSKY JAWFISH

4 stations; 9 specimens: 33 to 65 mm SL; 4 empty.

FOOD	VOLUME (%)
Shrimps	54.0
Fishes	22.0
Isopods	11.0
Ophiuroids	8.0
Crabs (juv.)	5.0

SCORPAENIDAE (Scorpionfishes)

The scorpionfishes are diurnal, solitary, and carnivorous. They sit upon the bottom, relying on their protective coloration and numerous dermal flaps and filaments to provide resemblance to the substratum. Characteristically, they wait for mobile prey to come within striking range of their relatively large mouths. In aquaria they have been observed to slowly stalk unsuspecting small fishes and crustaceans.

Scorpaena brasiliensis (Cuvier & Valenciennes)

BARBFISH

5 stations; 13 specimens: 111 to 164 mm SL; 6 empty.

FOOD	VOLUME (%)
Shrimps	35.7
penaeid	

Unidentified crustaceans	28.6
Stomatopods	14.3
Fishes	14.3
<i>Hippocampus</i> sp.	
Crabs	7.1

Remarks.—The barbfish is not common in the West Indies. The only individual which had eaten a fish was speared on a sand bottom in 65 feet of water off St. John, Virgin Islands, beside a thallus of *Avrainvillea*. It was 164 mm in standard length, and the seahorse that it had eaten measured 58 mm from the top of the head to the bottom of the coiled tail.

Scorpaena grandicornis (Cuvier & Valenciennes) GRASS SCORPIONFISH
11 stations; 15 specimens: 37 to 102 mm SL; 7 empty.

FOOD	VOLUME (%)
Shrimps	75.0
caridean	
stenopid	
Fishes	12.5
Unidentified crustaceans	12.5

Remarks.—*Scorpaena grandicornis* is a shallow-water fish most often taken in beds of seagrass. Like the preceding species, it appears to feed more on crustaceans than fishes.

Scorpaena inermis Cuvier & Valenciennes MUSHROOM SCORPIONFISH
6 stations; 28 specimens: 36 to 71 mm SL; 12 empty.

FOOD	VOLUME (%)
Shrimps	85.3
carideans	
palaemonids	
penaeids (2)	
<i>Penaeopsis</i> sp.	
Stomatopods	7.5
Unidentified animal material	6.3
Crabs	0.6
portunid	
Fishes	0.3

Remarks.—*Scorpaena inermis* is a small species that is most frequently found on coral rubble bottoms in the depth range of a few to 30 feet. Eschmeyer (1965), however, has recorded it to a depth of 40 fathoms. Two series of specimens were collected from a sand bottom dominated by *Halophila*. One 60-mm fish taken from the stomach of *Antennarius scaber* contained 11 small shrimps (penaeids and carideans including palaemonids), a portunid crab, and fish remains.

Scorpaena plumieri Bloch

SPOTTED SCORPIONFISH

19 stations; 28 specimens: 61 to 250 mm SL; 12 empty.

FOOD	VOLUME (%)
Fishes	42.2
<i>Acanthurus</i> sp. (larv.)	
congrid	
<i>Jenkinsia</i> sp.	
Crabs	31.3
majid	
<i>Mithrax coryphe</i>	
<i>Pitho</i> sp.	
<i>Portunus anceps</i>	
<i>Portunus ordwayi</i>	
Shrimps	18.7
penaeid	
<i>Penaeopsis goodei</i>	
Octopuses	6.2
Hermit crabs	1.6

Remarks.—*Scorpaena plumieri* is the most common species of the genus on shallow West Indian reefs. It is also the largest. Longley (in Longley & Hildebrand, 1941) wrote, "The body is hoary with dermal appendages like rags and tatters of weed. Among algae, combinations of green and yellow occur. I have sometimes found it almost necessary to brush the fish to convince myself that its color and covering were its own. The oblitative effect of its coloration is so pronounced that one may gaze almost directly at it without seeing it." He noted that it often remains motionless for long periods, but he saw it dash up from the bottom with rapidity to swallow a blenny that ventured too near. He found two such fishes, a portunid crab, and fragments of several other small crustaceans in the stomach of one specimen from Dry Tortugas.

Scorpaenodes caribbaeus Meek & Hildebrand

REEF SCORPIONFISH

9 stations; 21 specimens: 38 to 90 mm SL; 10 empty.

FOOD	VOLUME (%)
Shrimps	65.9
alpheids (2)	
carideans (3)	
Crabs	17.3
<i>Petrolisthes galathinus</i>	
porcellanid	
xanthid	
Unidentified crustaceans	9.1
Fishes	7.7
<i>Holacanthus</i> sp. (larv.)	

DACTYLOPTERIDAE (Flying Gurnards)

Dactylopterus volitans (Linnaeus)

FLYING GURNARD

6 stations; 7 specimens: 98 to 275 mm SL.

FOOD	VOLUME (%)
Crabs	61.7
majid	
parthenopids	
portunids (2)	
<i>Portunus</i> sp.	
Stomatopods	19.3
<i>Gonodactylus</i> sp.	
Pelecypods	7.2
Shrimps	5.4
penaeids (2)	
Fishes	5.0
Amphipods	1.4

Remarks.—The flying gurnard is a solitary benthic fish usually seen on sand bottoms. It is rare in the West Indies. Sluggish and easily approached, it "walks" on its pelvic fins and may utilize the free anterior rays of the pectoral fins like claws to scratch in the sand. When alarmed it spreads its long blue-spotted pectorals laterally, as if in a warning display (Breder, 1963). Beebe (1928) has attributed the ability to glide in the air to this fish. Longley & Hildebrand (1941) wrote, "It has been said at least since the time of Artdi that this fish flies. The statement seems scarcely credible, as the rays of the pectoral are so thin and flexible that the fin droops almost of its own weight."

EPHIPPIDAE (Spadefishes)

Chaetodipterus faber (Broussonet)

SPADEFISH

22 stations; 29 specimens: 129 to 350 mm SL; 7 empty.

FOOD	VOLUME (%)
Sponges	32.7
Zoantharians (except corals)	18.5
<i>Rhodactis sanctithomae</i>	
<i>Zoanthus</i> sp. (4)	
Polychaetes	13.7
<i>Sabellastarte magnifica</i>	
Tunicates	12.6
salps	
Gorgonians	6.3
<i>Muricea laxa</i>	
Algae	5.0
<i>Ceramium fastigiatum</i>	
<i>Cladophora</i> sp.	

diatoms	
<i>Giffordia mitchellae</i>	
Gastropod eggs	3.2
Holothurians	2.3
Corals	2.3
<i>Oculina diffusa</i>	
Seagrasses	2.3
<i>Cymodocea manatorum</i>	
Heteropods	0.5
Crab larvae	0.2
Spiny lobster larvae	0.2
Shrimp larvae	0.1
Amphipods	0.1
hyperiid	

Remarks.—The nearly ubiquitous spadefish is one of the most generalized of fishes in its food habits. The adults are usually encountered in small schools which often approach divers closely. Spadefish may occur in turbid areas over mud bottoms or clear water over offshore reefs. They may lurk in the crevices in reefs and feed on sponges, algae, etc. or swim well above the bottom and ingest the larger zooplankton and smaller nekton. The young are common in shallow brackish environments where they resemble red mangrove seed pods in form and color (Breder, 1946). Linton (1905) recorded the food from three stomachs of North Carolina fish as fragments of annelids, crustaceans, diatoms, a gorgonian (*Leptogorgia* sp.), and possibly foraminifera. Hildebrand & Schroeder (1928) examined the stomach-content material of four small specimens (68 to 82 mm) from Chesapeake Bay. This consisted chiefly of vegetable debris with a few minute crustaceans intermixed. Smith (1907-reference from Hildebrand & Schroeder) wrote of the spadefish, "It frequents rocky patches, wrecks, and piling in search of food, which consists of small crustaceans, worms, etc." Townsend (1929) stated that *C. faber* is a hardy fish which will live many years in captivity, adding that it is reported to feed on the Portuguese man-of-war (*Physalia*); fishermen at Trinidad supposedly capture it with this jellyfish as bait. Lowe (1962) reported hydroids, sponges, and feather stars (*Tropimetre carinata*) from specimens from British Guiana. None of the highly varied material from the stomachs of the West Indian specimens appears to have been accidentally ingested. The stomach of one 340-mm fish contained three pieces of sea cucumber and 21 pieces of manatee grass (the latter 13 to 53 mm long). Two fish (280 and 307 mm) had eaten only salps up to 10 mm long. Two others, 220 and 232 mm, contained only the coralliomorpharian anemone *Rhodactis sanctihomae*. The stomach of a 265-mm individual was filled with *Zoanthus* and one piece of live coral (*Oculina diffusa*) 12 mm long and 2 to 3 mm in width. A 185-mm fish contained only the tentacular crowns of five sabellids (*Sabellastarte mag-*

nifica). Two specimens (129 and 210 mm) taken with a trawl from a mud bottom off Mayaguez, Puerto Rico had eaten only an unidentified tube-dwelling polychaete.

CHAETODONTIDAE (Butterflyfishes and Angelfishes)

The chaetodonts are deep-bodied, compressed, colorful fishes which live on coral reefs. They are usually seen as solitary individuals or in pairs, and they are diurnal. The butterflyfishes (subfamily Chaetodontinae) in the West Indies seem to feed primarily on the tentacular crowns of polychaetes and on anthozoans, especially *Zoanthus*. No data were obtained on the food habits of *Chaetodon ocellatus*, a moderately rare species in the West Indies (although common in Florida). A small amount of animal material was noted in the stomach of one 118-mm specimen from the Dominican Republic, but no organisms could be identified. With the exception of *Centropyge*, the West Indian angelfishes (Pomacanthinae) feed mostly on sponges. Large amounts of algae may occasionally be found in the two species of *Pomacanthus*. The sponges which are eaten by angelfishes include species with numerous silicious spicules. One would expect, *a priori*, that the digestive tracts of the fishes consuming such sponges would be injured by the spicules. The fishes appear to have obviated any such abrasive effect, however, by secreting a heavy coat of tough mucous around the food mass. Juvenile angelfishes feed in part on the ectoparasites of other reef fishes (Randall & Randall, 1960). Such feeding has also been reported for some species of *Chaetodon*. The author has not observed this among West Indian species of the genus, but it would not be unexpected if it occurred. Hiatt & Strasburg (1960) noted that the chaetodonts in the Marshall Islands were divisible into three groups, herbivores, omnivores, and carnivores. They either grazed algae, ingested both coral polyps and algae, or browsed strictly on coral. Coral polyps were not found in the stomachs of any West Indian specimens, but individuals of the genus *Chaetodon* have been observed feeding on coral in aquaria. If reefs in the Caribbean were as dominated by corals as some of those in the Marshall Islands, it seems likely that coral polyps would appear as a prominent item of diet in at least some of the West Indian butterflyfishes.

Centropyge argi Woods & Kanazawa

CHERUBFISH

3 stations; 5 specimens: 36 to 56 mm SL; 1 empty.

Food	VOLUME (%)
Algae and detritus	100.0
<i>Cladophora</i> sp.	
<i>Enteromorpha</i> sp.	
<i>Lyngbya</i> sp.	
<i>Lyngbya majuscula</i>	

Remarks.—The cherubfish, sometimes called the pygmy angelfish, is a

Chaetodon capistratus Linnaeus FOUREYE BUTTERFLYFISH
11 stations; 29 specimens: 52 to 83 mm SL; 1 empty.

Remarks.—*Chaetodon capistratus* is the most common butterflyfish on shallow reefs in the West Indies and the smallest species of the genus in the region. The polychaetes which it had eaten consisted of the tentacles of serpulids and terebellids. Most of the unidentified tissue in the stomachs appeared to be coelenterate. The gorgonian material was only polyps (this fish has been observed to nibble at the fronds of gorgonians). Unidentified eggs were found in the stomachs of five specimens; none were fish eggs.

FOOD	VOLUME (%)
Unidentified animal material	43.3
Polychaetes	16.7
Shrimps	15.0
<i>Lucifer</i> sp.	
Amphipods	13.3
caprellids	
Hydroids	11.7

FOOD	VOLUME (%)
Polychaetes	58.7
sabellids (2)	
serpulids (3)	
terebellids (2)	
Anthozoans	32.5
<i>Bunodactis stelloides</i>	

<i>Zoanthus</i> sp. (2)	
Unidentified crustaceans	6.3
Mollusk eggs	2.5

Remarks.—Beebe & Tee-Van (1928) described the food of examples from Haiti as very minute crustaceans, algae, and other organic matter too disintegrated to identify. No plant material was detected in the 16 specimens reported above. All of the polychaete tissue consisted of tentacles.

Holacanthus ciliaris (Linnaeus) QUEEN ANGELFISH
19 stations; 26 specimens: 151 to 315 mm SL.

FOOD	VOLUME (%)
Sponges	96.8
Algae	1.4
<i>Dictyota dentata</i>	
<i>Dictyota divaricata</i>	
Tunicates	0.9
Hydroids	0.5
Bryozoans	0.4

Remarks.—This colorful species is not abundant, but it is universal on reefs from shallow water to depths of at least 200 feet. The stomachs of all specimens contained a variety of sponges (33 genera). These will be discussed in a separate paper by the author and Willard D. Hartman. The young, which have pale blue bars on the body, have been observed picking at the bodies of other reef fishes. The stomach of one small specimen from the Bahamas contained filamentous algae and a few calagoid copepods.

Holacanthus tricolor (Bloch) ROCK BEAUTY
12 stations; 24 specimens: 129 to 210 mm SL.

FOOD	VOLUME (%)
Sponges	97.1
Zoantharians	2.1
<i>Zoanthus</i> sp.	
Algae	0.8
<i>Avrainvillea rawsonii</i>	
<i>Dictyopteris</i> sp.	
<i>Lyngbya majuscula</i>	

Remarks.—Beebe & Tee-Van (1928) reported the food of this angelfish as "algae and scrapings."

Pomacanthus arcuatus (Linnaeus) GRAY ANGELFISH
27 stations; 34 specimens: 95 mm and 107 to 345 mm SL.

FOOD	VOLUME (%)
Sponges	70.2
Tunicates	10.1
didemnid (3)	

Algae	8.3
<i>Caulerpa mexicana</i>	
<i>Caulerpa cupressoides</i> (2)	
<i>Caulerpa prolifera</i> (2)	
<i>Caulerpa racemosa</i> (2)	
<i>Caulerpa sertularioides</i> (3)	
<i>Caulerpa taxifolia</i>	
<i>Coelothrix irregularis</i>	
<i>Colpomenia sinuosa</i>	
<i>Dictyopteris delicatula</i>	
<i>Dictyota</i> sp.	
<i>Dictyota bartayresii</i>	
<i>Dictyota divaricata</i>	
<i>Hypnea musciformis</i>	
<i>Penicillus pyriformis</i>	
<i>Pocockiella variegata</i>	
<i>Spatoglossum schroderi</i>	
<i>Ulva lactuca</i> (2)	
Zoantharians	4.4
<i>Zoanthus</i> sp.	
<i>Zoanthus sociatus</i>	
Unidentified animal material	3.3
Gorgonians	1.6
<i>Pterogorgia</i> sp.	
Unidentified eggs	1.5
Hydroids	0.4
Bryozoans	0.1
Seagrasses	0.1
<i>Ruppia maritima</i>	

Remarks.—The gray angelfish, sometimes referred to as the black angelfish, is a large reef fish. The young have vertical yellow bars. The stomach contents of a 95-mm juvenile from the Virgin Islands were not included in the above analysis. The fish contained five parasitic copepods, one free-living copepod (copepods 25 per cent by volume) and filamentous algae (75 per cent). Juveniles of the gray angelfish and the following species of *Pomacanthus* were often observed picking at the bodies of other fishes. Information on the food habits of adults has been presented in five previous works. Beebe & Tee-Van (1928) found the stomachs of Haitian specimens to be filled with algae, hydroids, etc. Breder (1948) stated merely that it feeds mostly on invertebrates and vegetation. Gudger (1929) emptied the contents of the alimentary tract of a specimen 18.75 inches long from Dry Tortugas. He found 240 cc of crustacean remains, pieces of gorgonians, and fragments of algae of various kinds. He added, "I am inclined to think that its principal food is algae." Longley & Hildebrand (1941) wrote that the diet of Tortugas fish includes algae and a great

variety of sedentary animals. Lowe (1962) reported sponges as the food of specimens of this species and *P. paru* from British Guiana. Sponges clearly dominated the food of the adult West Indian specimens listed above. In one 310-mm individual, however, algae represented 75 per cent of the total food mass in the stomach, and in another *Zoanthus sociatus* comprised 95 per cent of the stomach contents.

Pomacanthus paru (Bloch) FRENCH ANGELFISH
22 stations; 23 specimens: 59 mm and 95 to 328 mm SL.

FOOD	VOLUME (%)
Sponges	74.8
Algae	13.4
<i>Caulerpa cupressoides</i>	
<i>Caulerpa racemosa</i>	
<i>Caulerpa sertularioides</i>	
<i>Caulerpa taxifolia</i>	
<i>Centroceras clavulatum</i>	
<i>Cryptonemia crenulata</i>	
<i>Codium isthmocladum</i>	
<i>Dictyopteris delicatula</i>	
<i>Dictyota bartayresii</i> (2)	
<i>Halymenia florisia</i>	
<i>Hypnea musciformis</i>	
<i>Laurencia obtusa</i>	
<i>Padina gymnospora</i>	
<i>Sargassum platycarpum</i>	
<i>Spyridia filamentosa</i>	
Zoantharians	4.9
<i>Zoanthus sociatus</i>	
Tunicates	4.8
<i>Ascidia nigra</i>	
didemnids (2)	
Gorgonians	1.4
<i>Gorgonia flabellum</i>	
Hydroids	0.3
Bryozoans	0.2
Spermatophytes (including seagrasses)	0.1
<i>Cymodocea manatorum</i>	
<i>Halophila baillonis</i>	
Unidentified eggs	0.1

Remarks.—Like the gray angelfish, the French angelfish attains large size. It also displays vertical yellow bars in the juvenile form. The young feed in part by removing ectoparasites from fishes. The food of the 59-mm juvenile was not included with the data from the larger specimens. This small specimen had eaten calagoid copepods (40 per cent by volume) and

algae (60 per cent). The stomach-content material of larger angelfish was similar in composition to that of the gray angelfish. Sponges were the dominant food organisms. The stomach contents of a 95-mm individual consisted wholly of three species of sponges. The largest individual collected, however, had eaten only filamentous red algae, and a 128-mm fish contained 24 polyps of *Zoanthus* and a piece of ascidian.

Prognathodes aculeatus (Poey) LONGSNOUT BUTTERFLYFISH
6 stations; 8 specimens: 59 to 69 mm SL; 1 empty.

FOOD	VOLUME (%)
Polychaetes	38.5
serpulids	
Unidentified animal material	26.6
Echinoid pedicellariae and tubefeet	11.4
<i>Diadema antillarum</i>	
Shrimps	7.2
Unidentified crustaceans	5.7
Copepods	4.9
cyclopoids	
siphonostomes	
Mysids	4.7
Tanaids	1.0

Remarks.—*Prognathodes aculeatus* is not uncommon on West Indian reefs at depths greater than about 100 feet. Evidently its relatively long snout is useful to reach among the spines of echinoids to nip off the ends of tube-feet and pedicellariae. Hubbs (1963) reported (after Zaneveld) that it feeds on the tubefeet of echinoids. The stomach contents of two specimens examined by Hubbs and the author consisted of a nemertean, a mysid, a small caprellid, at least one copepod, and echinoid pedicellariae. Hubbs reported further (after Kristensen) that this butterflyfish feeds in aquaria on *Mysis* and often browses. Among the copepods taken from specimens from Puerto Rico were several siphonostomes. These are usually commensals of sponges and other invertebrates.

ACANTHURIDAE (Surgeonfishes)

The surgeonfishes are represented in the West Indies by three species of *Acanthurus* which are among the most common of reef fishes. They are herbivorous and diurnal. Their teeth are spatulate with denticulate margins, hence well adapted for feeding on filamentous algae. Their alimentary tracts are very long. Two of the species, *A. chirurgus* (usually listed as *hepatus* in the older literature) and *A. bahianus*, have thick-walled, gizzard-like stomachs. Their diet includes a large amount of inorganic sediment which probably serves to grind the algal food into finer particles and thus render more of the cell contents available for digestion. *A. coeruleus*, by contrast, has a thin-walled stomach, and it usually does not ingest sand.

Acanthurus bahianus Castelnau
11 stations; 23 specimens: 93 to 175 mm SL.

OCEAN SURGEON

FOOD	VOLUME (%)
Algae and organic detritus	91.8
<i>Bryopsis pennata</i>	
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp. (2)	
<i>Ceramium byssoideum</i>	
<i>Cladophora delicatula</i>	
diatoms (4)	
<i>Dictyota divaricata</i> (2)	
<i>Enteromorpha</i> sp. (2)	
<i>Enteromorpha flexuosa</i>	
<i>Eucheuma echinocarpum</i>	
<i>Galaxaura lapidescens</i>	
<i>Halimeda opuntia</i>	
<i>Herposiphonia</i> sp.	
<i>Hypnea musciformis</i> (2)	
<i>Hypnea spinella</i>	
<i>Jania capillacea</i>	
<i>Jania rubens</i>	
<i>Liagora ceranoides</i>	
<i>Lyngbya</i> sp.	
<i>Lyngbya majuscula</i>	
<i>Pocockiella variegata</i>	
<i>Polysiphonia</i> sp.	
<i>Polysiphonia ferulacea</i>	
<i>Rhizoclonium riparium</i>	
<i>Sargassum</i> sp.	
<i>Spyridia filamentosa</i> (2)	
<i>Ulva lactuca</i>	
Spermatophytes (including seagrasses)	8.2
<i>Cymodocea manatorum</i> (3)	
<i>Halophila baillonis</i>	
<i>Thalassia testudinum</i> (4)	

Remarks.—Beebe & Tee-Van (1928) remarked that the food of specimens from Haiti consisted of finely disintegrated organic matter with traces of algae and worm tubes. Longley & Hildebrand (1941) noted that *A. bahianus* is a bottom fish whose distribution in shallow water is essentially that of the algae on which it may be seen cropping all day long. They added that algae seems to constitute by far the greater part of its food. The author determined that about half of the stomach contents of the West Indian specimens was fine sand, along with tiny shells, etc. The percentage of inorganic material ranged from as little as 5 per cent to as much as 80 per cent. Although plant fragments were usually small, occasional large

pieces were found. Sections of *Cymodocea* in a 152-mm fish ranged from 7 to 25 mm in length. A 175-mm individual contained fragments of *Ulva lactuca* up to 37 mm long, *Eucheuma echinocarpum* to 10 mm, *Hypnea musciformis* to 8 mm, and *Thalassia* to 15 mm. Occasional gravel particles in this fish were as large as 3 mm in diameter.

Acanthurus chirurgus (Bloch)

DOCTORFISH

9 stations; 20 specimens: 135 to 237 mm SL.

FOOD	VOLUME (%)
Algae and organic detritus	93.9
<i>Amphiroa fragilissima</i>	
<i>Anacystis</i> sp.	
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp. (2)	
<i>Corallina cubensis</i>	
diatoms (2)	
<i>Dictyota</i> sp. (2)	
<i>Dictyota divaricata</i>	
<i>Gelidium corneum</i>	
<i>Herposiphonia</i> sp.	
<i>Jania capillacea</i> (2)	
<i>Laurencia obtusa</i>	
<i>Lyngbya majuscula</i>	
<i>Oscillatoria</i> sp.	
<i>Phormidium</i> sp.	
<i>Polysiphonia ferulacea</i> (2)	
<i>Sargassum platycarpum</i>	
<i>Spermothamnion investiens</i>	
<i>Ulva</i> sp.	
Seagrasses	5.7
<i>Cymodocea manatorum</i>	
<i>Thalassia testudinum</i>	
Annelid worm tubes (noncalcareous)	0.2
Gastropods	0.1
Nudibranch eggs	0.1

Remarks.—Of the food of specimens of this species from Haiti, Beebe & Tee-Van (1928) wrote, "The powerful gizzard-like stomach contained unidentifiable vegetable and animal matter." Townsend (1929) stated, "Although largely herbivorous the Aquarium [New York] has kept specimens as long as five years on a fish and clam diet varied occasionally with seaweed." Longley & Hildebrand (1941) reported *A. chirurgus* from Dry Tortugas to be almost entirely herbivorous. They indicated that foreign material constituted two-thirds to three-fourths of the stomach contents. The author found that sand and other inorganic matter such as dead *Halimeda* fragments, sponge spicules and gorgonian spicules comprised

25 to 75 per cent of the stomach contents of West Indian specimens examined by him. Individual pieces of gravel were as large as 5 mm in diameter.

Acanthurus coeruleus Bloch & Schneider

BLUE TANG

12 stations; 27 specimens: 88 to 157 mm SL; 2 empty.

FOOD	VOLUME (%)
Algae and organic detritus	92.8
<i>Amphiroa fragilissima</i>	
<i>Caulerpa racemosa</i>	
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp.	
<i>Ceramium byssoideum</i>	
<i>Ceramium nitens</i> (2)	
<i>Cladophora</i> sp.	
<i>Cladophora delicatula</i>	
<i>Coelothrix irregularis</i> (2)	
diatoms (3)	
<i>Dictyosphaeria favulosa</i>	
<i>Dictyota</i> sp.	
<i>Dictyota divaricata</i> (2)	
<i>Ectocarpus</i> sp.	
<i>Enteromorpha</i> sp.	
<i>Enteromorpha flexuosa</i>	
<i>Galaxaura lapidescens</i>	
<i>Gelidium rigidulum</i>	
<i>Halimeda incompressa</i>	
<i>Halimeda opuntia</i>	
<i>Hypnea spinella</i>	
<i>Lyngbya</i> sp. (2)	
<i>Lyngbya majuscula</i> (2)	
<i>Microcoleus</i> sp.	
<i>Oscillatoria</i> sp.	
<i>Phormidium</i> sp.	
<i>Polysiphonia</i> sp. (3)	
<i>Polysiphonia ferrulacea</i>	
<i>Rhizoclonium riparium</i>	
<i>Spirulina</i> sp.	
<i>Ulva</i> sp.	
Spermatophytes (including seagrasses)	6.8
<i>Cymodocea manatorum</i>	
<i>Halophila baillonis</i>	
Unidentified crustaceans	0.3
Gorgonian fragments	0.1

Remarks.—Longley, Schmitt, & Taylor (1925) first noted that *Acanthurus coeruleus* has a thin-walled stomach, in contrast to that of *A. chirurgus*.

They further observed that its algal food is "quite free" of foreign matter, in contrast to that of *chirurgus*. Only a trace of sand was found by the author in the stomachs examined by him. The few crustaceans that were detected were very small and could have been ingested accidentally with the algae. The yellow juveniles of this species were observed browsing freely on fine filamentous algae. Longley & Hildebrand (1941) stated that the blue tang is less of a bottom fish than the other two acanthurids previously discussed, although it often swims in the company of *chirurgus*. Breder & Clark (1947) briefly discussed and diagrammed the visceral anatomy.

BALISTIDAE (Triggerfishes)

The triggerfishes and other plectognaths have small mouths but powerful jaws with sharp cutting teeth. Their dentition enables them to prey upon a variety of armored invertebrates denied as food to most fishes. In spite of such advantage, one West Indian species shows a preference for feeding on plants and another on zooplankton. The balistids appear to be diurnal.

Balistes vetula Linnaeus

QUEEN TRIGGERFISH

65 stations; 95 specimens: 130 to 480 mm SL; 4 empty.

FOOD	VOLUME (%)
Echinoids	72.8
<i>Diadema antillarum</i> (43)	
<i>Echinometra</i> sp. (3)	
<i>Echinometra viridis</i>	
<i>Eucidaris tribuloides</i>	
spatangoids (3)	
Crabs	5.4
calappid	
<i>Mithrax</i> sp.	
Pelecypods	4.6
<i>Arca zebra</i>	
<i>Atrina rigida</i>	
<i>Barbatia domingensis</i>	
<i>Brachidontes</i> sp.	
<i>Chama sarda</i>	
<i>Isognomon radiatus</i>	
<i>Lithophaga bisulcata</i>	
<i>Ostrea</i> sp.	
<i>Spondylus</i> sp.	
<i>Volsella</i> sp.	
Ophiuroids	3.3
<i>Ophiactis</i> sp.	
<i>Ophiocoma</i> sp.	
<i>Ophionereis</i> sp.	
Unidentified animal material	2.5

Polychaetes	2.1
Hermit crabs	1.9
<i>Dardanus venosus</i>	
Gastropods	1.6
<i>Columbella mercatoria</i>	
<i>Crucibulum auricula</i>	
<i>Nassarius</i> sp.	
<i>Strombus gigas</i> (2)	
<i>Tegula fasciata</i>	
Asteroids	1.4
<i>Ophidiaster</i> sp.	
<i>Oreaster reticulata</i> (3)	
Algae	1.2
<i>Amphiroa fragilissima</i>	
<i>Corallina subulata</i>	
<i>Dictyopteris delicatula</i>	
<i>Halimeda incrassata</i>	
<i>Halimeda opuntia</i>	
<i>Laurencia obtusa</i>	
<i>Sargassum</i> sp.	
<i>Udotea flabellum</i>	
Sipunculids	0.9
Shrimps	0.8
alpheids	
Tunicates	0.6
Fishes	0.2
Corals	0.2
<i>Cladocora arbuscula</i>	
Unidentified crustaceans	0.2
Chitons	0.1
Scyllarid lobster	0.1
<i>Scyllarides aequinoctialis</i>	
Stomatopods	0.05
Amphipods	0.03
Anthozoans (except corals)	0.02

Remarks.—*Balistes vetula* is a common, benthic, solitary reef fish. It probably feeds mostly on reef-dwelling organisms but it makes occasional excursions over expanses of seagrass and sand. Randall (1963) reported it as the first species to appear as an adult on an artificial reef built in a seagrass bed in the Virgin Islands. The nearest natural reef was 120 meters away. Beebe & Tee-Van (1928) reported the food of two specimens from Haiti as *Thalassia* and small crustaceans. Randalls, Schroeder, & Starck (1964) listed it among the fishes which feed on *Diadema antillarum*. This echinoid is the principal item of the diet of adult queen triggerfish. The spines and test are eaten freely, along with soft tissue. The fish have been

observed to attack the urchin from the oval surface where the spines are shorter. The smaller triggerfish feed less upon *Diadema* than adults. Randall (1964a) included *B. vetula* among the fishes which eat the queen conch (*Strombus gigas*). A 202-mm fish contained the crushed remains of a conch about 70 mm long. A 330 mm-fish had eaten a 25-mm one. About half of the stomach contents of two adult fish consisted of a variety of algae. The remains of a scyllarid lobster taken from a 365-mm triggerfish consisted only of fragments of legs. The entire slipper lobster was estimated to have been about 6 inches long.

Canthidermis sufflamen (Mitchill) OCEAN TRIGGERFISH
5 stations; 5 specimens: 270 to 410 mm SL; 1 empty.

FOOD	VOLUME (%)
Echinoids	25.0
<i>Diadema antillarum</i>	
Pteropods	21.2
<i>Cavolina</i> sp.	
<i>Cavolina longirostris</i>	
Unidentified animal material	15.0
Gastropod larvae	13.2
<i>Cymatium</i> sp.	
<i>Tonna</i> sp.	
Siphonophores	8.5
Amphipods	6.0
hyperiids (2)	
Crab larvae	3.7
Isopod larvae	2.5
Algae	2.5
<i>Sargassum</i> sp.	
Shrimp larvae	1.2
Barnacle larvae	1.2

Remarks.—*C. sufflamen* was most often encountered in clear blue water over offshore reefs near drop-offs to deep water. It was usually observed in loose aggregations well above the bottom feeding on zooplankton. The unidentified animal material that constituted 70 per cent of the stomach contents of one fish was soft and gelatinous, hence probably salp, ctenophore, or scyphozoan. The largest specimen was speared in 10 feet of water in coral. It had fed entirely on *Diadema*.

Melichthys niger (Bloch) BLACK DURGON
11 stations; 17 specimens: 195 to 280 mm SL.

FOOD	VOLUME (%)
Algae	70.8
<i>Acrochaetium</i> sp.	
<i>Amphiroa fragilissima</i>	

<i>Calothrix</i> sp.	
<i>Ceramium byssoideum</i>	
<i>Ceramium nitens</i>	
<i>Corallina cubensis</i>	
diatoms	
<i>Dichothrix penicillata</i>	
<i>Dictyopteris delicatula</i>	
<i>Galaxaura</i> sp.	
<i>Galaxaura squalida</i>	
<i>Gelidium pusillum</i>	
<i>Gracilaria verrucosa</i>	
<i>Halimeda opuntia</i>	
<i>Herposiphonia secunda</i>	
<i>Hypnea musciformis</i>	
<i>Jania capillacea</i> (2)	
<i>Jania rubens</i>	
<i>Nitophyllum</i> sp.	
<i>Padina sanctae-crucis</i>	
<i>Peyssonnelia</i> sp.	
<i>Pocockiella</i> sp.	
<i>Pocockiella variegata</i> (2)	
<i>Polysiphonia</i> sp.	
<i>Sargassum fluitans</i>	
<i>Sargassum natans</i> (3)	
<i>Sargassum pteropleuron</i>	
<i>Sphacelaria tribuloides</i>	
<i>Spyridia filamentosa</i>	
Pteropods	5.5
<i>Cavolina</i> sp.	
<i>Creseis</i> sp.	
Crabs and crab larvae	4.9
Seagrasses	4.4
<i>Cymodocea manatorum</i> (3)	
Fishes	3.1
Unidentified crustaceans	2.9
Siphonophores	2.3
Tunicates	1.8
salps	
Gastropod larvae	1.3
Hermit crabs	1.2
Corals	0.6
<i>Colpophyllia</i> sp.	
Shrimps and shrimp larvae	0.6
Copepods	0.2
Barnacle larvae	0.2

<i>Lepas</i> sp.	
Foraminifera	0.1
Pelecypod larvae	0.1

Remarks.—*Melichthys niger*, sometimes classified as *M. radula*, is typically a species of outer reefs and clear water at depths of more than 50 feet; however, occasional individuals may be seen inshore in as little as 10 or 15 feet. Like *Canthidermis*, this fish is often seen well above the bottom. Both species are difficult to approach underwater. When sorely pressed, *M. niger* retires to the reef where it enters a small hole and wedges itself inside in typical balistid fashion. It is omnivorous but appears to feed more heavily on plants than animals. Most of the animals are planktonic. The algae in its diet may either be benthic or drifting at the surface. Individual fish may rise from the bottom in 70 feet or more of water to the surface to feed on *Sargassum* and fragments of seagrass. Some of the algae from the stomachs, such as *Calothrix* sp., *Dichothrix penicillata*, and *Nitophyllum* sp. are epiphytic on the floating *Sargassum*.

MONACANTHIDAE (Filefishes)

The filefishes are similar in dentition and general morphology to the triggerfishes, and their habits are also similar. They are not such strong swimmers, however, and thus are more closely associated with the bottom. Jordan & Evermann (1898) referred to the monacanthids as herbivorous shore fishes. Hiatt & Strasburg (1960) reported three species in the Marshall Islands to feed almost exclusively on corals. The West Indian species show a great diversity in their diet. Only one specimen was found with a small amount of coral in its stomach, although other benthic coelenterates were often encountered. Filefishes are usually seen as solitary individuals or in pairs.

<i>Alutera schoepfi</i> (Walbaum)	ORANGE FILEFISH
2 stations; 5 specimens: 345 to 350 mm SL.	
FOOD	VOLUME (%)
Seagrasses	67.0
<i>Cymodocea manatorum</i> (2)	
<i>Thalassia testudinum</i> (2)	
Algae	31.8
<i>Halimeda</i> sp. (2)	
Hermit crabs	0.6
<i>Clibanarius tricolor</i>	
Gastropods	0.6
<i>Columbella mercatoria</i>	

Remarks.—*Alutera schoepfi*, sometimes classified in the genus *Ceratacanthus*, is a rare species in the West Indies. The only specimens collected by the author in Puerto Rico were taken with a seine in a seagrass area in southwestern Puerto Rico. H. Smith (1907) reported that Linton examined

small specimens from North Carolina that had eaten bryozoans, shrimps, amphipods, and sea lettuce. He added that captive fish fed on algae. Beebe & Tee-Van (1928) found *Sargassum* in the stomach of one 17-inch specimen from Haiti. Hildebrand & Schroeder (1928) also listed only plant material from a 460-mm individual from Chesapeake Bay. Reid (1954) examined the stomach contents of juveniles from West Florida. He found undetermined vegetation, bryozoans, and copepods. The stomach contents of three of the Puerto Rican specimens taken at one station consisted of 36 per cent *Thalassia*, 31 per cent *Halimeda*, 19 per cent *Cymodocea*, 12 per cent algae epiphytic on the seagrasses, 1 per cent pagurids, and 1 per cent gastropods. The animals were small and may have been ingested incidentally with the plant material.

Alutera scripta (Osbeck)

SCRAWLED FILEFISH

8 stations; 8 specimens: 218 to 540 mm SL.

FOOD	VOLUME (%)
Hydrozoans	39.4
hydroids	
<i>Millepora alcicornis</i> (3)	
Algae	34.2
<i>Acanthophora spicifera</i>	
<i>Amphiroa fragilissima</i>	
<i>Caulerpa sertularioides</i>	
<i>Ceramium</i> sp.	
diatoms	
<i>Dictyosphaeria favulosa</i>	
<i>Dictyota bartayresii</i>	
<i>Dictyota divaricata</i>	
<i>Halimeda monile</i>	
<i>Halimeda opuntia</i> (2)	
<i>Hypnea spinella</i>	
<i>Laurencia obtusa</i>	
<i>Laurencia papillosa</i>	
<i>Valonia ventricosa</i>	
Gorgonians	12.6
<i>Eunicea calyculata</i>	
<i>Muricea</i> sp.	
<i>Plexaura flexuosa</i> (3)	
Seagrasses	9.0
<i>Thalassia testudinum</i> (2)	
Zoantharians	2.4
<i>Palythoa</i> sp.	
<i>Zoanthus</i> sp.	
<i>Zoanthus pulchellus</i>	
Tunicates	1.1

<i>Trididemnum savignii</i>	
Gastropods	0.6
<i>Anachis</i> sp.	
<i>Bailya</i> sp.	
<i>Cerithium</i> sp.	
<i>Epitonium</i> sp.	
Sponges	0.4
Shrimps	0.3
alpheid	

Remarks.—The scrawled filefish was also rarely encountered in the West Indies. It may be seen over reefs or beds of seagrass. The occurrence of large amounts of *Millepora alcicornis* in the gut of four specimens of this species was surprising in view of the powerful nematocysts of this so-called "stinging coral." In one 540-mm fish this branching hydrozoan constituted 97 per cent of the gut contents. The cylindrical pieces ranged from 5 to 48 mm in length. *A scripta* is also unusual in feeding on gorgonians. The gut of a 492-mm fish contained 34 sections of the fronds of *Plexaura flexuosa*, representing 52 per cent of the gut contents. This fish appears to feed with equal enthusiasm on plants; 95 per cent of the gut contents of a 508-mm individual consisted of *Thalassia* and ten different kinds of algae, particularly *Halimeda opuntia*.

Cantherhines macrocerus (Hollard) FALSE FILEFISH
7 stations; 10 specimens: 210 to 334 mm SL.

FOOD	VOLUME (%)
Sponges	86.5
Hydrozoans	5.0
hydroids (3)	
<i>Millepora alcicornis</i> (4)	
Gorgonians	4.8
<i>Gorgonia flabellum</i>	
Algae	2.9
<i>Amphiroa fragilissima</i>	
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp.	
<i>Dictyota divaricata</i> (2)	
<i>Dilophus guineensis</i> (2)	
<i>Enteromorpha flexuosa</i>	
<i>Gelidium pusillum</i>	
<i>Gracilaria debilis</i>	
<i>Liagora ceranoides</i>	
<i>Ulva lactuca</i>	
Holothurians	0.8

Remarks.—Although this reef-dwelling species is rare, it was more often noted as a pair than as separate individuals. Sponges clearly dominated the

food of all specimens, ranging from 58 to 91 per cent of the stomach contents. Much of the algae in the stomachs was found adhering to bite-sized chunks of sponge, indicating that the sponge and not the algae was the probable objective in feeding. Large cylindrical sections of *Millepora alcornis* were found in the stomach and intestines of four fish. In one 304-mm individual from Mona Island, they constituted 35 per cent of the total contents of the gut. The food-habit data of nine of the above ten specimens were reported on briefly by Randall (1964c) in a systematic review of the genus.

Cantherhines pullus (Ranzani)

ORANGE-SPOTTED FILEFISH

19 stations; 27 specimens: 46 to 170 mm SL; 1 empty.

FOOD	VOLUME (%)
Algae and organic detritus	42.8
<i>Amphiroa fragilissima</i> (4)	
<i>Bryopsis pennata</i>	
<i>Caulerpa vickersiae</i>	
<i>Ceramium</i> sp.	
<i>Ceramium byssoideum</i>	
<i>Cladophora</i> sp.	
<i>Coelothrix irregularis</i>	
diatoms	
<i>Dictyopteris delicatula</i>	
<i>Dictyota</i> sp. (2)	
<i>Dictyota divaricata</i>	
<i>Gelidium pusillum</i>	
<i>Gracilaria</i> sp.	
<i>Halimeda opuntia</i>	
<i>Jania rubens</i>	
<i>Liagora ceranoides</i>	
<i>Polysiphonia</i> sp.	
<i>Ulva</i> sp.	
Sponges	30.9
Tunicates	6.0
didemnids (7)	
<i>Trididemnum savignii</i> (3)	
Spermatophytes (including seagrasses)	4.6
<i>Halophila baillonis</i>	
<i>Thalassia testudinum</i> (4)	
Hydroids	3.1
<i>Sertularia</i> sp.	
Unidentified animal material	2.9
Bryozoans	2.3
Ophiuroids	1.9
<i>Ophiothrix</i> sp. (2)	

Gorgonians	1.7
Zoantharians (except corals)	1.7
<i>Zoanthus</i> sp.	
Unidentified crustaceans	0.8
Corals	0.7
Pelecypods	0.2
Gastropod eggs	0.1
Shrimps	0.1
alpheid	
Amphipods	0.1
Echinoids	0.1

Remarks.—*C. pullus* is the most common monacanthid fish of West Indian reefs. It is notably smaller than the preceding species. Beebe & Tee-Van (1928) reported the stomach contents of four specimens from Haiti as sponge spicules, minute crustaceans, and a portion of sea urchin. Randall (1964c) stated that this filefish "feeds on bottom growth, primarily sponge and algae, but stomachs often contain tunicates, bryozoans, and other sessile benthic invertebrates." His analysis was based on data from 20 of the 27 specimens listed above. All of the specimens examined had eaten at least some algae. The stomach contents of only two consisted entirely of algae. These two fish were juveniles, 46 and 65 mm in standard length. Sponges were found in all but two of the remaining specimens, the smallest of which was 98 mm in standard length.

Monacanthus ciliatus (Mitchill) FRINGED FILEFISH
6 stations; 14 specimens: 47 to 97 mm SL; 1 empty.

Food	VOLUME (%)
Algae and organic detritus	21.2
<i>Cladophora</i> sp.	
<i>Eudesme zosterae</i>	
<i>Lyngbya</i> sp.	
<i>Microcoleus</i> sp.	
Seagrasses	15.4
<i>Thalassia testudinum</i>	
Copepods	14.6
Shrimps and shrimp larvae	13.1
carideans	
Unidentified crustaceans	8.5
Amphipods	5.4
<i>Colomastix</i> sp.	
<i>Leucothoe</i> sp.	
Tanaids	4.6
Polychaetes	4.2
Stomatopod larvae	3.9
Isopods	3.1

Pelecypods	2.3
<i>Papyridea</i> sp.	
Unidentified animal material	1.9
Gastropods	1.5
Hydroids	0.3

Remarks.—As pointed out by Tabb & Manning (1961), this filefish is closely associated with vegetated areas, particularly *Thalassia*. Beebe & Tee-Van (1928) described the species as omnivorous and listed quartz pebbles, small crustaceans, algae and organic detritus from the alimentary tracts of specimens from Haiti. Reid (1954) collected more than 90 specimens from 13 to 60 mm in length at Cedar Key, Florida. He reported the food of individuals ranging from 39 to 55 mm in length as primarily copepods and mollusks. Shell debris from pelecypods and gastropods were found in most stomachs. Amphipods and ostracods were eaten by some of the fish. Springer & Woodburn (1960) also examined stomach contents of *M. ciliatus* from West Florida. They stated that their findings were essentially the same as Reid's.

Monacanthus tuckeri Bean SLENDER FILEFISH
4 stations; 4 specimens: 22 to 70 mm SL; 1 empty.

Food	VOLUME (%)
Unidentified organic material	41.3
Copepods	35.0
Gastropod larvae	6.7
Unidentified crustaceans	6.7
Tanaids	4.0
Isopods	3.3
Amphipods	3.0

Remarks.—*M. tuckeri* is the smallest West Indian filefish. It was occasionally seen on reefs, especially near fronds of gorgonians.

OSTRACIONTIDAE (Trunkfishes)

The trunkfishes are bottom-dwelling in various clear water habitats. They are slow swimming, as would be expected from the heavy external bony box with which they are encased and its limiting effect on body movement. Their food consists largely of sessile animals and plants. Some trunkfishes, at least, secrete a toxin from the mouth region and surface of the body. Possibly this toxic substance and the protective carapace give these fishes some immunity from predation. That this immunity is not complete is evident from finding *Lactophrys* in the stomachs of tiger sharks, a Nassau grouper, and a cobia (as juveniles in the latter two cases). Nevertheless, the occurrence of the larger species such as *Lactophrys trigonus*, *L. bicaudalis*, and *Acanthostracion quadricornis* in exposed areas such as seagrass beds and even sand flats suggests that these species enjoy some

freedom from predation. Other fishes that live as adults in the seagrasses are small, such as *Sparisoma radians* of the Scaridae and *Doratonotus* of the Labridae. The smallest of western Atlantic trunkfishes, *L. triqueter*, is primarily a reef-dweller.

Acanthostracion polygonius Poey

REEF COWFISH

3 stations; 4 specimens: 260 to 290 mm SL; 1 empty.

FOOD	VOLUME (%)
Tunicates	28.3
Unidentified animal material	25.0
Alcyonarians	23.3
Sponges	11.7
Shrimps	10.0
alpheid	
gnathophyllid	
<i>Synalpheus</i> sp.	
Gastropods	1.7
<i>Vasum muricatum</i>	

Remarks.—This species is the least common of the West Indian trunkfishes. It is usually seen on reefs. In most of the literature it has not been distinguished from *A. quadricornis*.

Acanthostracion quadricornis (Linnaeus)

COWFISH

6 stations; 6 specimens: 182 to 315 mm SL.

FOOD	VOLUME (%)
Sponges	30.7
Tunicates	18.3
Unidentified animal material	11.5
Zoantharians	10.8
<i>Bunodosoma granulifera</i>	
<i>Phyllactis flosculifera</i>	
<i>Zoanthus pulchellus</i>	
Hermit crabs	8.3
<i>Pagurus bonairensis</i>	
Algae	7.2
bluegreens	
<i>Halimeda opuntia</i>	
Gorgonians	4.2
<i>Muricea atlantica</i>	
Seagrasses	3.0
<i>Thalassia testudinum</i> (2)	
Scyphozoans	2.5
Polychaetes	1.8
Unidentified eggs	0.8
Pelecypods	0.3

Shrimps	0.3
Amphipods	0.3

Remarks.—Typically, *A. quadricornis* lives in seagrass beds. Beebe & Tee-Van (1928) reported the food of three Haitian examples, 72 to 260 mm in length, as algae, sponges, and the spines of a small club-spined sea urchin. Breder & Clark (1947) briefly discussed and diagrammed the visceral anatomy of this species. Reid (1954) wrote that the diet of specimens from West Florida ranging from 13 to 165 mm consisted of undetermined vegetation, algae, and pelecypods.

Lactophrys bicaudalis (Linnaeus) SPOTTED TRUNKFISH
12 stations; 12 specimens: 101 to 326 mm SL; 2 empty.

FOOD	VOLUME (%)
Tunicates	19.5
<i>Boltenia</i> sp.	
<i>Ecteinascidia turbinata</i>	
<i>Polycarpa insulsa</i>	
Holothurians	19.0
Ophiuroids	12.5
<i>Ophiocoma riisei</i>	
<i>Ophioderma rubicundum</i>	
Echinoids	10.0
<i>Diadema antillarum</i>	
Seagrasses	8.0
<i>Cymodocea manatorum</i>	
<i>Thalassia testudinum</i>	
Unidentified animal material	7.0
Algae	7.0
<i>Caulerpa racemosa</i>	
Polychaetes	6.0
Asteroids	6.0
<i>Oreaster reticulata</i>	
Crabs	4.0
Gastropods	1.0

Remarks.—Beebe & Tee-Van (1928) recorded the food of a 101-mm specimen from Haiti as algae and unidentifiable material. The only specimen of the above 12 which were examined that contained algae was a 166-mm individual; 70 per cent of its stomach contents consisted of *Caulerpa racemosa*. The largest specimen collected by the author contained only the orange-red tunicate *Polycarpa insulsa* (which R.H. Millar has indicated may be a synonym of *P. obtecta*). These tunicates were found from one end of the digestive tract to the other. Forty per cent of the gut contents of one 101-mm spotted trunkfish from Puerto Rico consisted of the viscera of a sea cucumber. There were no remains of the rest of the holothurian. One might speculate that the trunkfish harassed the sea

cucumber to such an extent (perhaps by biting it) that it eviscerated. The fish could then eat the viscera. Another trunkfish contained only holothurians, but these were small enough to be swallowed entire.

Lactophrys trigonus (Linnaeus)

TRUNKFISH

6 stations; 21 specimens: 109 to 395 mm SL.

FOOD	VOLUME (%)
Crabs	44.9
calappid (2)	
<i>Emerita</i> sp.	
majids (3)	
<i>Mithrax</i> sp.	
<i>Pitho</i> sp.	
portunids (2)	
xanthids (2)	
Pelecypods	10.1
<i>Atrina seminuda</i>	
<i>Codakia costata</i>	
<i>Musculus lateralis</i>	
<i>Tellina</i> sp.	
<i>Trachycardium muricatum</i>	
Polychaetes	8.6
glycerid	
pectinariid	
Echinoids	7.1
<i>Lytechinus variegatus</i> (2)	
Algae	4.9
<i>Acanthophora spicifera</i>	
<i>Centroceras clavulatum</i>	
<i>Ceramium</i> sp.	
<i>Ceramium byssoideum</i>	
<i>Dictyota</i> sp.	
<i>Halimeda</i> sp.	
<i>Halimeda monile</i>	
<i>Laurencia obtusa</i>	
<i>Spyridia filamentosa</i>	
Tunicates	4.5
<i>Microcosmus exasperatus</i>	
Seagrasses	3.0
<i>Cymodocea manatorum</i> (2)	
<i>Thalassia testudinum</i> (4)	
Unidentified animal material	2.9
Holothurians	2.6
<i>Holothuria arenicola</i>	
Asteroids	2.4
<i>Oreaster reticulata</i>	

Gastropods	2.1
<i>Acmaea pustulata</i>	
<i>Anachis sparsa</i>	
<i>Arene</i> sp.	
<i>Bulla</i> sp.	
<i>Haminoea elegans</i>	
<i>Nassarius</i> sp.	
<i>Olivella nivea</i>	
Amphipods	1.8
caprellid	
<i>Elasmopus</i> sp.	
Ophiuroids	1.6
<i>Ophioderma brevispinum</i>	
<i>Ophiothrix</i> sp.	
Unidentified worms	1.0
Unidentified eggs	1.0
Chitons	0.8
<i>Acanthochitona</i> sp.	
Hermit crabs	0.4
Shrimps	0.3
alpheid	

Remarks.—This species is also primarily a resident of the seagrass habitat. It appears to be the largest of the genus, attaining at least 18 inches in total length. It is principally a carnivore. In only one specimen did plant material exceed 5 per cent of the stomach contents. The food of this individual, 109 mm in standard length, was one-third algae. Seventy per cent of the stomach and gut contents of the largest specimen consisted of the echinoid *Lytechinus variegatus*. Inorganic sediment constituted 4 per cent of the stomach contents of a series of 8 adults which varied from 300 to 375 mm in standard length.

Lactophrys triqueter (Linnaeus) SMOOTH TRUNKFISH
13 stations; 17 specimens: 93 to 250 mm SL; 2 empty.

FOOD	VOLUME (%)
Polychaetes	29.2
onuphid	
syllid	
Sipunculids	15.7
<i>Aspidosiphon spinososcutatus</i>	
Crabs	9.0
majids (2)	
pinotherid	
<i>Upogebia</i> sp.	
Unidentified animal material	8.2
Shrimps	7.1

alpheids (2)	
carideans	
gnathophyllid	
Tunicates	6.7
<i>Ascidia nigra</i>	
<i>Trididemnum savignii</i>	
Sponges	6.0
Hemichordates	3.3
Gastropods	2.9
<i>Balcis intermedia</i>	
<i>Nitidella laevigata</i>	
<i>Trivia</i> sp.	
<i>Turbo castanea</i>	
Hermit crabs	2.3
<i>Paguristes</i> sp.	
<i>Spiropagurus</i> sp.	
Echinoids	2.3
<i>Lytechinus variegatus</i>	
Pelecypods	1.7
<i>Tellina</i> sp.	
Amphipods	1.3
Spermatophytes (including seagrasses)	1.2
<i>Halophila baillonis</i>	
<i>Thalassia testudinum</i>	
Unidentified worms	1.0
Algae	0.9
<i>Halimeda</i> sp.	
Chitons	0.7
Unidentified eggs	0.3
Ostracods	0.2

Remarks.—Beebe & Tee-Van (1928) recorded the food of *L. triqueter* from Haiti as comminuted vegetable matter. Longley & Hildebrand (1941) noted that this species is a reef fish which feeds on both algal and sand-covered bottoms. They found large quantities of sand and algae in the digestive tract of Tortugas specimens. Plant material represented a small percentage of the stomach-content material of West Indian specimens, however, and the highest percentage of inorganic sediment was 10. Longley observed that this species often blows a stream of water on to the bottom from a nearly vertical position, throwing up a cloud of sand. The author has recorded this mode of feeding on motion picture film. The localized current probably serves to expose worms and other invertebrates on which the fish feeds. Longley noticed that the wrasses *Halichoeres bivittatus* and *Thalassoma bifasciatum* often accompany the smooth trunkfish when it feeds in this manner; the wrasses probably capture animals that escape the trunkfish.

TETRAODONTIDAE (Puffers)

Sphaeroides spengleri (Bloch)

BANDTAIL PUFFER

17 stations; 31 specimens: 40 to 100 mm SL; 2 empty.

FOOD	VOLUME (%)
Crabs	20.4
majids (2)	
<i>Microphrys bicornutus</i>	
raninid	
Pelecypods	16.0
<i>Musculus lateralis</i>	
<i>Pinctada radiata</i> (2)	
Gastropods	9.6
<i>Bullata ovuliformis</i>	
Polychaetes	7.6
Echinoids	6.9
<i>Diadema antillarum</i>	
spatangoid	
Ophiuroids	6.0
<i>Ophiocoma riisei</i>	
<i>Ophioderma rubicundum</i>	
<i>Ophiothrix</i> sp.	
<i>Ophiothrix lineata</i>	
Amphipods	5.7
Shrimps	5.5
Spermatophytes (including seagrasses)	5.3
<i>Halophila baillonis</i>	
<i>Thalassia testudinum</i> (2)	
Algae and organic detritus	3.5
Hemichordates	3.4
Unidentified eggs	2.1
Unidentified animal material	2.1
Chitons	1.4
Isopods	1.1
Copepods	0.9
Tunicates	0.9
Hermit crabs	0.9
Fishes	0.7

Remarks.—This small puffer is not common but occurs in many different shallow-water habitats such as beds of seagrass or *Halophila*, sand or coral rubble, and reef. The jaws are armed with sharp beak-like plates with which it can crush crustaceans, small mollusks, etc. Plant material did not exceed 25 per cent of the stomach contents of any specimen; usually it was less than 5 per cent by volume of the contents.

CANTHIGASTERIDAE (Sharpnose Puffers)

Canthigaster rostrata (Bloch)

SHARPNOSE PUFFER

9 stations; 26 specimens: 36 to 88 mm SL.

FOOD	VOLUME (%)
Spermatophytes (including seagrasses)	16.1
<i>Cymodocea manatorum</i> (2)	
<i>Halophila baillonis</i> (2)	
Sponges	15.0
<i>Mycale</i> sp.	
Crabs	9.8
<i>Stenorhynchus seticornis</i>	
Unidentified animal material	8.2
Gastropods	7.8
alcidids	
<i>Alys</i> sp.	
<i>Alys riiseana</i>	
<i>Epitonium turritellulum</i>	
<i>Smaragdia viridis</i>	
Polychaetes	7.2
chaetopterid	
sabellids	
Pelecypods	5.2
<i>Crenella divaricata</i>	
<i>Musculus lateralis</i>	
<i>Tellina caribaea</i>	
Unidentified worms	4.6
Echinoids	3.8
<i>Diadema antillarum</i>	
Asteroids	3.8
<i>Astropecten</i> sp.	
Amphipods	3.1
<i>Corophium</i> sp.	
<i>Cymadusa filosa</i>	
<i>Photis</i> sp. (2)	
Shrimps	2.9
alpheid	
carideans	
Hydroids	2.7
<i>Pennaria</i> sp.	
Hermit crabs	2.3
Unidentified crustaceans	2.3
Algae and organic detritus	2.2
<i>Eucheuma echinocarpum</i>	
<i>Laurencia obtusa</i>	

Copepods	1.2
Pycnogonids	1.2
Tunicates	0.6

Trididemnum sp.

Remarks.—*Canthigaster rostrata* is a small omnivorous reef fish which may range into adjacent habitats such as seagrass beds. Plant material was clearly sought by the fish and not accidentally ingested; 78 per cent of the stomach contents of four fish from one station in Puerto Rico consisted of *Cymodocea manatorum*. The fish had nipped off the growing tips of the manatee grass. Twenty per cent of the stomach contents of another group of three fish was made up of the leaves of *Halophila*. The sabellid polychaete material from the stomachs of this puffer consisted only of tentacles. Hiatt & Strasburg (1960) reported the Indo-Pacific species *Canthigaster solandri* to be an omnivore; 81 per cent of its stomach contents was algae.

DIODONTIDAE (Porcupinefishes)

The porcupinefishes are bottom-dwelling and are usually found in reefs, although some species are often encountered over bottoms without cover. Like the related puffers, they are able to crush hard-shelled invertebrates with their powerful beak-like jaws. Because of their large size they can feed upon some of the larger mollusks, echinoids, and crustaceans which smaller fishes would be unable to eat.

Chilomycterus antennatus (Cuvier)
5 stations; 5 specimens: 65 to 216 mm SL.

BRIDLED BURRFISH

FOOD	VOLUME (%)
Gastropods	56.6
<i>Anachis</i> sp.	
<i>Arene</i> sp.	
<i>Astraea</i> sp.	
<i>Cerithium</i> sp.	
<i>Cerithium litteratum</i> (2)	
<i>Columbella mercatoria</i> (2)	
<i>Crassispira fuscescens</i>	
<i>Marginella</i> sp.	
<i>Mitrella lunata</i>	
<i>Modulus modiolus</i>	
<i>Nitidella ocellata</i>	
<i>Pusia</i> sp.	
<i>Pyramidella candida</i>	
<i>Smaragdia viridis</i> (2)	
<i>Tegula fasciata</i> (2)	
<i>Turbo</i> sp.	
<i>Turbo castanea</i> (2)	

Hermit crabs	21.4
diogenids	
pagurids	
Isopods	20.6
<i>Paracerceis caudata</i>	
Crabs	1.0
Shrimps	0.4

Remarks.—Beebe & Tee-Van (1928) recorded the food of two specimens 111 and 127 mm in length from Haiti as mollusks. The relatively large volume of isopods listed above was the result of inclusion of the stomach contents of the smallest specimen, 95 per cent of which consisted of isopods; 8 per cent of the food of an 88-mm burrfish was also isopod material.

Diodon holacanthus Linnaeus SPINY PUFFER
6 stations; 6 specimens: 97 to 380 mm SL; 2 empty.

FOOD	VOLUME (%)
Gastropods	67.7
<i>Acmaea leucopleura</i>	
<i>Astraea</i> sp.	
<i>Calliostoma</i> sp.	
<i>Cerithium algicola</i>	
<i>Cerithium litteratum</i>	
<i>Crassostrea rhizophorae</i>	
<i>Fissurella</i> sp.	
<i>Modulus modulus</i>	
muricid	
<i>Nassarius</i> sp.	
<i>Oliva reticularis</i>	
<i>Polinices lacteus</i>	
<i>Siphonaria</i> sp.	
<i>Tegula fasciata</i>	
<i>Turbo castanea</i> (2)	
Pelecypods	12.8
<i>Pinctada</i> sp.	
Echinoids	11.6
<i>Eucidaris tribuloides</i>	
Hermit crabs	4.2
Crabs	3.7
majids	

Diodon hystrix Linnaeus PORCUPINEFISH
38 stations; 42 specimens: 200 to 485 mm SL; 9 empty.

FOOD	VOLUME (%)
Echinoids	34.6
<i>Diadema antillarum</i>	

Echinometra sp. (3)
Echinometra lacunter (7)
Echinometra viridis
Eucidaris tribuloides (3)
Tripneustes esculentus

Gastropods

31.3

Acmaea sp.
Acmaea pustulata (2)
 acmaeid
Astraea sp.
Astraea caelata
Astraea longispina
Astraea tuber
Calliostoma sp.
Cerithium sp. (2)
Cerithium algicola
Columbella mercatoria (2)
Conus juliae
Fasciolaria tulipa
Fissurella sp. (2)
Fissurella barbadensis (5)
Fissurella nodosa
Hemitoma octoradiata
Littorina angulifera
Littorina ziczac
Melampus coffeus
Modulus modulus
Murex sp.
Murex pomum
Muricopsis hexagonus
Natica canrena
Nitidella sp.
Nitidella nitida
Oliva caribaeensis
Siphonaria sp.
Strombus sp.
Strombus gigas
Tegula sp. (3)
Tegula fasciata (3)
 turbinid
Turbo castanea (3)
Turritella sp.

Crabs

14.9

Arenaeus cribrarius
Calappa sp.

<i>Carpilius corallinus</i>	
grapsid	
majids (4)	
<i>Mithrax corphyæ</i>	
<i>Mithrax sculptus</i> (2)	
<i>Panopeus</i> sp. (2)	
<i>Percnon gibbesi</i>	
<i>Persephona punctata</i>	
<i>Portunus bahamensis</i>	
<i>Portunus ordwayi</i>	
xanthid	
Pelecypods	13.0
<i>Aequipecten gibbus</i>	
<i>Aequipecten lineolaris</i>	
<i>Antigona listeri</i>	
<i>Arca zebra</i> (2)	
<i>Brachidontes citrinus</i>	
<i>Chama</i> sp. (2)	
<i>Chione paphia</i>	
<i>Codakia pectinella</i>	
<i>Divaricella quadrisulcata</i>	
<i>Glycymeris pectinata</i>	
<i>Ostrea</i> sp. (2)	
<i>Pecten ziczac</i>	
<i>Pinctada</i> sp.	
<i>Pseudochama</i> sp.	
<i>Trachycardium magnum</i>	
Hermit crabs	5.9
<i>Calcinus sulcatus</i>	
<i>Calcinus tibicen</i>	
<i>Dardanus venosus</i>	
<i>Paguristes anomalus</i>	
<i>Paguristes grayi</i>	
<i>Paguristes wassi</i>	
<i>Pagurus miamensis</i>	
Unidentified animal material	0.3

Remarks.—This unique plectognath is the most frequently encountered species of the family on West Indian reefs, but it is not very common. Although primarily diurnal, it apparently feeds at least in part by night, for one collected in a trawl off Mayaguez, Puerto Rico at midnight was filled with pelecypods, gastropods, and the leucosid crab *Persephona punctata*. Beebe & Tee-Van (1928) listed the food of Haitian specimens as bottom debris, crustaceans, sponges, algae, etc. Two of the specimens examined by the author contained small amounts of seagrass, and one had ingested some algae (*Dictyota* sp.), but it seems likely that these plants

were not eaten intentionally. Hiatt & Strasburg (1960) found crushed gastropods, xanthid crab fragments, and foraminifera in a specimen 320 mm in standard length from the Marshall Islands. One would expect the spiny skin of this species and its ability to inflate itself to give it considerable freedom from predation. Beebe & Tee-Van (1928), however, noted that the following fishes fed upon this diodontid: *Haemulon plumieri*, *Peprilus paru*, *Lutjanus analis*, *L. griseus*, *L. synagris*, and *Tylosurus raphidoma* (= *crocodilus*). As a result of the present study the author is able to add *Galeocерdo cuvier*, *Epinephelus itajara*, *Lutjanus cyanopterus*, and *Sphyræna barracuda* to this list.

ANTENNARIIDAE (Frogfishes)

The frogfishes are well known for their sedentary nature and protective coloration, their "fishing" with a lure, and voracious habits. They are able to swallow prey of greater length than themselves. None of the species are abundant in the West Indies.

Antennarius multiocellatus (Cuvier & Valenciennes) LONGLURE FROGFISH
8 stations; 12 specimens: 31 to 99 mm SL; 7 empty.

FOOD	VOLUME (%)
Fishes	75.0
<i>Haemulon carbonarium</i>	
Crabs	12.5
<i>Percnon gibbesi</i>	
Stomatopods	12.5

Remarks.—This is the most common frogfish of rocky bottoms, coral reefs, pilings, etc. in the West Indies. Longley & Hildebrand (1941) reported a 50-mm clinid fish (*Malacotenus macropus*) from the stomach of a 60-mm specimen from Dry Tortugas, Florida. The specimen of *Haemulon carbonarium* listed above was taken from the stomach of a 97-mm longlure frogfish; the grunt measured 102 mm in standard length. F. Mago Leccia (personal communication) informed the author that the stomach of a 70-mm *A. multiocellatus* from Venezuela contained an 89-mm squirrelfish (*Holocentrus ascensionis*).

Antennarius scaber (Cuvier) SPLITLURE FROGFISH
6 stations; 11 specimens: 47 to 103 mm SL; 6 empty.

FOOD	VOLUME (%)
Fishes	100.0
<i>Diplectrum radiale</i>	
<i>Scorpaena inermis</i>	

Remarks.—This species may be found on a mud bottom as well as hard substratum. The specimen of *Scorpaena inermis* was taken from the stomach of a 63-mm frogfish; the scorpaenid measured 60 mm in standard length.

OGCOCEPHALIDAE (Batfishes)

Ogcocephalus nasutus (Cuvier & Valenciennes) SHORTNOSE BATFISH
6 stations; 9 specimens: 120 to 220 mm SL.

FOOD	VOLUME (%)
Crabs	47.5
<i>Emerita portoricensis</i>	
gonoplacids	
parthenopids	
Gastropods	25.9
<i>Haminoea elegans</i>	
<i>Mitrella nitens</i> (2)	
<i>Olivella</i> sp.	
<i>Sinum perspectrum</i>	
Algae	11.1
<i>Valonia utricularis</i>	
Fishes	8.8
tetraodontid	
Polychaetes	4.4
<i>Chloeia</i> sp.	
Pelecypods	1.7
<i>Corbula contracta</i>	
<i>Tellina</i> sp.	
Barnacles	0.6

Remarks.—This sluggish fish is not a reef species; however, it may occasionally be encountered on flat bottoms of sand, coral rubble, or seagrass near reefs. It also occurs in turbid water on mud bottoms. Reid (1954) examined 20 stomachs of specimens from West Florida. Large quantities of mollusks were found in 15, polychaetes in two, and three were empty. Those specimens which had ingested mollusks usually contained hundreds of a wide variety of small pelecypods and gastropods. Eight gastropods were identified to genus or species. Although this fish has a lure in the form of a small tentacle which is retractible into a cavity in the forehead, the above food habit data suggest that it is not used extensively in feeding.

DISCUSSION OF FOOD ORGANISMS

In the previous section of this report the food habits of 212 reef and inshore fishes have been analyzed from the standpoint of the species of fishes. Let us now examine the food organisms of these fishes by major groups in terms of the data of the present study.

PLANTS

Plant life, fundamental to all ecosystems, is not so clearly evident on coral reefs as in most other environments. When one views a well-developed reef, one is usually struck by the abundance of animals and the

paucity of plants. Depending on the type of reef, the corals, gorgonians, or sponges may dominate the scene. Tunicates, hydrozoans such as *Millepora*, soft corals, and zoantharians are also prominent among the sessile organisms, and fishes are the principal swimming forms. Plants may actually be hard to find, although there are reefs, of course, where benthic algae flourish. An ecologist contemplating a reef with an overwhelming preponderance of animal life may well ponder the plant support for the structure.

Six sources of plants are available as food to animals of coral reefs. These are benthic algae, boring algae, zooxanthellae, planktonic algae, plants drifting at the surface, and marine spermatophytes (primarily sea-grasses). The latter three sources are extralimital to the reef community. They enter the community via the zooplankton and fishes. Each is discussed separately below.

Benthic algae.—On reefs these algae grow primarily on rock and dead coral. They may, however, be seen on certain other dead invertebrates with hard parts such as mollusks, gorgonians, and *Millepora*. They even grow on the beaks of the larger parrotfishes (Winn & Bardach, 1960). All of the major groups of benthic algae, the bluegreens, greens, reds, browns, and diatoms, are well represented by many species in the West Indies. On reefs in which the sessile animals predominate, the larger species of algae are not often fully developed. Available substratum for algal growth may be so limited and the grazing activity of herbivorous fishes, gastropods, echinoids, and crustaceans so extensive that little more than a stubble of algae may be present. That algae on such reefs can actually be overgrazed has been demonstrated by Stephenson & Searles, 1960, and Randall, 1961a.

Three families of West Indian reef fishes are almost entirely herbivorous and depend on benthic algae as their primary source of food. These are the sea chubs (Kyphosidae), the parrotfishes (Scaridae), and the surgeonfishes (Acanthuridae). The blennies of the genera *Blennius*, *Entomacrodus*, and *Ophioblennius* are also herbivores. Algae form an important part of the diet (more than 20 per cent by volume) of the following omnivorous fishes: the porgies *Archosargus rhomboidalis* and *Diplodus caudimacula*, the damselfishes *Abudefduf taurus*, *Microspathodon chrysurus*, *Pomacentrus fuscus*, *P. leucostictus*, *P. planifrons*, and *P. variabilis*, the gobies *Coryphopterus glaucofraenum* and *Gnatholepis thompsoni* (and probably other gobiid species as well), the angelfish *Centropyge argi*, the triggerfish *Melichthys niger*, and the filefishes *Alutera schoepfi*, *A. scripta*, *Cantherhines pullus*, and *Monacanthus ciliatus*. Most of these fishes feed principally on filamentous algae. The large coarse algae such as *Sargassum* are eaten by only the larger herbivorous and omnivorous fishes such as the two species of *Kyphosus*, the two species of *Pomacanthus*, and *Melichthys niger*.

Boring algae.—These filamentous plants, sometimes called skeletal algae, grow beneath the surface of both living and dead coral. They account for

the green layer one sees upon breaking a piece of coral rock. In dead coral they include bluegreens, greens, and reds, whereas only greens are known from living corals. The importance of these algae to the nutrition of the coral and of the animals which feed by grazing on coral was not fully realized until the study of Odum & Odum (1955) in the Marshall Islands. In the Caribbean area the parrotfishes appear to be the only fishes which make use of boring algae; their feeding is directed almost entirely to dead coral rock. They are able to scrape into this layer with their strong beaks. As discussed in the section on the Scaridae, these fishes grind up the coral rock and coarse sediment with their pharyngeal mill along with the surface and boring algae. The ability to graze on low turf algae and boring algae probably gives the parrotfishes a noteworthy advantage over other herbivorous fishes when the algal food supply is scarce.

Zooxanthellae.—These algae grow in the tissues of corals and certain other coelenterates. They are eaten by the few fishes which feed directly on these coelenterates (see below).

Planktonic algae.—No fishes were detected which feed directly upon dinoflagellates or other planktonic algae. This microscopic food supply becomes available to the reef community principally through copepods and other herbivorous planktonic animals, which in turn form the prey of fishes, corals, and other plankton-feeding reef animals, and by filter-feeding sessile animals such as sponges, tunicates, and pelecypods.

Drifting plants.—These consist mostly of *Sargassum natans*, *S. fluitans*, fragments of the seagrasses *Thalassia testudinum* and *Cymodocea manatorum*, occasional masses of bluegreens mixed with diatoms, and epiphytes. The seagrasses are benthic, but pieces detached by wave action, decay, and the activity of animals may float to the surface and drift with wind and current. The kyphosids and *Melichthys niger* swim to the surface from depths at least as great as 70 feet in order to feed on the drifting weed. The ballyhoo (*Hemiramphus brasiliensis*), which lives at or near the surface, feeds heavily on the floating seagrass fragments. The drifting plants may become so heavily overgrown with calcareous epiphytes that they no longer float. The author has observed herbivorous reef fishes rise slightly above the bottom to feed on slowly sinking fragments of seagrass.

Marine spermatophytes.—Three species of seagrasses (*Thalassia testudinum*, *Cymodocea manatorum*, and *Ruppia maritima*) and *Halophila baillonis* have been found in the stomachs of West Indian fishes. Only *Thalassia* and *Cymodocea* are eaten in significant quantities, however. The most important fishes which graze on these four spermatophytes in the islands of the West Indies are the parrotfishes, the surgeonfishes, the sea bream *Archosargus rhomboidalis*, the filefishes *Alutera schoepfi*, *A. scripta*, and *Monacanthus ciliatus*, the puffers *Canthigaster rostrata* and *Sphaeroides*

spengleri, and the trunkfishes *Acanthostracion quadrirornis*, *Lactophrys bicaudalis*, and *L. trigonus*. In the latter four species seagrasses represented only 3 to 8 per cent of the gut contents of the specimens reported herein. The sea bream, the filefishes, the puffer *S. spengleri*, the trunkfishes, and the small parrotfish *Sparisoma radians* live as adults in the seagrass beds (although they may occur in adjacent habitats). The remaining parrotfishes and the surgeonfishes, when adults, are tied to reefs for shelter. Their grazing effect on seagrasses is therefore concentrated on the plants which grow near the reefs. When these fishes are numerous, they may eliminate the seagrasses completely in a zone 30 feet or more in width contiguous to reefs (Randall, 1965a).

ANIMALS

Protozoa.—A few fishes were found with foraminifera in their stomachs. In all except *Atherinomorus stipes*, these small organisms were probably not specifically selected as food by the fishes. They were mixed with sand and other bottom debris.

Sponges.—The pungent, disagreeable odor and spicules of most sponges would seem to protect them from predation; however, there are a few tropical marine fishes which feed extensively on them. Dawson, Aleem, & Halstead (1955) found sponges in the stomachs of the puffer *Arothron hispidus* and the butterflyfish *Chaetodon ephippium* at Palmyra, Central Pacific. Hiatt & Strasburg (1960) reported sponges as the principal item of food in the stomachs of two specimens of *Arothron mappa* and one of two specimens of the filefish *Amanes carolae* (= *Cantherhines dumerili*) in the Marshall Islands. Lowe (1962) listed sponges from the stomachs of the spadefish (*Chaetodipterus faber*) and the two angelfishes of the genus *Pomacanthus* from British Guiana. Bakus (1964) made observations on fishes which grazed sponges at Fanning Island. The stomachs of eight species of fishes from the West Indies contained more than 30 per cent sponges by volume. These fishes are as follows: *Chaetodipterus*, the two species of *Pomacanthus*, two of *Holacanthus*, two of *Cantherhines*, and *Acanthostracion quadrirornis*. In addition, 11.7 per cent of the stomach contents of *A. polygonius* consisted of sponge, as did 6 per cent of another trunkfish, *Lactophrys triqueter*; 15 per cent of the stomach contents of *Canthigaster rostrata* was sponge. Several other fishes had eaten traces of sponge, but hardly enough to be regarded as an intentional item of the diet. It is of interest to note that all of the sponge-feeding fishes are among the higher teleosts (the more specialized percomorphs and the plectognaths). By contrast, the sponges are the most primitive of multicellular animals.

Corals.—As pointed out by Hiatt & Strasburg (1960), coelenterates do not enter into the food web as intermediate forms in most marine communities. Probably their nematocysts discourage most potential predators. However, on reefs of the Marshall Islands in the tropical Pacific, where

luxuriant coral growth dominates the scene, certain fishes make substantial use of this food resource. Some chaetodonts and one monacanthid browse on the coral polyps; other species of *Chaetodon*, various scarids, one balistid, and another monacanthid graze directly on the living coral, scraping not only the soft polyps but also some of the individual corallites. Still other balistids, a monacanthid, several tetraodontids, and one species of *Canthigaster* bite off the tips of the branches of live coral.

In the West Indies, by contrast, corals are not utilized much for food by fishes. Only 10 species were found with corals in their stomachs, and in none of these did the coral volume exceed 2.3 per cent of the stomach contents (although a 5.1 per cent coelenterate polyp item from the stomachs of specimens of *Pomacentrus leucostictus* could have been from corals, at least in part). The fish whose stomach contained 2.3 per cent coral is the spadefish (*Chaetodipterus faber*). Only one specimen had eaten coral, however, and this consisted of a single piece of *Oculina diffusa*. Four damselfishes, notably *Microspathodon chrysurus*, grazed small amounts of living coral. Only two parrotfishes contained any coral tissues. In each of these fishes the corals represented only 0.2 per cent of the gut contents. Coral polyps were not found in the stomachs of butterflyfishes, although *Chaetodon capistratus* was observed to feed on coral polyps in an aquarium in Puerto Rico (personal communication, J. A. Rivero).

In view of the observations by Hiatt & Strasburg (1960) on the grazing of live corals by parrotfishes, as well as the algae on coral rock, a special effort was made to detect coral feeding by West Indian scarids. This was never observed, nor were their characteristic beak marks seen on live coral. A similar observation was made by J. H. Choat (personal communication; research for PhD thesis) who studied the ecology of reef flat fishes at Heron Island, Great Barrier Reef. He wrote, "I am regarding scarids as complete herbivores, as in this region at least, no parrotfish has been observed to feed selectively on living corals, conglomerate or otherwise." Instead they feed upon green, bluegreen, and red filamentous algae growing on calcareous surfaces. He noted that on occasions some individual parrotfishes grazed down to the living margins of corals, but both direct observation and subsequent examination of beak scars demonstrated that their grazing ceased fairly abruptly when the corals were encountered. Walter A. Starck, II (personal communication), on the other hand, has observed that parrotfishes occasionally scrape live coral in the Florida Keys. He added, "The amount of food taken in this way is insignificant compared to their normal grazing."

The greater utilization of corals by scarids in the Marshall Islands noted by Hiatt & Strasburg may be related to the high coral cover of the reefs there. When soft coral rock with a covering of algae is available as food, the parrotfishes may feed only on this. When such substratum is restricted

by the growth of corals, the fishes may then turn to the live corals for nutriment.

Zoantharians (other than corals).—Sixteen fishes (families Pomadasyidae, Pomacentridae, Ehippidae, Chaetodontidae, Balistidae, Monacanthidae, and Ostraciontidae) of the present study were found with the remains of zoanthideans and sea anemones in their stomachs. For six of the species these soft-bodied coelenterates represented more than 10 per cent of the volume of the stomach contents. The volume was in excess of 32 per cent for *Abudefduf saxatilis*, *Chaetodon capistratus*, and *C. striatus*. The great majority of this food material consisted of *Zoanthus*, large patches of which may be seen in many shallow reef areas. Only six fishes had eaten sea anemones.

Gorgonians.—Vast areas of hard substratum in the West Indies are dominated by a wide variety of gorgonians. In view of their abundance and the fleshy nature of many of the species, it was expected that a number of fishes would feed on them. This is not the case, however. Only 11 species were found with gorgonians in their stomachs, and in seven of these the amount was very small (less than 2 per cent). Only *Alutera scripta* had eaten more than 5 per cent by volume of gorgonians (12.6 per cent of the stomach contents of eight specimens of this filefish). In addition to possessing nematocysts and spicules, gorgonians may be strong-smelling. Possibly the odor serves to repel at least some fish predators.

Hydrozoans.—Hydroids are not abundant on West Indian reefs. They were found in nine species of fishes, although in less than 1 per cent of the volume of the stomach contents of five of them. The fish with the largest amount of hydroid in its stomach was *Chaetodon sedentarius* (11.7 per cent by volume). 3.1 per cent of the stomach contents of the filefish *Cantherhines pullus* was hydroid, as was 2.7 per cent of the stomach contents of *Canthigaster rostrata*. Another hydrozoan, the stinging coral *Millepora alcicornis*, was eaten by two filefishes, *Alutera scripta* (39.4 per cent of the stomach contents of eight specimens) and *Cantherhines macrocerus* (5 per cent). It is difficult to conceive of a less desirable food item than *Millepora*, in view of its powerful nematocysts and the high percentage of hard skeletal material. This hydrozoan is common on West Indian reefs. One might expect that any species of fish which could feed upon it and the numerous gorgonians would itself be abundant. However, *A. scripta* and *C. macrocerus* are among the least common of West Indian reef fishes.

Scyphozoans.—Only two species of fishes of this study fed upon jellyfishes, *Pomacentrus fuscus* and *Acanthostracion quadricornis*. Probably more feed occasionally on these soft-bodied animals, but jellyfishes are so rapidly digested that they would soon be undetectable in the fish stomachs.

Siphonophores.—Because of the distinctive pneumatophore of these planktonic coelenterates, which resists digestion, they are recognized with greater frequency in the stomachs of fishes than the preceding group. Ten fishes were found with siphonophores in their stomachs. The three most important species in this respect are *Clepticus parrae* (20 per cent by volume), *Inermia vittata* (16.7 per cent), and *Canthidermis sufflamen* (8.5 per cent). In addition, the spadefish (*Chaetodipterus*) is reported in the literature as feeding on *Physalia*.

Ctenophores.—The comb jellies are even more soft-bodied than the scyphozoans. Their transparent gelatinous tissue is soon rendered unidentifiable in fish stomachs. Only the yellowtail snapper (*Ocyurus*) was found with ctenophores in its stomach (2.7 per cent of total stomach contents). Also the author once observed tarpon (*Megalops*) from West Florida regurgitate ctenophores. Probably other West Indian fishes, particularly the larger plankton-feeders, feed at least occasionally on comb jellies. Frequently the unidentified animal matter in fish stomachs is gelatinous with little or no structure. In plankton feeders this is most likely jellyfish, salp, or ctenophore in origin.

Bryozoans.—The so-called moss animals are not among the more common benthic animals on West Indian reefs; therefore they were not expected to be prominent components of the stomach contents of fishes. They occurred in the stomach contents of six fishes, three of which are chaetodonts and two pomadasyids. Only the stomach contents of the filefish *Cantherhines pullus* contained more than 1 per cent by volume of bryozoans; its percentage was 2.3.

Sipunculids.—Twenty fishes of this study fed upon peanut worms. One is the stingray *Dasyatis americana* (20.6 per cent by volume sipunculids). Seven are pomadasyids of which *Haemulon album* is the principal species. Sipunculids were the foremost item of diet of 57 specimens of this grunt; these worms represented 25.2 per cent of its total stomach contents. Two of the sipunculid feeders are sparids, two are gerreids, two are mullids, one is the sand tilefish (*Malacanthus*), three are wrasses of the genus *Hali-choeres*, one is the queen triggerfish (*Balistes vetula*), and one the smooth trunkfish (*Lactophrys triqueter*) (15.7 per cent sipunculids). Several of these fishes have been observed to shove their snouts into the sand during feeding, at which time they would be most apt to encounter sipunculids. A number of fishes contained unidentified nonsegmented worms which were so digested that they could not be identified. These may have included nemerteans, priapuloids, echiuroids, hemichordates, and sipunculids.

Polychaetes.—These annelids are one of the most important food sources for West Indian reef fishes. Their segmented bodies, setae, and for some species horny jaws, distinctive opercula or crowns of tentacles enable one

to identify these worms in fish stomachs more often than most other soft-bodied animals. Sixty-two species of fishes, representing 24 families, were found with the remains of polychaetes in their stomachs. For seven of these fishes the polychaetes were the largest group of food organisms. These are listed as follows with the percentage of polychaetes that was found in their stomachs: *Chaetodon striatus* (58.7 per cent), *Halichoeres maculippina* (47.1 per cent), *Haemulon flavolineatum* (39.6 per cent), *Prognathodes aculeatus* (38.5 per cent), *Lactophrys triqueter* (29.2 per cent), *Pempheris schomburgki* (27.3 per cent), *Calamus calamus* (19.2 per cent), and *Mulloidichthys martinicus* (18.6 per cent). Other species in which polychaetes constituted more than 15 per cent of the stomach contents are the following: *Chaetodon capistratus* (31.4 per cent), *Haemulon aurolineatum* (31 per cent), *Harengula humeralis* (29 per cent), *Opisthonema oglinum* (22.4 per cent), *Eucinostomus argenteus* (19.5 per cent), *Haemulon chrysargyreum* (19.1 per cent), *Dasyatis americana* (17.3 per cent), *Priacanthus cruentatus* (16.8 per cent), and *Chaetodon sedentarius* (16.7 per cent). The polychaete material eaten by the spade-fish (*Chaetodipterus*), four damselfishes (*Abudefduf saxatilis* and *Pomacentrus* spp.), four butterflyfishes (*Prognathodes* and *Chaetodon* spp.), and the sharpnose puffer (*Canthigaster*) consisted entirely or in part of the tentacular crowns of sabellids, serpulids, and terebellids.

Chitons.—The distinctive mollusks of the class Amphineura were not common in fish stomachs. The occurrence of many of these animals in the intertidal zone, their tendency to hide beneath rocks, and their ability to adhere strongly to the substratum reduce the opportunity for predatory fishes to feed upon them. The stomachs of 24 fishes listed in the present report contained chitons. Six are labrids, five are pomadasysids, two are sparids, two are holocentrids, and two are ostraciontids. Chitons represented more than 5 per cent of the stomach contents of only the following six of these 24 fishes: *Labrisomus guppyi* (20 per cent, however only four specimens with food), *Holocentrus vexillarius* (10.3 per cent), *Haemulon carbonarium* (9.8 per cent), *Mulloidichthys martinicus* (7.9 per cent), *Haemulon flavolineatum* (5.7 per cent), and *Malacanthus plumieri* (5.7 per cent).

Gastropods (except pteropods).—Seventy-one species of fishes fed upon shelled gastropods, and ten on the larvae. In view of the protection afforded by the shell to these animals, 71 represents an unexpectedly high number of predators. The stomachs of 25 of these fishes contained more than 10 per cent by volume of gastropods. For the following 12 the percentage exceeded 20: *Diodon holacanthus* (67.7 per cent), *Chilomycterus antennatus* (56.6 per cent), *Aetobatis narinari* (53.4 per cent), *Calamus penna* (50 per cent), *Trachinotus falcatus* (47.8 per cent), *Lachnolaimus maximus* (39.7 per cent), *Hemipteronotus novacula* (38.5 per cent),

Diodon hystrix (31.3 per cent), *Ogcocephalus nasutus* (25.9 per cent), *Holocentrus vexillarius* (25.1 per cent), *Halichoeres poeyi* (21.3 per cent), and *Halichoeres radiatus* (21.3 per cent). Gastropods were the principal item of the diet of the first five of these fishes and *H. novacula*. Some of the fishes such as the holocentrids, mullids, and *Labrisomus* swallow the gastropods entire, and the shells are usually intact. Others such as *Diodon*, *Calamus*, and sting rays crush the shells in their jaws. Many such as the pomadasyids, labrids, and *Trachinotus* utilize their paryngeal teeth to render the mollusk shells into fragments. A few of the serranids and lutjanids had only the soft parts of gastropods in their stomachs. Since these fishes lack crushing dentition, it seems likely that they stole their prey from other predators after the soft parts were exposed.

Only one specimen of one species of fish, *Abudefduf saxatilis*, contained recognizable remains of opisthobranchs in its stomach. This fish had eaten three green and orange nudibranchs (*Tridachia crispata*) which accounted for the majority of its stomach contents and 5.3 per cent of the total stomach-content volume of the 33 specimens of this damselfish which contained food. Possibly nudibranchs occur more frequently in fish stomachs than would be indicated by these data. Like the jellyfishes previously discussed, they could not be expected to resist digestion long. On the other hand, nudibranchs are known, in general, to have noxious qualities which probably serve to discourage predators. Usually they are brightly hued and conspicuous; their color patterns may serve the purpose of warning coloration.

Pteropods.—These small pelagic gastropods were found in the stomachs of 13 species of fishes, most of which are plankton-feeders. Four are carangids, two are clupeids, and two are balistids. The four species with the highest percentage of pteropods in their stomachs are as follows: *Decapterus macarellus* (96.5 per cent; only two specimens), *Hemiramphus balao* (31.4 per cent), *Canthidermis sufflamen* (21.2 per cent), and *Clepticus parrae* (19.2 per cent). The bulk of the diet of one 12-pound horse-eye jack (*Caranx latus*) consisted of *Cavolina longirostris* 3 to 4 mm in length, which gave an overall percentage of pteropods to this species of 8.4. Evidently pteropods often occur as swarms in the plankton, thus an occasional fish will have a large number in its stomach.

Scaphopods.—Ten fishes were found with tooth shells in their digestive tracts, but all but one contained fewer than 1 per cent by volume of these small mollusks. The exception is the razorfish *Hemipteronotus novacula* whose stomachs contained 5.6 per cent scaphopods by volume.

Pelecypods.—Forty-four West Indian fishes of this study fed upon pelecypods, and two upon the larvae. For 17, these mollusks represented 10 per cent or more of the stomach contents. The stomachs of the following

six of the 17 contained more than 20 per cent by volume pelecypods: *Aetobatis narinari* (46.6 per cent), *Lachnolaimus maximus* (42.6 per cent and the main item of diet), *Hemipteronotus novacula* (27.9 per cent), *Halichoeres radiatus* (25.1 per cent and also the principal food item), *Halichoeres maculipinna* (24 per cent), and *Gerres cinereus* (23 per cent). The remarks above on the mode of feeding by fishes on gastropods apply also to pelecypods, in general.

Cephalopods.—Twenty-nine fishes fed upon octopuses and squids, only 10 of which were included among those which had eaten gastropods and pelecypods. The fishes which did not feed on the shelled mollusks are, for the most part, piscivorous types such as serranids, sphyraenids, and scombrids. Five of the 28 cephalopod-feeding fishes are lutjanids, four are pomadasyids, four are serranids, three are scombrids, two are priacanthids, and two are sphyraenids. Only five species, however, contained more than 10 per cent by volume cephalopod remains in their stomachs: *Ophichthus ophis* (50 per cent), *Euthynnus alletteratus* (36.6 per cent), *Sphyraena picudilla* (17.9 per cent), *Gymnothorax vicinus* (12.5 per cent), and *Ginglymostoma cirratum* (11 per cent). Relatively few specimens of all of these fishes were examined. Larger samples would probably reveal a lower percentage of cephalopods in the diet for most. Octopuses and squids are not abundant on West Indian reefs. The only squid observed in the vicinity of reefs by day is *Sepiateuthis sepioidea*. The squids in the stomachs of *Euthynnus* and *Scomberomorus* were mostly offshore pelagic species.

Crustaceans.—These arthropods are the most important food animals of the fishes of this report, both for plankton feeders and bottom feeders. They represent the dominant food class of 90 of these fishes. Apart from the unidentified crustaceans (which are listed from the stomachs of 74 species of fishes) and the Nebaliacea and the Euphausiacea (each found in only one species), the group is summarized briefly in the following 13 categories.

Copepods: Forty-seven West Indian fishes fed upon free-living copepods. For the following 17 of these, the percentage by volume of copepods in the stomachs exceeded 20: *Serranus tortugarum* (92 per cent; two specimens); *Allanetta harringtonensis* (89.2 per cent), *Chromis multilineata* (87.8 per cent), *Opisthognathus aurifrons* (85 per cent), *Inermia vittata* (76.7 per cent), *Jenkinsia lamprotaenia* (74 per cent), *Taenioconger halis* (66.3 per cent), *Hemipteronotus splendens* (60.8 per cent), *Decapterus punctatus* (60 per cent), *Harengula clupeiola* (55 per cent), *Chromis cyanea* (52.4 per cent), *Amblycirrhitus pinos* (45.8 per cent), *Clepticus parrae* (43.6 per cent), *Monacanthus tuckeri* (35 per cent), *Atherinomoropus stipes* (30 per cent), *Opisthonema oglinum* (26.6 per cent), and *Remora remora* (22 per cent). For all except *A. stipes* copepods were the

main item of diet. The species of copepods most commonly identified from fish stomachs were *Undinula vulgaris* and *Candacia pachydactyla*. A few calagoid copepods were found in the parasite-picking fishes.

Ostracods: Twenty fishes of this study fed upon ostracods. In only the following five did the percentage by volume of this crustacean subclass in the stomach contents equal or exceed 2: *Coryphopterus glaucofraenum* (12 per cent), *Decapterus punctatus* (8.5 per cent), *Halichoeres maculipinna* (5.9 per cent), *Taenioconger halis* (3.8 per cent), and *Gnatholepis thompsoni* (2 per cent).

Barnacles: Only two fishes were found with the remains of barnacles, including shells, in their stomachs, and the volumes were small. This is not surprising in view of the stout, fixed shell of the Cirripedia and the relative low number of individuals of this class on West Indian reefs. One of the two fishes is the large wrasse *Lachnolaimus maximus* (0.5 per cent barnacles by volume) and the other the batfish *Ogcocephalus nasutus* (0.6 per cent). In the former the barnacles were crushed. In one 145-mm specimen of the latter fish, which lacks crushing dentition, there was a single intact barnacle. Seven other fishes fed upon the thoracic appendages and/or the larvae of barnacles. The highest volume (10 per cent) was found in the silversides *Atherinomorus stipes*. This is a result of including one sample of three fish collected at Isla Venados, Venezuela, 30 per cent of the stomach contents of which consisted of barnacle larvae and a few appendages. The next highest volume of barnacle remains, 3 per cent barnacle appendages, was found in the sergeant major (*Abudefduf saxatilis*). This was due to the inclusion of a sample of these damselfish taken from beneath a pier off Crashboat Basin, Aguadilla, Puerto Rico. The fish evidently had been feeding by nipping off the thoracic appendages of the barnacles on the pilings. As pointed out by Newman (1960), the number of species of barnacles in tropic seas is high, but the number of individuals, particularly on coral reefs, is low. He attributes the paucity of barnacles on reefs to fishes which feed by rasping algae and other organisms on the limestone surface and remove substantial amounts of the substratum. The freshly-settled larval stages of barnacles and young individuals would be consumed even though they may not have been specifically sought by the feeding fishes. The same effect, of course, would be expected for the juvenile stages of other sessile animals.

Mysids: Swarms of opossum shrimps are frequently seen just off the bottom in and about Caribbean reefs. Often these little shrimps occur in the immediate vicinity of *Diadema antillarum* and move to a position among the spines of this formidable echinoid with the approach of danger (Randall, Schroeder, & Starck, 1964: Fig. 3). In spite of their apparent abundance and availability (as well as the ease with which they can be identified from their conspicuous statocysts even when partially digested), mysids were found in the stomachs of only 13 fishes. In only the following

six of these did the percentage by volume exceed 3: *Myripristis jacobus* (11.2 per cent), *Hypoplectrus puella* (8.9 per cent), *Priacanthus cruentatus* (7.8 per cent), *Hypoplectrus nigricans* (5.9 per cent), *Opisthognathus maxilloso* (5.4 per cent), and *Prognathodes aculeatus* (4.7 per cent). The long snout of the latter chaetodont is probably useful in feeding upon small crustaceans in crevices in reefs or among echinoid spines.

Tanais: The order Tanaidacea consists of small, slender, bottom-dwelling crustaceans allied to the isopods and cumaceans. They occurred in the stomachs of 14 fishes. In only the following four was the volume in the stomachs greater than 3 per cent: *Eucinostomus argenteus* (5.9 per cent), *Monacanthus ciliatus* (4.6 per cent), and *M. tuckeri* (4 per cent).

Isopods: Isopods were identified among the stomach contents of 43 fishes. In the following 12 the volume exceeded 5 per cent: *Gobiosoma* sp. (100 per cent, one specimen only), *Opisthognathus maxilloso* (28.6 per cent), *Chilomycterus antennatus* (20.6 per cent), *Echeneis naucrates* (20 per cent), *Remora remora* (20 per cent), *Odontoscion dentex* (17.8 per cent), *Opisthognathus whitehurstii* (11 per cent), *Pomacentrus variabilis* (10 per cent), *Anisotremus virginicus* (8.2 per cent), *Thalassoma bifasciatum* (6 per cent), *Mulloidichthys martinicus* (5.7 per cent), *Holocentrus vexillarius* (5.7 per cent), and *Apogon conklini* (5.3 per cent). The isopods from the stomachs of *Gobiosoma* sp. and *Thalassoma bifasciatum* were larval gnathiids which were probably removed by these "cleaning" fishes from host fishes.

Amphipods: These small crustaceans were found in 50 species of fishes considered in this report. Some such as the hyperiids were constituents of the food of plankton-feeding fishes. Most, however, are benthic types and appear in the stomach contents of bottom-feeding fishes. Amphipods represent more than 5 per cent by volume of the food of the following 13 species: *Eucinostomus argenteus* (41.8 per cent), *Apogon conklini* (18.8 per cent), *Bothus ocellatus* (15 per cent), *Chaetodon sedentarius* (13.3 per cent), *Hemipteronotus splendens* (12.5 per cent), *Remora remora* (8 per cent), *Haemulon parra* (7.1 per cent), *Canthidermis sufflamen* (6 per cent), *Haemulon chrysargyreum* (5.7 per cent), *Sphaeroides spengleri* (5.7 per cent), *Monacanthus ciliatus* (5.4 per cent), *Labrisomus nuchipinnis* (5.3 per cent), and *Halichoeres maculipinna* (5.1 per cent).

Stomatopods: Mantis shrimps occurred in the stomachs of 44 fishes, and their larvae in another 11 species. Because of their larger size they tend to constitute a higher percentage of the volume of the stomach contents than the groups of crustaceans previously discussed. More than 5 per cent of the volume of the stomach contents of 21 fishes consisted of stomatopods. For the following 11 the percentage was greater than 10: *Lutjanus synagris* (50 per cent, only two specimens), *Dactylopterus volitans* (19.3 per cent), *Myripristis jacobus* (17.4 per cent, all late

larval stomatopods), *Pempheris schomburgki* (16.7 per cent, also as larvae), *Epinephelus guttatus* (16.6 per cent), *Malacanthus plumieri* (15 per cent), *Scorpaena brasiliensis* (14.3 per cent), *Antennarius multiocellatus* (12.5 per cent), *Myrichthys oculatus* (12.5 per cent), *Cephalopholis fulva* (12.4 per cent), and *Bothus lunatus* (11.4 per cent). The stomatopod most commonly encountered in the fish stomachs was *Gonodactylus oerstedii* which displays a number of different color forms.

Shrimps: This category includes the decapod shrimps but not lobsters or anomurans. 115 species of fishes fed on shrimps and shrimp larvae; for 51 of these the percentage of shrimps in the stomachs exceeded 10; for 31 it exceeded 20, and for the following 22 it was in excess of 30: *Opisthognathus macrognathus* (100 per cent, one specimen), *Scorpaena inermis* (85.3 per cent), *Scorpaena grandicornis* (75 per cent), *Equetus acuminatus* (73.2 per cent), *Serranus tigrinus* (71.9 per cent), *Holocentrus coruscus* (70 per cent), *Scorpaenodes caribaeus* (65.9 per cent), *Equetus lanceolatus* (62.5 per cent), *Opisthognathus whitehurstii* (54 per cent), *Holocentrus marianus* (51.7 per cent), *Hypoplectrus chlorurus* (51.2 per cent), *H. puella* (51 per cent), *Apogon maculatus* (49 per cent), *Hypoplectrus aberrans* (43.8 per cent), *Odontoscion dentex* (38 per cent), *Haemulon parra* (37.6 per cent), *Scorpaena brasiliensis* (35.7 per cent), *Atherinomorus stipes* (35.6 per cent), *Priacanthus arenatus* (34.7 per cent), *Rypticus saponaceus* (34.2 per cent), *Haemulon aurolineatum* (33.6 per cent), and *Myripristis jacobus* (30.3 per cent). More shrimps from fish stomachs were identified as alpheidids than any other group of shrimps. This was due, at least in part to the distinctive snapping chela of these carideans which was often intact in a stomach even when the rest of the shrimp was digested. At times only a single chela was present, indicating autotomy.

Crabs: Anomurans such as porcellanids and hippids are included under this heading, along with the more numerous brachyuran crabs, but the hermit crabs are considered in a separate category below. A total of 114 species of this study had eaten crabs and crab larvae. In 68 of these fishes the percentage by volume of crabs in the stomachs exceeded 10; in 46 it exceeded 20, and in the following 25 it exceeded 30: *Echidna catenata* (96.3 per cent), *Myrichthys acuminatus* (86 per cent), *Alphestes afer* (77 per cent), *Holocentrus ascensionis* (73.3 per cent), *Labrisomus guppyi* (72.5 per cent), *Epinephelus adscensionis* (66.7 per cent), *Dactylopterus volitans* (61.7 per cent), *Myrichthys oculatus* (61.2 per cent), *Holocentrus rufus* (56.9 per cent), *Lutjanus synagris* (50 per cent), *Plectrypops retrospinis* (50 per cent), *Calamus penna* (50 per cent), *Ogcocephalus nasutus* (47.5 per cent), *Lactophrys trigonus* (44.9 per cent), *Lutjanus analis* (44.4 per cent), *L. griseus* (40 per cent), *Epinephelus guttatus* (39.5 per cent), *Haemulon carbonarium* (38.3 per cent), *Equetus punctatus* (34.4 per cent), *Haemulon parra* (33.3 per cent), *Epinephelus morio* (33.3 per

cent), *Bodianus rufus* (32.4 per cent), *Scorpaena plumieri* (31.3 per cent), *Holocentrus marianus* (30.6 per cent), and *Pseudupeneus maculatus* (30.2 per cent). Not infrequently, a single chela was the only remains of a crab found in the stomach of a fish.

Spiny lobsters: Only five fishes were found with the remains of lobsters in their stomachs, and one of these contained only the larval stage. The most important lobster predator is the jewfish (*Epinephelus itajara*). As many as five adult spiny lobsters (*Panulirus argus*) have been taken from a single fish. 45.6 per cent of the stomach contents of nine specimens of this large grouper consisted of *P. argus*. Second in importance, according to the data in the present report, is the dog snapper (*Lutjanus jocu*); 6.6 per cent of the stomach contents of 56 specimens consisted of lobsters, principally *P. guttatus*. One fish had eaten only parts of the antennae of this small species. The same is true for the Nassau grouper (*Epinephelus striatus*), 3.5 per cent of the stomach contents of which consisted of both species of lobsters.

Scyllarid lobsters: Slipper lobsters were fed upon by nine species of fishes, four of which had eaten just the late larval stage. Only the jewfish (*Epinephelus itajara*) contained more than 2 per cent volume of these highly-prized crustaceans; 23.3 per cent of the stomach contents of nine of these groupers consisted of scyllarids (primarily, if not entirely, *Scyllarides aequinoctialis*).

Hermit crabs: Thirty-eight fishes fed upon hermit crabs; four of these fishes ate only the larvae. Not unexpectedly, the fishes which fed on the adults were largely gastropod feeders as well. The 12 most important pagurid predators are as follows: *Chilomycterus antennatus* (21.4 per cent), *Calamus calamus* (13.4 per cent), *Equetus punctatus* (11.3 per cent), *Acanthostracion quadricornis* (8.3 per cent), *Calamus pennatula* (8 per cent), *Trachinotus falcatus* (6.1 per cent), *Diodon hystrix* (5.9 per cent), *Lachnolaimus maximus* (4.9 per cent), *Halichoeres radiatus* (4.5 per cent), and *Diodon holacanthus* (4.2 per cent). Most of the hermit crabs and their gastropod shells were found crushed in the stomachs of the diodontids, sparids, and labrids.

Echinoids.—The sea urchins and heart urchins represent another group which would seem, *a priori*, to be relatively free from attack by fishes. Once again, however, a surprising number of predators were demonstrated in the present study to feed on seemingly unappetizing prey. Thirty-four fishes were found with echinoid remains in their stomachs. Seven are pomadasyids, three are sparids, seven are labrids, and ten are plectognaths. The following 16 contained more than 10 per cent echinoids by volume: *Haemulon macrostomum* (86.8 per cent), *Balistes vetula* (72.8 per cent), *Anisotremus surinamensis* (53.5 per cent), *Calamus bajonado* (45.2 per cent), *Diodon hystrix* (34.6 per cent), *Canthidermis sufflamen* (25 per

cent), *Trachinotus falcatus* (25 per cent), *Haemulon album* (19.9 per cent), *Halichoeres radiatus* (19.9 per cent), *H. bivittatus* (17.9 per cent), *Bodianus rufus* (14.4 per cent), *Haemulon plumieri* (12.4 per cent), *Diodon holacanthus* (11.6 per cent), *Prognathodes aculeatus* (11.4 per cent), *Haemulon carbonarium* (10.9 per cent), and *Labrisomus nuchipinnis* (10.5 per cent). Echinoids represented the principal food of the first six of these fishes. Most of the fishes fed more heavily as large adults upon echinoids than as juveniles or subadults. Some of the wrasses such as the smaller *Halichoeres* and *Thalassoma bifasciatum* have been observed to feed on scraps of echinoids after the test had been broken by larger fishes such as the queen triggerfish.

Ophiuroids.—Brittlestars occurred in the stomachs of 33 fishes; the following 10 contained more than 10 per cent of these echinoderms: *Labrisomus kalisherae* (100 per cent, one specimen), *Malacanthus plumieri* (21.9 per cent), *Bodianus rufus* (19.5 per cent), *Anisotremus virginicus* (16.5 per cent), *Halichoeres garnoti* (15.5 per cent), *Calamus calamus* (15.5 per cent), *C. pennatula* (14.2 per cent), *Lactophrys bicaudalis* (12.5 per cent), *Labrisomus nuchipinnis* (12.3 per cent), and *Halichoeres poeyi* (10.2 per cent). Ophiuroids were the main food of *M. plumieri* and *A. virginicus*. *Ophiothrix* was the most common genus identified from the stomach contents. Part of the reason for this is the distinctive glassy spinules found on the arms. No matter how crushed and digested a brittlestar of this genus might be, its identity from the spinules is assured.

Asteroids.—Starfishes occurred in the stomachs of only five fishes. The largest amount, 6 per cent by volume, was found in the stomach of the trunkfish *Lactophrys bicaudalis*. This trunkfish had fed on *Oreaster reticulata*, a seagrass-dweller, as did *L. trigonus* and *Balistes vetula*. Only plecognaths such as these three fishes, with their cutting dentition and powerful jaws, would be expected to feed directly on this large, tough asteroid.

Holothurians.—Eight fishes utilized sea cucumbers as food, although only one, *Lactophrys bicaudalis*, consumed more than 4 per cent by volume. The stomach contents of ten specimens of this ostraciontid were 19 per cent holothurian in origin. As mentioned in the species account of this fish, 40 per cent of the food of one fish consisted only of the viscera of a large sea cucumber. It is possible that the fish secured this meal by sufficiently aggravating the sea cucumber to eviscerate. Another of these trunkfish had eaten several small holothurians which were largely intact.

Hemichordates.—Acorn worms were identified from the stomachs of only six species of fishes: *Haemulon album* (3.5 per cent), *Sphaeroides spengleri* (3.4 per cent), *H. plumieri* (3.3 per cent), *Lactophrys triqueter* (3.3 per cent), *Dasyatis americana* (2.3 per cent), and *Gerres cinereus* (1.9 per cent). All of these fishes feed in part on subsurface, sand-dwelling

invertebrates. The actual number of fishes feeding on these worms is probably higher, and the percentage volume in the stomachs is also probably greater than indicated. Hemichordates are soft-bodied and undoubtedly digested rapidly by fishes.

Tunicates.—Twenty-eight fishes were found with tunicates in their stomachs. Twelve of these fishes fed upon appendicularians and salps. The four whose stomach contained more than 10 per cent pelagic tunicates are as follows: *Chromis cyanea* (33.9 per cent), *Taenioconger halis* (18.6 per cent), *Chaetodipterus faber* (12.6 per cent), and *Paranthias furcifer* (12.2 per cent). Sixteen fishes fed in part on benthic tunicates. The three most important of these are the trunkfishes *Acanthostracion polygonius* (28.3 per cent, and the main food), *Lactophrys bicaudalis* (19.5 per cent, and also the principal food), and *Acanthostracion quadricornis* (18.3 per cent).

Fishes.—The stomachs of a total of 112 West Indian fishes contained the remains of fishes and fish larvae, and another 14 had fed on fish eggs. Fish represented 50 per cent or more of the stomach contents of 48 species of fishes of the present study, and it was the principal food of another ten species. These fishes are as follows: five sharks, *Dasyatis americana*, *Megaloops atlantica*, *Harengula humeralis*, three synodontids, two muraenids, *Ophichthus ophis*, four belonids, *Hemiramphus balao*, *Fistularia tabacaria*, *Aulostomus maculatus*, two sphyraenids, nine serranids, two priacanthids, four lutjanids, *Rypticus saponaceus*, *Rachycentron canadum* (one specimen), *Echeneis naucrates*, nine carangids, three scombrids, two bothids, *Scorpaena plumieri*, and two antennariids. Due to the emphasis placed in this study on the larger fishes and particularly those of value in sportfishing (see Introduction), a higher percentage of the piscivorous species is represented than other trophic groups. Several small open-water fishes such as *Atherinomorous stipes*, *Inermia vittata*, and *Selar crumenophthalmus* were found with fish scales (principally clupeoid) in their stomachs, but with no other fish remains. Probably these scales were eaten after they were detached from small schooling fishes as a result of the activity of predaceous species.

LITERATURE CITED

ANDERSON, W. W., J. W. GEHRINGER, AND E. COHEN

1956a. Physical oceanographic, biological and chemical data, South Atlantic Coast of the United States, M/V Theodore N. Gill, Cruise 1. Fish & Wildl. Serv., Spec. Sci. Rept., 178: 160 pp.

1956b. Physical oceanographic, biological and chemical data, South Atlantic Coast of the United States, M/V Theodore N. Gill, Cruise 2. Fish & Wildl. Serv., Spec. Sci. Rept., 198: 270 pp.

BABCOCK, L. L.

1951. The Tarpon. Ed. 5, 157 pp., privately printed.

BAILEY, R. M., et al.

1960. A list of common and scientific names of fishes from the United States and Canada. Amer. Fisher. Soc., Spec. Pub. no. 2: 102 pp.

BAKUS, G. J.

1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Found., Occ. Pap. no. 27: 29 pp., 1 fig.

BARDACH, J. E.

1959. The summer standing crop of fish on a shallow Bermuda reef. *Limnol & Oceanogr.*, 4 (1): 77-85, 2 figs.
1961. Transport of calcareous fragments by reef fishes. *Science*, 133 (3446): 98-99.

BARDACH, J. E. AND D. W. MENZEL

1957. Field and laboratory observations on the growth of some Bermuda reef fisheries. *Proc. Gulf & Carib. Fisher. Inst., Ninth Ann. Sess.*: 106-112, 1 fig.

BARDACH, J. E., H. E. WINN, AND D. W. MENZEL

1959. The role of the senses in the feeding of the nocturnal reef predators *Gymnothorax moringa* and *G. vicinus*. *Copeia*, no. 2: 133-139, 3 figs.

BEEBE, W.

1928. *Beneath Tropic Seas*. xiii + 234 pp., 38 illustr., Halcyon House, New York.

BEEBE, W. AND J. TEE-VAN

1928. The fishes of Port-au-Prince Bay, Haiti with a summary of the known species of marine fish of the island of Haiti and Santo Domingo. *Zoologica*, 10(1): 1-279, 1 pl., 268 text-figs.

BIGELOW, H. B. AND W. C. SCHROEDER

1948. Fishes of the Western North Atlantic. Pt. 1. Sharks. *Mem. Sears Found. Mar. Res.*, no. 1: 59-576, 101 figs.
1953. Fishes of the Western North Atlantic. Pt. 2. *Mem. Sears Found. Mar. Res.*, no. 1, xv + 514 pp., 117 figs.

BIGELOW, H. B., et al

1963. Fishes of the western North Atlantic, Pt. 3. *Mem. Sears Found. Mar. Res.*, no. 1, xxi + 639 pp., 139 figs.

BÖHLKE, J. E. AND J. E. RANDALL

1963. The fishes of the Western Atlantic serranoid genus *Gramma*. *Proc. Acad. Nat. Sci. Phila.*, 115 (2): 33-52, 3 figs.

BÖHLKE, J. E. AND L. P. THOMAS

1961. Notes on the West Atlantic jawfishes, *Opisthognathus aurifrons*, *O. lonchurus* and *Gnathypops bermudezi*. *Bull. Mar. Sci. Gulf & Carib.*, 11 (4): 503-516, 3 figs.

BREDER, C. M., JR.

1946. An analysis of the deceptive resemblances of fishes to plant parts, with critical remarks on protective coloration, mimicry and adaptation. *Bull. Bingham Oceanogr. Coll.*, 10 (2): 49 pp., 2 pls., 3 text-figs.
1948. *Field Book of Marine Fishes of the Atlantic Coast from Labrador to Texas*. G. P. Putnam's Sons, New York. xxxvii + 332 pp., 16 pls., 403 text-figs. [First published 1929].
1963. Defensive behavior and venom in *Scorpaena* and *Dactylopterus*. *Copeia*, no. 4: 698-700, 2 figs.

BREDER, C. M., JR. AND E. CLARK

1947. A contribution to the visceral anatomy, development, and relationships of the Plectognathi. *Bull. Amer. Mus. Nat. Hist.*, 88 (5): 287-320, 4 pls., 8 text-figs.

- BURKHOLDER, P. R., L. M. BURKHOLDER, AND J. A. RIVERO
1959. Some chemical constituents of turtle grass, *Thalassia testudinum*. Bull. Torrey Botan. Club, 86: 88-93.
- CARLSON, C. B.
1952. Exploratory fishing for the little tuna (*Euthynnus alletteratus*) off the Atlantic Coast of the United States. Proc. Gulf & Carib. Fisher. Inst., Fourth Ann. Sess.: 89-94.
- CLARK, E. AND K. VON SCHMIDT
1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci., 15 (1): 13-83, 18 figs.
- CLOUD, P. E., JR.
1959. Geology of Saipan, Mariana Islands. Part 4. Submarine topography and shoal-water ecology. U. S. Dept. Interior, Geol. Surv. Prof. Pap. 280-K: 361-445, 17 pls., maps.
- COURTENAY, W. R., JR.
1961. Western Atlantic fishes of the genus *Haemulon* (Pomadasyidae): systematic status and juvenile pigmentation. Bull. Mar. Sci. Gulf & Carib., 11 (1): 66-149, 17 figs.
- CROKER, R. A.
1962. Growth and food of the gray snapper, *Lutjanus griseus*, in Everglades National Park. Trans. Amer. Fisher. Soc., 91 (4): 379-383, 3 figs.
- CUMMINGS, W. C., B. D. BRAHY, AND J. Y. SPIRES
1966. Sound production, schooling, and feeding habits of the margate, *Haemulon album* Cuvier, off north Bimini, Bahamas. Bull. Mar. Sci., 16 (3): 626-640, 7 figs.
- DARNELL, R. M.
1959. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Pub. Inst. Mar. Sci., Univ. Texas, 5: 353-416, 17 figs.
- DAWSON, E. Y., A. A. ALEEM, AND B. W. HALSTEAD
1955. Marine algae from Palmyra Island with special reference to the feeding habits and toxicology of reef fishes. Allan Hancock Found., Occ. Pap., no. 17: 39 pp., 13 figs., 1 chart.
- DE SYLVA, D. P.
1963. Systematics and life history of the great barracuda *Sphyræna barracuda* (Walbaum). Stud. Trop. Oceanogr. Miami, 1: viii + 179 pp., 36 figs.
- DE SYLVA, D. P. AND W. F. RATHJEN
1961. Life history notes on the little tuna, *Euthynnus alletteratus*, from the southeastern United States. Bull. Mar. Sci. Gulf & Carib., 11 (2): 161-190, 10 figs.
- EBELING, A. W.
1957. The dentition of eastern Pacific mullets, with special reference to adaptation and taxonomy. Copeia, no. 3: 173-185, 3 pls., 7 text-figs.
- EIBL-EIBESFELDT, I.
1955. Über Symbiosen, Parasitismus und andere besondere zwaischenartliche Beziehungen tropischer Meeresfische. Zeit. Tierpsych., 12 (2): 203-219, 22 figs.

- EMERY, K. O.
1956. Marine geology of Johnston Island and its surrounding shallows, central Pacific Ocean. *Bull. Geol. Soc. Amer.*, 67: 1505-1520.
- ERDMAN, D. S.
1956. Recent fish records from Puerto Rico. *Bull. Mar. Sci. Gulf & Carib.*, 6 (4): 315- 340.
- ESCHMEYER, W. N.
1965. Western Atlantic scorpionfishes of the genus *Scorpaena*, including four new species. *Bull. Mar. Sci.*, 15 (1): 84-164, 12 figs.
- EVERMANN, B. W. AND M. C. MARSH
1902. The fishes of Puerto Rico, *Bull. U. S. Fish. Comm.*, 20 (part 1): 49-350, 49 col. pls., 112 text-figs., 3 charts.
- FEDDERN, H. A.
1965. The spawning, growth, and general behavior of the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Bull. Mar. Sci.*, 15 (4): 896-941, 33 figs.
- GUDGER, E. W.
1929. On the morphology, coloration and behavior of seventy teleostean fishes of Tortugas, Florida. *Pap. Tortugas Lab.*, 26 (Carnegie Inst. Wash. Pub. 391): 149-204, 4 pls.
- HARRINGTON, R. W., JR. AND E. S. HARRINGTON
1960. Food of larval and young tarpon, *Megalops atlantica*. *Copeia*, no. 4: 311-319, 2 figs.
- HIATT, R. W. AND D. W. STRASBURG
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.*, 30 (1): 65-127, 9 figs.
- HILDEBRAND, S. F. AND W. C. SCHROEDER
1928. Fishes of Chesapeake Bay. *Bull. U. S. Bur. Fisher.* 43 (1): 366 pp., 211 figs.
- HUBBS, C. L.
1963. *Chaetodon aya* and related deep-living butterflyfishes: their variation, distribution and synonymy. *Bull. Mar. Sci. Gulf & Carib.*, 13 (1): 133-192, 14 figs.
- IDYLL, C. P. AND J. E. RANDALL
1959. Sport and commercial fisheries potential of St. John, Virgin Islands. Fourth Internatl. Game Fish Conf., Nassau, Bahamas: 10 + 2 pp. (1960).
- JORDAN, D. S. AND B. W. EVERMANN
1896- The Fishes of North and Middle America. Pts. I-IV. *Bull. U. S. Natl. Mus.*, no. 47: 3313 pp., 392 pls.
- JORDAN, D. S. AND U. C. THOMPSON
1905. The fish fauna of the Tortugas Archipelago. *Bull. U. S. Bur. Fisher.*, (1904), 24: 229-256, 6 figs.
- KNAPP, F. T.
1949. Menhaden utilization in relation to the conservation of food and game fishes of the Texas Gulf coast. *Trans. Amer. Fish. Soc.*, 79: 137-144.

- KUMPF, H. E. AND H. A. RANDALL
1961. Charting the marine environments of St. John, U. S. Virgin Islands. Bull. Mar. Sci. Gulf & Carib., 11 (4): 543-551, 4 figs.
- LIMBAUGH, C.
1961. Cleaning symbiosis. Sci. Amer., 205 (2): 42-49, 11 figs.
- LINTON, E.
1905. Parasites of fishes of Beaufort, North Carolina. Bull. U. S. Bur. Fisher. (1904), 24: 321-428, 34 pls.
- LONGLEY, W. H. AND S. F. HILDEBRAND
1941. Systematic catalogue of the fishes of Tortugas, Florida with observations on color, habits, and local distribution. Pap. Tortugas Lab., 34 (Carnegie Inst. Wash. Pub. 535): xiii + 331, 34 pls.
- LONGLEY, W. H., W. L. SCHMITT, AND W. R. TAYLOR
1925. Observations upon the food of certain Tortugas fishes. Ann. Rept. Tortugas Lab., Carnegie Inst. Wash. Yearbk. no. 24: 230-232.
- LOWE, R. H.
1962. The fishes of the British Guiana continental shelf, Atlantic coast of South America, with notes on their natural history. Jour. Linn. Soc. London, Zool., 44 (301): 669-700, 4 figs.
- MARETZKI, A. AND J. DEL CASTILLO
1967. A toxin secreted by the soapfish *Rypticus saponaceus*. Toxicon, 4: 245-250, 1 fig.
- MAUL, G. E.
1956. Monografia dox peixes do Museu Municipal do Funchal. Ordem Discocephali. Bol. Mus. Funchal, 9 (23/24): 5-74, 5 figs.
- MCCLANE, A. J., et al.
1965. McClane's standard fishing encyclopedia and international angling guide. Holt, Rinehart and Winston, New York, 1057 pp., illustr.
- McKENNEY, T. W.
1959. A contribution to the life history of the squirrel fish *Holocentrus vexillarius* Poey. Bull. Mar. Sci. Gulf & Carib., 9 (2): 174-221, 12 figs.
- McKENNEY, T. W., E. C. ALEXANDER, AND G. L. VOSS
1958. Early development and larval distribution of the carangid fish, *Caranx crysos* (Mitchill). Bull. Mar. Sci. Gulf & Carib., 8 (2): 167-200, 7 figs.
- MENZEL, D. W.
1960. Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. Jour. Conseil Internatl. Explor. Mer., 25 (2): 216-222.
- MOFFETT, A. AND J. E. RANDALL
1957. The Roger Firestone Tarpon Investigation, Progress Report: 18 pp., 5 fig. Rept. to Fla. St. Bd. Conserv. (Mimeo Mar. Lab., Univ. Miami).
- NEWMAN, W. A.
1960. The paucity of intertidal barnacles in the tropical western Pacific. The Veliger, 2 (4): 89-94, 2 pls.

ODUM, H. T. AND E. P. ODUM

1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.*, 25: 291-320, 12 figs.

OLIVER, M. AND M. MASSUTI

1952. El rao, *Xyrichthys novacula* (Fam. Labridae). Notas biológicas y biométricas. *Bol. Inst. Español de Oceanogr.*, no. 48: 15 pp., 5 figs.

PLATE, L.

1908. *Apogonichthys strombi* n. sp., ein symbiotisch lebender Fische von den Bahamas. *Zool. Anz.*, 33: 393-399.

POSTEL, E.

1950. Pêche sur les côtes d'Afrique Occidentale. Rapport et note sur quelques poissons de surface de la presqu'île de Cap-Vert. Inspection générale de l'élevage, Dakar, French West Africa, (2): 77 pp.
1954. Le "Gérard Tréca" aux îles des Cap Vert. *García de Orta*, 2 (3): 311-318.

RANDALL, H. A.

1964. A study of the growth and other aspects of the biology of the West Indian topshell, *Cittarium pica* (Linnaeus). *Bull. Mar. Sci. Gulf & Carib.*, 14 (3): 424-443, 10 figs.

RANDALL, J. E.

1958. A review of the labrid fish genus *Labroides*, with description of two new species and notes on ecology. *Pacific Sci.*, 12 (4): 327-347, 1 col. pl., 6 text-figs.
1960. The case of the free-loading barracuda. *Sea Frontiers*, 6 (3): 174-179, 4 figs.
- 1961a. Overgrazing of algae by herbivorous marine fishes. *Ecology*, 42 (4): 812.
- 1961b. Let a sleeping shark lie. *Sea Frontiers*, 7 (3): 153-159, 4 figs.
- 1962a. Tagging reef fishes in the Virgin Islands. *Proc. Gulf & Carib. Fisher. Inst.*, Fourteenth Ann. Sess.: 201-241, 8 figs.
- 1962b. Fish service stations. *Sea Frontiers*, 8 (1): 40-47, 8 figs.
- 1963a. Additional recoveries of tagged reef fishes from the Virgin Islands. *Proc. Gulf & Carib. Fisher. Inst.*, Fifteenth Ann. Sess.: 155-157.
- 1963b. An analysis of the fish populations of artificial and natural reefs in Virgin Islands. *Carib. Jour. Sci.*, 3 (1): 31-47.
- 1963c. Notes on the systematics of parrotfishes (Scaridae), with emphasis on sexual dichromatism. *Copeia*, no. 2: 225-237, 3 col. pls., 4 text-figs.
- 1964a. Contributions to the biology of the queen conch, *Strombus gigas*. *Bull. Mar. Sci. Gulf & Carib.*, 14 (2): 246-295, 13 figs.
- 1964b. Sediment-producing fishes. *Underwater Naturalist*, 2 (1): 30-32, 1 fig.
- 1964c. A revision of the filefish genera *Amaneses* and *Cantherhines*. *Copeia*, no. 2: 331-361, 18 figs.
- 1965a. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology*, 46 (3): 255-260, 4 figs.
- 1965b. Food habits of the Nassau grouper (*Epinephelus striatus*). *Assoc. Is. Mar. Labs. Carib.*, Sixth Meeting: 13-16.
1966. The West Indian blennioid fishes of the genus *Hypleurochilus*, with the description of a new species. *Proc. Biol. Soc. Wash.*, 79: 57-71, 2 figs.

RANDALL, J. E. AND D. K. CALDWELL

1966. A review of the sparid fish genus *Calamus*, with descriptions of four new species. Bull. Los Angeles County Mus. Nat. Hist., Sci., no. 2: 47 pp., 24 figs.

RANDALL, J. E. AND H. A. RANDALL

1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bull. Mar. Sci. Gulf & Carib., 10 (4): 444-480, 15 figs.
1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica, 48 (2): 49-59, 2 pls., 2 text-figs.

RANDALL, J. E., R. E. SCHROEDER, AND W. A. STARCK, II

1964. Notes on the biology of the echinoid *Diadema antillarum*. Carib. Jour. Sci., 4 (2 & 3): 421-433, 3 figs.

RANDALL, J. E. AND G. L. WARMKE

- In press. The food habits of the hogfish (*Lachnolaimus maximus*), a labrid fish from the western Atlantic. Carib. Jour. Sci.

REID, G. K., JR.

1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf & Carib., 4 (1): 1-94, 13 figs.
1955. A summer study of the biology and ecology of East Bay, Texas. Part II. The fish fauna of East Bay, the Gulf Beach, and Summary. Texas Jour. Sci., 7 (4): 430-453.

ROBINS, C. R. AND J. E. RANDALL

1965. Three new western Atlantic fishes of the blennioid genus *Chaenopsis*, with notes on the related *Lucayablennius zingaro*. Proc. Acad. Nat. Sci. Phila., 117 (6): 213-234, 4 figs.

ROBINS, C. R. AND W. A. STARCK, II

1961. Materials for a revision of *Serranus* and related fish genera. Proc. Acad. Nat. Sci. Phila., 113 (11): 259-314, 8 figs.

RODRIGUEZ PINO, Z.

1962. Estudios estadísticos y biológicos sobre la biajaiba (*Lutianus synagris*). Centro Invest. Pesqueras, Nota sobre Investigaciones, no. 4: 1-89.

SATO, M.

1937. Preliminary report on the barbels of a Japanese goatfish, *Upeneoides bensasi* (Temminck & Schlegel). Sci. Rep. Tōhoku Imp. Univ., Biol., 11 (3): 259-264; Further studies on the barbels of a Japanese goatfish, *Upeneoides bensasi* (Temminck & Schlegel) *ibid*: 297-302.

SMITH, C. L.

1961. Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the western North Atlantic. FAO Fisher. Biol., Synopsis no. 23: vi + 61 pp., 19 figs.

SMITH, H. M.

1907. The Fishes of North Carolina. N. Carolina Geol. Surv., vol. 2, 453 pp., 19 pls., 186 text-figs.

SPRINGER, V. G.

1964. A revision of the carcharinid shark genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. Proc. U. S. Natl. Mus., 115 (3493): 559-632, 2 pls., 14 text-figs.

SPRINGER, V. G. AND K. D. WOODBURN

1960. An ecological study of the fishes of the Tampa Bay area. Fla. St. Bd. Conserv. Mar. Lab., Prof. Pap. 1: 104 pp., 18 figs.

STARCK, W. A., II

- In press. A contribution to the biology of the gray snapper, *Lutjanus griseus* (Linnaeus) in the vicinity of Lower Matecumbe Key, Florida. Stud. Trop. Oceanogr., Miami.

STEPHENSON, W. AND R. B. SEARLES

1960. Experimental studies on the ecology of intertidal environments at Heron Island. I. Exclusion of fish from beach rock. Austral. Jour. Mar. & Freshw. Res., 11 (2): 241-267, 3 pls., 4 text-figs.

STRASBURG, D. W.

1959. Notes on the diet and correlating structures of some central Pacific echeneid fishes. Copeia, no. 3: 244-248, 1 fig.

SUYEHIRO, Y.

1942. A study on the digestive system and feeding habits of fish. Jap. Jour. Zool., 10 (1): 1-301, 15 pls., 190 text-figs.

SZIDAT, L. AND A. NANI

1951. Las remoras del Atlantico Austral con un estudio de su nutricion natural y de sus parasitos (Pisc. Echeneidae). Rev. Inst. Invest. Mus. Argent. Cienc. Nat. Zool., 2 (6): 385-417, 14 figs.

TABB, D. C. AND R. B. MANNING

1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. Bull. Mar. Sci. Gulf & Carib., 11 (4): 552-649, 8 figs.

THOMSON, J. M.

1954. The organs of feeding and the food of some Australian mullet. Austral. Jour. Mar. & Freshw. Res., 5 (3): 469-485, 2 pls., 6 text-figs.

TORTONESE, E.

1961. Intorno a *Caranx fusus* Geoffr. (Pisces Carangidae) e ai suoi rapporti con le forme affini. Ann. Mus. Civ. St. Nat. Genova, 72: 149-160, 3 figs.

TOWNSEND, C. H.

1929. Records of changes in color among fishes. New York Aquarium Nat. Ser., N. Y. Zool. Soc., 60 pp., 27 col. pls., 15 text-figs.

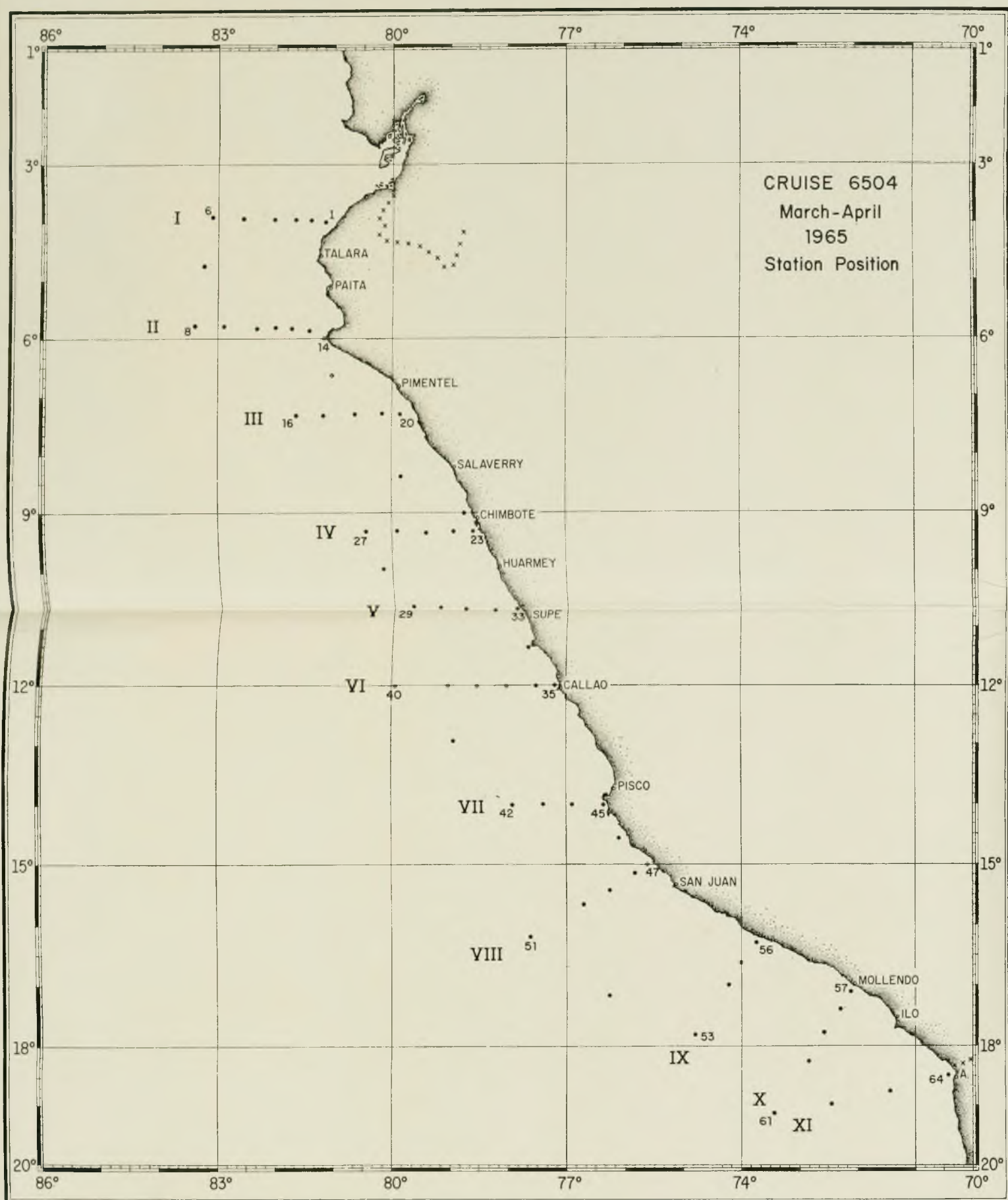
WINN, H. E. AND J. E. BARDACH

1959. Differential food selection by moray eels and a possible role of the mucous envelope of parrot fishes in reduction of predation. Ecology, 40 (2): 296-298.

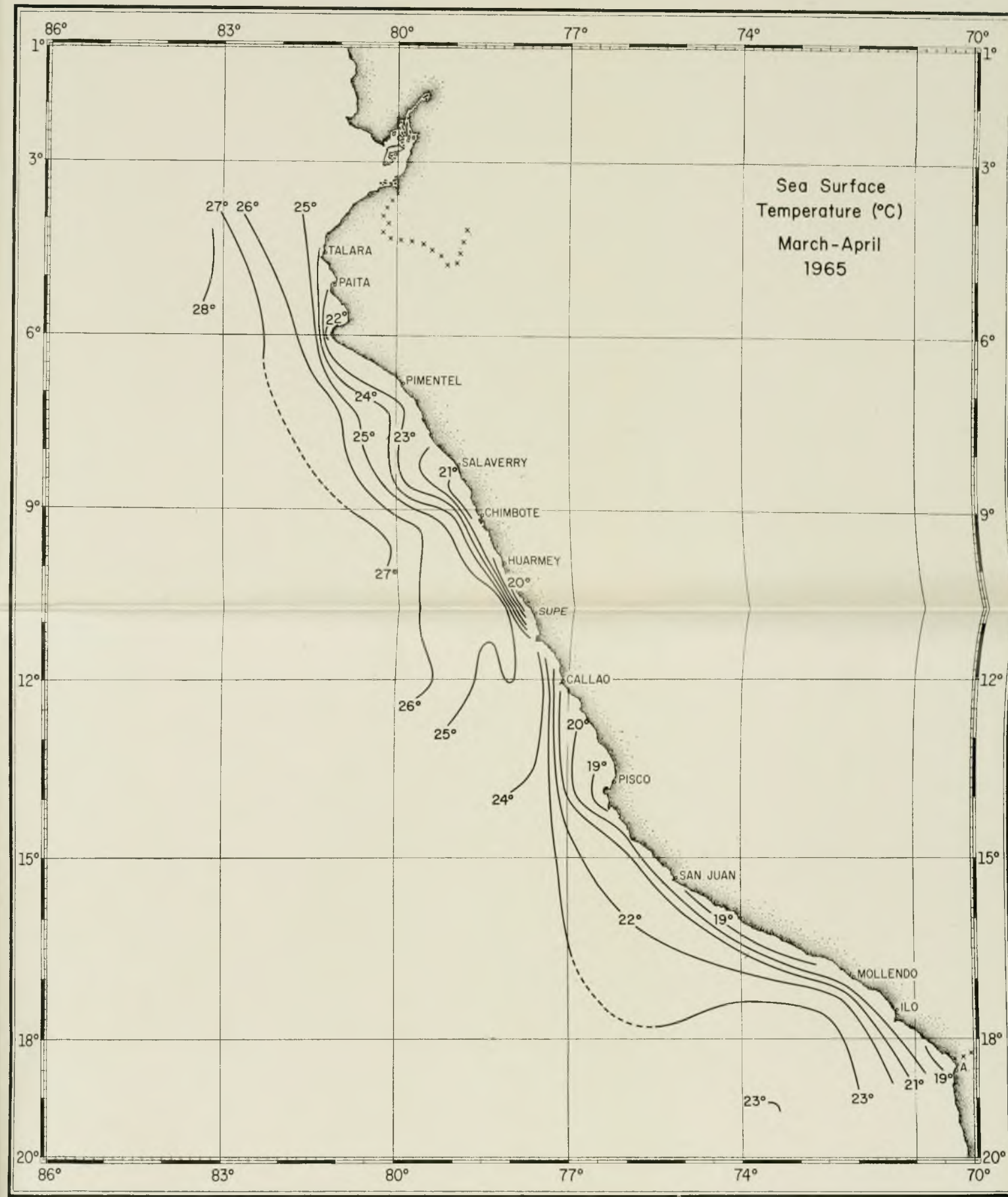
1960. Some aspects of the comparative biology of parrot fishes at Bermuda. Zoologica, 45 (1): 29-34, 1 pl.

WINN, H. E., M. SALMON, AND N. ROBERTS

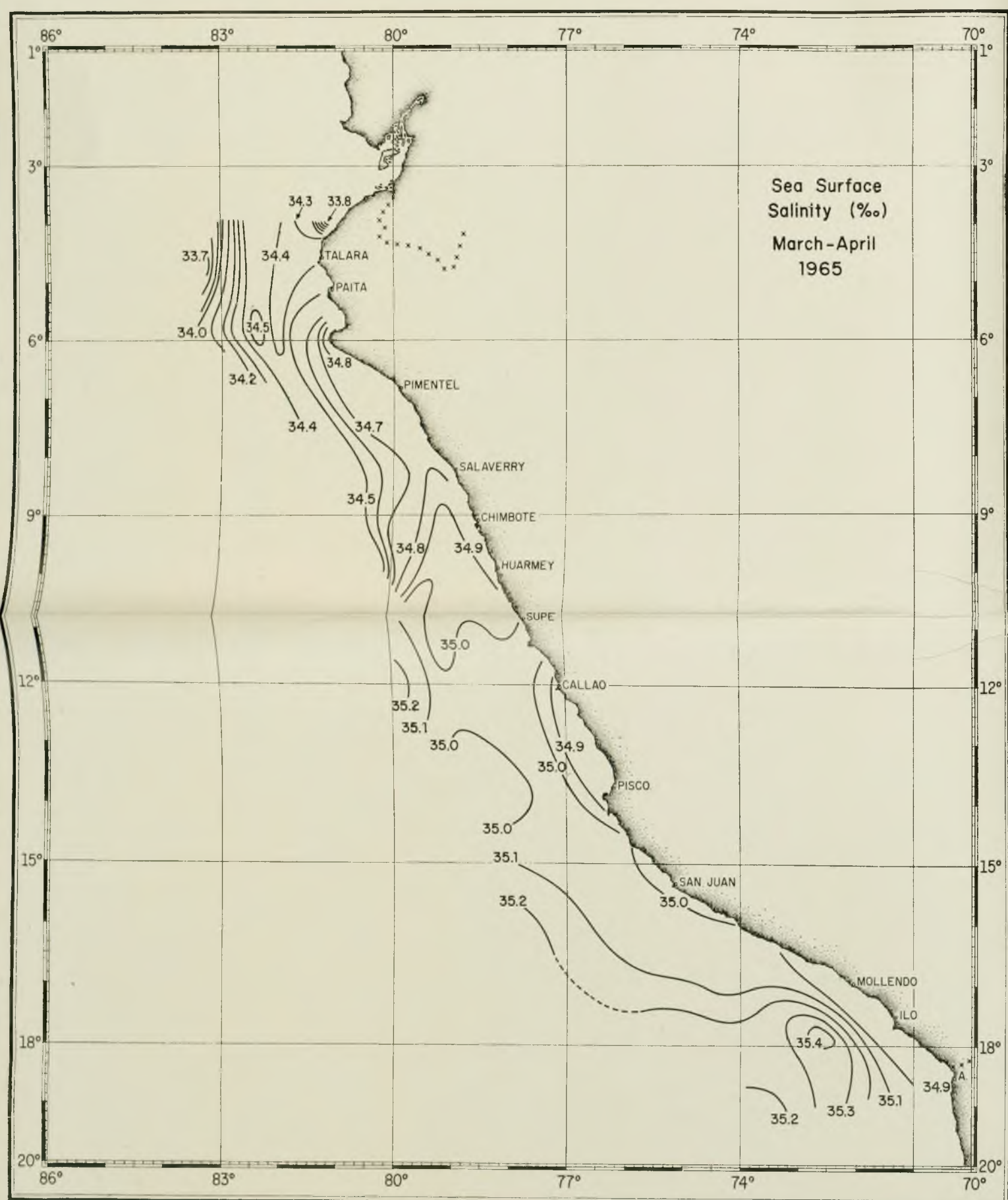
1964. Sun-compass orientation by parrot fishes. Zeit. Tierpsych., 21 (7): 798-812, 14 figs.



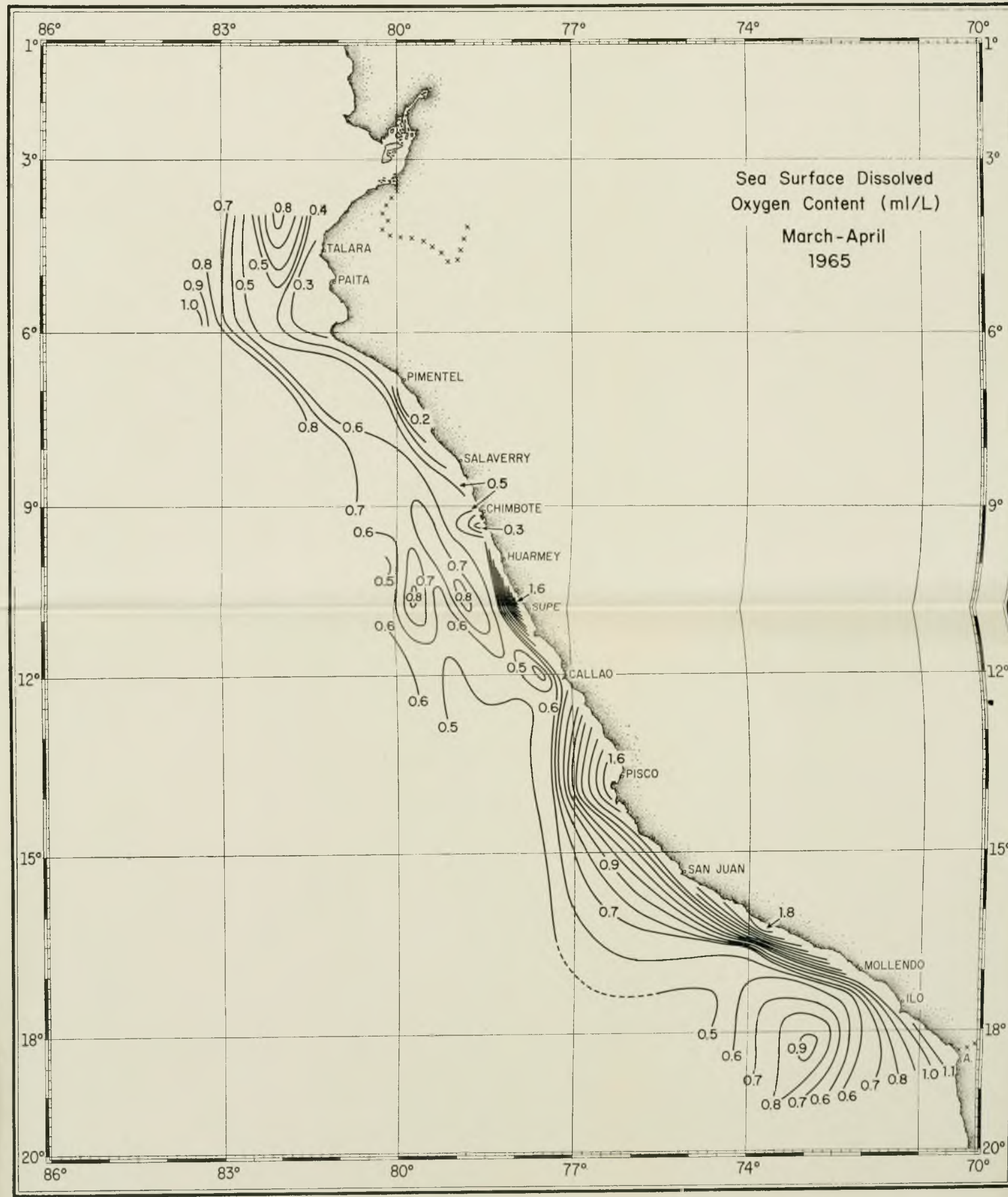
A



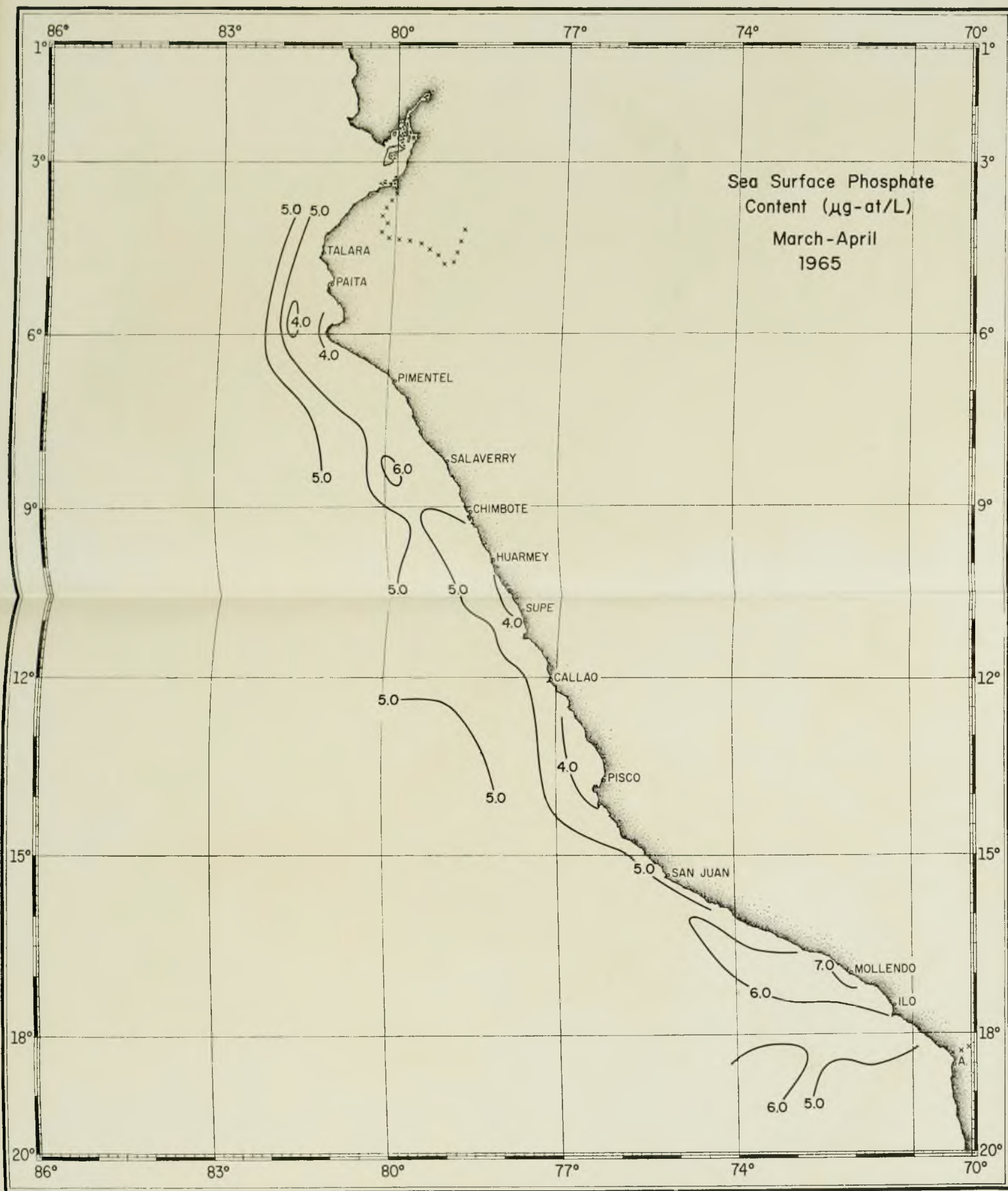
B



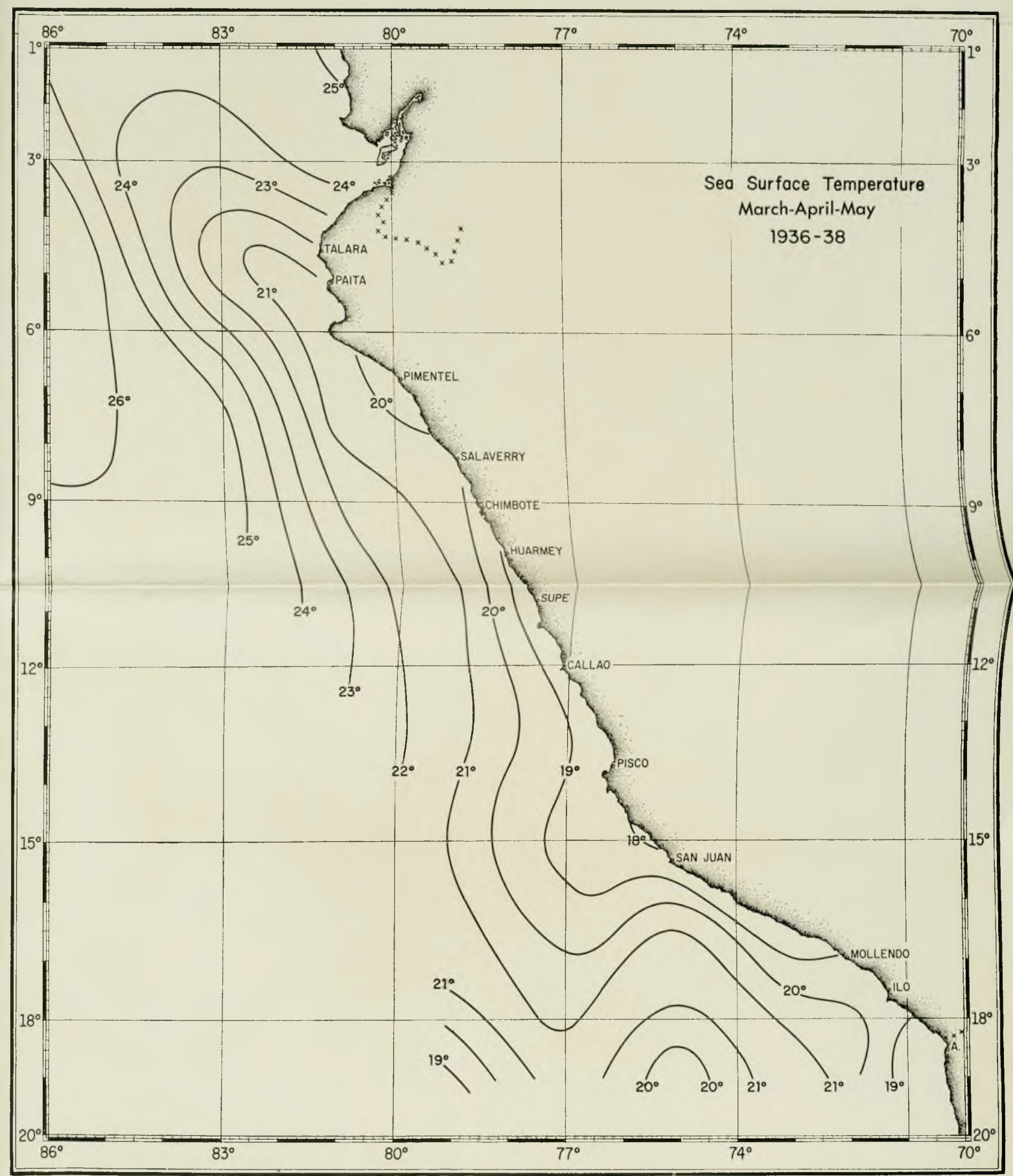
C



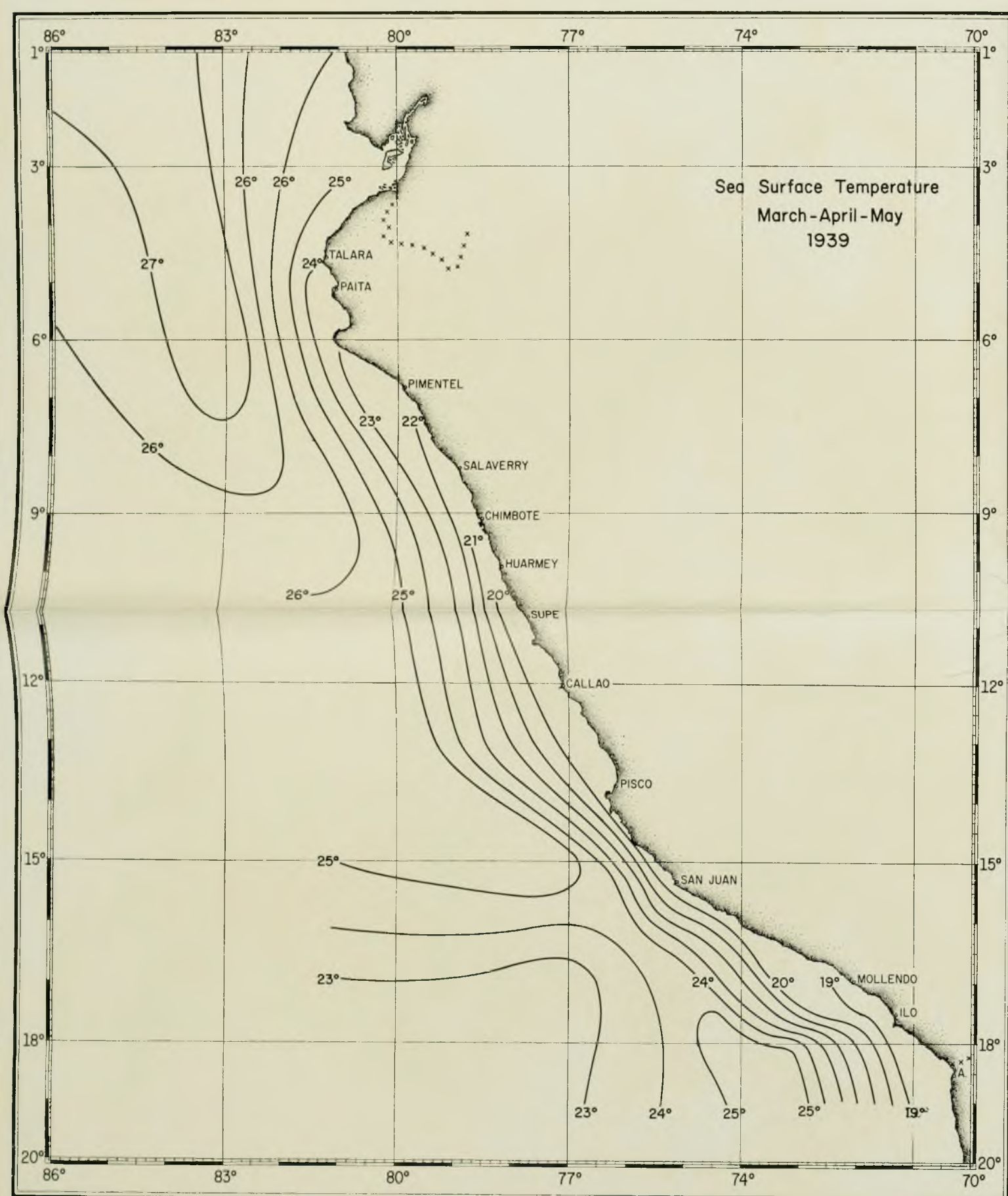
D



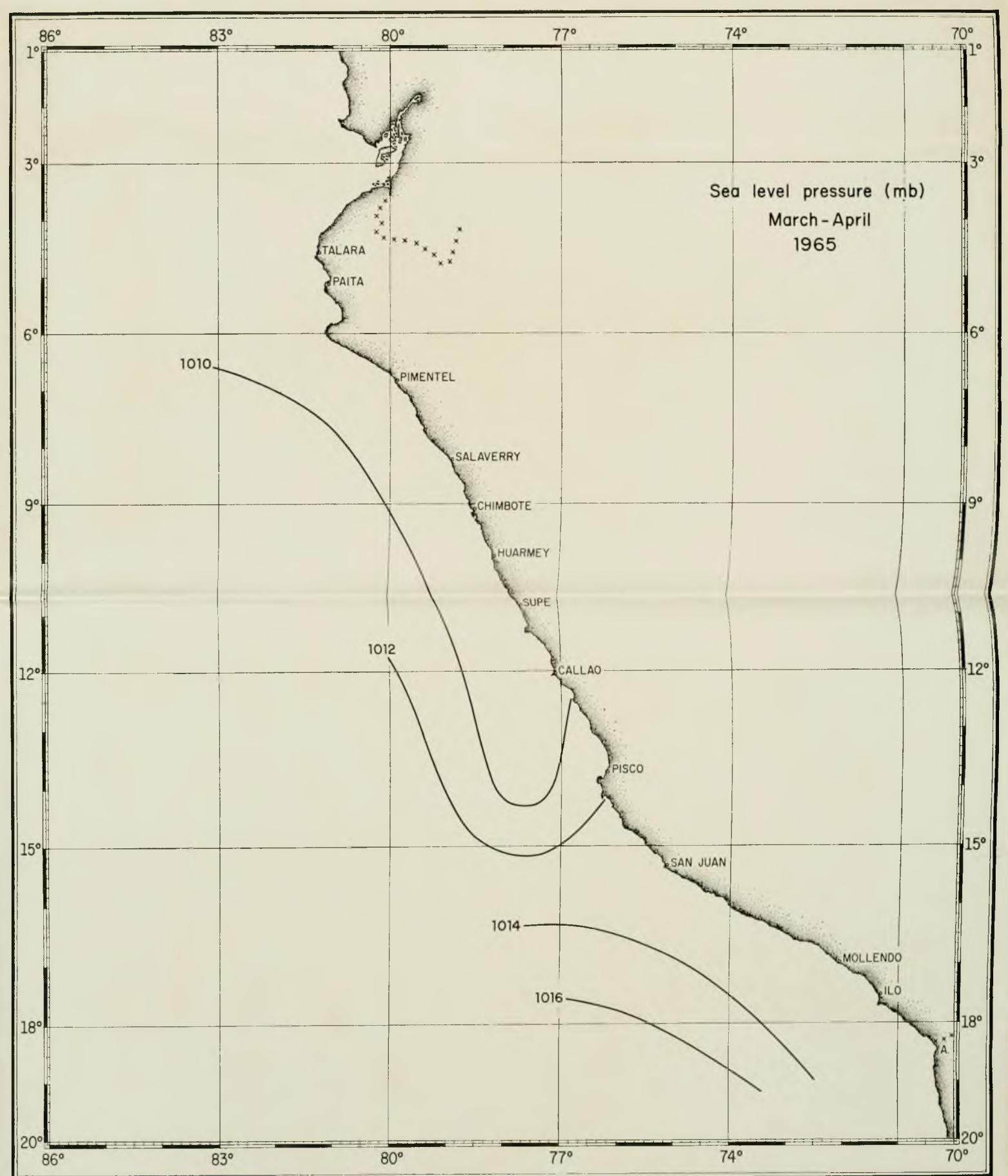
A



B



C



D