PREFACE

The past three decades have seen rapid advances in the ocean sciences. The development of new or improved techniques of observing and measuring in the ocean has greatly increased our understanding of this complex environment and, as well, posed many new challenges for the scientist. The influence of marine organisms on sound transmission in the ocean, particularly sound scattering by zooplankton and fish in the deep ocean basins has been a persistent and rewarding interest in recent years.

In the spring of 1970, the Maury Center for Ocean Science sponsored a three-day international gathering of scientists to assess our current understanding of biological sound scattering in the oceans. This book is the record of that assessment. It includes both formal invited contributions and informal discussion sessions. The participants first examined the biology of scattering layers, dealing with environmental, ecological and physiological aspects as well as the distribution and abundance of various scattering organisms. The acoustic manifestations of sound scattering, as well as some of its geographic features, were considered on the second day of the conference. The third day was given over to studies employing both biological and acoustic approaches. The participants convened on the evening of the third day for a review of the meetings.

The analysis of the phenomena of biological sound scattering requires several disciplines. This book presents our current understanding and many of our ideas about learning more in this fascinating and useful field of oceanography. I hope it will assist the ocean science community in continuing or reshaping its research in the biology and physics of the sea.

J. B. HERSEY
Director
Maury Center for Ocean Science

ACKNOWLEDGMENTS

As editors of all past volumes such as this, I have the monumental task of properly recognizing help in its preparation. It is a particularly difficult task for me since I have been so closely involved with this Symposium, even as an idea, and so many people have been involved with me in all of the formative stages of the conference, as well as during our deliberations at Airlie House. At the outset, I wish to extend my sincere appreciation to Dr. Robert E. Smith of the Florida Institute of Oceanography (formerly with the Office of Naval Research) and Mr. Kenneth W. Kaye of the U.S. Naval Oceanographic Office, who worked with me on an "Ad Hoc" basis more than three years before the Airlie House conference became a reality. Their interest and assistance were invaluable in ultimately framing the format for the meetings.

Dr. J. B. Hersey and Captain K. J. Carroll, USN, of the Maury Center for Ocean Science provided invaluable guidance and support. Mr. Donald Wilson of the Naval Research Laboratory, and Mr. Deane Holt and Mr. Charles Woodhouse of the Office of Naval Research provided able assistance in developing the program for the conference.

It goes without saying that the success of a meeting depends upon the participants. The vitality and spontaneity of our conference is, I feel, evident in the discussion portions of this volume. The dynamic and stimulating character of the Symposium is, I am sure, not fully captured, but it was there at Airlie House. For this, I thank each and every participant. My special appreciation is due the session chairmen; Dr. Richard H. Backus of the Woods Hole Oceanographic Institution, chairman of the Biology session; Mr. Robert S. Winokur of the U.S. Naval Oceanographic Office, who chaired the session on Acoustics; and Dr. Eric G. Barham and Mr. William E. Batzler of the Naval Undersea Research and Development Center, San Diego, who together chaired the joint session dealing with biological and acoustic considerations. They provided valuable aid in organizing the conference, in conducting the meetings, and in serving as a focal point for refereeing contributions and in associated editing chores.

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G.B.F.

LIST OF PARTICIPANTS

Dr. R. McN. Alexander
University of Leeds
Leeds, England

Dr. William Aron
Smithsonian Institution
Washington, D.C.

Dr. Richard H. Backus
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

Dr. Eric G. Barham
Naval Undersea Research & Development Center
San Diego, California

Mr. William E. Batzler
Naval Undersea Research & Development Center
San Diego, California

Dr. Peter C. Beamish
Bedford Institute
Dartmouth, Nova Scotia

Mr. Crest Z. Bluy
Defense Research Establishment
Halifax, Nova Scotia

Dr. Brian P. Boden
Scripps Institution of Oceanography
La Jolla, California

Dr. Margaret C. Bradbury
San Francisco State College
San Francisco, California

Mr. Charles Brown
Navy Undersea Systems Command
New London, Connecticut

Dr. Dail Brown
Smithsonian Institution
Washington, D.C.

Dr. Robert P. Chapman
Defense Research Establishment
Halifax, Nova Scotia

Dr. George L. Clarke
Harvard University
Cambridge, Massachusetts

Dr. William D. Clarke
Westinghouse Ocean Research Laboratory
Annapolis, Maryland

Dr. Daniel Cohen
Department of Interior
Washington, D.C.

Mr. Henry P. Cole
University of Alaska
College, Alaska

Dr. Sneed B. Collard
University of West Florida
Pensacola, Florida

Dr. James Craddock
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

Dr. Brian G. D'Aoust
Virginia Mason Research Center
Seattle, Washington

Mr. Edward E. Davis
Naval Oceanographic Office
Washington, D.C.

Dr. Max Dunbar
McGill University
Montreal, Canada

Calvin R. Dunlap, Lt., USN
USS Bainbridge (DLGN-25)
FPO San Francisco, California

Dr. Alfred W. Ebeling
University of California
Santa Barbara, California

Mr. G. Brooke Farquhar
Naval Oceanographic Office
Washington, D.C.

Mr. Norbert F. Fisch
Navy Undersea Systems Command
New London, Connecticut

Mr. William Friedl
Naval Undersea Research & Development Center
San Diego, California

Dr. Robert H. Gibbs, Jr.
Smithsonian Institution
Washington, D.C.

Mr. Kenneth Haigh
Admiralty Underwater Weapons Establishment
Dorset, England

Mr. John Hanrahan
Navy Undersea Systems Command
New London, Connecticut

Mr. William Hansen
McGill University
Montreal, Canada

Dr. J. B. Hersey
Maury Center for Ocean Science
Washington, D.C.

Mr. Vance Holiday
Scripps Institution of Oceanography
La Jolla, California

Dr. Osmund Holm-Hansen
Scripps Institution of Oceanography
La Jolla, California

Mr. Deane Holt
Office of Naval Research
Washington, D.C.

Mr. Burton G. Hurdle
Naval Research Laboratory
Washington, D.C.

Mr. Christian S. Jeannin
Laboratoire Acoustique
Le Brusc, France

Mr. Timothy W. Janaitis
Naval Oceanographic Office
Washington, D.C.

Mr. Richard Johnson
Scripps Institution of Oceanography
La Jolla, California

Dr. Elizabeth M. Kampa
Scripps Institution of Oceanography
La Jolla, California

Mr. Kenneth W. Kaye
Naval Oceanographic Office
Washington, D.C.

Dr. Johannes Kinzer
University of Kiel
Kiel, Germany

Dr. Richard H. Love
Naval Oceanographic Office
Washington, D.C.

Dr. Norman B. Marshall
British Museum (Natural History)
London, England

Dr. Roderick S. Mesecar
Oregon State University
Corvallis, Oregon

Dr. David Middleton
Cambridge, Massachusetts

Dr. Edward D. Mitchell
Fisheries Research Board of Canada
Quebec, Canada

Dr. Brian S. McCartney
National Institute of Oceanography
Surrey, England

Dr. Paul T. McElroy
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

Dr. Basil Nafpaktitis
University of Southern California
Los Angeles, California

Dr. Werner G. Neubauer
Naval Research Laboratory
Washington, D.C.

Dr. William G. Pearcy
Oregon State University
Corvallis, Oregon

Mr. Kenneth E. Perkins
Office of Naval Research
Washington, D.C.

Dr. George V. Pickwell
Naval Undersea Research
& Development Center
San Diego, California

Mr. Richard E. Pieper
University of British Columbia
Vancouver, British Columbia

Mr. W. Lawrence Pugh
Naval Oceanographic Office
Washington, D.C.

Dr. J. E. G. Raymont
University of Southampton
Southampton, England

Dr. Clyde F. E. Roper
Smithsonian Institution
Washington, D.C.

Dr. Morris Schulkin
Navy Undersea Systems Command
New London, Connecticut

Dr. Joseph Scrimger
Defense Research Establishment
Victoria, British Columbia

Mr. Lloyd W. Shearer
Naval Oceanographic Office
Washington, D.C.

Dr. Paul E. Smith
Bureau of Commercial Fisheries
La Jolla, California

Mr. Robert L. Swarts
Honeywell, Inc.
Seattle, Washington

Mr. Robert J. Urick
Naval Ordnance Laboratory
Silver Spring, Maryland

Mr. Peter Van Schuyler
Naval Oceanographic Office
Washington, D.C.

Mr. Robert J. Vent
Naval Undersea Research & Development Center
San Diego, California

Mr. David E. Weston
Admiralty Research Laboratory
Middlesex, England

Mr. Donald Wilson
Naval Research Laboratory
Washington, D.C.

Mr. Robert S. Winokur
Naval Oceanographic Office
Washington, D.C.

Mr. Charles Woodhouse
Office of Naval Research
Washington, D.C.

Mr. Bernard J. Zahuranec
Naval Oceanographic Office
Washington, D.C.

CONTENTS

Dr. Joseph Scrimger
Defense Research Establishment
Victoria, British Columbia

Mr. Lloyd W. Shearer
Naval Oceanographic Office
Washington, D.C.

Dr. Paul E. Smith
Bureau of Commercial Fisheries
La Jolla, California

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Washington, D.C.

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Naval Oceanographic Office
Washington, D.C.

Mr. Charles Woodhouse
Office of Naval Research
Washington, D.C.

Mr. Bernard J. Zahuranec
Naval Oceanographic Office
Washington, D.C.

ACOUSTIC ASPECTS OF SOUND SCATTERING

Mr. Robert S. Winokur, *Chairman*

JOINT ACOUSTIC AND BIOLOGICAL STUDIES

Dr. Eric G. Barham and Mr. William E. Batzler, *Co-Chairmen*

PELAGIC COMMUNITIES AND SOUND SCATTERING OFF SANTA BARBARA, CALIFORNIA

A. W. Ebeling, G. M. Cailliet, R. M. Ibara, and F. A. DeWitt, Jr.
University of California
Santa Barbara, California

and

D. W. Brown
Smithsonian Institution
Washington, D.C.

ABSTRACT

Factor analyses of occurrences of deep-sea animals, along with various measurements of their middepth environment off southern California, composed a system of four resident communities, interacting with more or less transitory groups of larvae and offshore species. Common silvery fishes, large reddish shrimps, orangish amphipods, and transparent medusae dominated a middepth community characteristic of the relatively shallow Santa Barbara Basin. Its counterpart in the deeper Santa Cruz Basin was associated with an oceanic group containing several offshore fishes and other animals characteristic of more tropical waters. The larger predators in these middepth communities are known to eat the smaller krill, sergestid shrimp, and other plankters in a shallower community of invertebrates as both groups ascend and tend to merge near the surface at night. A variety of fish and crab larvae, neritic krills, amphipods, salps, ctenophores, siphonophores, and silvery hatchetfishes with gas-filled swimbladders formed several transitory groups, which were associated among themselves and with the Shallow Invertebrate Community. At the deep end of the system in the Santa Cruz Basin, jet-black fishes and a vermilion shrimp dominated a community of bathypelagic animals, which was generally unrepresented in the inshore Santa Barbara Basin.

The measures of seasonal and water-mass changes had but few species correlates. Perhaps the resident communities, at least, were not greatly altered by local changes, which only indirectly reflected the characteristic movements of oceanic water masses further offshore.

The measures of the sound scattering layer were associated either with transitory groups containing fishes with gas-filled swimbladders or with the Shallow Invertebrate Community. In a separate analysis of the first year's samples, however, the SSL measures were generally associated with seasonal water-mass change. The SSL was shallower during the spring period of upwelling than during the fall period of thermal stratification. The relatively remote and stable Offshore Deep Community could not have contributed to the complex layers of sound scatterers in the middepths above.

INTRODUCTION

Elton (1966:81) presumed that "... communities of (the) open water ... seem to form an exception to any generalization about habitat structure, since their habitat has no structure .... Plankton has no cover structure in which predator hunts for prey, though in most other

communities it seems quite likely that without such cover the community would collapse before long." For this reason he believed that ". . . plankton is profoundly different in its organization from terrestrial and most aquatic communities . . .," and that ". . . its survival seems to necessitate very intricate vertical and other movements." Community ecologists, therefore, have generally despaired in describing ecological associations of plankton, presumably adapted to a "homogeneous" environment. Recently, however, plankton biologists have emphasized marked discontinuities in the oceanic fauna. Most major water masses contain assemblages of animals quite unlike other assemblages in adjacent water masses (Fager and McGowan, 1963; Beklemishev, 1969). Also, shallow animals differ markedly from deep animals in morphological, behavioral, and physiological ways (Marshall, 1960; Banse, 1964; Childress, 1968).

The middepth fauna off southern California is especially complex because it contains species from three converging water masses, as well as species endemic to the California Current system (Lavenberg and Ebeling, 1967; Ebeling et al., 1970). A counterclockwise current gyre, extending from the point of offshore deflection of the California Current at Point Conception to south of the Mexican border, moves inshore during a period of upwelling in spring and early summer (Brown, 1969). Here, some 13 depressions pit the relatively narrow continental shelf (Emery, 1960). Off Santa Barbara, the relatively shallow Santa Barbara Basin, 600 m deep, is located between the mainland and the Channel Islands about 20 miles offshore. The more typically oceanic Santa Cruz Basin, 2000 m deep, is located just seaward of the islands (Fig. 1). Here, resident animals meet transient animals from the north (subarctic group), south (equatorial group) and west (central group) (Brown, 1969). These residents and transients assort themselves both by depth and by basin.

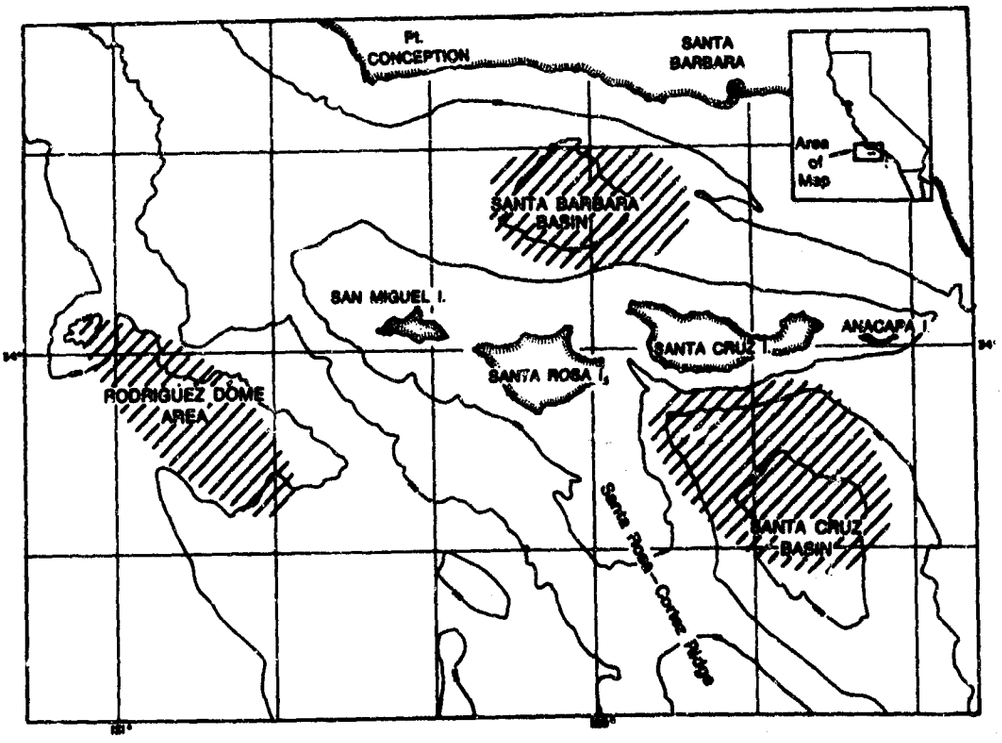

Figure 1. Deep-sea basins off Santa Barbara, California. Stations (hatched) included in the present analysis are in the shallow Santa Barbara Basin and the deeper Santa Cruz Basin. A third, more oceanic, station in the Rodriquez Dome area was analyzed in another study (Brown, 1969). Depth contours are measured in fathoms.

Perhaps the 12-kHz sound-scattering layers (SSL) observed off Santa Barbara have many contributors. In general, SSL's have been variously attributed to squids, crustaceans, fish with swimbladders, and siphonophores (Hersey and Backus, 1954; Naſpaktitis, 1968; Barham, 1963, 1966). The present multivariate analyses of abundances of species, estimates of biomass, and measures of the physical environment have resolved a complex system, into which fit selected measures of the depth and strength of the SSL.

METHOD

The two basins were sampled using a 6-foot Isaacs-Kidd midwater trawl fitted with electronic sensors of depth, temperature, and flow, and with a four-chambered cod-end sampler, whose gates were closed in sequence from on board the General Motors R/V *Swan* (Aron et al., 1964; Bourbeau et al., 1966; Brown, 1969). Each trawl haul optimally provided a series of "at-depth" and "oblique" samples. These were sorted into fish and invertebrate components, whose volumes were estimated by liquid displacement. Bottom and SSL depths were measured with a 12-kHz echo-sounder (PDR). Bathythermograph (BT) temperatures measured to 200 m for each haul provided indications of seasonal water-mass change.

Between fall, 1964 and spring, 1969, 56 cruises, about one a month during two main periods of sampling (August, 1964–October, 1965; July, 1966–October, 1967 and March, 1969), yielded 440 at-depth samples, about evenly distributed between the basins and culled to exclude those from long oblique hauls from depth to surface (Brown, 1969). Corresponding with the generally accepted ecological depth zones off southern California (cf. Paxton, 1967a), the sampled depths were classified as shallow (0-150 m), upper middepth (mesopelagic) (150-400 m), lower middepth (400-600 m), and deep (bathypelagic) (deeper than 600 m). Samples included in the analyses were either intrazone ("at depth") with vertical excursions less than 50-100 m or interzone (positioning) with excursions less than 200 m. Only shallow and middepth hauls could be made in the inshore Santa Barbara Basin, which lacks a true bathypelagic zone. The bathypelagic zone extends below 550-600 m in the Santa Cruz Basin. Greater vertical trawl excursions were allowed in the relatively homogeneous bathypelagic zone than in the complexly layered mesopelagic. The collections represented most daily and seasonal periods. From collection and environmental data sheets, all positional, temporal, physical, and biological measurements were punched on computer data cards for transcriptions and multivariate analyses.

The samples comprised two sets, one for each cruise series, containing 321 (for years 1966-67, 1969) and 119 samples (1964-65), respectively. For the set of 321 samples, 108 variables were measured in five categories: (1) *species*–captures of 80 species of small deep-sea fishes and invertebrates, standardized as numbers per kilometer flow, a measure of unit trawling effort or distance trawled as derived from the revolutions registered by the trawl's flow meter (Brown, 1969); (2) *biomass and diversity*–standardized fish volumes, invertebrate volumes, and numbers of species; (3) *SSL*–depths, intensity (scored from 1, weak, to 3, strong), and trawling excursion (sampling effort) within the upper and lower SSL; (4) *effort*–total kilometer flow per sample; and (5) *physical*–16 measures of season, time of day, location, depth, and water temperatures. All frequency distributions of species abundances were strongly skewed to the right as in a negative binomial distribution, indicating that the animals occurred in patches (Bliss and Fisher, 1953; Ebeling et al., 1970). Species captures and other variables, therefore, were transformed, usually to $\log(x+1)$, for statistical computations. Only 79 variables, including the abundances of 62 species, were analyzed for the second set of 119 samples.

Factor analyses were used to identify groups of associated species and environmental measures. The factors, which were derived from the correlations among all of these variables, were computed separately for the first and second sets of samples. They were computed in a way that

presumably explained the systems of intercorrelated variables as simply as possible; i.e., each factor was "positioned" so that it was strongly correlated with the smallest possible number of variables (Seal, 1964; Cattell, 1965; Harman, 1967). This means that the contributions of some variables to a given factor were maximized, while the contributions of others were minimized, and that, optimally, a given variable contributed substantially to but a single factor. The factors themselves were necessarily uncorrelated with one another.

The relative contributions of the variables to the factors were their correlations with the factors, called *loadings*, which were adjudged "significant" on a somewhat empirical basis (cf., Sokal and Daly, 1961; also see Table 1). Loadings of variables on factors, therefore, were either as large or as small as possible, so that the contrasts between large and small loadings were as important in identifying factors as were the actual sizes of the significant loadings themselves. That is, factors were meaningful only if most of their "non-significant" loadings were near zero. In the present analysis, non-significant loadings were usually less than 0.1, whereas significant loadings, which are listed in Table 1, were usually larger than 0.4 on a scale of 0 to 1.0.

Table 1. Factors of the Middepth Ecosystem off Santa Barbara

		1966-67, 69							1964-65	
		14	12	10	8	6	4	3	10	5
I.	INSHORE FISH VOLUME									
	Location (to offshore)	*–65						–79	–48	–68
	Bottom depth	*–50						–65	–48	–69
	Fish volumes	73						53	79	
	1(F). *Leuroglossus stilbius*	73						62	63	
	2(S). *Pasiphaea pacifica*	71							57	
	3(A). *Hyperia* spp.	71							67	
	4(F). *Stenobrachius leucopsarus*	65							64	
	5(S). *Pasiphaea emarginata*	63							69	
	6(A). *Paracallisoma coesus*	60							48	
	7(M). *Tlaropsidium kelseyi*	59							42	52
	8(M). *Aegina citrea*	50							69	
	9(F). *Parmaturus xanturus*	43							47	
	10(Si). "siphonophore bits"	*43							VII	II
	(S). *Sergestes similis*	*40			46			56	..	..
II.	OFFSHORE MIDDEPTH									
	Location (to offshore)	*..		..	33	46		(–I)	50	
	Bottom depth	*..		..	30	40		(–I)	50	
	1(S). *Pasiphaea chacei*	72				52		III	30	
	2(S). *Gennadas propinquus*	67				53	44	(–I)	71	42
	3(M). *Atolla wyvellei*	51						(–I)	62	50
	4(A). *Scina* spp.	51				43	35	III	–	–
	5(F). *Idiacanthus antrostomus*	50				44		..	IV	IV

Table 1. Factors of the Middepth Ecosystem off Santa Barbara (continued)

		1966-67, 69							1964-65	
		14	12	10	8	6	4	3	10	5
II.	OFFSHORE MIDDEPTH (continued)									
	6(My). *Gnathophausia ingens*	48				38		(–I)	40	
	7(F). *Cyclothone signata*	46				40		III	56	69
	8(M). *Colobonema sericeum*	*38	30				III	III	35	
	(F). *Triphoturus mexicanus*	*39			66			(–I)	74	59
	(F). *Lampanyctus ritteri*	*33			60			(–I)	34	46
III.	OFFSHORE DEEP									
	Upper trawl depth	62							54	92
	Upper trawl temperature	–55							–45	–87
	Location (to offshore)	*40							53	40
	Bottom depth	*39							49	40
	1(F). *Cyclothone acclinidens*	83						66	82	
	2(My). *Eucopia* spp.	82						64	–	–
	3(S). *Hymenodora frontalis*	81						57	79	
	4(My). *Boreomysis* spp.	76						62	–	–
	5(F). *Melanostigma pammelas*	62						45	49	
	6(O). *Conchoecia* spp.	60						46	..	..
	7(M). *Crossota rufobrunnea*	40							76	56
	8(F). *Scopelogadus m. bispinosus*	30						20	27	..
	9(F). *Sternoptyx diaphana*	23							39	..
	10(F). *Holtbyrnia melanocephala*	17						10	30	..
	(M). *Colobonema sericeum*	*39							..	..
IV.	CRAB LARVAE, KRILL SHRIMP									
	1(C). *Lepidopa myops*	90				73	VII	VII	76	
	2(E). *Nyctiphanes simplex*	89				74	VII	VII	X	..
	3(C). "porcelain crab"	53					VII	VII	85	
	4(C). *Blepharopida occidentalis*	*78					VII	VII	X	
	5(E). *Thysanoessa spinifera*	49					VII	VII	..	..
	6(C). *Emerita analoga*	*43			66	68	VII	VII	79	
V.	UPWELLING, WATER MASS									
	Upwelling	–85					II	..	–	–
	BT temperature, 200 m	83					..	..	95	
	BT temperature, 100 m	81					II	..	95	
	BT temperature, 50 m	81					II	..	89	

Table 1. Factors of the Middepth Ecosystem off Santa Barbara (continued)

	1966-67, 69							1964-65	
	14	12	10	8	6	4	3	10	5
V. UPWELLING, WATER MASS (continued)									
BT temperature, surface	*41	47			58	II	..	86	
Month (1-12)	*41	45			59	II	III	70	
VI. TRAWL HAUL OBLIQUENESS									
Trawl temperature range	86			VII	VII	..	VII	..	..
Lower trawl depth	*–68			X	IV	VII	VII	VII	III
Trawl depth range	68			X	..	..	..	III	III
Lower trawl temperature	*68			X	IV	VII	VII	VII	III
(C). *Emerita analoga*	*40			X	IV	VII	VII	..	..
VII. SHALLOW INVERTEBRATE									
BT temperature, surface	*52			41		..	..	..	..
Month (1-12)	*48		41	..	..	..	..	..	..
Lower trawl temperature	*40			72				78	(–III)
Invertebrate volumes	*41			62			72	63	(–III)
1(A). *Paraphronima crassipes*	76					II	58	IV	IV
2(E). *Nematocelis difficilis*	74							80	(–III)
3(Aw). "all arrowworms"	66					II	42	–	–
4(A). *Primno macropa*	57			45		..	39	–	–
5(S). *Sergestes similis*	*56					36	67	73	(–III)
6(E). *Euphausia pacifica*	53			67				68	(–III)
7(A). *Phronima sedentaria*	33			40		II	39	IX	..
VIII. SOUND SCATTERING LAYER (SSL)									
Depth lower SSL	83		68		VII	..	..	..	..
Strength lower SSL	–80		–70		..	..	..	–V	–V
Strength upper SSL	–49		–64		X	..	..	–V	–V
Effort sampling lower SSL	–47		–40		VII	..	..	–	–
Depth upper SSL	*29	37			..	..	..	–VII	..
Hours from midnight	*29				..	..	..	–VII	–III
IX. OFFSHORE FISH									
Location (to offshore)	*..	..	30	II	II	II	..	..	II
Effort sampling upper SSL	46			VII	VII	II	VII	–	–
Fish diversity	*36			II	II	II	VII	–	–

Table 1. Factors of the Middepth Ecosystem off Santa Barbara (continued)

		1966-67, 69							1964-65	
		14	12	10	8	6	4	3	10	5
IX.	OFFSHORE FISH (continued)									
	1(F). *Diaphus theta*	70			II	II	II	VII	40	II
	2(F). *Lampanyctus ritteri*	62			II	II	II	VII	40	II
	3(F). *Triphoturus mexicanus*	*51		60	II	II	II	(–1)	II	II
	4(A). *Vibilia* spp.	49			..	II	II	VII	86	II
	5(Sa). *Salpa fusiformis*	*46			II	II	II	VII	XI	..
	6(F). *Stomias atriventer*	44			..	..	..	..	II	..
	7(F). *Bathylagus wesethi*	43		34	..	..	..	..	–	–
	(E). *Euphausia hemigibba*	36	47		II	II	II	VII	–	–
	(O). *Macrocypridina castanea*	..	..	..	..	..	..	..	64	II
X.	LARVAL FISH									
	BT temperature, surface	*..	..	..	–40	VII	..	..	..	..
	Month (1-12)	*..	..	..	–42	..	..	..	..	..
	Fish diversity	*43				IV	VII	VII	–	–
	1(F). *Engraulis mordax*	79			62	IV	VII	VII	35	..
	2(F). *Sebastodes* spp.	75		67		IV	VII	VII	–	–
	3(F). *Merluccius productus*	55			47	IV	VII	VII	–	–
	4(F). *Citharichthys stigmaeus*	54			48	IV	VII	VII	45	IV
	5(F). *Microstomus pacificus*	35	39			..	..	..	40	..
	6(F). *Citharichthys sordidus*	*33	42		..	..	..	..	IV	..
	7(F). *Leuroglossus stilbius*	–	–	–	–	–	–	–	36	..
	(C). *Emerita analoga*	*36			58	IV	VII	VII	..	..
	(C). *Blepharipoda occidentalis*	*37				IV	VII	VII	..	..
XI.	FIRST HATCHETFISH									
	11(F). *Danaphos oculatus*	61		II	II	II	II	..	–	–
	2(F). *Argyropelecus pacificus*	53		II	II	II	..	..	71	II
	3(Si). *Vegrti* spp.	40		II	..	..	..	..	II	II
	4(F). *Argyropelecus intermedius*	38		..	..	..	..	..	40	II
	(F). *Benthosbella linguidens* (larvae)	33		..	..	..	..	..	–	–
XII.	CTENOPHORE									
	Depth upper SSL	*–38	XIII	..	..	..	..	..	–	–
	BT temperature, surface	*33	..	..	..	..	..	..	..	..
	1(Ct). *Pleurobrachia bachei*	56	XIII	X	X	IV	..	..	–	–

Table 1. Factors of the Middepth Ecosystem off Santa Barbara (continued)

	1966-67, 69							1964-65	
	14	12	10	8	6	4	3	10	5
XII. CTENOPHORE (continued)									
(F). *Citharichthys sordidus* (larvae)	*37	X	X	X	..	..	..	..	..
XIII. VOLUME JELLY CLOGGING									
Flow through trawl	−51	−45	VII	..	..	VII	VII	−	−
Invertebrate volumes	*46	———	VII	VII	IV	VII	VII	VII	−III
Upper trawl depth	−41	———	VII	VII	IV	VII	VII	VII	..
Upper trawl temperature	38	———	VII	VII	IV	VII	VII	VII	..
1(Ct). *Euphausia californiensis*	45	———	VII	..	..	..	VII	VII	−III
2(Si). *Praya dubia*	38	..	IV	..	..	..	..	IV	IV
3(Sa). *Salpa fusiformis*	*37	———	..	II	IV	VII	VII	XI	V
(Si). "siphonophore bits"	*30	XI	II	..	..	..	VII	VII	V
(C). galatheid larvae	27	VIII	..	VII	VII	..	..	−	−
XIV. SECOND HATCHETFISH									
11(F). *Argyropelecus lychnus*	49	VII	IX	VII	VII	II	VII	XI	..
2(S). *Sergestes phorcus*	45	XI	II	II	II	..	..	−	−
ARROWWORM (resolved from 1964-65 data set only, when arrowworms were identified to species)									
(Aw). *Sagitta scrippsae*	−	−	−	−	−	−	−	77	II
(Aw). *S. zetesios*	−	−	−	−	−	−	−	73	II
(F). *Argyropelecus intermedius*	XI	XI	XI	..	..	..	..	70	II
(Aw). *Sagitta maxima*	−	−	−	−	−	−	−	56	II
(F). *Cyclothone signata*	II	II	II	II	II	II	III	43	II
(F). *Argyropelecus pacificus*	XI	XI	II	II	II	..	..	36	II

Note:
Factors from the first analysis (1966-67, 69) are compared with others from the second analysis (1964-65). Columns indicate the number of factors used to represent the system. Identification of variables with the factors is indicated by their "loadings" on (correlations with) the factors (times 100). "Significant" loadings range from about 40 to 100, but smaller loadings are included if they are noticeably larger than zero on but a single factor. All other "non-significant" loadings (either not listed or indicated by two dots) are usually about zero and rarely exceed a value of 20. Horizontal lines indicate a series of loadings about equal in magnitude to the numeral on the left; dashes indicate variables not included in one or the other of the two analyses; asterisks indicate variables that load on more than one factor; and roman numerals indicate the alternate factors on which variables load in simpler representations or in the second analysis. Species are numbered as in figure 2 and their taxonomic groups are identified as: A, Amphipods; Aw, Chaetognaths (arrowworms); C, crab larvae; Ct, Ctenophora; E, Euphausiacea (krill); F, fishes; O, Ostracods; M, medusae; My, Mysidacea; S, decapod shrimps; Sa, salps; Si, Siphonophora.

Because we could make no *a priori* estimate of the number of groups of associated species and environmental measures in the present limited universe of trawl captures and on-station observations, we compared several representations of the system of intercorrelated variables, each composed by a different number of factors. Representations of 3-14 factors in the first analysis were compared with each other and with representations of 5 and 10 factors in the second analysis. All analyses were done using the program BMD 03M (Dixon, 1967) on the IBM 360-75 computer at the University of California, Santa Barbara.

The median depths of the upper and lower sound-scattering layers in each basin were averaged by pre- and post-noon periods of day and by pre- and post-midnight periods of night (Table 2). Shallowest and deepest depths were tabulated by day, night, and month (Table 3).

Table 2. Depths of Sound Scattering Layers at Day and Night in the Santa Barbara and Santa Cruz Basins

Basin	Upper Layer				Lower Layer			
Santa Barbara	Day = 50		Night = 31		Day = 100		Night = 69	
	am	pm	pm	am	am	pm	pm	am
	61(4)	46(12)	36(11)	22(7)	88(12)	111(11)	77(9)	56(5)
Santa Cruz	Day = 61		Night = 27		Day = 118		Night = 56	
	am	pm	pm	am	am	pm	pm	am
	75(10)	25(4)	25(11)	29(11)	128(7)	49(1)	55(6)	56(10)

Note:
Average depths in meters precede the number of observations (in parentheses) of distinguishable traces on the Precision Depth Recorder (12 kHz) for categories of daytime hours of pre-noon (am) and post-noon (pm), and of nighttime hours of pre-midnight (pm) and post-midnight (am). The "am" and "pm" averages are pooled for each pair of categories.

RESULTS

Our limited sampling universe was organized into a system containing about 10-14 groups of intercorrelated species and environmental measures (Table 1). The second analysis of observations made in 1964-65 substantiated the results of the first analysis of observations made later. In the first analysis, four groups remained intact no matter how many factors were used to represent the system, and so the species in these groups may be important members of four resident communities: one of middepth predators that prevail in the shallow Santa Barbara Basin, another of shallow invertebrate planktors that are equally abundant in both basins, and two others of middepth and deep predators that prevail in the mesopelagic and bathypelagic zones, respectively, of the deeper Santa Cruz Basin (Fig. 2). Species belonging to each of two communities indicated interactions between the communities (Fig. 2, double arrows). Other groups were more or less transitory, in that they were not identifiable when progressively fewer factors were used to represent the system, but merged with other groups or with the communities

Table 3. Extreme Depths of Sound Scattering Layers in the Santa Barbara and Santa Cruz Basins and the Months of their Occurrence

SSL Layer		Santa Barbara				Santa Cruz			
		Day		Night		Day		Night	
		Depth	Month	Depth	Month	Depth	Month	Depth	Month
Upper layer	Shallowest	16	IV	15	III, IV	10	IV, V	12	IV
	Deepest	100	VIII-X	122	X	160	VIII-XI	60	VII, XI
Lower layer	Shallowest	48	III	25	III	49	III	40	I, II
	Deepest	193	VIII	122	X, XI	170	XII	106	XI

Note:
The depths (arabic numbers), pooled from two or three observations each of midpoints on the PDR traces are listed by the months (roman numerals) when they were recorded.

(single arrows). "Transitory groups" usually contained animals that are seasonally abundant, such as exotic species with centers of distribution far outside the sampling area and shallow-water species represented only by their pelagic young and larvae, or contained animals that are atypical in their behavior, such as fish species that cannot ascend as rapidly as most others because they have large gas-filled swimbladders. A "physical group," containing only measures of seasonal change and water temperatures, reflected the annual oceanographic cycle.

I. **INSHORE FISH VOLUME COMMUNITY.** Increasing volumes of fish caught distinguished a resident community of middepth predators in the relatively shallow and inshore Santa Barbara Basin (Table 1 and Fig. 2: factor I). A silvery deep-sea smelt (factor I: species 1) and common lanternfish (4) abound within the region of the southern Californian basins, but rapidly dwindle in numbers outside this region. These fishes and a large reddish glass shrimp (5) appear pre-adapted to life in the inshore basins, which exclude many of the animals characteristic of the oceanic regions further offshore (Ebeling et al., 1970). [Clarke (1966) observed that "The migrating mesopelagic fauna of the (Santa Barbara Basin) is less complicated than that of the open ocean, and most of the truly bathypelagic species are absent."] Other common members of this community included a smaller and paler glass shrimp (2) and two light or orangish amphipods (3,6). Jelly-like animals were represented by two transparent medusae (7,8) and various pieces of siphonophores (10). Although numerically sparse, the relatively large pelagic young of a benthonic cat shark (9) substantially increased the fish volumes. The small and pale shrimp *Sergestes similis* also belonged to a shallower community of invertebrate plankters (factor VII). Perhaps the deeper and larger predators invaded the shallower communities of plankton, especially at night when populations of predators and prey tended to merge near the surface.

VII. **SHALLOW INVERTEBRATE COMMUNITY.** These abundant plankters, along with various jellies (see factor XIII), made up most of the invertebrate volumes and apparently flourished during the period of thermal stratification in the summer and fall. Two common krills of the California Current region (Brinton, 1962) may co-occur abundantly in this community because they feed in different ways: *Nematoscelis difficilis* (VII: 2) probably grasps its prey by its two long pincers, while *Euphausia pacifica* (6), which ranges farther northward,

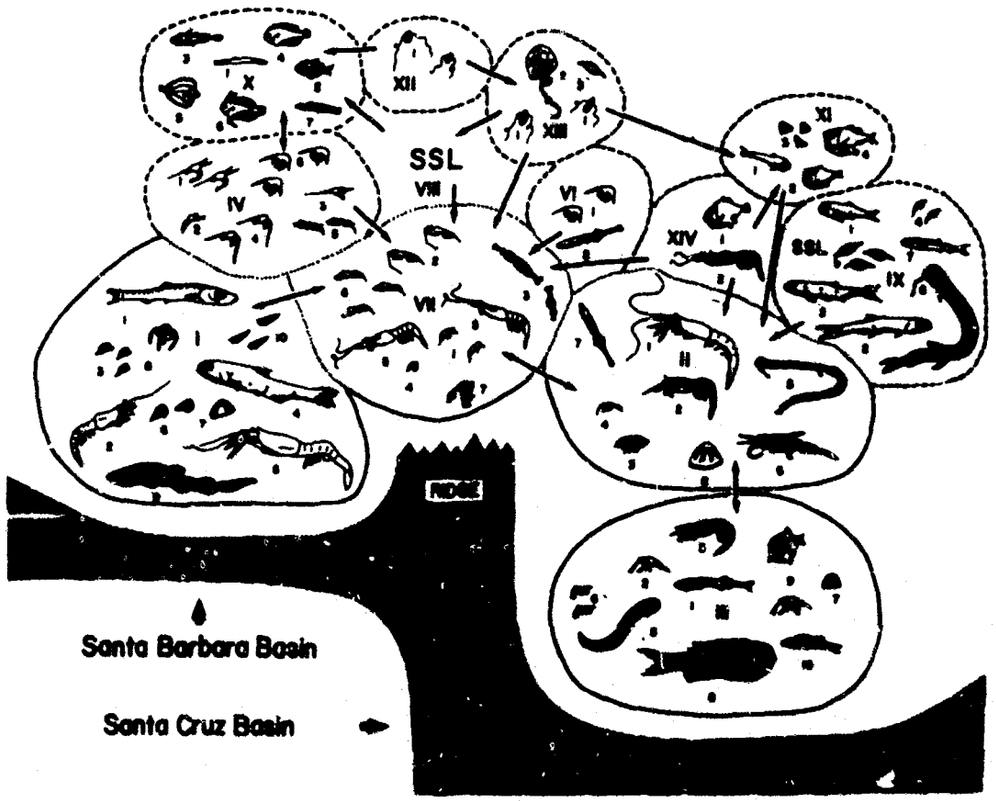

Figure 2. Animal associations in the middepths off Santa Barbara, California. Solid lines enclose species characteristic of resident communities; dashed lines enclose species characteristic of transitory groups. Dotted lines distinguish communities from juxtaposed groups. Double arrows indicate that the associations share (or probably share—dashed line) one or more species; single arrows indicate that species from transitory groups associate with other such groups or with communities, as progressively fewer factors are used to represent the system. Factors (roman numerals) and species (arabic numerals) are identified in Table 1. All parameters of the Sound Scattering Layer but one, which is in group IX, are assembled together by factor VIII (SSL). Stippling on the animals represents coloration of dark brown and black (fish) or of dark red and vermilion (crustaceans).

filters out its food by beating its sievelike legs (Barham, 1957). Within and below concentrations of the krill, the pale sergestid shrimp (5) ranged down into the daytime habitat of its predators. Small pale amphipods (1,5) and transparent arrowworms (3), which voraciously eat small zooplankton, occurred within the dense layers of krill. In the second analysis, the arrowworms, which were then identified to species, formed a distinct transitory group with three small fishes, which reportedly remain at about the same depth both day and night (Table 1: Arrowworm Factor).

II. OFFSHORE MIDDEPTH COMMUNITY. This community, together with a transitory group of offshore fishes which ascend toward the surface at night (IX:1-3, 6, 7), was more diverse than its inshore counterpart. The centers of distribution of its fish members are in oceanic waters to the south and west (Ebeling, 1962; Berry and Perkins, 1966; Pieper, 1967). Pearcy (1964) and Brown (1969) showed that the diversity of the mesopelagic fish fauna increases offshore over and beyond the continental slope, and that toward shore, the shoaling

bottom limits penetration of the more oceanic species. Two decapod shrimps dominated the resident community *per se*: a pale glass shrimp (II:1), which resembles *Pasiphaea pacifica* of the Inshore Fish Volume Community, and a bright red shrimp (2) which was almost never trawled inshore. The glass shrimp is concentrated above the darker-colored shrimp (Pearcy and Foras, 1966) and a large bright red mysid (6) (Childress, 1968). Other important members included a small, slender amphipod (4), two common medusae, one colored with patches of deep violet (3) and the other nearly transparent (8), an eel-like jet-black dragon fish (5), and the tiny semi-transparent bristlemouth fish (7) that associated with three species of arrowworms in the second analysis.

III. OFFSHORE DEEP COMMUNITY. Jet-black fishes (1, 5, 8, 10) and a vermilion shrimp (3) characterized this deep community of Santa Cruz Basin, which was sampled by deeper trawl hauls into colder water. Here, small mysids (2, 4) replaced the paler mesopelagic amphipods. Except for occasional strays, most of the bathypelagic species avoided the shallow Santa Barbara Basin, although an eelpout (5) belonging to a family of predominantly benthonic and littoral fishes, was commonly trawled in both basins. Even though they belong to the deep community (Ebeling et al., 1970), rare bathypelagic animals, like the deep-sea smelt *Bathylagus milleri*, did not appear in the final results of the analyses because they were caught so sporadically. And even most of the deep members (5-10) included in the final results were rare by middepth standards. They were less abundant by one or two orders of magnitude than the predominating bristlemouth fish (1) and shrimp (3). All fishes except the dusky hatchetfish (9) lacked gas-filled swimbladders. This community appeared relatively stable throughout the year. Its total biomass was considerably less than that of the middepth communities above (cf., Vinogradov, 1961; Banse, 1964). Many of the bathypelagic species are circumtropical or almost cosmopolitan in distribution (Grey, 1956; Lavenberg, 1964).

TRANSITORY GROUPS (IV, IX, X, XI, XII, XIII, XIV). Even though transitory species and community members generally live together at one time or another, their abundances often did not vary concordantly. Many of the transitory species behaved differently from community members, in that they did not appear to ascend at night. The silvery hatchetfishes (XI:2, 4; XIV:1) and tropical gonostomatid fish (XI:1) have large gas-filled swimbladders with relatively small gas-secreting organs (cf., Kanwisher and Ebeling, 1957; Marshall, 1960), and so would have difficulty adjusting their gas volume during rapid and extensive vertical migrations like those of some lanternfishes. In fact, there is little evidence that hatchetfishes ascend at night (Ebeling et al., 1970). Similarly, the group of fish larvae contained species like the hake (X:3) and rockfish (2) with large, balloon-like swimbladders.

Larval fishes (X) and zoea larvae of sand crabs (IV:1, 3, 4, 6) were segregated into two relatively well-defined but associated groups that contained all species represented only by larvae and young. Although group X contained only fish larvae, group IV included two species of krill. These small krills (2, 5) are mainly neritic in distribution, in contrast with the two common krills of the Shallow Invertebrate Community (VII:2, 6), which range abundantly into the California Current region further offshore (Brinton, 1962). Largest numbers of fish larvae were caught after most neritic and demersal fishes had bred during the winter mixing and spring upwelling periods when surface temperatures drop. The fish larvae added substantially to the diversity of the total fish catch.

Other transitory groups contained species with their centers of distribution located in more tropical waters farther offshore and southward. The Offshore Fish (IX) and Hatchetfish (XIV, XI) groups, however, entered the Offshore Middepth Community (II), especially in summer and fall when the California Current, containing cold subarctic water, was weakest (Brown, 1969). A cosmopolitan salp (IX:5) was also seasonally abundant. The oceanic krill *Euphausia hemigibba* was a possible indicator of tropical intrusions during summer and fall (Anon et al., 1967).

Various "jellies" (XII, XIII) occurred within and above the Shallow Invertebrate Community and its associated groups of zooplankters. The ctenophores (1) eat young krill, decapods, and fish (Fraser, 1962), and, in fact, *Euplokamis californiensis* (XIII:1) was associated with the shallow invertebrates in the second analysis. Decreasing flow of water through the trawl, increasing invertebrate volumes, and shallower hauls in warmer water identified the Volume Jelly Clogging Factor (XIII), which associated a predacious siphonophore (2) and herbivorous salp (3) with a ctenophore (1). During shallow hauls, these voluminous jellies often clogged the net, filling the cod-end chambers of the trawl and thereby obscuring the small crustaceans and fish larvae caught with them.

The transitory groups disseminated into other ecological groups and/or the middepth communities (Fig. 2, single arrows). Members of the Offshore Fish and Hatchetfish groups live among members of the Offshore Middepth Community. The jellies and groups of larvae associated among themselves, with parameters of the SSL, and directly or indirectly with the shallow invertebrates. The Trawl Haul Obliqueness Factor (VI) simply assembled the parameters distinguishing oblique hauls, usually to the surface through the habitat of the shallow invertebrates and their cohorts.

V. UPWELLING, WATER MASS FACTOR. Decreasing upwelling and rising water temperatures during summer and fall signified the annual oceanographic sequence from vertical mixing in late winter, through spring upwelling, to fall stratification (Barham, 1957; Brown, 1969). The sound scattering layer was shallowest and strongest during the upwelling months (Table 1, VII; Table 3). Barham (1957) observed that in Monterey Bay, blooms of phytoplankton follow the onset of upwelling by only one or two months, and that the peak bloom and its exploitation by grazers coincides with the predominance of a "solid type of scattering pattern."

VIII. SOUND SCATTERING LAYER (SSL) FACTOR. The upper and lower layers of the SSL descended with daybreak (see Table 2), when the intensity or "strength" of 12-kHz sound scattering diminished. The shallowest layers nearest the sound source were strongest and clearest, which may account for the apparent increase of trawling effort within them; i.e., broad and well-defined traces facilitated estimates of the proportion of a haul within the depth interval defined by the PDR trace. The measure of effort in sampling the upper SSL correlated with increasing abundances of offshore fishes, which included several diel vertical migrators (IX: SSL). Members of the Shallow Invertebrate Community and associated transitory groups varied in numbers concordantly with fluctuations in the SSL (Fig. 2: VIII). The second analysis substantiated the relationship between the migration of the upper SSL and the daily cycle of abundance of shallow invertebrates. It also showed that during the upwelling period both scattering layers were near the surface both during the day and at night (Table 3).

DISCUSSION AND CONCLUSIONS

The resident communities of deep-sea animals are presumably more stable in abundance, composition, and function than are the transitory groups. Although Fager (1963:418) defined a community simply as ". . . a group of species which are often found living together," he implied that these species coexist in well-organized, albeit open, systems having a definite structure and trophic function. MacFadyen (1963) suggested that communities should have a relatively stable composition, numerical hierarchy of species, and unity as secured by the many interlocking relationships among their member species and their environment. These relationships, which involve physiological tolerances, predator-prey interactions, and interspecific competition, account for ". . . mixtures of species which are unequally successful (because)...one or a few species, the dominants, overshadow all others in their mass and biological activity . . ." (Whittaker, 1965: 250). In the present study, for example, two species each of fishes and glass shrimps

numerically dominate the Inshore Fish Volume Community; a few krill, amphipods, and a sergestid shrimp dominate the Shallow Invertebrate Community; and a bristlemouth fish and dark vermilion shrimp dominate the Offshore Deep Community. Many of the transitory-group members, on the other hand, are either almost equally abundant or replace each other in abundance during the year and from one year to the next.

Although our model was derived indirectly through analyses of remotely collected samples, it still strongly indicates that deep pelagic animals live in associations having varying degrees of structure, even though their environment is essentially unstructured in the sense that it lacks a complex and firm substrate making up tangible cover. Beklemishev (1969) pointed out that pelagic communities differ from terrestrial or bottom communities, in that they occupy a three-dimensional, continuously moving medium containing few obvious landmarks. He concluded that pelagic communities are widespread geographically within the major oceanic water masses, which are maintained by vast current gyres as more or less permanent and closed systems. But in the present study, the relatively small and semipermanent southern California gyre may tend to integrate communities on a more local scale. Angel (1969) suggested that despite the vertical migrations of most of its members, an Atlantic community of ostracods is well organized and numerically stable within its total depth range. Also, Pearcy (1964: 96) concluded that off Oregon, "... a single community of upper mesopelagic fishes is suggested by the absence of drastic changes in the occurrence of species."

Other studies tend to substantiate the general composition of some of the communities and transitory groups resolved in the present study. Clarke (1966) distinguished three principal layers of vertically migrating animals in the Santa Barbara Basin: krills, shrimps, and lanternfish. He noted that ctenophores occur at the krill level; our second analysis indicated that ctenophores may occur with members of the Shallow Invertebrate Community, which contains the common krill. Clarke also showed that fishes and glass shrimps of the Inshore Fish Volume Community generally live below the main SSL at greater depths than do most of the shallow invertebrates (krill and sergestids). Ebeling et al. (1970) showed that four important members of the Offshore Deep Community were in a cluster of "typical bathypelagic species," that the two dominant fishes of the Inshore Fish Volume Community were invariably in the same cluster, and that the offshore fishes were often co-associated. Also, Brown (1969) and Ebeling et al. (1970) found similar pairs of co-occurring species of offshore fishes: the vertically migrating lanternfishes *Tarletonbeania crenularis* and *Diaphus theta*, the vertically migrating lanternfishes *Lampanyctus ritteri* and *Symbolophorus californiensis*, and the adult melamphaid *Melamphaes lugubris* and the pelagic young of the demersal rockcod *Sebastolobus altivelis*, both apparently non-migrators with large gas-filled swimbladders.

Vertically migrating members of the middepth communities may follow and eat the shallow invertebrates during the night, then descend at daybreak to escape predation and to rest (McLaren, 1963). Anderson (1967) and Holton (1969) showed that, during its ascent at night, the offshore lanternfish *Triphoturus mexicanus* (IX:2) eats various shallow invertebrates, including krill, sergestids, and copepods. Barham (1957) noted that the lanternfishes *Diaphus theta* (IX:1) and *Stenobrachius leucopsarus* (I:4) eat krill, young sergestids, and various copepods. Paxton (1967b) listed in order the preferred prey of common southern California lanternfishes: krill, copepods, and sergestids.

In general, species abundances were not correlated with the group of bathythermograph temperatures and seasonal parameters. This implies that although the parameters of depth, location, and time of day directly affect the associations and general behavior of the animals, the parameters of water masses such as temperatures at specific depths, affect the animals indirectly or not at all. Abundances of animals within the local, semienclosed basins vary with temporal

and physiographic changes, such as changes in time of day, location, bottom depth, and trawl depth and temperature. Perhaps the resident communities here are not greatly altered by local upwelling and water-mass flux, and the transient species move in and out of the basins according to oceanographic changes expressed more explicitly further offshore. Banse (1964: 111) suggested that "The vertical arrangement at a station . . . may not reflect the behavioral reaction of animals to actual conditions of life, but would be due to former conditions at other places."

Communities and groups relate to the 12-kHz SSL in several ways. Off Santa Barbara, strong upper and lower scattering layers were recorded in both basins (Tables 2, 3), with a third weak layer occasionally detectable below. A weak component of the second or third layer in the Santa Cruz Basin did not appear to migrate. Transitory groups of animals, some with gas-filled hydrostatic organs, seem to be associated with the SSL, which, in turn, seems to be more directly associated with the Shallow Invertebrate Community than with the other three communities. The shallow invertebrates, in turn, tend to intergrade with members of the middepth communities, probably through the vertical migrations of predators and prey. The relatively remote Deep Offshore Community which apparently interacts but little with the mesopelagic fauna, probably contributes few if any members to the complex layers of recorded sound scatterers. Its adult members are more or less restricted to the bathypelagic zone and rarely invade the middepths, although larvae and young often live in the mesopelagic zone (Marshall, 1960). Pearcy and Laurs (1966) observed that daily variations in fish abundance at different depths are noticeable only above 500 m off Oregon, implying that few mesopelagic fishes descend into the bathypelagic zone and vice versa.

Most of the sound scattering may be caused by a complex of various plankton groups and offshore fishes associated with the prevailing community of shallow invertebrates. However, the migrating component of the faint deepest layer may signify concentrations of larger predators following their prey as they ascend at night, and the weak, non-migrating component in the Santa Cruz Basin may signify small assemblages of hatchetfishes and other fishes with large, balloonlike swimbladders. Taylor (1968) observed that lanternfishes with gas-filled swimbladders were abundant in the main SSL off British Columbia, although fishes without swimbladders or with gasless swimbladders ranged below the main layer into the deep SSL. Barham (1957) attributed a solid SSL band in Monterey Bay off central California to a layer of krill and sergestids, a diffuse band to concentrations of an offshore lanternfish (IX: 1), whose swimbladder is only partly filled with gas (Capen, 1967), and a deep band to concentrations of this lanternfish and another lanternfish (I: 4) belonging to the Inshore Fish Volume Community. Davies and Barham (1969) trawled typical shallow invertebrates and siphonophores with gas-filled pneumatophores in a strong main scattering layer off San Diego. Hatchetfishes and amphipods ranged upward from this main layer into a weaker upper layer, while the mass of catchable fish was concentrated below the main layer. Barham (1963, 1966) observed physonect siphonophores and "silver" lanternfishes with gas-filled swimbladders in the main layers off San Diego and in more tropical waters to the south, respectively. In the Gulf of California, however, concentrations of lanternfishes and other middepth fishes, krill, and several shrimps apparently occur at the depths of the SSL (Dunlap, 1969).

Clarke's (1966) analysis of trawl samples from the Santa Barbara Basin substantiates the present conclusions that the Shallow Invertebrate Community forms some sort of nexus for the lower of the two main scattering layers, while most fish (1, 4) in the Inshore Fish Volume Community occur deeper. The shallow layer may be unrelated to either community. In general, Banse (1964: 103) concluded that "The main constituents of the DSL seem to be Euphausiidae [krill] in its upper portion . . . and fishes in the lower. Shrimps and squids can also be of importance." Also, Kinzer (1969) observed that the SSL in the eastern subtropical Atlantic is

composed mostly of two migrating layers, leaving a component at depth during the night. Krill and copepods are concentrated in the upper layer, while amphipods, ostracods, and arrowworms are more dispersed within, above, and below it. Aggregations of deeper fish are apparently attracted to the layer of shallow invertebrates. Nafpaktitis (1968) concluded from a literature review that two groups predominate in the SSL: shallower crustaceans (krill and sergestids) and deeper lanternfishes, especially those with gas-filled swimbladders.

Other investigators, however, found little or no correlation between catches made in the kind of midwater trawl used in the present study and depths of the SSL. Aron et al. (1967: 45) maintained that "The relatively poor correlation between biological and acoustical data [implies] that scattering at 12 kHz is not caused by zooplankton. The data further suggest that the trawl, although capable of producing large catches of lanternfishes, is not an effective device for sampling the low-frequency sound scatterers of the DSL." Pieper (1967) could find little relationship between catches of presumed sound scatterers (krill, lanternfishes, and siphonophores) and the recorded depths of the SSL. In the present study, the abundances of very few species varied directly with the parameters of the upper SSL. But copepods and other tiny herbivores (except for the crab larvae) were not included in the analyses because they were not sampled effectively in the trawl. Dense aggregations of such grazers may contribute substantially to the upper layer. Barraclough et al. (1969) showed that across the Pacific, dense concentrations of copepods, interspersed by a few krill, amphipods, and arrowworms, occur within the depth ranges of shallow layers, detected with a high-frequency (200 kHz) echo sounder.

We propose a four-dimensional spatial and temporal model of the deep pelagic ecosystem off Santa Barbara. The four resident communities are basic to its organization. Although they overlap in space and time, they are distinguishable from one another by the relatively stable concordant abundances of their member species, which are little affected by local water-mass changes. Transitory species move within and about the fundamental framework of communities and often segregate into relatively unstable groups by their different kinds of daily and seasonal movements. Many are either young of neritic and demersal species, or offshore species whose oceanic centers of distribution are located far from the distinctive local area of the southern California gyre. The complex interrelationships among the associations of middepth animals and the layers of sound scatterers imply that many species of invertebrates and fishes contribute to the SSL as they pursue their diverse activities within and between the communities and transitory groups. Therefore, the SSL *per se* may reflect many biological activities and is probably much more complex than indicated by the simple tracings of 12-kHz volume sound-scattering.

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THE DISTRIBUTION OF MESOPELAGIC FISHES IN THE EQUATORIAL AND WESTERN NORTH ATLANTIC OCEAN*

Richard H. Backus, James E. Craddock,
Richard L. Haedrich, and David L. Shores
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

ABSTRACT

Examination of about 290 midwater trawl hauls made to a depth of 1000 m in the equatorial and western North Atlantic Ocean from 1961 to 1968 suggests that at least 10 physical boundaries determine the ranges of mesopelagic fishes. The boundaries delimit six pelagic regions—the Slope Water Region, the Northern Sargasso Sea, the Southern Sargasso Sea, the Gulf of Mexico, the Caribbean Sea, and the Amazonian Region—and partly delimit four others—the Eastern Gyre and the Labrador, Lesser Antillean, and Guinean regions. It is rare for a fish species to be restricted to a single region. Rather, the fish distribution patterns noted result mainly from the occupancy of various combinations of regions by species. For warm-water species, seven distribution patterns have been noted, the most important of which are the *tropical*, the *broadly tropical* and the *Sargasso Sea* patterns. We have insufficient data for defining the distribution patterns of widespread species and species having essentially eastern and northern ranges in the North Atlantic. Each of these categories contains species that are distributed according to more than one pattern, and species in the northern group are tentatively divided into three subgroups on the basis of the southern range limit in the west. Each pelagic region has a more or less unique fish fauna with its characteristic assemblage of species in characteristic proportion, its characteristic diversity, and so on. Zoogeographically, the equatorial and western North Atlantic consists of a northern part (north of 35° N or 40° N) and a tropical part (the Gulf of Mexico through the Guinean Region), separated by a broad transition zone (the Sargasso Sea).

INTRODUCTION

Sampling the fishes of the mesopelagial, the dimly lit upper midwaters of the open ocean between about 100 and 1000 m, is difficult. Like all fishing gear, midwater nets are selective. Moreover, most mesopelagic species are daily vertical migrators, and there is evidence (e.g., Clarke and Backus 1964) that they are continually altering their depth, although most of the change comes at dusk and at dawn. Furthermore, the physical factors that appear to control the depths at which these fishes lie (transparency, temperature, and the like) vary horizontally over distances of a few miles. In short, the arrangement of fishes in the water column is continually changing from moment to moment and from place to place.

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It is for this reason, as well as for the sheer size of the area involved, that so little is known about the patterns of geographic distribution of North Atlantic mesopelagic fishes (or of any group of mesopelagic organisms in any ocean). Even less is known, of course, about what the physical factors controlling these distributions might be, although what can be called the "water mass" hypothesis is currently popular. This useful idea suggests that the ranges of pelagic animals conform to the water masses as defined by their temperature-salinity relationships. This concept was first used by Pickford (1946) and Haffner (1952) and has grown mostly as a result of Pacific Ocean studies (e.g., Bieri 1959, McGowan 1960, Brinton 1962, Ebeling 1962, Fager and McGowan 1963, Ebeling and Weed 1963, and Paxton 1967). Were the water mass hypothesis sufficient, however, the zoogeography of the North Atlantic pelagial would be very simple, for it consists almost wholly of one water mass—the North Atlantic Central Water. Our data indicate a far greater complexity, and we offer here some generalizations about the distribution of mesopelagic fishes in the equatorial and western parts of this ocean.

COLLECTING METHODS AND GENERAL DESCRIPTION OF COLLECTIONS

The principal data come from about 290 midwater collections made from the Research Vessels CHAIN and ATLANTIS II between 1961 and 1968 along the transects shown in Figure 6. Most of the collections were made with the 10-foot (3.05 m) Isaacs-Kidd midwater trawl (IKMT) (Isaacs and Kidd 1953). The mouth of the standard 10-foot IKMT is about 7.9 m^2; the bag is made of 63.5-mm (stretch) netting, with a 12.7-mm (stretch) liner in the rear. Recently we have used nets that are fully lined, with 12.7-mm mesh in the forward part and 9.5-mm mesh in the rear part. No adequate comparison has been made of the relative "catching power" of the two nets, but a small amount of data suggests that the fully lined net catches two to three times as many specimens per unit of effort as the half-lined net. In all cases a one-meter plankton net with 0.75-mm openings has been fitted to the cod-end of the trawl. The towing time per haul has ranged from two to four hours at a speed of about three knots. Net depth in most cases was measured by a time-depth recorder (Benthos Co.) attached to the trawl, but sometimes it was determined by triangulation (measuring wire angle and amount of wire out); the latter procedure is justifiable with towing warps of moderate length because the effect of the IKMT depressor is to take the belly out of the wire (Backus and Hersey 1956). Recently, net depth has been controlled by means of a telemetering depth meter (Benthos Co.).

Most of the samples have been collected in the upper 600 m, a few between 600 m and 1000 m. Daytime tows generally have been made at depths greater than 200 m. Shallower daytime hauls catch little or nothing, partly because most mesopelagic species lie at greater depths by day and partly because fish avoid the net when it is well illuminated (Pearcy and Laurs 1966). Night-time tows generally have been made at depths shallower than 300 m because many of the abundant mesopelagic species migrate at sunset to depths above this level. Hauls at twilight, when animals are vertically migrating rapidly, generally have been avoided; when made, the net has been towed between 200 m and 300 m, near the top of the range of our daytime tows and near the bottom of the range of our night-time ones. Because no opening-closing device has been used on the net, a haul may have been contaminated to some extent with specimens caught while the net was being set and hauled back. The time consumed in setting and retrieving the net has generally been less than 20 percent of the total time of the tow. The depth distribution of tows made on a representative cruise is shown in Figure 1.

In planning the sampling, approximate depths of tow were chosen so that a few successive tows would more or less cover the upper 600 m of the water column before the ship had changed geographic location too much. More refined sampling depths were chosen so as to

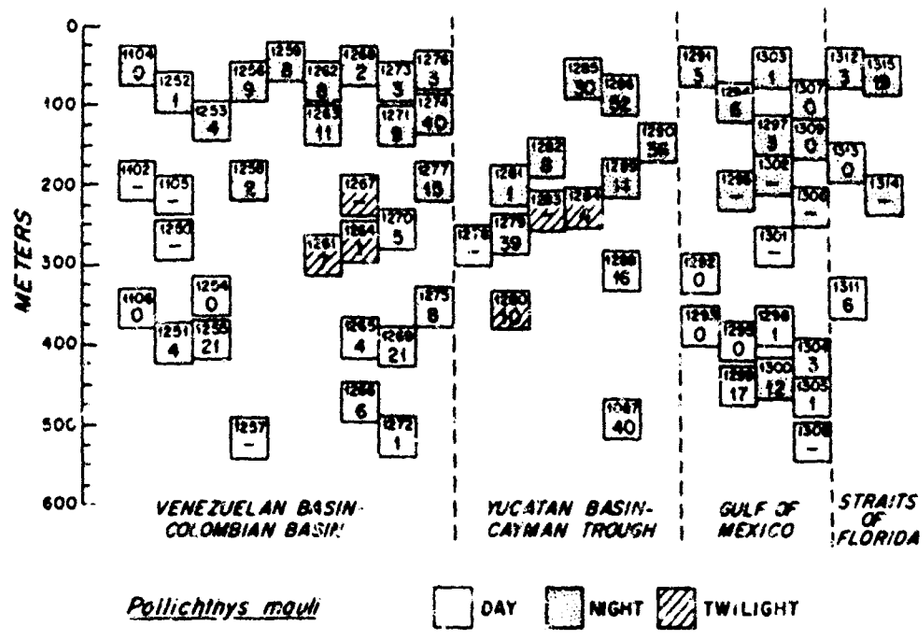

Figure 1. Sample of a worksheet showing the distribution according to depth and time of day of midwater trawl collections made on Chain Cruise 60 and upon which have been plotted captures of the gonostomatid *Pollichthys mauli*. The upper numbers within the boxes are collection numbers, the lower ones, numbers of specimens.

catch as much as possible. For help, we used the 12 kHz echo-sounder and the bathythermograph (BT). During daylight, the net was generally placed at some sound-scattering maximum (in a so-called "deep scattering layer"). During the night, when the animals sought are in that part of the water column where marked changes in temperature occur with depth, both the echo-sounder and the BT have been used. Experience has shown that sound-scattering maxima, temperature inversions, and the bottom of thermoclines and surface isothermal layers mark planes of concentration of midwater fish.

A few species of mesopelagic fishes migrate at night to the very sea surface. We have mainly caught these species in neuston nets (Bartlett and Haedrich 1968), which sample the upper 10 cm or so. Generalizations about the distribution of nine species (*Astronesthes niger, Centrobranchus nigroocellatus, Gonichthys cocco, Myctophum affine, M. asperum, M. nitidulum, M. obtusirostris, M. punctatum*, and *Symbolophorus veranyi*) are based principally upon material taken in about 115 neuston net hauls.

The fish in each collection have been sorted according to species and identified. For each species lot, the number of specimens, range of standard lengths, and displacement volume have been determined.

There is no good estimate of the distribution of sizes of the fish in the mesopelagial. It is certain, however, that many are large enough to easily elude our nets. On the other hand, it is equally well established that many mesopelagic species become sexually mature at a size as small as 25–50 mm in standard length (see, for instance, Tåning 1918, Grey 1964, and Nafpaktitis 1969). Thus, in spite of the fact that most of the fish that we have captured are small (Figure 2), adults and subadults of many species are included, especially from among the abundant and speciose families Myctophidae and Gonostomatidae.

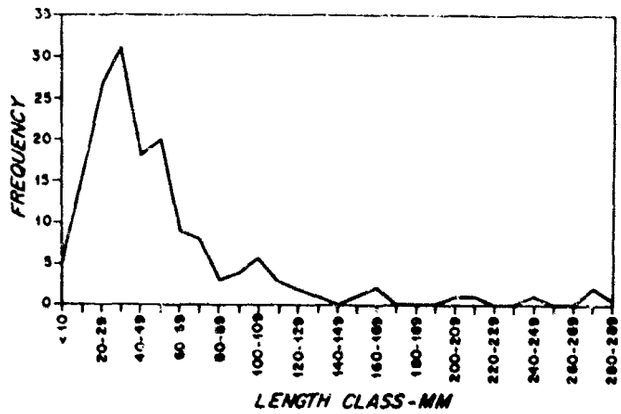

Figure 2. Frequency distribution of the maximum lengths of 155 species (about 80,000 specimens) collected between Massachusetts and the Azores on Atlantis II cruise 13.

Both the number of specimens caught and the displacement volume per unit of effort have varied widely. Figure 3 shows some of this variation in night-time collections and its relation to depth of tow and ocean region. The analysis of the relative abundance of species to one another as a function of region is made difficult by the region-dependent variation in the total amount of material caught.

The number of species taken in a collection has varied from fewer than 10 to several dozen. If the composition of a group of collections from a single ocean region is considered, it is seen that only a few species are abundant while many are rare.

After excluding from our collections epipelagic species and the young of certain littoral and benthic species that are only temporary inhabitants of the pelagial, about 350 species remain to be considered. Only about 80 of these have occurred in our collections with enough consistency so that we can remark upon their distribution with some confidence. Of these 80, three-fourths belong to the families Myctophidae and Gonostomatidae.

FAUNAL BOUNDARIES AND PELAGIC REGIONS

Our collections show that the 10 physical boundaries listed below have significance as faunal boundaries for mesopelagic fishes. In some cases, we assumed that a physical boundary had significance as a faunal boundary and then designed a cruise to test the hypothesis (especially numbers iii and v below). In other cases, faunal changes within transects were noted only after collection and study of the data. In these, if a faunal change was correlated with a physical change, the physical boundary was taken as the faunal boundary.

In order to objectively examine collection transects for faunal changes, we have developed a method of analysis based upon the distribution of the first and last captures of species within the transect (Backus et al. 1965). This method is based upon the simple principle that when a faunal boundary is crossed the first collection in the newly entered region shows a marked increase in the number of species collected for the first time during that particular transect. Similarly, the last collection made before crossing the boundary shows a marked increase in the number of species collected for the last time.

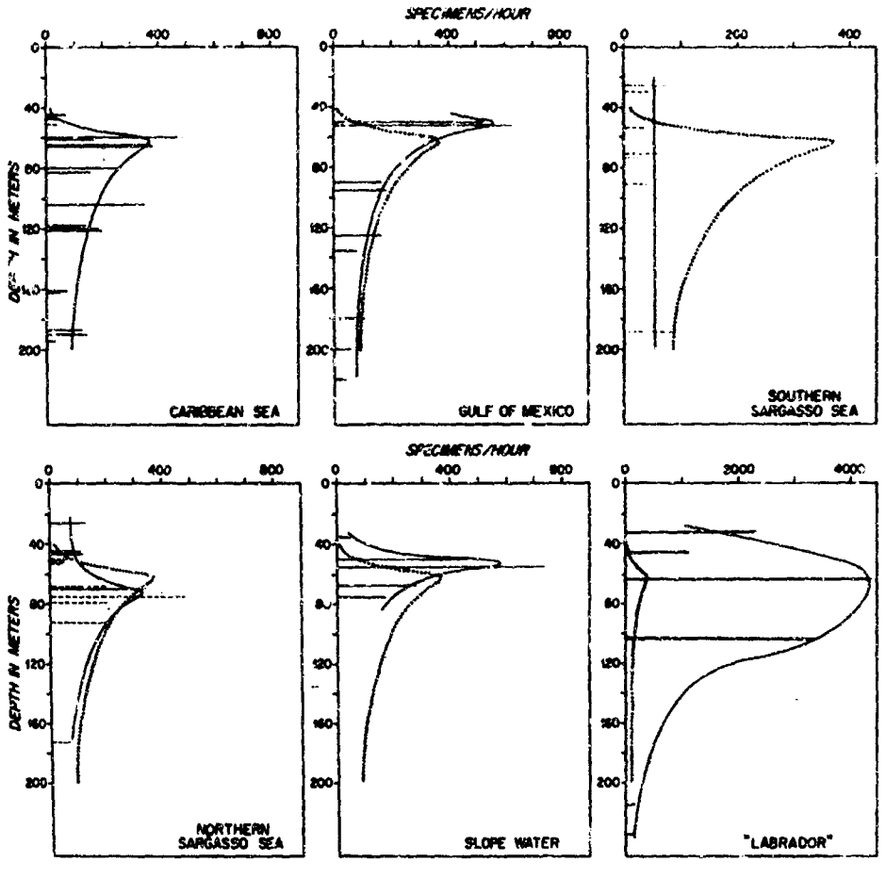

Figure 3. Number of specimens collected per hour in night-time collection in six pelagic regions of the North Atlantic plotted as a function of depth. The curves have been fitted by eye. The broken lines indicate catches that came from half-lined nets; these catches were doubled before plotting. The curve for the Caribbean Sea is used as a standard and is repeated as a broken line in the plots for the Gulf of Mexico, Southern Sargasso Sea, Northern Sargasso Sea, and the Slope Water and Labrador regions.

The following physical boundaries (together with the continental margin) mark off six pelagic faunal regions in the western and equatorial North Atlantic and partially mark off four other such regions. The regions are shown and named in Figure 4.*

i. The boundary between the Labrador-Coastal Water to the north and the Slope Water and Eastern Gyre to the south and running more or less parallel to the continental margin westward from the neighborhood of Flemish Cap to the longitude of central Nova Scotia, where it intersects the 200-m isobath. This boundary is set to follow the 200-m isotherm for 9°C. We follow Worthington (1964) in choosing this isotherm and Schroeder (1963) in drawing it.

ii. The boundary between the Slope Water to the north and the Gulf Stream and northern Sargasso Sea to the south. This boundary follows the 200-m isotherm for 15°C. Worthington (1964) is followed in choosing this isotherm, and Schroeder (1963) is followed in drawing it.

*The various attempts at dividing the world ocean into regions have been summarized by Laevastu (1963). None of the North Atlantic schemes bears much resemblance to ours.

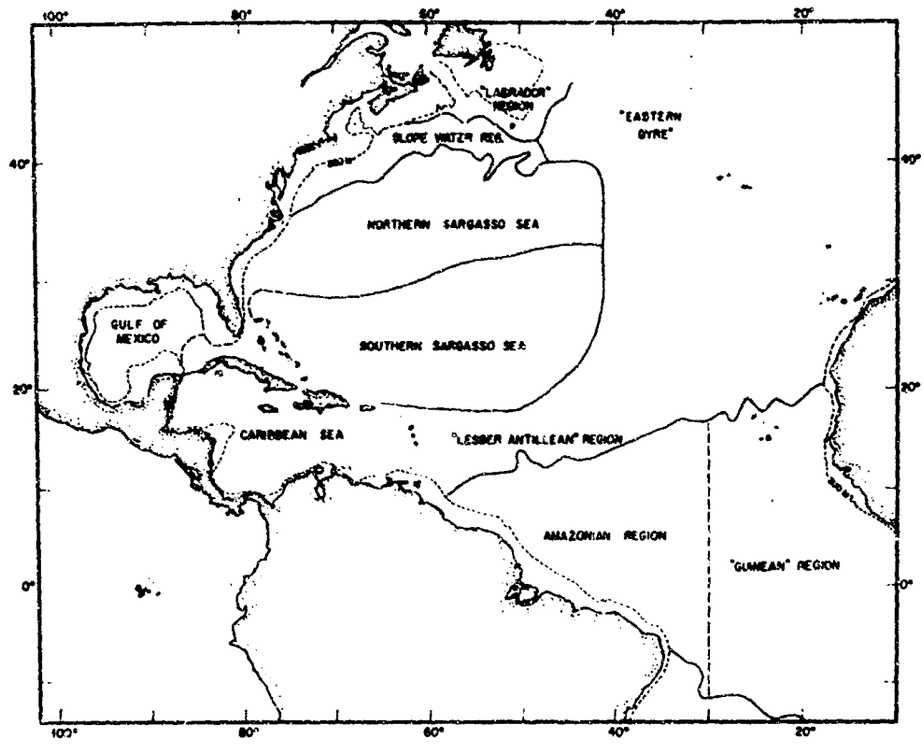

Figure 4. Pelagic regions of the western and equatorial North Atlantic. The broken lines indicate uncertainties described in the text. The names of incompletely bounded regions are enclosed in quotation marks.

iii. The boundary between the two North Atlantic clockwise gyres first described by Worthington (1962)—the southwestern (Sargasso Sea) gyre with Bermuda near its center and the northeastern gyre. The boundary follows the trough between the two gyres, running southeastward from the tail of the Grand Bank and connecting i and ii.

iv. The perimeter of the Sargasso Sea as defined by the temperature-salinity characteristics given by Worthington (1959). This boundary is used with ii to circumscribe completely the Sargasso Sea and begins at the junction of ii and iii, runs east to about 40°W, then south, southwest, and west to end near Puerto Rico.

v. The boundary corresponding to the area of the so-called thermal fronts (Voorhis and Hersey 1964), which may be the same as the North Atlantic Subtropical Convergence (Katz 1969); the boundary in Figure 4 has been drawn as the convergence is commonly drawn following Neumann and Pierson (1966: 425). This boundary divides the Sargasso Sea into northern and southern parts, the northern part being in the upper few hundred meters cooler, less stable, and more productive than the southern part (Backus et al. 1969).

vi. The boundary corresponding to the usual topographic limits of the Gulf of Mexico, except around the western end of Cuba, where the boundary is drawn to exclude from the Gulf of Mexico the region of strongest current. Because this last part of the boundary is not rigorously defined it is drawn with a broken line.

vii. The boundary corresponding to the usual topographic limits of the Caribbean Sea.

viii. The boundary between the North Atlantic Central Water and South Atlantic Central Water. This boundary is set to follow the 200-m isotherm for 14°C (Backus et al. 1965) as

drawn by Schroeder (1963). It runs from the coast of Africa at about 20°N west-southwestward to the offing of British Guiana.

ix. The northwestern boundary of the South Altantic Ocean counterclockwise gyre located off Brazil. This gyre is more or less homologous with the Sargasso Sea in the North Atlantic. This boundary is set to follow the 15°C isotherm for 200 m. The choice of this isotherm for limiting the gyre is made on the advice of W. G. Metcalf (personal communication) and is drawn following Wüst and Defant (1936).

x. A boundary running south along the meridian 30°W between boundaries viii and ix. This boundary is imprecisely drawn for want of information (and so is shown by a broken line). It is meant to divide the equatorial Atlantic into eastern and western parts, the eastern part in the upper levels of the water column being somewhat cooler and fresher and having less dissolved oxygen than the western part. These differences are associated with upwelling and the resulting increase in productivity in the waters off the African coast. It is probable that the difference in productivity is ultimately responsible for the faunal differences noted. The boundary shown follows the chart of primary production drawn by Fleming and Laevastu (1956) as modified by Ebeling (1962).

Although all these boundaries are defined and drawn as lines, it must be understood that they are not only broad ones due to the great irregularities always found, but also shifting ones. Figure 4 depicts an average situation, then, and a certain set of geographic coordinates may lie within one region on one occasion and within a second on another occasion.

DISTRIBUTION PATTERNS

Figures 6–17 are range maps exemplifying the North Atlantic distribution patterns noted so far. Each pattern results from the occurrence of species in a certain set of pelagic regions. The patterns noted and the assignment of species to them are based solely upon our own data. Seventy-eight species have been assigned a distribution pattern. Naturally, we are more confident of some of these assignments than of others. Therefore, we have used a question mark to distinguish those species about which we feel less sure. In the few cases in which published data have argued against an interpretation that we would have made from our own data, we have dropped the species in question from present consideration.

A map showing the occurrence of a species is useful only if it shows the distribution of the effort leading to the taking of the species; that is, such a map not only must show where a species was taken, but also, as far as possible, show where it might have been taken but was not. Our maps have been prepared in the following way: for each species, the number of specimens taken has been plotted, collection by collection, on work sheets that show the depth and time of day of the collections (Figure 1). From such plots the daytime and night-time depth limits of species as they occur in our collections have been established. Collections falling outside a species' depth limits have been considered everywhere inappropriate for taking that species, while collections falling inside a species' depth limits have been considered everywhere appropriate for taking a species even if specimens of that species were not actually caught in these collections. In Figures 6–17, collections deemed appropriate for taking a species, but which actually contained none, are represented by open circles; collections that contained specimens are entered as dots, with the number of specimens taken entered alongside each dot. The hazard attached to this procedure is the possibility that a species may have different depth limits in different parts of the ocean. An example is found in the phenomenon of tropical submergence, whereby certain animals living in nearsurface waters in far-northern seas are found in the tropics deep in the water column at the level of the appropriate temperature. However, the mesopelagic fishes that we have sampled well are mainly diurnal vertical migrators that come into the

epipelagial by night. We have noted only small changes in the vertical distribution of such species from one region of the ocean to another—changes insufficient to cause us to catch a species in one region but to miss it in another from want of sampling over a sufficiently wide range of depths. Figure 5, for instance, shows that *Pollichthys mauli* was not simply overlooked in the Amazonian and Lesser Antillean regions through our failure to sample at the correct temperature.

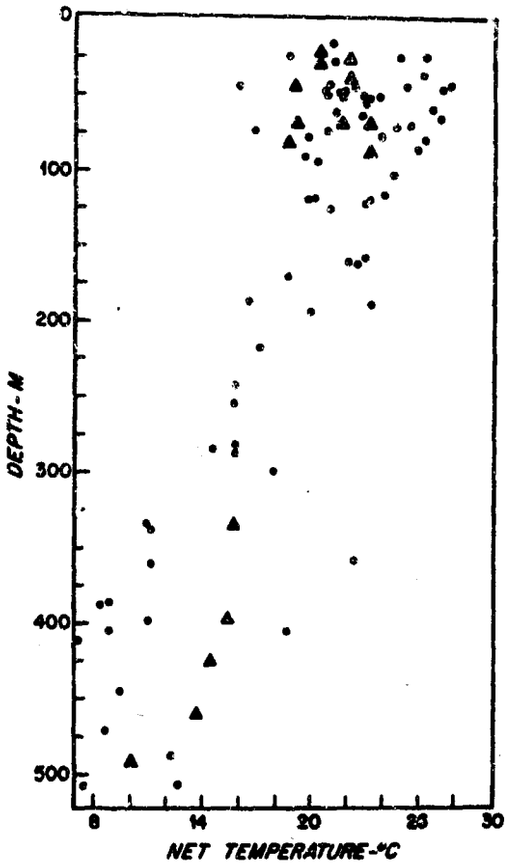

Figure 5. Temperature versus depth for collections including *Pollichthys mauli* (solid dots) and for collections over a similar range of depths in pelagic regions where *P. mauli* does not occur (triangles)

The *tropical* distribution is exemplified by the distribution of *Gonostoma atlanticum* (Figure 6). A *tropical* species is defined as one that regularly lives in the Guinean, Amazonian, and Lesser Antillean regions and in the Caribbean Sea and Gulf of Mexico. Such a species is mainly absent from the Northern and Southern Sargasso seas, although it can be found in small numbers in the northern part of the Northern Sargasso Sea, in the Slope Water Region, and even beyond the tail of the Grand Bank in the Eastern Gyre. It is presumed that such specimens are waifs, carried north to these places by the Gulf Stream. As a rule, a *tropical* species is more abundant in the Caribbean Sea than it is in the Gulf of Mexico. So far, 22 species have been assigned to the *tropical* pattern. These are the myctophids *Diaphus brachycephalus, D. dumerili, D. fragilis, D. lucidus, D. laeticeni, D. problematicus, D. splendidus, D. subtilis, Hygophum*

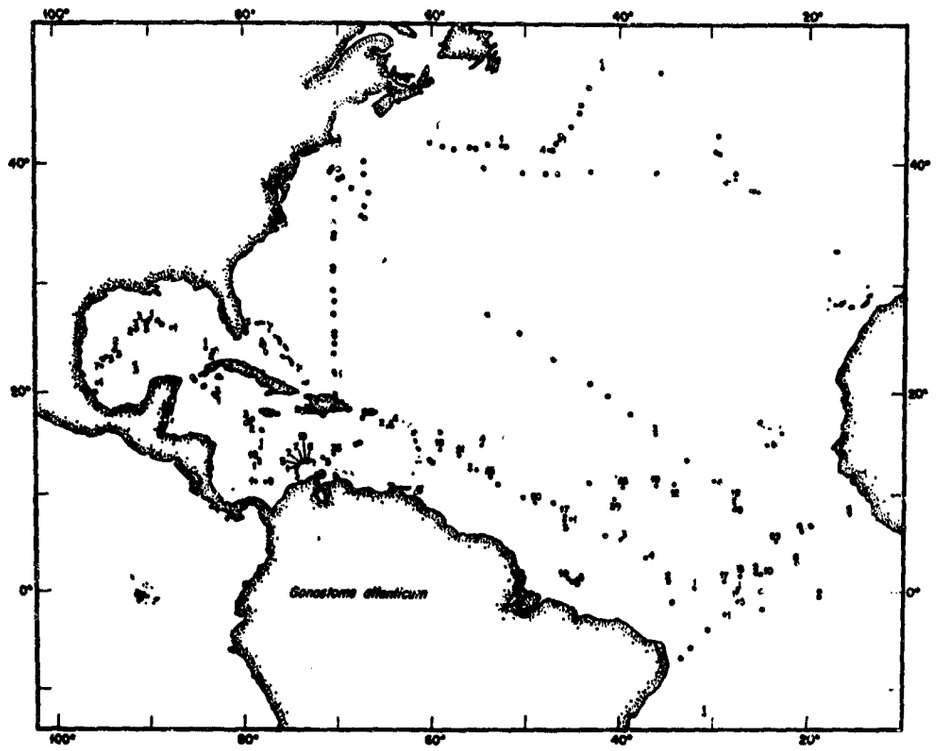

Figure 6. Distribution of *Gonostoma atlanticum* showing the *tropical* pattern. The numbers next to the solid dots show the number of specimens taken; these numbers have not been adjusted for variations in collection duration or for variations in net construction. A circle indicates that no specimens were taken in a collection at a depth deemed appropriate.

macrochir?, Lampanyctus alatus, Lampadena luminosa, Lepidophanes guentheri, L. suprolateralis?, Myctophum affine, M. asperum, and *M. obtusirostris,* the gonostomatids *Gonostoma atlanticum, G. elongatum?* and *Vinciguerria nimbaria?,* and the stomiatoids *Astronesthes richardsoni, Bathophilus pawneei,* and *Stomias affinis.*

The *broadly tropical* pattern is exemplified by the distribution of *Ceratoscopelus warmingi** (Figure 7). A *broadly tropical* species lives in the same regions where a tropical species lives but also occurs regularly in the Northern and Southern Sargasso seas and in the Slope Water Region. Small numbers are found just beyond the tail of the Grand Bank in the Eastern Gyre. As a rule, a *broadly tropical* species is more abundant in the Gulf of Mexico than it is in the Caribbean Sea (the converse being true for *tropical* species). To date, nine species have been assigned to the *broadly tropical* pattern. These are the myctophids *Benthosema suborbitale, Centrobranchus nigroocellatus?, Ceratoscopelus warmingi, Diaphus mollis, Myctophum nitidulum,* and *Notoscopelus resplendens;* also *Argytopelecus sladeni?, Diplospinus multistriatus,* and *Lestidiops affinis?*

The gonostomatid *Pollichthys mauli* has an interesting range (Figure 8). It is distributed according to the *broadly tropical* pattern except that, though present in the Guinean Region, it is wholly wanting in the Amazonian Region. We have also found *P. mauli* in the western South Atlantic, between about 23°S and the Subtropical Convergence in the offing of the Rio de la Plata. The range of *Coccorella atrata* may be similar to that of *P. mauli.*

*North Atlantic specimens of this species have generally been called *C. townsendi* (Eigenmann and Eigenmann). See Nafpaktitis and Nafpaktitis (1969).

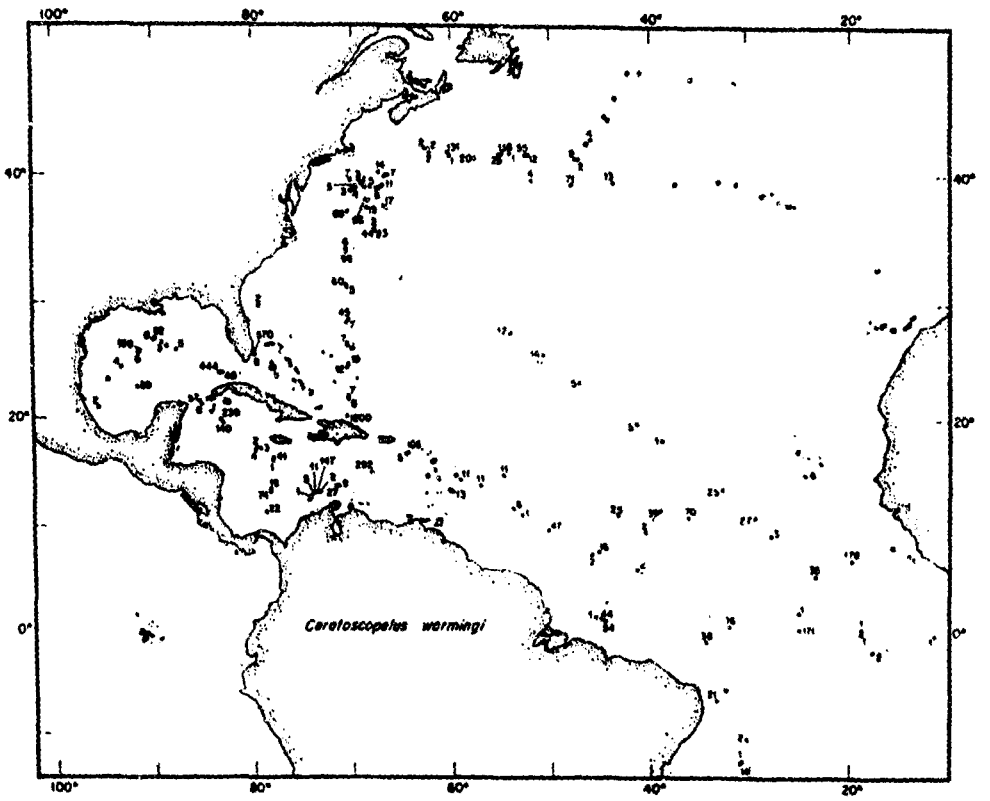

Figure 7. Distribution of *Ceratoscopelus warmingi*, showing the *broadly tropical* pattern. Compare this distribution with the distribution of its congener *C. maderensis* (Fig. 13).

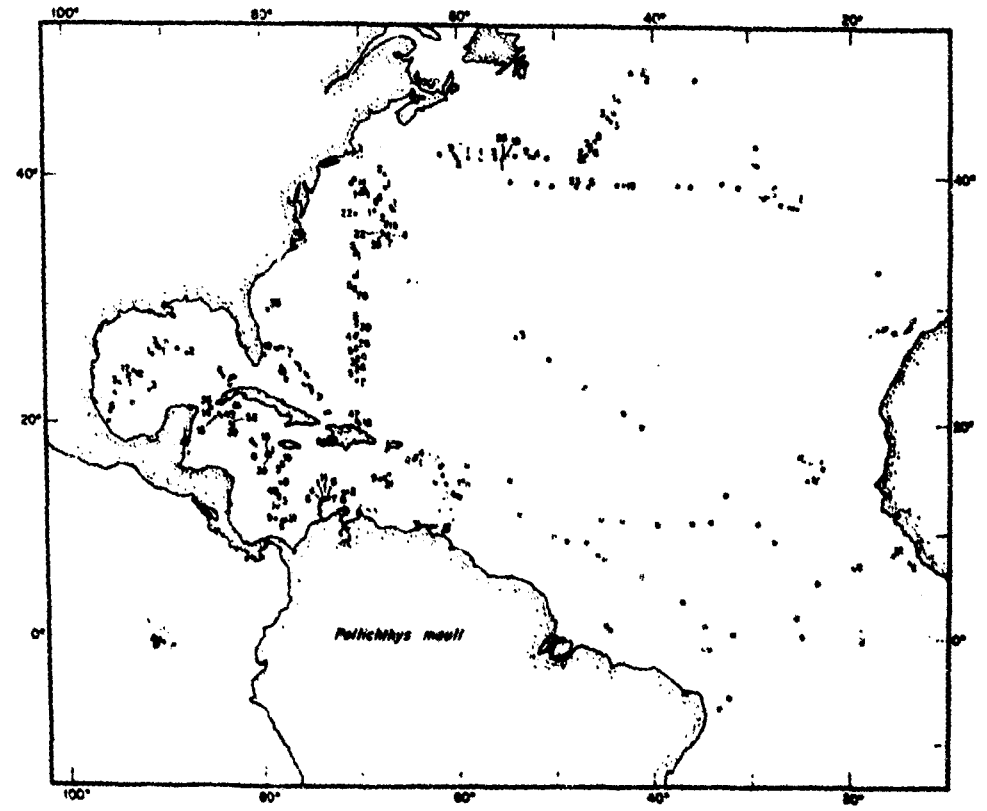

Figure 8. Distribution of *Pollichthys mauli*

Four other warm-water distribution patterns are evident, but none has had many species assigned to it. The range of *Lepidophanes gaussi* exemplifies the *Sargasso Sea* pattern (Figure 9). Such a species mainly occurs in our Northern and Southern Sargasso Sea collections. It has also been found in meagre numbers in the northern part of the Caribbean Sea, into which Sargasso Sea water spills via the Windward Passage (Worthington 1959). It is probable, however, that none of the five species assigned to this pattern (the myctophids *Diaphus effulgens* and *Lepidophanes gaussi*, and the stomiatoids *Chauliodus danae, Eustomias obscurus?*, and *Idiacanthus fasciola?*) finds its eastern limit at the edge of the Sargasso Sea as here defined. *C. danae* and *L. gaussi*, for instance, are among a list of eight "commoner" species found at 30°N, 22°W (Harrisson 1967). It is possible that fishes having this distribution pattern are adapted for living in the central least-productive regions of the North Atlantic, of which the Sargasso Sea forms but a part. *Diaphus effulgens, C. danae*, and *L. gaussi* are also found in the South Atlantic Ocean in the unproductive gyre off central Brazil.

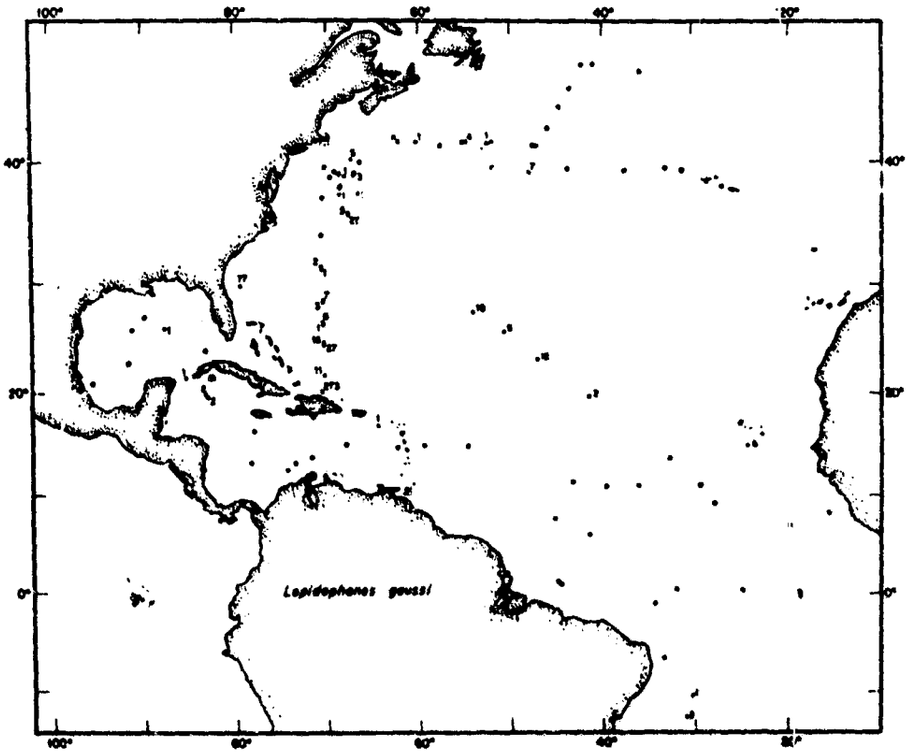

Figure 9. Distribution of *Lepidophanes gaussi*, showing the *Sargasso Sea* pattern

Diaphus garmani (Figure 10) and *D. elucens* appear to be restricted to the Caribbean Sea and Amazonian Region. *Diaphus termophilus* (Figure 11), *Astronesthes similis*, and *Cubiceps athenae* are found mainly in the Caribbean Sea and Gulf of Mexico. *Diaphus vanhoeffeni* (Figure 12) and *Chauliodus schmidti* occur only in our collections from the Guinean Region.

The essentially warm-water species, then, number 45 and are distributed according to seven patterns.

Twenty-two species have northern ranges. It is obvious that the species included are distributed according to several patterns, but it is not possible to describe these patterns because so

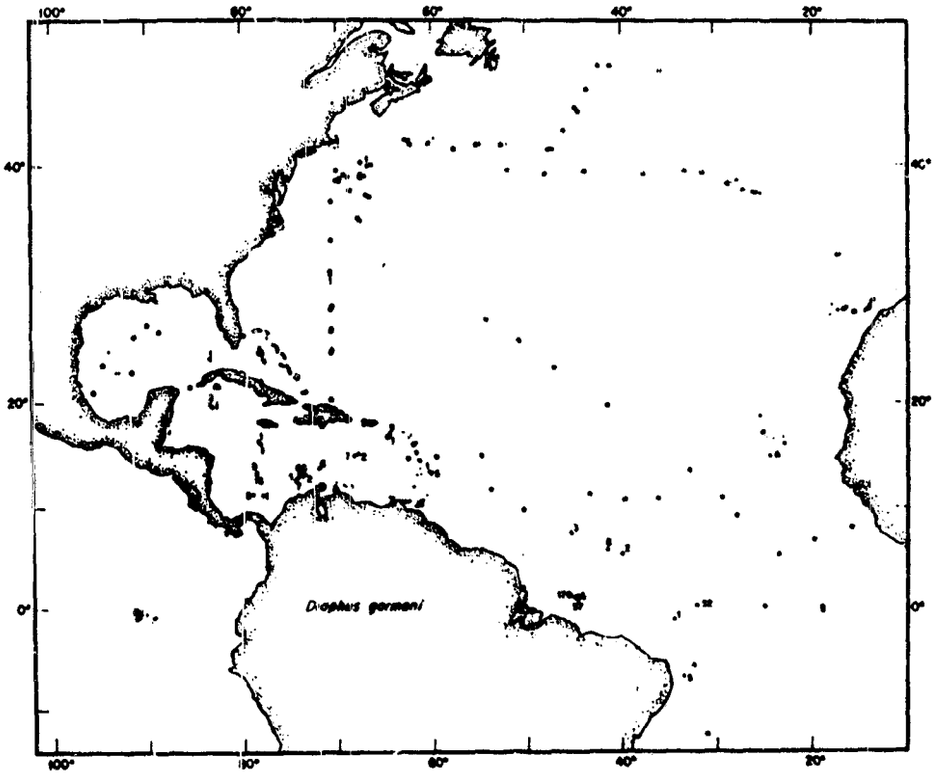

Figure 10. Distribution of *Diaphus garmani*, a series restricted to the Amazonian Region and Caribbean Sea

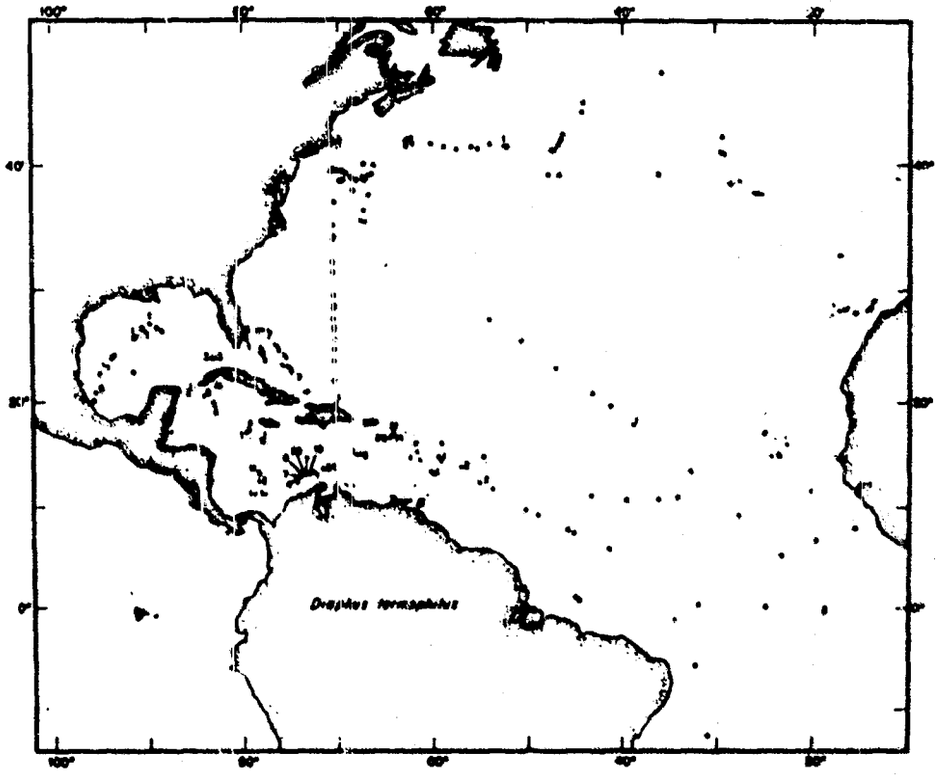

Figure 11. Distribution of *Diaphus termophilus*, a species restricted to the Caribbean Sea and Gulf of Mexico

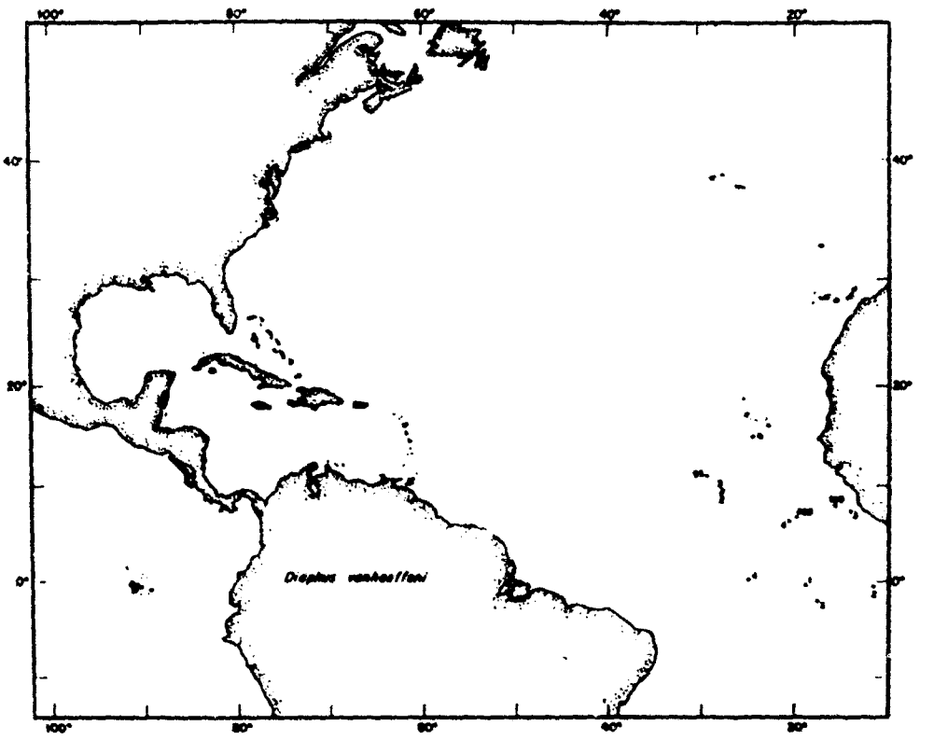

Figure 12. Captures of *Diaphus venhoeffeni*, a species frequenting the North Atlantic only in the Guinean Region. Circles indicating "no specimens" have not been used, because the amount of positive data is considered to be too small for setting reasonable depth limits for the species.

little is known about the northern and southern limits of these northern species in the eastern North Atlantic. All are widespread in European seas (Bolin 1959), and all, with two or three exceptions, are found in the Mediterranean Sea (Taning 1918). These species can be tentatively arranged in three groups according to the southern limit of their ranges in the western North Atlantic.

One group, exemplified by *Ceratoscopelus maderensis* (Figure 13), finds its southern limit at the Gulf Stream edge. This group includes the myctophids *Benthosema glaciale*, *Ceratoscopelus maderensis*, *Diaphus metopoclampus*, *Diaphus rafinesquei*, *Hierops arctic*, *Myctophum punctatum*, *Notoscopelus kroyeri*, and *Symbolophorus veranyi*, and the paralepidid *Notolepis rissoi*.

A second group finds its southern limit in the west at the boundary between Northern and Southern Sargasso seas. This group includes the myctophids *Lampadena chavesi?*, *Lampanyctus crocodilus*, *L. pusillus*, and *Lobianchia dofleini*, and the stomiatoids *Bathophilus metallicus* and *Stomias boa* (Fig. 14).

Species in the third group find their southern limit in the Gulf of Mexico although they are mainly absent from the Southern Sargasso Sea. The group includes the myctophids *Gonichthys cocco?*, *Hygophum benoiti*, and *H. hygomi*, the gonostomatids *Maurolicus muelleri*, *Vinciguerria attenuata*, and *V. poweriae*, and the stomiatoid *Astronesthes niger?*

Species of the first group tend to be endemic to the North Atlantic, species of the second group tend to be biantitropical, and species of the third group tend to range across the equator in the eastern Atlantic into the southern hemisphere. Because species of the last group can be waifed into the Amazonian Region by the westward-flowing South Equatorial Current, it may

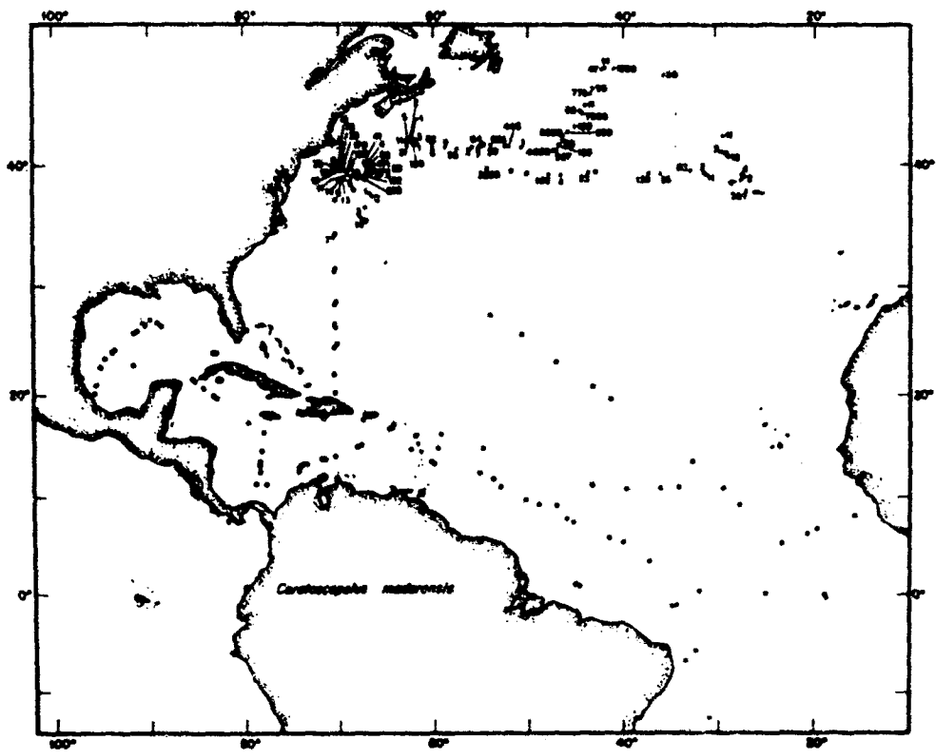

Figure 13. Distribution of *Ceratoscopelus maderensis*, showing the *northern* pattern in which the northern edge of the Gulf Stream forms the southern limit in the west.

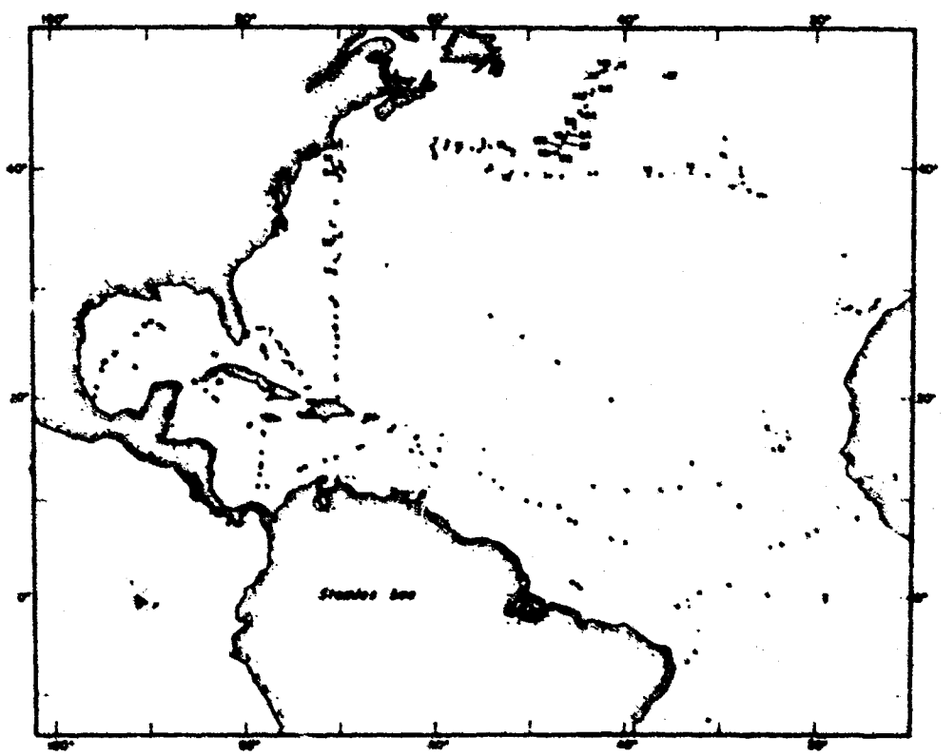

Figure 14. Distribution of *Stomias boa*, showing the *northern* pattern in which the area of the thermal fronts in the Sargasso Sea forms the southern limit in the west.

appear that such species are absent in the North Atlantic only from the Caribbean and Southern Sargasso seas.

The distribution of *Notolychnus valdiviae* (Fig. 15) is representative of a group of seven widespread species that includes the myctophids *Diogenichthys atlanticus*, *Lobianchia gemellari*, and *Notolychnus valdiviae*, the gonostomatids *Bonapartia pedaliota*, *Ichthyococcus ovatus*, and *Valenciennellus tripunctulatus*, and the sternoptychid *Argyropelecus hemigymnus*. These species have been found wherever we have collected. It is clear, however, that they are not ubiquitous in the North Atlantic, for some, if not all, have northern or eastern limits. Furthermore, certain ones inhabit the Mediterranean Sea while others do not, so that the assignment of these species to two or more distribution patterns at some time in the future is assured.

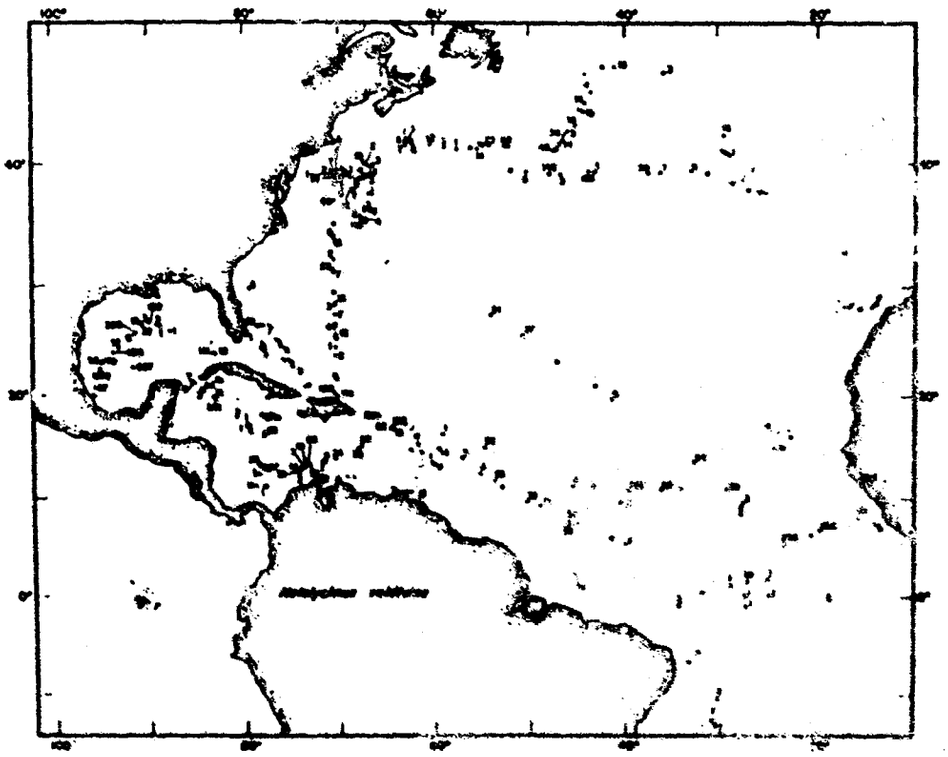

Figure 15. Distribution of *Notolychnus valdiviae*, a widespread species

A few species occur only in our few eastern collections. We can say very little about their distribution. Several patterns are involved. *Diaphus holti* (Fig. 16), for instance, is principally an inhabitant of the northeastern Atlantic and ranges south along the west coast of Africa to about 5°N, but not apparently beyond (Nafpaktitis 1969). *Electrona risso* (Fig. 17), on the other hand, crosses the equator and is said to occur all along the west coast of Africa to the Cape of Good Hope (Bolin 1959). Other species occurring only in our eastern collections are *Gonostoma denudatum* and *Argyropelecus olfersi*.

CONCLUDING REMARKS

From the variety of overlapping distribution patterns, it follows that each pelagic region is faunally distinct with its characteristic assemblage of species whose numbers are in characteristic

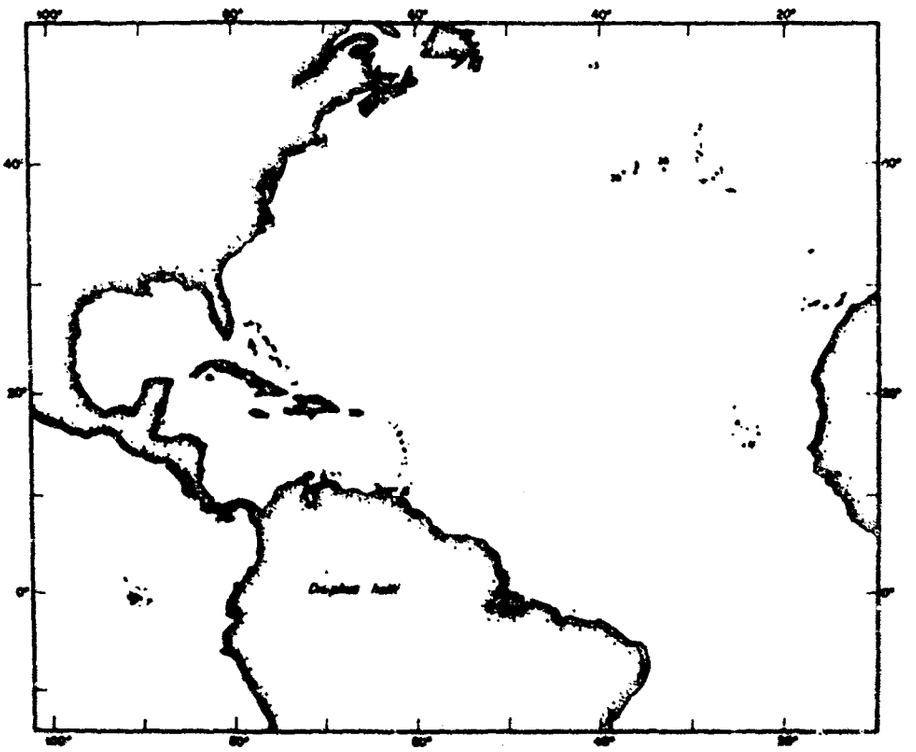

Figure 16. Captures of *Diaphus holti*, a species found only in our eastern collections. Circles indicating "no specimens" have not been used, because the amount of positive data is considered to be too small for setting reasonable depth limits.

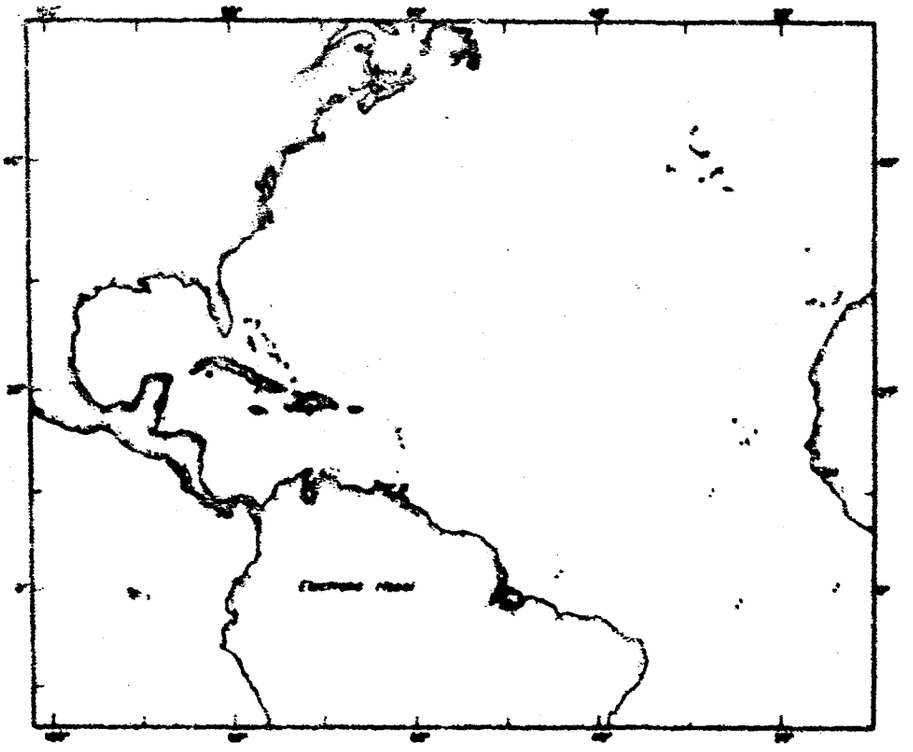

Figure 17. Captures of *Electrona risso*, another species found only in our eastern collections. Circles indicating "no specimens" have not been used, because the amount of positive data is considered to be too small for setting reasonable depth limits.

proportion, its characteristic diversity, and so on. A few inter-regional comparisons are presented in Tables I and II.

Tentatively, we can divide that portion of the North Atlantic with which we are familiar into a tropical part (Gulf of Mexico, Caribbean Sea, and Amazonian, Lesser Antillean, and Guinean regions) and a northern part (North of 35°N or 40°N), with the two parts separated by a wide transition region, the Sargasso Sea. The Sargasso Sea itself is divisible into a cooler and more productive northern part, having a mixture of northern and tropical species, and a warmer and less productive southern part, in which a few mainly tropical species live.

Table I. Some properties of shallow (<200-m) night-time collections according to region of origin. The number in parentheses is the number of collections entering each sample.

Pelagic region	No. of species	Specimens per hour	CC per hour	Diversity index (H)
Labrador (4)	56	2804	687	.71
Slope Water (5)	87	378	74	2.67
Eastern Gyre (10)	70	380	61	1.48
Northern Sargasso Sea (13)	98	149	35	3.08
Southern Sargasso Sea (7)	55	42	15	2.62
Gulf of Mexico (8)	127	260	95	2.92
Caribbean Sea (20)	153	171	58	3.35
Lesser Antillean (6)	67	97	55	3.00
Amazonian (13)	91	223	72	2.86
Guinean (8)	101	485	–	2.65

So far as the ecology of species goes, the distribution pattern is of first importance, and the principal question is why a given species is distributed in the way that it is. So far as community ecology goes, the pelagic region is of first importance, and we may ask why a certain region supports the complex of species that it does. We hope that information about the distribution and life histories of North Atlantic mesopelagic organisms will some day be adequate for answering these questions.

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Table II. Principal species in shallow (<200-m) night-time collections by pelagic region. The numbers in the first column under each region show the abundance rank within the region. The italic numbers in the second column under each region show the percentage of the total number of specimens in the region's collections that the species comprises. The species included are all of those having an abundance rank of five or less in any region.

Species	Pattern*	Region									
		Labrador	Eastern Gyre	Slope Water	Northern Sargasso Sea	Southern Sargasso Sea	Gulf of Mexico	Caribbean Sea	Amazonian	Lesser Antillean	Guinean
Benthosema glaciale	N 1	1 *82*	2 *10*	5 *5*							
Ceratoscopelus maderensis	N 1	2 *13*	1 *65*	2 *20*							
Lobianchia dofleini	N 2			1 *27*							
Lampanyctus pusillus	N 2	5 *.6*	3 *6*	3 *6*	4 *10*						
Stomias boa	N 2	3 *1*									
Lampanyctus crocodilus	N 2	4 *.8*									
Maurolicus muelleri	N 3		4 *5*								
Hygophum benoiti	N 3		5 *4*								
Diogenichthys atlanticus	W				1 *14*						
Ceratoscopelus warmingi	Bt				2 *13*	1 *57*		3 *11*	3 *11*		5 *5*
Notolychnus valdiviae	W				3 *12*	3 *9*	1 *19*	4 *10*		2 *13*	2 *14*
Pollichthys mauli	Sc				5 *6*	4 *3*					
Lepidophanes gaussi	SS					2 *15*					
Lampanyctus photonotus	?					5 *2*					
Benthosema suborbitale	Bt						3 *15*		5 *5*		
Diaphus dumerili	T							1 *12*	2 *11*		
Lepidophanes guentheri	T							2 *11*	1 *23*	1 *23*	3 *9*
Gonostoma elongatum	T ?			4 *5*						5 *6*	
Lampanyctus alatus	T						2 *16*		4 *5*		
Vinciguerria poweriae	N 3						4 *10*				
Melamphaes pumilus	?						5 *5*				
Vinciguerria nimberia	T ?							5 *6*			1 *32*
Lampanyctus nobilis	?									3 *8*	
Diaphus brachycephalus	T									4 *6*	
Diaphus vanhoeffeni	G										4 *6*

* N = Northern, W = Widespread, Bt = Broadly tropical, Sc = Special case, SS = Sargasso Sea, T = Tropical, G = Guinean. Question mark, when standing alone, indicates that it has not been possible to assign the species in question to a pattern; when following a pattern symbol, the assignment is questionable.

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DISCUSSION

Dunbar: One of my students has just finished a piece of work on the Cladocera, based mainly on the Edinburgh Oceanographic Lab collections with the plankton recorder. We find that their distribution and annual dispersal fit in extremely well with this gyre system of yours. They come out each season from the eastern part of the Atlantic, and stop at this trough. A little bit later they appear from the western side and go east, and they stop at that trough. Furthermore, there is a distinct barrier, apparently, between the northeastern trough and the Labrador Sea trough because the two populations that we find in the west Greenland area and the northeast Atlantic do not appear to coalesce at all.

Cohen: Could you tell us anything about your rationale for choosing these sampling depths?

Backus: Many midwater biological sampling programs are based on a rigid schedule of sampling depths. This has never made sense to me because the physical characteristics of the ocean change from place to place as a function of depth. That is, the only physical characteristic held approximately constant by sampling for hours at the same depth as one goes from one geographic location to another is pressure, and pressure is of small significance compared with temperature, light, dissolved oxygen, and so on. We tried to sample at a variety of depths before the ship changes location too much; we tried to sample at depths where we know there are concentrations of midwater organisms. We have used the echosounder for guidance in this, so our sampling has a strong bias in the direction of sound scatterers. At night when the organisms to be sampled are in the upper part of the water column, we have been guided by the bathythermograph, that is, the bottoms of isothermal layers or the bottoms of thermoclines, levels of temperature inversion – all seem to be planes of concentration of midwater organisms. Indeed, these often coincide with maxima of sound scattering on the echosounder recorder, and it is at these depths we have sampled in an attempt to collect as much material as possible. It all sounds very shaky, but I

think that the proof of the pudding is in the eating, in the fact that we have coherent interpretable results for at least eighty species of midwater fishes. This indicates that there is some value in this way of going about the sampling.

Mitchell: Literature indicates that the distribution of delphinid cetaceans also accords reasonably well with your faunal provinces, if you call them that, and my observations in the last four years in the central and western Atlantic, from the Equator to the Arctic, confirms that at least ten species of *Lagenorhynchus, Delphinus,* and many other delphinids, fit very well. In fact, this is the first clear indication that *Stenella caeruleoalba,* a striped porpoise that occurs up around Icelandic waters and also in the Caribbean, may follow very nicely one of your provinces.

LIGHT CONDITIONS IN THE SEA IN RELATION TO THE DIURNAL VERTICAL MIGRATIONS OF ANIMALS

George L. Clarke
Harvard University
Cambridge, Massachusetts

and

Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

ABSTRACT

Measurements of the intensity and spectral distribution of natural light as it enters the sea, as it penetrates to various depths, and as it is backscattered upward and out through the surface are reviewed. Changes in the spectrum caused by biological products, especially chlorophyll, can be detected both beneath the surface and above it to altitudes of at least 10,000 feet. The conditions of light at increasing depths are compared with the thresholds for important biological processes, including photosynthesis, color detection, phototaxis, vision, and bioluminescence. The relations of the foregoing to the control of the diurnal vertical migrations of animals are discussed.

The penetration of sunlight into the sea is of fundamental importance because it provides the energy, directly or indirectly, for the growth of all living things in the ocean. Furthermore, light exerts control over the vertical distribution, migration, and behavior of many marine animals, including those that produce or scatter sound. Therefore, a review of our knowledge of the conditions of the light in the sea and its changes with time and with depth forms a desirable background for a consideration of biological sound scattering in the ocean.

When light from the sun and sky falls upon the sea, a small percentage of it is reflected from the water surface itself. Most of the light, however, enters the sea, and the rays are refracted toward the vertical in the denser water medium. Beneath the surface, the light is absorbed and scattered by the water itself and by dissolved and particulate matter in the water, both living and nonliving. The rate at which the light is attenuated by the combined action of scattering and absorption is very different in different parts of the spectrum. The infrared and the far ultraviolet are absorbed very rapidly so that they are detectable only in the upper few meters. The red, the yellow, and the near ultraviolet penetrate more effectively, but not as effectively as the center of the spectrum. In the clearest ocean water, blue light is attenuated at the lowest rate, with the result that, below a depth of 20 or 30 m, almost all the energy is contained in this part of the spectrum. In waters that are less transparent, particularly if phytoplankton is abundant, the green part of the spectrum is the most penetrating.

If a spectrometer is placed in a watertight case with its receiving window directed upwards, the change in the spectrum of the ambient light at increasing depths can be measured. At the surface, the incident radiation from the sun and sky has its maximum intensity at a wavelength of about 495 nm. As the light penetrates the clearest ocean water, found particularly in tropical seas under most circumstances, the ends of the spectrum are rapidly reduced, and the maximum intensity moves to a wavelength of about 475 nm because that is the region of greatest transparency for pure water (Jerlov, 1968). In the temperate and polar seas and in coastal waters, the spectral region of greatest intensity moves toward the longer wavelengths, commonly coming to lie between 500 and 560 nm.

For the reactions of animals of the plankton and nekton, differences in the spectral distribution of the light at any one place are probably unimportant at depths greater than 30 m in the clearest water and at lesser depths in more turbid water, since the wavelength of greatest intensity is established within a relatively few meters and remains unchanged at greater depths in most instances (Smith and Tyler, 1967; Tyler and Smith, 1967; Jerlov, 1968). Except in localities in which a significant change in spectral distribution occurs at the depths at which the animals are migrating, measurements may be used that are made with a photometer sensitive to the whole of the visible spectrum. Using a photometer containing a photomultiplier tube, we have been able to make direct measurements in many parts of the world ocean of the ambient light for almost the entire range of intensities to which any living thing can respond.

A summary of our findings in relation to biological thresholds is presented in Figure 1 (Clarke and Denton, 1962; Clarke, 1968). Two heavy lines indicate the rates of light attenuation with depth for the clearest ocean water and for clear coastal water, respectively. The intensity of sun plus skylight incident upon the sea's surface in the middle of the day in the tropical regions or in the temperate zones in the summer is between 10^4 and $10^5 \mu w/cm^2$. The surface values for full moon and for the clear night sky are indicated. A heavy cloud cover can reduce the incident light to about 10 percent of that under clear conditions. The approximate intensity of the upward-scattered light is indicated in the case of the curve for the clearest ocean water.

The vertical dotted lines in Figure 1 show the depths at which biological thresholds of importance would be found in the clearest ocean water and in coastal water under conditions of maximum surface irradiation. The depths at which the same thresholds would occur in the clearest ocean water under conditions of full moonlight, clear night sky, and cloudy night sky are also shown. The possibility of an animal reacting to the upwelling light under the various circumstances also can be deduced from the diagram. The growth of green plants, as represented in the open sea by the phytoplankton, is seen to be limited to a depth of about 150 m under the very best conditions and is reduced sharply in the less transparent coastal water. Color vision would be possible for animals whose color sensitivity is the same as ours at depths as great as 500 m in the clearest water, but only to 100 m, or so, in coastal waters (Clarke and Denton, 1962). An intensity of light found just sufficient to cause the positive phototaxis of a pelagic crustacean (Nicol, 1959) is shown as occurring at about 650 m in the clearest water and 170 m in coastal water during the day time, but could occur at depths of over 200 m at night with a full moon or at about 70 m under starlight in the clearest ocean water.

The minimum depth at which an animal could see a small object or could tell the difference between day and night is of particular interest in relation to the ability to feed or to recognize friends and foes. The maximum depth at which animals could respond to broad-field differences in light has an important application in relation to the control of diurnal vertical migration.

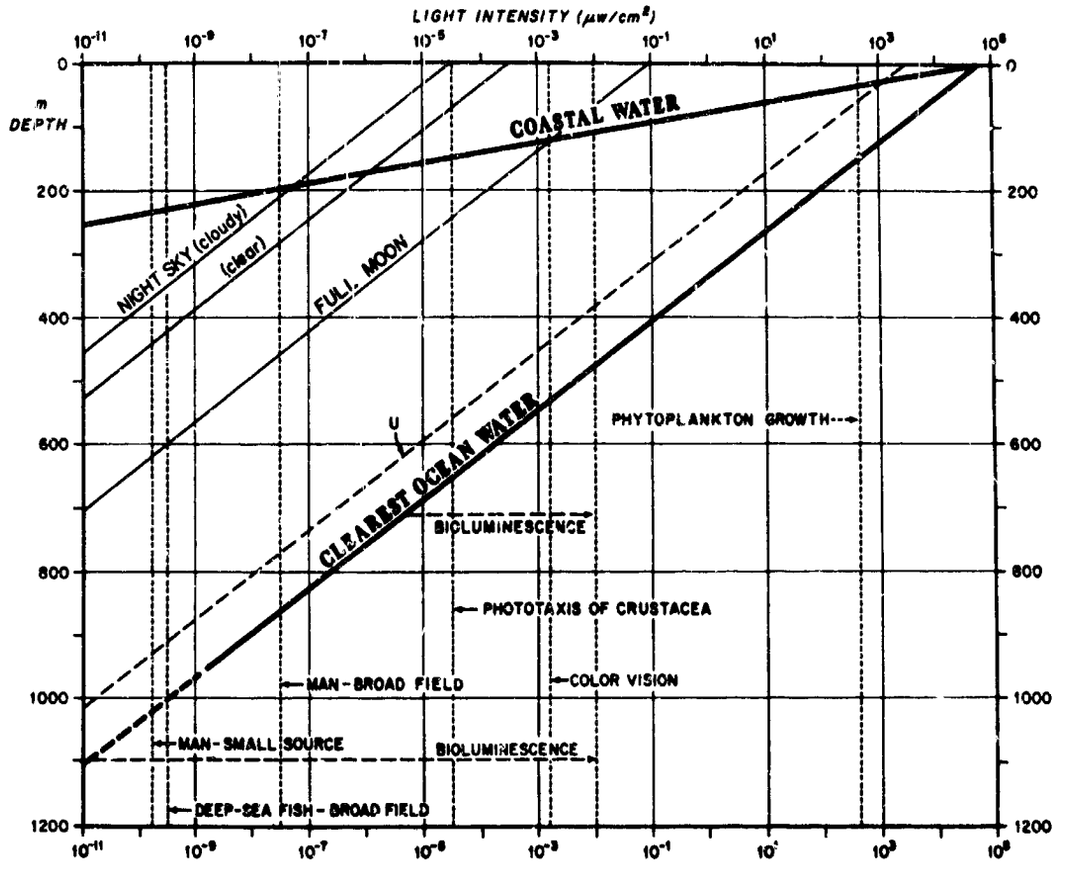

Figure 1. Schematic diagram to show the penetration of sunlight into the clearest ocean water (k = 0.033) and into clear coastal water (k = 0.15) in relation to minimum intensity values for the vision of man and of certain deep-sea fishes. The approximate minimum values for the attraction of crustacea, color vision in man, and for phytoplankton growth are indicated, as well as the range of intensity of bioluminescence in the sea. Curves are given for the penetration of light from the full moon and from the moonless night sky, when clear and when cloudy. A curve is also given for the approximate value of upward scattered sunlight (U). These curves are all for the clearest ocean water (Clarke, 1968).

Our most accurate information comes from tests on the human eye (Clarke & Denton, 1962). The threshold of illumination at which man could tell the difference between day and night would occur at a depth of about 860 m in the clearest water. The maximum depth at which light was directly measured by the photometer was 950 m; but because the optical properties of deep water are extremely uniform, it is safe to extrapolate the curve as has been done in the diagram. From anatomical and physiological considerations, it is believed that the eye of the deep-sea fish is probably about 100 times more sensitive than that of man (Clarke and Denton, 1962). If this be true, a deep-sea fish could probably tell the difference between day and night at a depth of 1,000 m in the clearest ocean water and could detect the light of the full moon at about 600 m. Even under the conditions of a cloudy night sky, the deep-sea fish could probably sense the light penetrating from the surface at a depth of over 300 m. The threshold intensity at which the human eye can detect a small source of light is indicated as about 10^{-10} $\mu w/cm^2$ (Clarke & Denton, 1962). Thus, probably both man and the deep-sea fish could recognize small objects at depths slightly greater than 1,000 m under ideal conditions, if the objects reflected or emitted light of this intensity or if they were effectively silhouetted.

The maximum intensity of flashes of bioluminescence has been measured and found to be 10^{-2} $\mu w/cm^2$ (Clarke and Denton, 1962), and this light level is indicated on the diagram. We can see that the intensity of luminescent flashes would be above that of the ambient light penetrating from the surface at depths greater than 500 m during the middle of a day in clearest water and greater than 100 m in coastal waters. The intensity of the brightest luminescence would be exceeded by the light penetrating from the full moon only at depths less than about 80 m in the clearest waters. At night without moonlight, bioluminescence is capable of exceeding the intensity of the ambient light at all depths, even including the surface waters (Clarke & Denton, 1962).

The diurnal vertical migrations of animals in the sea may now be considered in relation to the conditions of light just reviewed. The fact that the migrations recur with a daily periodicity shows that the fundamental timing must be on a day-night basis; therefore, it generally is agreed that they must be controlled primarily by light. The manner in which light acts, however, long has been a matter of disagreement. Early workers developed the theory that each population followed its own optimum light intensity as the isolumes moved toward the surface in the evening (as discussed by Clarke (1932) and by Nicholls (1933)). At night, when light fell below a threshold level, the animals moved downward. In the early morning they swam upward again toward their optimum illumination and then followed this downward to their noon depths, the actual value of which was modified by the season and the transparency of the water. This theory is illustrated in Figure 2, based on work of Nicholls (1933), which has been supported by later workers. The movements of deep scattering layers in some instances also seemed to follow certain isolumes, as shown, for example, by the observations of Boden and Kampa (1967).

Alternative theories propose that migrations are controlled by more complicated responses to the ambient light, sometimes with further modification resulting from other environmental factors, such as temperature or food (Banse, 1964). Chief among these is the theory that it is the *change* in light intensity, particularly a change above a certain rate, that acts as the stimulus that initiates this migration. Animals may undergo light adaptation or dark adaptation during the course of the day and night to alter the absolute intensity of the light at which the change is effective (Clarke, 1932). There are, however, usually upper and lower intensity limits, and the changes may be effective around a favored intensity that is optimal for each species. In most of the studies in which light has been measured, the position of each population is related to a particular isolume; but during periods of rapid light change, the animals are stimulated to swim vertically faster (or sometimes slower) than the movement of the isolume, as illustrated in Figures 3 and 4 (from Clarke and Backus, 1964).

Many other investigations of diurnal migrations, either in the field or in the laboratory, have been conducted and have been related to one or another of the foregoing theories. The more recent reports include the following: Banse (1964), Barham (1966), Boden et al. (1969), McNaught (1968), and Ringleberg et al. (1967). The studies show the paramount importance of light as a controlling factor. They also indicate how the vertical movement of large populations may cause changes in prey-predator relations and in other interdependencies at different depths and thus may influence the operation of the ecosystem in that segment of the ocean.

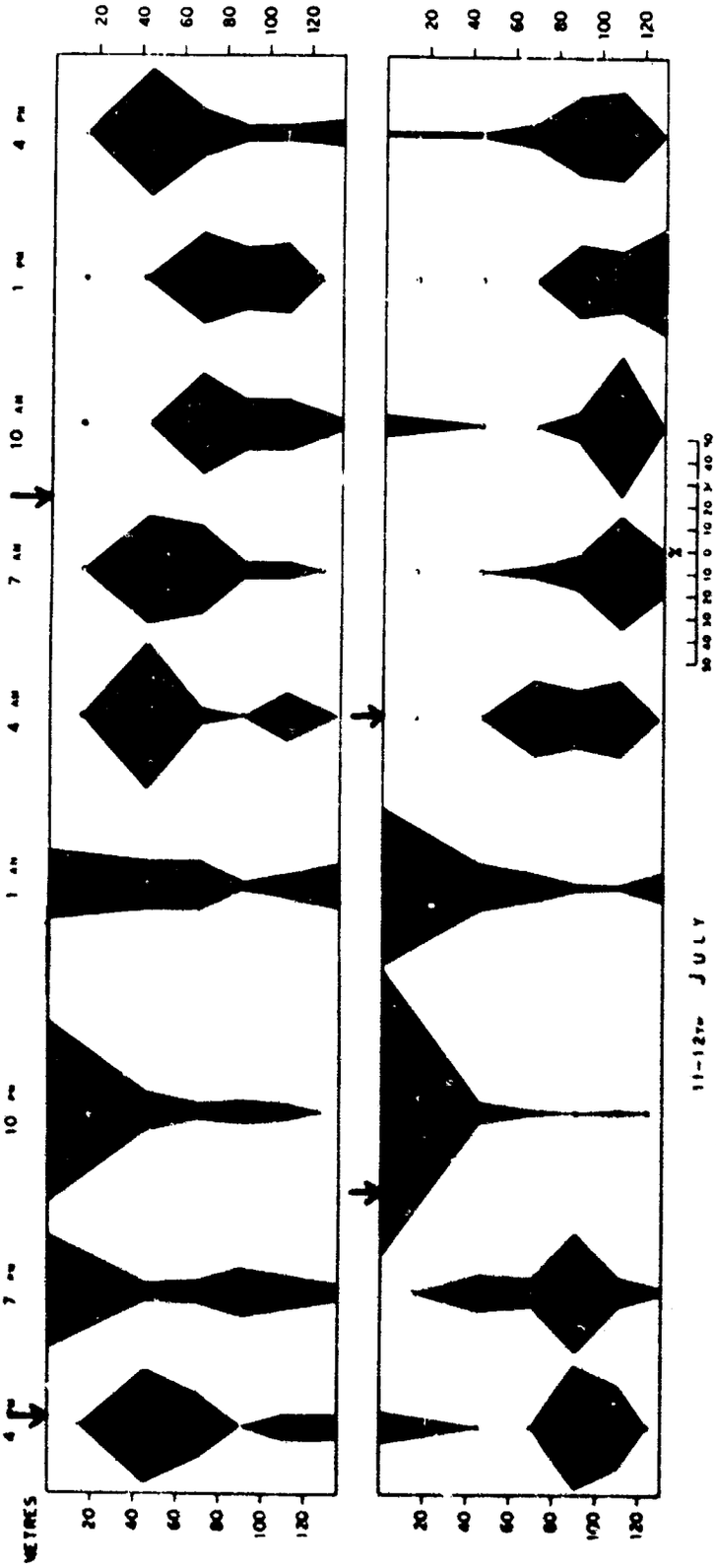

Figure 2. Diurnal vertical migration of a population of copepods (female *Calanus finmarchicus*) in the Clyde Sea area during 24-hour periods in January and in July. The times of sunset and sunrise are indicated by arrows. (Modified from Nicholls, 1933.)

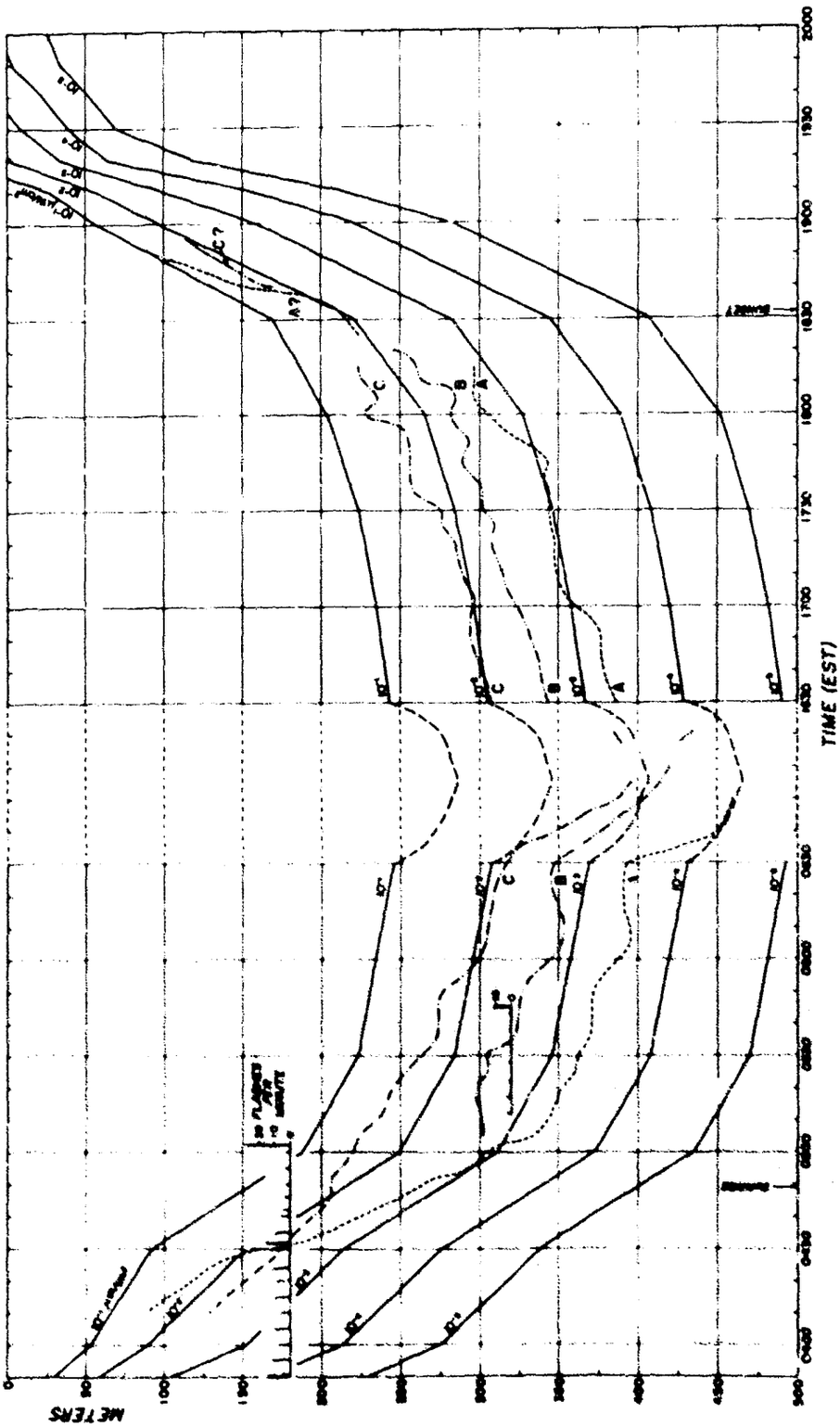

Figure 2. The vertical migrations of scattering layers A, B, and C in relation to the descent and ascent of the isolumes of ambient light during August 15, 1959, at a station 150 miles south of Nantucket. The numbers of luminescent flashes at times and depths of rapid migration and slow migration are indicated (Clarke and Backus, 1964).

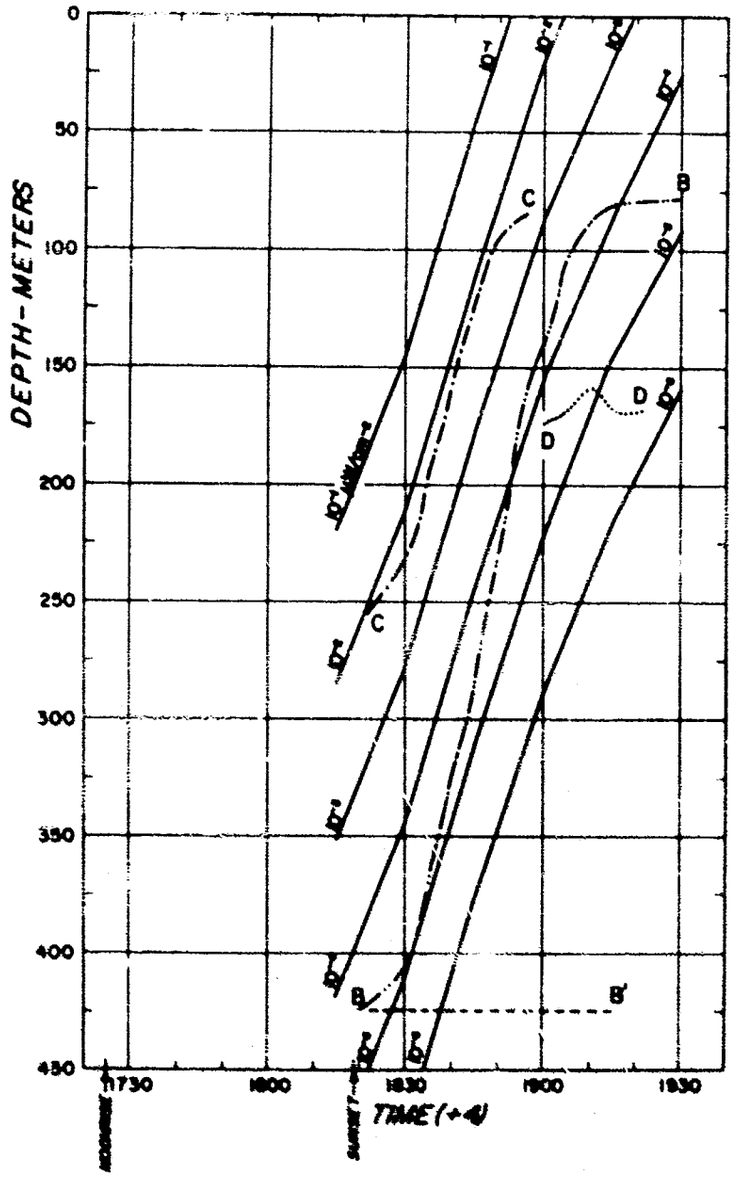

Figure 4. The vertical migrations of scattering layers B, C, and D in relation to the ascent of the isohumes during the evening of February 11, 1960, at a station 35 miles Southeast of Puerto Rico (Clarke and Backus, 1964).

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DISCUSSION

Kampa: At what intervals did you make those measurements? Were they made within minutes or half-hour periods during the trailing of the isolume?

Clarke, G.: You are talking about the last two figures?

Kampa: Yes.

Clarke, G.: These were continuous measurements.

Kampa: How are you making a continuous measurement?

Clarke, G.: We have an automatic recorder that traces the position of the deep scattering layers and of light.

time, and the light is recorded on the surface so that . . .

Kampa: Then are these surface measurements?

Clarke, G.: Surface measurements extrapolated to depth, and the positions of the isolumes are calculated from the surface measurements on the basis of transparency determinations made the day before, that day, and the following day. Transparency does not change in any important way within a few hours at any one locality. Also, there has been a feeling that the *change* in light at different depths might take place at different rates because of physical considerations, such as the effect of refraction or of scattering. To determine this, on one occasion we used three photometers simultaneously, hung at three different depths and recording continuously, and we found that the rate of dropping off of the light during the evening hours was parallel at the three depths.

Kampa: Were you using any color filters in the photometer?

Clarke, G.: No.

Kampa: What is the S-4 response of your photomultiplier? The 931A and its corollary that we have used have an S-4 response with a maximum sensitivity at about 450 nm. What is yours?

Clarke, G.: A maximum is in the blue, about 475 nm, at the region of the highest penetration of light.

Holm-Hansen: What is the effective depth at which you are measuring chlorophyll by your backscattering data?

Clarke, G.: This is a problem for the future. When we measure the backscattered light from above the surface, it is not yet known from what depth each portion of the light comes. Some comes from the first meter, some from the second meter, some from the third meter, and so on. Obviously the upper meters are the most important in contributing to the change in the spectrum, especially where there is a considerable amount of chlorophyll in the water.

Holm-Hansen: I realize that, but when you are trying to correlate your measurements with measurements of the particulate chlorophyll made by Lorenzen at sea, you got your sample at one depth. Now what depth are you sampling?

Clarke, G.: The ground truth sampling from the ship is determined by water coming in through an intake in the hull which is at a depth of two meters below the surface.

Holm-Hansen: I would like to make one comment. You described this as a new method for estimating total chlorophyll in the water column. It might be all right as an estimate of surface chlorophyll, but I think it would be very hard to extrapolate from surface chlorophyll to total productivity or total chlorophyll in the euphotic zone.

Clarke, G.: That is a very good point and one that would immediately appeal to all of us. It turns out that Carl Lorenzen has made a study in which he has investigated about 90 cases, and found that on the average the surface measure of chlorophyll was a good indication, in these instances, of the total amount of chlorophyll in the euphotic zone and of productivity.

Holm-Hansen: Could I have that reference please, if it is published and in the literature? From all the data I have seen in the literature as well as from my own data, it is rather hard to believe this relationship.

Lorenzen's report will appear in *Limnology and Oceanography*, Vol. 15, pp. 479-480, 1970. Another of his reports was published in *Deep-Sea Research*, Vol. 13, pp. 223-227, 1966, and a more recent report in manuscript form.

Holm-Hansen: I'm familiar with all of his publications, but I look forward to seeing this in print. At that time I hope I can be convinced that you and he are right.

Clarke, G.: I agree with you. I am skeptical about this, too. Certainly I think there would be circumstances when this would not be true, and I think that one would have to look into the relationship more carefully.

Raymont: I would like to make a small point about the chlorophyll. I take it that you cannot distinguish yet between what you could call active and degraded chlorophyll. This might also be a factor of considerable importance, certainly in some areas.

Clarke, G.: That is another good point, and again I have to rely on the work of Carl Lorenzen who is specializing in chlorophyll studies. He tells me that the degraded chlorophyll is 10 percent or less of the active chlorophylls in any body of water, so that even though it might have a slightly different spectral effect, it would not affect the overall picture.

Holm-Hansen: If you look at depth profiles, phaeophytin and degraded chlorophylls are usually very low, almost insignificant in the upper five or ten meters. Most of the degraded chlorophyll is deep in the water column, and so I think this will be rather insignificant for your general hypothesis.

Barham: I was wondering about changes in turbidity. I think you are absolutely right for the deep ocean, but I think we should point out that in shallow oceans you do get dramatic and sudden changes in turbidity near shore.

Clarke, G.: I certainly agree, but of course it is easier to keep track of conditions near shore. It is covering the huge areas far at sea by ship that is so time-consuming and that can be done much more rapidly from an airplane. As you already guessed, we are looking toward the application of this type of procedure to possible measurements from spacecraft.

Batzler: In your figure showing copepod distribution with time of day, I wonder if you could tell me the year that work was done. It seems to me that it is this sort of work that might have led Martin Johnson to say that the deep scattering layer migration must be biological in origin.

Clarke, G.: Well, I am sure it is. That piece of work was done in 1933.

Kampa: I will contradict the last statement because Martin Johnson has made it abundantly clear to us that he did not say that the sonic scattering layer was biological in origin. His hypothesis was that *if* this layer migrated toward the surface from various depths during the twilight period, it *might* be biological.

PHOTOENVIRONMENT AND SONIC SCATTERING*

Elizabeth M. Kampa
Scripps Institution of Oceanography
University of California at San Diego
La Jolla, California

ABSTRACT

The importance of ambient light to the vertical distributions of photo-oriented animals, some of which presumably comprise parts of sonic-scattering layers, has led biologists to trespass upon the territorial rights of physical oceanographers and to measure, rather than calculate, light at depth in the sea. Measurements of the attenuation of moonlight and sunlight with depth and of the spectral characteristics of such light have been undertaken in the coastal regions of the Atlantic and Pacific Oceans, the Mediterranean Sea, and the Gulf of California, and in the deep waters adjacent to oceanic islands (Bermuda, Madeira, and the Canaries).

Comparison is made of attenuation of light at depths greater than 200 m in the various regions, and inferences are drawn as to the photo-orientation of the animals in certain scattering layers.

INTRODUCTION

The importance of transmitted light, both natural (Boden and Kampa, 1958, 1965, and 1967; Clarke and Backus, 1956; Kampa and Boden, 1954) and artificial (Blaxter and Currie, 1967), to the behavior of certain communities of midwater animals that can be detected by echo sounders has been well established for a number of geographic regions. However, *in situ* measurements of the intensity and color of such transmitted light at the various depths inhabited by these photo-oriented, sonic-scattering layers throughout the 24-hour cycle of their migrations are relatively few. Many conclusions as to the intimacy, or lack thereof, of changes in photo-environment and vertical distribution of sonic scatterers have been based on data from midday observations of incoming solar energy at the sea surface, by human observations of sky state, times of sunrise and sunset given in nautical almanacs, tables presenting the average amount of incoming energy at sea level at various latitudes throughout the year, and, at best, extrapolations of near surface midday underwater light measurements. Changes in the state of incoming radiation from the night sky, except perhaps for lunar phases, have been disregarded. It also has been assumed that in tropical and subtropical regions, at least, the attenuation of daylight below 100 m is uniform for all oceanic regions (Jerlov, 1968).

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...transmitted light throughout the water ... recordings of incoming energy at the sea surface show a close correlation between photoenvironment and the vertical distribution of at least one sonic-scattering layer, seemingly ubiquitous in subtropical oceans. This paper summarizes some of these observations and questions the validity of assessing behavior of animal populations at depths greater than 200 m in terms of the attenuation of transmitted light in the surface layers.

INSTRUMENTS

The photometers used to obtain the data presented here have been described in detail by Boden, Kampa, and Snodgrass (1960) and by Kampa (1970b).

Mast Photometer

The collector on this instrument is a translucent plastic sphere; the sensor is a 931-A multiplier phototube. Schott BG12 and GG5 filters (1-mm thick) are in the light path at all times. A three-position shutter with a rectangular opening (exposing the entire photocathode), a pinhole (area approximately 0.001 that of the rectangular opening), and an opaque position can be changed at will from the control panel in the laboratory. By varying shutter position, it is possible to record incoming radiation throughout the 24-hour cycle and to monitor the dark current of the system.

Bathy-Thermo-Irradiance Meter

The light sensor is a 931-A multiplier phototube selected for low dark current and high sensitivity. In front of the phototube window is a free-flooding collimating tube with a flat-plate cosine collector at its outer end. Three of the shutter positions are identical with those in the mast photometer; the other two positions are opaque and are in the light path when depth and temperature are determined.

An eight-position filter holder carrying seven interference and tail-blocking filters is in the light path as well. The eighth position is left empty to allow for an easy check of filter sequence. The effective half-peak bandwidths of the filter combinations are 9 to 12 nm. The spectral regions from 410 to 537 nm can be examined with the filters in the instrument. The pressure sensor is a Bourdon-operated potentiometer, and a thermistor senses changes in temperature. Shutter (hence, function) and filter-changer positions are controlled from the ship's laboratory.

METHODS

Midday Transmission Measurements

Because multiplier phototubes are temperature sensitive, the instrument was lowered to several hundred meters with the shutter closed, and the dark current was allowed to stabilize. The shutter was then opened, and recordings were made of light at the seven wavelengths at that depth and temperature. The instrument was then raised in 50- or 100-m steps (depending on time available), and recordings were made at each level. From these records, curves representing the attenuation of light with depth were constructed, and the spectral distributions of light at the various depths were plotted.

Measurements of Photoenvironment During Periods of Change in Depth of a Selected Sonic-Scattering Layer

The submersible photometer was lowered, recording depth, until it reached the depth of the

[illegible] This passage [illegible] was [illegible] in the echo [illegible] a selected wavelength (usually between 460 and 470 nm) was [illegible] The [illegible] then was either lowered or raised, depending on whether light was [illegible] and the time and depth at which the first determined light level was [illegible] were recorded. From these observations, curves representing the change in depth of an isolume with time were plotted.

Surface Light Measurements

The surface scalar irradiance meter was introduced to the work recently, and its use is reflected in only six of the nine regions considered in this paper. The instrument is mounted as high as possible on the ship, and it records continuously. A time signal synchronized with that of the echo sounders allows a minute-by-minute comparison of changes in depth of the sonic-scattering layer with changes in incoming energy at the sea surface. This instrument is used as a monitor only and has not been calibrated in absolute units.

OBSERVATIONS

At a depth of 100 m (Fig. 1), intensities of light encountered in the nine regions sampled are separated into three groups; the average irradiance intensity of each group differs from that of the next by about one order of magnitude. The best lighted of the three 100-m groups, presumably representing water masses with the most transparent surface layers, were found in the open oceanic regions off Bermuda (Kampa, 1961), off the Madeiras, and off Tenerife and Fuerteventura in the Canaries (Kampa, 1970b). The maximum difference in peak intensity of the spectra for these four locations was threefold; the light in each was distinctly blue, with wave lengths of maximum transmission between 464 and 476 nm.

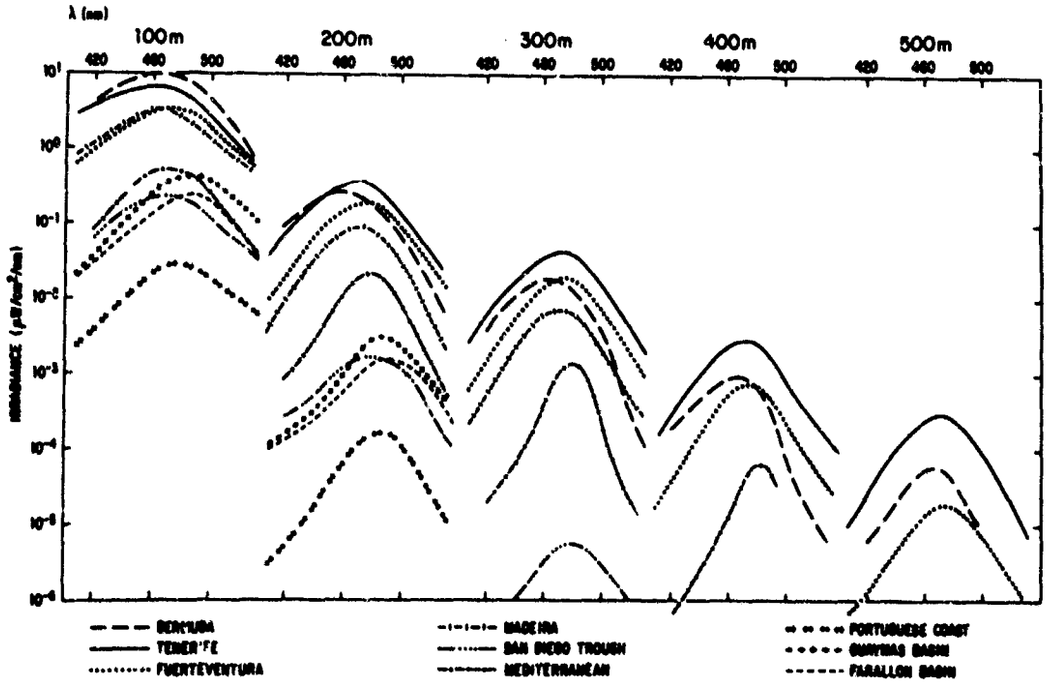

Figure 1. Intensity spectra of transmitted midday light at equivalent depths in nine oceanic regions.

The second group of regions with similar light intensities at 100 m included the more coastal deep waters of the Golfe du Lion in the Mediterranean, the San Diego Trough off southern California (Kampa, 1961), and the Guaymas and Farallon Basins in the Gulf of California (Kampa, 1970a). The range of intensities within this group varied by 2.5-fold, and the color of light at 100 m in these regions was somewhat more blue green, with maximum transmissions in the range of 476 to 486 nm.

The third group—if one region can constitute "a group"—was found in the continental slope waters off Portugal (Kampa, 1970b). There, the maximum transmission at 100 m was near 480 nm, midway between the extremes of color displayed by the waters in the second group.

At a depth of 200 m in the same nine regions, the pattern of distribution of light intensities into groups is less well defined. The four regions included in the highest intensity group at 100 m were still highest at 200 m, although light transmission in the 100- to 200-m layer had been greater in the waters off Tenerife than in those off Bermuda. Surprisingly, for the Madeiras are farther from the African coast than the Canaries, the waters in the 100- to 200-m layer off Madeira were optically denser than even those off Fuerteventura, and the light intensity at a depth of 200 m off Tenerife was four times that at the same depth off Madeira.

The transparency of the 100- to 200-m layer of the water column at the Mediterranean station was much greater than that of the California oceanic and Gulf of California stations, with which it appeared to be associated in the observations at 100 m. At 200 m, the intensity of irradiance in the Golfe du Lion, although still an order of magnitude lower than that observed off Fuerteventura, was a full order of magnitude greater than the average of intensities at the same depth in the San Diego Trough and the Guaymas and Farallon Basins.

At a depth of 300 m, the intensity of transmitted light off Fuerteventura and that off Bermuda were about equal, but the spectrum at the Bermuda station peaked near 462 nm, whereas the maximum transmission off Fuerteventura was greener near 478 nm. The irradiance level at this depth was again highest off Tenerife with a maximum intensity near 473 nm. The spectral distribution of transmitted light in the waters off Madeira was similar to that off Tenerife, but its intensity was about one-sixth the intensity off Tenerife.

The intensity of transmitted light at 300 m at the Mediterranean station was again approximately one order of magnitude dimmer than that at the same depth off Fuerteventura, but at this depth it was two orders of magnitude greater than that at the same depth in the San Diego Trough.

At 400 m, the intensity of irradiance in the waters off Tenerife was three times that in the waters off Bermuda. The light intensity at the Mediterranean station was more than an order of magnitude dimmer than that at the same depth off Fuerteventura and Bermuda.

At a depth of 500 m, the light off Tenerife was five times brighter than that at the same depth off Bermuda. The intensity at this depth off Fuerteventura in the Canaries was more than an order of magnitude dimmer than that off its neighboring island, Tenerife.

DISCUSSION

Prior to my 1970 papers, the effects of temperature on the responses of multiplier phototubes were not taken into account in our work. Instruments were calibrated in the laboratory at room temperature, measurements were made at sea, and direct inferences were drawn about the transparency of the waters off California, off Bermuda, and in the Mediterranean (Kampa, 1961). In all these, the intensity levels established for the upper 100-m layers seemed inordinately high. Calibrations of the photometers throughout the sea-temperature ranges encountered in all the observations made with instruments incorporating thermistor sensors have since been undertaken

(Kampa, 1970b), and only those measurements that could be corrected by use of information from concurrent temperature measurements are presented in this summary.

In his text *Optical Oceanography*, Jerlov (1968) contends that below 100 m, the attenuation of downwelling irradiance in the oceans is approximately uniform and that, with rare exceptions, the attenuation coefficients for all deep oceanic waters are within the narrow range of $k = 0.03$ to 0.04.

The observations presented here (Fig. 1) cast doubt on the first of these contentions. In the 100- to 200-m depth interval, significant differences in attenuation of light were observed at the nine stations, and regions that had shown similar photic structures at 100 m were quite dissimilar at 200 m. From these observations, it would seem that generalizations about photoenvironments cannot be made without direct measurements of the photic structures to depths of at least 200 m.

A comparison of the attenuation of transmitted downwelling irradiance at depths greater than 200 m in nine regions (Fig. 2) belies Jerlov's (1968) contention that the range of attenuation coefficients in deep waters is usually restricted to $k = 0.03$ to 0.04. The attenuation coefficient of transmitted light ($\lambda = 470$ to 480 nm) in the San Diego Trough approaches 0.06; that in the waters off Tenerife (0.024) is less than has been observed elsewhere. The attenuation curves for the remaining regions are distributed between these extremes. It should be noted here that the station on the continental slope off Portugal has been omitted from Figure 2

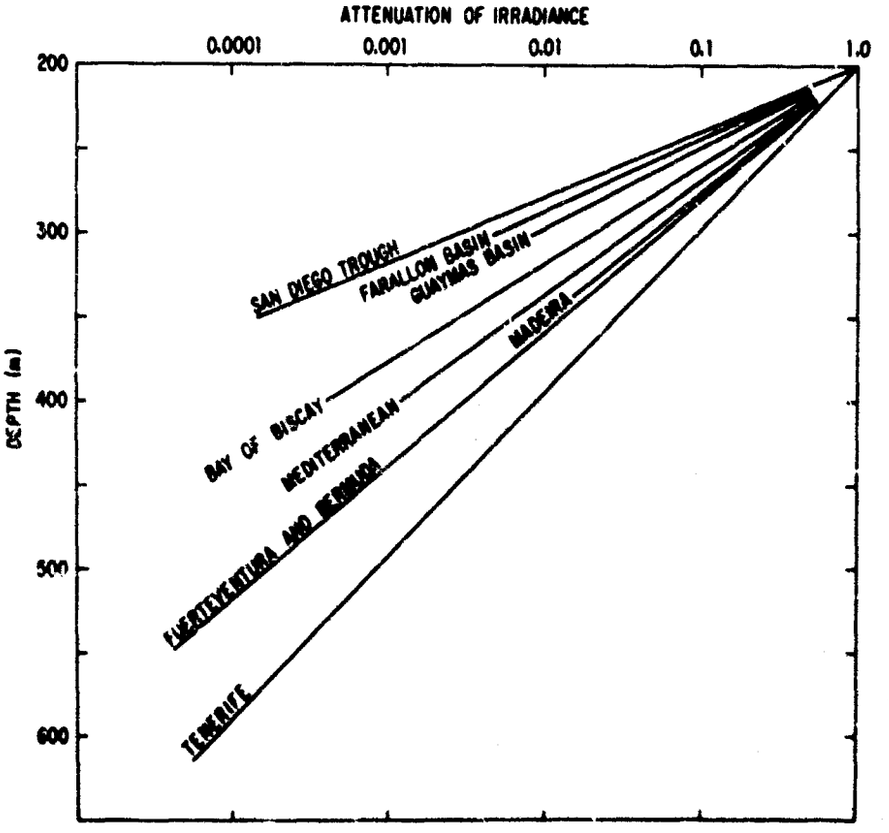

Figure 2. Curves representing attenuation of transmitted midday light ($\lambda = 470$ to 480 nm) at depths greater than 200 m in the regions illustrated in Figure 1. For ease of comparison, the values have been equated to 1.0 at the 200-m level.

because no measurements were made there at depths significantly greater than 200 m. Information on the transparency of waters below 200 m in the Bay of Biscay (Boden, Kampa, and Snodgrass, 1960) is included in Figure 2. These data were presented as percentages of surface irradiance and could not be corrected for inclusion in Figure 1.

This elaboration on conditions of underwater light may seem obscure to students of sonic scattering *per se*, but to the mesopelagic organisms responsible for the sonic scattering considered here and to biologists attempting to interpret the behavior of these animals, detailed information on the photoenvironment is essential. At the station off Fuerteventura, it was observed (Boden and Kampa, 1967) that, during twilights on successive evenings, the animals presumably responsible for a particular sonic-scattering layer could detect differences in sky state that were imperceptible to human observers aboard ship. These differences, recorded by both surface and submersible photometers (Fig. 3), were such that at the same time on successive evenings, the depth of the scattering layer and that of the isolume with which the layer had been associated on the two days varied by as much as 85 m.

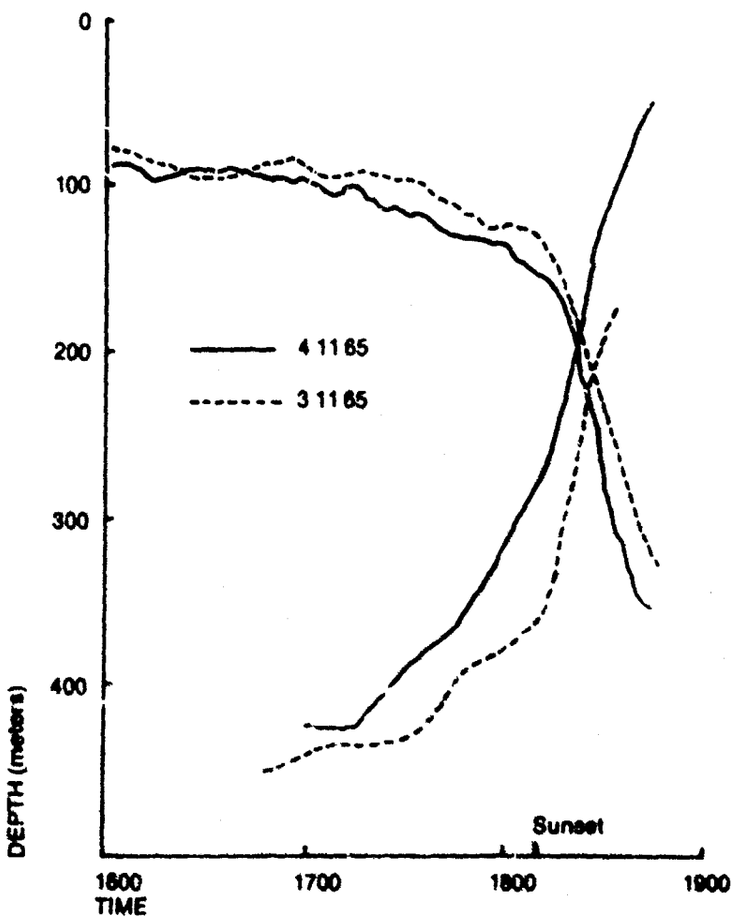

Figure 3. Curves representing the decrease of light intensity at the surface (upper left to lower right) and the corresponding rise of an isolume (λ = 474 nm) with which a sonic-scattering layer was closely associated during two successive dusks (lower left to upper right). (After Boden and Kampa, 1967.)

The remarkable similarity in the influence of photoenvironment on sonic scatterers that migrate diurnally, even in locations quite remote from one another, is emphasized by a comparison of the observed midday light-depth relationships (Fig. 4) of six sonic-scattering layers, four in the eastern North Atlantic (Kampa, 1970b) and two in the Gulf of California (Kampa, 1970a). Although the regions are remote from one another and the midday depths sought by the sonic scatterers differed by hundreds of meters, the intensity of irradiance encountered by these mesopelagic animals was at most six-fold at the wavelength of maximum transmission. If the most oceanic station off Madeira is disregarded as having a quite different fauna from that of the more coastal regions, the intimacy of the relationship between photoenvironment and midday depth of the sonic scatterers at the remaining five stations is even greater, and the extremes of irradiance intensities encountered by the layers differ only by a factor of two.

Observations such as these indicate that it is now time to measure, rather than calculate, light conditions at the depths of any sonic scatterers that appear to be photo oriented before drawing conclusions about their behavior.

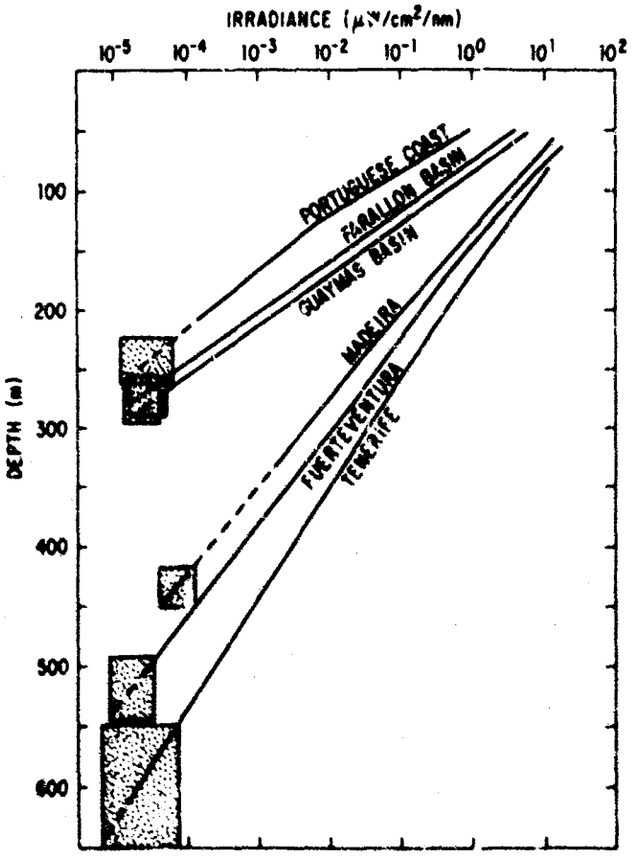

Figure 4. Relationships between irradiance at 480 nm throughout the water column and midday depth of a sonic-scattering layer in four regions of the eastern North Atlantic and in two regions of the Gulf of California. Stippled areas indicate vertical extent of scattering layers on echo-sounder records.

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DISCUSSION

Johnson: What acoustic frequency were you using to measure this layer?

Kampa: The ones in the eastern North Atlantic were all taken from the MUFAX precision echosounder working at 10 kHz, and the ones in the Gulf of California were done with a 714/715 Raytheon. It was operating at 25 kHz.

Barham: From the last figure is it your inference that there are distinct differences between scattering layers in deep oceanic areas and in coastal areas?

Kampa: Yes. This particular set of layers that we are watching and that I am concerned with I have found wherever I've gone, and although their depth range at midday may differ from place to place by as much as 250 meters, they are all associated with light that is within a very, very narrow range of intensity.

Clarke, G.: I don't quite understand the point that you are making about a difference in our results or interpretation. Would you kindly repeat it?

Kampa: I don't really see that there is any difference. It is just that I threw away my slide rule several years ago and I have been using a light meter instead.

Clarke, G.: I think that it is a very interesting observation that different scattering layers in different parts of the ocean seem to congregate at certain isolumes of absolute value, and that these isolumes occur at different depths according to transparency, so there must be something of general biological significance about these light levels. You are talking about different

geographical areas separated by many miles; we were talking about the control of the same scattering layer in the same place and at different hours of the day. We did not have facilities for making continuous records of the light at every depth throughout the day. We felt that this was not necessary because, having once determined the transparency, the transparency is not going to change within 24 hours; therefore a record at the surface, a continuous record, would be sufficient for determining the position of the isolumes.

Kampa: In every area where people are going to try to interpret the photo-orientation of animals, if such exists, I think that a continuous recording should be made of light at the surface because you and I don't have good enough vision to detect changes that the instruments and the animals at depth can, and I agree with you; but at midday one should examine the transparency of the water and preferably at a number of wavelengths.

Clarke, G.: I agree with you entirely, and this should be done with as much detail as is feasible under the circumstances. I think that a very important point has been brought out by your data: When we are talking about greater depths, that is, more than 200 or 300 meters, very slight differences in the attenuation coefficient will make very great differences in the position of a given isolume.

Kampa: That's quite right. The main thing is that anybody who is trying to interpret the behavior of animals at depth in terms of light should give up the notion that the attenuation in all oceans is the same at depths greater than 100 meters.

Clarke, G.: I think what you are saying is mostly a matter of misunderstanding. It is true that the deeper water is extremely transparent everywhere, but as I just said, little differences in transparency over great depths will have a very profound effect. In the ocean as a whole, the differences in transparency of the water in the deeper layers are relatively constant as compared to the surface layers of water, and I think that is where your argument is.

Clarke, W.: I think the thing we should look at is that we are progressing to more and more refined types of measurements. Admittedly, we started off very crudely, and I think we have to bear in mind that there is a history here we are working through. I agree with you that we should monitor the incoming radiation at the surface and also make these measurements at depth continuously in association with the scattering layers. But we have to remember that we started very humbly, and with the financial situation the way it is, we're still sort of humble.

Kampa: No, we don't need to be humble. I have a description of this little instrument. It can be reproduced for $1,500 including filters.

Clarke, W.: I agree, but I think that the one thing we are neglecting is that there was a history here and that we must look at things in perspective.

Kampa: I agree with you, but at the same time I don't believe in going on dealing with these generalizations when we have the equipment to do it now.

Clarke, W.: I'm not arguing with you on that point, and we are doing similar work at our laboratory, we are evolving a new type of system similar to yours.

BIOLUMINESCENCE IN SONIC-SCATTERING LAYERS

Brian P. Boden*
Scripps Institution of Oceanography
University of California at San Diego
La Jolla, California

ABSTRACT

Bioluminescent displays in sonic-scattering layers (detected by various types of echo sounders) are discussed. In the first experiment, a single photometer was employed in British Columbia waters. In recent experiments, dual meters have been used to determine spontaneous luminescence.

Spontaneous bioluminescence was monitored in the Gulf of California and in the San Diego Trough. The measurements were made simultaneously above, in, and below sonic-scattering layers. Such measurements were also made in the Eastern Atlantic.

INTRODUCTION

This paper is designed to emphasize the dependence of biological observations of mesopelagic fauna on acoustical techniques. It deals with bioluminescence in sonic-scattering layers (as portrayed by conventional echo sounders). The results presented here are not in chronological sequence but in geographical order.

Experiment I

In Saanich Inlet, British Columbia, a single photometer was used. For the detection of the scattering layers, we used two Furuno echo sounders, F7C1 and F7C5, operating at 50 and 200 kHz, respectively; an EDO echo sounder operating at 12.5 kHz, and a Minneapolis-Honeywell precision depth recorder operating at 12 kHz.

Scattering-layer patterns are rather peculiar in this fjord (Clary, B.M., W.E. Barraclough and R. Herlinveaux, 1962; Barraclough, W.E., Le Brasseur, R.J. and Kennedy, O.D., 1969). Between 80 and 100 m there is an abrupt oxygen deficiency that apparently discourages farther downward migration of the layers at the sunset twilight time. The ecological aspects of this have been discussed (Boden and Kampa, 1965).

Apart from a few spectacular flashes of luminescence, the general level was low. We attribute these flashes to perturbation by the meter, and the general low level to a sparsity of plankton at that season.

Because these results have been published, no figures are presented.

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Experiment II

Measurements of bioluminescence were made in the Gulf of California (lat. 22°33.7′ N, long. 109°06.0′ W) between 2005 and 2215 hours on January 9, 1968 from the R/V *Thomas Washington* (Scripps Institution of Oceanography),[1] and in the San Diego Trough (lat. 33° N, long. 30° W) between 1645 and 1745 hours in January 4, 1969 from the R/V *Velero IV* (University of Southern California).[2] These measurements were made simultaneously above, in, and below a sonic-scattering layer revealed by an echo sounder on board ship.

The purpose of the experiments was to obtain a comparison with similar determinations made off the Canary Islands on the SOND expedition of RRS *Discovery*, using the same technique and instruments (Boden, 1969). The technique is a simple scintillation technique. The prototype of the instrument was described briefly in *Nature* (Boden, Kampa, and Snodgrass, 1965). It was subsequently modified, and a detailed description is presented by Boden (1969).

In brief, the instrument consists of three pairs of radiance meters with collimating tubes restricting the angle of acceptance of their multiplier phototubes. Each meter contains a small wire recorder and its powerpack. The meters are mounted on a rack so that they have a squint vision (strabismical) and survey a roughly spherical, common volume of about 1 liter at a distance of about 1 m. They are interconnected, and both amplitude and frequency are monitored. Any luminescent flashing in the common volume is assumed to be spontaneous because it has not been disturbed by the instrument itself. These are the only flashes considered in the analysis, although each meter is capable of recording any flash in its own survey cone. The pairs of instruments are suspended at intervals on hydrographic wire and scan laterally.

The flashes are recorded by the wire recorder and later transferred to magnetic tape.

The final analysis requires a rather elaborate readback system. It is presented graphically on Speedomax and Sanborn recorders, numerically on a digital recorder, and is monitored visually on an oscilloscope. Auditory monitoring is also possible with a tape recorder. This systematization was deemed necessary for critical cross-reference, though reservations regarding the efficacy of the system are maintained (Boden et al., 1965).

Only one experiment was undertaken in the Gulf of California.

The number of coincident, presumably spontaneous, flashes per minute recorded by the Speedomax recorder is shown in Figure 1. The recorder is gated, and each bar of the histogram represents the total coincident flashes recorded in 1 minute. The digital recorder is similarly gated and provides the numerical countout of the flashes depicted in the histogram. Presentation in tabular form of the numerical countout is considered to be superfluous here because it is represented on the ordinates of the figures.

Wire to tape recording was at 7-1/2 inches per second (ips) and the readback was at 1-7/8 ips.

At the time of lowering, the echo sounder, a 714-715 Raytheon, operating at 21 kHz, revealed layers between 125 and 175 m. This is rather deep, but may be accounted for by clear water and a bright moon.

Figure 1A shows a record of the number of simultaneous flashes seen by the uppermost pair of meters while suspended at 100 m (just above the sonic-scattering layer). The cast was raised 75 m, and Figure 1B indicates considerably greater luminescent activity in the surface layers at 25 m.

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[1]Expedition MV 1968-I supported by National Science Foundation Grant GA-1300 and N.S.F. Grant GB-4672 to Prof. Carl L. Hubbs, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California.

[2]Cruise 990 of the R/V *Velero IV*, University of Southern California, Los Angeles, California.

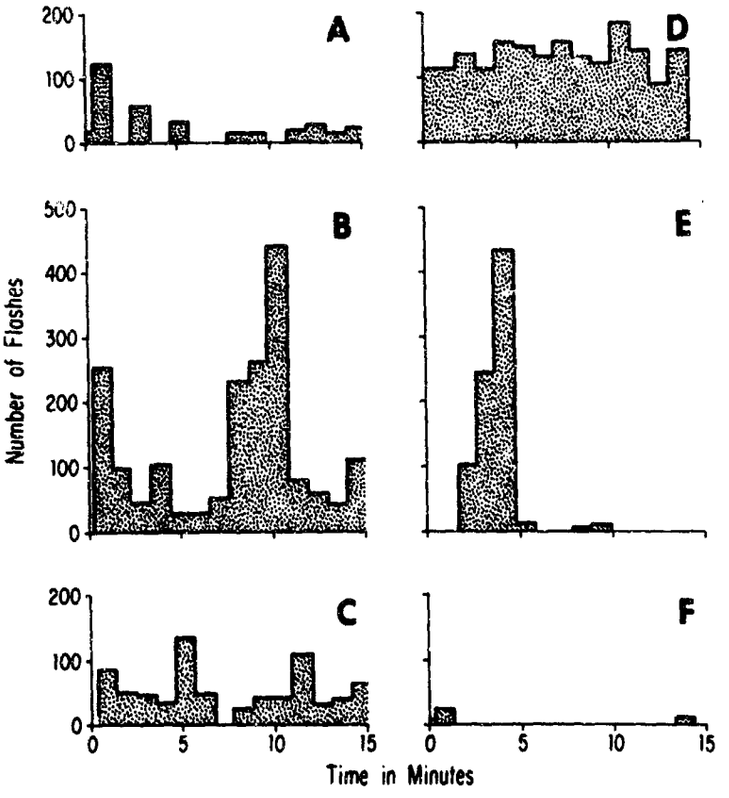

Figure 1. A. Number of simultaneous flashes recorded by uppermost pair of meters at 100 m. B. Simultaneous flashes recorded by same meters at 25 m. C. Simultaneous flashes recorded by middle pair of meters at 175 m. D. Record from same meters when raised to 125 m. E. Record from lower meters descending through surface layers. F. Record from lower meters at 275 m.

One bar of the histogram represents a time interval of 1 min. The numbers of flashes were provided by the counter.

The middle pair of meters was suspended at 175 m, at the apparent bottom of the sonic-scattering layer. At this level, there was very much more luminescence (Fig. 1C) than indicated by the uppermost meters when they were at 100 m. Figure 1D shows, however, that the degree of activity was surpassed when the meters were raised to 125 m, the uppermost component of the sonic-scattering layer. The signal on the Speedomax recorder was so consistently high that the pen did not return to zero throughout the record. The return to the base line in this figure denotes the termination of the record.

In Figure 1E, the record made from the lower pair of meters while descending through the surface layers is shown, and a few spectacular bursts of luminescence can be seen. The record at 275 m (Fig. 1F) shows very little activity. This depth is well below that of the sonic-scattering layer.

Experiment III

In another experiment, performed on the *R/V Velero IV* in the San Diego Trough, a somewhat different approach was taken. Recordings were made on a Gifft recorder at 12 kHz.

A single pair of meters was lowered to the depth of the sonic-scattering layer and maintained at that depth during the upward, twilight migration of the layer.

The instrument and scattering record were both clearly visible on the echo-sounder trace throughout this period (Figure 2). The instrument appears as a solid line. The descent of the instrument and its position in the layer is shown in Figure 2A. In Figure 2B, the instrument appears at the same depth, while the layer, augmented by a deeper community, undertakes its upward, twilight migration. Figure 2C shows the instrument at the same depth but now below the layer. Figure 2D shows the instrument being raised to the surface through the surface scattering.

The numbers of simultaneous flashes per minute recorded during each of these four time intervals are depicted in the histograms in Figure 3A through 3D. Figure 3A is the record for the 15-min period the instrument was in the layer. During the next 15 min the number of flashes increased greatly (Fig. 3B). Whether this was because of increased activity of the animals or recruitment from another community, or both, is speculation at this point. Figure 3C shows a reduction in the number of recorded flashes after the layer has passed the instrument. A great increase in luminescent activity in the surface layers is apparent in Figure 3D.

Experiment IV

Acoustic work

The objective of the main acoustic experiment was to measure quantitatively the scattering from different depths at different frequencies (2 kHz to 300 kHz, 3.3 kHz, 10 kHz, 26 kHz, 36 kHz, 54 kHz, 67 kHz, and 100 kHz) for comparison with the biological samples obtained with various nets. Echo sounders, when operational, were recording continuously, and all scientific personnel shared the sounder watches.

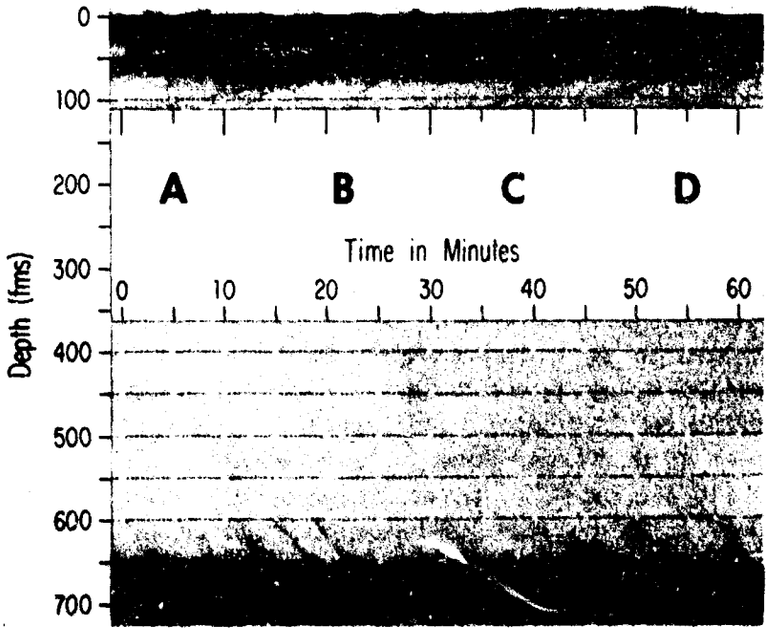

Figure 2. A fathogram made showing the upward, twilight migration of the sonic-scattering layer. A, B, C, and D indicate the four 15-min intervals during which observations were in the scattering layer, during migration, after migration, and in the surface layers.

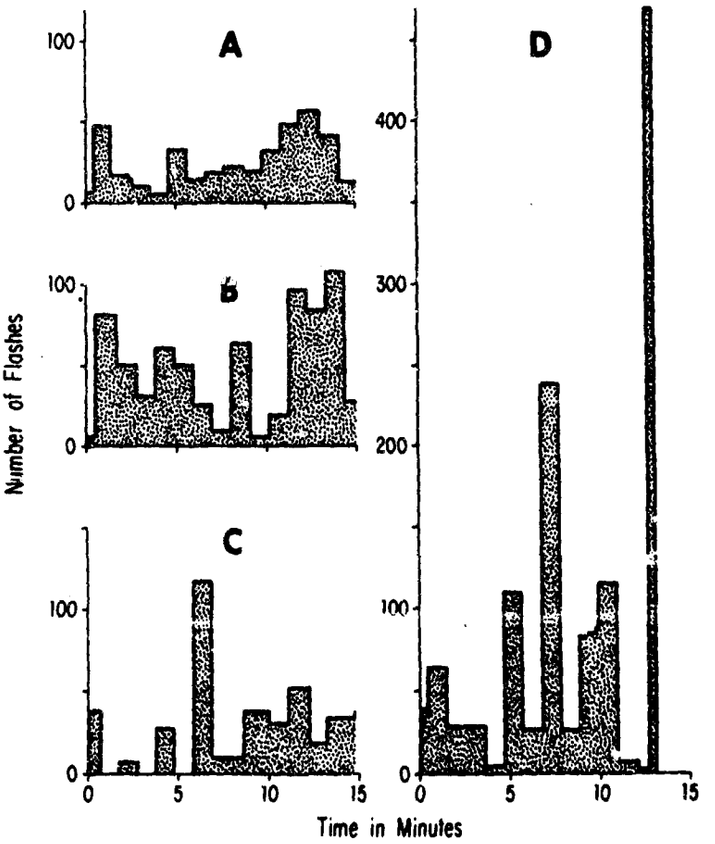

Figure 3. A. Number of simultaneous flashes recorded by a pair of meters situated in the scattering layer. B. Number of flashes recorded by same meters at same depth as the layer migrates past them. C. Number of flashes recorded by same meters at same depth after layer has passed them. D. Number of flashes recorded as the meters are raised through the surface layer.

Bioluminescence

This work has also been published (Boden, 1969), so the results are merely paraphrased here, and no figures are presented. In one experiment, a brace of meters was lowered to 180 m at evening twilight and held stationary. A considerable increase in luminescence was noted as the layer passed the meters, but this dropped to zero afterward.

In another experiment, three racks of instruments were lowered on one wire at midday. These were suspended at 110, 435, and 510 m. The densest part of the scattering layer shown by the fathometer was at 437 m. There was very little luminescence indicated by the upper and lower meters and negligible scattering at those depths. Increased activity was shown by the center meter.

In yet another experiment, a pair of meters was mounted on the vane of an Isaacs-Kidd trawl, surveying a common volume forward of it. Another pair scanned the contents of the net, one with meter looking upward and one downward. The downward-scanning meter recorded less activity than that of the upward-scanning one. The meters oriented forward and backward showed considerably more activity, and the latter, looking into the net, set the recorder off scale.

DISCUSSION

Rudyakov (1968) advocates the use of a photometer, towed at constant speed at varying depths, to determine the stratification of luminescent organisms. In his surveys, observations of luminescence and collections for identification of organisms were made concurrently, and some interesting narrow-layer stratification was demonstrated in the Mediterranean, the Red Sea, and Gulf of Aden. He rationalizes that such investigations are not only of great ecological interest but are also of importance in the solution of applied (presumably military) problems.

The results of these experiments substantiate previous observations made in the Pacific (Boden and Kampa, 1957; Boden et al., 1965) and in the Atlantic (Boden, 1969). These observations indicate a high degree of luminescent activity in surface waters and at sonic-scattering layer depths, and a lesser degree at intermediate depths and below the sonic-scattering layers. Such an agreeable confirmation of this phenomenon in yet another area of the oceans is most engaging.

The graphic presentation of the flashes has made it possible to examine their shape and has revealed a frequency of minor flashes within each major flash. Both frequencies and shape vary from flash to flash, but, in many cases, they were remarkably similar in any geographical area.

Figure 4A is a tracing, from the frequency channel of the record, of one of many similar flashes recorded in the Gulf of California. Figure 4B shows a flash recorded in the San Diego Trough. Differences in configuration, duration, and frequencies can be detected. Presumably, the meters were observing different communities in each case. The significance of this phenomenon is not yet clear, but laboratory work may show whether it is a specific characteristic.

The most exciting observations on shallow scattering layers are those by Tchindonova and Kashkin (1969) and Barraclough, LeBrasseur, and Kennedy (1969) in which it is shown that a relatively high frequency (200 kHz) reveals layers that cannot be detected by the usually operated low-frequency sounders.

These results all illustrate the dependence of biological oceanographers on physical oceanographers. I must quote, however, the words of the late Prof. Harald Sverdrup: "The major duty of a physical oceanographer is to provide a background for biologists."

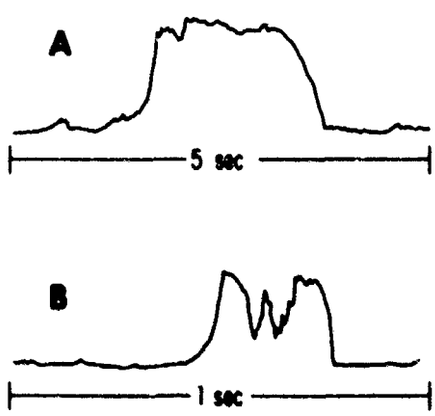

Figure 4. A. Configuration of a flash recorded in the Gulf of California. B. Configuration of a flash recorded in the San Diego Trough.

ACKNOWLEDGMENTS

The measurements in the Gulf of California were made by Dr. Elizabeth M. Kampa on an expedition under the leadership of Prof. Carl L. Hubbs. Both have scrutinized the manuscript, and I am thankful for their cooperation and comments. I also thank Prof. B.C. Abbott, University of Southern California, for making available the R/V *Velero IV,* for his help at sea, and for reading the manuscript.

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DISCUSSION

Pearcy: You show differences in flash rates at different depths. Are there also differences in the intensity of the flashes?

Boden: Once you get the meter up to the surface layers, it is certainly more intense, but I think we are probably dealing with dinoflagellates or something like that. At scattering layer depth, the frequency changes, but I think intensity does not change a great deal.

Holm-Hansen: When you speak of a flash, do you mean a flash which results from an on-off signal from one micro-organism, or do you mean a continuous bioluminescence and the instrument is just scanning that for a finite time?

Boden: The instrument really is scanning just a common volume. What the instrument is seeing, I don't know. Of course, each instrument can record flashers all the way through its scanning time, but it is only those we notice as being recorded by both instruments that we consider spontaneous luminescence. Whether this is one organism is uncertain, because you could get sympathetic flashing; something could flash and stimulate a flash elsewhere, so this is a very serious reservation that we are holding about the system. But I think it is better than anything we have done yet.

McElroy: I had just a comment concerning the stimulation effect. I have no idea of the quantities I am going to mention here, but this might be an interesting problem for a physicist. I can conceive of a couple of mechanisms occurring here as possible ways in which these additional emissions might occur. One would be that the animal is actually responding in some way through biological mechanisms. The other way that I am suggesting is through a strictly physical mechanism called stimulated emission of radiation. Stimulated emission carried to an extreme in a coherent sense is what is used in the laser. I am not suggesting that is exactly what is going on here, but there may be strictly a response on a physical basis with no real intervening biological mechanisms.

Boden: One thing I have run into in the last few months is that I cannot get any luminescent organisms, and I really don't know what the reason is. I bring the animals into the laboratory and I cannot make them flash. I don't know whether this is a seasonal thing or as has been suggested by some of our physical oceanographers, whether we are running into some sort of a problem with this tritium belt that comes right across from Japan, hits Seattle, and then apparently sinks down to form a peak off Baja California. But these creatures have to migrate through this belt, and of course this is going to upset oxidative metabolism. This could possibly be the reason why they are not luminescing.

Holm-Hansen: What organisms are these?

Boden: The ones I have been working on are mostly euphausiids.

Barham: I think you have already answered my question. I was just going to ask whether you get some kind of signature from them under laboratory conditions.

Boden: This is what I have been trying to do. They won't talk to me.

Backus: In connection with Paul McElroy's remarks, I would like to say that we have noticed two bioluminescent responses to the flashlight beam, one from the bow chamber of *Atlantis II* at night when shining the flashlight forward through the windows. Immediately upon turning on the flash, we've had large organisms, perhaps jellyfishes, bioluminesce in response to the flashlight beam. Also, from the *Alvin* during the day at depths of 600 and 700 meters, with all lights off and after having sat for awhile in a spot, upon turning the flash on and poking it out the window, we have had a sudden and dramatic flash of blue light from all around us. It is quite a spectacular thing.

Hersey: Brian, I was unaware of the apparent very strong correlation between the presence of the scattering layer as such and these bioluminescing animals. Have you made enough observations so that you would care to say how universal this observation is? Is it just one scattering layer where you know you can find bioluminescence, or are there many that display this correspondence?

Boden: What we have been doing is observing the migratory layer with which we are familiar. In a lot of the observations, particularly on *Discovery*, for instance, there were a lot of nonmigratory layers. This is also true in British Columbia. There, the nonmigratory layers which are right on the bottom of this oxygen-deficient layer were composed mainly of amphipods, which don't bioluminesce. The migratory ones are mainly *Euphausia pacifica*, and this is interesting in that it is a captive sort of group there because the salinity is very low and there is not much exchange of water between the fjord and the Pacific Ocean. These euphausiids seem to have developed a completely different spectral sensitivity.

Hersey: Now do you identify the euphausiids with the layer as scatterers of sound or is it something else?

Boden: I don't really know.

Hersey: One further question. The lanternfishes, by their very name, suggest that they could possibly be the signal both optically and acoustically.

Boden: Yes, they are probably chasing these little chaps up and gobbling them up.

Hersey: Well, I am wondering whether the light doesn't also come from the lanternfishes rather than from the euphausiids.

Boden: Well, I think it probably comes from all sorts of creatures.

Nafpaktitis: In reference to Backus' statement about flashing a light and getting a response, I would like to mention that in a recent letter, J. W. Hastings of Harvard University informed me that while in New Guinea he obtained six species of pony fishes, family Leiognathidae. These fishes have an organ surrounding the esophagus in which luminous bacteria are cultured. He was able to count the bacteria and also study the control of the system and how it flashes. He said that it can be triggered by a light flash to the eye.

Hansen: Did I understand you to say that amphipods were causing the scattering layer at the oxycline?

Boden: This is the idea that the Canadians had.

Hansen: This is a nonmigratory layer?

Boden: Yes. The other layer splits off and comes up.

SWIMBLADDER DEVELOPMENT AND THE LIFE OF DEEP-SEA FISHES

Norman B. Marshall
British Museum (National History)
London, England

ABSTRACT

In an earlier survey, fishes with a gas-filled swimbladder were found to be common at mesopelagic and benthopelagic levels of the deep ocean. In bathypelagic fishes the swimbladder is either regressed or absent. Of the mesopelagic fauna (centered between levels of 150 to 1,000 m), the most numerous forms with a swimbladder are stomiatoids (small gonostomatids and sternoptychids) and myctophids. A recently completed survey suggests that all but two of the trichiuroid fishes, nearly all of which are mesopelagic, can be added to the list of swimbladder containers, and there are others. Analysis of recent midwater trawl surveys in the North Atlantic shows that at least two-thirds of the individuals caught have a swimbladder.

Mesopelagic fishes may well be conspicuous components of deep scattering layers throughout the ocean. This seems remarkable, but most kinds of these fishes are small (and very adaptable). For instance, total catches of adult euphausiids are only about five times those of mesopelagic fishes. The mean size of the latter, and hence of swimbladders, is presumably lowest in the relatively sterile central water masses. Conversely, mean sizes are largest in areas holding expatriated individuals, as in the North Atlantic to the west of the British Isles. Joint acoustical and biological exploration of these areas should be rewarding.

Life in oceanic space may be assigned to four main levels: epipelagic (0 to ca. 150 m), mesopelagic (ca. 150 to 1,000 m), bathypelagic (ca. 1,000 to 4,000 m), and benthopelagic (near the bottom). There is also benthic life on, and just below, the interface of sea and land. Naturally, this neat scheme is transgressed by the animals. Each day about sunset, many mesopelagic fishes migrate up to the epipelagic zone, but beat a Puckish retreat before dawn. In the other direction, mesopelagic and bathypelagic fishes may sometimes live as near to the bottom as benthopelagic fishes. Even so, the scheme has some physicobiological basis. Epipelagic organisms live more or less in the euphotic zone, where primary production is concentrated. The mesopelagic zone is a twilight world containing most of the midwater fishes, especially stomiatoids and myctophids. Apart from sporadic bioluminescence, the bathypelagic zone is pitch dark, and the fish fauna is dominated in numbers by *Cyclothone* individuals and in species by ceratioid anglerfishes. The benthopelagic fauna consists largely of elongated, many-rayed fishes with a swimbladder, notably rat-tails and brotulids. Benthic deep-sea fishes, most of which are chlorophthalmids, bathypteroids, liparids, and zoarcids, have no swimbladder.

Since an earlier study (Marshall, 1960), I have now virtually completed a general survey of swimbladder development in deep-sea fishes. On the systematic side, there are close to 850

described species of mesopelagic fishes, most of which are stomiatoids (ca. 250 species), argentinoids (ca. 40 species), myctophids (ca. 200 species), alepisauroids (ca. 80 species), melamphaids (ca. 45 species), and trichiuroids (ca. 40 species). A gas-filled swimbladder is present in the adult stage of species comprising about a third of the mesopelagic fauna, notably in myctophids (ca. 180 species), stomiatoids (ca. 30 species, small gonostomatids (excluding *Cyclothone* spp.) and hatchetfishes), most trichiuroids, and some melamphaids. The volume of the swimbladder in these fishes (ca. 5% of the body volume) is such as to eliminate their weight in water. The swimbladder is purely a hydrostatic organ; there are no attached sonic muscles or linkages with the ears. The main kinds of mesopelagic fishes without a swimbladder are alepocephalids, searsids, alepisauroids, and most of the stomiatoids (*Cyclothone* spp., *Chauliodus* spp., *Stomias* spp., Astronesthidae (numerous species), Melanostomiatidae, *Idiacanthus* spp., and Malacosteidae).

Bathypelagic fishes, represented largely by black species of *Cyclothone* and ceratioid anglerfishes (ca. 100 species), amount to about 150 species. The swimbladder is either absent or regressed in the adults of all species. Regression occurs in the *Cyclothone* species, which have a gas-filled swimbladder during the postlarval phase, which is passed in the mixed layer. During metamorphosis and descent toward the adult living space, the swimbladder begins to regress and is gradually invested by fatty tissue. Though without a swimbladder, bathypelagic fishes must be very close to neutral buoyancy, a condition largely attributable to their weakly developed muscles and poorly ossified skeleton. These developments, *inter alia*, are correlated with a food-poor environment (Marshall, 1960).

Except for certain squaloid sharks, chimaeroids, alepocephalids, and ateleopids, fishes of the benthopelagic fauna have a well-developed, gas-filled swimbladder. Of some 750 species, the main groups are rat-tails (Macrouridae, ca. 300 species), deep-sea cods (Moridae, ca. 70 species), and brotulids (ca. 250 species). Even at depths beyond 3,500 m, 11 of 16 recorded species, represented by 88 of 117 specimens, have a swimbladder (depth records from Nybelin, 1957). (It is striking that most members of the two dominant groups have evolved drumming muscles on the swimbladders of males.) That neutral buoyancy is biologically advantageous in benthopelagic fishes is shown not only by the widespread development of the swimbladder, but also by the storage of squalene in such quantities that deep-sea squaloids and chimaeroids virtually achieve such buoyancy (Corner, Denton, and Forster, 1969).

Deep scattering layers (DSL) appear at mesopelagic levels, where fishes with a swimbladder are likely to be prominent components of echograms. Now that the survey of swimbladder development practically is complete, it is relevant to estimate the percentage of fishes at mesopelagic levels with this organ. Here we can do no better than consider data presented by Backus, Craddock, Haedrich, and Shores (1969).

Twenty-five tows with an Isaacs-Kidd midwater trawl (IKMT) were made at stations along the meridian 70°20′ W from off Hispaniola to the Gulf Stream, i.e., in the western Sargasso Sea. Of 7,676 fishes taken, about 60% belonged to species with a swimbladder. The most abundant forms were lanternfishes, *Ceratoscopelus warmingi* (1,547 specimens/14 stations); *Lampanyctus pusillus* (375/8); *Lepidophanes gaussi* (347/10); and *Notolychnus valdiviae* (489/15). The gonostomatid fish *Cyclothone braueri* was very abundant also (2,872/13), but I have excluded this from the percentage estimation. In fully mature individuals, the swimbladder contains no gas, though it may in stages between the postlarval and early adult phases. Moreover, there is no evidence that *Cyclothone* spp. migrate diurnally between daytime levels and the epipelagic zone. Of the migrating species, at least 80% of the total number of individuals will have a gas-filled swimbladder. Percentages of this order may be expected in other parts of the ocean.

Mesopelagic fishes with a swimbladder are likely to be conspicuous components of DSLs over most of the ocean. As we saw, most of the migrators have a gas-filled swimbladder and belong to the stomiatoid and myctophid groups. Moreover, most of these species feed on zooplankton ranging in size from copepods to euphausiids. Predatory migrators with a swimbladder are mainly trichiuroid and astronesthid fishes. Migrators without a swimbladder, such as *Chauliodus* spp., *Stomias* spp., and various melanostomiatids, are all predators, able to deal with relatively large prey. If *Gonostoma elongatum* may be taken as a paradigm, these forms are close to neutral buoyancy.

Beside this overall tendency to eliminate their weight in water, all kinds of migrators seem well equipped in other aspects for their seemingly strenuous up and down life. Along the flanks, often from dorsal to ventral midlines, the red muscle fibres of the myotomes are well developed. (Red muscles, which have inbuilt stamina, are the cruising motors of fishes.) All migrators have sensitive eyes of one kind or another, able, no doubt, to signal, *inter alia*, the approach of sunset and sunrise. Most species are luminescent, and we may expect to learn more of the significance of light display during diurnal vertical migrations. It certainly looks as though mesopelagic fishes are the marine counterparts of mice and owls: they "emerge" at night to seek their prey. During the daytime, as underwater observations suggest, they do nothing in particular, which is a good way to escape the notice of predators. Lanternfishes hang motionless in the water, often with little regard for set posture. Resting by day in cool waters has another advantage, according to McLaren (1963), who advances the hypothesis that as soon as the thermal stratification develops, vertical migration is profitable metabolically, for it is more efficient to feed at high temperatures and grow at low temperatures.

Large-scale variations in oceanic productivity are reflected in the numbers of mesopelagic fishes. For instance, in the western Sargasso Sea, Backus et al. (1969) found that catches were larger north of the "subtropical convergence" than to the south, where primary productivity is lower. One might also expect thin catches of mesopelagic fishes in the central water masses. In these gyrating "deserts," the dwarfing of certain species may well be part of their adaptation to food-poor surroundings. Presumably, the size spectrum of swimbladders is smaller than that in neighboring waters of higher productivity.

Certain regional differences in the mean size of mesopelagic fishes are very well marked. For instance, compare the size spectrum of the myctophid fauna from the Indian Ocean (Nafpaktitis and Nafpaktitis, 1969) with that from the Southern Ocean (Andriashev, 1962). (Both surveys used the IKMT.) Of the 18-odd species in the Southern Ocean, consisting mainly of *Protomyctophum* spp., *Electrona* spp., and *Gymnoscopelus* spp., all but three reach a maximum length of at least 50 mm. In the Indian Ocean, there is a more diverse myctophid fauna (of at least 54 species) assigned to 19 genera, but only eight species reach a maximum length of 60 mm. Moreover, the most abundant species, *Lepidophanes longipes* and *Hygophum proximum*, both reach a maximum size of about 40 mm. In proceeding, then, from the Southern Ocean to the Indian Ocean, there is a marked decrease in the spectrum of swimbladder size contributed by the lanternfish faunas. Given adequate frequency coverage, would this difference show on echograms? One might also expect a relatively large spectrum of swimbladder sizes from the mesopelagic fish fauna to the west of the British Isles.

The discovery that DSL's are widespread in the ocean caused some of us to think furiously. In a paper read to the Challenger Society in 1949 and in one published later (Marshall, 1951), I concluded that mesopelagic fishes with gas-filled swimbladders seem to occur over most of the ocean. It appears now that these fishes find a living everywhere except in extreme polar waters (the Arctic Ocean and waters fringing Antarctica). In a later paper (Marshall, 1960) and a book (in press) I have discussed the general adaptations of these fishes.

Euphausiid shrimps were the first pan-sound-scatterers to be considered. More recently, Barham (1963, 1966) has shown that physonect siphonophores, which are headed by a gas-filled float, are correlated nicely with certain sound-scattering layers off southern California. It will be relevant, then, to compare and contrast the organization and numerical distribution of euphausiids, physonects, and mesopelagic fishes.

Physonect siphonophores, like members of the calycophoran group, consist largely of gelatinous tissue. They are gelatinous carnivores par excellence, just as pelagic tunicates are gelatinous herbivores *par excellence*. In a physonect, the most expensive tissue system to maintain is that comprised by the muscle fibres, which are concentrated in the swimming bells, digestive members, stem, and tentacles. There are also the digestive tissues and the requirements of reproduction. But the entire mass of living tissue accounts for less than 5% of a physonect's weight. Compared to its size and polymorphic deployment, a physonect must be a very economical kind of predatory behaviour machine. Doubtless they are widespread throughout most of the ocean, but our knowledge is limited, largely because of their fragile nature.

Euphausiids and fishes are expensive predatory behaviour machines. Muscle comprises about a third of a euphausiid's weight and from a half to two-thirds of an active fish's weight. Much of a euphausiid's energy must be expended on diurnal migrations, food gathering, and keeping to a level, for they are negatively buoyant. Concerning their food, the emphasis in textbooks is on their herbivorous habits. Euphausiids range, however, from the near-herbivorous krill (*Euphausia superba*) to near-carnivorous forms (e.g., *Stylocheiron* and *Nematoscelis* spp.). In general:

> "It is apparent from 1) estimations of the biomass of euphausiids, 2) studies of the food of euphausiids, and 3) the array of predators dependent upon them for their nourishment, that euphausiids, along with the copepods, form the most important links between the primary producers and the primary, secondary, etc., predators in the marine food chains." (Mauchline and Fisher, 1969, p. 380).

Even so, the number of euphausiids under warmer oceanic waters (warm temperate to tropical) are not many times greater than the numbers of mesopelagic fishes.

Consider first the catches of the "Valdivia" Expedition with metre closing nets in the Atlantic and Indian Oceans. In 88 hauls, 15,368 euphausiids and 2,880 fishes were taken; i.e., the euphausiid/fish ratio was about 5:1 (the totals include larval stages). In the Atlantic Ocean, catches by the *Gauss* (German Plankton Expedition) with a metre net again gave a 5:1 ratio. Now compare these figures with some from a warm temperate sea, the Mediterranean. Here Danish Oceanographical Expeditions (1908-10), using mostly a Petersen young-fish trawl, took 149,887 euphausiids to 58,979 fishes, a ratio of about 3:1. (In comparing these catches, one must remember that the coarse-meshed net of this trawl did not take either euphausiids or fish below about 5 mm in length.)

What are the real numbers of euphausiids and mesopelagic fishes? One might argue that the ratios are biased because fishes are able more easily to avoid a net than euphausiids. Whatever the actual state of affairs, it is clear that the mesopelagic fish fauna, which consists largely of small-sized (25-150 mm) individuals dependent on zooplankton, has tried hard, as it were, to stay as close as possible to the euphausiid level of the food pyramid in the warm ocean. This is not altogether a difficult evolutionary feat, considering that all euphausiids depend to some extent on zooplanktonic food. Think also of fishes of the genus *Cyclothone*: they come close to being vertebrates without a backbone. The smallest species, *C. pygmaea*, has a brain of about the same volume as that of a honeybee.

In one way or another, sound scattering problems have led—and will lead—to deeper insight into the organization and ecology of the mesopelagic fauna. A final thought concerns the physonect siphonophores. They are designed very economically as deadly drift lines, but the

maximum number that can live together per cubic unit of the sea must be much lower than the corresponding figures for fishes and euphausiids. These animals have the right shape and sensory equipment to form schools or swarms, which is not to say that physonects are too sparse to give rise to DSL's. Biologists, of course, look forward to the day when fish and physonect traces can be identified as such. What about the contributions of the crustaceans, particularly euphausiids?

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SWIMBLADDER GAS SECRETION AND ENERGY EXPENDITURE IN VERTICALLY MIGRATING FISHES

R. McN. Alexander
University of Leeds
Leeds, England

ABSTRACT

A fish that has a swimbladder and makes vertical migrations must either adjust the quantity of gas in its swimbladder or suffer the penalty of changing density.

Gas that is to be secreted into the swimbladder must be obtained from solution in the sea, and work must be done to increase its partial pressure to the value in the swimbladder. An expression is obtained for the total amount of work that would be required in a descent if the volume of the swimbladder were kept constant throughout. Values are calculated for secretion of oxygen, using typical vertical distributions of partial pressure of dissolved oxygen.

If gas is not secreted, vertical hydrodynamic forces are required for equilibrium. Additional work must be done in swimming against the induced drag associated with these forces. It is shown that this work is greater than the work needed to secrete gas and keep the density constant for small daily migrations near the surface, but not for daily migrations to great depths. This is discussed in the light of existing evidence about the behaviour of vertically migrating fishes, including evidence from observations of sound scattering.

INTRODUCTION

Many species of teleost make daily vertical migrations, swimming toward the surface at dusk and away from it at dawn. The herring, *Clupea harengus* L., and other Clupeidae spend the night near the surface and the day at greater depths, which may be as much as 150 m (Blaxter and Holliday, 1963). Some smaller pelagic marine fishes, among which the Myctophidae are the most common, make daily vertical migrations of several hundred metres (Marshall, 1960). Some come right to the surface at night; others never come nearer the surface than 100 m or more. Myctophidae observed by Barham (1966) spent the night at around 50 m and the day at around 300 m. Various other teleosts such as cod (*Gadus morhua* L.), which live in relatively shallow water, spend the day close to the bottom and swim up some tens of metres at night (Beamish, 1966). Some freshwater fishes also make daily vertical movements (Northcote, 1967). Much of the information summarized in this paragraph has been obtained by echo sounding, and vertically migrating fishes appear to be a major constituent of the well-known deep scattering layers (see, for instance, Barham, 1966; Hersey, Backus, and Hellwig, 1962).

These fishes owe their sound-scattering properties largely to the possession of a gas-filled swimbladder. The swimbladder gives buoyancy; but as the volume of a swimbladder is affected by external pressure, a swimbladder containing a given quantity of gas will only give a fish exactly neutral buoyancy at one particular depth. The available evidence (Alexander, 1966, 1967) suggests that most vertically migrating fishes have neutral buoyancy at or near their minimum

(nighttime) depth, but it is doubtful whether any fishes adjust the quantity of gas in the swimbladder to maintain neutral buoyancy as they descend. Herring seem to be unable to secrete gas into their swimbladders (Brawn, 1962). They can add air to the swimbladder by gulping at the surface, but this addition would not enable them to maintain neutral buoyancy in any substantial descent. Several species that leave the bottom at night have been caught at the bottom by day and found to have too little gas in their swimbladders for neutral buoyancy at that depth (Scholander, Claff, Teng, and Walters, 1951). Observing shifts of scattering frequency during vertical movements of deep scattering layers, Hersey, Backus, and Hellwig (1962) suggest that some fishes maintain neutral buoyancy by secreting gas into their swimbladders as they descend, whereas others do not secrete at all; but this suggestion was based on an observation made on one occasion only.

This paper discusses whether it would be desirable for the fishes, if they were able to do so, to maintain neutral buoyancy by secreting gas into the swimbladder as they descended and removing it as they ascended. The question is one of energy. Consider a fish that has neutral buoyancy at a particular depth. Let it swim deeper so that the swimbladder gases are compressed and it becomes more dense than the water. It then has two alternatives: either it may compensate by using its fins to provide hydrodynamic lift as it swims, or it may secrete more gas into the swimbladder to restore neutral buoyancy. Either alternative involves expenditure of energy. I will estimate and compare the amounts of energy involved for fishes that make daily vertical migrations of various extents.

WORK FOR GAS SECRETION

I will estimate the work required to maintain by gas secretion the constant swimbladder volume required for neutral buoyancy in a vertical migration. Kanwisher and Ebeling (1957) attempted to estimate this work, but their attempt will be criticized.

The number of moles of gas, M, required to fill a swimbladder of volume V at pressure P and absolute temperature T is given by

$$M = \frac{PV}{RT}$$

where R is the gas constant. Hence it can be shown by partial differentiation that the number of moles δM that must be added to maintain the constant volume V when the pressure increases by a small amount from P to $(P + \delta P)$ is given by

$$\delta M = \frac{V \cdot \delta P}{RT} \qquad (1)$$

This gas must be obtained through the gills from the surrounding water, in which it is dissolved at partial pressure Q. When it is secreted into the swimbladder, its partial pressure is increased to $(P - K)$, where K is the partial pressure of other gases in the swimbladder. If only one gas is secreted, K will remain constant. The amount of work required to compress a mole of gas isothermally at temperature T from pressure Q to pressure $(P-K)$ is $RT \log_e [(P-K)/Q]$ (Glasstone and Lewis, 1962), so that the minimum amount of work δW that could accomplish the required secretion of δM moles of gas is given by

$$\delta W = RT \cdot \delta M \log_e \left[\frac{(P - K)}{Q} \right]$$

and from this and equation (1)

$$\delta W = V \cdot \delta P \log_e [(P-K)/Q] \tag{2}$$

Hence the minimum total amount of work W that is required to keep the swimbladder volume constant as the pressure increases from P_1 to P_2 is given by

$$W = V \int_{P_1}^{P_2} \log_e [(P-K)/Q] \cdot dP \tag{3}$$

In the simple case where Q and K do not change with depth,

$$W = V [(P_2 - K) \ln (P_2 - K) - (P_1 - K) \ln (P_1 - K) - (P_2 - P_1)(1 + \ln Q)] \tag{4}$$

If Q and K are not both constant, equation (4) does not apply, but W can still be obtained by numerical methods from equation (3).

Kanwisher and Ebeling (1957) gave an equation purporting to give W, but it seems to be an erroneous version of (2) with the symbol δ omitted from both sides of the equation, P_1 confused with Q, and K omitted. The values of W shown in their Figure 2 are considerably higher than those obtained in this paper.

The swimbladders of fishes generally are filled mainly with oxygen and nitrogen. At depths down to about 200 m, the partial pressure of nitrogen in the swimbladder is generally about 80 kN/m^2, the same as its partial pressure in the atmosphere (Scholander et al., 1951; but see Scholander and van Dam, 1953). Oxygen can be secreted into the swimbladder very much faster than nitrogen (Fänge, 1966), and a fish keeping its swimbladder volume constant in a descent presumably would secrete almost pure oxygen. We will assume that only oxygen is secreted and that the partial pressure K of other gases in the swimbladder is constant and equal to 80 kN/m^2.

The partial pressure of dissolved oxygen in the water is represented by Q. When photosynthesis can be ignored (as is generally true in the sea), Q will not exceed the partial pressure of oxygen in the atmosphere (20 kN/m^2) at any depth. In the most favourable conditions imaginable for the fishes we are considering, Q would be 20 kN/m^2 at all depths. Such ideal conditions do not occur; two observed distributions of partial pressure of oxygen are shown in Figure 1. The ideal Q is shown by the top line (a). Distribution (b), from the northern end of the Pacific Ocean, shows a moderate oxygen minimum; distribution (c), from near the Pacific coast of Mexico, shows a marked oxygen minimum.

Figures 2 and 3 show values of the work per unit swimbladder volume, W/V, required for secretion of gas in migration from the surface (Fig. 2) or from 100 m (Fig. 3) to various depths: (a), calculated from equation (4), assuming that the partial pressure of dissolved oxygen, Q, is 20 kN/m^2 at all depths; (b), obtained by numerical methods from equation (3) giving Q the values shown in Figure 1, curve (b); and (c) obtained in the same way, giving Q the values shown in Figure 1, curve (c).

As one would expect, these graphs show that the more marked the oxygen minimum, the more work is required to secrete oxygen while migrating through it. The work required, however, to migrate from the surface to a given depth in the least favourable conditions considered (c) is always less than twice the work required in the ideal conditions (a). The oxygen minimum makes less difference to the work required for secretion than one might suppose.

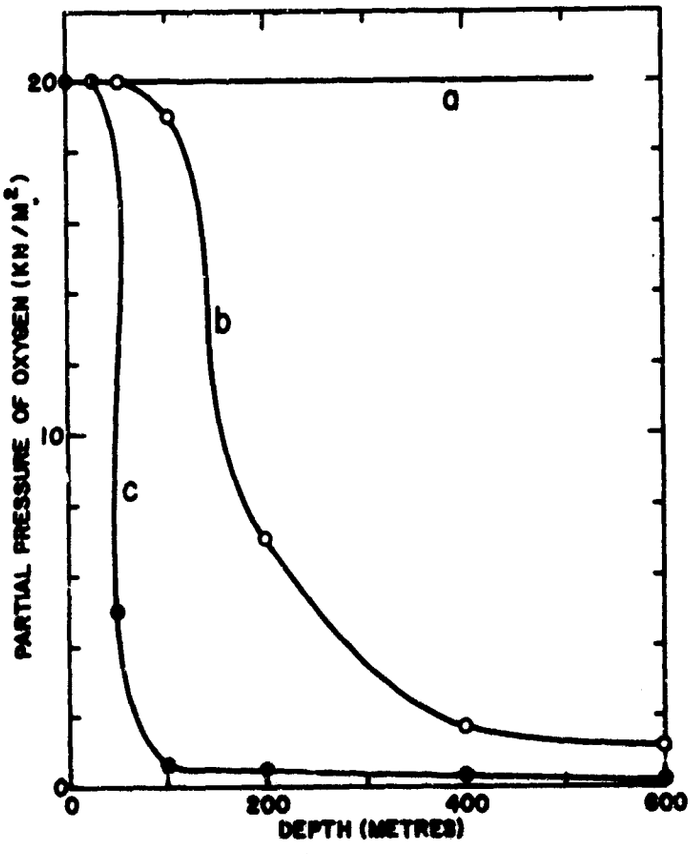

Figure 1. Graphs of partial pressure of dissolved oxygen against depth in the sea. The ideal situation, (a) with the water at all depths in equilibrium with the atmosphere, (b) as observed at 50°N, 175°W and (c) as observed at 20°N, 108°W. Data from Sverdrup, Johnson, and Fleming (1942).

WORK FOR HYDRODYNAMIC COMPENSATION

Suppose that the fish does not secrete oxygen, but leaves the quantity of gas in its swimbladder unchanged and compensates for loss of buoyancy by generating hydrodynamic lift. If the swimbladder has volume V at a depth where the pressure is P_1, it will have a volume $(V - \Delta V)$ at pressure P_2 where, by Boyle's Law

$$P_1 V = P_2 (V - \Delta V)$$

$$\Delta V = \frac{V(P_2 - P_1)}{P_2} \tag{5}$$

If the fish had neutral buoyancy at pressure P_1 it will have a weight in water $\rho g \cdot \Delta V$ at pressure P_2, where ρ is the density of the water. When it swims at this pressure, it must generate hydrodynamic lift $\rho g \cdot \Delta V = \rho g V (P_2 - P_1)/P_2$. This lift can be obtained only at the expense of drag, and the fish will be obliged to do work against additional drag as it swims.

Suppose that the fish swims all the time at the same speed. It could obtain the required lift by swimming with the body at a positive angle of attack but it seems from the work of Ohlmer

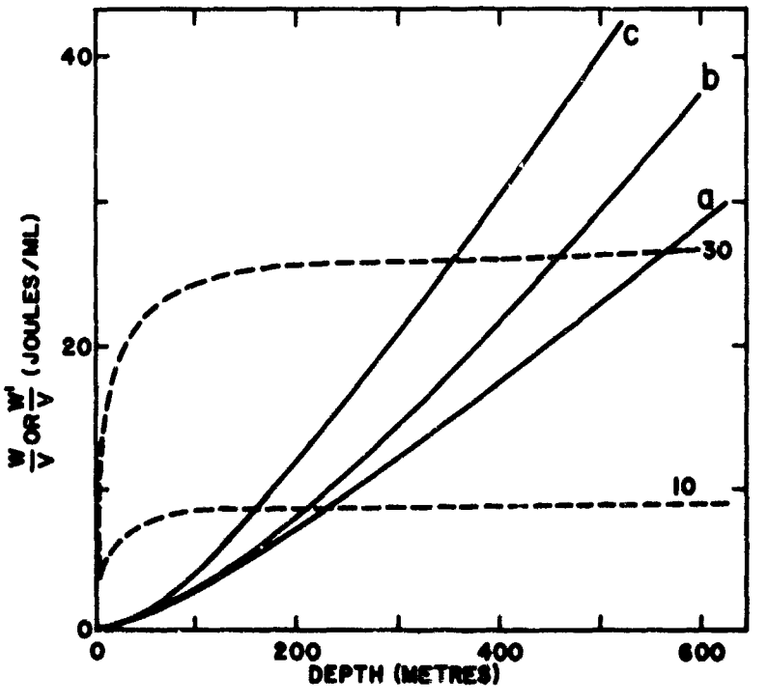

Figure 2. Estimated daily work requirements for fishes that make daily vertical migrations from the surface to the depths shown. The continuous lines show W/V (equations 3 and 4) for a fish that maintains buoyancy by secreting oxygen into the swimbladder, when the vertical distribution of oxygen is as shown in Figure 1 (a), (b), and (c). The broken lines show W'/V (Equation 6) for fishes that do not secrete but compensate for loss of buoyancy by generating hydrodynamic lift, at swimming speeds of 10 and 30 cm/sec.

(1964) that the ratio of lift to induced drag would be very low, making the energy cost of the lift high. It seems likely that the major part of the lift would be obtained by extending the pectoral fins and using them as hydrofoils. *Sarda* is known to use its fins this way: it has no swimbladder and consequently is always denser than sea water (Magnuson and Prescott, 1966). Consider a teleost between 10 and 30 cm long. The Reynolds number of its extended pectoral fins is of the order of 10^3 when it is cruising slowly at about 1 body length/sec. (On the relationship between fish length and swimming speed, see, for instance, Alexander, 1967.) Many insect wings work at similar Reynolds numbers. The maximum ratio of lift to drag obtainable with a locust wing at a Reynolds number of 4,000 is about 8; with a *Drosophila* wing at a Reynolds number of 200, about 2; and with butterfly wings at Reynolds numbers around 3,000, about 3 (see references in Alexander, 1968). Hence it seems unlikely that the fins could achieve a ratio of lift to drag better than about 5. The value of 10 previously suggested (Alexander, 1966) was based on information from aerofoils at higher Reynolds numbers.

We may thus estimate that the extra drag that the fish must suffer to obtain the lift is likely to be about 0.2 of the lift, or $0.2\,\rho g V(P_2 - P_1)/P_2$. If the fish suffers this drag for 12 hours (4.3×10^4 sec.) while cruising with velocity U, it will do work W', where

$$W' = \frac{9 \times 10^3\, g\, VU(P_2 - P_1)}{P_2} \qquad (6)$$

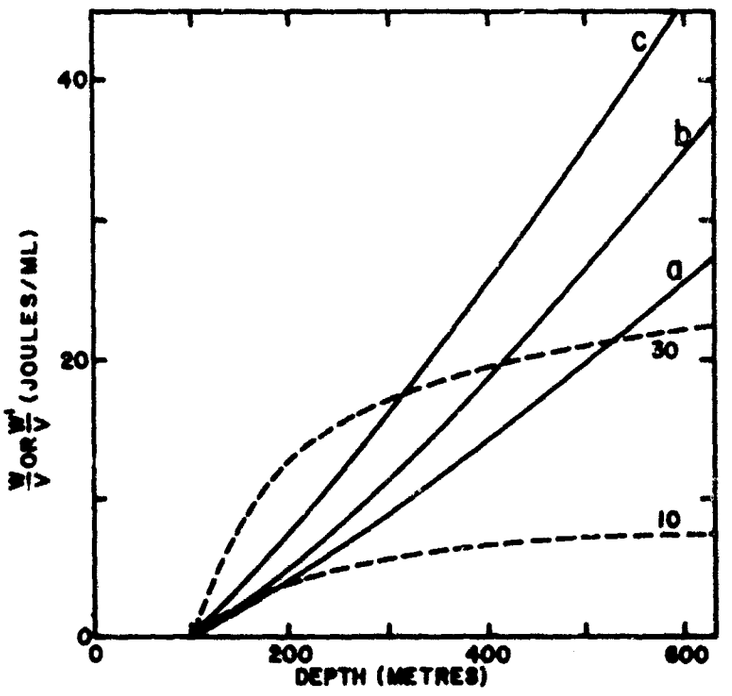

Figure 3. As Figure 2, but for vertical migration between 100 m and the depths shown

Values of W'/V for U = 10 cm/sec and U = 30 cm/sec are shown in Figure 2 for migration between the surface (P_1 = 100 kN/m^2) and various depths. Values are shown in Figure 3 for migration between 100 m (P_1 = 1.1 MN/m^2) and various depths. The curves in both figures approach asymptotically the values of 9 and 27 j/ml, which would apply for swimming at 10 and 30 cm/sec, respectively, if the swimbladder were compressed to the vanishing point.

We have made the assumption (which appears to be realistic, from the evidence cited in the introduction) that the fish has neutral buoyancy at the lesser of the two depths between which it is migrating. If we had assumed instead that the constant quantity of gas in the swimbladder gave neutral buoyancy at the greater of the two depths we would have found more work was needed to generate the hydrodynamic lift (which would in that case be negative). A swimbladder cannot be compressed beyond the vanishing point but it can expand at reduced pressures to many times the volume required for neutral buoyancy.

I have also assumed that the fishes being considered have the habit of swimming continuously. I could have assumed that when they have neutral buoyancy, they spend much of their time hovering motionless, but that they have to keep swimming when they descend so that they can generate lift. Using this assumption, larger values would have been obtained for the work needed. It would have been an unrealistic assumption that the fishes hover at all depths, using fin movements where necessary to compensate for changes of buoyancy: the teleosts that have been tested can compensate by fin movements only for small changes of swimbladder volume (Alexander, 1966).

DISCUSSION

We can now compare the work W done by a fish secreting oxygen to keep the swimbladder volume constant in its daily vertical migrations with the work W' that otherwise would have to

be done to overcome the drag incurred in generating hydrodynamic lift. Figures 2 and 3 suggest that W is less than W' for small vertical migrations near the surface, and greater than W' for migrations to substantial depths. Whether secretion or hydrodynamic compensation will be more economical of energy for a fish migrating between particular depths must depend on knowledge or assumptions about the efficiencies of the processes involved in doing these two very different types of work.

Measurements of the oxygen consumption of swimming fish indicate efficiencies of conversion of chemical energy to work against drag of 2.5% to 6% or a little more (Alexander, 1967; the figures given ignore pressure drag and ought to be increased accordingly.) There are no published values for the efficiency of the process of gas secretion in the swimbladder; but we might guess that it is not grossly unlike the efficiencies of other, admittedly very different, processes of secretion that have been investigated. Dr. C. R. Fletcher has contributed information about these efficiencies, and they seem unfortunately to be varied. Fletcher has calculated from data given by Holmes and Stanier (1966) and Rao (1968) that the efficiency of ion transport in osmoregulation in trout is 2.7% in water of 15‰ salinity and 11.1% in water of 30‰ salinity. The efficiency of ion transport in the rabbit gallbladder can be estimated as 27%, that of acid secretion in the frog gastric mucosa as 27% or more, and that of potassium secretion by the stria vascularis of the mammal cochlea as at least 40% (Keynes, 1969). Ignorance about efficiencies makes caution necessary in the following discussion.

A myctophid about 10 cm long may be expected to swim, when cruising slowly, at around 10 cm/sec. It makes daily vertical migrations of several hundred metres, with the highest point either near the surface or at a depth of a few hundred metres. Figure 2 indicates that a myctophid starting at the surface would require less work for hydrodynamic compensation at a swimming speed of 10 cm/sec than would be needed for maintaining buoyancy by gas secretion even in situation (a), so long as it descended to more than about 200 m (as myctophids seem to do). Figure 3 indicates that a myctophid starting at 100 m would also need less work for hydrodynamic compensation than it would for gas secretion, provided it descended to more than about 200 m. Provided that the efficiency of gas secretion is not too much higher than the efficiency of swimming, it is more economical for a typical myctophid to use hydrodynamic compensation than gas secretion. Maintenance of buoyancy by gas secretion would in any case require a very remarkable rate of uptake of oxygen at the gills (Marshall, 1960).

Adult herrings are about 30 cm long and probably would normally cruise at about 30 cm/sec in still water (they swim faster when necessary to keep station in tidal currents, Jones, 1962). They make much smaller vertical migrations than myctophids make. Figure 2 indicates that a herring starting at the surface would require more work for hydrodynamic compensation at a swimming speed of 30 cm/sec than it would require for maintaining buoyancy by gas secretion, unless it descended to depths far greater than the observed maximum of about 150 m. Provided that the efficiency of gas secretion is not too much lower than the efficiency of swimming, it would be more economical for a herring to use gas secretion instead of hydrodynamic compensation. Why has the herring not evolved the ability to maintain neutral buoyancy in its vertical migrations?

Let us see whether the rate at which it would have to take up oxygen from the sea would be excessive. Consider a rather large migration from the surface to a depth of 100 m. The mass of oxygen of density 1.3 mg/ml that would have to be added to the swimbladder to keep its volume constant at V ml would be $13V$ mg. The work required for its secretion (Fig. 2) would be about $3V$ j, which would require metabolism involving $0.2V$ mg oxygen (Bell, Davidson, and Scarborough, 1965) if the process were 100% efficient and $2V$ mg oxygen if it were 10% efficient. Hence the total quantity of oxygen required to provide the gas and energy for

secretion would probably be about $15V$ mg. (This total would not be affected very much by quite large variations in efficiency.) The volume of the swimbladder of a herring at neutral buoyancy is about 40 ml/kg body weight (Brawn, 1962); therefore this oxygen requirement is about 600 mg/kg body weight.

Brett (1964) found that 50-g *Onchorhynchus*, which used around 100 mg oxygen/kg hr when swimming slowly, could take up as much as 800 mg/kg hr when swimming fast. Such a fish could provide the swimbladder with 600 mg oxygen/kg body weight in a few hours if the swimbladder could use it. A fish the size of an adult herring (about 200 g) could not be expected to take up oxygen at a rate quite so high in proportion to the body weight (Fry, 1957), but the required rate of supply of oxygen to the swimbladder is still not beyond the likely capability of the gills.

Pomatomus, however, which secretes gas faster than any other teleost that has been investigated, takes about 4 hours to refill its swimbladder after it has been emptied (Wittenberg, Schwend, and Wittenberg, 1964). Thus, it could not maintain buoyancy by gas secretion in descents faster than 2.5 m/hour, which is much slower than the descent of herring. It is not clear why secretion should be so slow; it seems likely that faster secretion would be advantageous to fishes that make daily vertical migrations within 100 m of the surface of the sea.

SUMMARY

A fish that makes daily vertical migrations must either secrete gas into its swimbladder to maintain neutral buoyancy in its descents or compensate for loss of buoyancy by generating hydrodynamic lift. Secretion would require more work than hydrodynamic compensation in large vertical migrations, especially by fishes that swim slowly. The reverse is true of small vertical migrations by fishes that swim fast. Hydrodynamic compensation is probably more economical of energy for myctophids, but secretion (if fast enough secretion were possible) would probably be more economical for herring.

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DISCUSSION

Clarke, W.: We made some dives in the Gulf of Mexico looking at fish in the midwater community, and one of the things we noted about the lanternfish there was that they characteristically swam with their tails and folded their fins into the body. They would do two or three lunges like this and then, once their forward movement would stop, they would spread their fins again. Now admittedly this was under artifical circumstances, since they were within the light field of the submersible. But we repeatedly observed this behavior while watching them in midwater. Whether this is the case for all species of lanternfish I do not know, but in this particular instance they apparently were not using their fins for lift.

Alexander: But you say they were holding their fins out?

Clarke, W.: After they stopped.

Alexander: When they were stationary or when they were gliding forward?

Clarke, W.: They would fold their fins, swim with their tails, then once their forward motion stopped, they would spread their fins. But again, this is just an observation.

Alexander: It is a very interesting one. Do you know whether these particular fishes had gas-filled swimbladders?

Clarke, W.: That you would have to ask Haedrich, or Rosenblatt, or Pearcy. I am not sure what the species was, but we could probably run it down.

Pearcy: There are several bits of evidence suggesting that some myctophids with gas-filled swimbladders are neutrally buoyant at depth: (1) During *Alvin* dives, Backus and others observed that *Ceratoscopelus madarensis* hung motionless in the water, apparently neutrally buoyant, at daytime depths of 300-600 m. This species has a gas-filled swimbladder; (2) Hersey, Backus and Hellwig noted that peak resonant frequencies from scattering layers sometimes changed as the half-power of pressure during diel migration. This suggests that the size of the resonating swimbladder remains constant and neutral buoyancy is actively maintained by secretion and resorption; (3) The rete, gas gland and oval of fishes with gas-filled swimbladders that do migrate vertically are very well developed, as Dr. Marshall has shown; (4) Kanwisher and Ebeling found a very high percentage of oxygen in the gas from swimbladders of some lantern-fishes that were collected after they migrated to the surface at night. This is indirect evidence that the gas was secreted at depth before migration to the surface.

Alexander: I doubt whether the presence of a well-developed rete can be regarded as evidence that the fish maintains neutral buoyancy. If a fish has a gas-filled swimbladder and goes down to a substantial depth, then even if it allows its swimbladder to be compressed, there must be a loss of oxygen from the swimbladder by diffusion which must be made good by secretion. It might be that the rete was merely there to make up for what was lost accidentially in that way.

Barham: There is one thing that we have noticed on many occasions which tends to fit in with your hypothesis. Off the coast of Mexico, where we are dealing with scattering layers that we are quite convinced are comprised largely of myctophids, we see them migrate down in the daytime and after they reach their daytime depth, their trace disappears. The echogram that you were getting shows a beautiful layer, but when they reach daytime level, then in about half an hour, if you leave the gain alone and conditions stay the same, the layer disappears. Later in the afternoon it starts coming up again, and you start picking it up again. We have noticed this many times. It looks as if something were running out of gas.

Ebeling: We have made numerous measurements of the gas content in swimbladders of fishes that probably do not undergo diel vertical migrations, mainly rock fishes and perhaps hatchet fishes. The swimbladders of individuals recently trawled to the surface contained mostly oxygen, as much as 90%.

D'Aoust: There is another point that has not been mentioned, namely that oxygen consumption may be a rather poor estimate of the energy that the fish is expending at any one time. Glycolysis is a major energetic pathway in fish muscle, so oxygen consumption may be a conservative estimate of momentary work.

Alexander: You're not suggesting, are you, that fish behave like tapeworms, getting energy by glycolysis and then excreting fatty acids?

D'Aoust: I think that they would save the fatty acids.

Alexander. But if they save the fatty acids, then in the long term they are depending on oxidation.

D'Aoust: I don't think we can say that yet. The impression I get from what is known about fish metabolism, and this varies greatly, is that they can withstand a tremendous oxygen debt. I think that it makes difficult any estimation of efficiency because it is a matter of what is done with the waste over time, whether it is lactic acid or fatty acid.

Alexander: The particular figures I gave for efficiency of fish swimming were based on measurements of oxygen consumption over very substantial periods when oxygen debt was probably remaining more or less constant, that is, periods of several hours of constant swimming.

Aron: I have one set of observations. Two weeks ago we did some diving in the Santa Barbara Basin, which on the bottom is basically without oxygen and, according to quite a number of people, is abiological. We saw large numbers of the shark, *Parmaturus*, once we reached the bottom. But also on the bottom, and the sharks were clearly feeding on them, we saw at least three or four lanternfishes, probably *Diaphus*, that appeared to be dead. I haven't yet had a chance to talk to Eric Barham about this, but they were floating in every possible direction, hanging close to the bottom and a few feet off the bottom. Even when we approached them with the submarine, they showed no evidence of trying to move away. They looked dead but with no evidence whatsoever of any damage; they were just hanging. There was virtually no current there, and this would suggest that they are as close to neutrally buoyant as possible.

Alexander: If they were getting neutral buoyancy with a gas-filled swimbladder then they would be in a state of instability. They could not remain at a constant depth simply by staying motionless because any slight vertical movement would send them flying up or down.

Aron: You could push them with the boat. When they were caught up in the propeller drag, they were shoved, but they showed no evidence of an attempt to swim. I think they were dead.

Alexander: This suggests that if they were neutrally buoyant, they were depending on fats for their buoyancy rather than gas.

Kinzer: I would like to comment on what Dr. Clarke (W.) said. Most of the teleostean fishes actually keep their pectorals close to the body after the swimstroke. They do not use them as hydrofoils, and this would then give further evidence that pectorals do not contribute to keeping the fish in equilibration.

Alexander: One would have to suppose a less favorable lift-drag ratio.

Kinzer: But myctophids can behave differently, and one needs observation on this point. What I wanted to say is should we assume that myctophids go to the surface for feeding and if they feed and have quite some amount of food in their stomachs, this might add to their weight and would contribute on the way down?

Alexander: I don't think this would be substantially helpful to the fish because if it has neutral buoyancy up near the surface, it has only to swim down a little and the swimbladder will be compressed and will automatically give negative buoyancy that will help it on its way down.

Craddock: Are your equations based on the fact that they are neutrally buoyant?

Alexander: I am assuming that they are neutrally buoyant at the surface.

Craddock: Why are you assuming that? Why don't you try the same thing assuming neutral buoyancy at depth?

Alexander: Because far more energy would be involved. If you have neutral buoyancy at the surface, then as you go down, the swimbladder cannot be compressed beyond the disappearing point so there is a limit to the change of buoyancy that is possible. If you have neutral buoyancy at some depth and move upwards, the swimbladder may expand to many times its original volume, producing enormous excess lift, and consequently very much more energy would be required for maintaining constant level.

Nafpaktitis: Is there much energy involved in absorbing gas from the swimbladder?

Alexander: Energy is not required for absorbing gas from the swimbladder, or ought not to be, because the gas is then moving from a region of high partial pressure to a region of low partial pressure.

Craddock: Doesn't that in some way contradict what you just said before?

Alexander: Would you like to specify in what way it contradicts it?

Craddock: You said that if they went from neutral buoyancy at depth and went up, then they required a greater amount of energy.

Alexander: A greater amount of energy if you are supposing a constant mass of gas in the swimbladder. If you are assuming the other, then there is no difference between a fish which has neutral buoyancy at the top of its vertical range and maintains constant volume as it goes up and down and a fish that has neutral buoyancy at the bottom of its range and maintains constant volume as it goes up and down. They are the same thing. The fish that secretes gas to maintain constant swimbladder volume has neutral buoyancy at all depths.

Pickwell: I would like to ask you the source of your 15-mg per kilo figure. From what fish was that obtained?

Alexander: That was *Pomatomus*, measurements by Wittenberg.

Pickwell: I would like to add a cautionary note here. This kind of experimentation tends to be terminal, to be extremely drastic for the fishes involved. I think that we had better be quite cautious before we assign upper limits to the rate of gas secretion that any given age of any given fish can produce. For example, if you take a very sturdy, strong fish that allows itself to be dealt with in a very drastic manner and will tolerate terminal surgery for long periods of time, such as the Altantic Great Barracuda, you will see rather spectacular rates of gas secretion. I am sorry that I don't have figures to give you here, but I would be willing to bet that they would exceed the number you have just mentioned. So I think it is very important, of course, to take the best numbers you have, but I think that to some extent we may still be where we were in the middle fifties when Kanwisher and Ebeling produced their paper. The best numbers we have for some of the physiological parameters simply are not good enough and are not yet an indication of what the fishes in fact can do in the real world.

Alexander: I would agree with that.

PHYSIOLOGICAL CONSTRAINTS ON VERTICAL MIGRATION BY MESOPELAGIC FISHES

Brian G. D'Aoust
*University of California Naval Biological Laboratory**
Santa Barbara, California

The major factor limiting the extent and rate of upward excursion by mesopelagic fishes is the rate at which gas can be removed from the swimbladder. Downward migration carries only the burden of additional physical work of gas secretion and overcoming decreased buoyancy, whereas (depending on the size of the swimbladder) too rapid ascent involves the risk of embolism. Using simple decompression models of bubble resolution and considering present knowledge of swimbladder physiology, maximum possible rates of ascent are calculated for hypothetical fishes of different sizes over a range of initial:final pressure ratios. (P_i/P_f). Exceptions to the predicted limits are noted and discussed and the ecological advantage of a swimbladder to such species is considered.

INTRODUCTION

Almost ten years ago, Hersey and Backus (1962) suggested that physiologists consider more closely the problem of the deep scattering layer (DSL). At that time the evidence that mesopelagic teleosts were largely responsible for the migrating sound scattering layer was actually very good (Hersey and Backus, 1962; Marshall, 1951, 1960). However, the assumption that gas secretion and resorption capacities of the suspected species were equal to the task of vertical migration had been questioned. Evidence against sufficient rates of gas resorption was brought forth by Jones (1951, 1952), whereas Kanwisher and Ebeling (1957) indicated the magnitude of the problem of gas secretion with an approximate estimate of the energy that a fish would have to expend in order to resecrete the gas it had necessarily removed during ascent. Also, most laboratory data on the actual rates of gas secretion by surface fish showed the process to be too slow to account for the amount of gas needed (Copeland, 1952; Fänge, 1953; Scholander, 1954; Wittenberg, 1958).

Although few physiologists have had the rare opportunity to work on living specimens of such interesting but fragile species as the mesopelagic ones, definite progress has been made in explaining the mechanism of gas secretion (Kuhn et al., 1963; Steen, 1963; Enns et al., 1967). The details need not concern us here. Suffice it that the theory does predict secretory capacities well in excess of those actually observed. Moreover evidence that the suggested mechanism does operate has been provided (Fänge, 1953; Scholander, 1954; Ball et al., 1955; Steen, 1963; Kuhn et al., 1963; D'Aoust, 1970; Douglas, 1967, Enns et al., 1967). Two recent reviews (Alexander, 1966; Fänge, 1966) are useful for access to the literature.

*The author is now with the Virginia Mason Research Center, Seattle, Washington.

Yet, in spite of this development and also the rather widespread assumption that mesopelagic teleosts *do* secrete and resorb gases as required by their vertical migrations, one still senses a certain uneasiness about the phenomena of the DSL which, I think, stems from our unwillingness to accept the fact that it is all worth the fish's trouble. The physiological problems associated with migration might seem out of proportion to the nutritional or ecological benefits to be derived, and yet is it likely that such fish are unaware of a better way?

RESTRICTIONS ON VERTICAL MIGRATIONS

I think the question that sums up this perplexity can be phrased—Which of the processes of gas secretion or resorption are most limiting to the vertical migrations by mesopelagic teleosts? In considering the problem it would be useful to have a physical model—even if somewhat arbitrary—against which a fish's performance can be measured. Since the mechanism and work involved in gas secretion will be considered elsewhere in this symposium, the purpose of this paper is to provide such a model in considering the problem of vertical ascent.

The rate at which a fish can adjust its buoyancy in response to a decrease in pressure depends on the rate at which it can remove gas from its swimbladder. This was investigated by Jones (1952) who showed that the time necessary for a perch to adjust to a 40% reduction in pressure was of the order of 8 hours. Since members of the DSL often accomplish their migrations in less than 2 hours (Hersey and Backus, 19[illegible] Barham, 1966), we can assume with Jones that they must have a greater facility for removing gas. Jones (1952) suggested the importance of the ratio of the depth change to the depth to which the fish was adapted (i.e., neutrally buoyant) in determining the time necessary for migration. However, he appears to have ignored the importance of the magnitude of the gas partial pressure gradient in determining these rates. For example, one could conclude from his Figure 6 (p. 104) that it would take the same time for a fish to move from 40 m to 10 m as from 400 m to 100 m. (Both depth changes involve the same ratio of depth change/depth adapted.) This is not the case, because the rate at which a fish can remove gas ("B" in Jones' paper) depends primarily on the partial pressure gradient driving diffusion, and as mentioned by Alexander (1966), the maximum value of this gradient depends chiefly on the depth of the fish (since gases in the swimbladder are at ambient hydrostatic pressure). Also, as pointed out by Alexander (1966) the pO_2 of the blood perfusing the swimbladder and surrounding tissues will be a most critical determinant of the tension gradient in shallow water. Both of these considerations are conveniently illustrated by the data presented in Figure 1 (D'Aoust and Hogue, 1968). This shows the changes in Xe^{133} and O_2 concentration in the swimbladder of a salmon (a physostome) which was restrained just beneath the surface of a stream. Xe^{133} had been introduced via a canula through the pneumatic duct. The contents of the swimbladder were periodically sampled and analyzed for each gas. It is clear that the Xe^{133} disappeared in each fish at a rate *continuously determined by the gradient*. The constant k sums the effects of the diffusion barrier and the total area through which diffusion was occurring, so that at any one time the concentration of Xe^{133} could be given by the equation $C_t = C_0 e^{-kt}$, where C_0 is the initial concentration, and C_t is the concentration at time t. On the other hand, the concentration of oxygen, which should theoretically have increased since it was initially lower than in the surrounding water, changed in a way which suggests it was influenced by factors other than the water/swimbladder gas gradient. In a mesopelagic fish at a depth of several hundred meters, the pO_2 gradient is large and one might expect the gas—which is primarily oxygen—to initially disappear in the way indicated by the upper curve. On the other hand, the lower curves (O_2) illustrate the effect of respiratory and circulatory adjustments which can alter the rates of equilibration.

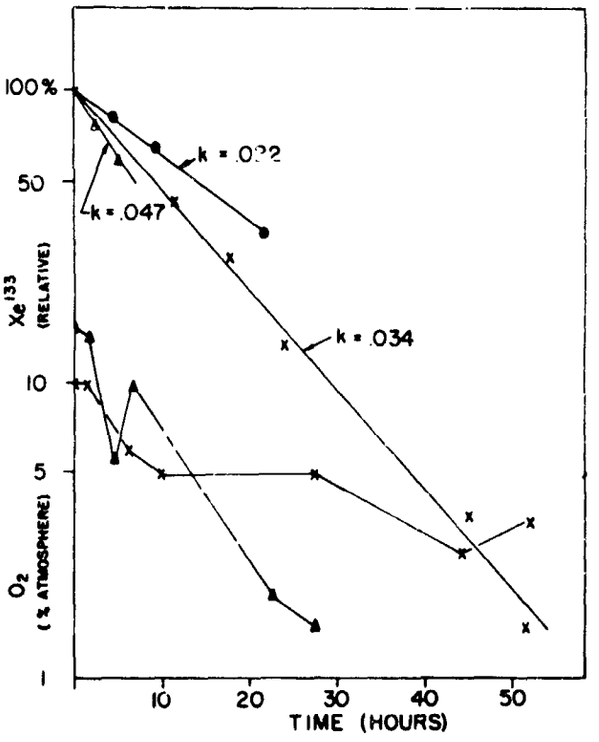

Figure 1. O_2 and Xe^{133} diffusion out of the swimbladder of the pink salmon, *Onchorynchus gorbuscha* restrained under 10 cm. of water. The concentration of Xe^{133} is expressed as a percentage of the original radioactivity present, while the concentration of oxygen is expressed as percentage volume on the same log scale. The values of k and Xe are given for each fish. Differences are probably due to differences in the surface/volume ratios in the swimbladder at the beginning of the experiments. Note the erratic behavior of the O_2 concentration, suggesting the effect of respiratory and/or circulatory adjustments, which however did not affect the rate of Xe^{133} escape. These curves illustrate the importance of the partial pressure gradient in driving diffusion and also the way in which perfusion may control the net rate of gas loss.

MAXIMUM POSSIBLE ASCENT RATES

To consider possible migratory rates it is convenient to regard the swimbladder as a bubble which must be brought upward with a constant volume V. This requires loss of an amount of gas which depends only on the difference in the initial and final depths of the migration. In physoclist teleosts this gas must be lost by diffusion, whereas in siphonophores, bubbles may be released through a sphincter (Pickwell, 1966, 1967). The number of moles of gas n which must be removed during an upward migration is calculated from Boyle's Law,

$$PV = nRT \qquad (1)$$

or

$$n = \frac{PV}{RT}, \tag{2}$$

where P is the pressure in atmospheres (atm.), R is the gas constant (0.082 liter atm. degree^{-1} moles^{-1}) and T is temperature in degrees Kelvin. Since P increases with depth we can write

$$P = ky + 1, \tag{3}$$

where k is a factor for the increase in pressure with depth and y is the depth in meters. The constant k is numerically equal to 0.10 if the standard atmosphere is combined with a seawater density of 1.033, and this value will be used here.

Then the number of moles n which must be lost from a bubble of volume V for each meter of upward travel is given by

$$n = \frac{V \cdot k}{RT}. \tag{4}$$

Thus a bubble of constant volume would have to lose or gain $\cdot k/RT$ moles per meter of depth per ml. volume, or an amount of gas that depends only on the depth change. In other words, a fish migrating vertically must remove or replace the same mass of gas whether the migration is from 600 m to 300 m or from 300 m to the surface.

As mentioned earlier, however, the time required for removal of this gas will be much greater for the upper 300 m than for the 600 to 300 m migration. This is because the loss of gas depends primarily on diffusion, which in turn depends directly on the gradient in chemical potential, or the partial pressure of the gas in the bubble minus that in the water outside the bubble. Since the gradient in gas pressure increases linearly with depth, loss of gas from the bubble should proceed at a greater rate at depth than near the surface.

This process was studied by Wyman et al. (1952), who described the effects of pressure on resolution of gas bubbles in seawater. They found that the process could be adequately described by the equation

$$\frac{dr}{dt} = -RT\delta \frac{P - P_0}{P}, \tag{5}$$

where dr/dt described the rate of change in the radius of the bubble with time, RT has the same meaning as before, δ is an effective diffusion constant which assumes a uniform concentration gradient at a steady state. It is equal to $\Delta\alpha/d$ where Δ is the "true" diffusion constant of dimensions cm^2/sec, α is the solubility coefficient (to convert partial pressures into concentrations), and d represents the thickness of the "unstirred" shell of water which is assumed to support the gradient in concentration. The expression $P\text{-}P_0/P$ is the partial pressure gradient divided by the total pressure where the bubble exists. It obviously tends to unity as the total pressure (or depth) is increased, and the rate of decrease in bubble radius dr/dt, similarly approaches a constant rate which from their data amounts to approximately 0.8 μm/sec or 8.0×10^{-5} cm/sec at 50 m.

Essentially the same treatment has been successfully used by Van Liew (1967) working with artificially produced subcutaneous gas pockets in rats.

Ultimately we are interested in the time necessary for migration of a bubble over a given depth-range. The essential requirement of such a migration is that the rate of gas loss or removal keep pace with the increasing volume of the bubble as depth decreases. Equation (5) applies at a constant pressure, whereas we are interested in times of migration during which the pressure

gradient is changing. However, we can conceive of an imaginary situation (ignoring buoyancy and drag) in which the increase in volume of the bubble due to decreasing pressure is just equal and opposite to the decrease in volume due to gas loss through diffusion. When such effects cancel, the *volume* will not change. Thus we need another equation for dr/dt describing the effects of pressure at constant mass of gas. This is available from equation (1), which is re-arranged to show how the radius of a bubble of gas depends on the pressure as follows:

$$r = \left(\frac{3nRT}{4\pi P}\right)^{\frac{1}{3}}. \tag{6}$$

P can be expressed at depth by using (3).

$$r = \left(\frac{3nRT}{4\pi(ky+1)}\right)^{\frac{1}{3}} = \left(\frac{3nRT}{4\pi}\right)^{\frac{1}{3}} \cdot (ky+1)^{-\frac{1}{3}} \tag{7}$$

Differentiating (7) with respect to time gives

$$\frac{dr}{dt} = -\left(\frac{3nRT}{4\pi}\right)^{\frac{1}{3}} \cdot \frac{k}{3(ky+1)^{\frac{4}{3}}} \frac{dy}{dt} \tag{8}$$

Thus (8) shows that the rate at which the radius of a bubble increases is proportional to the rate of change in depth (or pressure) and inversely proportional to the depth. Our requirement is that dy/dt is such that addition of equations (8) and (5) equals 0.

First, equation (5) can be stated in terms of (3), i.e., depth. Also, the assumptions will be made that (a) we are dealing with a bubble of pure oxygen since Douglas (1967) has thoroughly documented the fact that O_2 comprises 80-90% of the swimbladder gas below a depth of 50 m, and (b) that the oxygen partial pressure in the water (P_o) is 0.2 atm. throughout the water column.

Thus (5) becomes

$$\frac{dr}{dt} = -RT\delta \frac{(ky+1-.2)}{(ky+1)}$$

$$\frac{dr}{dt} = RT\delta \frac{(ky+.8)}{(ky+1)}. \tag{9}$$

If the effects of pressure reduction and diffusion loss are equal and opposite, addition of (8) and (9) gives 0, and we can equate the right-hand sides of equations (8) and (9) and rearrange to evaluate dy/dt at this null point;

$$\frac{dy}{dt} = \frac{3RT\delta}{k\left(\frac{3nRT}{4\pi}\right)^{\frac{1}{3}}} \frac{(ky+.8)}{(ky+1)} (ky+1)^{\frac{4}{3}}$$

$$\frac{dy}{dt} = \frac{3RT\delta}{kr} (ky + 0.8) \text{ and since } k = 0.1,$$

$$= \frac{3RT\delta}{r} (y + 8). \quad (10)$$

To evaluate (10) for any particular volume and depth, some assumptions must be made about the value of δ. Wyman et al. (1952) noted a gradual decrease in experimentally determined values of δ with depth which they showed was due to the mixture of gases present. Since only oxygen is considered here, their value for oxygen of 8.4×10^{-9} moles $cm^{-2}sec^{-1}atm^{-1}$ will be used. Equation (10) then works out to

$$\frac{dy}{dt} = \frac{5.65 \times 10^{-2}}{r} (y + 8) \text{ cm sec}^{-1}. \quad (11)$$

A 1.0 cm^3 bubble at 100 m could therefore rise at a rate of 9.8 cm/sec; at 10 m it could rise only at 1.6 cm/sec, and at 1 m depth it could rise only at 0.8 cm/sec. This relationship is shown in Figure 2 where depth is plotted on a log scale against dy/dt for several different bubble volumes. It is clear from the figure that, as expected, a fish with a swimbladder which behaves as a bubble could rise faster from 600 m to 300 m than from 300 m to the surface. Obviously the curves are imaginary at their extremes; drag would prevent a bubble travelling at the higher velocities shown and buoyancy would cause far greater vertical ascent rates than shown for shallow depths. What makes the curves still worth considering is that we are surrounding the "bubble" with a fish which can supply the necessary acceleration or restraint.

Figure 2 also indicates the restrictions of swimbladder volume on vertical migrations and the obvious advantage of a small swimbladder in accomplishing vertical migrations.

Inversion of (11) and integration over the limits y_1 to y_2 gives

$$T_{sec} = \frac{r\,2.303}{5.65 \times 10^{-4}} \log \frac{y_1 + 8}{y_2 + 8}. \quad (12)$$

which allows calculation of the time required by bubbles of various volumes to move upward under the assumed conditions. Figure 3 shows these times for bubbles of different sizes. Note that the figure assumes 100% oxygen in the swimbladder and therefore a minimum gradient at the surface of 0.8 atm. The times involved would be larger for bubbles of 85-90% oxygen. At any rate, the times shown in Figure 3 for bubbles of different sizes can be assumed to represent minimum times which a fish with a swimbladder of volume V and a diffusion constant approximating δ could be expected to take over any particular depth range. Thus a fish with a 1-cm^3 swimbladder migrating from 1000 to 500 m ($\log P_1/P_f = 0.297$) would require at least 10 min. whereas the same fish migrating from 500 m to the surface ($\log P_1/P_f = 1.81$) would need approximately 75 min.

Figure 3 thus provides a physical basis for comparison with observed rates of migration. It is an arbitrary but perhaps not unrealistic standard of comparison, and it is of some significance that the times shown are well within those observed for migrations of the DSL of 1-3 hours (Hersey & Backus, 1962; Barham, 1966). Since the members of the DSL appear to be well on the slow side as concerns gas removal it can be suggested that their "effective diffusion constant" δ (capacity to remove gas) must be much less than that assumed for a free bubble in the above

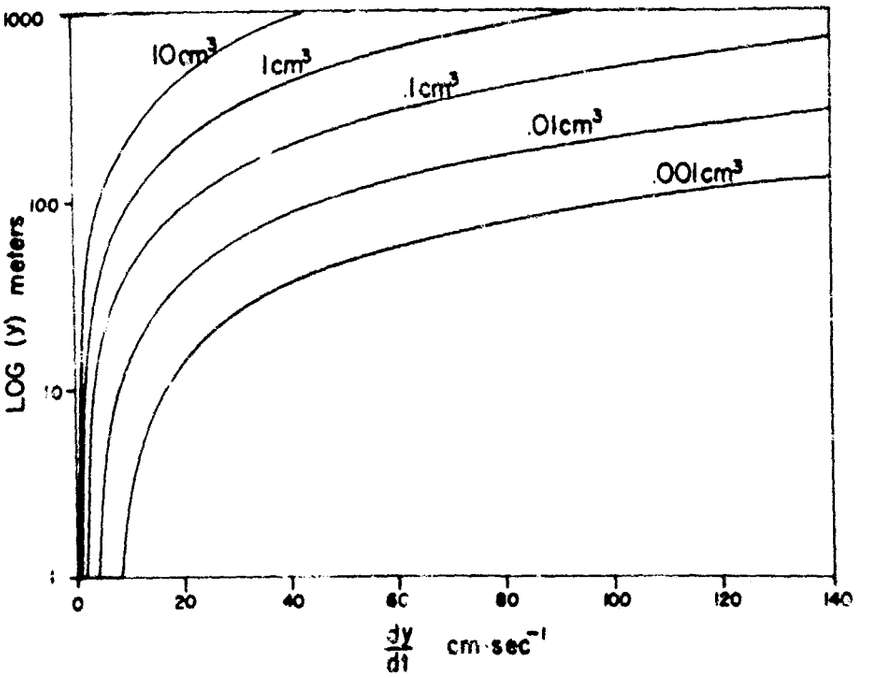

Figure 2. Rates of ascent dy/dt possible for different sizes of spherical bubbles such that the increase in radius $+dr/dt$ due to pressure decrease is exactly equalled by the decrease in radius $-dr/dt$ due to diffusion of gas out of the bubble in response to the pressure gradient. Based on equations developed in the text, assuming 100% oxygen in the bubble and 0.2 atmospheres of oxygen in the water, and neglecting buoyancy and drag. Note the relatively constant change in rates at the shallow and deep extremes of each curve.

calculations. This would improve their gas secretion efficiency (by minimizing gas loss), while still allowing them to remove gas at a sufficient rate to move upward at the rates observed. In fact, if it is assumed that a 0.1-cm^3 bubble took 2 hours to move from 300 m to the surface, then (12) would require a value for δ of 1.32×10^{-10} moles cm^{-2} atm^{-1} sec^{-1} or approximately $1/7$ of the values used in Figures 2 and 3. In other words, the rate of gas removal could be almost an order of magnitude slower than a free bubble without necessitating a slower migration rate.

POTENTIAL MEANS OF MAXIMIZING GAS RESORPTION AND SECRETION

The work of Marshall (1951, 1960), Kanwisher and Ebeling (1957), and Capen (1967) suggests that the actual volume of the swimbladders of mesopelagic fish seldom exceeds 1.0 cm^3 and is usually much less (a bubble of 1.0-cm^3 size would theoretically require only about an hour and a half to migrate at constant volume to the surface from 1000 m). Moreover, it appears that the often-quoted ratio of 5% (for swimbladder volume to fish volume) may not hold for some of these mesopelagic forms, many of which apparently lose the gas phase in their swimbladders on maturing, having largely substituted fat as a source of buoyancy (Marshall, 1951; Denton, 1961; Capen, 1967). These observations suggest that gas secretion is a

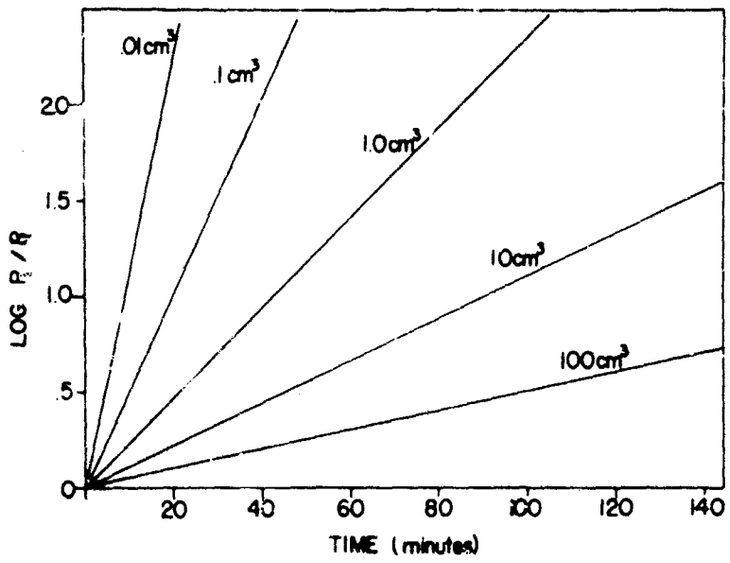

Figure 3. Theoretical time (abcissa) necessary for spherical bubbles of different size to move upward at constant volume over a particular range in depth (ordinate) given by log P_i/P_f where P_i is the initial pressure at the lower depth and P_f is the pressure at the final depth. Buoyancy and drag are neglected.

considerable burden. It is worthwhile to consider some of the adaptations which may favor both rapid secretion and resorption, keeping in mind that the enhancement of one might decrease the other.

High Fat Content

The first adaptation which comes to mind is to reduce the gas volume by partly or completely substituting fat for gas, as is done by *Lampanyctus*, *Gonostoma*, *Cyclothone*, and *Diaphus* (Ray, 1945; Marshall, 1951; Barham, 1957; Capen, 1967). The advantages of fat vs. gas as a source of buoyancy are obvious for species which must migrate over considerable depths. The urgent need for resecretion of gas is eliminated, and an added temporal degree of freedom is realized by the fish for which the energetic demands of gas secretion impose a considerable food requirement (Kanwisher and Ebeling, 1957). The interesting recent report by Malins and Barone (1970) which directly demonstrated synthesis of diacyl glyceryl ethers in preference to triglycerides as a response to negative buoyancy in *Squalus acanthias* suggests the possibility of similar controls by mesopelagic species. However, little or no fat is observed in juveniles which almost always have a gas phase (Capen, 1967). It appears then that the accumulation of fat is a gradual process taking place during maturation of the individual (Nevenzel et al., 1966). The dietary control of such accumulation is of considerable interest (Lewis, 1967; Nevenzel et al., 1969; Lee, 1970).

Surface Area/Volume Ratio

The more surface area relative to volume, the faster the gas transport; however, this effect should work both ways and render it that much more difficult to *secrete* gas at a sufficient rate. Nevertheless many of these species have an elongated swimbladder with length-to-width ratios

of up to 5:1, and Marshall, 1951, reported one of 40:1, *Photichthys argenteus*. (There are as yet few measured specimens which can be considered absolutely undamaged by the method of collection and/or preservation.) This would increase the possible rate of gas loss. However, it is obvious that the detailed histology of the swimbladder, surrounding tissue, gas gland, and resorptive surfaces is of most significance in determining the effective surface area for gas exchange.

The observations of Fänge (1953) and Dorn (1961) indicated a considerably villous organization of the gas gland epithelium in *Gadus* and *Anguilla* that showed a tendency to increase during gas secretion. This sort of organization would tremendously influence the effective area over which diffusion takes place, and would greatly accelerate gas transfer provided that adequate perfusion existed on the liquid side of the phase boundary. The advantage of such an organization is that its benefits can be switched on and off via circulatory and neural control.

In a complementary way a number of small gas pockets would be expected to increase the rate of gas removal provided, as before, that the interstices of such compartments were well perfused. This speculation is stimulated by the report of Capen (1967) describing a "fibrous cottony tissue" partially or totally filling the swimbladder in specimens of *Lampanyctus* and *Diaphus*. If such tissue actually consists of a number of gas pockets and the interstices are well perfused, a very great increase in effective surface area would exist. Capen (1967) also reported that the specimens he observed had oil-filled tissue around the swimbladder rather than inside it as first reported by Ray (1945).

It is of interest to consider the above points in relation to their probable effects on gas secretion and resorption. The diffusion coefficients Δ of gases in liquids are inversely proportional to the viscosity of the liquid (Glasstone, 1946). Although the solubility α of gases is higher in fats and oils, the viscosity of these substances is very much greater than water (10^2–10^3), and the diffusion of any gas through them is very much slower than for water. It can be assumed that an envelope of fat surrounding the swimbladder would provide a very effective diffusion barrier by lowering the value of Δ and increasing the value of d in the expression $\Delta a/d$. Decreasing the "passive" value of δ will increase the efficiency of gas secretion. Thus, as the fishes grow they may deposit such fat around the swimbladder where it acts as a diffusion barrier and provide auxiliary buoyancy, and, perhaps, an important energy reserve. Thus, the general direction of adaptation appears to reflect the most serious constraints of vertical migration, viz. the energy-consuming requirement to secrete gas.

The critical role perfusion must play is worth considering briefly. Wyman et al. (1952) estimated the effective thickness d of the "unstirred shell" to be approximately 33 μm, at the same time emphasizing that such a value only gave a rough estimate of the length of the "pure diffusion" path. Since capillaries are often smaller than 10 μm (Bard, 1960) it is very probable that during perfusion of the resorptive surfaces of the swimbladder the actual distance supporting a purely diffusive gradient is of the order of only a few microns. It is clear that the combined effects of increased perfusion and decreased values for "d" could greatly accelerate removal of gas from the swimbladder during ascent, the work necessary being chiefly that of cardiac output.

In fact, it has recently been suggested (Steen & Kruysse, 1964; Johansen & L'enfant, 1966), and more evidence is accumulating (Garey, 1967; Dawson & Garey, 1968) that teleosts are capable of extensive circulatory adjustments or shunts, such that the gill surfaces can either be bypassed or well perfused according to the fish's need. One can easily imagine shunts such that during ascent essentially O_2-free blood is supplied to the resorptive surfaces of the swimbladder and such circulation might amount to a very large proportion of the total cardiac output. During descent on the other hand, it can be supposed that *most* of the cardiac output goes to the gills and thence to the gas gland and *rete* circulation. In a situation where the blood perfusing

the gas gland had a very low pO_2 the *rete* would also provide a route for gas removal (Denton, 1961). For example, Marshall (1960) has described the swimbladder vasculature of a stomiatoid fish *Argyropelecus aculeatus* which lacks an oval (or gas resorptive organ); it features however an artery bypassing the *rete* with a venous return through the *rete*, and it can be assumed this serves the purpose of gas removal.

The above considerations seem to support the conclusion that once secreted, there need be no very great difficulty in removing gas at rates consistent with observed rates of vertical migration. Moreover, it can be suggested that if the fish does initially swim up a certain amount as suggested by Jones (1952) it could "float" the rest of the way and need expend only the cardiac energy to provide the required circulatory adjustments. In like manner, it could "sink" during descent and conserve energy for the task of gas secretion. It should be mentioned however, that actively swimming fish have been directly observed (Barham, 1966) in a layer which was descending at a rate (approx. 30 cm/sec) higher than the ascent (4.0 cm/sec.). Nevertheless gas secretion probably requires a large share of the fish's energy output during descent. Estimations of the total amount of work required (Kanwisher and Ebeling, 1957; Marshall, 1960) may however be too rigorous, as they are based on some assumptions regarding the fraction of cardiac output going to the gas gland. In view of the above considerations, it does not seem unreasonable to assume an overall higher efficiency for the process of gas secretion.

SUMMARY

(1) The need for an arbitrary physical model with which to compare the migratory behaviour of mesopelagic teleosts is suggested.

(2) The model chosen is that of a free spherical bubble, ignoring buoyancy and drag, rising at a rate such that its expansion rate due to pressure (depth) decrease is exactly cancelled by the decrease in volume due to diffusion loss.

(3) It is shown that for spherical bubbles of a size equal to or less than the volume of swimbladders normally found in mesopelagic fishes, the times theoretically necessary to rise 200 or 300 m are up to an order of magnitude less than those actually observed for the DSL.

(4) Some potential means of maximizing gas resorption and secretion are discussed in terms of existing physiological and anatomical evidence and ways are suggested in which dynamic physiological adjustments may assist gas removal or secretion.

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DISCUSSION

Alexander: I have three comments. First of all, it would be very nice if we had some really clear information as to what the fish actually do about their swimbladder volumes as they move up and down. Second, it seems likely that what limits the rate at which gas can be removed from the swimbladder may be the rate at which the blood can take the gas away. I did some calculations on this which are in a little book of mine called *Functional Design in Fishes*. These led to the conclusion that at shallow depths the rate of removal of gas should be extremely slow, and I got very good agreement with Jones's experimental figures. For greater depths, the blood was able to take away gas very much faster, largely because of gas being removed in physical solution in the blood. I am afraid I have not got the figures with me. The third point is that shunting out the gills would surely reduce the rate of removal of gas rather than increase it, because it would mean that the gas in the blood that was coming away from the swimbladder would simply be shunted back to the swimbladder again and would have no chance to diffuse out of the fish.

D'Aoust: I realize this, but I would get around it by saying that perhaps it is used or lost to the tissues in another way. The point I wanted to make is that, thinking of it in terms of the first time around with a shunt, you could consider almost an infinite gradient at the surface. I agree that this is the main restriction, but perhaps you can conceive some way of shunting which may get around the problem.

Alexander: I think that at any substantial rate of removal of gas, you might find yourself having to develop a fantastic metabolic rate to get rid of it.

Backus: The acoustical data of nine years ago in Hersey, Backus and Hellwig suggested that migrators would be heading both ways, that some were maintaining constant volume, and some were maintaining constant mass.

D'Aoust: I can think of another point. Just a slight change, an uncompensated expansion just for a meter or so, would allow the fish to be buoyant. This is an advantage in terms of work. By the same token, it is more useful to save energy and sink down, and secrete gas using the energy saved.

Smith: Would it be possible that bioluminescent flashes would assist in burning off this excess oxygen?

D'Aoust: You mean, why doesn't the fish explode?

McCartney: I have a comment relevant to gas bubbles, though not to fish swimbladders. Some time ago I worked on some data belonging to Brian Bary on gas bubbles rising from Saanich Inlet. The remarkable thing about these, which were observed on echo sounders, was that any given bubble seemed to be rising at a remarkably constant rate, although there were different rates for different bubbles.

D'Aoust: Yes, and I have neglected buoyancy and drag. There is a point in the ocean, probably, where parts of these curves would hold. Below it the drag would be too great to allow the bubble to rise; above it, the bubble would rise much faster due to buoyancy. So this is a hypothetical situation, and I agree it would require a fish for it to work.

Pickwell: I just want to make a couple of comments. One is that when you are dealing with certain adult myctophids that have a great deal of fat around the swimbladder, probably you are not dealing with a significant gas phase. Therefore as a diffusion barrier in that situation it is rather irrelevant. If there is gas there, in our observations at least, it is so small that possibly the fish could tolerate a passive expansion, perhaps throughout the entire vertical distance it is migrating. Second, as pointed out by Dr. Alexander, the business of diffusion is almost certainly controlled by rate of blood flow through the resorption mechanism in the oval. I consider it quite probable that the fish alters the rate of blood flow, within some range, so that towards the upper limit of its vertical migration, as it is resorbing gas, it is in fact pumping blood through this structure very much more rapidly than it found necessary to do when it began the migration. I do not think that there is any reason in the world why we should accept the idea that it does this at a uniform rate. Therefore, this changes the whole diffusion picture, and your rate of rise relative to diffusion is probably quite reasonable in that context.

D'Aoust: I assume you mean in the context that the diffusion coefficient you got would be something that lumped everything together. The actual diffusion coefficients involve surface area and circulation more than anything. But as you said, at the upper edge of the range it has to do a tremendous amount more circulatory work.

Pickwell: The reason I mentioned this is that in physiological experiments with gas secretion when we are observing the gas gland, it operates at different rates also, which lends credence to Dr. Alexander's supposition that there is an idling rate of maintenance of volumes. This is probably true. Nevertheless the swimbladder is after all a diffusion barrier, and in various species it is a rather good one, so I do not think we can assume that the fish, even at a considerable depth, is losing a huge quantity of gas and therefore has to idle at a very rapid rate; it has to idle at some rate, surely.

D'Aoust: Yes, the dimensions are pretty small.

Pickwell: This is my point.

D'Aoust: For water, for example, a millimeter or so, a millimeter is almost the thickness of the body wall in some of these fish. I should think it would be idling if it is maintaining neutral buoyancy at an appreciative rate, relative to the normal energy budget of the fish.

Pickwell: I don't think so. I think it is idling at a very small rate relative to what it can do when it wants to refill the bladder.

D'Aoust: I agree with you. I think we are saying the same thing differently.

Pickwell: Speaking in terms of one millimeter structures, just for fun since Eric Barham isn't on his feet yet, I thought I would throw in the physonect siphonophores. They do have a dimension roughly one millimeter in diameter, and they are carrying about 1 mm^3 of gas. As far as we can tell from observations both in the laboratory and from submersibles, within some rather tight limits they maintain a constant volume. Well, they can do this. They have a structure for putting out the gas. Nevertheless they are swimming rapidly, and their rate is still comparable to what the myctophids do. Let's not forget that both of these animals, these presumably resonant targets, are swimming. They're not just rising passively as this gas carries them upwards. Therefore, the rate or, at least the delimiting feature in rate of migration for a myctophid with a swimbladder, may be simply how fast it can take the gas out; certainly not in the case of the physonects, though.

D'Aoust: That is what I am suggesting. What I am saying is that we can make some measurements now, and even though the coefficients we get will not mean too much in terms of real diffusion coefficients, it will be something we can work with physiologically.

DEEP-SEA FISHES
LETHARGY AND VERTICAL ORIENTATION

Eric G. Barham
Naval Undersea Research and Development Center
San Diego, California

ABSTRACT

Over the past several years observations from deep submersible vehicles have provided new perspectives on the biology of mesopelagic fishes.

Many individuals of the myctophids, *Lampanyctus leucopsarus* and *L. mexicanus*, the deep-sea smelt *Bathylagus stilbius*, and *Cyclothone acclinidens* observed at middepths off southern California are passively drifting with their longitudinal axes at acute angles to the horizontal plane. If stimulated by the presence of the craft, such lethargic, vertically oriented fishes swim rapidly away. Thus, the frequency of these observations is related in part to the type of vehicle used, its equipment, and the way it is operated.

The adult myctophids have lumen-occluded, fat-surrounded swimbladders indicating that food storage and elimination of buoyant gas production are adaptations for diurnal reduction of metabolic and physical activity in response to environmental stress.

In some cases, vertical orientation of myctophids is polarized, the vast majority of individuals being oriented with their heads up in late afternoon and their heads down in the forenoon. This may be adaptive. Rhythmic opercular movements suggest that respiratory water currents jetted from their gill cavities are used to maintain their depth level or to "swim" up and down. A majority of myctophids that migrate into surface waters at night are seen actively swimming, but many adults remain immobile and vertically oriented near their daytime depths. Thus, some mesopelagic fishes may undergo periods of hibernation similar to known shallow water fishes.

Bathylagus stilbius lacks a swimbladder and that of *Cyclothone acclinidens* is fat filled. Vertical orientation in these fishes may result from a lack of sensory clues.

These observations suggest that: change of posture may affect the sound reflecting properties of fishes responsible for deep scattering layers; there are two behavioral types of myctophids, each with recognizable morphological features; photophores of vertically oriented fishes could not create a protective counter-shading, low-level bioluminescent glow against downcoming ambient light; and active fishes may be nearer their endurance limits and thus more easily captured by nets than those in a lethargic state that are rested and capable of rapid evasive movements.

INTRODUCTION

Diminutive mesopelagic fishes dwelling in the three-dimensional environment of oceanic middepths are, without doubt, the most abundant vertebrate animals in our world; and yet, understandably, little is known of their behavior. Few such fishes are removed uninjured from plankton nets and trawls, and even those species that nocturnally ascend into surface waters and are dipnetted carefully live, at the longest, only a few hours in shipboard aquaria; stressed and confined, their behavior is hardly typical. Thus, our concepts of the biology of these fishes by necessity have been based mainly on anotomical studies, net-catch data, and occasional glimpses of such fishes under ships' lights when they are in surface waters.

Mesopelagic fishes now can be studied in their own environment from deep submersible vehicles (DSV), and this paper draws from the experiences of over 50 dives in five different DSV's during a 6-year period. Most of the data presented are based on the results of a 19-dive series in the Westinghouse *Deepstar 4000* vehicle in the San Diego Trough, 30 June to 16 December 1966, because these observations were taken under better conditions and in the context of information gained from previous dives.

It is now apparent to this observer that in the California Current, numerous individuals of at least two species of myctophids, *Lampanyctus* (=*Stenobrachius*) *leucopsarus* and *L.* (=*Triphoturus*) *mexicanus*, some species of the gonostomatid genus, *Cyclothone*, and the deep-sea smelt, *Bathylagus* (=*Leuroglossus*) *stilbius*, normally are suspended lethargically, virtually motionless in the water, oriented with their long axes at the vertical or at steep angles from the horizontal. This behavior would seem to have important implications regarding the biology of these fishes. Thus, although other behavioral traits are noted, this paper deals mainly with what, for want of better terms, we will call "lethargy" and "vertical orientation." By necessity, much of the presented information is anecdotal. The possible relationships of fish behavior to the scattering of underwater sound are discussed, and interpretation of the reported behavior is placed in the context of problems that have long intrigued biologists. Conclusions, however, are tentative, and are given in the hope that they may stimulate further study and consideration of these prolific fishes, about which we know so little.

OBSERVATIONS

Trieste I

The kinds of organisms, and their behavior, that one observes from DSV's are affected greatly by the type of vehicle used and the way it is equipped and operated. Our experiences using the bathyscaphe, *Trieste I*, during six dives in the San Diego Trough (January to October 1962, approximately at 32°30′N, 117°28′W) are a case in point. Generally, the bathyscaphe rose or fell rapidly in her passages through middepths. In her dimly lit and partially obstructed field of view, objects the size and pigmentation of mesopelagic fishes could be seen and recognized only at distances of less than 5 m. Numerous mesopelagic fishes were sighted (Dietz, 1962; Barham, 1963), but these were seen either in rapid flight at the edges of the light field as *Trieste I* was descending, or they were caught up and momentarily tumbled about in the vortex created by the ascending bathyscaphe. As the craft rose, some fishes apparently were stunned or killed by the bathyscaphe's large, gasoline-filled float, and they were inert and turning slowly end over end as they passed by the viewing port.

The only opportunity for prolonged observation of midwater fishes occurred on two occasions when the bathyscaphe's descent had been slowed by an overdischarge of ballast. Small groups of yearling Pacific hake (*Merluccius productus*) swam slowly back and forth in front of the viewing port, occasionally erecting their dorsal spines. In this case they were obviously attracted to the craft, following it both up and down for short distances.

Trieste II

Conditions for viewing mesopelagic fishes were improved in *Trieste II* by installation of additional lights and more powerful motors, which permitted cruising at middepths. On a dive during early morning hours in the San Diego Trough, (5 March 1964, at 32°52′N, 117°27′W), large numbers of myctophids first were noted motionless in a vertical position, the majority with their heads down. These were seen at the fringes of the light field. The fishes that we

descended on at close range broke with a start from their lethargic state and rapidly swam downward in quick, jerky flights. When such fish could be kept in view, they were seen to resume again a vertical, immobile position, some with head up, others head down. This behavior was most surprising because myctophids at the surface at night under a ship's lights, are frequently darting at random, even leaping above the surface and leaving a shower of sinking scales behind while escaping an attacking squid.

Cousteau Saucer

The small Cousteau Soucoupe Sous Marine (Diving Saucer) is ideally suited for midwater observations. Buoyancy can be trimmed to maintain a constant depth, and an unobstructed, well-illuminated field of view is provided. By remaining motionless with all lights and motors turned off and then switching on the lights, a good impression of the normal behavior and posture of midwater organisms can be obtained. This technique of alternating light and dark periods was used to study the migrations of deep scattering layers (DSL) in four dives (3 to 4 February 1965) off Cabo San Lucas, Baja California, at about 22°50′ N, 109°40′ W (Barham, 1966). Swarms of a large (8 to 10 cm in length), silvery-scaled myctophid (probably *Myctophum aurolaternatum*) were observed swimming in a series of quick, random movements of about 1 m, alternating with motionless, short pauses. (This is similar to the behavior one sees when myctophids come to ships' lights at night in surface waters.) A few small (5 to 7 cm), black myctophids (probably *Lampanyctus mexicanus*) were seen also, vertically oriented, hanging motionless at the edges of the light field.

Deepstar 4000

With this background, we made a special effort to take data on mesopelagic fishes observed during the *Deepstar* dive series in 1966. *Deepstar* is essentially a larger Cousteau Diving Saucer with greater depth capability and payload. When an instrument rack is not in place, there is a good view, only partially obstructed by the overhanging brow. The observer lies comfortably on a couch behind the viewing port, dictates notes to a tape recorder, and can activate both a 70-mm still camera with slaved strobe flash and a 16-mm ciné-camera. Various lights can be turned off or on to provide best illumination for near- or far-field viewing. A second observer sits in the rear and can assist by reading instruments, taking notes, and maintaining communications with the surface support ship via underwater telephone. As in all deep submersible operations, the skill, interest, and motivation of the pilot, who lies beside the principal observer, viewing from his port, are of utmost importance in taking good data. (See Terry, 1966, for a detailed description of this craft and the other DSV's used.)

During the course of the program, we gained the impression that more midwater organisms could be seen, and in their natural postures, by drifting slowly up or down with the motors off. (Possible reasons for this effect will be discussed later.) The dives were planned, however, to study the depth relationship of organisms to DSL's and other acoustic features. With the ballasting system then in use, *Deepstar* could establish neutral buoyancy at only one depth after the descent weight was jettisoned. Thus, the dives were made in stepwise descending transects, running constantly on the motors to maintain a relatively stable level at several depths chosen on the basis of scattering conditions recorded by a surface ship previous to the dive.

The general posture and vertical distribution of all myctophids, *Cyclothone* sp. and *Bathylagus stilbius* observed during six dives over a 7-month period are shown in Figure 1. Based on similarity of dive pattern, these data were selected from a larger body of information. By running on the motors at speeds varying from 0.5 to 2.0 knots (0.95 to 3.7 km/hr) to maintain

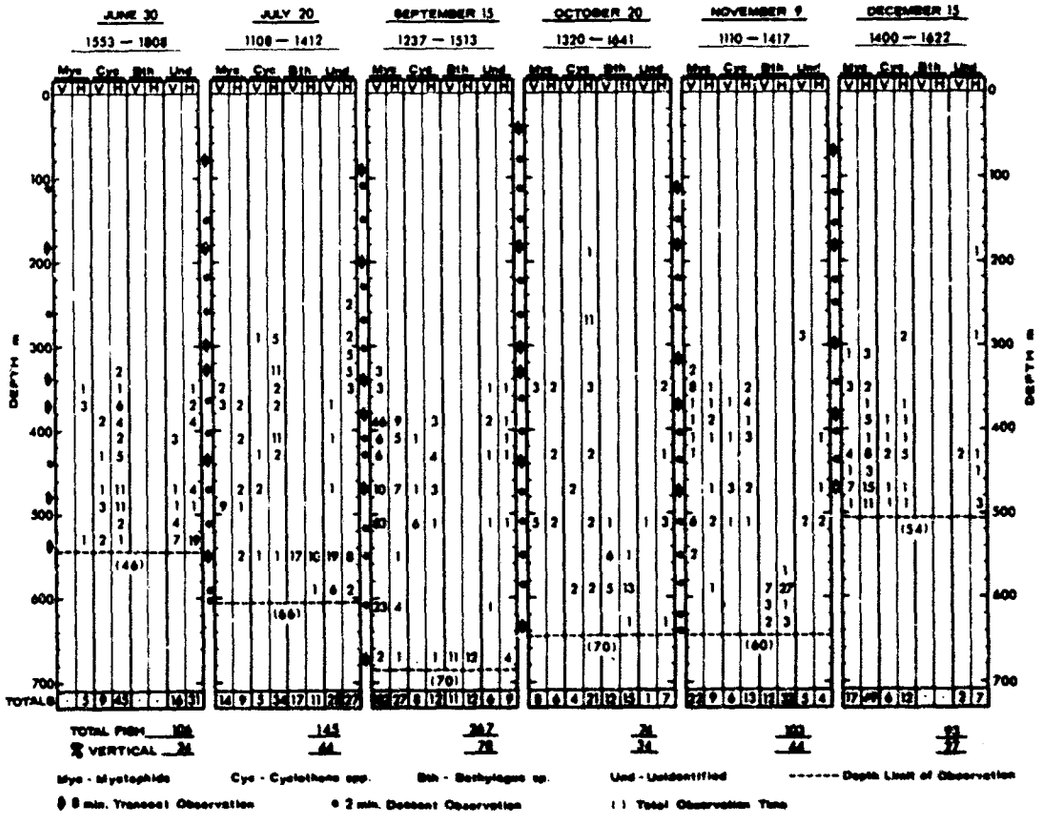

Figure 1. Vertical distribution and general orientation of mesopelagic fishes commonly observed in six Deepstar dives in 1966. The June to November dives were made within 1 km of 32°25' N, 117°30' W. The December dive was 15 km to the SE at 32°20' N, 117°19' W, but still in the San Diego Trough. Time span for the dives are shown at the head of each column, and total observation time for each dive is indicated in parentheses under the dotted line marking the lower limit of the dive. All quiescent fishes oriented at angles greater than about 30° from the horizontal are indicated in "V" columns; those fishes horizontal, either swimming or motionless, are scored in the "H" columns. Total fish counts for each dive and the percent of those that were vertically oriented are listed below each set of data.

the desired level, horizontal transects were made at the depths indicated by the arrows on Figure 1. Depth of *Deepstar* was recorded by an echo sounder directed upward. At each transect level, observations were made during four 2-min. periods of light (provided by 1,000-w and 500-w lamps) alternating with periods of darkness of the same duration. While descending, between transects, 2-min. lighted observations were made at the approximate 20-m intervals shown by dots. Time span for the dives are shown at the head of each column, and total observation time for each dive is indicated in parentheses under the broken line marking the lower limit of the dive. The vertical distribution of the fishes is plotted in 20-m groups.

The vast majority of the myctophids were either *Lampanyctus leucopsarus* or *L. mexicanus*, the latter species predominating at depths below 500 m. Those vertically oriented *Cyclothone*, identified with assurance, were large individuals of the black *C. acclinidens*, found generally below 400 m. The majority of *Cyclothone* sighted above 400 m were *C. signata*, a small, weakly swimming species with sparse pigmentation. This species can be recognized only within 2 m of the viewing port, where it usually is washed about helplessly by the DSV's pressure wave. Its

normal posture appears to be horizontal. Sightings of *Bathylagus stilbius* are, without exception, limited to depths below 500 m. Those fishes listed as "unidentified" were almost all members of these groups, but were seen either at such a distance or so fleetingly that a definite determination could not be made. Their relative numbers tended to decline following the July dive, a result of increasing confidence in our field identifications. Considerable numbers of hatchetfishes (*Sternoptychidae*) also were observed; these fishes were sometimes motionless, but always horizontally oriented. Most hatchetfishes appeared to be *Argyropelecus pacificus* or *A. intermedius*. A few were probably *A. lychnus* or *A. hawaiensis*. Lesser numbers were definitely *Sternoptyx diaphana*. When *Deepstar* was underway, most hatchetfishes were sighted in rapid flight. We have approached slowly, however, hatchetfishes that remained motionless (although their fins were vibrating) until almost in contact with the craft. They then turned rapidly back and forth three or four times within their own length before darting away. On other occasions when we were moving rapidly, hatchetfishes took flight, usually downward, at considerable distances from the boat. Several unidentified barracudinas (*Paralepididae*), and snipe eels (*Nemichthyidae*) were seen vertically oriented, but in a highly active state.

Above 550 m, the total numbers of fishes and the percent of those vertically oriented are clearly dominated by the fluctuations in the myctophid community. *Lampanyctus leucopsarus* and *L. mexicanus* populations appear to drift in loose aggregates. Because counts of the fishes taken on two consecutive dives made on the same day can differ more than the results of dives made at monthly intervals, these aggregations must be dispersed widely. (Apparently, estimates of population density based on individual dives are no better than individual net hauls.)

The results of the September dive deserve special attention. On this dive, following the deepest observations, the descending weight was dropped, and *Deepstar* climbed slowly (about 15 m/min) on its motors while other work was done. At a depth of 540 m, the ascent weight was dropped without motor noise. The DSV rose rapidly with the lights continuously on while the data on the left side of Figure 2 were obtained. *Deepstar* was tilted up at a steep angle, and we had a clear view (partially obstructed by the overhanging brow when the craft was in a horizontal or down position) of the undisturbed environment above and in front of us. Fully 97% of the 273 myctophids noted during the ascent were immobile and hanging in a vertical position. All but three individuals at the lower levels were oriented with their heads uppermost. The lanternfishes sighted between 350 and 260 m were young *Lampanyctus leucopsarus*, 4 to 5 cm in length. Only six individuals of this size class had been noted at the same depths during the descent transects of the same dive. During the ascent, notes were dictated continuously while the co-observer read off depths from a bourdon pressure gage. (*Deepstar*'s upward-looking depth recorder does not function properly when the boat is angled steeply in the ascent position.) In Figure 2 the fish counts (shown under posture symbols) have been bracketed to the depth notations.

As soon as *Deepstar*'s batteries could be recharged, another dive was made, this one entirely during hours of darkness. The data taken while descending in step fashion, as described earlier, are plotted on the right side of Figure 2. Only 31% of the 92 myctophids in the upper 100 m were in vertical position and inactive when first seen. The vast majority of these were the small size class of *Lampanyctus leucopsarus*. A few were mature specimens of the same species, and several of the active individuals looked like *Tarletonbeania crenularis*. Below 100 m, 68% of the 54 lanternfishes sighted were inactive and in vertical position. Most of these were mature individuals; *L. leucopsarus* predominated at shallower levels, and *L. mexicanus* at the greater depths.

Further considerations of the effects of DSV's and their mode of operation on the fishes seen is in order. When we were moving horizontally on *Deepstar*'s motors, lethargic, vertically oriented fishes were seen just as the lights were turned on. If at a distance, such fishes remained

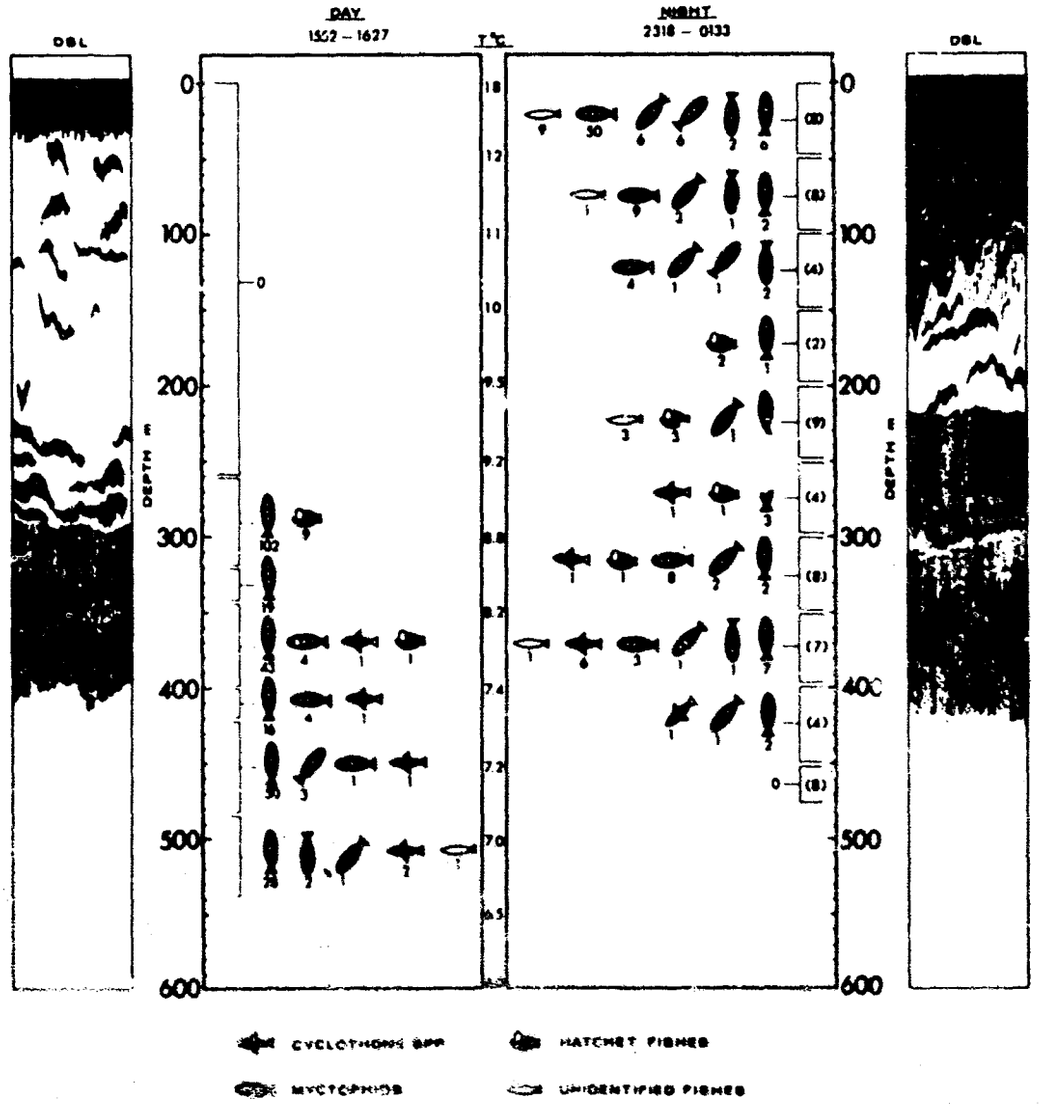

Figure 2. Comparative day-night vertical distribution and generalized posture of commonly observed mesopelagic fishes on *Deepstar* dives, 15 to 16 September 1966. The data in the left-hand column were taken while ascending to the surface. Posture symbols and counts are bracketed to depth readings taken from a pressure gage. The data in the right-hand column were taken while descending in stepwise fashion and alternating lights on and off. Posture symbols and counts have been bracketed to 50-m depth intervals, and the total observation time at each level is given in parentheses. Temperature readings from a thermistor taken at about 50-m increments on the daytime dive are given between the columns. Facsimiles of echograms recorded on a surface ship at the times of the observations are shown adjacent to the dive data.

unaffected by the craft's presence. But as *Deepstar* neared, they quickly reacted as they entered the intense region of the light field or when the photographic strobe light was activated. Myctophids responded to these stimuli by breaking from their torpor and swimming down and away from the craft in a series of rapid flights interspersed with short pauses and slight changes of direction. Bathylagids responded similarly, but they maintained a steadier course. *Cyclothone acclinidens* also took flight, although it is a slow, fluttering swimmer. Occasionally, all three

fishes resumed their vertical posture after making these rapid movements. As previously noted, they reorient with their heads either in the original position or reversed.

While *Deepstar* was quietly ascending or descending with the floodlights on, unseen fishes in the immediate path of the craft probably were stimulated into action before entering our field of view. Consequently, a higher percentage of those that were observed were seen undisturbed and in quiescent vertical position. We generally seemed to get higher fish counts when *Deepstar* was slowly drifting up or down, and the motor noise associated with horizontal transects may have altered some fishes, repelling them before they entered our light field. Apparently, fishes respond differently to the noise produced by different DSV's. The Cousteau diving saucer has a water propulsion system that has no noticeable effect on fishes. *Deepstar* has two propellers driven by electric motors; either the direct-to-alternating current-inverter "whine" or the "snap" of switch contacts when motor speed changes are made seems to repel fishes. This makes it difficult to position the boat so that lethargic, vertically oriented fishes can be photographed without triggering them into evasive action. When *Deepstar* was sinking slowly backwards, lethargic fishes occasionally drifted around from the shadow zone on the sides to a position just in front of the viewing port, where they could be observed critically, but were not in a position to be photographed by the fixed cameras. Numerous pictures of vertically oriented fishes were taken, but always at a distance. (Figure 3). They are not as revealing as short segments of motion pictures showing motionless, vertically oriented fishes and their quick evasive actions when we approached them.

On 24 September 1967, I had a brief opportunity to observe myctophids in the Atlantic Ocean off the New England coast (39°48′ N, 70°32′ W) from the Woods Hole Oceanographic Institution's *Alvin*. The objective of the dive was to study benthic fauna in collaboration with Drs. H. Sanders, R. Hessler, and R. Scheltema. On Dive 224, after a prolonged transect of the bottom, *Alvin* rose rapidly to the surface while I viewed constantly from the pilot's forward port. Between about 550 and 350 m, we first passed through scattered individuals and then tremendous concentrations of a large myctophid, all swimming rapidly downward and away from us, apparently in panic. At times it seemed as if the water literally was raining myctophids. These were, undoubtedly, the same populations studied in detail the following week by Backus et al. (1968). By homing on large targets with FM sonar, these workers clearly showed that this species, *Ceratoscopelus maderensis*, forms dense concentrations that are responsible for certain distinctive acoustic features.

In December 1967, we had further opportunities to observe mesopelagic fishes in waters other than the California Current using *Deepstar*. Some observations made on seven dives in coastal regions between Puntarenas, Costa Rica, and Acapulco, Mexico, are briefly summarized here. During most of these dives, perhaps to our observational advantage, *Deepstar's* inverters were inoperative. Without motors, the craft could only sink or rise slowly, or maintain a relatively steady position by ballasting.

Countless numbers of myctophids were observed. On some occasions these formed such dense swarms that they literally surrounded the boat. They behaved in a way similar to the behavior reported for *Ceratoscopelus maderensis* in western Atlantic slope water by Backus and his coworkers (1968). These myctophids *Benthosema panamense* were identified from specimens that lodged under the boat's fairings. In all cases, this species was highly active, swimming rapidly in typical myctophid fashion. The fishes were strongly attracted to the craft's lights and, on one occasion, followed us downward some 300 m. As off Cabo San Lucas in the earlier Cousteau saucer dives, only a few small, black myctophids were noted in the lethargic state and vertically oriented at the edges of the light field.

Figure 3. Lethargic, vertically oriented myctophids photographed with an externally mounted 70-mm camera on daytime *Deepstar* dives in the San Diego Trough. 1966. (A) September 15, at a depth of about 600 m. (B) November 9, at a depth of about 500 m.

Several snipe - eels (family *Nemichthyidae*) were seen vertically oriented with their heads uppermost and the midsections of their long snakelike bodies thrown into sinusoidal curves. On several occasions, between 150 and 250 m near the top of myctophid populations, large (25 to 30 cm) fishes were seen vertically oriented. Their heads were uppermost, and at times, rapid vibrations would run the length of their elongated, silvery bodies. Their bodies were so compressed that when their ventral or dorsal aspects were turned to the viewer, they seemed to disappear. These were probably cutlassfish (family *Trichiuridae*).

DISCUSSION

What have been the impressions of other underwater observers? Commenting on his pioneering observations from the bathysphere, Beebe (1935) was smitten by the "great activity of all the creatures except such as jellies and siphonophores," and, although he saw many gonostomatids and myctophids, he makes no mention of lethargy or vertical orientation. Many of the observers reporting on dives in the French bathyscaphes in the Mediterranean and adjacent Atlantic waters have noted that the barracudina, *Paralepis* (=*Notolepis*) *rissoi*, frequently holds itself rigidly upright, at times motionless but with fins vibrating, and then darts rapidly away oriented horizontally (Furnestin, 1955; Pérès, Piccard, and Ruivo, 1957; Trégouboff, 1956, 1958). Furnestin, who first reported on the odd behavior of *P. rissoi*, based on the identification on a specimen accidentally caught in the superstructure of the FNRS-3 bathyscaphe. The barracudina we have seen vertically oriented in the *Deepstar* dives is probably the subspecies *Paralepis rissoi rissoi.* Coincidentally, another paralepidid, *Paralepis atlantica,* observed swimming normally, was snagged between the *Deepstar's* sphere and cowling on the June 1966 dive. Bernard (1955) saw *Syngnathus* sp. in conjugating pairs actively swimming while vertically oriented, and Marshall (1960) quotes a letter from Pérès stating he had watched *Chauliodus sloani* hover obliquely in the water. There is no mention in these works of vertical orientation or its relation to lethargy in the types of fishes reported on here. Pérès (1958a) does note that *Cyclothone* sp. are frequently immobile, but both Pérès (1958b) and Trégouboff (1958) comment that myctophids are always in constant motion. It thus appears that the connection between lethargy and vertical posture in mesopelagic fishes has not been made previously in the literature.

In personal communications, however, several colleagues have informed me about seeing lethargic, vertically oriented fishes from DSV's. During a late afternoon dive on the day previous to ours in *Trieste II* in the San Diego Trough, Dr. R. Dill reported seeing many "small fishes" (very probably myctophids) oriented vertically with their heads up as the bathyscaphe rapidly descended to the bottom for geological studies. More recently, Dr. W. Clarke told me that while diving in *Pisces* in the Northeast Pacific off British Columbia and again in *Deepstar* in the Gulf of Mexico, he noted some myctophids in vertical position and immobile. Dr. D. Cohen informed me that in *Deepstar* dives in the Atlantic he saw many paralepidids and snipe - eels in vertical position, but not myctophids or other common mesopelagic fishes. Dr. R. Backus also told of seeing elongated, predaceous fishes in the vertical position. Concerning myctophids, Backus and his colleagues (1968) reported that the shoals of *Ceratoscopelus maderensis* were at rest. "They hung motionlessly in the water, sometimes horizontally, but often a little obliquely." The fish reacted to the presence of *Alvin* by swimming vigorously away. They also gained the impression that "Schools deep in the layer appeared to react more slowly and less vigorously . . . ." Clearly there are striking differences in the observed behavior of mesopelagic fishes, particularly the myctophids. We will attempt later to reconcile some of these conflicts, but first let us consider what roles lethargy and vertical orientation may play in the lives of these fishes.

Lethargy

The behavior and posture of many mesopelagic fishes observed in 1966 *Deepstar* dive series is quite similar to that observed by Russian fishery biologists in the North Atlantic from the submarine *Severyanka* of herring said to have been hibernating at relatively shallow depths. (Ryzhenko, 1962; Ryzhenko, Sokolov, Zolotov, and Khromov, 1961). Reportedly, the herring were completely immobile. Generally they are vertically oriented, although occasionally they are horizontal in posture, but with their ventral surfaces uppermost. Hibernation in other shallow-water marine fishes is known, typically in cold waters, and the fishes involved characteristically store large amounts of fat (Nikolsky, 1963). Interestingly, the adults of both *Lampanyctus leucopsarus* and *L. mexicanus* have regressed swimbladders copiously invested with fatty tissue (Capen, 1967), and this organ in adult *Cyclothone acclinidens* is filled with lipid material (Marshall, 1960).

Note in Figure 2 that about 70% of the myctophids seen in the upper 100 m at night were active and swimming horizontally. The majority of these fishes appeared to belong to the same population of adolescent *Lampanyctus leucopsarus* that had been observed the previous afternoon virtually all vertically oriented and immobile. This suggests that the fish's energy-expending activities are mainly restricted to their stay in shallow waters. As suggested by Marshall (1960), there is no rule that says all individuals of a population must migrate to the surface every night. Note again in Figure 2 that over half of the adult myctophids seen during the night dive at depths below 100 m were immobile and vertically oriented. Perhaps at certain stages in the lives of some myctophids, a state of suspended activity with little or no diurnal vertical movement is maintained for prolonged periods of time. Recall, however, that when triggered into action by an approaching DSV, these fishes are capable of rapid evasive movement. Perhaps then, these fishes have conformed to the stresses of their environment by developing a pattern of lethargic behavior, a modified type of hibernation that allows them to conserve energy, remain inconspicuous to their predators, and yet be capable of quick response to attack.

Regarding lethargy in *Cyclothone acclinidens* and bathylagids, as well as myctophids, work by Karineu (1965) shows that the activity of the respiratory enzyme, succinic dehydrogenase, is inversely related to the depth of capture of mesopelagic fishes. Thus, some degree of suspended activity might be expected in many deep-dwelling pelagic fishes.

Another line of biochemical research bears on this discussion. Nevenzel, Rodegker, Robinson, and Kayama (1970) have studied the lipids of eight species of myctophids. In four of these species, the lipid content of the whole fish is three to four times greater than in the others. Three of these four species, *Lampanyctus leucopsarus, L. mexicanus,* and *L. ritteri,* have atrophied, fat-surrounded swimbladders. The fourth species, *Diaphus theta,* is a dilemma. Capen's (1967) specimens were netted off Japan and had normal swimbladders, yet individuals of what is apparently the same species taken off California have swimbladders similar to *L. leucopsarus, L. mexicanus,* and *L. ritteri.* None of the four species with low total lipid content (*Hygophum reinhardtii, Tarletonbeania crenularis, Symbolophorus evermanni,* and *S. californiensis*) appear to have this type of swimbladder as adults. Nevenzel and his associates did not specifically analyze swimbladders, but the same general ratios of total lipid content hold for muscle tissue and viscera taken from the two sets of fishes. Thus it seems that high lipid content is associated with mesopelagic fishes in which lethargy and its related vertical orientation are well-developed.

In summary, Marshall (1960) has pointed out that the anatomical evolution of mesopelagic fishes has been shaped by their environmental stresses of hydrostatic pressure, dim light, sparse food, and, perhaps most important, cold water, which reduces metabolic activity and increases

the viscosity of the medium through which they must move. These factors have resulted in a degradation of their muscle and bone tissue. It appears that in some mesopelagic fishes, reduction of activity, such as discussed here, is a behavioral corollary.

Vertical Orientation

Odd body postures of fishes are hardly unknown. Some shallow-water marine fishes typically orient at odd angles in thigmotactic response to their physical environment. They align themselves in relation to sea urchin spines, coral, and gorgonian fronds in what appears to be a protective adaptation. As a possible extension of this function, a new gobioid fish has been reported recently by Cohen and Davis (1969) that, even when evading *Scuba* divers, maintains a vertical, heads-up posture while swimming several feet from a vertical underwater cliff. In other cases, there seems to be no apparent rationale for atypical orientation. For example, certain characins, though not bottom feeders, go around with the forepart of their bodies tilted down, and shrimpfish *Aeoliscus strigatus* live in schools and swim rapidly in the vertical position with their heads down. Immobility does tend to make mesopelagic fishes inconspicuous to the human eye (perhaps to their predators as well), and there may be a further protective advantage to vertical orientation. In the San Diego Trough, the water usually is filled with vertically hanging detrital "strings" about 10 cm in length. These strings strongly reflect light, and a quiescent fish at the edge of the light field in areas of such detritus is hard to recognize until it moves. The subjective impression one gets is that these little fishes, like so many rabbits, are hiding in the weeds. It should be noted, however, that vertical orientation is not confined to fishes. It is also common in chaetognaths, tomopterids, copepods, some squid, and certain siphonophores.

In the case of myctophids, another possible adaptive function of vertical orientation is related to buoyancy mechanisms and vertical migration. Freshly netted, moribund, adult *Lampanyctus leucopsarus* and *L. mexicanus* sink when placed in shipboard aquaria. Capen's (1967) sucrose solution experiments on a size series of freshly trawled *L. mexicanus* show that adults over 30 mm standard length (SL) have a density between 1.025 and 1.037 g/cm^3. Thus, they probably have a slight negative buoyancy in relation to sea water of density 1.026. The question then arises, how do the apparently inert, vertically oriented adults maintain their optimum depth.

We generally view the fishes from a moving platform, and it is difficult to verify whether lethargic, vertically oriented myctophids are maintaining a constant level. At times, however, when *Deepstar* was virtually motionless, no marked vertical movements were noted. Fin or body vibrations were not discernible. Obvious, however, were rhythmic opercular movements at 3- to 4-sec intervals that produced the flow of respiratory water over the gills. Shallow-water fishes keeping a fixed, midwater, horizontal position make reverse power strokes with their pectoral fins to compensate for the jet action of water forced through their gill chambers. It is reasonable to assume that myctophids use similar respiratory currents to maintain or raise themselves in the water column against their slight negative buoyancy. The young myctophids observed during the ascent from the daytime September dive were probably just beginning their evening ascent. They were, without exception, polarized with their heads uppermost. They may have been literally "breathing" their way to shallower depths.

Most young *Lampanyctus leucopsarus* and *L. mexicanus* float after capture, and studies of the latter species show that at intermediate growth stages, the fat deposits investing the swimbladders are only partially developed (Capen, 1967). Whereas their tissues are then denser than those of the adults, (ranging from 1.050 to 1.067 g/cm^3), a small gas phase is generally present

in specimens under 42 mm SL. Thus, though young adults use fat to compensate for most of their bulk, they still may secrete and resorb a small gas bubble for critical buoyancy trim.

A case of functional adaptation for vertical orientation of the swimbladderless *Bathylagus stilbius* is not made so easily as for the myctophids. Most tend to be oriented either head up or down, at 45° angles rather than strictly vertically, and spasmodic body tremors and fin movements are noticeable. Based on dives deeper than those discussed here, the large and consistently present *B. stilbius* population extends to about 1000 m. This species apparently does not regularly make extensive diurnal migrations, but at times they do come to the surface in large numbers. We took 48 specimens in early evening surface net hauls in the San Diego Trough, 13 January 1966. Forty-five of these were large (80 to 110 mm SL) heavily gravid females, one was an immature female, and two were small, immature males (35 to 55 mm SL). This suggests sex-related behavior similar to that of the myctophid, *Tarletonbenia crenularis* (Bolin, 1961). Apparently, mating is carried on at their lower depth levels, for on two occasions during dives in *Trieste II* (February to March 1964), several pairs of bathylagids were seen vent to vent, with tremors passing through their vertically oriented bodies.

What can be said of such fishes as paralepidids, snipe eels, and cutlassfishes in which vertical orientation seems to be so common? They all seem to lack swimbladders and upturned eyes, but have elongated, silvery bodies and predacous habits. Perhaps this posture is an advantage in stalking and capturing their prey from below, as suggested by Harrisson (1967) and others.

Bioluminescence

Dotting the bodies of myctophids and gonostomids are bioluminescent organs and glands, and the possible functions of these light-producing organs have long been the subject of conjecture (see McAllister, 1967, for a recent comprehensive review). In at least 72% of the 42 fish families known to be bioluminescent, these photophores tend to be concentrated along the ventral body surface (D.E. McAllister, personal communication). Because of this, Clarke (1963) has championed the idea that such light organs might produce constant, low-level luminescence that would protect them from deeper-living predators by matching the downcoming light level, thus providing a type of "countershading." Obviously, this would not work when such fishes are vertically oriented. On the affirmative side, however, note that hatchetfishes, *Cyclothone signata*, and the few melanostomiatids we have observed have never been seen in this position; these fishes better fit Clarke's conditions of association of photophores with pigmented body areas. Then, too, the principle still may apply to myctophids while they are in a horizontal position and in an active mode.

Our in situ observations so far have contributed little to the bioluminescence enigma. I have looked for bioluminescence associated with fishes at times when lights on submersible vehicles had failed or were turned out. With one exception, the only bioluminescent patterns I have been able to associate with large organisms have been in ctenophores, salps, and siphonophores. During a *Trieste II* dive, March 1964, at about 450 m in the San Diego Trough, a piece of equipment suspended from the bathyscaphe float hit a lethargic, vertically oriented myctophid. The fish gave off a bright blue flash of such intensity that it could be seen against the artificial light field of the craft. The flash very probably was from the caudal gland, or so-called "stern chaser." The fish then darted away. At certain times, when the DSV was moving forward or dropping rapidly, I saw small, unidentified objects strike against the front of the craft and emit a bright flash that was discernible against the artificial light field. Streamers of bioluminescent material may have lingered momentarily. From darkened *Deepstar*, I have noted relatively large, amorphous structures emitting a steady glow. When the lights were turned on, however, only

films of organic material could be associated with the regions where the glow was seen, suggestive of bioluminescent bacteria adsorbed to detrital material. My eyes were not fully dark adapted, however, and I could have failed to note other low-level light sources.

One other small point of interest. *Deepstar* was equipped with a xeon "flasher" to aid the surface ship's crew in locating the vehicle when it surfaced at night. This "flasher" usually would be turned on at about 50 m, and its first flash would evoke a bright bioluminescent response from the surrounding water. The response to subsequent flashes would be less and less intensity until they were no longer discernible.

Before postulating further adaptive functions for the bioluminescence of marine organisms, perhaps it is time to reconsider the basic biochemical role of this process, as suggested by Hastings (1968).

Net Avoidance

Studies show that catches of mesopelagic fishes in midwater trawls to 400 m of depth are generally more productive at night than during the day (Paxton, 1967; Pearcy and Laurs, 1966). This generally is thought to result from visual avoidance of the nets under brighter daytime light conditions. Observe a net being hauled to the surface at night. Usually the posterior region of the net is aglow with bioluminescing, captured organisms, and passage of the towing wire and the net's bridle and mouth-frame through the water are triggering "sparkle" and bright bioluminescent flashes. One would think that if a fish's visual equipment is capable of seeing an approaching net in the dimly lit waters of its daytime depths, it certainly should be able to sense such a "fiery apparition."

Consider another explanation for the day-night difference in catch. Harrisson (1967) has discussed in detail the relationship of fish orientation to net avoidance. If the swimming speed of a fish and velocity of a net are of about the same order, the most effective escape path for the fish is at right angles to the path of the net. As previously noted, when vertically oriented, lethargic fishes are stimulated into action by an approaching DSV, they swim rapidly downward. Thus, their escape path to horizontally towed nets is probably always at a high angle. If at nighttime, however, more of these fishes are actively swimming at random directions in relation to the net's course, then their chances of being captured are increased greatly.

Metabolic state may also play a role in net avoidance. Judging from the behavior of myctophids at the surface at night when attacked by squid under the ship's lights, the fish are capable of vigorous evasive action, even jumping clear of the water and skipping along the surface. They soon become exhausted, however, and usually are taken by repeated attacks, apparently being incapable of prolonged, hard activity. It would seem logical that fishes actively feeding or being fed upon at night might be nearer their exhaustion point and less capable of making that first critical evasive action (nets only "attack" once) than inactive, resting daytime fishes "cocked and primed" for escape.

In this context, the vulnerability of mesopelagic fishes to large objects coming up beneath them (as observed in the *Trieste I* dives) causes one to recall the amazingly heavy catches taken with the old, vertically hauled, standard meter nets compared, in terms of the volume of water sampled, to our present elaborate, but horizontally hauled, midwater trawls (see Harrisson, 1967, for a detailed discussion of sampling methods). In view of the behavioral characteristics of mesopelagic fishes discussed here, it might be rewarding to take a fresh look at the relative efficiency of these two modes of net hauling. At the least, metabolic state, state of aggregation, and associated behavior should be considered in population studies of mesopelagic fishes based on net-catch data.

Sound Scattering Aspects

Based on known distribution, habits, net catch data, and the presence of a potentially resonant gas-filled swimbladder in many species, the mesopelagic fishes, particularly the myctophids, long have been thought to be responsible for much of the middepth, midfrequency (12 to 24 kHz), diurnally migrating sound scattering in the oceans. (See Hersey and Backus, 1962, for a review of the early literature.) Much recent evidence from several lines of approach strongly substantiates this view. *In situ* observations clearly have established the spatial relationship between some myctophid populations and sound-scattering features (Backus, et al., 1968; and Barham, 1966), and acoustic experiments (Batzler and Pickwell, 1970; McCartney, 1970) reinforce the importance of resonance.

In this context, the situation off southern California, where much of our work has been done, is perplexing. At times, a strong migratory layer centered at about 300 m at its daytime depth is clearly caused by physonectid siphonophores with carbon-monoxide-filled pneumatophores, whereas observable myctophids are scarce or concentrated well below this level (Barham, 1963). A further complicating factor is that the adults of the dominant species of myctophids in this area have fat-occluded swimbladders; therefore, they should be relatively weak sound scatterers. The data obtained from all the *Deepstar* dives pertaining to scattering have not been analyzed completely, but it appears that at times physonects dominate at DSL depths, at other times, a mixed population of physonects and small myctophids or other fishes are present, and, more rarely, as in the September dives, large numbers of small myctophids are concentrated at these depths. In all cases, however, the fully grown adults are concentrated at deeper levels. When we recall that Capen's (1967) studies of *Lampanyctus leucopsarus* and *L. mexicanus* indicated that immature myctophids of both species contain potentially resonant small gas bubbles, this begins to make some sense.

Consider Figure 2 again. Adjacent to the dive data are facsimiles of echograms taken simultaneously from a surface ship using a 12-kHz transducer and a Gifft recorder. During the afternoon ascent (left side of Figure 2), all but one of the 121 myctophids sighted between 260 and 250 m, near the top of the scattering layer, were adolescents, whereas the mature individuals were concentrated below all recorded layers. At dusk, a component from this layer migrated upward, and the intermediate water levels filled with discrete targets. A more prominent DSL component rose only slightly, split in two, and maintained this level throughout the night (right side of Figure 2). Such "nonmigratory" layers (or components of layers) are common and widespread. Net hauls taken about 100 miles to the south of the San Diego Trough in the deep oceanic waters adjacent to Guadalupe Island showed that hatchetfishes inhabited such layers (Pickwell, Capen, and Sloan, 1968). The vertical distribution of these fishes as observed during the September 1966 *Deepstar* dives, provides additional evidence that associates hatchetfishes with nonmigratory layers. Note, as well, that the adult myctophids have apparently moved upward so that their populations also coincide with the nonmigratory layer components. In addition, Midttun and Hoff (1962) have demonstrated that the target strength of cod and coalfish is markedly reduced reduced (20 to 30 dB) when they are oriented at oblique angles in the sound cone. Changes in posture by myctophids, such as vertical orientation, may then affect volume reverberation levels.

Two Types of Myctophids

Some years ago, Marshall (1960) argued that myctophids must be highly active at their daytime depths to pass enough water over their gills for swimbladder inflation. Yet, in the same

work, he theorized that such fishes living in an oxygen-minimum layer suspend their activities during the day, and suggested that "daytime observations from a bathyscaphe might well be revealing."

Clearly, there are striking differences in the observed behavior of myctophids. This can be reconciled if we accept the view that there are two types of myctophids, each with related structures and behavior. One type can be termed the "active" or *Myctophum* type; the other the "inactive" or *Lampanyctus* type. Species of the active type apparently either lack swimbladders or have large, gas-filled swimbladders and well-developed related structures - gas gland, rete mirabilia, oval (Marshall, 1960). Lipid content of their swimbladders is relatively low. We can further generalize and say they have silvery or brassy scales, large eyes, and firm bodies, usually with a thin peduncle. They dwell at intermediate depths in tropical and subtropical waters and in the superficial layers in colder oceans. They migrate to the surface at night, where they are positively phototactic to light of medium intensity, collect around ship's lights, and can be dipnetted. The adults are concentrated at scattering layer depths during daylight hours, where occasionally they form large concentrations. They are attracted to the lights of the DSV and will follow the craft for long distances. Examples described in this paper would be *Myctophum aurolaternatum, Benthosema panamese,* and *Ceratoscopelis maderensis.* (Because I had no opportunity to observe *C. maderensis* when it was not being terrorized by the rapidly rising *Alvin,* this fish is added to the list with some reservations.) Species of the inactive type, on the other hand, have atrophied swimbladders, overgrown with fat and plugged with tissue. The organs have a high lipid content. They are darker in color, have small- or medium-size eyes, and are soft-bodied, usually with a thick peduncle. The fishes may migrate toward the surface at night, but only rarely reach the surface. They are not attracted to lights and seldom can be dipnetted. The adults are concentrated below scattering layer depths where they frequently drift passively in vertical position. In the California Current, the adolescents may be concentrated at DSL depths. They are negatively phototactic to the lights of the DSV and, when stimulated by the presence of such a craft, break from their topor and swim rapidly away. Examples would be *Lampanyctus leucopsarus* and *L. mexicanus.* Of the various anatomical characteristics associated with behavioral traits, the nature of the swimbladder would seem the most important.

These conclusions are generalities and represent clear-cut extremes. Inevitably, there will be intergrades and, perhaps, changes in behavioral patterns associated with stages in life cycle, season, and environmental conditions.

Having long pondered the problems and enigmas of the deep scattering layer, I conclude that to fully understand the complexities of this phenomenon, we must first understand the biology of mesopelagic fishes.

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DISCUSSION

Roper: I was interested in the comments about inactivity of fish with fat reserves rather than gas bladders. This is reminiscent of an observation that I have made in one species of deep-living cephalopod. It is a squid called *Bathyteuthis abyssicola* that occurs from about 500 to 2500 m. I was able to keep this animal alive for several days in an aquarium aboard ship in the Antarctic. One of the things that puzzled me at the time was that it was a very lethargic animal that did not swim around much, although it is not as weakly muscled as you might think. It would hang with its head down in the water. When I started to look at it in more detail, I discovered that the liver, instead of being a solid mass as in most other cephalpods, was a series of two chambers that were filled with oil. These squid hang vertically in the water presumably using the oil-filled chambers as buoyancy tanks. This is something I have wanted to follow up, but I have not been able to yet.

Barham: That is very interesting. We see a lot of squid, deep-sea squid, that are vertical in the water.

Roper: Right. Also, there are other kinds of squid that concentrate ammonium ions and that hang head up or head down in the water. One of the groups, the Chiroteuthidae, has extremely large arms where the lightweight ions are concentrated. I have observed a species of *Chiroteuthis* hanging head up in the water. Some of the others, the Cranchiidae, concentrate the ions in a sac

in the mantle cavity; they hang head down while "resting," but they do orient horizontally while swimming.

Cohen: Eric, I think what you really have to explain to us is why any of them orient horizontally, because if you have vertically migrating fishes that spend 3 hours a day going up and the another 3 hours going down, why in the world should they turn horizontal when they get up or down?

Barham: That is a very interesting point. I'm glad you brought that up, because there is one thing I forgot to mention which I think is rather speculative but worth throwing out. The only movement of myctophids that you will see when you really get a good look at them is opercular movements about every 2 or 3 sec, and I have toyed with the idea that these fishes are maintaining themselves in the water column. You see, they are just slightly negatively buoyant (the ones that Capen measured with his sucrose experiments); they relate to what we were discussing earlier. With these respiratory currents, if they breathed a little, it would hold them up. If they started breathing a little faster, why the next thing you know they would get these jets of water from their operculae and they would breathe their way to the surface. On one occasion we made a dive early in the morning and we did see them head down. We wondered whether they may breathe their way down again, but I'm not sure about this. I do think that here is something they might as well utilize, this work that they are doing, and we do see this very striking contraction of the opercular plates.

Craddock: Have you ever seen them light up?

Barham: No, I haven't, and I have looked for it. The only time I have ever seen bioluminescence from a myctophid is one that we hit with part of the vehicle. This was apparently the stern chaser (infracaudal gland) which went off with a big flash. You see a lot of bioluminescence in the water; I have played the game of turning off the lights, seeing something that is bioluminescent, and then flicking the lights on very rapidly to try and identify it. I have seen siphonophores that have been bioluminescent; I have seen ctenophores, medusae, and copepods, I think, that will hit up against the viewing port and bioluminesce so brightly that you can even see them when the lights are on. The only thing that I can see normally when playing this game is just a detrital film out there which has a steady state glow associated with it as if its elements were bioluminescent bacteria.

Craddock: Incidentally the *Ceratoscopelus* that we saw appeared to be sort of asleep, but they were not vertically oriented.

Clarke, W.: I was on some of those dives, too, with Craddock, Haedrich, and Backus. We used a flashlight out of the port to observe the fish. We were able to see the distances between eyeballs of the individual fish remain constant as long as the major light sources were off; in other words, they were inactive. As soon as we turned the main light sources on, they started swimming down out of the field. This is an observation we all made. The other thing concerning this luminescence is that on two occasions during the Gulf dives when we had lanternfish in view, we turned the lights off and caught an afterglow from them. I don't think that this was a residual image on the retina because one time I covered my eyes and had them turn the lights out, and I could see the glow of fish as soon as I uncovered; when they turned the lights on, the fish were there again. It would seem they had pulled up their luminescence to counter the intense light field; they were caught off guard, so to speak, and you could watch that luminescence gradually fade in the darkness when the lights were turned out.

Barham: I may have missed it Bill. I have never dark-adapted my eyes, and it has always been something we have done when the lights failed or something else.

Clarke, W.: One other thing in defense of this orientation business. I have seen this heads-up behavior quite commonly during midday inactive periods. There is no real need for the fish to use a countershading luminescence under these circumstances; they are essentially inactive. Hopefully, their predators are inactive. It would be rather like the terrestrial nocturnal animals during the day. They all sort of hole up and there is a truce for awhile. But during the migration period when the lanternfishes get to the surface and are feeding, everything is active and turned on, so to speak. At these times I would assume that you would have more horizontal orientation and predator pressures. This is the time when you would expect the countershading luminescence. I have never advocated that it be used continuously.

Backus: The vertically oriented fishes that I saw were all species that were very elongate, trichiuroids like *Diplospinus, Benthodesmus*, and some paralepidids or barracudinas, snipe eels like *Nemichthys*—one of which I saw go from head up position and swim over into head down position—all very elongate species that were precisely vertical in the water. Moderately elongate species like *Chauliodus* and *Stomias* were more or less horizontal. The *Ceratoscopelus madarensis* in the large schools were more or less horizontal, although sometimes head up a little or head down a little. These fit into Eric's second category of myctophids in that they were lethargic; they fit his other criteria for class two except that they do have a gas-filled rather than a fat-filled swimbladder and the orientation is somewhat different.

Kinzer: In the antagonistic behavior of *Nannostomus* we know from observations by Wickler that these fishes assume a head-down position, which is the characteristic gesture of these freshwater fish during fighting. They do this by altering their swimbladder volume. The sudden reduction in their specific weight is compensated by movement of pectoral fins or other fins.

OCEAN ACRE
PRELIMINARY REPORT ON
VERTICAL DISTRIBUTION OF FISHES AND CEPHALOPODS

Robert H. Gibbs, Jr.
Department of Vertebrate Zoology
Division of Fishes

and

Clyde F. E. Roper
Department of Invertebrate Zoology
Division of Molluscs

Smithsonian Institution
Washington, D.C.

ABSTRACT

Project "Ocean Acre," a joint enterprise of scientists from the Smithsonian Institution, University of Rhode Island, Navy Underwater Sound Laboratory, and Naval Oceanographic Office, is sampling the fauna of the water column beneath a one-degree square area southeast of Bermuda. The ultimate goal is to establish with precision the abundance, vertical distributions, and vertical migration patterns of all mesopelagic species and to relate these to acoustical, physicochemical, biological, and seasonal phenomena. Seven cruises were made between October 1967 and September 1969. The discrete-depth sampler developed by Aron et al. at General Motors was used whenever possible (three successful cruises to date). A 6-foot IKMT was used on two cruises; a 10-foot IKMT was used on the other five. A large Engel trawl was used on one cruise. Of 277 samples, 153 are from known discrete depths. Coverage is good for depths of 50 to 600 m both day and night, but sparse from 600 to 1300 m. Nondiscrete samples have been made to 2500 m.

The most abundant fishes are species of the families Myctophidae (lanternfishes, 58 spp.), Gonostomatidae (22 spp.), Sternoptychidae (hatchetfishes, 3 spp.), and Melamphaidae (9 spp.). Species with well-developed swimbladders can be correlated with 12-kHz scattering layers, and only a few species may be responsible for some layers. Two species, a hatchetfish, *Argyropelecus hemigymnus*, and a gonostomatid, *Valenciennellus tripunctulatus*, apparently migrate little or not at all and are most abundant between 400 and 600 m, where a broad scattering layer is seen both day and night. Several species live at this same level during daytime, but migrate upward at night (*viz.* the lanternfishes, *Notolychnus valdiviae, Diaphus mollis, Lobianchia dofleini*), accounting for nighttime diminution of this scattering layer. Many migrators inhabit deep thermocline depths of 700 to 1100 m during the day and migrate upward at night, although a few species remain at these depths at all times (e.g. *Sternoptyx diaphana*). The vast majority of migrators, regardless of daytime depths, occur in the upper 250 m at night. The complicated patterns of scattering layers during migration periods probably are due to these many different species migrating from different depths and reaching different levels at different times. Young of the gempylid *Diplospinus multistrictus* and juvenile puffers may be responsible for much sound scattering in the upper 200 m at all times.

Among the cephalopods, the enoploteuthid *Pyroteuthis margaritifera*, the most abundant cephalopod in Ocean Acre samples, exhibits diel migration, living at 300 to 500 m during the day and ascending to 100 to 200 m at night. *Pterygioteuthis giardi* occurs at 300 to 500 m during the day and at 50 to 200 m at night, with a peak concentration at 50 to 100 m. These species appear to move in coincidence with the major portion of the 12-kHz sound scattering layer. Data on less abundant species are not as complete, but indicate that both vertical migrators and nonmigrators exist.

INTRODUCTION

Sampling of midwater macroorganisms has been conducted for at least a century and has been particularly intense during the past two decades. This sampling generally has been the result of surveys or transects, where the area sampled has been visited only once or twice. With few exceptions, sampling has been accomplished with nonclosing nets, and the nets used in a given survey generally have been of one size only. Because of these limitations, precise information on the behavior of midwater organisms has been lacking. For example, knowledge about the vertical distribution of a species or a community had to be based on inference derived from open-net sampling, which, at best, yields insufficient data. Little reliable information was accumulated about life histories and seasonal variations of species.

With these problems in mind, biologists from the Smithsonian Institution, the Bureau of Commercial Fisheries, and the University of Rhode Island conceived the Ocean Acre project. The Ocean Acre concept was to select a single small area, to sample the water column of the area intensively with several types and sizes of collecting gear with particular emphasis on discrete-depth samplers, and to visit the designated area during all seasons of the year for a period of several years. With this approach we would be able to determine with precision the pattern of vertical distribution and abundance of individual species, to understand the community relationships of the species, and to ascertain how these aspects are related to acoustical, oceanographic, and other observed environmental phenomena. A comprehensive study of this sort would form the basis for comparative studies in other oceanic regions.

Early support for the Ocean Acre project came from the Smithsonian Institution and the University of Rhode Island. The bulk of the support since then has been provided by the U.S. Navy Underwater Sound Laboratory,[1] which, in addition to funding, has added acoustical expertise. Field assistance has been provided by all of the above institutions as well as the Bureau of Commercial Fisheries and the U.S. Naval Oceanographic Office.

THE AREA AND ITS OCEANOGRAPHY

The area selected for the Ocean Acre study is centered east of Bermuda at 32°N 64°W, and it encompasses a 1° square area. This site was selected because it has a relatively simple oceanographic regime (when compared with the Gulf Stream, for instance); physicochemical data are available for a period of more than 10 years (Schroeder and Stommel, 1969); and the fauna is relatively well known. The depth of water in the 1°-square area ranges from about 2000 m in the northwest corner to 4500 m in the southeast region. The following summary of the physical oceanography is based on our own measurements, Schroeder and Stommel (1969), Brooks et al. (1968), Stommel (1965), and Sverdrup et al. (1942).

The Surface Water Mass occupies the upper 600 m. Surface temperatures range from 20°–29°C, and the salinity is generally quite high–above 36.4‰. A seasonal shallow thermocline between 50 and 150 m is developed from about April to November, being most intense in August. Within this thermocline, the temperature can drop as much as 8°C in a vertical distance of 50 m. Below this thermocline both temperature and salinity are quite uniform to about 600 m–about 18-19°C and 36.2‰.

A permanent deep thermohalocline occurs from about 600 to 1100 m and has the general characteristics of North Atlantic Central Water. Within this depth range, the temperature changes from about 18°C to 6°C, and the salinity from about 36.2‰ to 35.0‰. Intermediate Water is present between 1100 and 2000 m, with temperatures between 5.5°and 4.0°C and

[1] U.S. Navy Contract Number N00140-69-C-0166.

a salinity of about 35.0°/₀₀. Below 2000 m the temperature drops below 3.5°C and the salinity is around 35.0°/₀₀; these are general characteristics of North Atlantic Deep Water.

Oxygen levels are generally between 4.5-5.5 ml/l at the surface and decrease until 700-900 m, where an oxygen minimum layer occurs with concentrations around 3.5 ml/l. Below this, oxygen concentrations rise to above 6.0 ml/l at 2000-3000 m.

Sound-scattering phenomena are more difficult to summarize. With a 12-kHz sound source, a weak and variable scattering layer is usually present at 0-150 m during the day and a deeper, stronger layer occurs between 400 and 600 m. At night the scattering layer is prominent between 0 and 250 m, and the 400-600 m layer, though diminished and narrower, is still intact.

BIOLOGICAL SAMPLING

Seven cruises have been taken to date. Discrete-depth samples were obtained during three cruises: on Acre 1, using a 6-foot Isaacs-Kidd Midwater Trawl (IKMT), and on Acre 4 and 6, using a 10-foot IKMT. All other cruises have used open IKMT's–6 foot on Acre 2, 10 foot on Acre 3, 5, and 7. In addition, neuston samples have been made using 1-m plankton nets. During Acre 7, trials were carried out using large Engel trawls, with the expectation of capturing the larger and swifter elements of the midwater fauna.

The discrete-depth sampler used is that developed by General Motors (Aron, Raxter, Noel, and Andrews, 1964). The environmental sensors have been inoperative, and depths during trawling have been estimated from wire angles or by a Benthos depth-telemetering pinger and checked by a time-depth recorder attached to the spreader bar.

The data-collecting program would ideally comprise four cruises each year in order to secure seasonal information. The collecting regime is set up to sample selected depths at least once during each cruise during the day, at night, and during both dawn and dusk migration periods. Each depth has been selected with respect to the observed acoustic and oceanographic characteristics of the water column. Day and night discrete-depth sampling is done at 12 depths down to 1500 m (Table 1). Five depth levels down to 1250 m (100-200 m, 300-400 m, 500-600 m, 800 m, 1250 m) are sampled during dawn and dusk migration periods. For reasons beyond our control, neither the full seasonal nor the full depth coverage have been realized.

During Acre 1, the sampling rationale with the discrete-depth gear was to employ one chamber to sample a given depth horizontally, the second chamber to sample diagonally to a second depth, the third chamber to sample the second discrete depth horizontally, and the fourth chamber to sample diagonally from the last depth to the surface. In this way, only two truly discrete-depth samples were obtained from each set of the trawl, although the first oblique sample (the second chamber) may also be considered discrete, particularly when the depth increment between the two horizontal tows is reasonably small.

On Acre 4 and Acre 6 the net was set to a given depth, and all three discrete-depth samples were made at this depth for one hour apiece. This method allows the collecting of three replicate samples at each sampled depth and minimizes the possibility of contamination.

The first seven cruises (Acre 1 through 7) have yielded 277 individual samples, of which 153 are from discrete depths (Table 2). The discrete-depth samples are almost entirely from the upper 600 m; only seven are from 600-1300 m. Open-net samples have been made to 2500 m. The depth and time coverage of the sampling program are shown in Fig. 1; the chart is used for the preliminary plotting of the vertical occurrence of species. Table 3 presents a summary of the sampling results in terms of the number of meter-hours of sampling at each depth stratum. Meter-hours, the standard used for comparing different samples regardless of size of net or duration of tow, is defined as the area in meters of the mouth opening of the net times the number of hours sampled. Differences in ship speed are not taken into account.

Table 1. Sampling Regime: Day and Night Sampling Depths

Depth in m	General Region
Surface	(Neuston Tows)
50	Above shallow thermocline
100	In thermocline
150	Below thermocline
200	Above daytime DSL
300	Above daytime DSL
400	Top of daytime DSL
500	Middle of daytime DSL
600	Lower daytime DSL
800	In deep thermohalocline
1000	Bottom of deep thermohalocline
1250	Below deep thermohalocline
1500	Below deep thermohalocline

Preliminary analyses in the following sections are made primarily on the basis of the charts (Fig. 1) for individual species. The general patterns of vertical distribution and of diel migration are indicated by blocking in the boxes that represent positive samples. Additional information is gained by adding numbers of specimens in the positive rectangles. Presently the data are being prepared for computer use, which will, for example, enable more precise and sophisticated analyses of distributions and community relationships.

FISHES

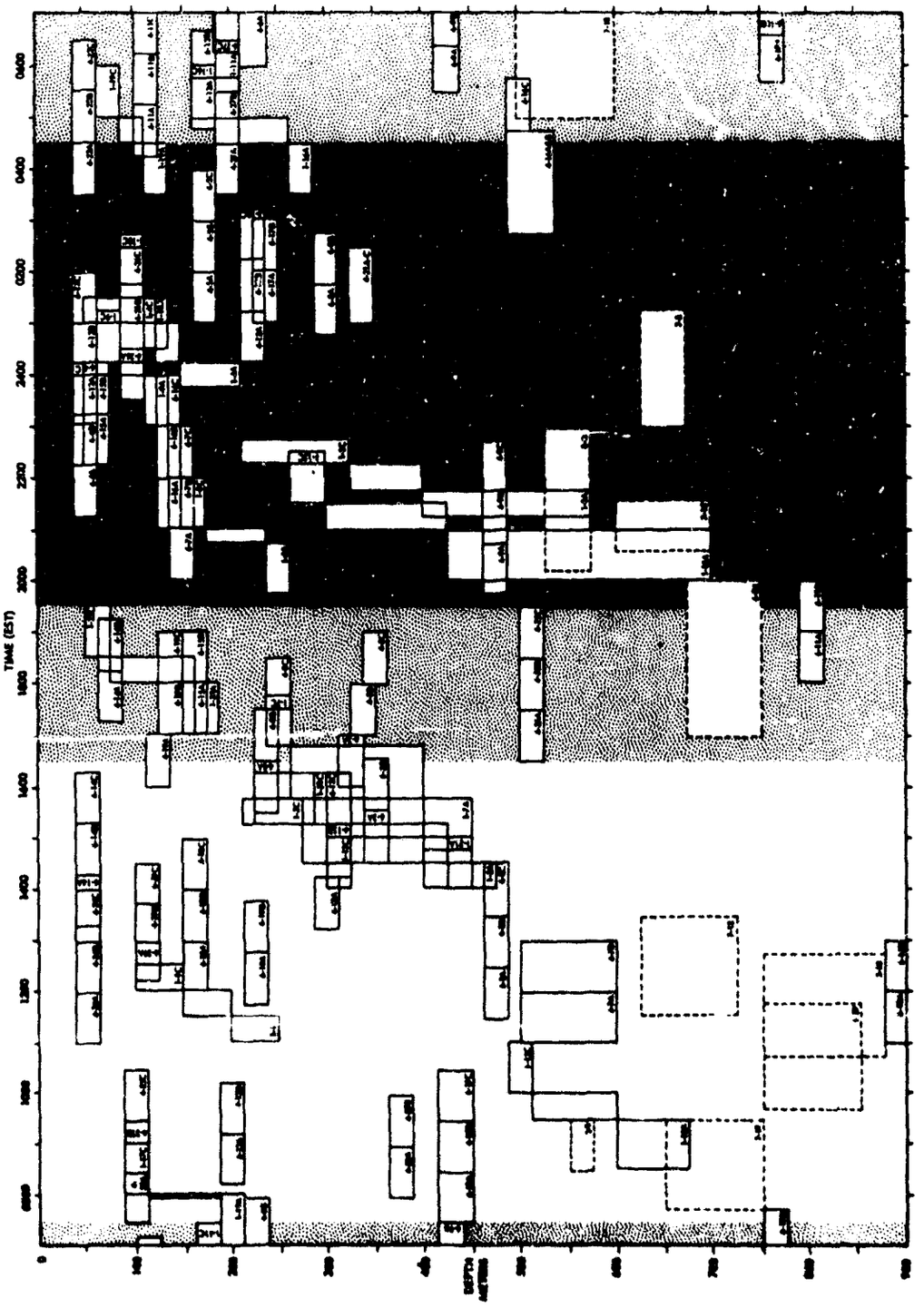
Based on our own determinations and those in the literature, we estimate the presence in Ocean Acre of more than 300 fish species belonging to about 80 families. Many of these, particularly in the upper 200 m, are larvae, postlarvae, and juveniles of shore fishes.

In terms of numbers of specimens in our samples, the most abundant families by far are Myctophidae (58 species), Gonostomatidae (22 species), Sternoptychidae (3 species), and Melamphaidae (9 species). These four families include more than one-quarter of all species expected in Ocean Acre. We estimate that they account for about two-thirds to three-fourths of the individuals caught. Most of the species in these families possess a gas-filled swimbladder, either as juveniles or at all stages of growth. Because of their obvious importance in interpreting sound-scattering phenomena, and because of their dominance in the ichthyofauna, we have concentrated our preliminary analyses on these four families.

Table 2. Biological Trawl Samples Taken on the First Seven Ocean Acre Cruises

	IKMT Discrete Depth Samples	IKMT Oblique Samples to Surface	IKMT Non-Discrete Samples	Engel Non-Discrete Samples	Unsuccessful Trawls	Total Number of Trawls	Sampling Dates
Acre 1*	48	16	10	-	5	31	26 Oct - 2 Nov. 1967
Acre 2*	-	-	5	-	1	6	6-7 Mar. 1968
Acre 3	-	-	14	-	-	14	3-6 July 1968
Acre 4	69	18	13	-	-	31	3-8 Sept. 1968
Acre 5	-	-	4	-	-	4	6-11 Dec. 1968
Acre 6	36	4	20	-	2	26	25-30 Apr. 1969
Acre 7	-	-	9	11	-	20	5-9 Sept. 1969
TOTAL	153	38	75	11	8	132	
GRAND TOTAL SUCCESSFUL SAMPLES						277	

*6-foot IKMT. All others 10-foot IKMT.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2200
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0200
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0600

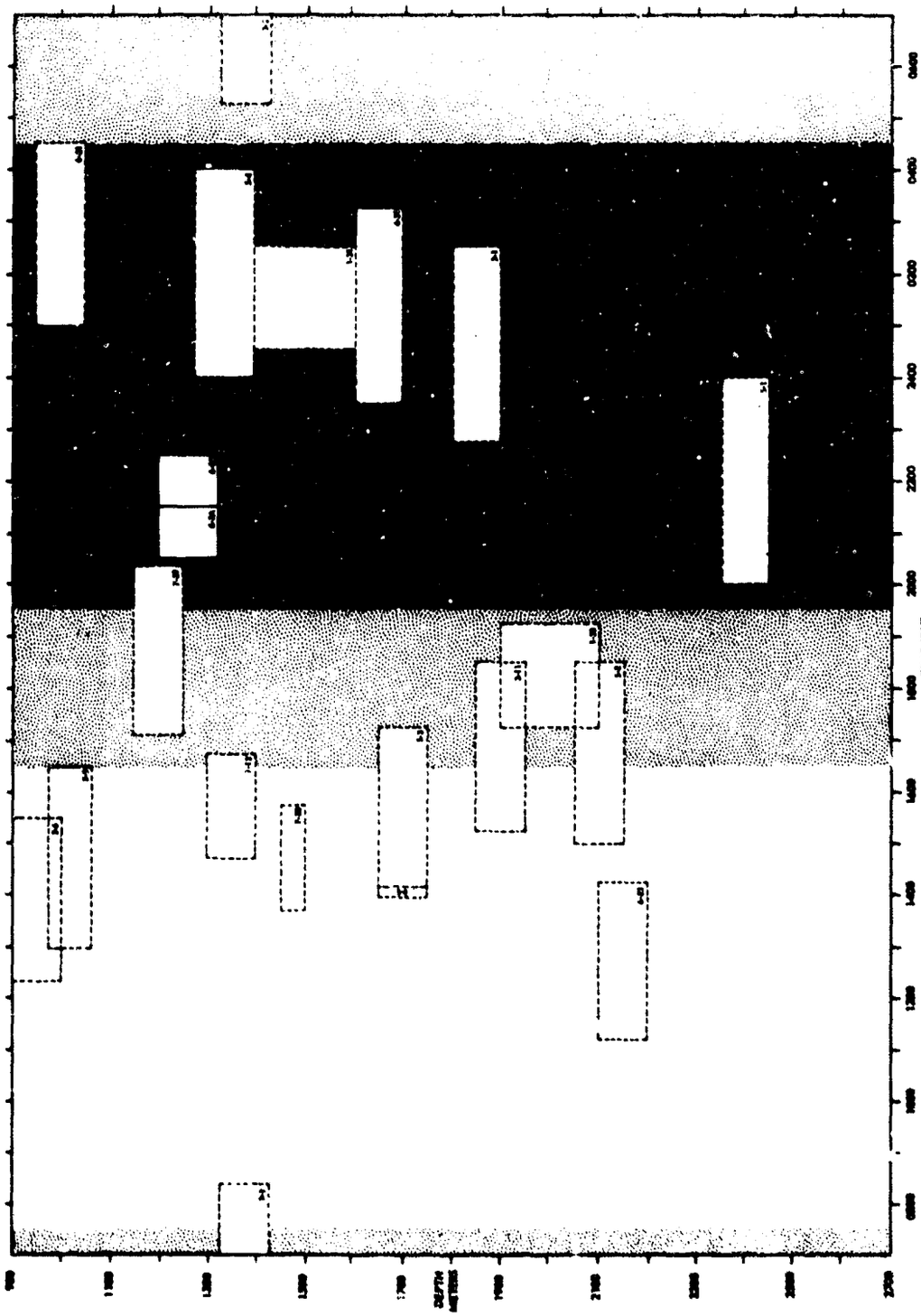

Figure 1. Discrete-depth samples (solid lines) and open IKMTs below 550 m (broken lines). Numbers and letters refer to cruise and sample number.

Table 3. Meter-Hours of Sampling by Depth During Acre 1 Through Acre 7*

Depth Range	Discrete-depth Samples								Oblique Samples						Open-net Samples (Both horizontal and oblique)					
	AM Migration		Day		PM Migration		Night		Day		Night		Overlap		Day		Night		Overlap	
0-50	9	(1)	–	–	–	–	36	(4)	–	–	2.8	(2)	–	–	–	–	17.7	(2)	9	(1)
51-100	4	(1)	80.8	(10)	22	(3)	78.5	(11)	7.5	(5)	5.5	(5)	1	(1)	–	–	26	(3)	9.8	(1)
101-150	33.2	(5)	22.3	(4)	19.7	(3)	41.7	(8)	6	(2)	1.5	(1)	–	–	–	–	67.7	(6)		
151-200	28	(6)	38	(5)	22	(3)	60.2	(8)	6.6	(3)	10.5	(2)	–	–	28.7	(3)	50.3	(6)	–	
201-250	37.4	(6)	31.3	(5)	12	(2)	60	(8)	4.5	(3)	4.1	(2)	–	–	18.8	(2)	19.4	(2)	26	(2)
251-300	–	–	4	(1)	–	–	28	(5)	3.8	(1)	4.7	(2)	–	–	–	–	9	(1)	–	
301-350	–	–	51	(7)	17.3	(2)	13.5	(1)	2	(1)	4.5	(1)	–	–	19.8	(2)	28.2	(2)	–	
351-400	–	–	36.7	(6)	9	(1)	3.4	(2)	6.8	(1)	9.8	(1)	–	–	8	(1)	–	–	27	(1)
401-450	18	(2)	29.7	(5)	–	–	–	–	–	–	–	–	–	–	27.4	(3)	18.2	(1)	–	
451-500	9	(1)	45	(5)	18	(2)	29.4	(4)	9.2	(2)	8.3	(1)	–	–	20.3	(2)	36	(2)	–	
501-600	–	–	22	(3)	9	(1)	13	(2)	–	–	12	(1)	–	–	17.6	(2)	25.5	(1)	18	(1)
601-700	–	–	5	(2)	–	–	–	–							18.5	(1)	57.3	(3)	–	
701-800	18	(2)	–	–	18	(2)	–	–							27	(2)	9	(1)	27	(1)
801-900	–	–	18	(2)	–	–	–	–							35.3	(3)	–	–	–	
901-1000	–	–	–	–	–	–	–	–							–	–	–	–	–	
1001-1100	–	–	–	–	–	–	–	–							41.5	(2)	26.9	(1)	–	
1101-1200	–	–	–	–	–	–	–	–							–	–	–	–	–	
1201-1400	–	–	–	–	–	–	18	(2)							–	–	45.2	(2)	58.5	(2)
1401-1600	–	–													36	(2)	8	(1)	35	(1)
1601-1800	–	–													27.3	(1)	61.7	(2)	–	
1801-2000	–	–													–	–	–	–	37.5	(2)
2001-2200	–	–													27	(1)	–	–	18.2	(1)
2201-2400	–	–													–	–	–	–	–	
2401-2600	–	–													–	–	36	(1)	–	
TOTALS	149.4	(24)	383.8	(55)	148.0	(19)	381.7	(55)	46.4	(18)	63.7	(18)	1	(1)	353.2	(27)	542.1	(37)	266.9	(13)

*Calculated from horizontal (at-depth) time only for open-net samples. Figures in parentheses are number of samples at depth.

Using discrete-depth samples, we have calculated the catch of fishes by depth intervals in terms of the volume in ml per meter hour (Table 4 and Figure 2). The small catch per unit effort above 600 m during the day is apparent and could be due to either small populations or net avoidance by some species or individuals. We are certain that, if large fishes occur here, our nets are not catching them. By contrast, the few daytime samples between 600 and 900 m have a relatively large catch per unit effort. The average size of individuals probably is larger at these depths than at shallower depths, although we have not yet substantiated this. It is noteworthy that the 12-kHz scattering layer at 400 to 600 m is not substantiated by large discrete-depth fish volumes, while the largest catches are below 600 m, where no 12-kHz scattering layer is recorded.

Catch per unit effort at night is much higher in the upper 500 m than in daylight, obviously due to the upward migration of populations from deeper levels. The largest increases over daytime catch are at 50-200 m and 350-500 m. The increases at 50-200 m are explainable by the migratory patterns of the majority of the species analyzed to date (see below). We do not yet have satisfactory explanations for the increases at the deeper level, but these could be due to species or larger individuals of a species that occupy deeper depths during the day and halt their upward migration at this level.

Catch per unit effort was also calculated for open-net tows. These data are not included here, but they show a picture similar to, although less reliable than, the discrete-depth data. One major difference is a relatively large daytime catch at 450-500 m (within the zone of the permanent scattering layer) that is not at all indicated by the discrete-depth samples. The largest daytime catches are still between 600 and 900 m with the peak at 600-700 m, confirming the discrete-depth data. The low discrete-depth catch at 500-600 m at night is also confirmed. Below 900 m, where discrete-depth samples are lacking, the open-net data suggest a concentration of fishes at 1000-1100 m, show a moderate catch down to 2000 m, and a low catch at 2400-2600 m. The effects of contamination during the long retrieval, however, render doubtful any conclusions based on samples from deeper than 1000 m.

In the upper 200 m, where sound scattering is prominent both day and night, juveniles of several species are relatively abundant in our collections. Among these are *Diplospinus multistriatus* and *Nealotus tripes* (both are gempylids with well-developed swimbladders) and young puffers (Tetraodontidae), which could account for much of the daytime scattering. At night, this upper stratum is occupied as well by migrators from deeper levels.

Between 200 and 400 m, where little is caught during the day, we have found juveniles of species that lack swimbladders, such as the alepisauroids, *Scopelarchus candelops* (Scopelarchidae) and *Evermannella indica* (Evermannellidae).

In the 400-600 m stratum, just above the deep thermohalocline in a permanent 12-kHz scattering layer, we find a moderate number of species. Some of these species migrate little or not at all and probably account largely for the night scattering. Such species include *Argyropelecus hemigymnus* (Sternoptychidae) and *Valenciennellus tripunctulatus* (Gonostomatidae), both of which display a diel pigment change: pale with contracted melanophores during the day and dark with expanded melanophores at night (Badcock, 1969; R.H. Goodyear, unpublished data). Other species occupy the 400-600 m stratum during the day but migrate to the upper 200 m at night. Such migratory species include the lanternfishes (Myctophidae) *Lobianchia dofleini, Lobianchia gemellari, Diaphus mollis, Diaphus effulgens, Notolychnus valdiviae, Hygophum benoiti,* and *Benthosema suborbitale;* and the gonostomatids, *Pollichthys mauli* and *Cyclothone braueri.*

The largest daytime fish populations occur in the 600-1100 m stratum, which is the North Atlantic Central Water and is characterized by the deep thermohalocline. Among the many species that inhabit this stratum are, as in the 400-600 m stratum, some species that migrate

Table 4. Fishes: catch per unit effort by discrete-depth sampler expressed as ml/meter-hour. Number of samples in parentheses.

Depth	Day	Night	Day-to-Night Increase
0-50	– (0)	5.39 (4)	–
51-100	0.64 (10)	4.97 (11)	4.33
101-150	0.12 (4)	*16.13 (8)	*16.01
151-200	0.16 (5)	3.29 (8)	3.13
201-250	0.29 (5)	2.19 (8)	1.90
251-300	0.25 (1)	2.84 (5)	2.59
301-350	0.50 (7)	2.22 (1)	1.72
351-400	1.06 (6)	4.43 (2)	3.37
401-450	0.45 (5)	– (0)	–
451-500	0.40 (5)	7.14 (4)	6.74
501-600	0.90 (3)	0.96 (2)	0.06
601-700	4.13 (2)	– (0)	–
701-800	– (0)	– (0)	–
801-900	2.33 (2)	– (0)	–
1201-1300		0.50 (2)	–

*Excluding one extremely large catch, the night and increase figures, respectively, become 3.44 and 3.32.

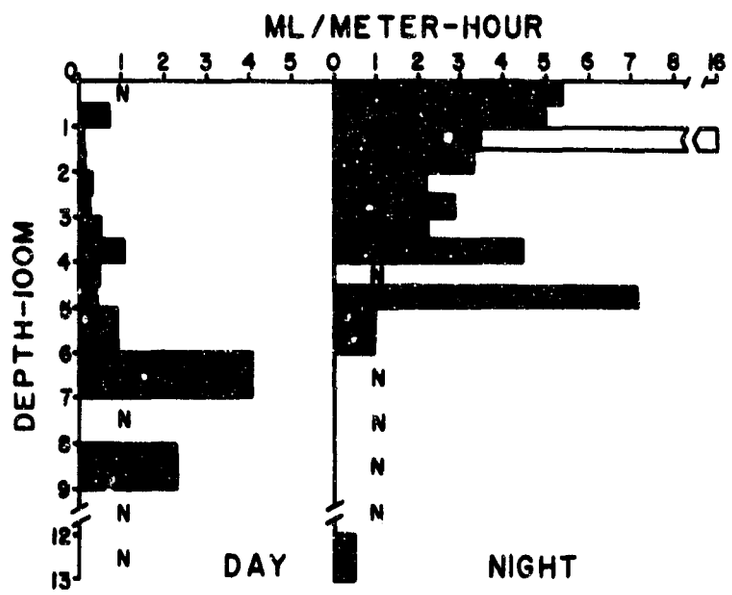

Figure 2. Fishes: catch per unit effort by discrete-depth sampler expressed as ml/meter-hour. An N indicates a depth increment where no tow was taken.

little or not at all and others that migrate at night. The nonmigrators include *Sternoptyx diaphana* (Sternoptychidae), *Scopeloberyx opisthopterus*, and *Scopeloberyx robustus* (Melamphaidae). A larger number of species migrate at night—most of them to the upper 200 m. These include the lanternfishes (Myctophidae) *Diogenichthys atlanticus, Ceratoscopelus warmingi, Ceratoscopelus maderensis, Lampanyctus pusillus, Lampanyctus festivus, Lampanyctus ater, Lampanyctus cuprarius, Lampanyctus photonotus, Lepidophanes guentheri, Lepidophanes pyrsobolus, Lampadena urophaos,* and *Taaningichthys minimus,* and the melamphaids, *Melamphaes pumilus* and *Melamphaes typhlops*. Some of these species apparently are most abundant between 50 and 150 m at night, while others are concentrated between 100 and 200 m. Still others, not mentioned here because of a paucity of data, appear not to reach the upper 200 m and may account for some of the increase seen in catch per unit effort between 350 and 500 m at night. A detailed study of the diminutive *Melamphaes pumilus* has shown that the depth of greatest abundance, both day and night, is deeper for adults than for juveniles or subadults (Michael J. Keene, unpublished manuscript). A similar phenomenon probably characterizes many or most midwater fishes with diel vertical migration patterns.

CEPHALOPODS

The cephalopods taken during Ocean Acre operations to date represent about 46 species in 23 families. Several species are new to science and will be described in a future work. The most speciose families, Enoploteuthidae and Cranchiidae, account for 70% of the total number of cephalopod species captured—40% and 30% respectively.

Enoploteuthids are prominent members of the midwater cephalopod fauna in warm-water regions of the world. When sufficient collections of particular enoploteuthid species exist, they indicate that these squid undergo a diel vertical migration.

Cranchiids are seldom caught as adults, and most species are known only from larval or juvenile forms. For this reason, little is known of their migratory habits. In Ocean Acre all cranchiids captured to date are larvae or juveniles which exhibit no apparent tendency toward diel vertical migrations. In fact, the majority of Ocean Acre cephalopods captured are larval and juvenile forms. The species that do exhibit migratory behavior begin migrating at a stage prior to full sexual maturity and continue to do so throughout adulthood.

The catch of cephalopods per unit effort, expressed in terms of milliliters per meter-hour, for discrete-depth samples to 600 m is shown in Table 5 and Figure 3. Daytime catches are relatively low, but by far the greatest catch per unit effort occurs at the 50-100 m level, where nearly the entire catch consists of larvae, primarily of cranchiid species. Below 100 m the catch drops sharply; between 200-300 m no specimens were captured despite 35 meter-hours of sampling. The catch increases to a low level in the 300-600 m layer. Below 600 m, 23 meter-hours of trawling failed to capture cephalopods. Other than the layer of abundant larvae at 50-100 m, the bulk of the specimens were taken in the 300-600 m layer which corresponds to the 12-kHz scattering layer.

The nighttime catches generally exceed by significant amounts the daytime catches. The greatest increases of night over day catches occur at 100-300 m, 350-400 m, and 500-600 m. The markedly higher nighttime catches at most levels—up to eight times greater than corresponding day catches—presumably reflect the general upward migration of cephalopods at night and almost certainly give an indication of the amount of net avoidance during the day. The larval cranchiids in the 50-100 m zone probably are incapable of avoiding the net because of their "floating" mode of life and their anatomical limitations against strong swimming. The

Table 5. Cephalopods: catch per unit effort by discrete-depth sampler expressed as ml/meter-hour. Number of samples in parentheses.

Depth	Day	Night	Day-to-Night Increase
0-50	– (0)	.167 (4)	–
51-100	.333 (10)	.203 (11)	–.130
101-150	.045 (4)	.384 (8)	.339
151-200	.052 (5)	.249 (8)	.197
201-250	0 (5)	.117 (8)	.117
251-300	0 (1)	.107 (5)	.107
301-350	.098 (7)	0 (1)	–.098
351-400	.136 (6)	.294 (2)	.158
401-450	.067 (5)	– (0)	–
451-500	.111 (5)	.136 (4)	.025
501-600	.055 (3)	.462 (2)	.407
601-700	0 (2)	– (0)	–
701-800	– (0)	– (0)	–
801-900	0 (2)	– (0)	–
1201-1400	– (0)	0 (2)	–

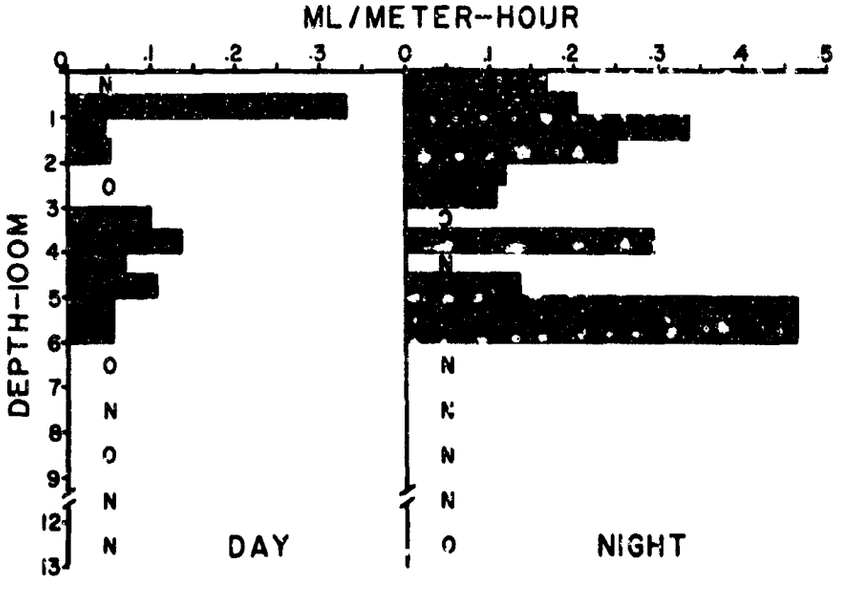

Figure 3. Cephalopods: catch per unit effort by discrete-depth sampler expressed as ml/meter-hour. An N indicates a depth increment where no tow was taken. A zero indicates that no specimens were captured in the depth increment sampled.

catch per unit effort in the upper 200 m at night is nearly equivalent to that in the entire upper 600 m during the day; this suggests that most of the population in the 300-600 m stratum may migrate to the upper 200 m at night.

The large night catches in 350-600 m are more difficult to explain. They may represent individuals (or species) that permanently inhabit this zone but avoid capture during the day, or they may be members of a deeper-dwelling community that ascends to that level at night.

It is interesting to note that the fish and cephalopod captures in terms of catch per unit effort follow similar patterns both day and night in the upper 450 m. Between 600 and 900 m in the daytime, however, the reverse is true: fish catches are at a maximum and cephalopods are at a minimum.

Data for vertically migrating species in the Ocean Acre area are most complete for two species of Enoploteuthidae. Discrete-depth samples show that *Pyroteuthis margaritifera* lives primarily between 300 and 500 m during the day and ascends to the 100-200 m zone at night. Large specimens of 20-mm mantle length or larger were caught only at night in shallow depths (Fig. 4) but were never caught during the day. These larger specimens probably are avoiding the net. *Pterygioteuthis giardi*, judging from discrete samples, also spends the daylight hours at depths of 300-500 m, then migrates toward the surface at night, where it occurs from 50-200 m, with a peak abundance in the 50-100 m zone (Fig. 5).

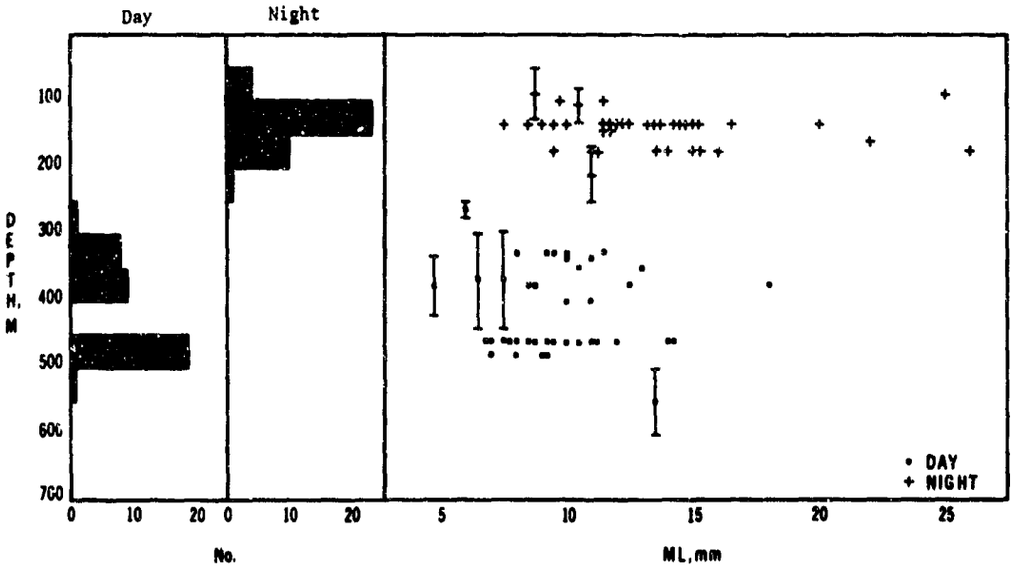

Figure 4. *Pyroteuthis margaritifera*. Vertical distribution based on discrete-depth samples for day and night. Left: depth vs. number of specimens; right: depth vs. size of individuals (ML = mantle length).

Open-net captures of *Pyroteuthis margaritifera* and *Pterygioteuthis giardi* follow a similar trend as that revealed by discrete-depth samples, except that the strata of occurrence are broader. Open-net samples also indicate a deeper vertical range for each species, but the deeper records probably are a result of contamination from the shallower layers as the open net passes through them.

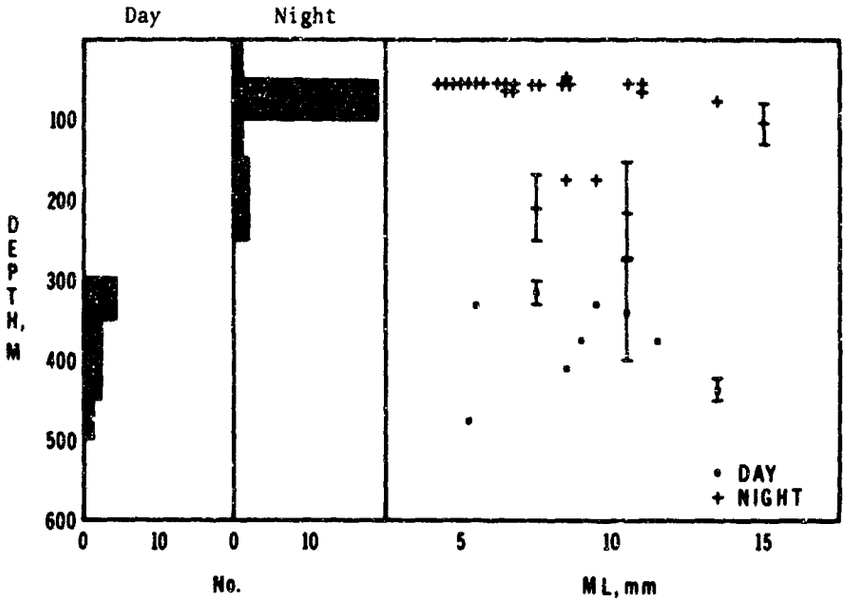

Figure 5. *Pterygioteuthis giardi.* Vertical distribution based on discrete-depth samples for day and night. Left: depth vs. number of specimens; right: depth vs. size of individuals (ML = mantle length).

The discrete-depth captures of *Helicocranchia papillata,* the most abundant cranchiid, nearly all occurred between 50 and 250 m both day and night. The only exceptions are two single captures at 375 m and 460 m during the day, but no significance can be placed on this as an indication of migratory behavior because all *H. papillata* captured to date are larvae and juveniles.

The role of cephalopods as true sound scatterers is unclear at the present, but at least some species, as the two enoploteuthids mentioned above, undergo a diel vertical migration that follows the movement of the 12-kHz sound-scattering layer.

SUMMARY

Our preliminary conclusions, based on 277 samples (153 of which are discrete-depth samples) taken during seven Ocean Acre cruises, are summarized as follows:

In the Surface Water Mass between 0 and 600 m, three distinguishable strata are identified. (1) In the upper 200 m, in which a seasonal thermocline is developed, daytime catches of fishes and cephalopods comprise mainly larvae and juveniles. A 12-kHz scattering layer is present in this stratum both day and night. At night the population is supplemented by vertical migrators, at which time the intensity of scattering increases. (2) Between 200 and 400 m the catches of fishes and cephalopods are small, and generally little or no scattering is recorded at 12-kHz. (3) At 400-600 m, where a 12-kHz scattering layer persists both day and night, catches of fish and cephalopods are moderate. Among fishes, several species migrate little or not at all and probably account for much of the nighttime scattering. A number of other fish and cephalopod species migrate to the upper 200 m at night. There is evidence that deeper-living fishes and cephalopods both migrate to and remain at this 400-600 m stratum at night.

The North Atlantic Central Water Mass, characterized by a deep permanent thermohalocline, is located between 600 and 1100 m. Fishes exhibit their greatest abundance in terms of species and numbers of individuals in this layer. Some species apparently do not migrate, while others migrate to the upper 200 m. Very few cephalopods have been captured in this layer; possibly larger specimens do inhabit this stratum but are able to avoid the net.

These data indicate rather clearly that temperature is not a barrier to the vertical migration of a number of species of fishes and cephalopods. For example, a species may migrate from the lower level of the deep thermohalocline to within 50 m of the surface and experience a temperature change of 15°C or higher. The vertical migrations of most species from the 400-600 m or the 600-1100 m stratum carry them well into or through the seasonal thermocline.

The migratory behavior of fishes and cephalopods from different depth strata at different times and different rates to different upper strata can easily be invoked to explain the complex sound-scattering phenomena observed during crepuscular periods as well as the relatively stable scattering layers observed during the day and night.

Most studies of scattering layers, and certainly those based on 12-kHz soundings, have given much attention to the layer represented by the 400-600 m community in our study. The region of greatest daytime fish concentrations that we find between 600 and 1100 m has been mentioned only rarely even in acoustical studies and has not been delineated in biological studies. This is an area deserving critical attention in future studies.

ACKNOWLEDGMENTS

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PROBLEMS OF THE FEEDING OF ZOOPLANKTON IN THE DEEP SEA

J. E. G. Raymont
University of Southampton
Southampton, England

ABSTRACT

Investigations of the composition and movements of deep scattering layers involve the feeding relations of both zooplankton and nekton. Although zooplankton may be broadly grouped into herbivores and carnivores, different species of such major groups as copepods and euphausids may range from almost pure herbivores to species living on a mixed diet and to some which are exclusively carnivores.

The vertical movements of species not only include those which migrate into the euphotic zone to feed on phytoplankton but also those which have more restricted movements into intermediate layers where they may be detritus feeders, carnivores, or rely on a mixed diet. Detritus may be carried to deeper levels during the vertical migration of zooplankton. This may be of special significance in relation to faecal pellets. The composition of food in faecal pellets may differ significantly from detritus, and bacteria may also use faecal pellets and detritus as surfaces from which they can absorb dissolved organic matter so contributing to the food supply, especially of the deep oceans. The general low concentration of detritus and bacteria in the open ocean is reviewed. Since many metazoans are unable to feed directly on the smallest organic particles, the role of protozoans may be significant as an intermediate link in the food chain. Some data are given of the abundance of foraminiferans and radiolarians and ciliates in this connection. Other possible trophic pathways from dissolved organic matter include relatively deep-living phytoplankton and organic aggregates.

Different populations of zooplankton exchange food material partly through vertical migration. Similarly, some of the oceanic nekton obtain part of their zooplankton food during depth migrations. The paper draws attention to the need for investigations on the quality of food in the oceanic environment, as well as to the quantity and problems of specific selection.

INTRODUCTION

Problems in investigating sound-scattering layers frequently include some consideration of relationships of feeding of oceanic plankton and nekton, especially in connection with vertical migration.

Trophic relationships in zooplankton communities are complex; the problems of the deep sea are particularly obscure. This paper, which is not intended to be a comprehensive review, attempts to draw attention to some of the important questions concerning zooplankton nutrition, including food selection and possible food sources, especially in relation to the deep sea and to migration patterns.

In the open ocean the zooplankton as secondary producers are regarded as feeding on the phytoplankton; small pelagic fishes feed on the zooplankton and are themselves consumed by larger fishes, some from the deeper levels. This picture of the food chain is, of course, excessively simplified.

Feeding Habits: Food Selection and Vertical Migration

The complications include complexities in the feeding in the zooplankton itself. Major groups of zooplankton animals are virtually exclusively carnivores—medusae, siphonophores, ctenophores, chaetognaths, pelagic polychaetes and nemertines; the heteropods and naked pteropods; probably the majority of the planktonic shrimps and amphipods; the great majority of the young stages of fishes. Though we know relatively little of the detailed requirements of carnivorous zooplankton, and many have very wide dietary abilities (cf. Wiborg, 1948 a and b and 1949), some species (e.g. some fish larvae) are more restricted in their food requirements (cf. Shelbourne, 1957; Ryland, 1964).

Apart from meroplanktonic larvae, certain major groups of holoplanktonic animals are usually regarded primarily as herbivores: copepods, euphausids and salps. This last group will not be considered further. The copepods may form some 70% of the total zooplankton, with even higher amounts at high latitudes; certain species of euphausids may also be enormously abundant. If these two major groups were entirely herbivorous, they would have to remain in the first 100-200 m (the main productive zone even for tropical waters) or could live somewhat deeper but must be able to migrate vertically to feed at night. But is this picture of an essentially herbivorous diet really true?

Among the copepods several species of *Calanus* have been studied in some detail. These copepods feed very widely on a whole range of phytoplankton food. However, even in *Calanus*, gut contents show at times small crustacean remains, and feeding experiments have shown that these animals will take animal food. Moreover, during winter scarcity at higher latitudes *Calanus* probably relies to some extent on animal food. What has been said for *Calanus* seems to apply to many similar forms in temperate and warmer waters. Species of *Rhincalanus*, *Neocalanus*, *Nannocalanus*, *Eucalanus* and *Pleuromamma*, for example, are essentially herbivores, though animal food (e.g. Radiolaria and crustaceans) may be taken at times (Mullin, 1966). In other genera (*Acartia*, *Centropages* and *Temora*) there seems a general tendency for a mixed diet to be more appropriate (cf. Petipa, 1959). The work of Anraku and Omori (1963) on the structure of feeding appendages and on experimental feeding bears out the idea that there is a gradual swing towards an omnivorous diet in these latter species, as compared with those which have very fine filtering appendages and are more or less confined mainly to plant food. Genera such as *Labidocera*, *Anomalocera*, *Candacia*, *Tortanus* and *Euchaeta* possess mouth parts which are much coarser and obviously ill adapted for filtration (cf. Gauld, 1964). Both field observations and experiments, as far as they have been carried out, suggest that these animals are exclusively carnivorous. This habit appears to apply particularly to bathypelagic genera (e.g. *Bathycalanus*, *Valdiviella*, *Megacalanus*, *Chirundina*, deep-sea species of the *Metridia* family, and probably some members of the *Augaptilidae*). Some fairly deep-living forms such as species of *Gaidius*, *Gaetanus*, *Euchirella* and *Haloptilus* appear to have a mixed diet, at least partly carnivorous.

Although copepods such as *Gaetanus*, *Gaidius* and *Euchirella* migrate vertically, they may not reach the surface. For deeper-living carnivorous copepods, the distance to the surface is very large and it seems extremely unlikely, though we do not have many accurate observations on vertical migration, that the animals migrate more than a few hundred metres. Certainly it

would seem impossible for all of them to reach near the surface. Thus Gueredrat (1969) has recently reported on four deep-living species from the tropical Pacific, all the copepods being essentially or exclusively carnivores. *Megaculanus princeps* never exceeds ca. 650 m but is usually absent from the upper 300 m by day and may migrate to become plentiful at night from 100-400 m. But *Pareuchaeta hanseni, Metridia princeps* and *Gaussia princeps* are generally deeper (even > 1000 m) by day and hardly ever rise above ca. 400 m at night. A few specimens of the last species have been taken at shallower depths. The question arises whether such deeper-living forms can find an adequate supply of animal food.

In the other major, apparently herbivorous, group, the euphausids, there appears to be a progression from essentially herbivorous, through omnivorous, to carnivorous species. One of the best-known euphausids, *Euphausia superba*, the krill of the Antarctic, is thought to be almost exclusively herbivorous; it feeds mainly on the diatoms of the Antarctic, though showing certain preferences as Nemoto (1966) suggests. Mauchline and Fisher (1969) have questioned what happens during the long Antarctic winter when phytoplankton is not available. Even this species may take animal food occasionally.

The mouth parts of all the euphausids, as well as the fine setules on the thoracic limbs, fit these animals extremely well for filtering particles. Many species undoubtedly take plant food; *Euphausia pacifica* for instance has been shown by Parsons, LeBrasseur, and Fulton (1967) to filter various phytoplankton food, certainly down to a size of about 12 μm. *Thysanoessa inermis, T. raschii, Meganyctiphanes norvegica,* probably *Euphausia mucronata,* and *E. similis* are among the many other species which appear to take phytoplankton. But all authorities on euphausids, especially Ponomareva (1955) have shown that many of these same species eat animal food. The exoskeletons of the prey (e.g. copepods), are often rejected and do not appear so abundantly in the contents of the stomach. Some euphausids, however, appear to take mainly animal food, and the genera *Stylochetron, Nematoscelis* and *Nematobrachion*, with their rather coarser feeding appendages, are essentially carnivorous forms (cf. Nemoto, 1967). Some warmer-water euphausids appear to rely far more on carnivorous or at best omnivorous feeding; this may to some extent reflect the lower standing crops of phytoplankton in tropical oceans.

Though a few euphausid species may show surface swarming (above all *E. superba*), most species live at a maximum of a few hundred metres from the surface, with the younger stages nearer the surface. The great majority of these euphausids migrate from these depths virtually to the surface at night, and Ponomareva has definitely found increased feeding at surface at night. Mauchline and Fisher (1969) summarize the work of other investigators and include *Meganyctiphanes norvegica*, two species of *Nyctiphanes, Pseudophausia latifrons*, eleven species of *Euphausia*, five species of *Thysanoessa* and three species of *Thysanopoda* in this migrating category. The species include tropical as well as cold-water forms and the distances travelled range from 50 to perhaps 400 m. Some of the forms appear to conform to the usual pattern of following the fading light, incidentally, moving up quite rapidly at dusk. A few species exhibit a midnight sinking, a rise towards the surface just before sunrise, followed by a rapid descent to the depths—the classical diurnal vertical picture. Though there have been so many arguments on the value of diurnal vertical migration, the very strong patterns which appear to hold for so many euphausids must surely allow them to feed much more effectively on the rich surface plankton at night, while during the day, at the much lower temperature of deeper water, their metabolism is reduced. This has been illustrated, for example, by the work of Small and Hebard (1967). McLaren (1963) also proposed that it was advantageous for zooplankton to remain at a lower temperature during the day, but related this in part to delaying maturity and to reducing metabolism.

Some euphausids (e.g. *Thysanopoda monocantha*) live deeper and others might be called mesopelagic (e.g. species of *Stylocheiron* and *Nematoscelis*) and while some appear to migrate, few reach the surface. Very few species of euphausids are really bathypelagic (exceeding 1000 m). These include *Bentheuphausia amblyops* and one or two species of *Thysanopoda*. Little is known of these bathypelagic species, but it seems probable that either they do not perform migrations or that the migration is slight. They certainly are unlikely tc reach the surface. The problem therefore emerges for these mesopelagic and bathypelagic euphausids, as for the bathypelagic members of any zooplankton group, that the deep-living species cannot rely on the rich surface plankton for food.

Detritus and Faeces as Food; Vertical Migration

Almost all euphausids rely to some extent on detritus for food. Detritus is an important food even for those species which feed on plankton at the surface during the dark hours. For the deeper-living species especially, it would appear likely that feeding on particles (essentially detritus) forms an important constituent of the diet. Detritus may be significant also in the nutrition of bathypelagic copepods. In addition to crustacean remains and protozoans, detritus occurs very frequently in their guts, but the contribution is very difficult to quantify.

Nemoto (1968) analyzed the ratios of active chlorophyll and degraded chlorophyll pigments found in a series of euphausids starting with those which are mostly near-surface living, and descending to those deeper-living species such as *Bentheuphausia amblyops*. He finds a fairly close correspondence: active chlorophyll is highest in a near-surface feeding form (e.g. *E. similis*), and the amount of degraded phaeophytin pigment is highest in bathypelagic species (*Bentheuphausia*). The deeper fauna relies to a considerable degree on faecal remains from species living in the upper levels (cf. Nemoto and Saijo, 1968).

Such studies are reminiscent of the theory of Vinogradov (1962). Although we now do not envisage the deeper fauna as relying for nutrition solely on the very thin rain of particles from the euphotic zone, Vinogradov considered that the difficulties encountered in the nutrition of deeper-living species were so great that a major contribution must come from food remains released by animals feeding in the upper zones. During feeding only part of the food was digested, and Vinogradov believed that as species descended during their diurnal vertical migrations, they carried a portion of the food from the rich upper levels which they released deeper down as faecal pellets. This material in turn supplemented the diet of deeper-living species which also performed diurnal migrations. A ladderlike series of migrating forms thus appears, extending down to considerable depths. Vinogradov's diagram suggests that some of the species could migrate 1000 m or more and this seems unlikely from an energetics point of view and from the few direct observations (cf. Gueredrat, 1969). Nevertheless, a series of species migrating at different levels is undoubtedly of great significance. Not only can deeper species benefit from the faecal pellets produced, but in this mixing of populations the carnivorous species, which represent a high proportion of the fauna, have the advantage of feeding on herbivores from higher levels.

The significance of faecal pellets becomes more obvious when the extremely slow descent of detritus particles in the open oceans is considered. Many authorities have suggested that relatively resistant materials (cellulose, chitin, lignin) form the residues of deep-sea detritus. The compacting of faecal material means that its rate of descent will be considerably accelerated, and its nutritive value will be in part retained. The significance of faecal pellets turns largely on the superfluous feeding theory put forward by Beklemishev (1957, 1962). Essentially herbivorous feeders such as many copepods were regarded as feeding virtually automatically.

At high phytoplankton concentrations, much of the food was not extensively digested, and thus superfluous feeding occurred with considerable nutriment voided as faeces. More recently laboratory experiments such as those of Mullin (1963) and others strongly indicate that feeding is reduced at high concentrations. Conover (1966) has also pointed out that such high food concentrations are rarely likely to be encountered in the sea. Nevertheless, Conover agrees, even though the assimilation efficiencies obtained from his experiments on copepods appear to be very high, that enough degraded chlorophyll and similar organic material might appear in faeces to contribute significantly to the nutritive value of these particles (cf. Paffenhöfer and Strickland, 1970).

Another aspect of faecal pellet feeding may be of significance. The observations of Newell (1965), Johannes and Satomi (1966), and others have suggested that some benthic marine animals are coprophagous and find considerable nutriment from faeces, especially since the faeces act as surfaces for a dense flowering of epiphytic bacteria. The bacteria feed by absorbing dissolved organic matter which is of course relatively plentiful in sea water. Zooplankton animals might make use of faecal pellets enriched in the same way by bacteria.

The quantity of general detrital material in the oceans, though present in relatively small amounts, is vastly greater than the biomass of plankton, as several authors have pointed out. Dead material forms an appreciable fraction even in the euphotic zone (e.g. Krey, 1961; Hagmeier, 1964; Beers and Stewart, 1969). For open oceans Menzel (1967) suggests the order of 0.1 mg C/litre as detritus, and though there are regional differences, all workers agree that there is a very rapid reduction in detritus below ca. 400 to 500 m. The quantities in deep water are to be reckoned in μg C/litre (e.g. Riley, Van Hemert, and Wangersky (1965) quote 10-20 μg/litre). Larger quantities may be derived however from deeper currents from high latitudes, etc.

The great reduction in particulate matter is certainly correlated with the enormous decrease in zooplankton in deep water. Bogorov (1958) dealing with the zooplankton mass in the northwest Pacific, shows a great reduction in biomass with depth. For example, in the upper 200 m he quotes a biomass of the order of 1000 mg/m^3; in the enormous zone extending from 500 to 6000 m the maximum is only of the order of 80 mg/m^3; below 6000 m depth the total amount is less than 1 mg/m^3. The vastly disproportionate amount of zooplankton especially in the first 200 m is obvious. Zenkevitch and Birstein (1956) and Vinogradov (1962), pointing to the same phenomenon, suggest that at high latitudes the biomass below 6000 m is only 0.001 that of the uppermost layers. Banse (1964) also suggests a reduction of two to three orders of magnitude for deep-water fauna.

Bacteria and Dissolved Organic Matter

Detritus may not be consumed directly by metazoans especially at the extraordinarily low concentrations in deep water. Bacteria might use the particles partly for surface attachment, since so many marine bacteria are apparently epiphytic, and the range of bacterial exoenzymes might permit the utilization of even some of the resistant detrital material. But in addition bacteria can utilize the dissolved organic matter, the amount of which is much greater than the particulate matter. The concentration in the surface of open oceans approaches 1 mg C/litre, about 10 times the amount of particulate matter. Differences in concentration seem to be relatively small below a depth of some 400 or 500 m. Menzel and Ryther (1968), for example, suggest that in all deeper waters the organic carbon does not vary very much from 0.5 mg carbon/litre.

The great resistance of this dissolved organic matter to bacterial action and oxidation is widely recognized. However, a much smaller proportion of the material is in a much more labile form. Khailov and Finenko (1968) demonstrated that some of the organic matter in the form of macromolecules is actively adsorbed on to natural detritus, and micro-organisms on the surface of the detritus might then assimilate a portion of the material adsorbed. The labile organic material also includes smaller molecules: a variety of carbohydrates, protein derivatives, and aminoacids and lipid materials, and though the quantities range only from 1 to 10 μg/litre, because they are relatively labile, they can provide food for heterotrophic organisms.

One of the main difficulties, however, in envisaging a food chain from detritus or dissolved organic matter through bacteria has been the emphasis in all literature that the density of bacterial populations in the deep sea is very low. But investigations such as those of Holm-Hansen and Booth (1966) using ATP as an indicator of living biological material, have suggested that the mean microbial population below the euphotic zone may approximate to about 1,000,000 or more cells per litre. This is many times higher than the densities of bacteria quoted by most microbiologists for plating counts. The great deficiencies of plating counts in estimating marine bacterial populations is now recognized. Although bacterial densities are not high, low multispecific populations appear to be possible at the poor nutrient concentrations in the ocean, though the rate of turnover is excessively low. How far the zooplankton could utilize bacteria directly is very difficult to resolve. Strickland (1965) states that Zhukova and Voroshilova and Donova have found success in the use of bacteria by zooplankton. On the other hand, the early experiments of Clarke and his colleagues (e.g. Fuller and Clarke 1936) and the numerous experiments on feeding bivalve larvae by Loosanoff all suggest that bacteria are rather unsuitable food for zooplankton. In fresh waters Takahashi and Ichimura (1968) have demonstrated that sulphur bacteria were definitely consumed by copepods; the bacteria were labelled and the copepods were found to possess the tracer. Possibly deep-sea marine filterers may act similarly.

Protozoa as Links in the Trophic Pattern

Foraminifera and Radiolaria

It is probably essential, however, to envisage further links in the chain from detritus and bacteria to metazoans. One possible link might involve Protozoa. Murray (1963) suggested that Foraminifera might feed on detritus and bacteria. However, experiments suggested that living phytoplankton was preferred and bacteria though ingested did not contribute apparently to the nutrition. How far Radiolaria may feed on detritus and/or bacteria is also unknown.

Although Foraminifera and Radiolaria have been cited as appearing often in the stomach contents of various zooplankton, it is very difficult to estimate their abundance in the oceans. Cifelli and Sachs (1966) studied a traverse in the Atlantic Ocean from the Nova Scotia shelf across the Sargasso to the Caribbean. The protozoans were present throughout the whole region, though in varying numbers, and in general Radiolaria were less abundant than Foraminifera. The average densities appear to be low, and judging from the frequent references in the literature to these protozoans as food of plankton, they must really be much more abundant. The answer to a large extent may be net mesh size.

Thus another indication of the abundance of these protozoans comes from the work of Beers and Stewart (1969) working offshore in the Californian Current area. Although they do not quote the precise abundance of Foraminifera and Radiolaria, we may calculate a mean number of Foraminifera and Radiolaria for a medium mesh net (more than 35 μm) of a few

thousands/m^3. In the finest net (less than 35 μm), one exceptional traverse showed some tens of thousands of Foraminifera per cubic metre. However, the protozoans were relatively sparsely represented in the coarse net (> 103 μm). Berger (1969) also investigated populations of Foraminifera; high densities were generally correlated with areas of high fertility, and he implies that these protozoans are essentially algal feeders. They were most abundant in the upper 100 m and decreased rapidly with depth, the mean density for a 160 μm net being ca. 10/m^3). But enormous variations in density were recorded (< 1 to 100,000/m^3) and a major factor in the variation would again appear to be net mesh size. A significant comment in Berger's work is that turnover time in Foraminifera may be relatively short.

Ciliata

But of greater importance among Protozoa perhaps are the ciliate populations. These are sometimes found in abundance in sea water, and their rate of turnover is high when compared with metazoa. By comparison with freshwater species, marine infusoria might be expected to feed partly on bacteria, perhaps also absorbing dissolved organic material to some extent.

Zaika and Averina (1968) found reasonable densities of infusorians in the admittedly shallow waters at the entrance to Sevastopol Bay. "Small" ciliates (20-55 μm) showed a mean density over four summer months of 6100/litre and "large" species (> 55 μm) some 350/litre. No evidence was obtained on their feeding habits, and Gold's experiments on culturing tintinnids suggest that these ciliates feed on phytoplankton. On the other hand, Lighthart (1969) working in the Puget Sound area, was able to isolate a few species of bacteriovorous Protozoa, including flagellates and ciliates, even in the water column.

An interesting quantitative survey is again that of Beers and Stewart (1969). Though the sampling was confined to the upper 100 m the total number of Protozoa is high, ranging from approximately 600,000 per m^3 to just under 200,000 per m^3 at the most offshore station. This may be compared with approximately 10,000/m^3 to 20,000/m^3 for total metazoans. More important, however, is the proportion of ciliates. In the finest samples (less than 35 μm) the ciliate groups together (chiefly small, nonloricate species) comprised 95% or more of the total Protozoa. In the next size category the larger tintinnids were much more important, but in all the samples together, tintinnids did not amount to more than about 20% of the total ciliate population. Although the contribution of ciliates, especially small species, to total biomass is admittedly very small, with their great rapidity of reproduction they could form an effective link in the food chain. Margalef (1963) has also emphasized the importance of ciliates (mostly small species) in the food chain in Western Mediterranean waters. His average density is nearly 900,000 per m^3.

Alternative Trophic Paths from Dissolved Organic Matter

Deep-Living Phytoplankton

There are one or two possible alternative paths, apart from bacteria, which could lead to the production of particulate organic matter from the relatively large amount of dissolved organic matter in the oceans. The works of Bernard (1948, 1953, 1963, 1967), of Wood (1963) and others have drawn attention to the existence of relatively deep living phytoplankton well below the euphotic zone. Bernard emphasizes coccolithophores, but a few Myxophyceae, flagellates, dinoflagellates, and even diatoms, also occur in some areas. Their occurrence has been confirmed recently in several different seas. Although the quantity may not be very large, if this

deep-living phytoplankton can live heterotrophically on the dissolved organic matter it represents a conversion to particulate matter. We cannot say how far such a population could be effectively grazed on by zooplankton, though Wood and Kenyon are quoted by Beklemishev, Neyman and Semina (1966) as reporting several phytoplankton species in the guts of animals caught at 4000 m in the Mediterranean. Although there is some doubt whether the cells contained living chlorophyll, there is a possibility that some zooplankton grazes on deep living phytoplankton.

Organic Aggregates

Another method of converting dissolved organic matter into "useful" particulate material comes from the work of Sutcliffe, Baylor and Menzel (1963); of Riley, Wangersky and Van Hemert (1964); and others on the formation of organic aggregates from dissolved organic matter. Although earlier investigations were concerned particularly with the formation of such aggregates in relation to bubbles and were, therefore, largely confined to the surface, we now know that aggregates can be formed at all levels by adsorption onto particles. Menzel (1966) has made a careful reappraisal of bubbling in aggregate formation, and has shown how artefacts appear owing to the adsorption of organic matter on filters. Barber (1966) demonstrated that bubbling did not cause aggregation under sterile conditions (cf. also Batoosingh, Riley and Keshwar, 1969).

Although the amount of organic aggregates falls very considerably in deeper water, some are present down to the greatest depth sampled (Riley, Van Hemert and Wangersky, 1965). The aggregates can adsorb bacteria and even phytoplankton cells at lesser levels, and certainly such aggregates are consumed by zooplankton, at least in shallow water. There is no need to suspect that they cannot be used also in deep waters.

Advantages of Mixed Diet—Role of Vertical Migration

Whatever the particulate food in the deep sea—detritus, bacteria, colloidal aggregates or deep-living phytoplankton—the rate of turnover appears to be very low. The deep-sea zooplankton population which can be supported is thus very low and the animals must in effect be filter feeders or carnivores which prey on these filtering forms. It seems virtually certain that a number of deep-sea zooplankton species combine both forms of feeding.

Vinogradov (1962) states that some bathypelagic plankton (> 2000 m by day) may show phytoplankton remains in the gut and claims this as evidence of extensive migrations, even to the euphotic zone. For example, some deep-sea mysids are claimed to be herbivorous. Perhaps the food, however, represents degraded phytoplankton, including faeces. Only two species of *Boreomysis* are stated by Vinogradov to be truly detritus eaters. On the other hand, many shallow water mysids such as *Neomysis integer* (Raymont, Austin and Linford, 1964) and *Schistomysis spiritus* (e.g. Mauchline, 1967) are clearly omnivorous, and although Mauchline's recent study (1970) has shown that *Mysidopsis gibbosa* and *M. didelphys* are essentially carnivorous, it seems probable that many deeper-living forms (e.g. *Eucopia* spp. *Gnathophausia gigas*) may incline to an omnivorous habit. Even the large pelagic prawns such as *Acanthephyra* spp. and *Systellaspis* spp. are at times apparently filterers since they show small particles in the gut, although they are largely carnivorous, especially on all kinds of crustaceans, chaetognaths, small fish and Radiolaria. Presumably from an energetics point of view a carnivorous diet is much more nutritious, provided not too much energy is expended in pursuing prey. Deep-sea ostracods are said to vary from filterers such as *Cypridina levis* to active carnivores such as

Gigantocypris mülleri. Vinogradov classes most as detritus feeders; in all probability many species combine both forms of feeding. Angel (1969), investigating ostracods in the northeast Atlantic, found a zone 0-250 m deep, rich in species and numbers, and a second maximum at ca. 450-625 m. The zones were to some extent recognizable even at night, although various species showed pronounced vertical migrations. He implies that the ostracods are mainly predatory but he states that the nutritionally poorer areas show greater species diversity. Presumably this might also relate to feeding habits. Beklemishev (1957) has reported *Conchoecia* species feeding on faecal pellets containing diatom remains.

A number of earlier workers (e.g. Jespersen, 1924, 1935; Leavitt, 1935, 1938) have noted in addition to a surface maximum of zooplankton, a second deeper maximum. This second rich layer might vary in depth from 500 m (northeast Pacific) to 800 m (western Atlantic) to 1000 m in depth (tropical Pacific).

This second maximum may perhaps be associated with the region near the permanent thermocline where often there appears to be an accumulation of detritus and sometimes lowered oxygen concentration. Perhaps the zooplankton finds better nutritional conditions near this zone than at deeper levels. Wickstead (1962), investigating the distribution of Indian Ocean copepods, also suggests that apart from a rich surface zone, a deeper (~ 600 m) rich zone exists, with many of these copepods migrating to the surface at night to feed. Below these, a deeper group (600-1500 m), also appears to move upwards to intermediate depths. They may feed on faecal pellets, detritus or even protozoans in this layer, but presumably many of the deeper migrating species are at least partly carnivorous.

Migration and Feeding in Nekton

We might extend this picture of a migrating trophic chain to include the nekton, especially the small mesopelagic fishes which prey to a large extent on the zooplankton. Though there are comparatively few detailed analyses of feeding habits of the upper mesopelagic fishes, and gut analyses may be misleading, it appears that some nine-tenths of these fishes living by day down to 600 m or 800 m, especially the small gonostomatids, the hatchet fishes, and above all the myctophids, are essentially plankton feeders, feeding on copepods particularly, but also on euphausids, amphipods, chaetognaths as well as on small squid and pteropods – possibly even on siphonophores and jellyfish. Most workers are agreed that a substantial diurnal vertical migration occurs in many of these oceanic fishes, though the hatchet fishes move relatively little. Marshall (1954, 1960) claims that this pattern is essential for myctophids if they are to obtain the necessary food supply in the surface layers.

A number of somewhat larger, essentially carnivorous, fishes also migrate surfacewards. These feed mainly on the smaller fishes but will take zooplankton also. Haedrich (1964) found that even the large active carnivorous species *Alepisaurus ferox* also migrates to the surface, and though they are markedly cannibalistic fishes, feeding on *Alepisaurus* of all sizes as well as on other fish species, they feed to some extent on zooplankton, particularly on hyperiid amphipods and heteropods.

Amongst other nekton which appear to use migration and the "nutrition ladder" to feed near the surface are the cephalopods. Some of the relatively small size species such as *Cranchia* live in the upper zones, together with the young of some deeper species, and others migrate from intermediate depths (cf. also migrations of *Pyroteuthis margaritifera* and *Pterygioteuthis giardi* (see paper, A.10, Gibbs and Roper). Many cephalopods consume zooplankton, including larger copepods, decapods and other crustacea and pteropods. Nesis (1965) investigating the feeding of young squid of *Gonatus fabricii* states that it consumes plankton (copepods, euphausids,

amphipods and sagittae) but there is an excellent grading of size of prey with increased size of the squid predator. Milliman and Manheim (1968) refer to concentrations which were probably sergestid shrimps, squid and myctophids, all showing vertical movements. Unfortunately there are no observations on whether this was partly a trophic relationship.

Sergestids certainly may act as intermediate carnivores in the food web. Thus Omori (1969) has recently shown that *Sergestes lucens* shows pronounced vertical migrations from >200 m by day to 10-50 m at night; the rise is rapid and great shoals accumulate. They feed on a wide range of material, detritus and even a few diatoms, but essentially they feed on zooplankton including copepods, decapods, euphausids and chaetognaths. At least two fishes, *Diaphus coeruleus* and *Gephyroberyx japonicus* migrate with them and feed very actively on them.

Even when we have investigated the quantities of food at all levels in the complex food chains and have accurate assessments of feeding preferences, this will still be insufficient. The *quality* of food is all important from the point of view of efficiency of turnover.

Our laboratory has, therefore, been investigating the proximate biochemical analysis of individual species of plankton over the past years. Despite probably accurate claims that high latitude zooplankton may be high in lipid, we have found many species ranging from neritic to deep-sea mysids, oceanic decapods, and high latitude euphausids and sagittae to be relatively rich in protein; some mysids may reach 70% dry body weight; euphausids and decapods average 50-60% dry body weight. Carbohydrate is almost invariably low (<5%) in all zooplankton species studied. Lipid, though variable (presumably with diet, reproductive stage, etc.) rarely exceeds 30% and is often <20% (cf. Raymont, Austin and Linford, 1966, 1967; Raymont, Srinivasagam and Raymont, 1969 a and b). The high protein content is, we believe, of the utmost significance to zooplankton feeders that appear, whatever the complexity of the food web and whatever the region, to play such a significant role in trophic relationships in the open oceans.

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MICROBIAL DISTRIBUTION IN OCEAN WATER RELATIVE TO NUTRIENTS AND FOOD SOURCES

Osmund Holm-Hansen
Institute of Marine Resources
University of California
La Jolla, California

ABSTRACT

This paper discusses the distribution and origin of organic substrates that may be important as food sources for the macrozooplankton and other metazoans in deep ocean water. Adenosine triphosphate determinations indicate that there is a microbial population in deep water that contains between 1 to 5% of the total particulate organic carbon. The respiratory activity of this biomass is estimated to be about 10 to 50 μl O_2/liter/yr, which compares favorably with respiratory estimates based on oxygen electrode measurements, electron transport activity, and heterotrophic CO_2 uptake. The distribution of phytoplankton in the euphotic zone is discussed briefly as it is influenced by nutrients, light, or grazing. Field observations of phytoplankton biomass generally indicate concentrations of algal carbon that are below those minimum concentrations required for good copepod growth as based on laboratory data. This disparity might be resolved if phytoplankton were distributed in patches or layers normally overlooked when determining chlorophyll concentrations with depth. Continuous chlorophyll profiles obtained by *in vivo* fluorometric measurements do indicate such a marked layering of algal cells.

INTRODUCTION

All animals discussed in this conference are herbivores, carnivores, or omnivores and thus are dependent upon preformed particulate food. The distribution and abundance of all animal forms responsible for the sound scattering layers in the oceans will thus be controlled to some extent by the distribution of available food sources. Although between the phytoplankton and the fish there may be many trophic levels that are detected by sonic devices, the base of the entire food chain consists of the photoautotrophic algal population in the euphotic zone. I wish to discuss the distribution and activity of these cells in the euphotic zone as well as organisms that may comprise the base of the food chain in deep water.

When considering the distribution of food materials with depth it is convenient to delineate four major zones of the water column as follows.

1. The euphotic zone, which extends from the surface to the depth at which photosynthetic reduction of CO_2 balances the respiratory losses of carbon. This depth is variable but is generally between 40 to 100 m in oceanic water.

2. In the depth interval from the lower portions of the euphotic zone to about 1,000 m (in the clearest ocean water) there is insufficient light for any net productivity by photosynthesis, but there is sufficient light penetration to serve as a stimulus for migrating animal populations.

The food levels in this zone may be quite high as a result of particulate matter settling down from the euphotic zone and also from migrating animal populations that feed in the euphotic zone and descend to depths approaching 1,000 m during the daytime.

3. From about 1,000 m to the bottom of the deepest trenches at over 12,000 m there is the zone where the only significant light is that of bioluminescence and where temperature and nutrients are quite constant. Our knowledge of the quantitative distribution of animal species in this zone is meagre, but we know there are zooplankton, fish, and other metazoans throughout this entire water column.

4. The fourth zone includes the sediments and the bottom-dwelling fauna. The macroscopic animals inhabiting this area are much better known (Sanders and Hessler, 1969; Vinogradova, 1962; Wolff, 1960) than the bathypelagic organisms higher in the water column, but very little is known concerning the micro-organisms of the sediments. These organisms comprising the bottom fauna are still dependent, of course, on the food materials in the water that passes over them and on that particulate matter that settles out of the water column.

Distribution of Organic Carbon

The sum of all the inorganic forms of carbon in sea water (e.g., H_2CO_3, CO_2, HCO_3^-, $CO_3^{=}$) is equal to about 50 times the sum of all the organic carbon. The three major components of the organic carbon fraction are (1) dissolved organic compounds (over 90% of total), (2) detrital particulate material (2 % to 4%), and (3) that found as constituents of living cells (approximately 1% or less). Both the dissolved compounds and detrital matter vary greatly in concentration in the euphotic zone, but they are quite uniform in all ocean water below a few hundred meters (Menzel and Ryther, 1968; Williams, 1969). The dissolved organic carbon averages about 500 μg C/liter in deep water (range is 0.2 to 0.8 mg C/liter), whereas the particulate carbon averages about 5 μg C/liter. Menzel (1967) has claimed that these organic fractions are uniform in time, space, and depth; but in view of data from various laboratories in recent years, his claim seems to be an invalid oversimplication. The concentrations of dissolved and particulate organic carbon in deep water do seem to be independent of the rate of photosynthetic production in the euphotic zone, but different water masses often have significant differences in concentrations of these carbon fractions (Williams 1969). The range of particulate carbon in the euphotic zone in oceanic areas is about 30 to 300 μg C/liter, of which from 20% to 90% may be found in living cells. The reservoir size of the dissolved and detrital organic carbon fractions is immense when calculated for all the oceans (Williams 1969), but the quantitative abundance of these chemical entities does not necessarily implicate them in deep ocean food chains. Elsewhere in this volume, Raymont speculates on the possible use of these reservoirs in deep water to support a microbial population that in turn would serve as food for carnivores. Most investigations, however, indicate that most if not all the dissolved and detrital carbon in deep water is refractory and cannot support the growth of microbial cells (Barber, 1968; Menzel and Goering, 1966). Further evidence for the refractory nature of these materials is furnished by Williams, Gaechter, and Kinney (1969) with C^{14}, which indicate a mean age of 3,400 years for the dissolved organic matter in deep Pacific Ocean water, and the results with C^{13}/C^{12} ratios (Williams 1968) which indicate a fairly uniform distribution of $\delta^{13}C$ in a deep water column. Although the above reports do suggest that a large part of the organic carbon in deep water is stable and not readily used by micro-organisms, it is possible that some small fraction of it is turning over rapidly and supporting a microbial population.

Food Sources for Deep Water Populations

The two hypotheses most commonly put forward concerning the nature of the first stages of the food chain in deep water are discussed separately, although it is likely that they are both important in various parts of the water column.

1. Vinogradov (1962a) has suggested that food materials are actively transferred from the productive euphotic zone to deep water through a series of interlocking zooplankton populations that show cyclic migrations. Thus, each migrating population consumes other zooplankton at its uppermost migratory position and then in turn is consumed by other zooplankters living below them in the water column. Studies on the feeding habits, the morphology of the feeding apparatus, and the gut contents of zooplankton caught at great depths have not given us as yet an unequivocal answer as to the validity of this hypothesis.

2. The other main alternative suggests that there is a heterotrophically growing microbial population in deep water that serves as the base of the food chain. The energy requirements for such a microbial population would depend upon either the dissolved or the particulate organic matter (Fig. 1). We do not know enough about the types of microbial cells found in deep water to say anything concerning the relative rates of carbon transfer through the two food routes shown in Figure 1. There has been much work on the bacterial populations in ocean water (Kriss, 1963; Sorokin, 1964; Zobell, 1968), but it is difficult to obtain any reliable estimate of bacterial biomass because of the lack of any suitable method for such determination. Microscopic examination of filtered samples of deep water reveal a very sparse but broad assemblage of microbial cells such as bacteria, fungi, yeasts, flagellates, and many small cells difficult to identify (Fournier, 1966; Hamilton, Holm-Hansen, and Strickland, 1968). There are very few data, however, on the quantitative biomass of any of these microbial forms. The numbers of ciliates that Raymont mentions elsewhere in this volume were obtained only between the surface and 200 m, and thus cannot be extrapolated safely to deep water (Beers and Stewart, 1967, 1969). It is much easier to get quantitative data on the macroscopic zooplankton that can be sampled with nets that open and close at the desired depth. Vinogradov (1962b) has described the distribution of copepods down to 4,000 m and shown that the copepod biomass decreases exponentially from approximately 20 μg fresh weight/liter at the surface to about 0.05 μg/liter at 4,000 m. The concentration of zooplankton in deep water generally does reflect the photosynthetic production rate in the euphotic zone (Banse, 1964).

Following is a discussion of recent methodology and results that bear upon the proposed food chain involving bacteria and ciliates as shown in Figure 1.

Biomass and Activity Estimates in Deep Water

Biomass Estimates

The methods commonly used to estimate the total mass of living cells in the euphotic zone (e.g., chlorophyll measurements and direct microscopic methods) are not feasible for deep water studies. The one method that does look promising involves the quantitative determination of adenosine triphosphate (ATP), which is a labile cellular intermediate in all live cells. ATP is found in fairly uniform concentrations in all living cells, but it is not found in detectable amounts in dead cells or in detrital material. The analytical method for determination of ATP in amounts as low as 1×10^{-5} μg is via a bioluminescent reaction involving firefly luciferin-luciferase whereby each molecule of ATP that is hydrolyzed yields one photon of light. The details of the ATP assay procedure have been described by Holm-Hansen and Booth (1966).

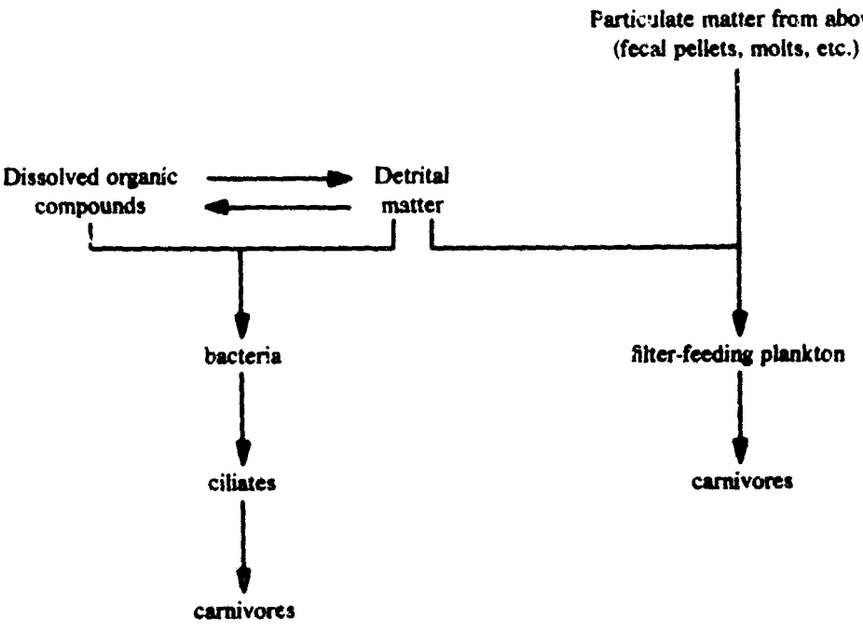

Figure 1. Possible food sources for organisms living in deep ocean water

A representative ATP profile with depth is shown in Figure 2. It is seen that ATP, which is directly proportional to biomass, is very high in the euphotic zone, decreases very rapidly between 100 and 200 m, and then declines at a much slower rate down to 3000 m. These concentrations of ATP may be extrapolated to cellular organic carbon by multiplying by the factor of 250, which is based on laboratory investigations in which ATP levels have been correlated with the cellular content of organic carbon. The biomass, as estimated by ATP determinations, generally account for 40% to 90% of the total particulate organic carbon in the euphotic zone, about 5% to 10% at 200 m, and about 1% at 3,000 m. These biomass estimates of cellular organic carbon can be further extrapolated to respiration values by applying respiration factors obtained from laboratory cultures. If one assumes an average rate of respiration and applies suitable temperature corrections, the deep ATP values indicate a respiration rate of about 5 to 50 μl O_2 /liter/yr.

Activity Measurements

1. Pomeroy and Johannes (1968) have measured the respiration of organisms in water samples down to 800 m by concentrating the particulate matter from 200 liters down to about 25 ml and then following the assimilation of oxygen directly with the oxygen electrode. In deep water these measurements seem to give slightly higher estimates of respiration rates than those estimated by ATP determinations.

2. Packard (1969) has estimated the respiratory activity of microbial cells in water down to 6,000 m in the Pacific Ocean by determination of the activity of the electron transport system in the particulate fraction. His depth profiles of respiratory activity are fairly similar to the depth profiles reported for ATP. In water below 2,000 m Packard's data indicate a respiratory rate of about 5 μl O_2/liter/yr.

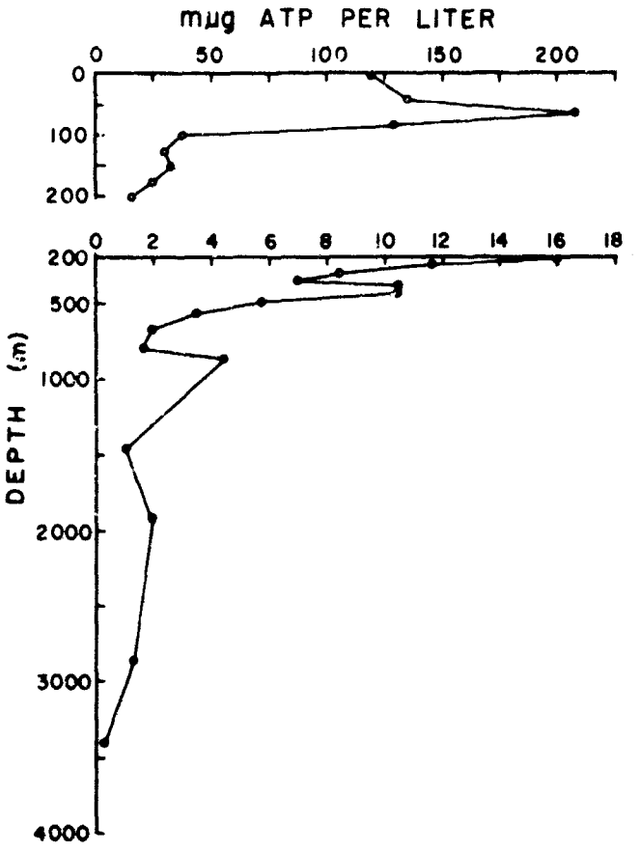

Figure 2. The distribution of adenosine triphosphate with depth in the eastern Pacific Ocean (31°45'N, 120°30'W). Note that different scales are used for the intervals 0 to 200 m and 200 to 3,500 m.

3. Sorokin (*personal communication*) has attempted to estimate the respiratory activity in deep water by determination of the rate of heterotrophic CO_2 uptake. His estimates of approximately 30 μl O_2/liter/yr are in the range of the above estimates.

From all these data, it appears that there is a deep-living microbial population that may be important as the first stage in deep-ocean food chains. To assess the food potential inherent in this microbial population, much more information is needed concerning the types of cells found in deep water, their distribution, and their metabolic turnover rates. With such information we may be able to conclude whether or not the rate of energy flow through this microbial population is sufficient to account for the observed concentrations of macrozooplankton and metazoans.

Biomass in the Euphotic Zone

Figure 3 shows a representative ocean profile of chlorophyll-*a* and phaeophytin-*a* concentrations as well as the biomass as estimated by ATP determination. In reference to our discussions this morning on the pigment concentrations at various depths, it is seen in Figure 3 that the chlorophyll-*a* concentration is low in the upper 50 m and reaches a maximum at 125 m. Phaeophytin was not detectable at the surface, reached its maximum concentration at about the same level as chlorophyll-*a*, and in deep water accounted for most of the pigments present. The depth

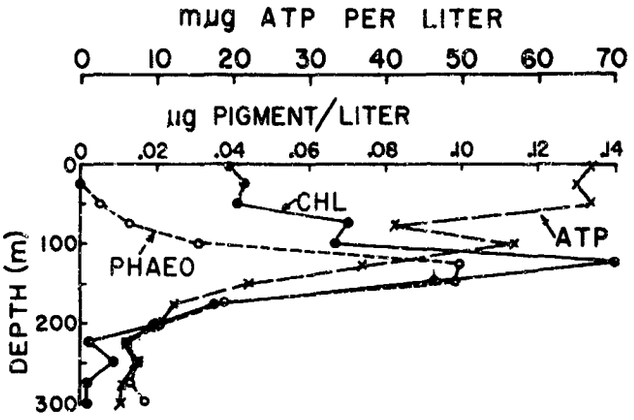

Figure 3. Profiles of chlorophyll, phaeophytin, and biomass as estimated by ATP in the Pacific Ocean (30°40'N, 120°02'W). Data from Holm-Hansen (1969).

of this chlorophyll maximum is deeper than usual, but there is almost always less chlorophyll in the surface waters than at depths between 10 to 50 m. Floristic analyses, in which the number and size of all recognizable cells are determined by microscopic examination, generally indicate a biomass directly proportional to the chlorophyll-*a* concentration (Holm-Hansen 1969). It is seen from Figure 3, however, that the biomass estimated by ATP measurements shows a maximum in the surface layers, with decreasing amounts deeper in the water column. This discrepancy between biomass as indicated by chlorophyll and ATP has been found in many profiles, both in marine and fresh-water environments. Studies on the rate of heterotrophic assimilation of C^{14}-labelled organic substrates also have indicated greatest metabolic activity in the surface waters. We do not know why there is such a discrepancy between phytoplankton biomass and biomass as indicated by ATP or activity measurements, but the most likely possibilities are as follows.

1. Phosphate and nitrate, the mineral elements most commonly found to be limiting for algal growth in natural waters, often are in very low or undetectable amounts in the upper portion of the euphotic zone, with increasing amounts with depth (Holm-Hansen, Strickland, and Williams, 1966). It is possible that phytoplankton abundance will be controlled to some extent by such nutrient availability. Thomas (1969) has described areas of the tropical Pacific Ocean where very low concentrations of fixed nitrogen seem to be limiting algal productivity.

2. Another alternative to explain the increasing amount of phytoplankton with depth is that the high light intensities in the upper portions of the euphotic zone are inhibitory. There is much laboratory data that indicate that many algal species are inhibited or killed by high light intensities, but how important this is for natural phytoplankton communities is not known. I do not think that high light intensities, *per se*, are the sole answer to this problem of phytoplankton distribution, but it is likely that the combination of nutrient availability coupled with light intensity may be controlling factors.

3. It is possible that the phytoplankton distribution does not reflect unfavorable growing conditions for the algal cells, but merely reflects differential grazing pressures. To demonstrate such a causal effect, however, demands much quantitative data for narrow depth intervals. At the present time we do not have the data available to indicate to what extent the phytoplankton biomass is controlled by the herbivorous zooplankton.

In regard to possible interactions between nutrient profiles, light intensity, and phytoplankton distribution, a series of chlorophyll profiles obtained off the coast of southern California is shown (Figure 4). This was during the late stages of a red water occurrence in which the dominant organism was the dinoflagellate *Ceratium furca*. Figure 4 shows that the chlorophyll-containing cells were mostly within the upper 2 m of the surface during the period of greatest illumination. With decreasing light intensities, the algal population migrated downward at a rate of 1 to 2 m/hr. Such a daily migration of dinoflagellates illustrates that for these species, at least, the high light intensities at the surface have no detectable deleterious effect on the cells. Such a daily migration up and down in the water column might have great survival value for motile algal cells, because it enables them to assimilate nutrients in the nutrient-rich deeper water and then to be exposed to high light intensities during the following day.

The fairly narrow layers of chlorophyll-containing cells seen in Figure 4 bring up the subject of the concentration of particulate matter in the oceans relative to zooplankton food requirements. Laboratory data (Paffenhöfer, 1970) indicate that various copepods require about 25 to 200 μg C/liter for good growth under simulated natural conditions. When such figures are compared to phytoplankton biomass as estimated from chlorophyll profiles in ocean water (Holm-Hansen, 1969; Lorenzen, 1966, 1967), it is obvious either that zooplankton in the sea can survive on algal concentrations much lower than that indicated by laboratory experiments or that our

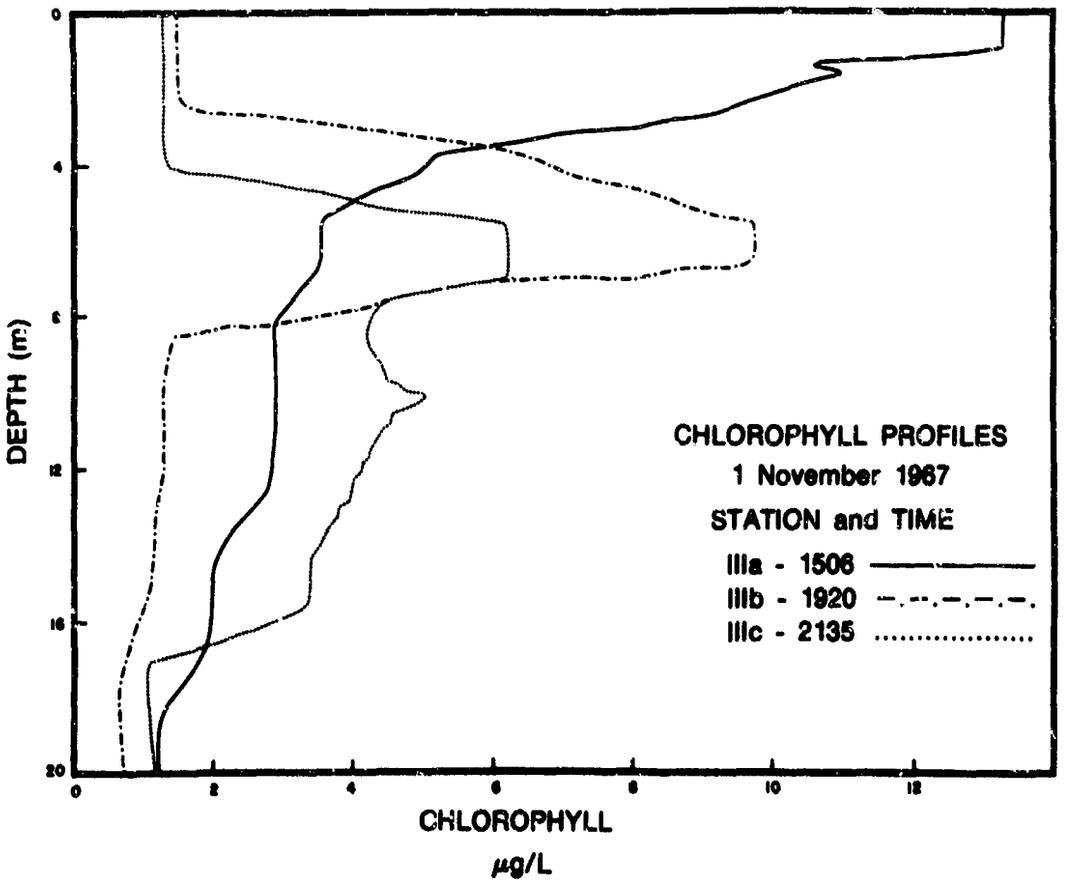

Figure 4. Changing profiles of chlorophyll distribution over a 6-hour period at one station off the coast of southern California (33°41′N, 118°07′W). Data from Eppley, Holm-Hansen, and Strickland (1968).

usual chlorophyll profiles are not detecting localized, higher concentrations of phytoplankton cells. With the use of the *in vivo* fluorometric determination of chlorophyll (Lorenzen, 1966), it is now possible to obtain continuous depth profiles for chlorophyll and thus to detect any significant amount of patchiness or layering of phytoplankton cells. Strickland (1968) has compared chlorophyll profiles obtained both by conventional bottle casts and by the continuous recording method and had demonstrated the likelihood of ecologically important layering of algal cells. Future work will be concerned with the relationship of such layers to the distribution of herbivorous microzooplankton and macrozooplankton. This aspect of studying the "fine structure" of the water column in regard to food sources is important not only for the euphotic zone inhabitants, but also for all the living animals in the aphotic zone.

ACKNOWLEDGMENTS

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DISCUSSION

Tuesday evening, 31 March 1970

Backus: In looking over Professor Clarke's shoulder at sea, I was always impressed by the nature of the trace the Sanborn recorder gave of bioluminescence at great depth. The impression that one gained from looking at this record was that the bioluminescence, at certain levels at least, was caused by a multitude of organisms, which suggests a multitude of microorganisms. So I would say that some of these organisms that Drs. Raymont and Holm-Hansen discussed are bioluminescent, if that helps in their identification.

Clarke, G.: I have two questions to ask Professor Raymont. I understand his reasoning in regard to a rain of fecal pellets not being very probable for providing nutriment for deeper levels, but I'm wondering why we have to look at it that way. Couldn't it be that there is a ladder of transfer of nutrient materials through the bodies, either living or dead, of a succession of migrating animals? Of those animals that started from the surface and went down 100 or 200 meters, some would die or would be captured by animals living between 200 and 300 meters. Some of the latter would serve as food for species migrating from 300 meters to greater depths, and so on down. Is there any reason why there couldn't be a chain of overlapping feeding migrations in that way without involving the fecal material at all? That's my first question. The other question is in regard to the nutrient aspect of the dissolved organic matter. I remember in the early days of the Woods Hole Oceanographic Institution several workers measured the dissolved organic matter and found that it was high, very uniform in all the lower levels of the ocean, and was highly resistant to attack by bacteria and other microorganisms. This suggested to them and to Dr. H. B. Bigelow, who was very astute with a common sense view of biological problems, that this dissolved organic matter could not be utilized very extensively if it remained uniform vertically and if it also was very resistant. What evidence is there that any of these microorganisms actually can and do use this dissolved organic matter for their own growth and hence as a part of a possible food chain deep in the water?

Raymont: I'll try to take the second question because I think at least I know a partial answer. As regards resistant material this comment is perfectly justified. There's work, for instance by Williams and his colleagues among many other people, which shows that a very large percentage of the very high amount (which Holm-Hansen was talking about) of the dissolved organic matter is very resistant material. But we have done a little work—not myself personally, but a biochemist on my staff—and there is certainly evidence accumulating from other laboratories suggesting that a small percentage of the dissolved organic fraction is what you might call in a reasonably labile state. If one wants some amplification of that remark: - I think that there are upwards of twenty amino acids which have been identified in sea water; there is a reasonable quantity of lipid material, (short and longer chain fatty acids) there are some carbohydrates (hexoses, pentoses and rhamnosides). It is these materials which I think one looks on as the substrates for bacterial action. Now I entirely agree that the amounts of these materials are of the order of micrograms carbon per litre, rather than the total amount of half a milligram carbon per litre which I think was the figure that Holm-Hansen suggested as a mean value. *(Holm-Hansen provided a table at this point for Raymont to use)* Table 1, Molecular Nature of the Dissolved Organic Matter in the Northeast Pacific Ocean (quantities in micrograms carbon per litre mean). The total organic carbon is one thousand microgram atoms per litre. The breakdown is: - amino acids 25μg-At./L., sugars (free) 10μg-At./L., fatty acids (free and combined) 40μg-At./L. and vitamins, 10^{-2} μg-At./L. (I've left out two of the smaller quantities). You can see that there is

a relatively small quantity of what I call the labile materials, and it is these that are the substrates for bacteria. I think that this sums up what I wanted to say.

Clarke, G.: Has anyone tried to grow anything on these sorts of materials at such concentrations?

Raymont: I'm speaking from memory now, but I think I must say "No". However, I think that Jannasch has shown in his experiments how you can get marine bacteria growing at much lower concentrations than we normally think of in laboratory cultures. In laboratory culture we think of big batch cultures with high densities of bacteria, but there would normally be one or two dominant species, probably succeeded then by other species. What Jannasch has been able to do is to grow a whole number of species together without an obvious dominance of one. These are then able to grow at much lower concentration of nutrients, though I admit not as low as those just quoted. Jannasch suggests that you get a much more balanced system, not perhaps an equilibrium, but somewhere approaching a dynamic equilibrium where a whole number of species is living at lower densities, and at much lower concentrations of nutrients. These concentrations might come somewhere near the sort of concentrations that we have in the open sea.

D'Aoust: The criteria for whether such material is utilizable is often based on bacteria that are not collected from deep down in the water column. It's known that there are some bacteria that can use raw petroleum, for that matter, albeit very slowly, but it's something to think about, and I think the point should be made.

Raymont: Yes, and I believe that in the case I was quoting, they were more or less near-surface bacteria.

Clarke, W.: In many observations while diving you see all this gelatinous and stringy material hanging in the water. I don't think that anyone has analyzed this material, but it might be proteinaceous or amino acids or what have you. All this material hanging in the water could act as a large surface area for bacterial growth, and it may be a scavenging surface for amino acids or other materials in the water and produce a focal point for these sorts of chemical reactions. When you put a plankton pump down in the ocean and you pump away, you're sort of integrating all of this. It may be that this detritus or snow that we commonly see is a focal point for this activity and an available food source which organisms can feed on. I must admit that I've never seen anything feeding on this material, but it certainly is abundant.

Marshall: One interesting aspect of dissolved organic material and the growth of organisms in the sea involves the Pogonophora, animals with no mouth, no anus, no gut. How, then, do they live? I think Dr. Little at Bristol has shown fairly well that they can live on amino-acids, so here is one group of organisms that lives on the deep-sea floor and probably depends on dissolved organic matter.

Raymont: I'm reminded that we have had a lot of papers from Stephens and his colleagues on the uptake of amino acids and similar compounds. The last paper I saw suggests that arthropods are apparently the least able invertebrates to take up dissolved organic matter from solution.

Clarke, W.: Leighton has been doing some work in sewer outfalls with sea urchin populations. I admit that this work isn't scattering layers or orientation, but these organisms are apparently able to take advantage of amino acids and other materials in the water when the natural kelp and algal supplies have disappeared. In the vicinity of the sewage outfalls they are apparently able to take advantage of this material that is in the water, somehow or other to take it up and incorporate it into their metabolisms. Admittedly echinoderms are not arthropods, but they are apparently very efficient in their metabolism.

Pearcy: Dr. Raymont, what is the evidence for small filter feeders in the detrital food chain of the deep ocean? If detritus or organic aggregates are the basis of the food chain, I would expect a trend toward small organisms with fine filtration mechanisms. However, deep euphausiids and copepods are often large and obviously carnivorous, with coarse feeding appendages.

Raymont: The evidence is against me here. The only thing I can plead is I think that until we do some direct experimentation it's dangerous to conclude from an examination of appendages what filter feeding organisms can feed on. I'd like to give an example though admittedly this is from the shallow sea: *Oithona* has mouth appendages which are coarse and which are well adapted for raptorial feeding; in other words, it is essentially a carnivore. As you probably well know, you can make *Oithona* filter; how it does I honestly don't know, but you can make it filter. Similarly, you can make *Centropages*, which is supposed to be an omnivore, filter almost entirely. All I'm suggesting is that if you can increase your particle size with aggregates fed on by a protozoan (perhaps a small ciliate), then you can get a form which may be more suitable as prey. I agree that I have no knowledge of this; what I'm offering is a model. Really what I'm pleading for is that in future investigations, somehow or other, one will use fine nets as well as the high-speed coarse nets and one will examine the really small plankton. At present, the sort of investigation that I was describing has been done down to about 200 or 300 metres. We need to do this in the deep sea, and it's going to be difficult.

Marshall: Some of the herbivorous copepods are able to seize individual diatoms. Why can't the deep sea ones seize an individual foraminiferan or a radiolarian or tintinnid? Are very fine filters necessary for this kind of existence? If *Calanus* can seize a diatom, why shouldn't the deep-living copepods seize their food, especially radiolarians?

Smith: We think that people are overestimating the amount of energy that is expended in the vertical migration. We think that some of the animals have to expend this amount of energy merely to clear the gill filaments and the small-scale viscous problems of this kind, and that the energy that is expended in vertical migration would be expended if they were to move 500 meters laterally. We have a paper (Vlymen, W. S., Limnology and Oceanography, Vol. 15, 348-356, 1970) out now which contends that vertical migration is quite free, almost extra expenditure. Do you have any reaction to this?

Raymont: No comment.

Holm-Hansen: In regard to the refractory nature of the dissolved organic matter in the ocean, Peter Williams at Scripps has done a lot of work regarding the age of the dissolved organic material and has come up with the age of approximately 3400 years for samples from 2000 m in the Pacific. This was estimated by determination of the natural radiocarbon activity of the dissolved organic carbon. Williams has also studied the $^{13}C/^{12}C$ ratios in the dissolved organic matter. His data indicate a uniform distribution of $\delta^{13}C$ with depth, which indicates that the dissolved organic material is very refractory; hence most of it would be unavailable for heterotrophic growth. One other thing in regard to the particulate matter: several investigators have collected the particulate matter by filtration and then used the *in situ* bacterial populations or have added bacterial populations to it and tested for the amount of material which can be degraded. Here again the evidence is that a very large proportion of it cannot be degraded by bacterial action.

Nafpaktitis: In my studies of midwater fish in general, and of lanternfish (family Myctophidae) in particular, I soon became interested in the extraordinary phenomenon of diel vertical migrations. I have always asked, as, no doubt, others have done, two main questions: *How*? and *Why*? By "how" I refer to the mechanism, or mechanisms, responsible for triggering these migrations;

and then, why do these creatures move up and down daily, what is the adaptive significance of this behavior.

By far the most difficult question to answer is and will for quite some time be the "why". It has repeatedly been proposed that "feeding" is the biological necessity underlying these vertical migrations. After having heard the excellent presentations by Drs. Raymont, Holm-Hansen, Kinzer and others during this symposium, I am less convinced today than ever before that "feeding" is the answer to the question. Among other things, this answer does not seem to explain the multiplicity of migratory patterns, some of which were discussed today by the participants to this symposium. Moreover, offered by itself, often emphatically, as *the* answer to the problem, it may discourage intensive search and study of other much more subtle, but equally as important biological factors underlying these vertical migrations. The thought that feeding in the upper, richer layer of the ocean may someday prove in many cases to be a matter of happy coincidence does no longer sound too far fetched.

While studying the various midwater fish my attention was drawn to an area in the frontal bone, on top of the head and between the eyes (Figure 1). In this area the bone is very thin (upper right in Figure 1), especially so in confirmed vertical migrators, with the overlying skin

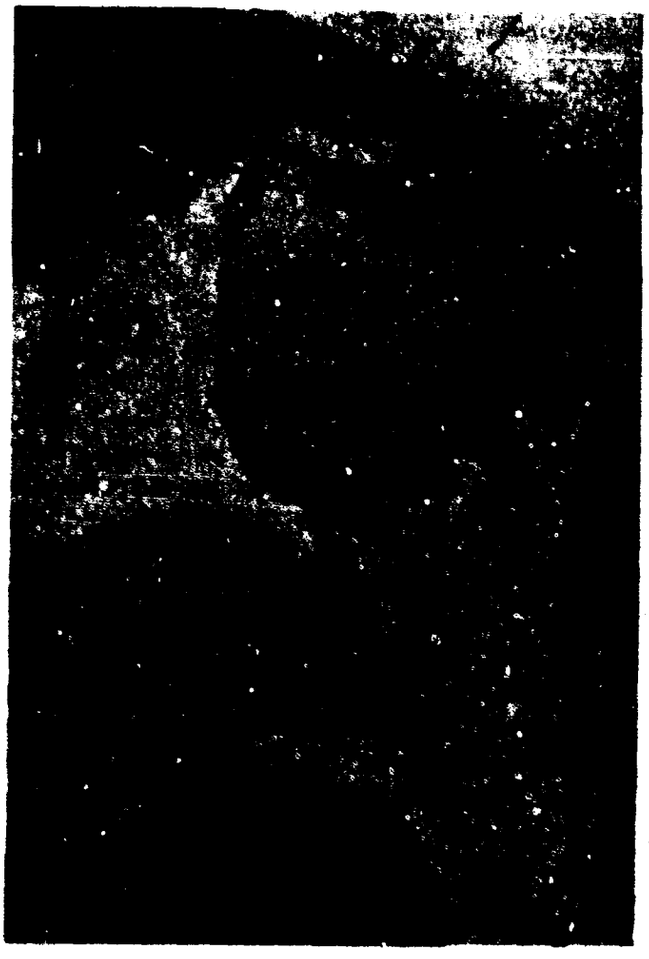

Figure 1. Photomicrograph: Sagittal section through the head of the lanternfish *Triphoturus mexicanus*

completely devoid of pigment. Beneath, and in contact with, the thin bone one may see the pineal organ. The apparent association between vertical migration and degree of development of the "pineal window" encouraged us to initiate a serious study of the pineal complex in midwater fishes and its possible implication as a photoreceptor and a "biological clock" triggering the migratory behavior.

It has been found that in the Western Fence Lizard, *Sceloporus occidentalis*, another diencephalic derivative, the parapineal, a structure analogous to the pineal of fish, plays a very important role in regulating the animal's exposure to solar radiation.

From the little work that has been done in deep-sea pineal structures (Holmgren, 1959) and from our preliminary histological studies there is reason to believe that the distal part of the pineal complex, the part which is in contact with the thin bone of the skull, includes at least two kinds of cells: secretory and supporting. Study of the ultrastructure, as well as biochemical and electro-physiological studies may reveal photoreceptors analogous to those found in the lateral eyes, and perhaps the presence of photosensitive pigments. At this time I can only say that the study of the pineal complex in midwater fish will prove very rewarding.

Cohen: Basil, you mentioned that the Western Fence Lizard, *Sceloporus*, has an analogous organ, and of course the tuatara does too. When we say it's analogous, we are talking about this structurally. What about functionally?

Nafpaktitis: They are analogous because their function is probably similar.

Cohen: But isn't that what we are talking about? There are not any lizards that are known to be diel migrators so far, are there? Why do they have these organs?

Nafpaktitis: No, but I may mention a recent study by people at Berkeley. First of all, let me clarify this analogy versus homology. In lizards the structure is called the parapineal or parietal organ. It is also a diencephalic derivative, but it is in front of the pineal which we find in fishes. So this is why I say the two structures are not homologous; they are analogous in that they probably have the same function. In *Sceloporus occidentalis*–the Western Fence Lizard–recent studies have shown that the organ includes cone-like structures with layers of membranes one on top of the other. Eakin, Stebbins and their associates at Berkeley have called this organ the "dosimeter of solar radiation". They have conducted field and laboratory studies in which they managed to derail the rhythmic behavior of lizards from which the parapineal had been surgically removed. In short, there is evidence that in lizards at least it is this structure that works as a "biological clock." The clock is there, and it's set by ambient phenomena, light, for example.

Marshall: Some myctophids migrate and some don't. Have you looked at the ones that don't migrate?

Nafpaktitis: Yes, primarily *Taaningichthys*. We're just beginning to study it. Externally the window does not seem to be as well developed as in shallower migratory forms. We have some *Lampadena* that do not migrate, and we have *Taaningichthys* that do not migrate. We also have the deep *Cyclothone*, the black ones, that don't seem to migrate, at least extensively. We're looking into them for comparative purposes. It is extremely well developed in those myctophids that live in the upper 400 meters, and we know definitely that they do migrate.

Holm-Hansen: I don't blame the lizards for being upset after cranial surgery like that. Why don't just put a black bandaid on top of their head?

Nafpaktitis: That has also been done, only instead of a bandaid they have used aluminum foil.

Holm-Hansen: What happened to the behavior?

Nafpaktitis: It was changed.

Clarke, W.: Are you stating then that you think that it's a light cue rather than a nutritional cue that's sending these organisms up and down?

Nafpaktitis: It's highly speculative, but I just venture the suggestion that it is.

Clarke, W.: I am being speculative, but I have seen other instances of lanternfish not making their migration. In other words, we passed the main body of them higher in the water column. They have migrated up, but there are still some sitting lethargically, as Eric Barham says, at depth not making their migration, so to speak. They're not with their light cue, and if we look at some of the invertebrates, euphausiid and sergestid shrimp in the Santa Barbara Channel migrate with light, but apparently for nutritional reasons since we find them with full guts when they get up to the surface. We also find that they miss cycles. In Saanich Inlet we found some euphausiids just sitting there at depth. The main body of euphausiids, at least from visual observations in a submersible, had migrated up to the surface. Here at daytime depths were some dormant euphausiids; apparently they had missed that diurnal cycle. To me this intuitively would spell a nutritional requirement rather than a light requirement.

Nafpaktitis: To expect clearcut cases in the ocean and in nature in general would be a little absurd. We're now getting to know more about digestion rates, metabolic rates, etc. Perhaps those that you saw staying behind had fed recently and were still digesting. And this, of course, may affect the nervous system, which is supposedly affected by the pineal organ which is affected by light. There is probably some complex feedback mechanism there.

Clarke, W.: Yes, and this behavior is quite striking, not only in the lanternfish and euphausiids but in the sergestids too. You will occasionally find them off base, so to speak. They're down; they don't make the migration. This turned up not only in visual observations from submersibles but also in some discrete depth plankton samples.

Nafpaktitis: That I know of, there's no evidence whatsoever that all the members of a species do migrate every day.

Clarke, W.: But you're still advocating a light stimulus or a nutritional stimulus or what?

Nafpaktitis: A light cue received by the pineal. That is the one that triggers when the animal is physiologically prepared to undergo migration.

Clarke, W.: But what would you say of the euphausiids and sergestids?

Nafpaktitis: I don't know.

Clarke, W.: They do migrate, apparently following an isolume. I am admittedly being sort of a devil's advocate.

Nafpaktitis: How deep are the ones, the euphausiids or sergestids, that do migrate to surface layers? What is the extent of migration?

Clarke, W.: We find sergestids right along with the lanternfish in the Santa Barbara Channel down to 400 or 500 meters.

Nafpaktitis: They do seem to migrate?

Clarke, W.: They're migrating with an isolume, at least on the basis of one year's work, which would seem to be just a slightly higher light level than that associated with the lanternfish, but there's a closer overlap between the lanternfish and the sergestid shrimp than there is between euphausiids and the sergestids. We have a layered cake here, but there's a lot more overlap between the sergestids and the lanternfish. This seemed to be the case in Saanich Inlet with the few sergestids and lanternfish that we saw there. And also in the Slope Waters, the sergestids and the lanternfish were more intimately associated than they were with euphausiids, but they were all making these migrations.

Nafpaktitis: I can't answer your question, but I would like to add that Dick Young, who is now in Hawaii, has been looking at the "VELERO" cephalopods, and entirely independently he came up with something similar. He is planning to study some light receptors in his cephalopods other than the eyes. I do not know any more details.

Roper: Dick Young is working with the parolfactory vesicles in cephalopods, particularly in the ones that migrate. Most of the enoploteuthids, for instance, are active migrators and have parolfactory vesicles; apparently the nonmigrators lack well-developed vesicles.

Nafpaktitis: He suspects that these may function as light receptors?

Roper: That's correct, but until recently he hasn't been able to do more than take a preliminary look.

D'Aoust: I think one good speculation deserves another, and there need be no either-or approach. None of us would go to dinner if we didn't see any food on the table, and it could be that the pineal apparatus, if it has a light role, simply neurologically indicates that it's time to eat. Now whether it's hungry is another matter. I don't see any contradiction in the fact that both nutritional and light cues can work, as you suggested.

Dunbar: Fascinated as I was by the second paper this morning, Dick, I wanted to ask a question about the first if Dr. Al Ebeling is here. Dr. Ebeling produced a scheme on a slide which I found very interesting indeed on the subject of the subdivision of an enormous oceanic ecosystem into units. This is a problem which has interested me for some time. I wanted to ask how he would define a pelagic marine ecosystem and, more than that, subdivide it into functional units.

Ebeling: I would define a pelagic oceanic ecosystem as the set of events that occur as oceanic organisms interact among themselves and with their environment. We defined functional units within the system, i.e., communities and ecological groups, by statistical analysis. The communities may interact through predator-prey relationships. For example, many of the larger fishes and shrimps in an "Inshore Fish Volume Community," which occupies the middepths of the Santa Barbara Channel, apparently eat smaller crusteceans in a "Shallow Invertebrate Community." Although the two communities may be more or less separated during the day, they integrate at night, especially near the surface when members are at the upper end of their diel vertical migration and are actively feeding. If the larger animals in the deeper communities are following the smaller animals in the shallower communities, what are the shallower, smaller animals doing? Some workers have suggested that they migrate to the food-rich surface waters to feed under the cover of night, then descend at daybreak to rest and hide in the dark and cool depths. All grazers, of course, are restricted to the euphotic zone near the surface. As suggested by Michel and Grandperrin, therefore, a "no-man's land" of transit may occur between two observed zones of maximum trawling success, one near the surface and the other near the bottom of the permanent thermocline. Our limited "ecosystem," of course, is defined relative to the

six-foot midwater trawl universe and to our limited series of environmental measures. But there is good evidence that seasonal and ontogenetic groups of animals occur within and about the stable communities whose members are abundant the year around. Therefore, the ecosystem is four-dimensional and fluctuates in both time and space.

Someone mentioned possible biological clocks and circadean rhythms with respect to diel vertical migration. One of my graduate students, Richard Ibara, has investigated such migrations of the midshipman fish, *Porichthys notatus*. Admittedly it's not a real deep-sea fish. It lives most of the year at depths of 100 meters or greater, buried in the sandy and muddy bottom during the day. It may ascend into the "Shallow Invertebrate Community" during the night and feeds mainly on small crustaceans like euphausiids and amphipods. It has a well-developed swimbladder, whose volume must be adjusted during the ascent. The interesting thing is that young individuals in laboratory aquaria become active periodically according to a diel cycle. They will uncover themselves, swim about or hover motionlessly, snap at live shrimp, then bury themselves again. But their circadean activities require entrainment by some sort of light-dark cycle, and they are out of phase under constant conditions of light or dark.

Clarke, W.: On this business of whether we can recognize a community *per se*, the fact that we can go in now and predict essentially what we will catch at a certain light level, I think, adds some credence to the fact that we do have something here that's material. In other words, we can select a particular isolume in the Santa Barbara Channel and, say, ninety-nine times out of a hundred predict what organism will dominate that particular catch on the basis of the light regime. Through my year's work we found out that the euphausiids are associated primarily with one isolume, sergestids with another, and lanternfish with another. And these layers maintain their integrity throughout the diurnal cycle even though, in the case of the euphausiids, the light regime they're following goes through the surface of the ocean at night and they cannot follow it. They can't swim any higher. But the sergestids and lanternfish layers maintain their integrity throughout this period whether it's a moonless night or not, so you can associate a certain predictability with this. You can turn the table around and say, "Okay, if I fish at this light level, I will find these organisms in association with one another, and they will dominate the catch." So I think again we have a reverse indication that these communities actually are existing here.

McCartney: I would like to ask whether anybody has any data on migrations during eclipses. That's the first point. The second point is concerned with hearing in swimbladder fish. I think that Dr. Marshall mentioned that there was no obvious connection between the swimbladder and the ears, and I don't believe that it is necessary that there be any obvious connection, as in the Weberian apparatus, for the swimbladder to affect the hearing or perhaps improve it at low frequencies. Related to that, perhaps I might ask Dr. Barham whether he feels that the motor noise from his submersibles was being sensed by the fish in addition to their response to the light. Further, does anybody feel that these deep sea fish are escaping the nets in the same way that fishes in shallow depths can sometimes hear the trawl nets coming along, especially bottom trawls?

Marshall: About the swimbladder and the hearing, there are some deep sea fish, deep sea cod, which have a connection between the swimbladder and the ears, a very close connection. It's true that there's not a close connection in the lanternfish, but the swimbladder could function as a hearing aid, although presumably not as well as in the deep sea cod. Actually, I think that Dr. Alexander would have some data on this. I think he worked out some properties of the swimbladder and hearing, however with a close connection, if I remember rightly.

Alexander: But it falls off very rapidly in the near field.

McCartney: Agreed. It falls off very rapidly in the near field, but the presence of the swimbladder means that the particle velocity at the ear at these low frequencies is many orders of magnitude greater than it would be if the swimbladder were not present.

Alexander: I don't think there's a possibility of more than about two orders of magnitude and that only when you have a close connection between the swimbladder and the ear. If the swimbladder is removed from the ear by a substantial distance, you get a falling off as the near field falls off around a source.

Barham: Subjectively, we get the feeling that there is a great deal of difference between different submersibles and the motors that drive them and the organisms' reactions to them. For example, the Cousteau saucer had a water propulsion system. It was driven by electric motors, that is true, but they were DC motors which are not highly efficient but worked beautifully. They couldn't go very fast but had a great deal of control. We had very good luck using this vehicle in the dives off Cabo San Lucas, where we took up a station and allowed a scattering layer to migrate by us. We just sat there and turned the lights off and on at one or two-minute intervals, and this worked out beautifully. We then worked with DEEP STAR. We thought we could play the same game, but it didn't turn out quite that neatly at all. DEEP STAR had DC-AC inverters on it, and we had a lot of trouble with them, as anybody associated with that program knows. It kept failing all the time. Eventually they got it whipped. At any rate, this leads off into another crazy theory which I shan't bore you with, but I do think that lots of organisms are extremely susceptible to electric signals, and whenever these damed inverters would turn on, they would create a whine. Whenever they would run through their various step gains on their motors, the switches would snap and pop, and things were different. There were times, particularly when we were working with Bill Batzler, when we were sitting at a certain level and pinging upward with the sound devices, that, expecting the scattering layer to come by us very neatly and nicely, we would turn on the lights, look at these things, and identify and count them. But we would hardly see anything, and then we would get the word from the surface: Everything is up, fellas. Come home, It's all over. And we'd start up, and we'd pass these things. They had already gotten by us somehow, and we hadn't seen them; they seemed to detour around us. Perhaps because they could see the glow from our lights every two minutes as they were moving upward, they took off in slightly different directions and we missed them. Another thing you have to bear in mind is that sometimes these populations that some of us feel are basically responsible for scattering layers can be very diffuse. There doesn't have to be a lot of them. It's very subtle. You can miss it very easily. You are obviously trying to get enough numbers to be convincing. If you don't get those numbers, you are left with something of an uncertainty. At other times things look very clear and very distinct. It all depends.

I would go back to another question now that I am here and direct this to the people who are studying communities in the California Current system. If you do not consider physonect siphonophores in your system, associated with *Euphausia pacifica* and *Sergestes similis* as a triumvirate, I think you are missing a bet. I beseech you to devise collecting methods to go out and take these things so that you can take a good look at them because they are there and they are a very dominant, important predator in this system.

Backus: I might say a word about the question relevant to the behavior of deep scattering layers during solar eclipses. We made some observations during the solar eclipse of July 20, 1963. The eclipse was on the order of 90 percent coverage of the sun at the location of the ship. The time of maximum occlusion was well into the afternoon, as I remember it. The scattering layer began

to behave as it would at sunset and then started back down. Then proper sunset came and it came on up. We wanted to do some fishing experiments during the recent solar eclipse, but the ship wasn't available and I considered it a bore to turn just the echosounder on again. But one of our ships was at sea where the maximum occlusion occurred closer to the middle of the day and was not so extensive as on the earlier occasion; the echosounder records weren't very good, but little or no response was indicated. Like most things, it is rather complicated.

Kaye: I think ONR asked for reports during the past eclipse, and I wonder if they received any results.

Holt: Nothing.

Farquhar: I would like to go back for just a moment to the discussion by Basil Nafpaktitis regarding the pineal complex. If this complex is to be of particular advantage to the animal as a light collector, then it seems to me that its optical properties ought to be better, perhaps, than the eye. I wonder if you looked at a comparison between the transmissivity of the pineal covering as opposed to the eye of the animal.

Nafpaktitis: As I said, we are just now beginning to go into the pineal. I do not belittle the importance of the eye. There is no doubt about it, but the pineal body might prove as important, if not more important, in terms of sensitivity.

Hansen: This would mean that the eye is an information gathering organ in terms of a visual image—you used the term light dosimeter. This would not be an image-making device but a summating device for triggering the migratory behavior. In vertical migration studies dating as far back as 1898, there is a recurrent theme stating that the sign of migration—in other words, the direction—is changed by a salinity change such that vertically migrating plankton would take off on a triggering light signal, quite probably going faster than the isolume, but would eventually cut off not to a light signal but to some physiological osmotic effect such as a salinity change near the surface. This problem I find very interesting because Bill Clarke explained the delay by saying that the isolume would go on through the surface. Obviously our organisms can't. So what do they do when the isolume trigger is stopped and they are all stuck up there at the surface? You then have to reverse the sign to move them back down again to reverse the behavior pattern. I wonder if anyone else has any thoughts on this.

Clarke, W.: What we usually noticed was that the light level would come up again, the sign would reverse, and the euphausiids would start moving down, essentially associated with the same isolume. Their migration was stopped because of an interface which they couldn't go through. In the case of the sergestids and lanternfish, that isolume never reached the surface. They would come to the apogee so to speak, in their migration but they would not start migrating down until the light level increased again. We made a series of oblique tows at these dark times well below their preferred light levels right up through the whole water column. They would not start downward migration again until light levels rose to a point at which the isolume they followed was being depressed again. Moore has stated in literature that a thermocline will often stop the migration in tropical waters. We never saw this happen in the Santa Barbara Channel.

Hersey: Were these inferred light levels or measured light levels?

Clarke, W.: We were using the six-foot Isaacs-Kidd midwater trawl with the GM-developed system, and the photometer was located in the spreader bar so that light measurements were being

made *in situ* at depth. We were also using a depth sensor that was telling us where the trawl was relative to light level and a temperature sensor telling us what the temperature was at that point. So all of these were being measured *in situ* at the time that the collections were being made.

Raymont: Could I just make a brief comment on that remark about reversal of sign with salinity? I seem to remember that Rose was one of the early workers who proposed salinity, among a lot of other factors, causing a reversal of sign. But I think that most of the work that's been tried out subsequently hasn't borne a great deal of fruit in this connection. I'm particularly reminded here of Harder's work in Germany where he had very sharp salinity gradients. He shows that a number of plankton animals actually collect above and below the salinity barriers. Some gather in gradients; others will go through a gradient and will then stay there. This doesn't sound as though you have a reversal of sign.

Hansen: You are perfectly right regarding Rose's work. However, Joan Lance in 1963 did find this effect of the reversal of sign. As far as Harder's work is concerned—why I'm bringing this up is that we're not going to have time to discuss one of the topics that I want to bring up in our paper which concerns pteropod vertical migrations as recorded on the depth sounder—we have an effect of accumulation of the pteropods on a pycnocline which gives a very, very hard scattering layer at about 50 meters, and one can see the pteropods come up in vertical migration, hit the pycnocline, and stick there. But the pycnocline scattering layer stays there day and night, and this will be at equinoctial times so that we have day and night in the Arctic. There's an effective segregation of the population at the pycnocline because at night you see a component come up to the pycnocline and the pycnocline-thick scattering layer thickens. A little later you see migration continuing up toward the surface. This then drops off a bit, responds at dawn, and comes back down. But the pycnocline scattering layer remains present at all times. Thus at all times we believe we have pteropods stuck on the pycnocline. In his examination of stratified water columns and accumulation of plankton under these conditions, Harder suggested that the detrital material had accumulated on density boundaries and that in fact we had a filter feeding response in the plankton under these conditions, which would be why they accumulate above and below. Unfortunately there doesn't seem to be very strong evidence in the open sea of detrital accumulations on interfaces as far as I know, and we certainly have no example of this in the Arctic. Even though we have a very strong pycnocline, there seems to be no detrital accumulation at least from the nephalometry. So I think that it is still an open question why one gets accumulations at interfaces other than those due to physiological constraints of osmotic effects, or density, perhaps.

Pieper: I don't really want to get into this in any great detail at the moment, but I hope to convince you on Thursday that we are watching the distribution of euphausiids with high frequency echosounders. Now if I can convince you of this fact, there are two things that you probably remember reading about Saanich Inlet where we are presently doing our work. One is that there is a very strong oxycline at around 100 meters during most periods of the year, and the oxycline is a parameter that we can measure, which limits the downward movement of euphausiids to around 90 to 100 meters. Why are they stopping here? Experiments that have been completed recently at the University of British Columbia indicate that it is not the low oxygen that is stopping the downward movement of the euphausiids from going right into the deeper waters; if you take surface water and in some way remove the oxygen, they can live in this kind of water. Similarly, if you take the bottom water from Saanich and oxygenate it, the euphausiids do not like it. Their respiration rates will increase drastically, and they will die. What I would like to suggest is that something like an oxycline or a pycnocline is probably more

of an indication of different water types, which is something that maybe the animals cannot adapt to or something that they do not wish to go into, and it is this that is stopping the movement rather than a density layer.

Barham: I want to mention a short piece of work of one of our people, I. E. Davies, on a cruise just outside of the Okhotsk Sea where there was a positive thermocline, an extremely strong one, with a layer of extremely cold water overlying warmer water. We had scatterers there that would come right up to this barrier but would not come through it; this was observed for about three or four nights. Davies assumed, and I agreed with him, that it was a thermal barrier that was stopping this migration. So it can be lots of things.

Holm-Hansen: I very much enjoyed Bill Hansen's comments about the reversal of sign and how to get things back down. I wish I had some answers, but I don't. I do have some complicating factors. In motile unicellular algae Halldal has lots of evidence for reversal of sign by the magnesium/calcium cation ratio. Changing this ratio, he can get them to go either toward or away from the light. In studies at Scripps in a 70,000 liter outdoor tank (ten meters deep and three meters wide) we also have evidence that nitrate-deficient dinoflagellates will not migrate. Throw in nitrate and they'll start migrating right to the bottom of the tank at night and on up to the surface in the daytime. It is obvious that migration is a complicated affair and is influenced by intracellular physiological conditions as well as by physical and chemical conditions of the milieu.

Alexander: Might I be allowed to do a little horizontal migrating toward that blackboard? I want to come back if I may to this problem that Dr. McCartney raised about the advantage or otherwise of getting a swimbladder nearer to an ear. I've just been thinking about the proportions of a fish. There's a fish. There's its swimbladder. There's its ear. This is a fish without any special connection between the swimbladder and the ear. If you start off at the center of gravity of the swimbladder, measure the distance to the ear—call it x, measure the distance from the center of gravity of the swimbladder to the surface of the swimbladder—that might be just about, taking a guess, 0.7x. If these proportions are right, then in fact the amplitude at the ear is only going to be a factor of 2 less than the amplitude at the surface of the swimbladder, and maybe these extensions of the swimbladder right to the ear aren't really being as helpful as they look.

Backus: Any comments on the proportions?

Marshall: I'd merely like to suggest an experiment. There are two kinds of mackerel; *Scomber* and *Pneumatophorus*, the latter with a swimbladder (*Pneumatophorus*), the other without. These fishes are extremely alike, and I'd like to suggest experiments on conditioning and hearing in these species of fishes. And they are fairly easy to keep.

RESONANT ACOUSTIC SCATTERING FROM GAS-BLADDER FISHES

W. E. Batzler and G. V. Pickwell
Naval Undersea Research and Development Center
San Diego, California

ABSTRACT

Live fish, their swimbladders, and rubber balloons the size and shapes of fish bladders have been used as targets in acoustic scattering measurements made in the frequency range 400 to 4,000 Hz. Our chief interest is the frequency of resonant response, the Q of that response, and the strength of the target. All fish were small compared with the acoustic wavelength. The balloon targets exhibited a fairly sharp resonant response with Q's as high as 20, corresponding to a target strength enhancement of about 32 dB. The resonance curves for the scattering from fish were broader; Q's in the range 3 to 5 were observed. Results obtained using a 10.6-cm anchovy as a target are typical: resonance frequency, 1,275 Hz; Q, 4.5; and target strength, −35 dB at 1 m. Results using the gas bladder as a target are: resonance frequency 1,250 Hz, Q, 21; target strength, −22 dB. With the bladders completely deflated the fish produced no measurable response. The values of resonance frequency determined acoustically were used to predict the volume of gas in the fish bladders by applying the theoretical expression relating the resonant frequency to the bladder size. These predictions show good agreement with the measured gas volumes. Comparison of the Q of the whole fish with that of its bladder gives an estimate of the damping effect of the fish tissue surrounding the bladder. Tests made in a sound-transparent pressure chamber clearly demonstrate the upward shift in resonance frequency expected with an increase in water depth.

INTRODUCTION

It seems well established at present that acoustic volume scattering, especially that associated with the stronger scattering layers of the deep ocean, is produced by resonant or near-resonant scattering from certain relatively small gas-bladder fishes and possibly by other organisms, such as siphonophores, which contain entrapped bubbles of gas. The work of Hersey, Backus, Chapman, Andreeva, and their associates in establishing this belief is well known (1,2,3). Net hauls and visual observations from deep submersibles tend to support this belief since gas-bladder fishes of appropriate size have been netted in the layers and have been sighted from submersibles passing through the layers (4,5,6). A comprehensive review and further development of the experimental and theoretical aspects of scattering from bladder fishes has been published recently by Weston (7). Thus a considerable body of information regarding this interesting phenomenon is available. As far as we know, however, there have been few if any tests of single fish to give further confirmation to this belief by determining the frequency of resonant scattering, the damping effect, and the target strength of these individual targets. This situation is understandable since the individual fish is a very poor target even when the expected 15- to 20-dB enhancement at resonance is present. Thus, for example, resonant scattering from a near-surface fish at 3 kHz requires a bladder of volume equal to that of a sphere having a diameter of only 3.5 mm. Assuming an enhancement of 18 dB, the target strength would be −43 dB. Measurement of this target by the usual methods is difficult if not impossible under the conditions imposed by low signal frequency, long pulse

lengths, and high background levels. A procedure for overcoming this difficulty was described in two recent papers (8,9). The present paper reviews the experimental procedure and test results of those papers and presents additional information concerning procedure, tests results, and comparison of these results with theory. All experimental data considered were obtained in the Transdec (10) calibration pool at the Naval Undersea R&D Center using live fish, fish bladders, and rubber balloons as targets.

EXPERIMENTAL PROCEDURE

The sketch in the upper-right corner of Figure 1 suggests the experimental procedure. The target—a balloon in this example—is placed in close proximity to a probe hydrophone. The J-11 source used provides a continuous signal varying in frequency over the range within which resonance is expected. A sample record showing the frequency response obtained with and without the balloon target is shown in the lower part of this figure. A sharp increase in pressure level is seen near 500 Hz. This is followed by a sharp decrease in level as the incident and scattered pressures interfere, reaching a minimum level at about 700 Hz. Small oscillations in the probe and the target response are principally a result of specular reflections from the water surface and reverberations in the pool. If the probe response alone (dotted curve) is subtracted from the target response much of this fluctuation is eliminated. The normalized curve that results is shown in Figure 2. In the form seen here the levels above and below the dotted reference line give a direct comparison between the measured and the incident pressure, here designated as p_m and p_i, respectively. Frequency response curves shown in later illustrations will also be given in this normalized form.

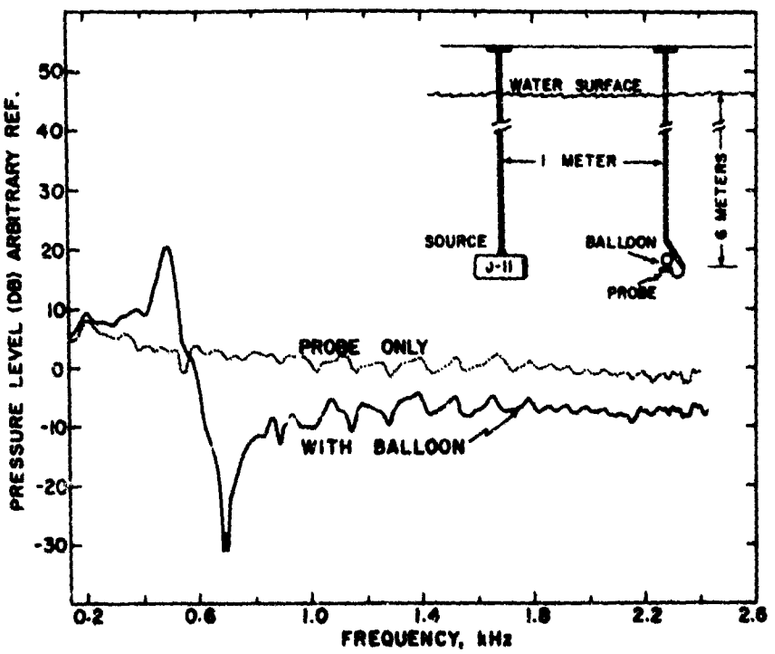

Figure 1. Experimental procedure and sample record of resonant scattering from an air-filled balloon

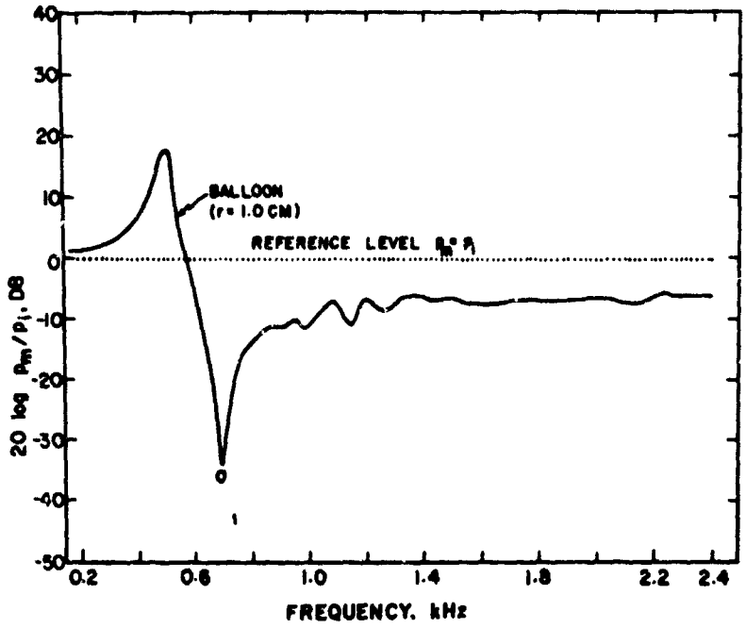

Figure 2. Normalized form of the frequency response of the acoustic scattering from an air-filled balloon

Simple theory for scattering from a spherical gas-filled cavity in water is expressed by the relation (11),

$$\frac{B}{A} = \frac{p_s}{p_i} = \frac{R}{\left(\frac{f_r^2}{f^2} - 1\right) + i\delta}$$

where

$B = p_s$ = scattered pressure at 1 cm from the center of the cavity

$A = p_i$ = incident pressure

R = radius of the gas cavity in centimeters

f = signal frequency in hertz

f_r = resonance frequency

$\delta = \frac{1}{Q}$ = damping constant

This relation is expressed diagramatically in Figure 3, where p_m is the measured sound pressure and, as before, p_i and p_s are the incident and scattered sound pressures. Assumption of this model provides a means of obtaining the scattered pressure level from the measured and incident levels. The procedure, stated briefly, is as follows: Peak measured pressure ratios such as that

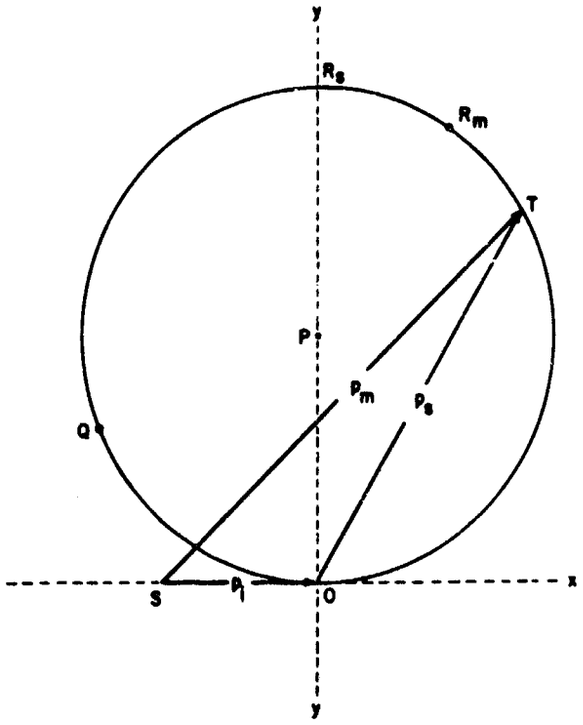

Figure 3. Circle diagram illustrating the relationship among incident, scattered and measured pressure with change in frequency

at about 500 Hz, Figure 2, determine the size of the circle corresponding to a given incident pressure, p_i. With this relation established, the magnitude and phase of the scattered pressure can be determined for any given value of p_m. The points R_m and R_s in Figure 3 show the positions where the pressures p_m and p_s are at maximum, respectively, and point T is any other arbitrary point on the circle.

TESTS RESULTS AND DISCUSSION

The responses of gas-bladder fish were, of course, the chief interest. In these tests a live fish was placed in close proximity to the probe hydrophone, replacing the balloon pictured earlier. The target fish was secured in a copper-screen pocket with the probe hydrophone close to the bladder position.

Figure 4 shows the frequency response curves obtained from two goldfish, one somewhat smaller than the other. Also shown in each case is the response of the bladder. The bladder was easily removed from the fish, usually without loss of gas. The bladder response shows an increase in the Q of the response and thus provides a measure of the damping caused by the fish tissue. In all cases the bladderless fish was also tested. No discernible deviations from the zero reference line resulted; that is, the presence of the bladderless fish was not detectable. Note also in this figure that the peak response for the smaller fish comes at a higher frequency, as is expected.

Figure 5 shows the response from a live anchovy 10.6 cm long and from its bladder. Again the bladder response shows a marked increase in Q over that for the fish. In the table (lower left, Fig. 5) are listed the resonance frequency, the Q, the target strength enhancement (12) over geometrical scattering—designated by E and obtained from $E = 10 \log (4Q^2)$—and the overall

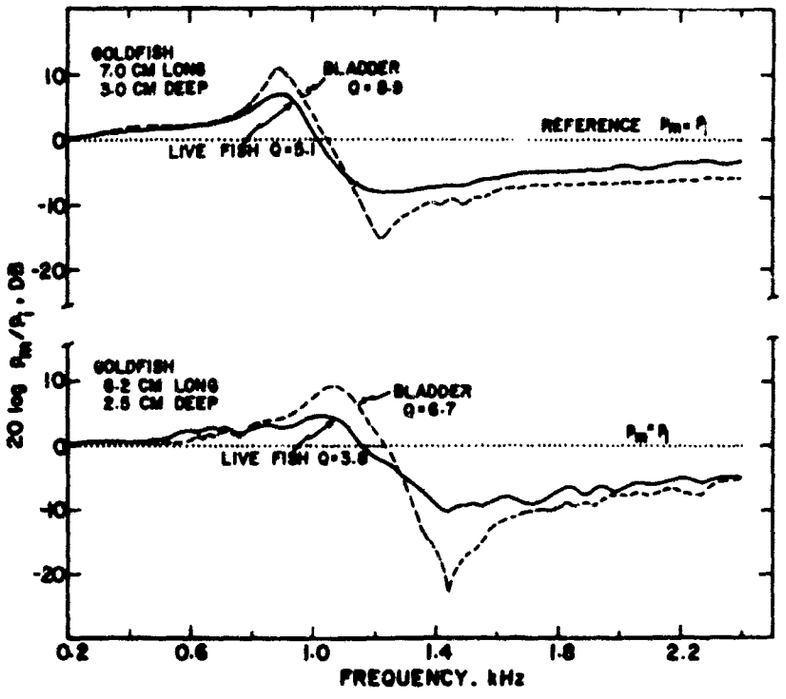

Figure 4. Frequency response of the acoustic scattering from two live goldfish and from their bladders

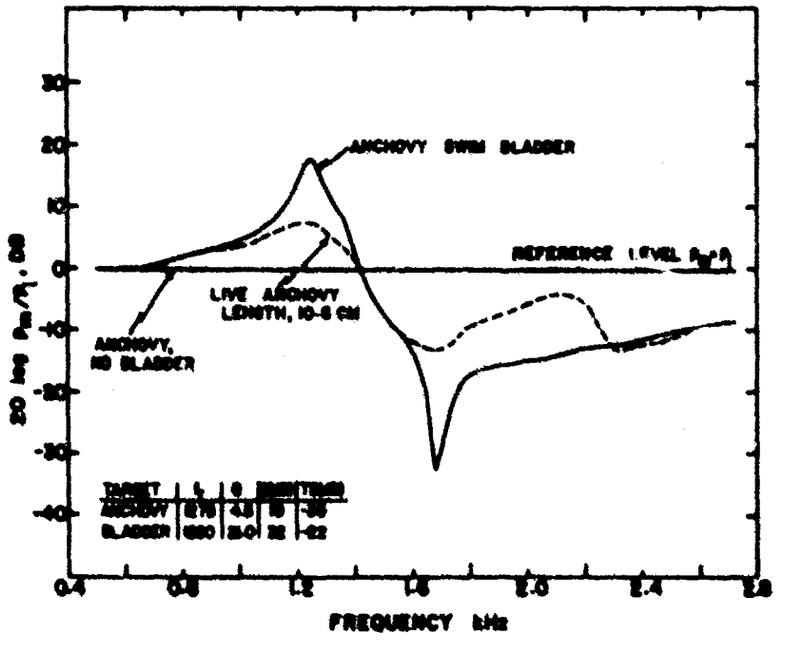

Figure 5. Frequency response of the acoustic scattering from a live anchovy and from its bladder

calculated target strength, for each target. The latter value is for a distance of 1 m. The geometrical scattering cross section used in this last calculation was that for a sphere having the same volume as the fish's bladder. Some error is expected here because all bladders tested were elongated and were usually bilobar in shape.

Let us consider for a moment the target strength of −35 dB estimated for this anchovy. Is this target strength consistent with the volume scattering strengths produced by a strong scattering layer? Assuming a volume scattering strength of −65 dB (that is, the average target strength of each cubic meter of insonified water) and assuming incoherent addition of the individual echoes, it is seen that the presence of only one fish of this size in each 1,000 m^3 of water would be sufficient to produce the relatively high assumed value of −65 dB.

While anchovy are not usually found at depths greater than 100 to 200m, gas-bladder fish of a similar size are observed in the deeper scattering layers. Anchovy, off California, are observed both in schools and as more widely dispersed individual fish. In schools they may be strong acoustic targets but the echo level varies with frequency and several other parameters; incoherent addition of individual target strengths is no longer valid (7).

The quality factors, Q, listed in Figure 5 can be used to estimate the damping effect of the fish tissue surrounding the bladder. Following Weston (7, p. 67).

$$Q^{-1} = Q_b^{-1} + Q_f^{-1}$$

where,

Q^{-1} = overall damping constant

$Q_b^{-1} = Q_r^{-1} + Q_t^{-1}$ = bladder damping constant

Q_f^{-1} = fish tissue damping

Q_r^{-1} = radiation damping

Q_t^{-1} = thermal damping

Substituting the tabulated values,

$$Q_f^{-1} = \frac{1}{4.5} - \frac{1}{21} = 0.185$$

$$Q_f = 5.4$$

The latter value compares favorably with that predicted from Andreeva's work (7, p. 71). Values of Q_f obtained in a similar manner for the two goldfish (Fig. 4) show poor agreement with the value predicted from Andreeva.

Frequency response curves of the type shown in Figures 4 and 5 were also made at other simulated water depths. These depths were simulated by the use of the sound transparent pressure chamber (13) seen in Figure 6. The probe hydrophone and target are placed in this chamber which is then closed and lowered to the usual test depth of 6 m. The pressure inside this chamber can be varied as desired up to a maximum of 600 psig. The probe hydrophone used at present limits the tests to depths equivalent to 200 psig. The fiberglass walls of the chamber are practically

Figure 6. Sound-transparent pressure chamber used in depth-simulating tests

transparent to the acoustic signals used in the tests. Thus essentially the same procedure already described was used in measuring the effect of pressure.

Figure 7 shows the results obtained when a rubber balloon of 1-cm radius (at atmospheric pressure) was used as a target in the pressure chamber. The vertical scale is magnified compared with that in previous response curves, increasing the apparent sharpness of the response. As expected from the theory, the resonance frequency increases as the pressure is increased from 0 to 200 psig, a simulated depth range of about 140 m. The increase in resonance frequency is a result of the pressure-induced decrease in radius as well as to the increase in ambient pressure.

With one exception, the level of the peak response seen in Figure 7 decreases with pressure. This may result from the decrease in balloon size with pressure and to an increase in damping factor with frequency, an effect known to exist in the case of air bubbles. Although the Q of the response varies somewhat in these tests all but two values are near 14. At a pressure of 200 psig the radius has decreased to about 4 mm, less than half its original size. The elastic properties of the balloon may be quite different after reduction to this size. Similar tests at constant volume over a wider range of pressures may help in resolving some of these questions.

The pressure effect using fish as targets was also tested. Figure 8 shows the frequency response curves obtained when a live goldfish, and then its bladder, were used as targets in the pressure chamber. It is seen that the peak response of the bladder occurs at a higher frequency than that for the fish. It is believed that some air was lost from the bladder in the dissection process. It is also possible that the fish was partially successful in maintaining the volume of its bladder when subjected to pressure. The latter possibility seems unlikely because little more than 15 min. elapsed between successive records. Biologically this is considered too short a

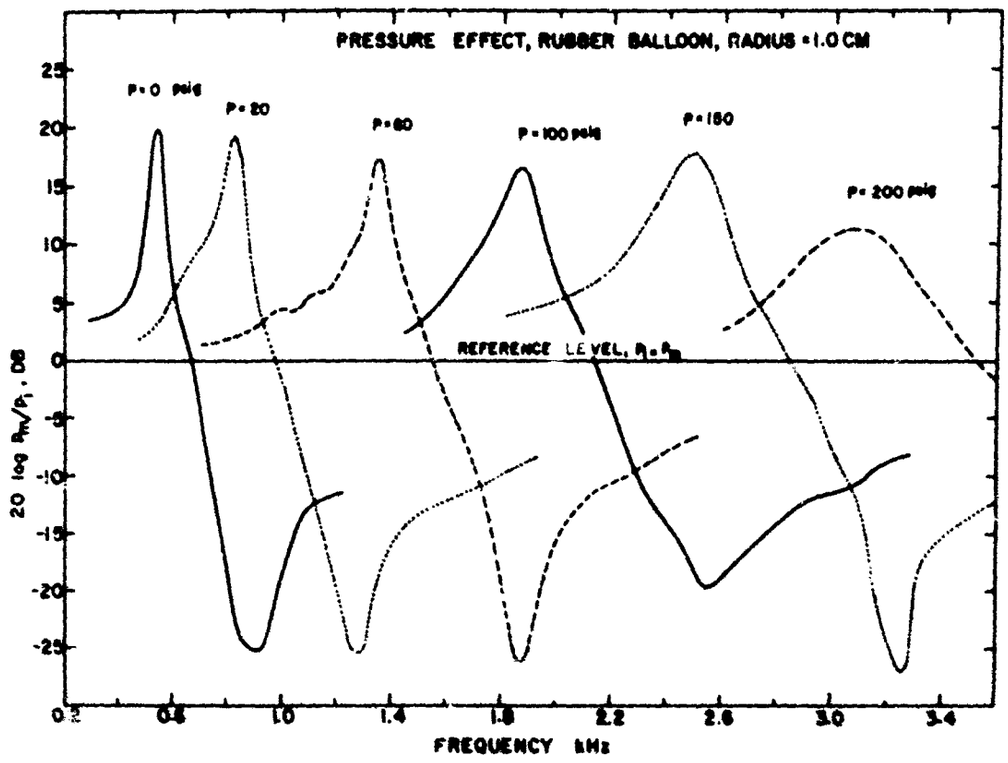

Figure 7. The variation in frequency response of the acoustic scattering from an air-filled balloon as the ambient water pressure is increased

time for an appreciable reaction by the fish. Furthermore, recent tests in which the chamber was held at a pressure of 150 psig for about 1 hour showed no change in resonance frequency for the goldfish target used. The quality factor, Q, for the bladder response (Fig. 8) is again in the range 5 to 10, similar to that for the other goldfish tested but considerably lower than that found for the anchovy bladder.

How well do our experimental results agree with those expected from theory? In particular can the volume of the fish bladder or the balloon be predicted from a measurement of the resonance frequency and vice versa? The graph in Figure 9 compares measured resonance frequencies (on the vertical scale) with those calculated from the relation derived by Andreeva (3) shown in the lower-right corner of this figure. As shown by the legend, upper left, a value of $\mu_1 = 10^6$ dynes/cm^2 was used for the fish and the bladders while a value of $\mu_1 = 0$ was used for the balloons. The agreement is seen to be quite good; all but 3 of the 26 cases fall within the ±150 Hz limits given by the dashed lines and 20 of the points are not more than ±100 Hz from perfect agreement. The reduction in size of the gas cavity because of pressure was included in the calculations. The term μ_1, which is the real part of the complex shear modulus of fish tissue, has a value, according to measurements by Lebedeva (14), somewhere in the range 10^5 to 10^7 dynes/cm^2. The present results indicate that 10^6 dynes/cm^2 is a better value of μ_1 than either 10^5 or 10^7. A value of 5×10^5 dynes/cm^2 may be an even better value. Gas volumes were not measured closer than ±0.1 cc and measurement of f_r is not precise at low values of Q. Improvement in the measurement techniques used may provide a more precise check on the appropriate value of μ_1.

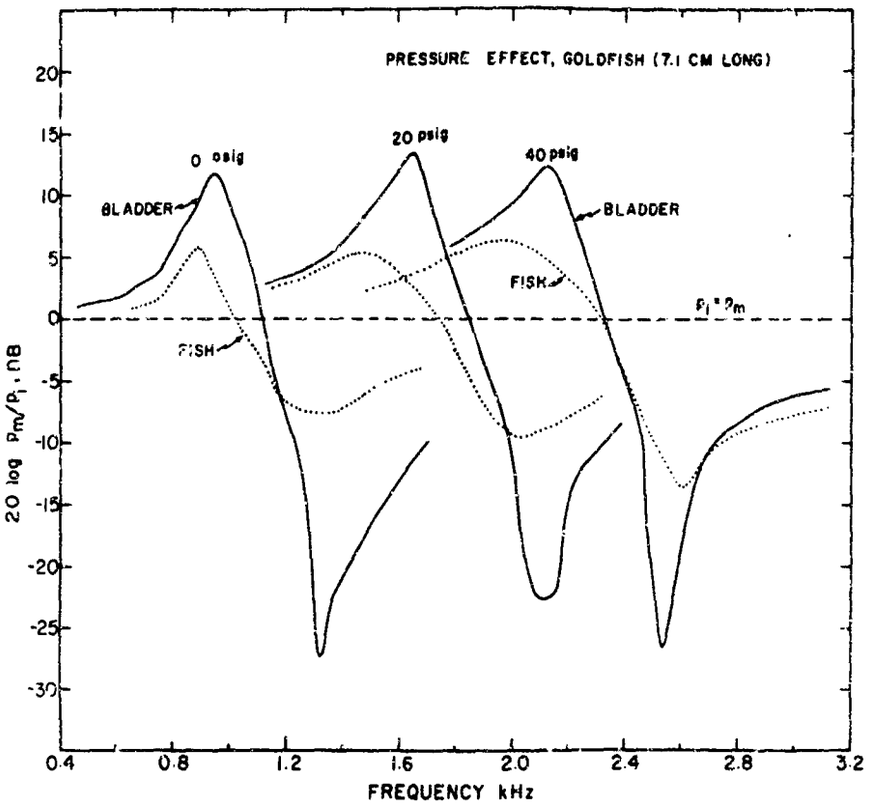

Figure 8. The variation in frequency response of the acoustic scattering from a goldfish and from its bladder as the ambient water pressure is increased

CONCLUSIONS

More accurate measurements, a more complete coverage of pressure effects, and the testing of additional species of fish, especially those inhabiting deep scattering layers, will increase the value of this study. Nevertheless, it is believed that the present effort has done much to clarify the major problems concerning resonant scattering from fish. The results obtained show, perhaps for the first time, that:

1. Resonant scattering with Q's in the range 3 to 5 may be expected from gas-bladder fishes.
2. Decrease in bladder volume or increase in water depth increases the resonance frequency of scattering from the fish.
3. Removal of the bladder eliminates the resonant response of the fish.
4. The volume of gas in the fish bladder can be predicted fairly closely from the resonance frequency and vice versa.
5. Comparison of the response of the fish with that of its bladder provides a means of estimating the damping effect of the fish tissue.
6. Small fish, even when thinly distributed, have a target strength at resonance high enough to account for even the highest observed scattering strengths.

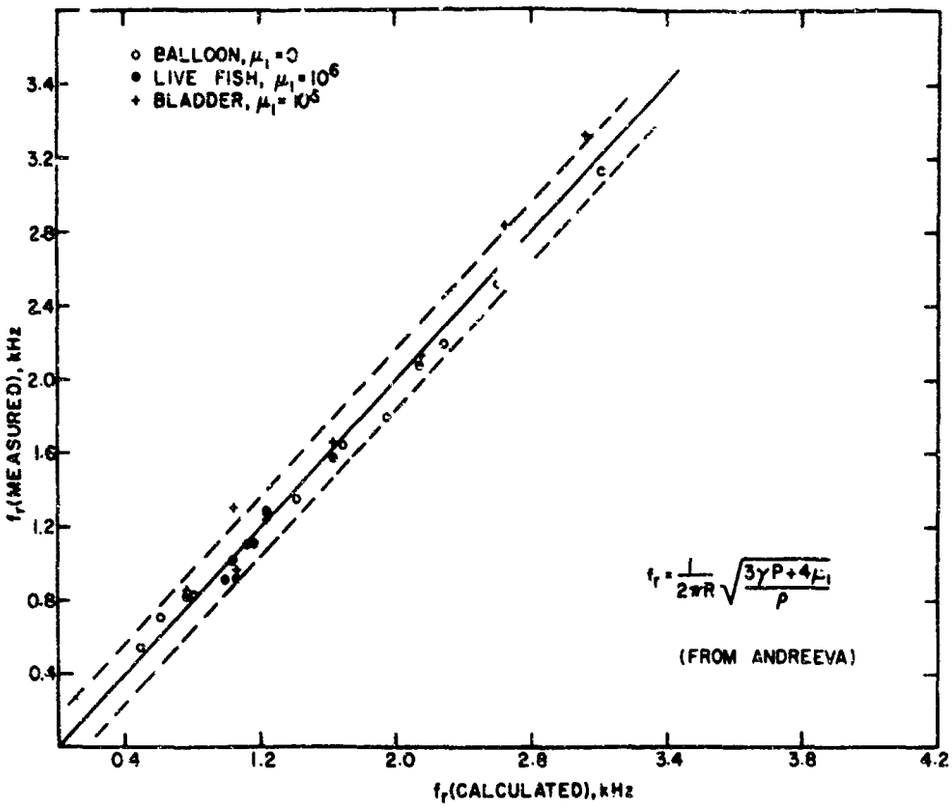

Figure 9. Comparison of the measured resonance frequency of acoustic scattering from air balloons, fish, and fish bladders with that calculated from the volume of the cavity

ACKNOWLEDGMENTS

We are indebted to John Hickman, John Roshon, Arthur Huntley, and Charles Green, all members of NURDC's Transducer Division, for help and advice during this study. Their Transdec facilities were indispensable in our tests. Our thanks also go to Mrs. Grace Wofford who prepared the illustrations and to Mrs. P. A. O'Neal (née Maria Regan) who formerly collaborated in this project.

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DISCUSSION

Van Schuyler: Do you have any plans in the future for working with smaller organisms and at higher frequencies than what you have presented here?

Batzler: No, I have none.

Schulkin: Not being a biologist, the question occurred to me whether the fish has air or oxygen in its bladder, and whether you filled its bladder with the same proportion of gas mixture.

Batzler: The bladder was not deflated. Dr. Pickwell removed the bladder intact, so its was not a matter of filling the bladder.

Schulkin: Did you pierce the bladder and investigate the gas content afterwards?

Pickwell: Actually, the goldfish swimbladder and the anchovy swimbladder have a percentage of oxygen somewhat exceeding air, usually approximately 30 percent. We did not exchange the gas in the swimbladder. We wanted to take the swimbladder out of the fish with the same volume that it had in the intact fish, so we never purposely deflated it. We did analyze the gas in a few situations in these comparatively surface-dwelling fishes. The percentage of oxygen is always very close to 30 percent. I should also emphasize the fact that in a few carp that we used, and in the goldfish, the bilobar, or dumbbell shape of the swimbladder, did not seem to have any effect on the final results. We measured the total volume of gas in the swimbladder even though the constriction between the two lobes was in fact rather pronounced. The volumes of gas we are dealing with, both in the anchovies and in the goldfish, are very comparable to the volumes of gas seen in hatchetfishes, particularly of the genus *Argyro pelecus*, which are characteristic of the nonmigratory scattering layers off San Diego.

Alexander: The goldfish belongs to the group of fish known as the Ostariophysii, which have a swimbladder that is pressurized and blown up to 1/2 to 1 psi above ambient pressure, and the swimbladder wall is made of rather inextensible material. It does not stretch nearly as easily as the swimbladder walls of most other species. I wonder to what extent this affected your results.

Batzler: No effect that I know of. I am sure that there is some effect there. You saw the limits in which we measured these, and although I perhaps belittled the ±150 Hz, I am sure there are effects that we have not measured. I can assure you that Dr. McCartney has looked at some of these things more closely, but I wonder if George Pickwell has a comment here.

Pickwell: Only that in the goldfish with which we dealt, the foreward lobe of the swimbladder is not very extensible, as you correctly stated. The after lobe tends to be, but in either case if the volume had increased, this would have shifted the resonant peak in the opposite direction from which we actually saw it move, if it deviated at all from what the resonance had been in the intact fish. In the case of the anchovy, again you are correct. The swimbladder is comparatively diaphanous and might be expected to stretch, but again, the frequency shifted in the wrong direction.

Alexander: I was wondering whether these swimbladder walls of very different properties led to any measurable differences in the values of Q for the isolated bladders of the two fishes.

Batzler: There certainly was a difference in Q between the bladder and the fish, but that is not quite your question.

Alexander: No, between the bladder of one fish and the bladder of another.

Batzler: Oh yes. This may be true. I really feel that we do not have a big enough statistical sample to be sure that this is generally true, but I see your point much better, and it is something to look for.

MEASUREMENTS OF THE TARGET STRENGTH OF FISH IN DORSAL ASPECT, INCLUDING SWIMBLADDER RESONANCE

B. S. McCartney and A. R. Stubbs
National Institute of Oceanography
Wormley, Godalming, Surrey, England

ABSTRACT

The need for measurements of the target strength of fish is discussed. The phenomenon of swimbladder resonance of deep-ocean fish is well known and is a useful means of estimating their sizes. For larger commercial fish in shallower seas, the resonant frequency is much lower and resonance is very difficult to observe in the field. A method of observing and measuring the swimbladder resonance of a captive live fish in controlled conditions is described and results on several gadoids are given. Reasons for the higher resonant frequencies than predicted are given, and the damping of resonance is high, which is expected. Application of these results to acoustic sizing at sea appears remote. The experimental technique is offered as a useful tool in physiological studies involving swimbladder function.

Measurements at higher frequencies in the diffraction and geometrical regions are also presented, resulting in an empirical equation for target strength as a function of length of the fish and wavelength. It is believed that this equation is useful for acoustic fish sizing with the use of echo sounders at sea. The swimbladder is the major scatterer over the whole frequency range.

TARGET-STRENGTH PROBLEM AND PREVIOUS WORK

When sound energy is incident on a fish, some energy is dissipated by absorption and the rest is scattered in all directions. The proportion of re-radiated to incident intensity is dependent upon frequency, the incident and reflected angles, and the dimensions and mechanical properties of the fish structures. The number, complexity of shape, and relative motion of these structures in a living fish make it impossible to calculate completely the scattered field; even to estimate it with much confidence is difficult because the acoustic impedances of the various parts are uncertain and difficult to measure. Experimental determinations of target strength are thus essential. Over most of the useful spectrum, little more than an order-of-magnitude agreement with the scattering calculated from simple geometrically shaped models can be expected.

Fortunately, the number of parameters can be reduced to make a worthwhile practical investigation manageable. First, it is the back-scattered echo level that is invariably of interest, and re-radiation in other directions need not be measured. Second, echo sounders detect fish principally at or near dorsal aspect, and here we concentrate on this aspect though this emphasis does not deny the need for measurements in azimuth at low elevations for forward search and scanning sonar applications. Third, measurements by Haslett (1962b) on whiting *Merlangius merlangus* (L.), showed that the dimensions of the acoustically important components of this species can be scaled as proportions of the fish length L, leading to the useful idea (Haslett,

1965) that the plot of acoustic backscattering cross-section σ, normalized by L^2, versus L/λ (fish length/wavelength) should be the same for all whiting; in practice, this idea means that the range of frequencies covered with each fish size, or vice versa, can be reduced. Caution is required when absorption losses become significant, because these losses may not scale. Though many fish of other species have similar proportions to whiting, there are also some significant differences, even within the gadoid family, particularly in the shape of the swimbladder.

The results of target-strength measurements on *dead* fish in dorsal aspect by six authors were plotted by Haslett in the normalized manner in Figure 1, taken from Figure 3 of Haslett (1965), covering mainly the range $4 < L/\lambda < 20$, with some results down to $L/\lambda = 2$ and up to $L/\lambda = 60$. The main feature of this summary is the wide scatter, the extreme example being a factor of 5×10^3 between two results differing by only 20% in L/λ. This result cannot be explained by selective absorption or resonance phenomenon but rather indicates that scattering components from two or more parts of the fish are interfering, causing large variations in re-radiation, either at a fixed aspect as frequency is varied or at a fixed frequency as aspect is varied. Variability in σ/L^2 tends to be worse at higher values of L/λ, as each scattering component becomes more directional. Maximum values of σ/L^2 increase with L/λ, which is another indication of directivity. Values of σ/L^2 for smaller fish at high frequencies tend to be lower than the values of σ/L^2 from larger fish at lower frequencies having the same value of L/λ; this finding might indicate that increased absorption losses at the higher frequencies are becoming significant, in which case the sound may not be penetrating the fish flesh to reach other major scatterers, such as the swimbladder and the backbone; alternatively, different experimental conditions make absolute comparisons difficult.

NEED FOR TARGET-STRENGTH DATA

It would be desirable for acoustic systems to obtain information on the presence, position, quantity, size, and species of fish in the sea. A knowledge of the acoustic backscattering cross-section area of fish is required:

1. For the detectability specification of fishing sonars and echo sounders.
2. For the size determinations necessary for stock estimation.
3. For classification of species by their echo properties.

Detectability

From Figure 1, for sounders operating within $4 < L/\lambda < 20$, the minimum detectable target to aim for at maximum range may be specified as $\sigma = 10^{-4}L^2$, though to achieve $\sigma = 10^{-3}L^2$ would be worthwhile.

Sizing

Cushing (1968) has obtained a statistical estimate of fish population by converting target strengths observed at sea at a fixed frequency into the corresponding distribution of fish sizes. For this purpose, the most convenient form of representing the data is an empirical equation relating target strength T to L and λ; T is defined by

$$T = 10 \log_{10} (\sigma/4\pi). \quad (1)$$

This representation has been done in the section on Measurements at Higher Frequencies with our own data and that from Figure 1, in a manner similar to that used by Love (1969) for the maximum side-aspect target strength.

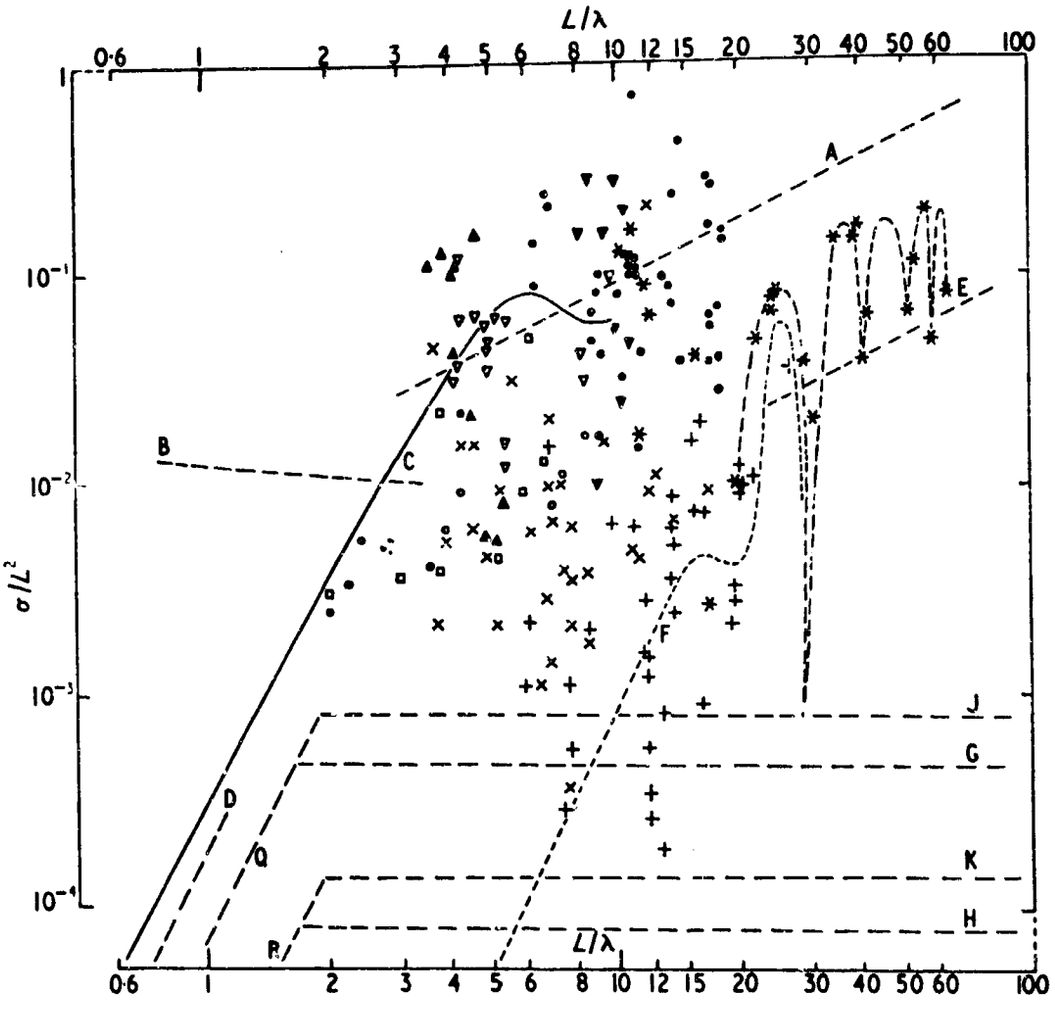

Figure 1. Normalized backscattering cross section σ/L^2 of fish in dorsal aspect. Results from six observers, taken from Figure 3 of Haslett, 1965.

It is now widely accepted (Andreeva, 1964; Chapman and Marshall, 1966; Hersey and Backus, 1954; Weston, 1967) that the peaks in the volume scattering coefficient spectra of many sonic scattering layers in the deep ocean result from the resonances of fish swimbladders. Because the resonant frequency is a function of the swimbladder volume and this volume in turn is directly related to the size of the fish, measurement of the resonant frequency is an attractive direct method of fish sizing, being independent of equipment gain levels and fish aspect.

Resonance occurs because, like a gas bubble, the swimbladder is a compliance whose acoustic loading at long wavelengths is predominantly the inertia of the surrounding water. For a bubble of radius a, the resonant frequency f_0 is given by Minnaert's formula (Weston, 1967).

$$f_0 = \frac{1}{2\pi a}\sqrt{\frac{3\gamma P}{\rho}} \tag{2}$$

where γ is the ratio of specific heats for the gas, P is the absolute static pressure, and ρ is the water density.

For deep scattering layers between 100- and 1000-m depth, resonant frequencies occur between 3 and 20 kHz (Andreeva, 1964) and it is estimated that the fish responsible are between 10 and 1 cm in length. If the sizes of such small fish can be estimated at 1000-m depth, it seems reasonable to enquire whether the sizes of larger fish of commercial interest found at the shallower shelf depths may also be determined acoustically. For fish of length between 1 m and 10 cm, resonant frequencies are expected to fall in the range 100 Hz to 1 kHz. After some experiments (McCartney, 1967; McCartney, Stubbs, and Tucker, 1965) with wide-band sources on fish shoals located at sea, it was realized that not enough was known about the effects of acoustic interaction between fish within the shoal, so that the aggregated scattering from the shoal did not necessarily have the same spectral form as did that from a single fish; and this form itself was insufficiently well known. This situation contrasts with the case of the deep scattering layers, in which the packing density is too small for interaction to be troublesome, and where at long wavelengths, the individual scatterer may be represented fairly well by a moderately damped, spherical gas bubble. In the following sections on swimbladder resonance measurements, we have determined experimentally, for single *live* fish in controlled conditions, the relationship between length, depth, and resonant frequency and the damping of resonance. It should be noted that the work complements theoretical studies by Weston (1967) and Andreeva (1964), who predict large damping for resonance at shallow depths.

Classification

The echo sounder has been used by the fishing industry for 30 years to detect fish, and reports (Balls, 1947; Hodgson, 1950) of fishermen able to identify successfully many of the echo traces are too numerous to be dismissed. In addition to their echo sounder information, the fishermen are undoubtedly using local knowledge of the grounds and past experience of catches. It is not easy to assess the relative contributions of the acoustic data and fishing knowledge to classification. The need to spend perhaps 10 months each year on commercial fishing vessels extracting subjective information from busy skippers without getting in the way is a daunting prospect. It is therefore not too surprising that there does not appear to have been any scientific investigation of these abilities, possibly leading to changes of echo-sounder design for improved classification.

The few attempts (Berktay, Dunn, and Gazey, 1968; La Fond, 1965; Tucker and Barnickle, 1969) to create acoustic classification systems have employed wide bandwidths to obtain echo spectra expected to be characteristic of the target, but results with these are too sparse to be assessed at the present time.

SWIMBLADDER RESONANCE EXPERIMENTS

The conventional method of measuring target strength is to transmit a pulse, several cycles long and of known intensity, and to measure the range and amplitude of the returned echo, which is separated in time from the transmission pulse. When this procedure is attempted with small scatterers at very low frequencies, difficulties arise because the pulse, being several cycles long and therefore several wavelengths long, is still being transmitted when the received echo is returned, unless the fish is at a great range. In the latter case, the signal level may be so low that detection is poor against the background noise, which usually is high at low frequencies. A short, impulsive wideband source would be attractive, allowing determination of the spectral response in one pulse, but all sufficiently energetic sources available to date in this frequency band have rather large, long, and unreliable tails, so that the same objection as for the monofrequency pulse applies.

Objects smaller than a wavelength may be considered to consist of connected lumped parameters such as masses, compliances, and loss resistances; and if the complex mechanical impedance of an object is known, then the target strength at low frequencies can in principle be estimated. Several techniques (Hund and Kuttruff, 1962) using enclosed volumes or tubes are available for the measurement of complex acoustic compliance, but the technique we have adopted is a free-field method in which corrections for a chamber are not required and so that plane incident waves can be used.

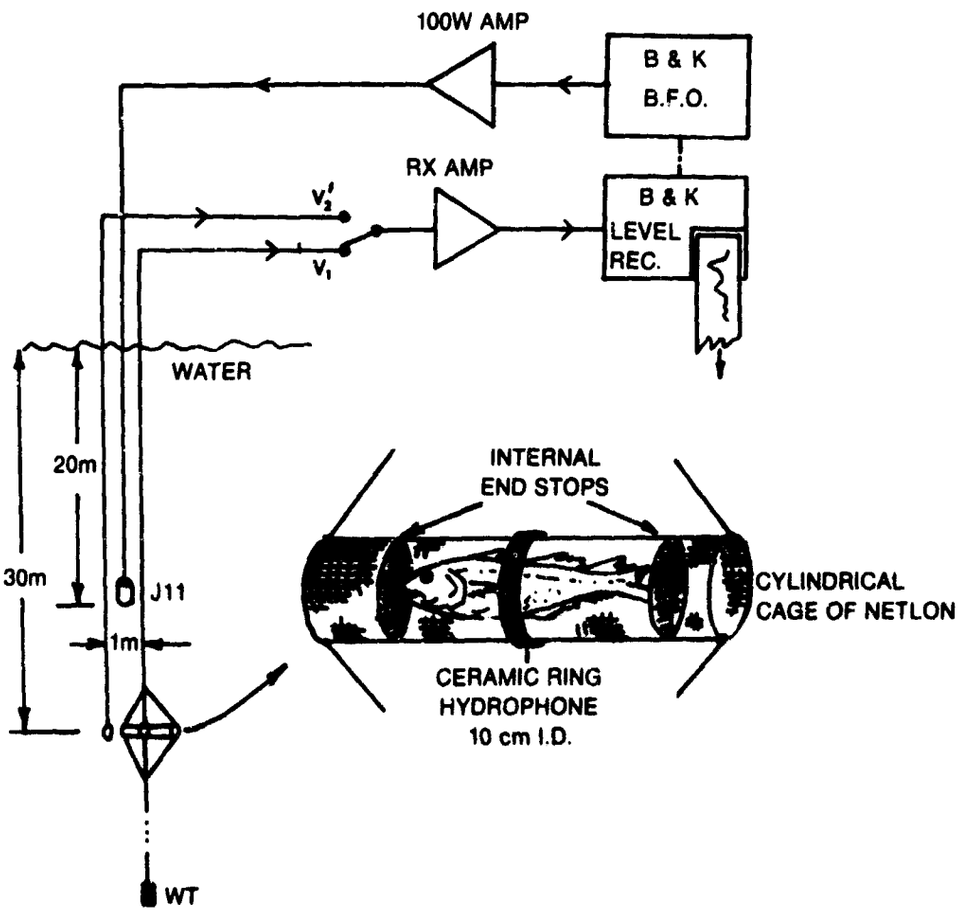

Figure 2. C.W. experiment from F.R.S. *Mara*, moored in Loch Torridon

The method shown in Figure 2 was employed from F.R.S. *Mara*, moored in Loch Torridon and operating as nearly as possible as a "silent" ship. The basic principle is to measure the acoustic waveform at some distance from a wideband sound source with a hydrophone close by the fish and then to repeat the measurement after removing the fish. After considerable difficulty with the technique in 1967, with the use of pulses from a pneumatic sound source and with omnidirectional spherical hydrophones, a more successful arrangement was found in 1968 with a CW source (a J11 underwater loudspeaker) and with a ceramic ring hydrophone 10 cm in diameter, inside which the fish is centrally placed. The signal from a B.F.O., sweeping from 20 Hz to 20 kHz, is amplified and fed to the loudspeaker. The amplitude of the received hydrophone signal $|v|$ is recorded on an ink-pen recorder whose paper drive is synchronized mechanically to the

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B.F.O. The second ring hydrophone, 1 m away, is used to monitor the source level transmitted, while the output of the first is recorded with and without a fish present in the cage. This cage, made from moulded plastic mesh Netlon, was found to be better than a polythene bag, used in some of the earlier experiments; the fish could be inserted easily into the cage and its movement could be restricted, yet water could flow to allow respiration, and it did not trap air bubbles. The acoustic interference from the cage was negligible below 5 kHz. By definition,

$$\sigma = \frac{4\pi R^2 \overline{p_s^2}}{\overline{p_i^2}} \tag{3}$$

where p_s is the scattered pressure at a distance R from the fish and p_i is the pressure incident on the fish. With the geometry of this experiment, $R = 5$ cm, p_i is a plane wave incident "edge on" to the ring hydrophone, with sensitivity S_p, while p_s is a wave spreading spherically from the centre of the ring, whose sensitivity in this case is S_s; the relationship between S_p and S_s is frequency dependent in the band of interest (Appendix 1 and Fig. 16). Using subscript 1 when the fish is present and 2 when absent, we have the hydrophone voltages

$$v_1 = S_p \cdot p_i + S_s \cdot p_s \tag{4}$$

$$v_2 = S_p \cdot p_i \,. \tag{5}$$

Combining (3), (4), and (5),

$$\sigma = 4\pi R^2 \left(\frac{S_p}{S_s}\right)^2 \frac{\overline{(v_1 - v_2)^2}}{\overline{v_2^2}} \,. \tag{6}$$

v_1 and v_2 are both vectors, but because they are not available simultaneously, subtraction is impossible from records of $|v_1|$ and $|v_2|$ unless phase differences are known. One possibility is to assume that the monitor hydrophone voltage approximates v_2, because it is some way from the scatterer, and then use a phase meter at fixed frequencies sequentially. This method was employed once, but a more convenient method is available because $S_s \gg S_p$ and hence, particularly around resonance, $|v_1| \gg |v_2|$, so that regardless of phase, $\overline{(v_1 - v_2)^2} \simeq \overline{(v_1)^2}$, and we can write, from (1) and (6),

$$T \simeq 20 \log_{10}\left(\frac{R S_p}{S_s}\right) + 20 \log_{10}\left|\frac{v_1}{v_2}\right| . \tag{7}$$

The second term is obtained directly from the level recordings and the first is a calibration factor. In practice, a reasonable approximation results if $20 \log_{10} |v_1/v_2|$ exceeds 10 dB. Then the phase angles are such that below resonance, T is overestimated by less than 1.8 dB; at resonance, T is overestimated by less than 0.4 dB; and above resonance, T is underestimated by less than 1.3 dB. Most of the results here are uncalibrated plots, but they do give resonant frequency and damping with acceptable error in most cases. Calibrated plots are included in the summary, Figure 11, for three fish.

Cod, *Gadus morhua* (L.), ling, *Molva molva* (L.); pollack, *Pollachius pollachius* (L.); and coalfish (or saithe), *Pollachius virens* (L.) were caught on hand lines and then either brought to the surface or removed from the hook at depth by divers and placed directly into the keep cage at 30 m. The latter method is the more satisfactory because there is a much reduced chance of damage to the swimbladder. At the end of the experiment, three fish were brought to the surface, killed, measured, and the swimbladder was examined; two fish were dissected in situ at 30 m, three fish escaped during handling, and one was kept alive indefinitely. An experiment with herring, *Clupea harengus* (L.), caught in a drift net failed because of the poor condition of the fish, which died during the experiment.

RESULTS OF RESONANCE MEASUREMENTS

The results for three cod, plotting 20 log $|v_1/v_2|$ versus frequency, are shown in Figure 3. The main feature of these results, in which resonance is clearly demonstrated, is that the 35-cm cod has a lower resonance than does the 32-cm cod but that the resonance of the 39-cm cod, which would be expected to be even lower, fell in between the two; this fish was later found to have a ruptured swimbladder, which fact might explain the greater losses and the higher resonance because of lost gas.

Figure 4 shows how the resonant frequency of the 32-cm cod increased by 50% with time, reaching a stable value (which was then held overnight), and shows the corresponding estimated change in swimbladder volume estimated from Equation 2. This change could result from slow loss of gas from a ruptured bladder or, more speculatively, perhaps could have occurred because the fish was absorbing oxygen from its swimbladder during the period up to 19.00 hours, after which the residual gas was mainly nitrogen. This experiment was one of the earliest made with a polythene bag pierced by several small holes, which may have been insufficient to allow adequate water flow for respiration. The estimate of volume is not too accurate because of uncertainties about the effects of tissue elasticity and shape, discussed further below.

The results of Figure 5 were obtained from the largest fish used, which was a 55-cm ling, and show the resonance at 500 Hz with, in this case, a small decrease in frequency overnight.

The results for a 35-cm pollack (Fig. 6) shows an increase in resonant frequency and in Q, or decrease in damping, as the fish is placed deeper. A further, large increase in Q is shown after the fish is killed in situ and the gut below the swimbladder is removed, leaving the swimbladder intact. Because the Q doubled when the gut was removed, it follows that half the damping previously resulted from the viscous losses within the gut. The accuracy in resonant frequency is not good enough to imply reduced mass loading on the swimbladder when the gut is replaced by the less dense water.

The results in Figure 7, for saithe or coalfish, again indicate increased damping when the swimbladder is burst, and a slightly higher resonant frequency. When the fish with an intact swimbladder is raised from 30 to 20 m and then to 10 m quickly enough to prevent gas resorption at the new static pressures, the resonant frequency drops and the damping becomes larger, suggesting that losses within extended tissue are responsible.

The presence of the fish with a swimbladder effectively alters the sensitivity of the hydrophone to incident acoustic waves, converting plane waves to spherical waves, especially at resonance. In Figure 8, the ambient noise level recordings in one-third octave bands with and without the pollack are shown. The reduction in sensitivity at the ring resonance at 6 kHz is evident, and the increase between 450 and 2000 Hz, peaking at the resonance around 800 Hz, results from the resonance of the pollack.

A third method of demonstrating swimbladder resonance is illustrated by Figure 9. It shows the waveform obtained 30 m below an air-gun sound source with a ring hydrophone. The lower

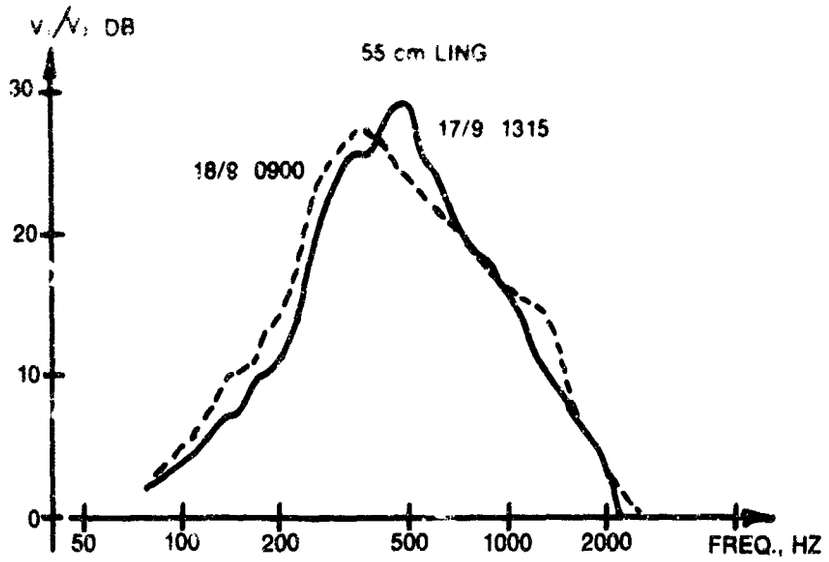

Figure 5. Resonance curves for the 55-cm ling on two consecutive days

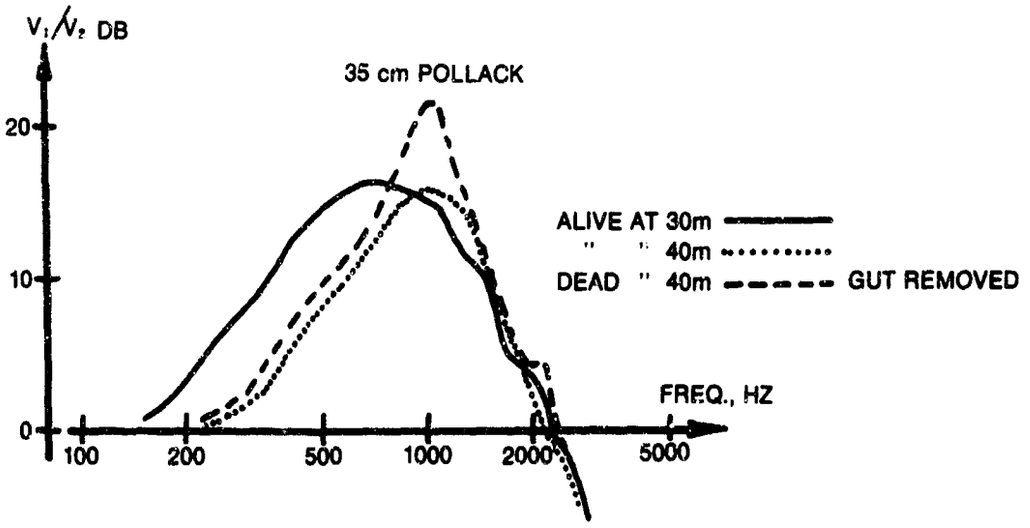

Figure 6. Resonance curves for the 35-cm pollack

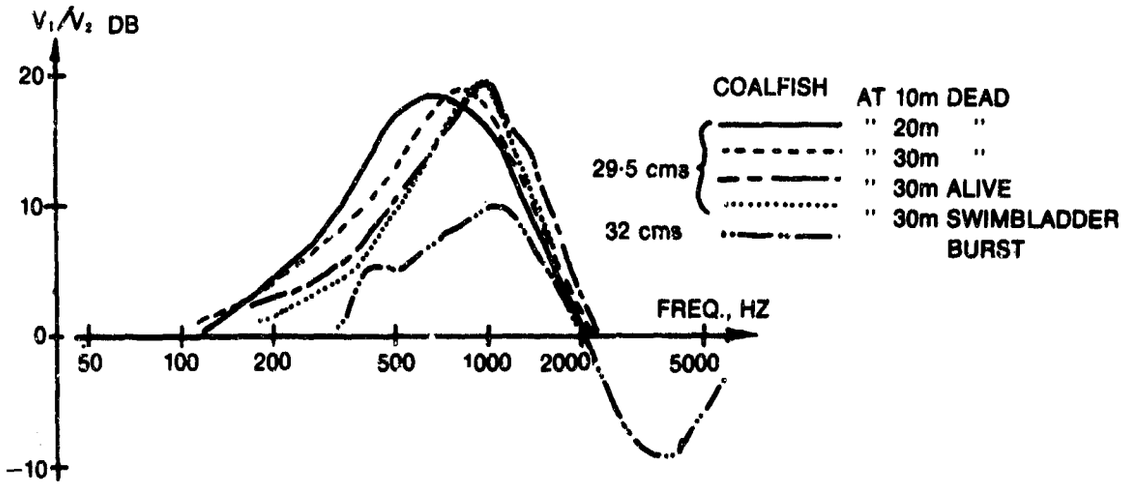

Figure 7. Resonance curves for coalfish

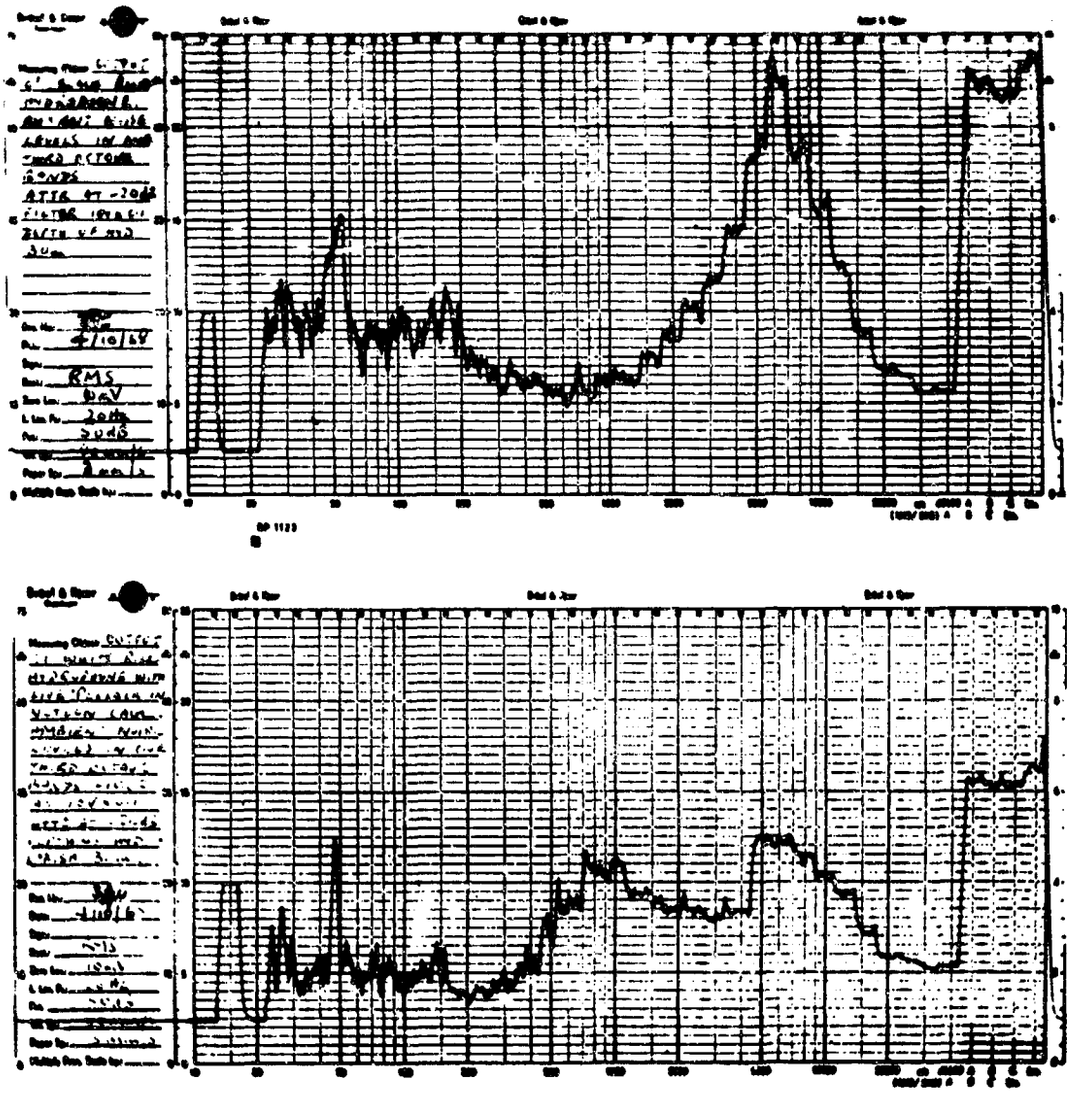

Figure 8. Ambient noise-level recordings in one-third octave bands with the ring hydrophone, at 30 m. Upper record: without fish. Lower record: with a pollack inside the ring.

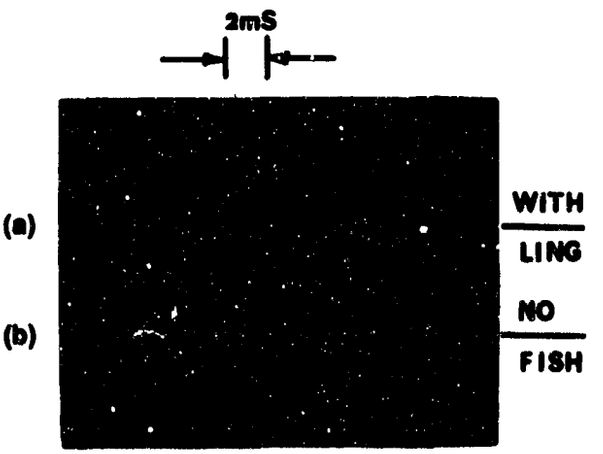

Figure 9. Voltage waveforms from the ring hydrophone 30 m below the air gun, a pneumatic sound source, (a) with ling inside the ring, (b) without fish

trace, *b*, is the absence of the fish and shows that the air-gun waveform is essentially one cycle at 400 Hz, preceded by a small pre-pulse. The high-frequency waveform superposed results from the high sensitivity of the ring hydrophone at its resonant frequency around 6 kHz. The upper trace, *a*, shows that the high-frequency ring resonance is suppressed because of the pressure-release effect of the swimbladder above resonance. The waveform is mainly a heavily damped pulse at 500 Hz, the resonance of the Ling swimbladder. Spectrum analyses of these waveforms, followed by division of each harmonic level of *a* by the level of the same harmonic of *b*, yields the same spectral shape of $|v_1/v_2|$ as the CW technique.

DISCUSSION OF RESONANCE EXPERIMENTS

The measured values of the resonant frequencies (Table 1) of all the fish are higher than one would expect on the basis of representing a fish swimbladder by a spherical bubble of the same volume required to give the fish neutral buoyancy. For a marine fish, the radius of such a bubble would be (Haslett, 1962b)

$$a = 0.043\, L. \tag{8}$$

From equations 2 and 8, using $\gamma = 1.40$ (oxygen) and $\rho = 1.08$ gm/cc (Alexander, 1966), for fish flesh, which has greater influence than the water because of its proximity, we have

$$f_r = 23.0 \sqrt{D_f + 10}\times \left(\frac{1}{L}\right), \tag{9}$$

where f_r, is in hertz, L in metres and D_f is the depth of the fish in metres. Thus, for $D_f = 30$ m, $f_r L = 145$. Observed values are 40% to 100% higher. The validity of (8) for these fish is not known. Also, the swimbladder may not be fully inflated, or it may be under tension, or the effect of shape may be more than predicted. These uncertainties pointed to the need for some control experiments with artificial targets, and for this purpose, slightly inflated toy balloons were stretched to approximate prolate spheroids.

The results for a constant volume balloon at four values of length-to-diameter ratio *e* are given in Figure 10a. The proportional increase in resonance, which is now at a high Q of around 10 because of reduced tissue losses, is plotted in Figure 10b as a function of *e*. Though they are not exactly prolate spheroids, the agreement with Weston's calculations (Weston, 1967) is quite close. The curve in Figure 10a labelled σ is the acoustic back-scattering cross section after sensitivity corrections have been applied for the nearly spherical balloon of radius 1.9 cm at 30 m. The resonant scattering cross section is very close to the theoretical value for a bubble of this size with a Q of 10. The balloon experiments confirm that the experimental technique is valid and that the high resonant frequencies of fish are genuine and, moreover, for the typical length-to-diameter ratios of fish swimbladders (Table 1), it is clear that elongation can account for only 20% to 30% of the increase in $f_r L$.

Unfortunately, detailed measurements of the swimbladder sizes and shapes at the surface are available for only two of the intact fish, coalfish A and the pollack; it is most significant that these swimbladder volumes at the surface, calculated from the measured dimensions, are less than the nominal neutral buoyancy volume $4.1 \times 10^{-4}\, L^3$ which is based upon the dimensions of whiting (Haslett, 1962b) and the average specific gravity of fish flesh. The divers reported on several occasions that fish appeared to be "heavy" at 30 m depth, where the swimbladder volumes must have been even lower.

TABLE I

FISH	Coal-fish A	Coal-fish B	Coal-fish D	Ling	Cod A	Cod B	Cod C	Pollack
Length (cm)	29.5	32	30	55	32	39	35	35
Handling procedure	A	A	B	A	A	C	A	D
Swimbladder condition	I	R_o	? E	I	? E	R_{30}	? E	I
Swimbladder length (cm)	8.9	10.4	–	–	–	–	–	14.5
Aspect ratio at surface	6.4	10.0*	–	–	–	–	–	8.5
Aspect ratio at 30 m	8.2	–	–	–	–	–	–	12.0
Measured volume at surface (ml)	10.1	8.0#	–	–	–	–	–	11.0
Estimated volume of swimbladder at 30 m (ml)	4.6	–	–	17†	–	5.9†	14.7†	5.5
$V_N = 4.1 \times 10^{-4} L^3$ (ml)	10.5	13.4	11.1	68.2	13.4	24.3	17.6	17.6
f_r at 10 m (Hz)	660	–	–	–	–	–	400	–
at 20 m	830	–	–	400	–	550	470	–
at 30 m	950	1000	800	500	910	700	560	766
at 40 m	–	–	–	–	–	–	–	921
at 55 m	–	–	–	–	–	–	–	1120
D_T (±2 m of water)	15	–	–	2	–	1	8-15	2
Q at 30 m	2.5	~1	~1	2.5	3.5	1.8	2.0	~1
$f_r L$ at 30 m (Hz m)	280	320	240	275	290	270	200	270
f_r at 30 m, calculated from equation (10)	898	–	–	–	–	–	–	791

Note: Handling Procedures:

A–Fish removed from hook at surface, transported across Loch to ship at surface pressure in tank, lowered to working depth in stages and allowed time to equilibrate. After experiment, raised to surface for examination (or escape!).

B–Fish removed from hook at depth, transported across Loch at working depth to site.

C–As A, but examined in situ at 30 m.

D–As B, but examined in situ at 30 m.

E–Escaped.

I–Intact.

R_o–Ruptured at surface.

R_{30}–Ruptured at 30 m.

*–High because of rupture.

#–Low because of rupture.

†–Calculated from equation (10) using measured f_r.

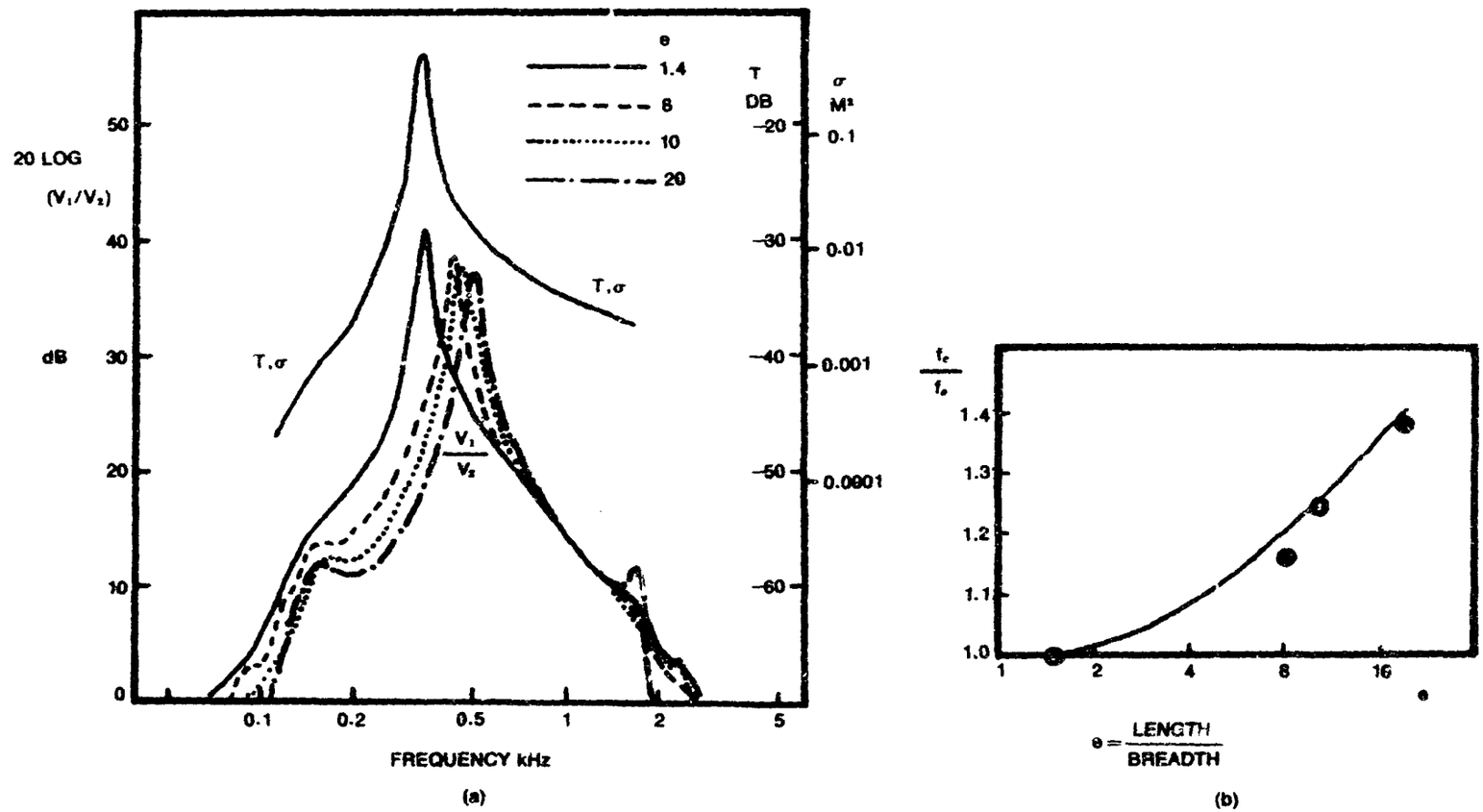

Figure 10. (a) resonance curves of constant volume balloon at various elongations, together with the calibrated target strength and σ of the nearly spherical balloon. (b) ratio of the resonant frequency of an elongated balloon to that of a spherical balloon having the same volume. o experimental, ——— theoretical ratio for prolate spheroid (Weston 1967)

In general, [illegible] hydrostatic pressure (2) an increase in the internal dynamic stiffness to radial vibration and (3) an increase in viscous damping. The first two tend to increase the resonant frequency and together may be represented by an excess internal pressure, equivalent to D_T meters of water pressure, which will depend on the elasticity of the swimbladder, the mass of gas and the unextended size of the bladder. The apparent values of D_T were obtained for five fish (Table 1), and for the balloon as follows. Changes in resonant frequency of a constant mass of gas have a 5/6th power law dependence on absolute pressure, so that a plot of $f_r^{1.2}$ against depth should be a straight line (Weston, 1967), if D_T is constant. The results for a balloon and a coalfish are shown in Figure 11. The excess pressure in the balloon is very small; this fact was confirmed by a manometer measurement. For the coalfish, the straight line may be fortuitous since the accuracy of f_r is poor when measured from plots of $\log_{10}|v_1/v_2|$; accuracy can be improved by manually tuning for the resonant peak using a voltmeter for v_1, and a frequency meter connected to the B.F.O. For the ruptured cod B, D_T was very small as would be expected; for cod C the plot was not linear and it is estimated that $D_T = 8$ m at $D_f = 30$ m and $D_T = 15$ m at $D_f = 10$ m. The value of D_T for the ling is not accurate as frequencies at only two depths were available; but for the pollack, frequencies at greater depths than 30 m give a good line with $D_T = 2$ m. From Appendix 2 it may be seen that a straight line can only be expected if the static excess is zero, in which case

$$D_T = D_t = 4\mu_1 \frac{t}{\gamma a} \times 10^{-5}$$

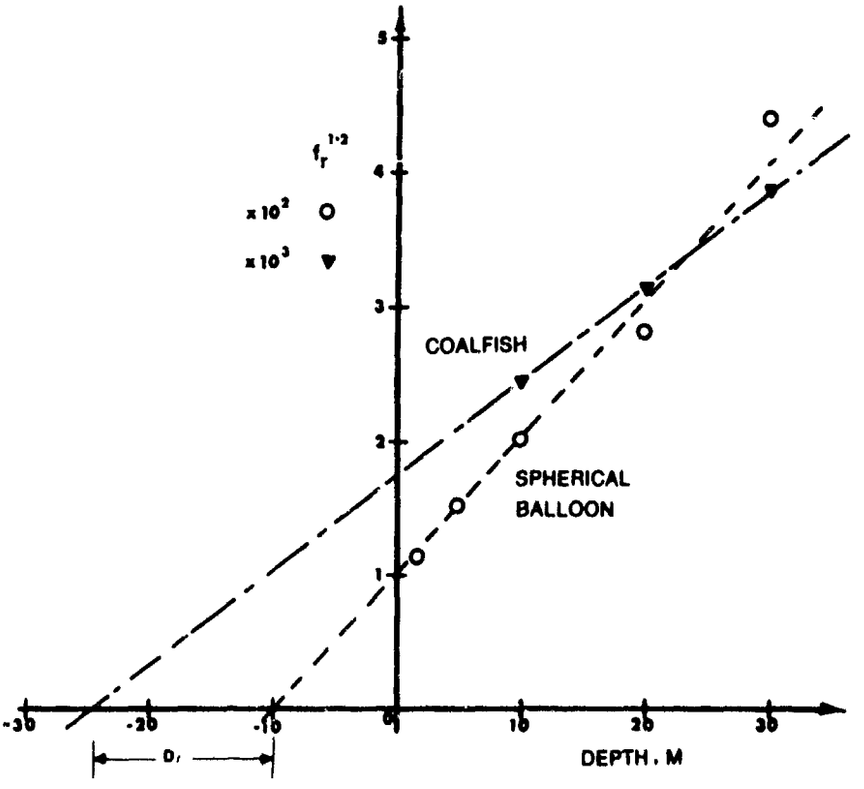

Figure 11. Variation in resonant frequency with depth for a coalfish and the spherical balloon, to determine D_T

and

$$f_r = (2\pi a)^{-1} \rho^{-1/2} \left[3\gamma P + 4\mu_1 \left(\frac{3t}{a} \right) \right]^{1/2}$$

where μ_1 is the real part of the complex shear modulus of the bladder wall and associated tissues whose thickness is t, which probably is of the order $0.2a$. The stiffness correction due to μ_1 is $(3t/a)$ times that used by Andreeva (1964). Using $t/a \simeq 0.2$ gives $\mu_1 \simeq 2.6 \times 10^6$ dynes/cm^2 for coalfish A and $\mu_1 = 3.5 \times 10^5$ dynes/cm^2 for the pollack. Cod C apparently had a static excess pressure and μ_1 is less than 1.4×10^6 dynes/cm^2. Andreeva quotes direct measurements of μ_1 in the region of 10^6 to 10^7 dynes/cm^2.

The ability of fish to withstand these sudden involuntary changes in depth seems to vary. Out of four coalfish, two had ruptured swimbladders at the surface; one exploded 2 feet from the surface as a diver brought it up, having previously killed the fish at depth and then watched the bladder expand. No haddock, *Melanogrammus aeglefinus* (L.), were caught during these experiments in 1968, but in previous years each one caught had a ruptured swimbladder at the surface. One out of two cod examined was ruptured, while the ling and pollack were intact. Ling have been observed to have bladders ballooning from their mouths when brought up from the depths in fishing nets. It is unlikely that the swimbladder wall is uniformly elastic, especially in view of the manner in which it is attached to the vertebral column, and it probably extends little in length and rather more in diameter to both static and dynamic pressures. From the above and other evidence (Alexander, 1966) it is thus unlikely that the swimbladder volume and the external pressure follow Boyle's law, especially for fish brought to very shallow depths. A hypothetical characteristic is sketched in Figure 12 for a fish initially settled at 30 m depth. Without the tension of the walls, the mass of gas would occupy the volume at B, and the curve ABC is the isothermal gas characteristic for constant mass. With tension in the swimbladder wall, the internal pressure exceeds the external pressure by DB' and the volume is reduced to V_E so that the gas conditions are at B'. If now the fish is placed deeper, not having time to absorb or secrete gas, the excess pressure will gradually drop to zero and the walls become flaccid, as at A. For further increases in depth, the volume V and external pressure will follow the gas law. If instead the fish is raised from 30 m to 10 m depth, the bladder will come under greater stress, the volume increasing and the pressure decreasing to the point C'. The excess pressure is now FC' which exceeds DB'. The curve $ADFR$ is the volume/depth characteristic, rupture possibly occurring at R just before atmospheric pressure is reached externally. The neutral buoyancy volume V_N, which is essentially constant at all depths for a given fish, may be exceeded by the time the surface is reached; live swimbladder fish brought to the surface often float. Given time, the fish could presumably secrete gas to reach A' or absorb gas to reach F' and regain its volume V_E such that $GA' = EF' = DB'$. The stiffness of the swimbladder characteristic in Figure 12 has been made high in order to separate the two curves for illustration purposes, and the relative values of V_R, V_N, V_E and V_A are speculative. The possession of a fairly stiff swimbladder by the fish has obvious advantages with regard to depth stability, and the low buoyancy helps to increase the vertical range of a fish. While low buoyancy has rarely been reported (Alexander, 1966), it is evident that observations on live fish in shallow aquaria, or on fish brought up to the surface from deep water, are difficult to apply to the fish at depth. With refinements, the technique evolved here may be used by fish physiologists to obtain independent estimates of swimbladder volume in live experimental fish in situ. Fish audiologists from the Marine Laboratory, Aberdeen, have already used the technique to monitor the swimbladder condition before hearing tests.

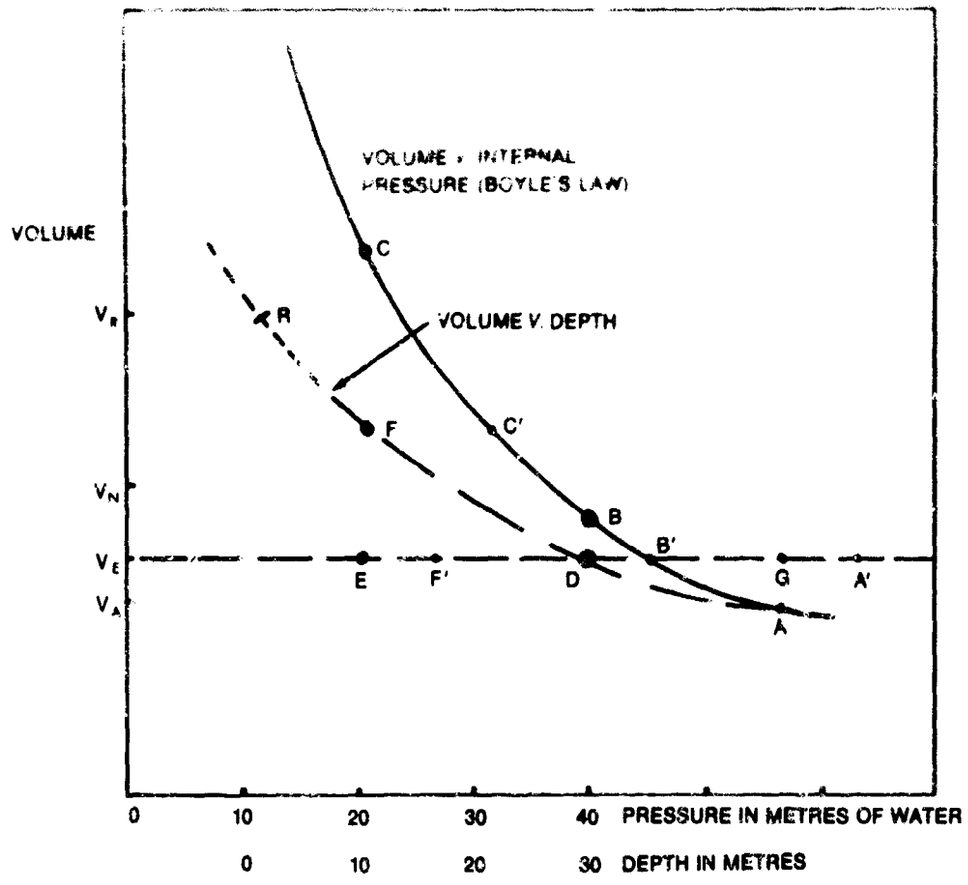

Figure 12. Hypothetical depth, volume characteristic for a stiff swimbladder

Allowing for the measured values of D_T, the volumes of the swimbladder of coalfish A and the pollack at 30 m depth can be estimated from the surface dimensions to be 4.6 cm³ and 5.5 cm³, respectively. In view of the strong attachment to the rigid backbone, the length is probably constant with depth, so that the reduced volumes are achieved with slightly larger aspect ratios of 8.2 for the coalfish and 12 for the pollack; the resonant frequencies calculated from (2) must thus be increased by 20% and 28% to 898 Hz and 791 Hz compared with the measured values of 950 Hz and 766 Hz, respectively. These discrepancies of −6% and +3% are well within the experimental errors. Cod swimbladders have lower aspect ratios (e) (Midttun and Hoff, 1962) than do coalfish and pollack, which may partially account for the low value of $f_r L$ for cod C. Cod B and coalfish B were ruptured, which probably explains their high resonant frequencies. Though cod A escaped before it could be examined, it is evident from Figure 4 that it was either using gas or losing it from a rupture and may have been doing so for some time before the high resonant frequency was first measured. The ling was kept alive for use in audiogram experiments, and subsequently lived a considerable time before release, so an intact bladder is assumed. In Table 1 the volumes of three swimbladders which were not examined have been calculated from values f_r and D_T using

$$f_r = \frac{1.25}{2\pi a} \cdot \sqrt{\frac{3\gamma (D_f + 10 + D_T)}{\rho}} \times 10^5, \qquad (10)$$

which allows a 25% increase for shape. These volumes, determined from acoustic measurements, range from 25% to 83% of those which would be calculated for the neutrally buoyant standard fish shape. It should be noted that the length-to-weight relationships of fish are known to vary even within a species, depending upon season and condition of the fish.

The highest Q observed at 30 m was 7.5 for cod A, and the lowest values correspond to overdamped systems. In general, cod and ling had the lowest, and coalfish and pollack the highest damping. Damping consistently increased as a fish was raised and consistently decreased as it was lowered. Damping is principally due to shear losses within the tissue of the swimbladder wall, especially when this wall is under tension, and to viscous losses between the surrounding fish materials of differing density in a local acoustic field having high particle velocities. The radiation and other losses (Andreeva, 1964; Devin, 1959; Weston, 1967) were negligible in comparison with the fish tissue losses. According to Andreeva the tissues can be characterized by a complex shear modulus $\mu_0 = \mu_1 (1 + j\mu_2)$, in which case the tissue damping, for a spherical bladder completely surrounded by the viscoelastic material of thickness greater than the bladder dimensions, is

$$\delta_f = \frac{4\mu_1\mu_2}{(3\gamma P + 4\mu_1)} . \tag{11}$$

Our calculations (Appendix 2) based on a thin-walled spherical viscoelastic shell, allowing for possible excess static pressure, give, at resonance

$$\delta_f = \frac{\mu_2 \cdot D_t}{(D_f + 10 + D_s + D_t)} = Q^{-1} . \tag{12}$$

While either (11) or (12) would both predict the observed reduction of Q as the fish is raised and vice-versa, the values of μ_2 necessary to explain the high damping are an order of magnitude larger than in Andreeva, for other fish, though approaching values for a plastic material (Workman and Hayek, 1969). No allowance has been made for viscous losses in the other body parts, which will not be depth dependent and which the single experiment with the pollack showed to be significant. The damping must also be higher for an elongated bladder than for a spherical one. Since the accuracies of the measurements are not very great there is little point in pursuing these aspects further.

MEASUREMENTS AT HIGHER FREQUENCIES

The backscattering cross-sections of the same and other live fish at higher frequencies were measured using a different method. An array of four transducers, mechanically resonant at 6.5 kHz, was used as a sound source over the band 4 kHz to 20 kHz. Short pulses 1 msec long were transmitted at a frequency which was changed at one-third octave intervals. The source was placed just below the surface and vertically above the live fish, which was contained at 30 m depth in a large polythene bag about 1 m long and 40 cm in diameter; the fish could swim around in this bag, which was holed to allow respiration. In the same vertical line at 20-m depth, an omnidirectional hydrophone was positioned between the sound source and the fish.

The incident and scattered pulses, separable in time, were received by the hydrophone and recorded via the same tuned amplifier on the same polaroid film from a C.R.O. trace. In this way, the ratio of the incident and reflected pressures can be measured directly from the film,

together with the setting of a calibrated attenuator in the path of the larger incident pulse, the ratio of the pulse amplitudes is independent of source levels, hydrophone sensitivity, amplifier and C R O gains and frequency responses. The acoustic backscattering cross-section is then determined from

$$\sigma = 4\pi \left(\frac{d_f (d_s + d_f)}{d_s} \right)^2 \left(\frac{v_s}{v_i} \right)^2 \qquad (13)$$

where d_f and d_s are the distances from the hydrophone to the fish and sound source, respectively, and v_s and v_i are the scattered and incident pulse voltages. It is considered important that this method of absolute measurement of σ is not dependent upon standard or reference targets. The distances were known to ±1% but could have been measured by the pulse travel times.

The directions of the pulses incident on the fish and hydrophone differed by less than 1.5°, so that even at the highest frequency, the error in v_i caused by the directivity of the transmitting transducer is less than 0.6 dB. At each frequency, the value of v_i was very steady from pulse to pulse. Because of movement of the fish within the bag, the angle between the incident wave and the scattered wave as observed at the hydrophone could vary between 3° and 6.5°, and the incident wave may vary from 0° to 2° from the vertical. Also, the live fish can pitch an unknown angle during the experiment, and the major acoustic reflectors may be tilted relative to the mean horizontal axis of the fish (Midttun and Hoff, 1962), so that the angles of vertical incidence, dorsal aspect, and maximum backscattering do not necessarily coincide. Thus, directivity and fish movements cause variations in v_s from pulse to pulse. The maximum value of v_s over eight pulses superimposed on the film was used. In most cases, v_s was well above background level; in cases where the fish echo was detectable, but comparable with the noise or reverberation level, corrections were made on an energy basis; occasionally, σ was too small for v_s to be detectable. It is estimated that errors in (v_s/v_i) and target strength do not exceed ±2 dB, though there is no guarantee that the absolute maximum value in the pitch plane has been recorded, especially at high L/λ. Nevertheless, the values obtained are probably fairly representative of what would be measured by an echo sounder at sea. In a separate experiment, looking at fluctuations over 25 pulses, a minimum spread of 2.7 dB at one frequency and a maximum spread of 14 dB at a higher frequency were observed, but the spread did not consistently vary with frequency, and it is felt that more data on variability are needed.

In the range $0.8 < L/\lambda < 16$, 199 measurements on six species of swimbladder fish indicate considerable variability from frequency to frequency, fish to fish, and day to day. Absolute values occur with a similar spread to those found by other authors (Fig. 1), and it is considered that an alternative presentation and some further data reduction might be worthwhile; two methods are demonstrated. Values of σ/L^2 were first averaged in one-third octave bands of L/λ and plotted as the "mean" in Figure 13, which also shows the maximum and minimum observed in each band. A few results for a mackerel, *Scomber scombrus* (L.), not a swimbladder fish, fall well below the mean of the swimbladder fish: this observation offers support for the conclusion of other workers that the swimbladder is a major scattering component of fish in this band, though it is also possible that the mean density and acoustic impedance of mackerel are less than those for the body of a fish supporting a swimbladder.

All the measurements were then plotted as in Figure 14, normalizing σ by λ^2 instead of L^2 after Love (1969), (who remarks that this procedure improves the presentation of the data). Of course the quality of the data is unaltered, but though the σ/L^2 plot illustrates the frequency

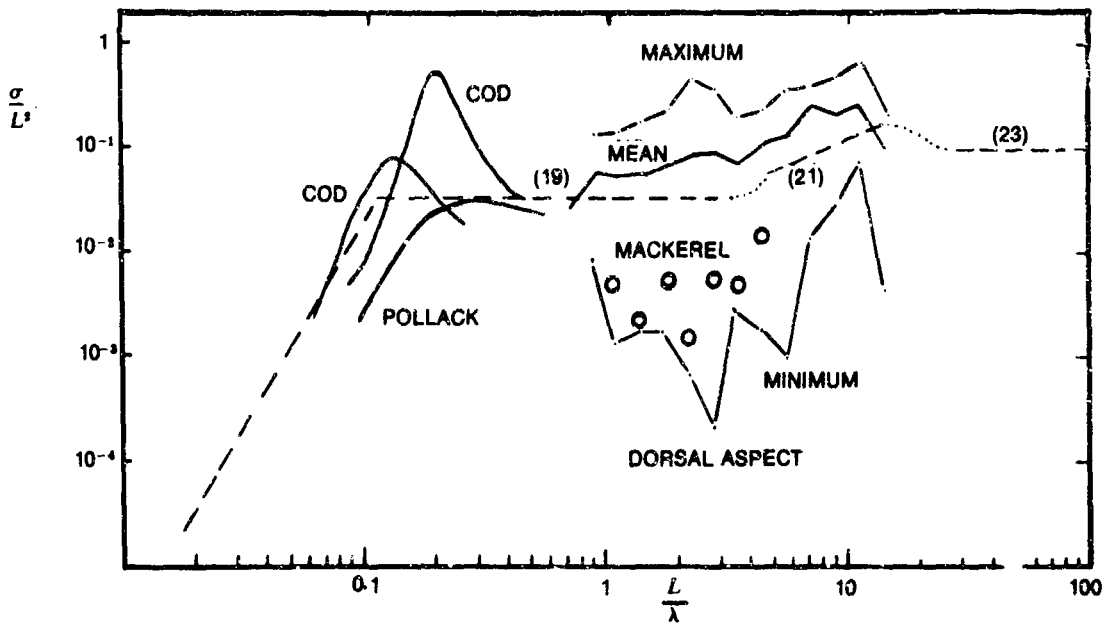

Figure 13. Summary plot of scattering normalized by length from fish in dorsal aspect at 30 m. Bracketed numbers refer to equations in the text.

dependence, the σ/λ^2 plot illustrates the fish-length dependence; it is apparent from the data that L is the more important parameter. A least mean-square regression of $10 \log (\sigma/\lambda^2)$ on $10 \log (L/\lambda)$ gave the line shown in Figure 14, for which the equation is

$$\frac{\sigma}{\lambda^2} = 0.029 \left(\frac{L}{\lambda}\right)^{2.45}. \tag{14}$$

Using equation (1), this expression can be rewritten as

$$T = 24.5 \log_{10} L - 4.5 \log_{10} \lambda - 26.4 \tag{15}$$

or

$$T = 24.5 \log_{10} L + 4.5 \log_{10} f - 27.2, \tag{16}$$

where L and λ are in metres, f is in kilohertz, and T is in decibels re: $4\pi m^2$, the cross section of a perfectly reflecting sphere of radius 2 m. The 4.5-dB per decade increase with frequency is approximately the slope of the mean on Figure 13, as would be expected from the same data. The regression line is slightly lower in level than the arithmetic mean because it was obtained from log σ and thus is nearer a geometrical mean.

The data collated by Haslett (1965) in Figure 1 have been replotted in Figure 15 as σ/λ^2, and the regression line obtained for this dorsal aspect data is

$$T = 25.3 \log_{10} L - 5.3 \log_{10} \lambda - 33.4 \text{ dB}. \tag{17}$$

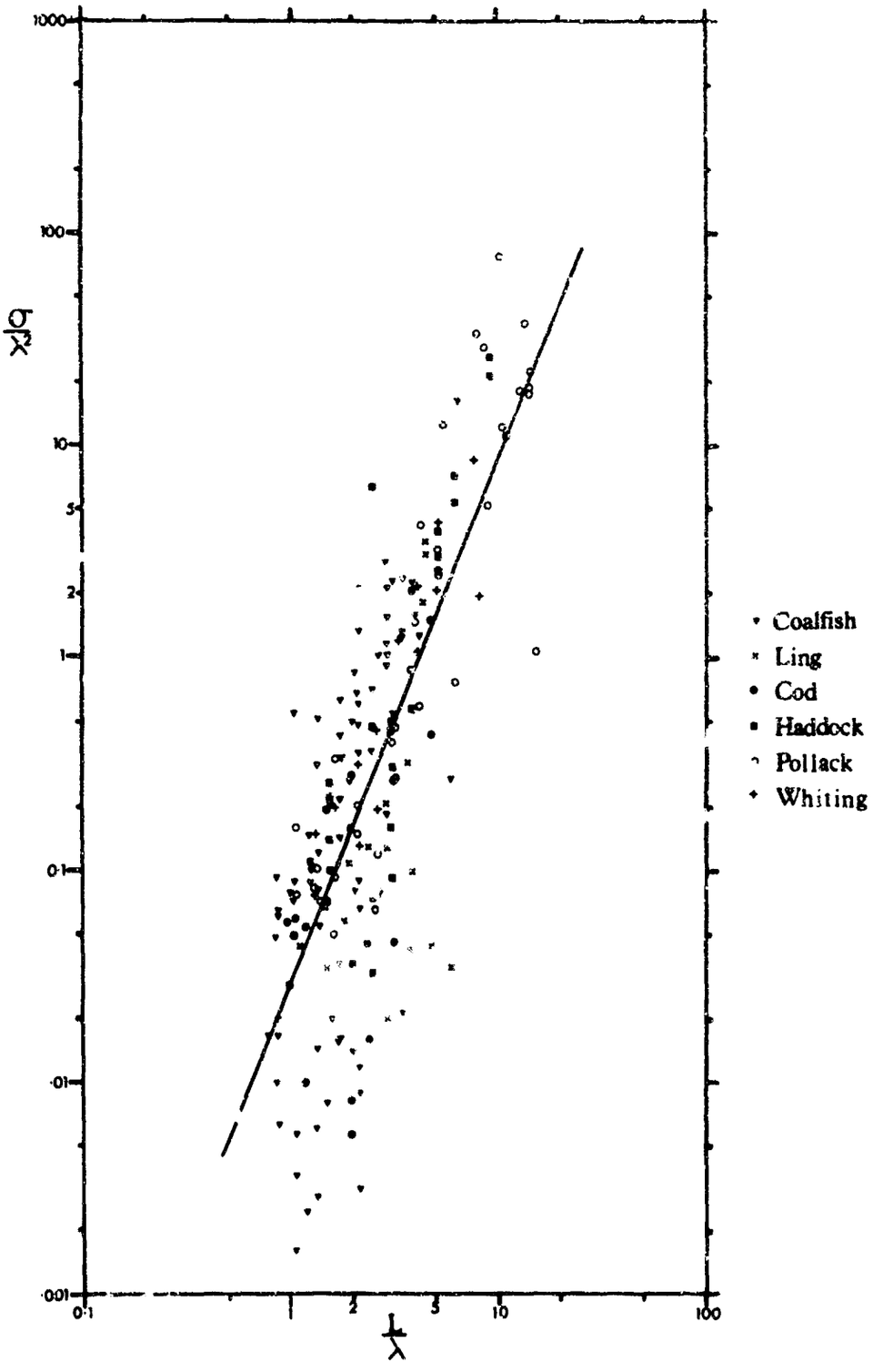

Figure 14. Results of scattering measurements on six species of fish, normalized by wavelength, and the regression line, equation (14)

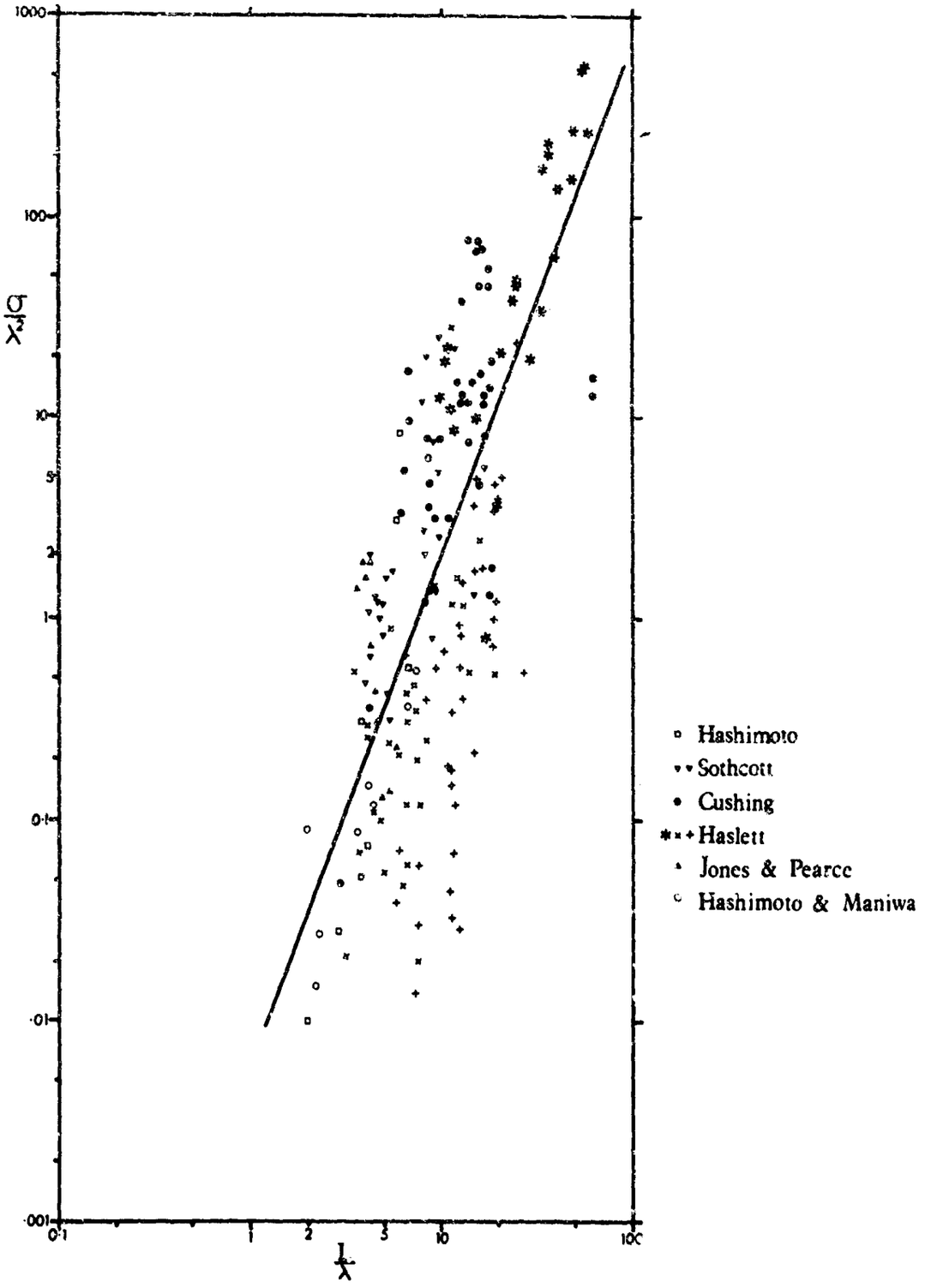

Figure 15. Results of scattering measurements by six authors on a wide variety of fish; data taken from Figure 1 and replotted normalized by wavelength instead of fish length. The regression line is equation (17).

These results, equations (15) and (17), can be compared with those of Love, whose regression line for various fish in maximum *side* aspect is

$$T = 24.1 \log_{10} L - 4.1 \log_{10} \lambda - 23.5 \text{ dB}. \tag{18}$$

There is close agreement on the length and frequency coefficients. The constant for maximum side aspect is 3 dB larger than our value for dorsal aspect, which is reasonable because fish generally are deeper than they are broad. However, the large difference in constants for the two sets of dorsal data cannot be explained easily. Our data were obtained using *live* fish in good condition; the data of Figure 1 and equation (17) were from *dead* fish, some with artificial swimbladders.

The individual points are by no means distributed normally about the regression line. In Figure 14, there are more points above and closer to the line than below it, suggestive of multiple scattering with broad maxima and deep interference minima. The standard error in the slope of Figure 14 is 1.4 dB/decade and the standard error of the constant is 0.7 dB.

Haslett (1965) has calculated in some detail the contributions from various component structures of the fish, using approximate geometrical shapes. We shall be content to calculate the contribution in several frequency bands from simple models representing the swimbladder, for which the amplitude reflection coefficient, μ, can reasonably be taken as -1. Below resonance, in the Rayleigh scattering region, σ is proportional to $L^6\lambda^{-4}$. Above resonance and below frequencies where the swimbladder dimensions are less than a wavelength, Weston (1967) has shown that the acoustic cross section is equal to the surface area for a soft spheroid of any aspect ratio. Thus, a prolate spheroid of length $0.36L$ and diameter $0.036L$ would have

$$\sigma = 3 \times 10^{-2} L^2, \; f_r < f < \frac{2.8c_0}{L}. \tag{19}$$

The upper frequency limit is near $L/\lambda = 3$. Above this frequency, as first the swimbladder length and then other dimensions become comparable with a wavelength, the diffraction region is difficult to approximate simply. Modeling the swimbladder on a cylinder of length $\ell = 0.36L$ and diameter $2b = 0.03L$, the latter less than the prolate spheroid minor dimension in order to give the same volume, $2.5 \times 10^{-4} L^3$, which is somewhat lower than neutral buoyancy volume in accordance with Table 1, we can use the scattering cross section of a finite cylinder (Haslett, 1964; Tucker and Stubbs, 1958)

$$\sigma = \frac{2\pi b \ell^2}{\lambda} \mu^2, \tag{20}$$

giving then

$$\sigma = 1.2 \times 10^{-2} \frac{L^3}{\lambda}, \; \frac{5.3c_0}{L} < f < f_u. \tag{21}$$

The lower frequency limit is determined from $2\pi b > \lambda/2$ and corresponds to $L/\lambda > 5.3$. It should be noted that equations 19 and 21 intersect at $L/\lambda = 2.5$, so that it is reasonable for σ to be less than equation (21) and more than equation (19) in $2.5 < L/\lambda < 5.3$. The upper limit f_u of the finite cylinder approximation will depend upon the curvature of the long axis

of the bladder and at high frequencies, scattering is specular. Using the laws of geometrical optics, Tucker and Stubbs (1958) calculate that for an ellipsoid of length ℓ, b.eadth $2b$, and depth $2c$,

$$\sigma = \frac{\pi \ell^2 b^2}{16c^2} \mu^2. \tag{22}$$

This expression arises because the two principal radii of curvature are $\ell^2/8c$ and $b^2/2c$. In this case of prolate spheroid, $b = c$, $\mu = -1$, and $\sigma = \pi\ell^2/16$, which, surprisingly, is independent of b and gives

$$\sigma = 10^{-1} L^2, \quad f_u < f. \tag{23}$$

For this approximation to apply, $2b > \lambda$, and the lower limit will correspond to $L/\lambda > 28$. Because equations 21 and 23 intersect at $L/\lambda = 8$, σ is somewhat uncertain in the region $8 < L/\lambda < 28$. However, the geometrical optics approximation takes no account of surface creeping waves, which Senior (1966) has shown can enhance high-frequency scattering from prolate spheroids for "end" or "nose on" incidence. At all events, the frequency range in which a 10-dB/octave slope can be expected is quite restricted, probably to less than the range over which the regression lines have been forced. Some more recent broadside measurements by Haslett (1969) at high L/λ values show very low or zero frequency dependence. It is apparent in broad outline and general level, if not in precise detail, that the swimbladder can account for practically all the scattering from these fish. Higher values than these approximations can be expected if the fish is nearer neutral buoyancy, if the swimbladder is concave along its length, or if it is broader than it is deep.

Though the rest of the fish is bulkier than the swimbladder, this factor is more than offset by the much reduced amplitude reflection coefficient, so that scattering is an order of magnitude at least below that from the bladder. There is some uncertainty about the value of μ for fish flesh and bone in sea water. Haslett (1962a, 1965) has obtained $\mu = 0.019$ by measurement at a high frequency on small samples of flesh, whereas Mahrous and Cushing find a sound velocity in fish flesh of 1,620 m/sec, which would give $\mu \simeq 0.064$. For cod bone, Haslett measures $\mu = 0.25$ to give $c_0 = 1{,}280$ m/sec, while Mahrous and Cushing measure $c_0 = 5{,}650$ m/sec, giving $\mu = 0.76$.

CONCLUSIONS

1. A technique has been developed whereby the swimbladder resonance of a live or dead fish may be observed and measured at sea.

2. By this method, the resonant frequency of several live gadoid fish were found to be higher than would be predicted for a neutrally buoyant fish with a spherical swimbladder.

3. The three major reasons for the higher frequency of resonance are (a) the elongation of the bladder, (b) an excess internal pressure because of the stiffness of the bladder wall, and (c) the fact that apparently the bladders of the experimental fish were insufficiently inflated to provide neutral buoyancy.

4. The damping of resonance in all cases was high and was in roughly equal measure the result of the viscous losses in the bladder wall tissues and the surrounding gut.

5. Measurements on elongated balloons confirmed the validity of the resonance technique and showed that the effect of aspect ratio was close to the theoretical calculations of Weston.

6. Application of swimbladder resonance for the sizing of commercial fish at liberty in the sea is not a practical proposition because of severe and fundamental transducer and resolution limitations. The in situ resonance technique described here is considered to be a valuable method of monitoring the swimbladder function.

7. An absolute method of measuring the target strength of fish at higher frequencies has also been developed; it does not depend upon calibrated transducers or upon "standard" targets.

8. Measurements in dorsal aspect on live fish in the range $0.8 < L/\lambda < 20$ give an empirical equation,

$$T = 24.5 \log_{10} L - 4.5 \log_{10} \lambda - 26.4$$

It is recommended that this equation be used when sizing by target strengths with calibrated echo sounders at sea.

9. The major cause of scattering over the whole frequency band is the swimbladder.

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APPENDIX 1

HYDROPHONE SENSITIVITIES AND CALIBRATION CONSTANT

In order to convert the uncalibrated plots of Figures 3,5,6,7, and 10, it is necessary to know the hydrophone sensitivities S_s and S_p and hence the calibration factor of equation (7),

$$20 \log_{10}\left(\frac{RS_p}{S_s}\right).$$

It was not possible to calculate theoretically the sensitivities with any confidence because of the complex boundary conditions. The edge-on sensitivity to plane waves S_p was determined (Fig. 16) by a conventional substitution calibration. To obtain S_s a small piezoelectric sphere was placed at the centre of the ring and used as a transmitter over the frequency band 100 Hz to 10 kHz. The voltages from the ring and another small calibrated hydrophone some distance away were measured. The ring sensitivity was therefore obtained (Fig. 16) relative to the hydrophone for spherical waves originating at the centre of the ring. The resulting calibration factor (Fig. 16) has been used in Figure 10 for the nearly spherical balloon and the measured target strength is very close to the theoretical values for a Q of 10. Application of the calibration factor to the elongated balloons and the fish is less certain. Well away from the scatterer, the field is spherical, because it is a monopole smaller than a wavelength. However, at the position of the ring, which is separated from the scatterer by the same order as the length of the scatterer, the field is more complex and a proximity correction might be necessary, depending upon the aspect ratio. The calibration factor, uncorrected, was applied to the cod that had the highest Q, the pollack having the lowest Q, and to another cod with the lowest normalized frequency, all plotted in Figure 13. Taking account of the higher resonant frequency discussed under Measurements at Higher Frequencies, the calibrated and normalized results at low frequencies on Figure 13 fit the theoretical values of equation (19) and the Rayleigh scattering below resonance sufficiently closely to suggest that any corrections from the proximity of the ring are small.

Radial and axial displacements of the target from the centre of the ring were shown to have no effect on the resonant frequency and a small effect on amplitude, so that providing the ring is placed around the bladder, further accuracy in positioning is unnecessary.

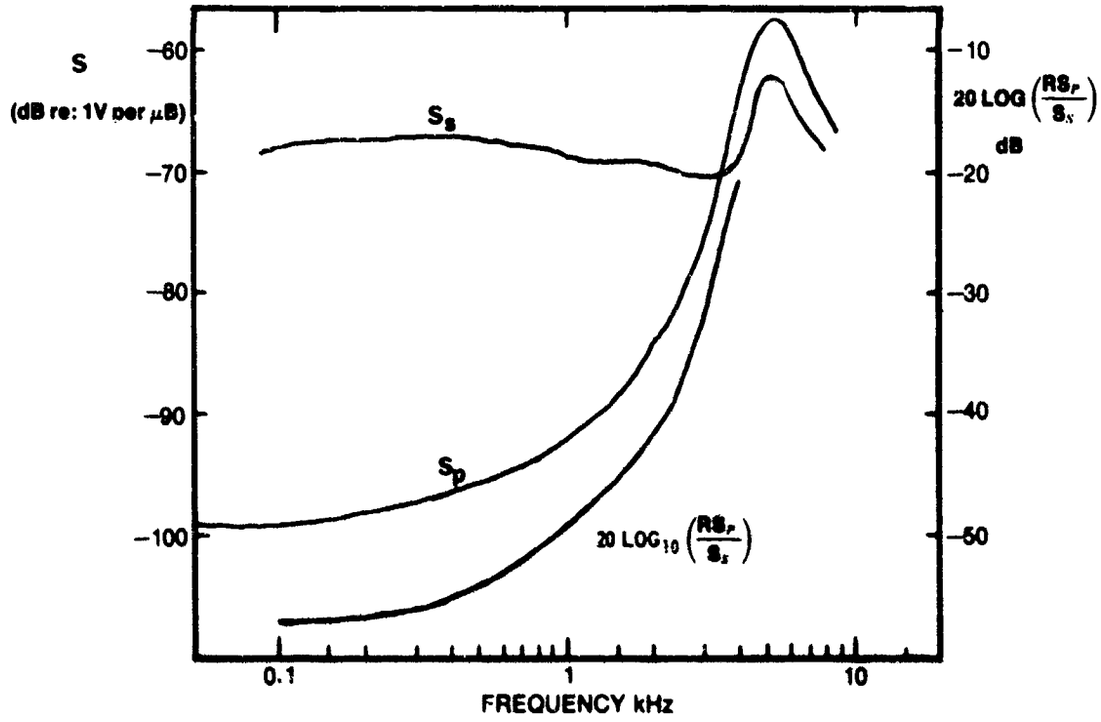

Figure 16. Measured sensitivities of ring hydrophone: S_s to spherical waves from the centre of the ring, S_p to "edge-on" plane waves. $20 \log_{10}\left(\frac{R S_p}{S_s}\right)$ is the calibration term in equation (7)

APPENDIX 2

THE EFFECTS OF SWIMBLADDER TISSUE ON RESONANCE

For simplicity the fish is modeled on a spherical viscoelastic shell (swimbladder) surrounding a gas volume V and surrounded by an infinite body of water. If the shall density is the same as water the radiation load on the bladder is the same as that on a spherical bubble of the same size, but the mechanical stiffness is altered because of both an increased internal static pressure and elastic energy storage in the shell, and the damping is increased due to incomplete recovery of stored energy within the shell.

The radial displacement of a spherical elastic shell is given (Love, 1927) by

$$U_r = \frac{1}{3B}\left(\frac{p_1 r_1^3 - p_0 r_0^3}{r_0^3 - r_1^3}\right) r + \frac{1}{4\mu_0}\left(\frac{r_0^3 r_1^3 (p_1 - p_0)}{r_0^3 - r_1^3}\right)\frac{1}{r^2}$$

where p_1 and p_0 are the internal and external pressures at radii r_1 and r_0 respectively, B is the bulk modulus of compressibility, μ_0 is the shear modulus and $r_1 \leqslant r \leqslant r_0$. For viscoelastic materials B is taken to be real, and μ_0 is complex and frequency dependent (Workman and Hayek, 1969). Andreeva (1964) defined $\mu_0 = \mu_1 (1 + j\mu_2)$ and considered the bladder material to have dimensions larger than the bladder, so that putting $p_0 = 0$ at $r_0 \to \infty$, gives

$$U_{r_1} = p_1 \frac{r_1}{4\mu_0}.$$

However this approximation does not seem too satisfactory, in view of the experiment in which the gut below the pollack was removed, causing decreased damping but not affecting the resonant frequency. Let the wall be thin so that $r_0 - r_1 = t$ and $(r_0^3 - r_1^3) \simeq 3r_1^2 t$, giving

$$U_{r_1} \simeq (p_1 - p_0)\frac{r_1^2}{3t}\left(\frac{1}{3B} + \frac{1}{4\mu_0}\right).$$

It is probable that, like natural rubber (Workman and Hayek, 1969), $B \gg \mu_0$ for the bladder wall tissue, giving

$$U_{r_1} \simeq (p_1 - p_0) \cdot \frac{r_1}{4\mu_0} \cdot \left(\frac{r_1}{3t}\right),$$

which indicates an extension $(r_1/3t)$ times that produced by Andreeva's approximation. Now if the bladder is initially extended U beyond the flaccid state then the excess internal pressure is $\Delta P = 4\mu_1\left(3t/r_1^2\right)U$, where it has been assumed that $\mu_2 = 0$ at zero frequency. Devin (1959) and Weston (1967) derive formulae for the resonant frequency and damping of gas bubbles and Weston (1967) and Andreeva (1964) discuss damping coefficients due to fish tissue, so that it is not necessary to write down the derivation here in full, except to point out

that the difference between the gas pressure and the sum of the incident and scattered pressures at the radius a must equal $4\mu_0 (3t/a^2) u_a$ instead of zero, where u_a is now the acoustic displacement of the wall and $a = r_1 + U$. The resonant frequency is then given by

$$f_r = (2\pi a)^{-1} \rho^{-1/2} \left[3\gamma (P + \Delta P) + 4\mu_1 \frac{3t}{a} (1 - k_0 a \mu_2) \right]^{1/2},$$

the damping by

$$\delta = \delta_r + \delta_f ,$$

where δ_r, the radiation damping is $k\ a\ \omega_o^2/\omega^2$ and the tissue damping is

$$\delta_f = \frac{4\mu_1 \mu_2}{\rho \omega^2 a^2} \frac{3t}{a} .$$

Now $k_o a \mu_2 \ll 1$, so that we obtain

$$f_r = (2\pi a)^{-1} \rho^{-1/2} \left[3\gamma P + 12\mu_1 t \left(\frac{3\gamma U}{(a-U)^2} + \frac{1}{a} \right) \right]^{1/2},$$

or, if Andreeva's assumption was used,

$$f_r = (2\pi a)^{-1} \rho^{-1/2} \left[3\gamma P + 4\mu_1 \left(\frac{3\gamma U}{(a-U)} + 1 \right) \right]^{1/2},$$

which reduces to her formula if $U = 0$.

It is interesting to note that in the case of a small gas bubble for which surface tension σ_t is significant

$$f_0 = (2\pi a)^{-1} \rho^{-1/2} \left[3\gamma \left(P + \frac{2\sigma_t}{a} \right) - \frac{2\sigma_t}{a} \right]^{1/2} ;$$

The term $+ 2\sigma_t/a$ is the static excess internal pressure, but the term $- 2\sigma_t/a$ is a consequence of σ_t remaining constant as the bubble oscillates, so that during the expansion cycle the total excess internal pressure is being reduced.

Returning to the experiment in which f_r is measured as the fish depth is altered, and if μ_1 is in dynes/cm^2, the apparent excess pressure in terms of metres of water is given by

$$D_T = (3\gamma)^{-1} \times 10^{-6}\ 12\mu_1 t \left(\frac{3\gamma U}{(a-U)^2} + \frac{1}{a} \right).$$

That is

$$D_T = D_s + D_t ,$$

where the static excess head of water is

$$D_s = 12\mu_1 \frac{t\,U}{(a-U)^2} \times 10^{-5},$$

and the effective contribution due to tissue rigidity is

$$D_t = 4\mu_1 \frac{t}{\gamma a} \times 10^{-5}.$$

$D_s \sim D_t$ if $U/a \sim 0.2$, which is a large strain but not an impossible one for the fish raised from 30 to 10 m. For a fish forced to undergo rapid changes in depth, U will change and though this could be calculated, it requires the assumption of linear elasticity, which is doubtful since a large proportion of bladders ruptured. If a plot of $f_r^{1.2}$ versus D_f is a straight line then it suggests that $U = 0$ over the range of D_f, that $D_s = 0$ and that $D_T = D_t$.

At resonance the tissue damping is

$$\delta_f = \frac{\mu_2 D_t}{(D_f + 10 + D_t + D_s)}.$$

μ_2 is probably frequency dependent.

These calculations based on a spherical bladder can only serve as a guide to the real fish, whose swimbladder is, in general, a more complex shape and stiffened by the vertebrae, whose tissues do not have uniform thickness or elastic properties and whose recent pneumatic history is so important.

APPENDIX 3

NOMENCLATURE

a	radius of bubble or swimbladder
B	bulk modulus of tissue
$2b$	diameter of cylinder or breadth of ellipsoid
$2c$	depth of ellipsoid
c_o	velocity of sound
D_f	depth of fish
D_s	actual excess static pressure in metres of water
D_T	equivalent total excess internal pressure in metres of water
D_t	equivalent excess pressure due to tissue elasticity
d_f	distance between hydrophone and fish
d_s	distance between hydrophone and source
e	ratio of length to diameter for prolate spheroid
f	frequency

f_e resonant frequency of spheroid

f_o resonant frequency of spherical bubble

f_r resonant frequency of fish swimbladder

f_u upper frequency limit of cylindrical approximation

L length of fish

ℓ length of cylinder or ellipsoid

P absolute static pressure

ΔP excess static pressure

p_i incident acoustic pressure

p_s scattered acoustic pressure

Q ratio of resonant frequency to 3 dB bandwidth

r radius of shell

R radius of ring hydrophone, distance from fish.

S_p sensitivity of ring hydrophone to 'edge-on' plane waves

S_s sensitivity of ring hydrophone to spherical waves

t thickness of tissue

T target strength

U initial radial displacement of spherical bladder

u_a acoustic displacement of bladder wall

V volume of swimbladder

V_E original volume of bladder before change in depth

V_N neutral buoyancy volume

V_R volume of bladder at rupture

v hydrophone voltage

v_1 ring hydrophone voltage with fish present

v_2 ring hydrophone voltage without fish

v_i incident pulse voltage

v_s scattered pulse voltage

γ ratio of specific heats of gas

δ damping factor

δ_f damping factor at resonance due to fish tissue

δ_r damping factor at resonance due to acoustic radiation

λ wavelength

μ amplitude reflection coefficient

$\mu_c = \mu_1 (1 + j\mu_2)$ complex shear modulus of tissue

ρ density

σ acoustic backscattering area

σ_t surface tension

ω $= 2\pi f$

DISCUSSION

Winokur: Thank you, Brian. I know that Richard Love has done some additional work on dorsal aspect target strengths, and we will save his remarks until this evening. He does have a few slides to show of his data, and has developed an equation similar to Dr. McCartney's.

McCartney: Richard Love's equation for maximum side aspect is very similar to mine in frequency dependence and length dependence. There is a 3 dB difference in the constant, which acoustically is reasonable. One might say that the fish are rather deeper than they are wide, and that might account for 3 dB, but I doubt it. I think it is probably experimental error.

Shearer: Dr. McCartney, I wonder if you could elaborate on a statement that you made at the beginning of your presentation. You said that the volume of the swimbladder is directly related to the length of the fish. What kind of correlation did you find?

McCartney: By length I really should have said length cubed. This was the naive assumption which we had made originally. The basis of this is that if the fish is neutrally buoyant, it is because of the specific gravity of the rest of the fish. The swimbladder has to be of the order of 5% of the total volume of the fish. If you have a fish of a certain shape, then the volume is proportional to the length cubed. For the fish we were dealing with, we were talking in terms of $4 \times 10^{-4} L^3$ for the volume of the swimbladder.

Shearer: Your first equation then was Haslett's equation based on the six specimens of whiting?

McCartney: Yes.

Barham: On the matter of 5 percent, some years ago I ran up some curves on this sort of thing where we measured displacement of the fish, then assumed the 5 percent factor for the volume of the swimbladder. Then, when we actually made measurements, we never really quite came up with this 5% figure. We were always a little short, it seemed, in the vast majority of cases. I assume that these are gadoid fishes and the swimbladder would be similar to that of a Pacific hake, which has a highly muscular wall around it. Maybe I missed it, but you make special note that what you measured is the dorsal aspect. Would you say again how important the angle of incidence of sound on the target would be?

McCartney: The angular dependence in the resonance scattering region is zero. The scattering is omnidirectional, or isotropic, if you like. In the region where the length of the fish or the length of the swimbladder begins to be comparable with the wave length, then scattering does become directional; there are lots of measurements on the directional properties. There are quite a lot of results which show angular dependence in the high frequency region, e.g., Love

and Haslett and some Norwegian results. We have concentrated on dorsal aspect because it is the most important from the point of view of echo sounding.

Winokur: I believe that in some of the data Richard Love will present later this evening, he does show a difference between the side- and dorsal-aspect target strengths. The dependence ranges from about 1 to 8 or 9 dB for ranges of L/λ from about 1 to 80.

SOUND EXTINCTION BY FISH IN ONE-WAY SHALLOW-WATER PROPAGATION

David E. Weston and Pamela A. Ching
Admiralty Research Laboratory
Teddington, Middlesex, England

ABSTRACT

Biological sound scattering is usually thought of in connection with reverberation; however, the effect may be important in one-way propagation as well, and therefore transmission measurements may also be used to study the scatterers. It is the acoustic extinction cross section that matters, since energy is lost because of both scattering and absorption. The effect appears to be of significance only for shallow water, because of the presence of fishes having swimbladders. Five different aspects or approaches are described below, drawing heavily but not entirely on experiments in the Bristol Channel.

(1) The best information relates to diurnal changes in level, broadly speaking the summertime level drops near sunset and rises near sunrise. This occurs because the fishes are in shoals by day, but at night they are dispersed and more effective in extinguishing the sound. The phenomenon is complicated, with at least seven diurnal patterns being distinguished, and also highly variable. The attenuation can be very large, e.g., at 700 Hz it is up to 2 dB/km. The latter is a result of a concentration of one 24-cm pilchard to approximately 10 m^3 of sea surface. (2) The dependence of level on range (and frequency) is governed by the sum of the boundary and the volume losses, and it is sometimes possible to assess the magnitude of the volume losses caused by the fishes. (3) The seasonal variation in transmission loss may provide similar information. (4) The presence of fish has been observed to affect the frequency dependence of the extra attenuation caused by high winds. (5) A fluctuation of a few minutes' period occurring in the summer daytime is also tentatively ascribed to fishes, although the mechanism may not be closely related to the fish attenuation already described.

INTRODUCTION

There are two fundamental points to be made about biological sound scattering, if a balanced picture is to be obtained.

1. The subject is of comparable importance for marine biologists and for physicists or oceanographers studying underwater acoustics. For the biologist the scattering of sound can be used as a tool for the study of marine organisms. For the physicist biological scattering plays a controlling part in many acoustic phenomena and can provide the solution to many mysteries. It is believed that this dual importance is now recognised.

2. Biological sound scattering may be investigated through echo-sounding, echo-ranging, or reverberation experiments. When it combines with biological sound absorption, however, it can

becomes a significant cause of attenuation. Thus we should pay almost equal attention to one-way and two-way effects.

It appears that sound attenuation resulting from marine organisms is not usually important in the deep sea (1,2). The present paper considers attenuation resulting from fishes in the shallow waters of the Continental Shelf and gives the story below split under five headings. Much of this relates to an extensive series of propagation experiments carried out in the Bristol Channel (3,4). This work is still in progress, so the object here is to summarize what has been published and also to bring the account up to date. The references happen to comprise a complete bibliography of papers on this subject from the Admiralty Research Laboratory, published or in an advanced state of preparation.

As general background it may be noted that the frequencies investigated lie mainly between 700 Hz and 3.5 kHz, and ranges extend to 137 km (74 nautical miles). Eleven different fluctuation mechanisms have been identified, including those of biological origin. This large number of effects makes it very difficult to study any given effect on its own, without ambiguity in interpretation.

DIURNAL EFFECTS CAUSED BY FISHES

The main evidence for fish attenuation comes from the difference between the propagation during the day and during the night. Large changes in received signal level may often be noticed at sunrise and sunset, as first discovered in 1963 (3). The patterns are attributed to fishes largely because of the timing relative to light intensity, and the knowledge that fish shoals break up when it gets dark and re-form when it becomes light. The scattering and absorption of sound by the fishes depends on their degree of aggregation; this is particularly important for pelagic fishes having swimbladders. At night the fishes swimming as individuals can produce a high overall attenuation. In the daytime when they are packed into shoals there is acoustic interference between the scatterers, and the attenuation they produce is less.

A systematic series of multifrequency amplitude fluctuation experiments was carried out in the Bristol Channel at regular intervals between May 1967 and September 1968 (5). A sequence of pulses of 4 sec duration at frequencies between 700 Hz and 3.5 kHz was transmitted every 100 sec, and received at ranges of 23 and 137 km. Sample curves from (6) are reproduced as Figure 1 and show the magnitude of the day-night differences over the 23 km (13 nautical mile) path.

Seven different diurnal patterns of attenuation against time have been distinguished, and a schematic representation of these patterns is shown in Figure 2, taken from (4). It is convenient to show patterns as centred about local midnight rather than midday. The first two patterns are the most common, and together outnumber the rest. Pattern 1 is an abrupt drop in signal level after sunset, often between 15 and 25 dB, followed before sunrise by a similar abrupt rise in level. Pattern 2 is a dip in signal level of between 10 and 20 dB, after sunset and before sunrise. Pattern 3 is a bowl-shaped gradual change in signal level of between 5 and 15 dB giving a reduced signal level at night. Patterns 4 to 7 grow progressively more complicated as shown, and the last two are also rather rare.

The character and magnitude of the patterns is extremely variable and is a partial result of changes in number, type, and aggregation behaviour of pelagic fishes. There may also be a contribution from bottom-living fishes that may swim upwards in the water column around twilight. In addition, pelagic fishes will often assume a shallower depth near dusk. Acoustically the depth of the fishes is important for three distinct reasons. First, the bladder resonance frequency is a function of depth. Secondly, there is the Lloyds mirror interference effect occurring near both the surface and the sand bottom. The acoustic pressure is reduced, the fishes are partly decoupled from the acoustic medium and the attenuation is reduced. Third, the sound velocity

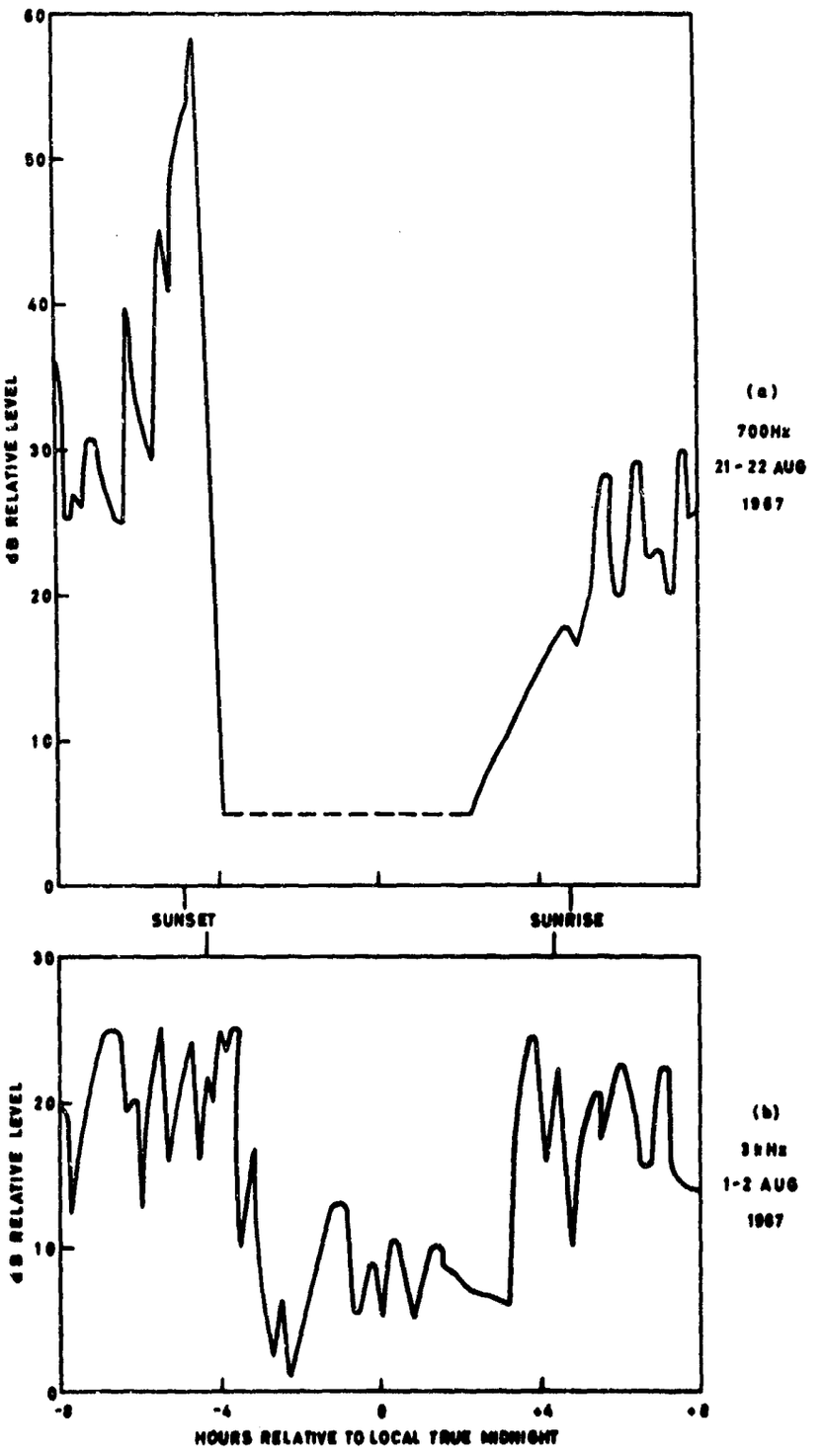

Figure 1. Examples of fish attenuation changes at a range of 23 km, illustrated by pulse envelope curves

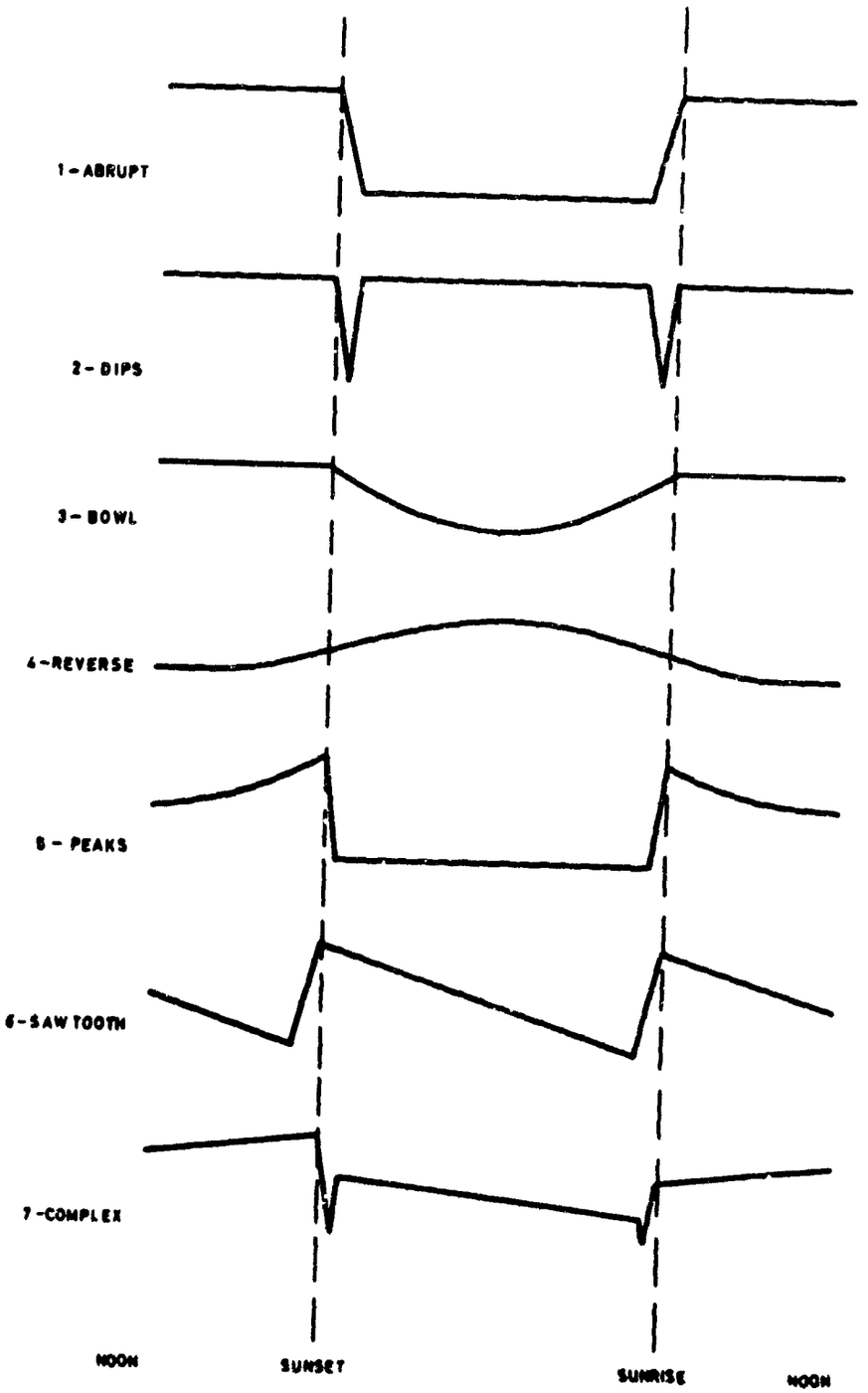

Figure 2. Schematic representation of attenuation patterns caused by fish (the scale of the level changes is highly variable, but perhaps 15 dB is typical)

structure may channel the sound, usually in the colder water in the lower half of the water column. This is important for the 137-km path, particularly in the summer months, and deep fishes can than have much more effect than shallow fishes.

The amplitude of the change in signal level for each pattern has been plotted against the time of year in Figure 3 (4) for the short-range 23-km path. The pattern may involve an increase or decrease in signal level at night. The main effects over this path occur between July and September, the higher frequency transmissions being affected about a month earlier than the lower frequencies. The maximum observed attenuation of at least 45 db occurred at 700 Hz, which is the lower limit of the measurements. It does seem as if the effect peaks near this frequency, with a Q-factor of about 2. A bladder resonance of 700 Hz corresponds, with a few reasonable assumptions on depth and tissue elasticity (1), to a fish length of 24 cm, almost certainly the Cornish Pilchard (*Pilchardus sardinus*). There is a second frequency peak which early data suggest is at about 3.2 kHz, corresponding to a 5.3-cm length, with no obvious fish candidate responsible.

From the measured attenuation and frequency it was possible to estimate the mean numbers of fishes in the 24-cm category as at least 0.12 per m^2 of sea surface with mass about 12 gm/m^2, or 107 lb/acre.

For the 137-km path the attenuation patterns are not limited to the summer months, and there are no marked frequency dependence effects as for the 23-km path.

RANGE-DEPENDENCE OF TRANSMISSION

If one tries to explain the shape of the curve of shallow-water signal level against range as resulting mainly from losses on boundary reflections, one runs into difficulties (7). One possibility is to suppose a significant bulk attenuation, perhaps because of fishes. This explanation can still work in the daytime because the diurnal variation of the fish effect is not necessarily a full-depth modulation, i.e., there may still be some fish attenuation remaining in the daytime. An experimental approach to this problem involves, first, an assessment of absolute transmission loss, and, second, an estimate of the losses due to the boundary. The latter follows from the number of normal modes that remain effective as carriers of energy, and this number can be obtained from dispersion, interference or depth-dependence measurements. Quantitative work of this type (5) has indicated that fish or other bulk attenuation is indeed important. The answer depends among other things on the frequency; well below our present frequency range ($<$700 Hz) boundary losses will predominate, and well above it ($>$3.5 kHz) the main loss is a result of the magnesium sulphate relaxation.

SEASONAL VARIATION IN PROPAGATION

The above ideas on the basic mechanisms of shallow-water sound propagation are supported by the seasonal dependence of the daytime transmission, which is much worse in the summer. The increased losses in the summer are apparently a result of a mixture of thermal and fish mechanisms (3,5).

WIND ATTENUATION

High winds, or rough seas, attenuate the signal level, affecting the higher frequencies first (3). It has been observed at times that the lower frequency transmissions are attenuated first in the daytime when the diurnal fish patterns are present. This is presumably because the fish shoals have been dispersed by the rough seas, and this dispersion has caused the attenuation.

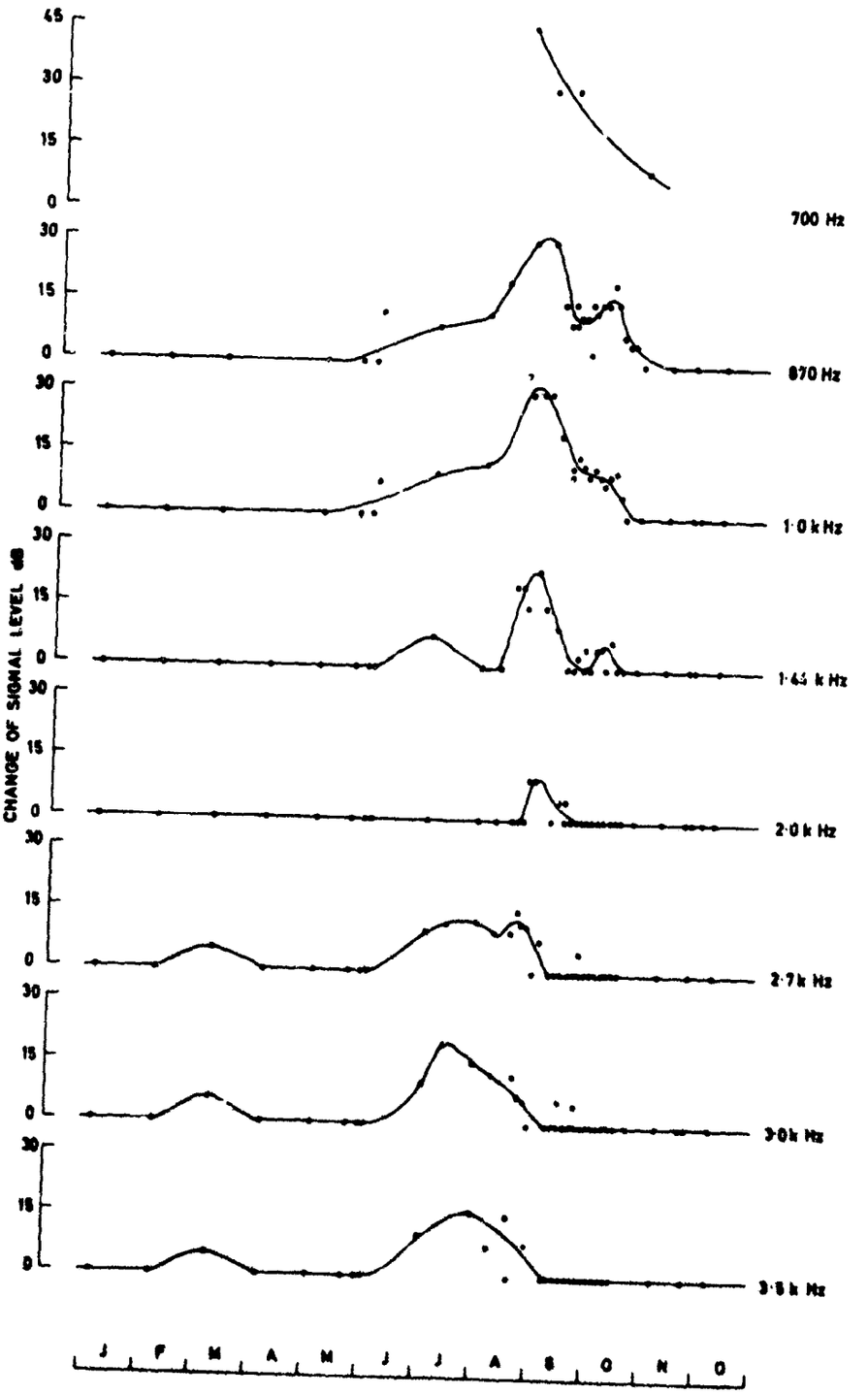

Figure 3. Seasonal dependence of diurnal level changes over 23-km path

FAST FLUCTUATIONS

Another fluctuation effect occurs in the summer daytime over the short-range path (3). During the night the envelope of the pulses is smooth, but during the day the amplitude variation is considerable and the envelope is rough, with a typical period of some minutes. The timing of the effect is closely allied to the attenuation patterns, suggesting that the cause again is fishes. This effect occurs over the whole frequency range and is most pronounced in August.

CONCLUSIONS

It is hoped that enough has been said to establish the fundamental part played by fish attenuation in all aspects of shallow-water propagation to medium and long ranges. There is the further possibility of gaining information on the fish populations.

ACKNOWLEDGMENTS

The experiments quoted are the work of a team, and we particularly wish to acknowledge the contribution of our colleagues whose names appear in the references.

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DISCUSSION

Batzler: I wondered if you have marked internal waves in this area and if so, if you associate any of your effects with these waves. If you do see some effect, how do you compare it with others more or less marked?

Weston: We do have internal waves in the area. We can see internal waves of both the semidiurnal tidal period and of shorter periods, that is, several minutes. We can see acoustic fluctuations due to these waves, but I would say that they are due to the direct effect of the internal wave in that one gets a variable refraction through the wave. I have not managed to find a tie-up between internal waves and fish of the sort that you are hinting at. Incidentally, we can use scattering layers to mark the internal waves on occasions.

Smith: Have you noted any lunar effects in the fish behavior?

Weston: The short answer is "No, we have not," and I think these are difficult to look for because there are so many other things happening. I suspect that there probably are such effects, but we haven't identified them.

Van Schuyler: In the initial portion of your paper you talked about these two peaks, resonant peaks, that I believe you associated with two particular sized individuals. I believe you also quoted a Q of 2.

Weston: Yes.

Van Schuyler: I just want to clarify a point. I may just have missed this, but is this what you term the group Q rather than an individual Q?

Weston: This is effectively a group Q, and it allows for the Q of the fish, the spread in depth of the fish, the spread in size of the fish, and anything else that happens. I'm just going by the attenuation measured as a function of frequency.

Van Schuyler: In some of the work you have done, you talked about a Q for a fish school as opposed to a Q for an individual. Was the Q of 2 for the whole fish school, or were you associating this with an individual animal?

Weston: The Q as measured here does not apply to a compact school of fish as such because when the fish are schooled, they are not producing a very large attenuation. It applies to the fish at night when the fish are dispersed, they are dispersed in both horizontal position and depth, and of course they have a spread in size, and this dispersed group is what the Q refers to.

SCATTERING RETURNS IN THE MEDITERRANEAN AND EASTERN ATLANTIC—DATA AND INSTRUMENTATION

Paul T. McElroy and Asa Wing
Woods Hole Oceanographic Institution
*Woods Hole, Massachusetts**

INTRODUCTION

While carrying out acoustic measurements in the ocean, investigators have repeatedly observed scattering of acoustic energy from discontinuities in the water volume itself. The most usual measurement is made with a common source and receiver. This monostatic geometry detects backscattering, whereas bistatic measurements (separate source and receiver) detect scattering at other angles. The scattering is generally due to discrete scatterers in the water volume; these scatterers have been identified as biological by several investigators. The effect is called volume reverberation to distinguish it from the scattering occurring at the water surface and ocean bottom and to distinguish it from a specific target of interest within the water volume. In many cases, particularly those reported in this Symposium, it is the reverberation itself which is of primary interest.

The usual parameter used to describe the reverberation is the volume scattering strength—the scattering area over 4π per unit volume—given as a function of depth and frequency. Many investigators report the integral of the volume scattering strength over the entire portion of the water column where it has significant value. This is usually the upper 500 fathoms (fm) of the column.

The authors have measured volume scattering returns at 12 kHz during Cruise 49 of the Research Vessel *Atlantis II*; during May and June of 1969, the *Atlantis II* steamed from Libya to the Strait of Gibraltar and thence to the Azores. The returns were tape recorded, and, upon being processed to give the integral of the volume scattering strength, showed some interesting geographical anomalies such as peaks in nutrient-rich regions. These results are reported here in the latter part of this paper.

The analog instrument used for this processing gives the integral of the volume scattering strength in real time**, the integral can be made between any two depths selected by the operator. Barham and Dullea (1970) are nearing completion of combined analog and digital systems, capable of real-time displays of the volume scattering strength. Until recently, it has not been possible to compute and display scattering strength in real time, so that echo-sounder records have been the only real-time display of scattering.

While the scattering results are what is of primary interest, the instrument—called the Integrator—is described here in some detail for two reasons: (1) this is the first reported use of

*Contribution No. 2495 from the Woods Hole Oceanographic Institution.

**Real-time measurements were made with this instrument during Cruise 1 of the Research Vessel *Knorr* in May 1970.

an instrument which the authors intend to use during future cruises, and (2) the description permits readers to evaluate the technique and its errors for comparison of the data with that of other workers.

THEORETICAL BACKGROUND

Adequate theoretical background for the measurement of the volume scattering strength with a piston-type transducer is given by Machlup and Hersey (1955), Hersey and Backus (1962), and the National Research Council (1947). Equation 30 from Hersey and Backus (1962) (combined with the unnumbered equation on page 524) gives the pressure $p(t)$ scattered back to the receiving transducer. It is

$$p^2(t) = \frac{V^2(t)}{B_{f_0}^2} = \frac{4\pi \times 10^4}{ct^4} \frac{P_0^2}{2} \tau_0 \alpha \beta \int_0^{\pi} s_v(r\cos\theta)\, b^2(\theta) \sin\theta\, d\theta. \qquad (1)$$

Most of the terms in this equation are defined in Fig. 1. In addition, $V(t)$ is the open-circuit received voltage at the transducer and B_{f_0} is the receiving sensitivity at $f_0 = 12$ kHz.

$s_v(r, \theta, \phi)$ is the volume scattering strength* at a position defined by r, θ, ϕ. It is the cross-sectional area per unit volume of scatterers effective in removing energy from the incident beam and returning it into a unit solid angle.

α and β are terms not found in Eq. 30 of Hersey and Backus (1962). That derivation assumes that the outgoing pulse has an ideal boxcar shape (see Fig. 1) of peak amplitude P_0. Due to transducer characteristics the actual pulses generated had more the teardrop shape shown in the top right of Fig. 1. If the peak of the teardrop is P_0, then the teardrop will have less energy than the boxcar. α is just the ratio of these two energies and is used to correct the source level in the experiments reported here.

β is a filter corrective factor compensating for the filters in the processing system. They are a little narrower banded than the ideal, which would pass most of the energy in the source pulse.

The assumptions necessary in the derivation of Eq. 1 are found in the literature (Hersey and Backus, 1962; National Research Council, 1947; Urick, 1967). Some that seemed particularly important in the operation of the Integrator are discussed here.

1. There must be enough scatterers in the volume insonified by the pulse that the scattered return represents an average property of the water volume rather than the return from a few individual targets. The Integrator averages variations from pulse to pulse by summing the returns from 100 separate pulses.

2. r must be $\gg c\tau_0/2$ so that source intensity does not change significantly over pulse length. For pulse lengths τ_0 of 2.67 msec the inner range limit has been set at 20 msec of two-way travel time.

3. Attenuation in the 12-kHz signal is ignored, introducing errors generally less than 1 dB.

4. To determine s_v, it must be removed from under the integral sign. Since the transducer beam pattern $b(\theta)$ is not infinitely sharp, $s_v(z)$ is averaged over some finite depth interval, that interval increasing linearly with depth:

*Those referring to Hersey and Backus (1962) will note that s_v, the present-day symbol for the volume scattering strength, has been substituted for m used in that paper. The m in that paper is the scattering strength, not coefficient despite normal usage, as is made clear by reference to pp. 2 and 4 of Machlup and Hersey (1955).

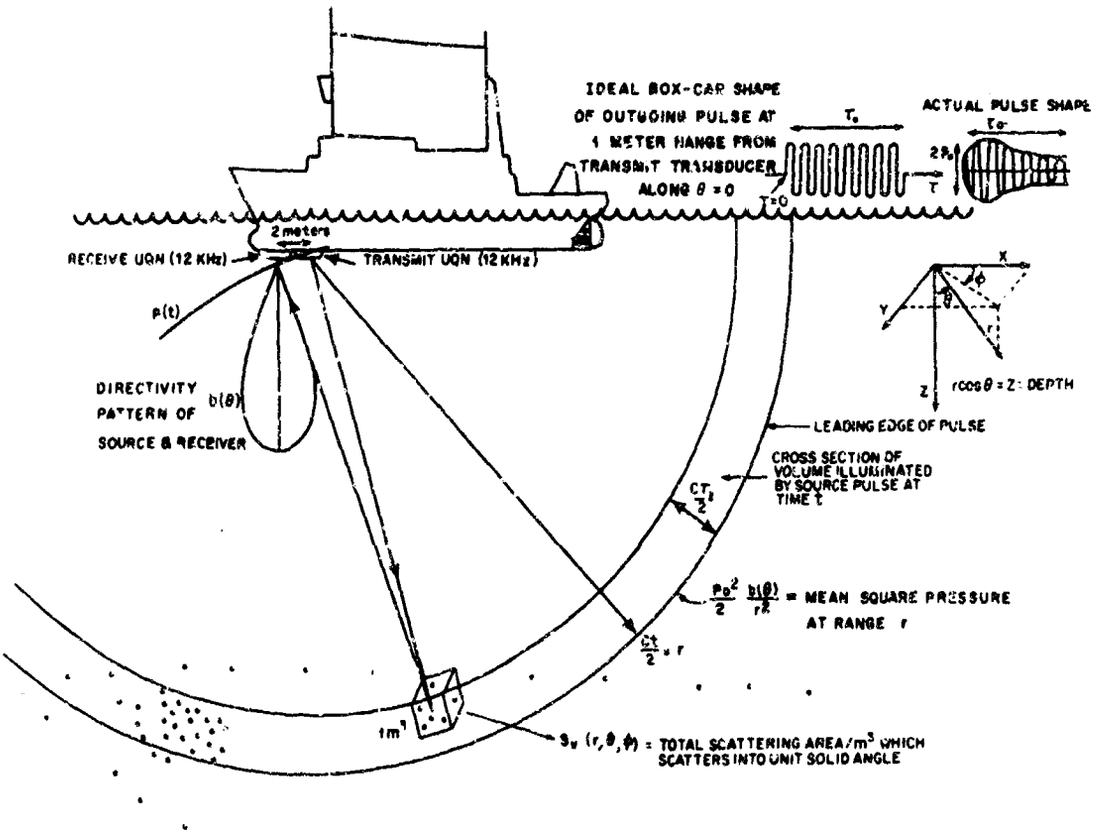


Figure 1. The geometry for integrator scattering measurements

$$\int_0^{\pi} s_v(r\cos\theta)b^2(\theta)\sin\theta\,d\theta \equiv \langle s_v(z)\rangle \int_0^{\pi} b^2(\theta)\sin\theta\,d\theta. \qquad (2)$$

The brackets $\langle\ \rangle$ are meant to emphasize that $s_v(z)$ is averaged over a depth interval.

A failure to appreciate the significance of the $b^2(\theta)\sin\theta$ integral can result in errors in setting the depth of fishing nets in relation to the scattering layers. In Fig. 2, notice that there is no contribution to the integral at zero degrees, the direction of maximum intensity in $b(\theta)$. This is because the volume element which depends on $\sin\theta$ goes to zero as can be seen in the right-hand portion of the figure. Rather the angle corresponding to maximum return is closer to θ_{max} = 12 degrees. r, the slant range to the layer at θ_{max} = 12 degrees, might be interpreted as its depth z as shown at the top left in Fig. 2. The difference $r\text{-}z/r = 1 - \cos\vartheta$ is a measure of the fractional depth error, only $1 - 0.98 = 0.02$ for the 12-kHz UQN. However, depth errors for scattering layers measured using transducers with broader directivity patterns could be sizable.

INTEGRATOR DESIGN

Combining Eqs. 1 and 2 and integrating over the depth interval z_1 to z_2 gives the integral of the volume scattering strength:

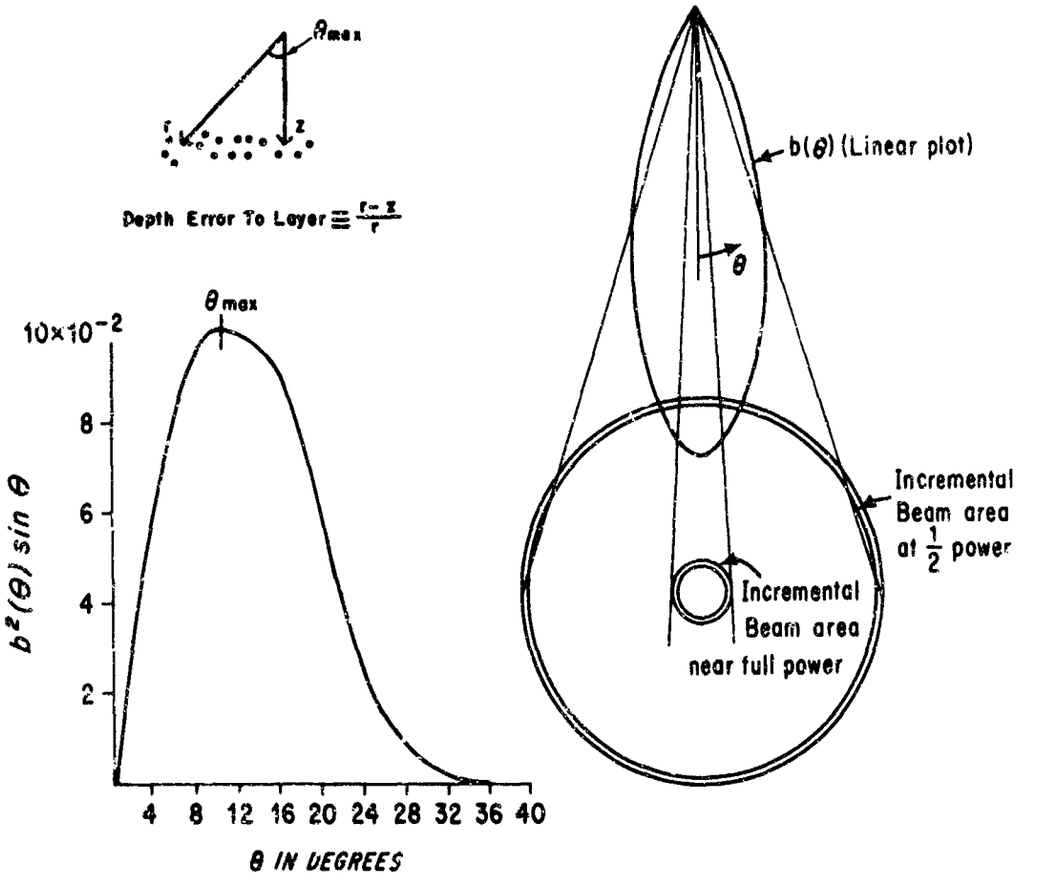


Figure 2. Directivity characteristics of the 12-kHz UQN transducer

$$\int_{z_1}^{z_2} \langle s_v(z) \rangle dz = \int_{t_1}^{t_2} V^2(t) t^2 dt \; \frac{1}{B_{J_0}^2} \left[\frac{P_0^2}{2} \tau_0 \alpha \right]^{-1}$$

$$\left[\frac{C^2}{8\pi 10^4} \right] \left[\int_0^{\pi} b^2(\theta) \sin\theta \, d\theta \right]^{-1} \beta^{-1}. \quad (3)$$

The Integrator is an analog instrument which evaluates this equation. It incorporates one additional feature, the summing of 100 successive integrations, to give an average value of the integral;

$$\frac{1}{100} \sum_{i=1}^{100} \int_{z_1}^{z_2} \langle s_{v_i}(z) \rangle dz. \quad (4)$$

Figure 3, the Integrator block diagram, is laid out in five major segments--pulse generation, received signals, timing, signal processing, and display. The quantities in parentheses are variables or parameters found in the $s_v(z)$ equation.

For instance in the transmit section, a reference time t_0 necessary to correct for spherical spreading is generated, and source pulse shape is measured. The transducer is calibrated at the end of the cruise. By using reference hydrophones, it was determined that the voltage magnitude and shape across the calibration resistor of a particular transducer are linearly proportional to the pulse in the water. Thus oscilloscope photos of this voltage during the cruise provide a calibration in source level, namely P_0 and α. Any variation is minimized by driving the transducer with a tone burst generator. There is always the problem of changes in transducer characteristics such as aging during the cruise. However, quenching was not a problem since data were collected while hove to in low sea states.

The receive section gives a $V(t)$ which contains both the scattering return and noise. In addition an electronics calibration signal is injected at this point. Transducer calibration at a later time gives B_{f_0}, the receiver sensitivity.

The timing section generates a signal gate at times t_1 and t_2 after t_0, corresponding to z_1 and z_2. In addition a ramp voltage proportional to t is generated and used to correct for spherical spreading. The timing section also counts the total number of integrations and shuts the system down when either 40 or 100 is reached.

Signal processing is straightforward. First there is a gate to remove the outgoing pulse from the receive transducer--to prevent amplifier overload. Note that there is the option of either tape recording or direct processing. An amplifier, tuned to match the source spectrum of the 2.67-msec source pulse, removes much of the broadband sea noise. The signal is next gated in the interval t_1 to t_2. It is then multiplied by the ramp voltage in a Philbrick analog multiplier. Squaring follows and then integration, using a high quality capacitor as feedback element in an operational amplifier circuit. Not only does the capacitor integrate a particular scan, but it sums all 100 scans. Readout is on a digital voltmeter.

There follows some further manipulation of Eq. 3. The final equation will relate readings on the digital voltmeter to the value of the volume scattering strength integral.

DVM (Signal) = digital voltmeter reading when scattering signal return is processed

DVM (Cal) = digital voltmeter reading when a calibration signal of 1 mv rms is applied across a calibration resistor at the receive transducer

K = constant of proportionality between signal at receive transducer and the digital voltmeter reading

$$\text{DVM (Signal)} = K \sum_{i=1}^{100} \int_{t_1}^{t_2} V_i^2 \,(\text{Sig}, t)\, t^2 \, dt \tag{5}$$

$$\text{DVM (Cal)} = K \sum_{i=1}^{100} \int_{t_1}^{t_2} V_i^2 \,(\text{Cal}, t)\, t^2 \, dt = K \times 100 \times 10^{-6} \int_{t_1}^{t_2} t^2 \, dt . \tag{6}$$

Combining Eqs. 3 through 6 gives a 100-sample ensemble average of the integral:

$$\left[\int_{z_1}^{z_2} < s_v(z) > dz\right]_{\substack{ensemble\\ average}} = \frac{1}{100}\sum_{i=1}^{100}\int_{z_1}^{z_2} < s_{v_i}(z) > dz$$

$$= \frac{1\ \text{DVM (Signal)}}{100\ \text{DVM (Cal)}} \times 100 \times 10^{-6} \int_{t_1}^{t_2} t^2\, dt \frac{1}{B_{f_o}^2}$$

$$\left[\frac{P_0^2}{2}\,\tau_0\alpha\right]^{-1} \frac{C^2}{8\pi 10^4}\left[\int_0^{\pi} b^2(\theta)\sin\theta\, d\theta\right]^{-1} \beta^{-1}. \quad (7)$$

Then, taking 10 log and evaluating each term yields

$$10\log\left[\int_{z_1}^{z_2} < s_v(z) > dz\right]_{\substack{ens.\\ av.}} = 10\log \text{DVM (Sig)} - 10\log \text{DVM (Cal)} - 60 + 10\log$$

$$\left[\frac{t_2^3 - t_1^3}{3}\right] + 77.9 + \left[-107.7 + 25.8 - 10\log\alpha\right]$$

$$+\left[49.5\right] + \left[15.1\right] + 1.0 = 10\log \text{DVM (Sig)}$$

$$- 10\log \text{DVM (Cal)} + 10\log\left[t_2^3 - t_1^3\right]$$

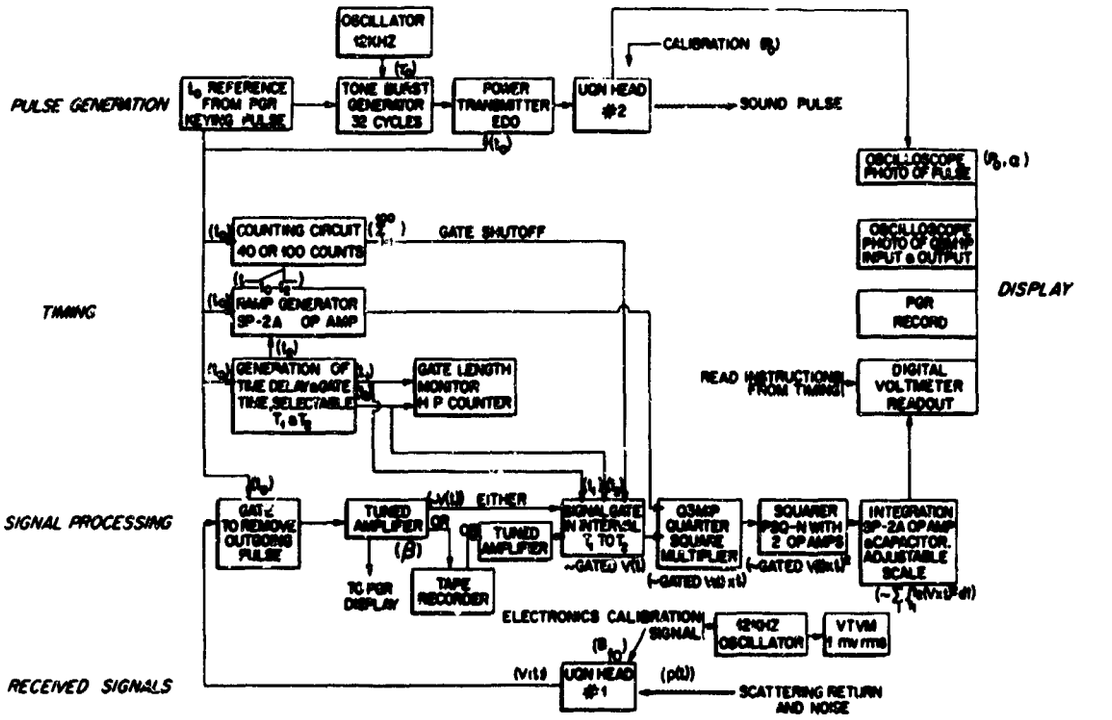
$$- 10\log\alpha - 3.2 \quad (8)$$

α is 1/3. The factor 3.2 dB applies only for the particular source levels and receive sensitivities in the transducers during Cruise 49 of *Atlantis II*.

ERROR AND ANALOG PROBLEMS

One serious problem was insuring that voltages were within the proper operating range for the analog components. The multiplier works best when both voltages are large. However with spherical spreading, the t ramp is small when the $V(t)$ signal is large and vice versa. The first step was dividing the processing interval into two segments: 0.02 to 0.1 sec and 0.1 to 1 sec. Then the ramp peak and the maximum $V(t)$ value were adjusted to just short of saturation levels. Generally the Integrator gave the same answer within ±2% over a 4-dB range in the attenuator used to set the $V(t)$ level. Outside this range the deviation would increase.

Reproducibility is quite good. The same answer is found within ±1/2% for a given signal processed repeatedly under the same conditions. The primary source of error is jitter in t_1 and t_2, a resolvable problem.



NOTE: 1. Numerous Monitor Points Incorporated. 2. Quantities in Parentheses are Parameters and Variables in Analytical Equations.

Figure 3. Integrator block diagram. Numerous monitor points have been incorporated. Quantities in parentheses are parameters and variables in analytical equations.

Noise is an important factor in the overall error of the system. Noise is measured during each data run and processed over the same $t_1 - t_2$ interval as that used for the scattering return. The digital voltmeter reading corresponding to this noise power is then subtracted from the voltmeter reading for scattering signal plus noise power described in Eq. 5. It is this noise-corrected signal which was used in Eq. 8 to give the ensemble average of the volume scattering strength integral. This procedure is that normally followed when noise data are available. For a simple squarer, this correction would be the one appropriate for an infinite ensemble, and hence the best guess for the finite sample of 100 scans.

However, in this instrument and perhaps in others, this procedure gives a low estimate of the noise correction as was shown by a simple test. A 12-kHz sine wave as signal and nearly Gaussian noise were combined in a passive adder and processed in three ways: signal, noise, and signal plus noise. The digital voltmeter reading for signal plus noise was always greater than that given by summing the readings for signal power plus noise power, whereas one would have expected it to be sometimes greater, sometimes less: greater when the cross products of signal and noise created by the squarer are greater than zero, less when the cross products are less than zero.*

The probable cause of this anomaly is the imperfect performance of the squaring unit which has a dynamic range of 34 dB. Weak noise signals are not properly processed.

In the experimental results reported in the following section noise power was very low, so that the errors introduced by improper correction will be small – less than 2%.

*The details of the signal-to-noise characteristics of a perfect squarer are found in Davenport and Root (1958). The contribution of the cross products of signal and noise to the deviation from the mean power are discussed; however, these cross products do not affect the mean power.

Other errors in the system are

1. Averaging of $s_v(z)$ over depth described in Eq. 2.
2. Errors in the calibration of source and receiver which could be ±2.5 to 3 dB. This affects the comparison of results with other investigators, and of results in two different cruises. It is not significant in comparing results within a cruise. There, relative errors are around ± 1 dB. Values may also be low in an absolute sense by up to 1 dB since there is no correction for attenuation.

RESULTS FROM CRUISE 49 OF ATLANTIS II

Taped records at 12 kHz taken during Cruise 49 of the Research Vessel *Atlantis II* from a point near Libya to the Azores during May and June of 1969 have been processed. Measurements were made between 2 and 3 p.m. local time each day, at silent ship. Figure 4 shows the track and values of the $s_v(z)$ integral in the range of 0.1 to 1 second of two-way traveltime, that is, a depth range of 75 to 750 m. The numbers are in decibels and are offset by 34 dB to better demonstrate the variation. Between extremes over the track, there is a range of 17.5 dB. It is −36 dB near Azores, 12 dB higher than typical values for this integral found by Marshall and Chapman in the western North Atlantic in the range of 6.4 to 12.8 kHz (Chapman and Marshall, 1966). It is uncertain whether this is a real difference or is somewhat a consequence of the fact that the results of two very different experimental geometries are being compared.

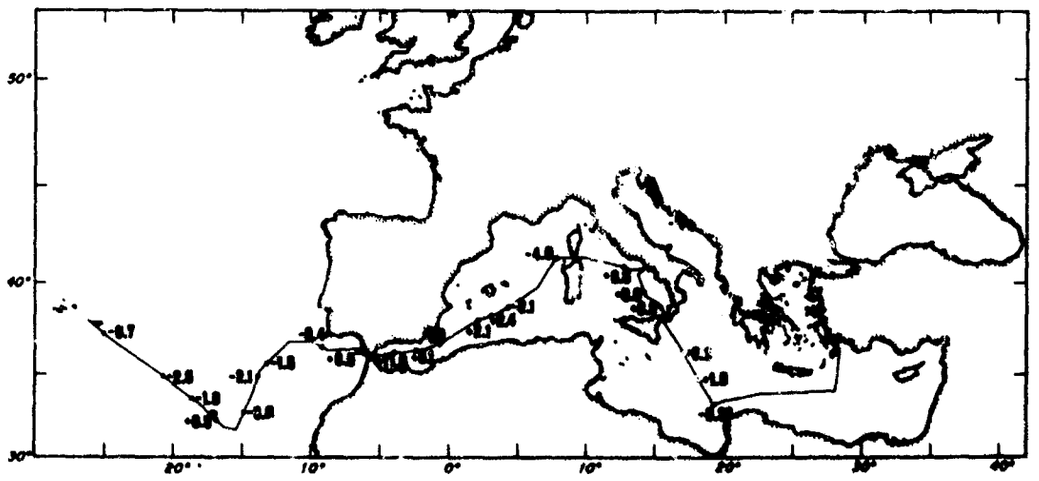


Figure 4. 10 log $\int_{z_1}^{z_2} s_v(z)\,dz$ + 34 DB along the track of cruise 49 of *Atlantis II* in the depth interval 75 to 750 meters

The measurement off Libya is in question since it was the first of the cruise and was subject to more errors. The peak near the Strait of Gibraltar is understandable from the known richness of that area. However, the peak near Stromboli is an interesting anomaly. According to E. F. K. Zarudzki (1970) the Mediterranean near Stromboli has unique qualities; there is underwater heating due to volcanic activity, and the area is a strong focus for swordfisherman. Perhaps vertical mixing due to heating at the bottom in this small region results in an area of high productivity accounting for the peak in scattering.

Figure 5 is another plot of the data found in Fig. 4. The offset value of the $s_v(z)$ integral is plotted against distance measured between acoustic stations along the track, a track chosen to

sample various parts of the Mediterranean and eastern Atlantic waters. The plot serves three purposes: (1) it displays more clearly the character of the variation in the data, particularly in passing from one region to another, (2) it facilitates the comparison with Fig. 6 made below, and (3) it shows that the major daytime scattering is between 75 and 750 m and not in a shallow dominant layer. The upper curve is for the time interval 0.1 to 1 second or 75 to 750 m in depth. The lower is for the interval 0.02 to 0.1 second or 15 to 75 m in depth. (Four data points are restricted to the interval 0.035 to 0.1 sec.) The processed value at each station is represented by the dots; these dots have been connected by straight lines to facilitate reading the curve. However, one should not infer that these straight lines accurately represent scattering values between stations, since local "hot spots," such as that found near Stromboli, might have caused significant deviations.

The lower curve, for near surface scatterers, shows structure markedly different from the upper curve. There is a general downward trend from Stromboli all the way west to the Azores. East of Stromboli, within the eastern Mediterranean, there is a sharp drop.

Figure 6 summarizes the character of the scattering as seen on the graphic recorder at each acoustic station. The horizontal axis is the same as in Fig. 5. The vertical axis is depth and the plots indicate relative intensity over depth of the scattering returns. The width of each block is a rough measure of the relative darkening of the record. Darkened rectangles are representative of diffuse scattering, while the hollow ones represent the crescent or irregular echoes representative of individuals or schools.

One interesting feature is the general rise in the bottom of the deepest layer as one approaches the Strait of Gibraltar from the east. At the station closest to the Strait, still some 70 mi away, the bottom of the deepest layer is at 340 m, the shallowest of any station, while the bottom is at 840 m. The sill depth is 300 m (Leroy, 1967). The upper water is Atlantic water, the lower the more saline Mediterranean, specifically, the Levantine water (Wüst, 1961). This Levantine water attains velocities of 100 cm/sec at the Strait at 275 m (Wüst, 1961). Perhaps the 12-kHz scatterers in the region of the Strait find the lower Mediterranean water inhospitable to them. It is a question worthy of further examination.

Recently, Barraclough, LeBrasseur, and Kennedy (1969) discussed the relative darkening of echo-sounder records along a cross-Pacific track and coupled it with a discussion of biomass. They limit themselves to three categories of echo-sounder record—dense, patchy, and absent—in suggesting possible biomass variations.

Such measurements, based on echo-sounder records alone, may be deceptive. Reference to the echo-sounder records of Cruise 49 would lead one to erroneous conclusions concerning scattering strength, let alone biomass. In Fig. 6 the strongest returns appear to be in the western part of the track, and the weakest in the central. Yet, exactly the opposite in measured scattering strength is seen in Fig. 5.

This unreliability in using uncalibrated echo-sounder records as a predictor of scattering strength from one day to the next should come as no surprise; there are too many variables affecting the quality of the records such as noise level and amplification.

ACKNOWLEDGMENTS

We offer special thanks to Richard H. Backus, who was instrumental in the original conception of the Integrator and who has maintained a steady interest in its development and use. Hartley Hoskins and James Heirtzler offered a number of valuable suggestions for improving this manuscript.

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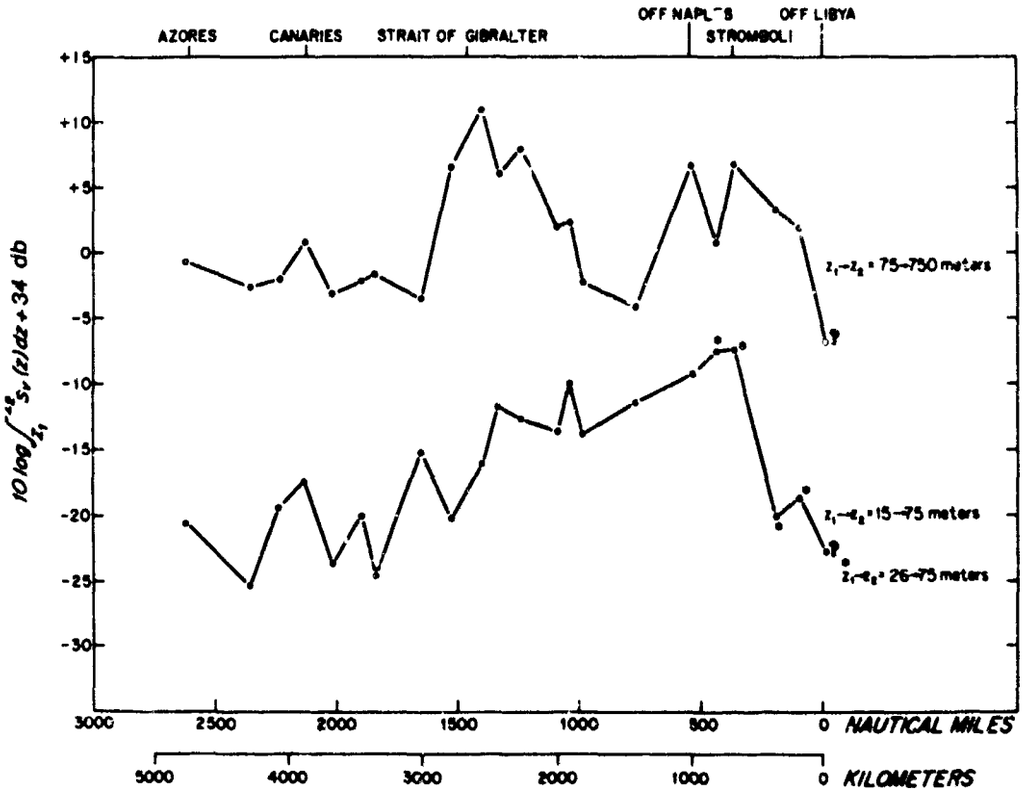

Figure 5. $10 \log \int_{z_1}^{z_2} s_v(z)\,dz$ versus distance along a line connecting acoustic stations during Cruise 49 of *Atlantis II*

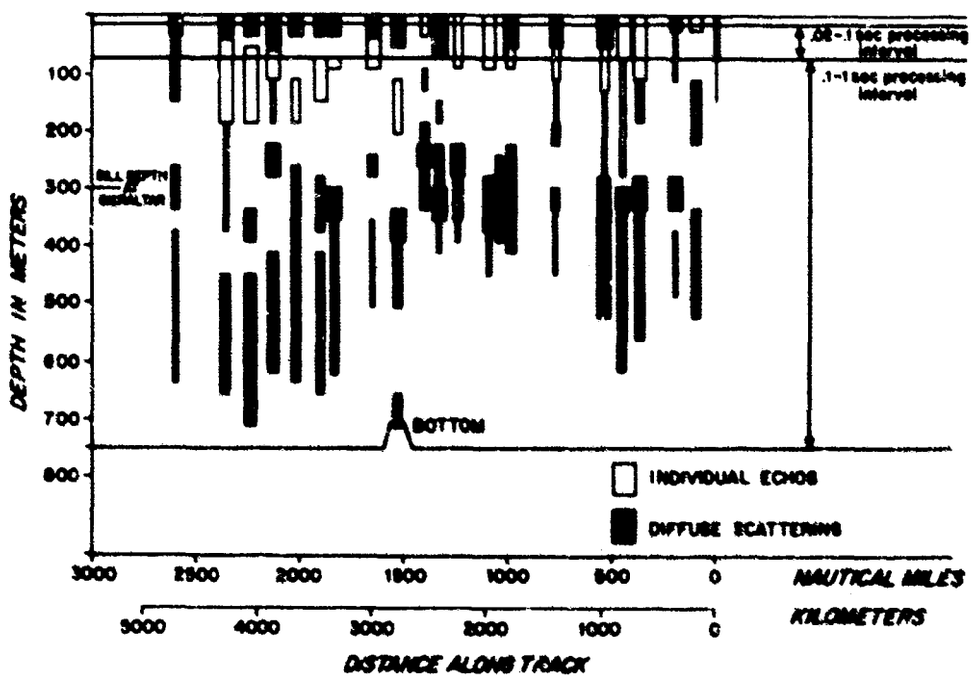

Figure 6. Scattering returns from the echo-sounder record taken during Cruise 49 of *Atlantis II* plotted versus distance along a line connecting acoustic stations

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DISCUSSION

Hanrahan: Paul, did I understand you to say that the minimum depth at which you see volume scatters is 225 ft, or 75 m, because of the blank in time of the receivers.

McElroy: You are talking about this last slide?

Hanrahan: I think midway through the paper you said that you were looking at the scattering from a depth of 75 m to something in the neighborhood of a 1000 ft.

McElroy: The maximum depth was 750 m, 75 to 750 m. At least as far as our echo-sounder records were concerned, at this particular frequency, which was 12 kHz, there was no indication on those records or on the oscilloscope photos of anything below that depth. But the last slide (Figure 6) shows the distribution, and it extends pretty well down to the maximum.

Hanrahan: Well, the point of my question is the minimum depth at which you see the scattering. Are you not limited to something on the order of 100 ft—you only see those scatterers below 100 ft?

McElroy: Yes, just because of the blanking, overloading, and so on. We tried to minimize that problem as shown in the block diagram. We had a gate right at the very beginning which was designed to remove the outgoing pulse. I should mention specifically that we used two different transducers. We transmit on one and receive on another, so that we were able to shrink that

gate time quite a bit. Our shortest gate time is looking at things after, say, 20 msec, which is a two-way distance of 50 ft, but I think that is reasonable just because we could see differences from day to day by using the gate. It was only because we used the gate and could protect our electronics that we could do this.

Hanrahan: My concern is that, in a place like the Mediterranean, unless your recovery time is sufficiently fast so you can see from 30 ft on down, an echo-sounder will give you a very optimistic value for scattering strength. There is work by La Spezia showing that the predominant scatterers, around 3.5 kHz at least, come up to a depth of about 20 ft at night.

McElroy: Yes, I think part of the questions on the recovery time of the transducer may be taken care of by the fact that we are using a different transducer to receive. There is no recovery time of the electronics because I do not hit them with too hard a signal.

Batzler: Have you seen successful in using this instrument underway?

McElroy: No, but I think that we are at that point now. We have taken unprocessed data at sea and run it through the instrument later. The real issue in running signals through it is whether you can believe what you get. The time we spent on our tape records has essentially developed some criteria in our own minds which would permit us to do a more intelligent job of using it underway. Of course the problem under way is that you get one crack at it. You have to set things up properly to process within the selected time interval. With tape records you can run over and over.

Batzler: I am not familiar with integrated scattering strengths in these areas, but if I interpreted your numbers correctly, these seem low to me.

McElroy: That is correct. Quite frankly, they seem low to me, and I spent a fair amount of time going over the equations making sure I was defining terms properly to see whether I left out a factor. That is still bothering me. For instance, just to amplify that point, the maximum value of the integrated coefficient over the 1-sec time was around -61 dB. If you take Chapman and Marshall's data from the western North Atlantic in the frequency range 6.4 to 12.8 during daytime, their value is -48 dB. I am bothered by it, and I do not know why at this point.

Batzler: A lot of people have been bothered by things like this in scattering. Maybe the third comment is the most important. Although you defined it clearly, you have spoken of scattering coefficient. I believe that if we go back far enough historically, it is scattering strength that you are talking about.

McElroy: Yes. I am referring to scattering into a unit solid angle rather than into 4π. I made sure I was not off by the 4π factor, although if I had been, it would have reduced my scattering strengths rather than increase them.

Batzler: I am sure you did not confuse any of the people who have been working in this field, but just let me emphasize that we talk about scattering coefficient, we talk about scattering strength, and we talk about column strength. The column strength is integrated, the scattering strength is what you talked about, and the scattering coefficient is different by 11 decibels.

McElroy: Right. It is the 4π factor.

A STATISTICAL THEORY OF OCEAN REVERBERATION*

David Middleton†
Cambridge, Massachusetts

ABSTRACT

A brief outline of a general theory of reverberation and similar types of first-order scattering is presented. The scatter propagation is expressed as a Poisson process in space and time and includes volume and surface reverberation for general geometries and monostatic and bistatic operation and for a variety of physical conditions. A summary of the approach used in the construction of the theory is given as well as some quantitative results. Scatterer structure is then discussed in relation to general mathematical models.

INTRODUCTION

A statistical theory of reverberation and similar first-order scattered fields has been developed from the assumption that primary (i.e., first-order) scattering is the principal mechanism, whether caused by organic, inorganic, or geometrical effects or their combinations (Middleton, 1967, 1972). In this paper, we present a very short summary of some of the principal concepts that are pertinent in various aspects to the problems encountered in the measurement and interpretation of scattering phenomena observed in the ocean. The motivation for this work comes originally from the field of statistical communication theory (SCT), which is concerned primarily with the transfer and processing of information from one point in space-time to another (Middleton, 1960), and where in applications like the present, one must deal with space-time *fields*, not with time processes alone (Middleton, 1970). Because measurement and observation are communication processes in this broad sense, it is entirely natural that the methods and ideas of SCT should prove essential in both the investigation of the physical details of scatter mechanisms and the inevitable and often formidable problems of data processing that follow upon data acquisition. In brief, our task is to develop a model of the scatter process (Middleton, 1967, 1972) that will adequately account for such controlling factors as geometry and propagation and will permit us to examine the scatter process itself. Coupled with this, of course, there must be appropriate experimental acquisition, support, and interpretation. Here theory and experiment mutually reinforce each other – the former providing the "macrostructure" (the general propagation model) and the latter, the "microstructure" (the physical detail and properties of the scatterers themselves, which must be phenomenologically introduced into the former). In this regard, the

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†Consulting Physicist 35 Concord Ave., Cambridge, Mass. 02138. Prof. of Communication Theory at the University of Rhode Island.

many studies of the biological scattering mechanisms presented in this volume provide essential data for the mathematical modeling of the effects of typical scatterers. In return, we expect that these analytical models may offer needed quantitative apparatus for experimental design, data processing, and interpretation.

A SUMMARY OF THE APPROACH

Let us begin with a very brief account of the approach used in the construction of the theory. The details are amply developed by Middleton (1967, 1972) with many references to current and previous work therein for those wishing to pursue these matters further.

The scatter propagation is expressed as a Poisson process in space and time. Both volume and surface reverberation are included for general geometries and monostatic and bistatic operation (in the far field) and for a variety of physical conditions. These are principally zero and nonzero (vertical) velocity gradients, scatterer and platform dopplers, multiple reflections from surface and bottom, and absorption in the medium (as well as in the scatterer). The medium (ocean) in this case is characteristically dispersive because of random scatterer and platform motion and the presence of nonzero velocity gradients (when turning points in the ray paths occur). The scatter mechanism is expressed canonically as a time-varying (linear) stochastic filter, whose properties may depend on location and direction of "illumination," as well as upon an intrinsic biological or inorganic structure. The model is "macroscopic" in that simple, equivalent point scatterers are used to represent the actual scattering objects (and/or interfaces between water, air, and bottom). The coupling of the signal source to the medium is represented by general transmitting and receiving apertures (arrays), which can be frequency dependent. Both broadband and narrowband illuminating signals are considered.

Next, a combination of ray theory and wave theory is used to obtain the typical form (in space-time) of the scattered radiation for general sources and geometries. The ray-theory approach gives us the geometric bounds on the propagation, while wave theory provides the more detailed physical structure. Ultimately, our useful observables are statistical—the means, covariances, and probability distributions of the resultant received scattered process $X(t)$. These are obtained by suitable averaging (under the original Poisson assumption). For sufficiently dense scattering, the resultant process is gaussian, so that the process covariance $K_X(t_1,t_2)$ gives essentially a complete statistical description. In any case, the mean $\langle X(t)\rangle$ and the covariance $K_X(t_1, t_2) = \langle X(t_1)X(t_2)\rangle - \langle X(t_1)\rangle\langle X(t_2)\rangle$ are among the most important macroscopic quantities to be estimated experimentally; and through them in turn the intrinsic or "microscopic" properties of the scattering mechanisms may be explored; i.e., their doppler, filter-response parameters (Q, resonant frequency), cross section (e.g., level), absorption, etc. A corollary question of central importance in dealing with data is the validity (physically, the stability of the underlying physical mechanism) of the experimental data ensemble from which we work to make our statistical estimates. We must test for this validity before going on to other statistical measures. This in turn requires a tighter hold on "ground truth" than heretofore, if the data are to be interpreted reliably (Middleton, 1969).

Of particular importance to operational tasks, including measurement, is the fact that the scatter processes are themselves nonstationary and often nongaussian. Nonvanishing means represent specular (i.e., coherent) scattering available practically only in the specular direction when the interface or scattering layers are sufficiently smooth. Also critical is the vertical speed profile with depth, because deviations from zero gradient can radically alter the propagation paths and hence the volume and surface domains of illuminated scatterers. This is illustrated by such varied modes as sound fixing and ranging (SOFAR), convergence zone (CVZ), surface duct, (SD), bottom-bounce propagation, and combinations of these (discussed with examples in Middleton

(1967, 1972), Part III). Again, geometry is controlling because one needs to know where, and would like to determine what, the scatter mechanisms are. The formulation of the theoretical model is broad enough to permit us to handle complex operational conditions and to provide needed structure for experimental design and evaluation of the results, as well as for the optimization or near optimization of the systems (signals, apertures, geometries) employed to obtain the desired data.

SOME QUANTITATIVE RESULTS FOR THE RECEIVED SCATTERED FIELD*

The basic wave equation governing propagation in an ocean with absorption and vertical (z-) inhomogeneity in the propagation speed c is

$$\left(1 + \frac{\alpha}{c^2(z)} \frac{\partial}{\partial t}\right) \nabla^2 p - \frac{1}{c^2(z)} \frac{\partial^2 p}{\partial t^2} = \begin{cases} -G_T(t,\xi); & \text{in source domain} \\ 0 & ; \text{outside source region} \end{cases} \quad (1)$$

where $p(t, \mathbf{R})$ is the ambient pressure field at a point $P(\mathbf{R})$, measured from the origin (O_T) of the primary (rectangular) coördinate system centered on the transmitting aperture; $\mathbf{R} = \hat{\mathbf{i}}_x x + \hat{\mathbf{i}}_y y + \hat{\mathbf{i}}_z z$ is the vector from O_T to $P(\mathbf{R})$, and ∇^2 is the usual Laplacian operator. Here $G_T(t,\xi)$ is the source function

$$G_T(t, \xi) = \int_{-\infty}^{\infty} A_T(\xi, f)\, S_{in}(f, \xi)\, e^{j\omega t}\, df, \quad (\omega = 2\pi f), \quad (2)$$

in which $A_T(\xi, f)$ is the aperture weighting of the transmitter, and $S_{in}(f, \xi)$ is the amplitude (spectrum) of the driving signal, applied to element $d\xi$ (at ξ) of the aperture. The far-field solution of (1) (valid within the conditions of the WKB approximation) is**

$$p(t, \mathbf{R}) \doteq \frac{1}{4\pi \ell_0(\mathbf{R})} \int_{-i\infty+d}^{i\infty+d} \mathcal{A}'_T \left[\left(\frac{\hat{\mathbf{i}}_T s}{2\pi i c_0}\right), \left(\frac{s}{2\pi i}\right) \middle| S_{in}\right]$$

$$Y_{path}(s \mid \mathbf{R})_{\nabla c}\, e^{s(t - \tau_{\ell 0})} \frac{ds}{2\pi i} \quad (3)$$

*From Middleton 1967, 1972, Part III.

**When the angles of the rays emitted from (and received by) the aperture surfaces are not close to $\pi/2$ (i.e., are not near the horizontal) we must replace $\hat{\mathbf{i}}_T/c_0$ and $\hat{\mathbf{i}}_R/c_0$ in (3) and (6) by $-\mathbf{a}_T$ and $\mathbf{a}_R$, $(1/c_0) \times$ (approx.) unit vectors *in the directions of the ray*, emitted and received at the respective apertures; $\mathbf{a}_R = \mathbf{a}_T$ for monostatic operation. See Part III of Middleton (1967, 1972) for details.

where for frequencies below O $(4\times10^4$ Hz)

$$Y_{\text{path}}\Big|_{\nabla c} \doteq \exp\left[\left(\frac{\hat{\tau}_0 \ell_0 s^2}{2c_0}\right) + \left(\frac{i\pi k}{2}\right)\right], \quad k = 0,1,2,\ldots . \tag{4}$$

Here c_0 is the sound speed at O_T; $\tau_0 = \tau_0(\mathbf{R})$, and $\ell_0 = \ell_0(\mathbf{R})$ are respectively the time along the path taken by the wavefront going from O_T to $P(\mathbf{R})$ and this path length. The explicit forms of ℓ_0, τ_0 of course depend on $c(z)$ (and thus on ∇c) and depth; for the convenient approximation of the speed profile by linear segments (in z), ℓ_0 is made up of suitably matched arcs of circles.

The quantity $\mathcal{C}'_T$ is a generalized beam pattern, defined by the spatial Fourier transform

$$\mathcal{C}_T \equiv \int_{V_T} A_T(\xi,f)\, S_{in}(f,\xi)\, e^{2\pi i \nu\cdot\xi}\, d\xi \tag{5}$$

where $\nu = \hat{\imath}_x \nu_x + \hat{\imath}_y \nu_y + \hat{\imath}_z \nu_z$ is a vector wave number defined in the direction of $P(\mathbf{R})$; e.g., where $\hat{\imath}_T$ is the unit vector* $\hat{\imath}_T = \mathbf{R}/|\mathbf{R}|$; $R \equiv |\mathbf{R}| = \sqrt{x^2+y^2+z^2}$, in the usual way. In (4), $\hat{\tau}_0$ is the *relaxation time* of the medium [$O(10^{-6})$ seconds or somewhat less in salt water], while $k \neq 0$ measures the number of turning points (changes of direction vertically) that a typical ray in the beam undergoes in getting to $P(\mathbf{R})$. The ocean, as is well known, acts like a linear filter, where the absorption is (logarithmically) proportional to range $\sim \ell_0$ and to the square of the frequency $\sim s^2$, cf. (4).

In the more general bistatic cases, where the receiving aperture R is not collocated with that of the transmitter T, we find on regarding a typical j^{th} point scatter (on a surface or in the volume) as a new source reradiating the field incident upon it, that the received scattered wave (now only a function of time because it has passed through the receiving aperture A_R) can be expressed (again for far-field operation)* as

$$\begin{aligned} U_j(t)_{\nabla c\neq 0} \doteq \frac{1}{4\pi^2 \ell_{01}\ell_{02}} &\int_{-i\infty+d}^{i\infty+d} \mathcal{C}_R\left(\frac{\hat{\imath}_{Rj} s}{2\pi i c_0}, \frac{s}{2\pi i}\right) Y_{\text{path}}\left(s\,\middle|\,\mathbf{R}_{2j}\right)_{\nabla c} e^{st}\frac{ds}{2\pi i} \\ &\times \int_{-i\infty+d}^{i\infty+d} \psi_M\left(\frac{s'}{2\pi i}, \frac{s-s}{2\pi i}\,\middle|\,\mathbf{R}_{1j}\right) \mathcal{C}'_T\left(\frac{\hat{\imath}_{Tj} s}{2\pi i c_0}, \frac{s'}{2\pi i}\,\middle|\,S_{in}\right) \\ &\times Y_{\text{path}}\left(s'\,\middle|\,\mathbf{R}_{1j}\right)_{\nabla c} \frac{ds'}{2\pi i} \end{aligned} \tag{6}$$

Here $\mathbf{R}_{1j}$, $\mathbf{R}_{2j}$ locate the jth scatter vis-a-vis O_T and O_R (the origins of the transmitting and receiving apertures, respectively), while $\hat{\imath}_{Rj}$ is a unit vector* in the direction of O_R along $\mathbf{R}_{2j}$.

*See footnote (**) p. 234.

in which

μ_j = $\left\{1 + \Sigma \text{ (relative doppler velocities)}\right\}_j \equiv 1 + \epsilon_j$

γ_{0j} = dynamic cross section of the j^{th} scatterer; a purely statistical parameter (over all j) with the dimensions of "speed".

Thus, a typical received scattered waveform is

$$U_j(t) \doteq \frac{\mu_j A^2 \, Q_{RTj} e^{i\mu_j \omega_0 (t - 2\tau_{\ell 0j})} \, S_{in}\left[\mu_j (t - 2\tau_{\ell 0j})\right]_0}{\left(4\pi \ell_{0Tj}\right)^2} \tag{11}$$

where

$$A = \exp\left[\left(-\hat{\tau}_0 \, \omega^2{}_0 \, \ell_{0T}/2c_0\right) + ik\pi/2)\right] \text{(absorption along the path)} \tag{12a}$$

and

$$Q_{RTj} \equiv \gamma_{0j} \mathcal{G}_R \left[\frac{-\hat{\mathbf{i}}_T f_0}{c_0}, f_0\right] \mathcal{G}_T \left[\frac{\hat{\mathbf{i}}_T f_0}{c_0}, f_0\right] \tag{12b}$$

is the (coupled-system) *scattering cross section* (dimensions of "area") relating transmitting and receiving apertures and the scatterer. The quantity f_0 is the carrier or central frequency of the driving signal whose (complex) envelope is $S_{in}(\ )_0$.

For this case (and our assumed Poisson statistics) the covariance function of the received scattered wave is found to be (Middleton 1967, 1972, Part IV)

$$K_X(t_1, t_2) \equiv \langle X(t_1) X(t_2)\rangle - \langle X(t_1)\rangle \langle X(t_2)\rangle \tag{13}$$

or

$$K_X(t_1, t_2) = \frac{1}{2} \operatorname{Re}\left\{B_X^* \; e^{i\omega_0 \tau}\right\} = R_X(t_1, t_2) \cos \omega_0 \tau + \Lambda_X(t_1, t_2) \sin \omega_0 \tau \tag{14a}$$

$$\tau = t_2 - t_1 \tag{14b}$$

and (*) denotes the complex conjugate. Specifically, we have

$$B_X(t_1, t_2) = \langle e^{i\omega_0 \epsilon \tau}\rangle_\epsilon \frac{1}{(4\pi)^4} \int_{\Lambda'(S \text{ or } V)} \sigma'[S \text{ or } V] \frac{A^4 < \left|Q_{RT}(\mathbf{R} f_0)\right|^2 >_{\gamma_0}}{\ell_{0T}(\mathbf{R})^4}$$

$$\times K_0\left[t_1, t_2 \;\middle|\; \tau_{\ell 0}(\mathbf{R})\right] d\mathbf{R} \tag{15}$$

with $d\mathbf{R} = dR\, d\varphi$, or $dR\, d\theta\, d\varphi$ (for surfaces S or volumes V, respectively); Λ' is the jointly illuminated *and* viewed domain of scatterers; σ' is the effective density of scatterers (and like A, can depend on geometry), and

$$K_0 = \left\langle S_{in}(t_1 - 2\tau_{\ell 0})\, S_{in}(t_2 - 2\tau_{\ell 0})^*_0 \right\rangle_{\text{signal}}$$

$$= \text{covariance of the complex signal envelope where } S_{in}(t) = S_{in}(t)_0\, e^{i\omega_0 t}. \tag{16}$$

The quantity

$$\langle e^{i\omega_0 e\tau} \rangle_e = \text{the characteristic function of the doppler distribution}$$

$$= \int_{[e]}^{\circ} e^{i\omega_0 e\tau}\, w(e)\, de;\ e \equiv \mu - 1\,. \tag{17}$$

With (15) to (17) in (14) we have a full "anatomization" of the covariance, showing its detailed structure and the role that geometry plays in problems of this type.

For signals of short duration we have a nonvanishing value of K_0 only in the ranges (along the path) within the duration time of S_{in}; i.e., about the range $t_1 \approx 2\tau_{\ell 0}$ so that

$$K_0(t_1, t_2 \,|\tau_{\ell 0}) \doteq K_0(\tau) = \langle S_{in}(0)_0\, S_{in}(\tau)_0{}^* \rangle \tag{18}$$

and (15) becomes

$$B_X(t_1, t_2) \doteq K_0(\tau) \langle e^{i\omega_0 e\tau} \rangle_e \cdot B_0(t_1) \equiv B_X(\tau \,|\, t_1 = 2\tau_{\ell 0}) \tag{19a}$$

with

$$B_0(t_1) \equiv \frac{(\sigma' A^4 \langle |Q_{RT}|^2 \rangle)_{R_1}}{(4\pi)^4\, \ell_0(R_1)^4} \tag{19b}$$

where $t_1 = t_1(\mathbf{R}) = 2\tau_{\ell 0}(\mathbf{R})$ and $|\mathbf{R}|$ locates the physical *geometric* (≠ path) range vis-à-vis the receivers. Thus, $K_X(t_1, t_2) \doteq K_X(\tau \,|\, t_1)$ is now the covariance of a locally stationary process X, whose statistical properties, of course, still depend on range (t_1). The comparative simplicity of $K_X(\tau \,|\, t_1)$ [Eqs. (19a, b) in (14)] makes it very convenient when signals of short durations are used.

Finally, for many oceanographic applications, particularly in the study of scattering layers in the ocean, the geometry becomes quite simple. Beams directed vertically down from at or near the surface are employed. For reasonable beam widths the effects of nonzero (vertical) velocity gradients are negligible, and we can replace path length ℓ_{0T} by the geometric distance R_j from

source to scatterer. The various terms in K_X that depend on path length and time along the path are correspondingly simplified.

SOME REMARKS ON SCATTERER STRUCTURE

Clearly, a key element in the theory is our choice of response function (h'_M) for a typical scatterer. Probably the most general model we need consider has the structure

$$h'_M = \gamma(t)\, h_F(\tau) \tag{20}$$

where $\gamma(t)$ represents a possible time-variation expressed as a variable level, and h_F is the (linear) circuit representation of the scatterer. Thus, for example, if the scatterers are a body (or school) of fishes, moving through the beam, and changing aspect while in it, $\gamma(t)$ will change. Furthermore, if like so many such scatterers, these fishes have airbladders, they will act like resonant LCR circuits of moderate (to low) Q where

$$h_F(\tau) = \frac{e^{-\alpha\tau} \sin \omega_1 \tau}{\omega_1 LC} \tag{21}$$

where

$$\omega_1 = \sqrt{\omega_0^2 - \omega_F^2}$$

$$\omega_F = \alpha = \frac{R}{2L}$$

$$\omega_0^2 = \frac{1}{LC} \quad (> \omega_F^2 \text{ here}).$$

For simplicity let us suppose that the change of aspect of the fishes in the beam is slow with time, so that $\gamma(t) \doteq \gamma_0$. Then, with weak doppler (the usual case), (10) can be shown to be

$$\Psi_{Mf} \doteq \mu_f \gamma_0 e^{-2s'\mu_f \tau_{0f}} \delta\left(s - \mu_f s'\right) \left\{ \frac{2\pi i}{LC\left[(\alpha + s)^2 + \omega_1^2\right]} \right\} \tag{22}$$

which from (6) in our narrowband example [(10) et seq.] yields the modified waveform

$$U_f(t) \doteq \frac{\mu_f A^2 Q_{RTf} \displaystyle\int_{-\infty}^{\infty} e^{i\mu_f \omega_0 (\tau - 2\tau_{0f})} S_{in}\left[\mu_f(\tau - 2\tau_{0f})\right]_0 h_F(t-\tau)\, d\tau}{\left(4\pi \ell_{0Tf}\right)^2} \tag{23}$$

with h_F given by (21) in the expected way. The typical scattered wave is, in effect, filtered by the scatterer, with a consequent modification of waveshape. Where the input signal to the medium is tuned to the resonant frequency of the fish bladder (or more precisely, to that of the fish, which is close to it), $f_{0\text{-sig}} \approx \omega_1/2\pi$, we may expect the largest return, with smaller returns as $f_{0\text{-sig}}$ departs from $\omega_1/2\pi$. Again, this is entirely to be expected.

Other models must be constructed for scattering caused by random interfaces, but the same general type of model may be postulated: At the sea surface we should introduce an absorbing

or RC filter, ($h_F = \alpha e^{-\alpha\tau}, \alpha = 1/RC$), when the sea state is heavy and there is consequently a noticeable bubble layer below the air-water interface. In other cases, where this bubble layer is absent or negligible, the single point-scatterer model of our narrowband example in the previous section appears a good initial choice. Again, for bottom scattering, we may expect a similar absorbing filter with different parameters. All this is clearly phenomenological and guided by our present concepts and knowledge. Actual numbers and often the applicability of our choices must be obtained and established by experiment. The data on biological scatterers (fishes, etc.), for instance, presented in many of the accompanying papers of this Symposium should prove a valuable source of information, from which we may hope to obtain useable models and parameters along the lines just indicated.

CONCLUDING REMARKS

A very brief outline of a general theory of reverberation and similar types of first-order scattering has been presented to call attention to the fact that workable, quantitative models of the scattering processes in the ocean are available for study and use, not only for the ultimate purposes of information processing and communication, but also for the guidance and interpretation of experiments directed toward a detailed examination of the scattering mechanisms themselves. In conjunction with adequate statistical tests as to the validity of the data (Middleton, 1969), available biological information should play a critical role in determining the pertinent parameters of our phenomenological scatter models; and this in turn should make possible a realistic description of reverberation, which is needed in a variety of other signal processing problems. No attempt at completion is intended here; the technical details are fully covered in Middleton (1967, 1972).

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TIME VARIATIONS OF SOME ACOUSTIC VOLUME REVERBERATION PARAMETERS*

Robert L. Swarts
Honeywell Inc.
Seattle, Washington

ABSTRACT

In recent experiments in the Strait of Juan de Fuca, north of Seattle, Washington, sequential reverberation records were produced using pulsed continuous-wave signals and a vertically oriented, bottom-mounted, narrow-beam transducer. Several hundred pulse sequences were transmitted on the hour for 250 consecutive hours. The resulting reverberation was demodulated in quadrature and recorded on analog tape. The tapes were returned to the laboratory and digitized. Estimates of data parameters were then obtained using ensemble averaging techniques, and the behavior of the estimates as a function of time was studied. Special attention was given to the determination of probability density functions, detection of environmental nonstationarity by testing the data for statistical inhomogeneity, and isolation of spatial-temporal patterns in the volume backscattering strengths. Volume scattering strengths for the whole 250-hour period were obtained as a by-product of the latter activity. Diurnal variations as well as higher frequency space-time changes are clearly indicated.

INTRODUCTION

The work leading to the material discussed in this paper began in 1967 as an attempt to ascertain the validity of a theory of first-order reverberation developed by Dr. David Middleton (1967). Dr. Paul Moose (1968, 1970), using Middleton's results, investigated the behavior of the autocovariance function of the reverberant signal when certain simplifying assumptions were satisfied. He devised experiments similar to those subsequently announced by Ol'shevskii (1967) for estimating that function. The results of the experiments (Swarts, 1969a; Moose and Swarts, 1969) led to the supposition that in most cases the environment was neither homogeneous nor stable enough to allow valid estimates to be obtained.

This led to another series of experiments, under the ONR sponsorship, aimed at a more direct approach to the determination of environmental stability. Recordings of the reverberation were made over an extended period; these were returned to the laboratory and processed on a digital computer. Acoustic backscattering strengths and target strengths were obtained, and the demodulated data were tested for statistical homogeneity using a nonparametric test.

The results of these experiments are contained herein. The reader interested in equipment details, calibration, error analysis, and supporting environmental data is referred to Swarts (1969b).

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THEORY

Figure 1 is a functional description of the significant aspects of our experimental hardware. The signal to be transmitted is generated, as shown on the left-hand side of the figure, by amplifying the gated output of a sinusoidal signal source. That signal is conveyed via a transmit/receive relay switched in synchronism with the gate, to an underwater sound transducer mounted on the sea bed. The resulting reverberation signal is received by the same transducer; and, with the transmit/receive relay in its receive mode, this signal is preamplified and demodulated in quadrature. The outputs of the demodulator are low-pass filtered and recorded on a precision analog tape recorder for processing in the laboratory.

If it is assumed that within the beam width of the transducer, the medium is homogeneous and isotropic, and if multiple scattering is insignificant, then it can be shown (see Appendix A) that the demodulated signal caused by a small volume element containing N point scatterers is as indicated in equation (1), Figure 2.

In equation (1)

α = system gains and conversion factors
$\tilde{f}(\theta,\phi)$ = pressure beam pattern of transducer
θ,ϕ = angular coordinates of elemental volume
R_i = range to ith scatterer
$\beta_i = 2v_i/c$ = ith scatterer doppler factor
v = on-axis velocity component
$|\tilde{\sigma}_i|$ = reflectivity of ith scatterer

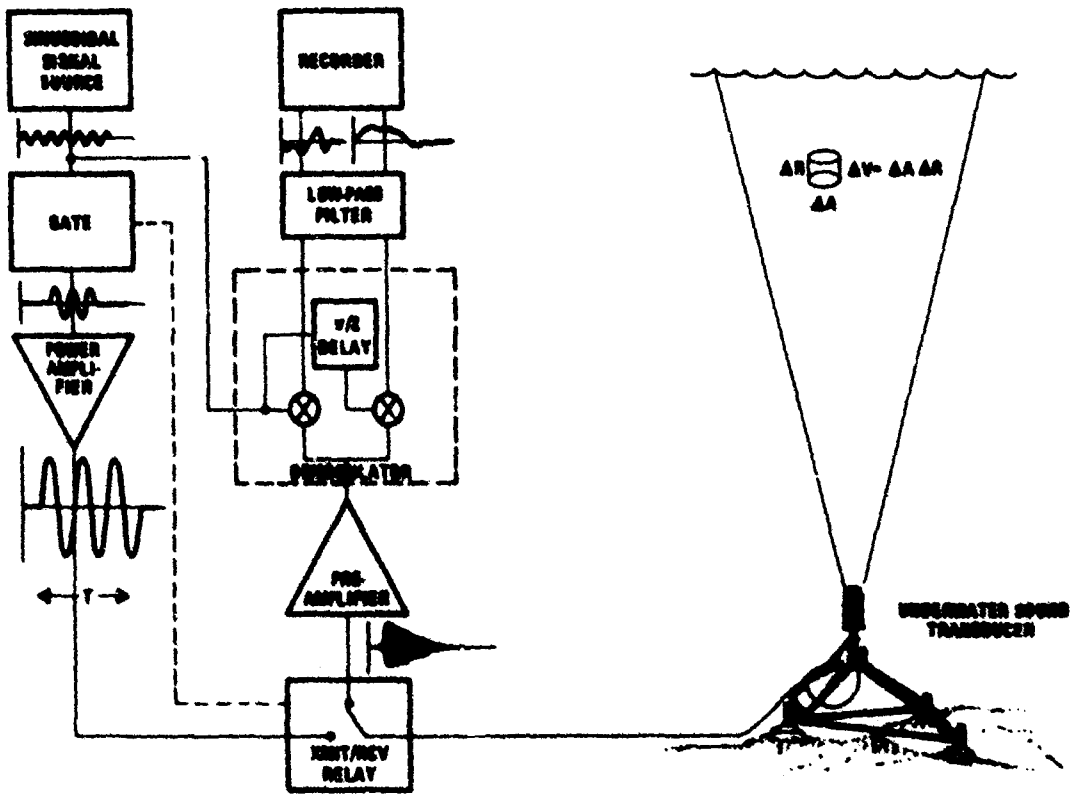

Figure 1. Functional description of experimental system

Output of Low-Pass Filters

$$\tilde{r}(t) = \alpha \tilde{f}^2(\theta, \phi) \sum_{i=1}^{N} x\left(t - \frac{2R_i}{c}\right) \frac{\tilde{\sigma}_i}{R_i^2} e^{j\omega\beta_i t} e^{-j\omega \frac{2R_i}{c}} \quad (1)$$

$$\tilde{r}(t) = \alpha \tilde{f}^2(\theta, \phi) \sum_{j=1}^{M} \sum_{i=1}^{N_j} x\left(t - \frac{2R_{ij}}{c}\right) \frac{\tilde{\sigma}_{ij}}{R_{ij}} e^{j\omega\beta_{ij} t} e^{-j\omega \frac{2R_{ij}}{c}} \quad (2)$$

Autocovariance of $\tilde{r}(t)$

$$\tilde{K}_{rr}(t, \tau|N) = E[\tilde{r}(t)\tilde{r}^*(t+\tau)] \quad (3)$$

$$\tilde{K}_{rr}(t, \tau/N) = \sum_{j=1}^{M} \tilde{K}_{rr}^{(j)}(t, \tau|N_j) \quad (4)$$

$$\tilde{K}_{rr}(t, \tau) = \sum_{j=1}^{M} \int_{\text{All Directions}} \frac{\tilde{K}_{rr}^{(j)}(t, \tau|N_j)}{N_j} \rho_j(t, \theta_k, \phi_k)\, dV_k \quad (5)$$

$$\tilde{K}_{rr}(t, \tau) = \frac{\alpha^2 4\pi}{d} \sum_{j=1}^{M} \tilde{K}_{\sigma_j}(t, \tau) \tilde{\Psi}_{\beta_j} \rho_j(t) \frac{1}{R^2} \int_{R - \Delta R/2}^{R + \Delta R/2} x\left(t - \frac{2R_i}{c}\right) x\left(t + \tau - \frac{2R_i}{c}\right) dR_i \quad (6)$$

$$\hat{\tilde{K}}_{rr}(t, \tau) = \frac{1}{P} \sum_{\ell=1}^{P} \tilde{r}_\ell(t') \tilde{r}_\ell(t' + \tau) \quad (7)$$

$$\sigma_{rr}^2(t) = \frac{4\pi \alpha^2 A^2}{dR^2} \frac{cT}{2} \sum_{j=1}^{M} \overline{|\tilde{\sigma}_j(t)|^2} \rho_j(t) \quad (8)$$

Figure 2. System-environment relationships

If there are M classes of scatterers present, then $\tilde{r}(t)$ can be written as in equation (2), where the sum of the N_j is N.

The autocovariance of $\tilde{r}(t)$ is defined in equation (3). The asterisk denotes complex conjugation.

If the scatterer classes are independent, equation (4) results from noting that the expected value of a sum of independent random variables is the sum of the individual expectations. The (j) denotes the covariance from the jth class alone.

It is shown in Appendix A that if the scatterers within a class are independent and uniformly distributed throughout ΔV, and if the scatterer parameters $\tilde{\sigma}$ and β are independent and identically distributed for each scatterer, then $K_{rr}^{(j)}$ depends directly on N_j. If we (a) substitute for N_j, the product of the scatterer density in the kth elemental volume and the volume of the element, (b) let the base of the element ΔA shrink to the limit, and (c) integrate over all directions, we obtain the total unconditional autocovariance as indicated in equation (5). R is the range to the kth element and θ_k, ϕ_k its coordinates; $\rho_j(t)$ is the local jth class scatterer density at time t.

Making use of equation (2), and requiring $R >> \Delta R$, Equation (5) has been solved yielding equation (6); where d is the directivity factor of the transducer, $\tilde{R}_\sigma$ the scatterer reflectivity autocovariance, and $\tilde{\psi}_\beta$ the doppler characteristic function.

Some care must be taken in using this equation. In words one can say that equation (6) represents the autocovariance of the complex reverberation envelope at range R and at time t for a delay of τ. Suppose a sequence of pulses, each of width T, centered in time about t is transmitted with sufficient time between pulses so that the reverberation from one pulse has died away before the succeeding pulse is transmitted. Let P be the total number of pulses and D the interval between them. The autocovariance can then be estimated as in equation (7), where $t = (2R/c)$ is the time required for each pulse to travel from the transmitter to range R and return. Unfortunately, implicit in this estimation technique is the requirement that the statistics involved be stationary over the time required for the transmission of all pulses, PD; and that the scattered field be homogeneous over the range interval ΔR; that is cT.

It is precisely because the environment is neither sufficiently stationary nor homogenous that previous attempts to obtain valid estimates of the autocovariance failed.

To obtain a necessary condition for the estimation of the autocovariance, let $\tau = 0$ in equation (6) and let the transmitted envelope $x(\cdot) = A$, a constant, if its argument lies between 0 and T. Noting that the autocovariance for zero delay is the variance of the signal, equation (8) results.

This equation is important for two reasons. First, it says that if only one type of scatterer is present, the autocovariance can be estimated only if the product of the mean square scatterer reflectivity and scatterer density do not vary over the estimation period. If those parameters change with time, so does the variance of the complex reverberation envelope and thus so does any statistic of second or higher order that depends on the output of our receiver. Further, if more than one class of scatterers is present, the same argument holds for the sum of the products.

Second, by comparing equation (8) with the expression for the received reverberation intensity level from volume backscattering given in *Physics of Sound in the Sea*, we note that the summation is equal to the scattering cross section divided by 4π, which Urick (1967) gives as the antilog of the scattering strength. Because scattering strength is equivalently target strength per unit volume, we conclude that $10 \log |\tilde{\sigma}(t)|^2$ is the average target strength of a scatterer. Observe, however, that if the scatterers are not uniformly distributed throughout the insonified volume, this latter conclusion is invalid. In the limiting case of a single scatterer, interpretation of $|\tilde{\sigma}(t)|^2$ in equation (8) as target strength will result in a value that is far too small.

EXPERIMENT

Using the results just discussed as a guide, an experiment was developed to test directly the period over which the statistics of a reverberation signal might be considered stationary. In the sense expressed by equation (8), that period may also be considered the period of environmental stationarity.

Our acoustic equipment was deployed in the Strait of Juan de Fuca, north of Seattle, Washington, in water about 280 feet deep. Data were collected over a 10-day period at 28 kHz; pulse widths were either 1.6 or 3.2 msec. Data processing during each ping interval was terminated prior to the first surface return. On-site measurements showed that the fourth surface-bottom return could not be detected. The pulse repetition time was accordingly set at 0.4 sec.

Individual pulse and N-ping average scattering strengths were computed as a function of range. Figure 3 is a typical plot. In this case, data have been averaged over 200 pulses. Because the pulses were spaced 0.4 sec apart, the plot reflects data from an 80-sec period. If this plot is used to compute an approximate value for the scattering strength of the water column, the result is about 4 dB higher than that reported by Chapman and Marshall (1966) at 15 kHz and about 13 dB higher than that reported by Gold and Van Schuyler (1966) at 20 kHz. The discrepancy may be explained in part by the difference in frequency, but is more probably attributable to the presence, in our case, of a relatively dense, uniform scatterer population rather than the layered structure felt to be present in the cited experiments. The scattering strength of the total water column when the scattered signal stems largely from a layer of thickness less than the total water depth must necessarily be less than the scattering strength of the water column within the layer. The extent of the difference depends strongly on the ratio of the thickness of the layer to the depth to the bottom of the layer. The same effect tends to mask large diurnal variations in scattering strength with depth.

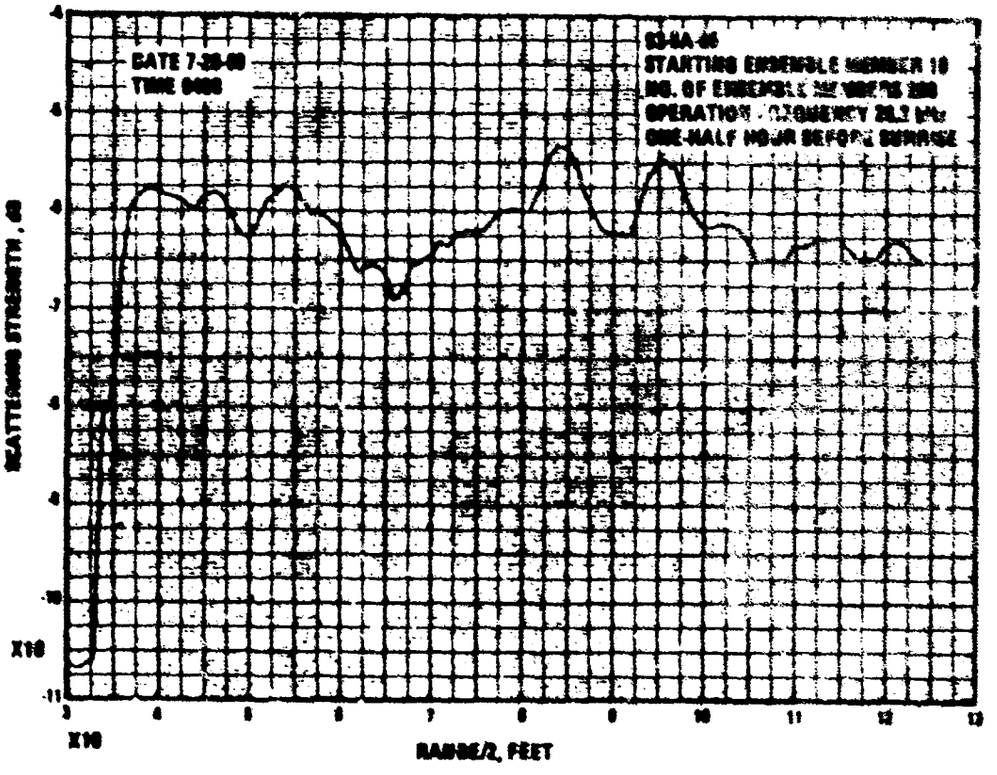

Figure 3. Average scattering strength as a function of range from the transducer

Two hundred-ping average scattering strengths were also computed at three ranges and for 39 times within a 7-day period. The values are plotted in Figure 4 as a function of time. The maximum value of the marked diurnal variation (−59 dB to −86 dB) is in relatively good agreement with the maximum value observed by Anderson (1967) at 25 kHz and about 6 dB greater than the maximum variation seen by Scrimger and Turner (1969) at shallow depths in a 5- to 10-kHz band.

Sheer bulk of data prevented the computation of a continuous curve over the whole time period, but selected portions were considered in great detail. Using data collected over 40-minute intervals near midnight and midday, we were able to compute average scattering strengths as a function of range for ensembles of 30 pulses for sets of 85 contiguous ensembles. One such record spans about 10 min and is shown in Figure 5.

It can be argued from the sharpness of the leading and trailing edges of the lobes in this figure that they are the result of single objects, and thus the target strength rather than the scattering strength should be computed.

Unfortunately, at present we do not have a pattern recognition criteria built into our computer, and therefore had to be satisfied with treating all data equally. If, however, the target strength is computed for all range points, then at least those echoes from single fish will yield correct target strength measurements. This has been done for fourteen targets. Values varied from −27 to −40 dB. Indicated fish lengths for these values are given in Table 1 (Tucker, 1967).

If fish of all sizes are uniformly distributed in range, the peaks of the scattering-strength lobes should diminish with range in general at the rate of 6 dB per range octave. If the targets all move with nearly the same velocity, then the persistence should increase directly with range. Although the plot shows a tendency towards this behavior, longer records are necessary before a definite answer can be reached.

The data for Figure 5 were collected during the night. Figure 6 is a similar plot, but the data in this case were collected during daylight hours. The smoothing out of the area near the surface and the marked reduction of individual target persistence is immediately obvious. Not so obvious from the plot is the fact that the area near the surface displays a higher average scattering strength than does the same area during the night. This is, however, in agreement with Figure 4.

The portion of the plot marked for an expanded view is shown in great detail in Figure 7. Each trace is the scattering strength computed for a single pulse. The cause of the peak at the beginning of Figure 6 is seen to be a target that persists throughout the 30-sec period spanned by this plot. A second individual target, already in the transducer beam, is seen to fade out about halfway through the interval. The remainder of the plot appears to be a jumble of small scattered returns.

In contrast, Figure 8 displays a host of persistent characteristics, not all of which, though, can be considered single targets. The data for this plot were collected at night.

The next step was to determine a quantitative estimate of the period of time over which the environment might be considered stable or stationary. Assuming constant equipment parameters and a reverberation level well above hardware self-noise, any variation in the output of the low-pass filter is a result of some variation in the environment. Suppose, then, that one of the low-pass filters is sampled a fixed time after the transmission of each of a sequence of pulses. If the data so generated are not statistically homogenous, we conclude that the environment has changed significantly.[1]

[1] Significantly means changed to the extent that the low-pass filter output is not homogenous. Because information concerning the phase of the complex envelope is present in the output of the filter, the scattering strength need not have changed. However, as previously pointed out, a significant change in the scattering strength will definitely result in the data being inhomogenous.

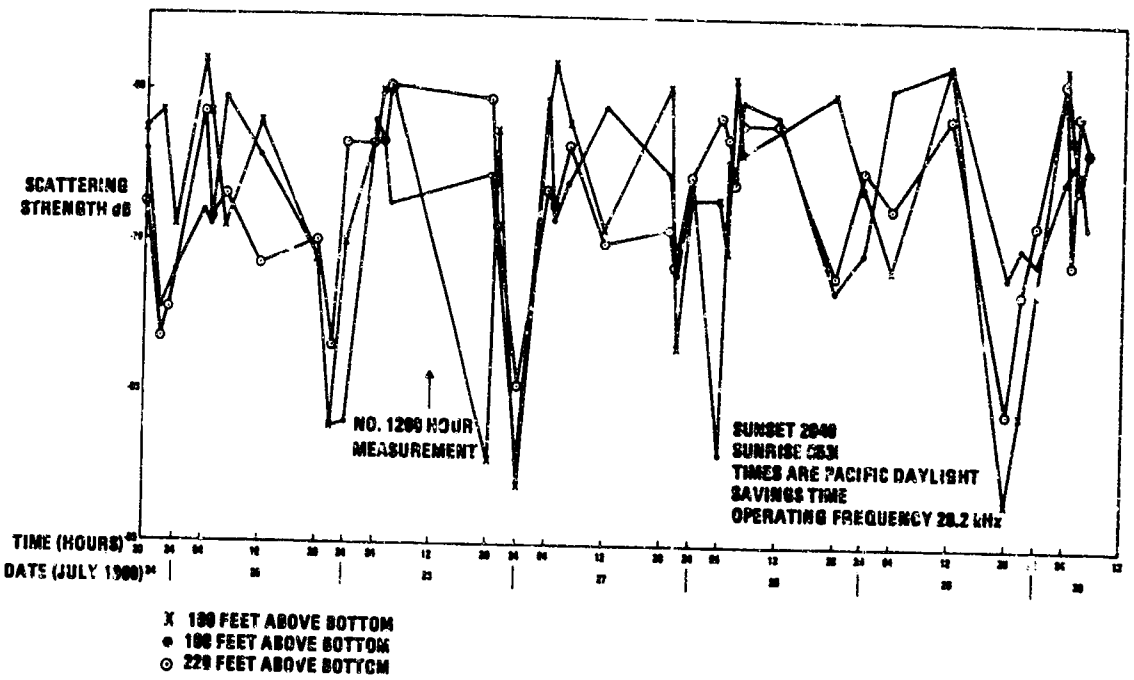

Figure 4. Average scattering strength as a function of time at three depths

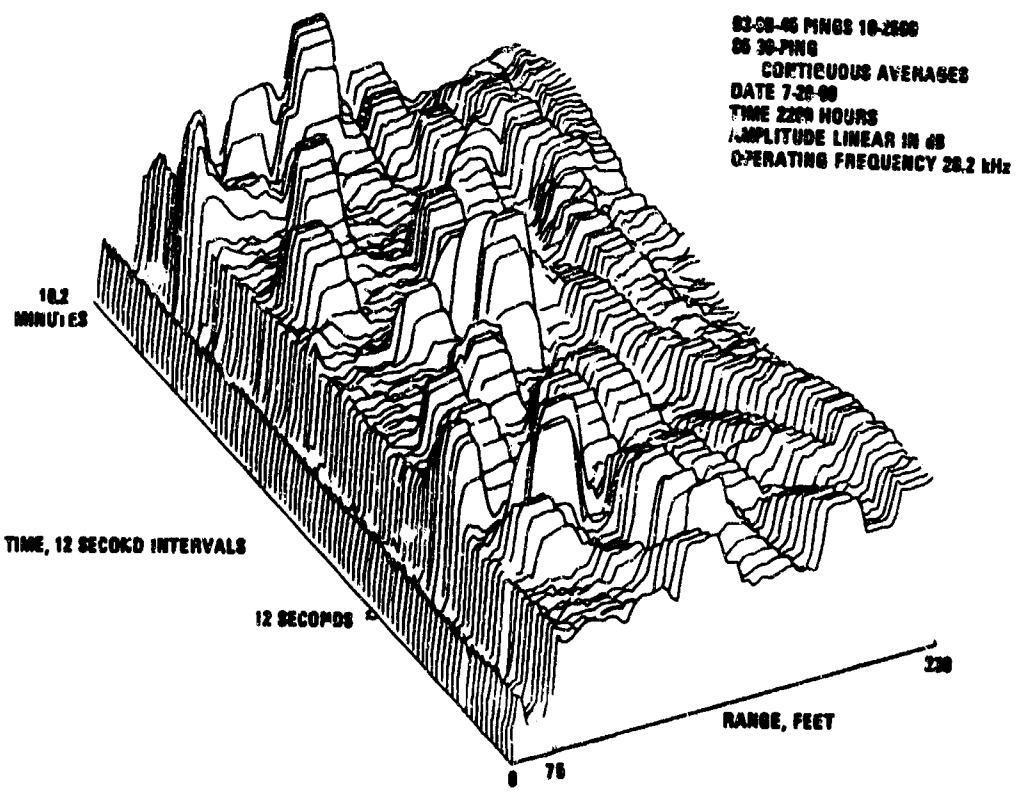

Figure 5. Relative average scattering strength as a function of range over a 10-min period

Table 1. Indicated Fish Lengths

Target strength, dB	Fish length, inches	
	Lower limit	Upper limit
−17	31	71
−40	4.7	9.8

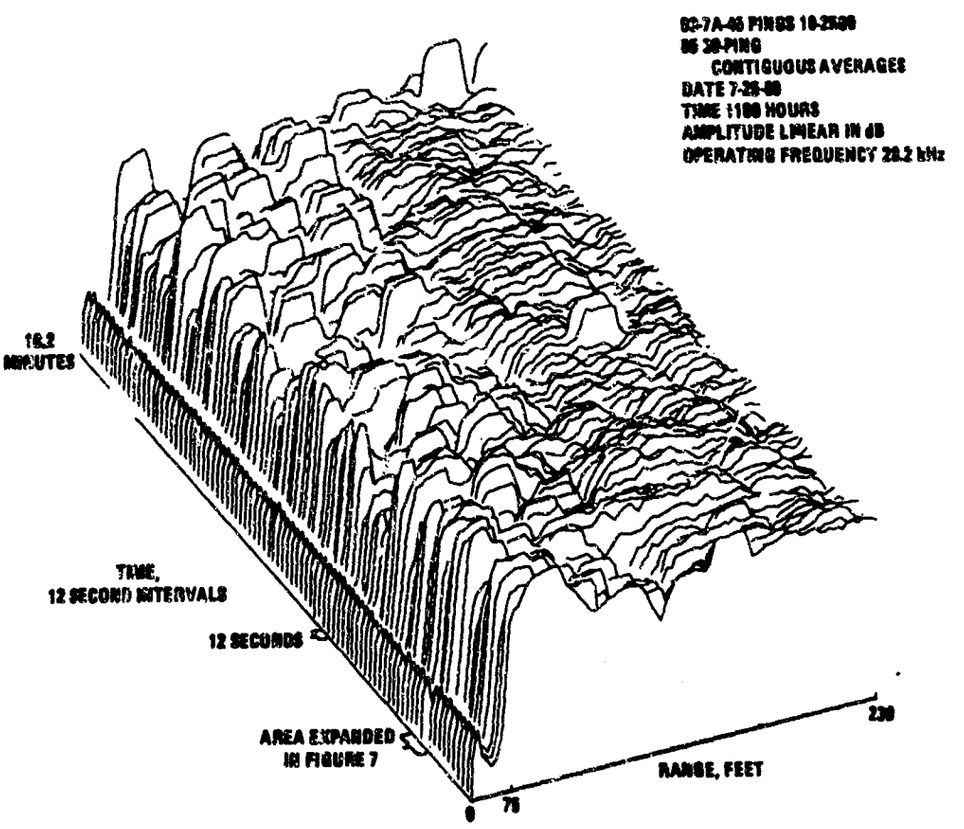

Figure 6. Relative average scattering strength as a function of range over a 10-min period

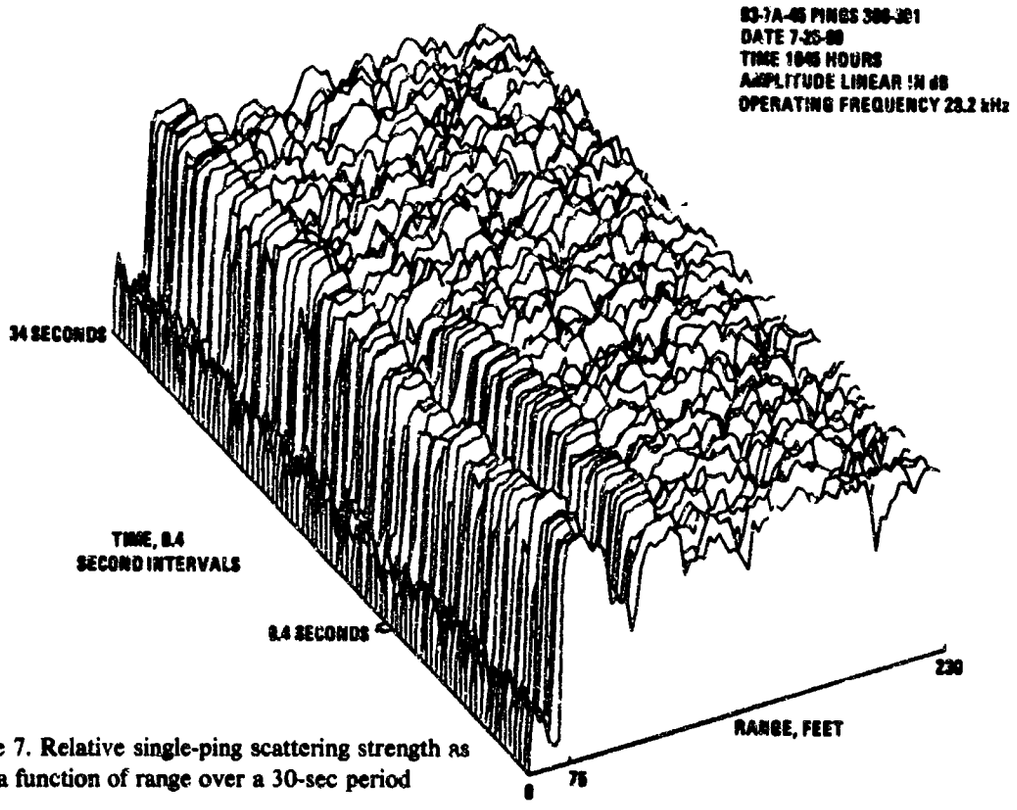

Figure 7. Relative single-ping scattering strength as a function of range over a 30-sec period

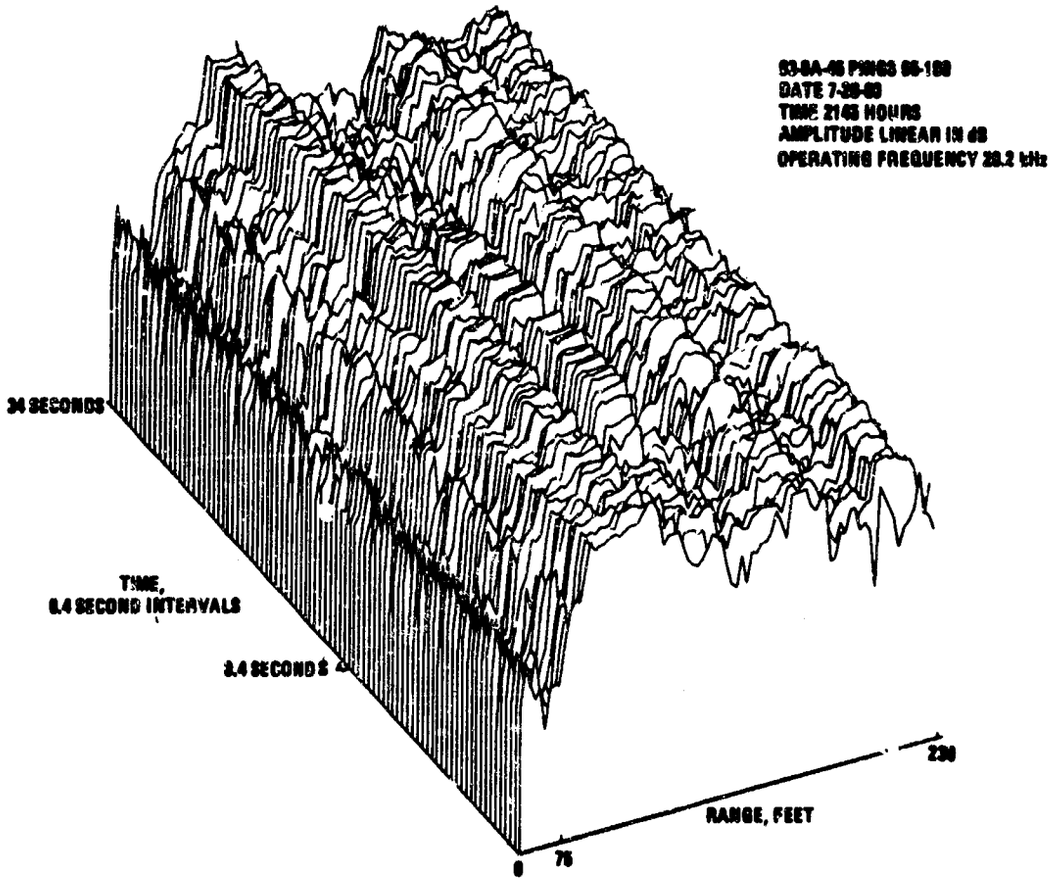

Figure 8. Relative single-ping scattering strength as a function of range over a 30-sec period

Data obtained as indicated was tested for homogeneity using the Kolmogorov-Smirnov statistic (Middleton, 1969; Arase and Arase, 1968). This test was used because it is nonparametric, computationally simple to implement, and generally more powerful (Massey, 1951) than the traditional chi (χ) square statistic. It tests the maximum difference between two sample cumulative probability distributions. If the difference exceeds a threshold that is dependent upon the significance level in which one is interested, then the data are said to be inhomogenous at that significance level; and it is concluded that there has been a significant change in the environment.

Plots of the cumulative probability distribution for two subensembles of 500 samples taken from nighttime data are shown in Figure 9. The plots differ by a maximum of 0.0836 as indicated on the figure and thus just pass the test at the 5% significance level.

Similar plots were compiled and tested at four ranges for ensemble sizes of 60 to 2,000 points. The results for samples taken from daylight data are shown in Figure 10. Two trends are obvious: The data begin to appear significantly inhomogenous for sample sizes greater than 60 and tend to be more homogenous with increasing range. It can be argued that the latter trend is a result of the expected greater persistence of targets at longer ranges. However, this hypothesis is belied by Figure 11, which presents the results of the tests for data collected at night. Here, the trend towards inhomogeneity with increasing sample size is reinforced, but the range dependence is virtually eliminated. Because data inhomogeneity for sample sizes larger than 60 implies environmental nonstationarity for times greater than 24 sec, it becomes apparent that the decision to plot scattering strengths averaged over 30 pulses was a fortuitous one.

An attempt was also made to determine whether or not the data could be considered normally distributed. A test by Pearson (1930) on the skewness and kurtosis of the data proved particularly simple to implement and was used despite the fact that it tends to exaggerate the weight of large data values. Only sets of ensembles of 120 or more samples that showed a failure rate of 10% or less under the Kolmogorov-Smirnov test for homogeneity were considered. As it turned out, only that data collected during daylight hours and sampled at ranges of 180 or 230 feet could qualify. The results of 31 such tests are indicated in Table 2.

Certain other patterns were clear. At both ranges, the skewness was negative in two-thirds of the cases tested. However, because the tendency was slight and the failures displayed no preference for either polarity, the negative trend may be statistically permissible. At 230 feet, the kurtosis was never less than 3, even in those cases that passed the test; in fact, it was less than 4 only one-third of the time.

At 180 feet the kurtosis appeared rather evenly distributed about 3, except in one of the failures where it reached a value of 7.9, the maximum observed at either range.

We conclude from this that even when the data are homogenous, it can not in general be considered normally distributed, except in a very coarse sense. We also note that the processes operating at different ranges may be physically different as attested by the significant differences in computed kurtosis for two ranges.

Additional plots have been included as Appendix B to show the variability of the data.

RESULTS AND CONCLUSIONS

We have shown that stationarity of the acoustic backscattering strength is a requirement if the data at the output of a sonar receiver are to be statistically homogenous. Changes in the scattering strength parameter over durations ranging from seconds to days have been demonstrated; a periodic diurnal variation has been shown. A nonparametric statistical test was used to place a lower limit on the duration of environmental stationarity by determining the duration

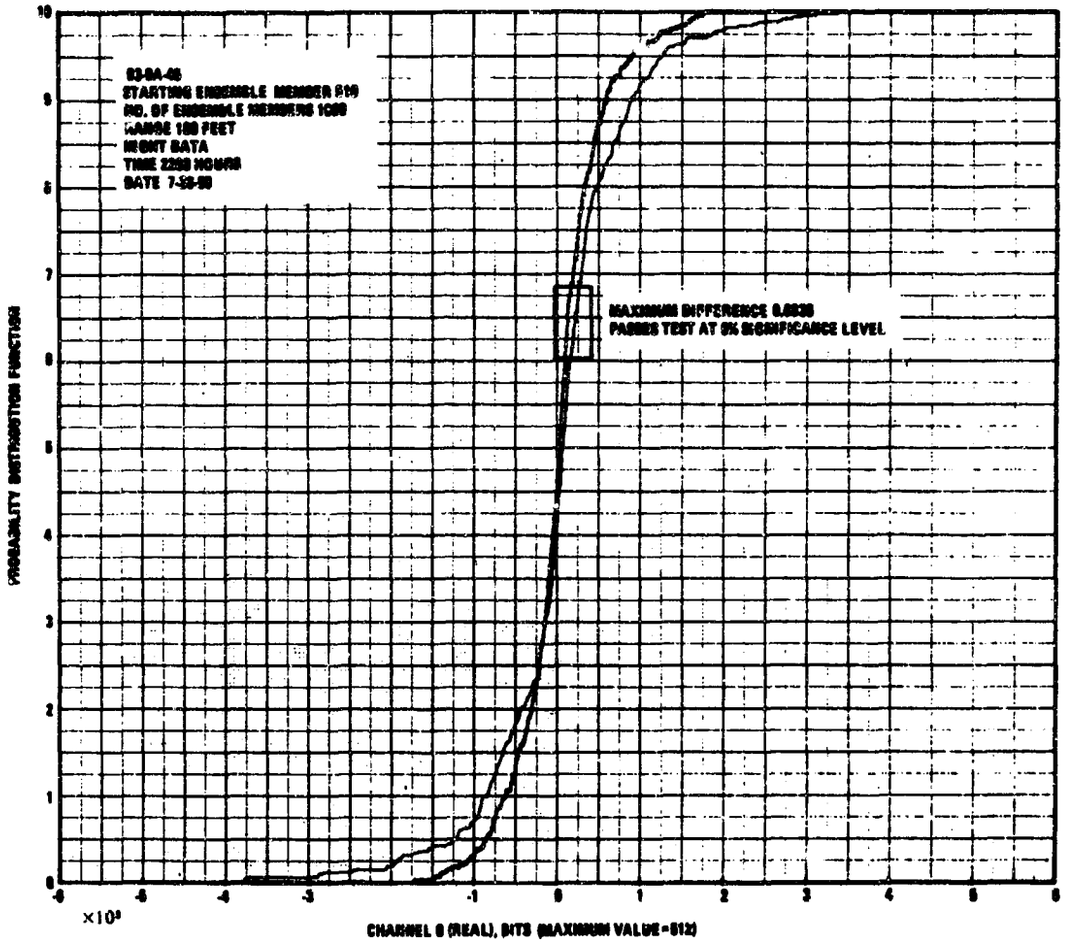

Figure 9. Sample cumulative probability distribution functions for two contiguous subensembles of 500 members each

Table 2. Results of Tests for Normality

Range	Number of tests	Number of times parameter failed at 5% level		Total number of tests failing either criteria
		Skewness	Kurtosis	
180	16	3	3	5
230	15	3	12	12

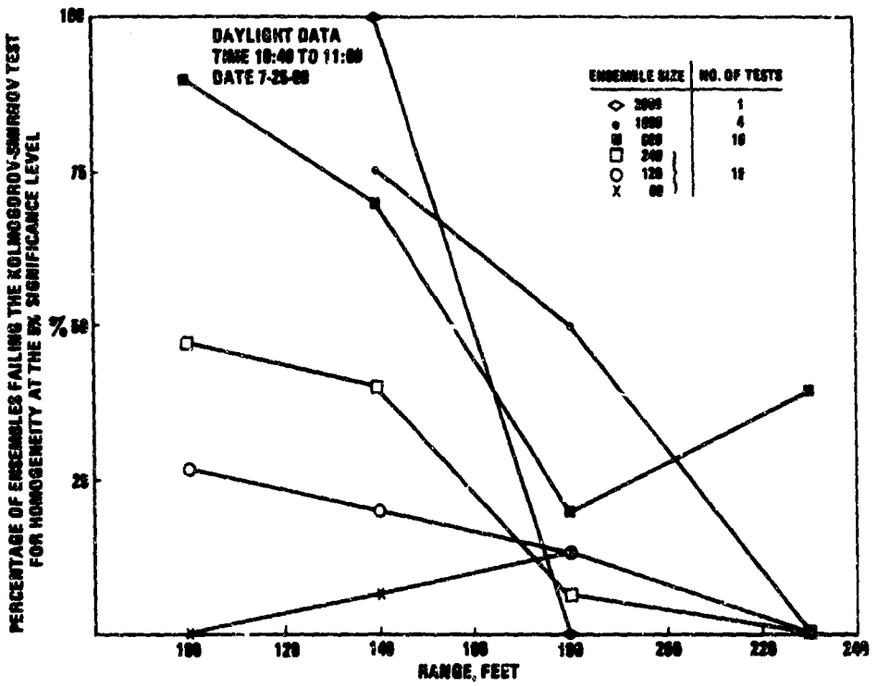

Figure 10. Results of Kolmogorov-Smirnov test as a function of range and ensemble size

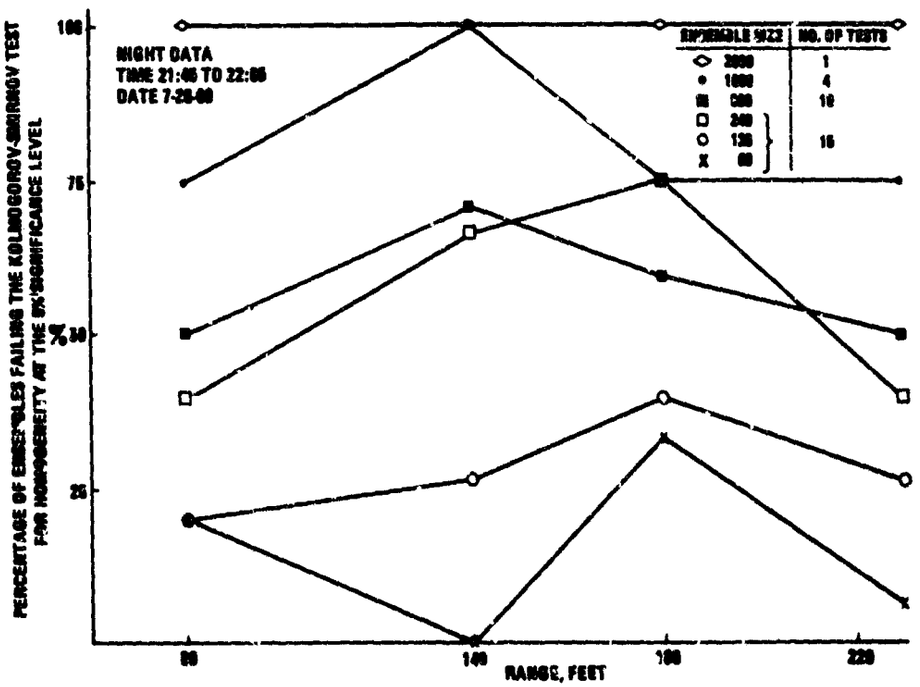

Figure 11. Results of Kolmogorov-Smirnov test as a function of range and ensemble size

over which data sampled at the output of our receiver could be considered homogenous. Where the data proved homogenous, it was shown that in general the data could not be considered normally distributed.

The results indicated are limited, of course, by the location, duration, time of year, and experimenter-controlled conditions. In addition to the need to generalize the results in these respects, there is also a necessity for more compact data-reduction techniques and simple devices to display multidimensional reverberation (scattering) data.

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APPENDIX A

DERIVATION OF ENVIRONMENT SYSTEM RELATIONSHIPS

Allow the transmitted signal the representation

$$s(t) = \mathrm{Re}\left\{ x(t) e^{j\omega t} \right\}.$$

Assuming an homogenous, isotropic medium, the signal received back at the transmitter, after being scattered by a slowly moving point target of reflectivity $\tilde{\sigma}_i$ at initial range R_i, is

$$r_i(\gamma) = \mathrm{Re}\left\{ s(\gamma_i) \frac{1}{R_i^2} \tilde{\sigma}_i \alpha \tilde{f}^2(\theta,\phi) \right\}$$

where $\tilde{f}^2(\cdot)$ is the (monostatic) transducer beam pattern; α, the necessary system gains and conversions; and θ and ϕ are the angular coordinates of the incremental volume in which the scatterer is located relative to the transducer axis.

Moose* has shown that for targets moving with on-axis velocity components v very small with respect to C

$$\gamma_i \simeq \left(1 + \frac{2v}{C}\right) t - \frac{2R_i}{C}.$$

In practical situations, however, it is generally sufficient to allow

$$s(\gamma_i) = \mathrm{Re}\left\{ x\left(t - \frac{2R_i}{C}\right) e^{j\omega \left[(1+\beta_i)t - \left(\frac{2R_i}{C}\right) \right]} \right\}$$

where

$$\beta_i = \frac{2v}{C}$$

If there are N scatterers in some incremental volume $\Delta V = (\Delta A)(\Delta R)$ centered at θ, ϕ, R, then assume that the total signal is simply the linear superposition of the individual scattered returns

$$r'(t) = \sum_{i=1}^{N} r_i'(t) = \sum_{i=1}^{N} \mathrm{Re}\left\{ x\left(t - \frac{2R_i}{C}\right) e^{j\omega(1+\beta_i)t} e^{-j\omega(2R_i/C)} \frac{\tilde{\sigma}_i}{R_i^2} \alpha \tilde{f}^2(\theta,\phi) \right\}.$$

*Moose, P. H. Characterization of moving acoustic targets as linear time-varying filters. Letter to Editor, *J. Acoust. Soc. Am.*, Vol. 43, No. 5, 1968.

Notice that $r'(t)$ can always be reduced to the form

$$r'(t) = \sum_{i=1}^{N} \operatorname{Re}\left\{A_i x\left(t - \frac{2R_i}{C}\right) e^{j(\omega t - \delta_i)}\right\}$$

$$= \sum_{i=1}^{N} A_i x\left(t - \frac{2R_i}{C}\right)[\cos \omega t \cos \delta_i + \sin \omega t \sin \delta_i] .$$

If $r'(t)$ is multiplied by $2 \cos \omega t$, and the result is low-pass filtered to attenuate the double frequency terms, the result is

$$r_p(t) = \sum_{i=1}^{N} A_i x\left(t - \frac{2R_i}{C}\right) \cos \delta_i .$$

Similarly, if $r'(t)$ is multiplied by $2 \sin \omega t$

$$r_q(t) = \sum_{i=1}^{N} A_i x\left(t - \frac{2R_i}{C}\right) \sin \delta_i .$$

Represent the total signal as a complex signal vector

$$\tilde{r}(t) = r_p(t) + j r_q(t) = \sum_{i=1}^{N} A_i x\left(t - \frac{2R_i}{C}\right) e^{j \delta_i} .$$

Comparing this expression to that for $r'(t)$, observe that

$$\tilde{r}(t) = \sum_{i=1}^{N} x\left(t - \frac{2R_i}{C}\right) \frac{\tilde{\sigma}_i}{R_i^2} \alpha \tilde{f}^2(\theta, \phi) e^{j\omega \beta_i t} e^{-j\omega (2R_i/C)}$$

$\tilde{r}(t)$ is known as the complex envelope of $r'(t)$.

The autocovariance of $\tilde{r}(t)$ is defined as*

$$\tilde{K}_{rr}(t, \tau \mid N) = E\left\{\tilde{r}(t)\, \tilde{r}^*(t + \tau)\right\}$$

*The asterisk within the equation denotes complex conjugation, and, E is the expected value.

$$\tilde{K}_{rr}(t,\tau\,|N) = E\left\{\sum_{i=1}^{N}\sum_{j=1}^{N} x\left(t-\frac{2R_i}{C}\right)x\left(t+\tau-\frac{2R_j}{C}\right)\right.$$

$$e^{j\omega\,[\beta_i t-\beta_j(t+\tau)]}\; e^{-j\omega 2(R_i-R_j)/C}\;\frac{1}{R_i^2}\,\frac{1}{R_j^2}\;\alpha^2\,|\tilde{f}\,(\theta,\phi)|^4$$

$$\left.\tilde{\sigma}_i(t)\,\tilde{\sigma}^*_j(t+\tau)\right\}.$$

If the scatterers are independent

$$\tilde{K}_{rr}(t,\tau\,|N) = E\left\{\sum_{i=1}^{N} x\left(t-\frac{2R_i}{C}\right)x\left(t+\tau-\frac{2R_i}{C}\right)e^{-j\beta_i\omega\tau}\right.$$

$$\left.\frac{1}{R_i^4}\;\alpha^2\,|\tilde{f}\,(\theta,\phi)|^4\;\tilde{\sigma}_i(t)\,\tilde{\sigma}^*_i(t+\tau)\right\}.$$

If, in addition, there are M classes of scatterers present, and if the parameters of the scatterers (σ,β) within any class are identically distributed, then

$$\tilde{K}_{rr}(t,\tau\,|N) = \alpha^2\,|\tilde{f}\,(\theta,\phi)|^4\sum_{j=1}^{M}\tilde{K}_{\sigma_j}(t,\tau)\,\tilde{\psi}_{\beta_j}(\omega\tau)$$

$$E\left\{\sum_{i=1}^{N_j}\frac{1}{R_i^4}\;x\left(t-\frac{2R_i}{C}\right)x\left(t+\tau-\frac{2R_i}{C}\right)\right\}$$

where

$$N = N_1+N_2+\ldots+N_M$$

$$\tilde{K}_{\sigma_j}(t,\tau) = E\left\{\tilde{\sigma}_j(t)\tilde{\sigma}^*_j\,(t+\tau)\right\}$$

$$\tilde{\psi}_{\beta_j}(\omega\tau) = \text{doppler factor characteristic function}.$$

The expected value term is defined

$$\int_{R-(\Delta R/2)}^{R+(\Delta R/2)}\!\!\cdots\!\int\;\sum_{i=1}^{N_j}\frac{1}{R_i^4}\,x\left(t-\frac{2R_i}{C}\right)x\left(t+\tau-\frac{2R_i}{C}\right)p\,(R_1,R_2,\ldots R_{i_j})\,dR_1\,dR_2\ldots dR_{N_j}.$$

By virtue of independence, the joint probability

$$p(R_1, R_2 \ldots R_{N_j}) = p(R_1)\, p(R_2) \ldots p(R_{N_j})$$

equals the product of the marginal probabilities. If the scatterers are locally uniformly distributed in range

$$p(R_i) = \frac{1}{\Delta R} \text{ and } p(R_1, R_2 \ldots R_{N_j}) = \left(\frac{1}{\Delta R}\right)^{N_j}.$$

Interchanging order of summation and integration, and noting that in each term of the sum, $N_j - 1$ of the integrals are independent of the variable being integrated, the expectation becomes

$$\frac{N_j}{\Delta R} \int_{R-(\Delta R/2)}^{R+(\Delta R/2)} \frac{1}{R_i^4}\, x\left(t - \frac{2R_i}{C}\right) x\left(t + \tau - \frac{2R_i}{C}\right) dR_i$$

By replacing N_j by $\Delta V \rho_j(t)$, $\rho_j(t)$ being the local scatterer density at time t, and noting that $\Delta A = R^2\, \Delta \Omega$, where $\Delta \Omega$ is the solid angle subtended by ΔA, the autocovariance is

$$\tilde{K}_{rr}(t, \tau, \mid N) = \alpha^2 \mid \tilde{f}(\theta, \phi) \mid^4 \sum_{j=1}^{M} \tilde{K}_{\sigma_j}(t, \tau)\, \tilde{\psi}_{\rho_j}(\omega \tau)\, \rho_j(t)\, R^2\, \Delta \Omega$$

$$\int_{R-(\Delta R/2)}^{R+(\Delta R/2)} \frac{1}{R^4}\, x\left(t - \frac{2R_i}{C}\right) x\left(t + \tau - \frac{2R_i}{C}\right) dR_i$$

If the scatterer field is homogenous, or if the transducer beam width is sufficiently narrow for angular homogeneity of the scatterer field to prevail within it, $\tilde{K}_{rr}(t, \sigma \mid N)$ can be integrated over all space to obtain $\tilde{K}_{rr}(t, \tau)$.

All of the foregoing assumptions make $f(\theta, \phi)$ the only direction-dependent variable in $\tilde{K}_{rr}(t, \tau \mid N)$. Because the directivity factor is defined as

$$d = \frac{4\pi}{\int_0^{4\pi} f^4(\Omega)\, d\Omega}.$$

$\tilde{K}_{rr}(t, \tau)$ may be written

$$\tilde{K}_{rr}(t,\tau) = \frac{\alpha^4 4\pi}{d} \sum_{j=1}^{M} \tilde{K}_{a_j}(t,\tau)\,\tilde{\psi}_{\beta_j}(\omega\tau)\,\rho_j(t)\,R^2$$

$$\int_{R-(\Delta R/2)}^{R+(\Delta R/2)} \frac{1}{R^4} x\left(t-\frac{2R_i}{C}\right) x\left(t+\tau-\frac{2R_i}{C}\right) dR_i .$$

Asymptotically, if $R >> \Delta R$

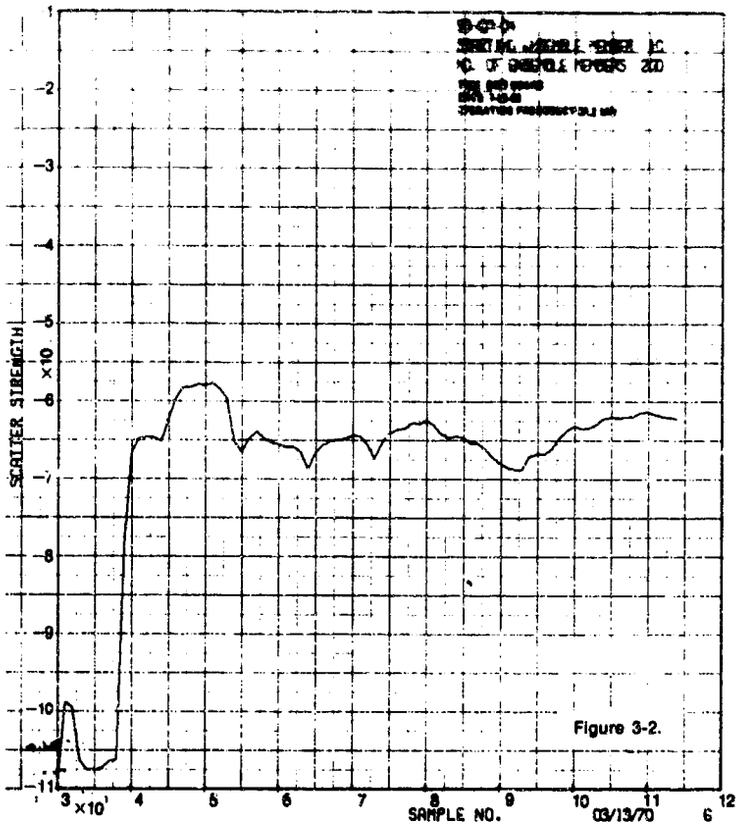
$$\tilde{K}_{rr}(t,\tau) = \frac{\alpha^2 4\pi}{d} \sum_{j=1}^{M} \tilde{K}_{a_j}(t,\tau)\,\tilde{\psi}_{\beta_j}(\omega\tau)\,\rho_j(t)\,\frac{1}{R^2}$$

$$\int_{R-(\Delta R/2)}^{R+(\Delta R/2)} x\left(t-\frac{2R_i}{C}\right) x\left(t+\tau-\frac{2R_i}{C}\right) dR_i .$$

If this expression is evaluated at $\tau = 0$ for a gated continuous-wave signal of duration T and amplitude A, then

$$\tilde{K}_{rr}(t,0) = \bar{\sigma}_{rr}(t) = \frac{4\pi\alpha^2}{dR^2} \frac{CT}{2} A^2 \sum_{j=1}^{M} \overline{|\tilde{\sigma}_j(t)|^2}\,\rho_j(t)$$

which relates signal strength to the mean square scatter reflectivity and density.



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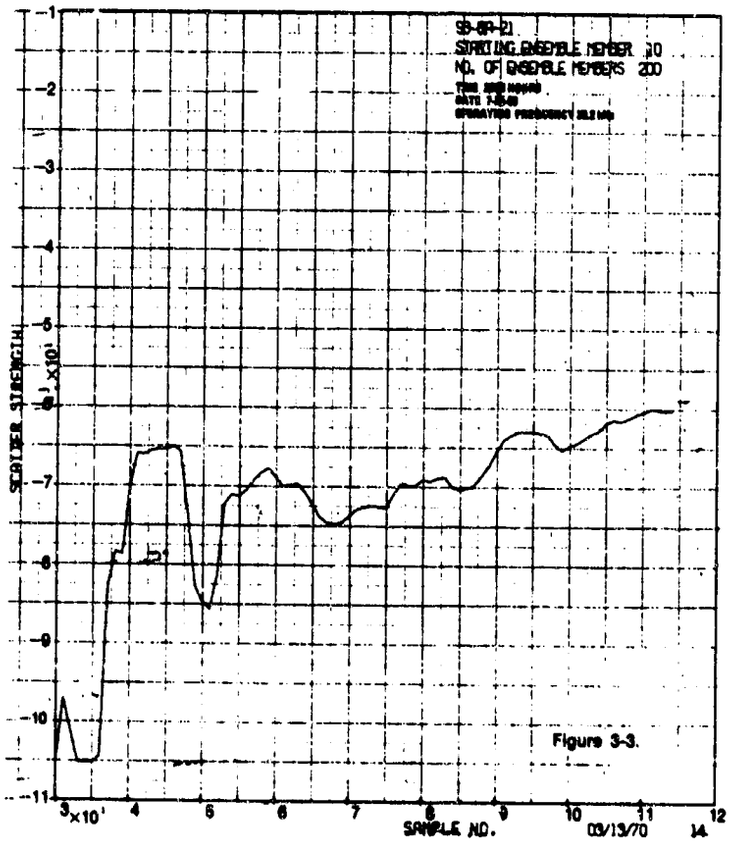

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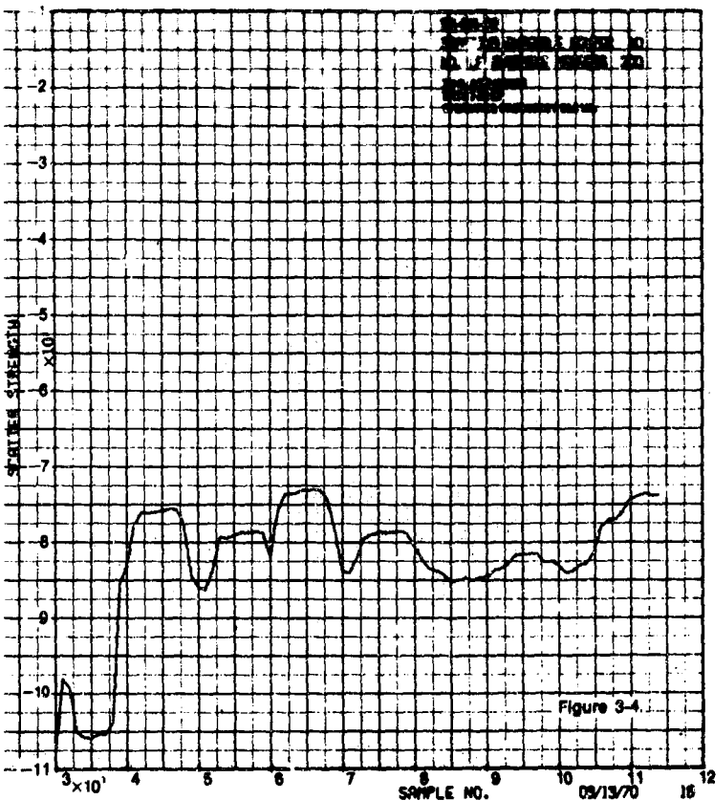
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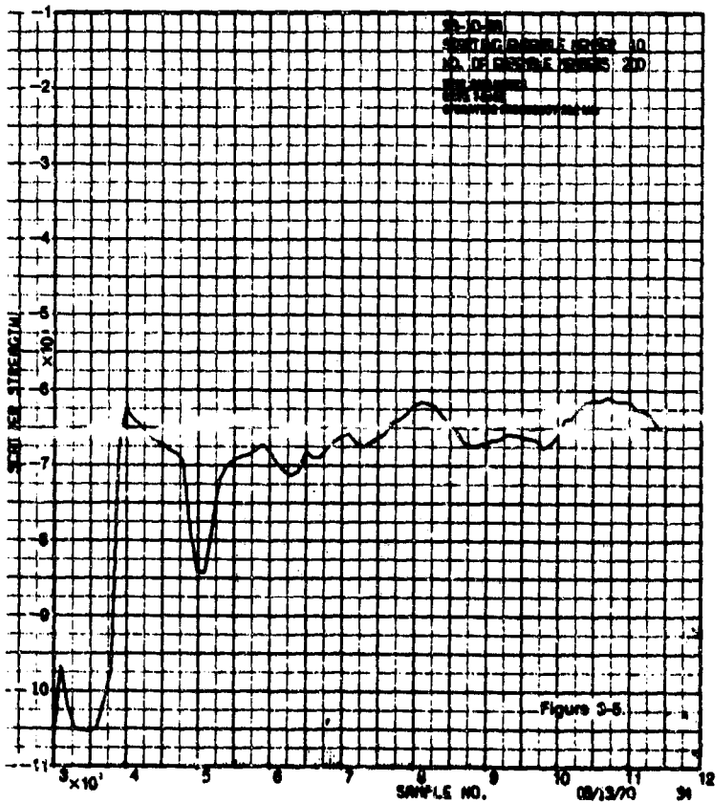
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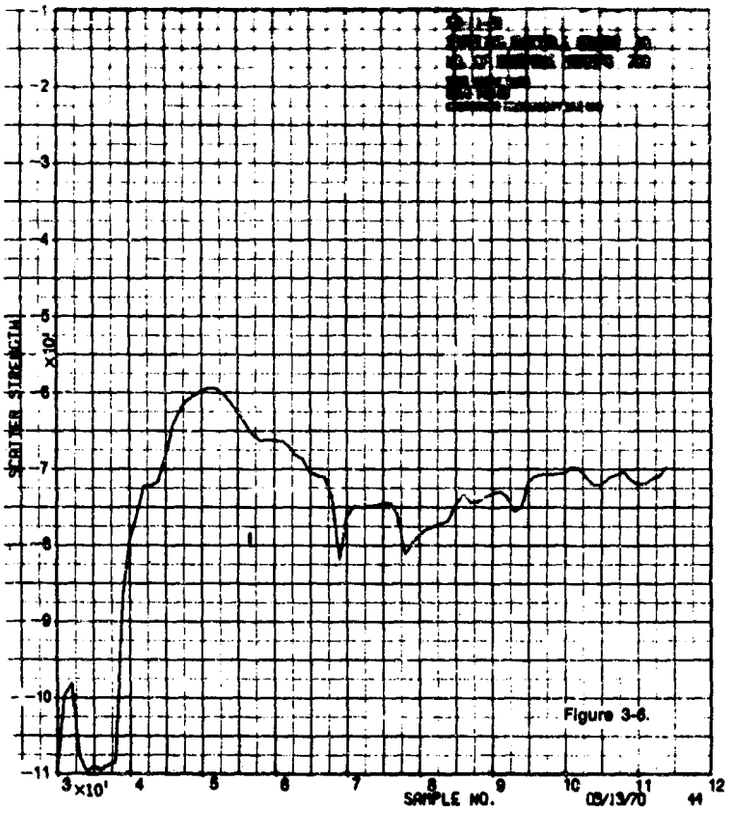


Figure 3-6.

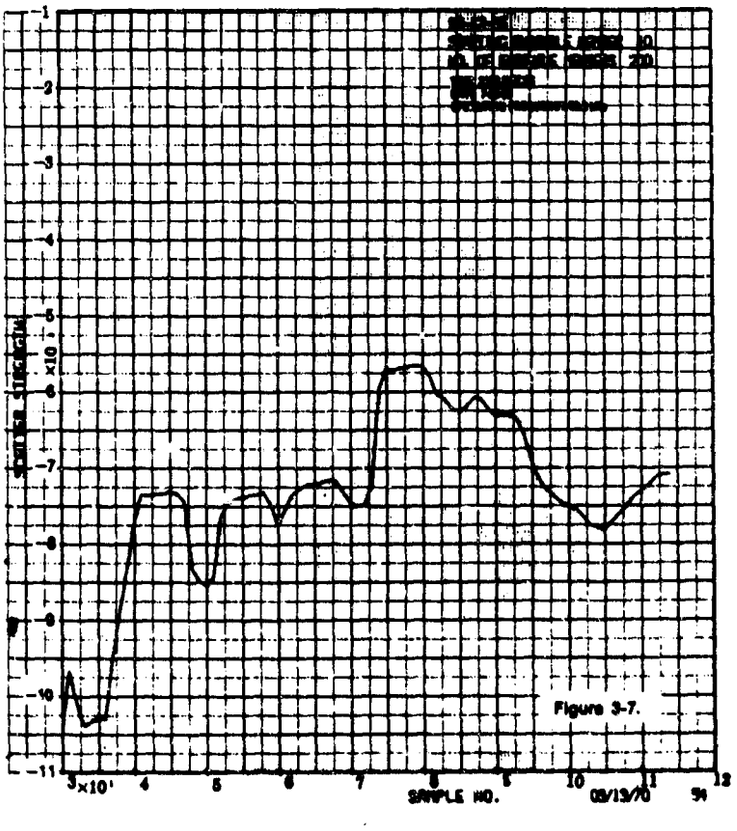
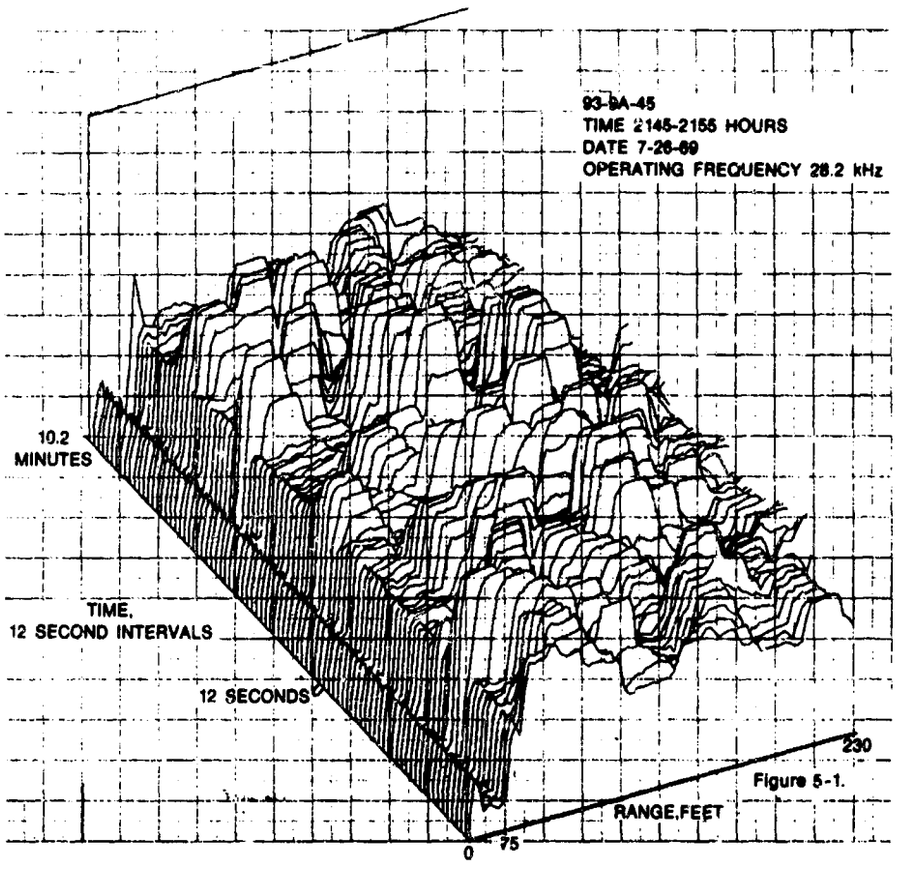


Figure 3-7.



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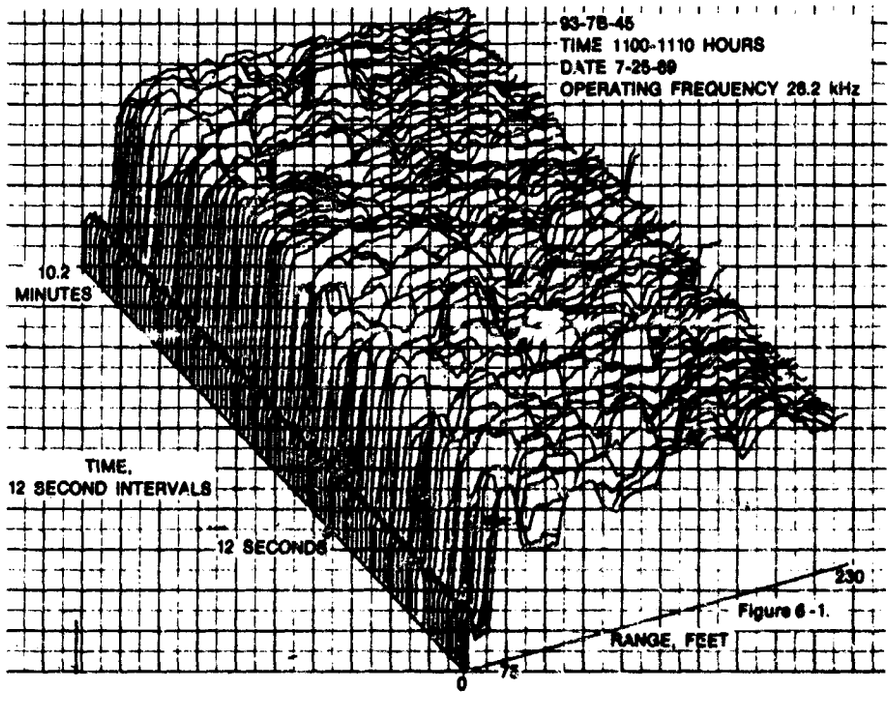

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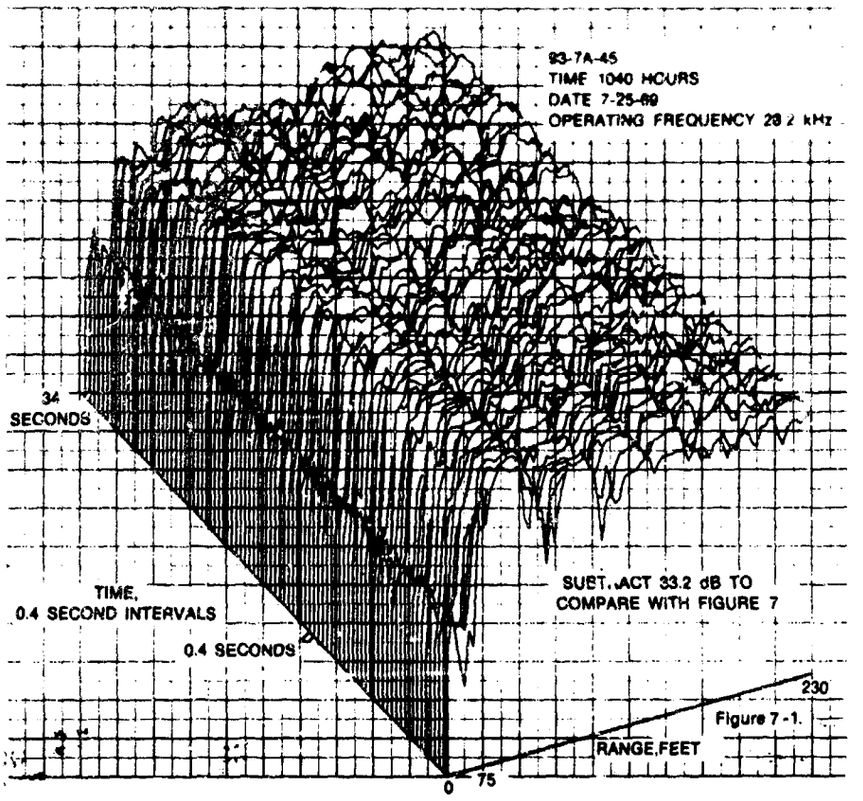

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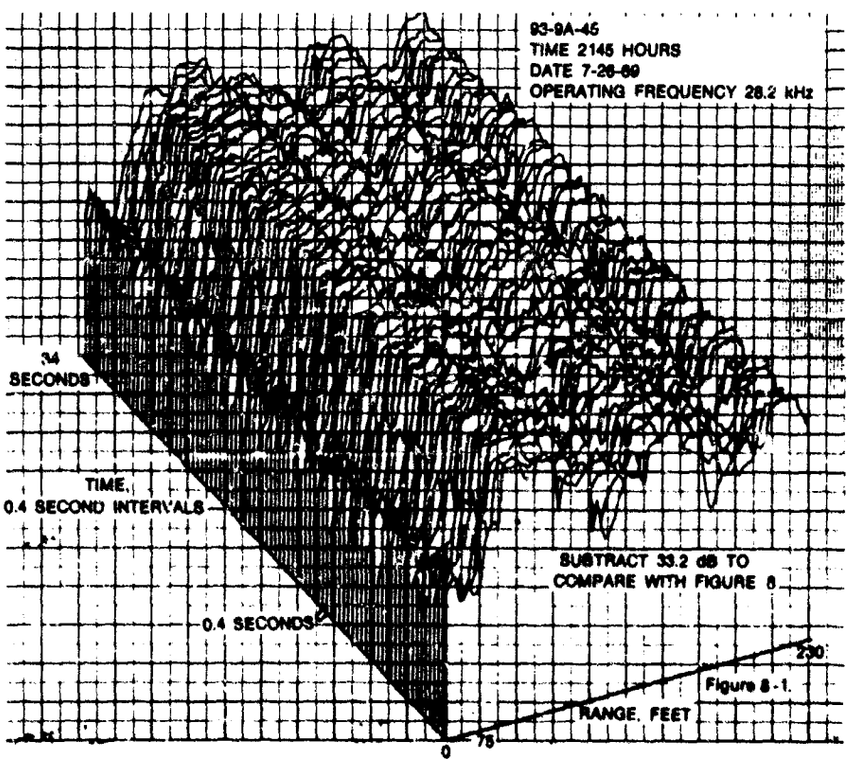

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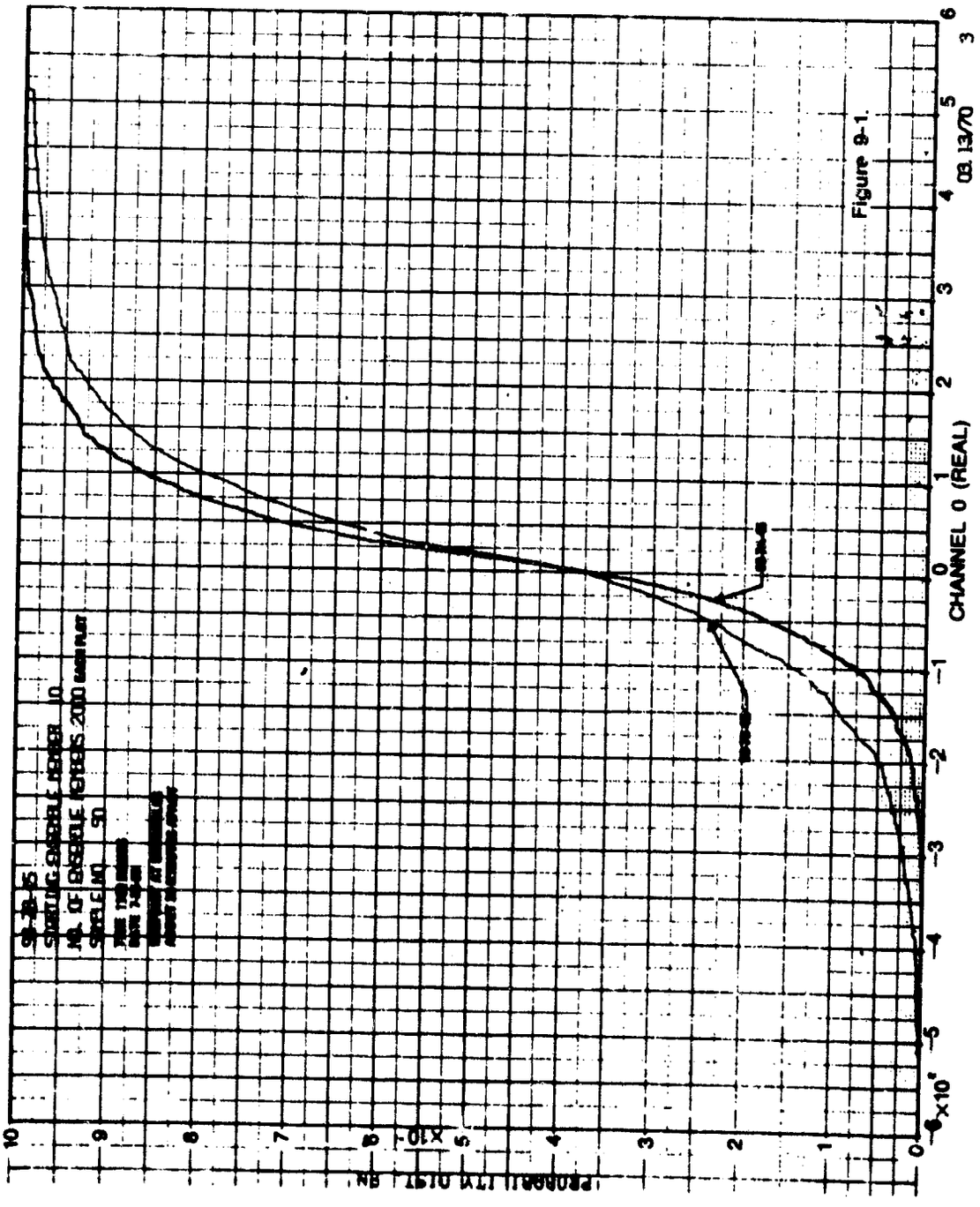

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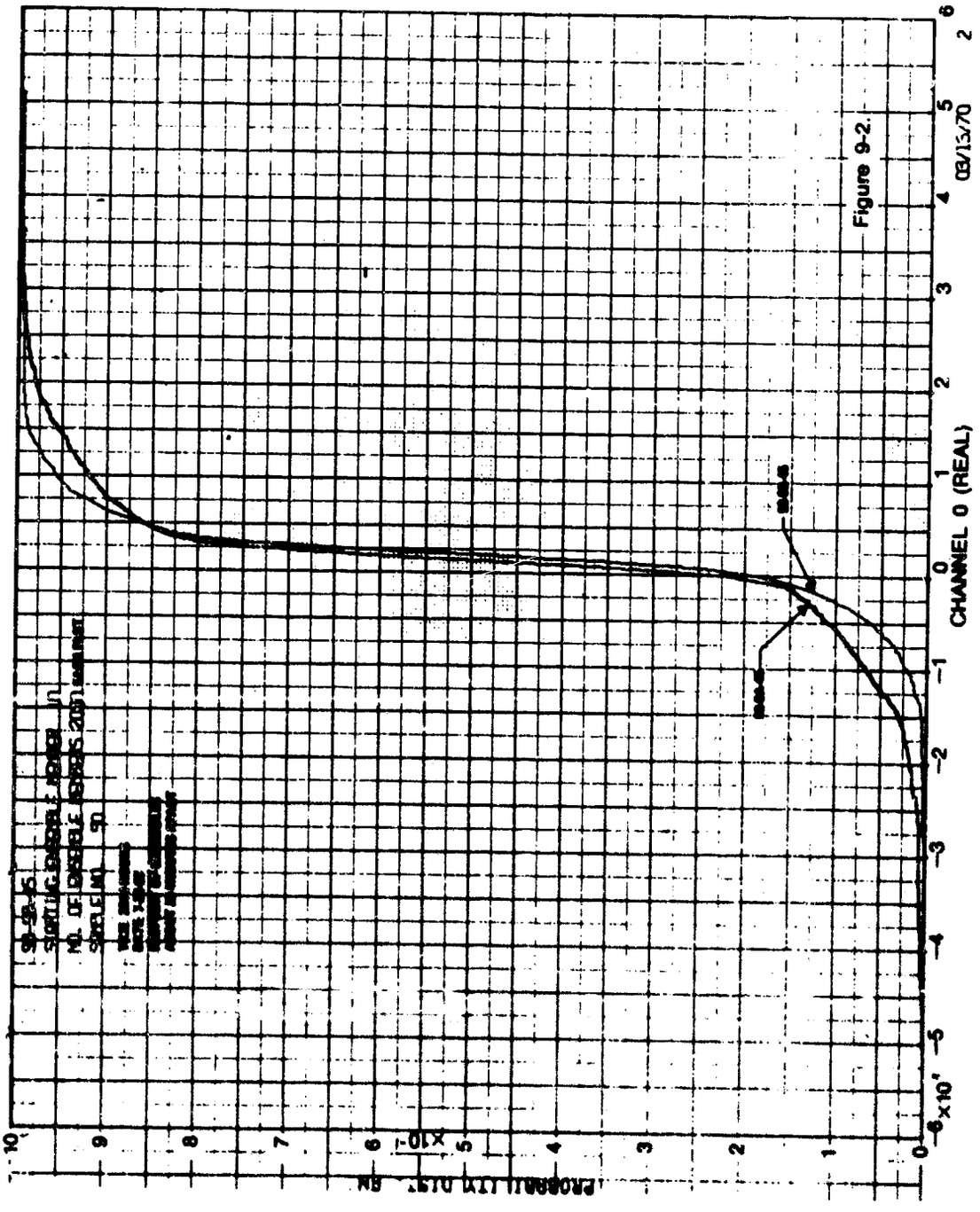
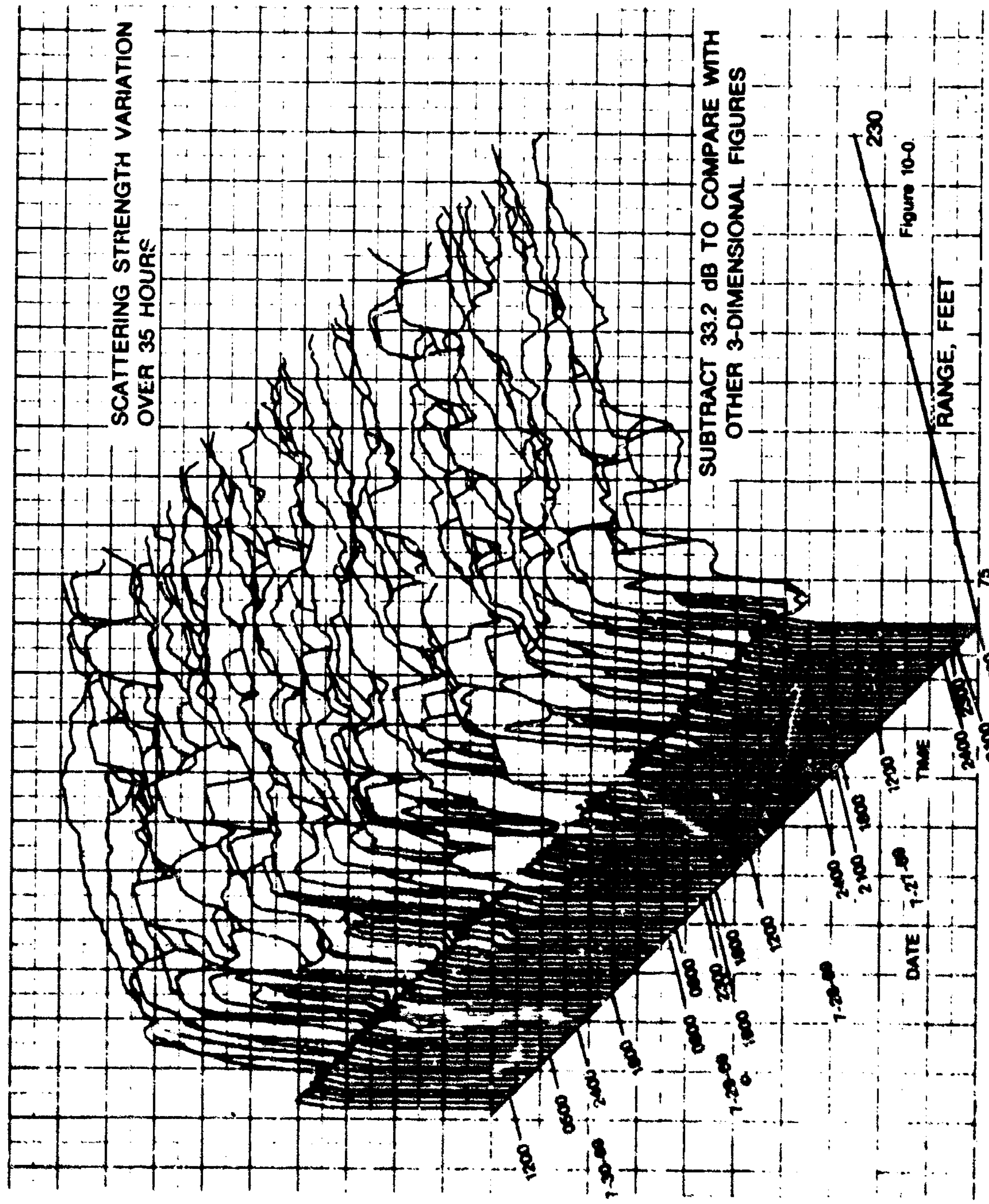


Figure 9-2.


SCATTERING STRENGTH VARIATION OVER 35 HOURS
SUBTRACT 33.2 dB TO COMPARE WITH OTHER 3-DIMENSIONAL FIGURES
230
75
RANGE, FEET
DATE
TIME
Figure 10-0

GEOGRAPHIC, SEASONAL, AND ANNUAL PATTERNS OF MIDWATER SCATTERERS BETWEEN LATITUDES 10° AND 68° NORTH IN THE ATLANTIC

Kenneth K. R. Haigh*
Admiralty Underwater Weapons Establishment
Dorset, England

ABSTRACT

A 3-year survey of the North Atlantic has enabled patterns of the depth of midwater scatterers to be described with respect to geographic position and seasonal and annual variation. These data are qualitative, obtained from echo-sounder records, but some quantitative target strength data in the northernmost latitudes are presented. Most of the patterns can be correlated with the results of other workers in local regional areas.

INTRODUCTION

Between 1963 and 1967 the Admiralty Underwater Weapons Establishment in Portland, Dorset, in association with the Hydrographer of the Royal Navy, carried out an extensive hydrographic and oceanographic survey of the North Atlantic between latitudes 10° and 68° N. Research ships from the United States, the Netherlands, Norway, and the United Kingdom took part in the operation, which was known by the acronym NAVADO. Throughout the survey, Precision depth recorders (PDR) were in operation, recording qualitatively the presence of any deep scattering layer (DSL). The PDR was concerned primarily with the bottom topography and the bottom acoustic reflectivity. Equipment used to measure the bottom reflectivity (Ref. 1) also could be used to measure the DSL target strength, but, in general, quantitative DSL data were not obtained except on the northmost crossings of the Atlantic.

The general pattern of the survey was to steam on lines of latitude 3° apart, but during the course of the long operations, some lines were traversed up to three times. This, together with some north-south runs, has enabled a description to be made of geographic, seasonal, and annual patterns of the depth of the DSL in the North Atlantic. Figure 1 indicates the geographic area covered, the lines of latitude surveyed, and the dates on which these were accomplished.

EQUIPMENT

The PDR's in use throughout the survey operated at 10 kHz, with a pulse length of 20 msec and a beamwidth of 30°. DSL information is, therefore, qualitative only, except as previously noted. Additional information at other frequencies was obtained on the northern lines.

*Paper presented by Timothy W. Janaitis, U.S. Naval Oceanographic Office.

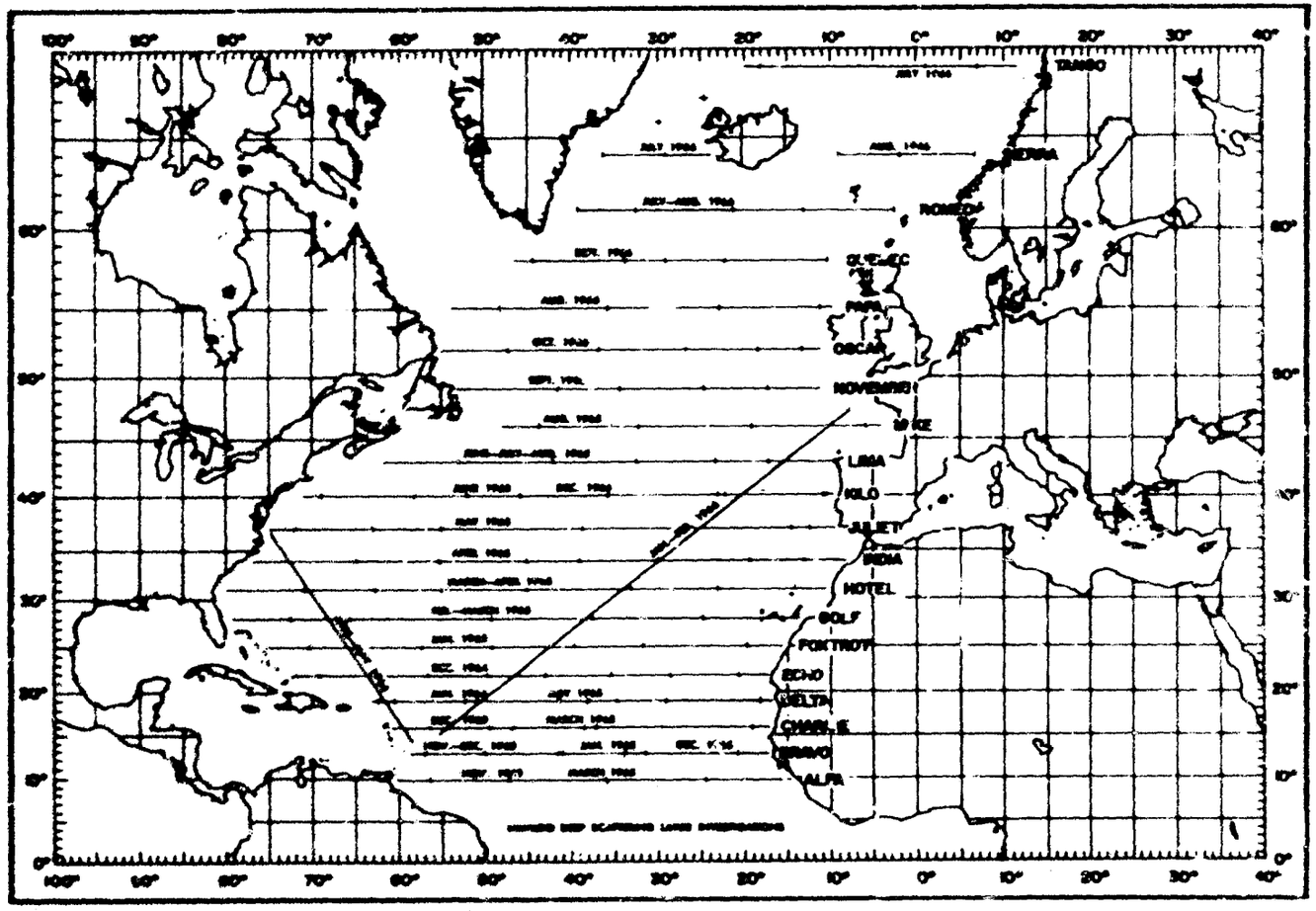


Figure 1. NAVADO survey area

In this type of investigation, the well-known limitations of echo sounders, such as excessive beamwidth, limited dynamic range of recording paper, and quenching by the ship's hull, require no explanation other than to reiterate their presence. Inevitably, gaps occurred in the continuity of the echo-sounder traces, caused by a variety of factors, among which were the PDR stopping while on an oceanographic station and a seabed echo obscuring the DSL. An estimate of the thickness of the DSL was made from the extent of the trace darkening on the PDR paper, but it must be remembered that this measurement was highly subjective because of its dependence on the PDR gain and echo-sounder pulse length.

DATA REDUCTION

A number of methods were explored for reducing and presenting to the scientific community the DSL information obtained on many thousands of miles of ship track. The scheme finally adopted consisted of transcribing the PDR DSL information, sampled at 3-hour intervals during each transverse, to a graphic form as shown in Figure 2 for line ECHO (lat 22 ° N). Complete information for all the ship's tracks is contained in Ref. 2. Each graph is shown with depth (fathoms) as the ordinate and date/time and associated longitude as the abscissa. In all the graphs except for the north-south tracks, a west-east progression along each traverse is represented from left to right along the horizontal ordinate. The shaded portions of each graph represent the depth and thickness of the DSL. Gaps in the graphic presentations usually indicate an oceanographic station or a merging of the DSL on one phase of the PDR record with the bottom echo on a different phase. Diurnal migrating patterns are observed easily from the graphic record. Upper limits of the diurnal patterns were not discernible in many cases because of merging of the different layers into the initial reverberation pattern of

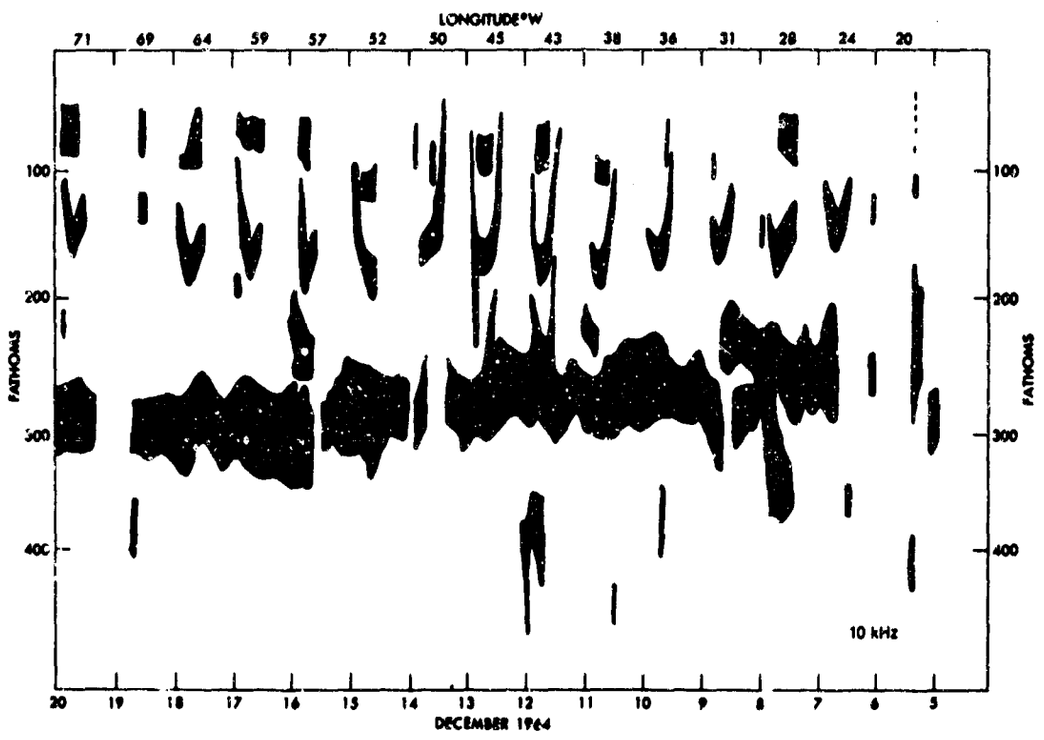


Figure 2. NAVADO DSL line ECHO (lat 22° N)

the echo sounder. Some minor fluctuations in depth, thickness, and occurrence are not shown because of the effect of the 3-hour sampling of the PDR information.

Scant attention was paid to the diurnal patterns of the DSL as these phenomena have been studied intensely in the past. Effort was directed to the geographic, seasonal, and annual patterns. By ignoring the season and sampling the number of layers and their maximum depth, we were able to build patterns of their geographic distribution.

The number of layers present for 5° increments of longitude along each latitude traverse is shown in Figure 3. Five types of distinct scattering layers, designated as layers A, B, C, D, and E, were found within the depth range 100 to 500 fm. These layers are shown in Figures 4 through 8, in which the maximum midlayer depth is shown for the same 5° increments of longitude used in Figure 3. Contours of equal midlayer depth are drawn on the charts at 25-fm intervals for the two most widely distributed layers, B and D, in order to show the depth variation with geographical position. The two north-south traverses of Ref. 2 yielded valuable clues to isolating these layers.

Part of line KILO, latitude 40° N, was surveyed during both summer and winter, June 1965 and December 1966. This duplication enabled us to investigate any seasonal effects. Data from these two occasions are superimposed in Figure 9. Annual conditions over a 3-year period were available between latitudes 10° and 16° N; these are presented for line BRAVO, latitude 13° N, in Figure 10.

The foregoing data have been qualitative, but around Iceland, quantitative data were obtained by using equipment described in Ref. 1. Figure 11 shows a PDR trace of the DSL being mea-

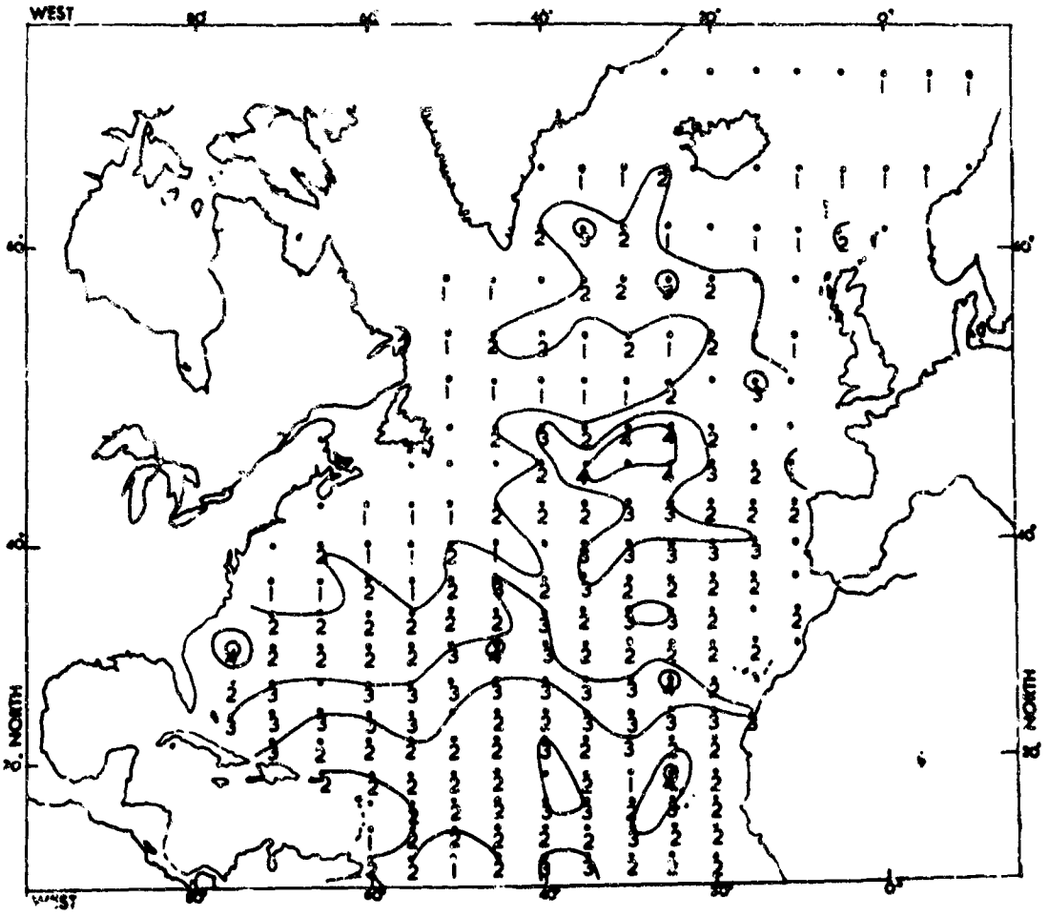


Figure 3. Number of DSL's present

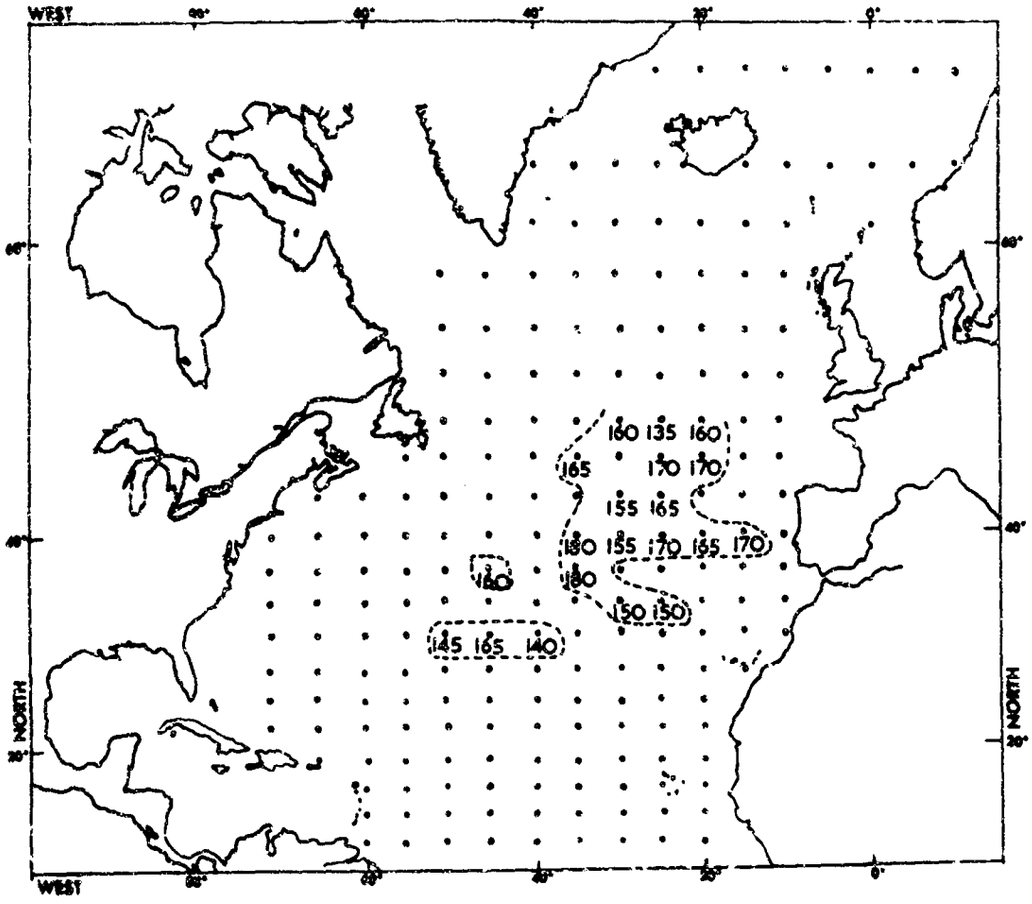


Figure 4. Maximum midlayer depth of layer A

sured, with the DSL bracketed by the opening and closing marks of the measuring gate. During the open period of this gate, the peak echo signal from the DSL is measured and then converted into target strength. Table 1 indicates typical target strengths.

During the traverses of latitudes 61° and 68° N, qualitative information at 30 and 50 kHz was obtained, in addition to that at 10 kHz. These data are presented fully in Ref. 2, while that at 30 kHz at latitude 61° N is shown in Figure 12.

DISCUSSION

Layers A, B, and C

Layers A, B, and C (Figures 4-6) were purely migratory and were found in latitudes south of 49° N. These layers of small vertical thickness (20 to 30 fm) generally produced considerably more darkening of the 10-kHz PDR than did the deeper, more diffuse, and thicker layer D. Occasionally, discrete groups of more intense scattering were found in layers A, B, and C, particularly in late and midafternoon. Layers A and C were identified only in localized areas in the North Atlantic, but they usually were found with layer B. Moore (Ref. 3), who found similar instances of multi-layers in the Mediterranean and near the Azores, suggested that each layer contains a different subspecies of the same marine organism, in his case, euphausiid, but in this current study more likely to be swimbladder-bearing fishes. According to Marshall (Ref. 4) the different types of scatterers may be competing for living space.

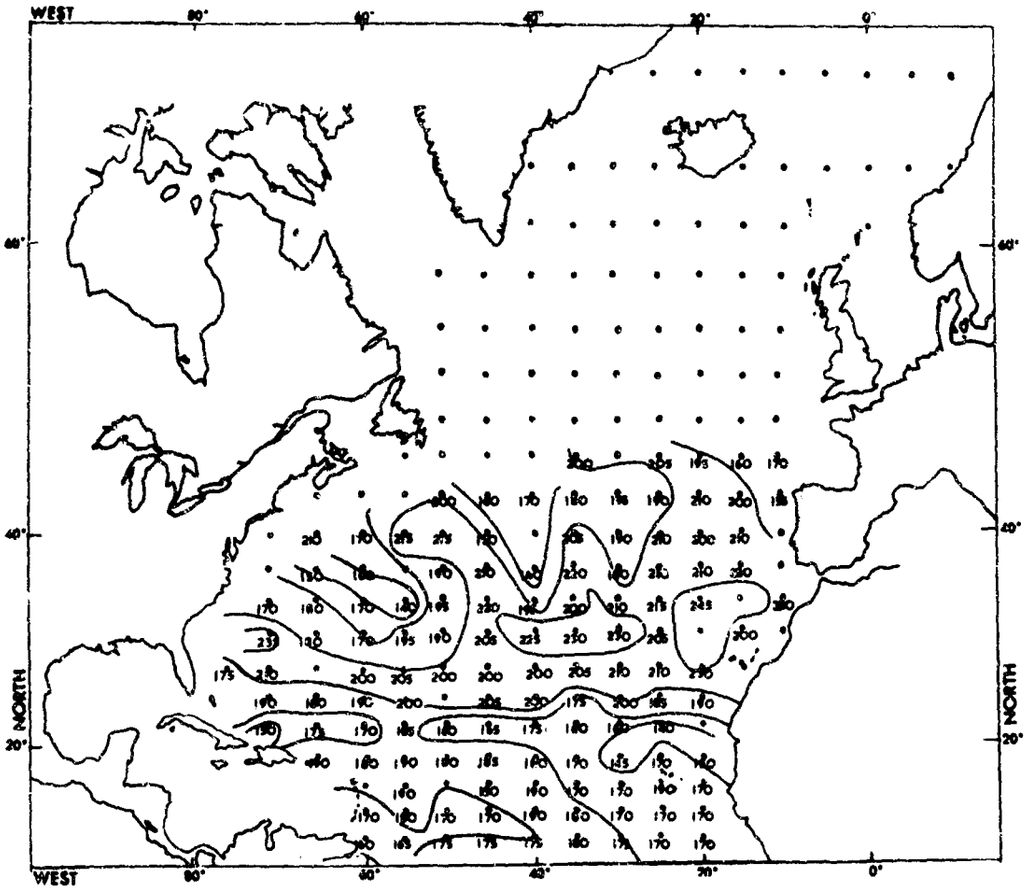


Figure 5. Maximum midlayer depth of layer B

Layer A was concentrated north of 31° N, and layer C, south of 29° N. Layer B was the most widely distributed of the three; it was found in North Atlantic areas south of 46° N, and had a maximum midlayer depth ranging from 140 to 245 fm. Layer A was generally shallower than layer B, with a maximum midlayer depth ranging from 135 to 170 fm. Layer C was deeper than layer B, with maximum midlayer depth of 215 to 280 fm.

Layer B probably can be identified with the shallower layer of the two found by Hersey and Backus (Ref. 5), who used a 12-kHz echo sounder. The extremes of the depth variation of the layer that they discovered in the western North Atlantic were 131 and 220 fm. This range is similar to that of layer B in the same area. The deepest migrations of layer B occurred along latitudes near 31° N, with a corresponding decrease in depth north and south of this line. Pronounced minima of the vertical extent of the migration depths occurred off the North African west coast and the U.S. eastern seaboard in areas of upwelling and heavy current movements respectively. Data published by Chapman and Marshall (Ref. 6) may provide a clue to the resonant frequency and scattering of layer B, at least in the western North Atlantic. These investigators found three predominant layers in the ocean on a line between Bermuda and Nova Scotia. The shallowest layer, which occurred at all the sites investigated, had a resonant frequency near 13 kHz and lay at a depth that decreased with increase of latitude from 295 fm in the south to 195 fm in the north. These depths were, in general, greater than those of layer B at 10 kHz, but the depth variations with latitude and migratory behaviour were similar. Chapman and Marshall (1966) found that this shallowest layer probably dominated the scattering in the octave band 6.4 to 12.8 kHz with a strength of −55 to −60 dB.

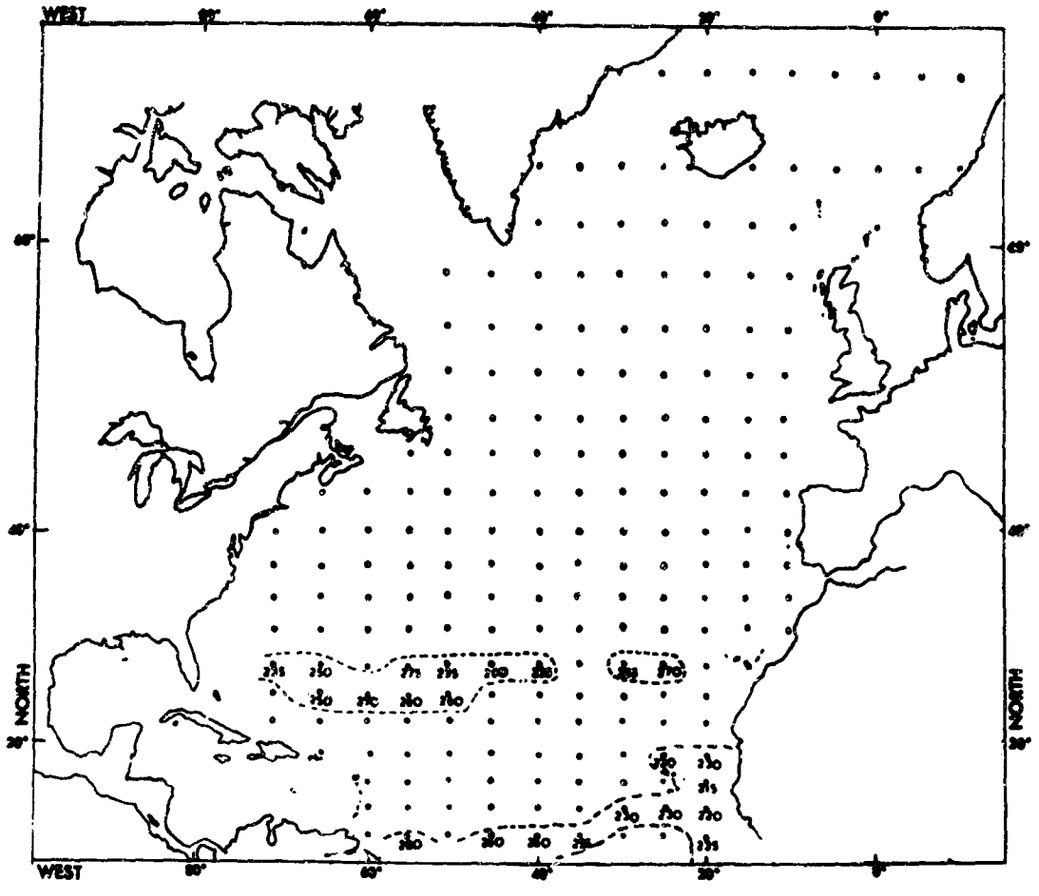


Figure 6. Maximum midlayer depth of layer C

Layer D

Layer D (Figure 7) was found to be the most widely occurring layer. It is characterised mainly by its partially migratory nature and greater thickness (30 to 60 fm). It attained a maximum depth of about 345 fm in the area 25° to 28° N and lay nearest the surface in the mid-Atlantic south of Iceland and off the east coast of Canada and the United States. Of the two layers discussed in Ref. 5, the deeper layer with its semimigratory pattern and depth range of 222 to 323 fm may be compared to layer D. Chapman and Marshall (Ref. 6) found a layer in the Sargasso Sea similar in character to layer D; the Sargasso Sea layer had a middepth of 330 fm and resonant frequency of about 7 kHz. The suggestion has been made that the constituents of this semimigratory layer may have been neutrally buoyant particles of organic detritus floating on a density discontinuity in the main thermocline. That migration occurs to and from the layer indicates, however, that at least some of the scatterers were living organisms. It is also probable that layer D does not consist solely of one species of scatterer throughout its wide geographic distribution.

Layer E

Layer E (Figure 8) was mainly migratory and was discovered only in localized areas of the North Atlantic. This layer often was revealed only during its migration to and from its maximum depth, which ranged from 300 fm near Iceland to nearly 500 fm further south. Moore (Ref. 3)

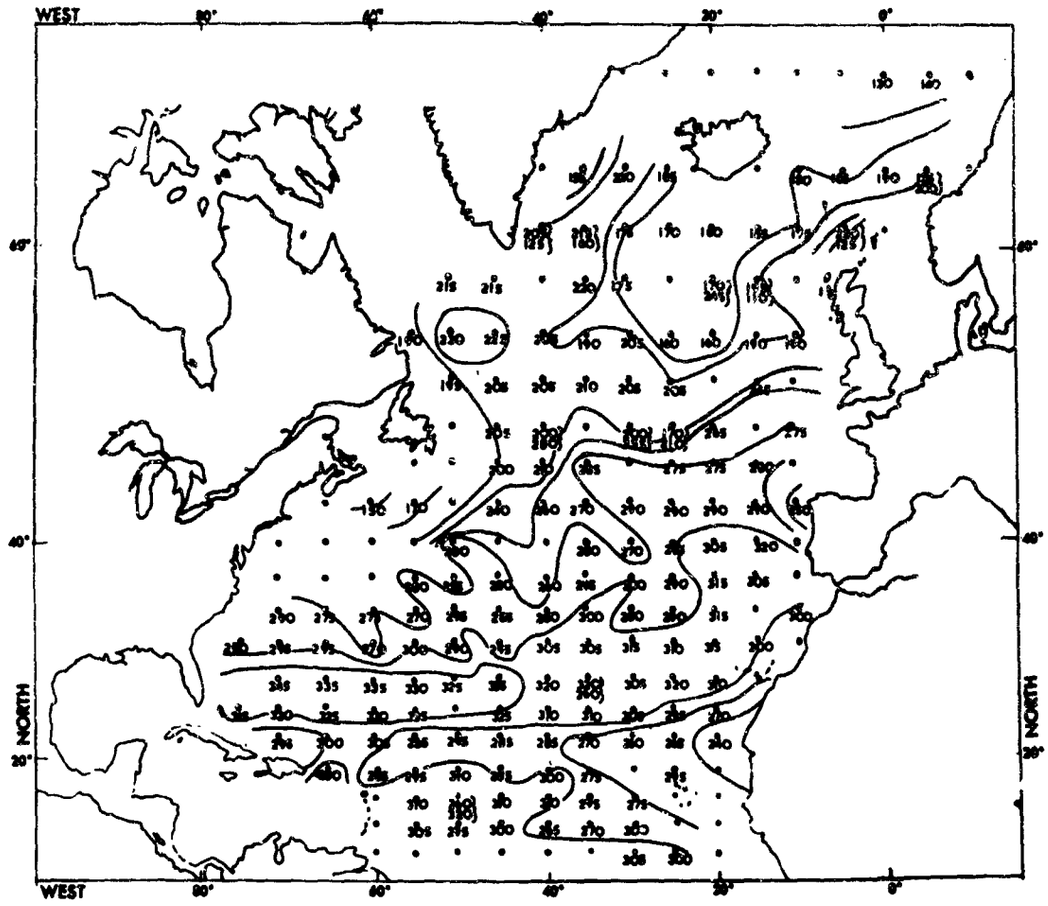


Figure 7. Maximum midlayer depth of layer D

remarked on the presence of such a deep layer and suggested that the scattering may be caused by a large red prawn. Chapman and Marshall (Ref. 6) found a layer resonant at 5 kHz whose depth corresponds roughly to that of Layer E, but their interpretation of the cause was a resonant swimbladder.

Areas With No Well-Defined Layers

The only area found in the whole of the North Atlantic Ocean that did not have the distinct 10-kHz scattering layers was the area north of Iceland. In this area there was a well-defined boundary between the north-flowing Irminger current and the south-flowing East Greenland current. The period spent at 68° N was during 20-hour sunlight, and the normal diurnal patterns could not be reasonably expected; however, such patterns did appear at 30 and 50 kHz.

Scattering Layers and Plant Life

As part of the ecological chain, the animals making up or comprising the scattering layers may be feeding on phytoplankton which in turn must be dependent on the abundance of nutrients. The distribution of phytoplankton should therefore correlate with the distribution of herbivores (most likely planktonic) or perhaps first or second order carnivores (not necessarily planktonic) in either a positive or negative manner. However, since it is reasonable to be expected that not all organisms (planktonic or otherwise) are sound scatterers there is no reason to think that the presence of phytoplankton will correlate with the distribution of those organisms in particular, that happen to scatter sound. A great deal of information on plankton distribution has been published in the Dana Reports and has been summarised and processed by Backus and Hersey (Ref. 7).

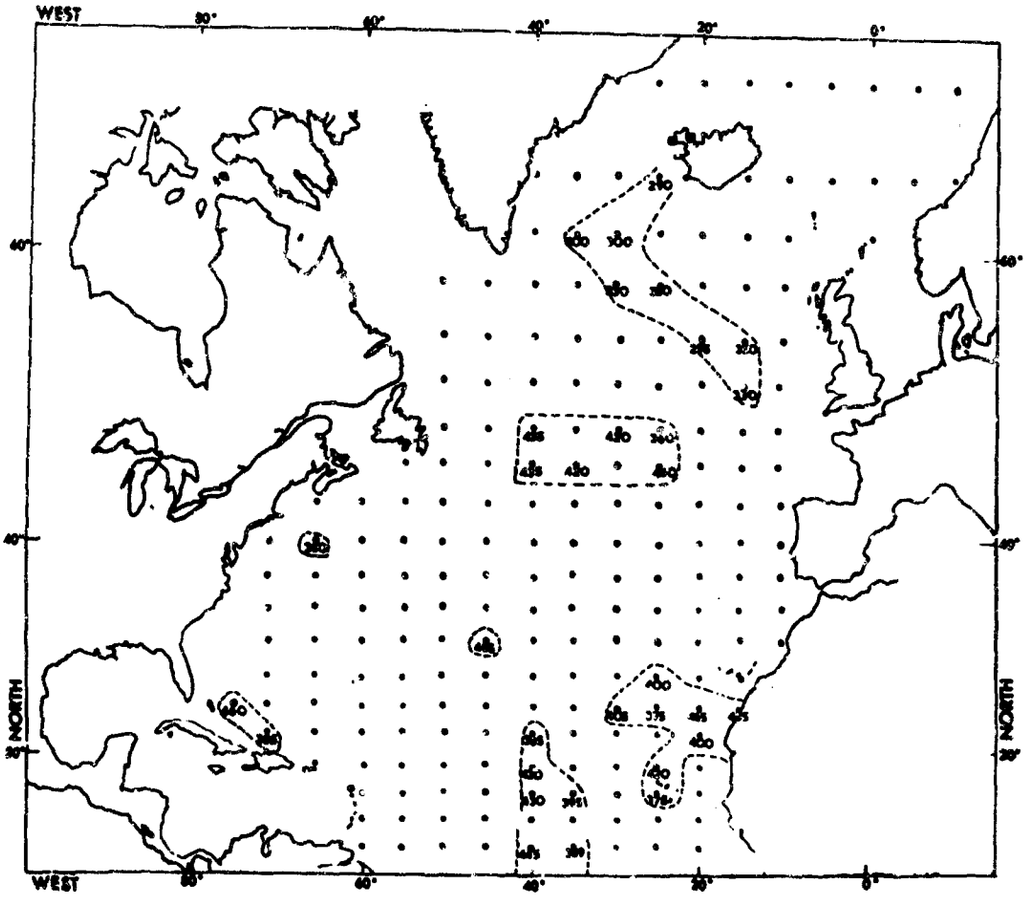


Figure 8. Maximum midlayer depth of layer E

Very little correlation exists between this processed data and the present results. Backus and Hersey predicted very heavy scattering in the northeast Atlantic, decreasing to a low level in the south of the area covered by this survey.

Seasonal Variation

The seasonal scattering layer depth variation along latitude 40° N (line KILO) between longitudes 12° and 43° W shows surprisingly little variation other than that the maximum layer depth at the eastern end was some 30 fm deeper in the summer months (Figure 9).

Annual Variation

There appears to be good correlation of scattering layer depth along line BRAVO for information obtained over a span of 3 years (Figure 10). Information was obtained in November and December 1963, January 1965, and December 1965. The DSL patterns are remarkably consistent in their appearance from year to year. The outstanding features are a layer that migrates to a depth rather less than 200 fm and a deeper, semimigratory layer around 300 fm. This deeper layer shows a definite trend each year toward becoming shallower from west to east by as much as 30 fm.

CONCLUSIONS

1. There are two main scattering layers in the North Atlantic which are identified in this report as layers B and D.

2. There is a variation of maximum scattering layer depth with geographic location that in all probability is correlated with the hydrography.

3. Seasonal variation of scattering layer depth patterns for a fixed location in the tropics vary in minor detail only between the months of June and December.

4. Annual patterns of the scattering layer depths for the months November to January, over a 3-year period, are repeatable.

Table 1. Typical DSL Target Strengths Around Iceland

Latitude	Longitude	Target strength (dB)
68°33′ N	18°22′ W	51.47
67°17′ N	23°42′ W	54.5
67°11′ N	23°47′ W	48.2
66°00′ N	28°04′ W	53.9
65°57′ N	28°14′ W	62.8
65°55′ N	28°25′ W	50.7

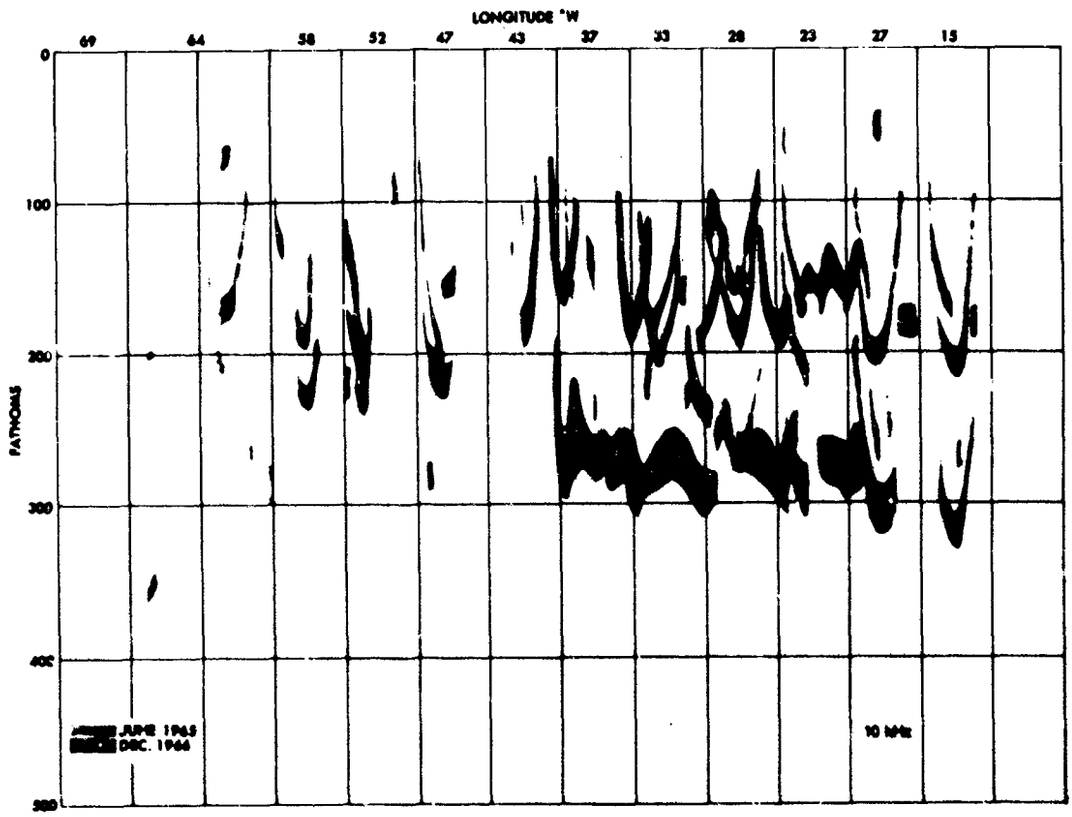


Figure 9. Seasonal variation of the DSL on line KILO (lat 40° N)

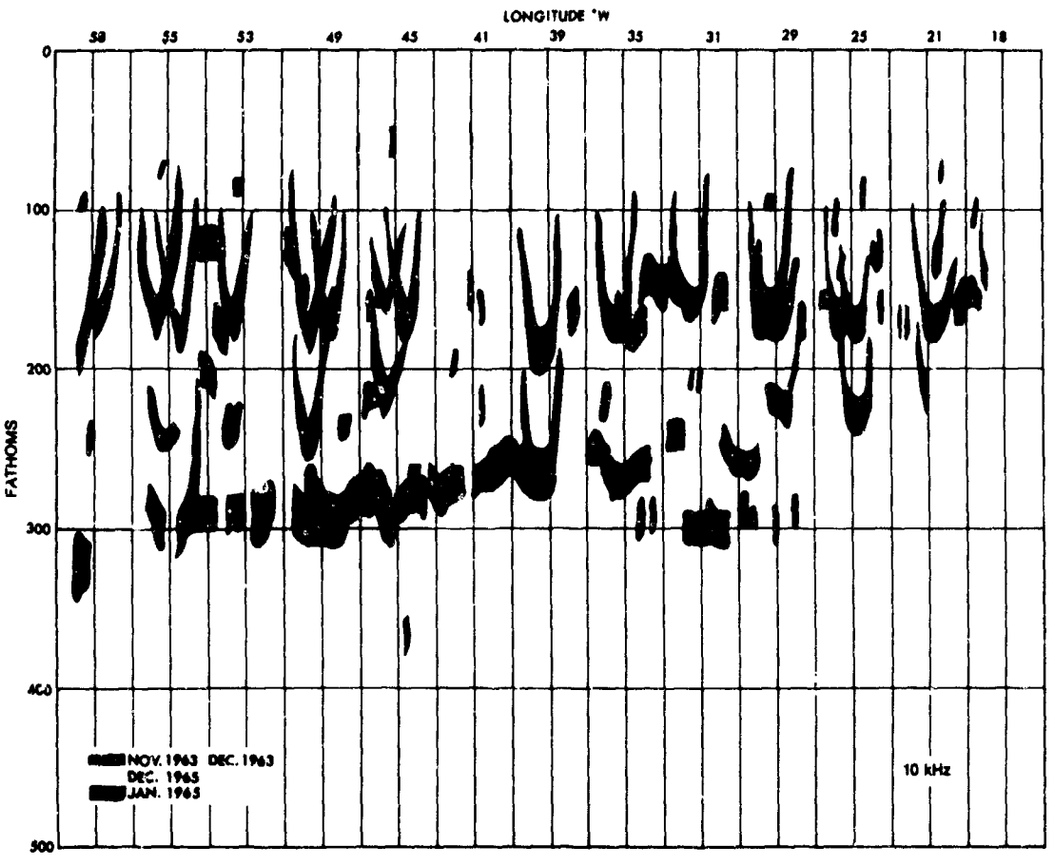


Figure 10. Annual variation of the DSL on line BRAVO (lat 13° N)

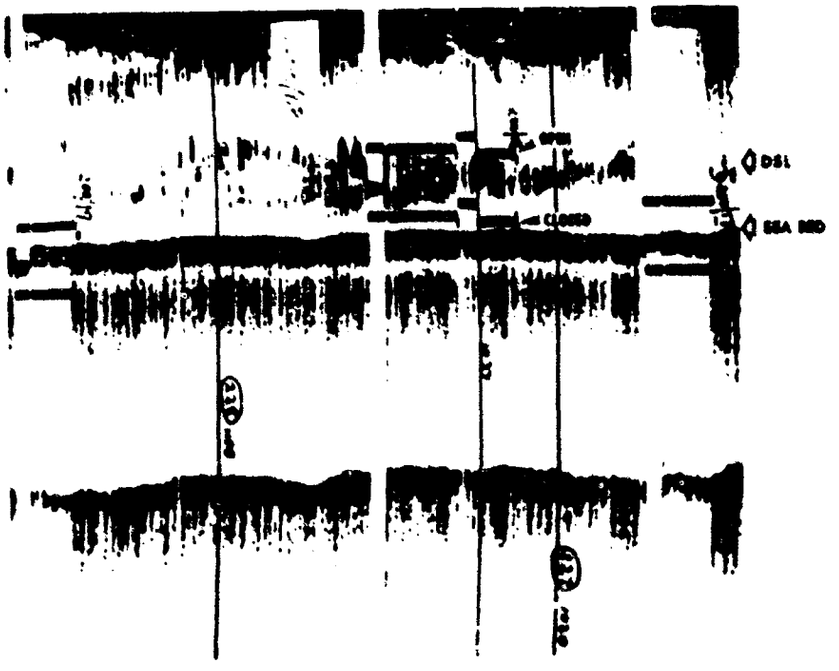


Figure 11. DSL showing measuring gate

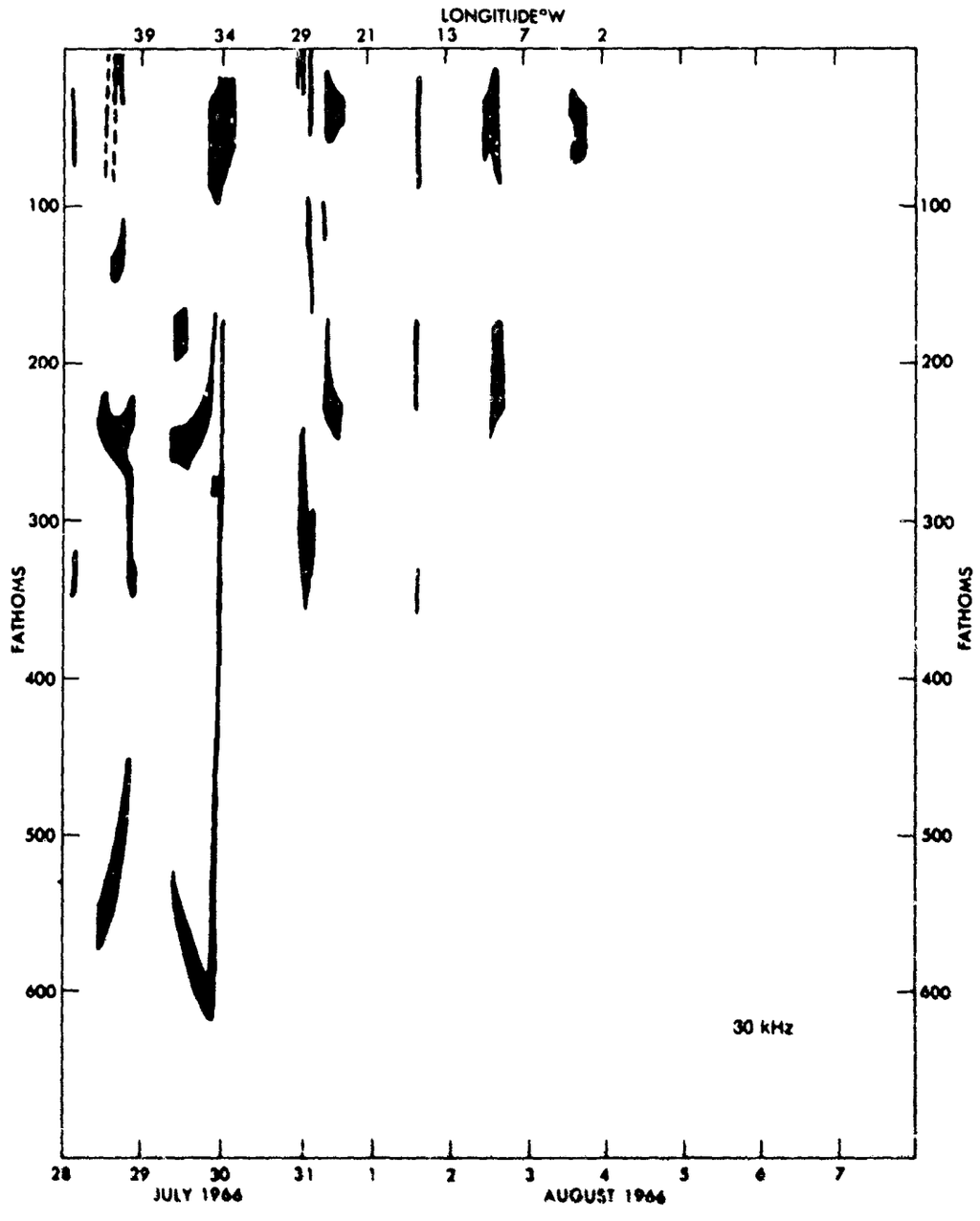


Figure 12. 30-kHz DSL on NAVADO line ROMEO (lat 61° N)

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DISCUSSION

Clarke, W.: What was the upper limit of layer D?

Janaitis: That was approximately 330 fathoms from 25° to 28° North.

Barham: In characterizing your layers, do you distinguish between diffuse scattering layers and layers that are formed by hard targets like the echo groups, or tent fishes as we sometimes call them?

Janaitis: I really couldn't answer that question. I haven't had access to all of the data, and I actually had only an hour to discuss this paper with Ken (Haigh). However, I am going to be seeing him within the week, because I will be going out to California. I know this is a little hardship, but if you could write your questions on paper, I could carry them out to him. I'm sorry I couldn't help you there.

Farquhar: You mentioned the term "midlayer depth." I wondered just how you determine the depth, whether it was the top of the trace as it appeared on the echo-sounder record, or did you use some other means?

Janaitis: I believe that Ken (Haigh) just took the average between the top and the bottom. As you said, the thickness was highly subjective due to its dependence on the pulse length and the gain. I believe he just took an average.

Cole: Do you know how happy he was with the use of the numbers of layers as a parameter to characterize these things?

Janaitis: No, I don't.

Cole: It seems to me that the main problem in some of these studies is in trying to fix on a variable which will accurately represent a meaningful condition in the DSL. In some of the work that we did, the number of layers seemed to be a less reliable and less interesting variable. For example, in plotting the number of layers we obtained few layers toward the North around Iceland and the Revkjanes Ridge, which graded into more and more layers in the Sargasso Sea region, but this parameter seemed to have too much variability to be useful.

Janaitis: No, Ken never brought this up. He mentioned the fact that the survey wasn't set up to measure the DSL, but they had obtained these data as they were measuring bottom topography and acoustic reflectivity. He was a little disappointed in that aspect because the trip wasn't equipped solely for the DSL.

THE DEEP SCATTERING LAYER: PATTERNS ACROSS THE GULF STREAM AND THE SARGASSO SEA*

H. P. Cole,† G. M. Bryan and A. L. Gordon
Lamont-Doherty Geological Observatory of Columbia University
Palisades, New York

ABSTRACT

The depth configuration of the acoustic reverberation caused by the sonic scattering layers has been examined by means of 12-kHz echograms recorded on several cruises between New York and Bermuda. A distinct change in the depth and migratory behavior of certain scattering layers occurs upon crossing the Gulf Stream. The deep nonmigrating layer present from 220 to 320 fathoms (fm) in the region south and east of the Gulf Stream, vanishes in the slope water to the north and west where it is replaced by a migratory layer whose daytime maximum depth is 300 fm. At the point of crossing the maximum temperature gradient on the North Wall of the Gulf Stream, all intermediate and deep scattering layers are absent. Vertical temperature profiles of the Sargasso Sea from the *Gibbs* indicate that the deep scattering layer (220-320 fm) lies at the depth of the relatively homogeneous 18°C -36.5 °/₀₀ water layer, and, therefore, in the western North Atlantic Ocean the 220- to 320-fm nonmigrating scattering layer is a useful indicator of the presence of this water mass. The northern termination of this layer marks the position of the Gulf Stream.

INTRODUCTION

Many investigators of the sonic scattering layers of the oceans have dealt with questions relating to the identification of the scattering agent (Barham, 1963a, b; Hersey and Backus, 1954, 1962; Millman and Manheim, 1968; Kinzer, 1969), the acoustic properties of suspected scattering species and reverberation measurements (Cushing and Richardson, 1955; Hersey, Backus and Hellwig, 1962; Haslett, 1965; Chapman and Marshall, 1966) or, in fewer cases, with the consideration of the oceanwide pattern of scattering layer depths (Beklemishev, 1964; Chapman and Marshall, 1966). During one series of reverberation measurements, between Nova Scotia and Bermuda Chapman and Marshall (1966) noticed a deep nonmigratory reverberation layer which seemed to occur only south of the Gulf Stream. The relationship between scattering layer depths and hydrography has been investigated by Weston (1958); Fraasetto, Backus and Hays (1962) and Bary (1966) among others, and correlations have been found within particular areas, for example, the Mediterranean Sea and Saanich Inlet, British Columbia.

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*L-DGO Contribution Number 1533.

†Presently at the Geophysical Institute of the University of Alaska, College, Alaska 99701.

In the deep ocean, however, broad hydrographic dependence of the deep scattering layers has not previously been investigated, nor has a major boundary current, such as the Gulf Stream, been examined in detail for its effect on scattering layer patterns. In this report, we propose to examine the variations in 12-kHz scattering patterns within and peripheral to the Gulf Stream and, by relating them to the local hydrography, demonstrate that the position of the Gulf Stream and of the characteristic 18°C water of the Sargasso Sea (Worthington, 1959) may be determined from the acoustic record alone.

METHODS

Three sets of echograms of acoustic scattering layers were obtained on the following research cruises between New York and Bermuda: *Gibbs*, Oct. 25, 1968 to Nov. 10, 1968 (Fig. 1); *Vema*-25, Dec. 1, 1966 to Dec. 5, 1966; *Vema*-26, July 25, 1968 to Aug. 1, 1968 (Fig. 2). The *Gibbs* obtained concurrent hydrographic measurements consisting of five complete hydrostations and fifty expendable bathythermograph (XBT) measurements taken at intervals of 10 n.mi. (nautical miles) along the track in deep water.

The *Vema* and *Gibbs* were both equipped with continuously recording 12-kHz Precision Depth Recorders (PDR) employing hull-mounted transducers pointing directly downward. The transducer output beam pattern has a half-power point 17° off the vertical axis; the input signal is filtered for a narrow bandpass centered at 12 kHz so that what appears on the record is reverberation at this frequency which is, however, uncalibrated with respect to acoustic energy

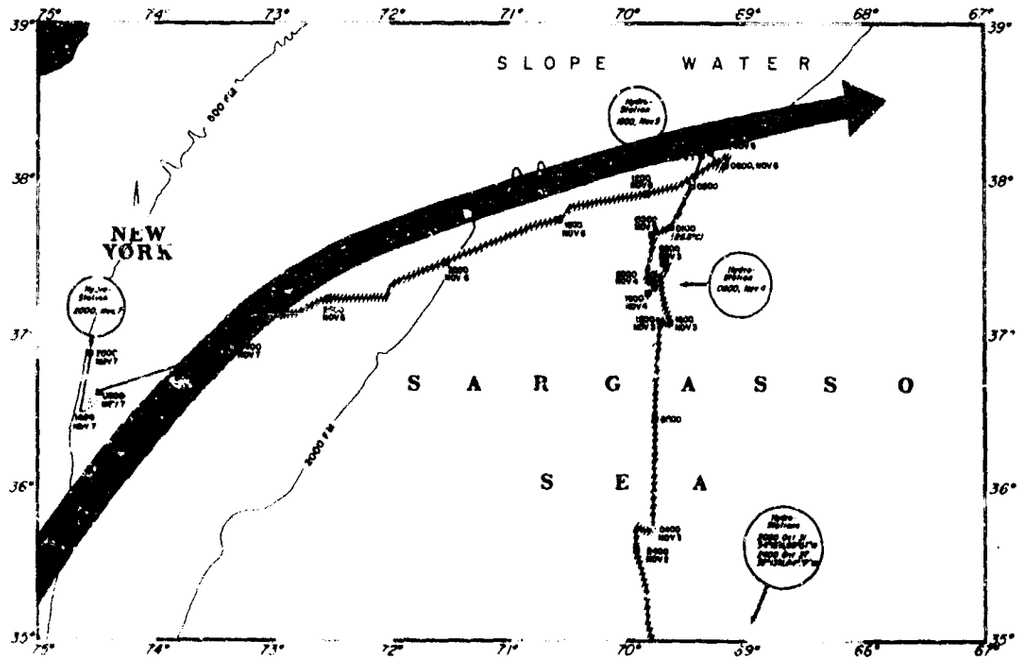

Figure 1. Track chart for the November, 1967, *Gibbs* cruise from Bermuda to New York. Times and dates are marked at intervals along the track along with hydro-station positions. Crosshatching along the track indicates the presence of the deep (220 to 320 fm) nonmigratory layer on echogram records. The general position of the boundary between the Gulf Stream and slope water is indicated by the broad arrow. The precise point where the north wall is crossed is determined from the temperature profile (Fig. 6). This position coincides with the disappearance of the deep layer. Letters correspond to points on Fig. 5.

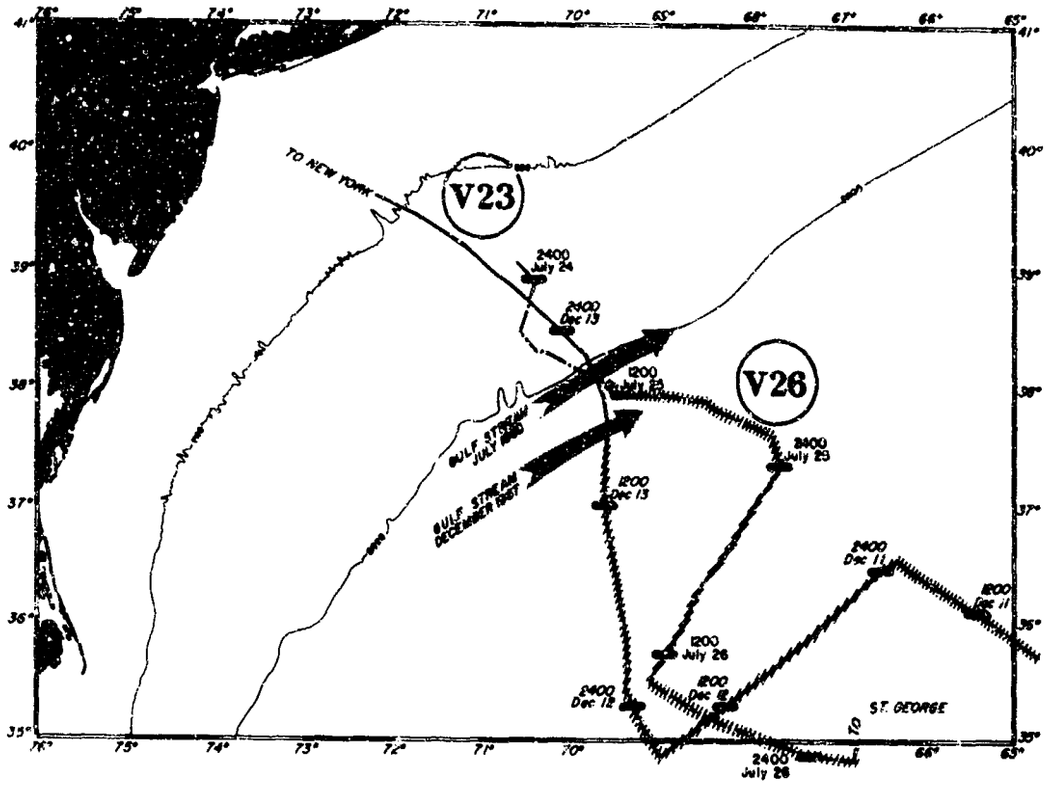

Figure 2. Track chart for the *Vema* cruises with time marks at 1200 and 2400 hrs each day. Crosshatching along the track indicates presence of deep (220 to 320 fm) nonmigratory layer on echogram records. For each cruise, the general position of the boundary between Gulf Stream and slope water, established from temperature data, is indicated by the broad arrow. This position coincides with the disappearance of the deep layer.

levels. The recorder stylus normally moves in a 1-sec mode which displays the upper 400 fm of the water column. Previous experience in this geographical region using a 10-sec sweep has shown that the scattering layers do not appear on our records below 400 fm so that a 1-sec sweep is sufficient. This is not to say that layers of biological origin are not present below 400 fm, but rather that these instruments do not record them as acoustic scatterers at depths greater than 400 fm in the western North Atlantic.

The echograms from all cruises were inspected at hourly intervals for the depth, thickness and density* of the layers and these results were catalogued on punched cards. These data were combined with those previously obtained from echograms from oceanwide cruises over the whole North Atlantic. In order to procure the most useful and meaningful variables with which to describe acoustic scattering, a number of scattering layer parameters were devised: total thickness (equal to the sum of thickness of each layer), a weighted thickness of all layers (produced by weighting the thickness of a layer with a density factor), depth and thickness of

*"Density" was a qualitative judgement of the blackness of the record but due to its subjective nature was eliminated as a factor in the data of this report.

individual layers, and depth of the bottom of the deepest layer.* Preliminary plots along a particular ship's track and contouring of these variables over the whole North Atlantic indicated that most of them had too much short-term time variability and did not seem to cluster well into homogeneous groups with distinct variations from area to area in the Atlantic Ocean. Beklemishev's (1964) success in establishing scattering layer provinces in the Pacific indicated that it was not unreasonable to expect similar geographical homogeneity in the North Atlantic. In our study, the two most useful variables turned out to be the total thickness of all layers and the depth of the deepest layer Along cruise tracks these variables were relatively stable and, when contoured, they demonstrated interesting homogeneity within hydrographically similar areas of the North Atlantic. Of the two variables, the behavior of the deepest layer, as monitored by the depth to its lower boundary, is used as the primary tool in analyzing the variation of scattering across the Gulf Stream.

RESULTS

The results of examining the records indicate the remarkable uniformity of the scattering layer pattern in the northwest quadrant of the Sargasso Sea, a fact which may be illustrated most clearly by the *Gibbs* echo-sounding records (Fig. 3).

In each case, the day scattering layer pattern consists of a surface layer from the surface to 80 fm; one or two random intermediate scattering layers at depths from about 100 to 140 fm, and a deep scattering layer occupying depths from 200 to 320 fm. The night scattering layer pattern has a more dense surface layer extending to 140 fm, which then merges with a very finely laminated horizontal structure from 140 to 200 fm; and a deep scattering layer (DSL) from 220 to 320 fm. The significant feature is the great similarity of all the day patterns and all the night patterns and the ubiquitous occurrence of a deep scattering layer from 220 to 320 fm.

As one examines the records along the *Gibbs* track, the scattering pattern in the Sargasso Sea at 0800 on Nov. 4 (Fig. 4a) is the standard Sargasso Sea daytime pattern which becomes the standard, but less dark, nighttime pattern in the evening (2000-2300) of Nov. 4 (Fig. 4b). Three hours later (a distance of 30 n.mi.) (Fig. 4c, 4d), at 0200 on Nov. 5 nothing is visible except a layer from 0 to 100 fm and faint patches of layering extending to 160 fm. After viewing a characteristic scattering pattern unbroken for a track distance of 500 n.mi. in the Sargasso Sea, a distinct interruption in the intermediate and deep layers occurs on the records for the very early morning of Nov. 5 from 0000 to 0600. By 0900 on Nov. 5 intermediate layering is again present (Fig. 4e) at a depth of 120 to 220 fm and is migratory. A deep migratory layer at 200 to 300 fms exists but could not be reproduced photographically from the original record. On the night of Nov. 5 the deep layers extended only to 120 fm (Fig. 4f).

The scattering layer data obtained by the *Gibbs* can be divided into three types:

(1) A deep layer with a significant nonmigratory component,
(2) Absence of a deep scattering layer, and
(3) A deep layer with only a migratory component.

Figure 5 shows the extent of each of these regimes along the *Gibbs* track. To what, if anything, can we relate the abrupt changes in the scattering pattern? According to the bathythermograph profile taken on the *Gibbs* cruise (Fig. 6) at 0200 Nov. 5 when the PDR showed no DSL at all, the research vessel passed out of the Gulf Stream into the slope water to the north. The deep layer

*Due to geometric effects with the conical beam pattern, a scatterer may appear to lie at a greater depth and hence a layer of a certain thickness will be represented as thicker on the echosounder. For a 17° half-power point, the change in thickness is about 5% and will not invalidate our arguments.

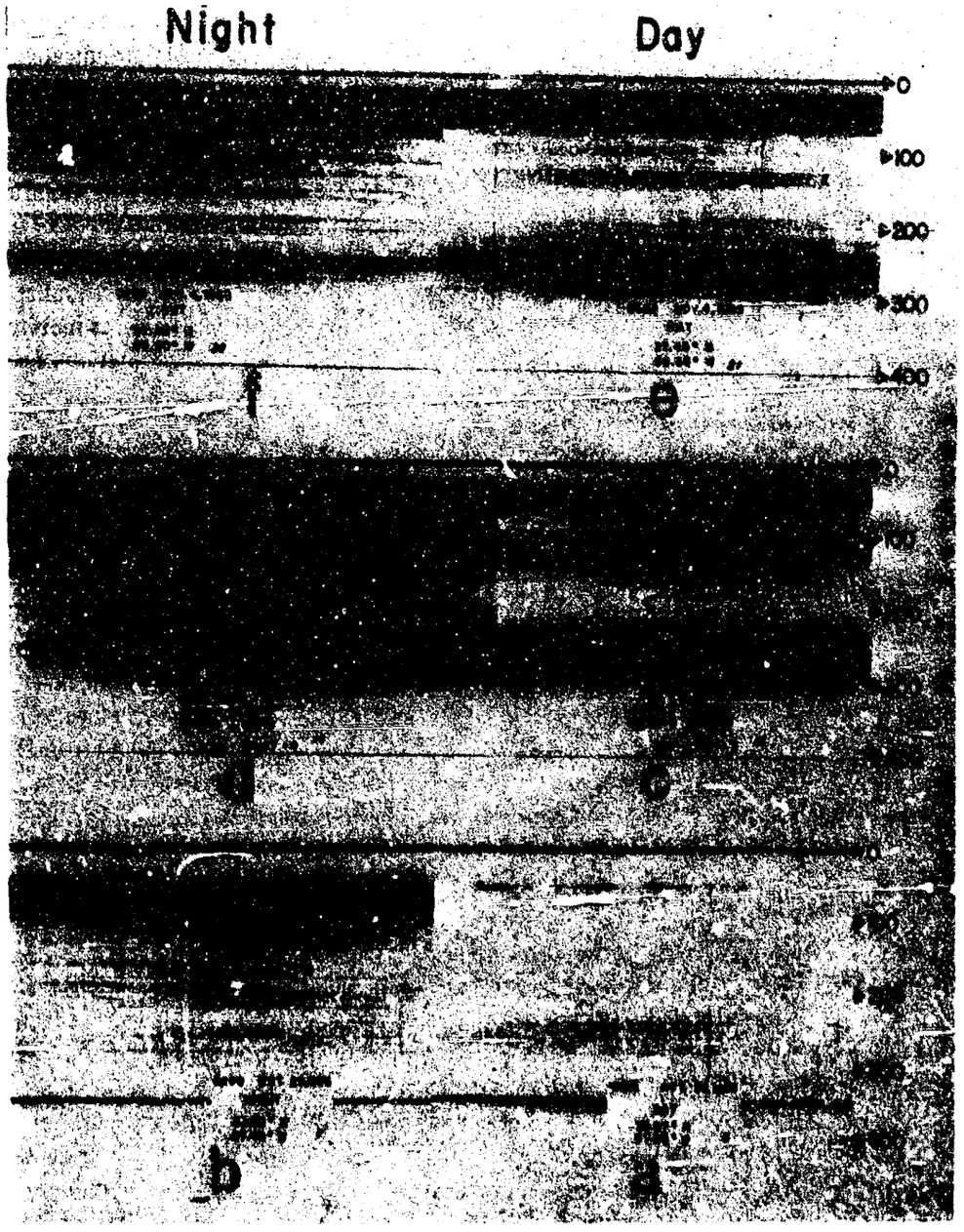

Figure 3. *R/V Gibbs* echograms of the acoustic scattering layers. These are all from Sargasso Sea waters; a, c, e, are daytime records. Oct. 29, Nov. 1, Nov. 4; b, d, f are nighttime records of the same dates. Each record covers a track distance of 15 n. mi. A blank occurs at the top of each record from the surface to 40 fm due to a malfunction of the electronics of the PDR. Photos a, b, e, and f show the bottom in a position which apparently is at the same depth with the deepest scattering layer and partially obscures it. The notable fact in these six records is the ubiquitous presence of the deep scattering layer at a depth of 220 to 320 fn..

Figure 4. *R/V Gibbs* echograms of the acoustic scattering layers obtained in three water masses: Sargasso Sea, the Gulf Stream and slope water (see caption for Fig. 3). The bottom partially obscures the scattering layer in a, b, and c. Picture b shows line due to the Benthos depth telemetry pinger and e shows acoustic reflection from the lowered instrument. Echogram d is a direct continuation of c. Echograms c and d do not have sufficient resolution to indicate fine layering to 160 fm which is visible on the original records.

Figure 5. Depth to the bottom of the deepest layer (plotted downward from a base line) for *R/V Gibbs* cruise between New York and Bermuda. Crosshatching indicates a nonmigratory DSL component, small dots indicate no DSL, and large dots regions of only migratory DSL. Letters correspond to positions along the track chart (Fig. 1).

lying at 220 to 320 fm, which was ubiquitous south of the Gulf Stream, disappeared, and the characteristic pattern of day and night deep scattering layers associated with the waters of the Bermuda area had totally vanished. The reestablishment of scattering occurred at daylight (0700) on Nov. 5 with a migratory bottom layer, as the ship entered the colder water to the north of the Gulf Stream.

A particular aspect of the DSL at 220 to 320 fm in the Sargasso Sea region may be understood by referring to a record of the DSL at dusk at 1800 Nov. 1, 1968 (Fig. 3d). It is obvious that there is a migratory component from the DSL which ascends at dusk and joins the intermediate and surface layers, and also a nonmigratory component which remains at the daytime level, becoming slightly less dense. The significance is that as the ship passed out of the Sargasso Sea, only the nonmigratory component of the DSL at 220 to 320 fm vanished while some sort of migratory deep layer remained and exhibited diurnal migration to 250 fm in the slope water to the north of the Gulf Stream.

Another example of this behavior is shown in the *Gibbs* scattering layer record for Nov. 6 and 7 (Fig. 6), as the ship obliquely reentered the Sargasso Sea by traveling at a small angle to the axis of the Gulf Stream. (See track chart Fig. 1.) The isotherms (Fig. 6) are not steep and the characteristic Sargasso deep layers were not encountered until 1600 to 2000 Nov. 6. That this is a nonmigratory layer is obvious since the layer attained the characteristic 300 fm depth at night. The ship then entered the slope waters at 0200 Nov. 7 and the normal migratory deep layer was present. It should be noted that the three *Gibbs* crossings mentioned occurred at positions separated by distances of as much as 300 n.mi. A summary of these comparative patterns is presented in Table 1.

The echograms obtained on *Vema* 23 and 26 can also be divided into the same three regimes found on the *Gibbs*. Since no bathythermograph data are available, these profiles are related to the continuously recorded surface temperature trace and engine induction temperature obtained aboard the *R/V Vema* (Fig. 7). These cruises were chosen because of the good quality of the records and because the tracks intersected the mean position of the Gulf Stream at nearly right angles. A constant value of the depth of the bottom of the DSL throughout a 24-hour period indicates that the DSL has a nonmigratory component. In each case, it is seen that as the surface temperature drops from the characteristically high Sargasso Sea values indicating passage across the Gulf Stream and into the slope water, the DSL bottom depth decreases from 320 fm to between 50 to 100 fm and then establishes a diurnally fluctuating value with a maximum depth of

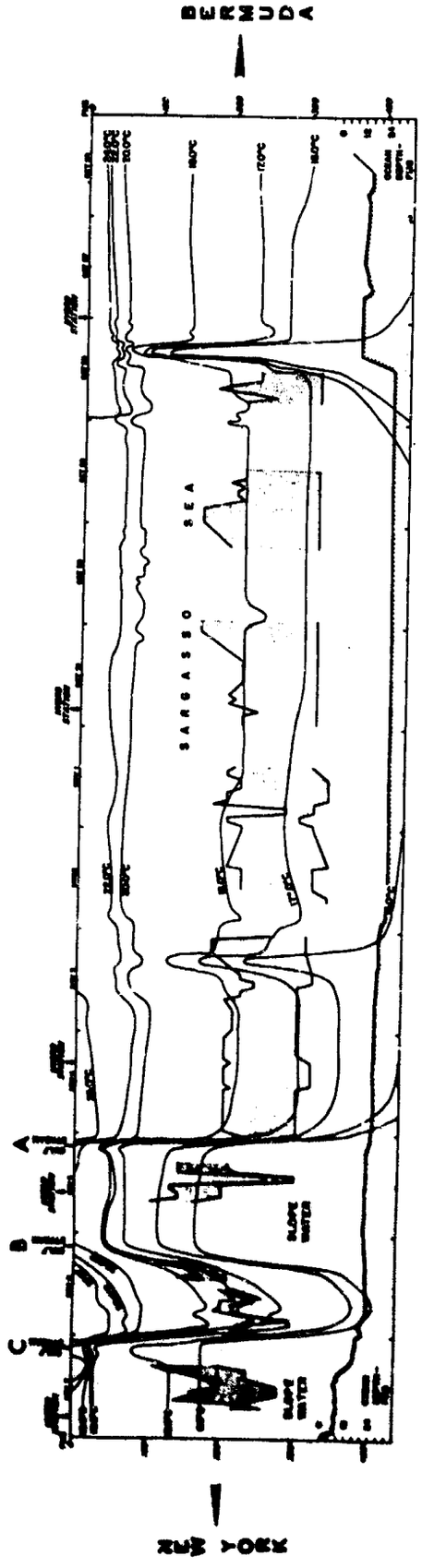

Figure 6. Temperature profiles based on BT data obtained by the *Gibbs* super-imposed (in patterned area) on a profile of the deepest DSL layer. Letters correspond to positions along track chart (Fig. 1).

Table 1. Tabulation of Scattering Layer Levels Across the Gulf Stream (values in fathoms)

Layer	Slope Water		Gulf Stream		Sargasso Sea	
	Day	Night	Day	Night	Day	Night
Surface Scattering Layer	0-80	0-120	0-100	0-80	0-80	0-140
Intermediate Scattering Layer	120-220	0	0	0	100-120 120-140	140-220
Deep Scattering Layer (DSL)	260-300 (migratory)	150-200	0	0	220-320 (migratory) 220-320 (nonmigratory)	50-200 220-320

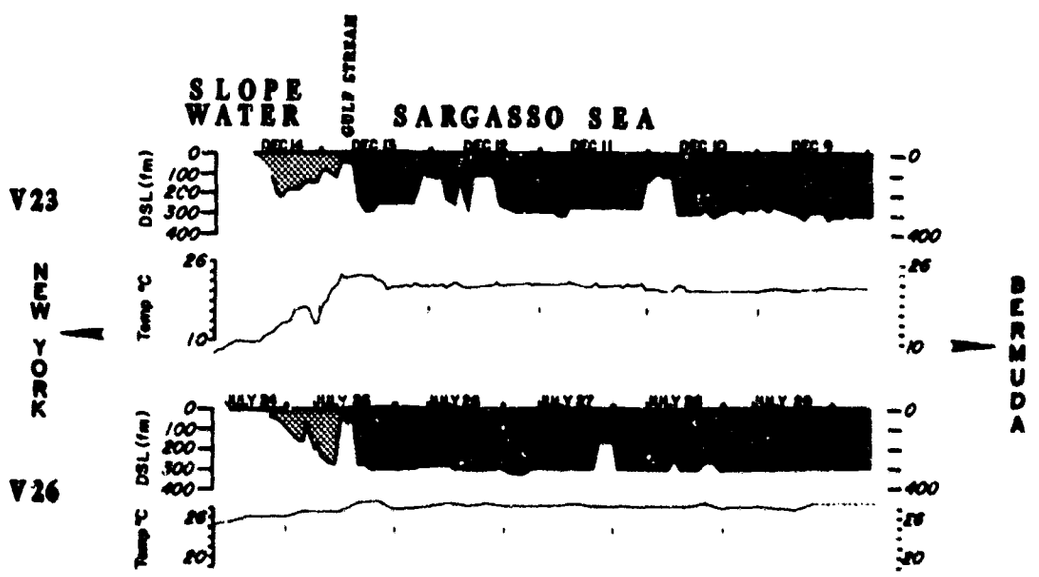

Figure 7. Depth to the bottom of the deepest layer and surface temperatures along the *Verna* 26 tracks. For *Verna* 26 it should be noted that on crossing into the Sargasso Sea the temperature increase is very small due to high summer slope water temperatures. The patterned areas are described by the caption for Fig. 5.

about 250 or 300 fm. Hence, on the records for these three crossings for summer, autumn, and winter, the existence of the 220- to 320-fm deep nonmigratory layer is characteristic of the Sargasso Sea, and the northern termination of this layer marks the position of the Gulf Stream.

DISCUSSION

Referring to the graph of temperature and depth of the deepest scattering layer for *Gibbs* (Fig. 6), it is interesting to note how precisely the low scattering lies between the 17°-18°C

isotherms of the Sargasso Sea. Even as the *Gibbs* reentered the Sargasso Sea on November 6 the depth and thickness of the deep layer appears to respond to small fluctuations in the depths of the isotherms.

Since the definition of water masses depends on both temperature and salinity, it could be interesting to see if the deep layer resides within not only a particular temperature range but salinity range as well, i.e. a particular water mass. At depths of 220 to 320 fm at five *Gibbs* hydro stations (shown on Fig. 6) the salinity values were determined to be 36.4 ± 0.1 °/₀₀ in the Sargasso Sea and, 35.0 ± 0.1 °/₀₀ in the Gulf Stream. The Sargasso Sea temperature and salinity data agree with that of the characteristic Sargasso Sea water mass, i.e., 17.9 ± 1°C and 36.5 ± 0.1 °/₀₀, discussed by Worthington (1959). The significance, therefore, seems to be that the nonmigrating deep layer corresponds, over the area investigated, with the "18°C water" of the Sargasso Sea.

A more oceanwide connection between the DSL and the thermal structure of the water column shows that the correspondence with 18° water tends to deteriorate toward the east from Bermuda. This may be seen by comparing the contour plot of the depth of the deepest layer and the depth of the 18°C isotherm in the Sargasso Sea (Fuglister, 1960) (Figs. 8 and 9, respectively). It is evident from the *Gibbs* data (Fig. 6) that the depth of the 18°C isotherm corresponds to the top edge of the deep nonmigratory layer (220 to 320 fm). These contours of DSL and 18°C isotherm depth are stable seasonally. Histograms of "depth of DSL basement" derived from records obtained from 1955 to 1969 were plotted monthly and indicate that there is no seasonal change in the depth to the bottom of the nonmigratory DSL. Similarly Schroeder, Stommel, Menzel, and Sutcliffe (1959) cited the extreme stability of the properties of the 18° water throughout the 85 years considered in their investigation. The concentric contours of both plots lead to the striking results that both distributions are lenticular but the positions of their maximum depth centers do not coincide. The DSL configuration has a depth of over 340 fm which is located in the area of 35°N, 50°W. But the maximum depth of the 18° water is far closer to North America at 30°N, 70°W as result of the westward intensification of the North Atlantic Gyre. For comparative purposes the temperature and salinity values at 220 to 340 fm at the center of the DSL depression are in the range of 15° to 17° and 36.0 to 36.4 °/₀₀ salinity, respectively.

A speculative answer to the question as to why the DSL center is shifted to the east may be found by considering the effect of variations of light levels at 220 fm in the North Atlantic. From the examination of transparency data over the North Atlantic in Schott (1944), an approximate center of transparency would be in the region of 25°N, 45°W, a spot east of the position of DSL maximum (Fig. 8). These data show the transparency to be constant in the central North Atlantic and decreasing near the coasts. Greater transparency results in a given level of light intensity being found at greater depths in the ocean. Since the DSL is highly photosensitive, increased light levels force the nonmigrating DSL deeper to a depth of 340 fm. On the other hand, at the center of maximum transparency, the T-S values of the water in the 220 to 320-fm layer are 13° to 15°C and 35.9 to 36.0 °/₀₀ salinity (Fuglister, 1960), values still lower than those at the lower DSL level. Hence, the difference may be related both to light levels and to the T-S characteristics of the water mass at that level. The position of maximum DSL basement depth may represent a balanced response to these two sets of stimuli.

One important problem in the above hypothesis is that if the variations in light levels, due to variations in transparency, are sufficient to override the T-S dependence characteristics to some extent, why then does the much greater diurnal variation in light levels produce no diurnal response in the nonmigratory layer? Possibly this implies the existence of organisms in the deep layer which have response times on the order of days and are not susceptible to short-term light

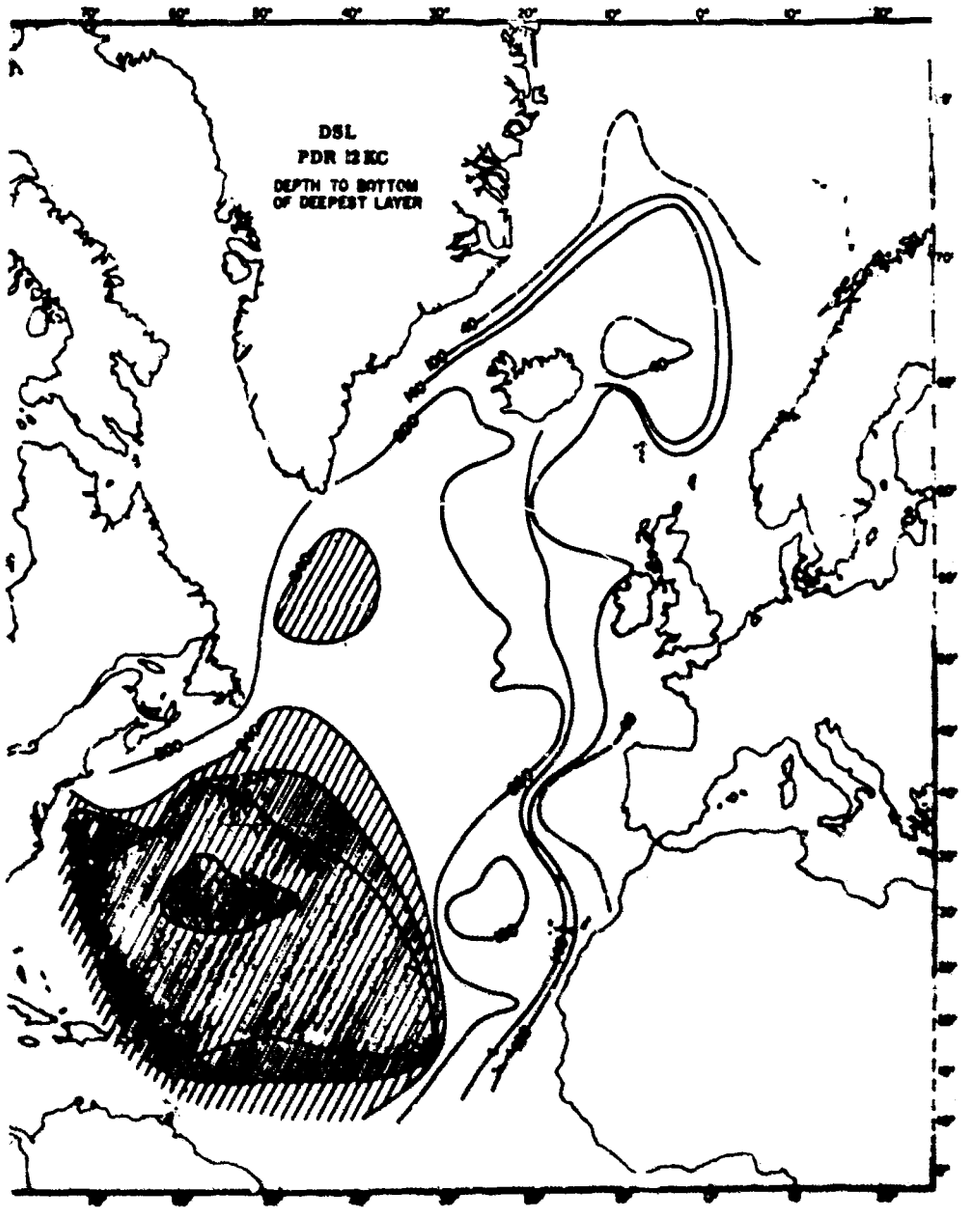

Figure 8. A contoured plot of the depth to the bottom of the deepest layer. This plot was derived from some 3000 12-kHz DSL observations over the North Atlantic, primarily from *Verna* cruises. On a preliminary plot individual DSL readings were mapped and the maximum value of the parameter occurring in a 1° (lat.) X 5° (long.) area was chosen as the value to be the contoured on the present chart. Hence, from original values of, say, 300, 300, 320, 260 and 200 fm within a 1° X 5° rectangle from the preliminary plot, the value 320 would be used here.

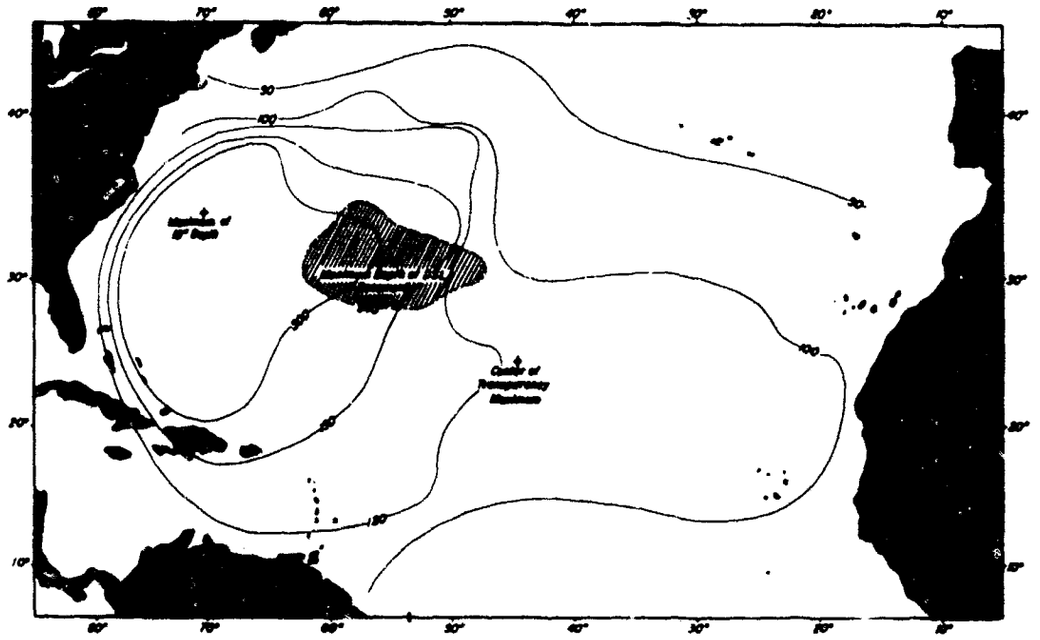

Figure 9. The contoured plot of the depth in fm of the 18° isotherm (from Fuglister) plotted concurrently with the position of the DSL maximum and a center of transparency for the North Atlantic (Schott, 1944).

variations, or organisms which have no migratory response to light levels whatever and position themselves with respect to the lower limits of the species which do migrate. Figure 3d could portray this behavior.

Recently Masuzawa (1969) showed that "18°C water" exists in the western subtropical Pacific Ocean. It would be of interest to discover if there were any nonmigratory layers in the Pacific associated with this homogeneous water type.

The absence of any scattering along the 50-mi. transition from the Sargasso Sea to the slope waters was clearly evident on our four crossings. This absence is due to the simple fact that the Gulf Stream marks a severe hydrological boundary (particularly noticeable at the north wall) which clearly separates the biological community of the Sargasso Sea from that of the slope water. The abrupt nature of the discontinuity across the north wall is cited by Stommel (1966) who states that the Gulf Stream maintains its integrity and identity to a remarkable degree and "small scale turbulent processes tending to transfer properties across the stream in the upper layer are inconsiderable." Biota which are indigenous to the Sargasso Sea or slope waters apparently cannot adapt to the sharp gradients of salinity and temperature encountered in crossing the Stream itself.

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QUASI-SYNOPTIC MEASUREMENTS OF VOLUME REVERBERATION IN THE WESTERN NORTH ATLANTIC

Edward E. Davis
U.S. Naval Oceanographic Office
Washington, D.C.

ABSTRACT

During May 1969 a quasi-synoptic measurement study using airborne techniques and instrumentation was undertaken in the western North Atlantic to measure volume reverberation at frequencies between 0.8 and 3.2 kHz. The sites selected for this study were chosen to transect the estimated position of the Gulf Stream along three tracks north of Bermuda. A correlation was attempted between the measured reverberation levels and this boundary.

Scattering-strength contours for daytime and nighttime measurements as well as diurnal variation were examined within the boundary constraints of the experiment. An interpretation of the resultant scattering-strength contours for frequencies between 0.8 and 2.5 kHz and temperature regimes or water masses observed indicate that scattering may be influenced by the Gulf Stream position. Day measurements indicated a high scattering center north of the Gulf Stream, and a low scattering center to the south. Maximum diurnal variation was observed where maximum nighttime scattering was measured and generally occurred south of the Gulf Stream. No direct relationship between the Gulf Stream boundary and the measured reverberation levels was observed for the highest frequency investigated, in particular 3.2 kHz.

INTRODUCTION

In recent years observations of volume reverberation produced by the re-radiation of impinging sound upon swimbladder-bearing organisms associated with the deep scattering layer (DSL) have been reported by various investigators as a function of geographic area, season, and acoustic frequency (Adlington, 1967, Marshall and Chapman, 1964, Gold and Van Schuyler, 1966, Hersey, Backus and Hellwig, 1962). Because oceanographic boundaries may affect the distributional characteristics of biological organisms commonly found within the DSL, as suggested by Ebeling (1962), an airborne quasi-synoptic study was undertaken in May 1969 to investigate the effect of an oceanographic boundary, in particular the Gulf Stream, upon volume scattering conditions. Because the primary scattering organisms often exhibit diurnal depth migrations that affect the frequency-dependent characteristics of volume reverberation, measurements were made during day and night conditions. The measurement sites were chosen to transect the estimated position of the Gulf Stream between Bermuda and Nova Scotia along three longitudes as shown in Figure 1.

EXPERIMENTAL METHOD AND DATA ANALYSIS

At each measurement site shown in Figure 1, a modified sonobuoy (Davis, Parham, and Kelly, 1968), an air expendable bathythermograph (AXBT), and a series of three explosive

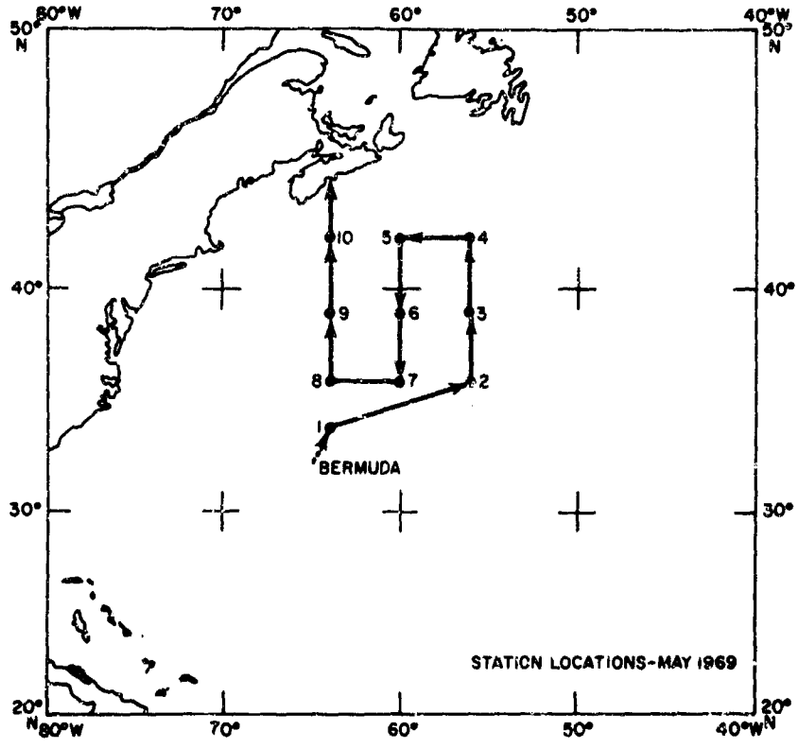

Figure 1. Airborne reverberation stations

sound signals were dropped from an aircraft during day and night hours. Daylight hours are defined as 1-1/2 hours after sunrise until 1-1/2 hours before sunset. Night hours are defined as 1-1/2 hours after sunset until 1-1/2 hours before sunrise. The sea conditions observed during the measurement period were less than or equal to sea state 1. Temperature variations observed from the AXBTs taken at each test site were used to estimate the position of the Gulf Stream.

The SSQ-41 sonobuoy is a modified electronic package with a frequency response between 0.8 and 3.2 kHz that activates on contact with the water and deploys an omnidirectional hydrophone to a depth of 60 feet. A radio link between the monitoring aircraft and sonobuoy is used to telemeter all acoustic information, as well as a calibration pulse that is used for system linearity checks and data analysis.

The explosive sound signals used were broadband, omnidirectional sources containing 1.8 lbs of TNT with a 0.07 lb tetryl booster and were detonated at a depth of 60 feet. The resulting reverberation levels produced by insonification of the DSL by these sound signals, which were dropped in close proximity to the sonobuoys, are transmitted to the monitoring aircraft and recorded broadband on magnetic tape as shown in Figure 2.

The analog data recorded broadband in the field (Figure 2) were analyzed using one-third octave bandwidth filters over the frequency range from 0.8 to 3.2 kHz. These filtered data were displayed on a logarithmic recorder from which reverberation levels were determined, utilizing the calibration pulse transmitted by the sonobuoy. A typical logarithmic reverberation record as well as the equation for determining scattering strength from explosive sound signals are given in Figure 3 with its legend. Each series of reverberation-level curves similar to that shown in Figure 3 were read where the reverberation exhibits a $-30 \log t$

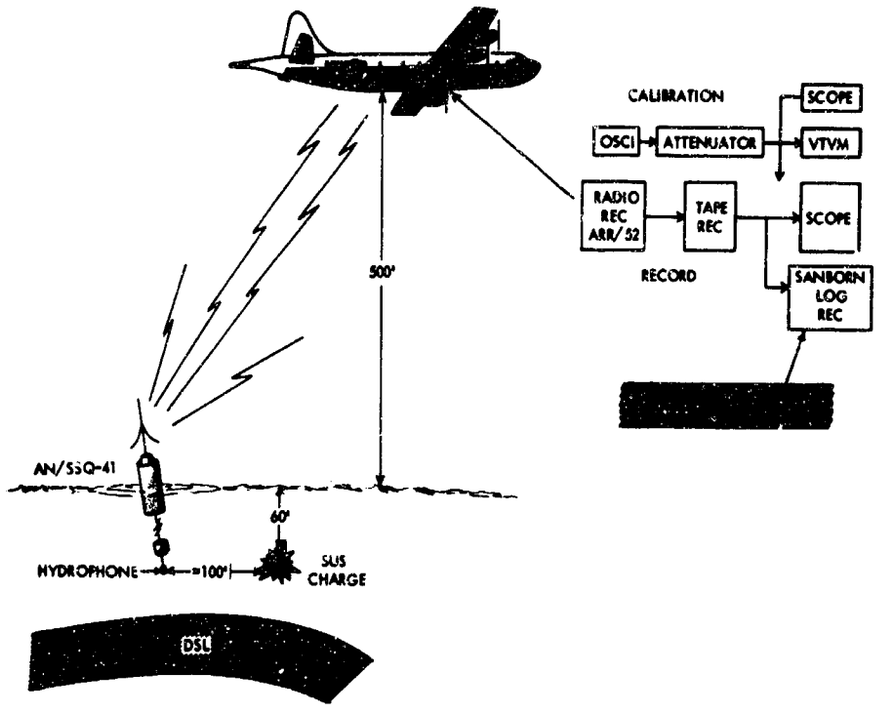

Figure 2. Airborne acoustic system

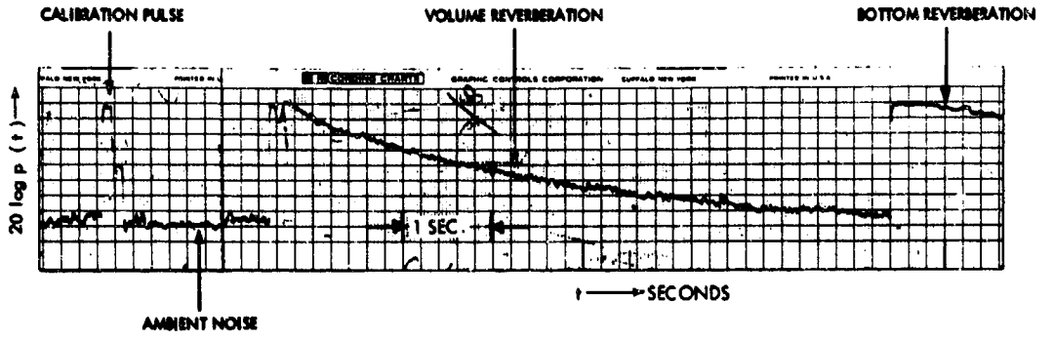

Figure 3. Logarithmic record of volume reverberation versus time. The reverberation pressure level equation is:

$$20 \log p(t) = 10 \log \int_0^d M(z)\, dz - 30 \log t + 10 \log E + K$$

where:

$20 \log p(t)$ = rms reverberation level dB re 1 dyn/cm^2
$M(z)$ = volume scattering coefficient for a layer, in meter^{-1}
z = vertical depth, in meters
t = time after explosive detonation, in seconds
E = energy per unit area of sound source, in erg/cm^2
K = constant (48 dB)

decay and at times when the surface scattering was negligible. The scattering strength of the water column has been presented as 10 log $\int_0^d M(z)dz$ by Chapman and Marshall (1966), Machlup and Hersey (1955), and others and is determined from the measured reverberation levels that characteristically decay at a rate of -30 log t. This equation was used to describe the amount of reverberation produced by all scatterers in a water column of depth d and of $1\text{-}m^2$ cross section. If the reverberation is caused by a series of horizontally stratified isotropic scatters present in a nonattenuating, nonrefracting medium, and if its distribution is a function of depth only, the scattering-strength equation is written as shown in Figure 3, where the constant K in the equation, in this case 48 dB, includes a correction for energy reaching the scatterers by surface-reflected paths and 10 log E is the energy per unit area at 100 yards from the sound source (Stockhausen, 1964). Scattering strengths were computed for all frequencies analyzed unless reverberation not consistent with a -30 log t decay was present (as at Station 4), or a poor signal-to-noise ratio was observed.

DISCUSSION OF RESULTS

Scattering strengths as a function of frequency were determined for the day and night measurements. In addition, the scattering-strength results were examined for the water masses north as well as south of the Gulf Stream, and a synoptic analysis using contours was attempted to enable a quantitative interpretation of the observed results in the area under study. The analyses were performed at frequencies from 0.8 to 3.2 kHz, and a relationship between scattering conditions and the estimated position of the Gulf Stream and its associated water masses was investigated.

Figure 4 illustrates the isotherm contours, determined from the AXBTs, at 100 feet, with the estimated Gulf Stream position superimposed as a boundary between cold and warm water masses. From this data it appears that the Gulf Stream was transected during the measurement study.

Scattering-Strength Variations

Figures 5 and 6 illustrate typical scattering strength and diurnal variation versus frequency curves where diurnal variation is defined as the difference between nighttime and daytime scattering strengths. The curves are presented for two longitudes, 64°00′ W and 60°00′ W, where transects of the Gulf Stream were completed and are annotated as to their relative position with respect to the Gulf Stream.

Figure 5 shows typical scattering strength and diurnal variation curves for three stations along longitude 64°00′ W. It is observed that the scattering strengths for day and night generally increase with increasing frequency for all stations. Stations 9 Day, 10 Day, and 10 Night also exhibit a knee or peak at frequencies between 1.25 and 2.5 kHz. Nighttime scattering strengths for Stations 8 and 9, to the south of the Gulf Stream, are as great as 15 dB higher than daytime measurements. Station 10, north of the Gulf Stream, generally has scattering strengths lower than Station 9 (just south of the Gulf Stream) and exhibits little or no diurnal variation at frequencies below 1.25 kHz. Above 1.25 kHz the diurnal variation increases rapidly with a maximum of 13 dB at 3.2 kHz. For stations along this longitude it is observed that diurnal variation generally decreases northward over the range of frequencies analyzed.

Figure 6 illustrates scattering strengths and diurnal variations for the three stations along longitude 60°00′ W. It is observed that Stations 5 and 6 exhibit several unusual scattering-strength characteristics. Station 5, north of the Gulf Stream and in the coldest water mass observed ($T = 37$°F), has daytime scattering strengths that decrease with increasing frequency from 0.8 to 2.0 kHz and then increasing with frequency to 3.2 kHz. The nighttime scattering

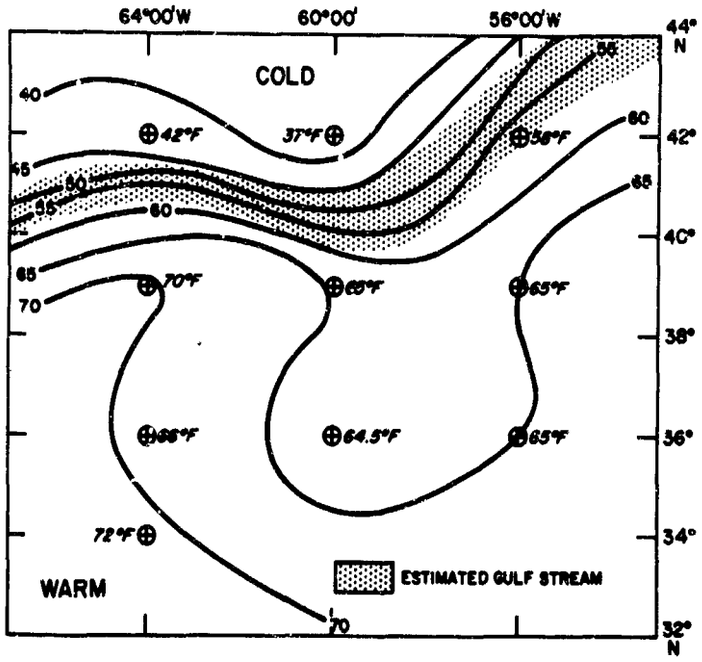

Figure 4. Isotherm contours at 100 feet

results for this station were estimated from contour plots discussed later. The estimated nighttime scattering strengths at this station also show scattering frequency reversals for frequencies between 0.8 to 2.5 kHz. A peak in nighttime scattering that is observed at 2.0 kHz has been determined from the contour plots.

Scattering-strength measurements at Station 6, just south of the Gulf Stream, indicate scattering strengths that increase with increasing frequency for day observations. Night measurements for Station 6 indicate a strong scattering peak at 1.6 kHz with a diurnal variation of 25 dB present at this frequency. The presence of such a dominant peak in nighttime scattering may indicate the vertical migration of a large number of potential sound scatterers producing a strong low-frequency resonance at 1.6 kHz. The scattering curves for Station 7 exhibit a general increase with frequency with a knee or peak at 1.6 kHz and diurnal variations between 10 and 15 dB.

Quasi-Synoptic Contour Analysis of Scattering Strengths

Figures 7 through 9 illustrate the scattering-strength contour analysis for day and night measurements, as well as diurnal variations, for frequencies between 0.8 and 3.2 kHz. All scattering strength values (in decibels) shown in the figures are negative, and "H" and "L" designations indicate relative high or low scattering. For discussion purposes it was found that contour patterns for frequencies of 1.25, 2.5, and 3.2 kHz are representative of low-, mid-, and high-frequencies over the range of frequencies analyzed.

The Gulf Stream boundary delineated by the isotherms at 100 feet and occurring between cold water with a sharp temperature gradient to the north and warm water with a weak temperature gradient to the south is also superimposed on each figure.

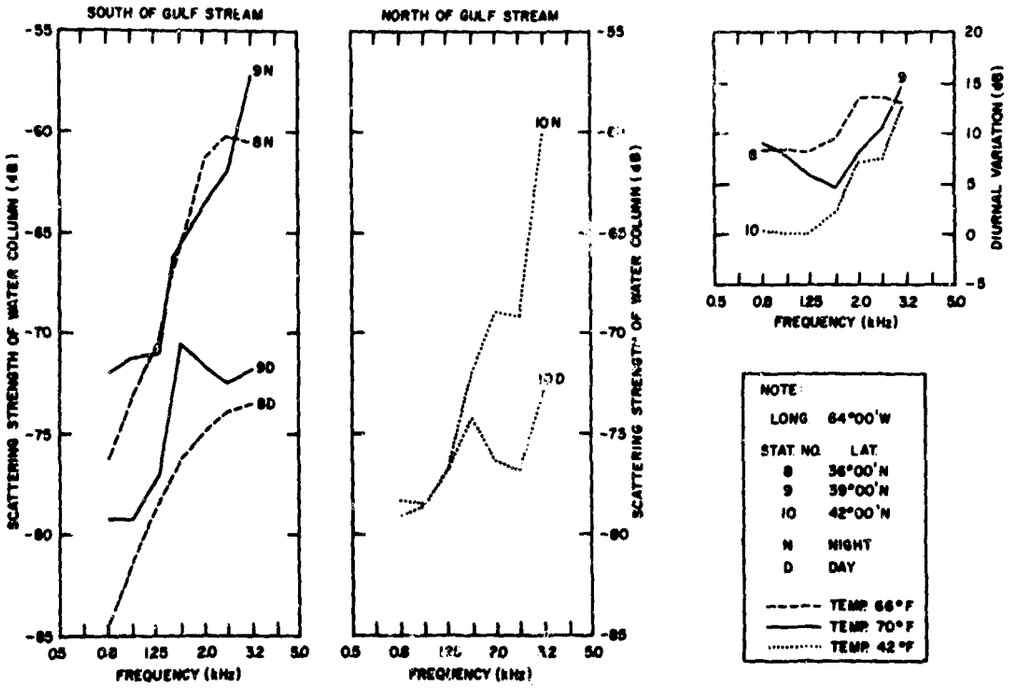

Figure 5. Scattering-strength curves for longitude 64°00′ W

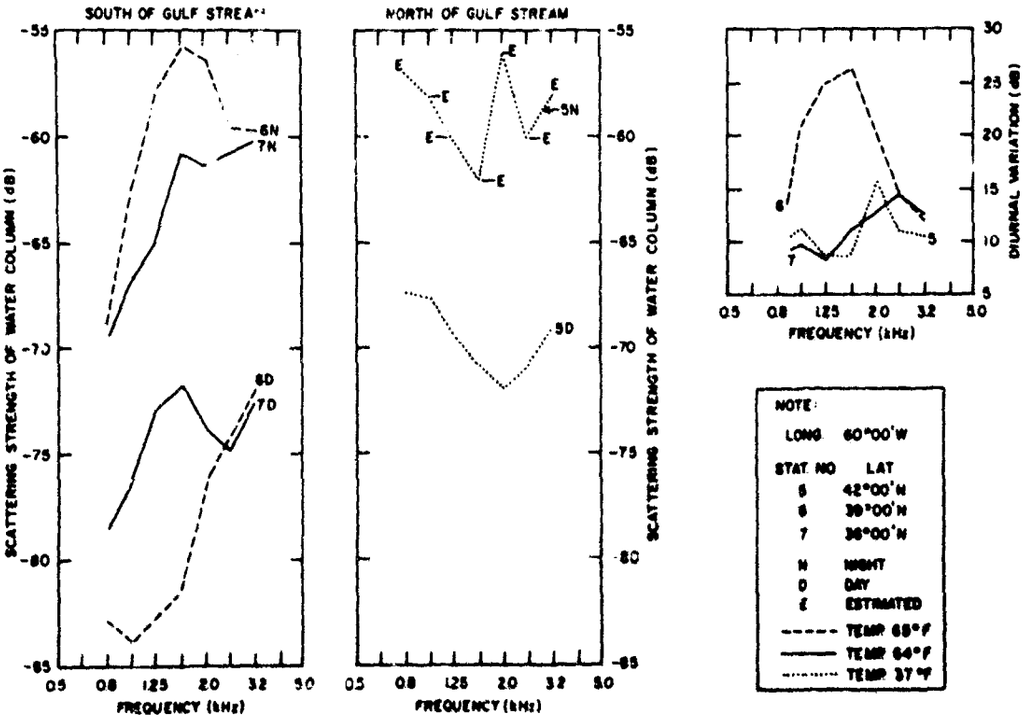

Figure 6. Scattering-strength curves for longitude 60°00′ W

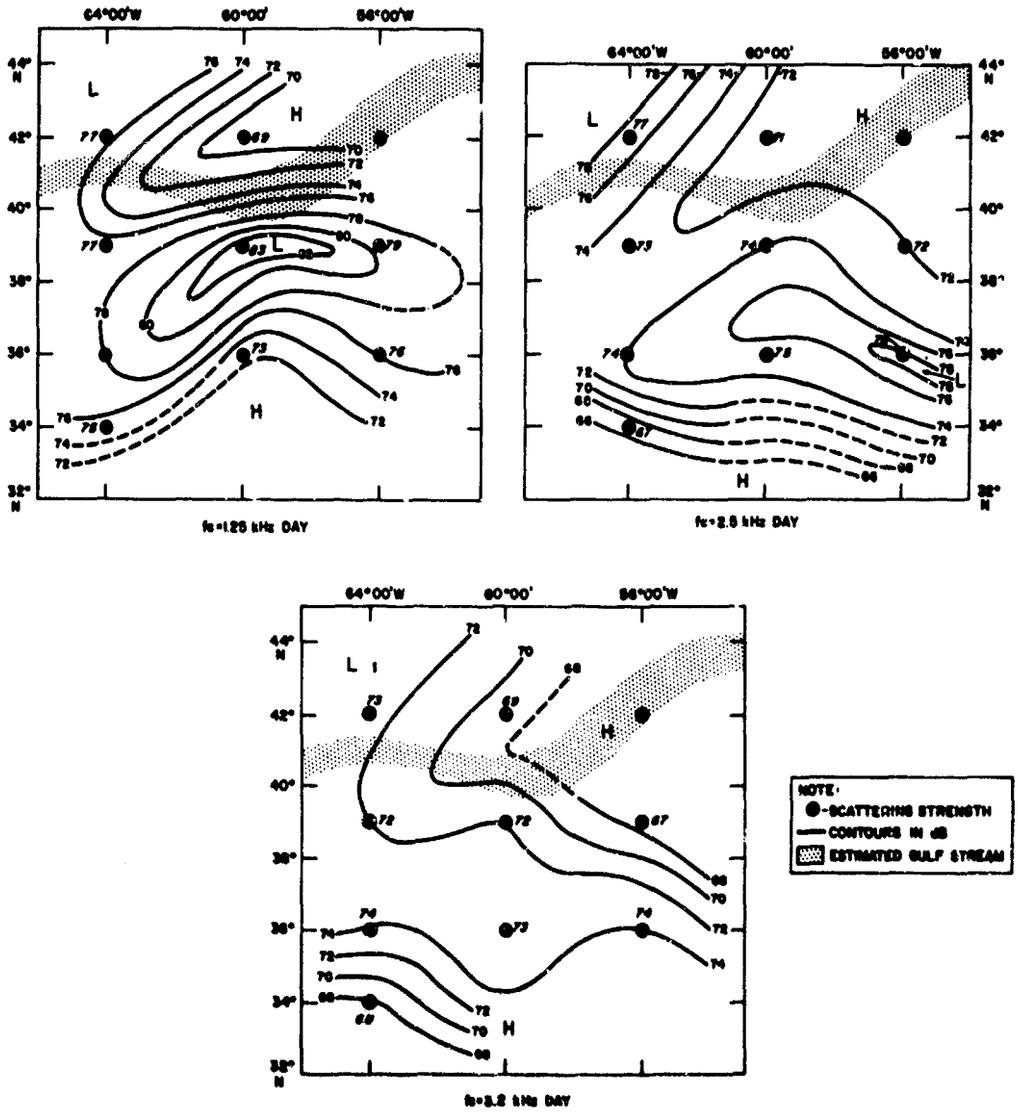

Figure 7. Scattering-strength contours for day measurements.

Day Measurements

Although it was observed that the scattering strengths at frequencies between 0.8 and 2.5 kHz have some variance in contour patterns the resultant data indicate the presence of two scattering centers; a region of higher scattering to the north of the Gulf Stream and a region of lower scattering to the south of the Gulf Stream. The representative contour patterns shown in Figure 7, indicate the presence of these scattering centers which appear to change with increasing frequency. With increasing frequency the scattering gradients become weaker and a degradation of distinct scattering centers occurs. At a frequency of 3.2 kHz there is no indication of the scattering centers observed at the lower frequencies, and the highest scattering strength values are found to occur to the northeast and southwest.

Night Measurements

At all frequencies between 0.8 and 2.5 kHz, night scattering strengths are higher than day and indicate a region of highest scattering in the center of the area under study as shown in Figure 8. As frequency increases, scattering-strength contours show a varying north-south orientation around the region of high central scattering. At 3.2 kHz, the highest scattering occurs to the northwest and no distinct scattering center is present.

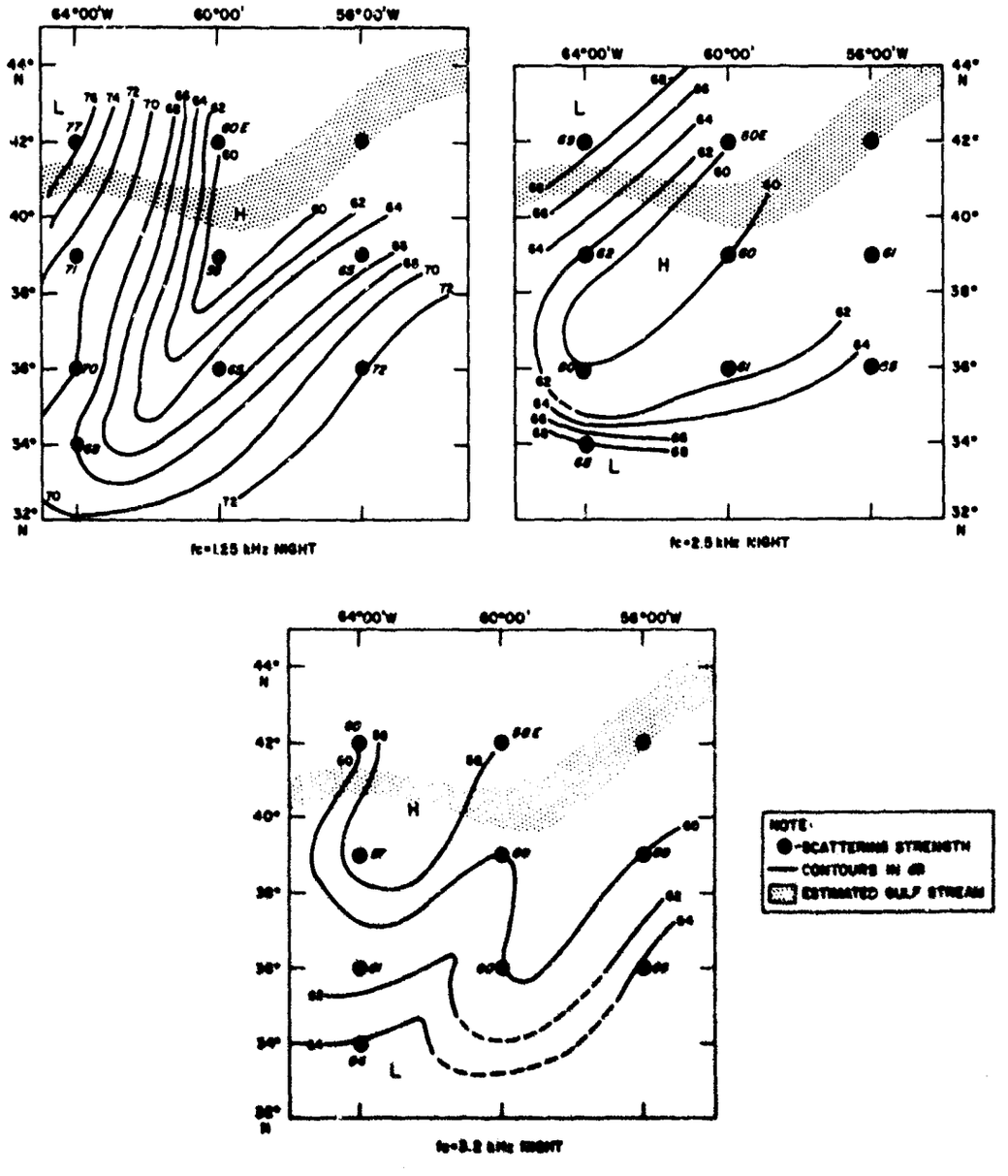

Figure 8. Scattering-strength contours for night measurements

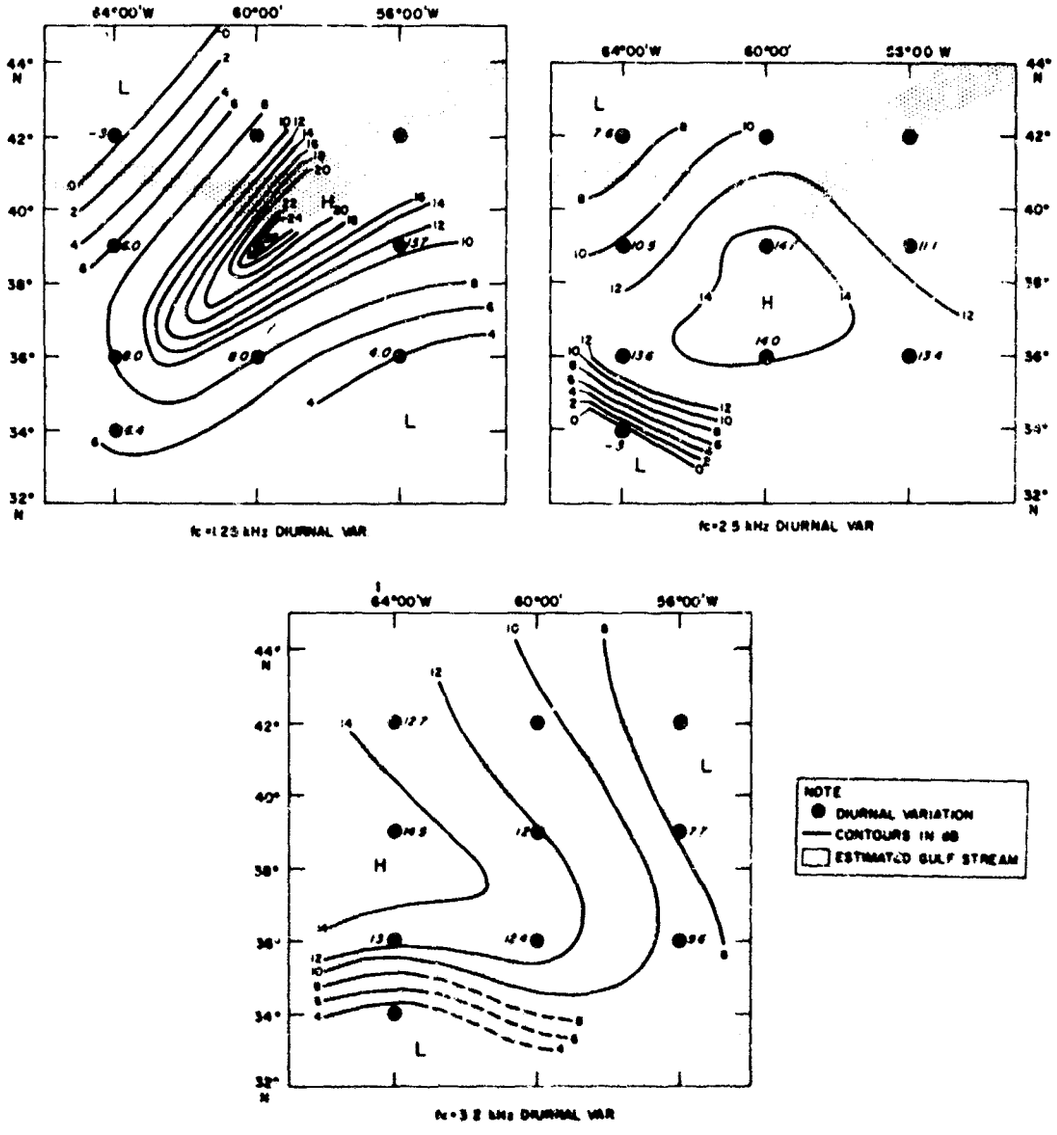

Figure 9. Scattering-strength diurnal variation contours

The high nighttime scattering observed for 1.25 kHz in the center of the area under study occurs near or at the Gulf Stream boundary. At 2.5 and 3.2 kHz, nighttime scattering strength characteristics cannot be directly related to the Gulf Stream boundary.

Diurnal Variation

At frequencies between 0.8 and 2.5 kHz, diurnal variation generally exhibits contour patterns that indicate greatest variation occurring in the region of highest nighttime scattering (approximately 61°00′ W, 38°00′ N) as indicated in Figure 9. A gradual change in contour patterns occurs with increasing frequency, and it is observed that 3.2 kHz shows no indication of the high central variation present at other frequencies. At 3.2 kHz the highest variation occurs to the west and decreases to the southeast.

The maximum diurnal variation at frequencies of 1.25 and 2.5 kHz appear to be located near or below the southern boundary of the Gulf Stream, whereas at 3.2 kHz the highest diurnal variations occur to the west. The high diurnal variation observed may be a result of a large aggregation of local migratory scattering organisms found near this oceanographic boundary.

SUMMARY

The results of a quasi-synoptic study to investigate volume scattering strength in the vicinity of the Gulf Stream indicate the following.

1. Day scattering strength contours generally indicate two local centers of scattering for frequencies between 0.8 and 2.5 kHz; a high scattering center in the cold water north of the Gulf Stream and a lower scattering center in warm water south of the Gulf Stream.
2. Night measurements indicate maximum scattering strengths at approximately 61°00′ W, 38°00′N.
3. The diurnal variation is observed to be greatest where maximum nighttime scattering is observed. This may indicate the presence of large aggregations of migratory sound scatterers near the Gulf Stream.
4. High diurnal variations south of the Gulf Stream may mask the influence of the oceanographic boundary on the two scattering centers observed during daytime measurements.
5. From the contour plots it appears that scattering strength variations along longitude or latitude circles may produce sharp scattering gradients over short distances.
6. Changing contour patterns at the highest frequency investigated during this study (3.2 kHz) did not indicate that a direct relationship exists between the Gulf Stream boundary and the measured reverberation levels.

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DISCUSSION

Johnson: The data for each station consist of results from three charges?

Davis: That is correct.

Johnson: And they are dropped within 100 ft of the sonobuoy. How did you manage to place them at 100 ft?

Davis: A navigational system on the aircraft used for operational exercises can triangulate on a sonobuoy and drop the SUS charge within 100 ft of the buoy. Charges have often dropped within 30 ft and many times they have hit the buoys. We work with an operational test and evaluation squadron that does this on a continuing basis, so they have quite a bit of practice doing this.

Batzler: I am sure you have made some comparisons with the shipboard method of measurement. Would you comment on this?

Davis: Airborne measurements in an area where some data were collected by ship produced scattering results that were comparable within a couple of decibels. This area was east of the Bahamas. Some data compared with data collected by Dr. Chapman and his associates indicate large unexplained differences (sometimes as great as 15 dB) at the Gulf Stream boundary. Seasonal dependence in the North Atlantic Ocean may be responsible for some of the observed differences. Perhaps Dr. Chapman has some information of that type.

Chapman: The more you look at deep scattering layer data, the more tolerant you become about the differences.

Winokur: I might add that comparison of some data collected south of Bermuda using the airborne technique with data collected by Dr. Chapman indicates some very excellent agreement, within a few decibels.

Davis: Mr. Adlington of the Defense Research Establishment conducted an acoustic study along 65° west longitude, and I conducted one along 75° west in the same oceanographic province, south of Bermuda. I understand that the biological scattering organisms in these localities are very similar, and my scattering strength curves versus latitude are very similar to his. The Gulf Stream seems to be the area of contention. We have examined the temperature profiles at each station to determine whether there is any kind of irregular sound velocity profile that might produce shadow zones or some unusual ray plots, but this is not indicated in any of the stations I have shown here.

Hersey: I, too, could be very sympathetic with variations of 15 dB, but I am curious to know about the consistency between groups of observations of the peak frequencies of the scatterers. I would hope that there is greater consistency there.

Davis: Well, most of the peaks that I have observed in my scattering data were primarily at 1.6 kHz, and I cannot correlate it with any of the migrating organisms in the water column, if that is what you mean.

Hersey: Excuse me. My question, I guess, was directed really to you and Dr. Chapman as to whether these large differences that you note where you both observed in the same place are only characteristics of the levels. Do you observe your frequency peaks at the same frequency?

Chapman: I have a comment which I think is relevant. I will make it in my paper.

Davis: Most of my data is at lower frequencies than Dr. Chapman's data, so it's difficult to make a direct comparison. I have observed similar trends at some of the same frequencies at which Mr. Adlington has collected data, but most of my data are below 3.2 kHz, and I believe Dr. Chapman's usually extend in a band between 1.6 kHz and 20 kHz. For the crossover frequency bands, I have few comparisons.

Hersey: This is more for clarification, but your 1.6 kHz peak, as I recall, was consistently observed throughout the whole area, was it not, independently of whether it was north or south of the Gulf Stream?

Davis: Yes, it was.

Winokur: As I recall, Dr. Chapman's data are reported in octave bands, and these data are for one-third octave bands, so there's only one point of comparison over the range of frequencies.

GEOGRAPHIC VARIATIONS IN THE ACOUSTIC CHARACTERISTICS OF DEEP SCATTERING LAYERS

R. F. Chapman, O. Z. Bluy, and R. H. Adlington
Defence Research Establishment Atlantic
Dartmouth, Nova Scotia, Canada

ABSTRACT

Since 1959, an acoustic investigation has been made of the characteristics of scattering layers in the deep ocean. Marked variations of scattering strengths and layer depths were observed as a function of time of day, frequency, and location. The greatest variations in scattering strengths with location took place near oceanographic boundaries. Sound sources for the experiments were explosives fired near the surface. Measurements were made with both omnidirectional and directional wideband receivers. The measurement and analysis techniques are illustrated using data collected in the North and South Atlantic and in the North Pacific.

Since 1959, the Defence Research Establishment Atlantic has been engaged in a program to measure the acoustic properties of deep scattering layers. Most of the measurements have been made in the North Atlantic, although within the past 6 months, the investigation has been expanded to include sites in the South Atlantic and the North Pacific. As the analysis of the most recent data has yet to be completed, most of the experimental results presented in this paper were obtained in the North Atlantic and adjacent seas.

The extent of our coverage of these areas is shown in Figure 1. A total of 136 sets of measurements, usually beginning 2 hours before and ending 2 hours after sunset, was made during 16 cruises. A number of sites, particularly those between Halifax and Bermuda and Halifax and the Azores, were visited more than once.

The shaded areas are oceanographic boundaries: that north of Iceland, the polar front; that extending from Iceland to just south of Nova Scotia, the secondary polar front; and that south of Bermuda, the subtropical convergence. Farquhar (1) examined the information available on the geographic distribution of various species of fish likely to make major contributions to the reverberation from deep scattering layers, and concluded that they would tend to be confined by these boundaries. Thus, one might expect to have reverberation provinces with fairly well defined boundaries.

The sites visited in the North Pacific in November 1969 and in the South Atlantic from November 1969 to January 1970 are shown in Figure 2. Thirty-two sets of measurements were made in the North Pacific between the mouth of the Columbia River and the Panama Canal, and forty-five sets of measurements were made in the South Atlantic between the Equator and the

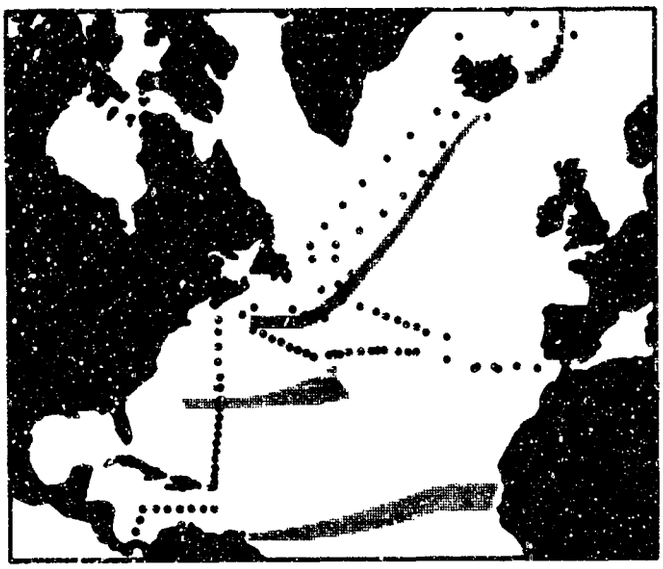

Figure 1. Reverberation measurement sites in the North Atlantic and adjacent seas

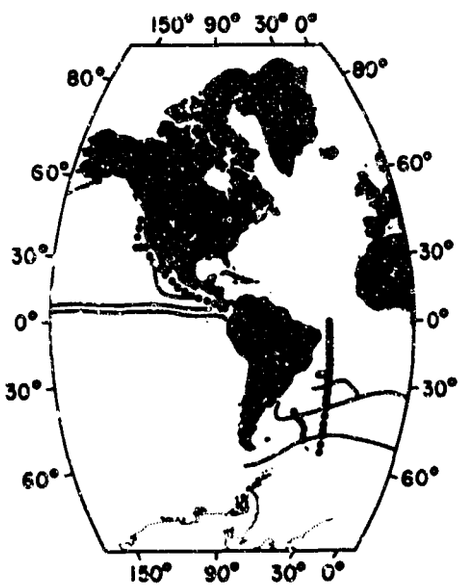

Figure 2. Reverberation measurement sites in the South Atlantic and North Pacific

island of South Georgia. The solid lines in the figure are oceanographic boundaries (2). In the Pacific, the line of stations intersects the northernmost boundary at approximately 30° and 10° N. In the Atlantic, the measurement sites span both the subtropical convergence that lies between 30° and 40° S. and the Antarctic convergence near 50° S.

In this paper, information will be presented on the scattering strength and depth of deep scattering layers and their dependence on location, time of day, and frequency. The data presented lend support to the reverberation province hypothesis. Some data also will be presented on the size of scatterers responsible for the observed reverberation.

Various experimental arrangements have been used, evolving into that shown in Figure 3. The sound sources for the experiments were 1-lb TNT charges fired approximately 0.5 m below the sea surface. This permitted the bubble to break through the surface before the emission of the first bubble pulse, thus eliminating the ambiguities in layer depth associated with a multiple pulse source. The backscattered sound was received on an omnidirectional hydrophone and on a wideband, directional receiving array; both operated at a depth of 10 m and over a frequency range from a few hundred Hz to 25.6 kHz.

The array consists of a line hydrophone on the axis of a 90° cone of 2-m aperture. The effective aperture and, hence, the beamwidth is varied by selecting different lengths of the line hydrophone. For example, a beamwidth of 11° can be obtained at the geometric mean frequency of each of the three octaves covering the range from 3.2 to 25.6 kHz. This arrangement has been used in all experiments carried out during the past 2 years in cruises off the Grand Banks, between Halifax and the Azores, in the North Pacific and Caribbean, and in the South Atlantic. In a number of earlier experiments, the high-frequency cutoff of the omnidirectional hydrophone was one to two octaves lower; two ship-mounted, narrowband, echo-sounder arrays operating at 5 and 12 kHz were used as receivers instead of the cone.

All data were recorded wideband in analog form on magnetic tape. Later they were played back through octave-band filters and a variety of spectrum analyzers. The octave-band data were displayed on level recorders to provide traces of the form shown in Figure 4.

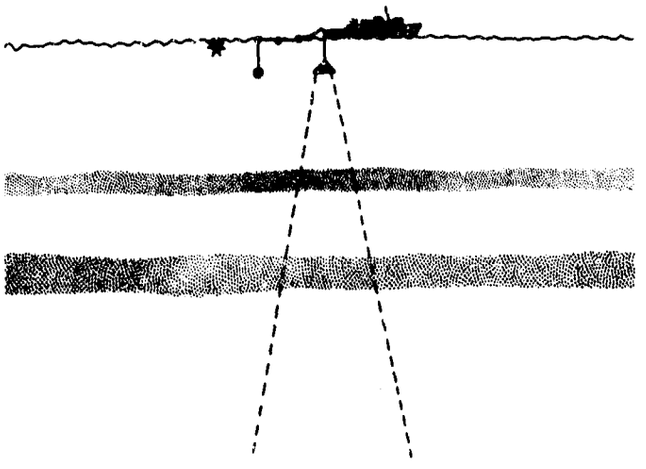

Figure 3. Experimental arrangement used in recent experiments

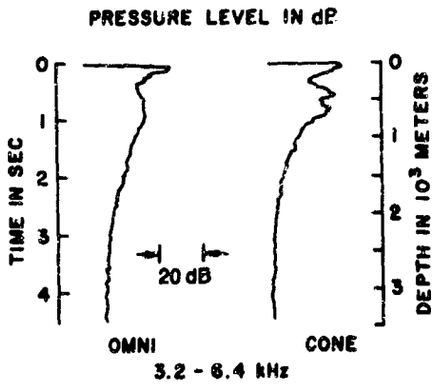

Figure 4. Reverberation level versus time and equivalent depth measured with the "cone" in the Caribbean

The traces are of reverberation level in the 3.2- to 6.4-kHz octave versus time t after the explosion, measured in the Caribbean south of Haiti. The equivalent depth scale is shown on the right. In the trace on the left, obtained with the omnidirectional hydrophone, there is evidence of layers at depths of 450 and 650 m. Below the bottom layer, the reverberation falls off at $-30 \log t$, consistent with the decay of reverberation from horizontal layers of isotropic scatterers. The trace on the right shows the increased definition of the scattering layers obtained using the full aperture of the cone. From the portion of the omnitrace that decays at $-30 \log t$, a quantity can be readily computed that we call the scattering strength of the water column (3). This quantity, $10 \log \int_0^d M_z \, dz$, is the target strength of a column of water 1 m^2 in cross section extending from the sea surface down to a depth d. The depth of the column is sufficiently great to include all the scatterers that make a significant contribution to the reverberation in the frequency band considered. The scattering strength of the water column has turned out to be quite a useful quantity, which can be obtained with extremely simple measurement and analysis techniques. It is convenient for indicating gross changes in reverberation conditions with location, time of day, and season.

If more details are required, such as scattering layer depth or the distribution of the volume scattering strength M_z with depth z, it is better to go to the additional complication of using directional wideband receivers such as the cone (4,5), or to make measurements at short ranges using sound sources and receivers lowered into the layers (6,7).

In the North Atlantic, three cruises were made over a limited range of latitudes: Halifax to Gibraltar in August 1964, Halifax to the Azores in April 1969, and through the Caribbean in December 1969. In each cruise, considerable distances were covered in the same water mass in For example, $10 \log M_z$ versus depth profiles obtained using near surface fired charges and the 5-kHz directional receiving array on the cruise between Halifax and Gibraltar are shown in Figure 5. The recovery characteristics of the system were such that data are reliable only for depths greater than 50 m. The daytime profiles are on the top and the nighttime profiles are on the bottom of the figure. The shaded areas indicate scattering strengths per unit volume exceeding -80 dB. At this frequency, there is a nonmigrating layer at a depth of approximately 600 m extending from 10° to 37° W. At night there is appreciably more scattering at shallow depths, presumably caused by scatterers that resonate near 5 kHz but which are deeper and resonate at higher frequencies during the day.

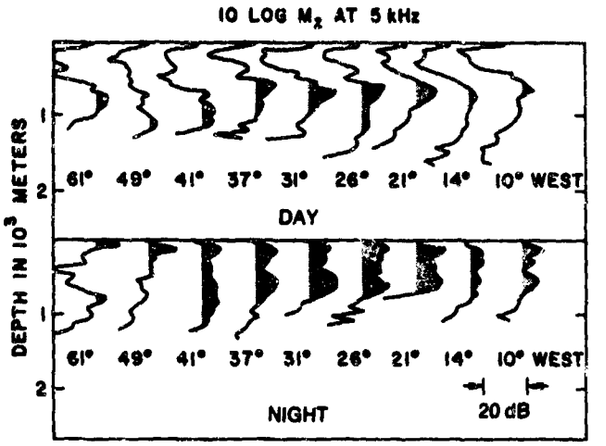

Figure 5. Profiles of volume scattering strength versus depth between Halifax and Gibraltar

Nighttime values of the octave-band scattering strengths of the water column for the same cruise are shown in Figure 6. The scattering strengths in the top octave have been increased by 10 dB to keep them separate from those in the middle octave. There is a consistent decrease in scattering strength from the Azores to Gibraltar, which may be associated with the outflow of Mediterranean water.

Somewhat larger variations in scattering strengths have been experienced in going from north to south in the North Atlantic. For example, volume scattering strength versus depth profiles measured with explosives and the 5-kHz array at the sites visited just south of Iceland and just north of Puerto Rico are shown in Figure 7. The traces on the left are representative of those for all stations between Bermuda and Puerto Rico; those on the right are representative of those stations between Newfoundland and Iceland, except for the four closest to Newfoundland.

The dashed lines represent the daytime values of scattering strength and the solid lines, the nighttime values. During the day, the dominant layer is deeper and has a higher scattering strength at the northern station; the peak value of scattering strength is 15 dB greater, whereas the scattering layer depth of 400 m is approximately half that of the southern station. At night at both stations, the scattering strength increases at the shallower depths, but again, not at the expense of the scattering strength of the deepest layer. This is a common feature at nearly all the sites that we have visited; there are usually an appreciable number of the larger scatterers that undergo little or no change in depth with time of day.

That very large changes in scattering strength can take place over relatively short distances is illustrated in Figure 8. Here we have daytime values of scattering strength (open triangles) and nighttime values (solid triangles) in the 1.6- to 3.2-kHz octave for the line from Halifax to Puerto Rico. Halifax is on the right and Puerto Rico is on the left; the dashed line is at the latitude of Bermuda. The differences between the values of the scattering strength of the water column measured during the day and those measured at night are large at the southern stations (of the order of 20 dB) and decrease toward the north. There is a very striking change in scattering strength south of Bermuda near the location of the subtropical convergence.

The nighttime values of scattering strength in this octave for all the stations visited in the North Atlantic and adjacent seas are shown in Figure 9. The various shadings correspond to groupings of scattering strengths in 6-dB intervals; the darker the shading, the higher the scattering strength. The dominant features shown here occur in the other frequency bands studied.

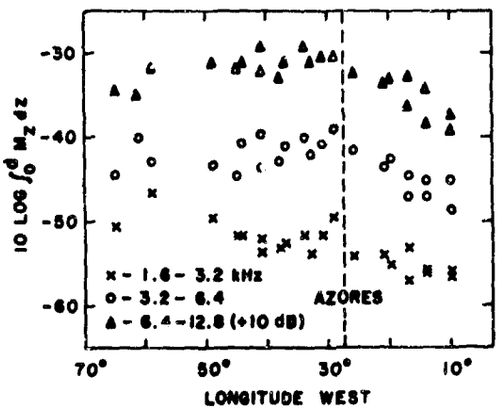

Figure 6. Nighttime values of octave-band scattering strengths of the water column between Halifax and Gibraltar

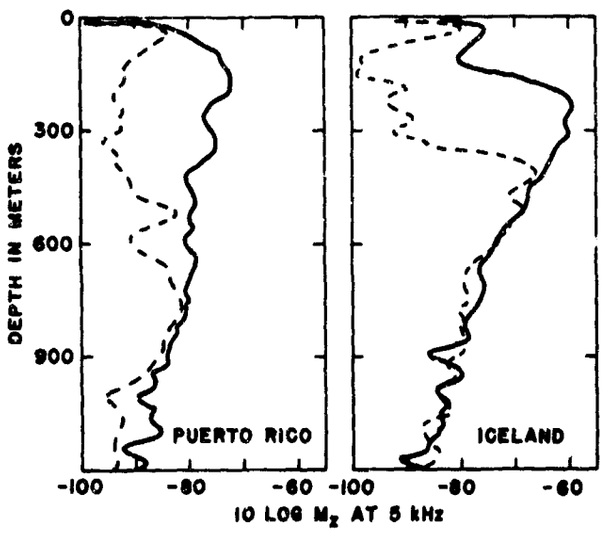

Figure 7. Volume-scattering strength versus depth profiles for typical sites south of Iceland and north of Puerto Rico (dashed lines = day, solid line = night)

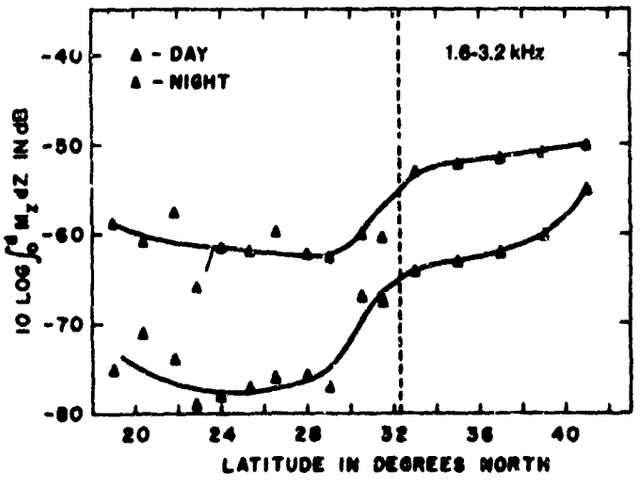

Figure 8. Scattering strength of the water column between Halifax and Puerto Rico

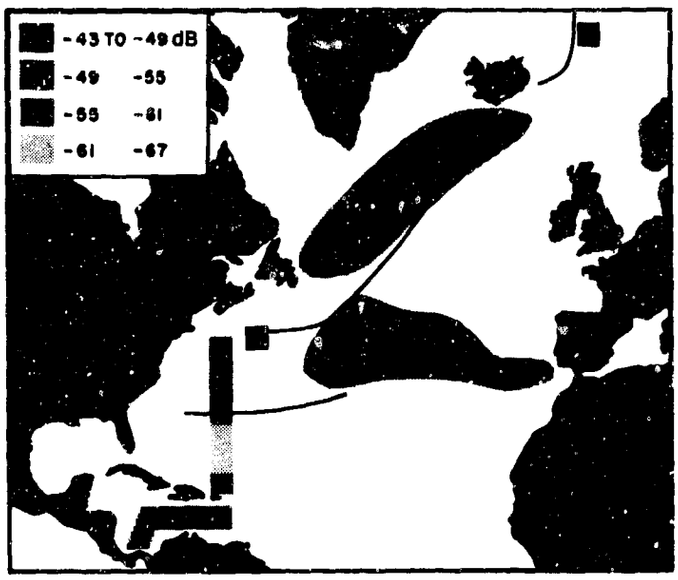

Figure 9. Nighttime values of the scattering strength of the water column in the 1.6- to 3.2-kHz octave for the North Atlantic and adjacent seas

Scattering strengths can be relatively constant over large distances; but they may exhibit sharp discontinuities, frequently occurring near the boundary separating two water masses. The decrease in scattering strength between the Azores and Gibraltar and the abrupt discontinuity near the subtropical convergence south of Bermuda have been discussed earlier in the paper. The scattering strength starts to increase near Puerto Rico, and these higher values are maintained in the Caribbean. There is a decrease in scattering strength in crossing the secondary polar front from east to west near Newfoundland; there is a gradual increase toward the northeast. North of Iceland there are significant differences in sound scattering on the opposite sides of the polar front, the deep scattering layers tending to disappear on the western side (8).

As the analysis of the data from the South Atlantic has just begun, only one figure will be presented showing the geographic variation of the scattering strength of the water column in the 3.2- to 6.4-kHz octave. In Figure 10, the dependence of scattering strength on latitude is shown for the line of stations along 30° W. The dominant features shown here occur in all frequency bands studied. As a point of reference, the scattering strengths and their dependence on frequency at the northmost stations are very similar to the stations just north of the Azores. In this figure, a fairly well-behaved dependence of scattering strength on latitude is shown. Some of the more dramatic changes take place near oceanographic boundaries. There is a rapid increase near the location of the subtropical convergence between 30° and 40° S and a peak in scattering strength at 48° S near the Antarctic convergence, followed by a very rapid decrease towards the south. This peak also occurs 10° to the west on the line between South Georgia and Buenos Aires.

Figure 11 shows the scattering strength of the water column in the 1.6- to 3.2-kHz octave for the sites visited in the North Pacific. Again, there is a very pronounced and fairly well-behaved dependence of scattering strength on latitude, rapid decreases and increases occurring between

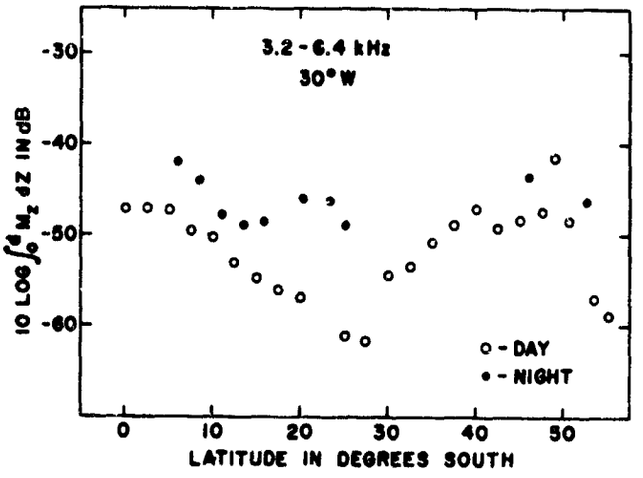

Figure 10. Scattering strength of the water column along 30° W in the South Atlantic

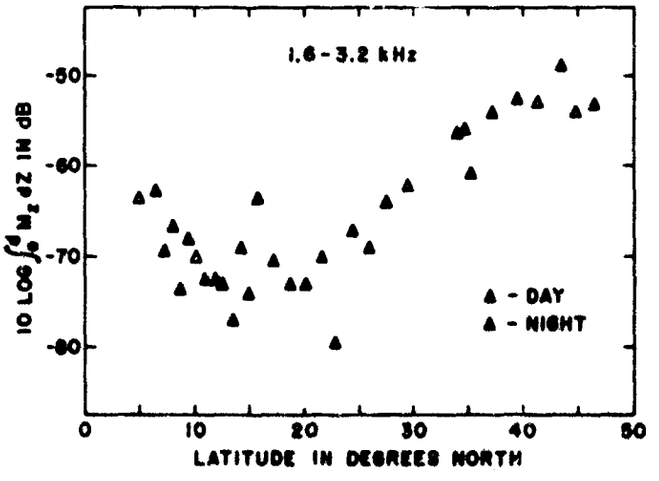

Figure 11. Scattering strength of the water column in the eastern North Pacific

5° and 10° N and 20° to 40° N, respectively. The overall change of scattering strength in this octave band with latitude is quite large, exceeding 25 dB. The diurnal variation in scattering strength in this octave is much smaller than that observed in the Atlantic. This is consistent with the ±2 dB variation at 3 kHz observed by Batzler (9) at a location 200 miles southwest of San Diego.

To obtain insight into how these changes in scattering strength are related to changes in layer structure, the octave-band reverberation levels measured with the cone were examined. Representative traces measured in midmorning are shown in Figure 12. Traces for the 1.6- to 3.2-kHz octave are shown at the top of the figure, and those for the 6.4- to 12.8-kHz octave at the bottom. The shaded areas indicate reverberation levels exceeding an arbitrary reference level, which is the same for each trace. The traces labelled 45° N on the left of the figure are representative of those found between the mouth of the Columbia River and an area about 200 miles south of San Diego. Strong layers appear in the 1.6- to 3.2-kHz band at depths of 500 and 1,000 m. The former layer undergoes some changes with location: it divides into two layers at about 35° N, then reunites to become a single, shallower, and weaker layer at 29°N, and is not evident at the southmost stations. This and the prominent layer at about 1,000 m undergo little, if any, diurnal migration. The 1,000-m layer weakens toward the south and disappears off Baja California.

In the higher frequency band, a layer at about 350 m persists at all stations. There is some evidence that this layer does not migrate, although generally the reverberation trace fills in and individual layers tend to be masked at night. At about 29° N, where the low frequency scattering layer at about 1,000 m begins to weaken, a new layer can be seen forming at essentially the same depth in the 6.4- to 12.8-kHz octave. This scattering layer also eventually weakens and is not seen at the stations at or below 9°N. The transition stations at 29° and 9°N correspond to the locations where an oceanographic boundary shown in Figure 2 crosses our line of stations.

From what we have seen so far in all three ocean areas visited, scattering strengths tend to change in a fairly well-behaved manner over distances of many hundreds of miles. On a number of occasions, the more dramatic changes take place in the neighborhood of oceanographic boundaries.

The deep, nonmigrating scattering layers that are effective at low frequencies imply the existence of relatively large scatterers. The effective radius of the dominant scatterer in the 1,000-m, low-frequency layer shown in Figure 12, calculated using Minnaert's equation for a spherical bubble (10), is 1.8 cm. This can be compared with 0.54 cm, which is the radius of the largest scatterer found in our earlier measurements between Halifax and Bermuda (3). Since then, however, we have obtained evidence of larger scatterers at a number of other locations: northeast of Newfoundland, in the Norwegian Sea, near the Azores, and in the western North Atlantic south of the Gulf Stream and off the tail of the Grand Banks. They were approximately 1,000 m deep except in the Norwegian Sea and off the tail of the Grand Banks, where they were found at depths of approximately 180 and 400 m, respectively. The estimated sizes of the effective radii of the gasbladders are 0.72 cm in the Norwegian Sea, 1.1 cm northeast of Newfoundland, and 1.5 to 2.0 cm off the Azores and in the western North Atlantic.

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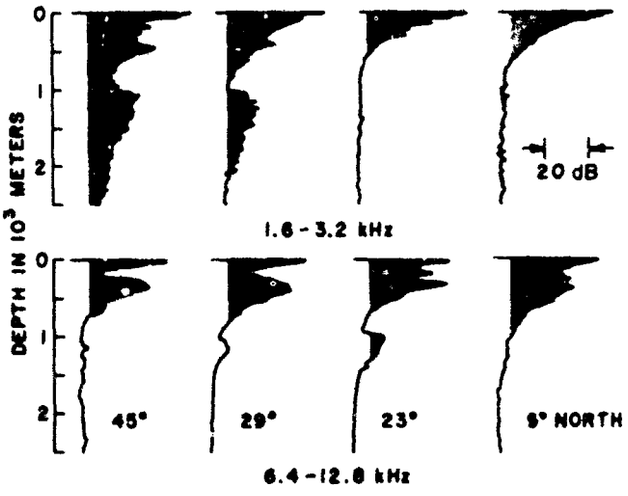

Figure 12. Typical reverberation level versus depth profiles for the eastern North Pacific

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DISCUSSION

Winokur: Can you explain the lack of diurnal variation, or do you have any indication of why there is a lack of diurnal variation in the Pacific?

Chapman: In this 1.6- to 3.2-kHz octave, there is appreciably less diurnal variation in the Pacific than in the Atlantic data. In the next higher octave, 3.2 to 6.4 kHz, the situation is reversed. The variations are obviously related to the sizes of the scatterers present and their migration characteristics, but we do not have a detailed explanation.

Pearcy: Do any of these 1,000-m layers that you report show any day-night migrations? Also, how far offshore were you in the northeastern Pacific?

Chapman: The stations are approximately 140 miles off the coast. As far as we have been able to determine from the records, there is no diurnal migration of the 1,000-m layers.

Dunlap: I would just like to confirm with you the boundaries in the Pacific. Maybe I could talk with you later, but some of the boundary lines that you drew there look fairly familiar. I would like to confirm what you are using as a basis there.

Chapman: This was in a textbook, Deitrich's *General Oceanography*; in fact, we took the boundaries of current systems, and I appreciate that this probably may not be the right way.

Dunlap: My comment is that you were mentioning water masses, whereas it is mainly one general water mass. It depends on how you define it.

Chapman: This may not be the right way to do it, but these data came back within the last month, and we had to take a little shortcut in defining our boundaries, I'm afraid.

Barham: I think part of the problem we have is that most biologists are familiar with the scattering layer when we record it on an echo sounder, originally at 24 and 18 and now usually at 12 kHz. So this is our concept, and when we look at data at the frequencies that you show us, we have a hard time equating what we know. The net hauls, the submersible dives, etc., are directed primarily to features that traditionally we have been able to record with a good echo sounder from a surface ship. And I wonder whether in fact we should not attempt to delineate between these midfrequency scatterers which form the strata that we call scattering layers and these much lower frequency things that apparently just stay pretty close to one constant depth. Of course, we also have scatterers at the familiar frequency that migrate but little if at all. Would you comment on that?

Chapman: I do not know really what to say on that. I think that the sort of techniques that we had here are not that complicated. The cone that we use has become a fairly standard operation. I really think one ought to use a wideband directional projector.

Winokur: I might point out that the geologists and geophysicists have switched to a lower-frequency directional echo sounder, and perhaps the biologists should consider doing the same thing.

Hersey: My first comment is on the graph you have shown of variation in the Pacific where the low-frequency layer in high latitude, I believe it was, terminates south of 29° N and was replaced by a higher frequency one. At least with the resolution that you provided there, this agrees rather well with a marked thermal front. Whether it is a legitimate oceanographic boundary, I will leave to somebody else. But that is a very sharp boundary.

Chapman: Yes. And there seemed to be something else at 10° N too.

Hersey: I would certainly second Bob Winokur's urging that the biologists start using lower frequency echo sounders which are more and more available. These instruments are at first discouraging. You seldom see any scattering layers on them during daylight, but commonly must wait until after sunset when they usually are evident. My third comment is that Bob Chapman and his Canadian colleagues are certainly to be congratulated for their overwhelming and brilliant coverage of the Atlantic and now the Pacific Ocean. I certainly congratulate you.

Chapman: Thank you.

Clarke, W.: I would like to add one more thing on 29° N. Wooster at Scripps described this same front. It lies off Cabo San Lazaro, Baja California; south of that you have an extreme O_2 minimum which goes down to 1,000 m. In fact, that is about the bottom of it. If you look at

the zoogeography in the area, there is quite a change in fauna. There is a very distinct fauna in that widespread O_2 minimum layer. And below the layer you get some elements that cross through the tropical region underneath it. Other midwater species are stopped because their vertical range is at the same level as the O_2 minimum layer, but they do cross the tropical region in the western Pacific, so that O_2 minimum body of water in the eastern Pacific is quite an effective biological barrier.

Batzler: Let me also express my admiration—and I have to say envy—for what Bob has done in the Pacific. I might say that we have occasionally seen this deep layer, and I think it is pertinent because of his suggestion that we use broadband sources. We have some that cover a fairly wide frequency band, but I do not think that they will work as well as the explosive source with the cone, because, as I say, we have seldom seen this deep layer. I might also say that we are doing broadband work off San Diego in a seasonal study that we have started, and his paper has given us many points that I hope we will be able to use in making seasonal comparison.

McCartney: I would like to confirm the statement made by Dr. Hersey that on low-frequency equipments used for subbottom profiling, we have seen very little evidence of any scattering layers. I would like to ask Bob Chapman whether he has made any estimates of the number of scatterers in these low-frequency resonant layers. Knowing the resonant frequency, you have a good idea of the size and hence of the target strength of one individual, and you know the scattering coefficient. How many fish per unit volume does this correspond to?

Chapman: Well, I think Orest Bluy will provide us with the numbers corresponding to the layer northeast of mid-Newfoundland.

Bluy: The peak densities of the large, low-frequency resonant scatterers at several stations northeast of Newfoundland are about $10 \times 10^{-6}/m^3$ or ten fish per million cubic meters. At one station where the layer was particularly prominent, peak densities of $100 \times 10^{-6}/m^3$ were observed.

VOLUME BACKSCATTERING MEASUREMENTS AT 12 kHz IN THE MEDITERRANEAN SEA AND DESCRIPTION OF A MULTIPLE FREQUENCY SOUNDER FOR FURTHER INVESTIGATIONS

Christian Jeannin
Laboratoire de Detection Sous-Marine
du Brusc, France

ABSTRACT

Observations of scattering layers have been conducted for two years in an area of 100 x 25 miles near Toulon in connection with temperature–salinity measurements and biological sampling. Volume backscattering at 12 kHz, measured with an echo sounder, is expressed as reverberation index versus depth (50 to 1500 m); it exhibits the following general features: (a) *Stratification and statistical properties* – three layers. Upper - from surface to 100 m, diffuse and discrete scattering. Intermediate - mean depth 350 m, thickness 100 to 300 m, index -80 to -70 dB/m^{-3}, partial diel migration and diffuse scattering even at night near surface. Deep - mean depth 800 m, thickness 200 to 400 m, index -90 to -75 dB/m^{-3}, diffuse scattering; (b) *Diurnal migrations* – regular ascent at sunset, dependence with meteorological conditions for descent at sunrise; and (c) *Seasonal variations* – increased scattering between the upper and intermediate layers in May and June. Such acoustic measurements will be extended in depth, frequency and area by using a specially designed towed sounder with following characteristics: frequency range 2.5 kHz to 5 kHz by 100 Hz steps, acoustic level 126 to 130 dB re 1 μbar, pulse length 10, 100, and 500 msec, automatic recording.

INTRODUCTION

Depuis la fin de l'année 1967 le Laboratoire de Détection Sous-Marine du Brusc étudie en liaison avec la Station Marine d'Endoume (Faculté des Sciences de Marseille) les propriétés des couches diffusantes du milieu marin.

Le présent exposé a pour but de dégager les traits principaux des observations et mesures acoustiques faites avec un sondeur grand fond à 12 kHz au rythme de 24 heures tous les deux mois en 1968 et de trois à quatre jours tous les trois mois par la suite, sur une zone s'étendant de Marseille à Villefranche jusqu'à une distance de 25 Nautiques de la côte.

INDEX DE REVERBERATION

Définition

Le pouvoir de rétrodiffusion acoustique d'un volume V est caractérisé par son index de réverbération r_v tel que:

$$r_v \cdot V = \frac{I_D}{I_i} = \frac{\text{intensité rétrodiffusée}}{\text{intensité incidente}}$$

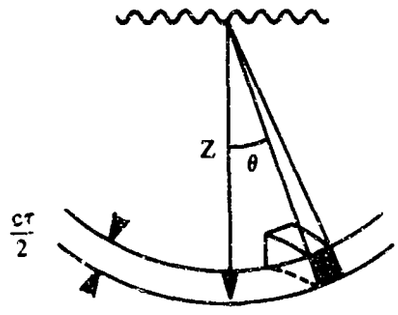
Soit en décibels: $R_v\ dB/m^{-3} = 10 \log \frac{I_D}{I_i} - 10 \log V$

Lorsque les éléments diffusants sont répartis au hasard l'enveloppe du signal réverbéré est une grandeur aléatoire dont la densité de probabilité suit une loi de RAYLEIGH (Réference 1 page 64), loi à une dimension telle que le coefficient de variation:

$$\gamma = \frac{\text{déviation standard}}{\text{valeur moyenne}} \text{ est égal à } 0.52.$$

Calcul

Dans le cas du sondage vertical, la perte de propagation par divergence géométrique est égale à $(1/Z^2)$ et le calcul général (Référence 2 page 190) se simplifie. L'intensité $I_R(\theta)$ réverbérée dans la direction θ par le volume élémentaire de révolution hachuré est:



$$I_R(\theta) = r_v \cdot I_o \cdot b^2(\theta) \sin\theta\ \pi c\tau \frac{1}{Z^2} \cdot e^{-2\alpha Z}$$

avec I_o = intensité dans l'axe à l'émission
$b(\theta)$ = fonction de directivité du sondeur
τ = durée d'émission
c = vitesse du son

On peut remarquer que l'intensité réfléchie, répartie en $b^2(\theta)$ pour un réflecteur seul, l'est ici suivant $b^2(\theta) \cdot \sin\theta$.

La loi de variation en fonction du temps t de l'intensité totale I_R s'obtient en intégrant et en remplaçant Z par $(ct/2)$ et s'exprime en logarithmes:

$$10 \log \frac{I_R}{I_o} = R_v + 10 \log \frac{4\pi}{c} + 10 \log \tau - 20 \log t - \beta ct +$$

$$\int_o^{\tau/2} b^2(\theta) \cdot \sin\theta \cdot d\theta$$

L'amortissement du son est $\beta = 1$ dB/km à 12 kHz et une vitesse moyenne de propagation $c = 1510$ m/s donne en Méditerranée une erreur sur l'immersion inférieure à 1 mètre jusqu'à 750 mètres et croissant ensuite jusqu'à 8 mètres à l'immersion de 1500 mètres.

MESURES ET DEPOUILLEMENT

Matériel de mesure

Les mesures faites avec un émetteur-récepteur enregistreur (GDR-T) Oceansonics associé à un transducteur EDO 353 monté sur poisson ORE, sont exploitées qualitativement sur le graphique

et quantitativement par enregistrement magnétique analogique et calcul numérique en Laboratoire.

Le sondeur grands fonds a pour caractéristiques:

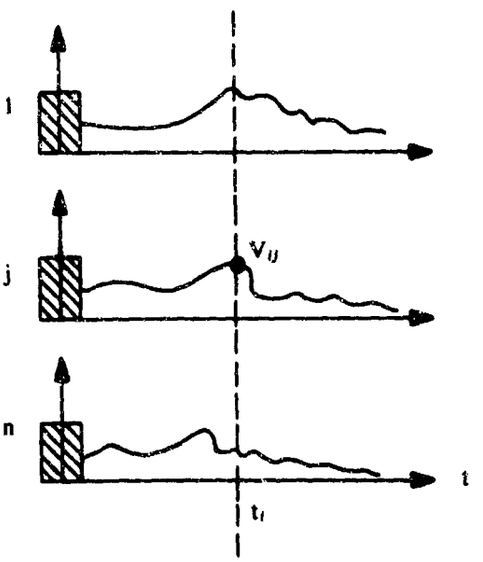
- Emission: Niveau $10 \log I_o = 110\,dB$ re 1 μbar

  Impulsions de durée $\tau = 1$ à 50 ms à la fréquence 12 kHz

- Réception: Sensibilité $Sh = -72$ V/μbar

- La directivité émission réception de 23° à 3 dB donne un volume insonifié théorique $V_{m^3} = (\tau_{ms} \cdot Z^2{}_m/10{,}3)$ pour une répartition en $b^2(\theta)$ mais en fait environ trois fois plus grand soit $\tau \cdot Z^2/3{,}5$ pour la réverbération (répartition $b^2(\theta) \cdot \sin\theta$); ainsi par exemple: $V \sim 3.10^4 m^3$ pour $\tau = 10\,ms$ et $Z = 100\,m$.

Dépouillement numérique



Soient n émissions successives et V_{ij} le niveau du signal réverbéré à l'instant t_i après la jième impulsion. L'index de réverbération Rv_i et le coefficient de variation γ_i correspondants se déduisent de l'amplitude moyene:

$$<V_i> = \frac{\sum_{j=1}^{n} V_{ij}}{n}$$

et de l'intensité moyenne:

$$<V_i^2> = \frac{\sum_{j=1}^{n} V_{ij}^2}{n}$$

par les expressions:

$$Rv_i = -10 \log G + 10 \log <V_i^2> + 20 \log t_i + \beta c t_i$$

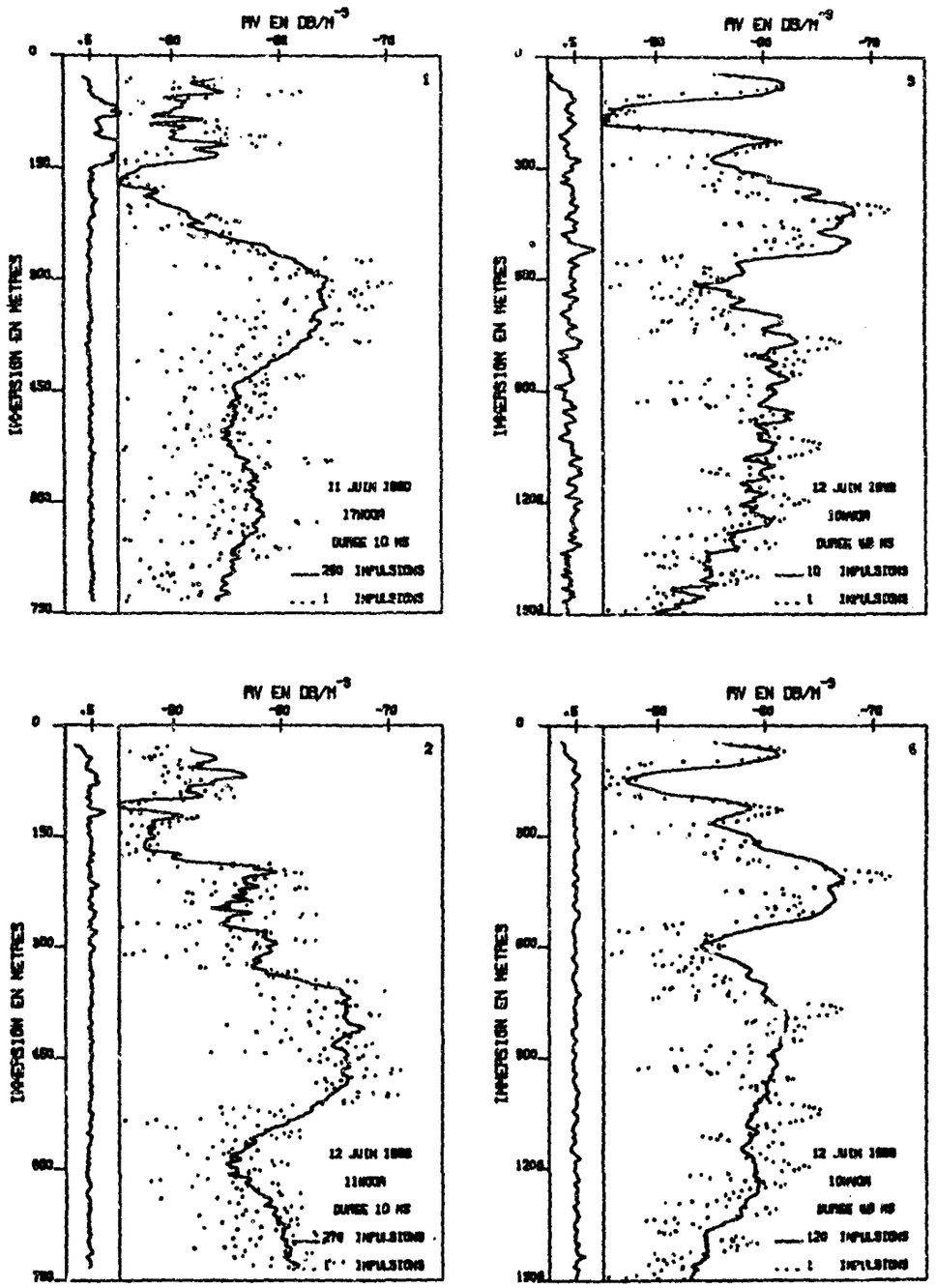
où G est une constante

$$\text{et} \quad \gamma_i = \sqrt{\frac{n}{n-1}\left[\frac{<V_i^2>}{(<V_i>)^2} - 1\right]}$$

RESULTATS

Propriétés statistiques

Les courbes de la Figure 1 mettent en évidence l'influence du nombre d'impulsion pris en compte et de la durée d'émission sur les valeurs de l'index et du coefficient de variation (à gauche sur les graphiques).



INDEX DE REVERBERATION DE VOLUME ET COEFFICIENT DE VARIATION

EN FONCTION DE L'IMMERSION

FREQUENCE:12KHZ ZONE:NORD MEDITERRANEE OCCIDENTALE

Figure 1

La réflexion des ondes sur un élément diffusant présent pendant une partie seulement de l'enregistrement ou variable en immersion donne un γ supérieur à 1 et correspond souvent à un écho discret sur le graphique. Ceci se produit lorsque le volume insonifié et la densité des diffuseurs son faibles, c'est-à-dire de jour aux petites immersions pour des impulsions courtes (Fig. 1 jusqu'à 150 mètres). Dans les autres cas, la réverbération suit une loi de RAYLEIGH avec γ voisin de 0,52 et donne un écho diffus sur le graphique.

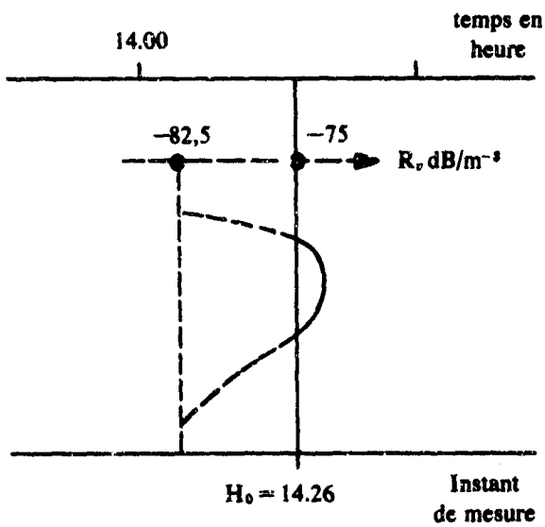
Les profils de réverbération, obtenus avec des durées d'émission différentes, sont comparables avec une mise en valeur de la structure fine pour les impulsions courtes et une diminution du bruit de fond pour les impulsions longues (ex. courbes n° 2 et 4).

Lorsque le nombre d'enregistrements pris en compte pour le calcul de la moyenne est petit, le coefficient de variation n'est plus égal à 0,52, mais la comparaison des courbes 3 et 4 montre que le tracé avec 10 impulsions est déjà une bonne approximation du tracé avec 120 impulsions.

Dans le cas général, la moyenne a été faite sur une vingtaine d'impulsions de 50 ms. Ces mesures sont complétées par des mesures à 10 ms la nuit (Mai et Octobre 1968) ou pendant les migrations (Mars et Juin 1969).

Evolution journalière

Les Figures 2 à 4 donnent quelques exemples d'évolution de l'index sur des périodes égales ou supérieures à 24 heures.



A la partie supérieure, le temps est porté en heure locale (temps universel plus une) en ne tenant pas compte des heures de nuit sans mesures. Les courbes d'index ont pour référence $R_v = -75$ dB sur la vertical H_o = instant de mesure indiqué au bas du graphique et sont tracées à l'échelle 30 dB/cm en ne considérant que les valeurs supérieures à − 82,5.

La date des mesures, leurs, coordonnées moyennes et les heures de lever et coucher du soleil sont indiquées dans le cartouche.

Ces courbes sont caractéristiques des enregistrements faits depuis 1967 et mettent en évidence trois maximum de l'index, correspondant sur le graphique à trois couches : superficielle de 0 à 150 mètres, intermédiaire en moyenne à 350 mètres et profonde vers 800 mètres. Le phototactisme des éléments diffusants se manifeste par leurs mouvements au lever et au coucher du soleil, leur contraction et dilatation de jour ou de nuit et immersion variable d'un jour à l'autre.

Ce comportement est particulièrement net pour la couche intermédiaire : dans l'après-midi, certains éléments remontent d'abord lentement en provoquant une contraction de la couche (diminution de l'épaisseur, augmentation de l'index), puis la migration s'accélère jusqu' à 3 mètres par minute en fin d'après-midi pour se terminer au moment du coucher du soleil en venant combler la zone sans diffusion observée de jour vers 150 à 250 m. La diminution d'index qui devrait en résulter est compensée par la remontée d'éléments profonds, migration que l'on peut observer sur certains enregistrements graphiques. Pendant la nuit, cette couche supérieure se modifie en se séparant en deux parties : l'une près de la surface est plus épaisse que le jour,

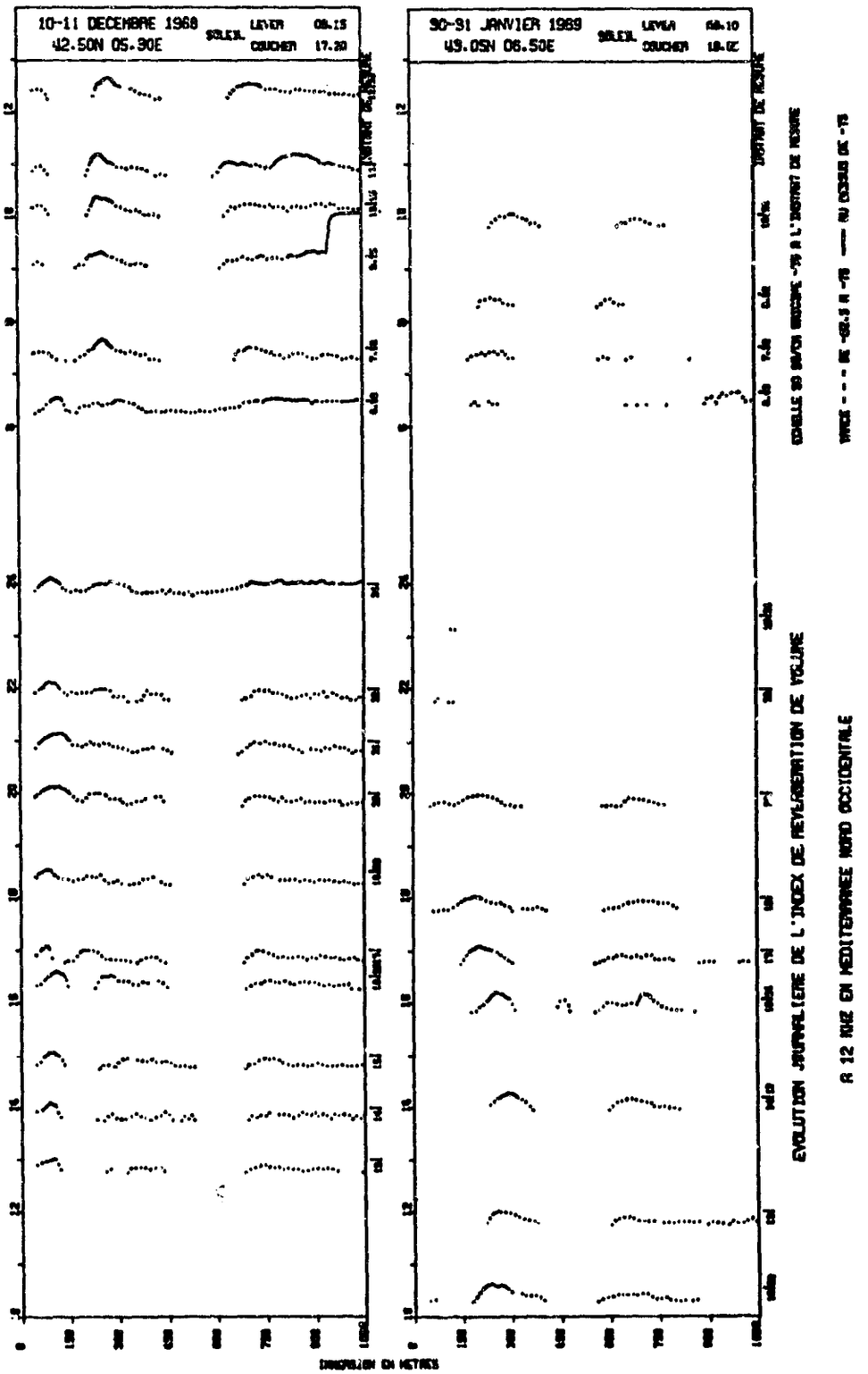

10-11 DECEMBRE 1968
42.50N 05.90E
SOLEIL LEVER 08.15
COUCHER 17.20
30-31 JANVIER 1969
49.05N 06.50E
SOLEIL LEVER 08.10
COUCHER 18.02
DISTANCE EN METRES
EVOLUTION JOURNALIERE DE L'INDEX DE REVERBERATION DE VOLUME
A 12 KHZ EN MEDITERRANEE NORD OCCIDENTALE

Figure 2

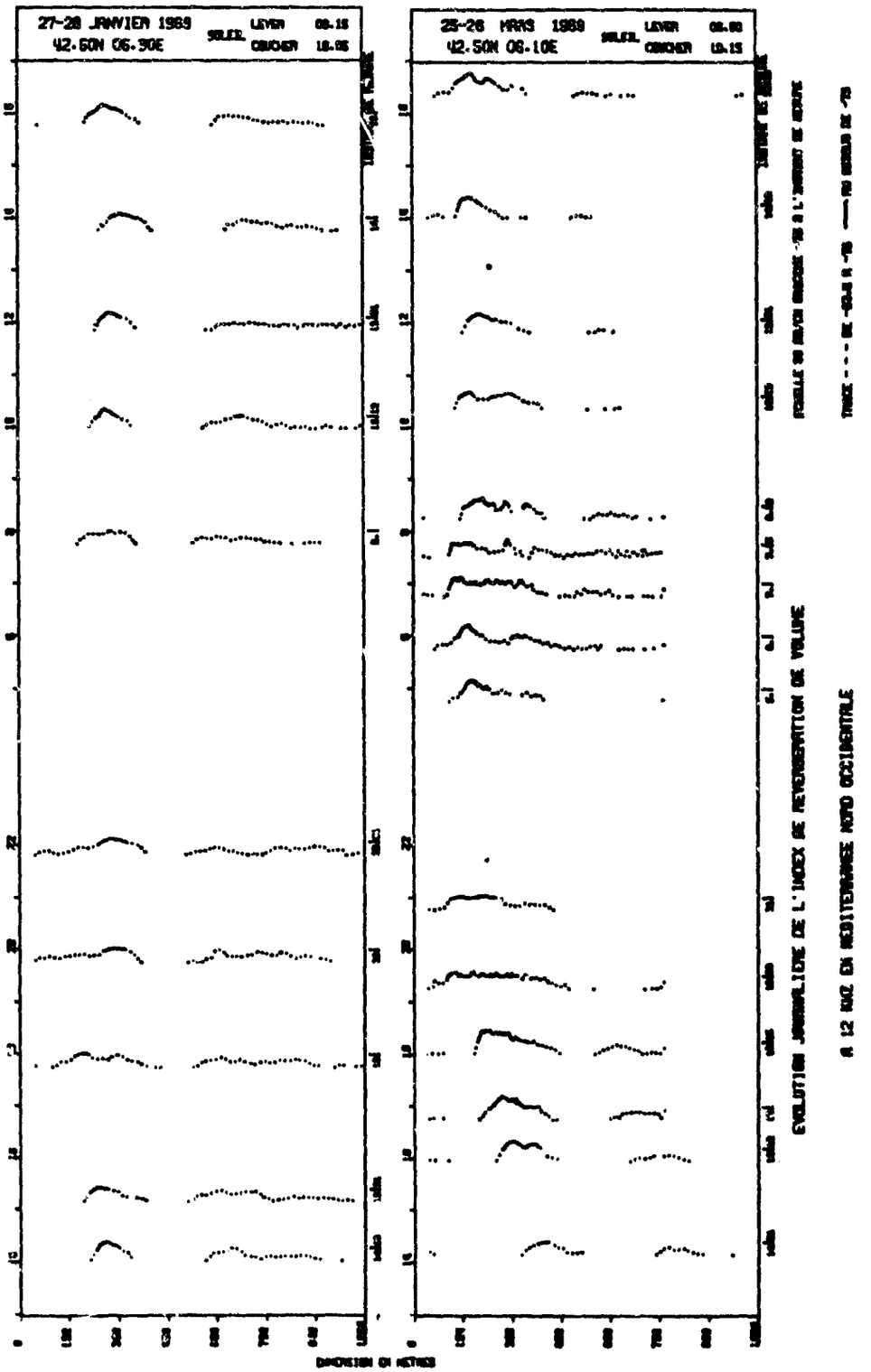

27-28 JANVIER 1989
42.50N 06.30E
SOLEIL LEVER 08.15
COUCHER 18.05
25-26 MARS 1989
42.50N 06.10E
SOLEIL LEVER 06.00
COUCHER 19.15
EVOLUTION JOURNALIERE DE L'INDICE DE RENORMALISATION DE VOLUME
A 12 KHZ EN MEDITERRANEE NORD OCCIDENTALE

Figure 3

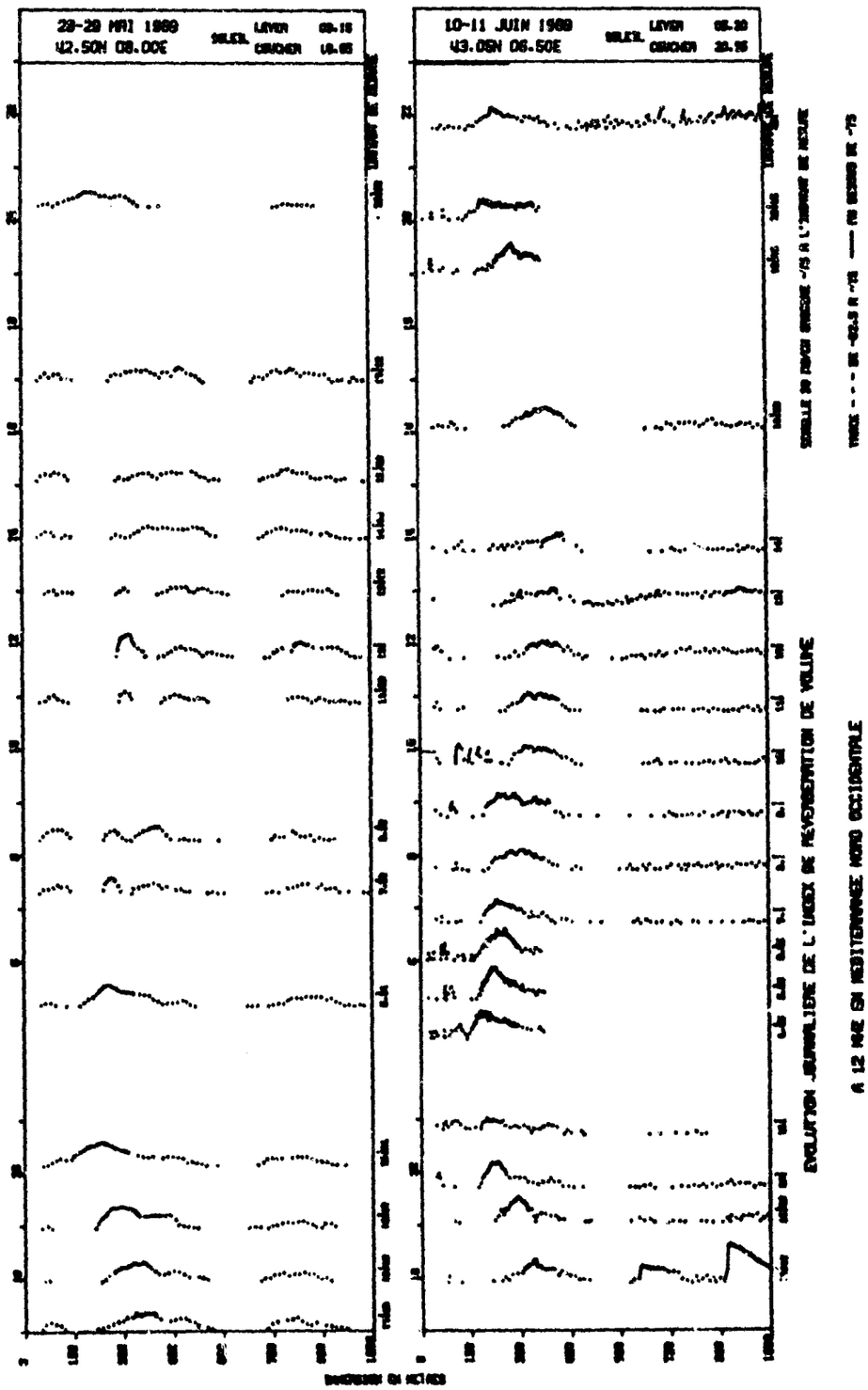

28-29 MAI 1989
42.50N 08.00E
10-11 JUIN 1989
43.05N 08.50E
EVOLUTION JOURNALIERE DE L'INDEX DE REVERBERATION DE VOLUME
A 12 KHZ EN MEDITERRANEE NORD OCCIDENTALE

Figure 4

et certains de ses éléments migrent régulièrement vers la seconde partie environ deux heures avant le lever du soleil ; la descente de la couche intermédiaire formée la nuit dépend de l'ensoleillement de sorte que l'immersion maximum atteinte entre 12 H 00 et 14 H 00 varie d'un jour à l'autre, en Mars 1969 par exemple (Figure 3, tracé inférieur) où les conditions météorologiques étaient très mauvaises, cette couche est restée près de la surface.

Variations saisonnières et spatiales

Sur la Figure 5, nous avons porté quelques courbes caractéristiques de mesures s'étendant chacune sur deux à trois jours avec en traits pleins deux profils relevés en milieu de journée et en pointillés un profil pris en début de nuit avant la séparation de la couche supérieure.

Les couches n° 1 et n° 2 relevées à la même époque sur des zones distantes de 60 Nautiques sont très voisines alors que les couches n° 2 et n° 4 relevées au même point en Janvier et Juin sont différentes et présentent les caractéristiques suivantes :

	29 – 31 JANVIER 1969			10 – 12 JUIN 1969		
	Immersion moyenne	Epaisseur	Index (dB)	Immersion moyenne	Epaisseur	Index (dB)
Zone superficielle	25 m	50m	−86	30 m 150 m	60 m 30 m	−78 −80
Zone intermédiaire	300 m	100 m	−74	400 m	200 m	−73
Zone profonde	700 m	150 m	−78	900 m	300 m	−81

On observe donc en Juin un élargissement des couches et une plus grande diffusion dans la zone de la surface jusqu' à 300 mètres ; cette augmentation est particulièrement nette sur l'enregistrement graphique correspondant.

Bien que les mesures considérées s'étendent sur plusieurs jours, l'interprétation des variations saisonnières et spatiales est limitée par les conditions météorologiques du moment (par exemple Mars 1969 tracé n° 3 Figure 7) et de nombreuses observations sont nécessaires avant de pouvoir tirer des conclusions.

A fortiori, ceci rend difficile l'étude des fluctuations d'une année à l'autre.

SONDEUR à FREQUENCE VARIABLE

Cette étude préliminaire à 12 kHz dans la région de TOULON sera étendue en immersion, fréquence et zones océaniques par l'utilisation d'un sondeur vertical conçu spécialement.

Ses caractéristiques sont les suivantes :

Fréquence de travail de 2,5 kHz à 5 kHz variable par pas de 100 Hz

Durées des impulsions : 10 – 100 et 500 ms

Niveau d'émission : 126 à 130 dB re 1 μbar

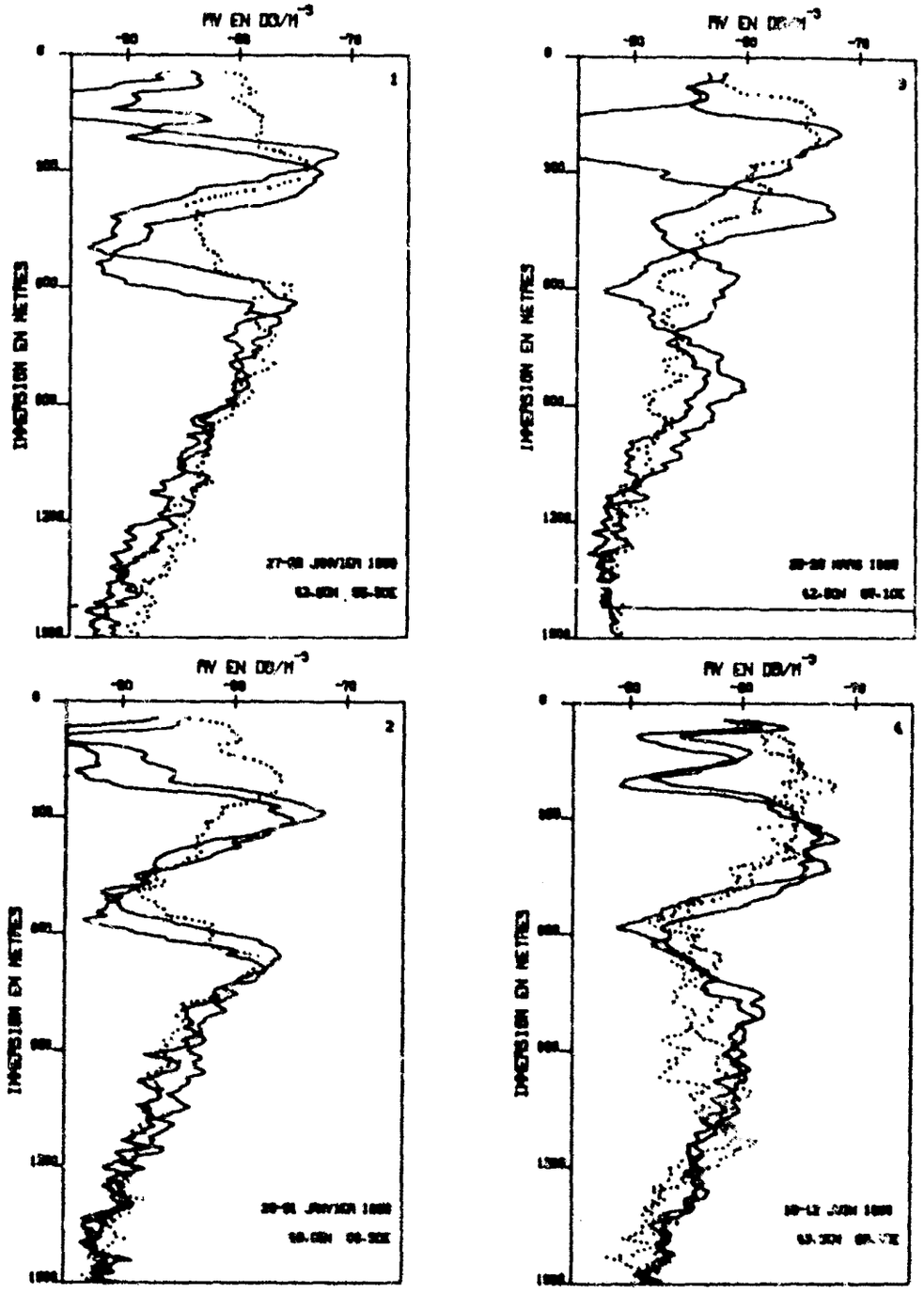
Corrections automatiques du gain à l'enregistrement.

Enregistrement digital des paramètres : heure de mesure, coordonnées, vitesse et immersion du sondeur.

Grande surface du transducteur donnant une ouverture de lobe égale à 20° à 2,5 kHz.

Stabilité du remorquage à 30 mètres, assurée par la forme du poisson et controlée par un capteur d'immersion et deux inclinomètres.

Mesure de l' éclairement par photomètre incorporé au poisson et dirigé vers la surface.



VARIATION SAISONNIERE DE L INDEX DE REVERBERATION DE VOLUME A 12 KHZ
EN MEDITERRANEE NORD OCCIDENTALE

Figure 5

CONCLUSION

Les mesures de réverbération faites dans la région de TOULON depuis deux ans ont permis de dégager quelques propriétés qui seront complétées par une étude de correlation avec les prélèvements biologiques et les paramètres physiques. L'interprétation de ces résultats est limitée par l'emploi d'une seule fréquence, le manque de mesure de l'éclairement et le faible niveau d'émission du sondeur. Ces lacunes seront comblées par le sondeur à fréquence variable qui, grâce au nombre de données recueillies, permettra de préciser les lois de variation de la diffusion acoustique et contribuera ainsi à une meilleure connaissance du milieu marin.

AN ACOUSTICALLY DETERMINED DISTRIBUTION OF RESONANT SCATTERING NORTH OF OAHU

Peter Van Schuyler
U.S. Naval Oceanographic Office
Washington, D.C.

ABSTRACT

This paper summarizes the results of an explosive echo study of deep scattering layers located at 24°31′N, 157°50′W. The parameters considered are the depths and thicknesses of the layers of maximum acoustic scattering, their scattering strengths in the frequency range 0.8 to 20 kHz, and their daily vertical excursions; also the resonant frequency, swimbladder size, and population density of the dominant scatterers. A hypothesized resonant scatterer size-distribution curve, developed by extending existing mathematical formulations is presented.

INTRODUCTION

Deep scattering layers have become the subject of extensive field investigations (1-6) and theoretical work (7-10). Evidence relating the dependence of these scattering layers upon variables such as time of day, season, geographic location, and oceanographic data has accumulated rapidly. Further, various investigators (3, 5, 9, 11) have concluded that mesopelagic fishes are primarily responsible for this backscattering of underwater sound, particularly those possessing swimbladders.

This paper summarizes the acoustic results from a study conducted during May 1968 of a deep scattering layer in an area located approximately 200 nautical miles north of Oahu at 24°31′N, 157°50′W. The objective of the paper is to describe the size and depth distribution of those individuals comprising the scattering layer, based on the analysis of explosive source reverberation data.

EXPERIMENTAL METHOD

Omnidirectional explosive "point" charges were detonated in close proximity to a broad band omnidirectional receiving hydrophone, with both located at a nominal depth of 60 feet. Approximately 120 charges were detonated in completing acoustic measurement sequences to determine the scattering strength of the water column for daytime, nighttime, and transition periods. Full daytime followed by full nighttime measurements were completed on one day and then repeated several days later. The maximum areal separation for all sequences did not exceed 7 miles. All measurements were conducted under "quiet ship" conditions, with the ship hove to

and drifting at 1 knot or less. Each daytime and nighttime measurement sequence was accomplished by detonating 10 explosive charges over a relatively short interval of about 1 hour at times when the scattering layers were most stable.

THEORY

Because most of the applicable scattering theory and equations are taken from Weston (7), Chapman (8), Andreeva (9), and Mohammed (10), the discussion here is limited to the development of the scattering layer results presented.

Acoustic Properties of Fish with Swimbladders

The resonant frequency of a gas-filled fish swimbladder is given by Andreeva (9) as:

$$f_r = (2\pi R)^{-1}\left(\frac{3\gamma P_0 + 4\mu_1}{\rho}\right)^{1/2} \tag{1}$$

where f_r is the resonant frequency in cycles per second, R is the effective radius of the swimbladder in centimeters, P_0 is the hydrostatic pressure in dynes per square centimeter, γ is the ratio of specific heats of the swimbladder gas at constant pressure and volume, ρ is the density of sea water in grams per cubic centimeter, and μ_1 represents the real part of the complex shear modulus of fish tissue varying between limits of 10^6 and 10^7 dyn/cm^2 (9).

Similarly, the expression relating the acoustic scattering cross section of the fish swimbladder to frequency is given by:

$$\sigma(f) = (4\pi R^2)\left[\left(\frac{f_r^2}{f^2} - 1\right)^2 + \frac{f_r^2}{Q^2 f^2}\right]^{-1} \tag{2}$$

where Q accounts for the influence of reradiation, thermal, and viscous losses upon the fish-swimbladder system (9). The major loss mechanisms are viscosity near the surface, and reradiation for depths exceeding 200 meters (9). Further, the small thermal losses render the Q virtually independent of frequency with a maximum value approaching 10 at a depth of 200 m.

Number of Resonant Scatterers

It can be shown that each cubic meter of ocean, specified at a depth z, and containing n scatterers, each of acoustic cross section σ, can be characterized by a backscattering coefficient given by:

$$M_{zf} = \frac{n(z)\,\sigma(f)}{4\pi} \tag{3}$$

The assumptions implied in equation (3) are: (1) the total number of scatterers is a function solely of depth, (2) their acoustic cross sections at depth depend only on frequency, and (3) there is negligible acoustic interaction between scatterers, i.e., multiple scattering and coherent scattering does not occur. These qualifications will be met for a sufficiently diffuse concentration of approximately equal swimbladder size scatterers in a layer "thin" enough so that the Q and, consequently, f_r remains essentially constant over the thickness of the layer.

The average backscattering coefficient, for a vertical distribution of sound scatterers extending from the surface down to depth d is given by:

$$\int_0^d M_z\,dz = \frac{\int_0^d \int_0^\infty M_{zf}\,G(f)\,|H(f)|^2\,df\,dz}{\int_0^\infty G(f)\,|H(f)|^2\,df} \tag{4}$$

where $G(f)$ is the power spectrum of the sound source and $|H(f)|^2$ is the power spectrum of the filter (10).

Determination of the primary scattering layer's depth and also its scattering strength as a function of frequency makes possible the segregation of the dominant scatterers within the layer according to their effective swimbladder radius R. This results in a biological scatterer size-population density curve for the layer. Equations (2), (3), and (4) can then be combined to obtain:

$$\int_0^d M_z\,dz = \frac{NR^2 \int_0^\infty \left\{ G(f)\,|H(f)|^2 \left[\left(\frac{f_r^2}{f^2} - 1 \right)^2 + \frac{f_r^2}{Q^2 f^2} \right]^{-1} \right\} df}{\int_0^\infty G(f)\,|H(f)|^2\,df} \tag{5}$$

where $N = \int_0^d n(z)\,dz$ and expresses the number of resonant scatterers of radius R present in a 1-m² cross section column of water extending from the surface to the layer bottom d. Given the layer thickness Δ, the number of scatterers per cubic meter in the layer can be determined by:

$$N_L = \frac{N}{\Delta}. \tag{7}$$

The results presented here for sound scatterer densities were derived from a one-third octave band frequency analysis of the explosive source scattering results and the numerical integration solution of equation (5) derived by Mohammed (10).

Scattering Strength of the Water Column

The applicable equation for analysis is:

$$10 \log \int_0^d M_z\,dz = 20 \log P - 10 \log E + 30 \log t + a\,ct - 48 \tag{8}$$

where P is the RMS pressure in dynes per square centimeter of the reverberation level for the analysis bandwidth, E the source energy per unit area in ergs per square centimeter measured at 100 m for a similar bandwidth, t the time after detonation in seconds, a the attenuation coefficient in dB/m, and 48 is a constant dependent upon experimental geometry.

The scattering layers are treated as occupying horizontal segments of the water column bounded by the sea surface and the bottom of the deepest layer present. Further, within any

given horizontal plane the scatterer concentration is assumed both isotropic and constant. The time-variant signal produced by insonification of ordered layers is predicted to decay exponentially at $-30 \log t$ (in decibels) after penetration of the bottom of the deepest layer present. Prior to this time/depth the scattering return is changing because of contributions from successively deeper layers. Therefore, the "scattering strength of the water column," i.e., the integrated or total backscattering strength of a 1-m-sq cross section water column extending from the sea surface to the depth d of the bottom of the deepest layer for the analysis bandwidth used, must be determined after penetration of the deepest layer present has occurred.

Identification of Scattering Layers

For an omnidirectional hydrophone-source combination located above the scattering layers a spectrum comparison of selected samples of the scattered return can be used to identify the major scattering layers. A sample of the reverberation taken at time t_1 after detonation will consist of scattering produced by all insonified targets present between the surface and the depth d_1 given by $ct_1/2$. Another sample taken at t_2, $t_2 > t_1$, will consist of all those scatterers responsible for the first sample plus those in the interval $d_1 - d_2$, and so on. Using this technique and others discussed in the following section, the dominant layer of this study was identified.

RESULTS

Frequency Dependence of Scattering Strength

Scattering strength versus frequency in one-third octave bands between 0.8 and 20 kHz was determined for each measurement sequence using equation (8). Daytime scattering strength values in the area studied never varied by more than 4 dB; the same maximum difference was observed when all the nighttime values were compared. Consequently, the two sets of repetitive data were averaged and the respective daytime and nighttime mean values of scattering strength versus frequency were plotted. The similar results obtained from the two daytime and nighttime measurement sequences is indicative of both experimental reproducibility and the relatively stable nature of the scattering layers during the period this study was conducted. The daytime results are shown in Figure 1. A prominent peak in scattering strength is observed in the frequency range 5 to 6.3 kHz, and the values appear to be increasing again at 20 kHz. The greatest variation in scattering strength is found for frequencies between 2 and 5 kHz.

The corresponding results obtained under nighttime conditions are illustrated in Figure 2. The daytime characteristics of a peak at 5 to 6.3 kHz and greatest frequency dependence in scattering strength below 5 kHz are evident in the night data also. A secondary peak is observed near 12.5 kHz. The nighttime scattering strength values shown are greater than the corresponding daytime values by about 2 to 16.5 dB.

Figure 3 snows the diurnal variation of scattering strength as a function of frequency for the area under study. The data shown were determined by subtracting daytime scattering strengths from nighttime values and clearly indicate a nighttime increase resulting from the upward diurnal migration of the scattering layer during sunset. The smaller scatterers, contributing to the diurnal variation at frequencies above 5 kHz, appear to undergo only "slight" upward movement, as they account for relative scattering increases of about 3 dB. The majority of the increased scattering at night is apparently a result of those scatterers resonant at frequencies below 5 kHz. A pronounced maximum increase in nighttime scattering is shown for the 2.5-kHz scatterers.

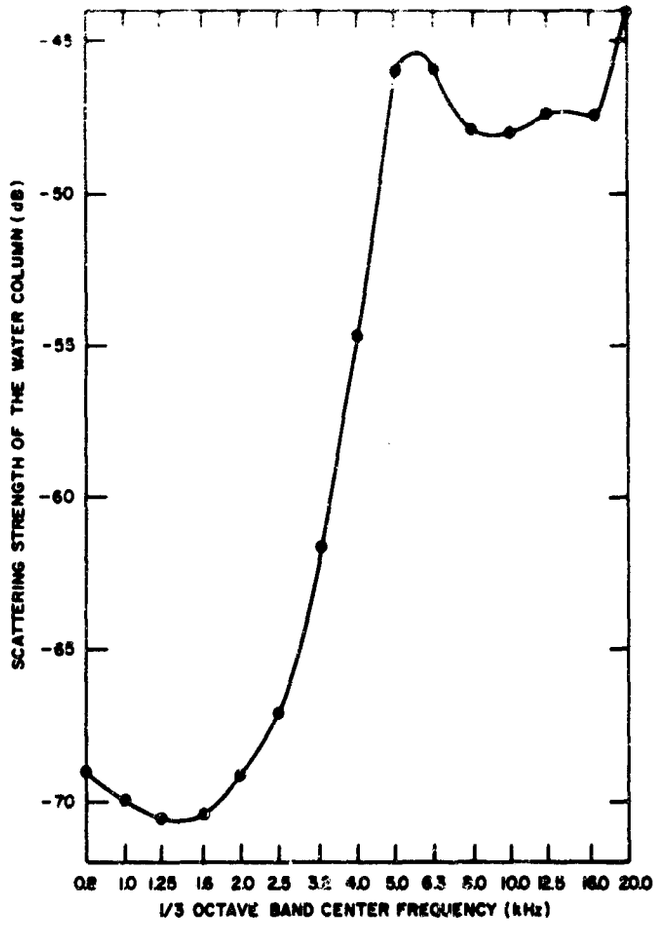


Figure 1. Mean scattering strength versus frequency, day sequence

Identification of Dominant Scattering Layer

The one-third octave band analysis of a shot from a daytime sequence, which can be used to determine the depth of the bottom of the deepest layer insonified, is shown in Figure 4. Scattering from the deep layer is first received at approximately 0.7 sec after detonation; thereafter, the reverberation levels continue to increase, reaching a maximum at 0.9 sec, where penetration of the layer bottom occurs. The reverberation level then decays at the rate of $-30 \log t$. The maximum level was identifiable for all the daytime frequency bands investigated, but was most marked in the 5 and 6.3 kHz bands. The nighttime scattering returns, when subjected to similar one-third octave band-pass analysis, showed evidence of a definite "filling in" of the low-frequency traces, because of the upward migration of the layer. The resultant effect is that the depth of the bottom of the nighttime scattering layer could not be identified on the acoustic records.

Another daytime shot was processed using a narrow band vibralyzer to produce the three-dimensional plot shown in Figure 5. Again at approximately 0.7 sec after t_0, sound scattered from the deep layer is discernible. An estimate can be made of the depth to the surface of the layer from this type of plot, but information regarding the bottom of the layer is totally obscured.

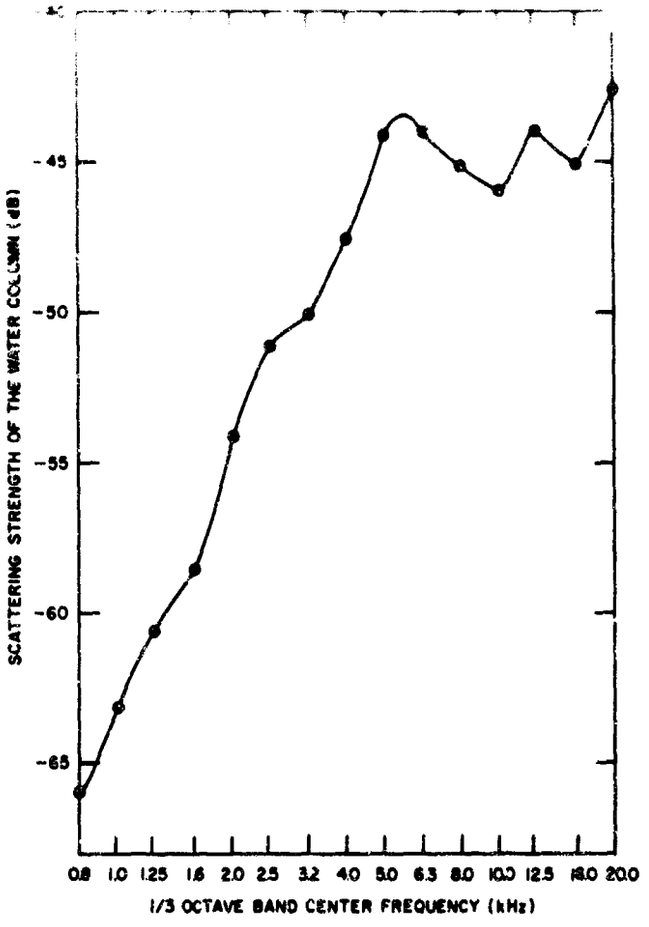


Figure 2. Mean scattering strength versus frequency, night sequence

Scattering strength spectra computed for selected times after detonation for a day sequence are presented in Figure 6. The data indicate that relatively few scatterers are present between the surface and 430-m depth, with most of the scattering occurring in the depth interval from 580 to 690 m, followed by negligible contributions from scatterers at depths greater than 764 m. Additionally, the strongest scattering returns are produced by those scatterers resonant near 6.3 kHz. A similar plot for the nighttime results is shown in Figure 7. In general, the scattering at night appears almost wholly confined to the upper 305 m. The nighttime layer thickness depicted is almost three times the thickness of the dominant daytime layer identified. It should perhaps be noted that little significance is attached to the trend of the data obtainable for frequencies below 1.25 kHz at the shallow depths because of difficulties in data interpretation in this region.

The ship's 12-kHz echosounder system using a downward looking transducer with a 30° conical beamwidth was operated throughout most of the cruise. The fathograms produced were of inferior quality because of equipment malfunctions, but nevertheless certain recurrent patterns of the 12-kHz scattering population were amply displayed. Most prominent of the daytime features was a concentration of scatterers located at a depth of 504 m and an apparent thickness of of 60 m. On one occasion a surface layer was noted after sunrise extending down to 54 m while on two other days a third, 180-m thick layer was seen between 110 and 290 m.

During upward migration across sunset the scattering pattern seen on the echosounder changed significantly, and showed a persistent concentration of scatterers from the surface to an

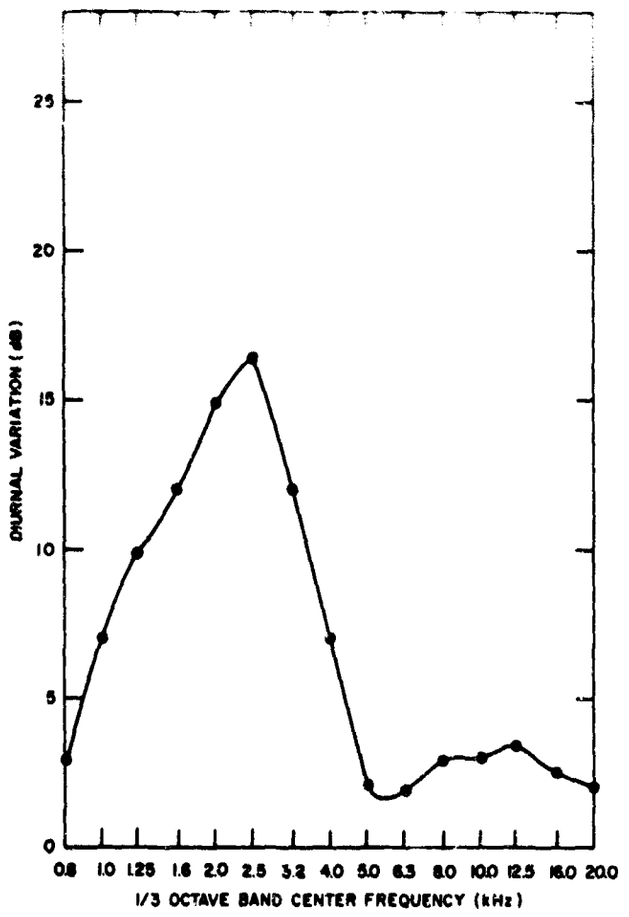


Figure 3. Diurnal variation of mean scattering strength as a function of frequency

average depth of 340 m. A deep scattering concentration was also noted near 580-m depth and of 67-m thickness. An intermediate third layer was sometimes observed at night near 440-m depth, with a thickness of 45 m.

The daytime and nighttime dominant scatterer concentrations, as determined from the reverberation spectra, agree very well with the 12-kHz echosounder records. This is not an unexpected result for this location as a 12-kHz peak is observed in the scattering strength curve of Figure 2. In addition, the scattering strength at 12 kHz is high compared to the lower frequencies. The deep nighttime scattering layer at 580 m, explicit in the 12-kHz echosounder results but not implied by the reverberation spectra of Figure 7, could easily be explained by the hydrophone receiving sound scattered from the surface layer at exactly the same time as returns from the deep layer. Further, the location of the daytime layer together with the observation of little diurnal variation at 12-kHz indicate a nonmigratory component that would not be resolved by the receiving system. However, it is also apparent that such a nonmigratory concentration of small scatterers could be completely masked by the strong nighttime "surface" layer. Admittedly then, the possibility of a depth ambiguity does exist in the nighttime results of Figure 7.

Size Distribution of Resonant Scatterers

It is assumed, at least for this discussion, that all the scatterers insonified by the explosion shock wave are forced into damped oscillation at their respective resonant frequencies. This

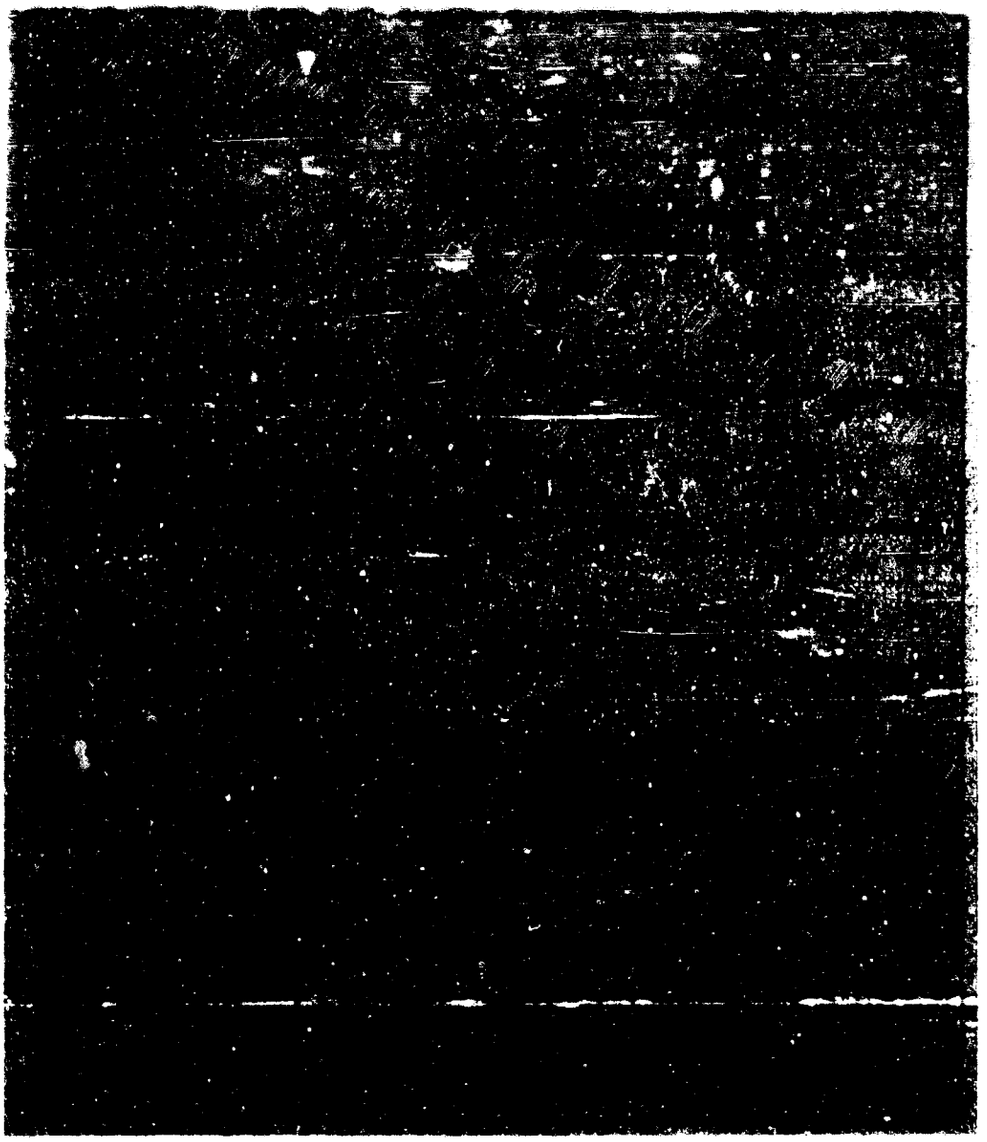


Figure 4. Representative one-third octave bandpass analysis of a daytime measurement

stipulation is needed to assure that the intensity of backscattered sound produced at a specific frequency is a function solely of the number of scatterers of swimbladder radius R equivalent to that specific frequency of resonance. Combining the numerical integration results of equation (5) with the calculated scattering strength, resonant frequency, and depth values for the main layer considered produces a curve relating the number of scatterers per cubic meter (N_l) of a certain size swimbladder in the layer to the radius R of that swimbladder. Certain simplifications and assumptions have been allowed for ease in computation. First, the Q was determined from the mean depth of the layer and assumed constant. Second, the shear modulus of fish tissue was ignored, and, third, the ratio of the scatterer resonant frequency to the individual one-third octave filter center frequency was always unity. The latter two simplifications were not violated for the data presented, but the initial assumption of constant Q does cause concern in the nighttime case. To clarify, the variation of Q as a function of depth for the uppermost 200 m of the nighttime layer is significant. The nighttime curve was calculated using a mean value of Q near

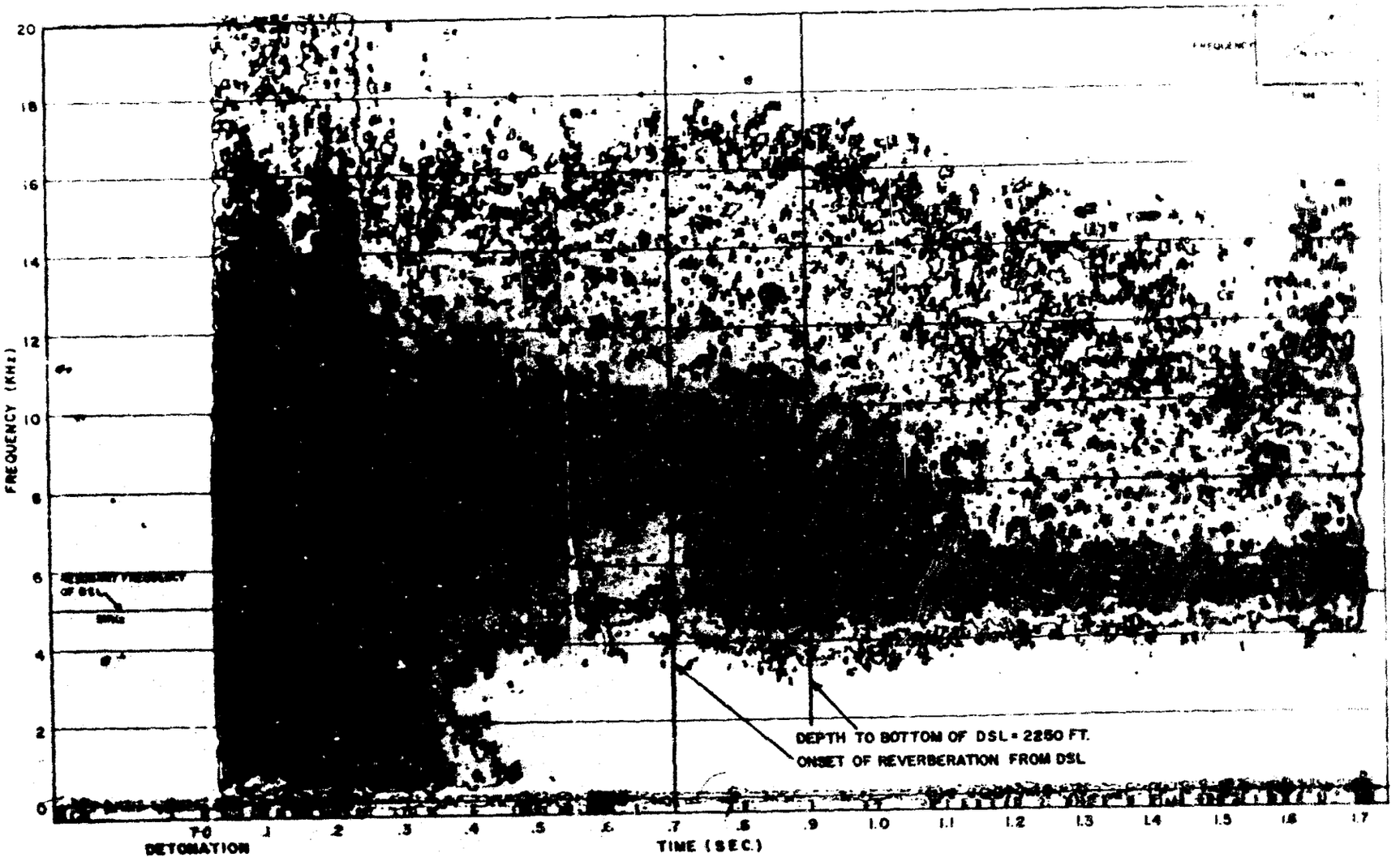


Figure 5. Typical narrow band spectrum analysis of daytime measurement

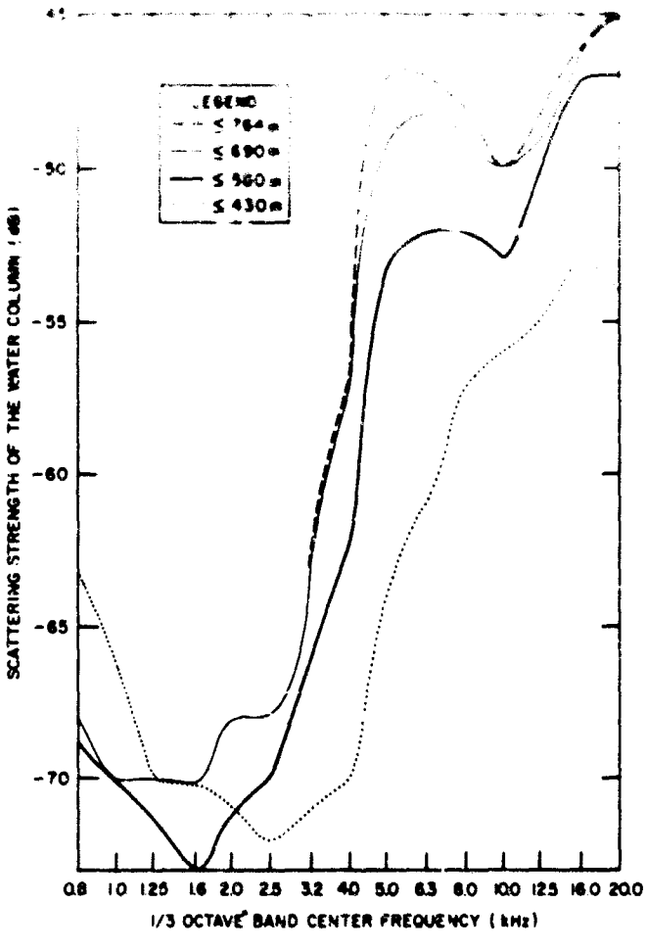


Figure 6. Daytime scattering strength spectra as a function of frequency for selected times after detonation

10. The results for the layer populations are shown as Figures 8 and 9, with the scatterer densities presented as $\log N_L$.

No conclusions regarding biological species composition are possible, but the calculated concentration shown does possess a range of values exceeding several orders of magnitude while the associated swimbladder variation remains small. It therefore seems reasonable to assume that most size components of the layers are represented. Extrapolation of these curves to even smaller sizes would seem to produce significantly higher concentrations but the minimal values shown for the large radii would probably persist well out into the "tail."

A comparison of the $\log N_L$ values reveals little difference between the day and night concentrations. Because we are effectively looking at the same scatterers in each case and because the relatively wide analysis bandwidth used tends to obscure the frequency shift resulting from migration, this presents no contradiction.

CONCLUDING REMARKS

In summary, volume scattering measurements were made in an area 200 miles north of Oahu. Detailed analyses of the explosive source scattering strength data permitted calculations to be made to determine the daytime and nighttime depths of the scattering layer and their respective thicknesses. By assuming resonant scattering for swimbladder bearing fishes, a method was

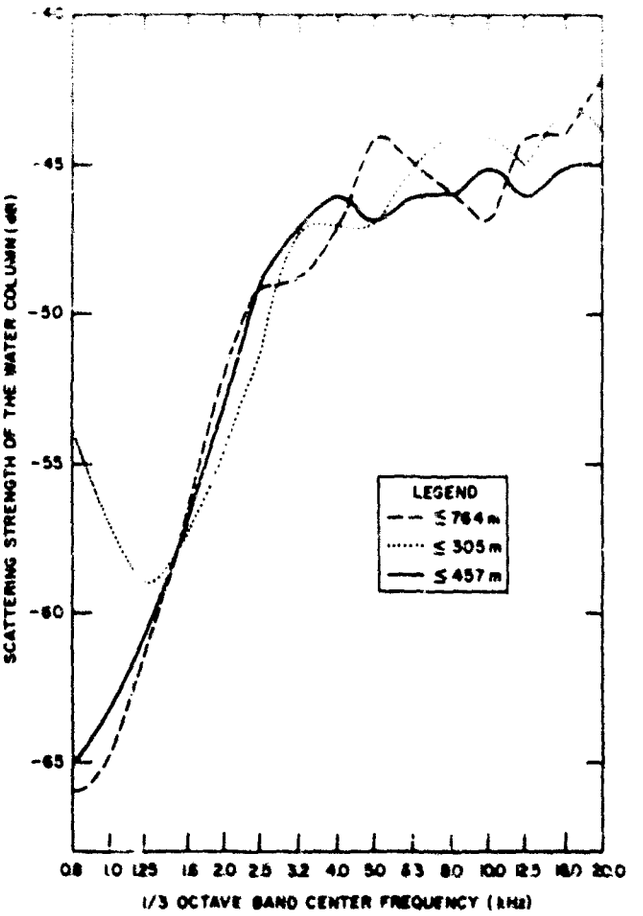


Figure 7. Nighttime scattering strength spectra as a function of frequency for selected times after detonation

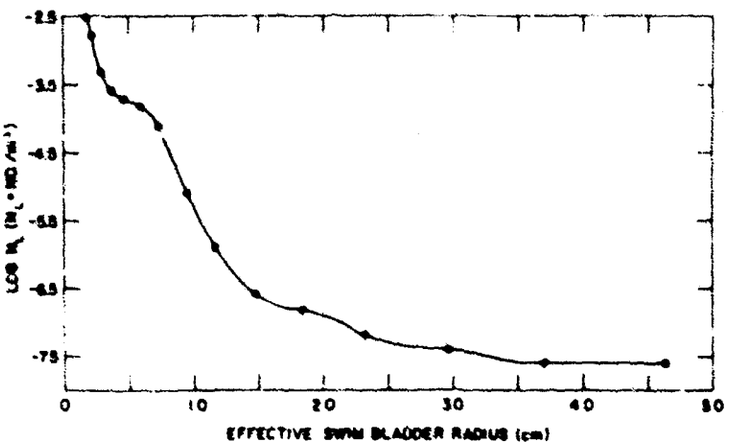


Figure 8. Daytime size distribution of resonant scatterers

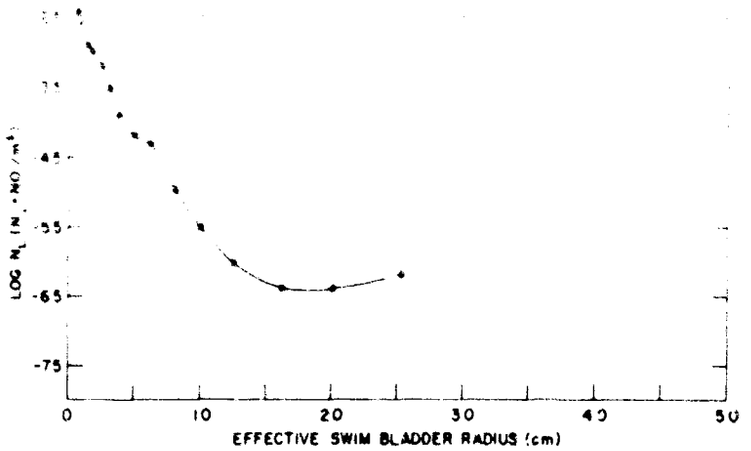


Figure 9. Nighttime size distribution of resonant scatterers

presented for determining the size and concentration of those individuals comprising the scattering layer.

The treatment presented here is not intended to be either complete or conclusive. Certainly, more experimental validation, possibly through biological net hauls and directional acoustic measurements, is required. The significance of the acoustically derived scatterer size distribution, assuming its validity, will most probably become clearer as it is further applied. For example, if biological net haul data are combined with acoustic results, it may be possible to derive a relationship of computed *in situ* swimbladder size versus fish length. Such a relationship would provide validation for the application of similar equations, derived from laboratory swimbladder measurements, to *in situ* conditions. At present, the application of these latter equations is dependent upon exact knowledge of the physiological characteristics of the swimbladder bearing fish. In addition, a study of the statistics of the derived distributions could yield valuable information on the coherent character of the actual scattering response.

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DISCUSSION

Smith: Sorry to start off with such a simple and technical question, but what is the origin of your choice of sixty feet for the source and receiver depth?

Van Schuyler: We make use of Navy signal underwater sound (SUS) signals, and they are set to pressure detonate. It is detonated merely by means of hydrostatic pressure on a piston face in the explosive, and it is just set to actuate at 60 ft. They come in various detonation depths, and 60 ft, it happens right now, is the shallowest we can go.

Winokur: I might add that in the measurement of this type, it is most desirable to utilize a source as close to the surface as possible, and Dr. Chapman uses explosives that detonate very near the sea surface. By using a shallow source it is possible to reduce the effect of surface reverberation on the volume scattering measurement.

Batzler: I wonder how close this area is to MGS 4 measurements in this general area.

Winokur: It coincides with one location.

Batzler: I remember that their results a little earlier in the year, probably April or March, had very high integrated values, column strengths. At 3.5 kHz I think it was −38 dB. They had a test later on, maybe September, where this went down to about −55 dB, and I have some single frequency measurements from August which agree pretty well with their September data, but I wonder how your values agree or disagree with their very high values. They're quite high

Van Schuyler: I had originally included for comparison the results of the Alpine data. As I remember, the reason I didn't include them was because the data as I had it from them only consisted of one or two, I think three frequency points, and I did not like the idea of trying to draw a comparison for the three frequency points. But at those frequency points, there seemed to be fairly good agreement at the higher frequencies; I believe it was at 8 and 12 kHz. I'm not sure about those two numbers. But at the low frequency, there is a substantial difference. It's kind of nebulous to try to talk about a trend on three data points for a 20-kHz range.

Batzler: It may point up the fact that in certain areas, principally off southern California, there is a distinct difference with season. The month of May may be late enough so that you have quite a difference between it and their measurements in April, I believe.

THE DEPENDENCE OF ACOUSTIC VOLUME SCATTERING ON DEPTH, FREQUENCY, AND TIME IN THE NORTHEAST PACIFIC OCEAN

J.A. Scrimger and R.G. Turner
Defense Research Establishment Pacific
Victoria, British Columbia

ABSTRACT

Measurements of the acoustic scattering characteristics of the ocean volume have been made in the northeast Pacific Ocean. Some limited measurements of total scattering of the water column are presented. A recently developed technique that enables volume scattering strength to be measured in situ as distinct from methods using downward-looking, near-surface equipments is described. Frequency- and depth-dependence of scattering is shown for a site off Point Reyes (San Francisco). Data were collected over almost a full day, enabling diurnal variations to be examined.

INTRODUCTION

The scattering of acoustic waves from the ocean volume has been studied at the Defense Research Establishment Pacific (DREP) since about 1967. Most of the measurements have been made in local waters, which means—since DREP is situated on the southern tip of Vancouver Island—the northeast Pacific Ocean. Our initial approach to this problem was to adopt the technique that had been developed by Chapman (1967) and his coworkers with a view to looking for differences or similarities that might exist in the reverberation characteristics of the Pacific and Atlantic Oceans. We were soon to discover that the scattering phenomenon was a complex one and that oceanic comparisons were not easily made, except in terms of the commonly used parameter—scattering strength of the water column, $10 \log \int_0^{Z_{max}} M_v(z)dz$, where Z_{max} is a depth above which the majority of the scatterers reside and at which depth the integral attains a maximum value. Accordingly, we developed a means of obtaining measurements of the scattering strength explicitly, i.e., $10 \log M_v(z,f)$—a function of both depth z and frequency f.

Figure 1 shows the locations that we have examined in the northeast Pacific Ocean. Cruise 8/69 (Stations IV to VII) was carried out to look for changes in scattering characteristics with latitude without the concomitant seasonal variation that may be contained in the data from other stations. Analysis of data from these areas is nearing completion, however only data from two stations (Stations I and II) will be presented in this paper. At Station I we obtained data yielding integrated scattering strengths (Scrimger and Turner, 1969), while at Station II a time series of measurements of the value of $10 \log M_v(z,f)$ was obtained. Station III, incidentally, was occupied when the technique of measuring scattering strength directly was first tried out in 1968, and the results of that trial have been reported elsewhere (Scrimger and Turner, 1969b). Results obtained from Station VIII will also be reported on separately.

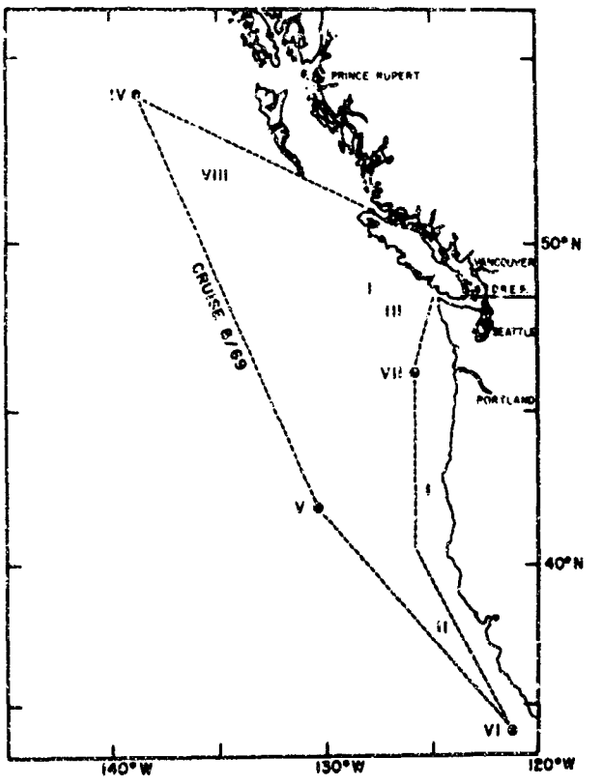

Figure 1. Site locations for the measurement of volume scattering from DREP

INTEGRATED STRENGTH MEASUREMENTS

Integrated scattering strength measurements are made using explosive charges, fired near the surface, as an acoustic source and a hydrophone suspended close to the firing point to detect the backscattered returns. The latter are produced within an expanding hemispherical shell corresponding to the shock wave of the explosion. Observation of the decaying intensity of the returned sound for several seconds enables information on the scattering characteristics at almost any desired depths to be obtained. It may be shown that the scattering strength derived from the scattered returns from the hemispherical shock wave is equivalent to that which would be obtained by integrating along a vertical column of unit cross section and of the same length as the radius of the shock wave. Such scattering strength measurements are thus generally referred to as integrated or column strength values. Figure 2 shows integrated scattering strengths, in three octave bands covering the frequency range 1.25 to 10 kHz obtained at Station I. These are plotted as a function of the column length (i.e., depth z). The column strength usually reported is the maximum value of scattering strength that may be read at the bottom of these curves. Our interest in plotting the integral in this way (essentially as a function of the upper limit of the integral) was to look at the distribution of scattering with depth in the water column. Because contributions of scattered energy received at a near-surface hydrophone from the horizontally stratified scattering layers can only add to the integral, it must always be positive-going when generated as a function of depth and prominent "shoulders" on this curve are indicative of the depth and strength of scattering layers. In fact, differentiation of this curve will, in principle, yield the scattering strength profile. Deriving scattering strength profiles in this way, however, proves unrewarding. As can be seen from Figure 2, a considerable portion of the integrated-strength profile near the surface is negative-going because of contamination from surface scattered energy, and the depth to which this contamination is effective is determined by the

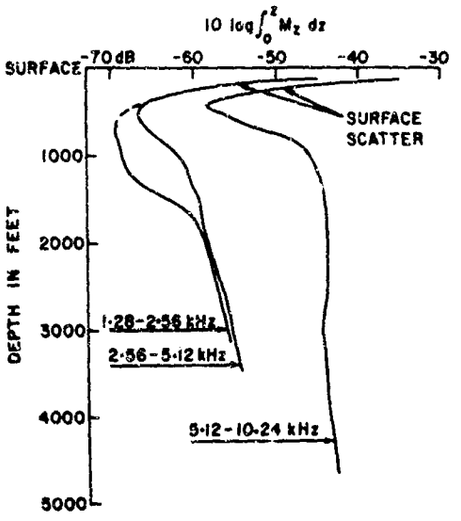

Figure 2. Integrated strength vs depth in the three octave bands between 1.28 and 10.24 kHz taken near sunrise in October

hydrophone depth, by the acoustic frequency being observed (since surface scattering strength is frequency dependent), and by the surface roughness or sea state. At the bottom end of the curves, the depth to which the data are valid depends on the signal-to-noise ratio of the decaying reverberation signal; and in the middle portions of the curve only the strongest layers yield slopes in these curves that can be readily measured.

IN SITU MEASUREMENTS

Method

In 1968 efforts were concentrated on a technique that would permit the measurement of volume scattering strength in situ and, as mentioned earlier, a description of this technique along with the results from its first use have already been reported (Scrimger and Turner, 1969b). Because the method is new and different from that used by other workers in the field, a brief description will be given here. The technique is to detonate a small explosive charge close to (<10 ft) a hydrophone and observe the broad band (at present 0.2 to 10 kHz) scattered returns for a short time interval after detonation. In fact the data samples used in deriving scattering strengths are 12.5 msec in length and begin 40 msec after detonation. We are therefore dealing with the returns scattered from a spherical shell about 200 feet in diameter with a volume of about 50×10^3 yd^3. It is thus possible to measure in situ values of scattering strength with a resolution of about 200 ft. This type of experiment is shown in Figure 3. The inset to this figure shows a pod of explosive charges and hydrophone, which may be lowered together to various depths in order to observe the amount of scattered energy produced by detonating units of the pod. In this way it is possible to obtain a profile of scattering strength versus depth, with good depth resolution, down to the present limiting depth of 2,000 ft. This depth limit is currently imposed by the type of charge that will not fire reliably below 2000 ft and also by an arbitrary choice of cable length.

The expression that relates volume scattering strength to the observed pressure for this type of experiment is

$$20 \log p = 10 \log M_v + 10 \log E_{100} - 20 \log t + 73.7$$

where p is the pressure, M_v is the volume scattering strength, E_{100} is the energy flux at 100

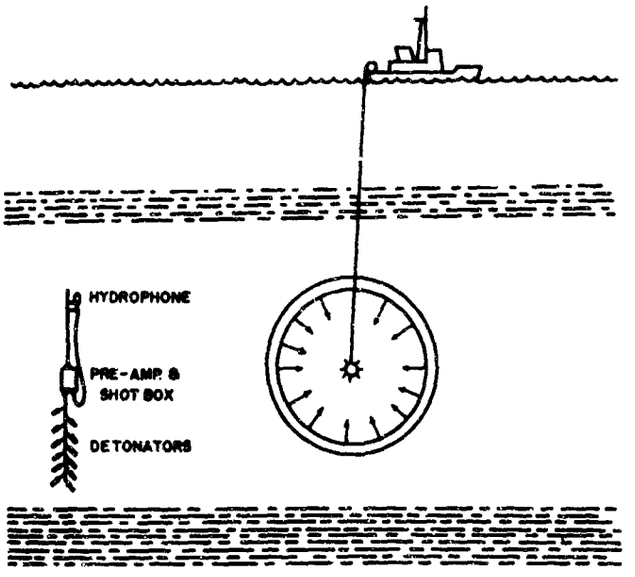

Figure 3. Backscattered energy (arrows) from the expanding spherical shock wave geing received by the hydrophone a few milliseconds after charge detonation. The picture is not to scale and the scattering shell would generally be small compared with the layer thicknesses. The inset shows the arrangement of the hydrophone and charge pod.

yards, and t is the time after detonation, all in cgs units. The derivation of this expression assumes that the measurement takes place in a region of uniform scattering and a decay of 20 log t is predicted, which differs from the more familiar 30 log t decay observed in the widely used, surface-fired charge technique. If the region does not possess uniform scattering characteristics, a 20 log t decay will not be observed but the method will still yield an average value of the scattering strength for that small volume of the ocean from which the acoustic returns originate. The above expression may be obtained by making the proper substitutions in the general equation given by Urick (1962). It was deemed necessary to consider the effect of pulse length, since our scattering observations are made close in to the charge-hydrophone pair. We have therefore made a separate derivation (Scrimger and Turner, 1969b) of the above scattering equation, which allows limits to be placed on the magnitude of errors to be expected when pulse length effects are ignored in our type of experiment. If the acoustic pulse length is assumed to be represented by one bubble pulse interval, which for our charges varies from 5 msec at 200 feet to 1 msec at 2000 ft, then Figure 4 depicts the magnitude of the pulse length errors that might be encountered for various times of observation.

Because this method of measuring scattering strength involves the firing of our explosive charge sources (C.I.L. Seismocaps, T.N.T. equivalent–0.00146 lb) over a range of depths from 200 to 2000 ft and because the energy spectrum level of an explosive charge is known to vary with depth (Christian, 1967), it has been necessary to make energy-spectrum measurements for these particular charges. A description of the method and the results of these measurements has been reported on separately (Turner and Scrimger, accepted for publication), but a series of energy spectra for groups of charges fired at five different depths and monitored by a hydrophone spaced at a range of about 100 yards for the shallowest group and about 300 yards for the others is shown here in Figure 5, all scaled to a distance of 100 yards. This series of curves dramatically illustrates the shift of the peak of the energy spectrum toward higher frequencies as the increasing depth shortens the bubble-pulse interval. In addition, it will be seen that the high-frequency end of the spectrum has about a minus 3-dB-per-octave slope, which decreases with increasing depth rather than the familiar minus 6-dB-per-octave falloff such as is found in the energy spectra of 1-lb charges. This depth variability of the source characteristics has been included in arriving at our volume scattering strength spectra.

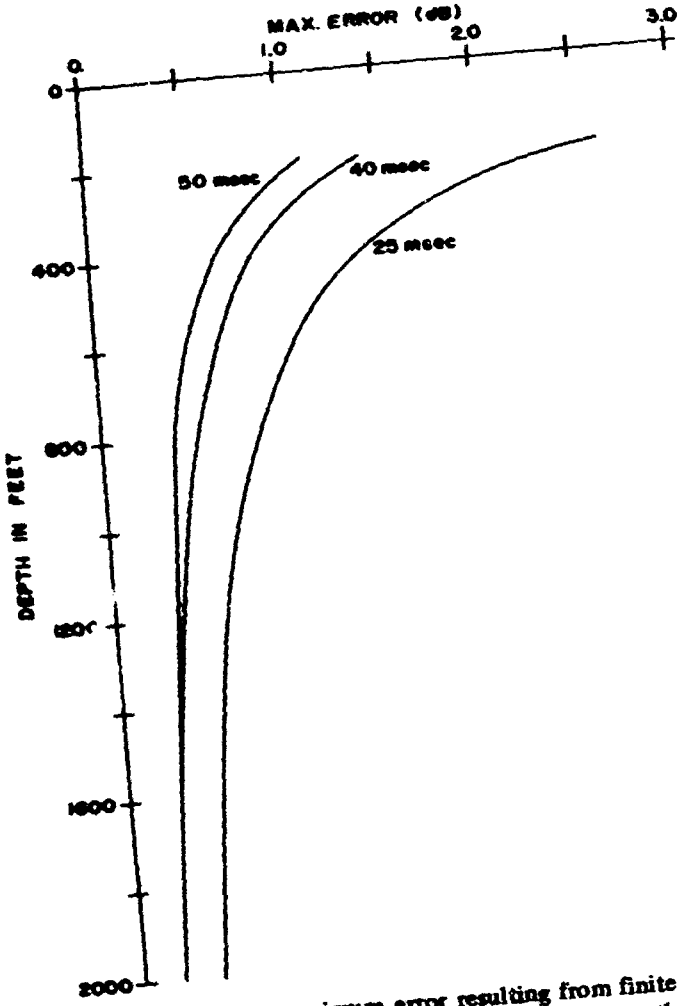

Figure 4. The maximum error resulting from finite pulse length to be expected in scattering strength values derived from intensity measurements taken at three different times after initiation of the pulse plotted as a function of the depth of detonation of the explosive source

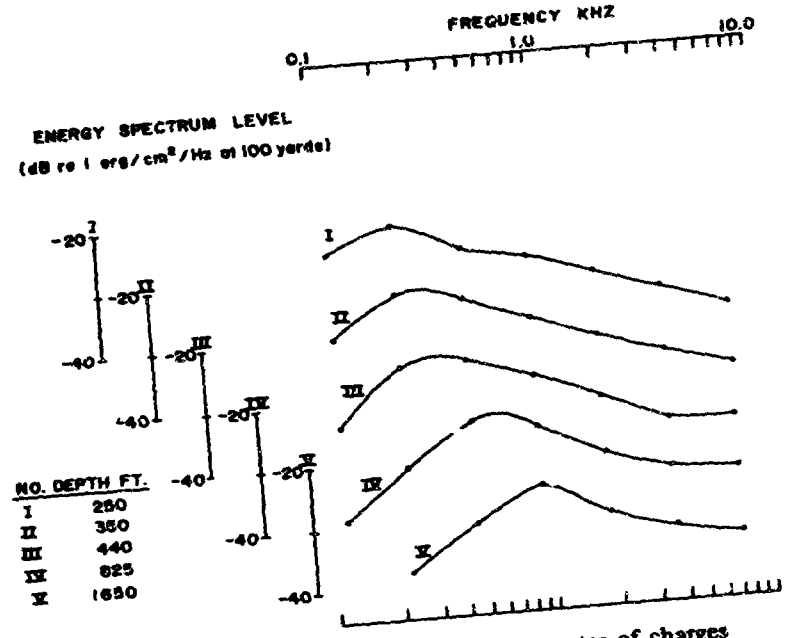

Figure 5. Depth dependence of energy spectra of charges used in the experimental method

Results

In December 1968, we had occasion to carry out deep-anchoring trials off San Francisco and at that time were able to obtain measurements over almost a full day at Station II where the water depth was 1,930 fm. These measurements, which have recently been reported (Scrimger and Turner, submitted for publication), permitted some insight into the mechanism of the diurnal variation of volume scattering. The hydrophone-pod combination was lowered a total of eight times between 0600 hours P.S.T. (about 1.5 hours before dawn) and 2000 hours P.S.T. (about 2 hours after sunset). Beginning at a depth of 200 ft, 10 shots spaced at 200-ft intervals were fired in each lowering, which took about 30 min. The analysis techniques used, although similar to those mentioned in our earlier paper (Scrimger and Turner, 1969b) have undergone slight changes that now allow our complete data analysis to be carried out digitally with relative ease and speed. These changes have been stimulated by the acquisition of a third-generation computer with which the Fast Fourier Transform technique of power-spectrum analysis could be implemented at our laboratory. The broadband, magnetic-tape recordings of the back-scattered sounds from each charge firing are first digitized and then scattering-strength spectra having a resolution of 400 Hz are generated from short (12.5 msec) samples of the scattered signals beginning at 40 msec after detonation. This procedure resulted in the production of 80 spectra. Because scattering characteristics can be expected to show a depth dependence, these spectra were grouped according to the 10 depths at which firings were made and these groupings are shown in the next 10 figures—Figures 6 through 15. Because of a malfunction in the calibration system during the time we were gathering data for profile 5, only seven out of a total of eight spectra were plotted in each group. Profile 5 was also omitted from Figure 18 for the same reason.

In Figure 6, spectra obtained at the 200-ft level are presented. Here we note that the only difference between all spectra observed over the diurnal period is the level shift that occurs between spectra. Characteristics that are common to all the spectra are the minimum at 2.5 kHz, the sharp low-frequency rise in level and the linear increase of level with frequency of about 5 dB/kHz on the high frequency side of the minimum. At the 400-ft level (Figure 7), the overall shift among the spectra is notably smaller than that at 200 ft; the minimum has virtually disappeared and the slope has decreased slightly. At the 600- and 800-ft levels (Figures 8 and 9) the spectral characteristics fall into two frequency regimes—one above 5 kHz and one below. In the higher frequency regime the spectra are tightly grouped and have a common slope, the slope of the 800-ft data being less than that of the 600 ft. Below 5 kHz the large (25 to 35 dB) spread among the spectral levels obtained at different times of the day is again apparent. Figure 10 shows the spectra obtained at 1000 ft. At this depth the spectra of scattered returns are virtually flat between 2 and 10 kHz and show a marked fall in level below this frequency. The spread in average values remains high. Spectra associated with the 1200- and 1400-ft levels (Figures 11 and 12) show only a small change from the 1000-ft spectra, but the trend to decreasing slope with increasing depth continues so that now slopes above 3 kHz have become negative. At 1600 ft, the levels of all but one spectrum have decreased and a well-defined line component appears in the spectra (Figure 13) at 9.6 kHz. This component persists in the spectra observed at the 1800- and 2000-ft levels (Figures 14 and 15) at which depths three additional spectral lines become apparent at frequencies of 1.2, 3.2, and 4.8 kHz. To be sure of the origin of such line components, we recorded a small sample of noise immediately before firing each shot and subsequently subjected each noise sample to the same analytical procedure undergone by the signal. Plotting families of the noise spectra at each of the above depths enabled spurious single-frequency noise components to be identified. This technique shows the lines at 1.2 and

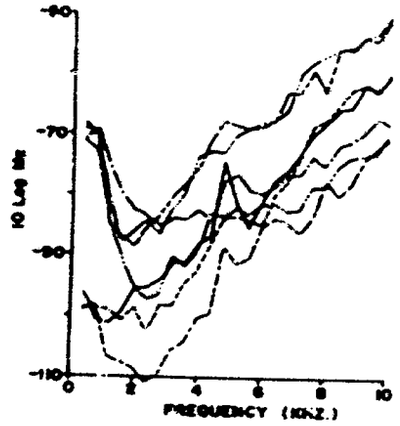

Figure 6. Scattering strength spectra obtained at 200 ft.

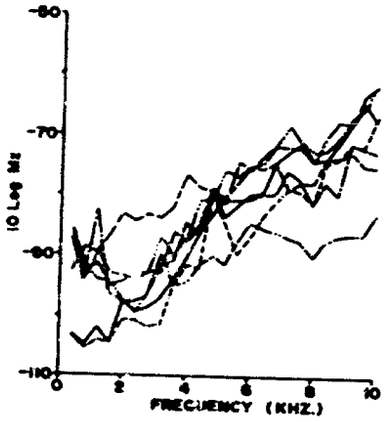

Figure 7. Scattering strength spectra obtained at 400 ft.

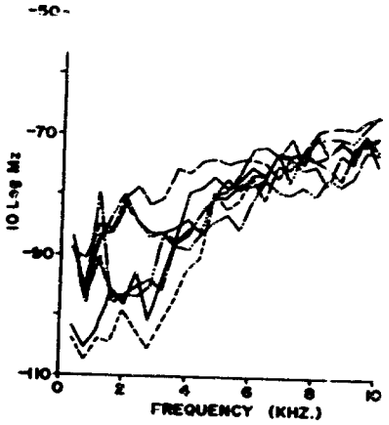

Figure 8. Scattering strength spectra obtained at 600 ft.

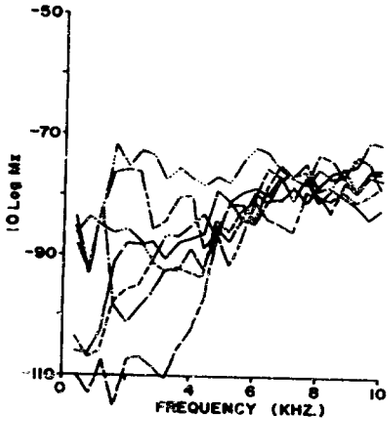

Figure 9. Scattering strength spectra obtained at 800 ft.

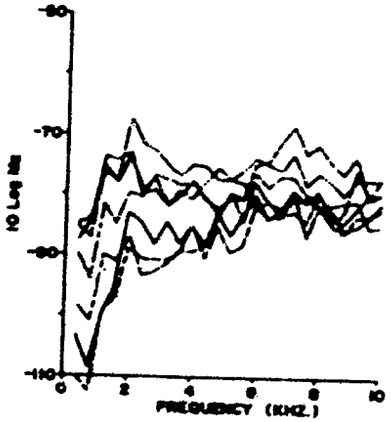

Figure 10. Scattering strength spectra obtained at 1,000 ft.

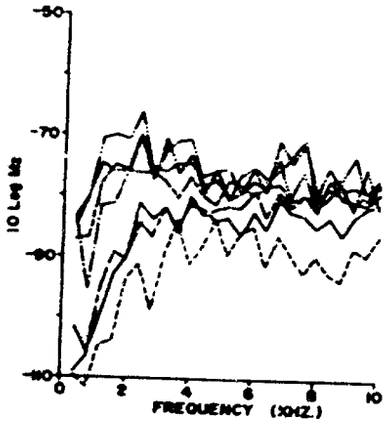

Figure 11. Scattering strength spectra obtained at 1,200 ft.

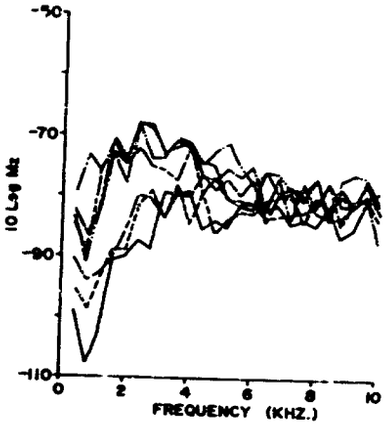

Figure 12. Scattering strength spectra obtained at 1,400 ft.

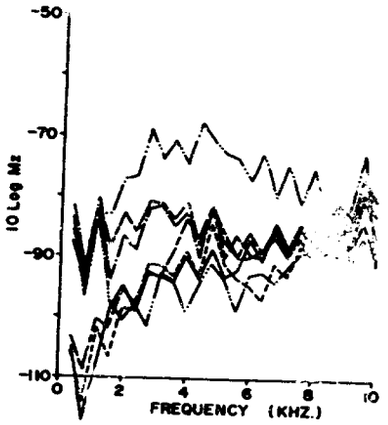

Figure 13. Scattering strength spectra obtained at 1,600 ft.

(Key for Figures 6-15: profile number: 1, —, 2 — —, 3 - - -, 4 — . . —, 6 — . —, 7 — . . . —, 8 — — — —.)

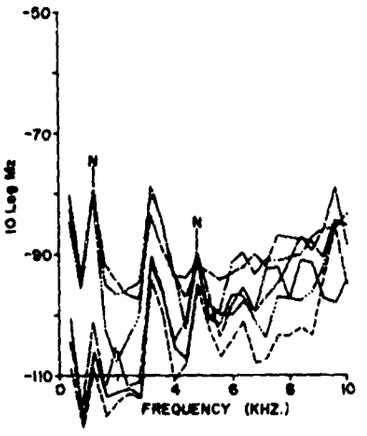

Figure 14. Scattering strength spectra obtained at 1,800 ft.

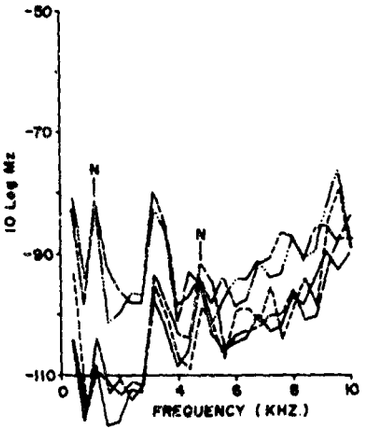

Figure 15. Scattering strength spectra obtained at 2,000 ft.

4.8 kHz, which are marked N in Figures 14 and 15, to be a result of noise, whereas noise spectra in the vicinity of the other lines at 3.2 and 9.6 kHz were flat. Close examination of some of the shallow spectra also reveals traces of these noise components.

Integration under any of these scattering strength versus frequency curves between any arbitrarily chosen pair of frequencies gives the scattering strength in any desired frequency band. Thus scattering strength versus depth profiles may be derived, and we have chosen to do so for the four octave bands between 0.625 and 10 kHz shown in the next four figures (i.e., Figures 16 through 19). In Figure 16, profiles in the 5- to 10-kHz band are plotted, the reference ordinates for these profiles being spaced horizontally in proportion to their temporal spacing during the day. Because the profiles take about 30 min to complete, the reference ordinate was taken at the mean time of the lowering. The scattering-strength values are absolute and are given by their horizontal displacement from the reference ordinate, in terms of the decibel scale factor shown in the figure. The upward migration of scatterers is readily seen and produces, at least at this position, an increase of scattering strength in the upper 200 ft of the water of as much as 20 dB. Other notable features in these profiles are (1) the near-linear increase in scattering strength as the surface is approached from depths as great as 1200 to 1600 ft at night, as distinct from the vertical character of the profiles during daytime; (2) the relatively small variation in level in the 600- to 1500-ft depth range that was seen in the spectral curves discussed above; and (3) layers evident near the surface, at 600 and 1400 ft. Comparison of these profiles with the echogram taken with a 12-kHz echosounder gives fair correlation for layer position and movement. Lack of correlation is likely to be because the echosounder frequency lies outside the band used for these profiles. Profiles in the 2.5 to 5 kHz band (Figure 17) show little resemblance to those in the higher octave band of Figure 16 and show the near-surface increase in strength only during the postsunset period. A well-defined layer centered at 1400 ft persists throughout most of this record, but it is certainly not symmetrical about the daylight hours. The layer is weak in the pre-dawn period, becomes stronger and wider in the course of the day and by sunset extends over almost 1000 ft in depth between 600 and 1600 ft. The scattering picture that appears as we pass to the next lower octave band (i.e., the 1.25- to 2.5-kHz band, Figure 18,) is again different from those seen in the higher octave bands. Here we find variations in profile structure occurring from profile to profile—especially in the first five observed. Generally a minimum in scattering strength is found in the 400- to 500-ft depth interval, except in profile 3 where a large increase in scattering strength occurs at this level. It is tempting to at-

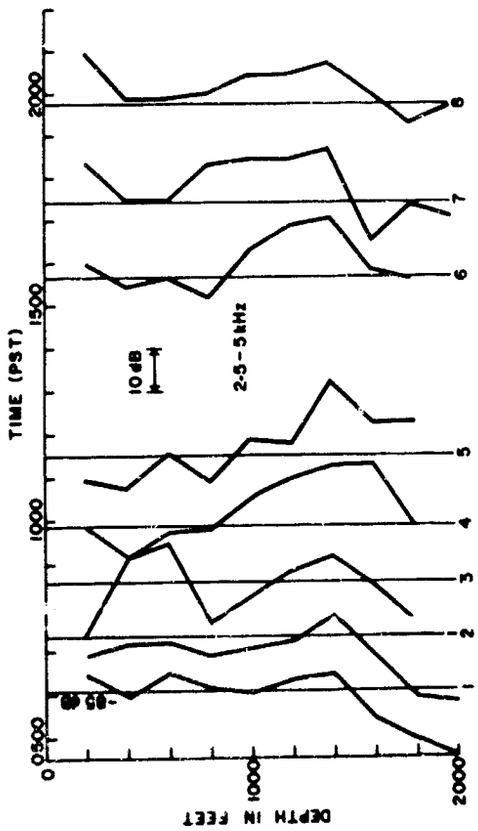

Figure 17. Scattering strength profiles in the 2.5- to 5-kHz band

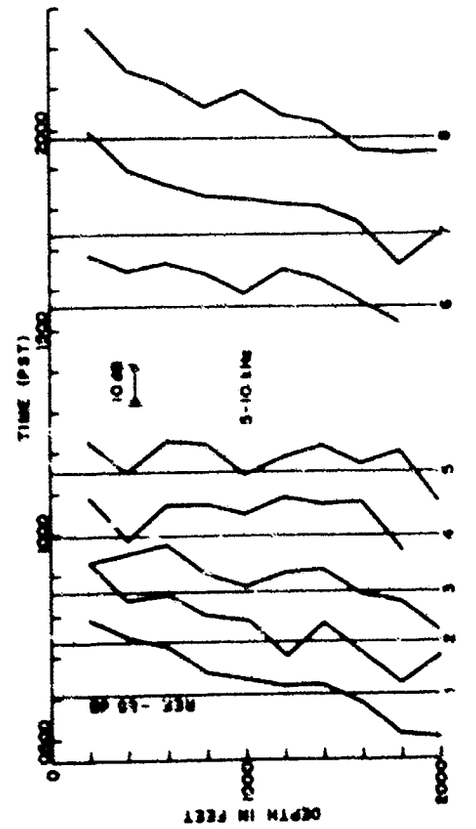

Figure 16. Scattering strength profiles in the 5- to 10-kHz band

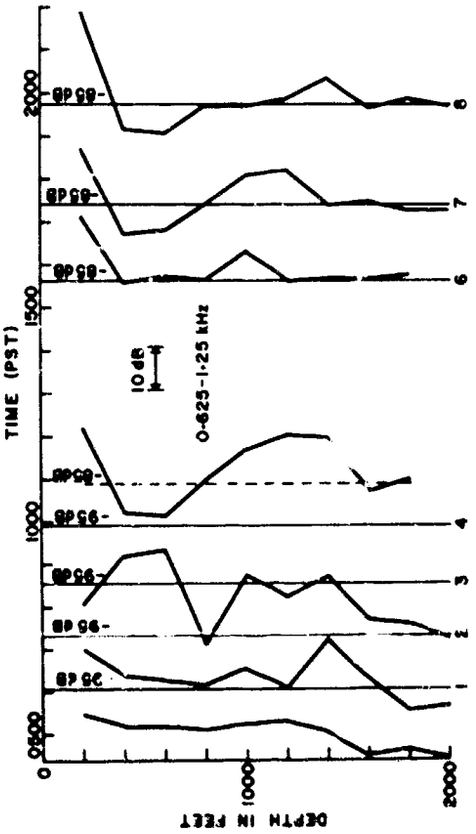

Figure 19. Scattering strength profiles in the 0.625- to 1.25-kHz band. (Note profile 5 was not included in this band).

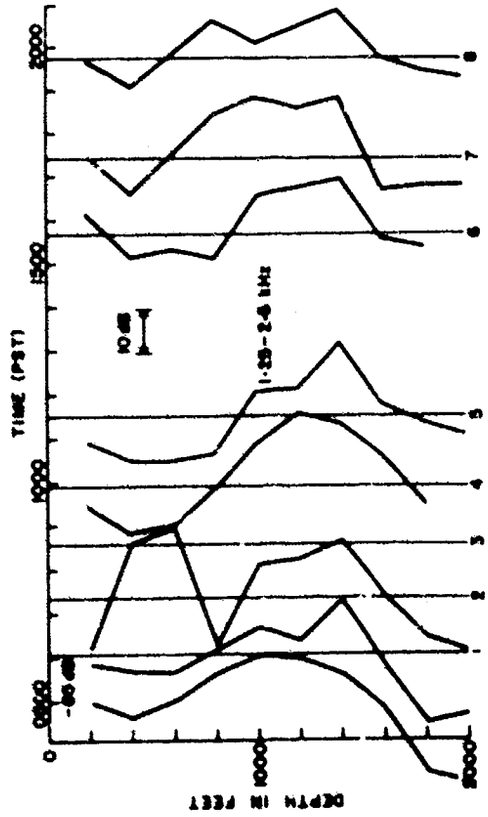

Figure 18. Scattering strength profiles in the 1.25- to 2.5-kHz band

tribute such large and sudden changes to fish shoals. No signatures that might be associated with shallow-swimming fish appear in the spectra, however. One feature of this series of profiles that can be seen at once in the spectral presentation is the gross increase in level that occurs in all profiles after the first three. This average low level of scattering for the first three profiles of the day is again evident in the 0.625- to 1.25-kHz b...d (Figure 19). It will be seen in Figure 19 that the reference ordinate drawn for these profiles is 10 dB lower than that used elsewhere. A near-surface layer may be seen in profiles 4, 6, and 7, the scattering strength of which increases by some 8 dB in profile 8. This layer is missing in the pre-dawn and early-morning profiles (evidently we should have taken a few more measurements during the night in order to see when the near-surface layer dispersed). In this frequency band, the deeper layers are present at about 1000 and 1400 ft. By 1000 hours (profile 4), these layers have coalesced into one thick layer extending from 100 to 1500 ft. Between 1500 and 2000 hours (profiles 6, 7, and 8) a thin layer appears to sink from 1000 to 1400 ft.

CONCLUSION

We see then that the phenomenon of scattering of acoustic waves from the volume of the ocean most certainly cannot be represented by a picture of a medium consisting of stable scattering layers. The statistics available in the data obtained over the diurnal period that we have discussed above are insufficient to reveal cyclic components in the variability other than the post-sunset increase in the scattering near the surface caused by the upward migration of biological species. Hopefully, with the acquisition of more data, we will be able to identify fish sizes and size distributions (if not species) in terms of the broadband spectra. For example, the line components in the spectra obtained at the 1600- and 1800-ft levels can be presumed (assuming the relationship between bubble resonant frequency, depth and radius given by Minnaert (1933)) to be a result of resonant scattering from swimbladders or gas bubbles of 0.74- and 0.25-cm radius for 3.2 and 9.6 kHz, respectively, and it may be possible to interpret the uniformity of the spectral slopes over various frequency ranges at most of the depths examined in terms of fish bladders and their spacing in an array or shoal as discussed by Weston (1967). Further study will doubtless produce a clearer picture.

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DISCUSSION

Wednesday evening, 1 April 1970

Winokur: I have asked a few people to make some comments and to present additional data this evening related to the papers that we heard earlier before we get into any critical discussion or comment about what we have heard so far in this session. In order to start off this evening's session then, I have asked Mr. Richard Love of the U. S. Naval Oceanographic Office to take a few minutes to present the results of some of the dorsal aspect work that he has done because it is very closely related to what Brian McCartney reported on earlier.

Love: Today's papers have concerned the resonant scattering from air-bladder fish. However, the range of resonance is not usually the range of interest where discrete fish echoes are received by a sonar. In this range the target strength of fish can vary widely with small changes in fish length or acoustic frequency, and fish of the same size and species may have target strengths varying by as much as 10 dB.

To approximate the target strength of an individual fish, I have conducted experiments on a number of live fish of 12 different species, ranging from 2 to 9 inches in length. The incident acoustic frequency ranged from 12 to 200 kHz.

I have combined the results of these experiments with all other available data into non-dimensional regression lines, which can be used to determine the maximum side-aspect and dorsal-aspect target strengths of an individual fish. Figure 1 shows these regression lines. The side aspect data were published in the September 1969 issue of the Journal of the Acoustical Society of America, and the dorsal aspect data is new. Here, σ is the acoustic cross section, L is the fish length, and λ is the acoustic wavelength.

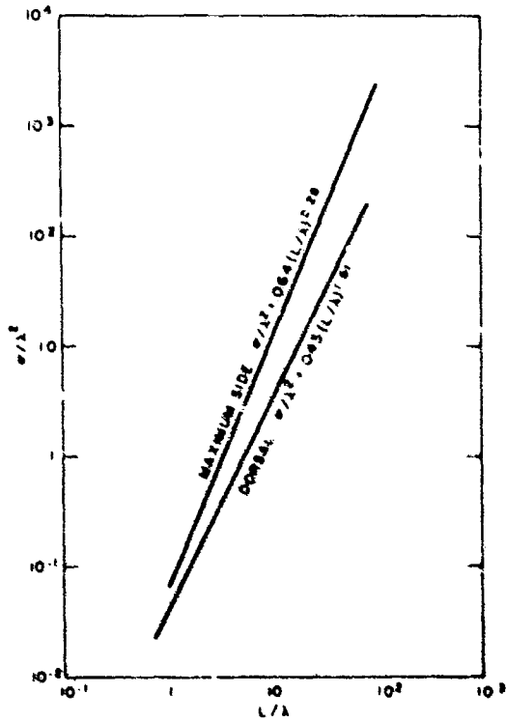

Figure 1

For the dorsal aspect the regression line is

$$\frac{\sigma^2}{\lambda} = .043\left(\frac{L}{\lambda}\right)^{1.91}$$

in the L/λ range of 0.7 to 90, and for the maximum side aspect it is

$$\frac{\sigma^2}{\lambda} = .064\left(\frac{L}{\lambda}\right)^{2.28}$$

in the L/λ range of 1 to 100. This equation for the maximum side aspect is a slightly modified version of one that appeared in JASA, the modification being a result of the addition of recent data.

The target strength of an individual fish can be calculated from the regression lines by using the relation

$$T = 10 \log\left(\frac{\sigma}{4\pi}\right)$$

where T is measured at one yard and σ is in square yards.

For the maximum side aspect

$$T = 22.8 \log L - 2.8 \log \lambda - 32.4$$

and for the dorsal aspect

$$T = 19.1 \log L + 0.9 \log \lambda - 34.2$$

Over the common L/λ range of 1 to 90, the side aspect target strength increases from 1.8 dB greater than the dorsal aspect at $L/\lambda = 1$, to 9.0 dB greater at $L/\lambda = 90$.

Comparing Dr. McCartney's equation presented this morning to my dorsal aspect equation over their common L/λ range of 0.8 to 20, Dr. McCartney's is 2.2 dB lower than mine at $L/\lambda = 0.8$ and is 5.3 dB higher than mine at $L/\lambda = 20$.

Figures 2 and 3 show the relation of the regression lines to resonant scattering.

The resonance peak shown is calculated from Andreeva and Chindonova's equations for a fish at a depth of 20 feet, with a $Q = 5$ and with an equivalent spherical swimbladder radius equal to 1/20 of the fish length. The portions of the curve off resonance are approximated by a spherical bubble equal in volume to the fish's swimbladder.

It can be seen in Figure 2 that at any specific frequency, a large non-resonant fish can have a greater acoustic cross-section than a small resonant fish. However, as is shown in Figure 3, where the ordinate has been changed from σ/λ^2 to σ/L^2, the acoustic cross-section of a fish of specific size is probably greater at the resonant frequency than at any other frequency for which $L/\lambda < 100$.

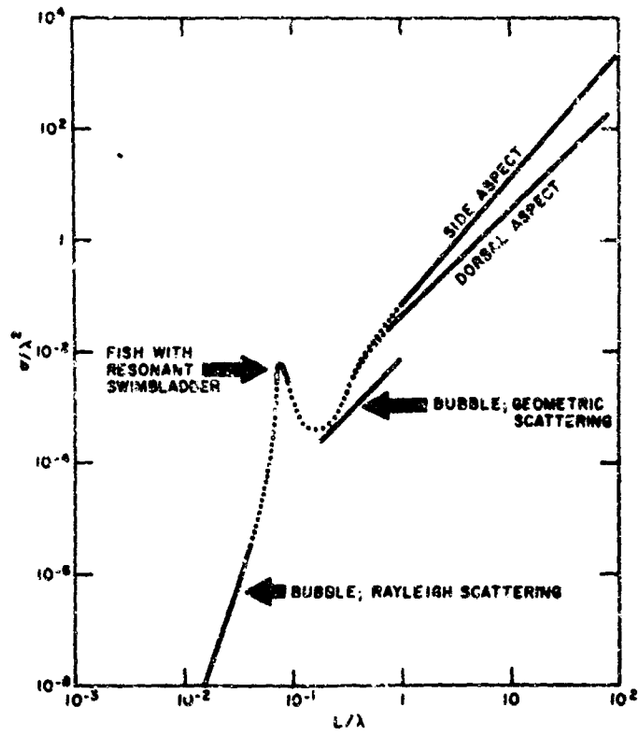

Figure 2

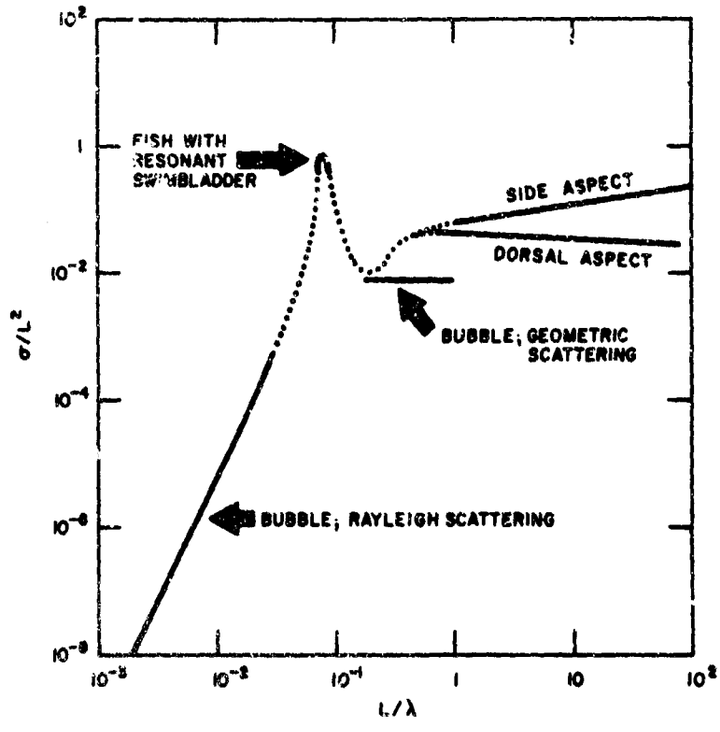

Figure 3

Johnson:

Some Mid-Ocean Acoustic Scatterers

An acoustic system has been developed at the Marine Physical Laboratory that can provide data on sound scattering in the ocean (1,2). Uniform depth resolution is achieved through the use of an electronic package equipped with sources and receivers which is lowered into the ocean. Recent work at a location in the San Diego Trough has provided some estimates of target strength, swimming speed and population density for individual scatterers to depths of 1600 meters. In data collection, a single frequency ping is generated; then samples are taken corresponding to returns from sections of spherical shells around the underwater package limited vertically by the 40° beamwidth of the horizontally omnidirectional transducers. All of the data were obtained using a 2-msec pulse length with instantaneous envelope samples spaced 1-msec apart.

The displays presented here are organized around four frequency pairs: 4.5 and 6.3 kHz, 8.9 and 10.5 kHz, 15 and 16.7 kHz, 24 and 27 kHz (Figures 1-3). Data returns at the top of each band come from 30 meters range and those at the bottom from 80 meters. The median of the returns from each ping is encoded in the stripe above each frequency band. The computer compares each sample to the median, and assigns the seven available grey shades to samples from one to seven dB above the median. Samples at or below the median are written as white, while anything more than seven dB above the median is written with the darkest shade of grey. Steady darkening with increasing range is the effect of the range corrections on ambient noise in the absence of scatterers.

Because of the experiment's geometry, identifying a single return with an individual scatterer would be unjustified. But by observing a small volume for several minutes, we can track scatterers and, hopefully, average out interfering effects.

All the numbers should be treated with some skepticism. The movement rates are not absolute, since we have no measurements of current speed. Target strengths are subject to off-axis distortion and represent averages of strong scatterers to the nearest 5 dB. Population densities are low estimates for these same strong scatterers, but they should be within a factor of two. Finally, the observations at each depth lasted only 20 minutes and may not represent the ocean or even the San Diego Trough in general.

Of the animals observed, only those at 1600 m seem to be clearly affected by the presence of the acoustic package. At that depth they are typically attracted rather than repelled.

Summary of Results

	Target Strength dB	Population per $10^6 m^3$	Movement m/sec
1000 m			
15 & 16.7 kHz	-55	2	0 - 0.1
24 & 27 kHz	-40	3	0 - 0.1
1300 m			
4.5 & 6.3 kHz	-35	2	0.1 - 0.2
8.9 & 10.5 kHz	-35	12	0 - 0.1
15 & 16.7 kHz	-40	12	0 - 0.1
24 & 27 kHz	-35	8	0 - 0.1
1600 m			
4.5 & 6.3 kHz	-35	4	0.1 - 0.2
8.9 & 10.5 kHz	-40	5	0.1 - 0.3
15 & 16.7 kHz	-45	7	0.1 - 0.3
24 & 27 kHz	-40	5	0.1 - 0.3

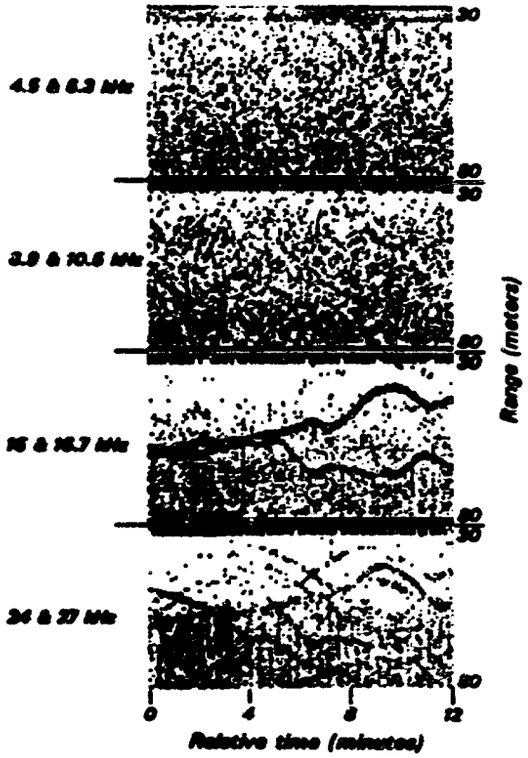

Figure 1. Results from 1,000 meter drift run displayed on a Ross recorder after computer processing

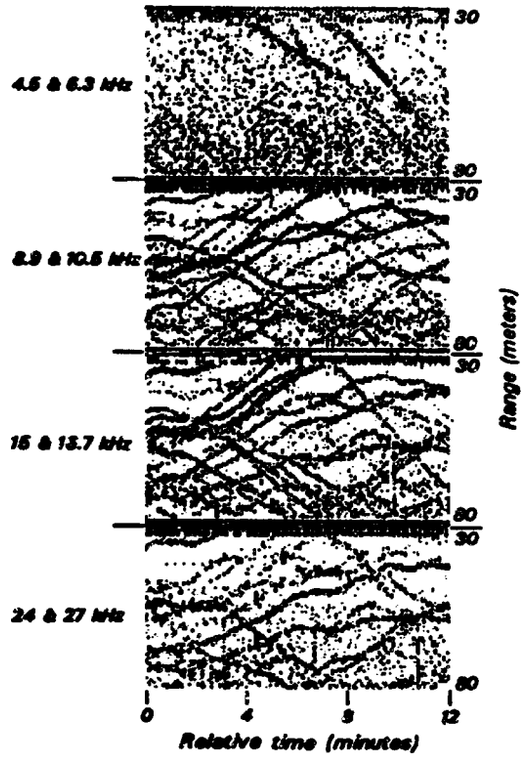

Figure 2. Results from 1,300 meter drift run displayed on a Ross recorder after computer processing

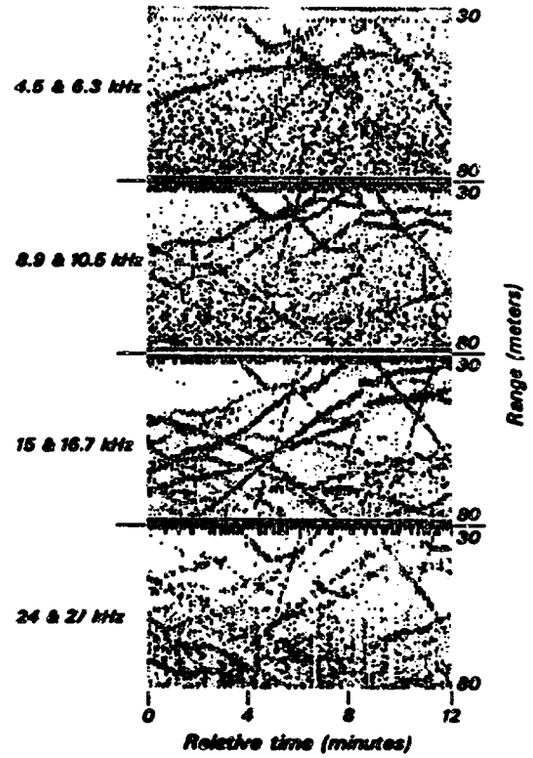

Figure 3. Results from 1,600 meter drift run displayed on a Ross recorder after computer processing

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McCartney:

CHANGES IN SCATTERING LAYER STRENGTH DURING DEPTH MIGRATION

Useful information on the sizes of sound scattering organisms has been obtained by measurement of acoustic back scattering strength, particularly the use of resonant peaks and the changes thereof during the diurnal migration periods. There is considerable interest in the migration behaviour and whether constant mass, constant volume or other constraints apply. To resolve this, good accuracy in depth and resonant frequency are required simultaneously. Generally, wide-band explosive sound sources have been used, enabling resonant peaks to be observed up to 20 kHz, but owing to the lack of directionality in the source, the depth resolution is relatively poor. Fixed frequency echo-sounders can give better depth resolution, but there is no guarantee that the scattering observed is resonant, unless a battery of echo-sounders are used simultaneously to cover the spectrum. The purpose of this contribution is to suggest that the depth variation of scattering strength at the centre of a layer may provide useful clues when only a single sounder is available.

The acoustic scattering section σ of a gaseous sphere of radius R (swimbladder approximation) is well known to be

$$\sigma = 4\pi R^2 \left[\left(1 - \frac{f_0^2}{f^2} \right)^2 + Q^{-2} \left(\frac{f_0}{f} \right)^4 \right]^{-1} ,$$

and the resonant frequency to be

$$f_0 \propto D^{1/2} R^{-1} ,$$

where Q is the quality factor at resonance and D is the depth (including correction for atmospheric pressure).

For a constant volume migrator, R is independent of D and the scatterer will pass its resonant depth D_0 when the sounder frequency $f = f_0$. Then approximately we can write:–

(A) Constant volume case,

$\sigma \propto D^{-2}$,	$f < f_0$,	$D > D_0$,	$M \propto -20 \log_{10} D.$
$\sigma \propto Q^2 D^{-2}$,	$f = f_0$,	$D = D_0$,	
$\sigma \propto$ const,	$f > f_0$,	$D < D_0$,	M const

For a constant mass migrator $R \propto D^{-1/3}$, so that $f_0 \propto D^{5/6}$ and we obtain

(B) Constant mass case

$\sigma \propto D^{-4}$,	$f < f_0$,	$D > D_0$,	$M \propto -40 \log_{10} D$.
$\sigma \propto Q^2 D^{-4}$,	$f = f_0$,	$D = D_0$	
$\sigma \propto D^{-2/3}$,	$f > f_0$,	$D < D_0$,	$M \propto -6.7 \log_{10} D$.

For these ideal cases, A and B, a plot of the volume scattering strength $M = 10 \log (n\sigma/4\pi)$ versus $\log_{10} D$ at the centre of a layer containing n similar scatterers per unit volume would be expected to have slopes of -20 and 0 dB per decade or -40 and -6.7 dB per decade either side of a resonant peak. The values of Q will probably depend upon depth.

Figure 1 contains two contoured plots of scattering coefficient ($m = n\sigma$) at 10 kHz during the sunrise and sunset migrations one day during the DISCOVERY SOND cruise in 1965. The analogue scattering level for four successive pulse transmissions was obtained on an ultra-violet paper recorder every five minutes. The traces were read and averaged over the four pulses and over each 20-m depth interval between 0 and 700 m; scattering coefficient was computed and plotted, and subsequently contoured.

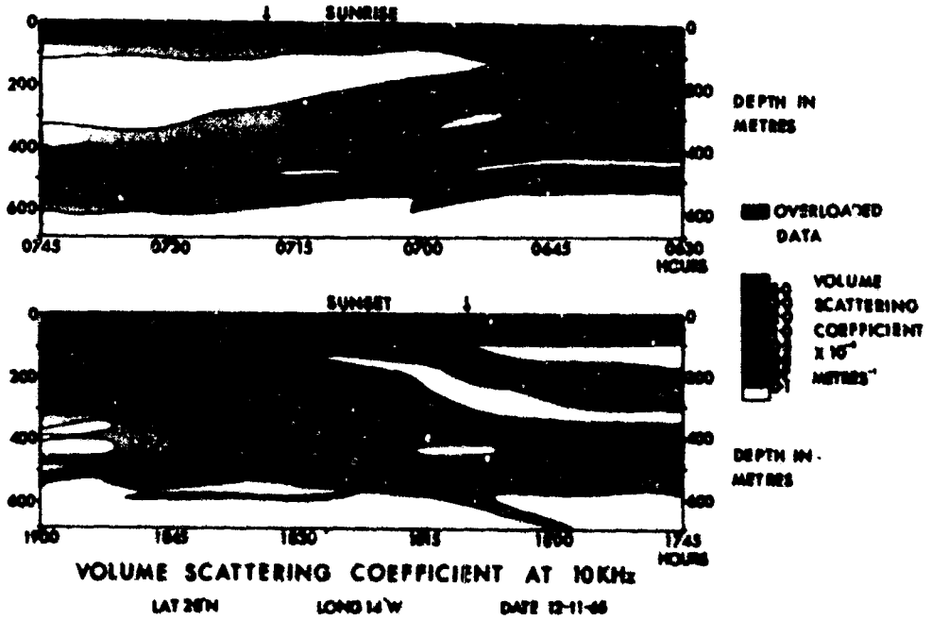

Figure 1

The plots of scattering strength versus depth in Figure 2 were obtained from the more obvious layers of Figure 1. Open and solid symbols refer to sunrise (downward) and sunset (upward) migrations respectively, while the same symbols have been given to layers which have the same mid-day depth, as observed on the original echo-sounder intensity record. Slopes vary from 0 dB per decade to -60 dB per decade of depth, and separate peaks are observed at 250 m

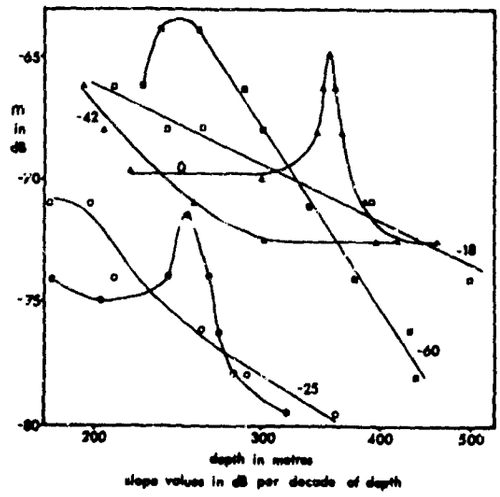

Figure 2

(twice) and 360 m depth, corresponding possibly to resonant radii of 1.7 mm, and 2.0 mm. None of the examples show identical sunset and sunrise patterns, though there is a tendency for the end points of corresponding layers to be at the same values, which is expected if there is little depth migration outside these periods.

Variations from the above theoretical strength/depth rates would be expected if the layers contain a fish population mixed in size or behaviour, but migrating together, if there is a change in thickness of the layer as it migrates, if layers merge, or if there is an appreciable non-migratory component of scattering. The results shown are not a very conclusive demonstration of whether this method of examining scattering layers has merit. A wider dynamic range in recording and better resolution in time and depth are required. The first two are possible but a compromise on depth resolution has to be achieved. At large depths resolution may be affected more by the difference in depth between the axis and the edges of the beam than the pulse length, but reducing the beamwidth can make the pulsed sampling volume too small at the shallower depths. Perseverence with the measurement of scattering strength at a fixed frequency during migration periods is perhaps worthwhile because most research ships have echo-sounders; few are able to use the wide-band explosive techniques, especially during biological sampling cruises.

Hersey:

I am afraid that I have rather serious worries about the fundamentals of an analysis of this type. For example, ask yourselves how many times you have stopped your ship and allowed it to drift while continuing to record the scattering layer. Usually when someone stops the ship, the reason is that the hydrographer is going to take a station and you are asked to turn things off and get out of the way so far as the scattering layer observations are concerned. But if you keep the records running, many times instead of seeing the familiar salt and pepper aspect of the deep scattering layer, you have learned that it changes its character altogether. What you are seeing are correlatable echo trains that come from individuals either randomly scattered or grouped in depth. Since you can discern them quite far away, I don't know just what analysis you are advocating regarding these interlacing echoes like the very pretty pictures that we were

just shown a few moments ago. Obviously it is worth making some kind of a measurement like your contours. I have done the same thing. It is very rewarding as long as you are sure what it is you are measuring. I want to remind you again that very often that which looks like diffuse scattering on a record made from a ship underway has that appearance only because you are passing very rapidly over the scattering. If you slowed down, the appearance of diffuse scattering disappears altogether and only single patches of scatterers are to be seen. Just to make things more confusing, of course, that picture is not universally true. In some places when you slow down and you simply drift, the salt and pepper pattern continues and individuals are not resolved, so I think it is necessary to think ahead to these several possibilities and work out the fundamentals of the measurements so you can deal with either kind.

BIOLOGICAL RESULTS FROM SCATTERING LAYER INVESTIGATIONS IN THE NORWEGIAN SEA

Bernard J. Zahuranec and W. Lawrence Pugh
U.S. Naval Oceanographic Office
Washington, D.C.

ARSTRACT

In August 1967 collections were made of midwater organisms at four stations in the Norwegian Sea. A 6 foot Isaacs-Kidd Midwater Trawl was towed open at three of the stations and a closing device was used at the cod end at the first station.

The collections contained few species but large numbers of organisms, consistent with the high productivity reported for this region. The only fish caught in abundance were specimens of the lanternfish *Benthosema glaciale*, which increased in numbers as well as in depth of occurrence from northwest to southeast. The invertebrates also seemed to occur in greater abundance at shallower depths at the western stations than at the eastern stations.

Depth recorder records showed two kinds of scattering: (1) a diffuse scattering layer most pronounced at the easternmost stations, and (2) discrete echoes, generally at shallower depths, tending to coalesce into a layer at the westernmost stations. The discrete echoes may result from individuals or schools of larger fishes, such as herring or the cod *Micromesistius poutassou*, which, for the most part, could successfully avoid the net. Investigation of the largely fat-invested swimbladders of specimens of *Benthosema* revealed varying degrees of occlusion of the lumen. Investigation of the otoliths and the length-frequency distribution of the specimens of *Benthosema* indicated the presence of year classes I through III and possibly IV.

INTRODUCTION

In the course of investigating acoustic scattering layer phenomena, the U.S. Naval Oceanographic Office collected biological and oceanographic data in the Norwegian Sea in August 1967 aboard the USNS *Gillis*. The Norwegian Sea was chosen for investigation as a boreal region of reportedly high productivity. Because boreal regions tend to have fewer species than tropical or temperate regions, an investigation of such a region held promise of providing insight into some of the biological problems associated with sound scattering in the ocean.

The locations investigated in the Norwegian Sea were selected to sample the transition from the cold water of Arctic origin to the warmer and more saline water of North Atlantic origin. Station 2 (Fig. 1) is located at the western edge of the Icelandic Basin and well within the limits of colder water. Station 2A is located at the eastern edge of the Icelandic Basin, just over the western rim of the sill separating the Icelandic and Norwegian Basins, in an area of some mixing of colder and warmer waters. Station 3 is located in the western part of the Norwegian Basin and Station 4 is located in the eastern part of the Norwegian Basin in typical North Atlantic Water.

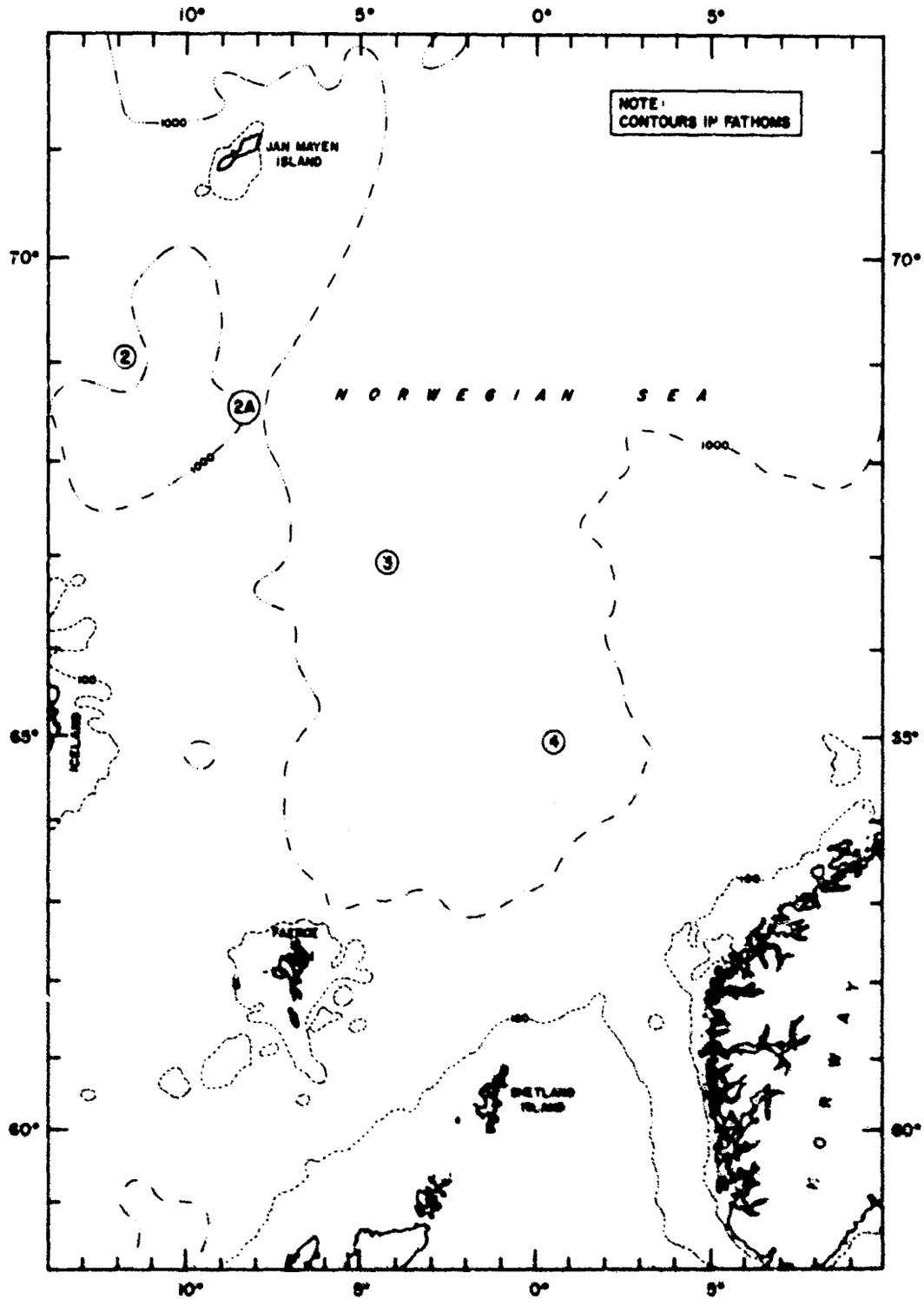

Figure 1. Location of stations in the Norwegian Sea

At all four stations biological tows and hydrographic casts were made. This paper reports the biological data taken, principally the data on fishes. The hydrographic data will be reported separately.

In studies involving midwater fishes as possible sound scatterers, the presence or absence of a gas-filled swimbladder and the size of the swimbladder are important because of acoustical theory that relates volume reverberation to gas bubbles in the water column. The entire swimbladder is not necessarily filled with gas but may become occluded, especially as the fishes age. Marshall (1960) showed that in many species the swimbladder becomes invested with fat. Capen (1967) reported that in several lanternfishes from off the southern California coast, the swimbladders in large specimens become filled or partly filled with a "cottony tissue" outgrowth from the gas gland.

To understand the situation in the common Norwegian Sea lanternfish, *Benthosema glaciale*, the swimbladders of a number of preserved specimens caught in the Norwegian Sea were examined. Because the swimbladder size is related to the size and age of the fish, the ages and peaks of abundance for *B. glaciale* were determined.

Appendix I is a list of fishes collected.

METHODS

All biological collections were made with a standard 6-foot Isaacs-Kidd Midwater Trawl (IKMT), fully lined with 1/4-inch (bar) knotted nylon netting. The cod end was a half-meter net of knotless nylon with about 1/8-inch openings. At Station 2, a four-chambered General Motors Mark II Discrete Depth Plankton Sampler (DDPS) (Aron et al., 1964) was attached to the IKMT. At all other stations, the open IKMT was used with the cod end tied off.

Depths of collection were estimated by triangulation from length of wire and wire angle by use of a hand-held inclinometer. All organisms were preserved in 10% formalin and returned to the laboratory for sorting, identification, and analysis. All fishes were identified by the authors. The invertebrates have not been identified as to species at this time, but they were sorted at the Smithsonian Oceanographic Sorting Center into six major groups: chaetognaths, pteropods, copepods, amphipods, euphausiids, and carideans.

A Gifft Depth Recorder was operated continuously, providing a record of the acoustic returns at 12 kHz. Standard hydrographic casts were taken at each station, providing measurements of temperature, salinity, dissolved oxygen, and selected nutrients in the water.

The specimens of *Benthosema glaciale* examined for swimbladder morphology ranged in size from 19.5 mm standard length (SL) to 64 mm SL. They were dissected under a binocular microscope, and measurements were made of the major and minor axes of the swimbladder. The swimbladders were then removed and opened to determine the gas-gland development and amount of fat.

RESULTS

In general, two characteristics of the Norwegian Sea biological collections were evident. First, the number of species was very small, whereas the number of individuals was great; second, among the fishes, relatively few individuals were captured.

Fishes

Almost all the fishes taken were specimens of the myctophid *Benthosema glaciale*. In addition to a few unidentified larvae, single specimens were taken of another myctophid, *Hierops*

arctica, at Station 3; a gonostomatid, *Maurolicus mulleri*, at Station 4; and a cod, *Micromesistius poutassou*, at Station 2A.

Benthosema glaciale was most numerous in the collections at Station 4, the easternmost station. Fewer specimens were taken at Station 3, very few at Station 2A, and none at Station 2, the westernmost station. The results of these collections will be examined and discussed, considering the easternmost station first.

At Station 4, 401 fishes were taken in nine tows, which sampled from the surface to depths of about 85 to 940 m (Fig. 2). Of this total, 390, or about 97%, were *B. glaciale*.

Three tows (T4, T6, and T7) accounted for 351 of the fishes or 87.5% of the total catch. Tows T4 and T7 were nighttime tows, whereas tow T6 was a daytime tow. Tow T4, collected down to a depth of about 300 m, and caught 73 *B. glaciale* and 9 unidentified larvae, giving a concentration of 2 fishes/1000 m^3. Tow T7, which collected down to a depth of about 185 m, caught 110 *B. glaciale*, giving also a concentration of 2 fishes/1000 m^3.

There were three other tows made during the night (T3, T8, and T9). All had much lower fish concentrations, with the two deeper tows having somewhat heavier concentrations than the single shallower tow. These results indicate that the depth of maximum concentration of *B. glaciale* at night is between 185 and 300 m. However, whether all individuals of *B. glaciale* take part in the upward migration is questionable. Tow T8 which sampled down to about 470 m, caught 24 *B. glaciale* giving a concentration of 0.5 fishes/1000 m^3, which is intermediate between the three tows with heavy concentrations and the other tows. There are two possible explanations why so many fishes were found in this collection after *B. glaciale* had migrated up to the nighttime level. The distribution of *B. glaciale* could be very patchy and, by chance, dense patches were sampled as the open-net haul went through the depth of maximum concentration on setting and retrieving the net. Alternatively, only a portion of the fishes may have migrated upward, leaving some at the daytime depths.

There were four tows taken during the day (T1, T2, T5, and T6). During tow T6, which collected down to a depth of about 500 m, 159 *B. glaciale* were taken, giving a concentration of 3 fishes/1000 m^3. Two of the other daytime tows sampled shallower than tow T6, and the third tow sampled deeper. They all had much lower fish concentrations, but, again, the deeper haul had more fishes than either of the shallower hauls. The indication is that *B. glaciale* seems to be concentrated at a depth of approximately 500 m during the day.

At Station 3, there were only 113 fishes taken in a total of 12 tows, sampling from the surface to depths of about 25 to 1350 m (Fig. 3). This is only about 28% of the fishes taken at Station 4 in 30% more towing time. Of the 113 fishes, 111 or more than 98% were *B. glaciale*, one was another myctophid *Hierops arctica* and one was an unidentified larval fish. The situation for *B. glaciale* at Station 3 was similar to that found at Station 4 in that 103 of the 111 fishes (about 93%) were taken in only three tows (T1, T7, and T9). Tows T1 and T7 were daytime tows, while T9 was a nighttime tow. Tow T9, collected from 0140 to 0405 hours down to a depth of about 275 m and caught 25 *B. glaciale* and one unidentified larval fish, giving a concentration of 0.6 fishes/1000 m^3. There were three other tows (T3, T4, and T8) taken during the night; one shallower, one at comparable depth, and one deeper than T9. All three had much lower concentrations of fishes than T9, with the deepest tow (T8) having the highest concentration. Tow T1 collected down to a depth of about 500 m and caught 23 *B. glaciale* and one *Hierops arctica*, giving a concentration of 0.5 fishes/1000 m^3. Tow T7 collected down to a depth of about 500 m from 1515 to 1900 hours and caught 53 *B. glaciale*, giving a concentration of 0.8 fishes/1000 m^3. There were four other daytime tows taken, one shallower and the other three deeper than T7. All four had much lower concentrations than the two tows of 500 m.

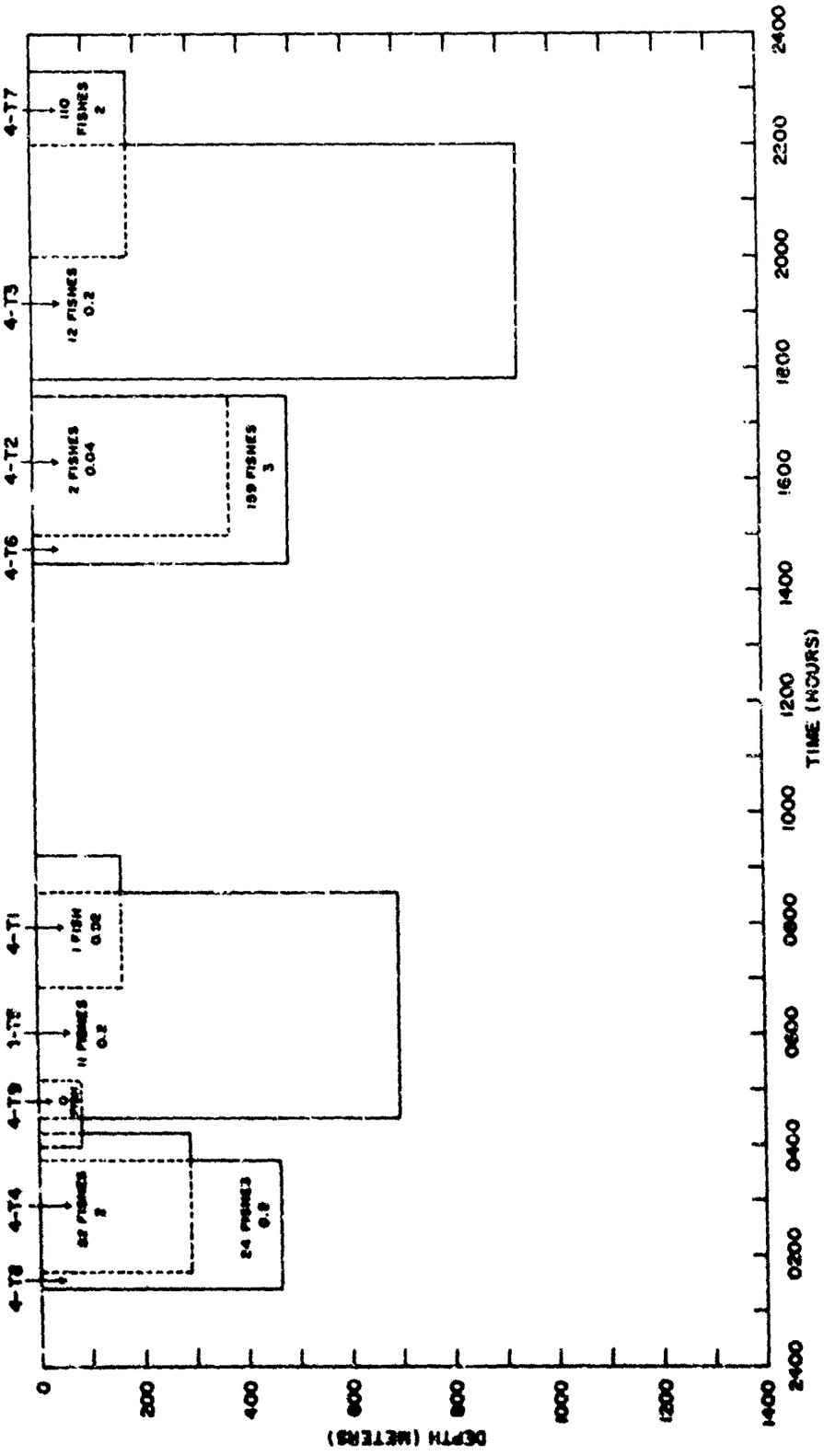

Figure 2. Diagrammatic representation of nci hauls at Station 4 showing number of fishes in each haul and calculated concentration of fishes per 1000 m^3 of water sampled

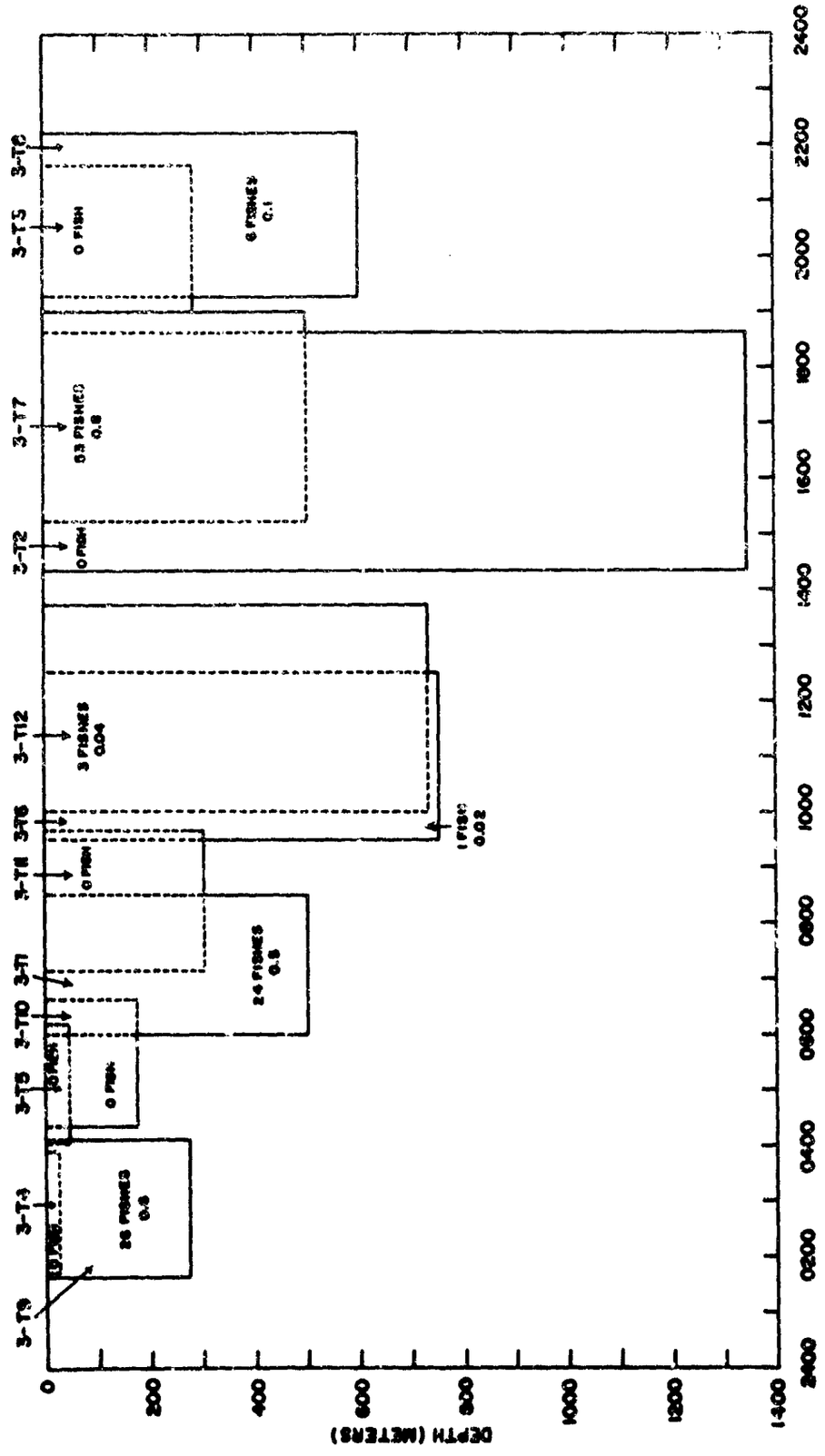

Figure 3. Diagrammatic representation of net hauls at Station 3 showing number of fishes in each haul and calculated concentration of fishes per 1000 m^3 of water sampled

These collections indicate that the maximum concentration of *B. glaciale* at Station 3 is at a depth of about 275 m at night and 500 m during the day, which fits the pattern seen at Station 4.

At Station 2A, in 11 tows which sampled from the surface down to depths of from 15 to 1160 m (Fig. 4), only 6 fishes were taken, 5 of which were *B. glaciale*. The only other fish caught was a cod, *Micromesistius poutassou*. It was taken in tow T1, which sampled from the surface to about 25 m, and was the only fish caught during the night. There were four nighttime tows (T1, T6, T7, and T8), with the deepest going to a depth of only 40 m.

While there were five daytime tows (T3, T4, T9, T10, and T11), only two caught any fishes. Tow T10 sampled from the surface to a depth of about 387 m and caught 4 *B. glaciale*, giving a concentration of 0.1 fishes/1000 m^3. This was much shallower than the depth at which *B. glaciale* was found during the day at Stations 3 and 4. The only other fish caught in daytime was a single specimen of *B. glaciale* taken during T11.

There were seven tows made at Station 2, two at night and the other five during the day (Fig. 5). Even though the water column was sampled down to a depth of about 500 m, no fishes were taken during the day or night.

Zooplankton

Euphausiids–Because of their abundance and ubiquitous occurrence the distribution of the euphausiids can be examined in some detail.

Two of the daytime hauls at Station 4 (Fig. 2) had notably heavier concentrations of euphausiids. Tow 4-T2 with a concentration of 100/1000 m^3 and tow 4-T6 with a concentration of 50/1000 m_3 indicate a possible daytime depth of occurrence between 380 m and 500 m.

Two of the daytime hauls at Station 3 (Fig. 3) also had somewhat heavier concentrations of euphausiids: 3-T1 and 3-T7 with 50 and 40/1000 m^3, respectively, indicate a daytime depth of occurrence at about 500 m and agree with the situation at Station 4. All the other daytime tows made at Stations 3 and 4 sampled much lower concentrations of euphausiids, ranging from none to 20/1000 m^3.

All daytime tows at Station 2A showed concentrations ranging from none to 10/1000 m^3 except tow T10 (Fig. 4), which had a somewhat heavier concentration: 30/1000 m^3. This sampling depth of 390 m agrees with the depth of maximum concentration seen at Stations 3 and 4.

At Station 2, two chambers from tow T4 showed euphausiid concentrations of 60 and 100/1000 m^3, and sampled between 400 m and 550 m. These depths agree with those of maximum daytime concentrations at the other stations. However, chamber A from tow T3, sampling at around 100 m, had a concentration of 50/1000 m^3, suggesting a possibly shallower daytime depth of occurrence at this station. The oblique hauls to the surface showed concentrations ranging from 6 to 1200/1000 m^3, suggesting patchiness in the near surface waters.

Nighttime hauls were made at Stations 2A, 3, and 4. Virtually all hauls had moderate concentrations of euphausiids ranging from 5 to 20/1000 m^3. Only tow T3 at Station 3 had a slightly greater concentration: 30/1000 m^3. Thus, our collections give little indication of nighttime depth of concentration for euphausiids.

Chaetognaths–These were the most abundant invertebrates represented in our collections. However, large numbers were caught in the mesh near the cod end of the net. Thus, the data from the closing net samples at Station 2 were not reliable and had to be treated as open-net hauls with the data from the different subsamples of each haul lumped together.

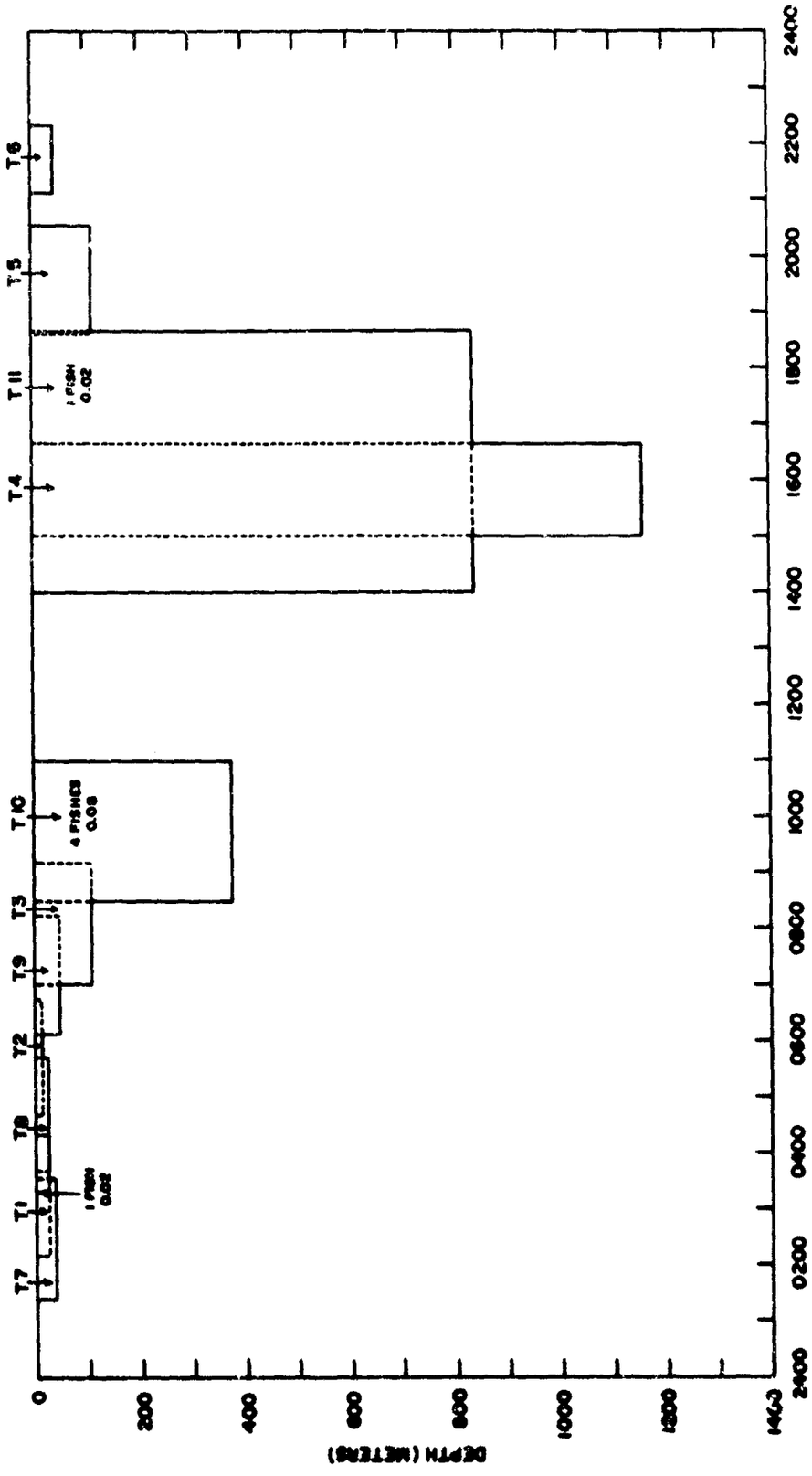

Figure 4. Diagrammatic representation of net hauls at Station 2A showing number of fishes in each haul and calculated concentration of fishes per 1000 m^3 of water sampled

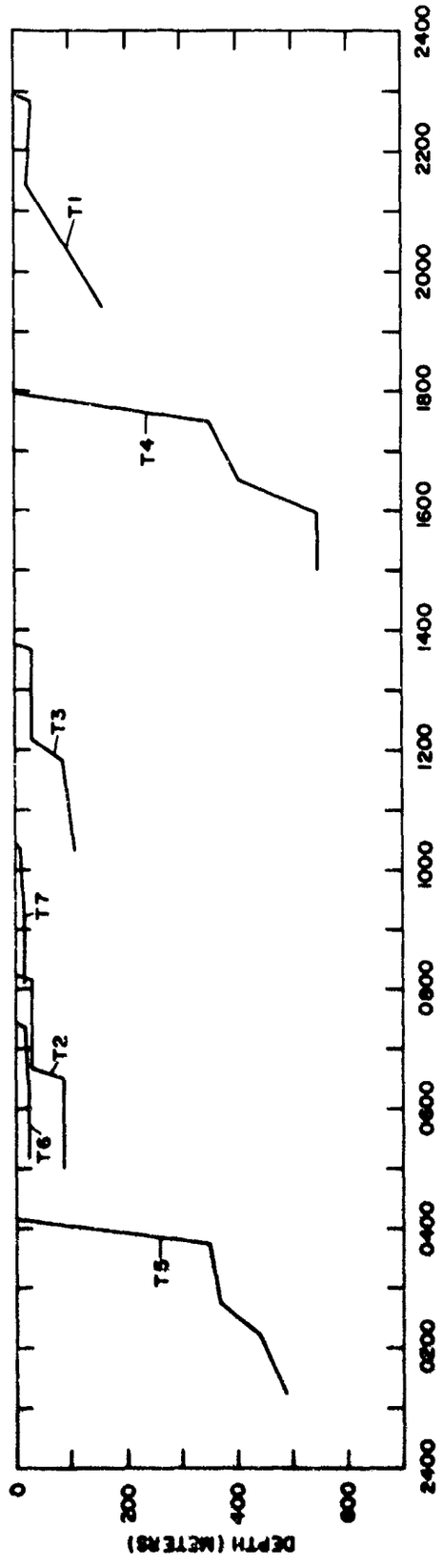

Figure 5. Diagrammatic representation of towpaths of net hauls at Station 2

Chaetognaths were particularly abundant in the deeper hauls at all stations. At Station 4 (Fig. 2) hauls deeper than 350 m contained concentrations of 100 to 200/1000 m^3. At Station 3 (Fig. 3), hauls deeper than about 250 m contained concentrations of 90 to 200/1000 m^3. At both stations, the shallower hauls showed concentrations ranging from 5 to 60/1000 m^3. At Station 2A (Fig. 4) all hauls contained concentrations of at least 80/1000 m^3 while the two hauls deeper than 400 m contained concentrations of 300 and 400/1000 m^3. At Station 2 (Fig. 5), the two deep hauls contained concentrations that ranged from 60 to 300/1000 m^3.

These collections indicate that chaetognaths are more abundant at the westernmost stations and in the deeper hauls. They also suggest that the distribution of chaetognaths may be patchy, especially at shallower depths.

Pteropods–The only large concentrations of pteropods encountered were in some of the oblique tows to the surface at Station 2 (Fig. 5) where the concentrations ranged from 6 to 300/1000 m^3. At Station 2A (Fig. 4), those tows sampling from the surface down to about 50 m contained concentrations ranging from 1 to 20/1000 m^3. All other tows at Stations 2 and 2A as well as all tows at Stations 3 and 4 had lower concentrations, ranging from none to 10/1000 m^3.

The numbers of pteropods in the collections from Stations 3 and 4 are too sparse to indicate anything definite about their distribution at those stations. However, from the collections made at Stations 2 and 2A it appears that the pteropods there may be distributed in dense patches very near the surface.

Copepods–In general, at all four stations the copepods showed some heavy concentrations in two layers, one from the surface to 200 m and one between 700 and 1300 m. In between these depths, only small or intermediate concentrations were encountered. The collections in the shallow layer, above 200 m, had concentrations ranging from none to 400/1000 m^3, whereas those in the deeper layer showed concentrations ranging from 1 to 20/1000 m^3, with two exceptions at Station 2 that collected between 350 and 550 m. There, chamber B in tow T4 and chamber B in tow T5 contained the somewhat greater concentrations of 30 and 50/1000 m^3, respectively.

The pattern from our collections suggests that the copepods may be concentrated in patches at shallow depths (less than 200 m) and at deeper depths (perhaps 700 m to 1300 m).

Amphipods–Amphipods were generally found in moderate abundance in those tows that reached around 400 m or deeper at all four stations, their concentrations ranging from 3 to 20/1000 m^3. At Stations 2A, 3 and 4 the tows shallower than 400 m contained very few amphipods except one nighttime haul at Station 3, T9, which contained 20/1000 m^3, suggesting a possible shallower nighttime concentation.

At Station 2, the oblique hauls near the surface contained concentrations ranging from 6 to 100/1000 m^3, suggesting that amphipods may occur in rather dense patches near the surface at Station 2.

Carideans–Larger concentrations of caridean shrimps occurred only in those collections that sampled below 600 m. At Stations 2A, 3 and 4 the concentrations of carideans in the hauls that reached 600 m or deeper ranged from 2 to 10/1000 m^3. Concentrations in the shallower hauls ranged from none to 1/1000 m^3. No carideans were caught at Station 2 where the deepest haul reached 550 m.

Scattering Layers

Echo-sounder data obtained using the Gifft Depth Recorder were examined in detail. The records from Stations 4 and 3 show two layers (Figs. 6 and 7): a deep diffuse layer centered at

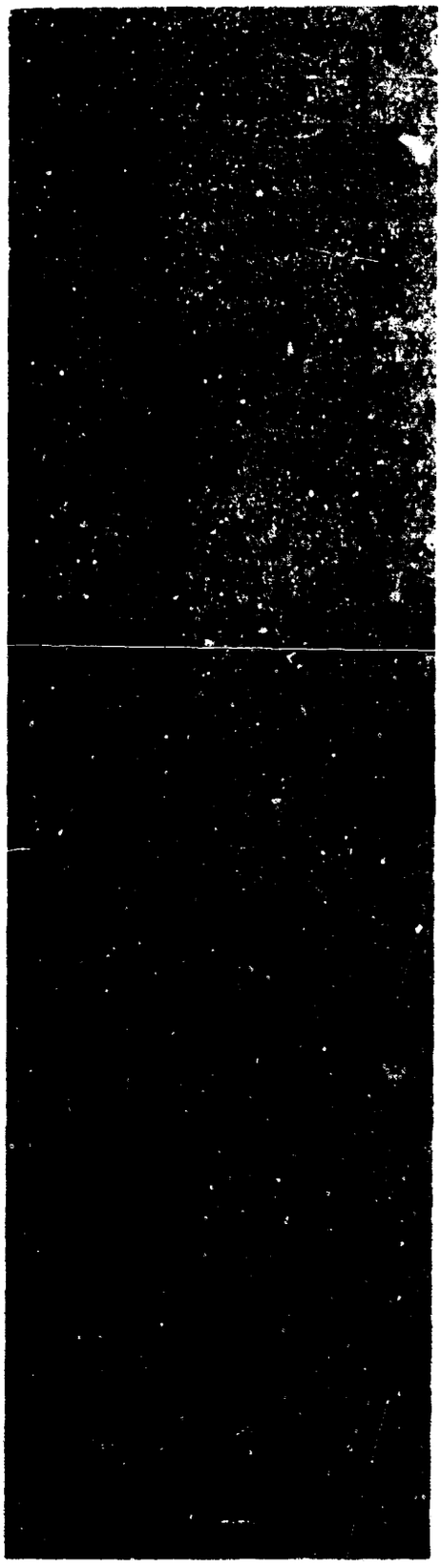

Figure 6. Schematic representation of 12-kHz echo-sounder record at Station 4

Figure 7. Schematic representation of 12-kHz echo-sounder record at Station 3

around 225 m during the day and near the surface at night, and shallower discrete echoes that tended to coalesce into a solid layer at about 200 m during the day and 25 to 50 m at night. Both layers migrated over the sunrise and sunset periods. The layers at the two stations differ in that the shallow layer is somewhat less continuous at Station 3. The scattering layer records from Stations 2 and 2A show few similarities to those from the other two stations. There is no deeper diffuse layer at either Station 2 or 2A. The discrete echoes that do occur at Station 2A (Fig. 8) are sparser and have less tendency to form a solid layer. They are recorded as a 50-m wide band centered at a depth of about 100 m and show no sign of any migrating activity. The discrete echo pattern at Station 2 is similar, but the echoes are even sparser than those at Station 2A and are shallower, being centered at 30 to 40 m depth.

Chemistry

Oxygen and nutrients were in plentiful supply throughout the water column at each station. No correlation was seen between the vertical distribution of organisms taken in our hauls and the oxygen and nutrient concentrations.

Swimbladder Morphology of *Benthosema glaciale*

Examination of the swimbladder of *Benthosema glaciale* showed that at about 20 mm SL (Fig. 9A) the swimbladder measures about 2.5 X 0.75 mm, and no fatty tissue can be seen associated with it. At this size, the gas gland is a thin layer that covers almost the entire inner surface of the swimbladder. By the time *B. glaciale* has attained a length of 30 mm (Fig. 9B), the swimbladder has increased in size to about 4 X 1.5 mm. The anterior part of the swimbladder containing the three retia mirabilia has become completely invested with fatty tissue and some patches can be seen extending posteriorly along the ventral surface of the organ. The gas gland has increased in volume, forming a thicker layer over the inner swimbladder wall. At about 40 mm SL (Fig. 9C) the swimbladder size is about the same, but the fatty tissue and gas gland have continued to increase in volume. Adipose tissue completely surrounds the swimbladder and extends ventrally in two large lobes that run the entire length of the swimbladder. The gas gland has also increased in volume and occupies all but a small lumen at the posterior end of the organ. At this stage, adipose tissue development associated with the organ seems to stop and the gas gland volume increase levels off until *B. glaciale* has grown in size to over 50 mm SL. Then, the swimbladder increases slowly in length while the gas gland starts to regress with a net effect of an increase in the size of the lumen. When *B. glaciale* has attained a size of about 55 mm SL (Fig. 9D), there is a small lumen that extends throughout the posterior two-thirds of the organ. This is formed by a combination of an increase in the swimbladder size to about 5 X 1.5 mm and some decrease in the volume of the gas gland. By 60 mm SL (Fig. 9E) the gas gland appears only as a thickened layer investing the inner walls of the organ leaving a lumen the entire length of the swimbladder. At 64 mm SL which is the maximum size for *B. glaciale* taken during our net hauls in the Norwegian Sea, the swimbladder size has increased to 5.5 X 1.5 mm, but no difference can be seen in the lumen size as compared with that at 60 mm SL.

Size Distribution and Age Groups of *Benthosema glaciale*

An investigation of our material concerning the size distribution of *B. glaciale* indicates peaks of abundance for specimens of approximately 30, 40, 50, and perhaps 60 mm SL (Fig. 10). Johnsen (1945, p. 51) had limited material collected in the summer from the Norwegian Sea and

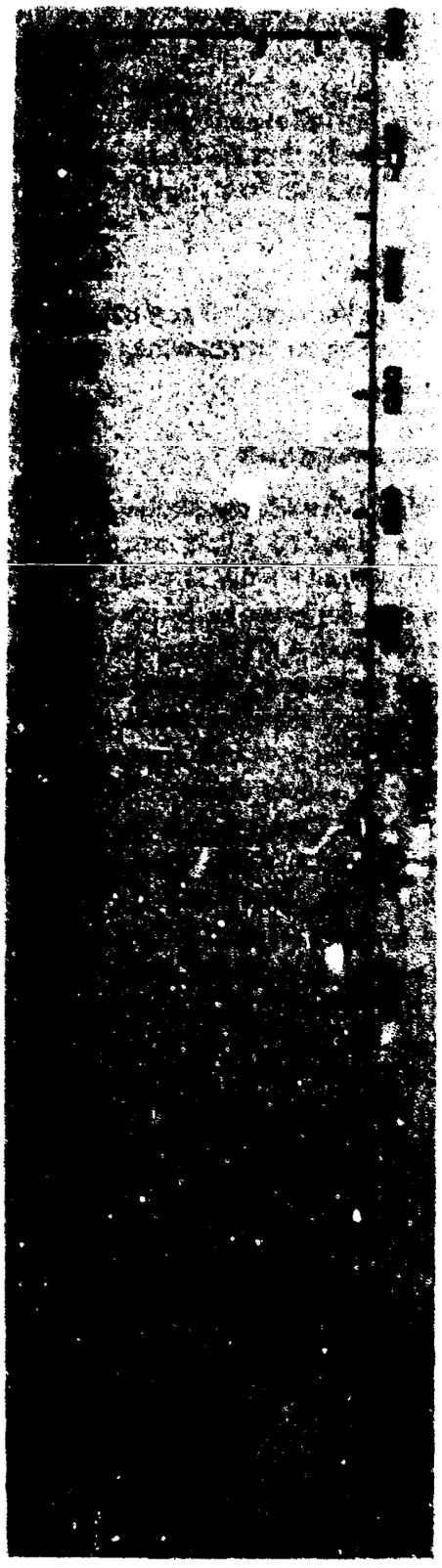

Figure 8. Schematic representation of 12-kHz echo-sounder record at Station 2A

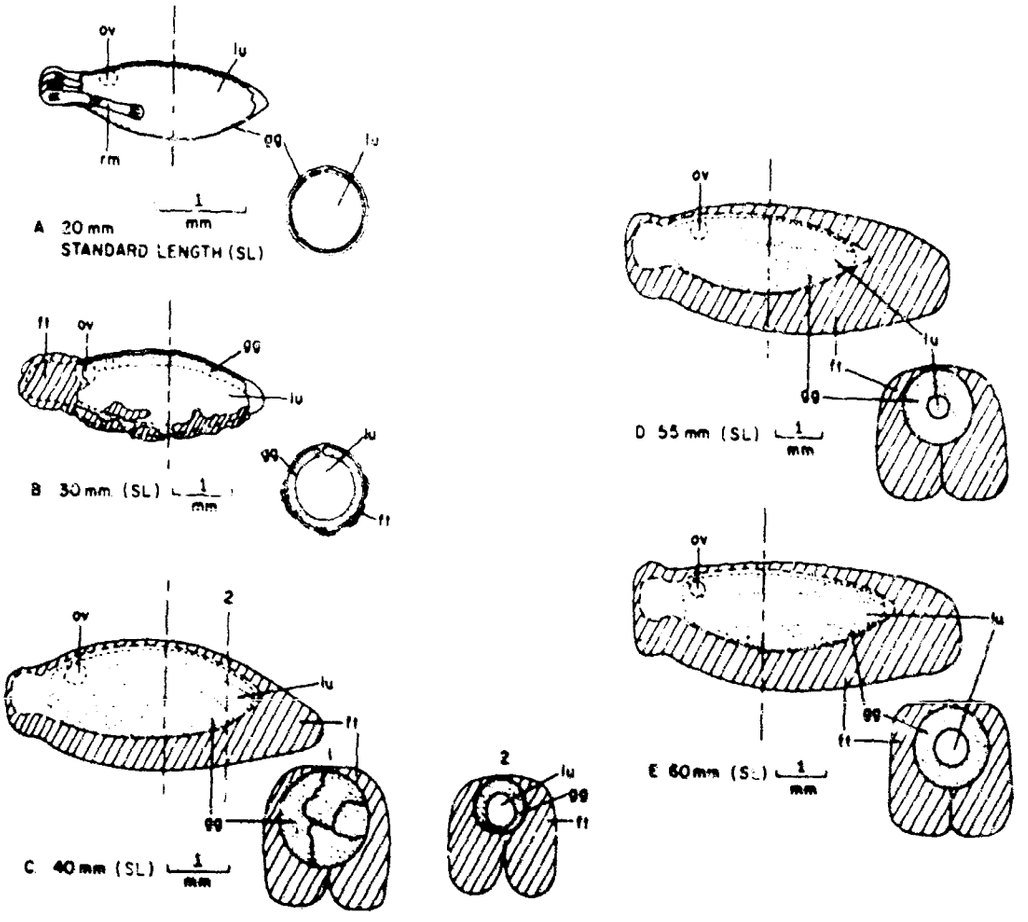

Figure 9. Schematic representation of the growth stages in *Benthosema glaciale* swimbladders showing lateral and cross-sectional views. Labeling is as follows: ov, oval; rm, rete mirabile; gg, gas gland; lu, lumen; ft, fat.

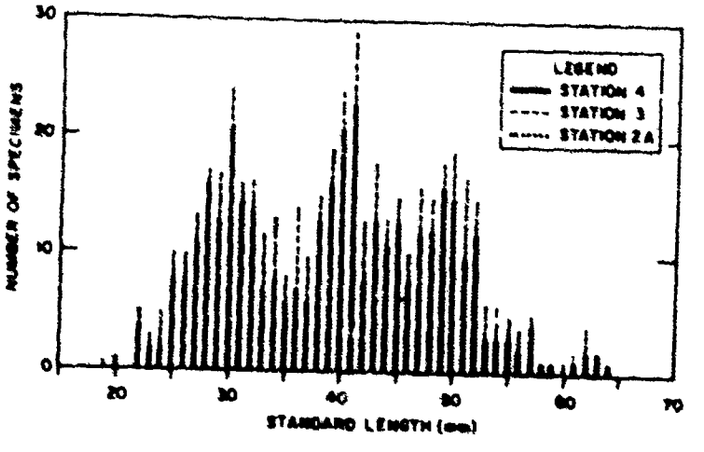

Figure 10. Size distribution of specimens of *Benthosema glaciale* from the Norwegian Sea, August 1967

adjacent waters showing peaks of abundance at approximately 25, 50, and 70 mm, which he regarded as age groups I, II, and III. Halliday (1970) divided extensive material from the northwestern Atlantic into year classes based on the number of transparent rings in the otoliths. For material collected in July 1968, he found the mean lengths of the first, second, and third-year classes to be 33.5, 44.3, and 48.9 mm, respectively. Otoliths from our material in the Norwegian Sea were found to be in good condition. Those specimens examined that were around 30 mm SL belonged to age group I, those around 40 mm belonged to age group II, and those around 50 mm belonged to age group III. However, the largest specimens examined, around 60 to 64 mm, could not be placed in age group IV with certainty. Nevertheless, our peaks of abundance more closely resemble those of Halliday than of Johnsen.

In the Norwegian Sea, Johnsen (1945) considered a few individuals in his age group II (peak at around 52 mm) and probably all in his age group III (65-75 mm) to represent mature adults. In the Atlantic he considered his age group II (peak at around 52 mm) to represent mature adults. Halliday reported that some females spawn at two years while all spawn at three years and older (greater than around 38 mm). None of our examined specimens show well-developed gonads, nor could they be expected to if they spawn in the spring, as Halliday found in the northwest Atlantic. Johnsen reported that breeding occurs in the fjords along the coast of Norway and widely in the North Atlantic, perhaps including the Faeroe Channel. It is not known whether the population in the open Norwegian Sea is a breeding population or expatriates maintained by the influx of individuals from the fjords and Faeroe Channel.

DISCUSSION

Oceanography

The oceanography of the Norwegian Sea is complex (Alekseev and Istoshin, 1959; Metcalf, 1960; and Stefansson, 1962). The Norwegian Sea south of Jan Mayen Island is divided by the Iceland-Jan Mayen Ridge into the Icelandic Basin in the west and Norwegian Basin in the east. Although the two basins are connected across a deep sill, they are very different oceanographically in the upper layers. The Norwegian Basin is dominated by a large cyclonic eddy made up of North Atlantic Water that flows over the Wyville Thompson Ridge between the Faeroe and Shetland Islands. The Icelandic Basin on the other hand, is dominated by Arctic Intermediate Water that flows from the north (Hunger, unpublished data).

Fishes

Many investigators, including Murray (1886), have pointed out the depauperate nature of the Norwegian Sea deep-sea fauna compared with that of the adjacent North Atlantic. The Wyville Thompson Ridge with a sill depth of only about 500 m, acts as a barrier to the movement of Atlantic deep-sea organisms into the Norwegian Sea. The "Michael Sars" North Atlantic Deep Sea Expedition of 1910 collected biological material at one station south of the ridge (Station 101) and one station just north of the ridge (Station 102). At all depths, the collections made at Station 101 closely resembled those made further south and west in the Atlantic. However, at Station 102 just to the north of the ridge, tows were made at 50, 100, 150, 200, 300, 500, 700, and 750 m and no specimens of deep-living Atlantic organisms were taken. Comparing the faunas at these two stations, Murray and Hjort (1912, p. 126) found that only 48 species out of a total of 433, or about 11%, were common to both sides. Among the fishes, about 13% of the species were common to both sides. An examination of the various published "Michael Sars"

Expedition reports dealing with midwater fishes reveals that only one 11-mm specimen of *Maurolicus mulleri* and eight specimens of *Benthosema glaciale* were taken at Station 102. However, a few other Atlantic midwater fish have been recorded along the Norwegian coast.

Murray and Hjort (1912, p. 643) give a list of Atlantic forms found in Norwegian waters, along with their relative frequency of occurrence and point out that most are rare visitors seldom found in great numbers. Among the midwater fishes mentioned are *Myctophum glaciale* (= *Benthosema glaciale*), *Myctophum elongatum* [= *Notoscopelus kroyeri* (see Bolin, 1959, p. 40)], *Argyropelecus olfersi*, *A. aculeatus*, *A. hemigymnus*, and *Nerophis aequoreus*. They also state that "only *Myctophum glaciale* and *Nerophis* were observed" in the large amount of work done by the "Michael Sars" in the Norwegian Sea prior to the 1910 expedition. Johnsen (1923, 1945) reported on numerous specimens of *B. glaciale* from the Norwegian Sea, and Becker (1967) discussed the results of one station made by the *Peter Lebedev* at 68°30′ N, 6° W which was near our Station 2A. He reported that 58 specimens of *B. glaciale* and one *Lampanyctus macdonaldi* were taken in five hauls. In light of these previous findings it is not surprising that our collections from the Norwegian Sea contained so few of the Atlantic midwater fishes, but it is somewhat surprising that they contained such large numbers of *B. glaciale*.

B. glaciale in the Norwegian Sea appears to be confined to the upper layers comprised of a mixture of two water masses, Arctic Intermediate Water and varying amounts of North Atlantic Water. Our collections indicate that *B. glaciale* may not occur in the colder and less saline Arctic Bottom Water. At Station 2A, the Arctic Bottom Water was found at a depth of about 400 m (Hunger, unpublished data) whereas the maximum daytime collection of *B. glaciale* was taken in a tow from the surface to a depth of 387 m. At Station 3, the Arctic Bottom Water was deeper, occurring at about 750 m, while at Station 4 it was found at about 650 m. At both Stations 3 and 4, *B. glaciale* was found concentrated at around a 500-m depth during the day and at 185 to 300 m at night, well within the mixed North Atlantic and Arctic Intermediate Waters. This agrees well with Johnsen (1923, p. 14), who regarded the depth of occurrence of *B. glaciale* in the open Atlantic to be from the surface in the daytime to about 500 m. Johnsen also noted (ibid., p. 18) the correlation of frequent catches of this species with the presence of water of Atlantic origin.

Zooplankton

In actual numbers of individuals, most of the invertebrates tended to be more abundant at the shallower tows of the westernmost stations than at any of the tows of the easternmost stations.

There is an indication that some of the invertebrates are also limited to the same water masses as *Benthosema*. In particular, the euphausiids fit this pattern, with abundances at depths of 500 m or less at Stations 3 and 4 and less than 400 m at Station 2A. On the other hand, the distribution of the carideans indicates that they may be excluded from these water masses and confined to the Arctic Bottom Water.

The distribution patterns of the other invertebrates that were studied are more complex. All suggest that patchiness may be a factor, especially dense patches near the surface for the chaetognaths, pteropods, and amphipods. Furthermore, it is likely that several species are to be found in each of the major groups of invertebrates studied. Differing ecological requirements reflected by various distribution patterns within a single group could easily account for some of the complexities observed. This is particularly prominent in the distribution pattern shown by the copepods: higher abundances in those tows that sampled the Arctic Bottom Water as well as in some of the shallow, near-surface tows.

Scattering Layers

The depths of the 12-kHz scattering layers seen on the echo sounder did not correlate with the depths of maximum concentration for *Benthosema* nor with the distribution patterns found in those invertebrates examined. The diffuse echo returns prominent at Stations 3 and 4 may have been caused by small organisms, but the patterns of discrete echo returns probably represent sound scatterers of a much larger size than *Benthosema* or the invertebrates studied. There are several possible sound scatterers that occur in sufficient numbers in the Norwegian Sea to account for this pattern. The single specimen of the gadid fish *Micromesistius poutassou* that was caught at Station 2A confirms their presence in the area, suggesting that this species may account for at least some of these discrete echoes. *Micromesistius* is abundant enough in the Norwegian Sea that a commercial fishery has developed for them (Zilanov and Salnikova, 1967). Perhaps of equal or greater importance are the schools of herring that are found in the Norwegian Sea in the summer (Marty, 1956). The herring schools concentrate to feed in this region and consist of fairly large fishes from 23 to 35 cm in length (Marty, 1958). That the herring schools gather near the edge of the cold Arctic water (sometimes called the Polar Front) is well known to Icelandic fishermen who depend on this fact to exploit the stock with good yields per unit effort (G. B. Farquhar, personal communication). As Berge (1958) has pointed out, there is a good correlation between the feeding area of the herring in summer and the area of highest productivity.

Productivity

In common with other boreal waters, the Norwegian Sea is a region of high primary productivity. Using Steeman Nielsen's Carbon 14 method, Berge (ibid.) found the primary production to be 0.8 to 1.8 g C/m^2/day in the central Norwegian Sea based on measurements in May and June. Most of his measurements outside this high productivity area still indicated a productivity of 0.4 g C/m^2/day or greater.

Our measurements did not include primary productivity and although the relationship between primary productivity and standing crop is problematical, the quantity of material in our biological collections was abundant enough to be consistent with the concept that the Norwegian Sea is a region of high productivity. Undoubtedly, a great deal of the primary productivity in this region is converted to herring, *Micromesistius*, and other large fishes, all unavailable to us because of the small size of our midwater net.

An intensive survey of the area is needed to better understand the biological conditions in the Norwegian Sea. Such a survey should include a sampling program over all four seasons and should use larger and more sophisticated nets which the larger fishes, such as the herring and *Micromesistius*, could not avoid.

CONCLUSIONS

Examination of 12-kHz echo-sounder records from the Norwegian Sea showed that there were two layers at Stations 3 and 4 in the eastern portion with both layers showing evidence of migration over the sunrise and sunset periods. At Stations 2 and 2A in the western portion, only one layer was found which showed no evidence of migration over sunrise and sunset. No correlation was noted between the echo-sounder records and the distribution of organisms.

The deep midwater fish fauna of the Norwegian Sea consists almost exclusively of the myctophid *Benthosema glaciale*. Larger, commercially valuable fishes, including herring, also occur in the midwaters, probably at shallow depths.

Specimens of *Benthosema glaciale* were most numerous in the eastern part of the Norwegian Sea, with a center of occurrence at a depth of about 500 m in the daytime and 185 to 300 m at night.

Investigations of swimbladder morphology of *Benthosema glaciale* indicated that as individuals increase in size, the swimbladder becomes invested with fatty tissue. Because of enlargement of the gas gland, the lumen decreases in volume to a minimum in 40-50 mm (SL) individuals. The lumen then was found to be somewhat larger in the largest fish examined.

Our collections of *B. glaciale* showed peaks of abundance at Standard Lengths of approximately 30, 40, 50, and possibly 60 mm, whereas investigations of otoliths indicated the presence of year classes I through III and possibly IV.

In general, the invertebrates were more abundant in the shallower hauls at the western stations than in those at the eastern stations in the Norwegian Sea.

No correlation was noted between the distribution of organisms and the vertical distribution of nutrients, although *B. glaciale* and perhaps the euphausiids seemed to be excluded from the cold Arctic Bottom Water and restricted to waters that have some admixture of North Atlantic Water. In contrast, the carideans seemed to be restricted to the Arctic Bottom Water. The other invertebrates examined showed more complex distribution patterns, probably reflecting patchiness as well as the effects of the combined distributions of two or more species of differing ecological requirements.

ACKNOWLEDGMENTS

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APPENDIX I

FISHES CAUGHT IN THE NORWEGIAN SEA

Salmoniformes
Gonostomatidae
Maurolicus mulleri (Gmelin, 1788). 4-T1 (1, 16 mm).

Myctophidae
Hierops arctica (Lutken, 1891). 3-T1 (1, 34 mm).
Benthosema glaciale (Reinhardt, 1837). 2A-T10 (4, 22 to 46 mm), 2A-T11 (1, 46.5 mm), 3-T1 (23, 26 to 61.5 mm), 3-T6 (1, 62 mm), 3-T7 (53, 20 to 63 mm), 3-T8 (6, 35 to 55 mm), 3-T9 (25, 25 to 63.5 mm), 3-T12 (3, 42 to 56 mm), 4-T2 (1, 30 mm), 4-T3 (12, 27 to 55 mm), 4-T4 (73, 27 to 65 mm), 4-T5 (11, 31 to 62 mm), 4-T6 (159, 23 to 57 mm), 4-T7 (110, 25 to 62 mm), 4-T8 (24, 22 to 65 mm).

Gadiformes
Gadidae
Micromesistius poutassou (Gill, 1863). 2A-T1 (1, 262 mm).
Gaidropsaras argentatus (Reinhardt, 1838)
Found on deck, 65°10′ N, 00°04′ E (1, 37 mm).

DISCUSSION

Hersey: As an acoustician I would appreciate it, and I suspect others would also, if the authors could identify the part of the organ that is likely to be filled with gas.

Pugh: If a gas bubble were present, it would be found in the lumen. The lumen is the area labelled "lu.", as can be seen on the cross sections in Fig. 9. The lumen is not necessarily filled with gas, but may be partially or completely filled with an amorphous cottony tissue outgrowth of the gas gland.

Alexander: Have you any information on the chemical nature or specific gravity of the fat?

Pugh: No.

Alexander: And the histological nature of the gas gland?

Pugh: We have not done any histological studies on swimbladders. However, Marshall has done extensive work on swimbladders including the histology. He could better answer your question.

Marshall: What is the specific question?

Alexander: What is the histological nature of this very much enlarged gas gland?

Marshall: It looks very much like any gas gland. Gland cells in the myctophids are usually quite small.

D'Aoust: I am naturally delighted to see another report of the fat surrounding the bladder as the fish gets older. It is speculation, but I think it could be interpreted as a diffusion barrier. One other point—did you notice an oval in these fish? Specifically, was there a resorptive area differentiated from the gas gland?

Pugh: The oval could be seen at the anterior end of the swimbladder where its position was represented schematically by a dotted circle (ov.).

Ebeling: I will comment on the composition of fat associated with swimbladders. Dr. Judd Nevenzel analyzed the fat that invests swimbladders of *Triphoturus mexicanas*, *Diaphus theta*, and other California Current lanterfishes and found that a relatively large proportion was composed of wax esters of relatively low density. Perhaps such low-density fats invest the swimbladders of many other lanternfishes.

Barham: I do not believe he took them directly from the swimbladder; he pooled the analysis of lipids by whole fish, muscle, and viscera and did not get values for the swimbladder itself.

(NOTE: It was later determined that Barham is correct.)

SCATTERING LAYERS AND VERTICAL DISTRIBUTION OF OCEANIC ANIMALS OFF OREGON

William G. Pearcy and Roderick S. Mesecar
Department of Oceanography, Oregon State University
Corvallis, Oregon

ABSTRACT

This paper reviews some of the distributional features of vertically migrating micronekton off Oregon; describes a new, conducting-cable, midwater-trawl system using an eight-net, opening-closing cod-end unit; and gives some preliminary results on trawl catches relative to sound-scattering layers.

A variable complex of organisms, including euphausiids, a sergestid shrimp, and mesopelagic fishes, was often common in 12- and 38.5-kHz scattering layers. The depth range of many species was broad, and sometimes the largest catches were made at depths above or below scattering layers. Variability was large among nets that fished either horizontally or vertically during single tows.

DISTRIBUTION OF MESOPELAGIC ORGANISMS OFF OREGON

Only a few species of oceanic micronekton predominate our nighttime-midwater trawl collections in epipelagic waters off Oregon. The lanternfishes *Stenobrachius leucopsarus*, *Diaphus theta*, and *Tarletonbeania crenularis;* the melanostomiatid *Tactostoma macropus;* the sergestid shrimp *Sergestes similis;* and the euphausiid *Euphausia pacifica* are all abundant. All these species (except *T. macropus*) have been correlated with biological sound scattering in other areas (Barham, 1956 and 1963; Kampa and Boden, 1954; Taylor, 1968; Tucker, 1951).

Of the fishes, *Stenobrachius leucopsarus* juveniles (less than 30-mm standard length) have a gas-filled bladder, but the swimbladder of adults is regressed and surrounded by fatty tissue (Capen, 1967; Butler, 1970). We have found gas in the swimbladders or body cavities of some *Diaphus theta* and *Tarletonbeania crenularis;* gas usually occurred in small individuals but was found in individuals larger than 30 mm. All *Hierops (Protomyctophum) crockeri* and *thompsoni* examined at sea had gas-filled swimbladders (Butler, 1970).

Studies with an opening-closing cod-end unit on a 6-foot Isaacs-Kidd midwater trawl (IKMT) provide good evidence for vertical migration of the four common mesopelagic fishes and *Sergestes similis* between broad depth intervals off Oregon. In the upper 150 m, nighttime catches exceeded daytime catches; between 150 and 500 m, daytime exceeded nighttime catches (Pearcy and Forss, 1966; Pearcy and Laurs, 1966). Catches of these species between 500 and 1,000 m were low, and no diel differences were evident. The ratios of night to day catches per m^2 in the water column to 1,000 m for all species were greater than 1.0, indicating avoidance of

the trawl during the daytime. Although only slightly more *Diaphus theta* were collected per m^2 at night, over four times as many *Tarletonbeania crenularis* were caught at night than during the day.

The average size of mesopelagic fishes also varied with depth; individual weight was lower in 0- to 150-m collections than in 150- to 500-m and 500- to 1,000-m collections (Pearcy and Laurs, 1966). These studies also show broad depth ranges for mesopelagic species. During the night, for example, lanternfishes and shrimps were caught at all depths within the upper 1,000 m and were not concentrated solely near the surface. Vertical migrations and distributional patterns *within* these broad depths undoubtedly occur. Pearcy (1964) found that the three common lanternfishes sometimes have different distributions within the upper 100 m at night.

In any quantitative study of pelagic animals, distributional patterns and catch variability are important considerations. Repeated tows during night or day periods suggest patchy or clumped distributions of mesopelagic fishes (Pearcy, 1964; Pearcy and Laurs, 1966). Ebeling, Ibara, Lavenberg, and Rohlf (1970) reported that most mesopelagic fishes off southern California were more clumped at middepths during the day than near the surface during the night. Donaldson (1968) found that the thickness of 38.5-kHz scattering layers was less during the day than at night off Oregon, a trend that suggests that the density of organisms within layers may be higher by day (Taylor, 1968).

The number of scattering-layer organisms may vary seasonally and annually. Significant differences in the number and biomass of midwater animals have been reported off Oregon (Laurs, 1967; Pearcy, 1964, 1965; Pearcy and Forss, 1966; Pearcy and Laurs, 1966; Pearcy and Osterberg, 1967). In oceanic waters over and beyond the continental slope, the highest biomass of small nektonic fishes, squids, and shrimps generally occurred in the summer; the lowest biomass occurred in the winter. Over the outer edge of the shelf, however, the reverse was true. Usually higher catches were made in winter than in summer.

These inshore-offshore and seasonal changes also may be related to changes in size structures of populations. The decrease in biomass in winter offshore catches was correlated with an increased recruitment of small *Stenobrachius leucopsarus*. Small lanternfishes of this species have gas-filled swimbladders, but large individuals do not. The sound-scattering potential offshore, therefore, may be higher during winter than during summer, even though the total micronekton biomass may be lower in winter.

MIDWATER TRAWL SYSTEM

A conducting cable system using a 6-foot IKMT with an eight-bar multiple plankton sampler (MPS) (Bé, 1962; Pearcy and Hubbard, 1964) as an opening-closing cod-end device sampled oceanic animals to 1,000 meters (Fig. 1). Pressure (depth), temperature, flow (revolutions), and net opening were scanned sequentially and transmitted as frequency-modulated (FM) signals from transducers on the IKMT-MPS to recording units on deck.

The electrical system is illustrated in Figure 2 as a block diagram. One hundred fifty milliamperes at 50 volts direct-current is transmitted down the 4,600 m of 11-mm coaxial cable (U.S. Steel Corp.) into the pressure housing on the MPS. This housing contains the net actuator, transducer, and scanning and signal transmission electronics. When a net release button is pushed on shipboard, a polarity reversal of the voltage to the MPS takes place. When the net release button is returned to its normal position, the motor circuit actuates a 2-rpm gear motor for one shaft revolution that opens one net and closes another. Cams located on top of the MPS are coupled directly with the motor shaft in the electronics package. During one motor-shaft revolution, one cam turns 360°, releasing one lever bar that holds the net bar in a cocked position.

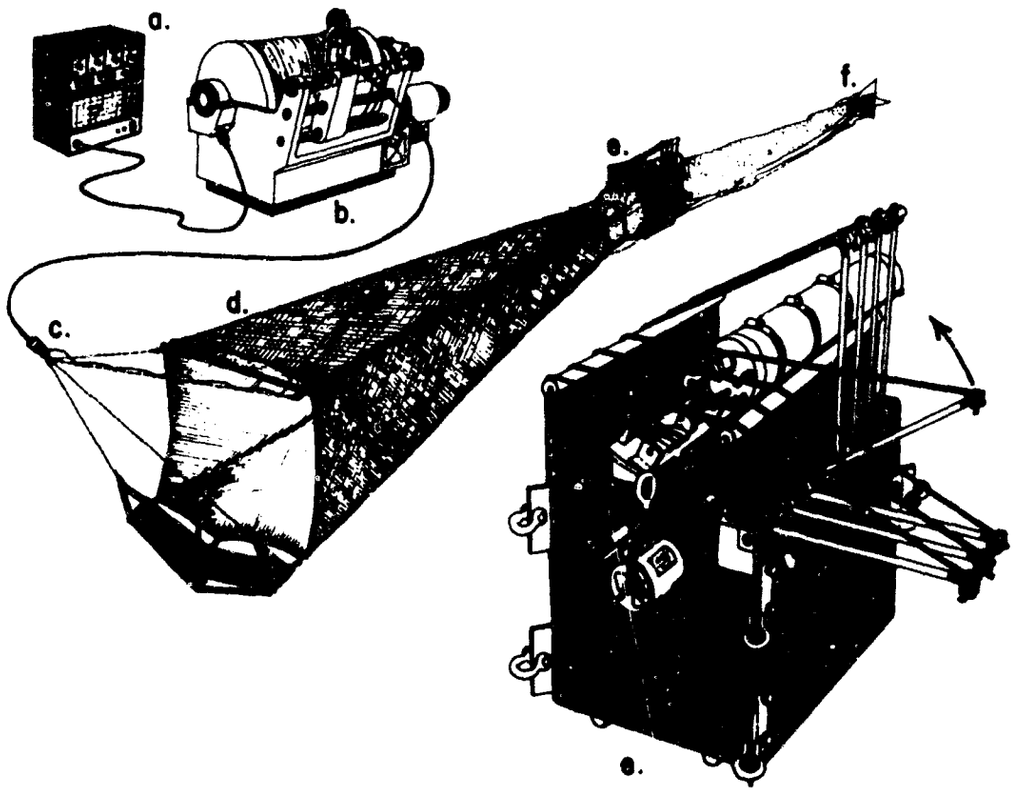

Figure 1. A conceptual drawing of the components of a conducting-cable, midwater-trawl MPS system with the following parts: (a) deck readout recorders, (b) deck winch with slip rings and conducting cable, (c) electric swivel, (d) 6-foot IKMT, (e) eight-bar MPS, and (f) eight sample nets.

This operation is repeated eight times for release of eight nets. During the motor operating period, an FM signal that identifies which net is opened is transmitted to the surface.

Actuation of the net release motor interrupts the automatic scan sequence of the transducer outputs. Between net actuations, the electronic scanner sequentially connects the transducer outputs for discrete periods of time to a voltage-controlled oscillator (VCO) generating FM signals. The VCO output is coupled through an electronic driver stage to the coaxial cable. Signals are displayed aboard ship in two ways: on an analog strip-chart recorder, and on a digital counter. The recorder offers a quick observation of a tow pattern of the trawl. The digital readouts, which are periodically written on the strip-chart record, give the greatest resolution. The maximum resolving capability in the monitoring system is one part in one thousand of transducer output signal.

Depth was monitored with a potentionmetric type Servonic model H-172-5 pressure transducer. The transducer was calibrated in the lab with a temperature-corrected Heise pressure gage. The depth resolution was ± 1 m and was transducer limited.

Water temperature was sensed by a 10-kΩ thermistor (Yellow Springs Instrument Corp.) at 25°C. It was calibrated to ±0.02°C in an ice bath with a Hewlett-Packard quartz thermometer and referenced by a platinum thermometer and Mueller bridge. The thermistor time constant was 1.3 min.

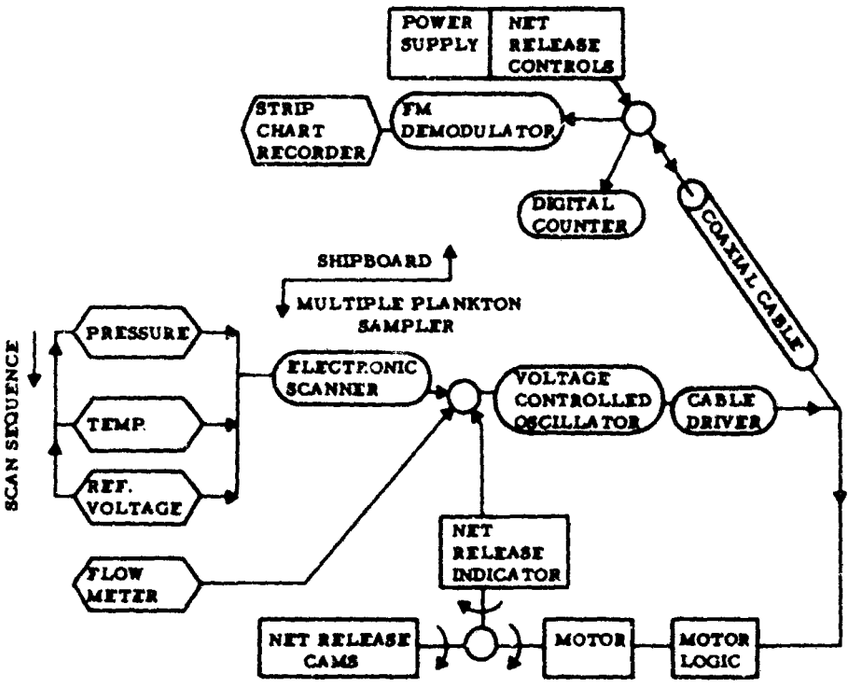

Figure 2. Block diagram of the electronic modules inside the MPS electronics case

A voltage reference was used to excite the pressure and temperature transducers and to act as a figure of merit. This reference is monitored each scan cycle along with the transducer signals. If our reference has changed during a tow, it indicates not only an error in data but an electrical malfunction in the transmitting electronics.

The electronics scanner was set to sense pressure for 20 sec and temperature and reference for 10 sec each. As indicated in Figure 2, however, the flowmeter has a priority to interrupt the scanner at any time. This is because the flowmeter is a revolution counter, recording a signal every 1,000 revolutions of an impellor by causing the VCO input to go to zero. On the strip-chart recorder, the flowmeter signals appear as event marks that interrupt the regular analog records of pressure and temperature.

The MPS box (40 X 40 X 51 cm) is made of 7-mm aluminum and weighs 30 kg complete with the electronic package on top. The MPS nets, 3 m long, are of 0.571-mm Nitex. The liner of the IKMT is 5-mm mesh.

The electrical IKMT-MPS system was used successfully on a cruise from 12 to 18 November 1969. Twenty-six separate tows were made; opening-closing malfunctions occurred on five tows, usually because of human error in resetting the equipment. The flowmeter, mounted inside the MPS box, worked on only eight tows because of a short in the magnetic switch. The flow through the MPS on these eight tows was fairly uniform throughout an entire tow. There was no evidence for closure of the MPS mouth caused by twisting of the net. However, in one case, an interruption in the flow was caused by a squid caught in the impellor.

Catches were calculated on the basis of grams (wet weight) collected per minute. Tow speeds were fairly constant within a single tow and ranged from 3.4 to 4.6 knots among tows. At this speed, a 6-foot IKMT (mouth area of 2.9 m^2) with a filtration efficiency of 85% (Pearcy and

Laurs, 1966) filters about 260 to 350 m^3/min. All tows were beyond the continental slope off central Oregon between latitudes 44°12′ and 44°55′ N and longitudes 125°25′ and 126°05′ W).

When the trawl descended to the maximum tow depth, the first MPS net fished obliquely over a large depth range. Because of this, and the fact that flow rate was usually lower in this net, the first net often was not included in the catch results of all tows.

Two echo sounders were used during this cruise: (1) a 12-kHz Edo model 248 transceiver with a pulse power of 1,400 watts and an Edo 333B recorder and (2) a 38.5-kHz Simrad 510-5 echo sounder with a pulse power of 450 watts. Gain was reduced in surface waters of both recorders to accentuate subsurface scattering layers; hence, surface scattering layers in the upper 36 m usually were not recorded.

SCATTERING LAYER VARIATIONS

The depth and thickness of 12-kHz scattering layers for two diel periods during the cruise are replotted in Figure 3. Variability is pronounced. Layers were recorded within the upper 100 m during both day and night periods. Sometimes these surface layers deepened or shoaled within day or night periods. Migration of layers occurred during twilight periods (sunrise was about 0600 hours; sunset, 1730 hours, local mean time). The descent on 18 November was to greater depths than on 14 November. Ascent toward the surface occurred during midafternoon on both days. Note that a layer descended from the main ascending migratory layer at about 1800 hours on 18 November; it migrated downward to about 400 m, but then ascended to rejoin the main layer at 2400 hours. This descent of a secondary layer from a main ascending layer was observed on another day; but in this second instance, it remained at 400 m and did not ascend to join the main layer. Echo groups or "tent fish" were recorded near the surface after descent of the mi-

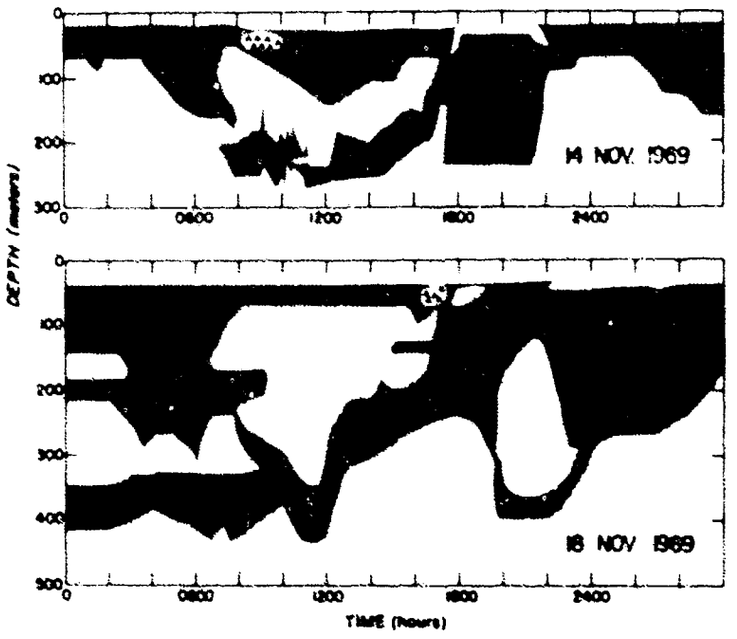

Figure 3. Depth distribution of 12-kHz sound-scattering layers over two diel periods of the November cruise. ^^ indicates echo groups.

gratory scattering layers on 14 November and before ascent of the migratory layer on 18 November (see also Fig. 4).

MIDWATER TRAWL CATCHES AND SCATTERING LAYERS

The catches of midwater animals relative to sonic-scattering layers are summarized for six of our IKMT-MPS tows in Tables 1 through 6 and Figures 4 through 9. These tows indicate some of the spatial and temporal variations of the catches.

Variability within Depths

Repeated collections were made at 40 m within a scattering layer after it ascended into surface waters (Fig. 4 and Table 1). Each net in this series sampled for 20 min, filtering approxi-

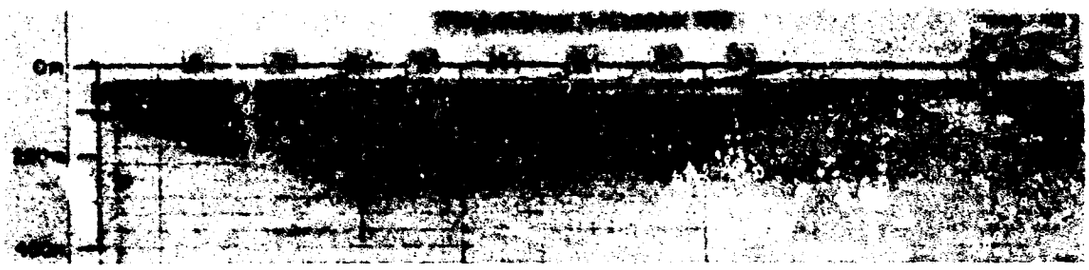

Figure 4. A 12-kHz echogram taken from 1730 to 2025 hours on 18 November 1969. In Figures 4 through 9, the echogram is superimposed on the trajectory of the trawl and numbers of the MPS nets. The times given apply to the duration of the tow, time increasing from right to left.

Table 1. Catches of Midwater Animals from 1730 to 2025 Hours on 18 November 1969

Depth range of sound-scattering layer (m)		Depth of each net fished		Biomass[a] (grams wet weight/minute)				Number of *S. leucopsarus*
38.5 kHz	12 kHz	Net	Depth (m)	F	S	E	P	
10–60	36–250	2	40	0.11	0	3.20	0.54	6
		3	40	0.30	T	2.25	0.40	0
		4	40	T	T	4.80	0.26	8
		5	40	T	T	5.32	0.61	2
		6	40	T	T	1.05	0.70	1
		7	40	0.06	0.05	4.36	0.38	3
		8	40	0	0	4.80	0.30	0

[a]Catches are represented as follows: F = Fishes, S = shrimps, E = euphausiids, and P = plankton. Large catches are underlined. T indicates trace, less than 0.01 g/min. S or L refers to the numbers of small (less than 30-mm standard length) or large (greater than 30-mm standard length) *Stenobrachius*. Genera in parentheses were common but did not predominate the catch.

mately 5,000 m^3 at 3.4 knots. Variations in the biomass (grams wet weight per minute) of fishes and shrimps were large among samples. Catches of euphausiids and plankton, however, were less variable. The numbers of the common lanternfish *Stenobrachius leucopsarus* also indicated a clumped or patchy distribution.

The tow depicted in Figure 5 and Table 2 shows both horizontal and vertical variability of catches. The largest catches of fishes, shrimps, euphausiids, and plankton were made in the first net at 0 to 35 m. Although the 12-kHz scattering layer started 18 m from the surface and the 38.5-kHz layers started 10 m from the surface, the layers probably continued to the surface through the gated-out portion of the echograms. Two of the three samples at 35 to 38 m had large fish biomasses; only one of the three samples below the scattering layer at 77 m had a large *Sergestes* biomass. The biomass of *Euphausia pacifica*, on the other hand, was uniformly large between 35 and 77 m and small below 77 m. Thus, large catches were made within the scattering layer, and smaller catches were made below the scattering layer. Variability within horizontal strata was again large, and variability was larger for fishes and shrimps than for euphausiids.

Table 2. Catches of Midwater Animals from 2040 to 0010 Hours on 14 November 1969

Depth Range of sound-scattering layer (m)		Depth of each net fished		Biomass[a] (grams wet weight/minute)				Abundant genera	
38.5 kHz	12 kHz	Net	Depth (m)	F	S	E	P		
10–50	18–70	1	0-35	5.56	1.95	20.56	24.01	*Stenobrachius* (S > L)	Medusae
		2	35	2.46	0.30	3.00	0.71	*Tectostoma*	*Euphausia*
		3	35-38	2.38	0.58	5.40	0.13	*Diaphus*	*Sergestes*
		4	38	0.79	0.06	3.99	0.04	*Tarletonbeania*	
		5	38-77	2.11	0.43	3.18	0.76	*Tectostoma*	
		6	77	0.13	0.46	0.18	0.15		
		7	77	0	0.06	0.59	0.06		
		8	77	0.67	1.17	0.20	0.28	*Sergestes*	

[a]See Table 1.

Figure 5. A 12-kHz echogram taken from 2040 to 0010 hours on 14 November 1969

Variability Among Depths

Two tows sampled similar depths and fished through and below a scattering layer during one night (Figs. 6 and 7 and Tables 3 and 4). The layer, which first shoaled and then deepened, was from 18 to 90 m on the 12-kHz Edo. Two layers within this depth range appeared on the 38.5 kHz Simrad echogram. In the first tow *Sergestes similis* biomass peaked between 10 and 45 m; the *Euphausia pacifica* biomass was largest at 45 m (within both the 38.5- and 12-kHz layers); and the fish biomass (mainly *Tactostoma macropus*) was largest between 96 and 144 m, near the lower edge of the thick portion of the layer (Table 3).

Table 3. Catches of Midwater Animals from 2048 to 2351 Hours on 13 November 1969

Depth range of sound-scattering layer (m)		Depth of each net fished		Biomass[a] (grams wet weight/minute)				Abundant genera	
38.5 kHz	12 kHz	Net	Depth (m)	F	S	E	P		
10–25		7	10-45	5.54	3.09	0.13	0.34	*Sergestes*	(*Stenobrachius*)
40–50	18–70								
		6	45	0.74	0.52	0.21	1.09	*Euphausia*	*Stenobrachius*, *Tactostoma*
		5	45-91	0.68	1.10	0.10	0.14		*Euclio*
		4	91-96	0.49	0.70	0.02	0.10		
		3	96-144	1.20	0.29	0.01	0.18	*Tactostoma*	
		2	141-145	0.41	0.17	0	0.35		

[a]See Table 1.

Figure 6. A 12-kHz echogram taken from 2048 to 2351 hours on 13 November 1969

The second tow (Table 4, Fig. 7) which started about 2 hours after the end of the first one, had the largest catches of fishes, shrimps, and euphausiids in the 97-145 m net, below or in the lower edge of the scattering layer. Most of the fish biomass caught at the depth of the scattering layer was from *Tactostoma macropus*. These changes in vertical distributions may be caused by horizontal patchiness or the descent of *Sergestes* and *Euphausia* within the scattering layer during the sampling period.

Table 4. Catches of Midwater Animals from 0200 to 0535 Hours on 14 November 1969

Depth range of sound-scattering layer (m)		Depth of each net fished		Biomass[a] (grams wet weight/minute)				Abundant genera
38.5 kHz	12 kHz	Net	Depth (m)	F	S	E	P	
15-25		1	0-10	0.08	0.25	0.06	0.58	
40-50	18-90	2	10-50	0.76	0.04	0	0.15	(*Tactostoma*)
		3	50	0.62	0.04	0.08	0.30	
		4	50	0.41	0.06	0.23	0.25	
		5	50-97	0.15	0.28	0.14	0.21	
		6	97	0.05	0.46	0.26	0.20	
		7	97-145	1.17	0.86	0.49	0.39	*Stenobrachius*(S) *Tactostoma* *Sergestes* *Euphausia*

[a]See Table 1

Figure 7. A 12-kHz echogram taken from 0200 to 0535 hours on 14 November 1969

Deep Scattering Layers

Sometimes during the day, and less commonly at night, a deep scattering layer (DSL) was apparent on 12-kHz echograms at 350 to 420 m (Figs. 8 and 9). Tables 5 and 6 show the catches above and within such a deep layer on two consecutive tows.

During the daytime tow (Figure 8 and Table 5), catches of fishes and shrimps were larger in samples in the DSL than above the DSL. (Nets 1 and 2 fished in the surface scattering layer but caught almost nothing.) Euphausiids were most numerous in and just above the DSL (324 to 410 m). The large plankton biomass in net 4 resulted from *Lensia*, a nonphysonect siphonophore. The most numerous fish in the DSL was small *Stenobrachius leucopsarus* (less than 30 mm).

The DSL started to rise toward the surface at 1400 hours on 17 November (Fig 8). The migration of this layer continued toward the surface and is apparent between 200 and 300 m in Figure 9. A portion of this migratory layer appeared to split off at 1630 hours (just below start of net 2 in Fig. 9) and descend to 360 to 420 m, the original day depth of the layer in Figure 8. A second layer also appeared to descend from the main layer at 1730 hours (end of net 3) to form an intermediate layer at about 200 m.

The IKMT-MPS was towed horizontally at 173 to 180 m while the main layer migrated upward (Fig. 9 and Table 6). Catches in net 2, which appeared to fish in the densest part of the layer, were low. Many euphausiids were caught in net 3 after the main layer migrated above the tow depth and when the net fished in the vicinity of the intermediate layer. *Sergestes* also was caught at 175 m, but mainly in net 4. The largest fish biomass was caught in the two nets that fished the DSL, which was located between 360 and 420 m.

Figure 8. A 12-kHz echogram taken from 1024 to 1445 hours on 17 November 1969

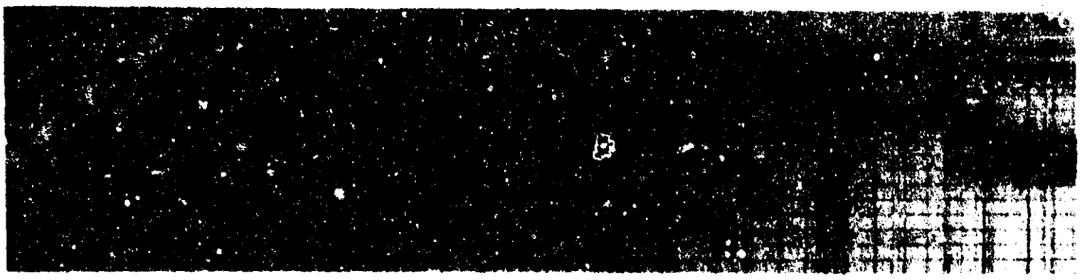

Figure 9. A 12-kHz echogram taken from 1610 to 2110 hours on 17 November 1969

Table 5. Catches of Midwater Animals from 1024 to 1445 Hours on 17 November 1969

Depth range of sound-scattering layer (m)	Depth of each net fished		Biomass[a] (grams wet weight/minute)				Abundant genera
12 kHz	Net	Depth (m)	F	S	E	P	
37–70	2	53–48	0	0	T	0.14	
	3	48–277	T	T	0.01	0.23	
	4	277–256	0	0	0.04	5.16	*Lensia*
	5	256–324	T	T	0.01	0.48	*Euclio*
	6	324–330	0.03	0	0.16	0.53	
350–420	7	330–405	0.12	0.12	0.16	0.27	*Diaphus*, *Sergestes*, *Euphausia*
	8	405–410	0.42	0.11	0.17	1.09	*Stenobrachius* (S)

[a]See Table 1.

Table 6. Catches of Midwater Animals from 1610 to 2100 Hours 17 November 1969

Depth range of sound-scattering layer (m)		Depth of each net fished		Biomass[a] (grams wet weight/minute)				Abundant genera
38.5 kHz	12 kHz	Net	Depth (m)	F	S	E	P	
down to 175	down to 175	2	173–180	0	T	0.32	0.23	
		3	173–175	0.33	0.32	1.08	0.35	*Euphausia*
		4	175	0.17	0.89	0.12	1.64	*Sergestes*, siphonophore
		5	175	0.11	0.43	0.10	0.21	
	360–420	6	175–400	0.66	0.57	0.15	0.89	*Stenobrachius* (S > L), siphonophore, *Tactostoma*
		7	400–410	0.58	0.12	0.06	0.57	*Stenobrachius* (S > L), *Hierops*, *Chauliodus*

[a]See Table 1.

Small *Stenobrachius leucopsarus* were numerous in the DSL (350 to 420 m) during both the daytime and nighttime tows (Tables 5 and 6). These fish have gas-filled swimbladders (Capen, 1967) and may be principal contributors to this 12-kHz sound-scattering layer off Oregon. *Sergestes* and *Euphausia*, on the other hand, were common within depths of the DSL during the day but were most common above the deep layer at night. Small *S. leucopsarus* of the same age group also were caught in large numbers near the surface at night. They were common in a scattering layer in the upper 50 m later during the night of 17-18 November, the same night they were captured in deep water (Table 6). This suggests two centers of abundance or migratory and nonmigratory individuals of this age group within the population.

Summary of Occurrences Relative to Scattering Layers

Table 7 shows how frequently common groups of animals had peak abundance in, above and below scattering layers. These data are only from tows that sampled through layers.

Table 7. Occurrence of Maximum Catches of Various Midwater Animals

		Euphausiids	*Sergestids*	*Siphonophores*	*Pteropods*	*Stenobrachius*	*Lampanyctus*	*Diaphus*	*Tarletonbeania*	*Hierops*	*Tactostoma*	*Chauliodus*
0–100 m Night	12 kHz	AA IIIII BB	AAA III BB	B	AA II	A IIIII* BBB		III B	II		III BBBB	
	38.5 kHz (8 tows)	IIIIII B	IIIII BB		III	A IIIII*I* BB		A III B	I		II BBBB	
Day	12 kHz (4 tows)	I BB	B	B	I B	BB	B	B	B			
	38.5 kHz (4 tows)	I BB	B	B	I B	BB	B	B	B			
100–275 m Day/night	12 kHz (4 tows)	A II B	II B	II		I BBB*		II B	B	B	B	BB
Day/night	38.5 kHz (3 tows)	A I B	BB	A B	A	A B		A	BB	B		B
350–420 m Day/night	12 kHz (4 tows)	A III	AA I	AAAA		IIII B*		I		II		I

*This table shows how often the maximum catches of various common midwater animals occurred in (I), above (A), and below (B) the sound-scattering layer sampled. Night and day tows were tabulated separately when four or more tows could be included. An asterisk indicates a preponderance of *Stenobrachius* larger than 30 mm.

Within the upper 100 m at night, euphausiids, *Sergestes*, and *Stenobrachius* peaked at scattering-layer depths more frequently than other animals. Euphausiids, for example, were common at scattering-layer depths in seven out of eight tows through 38.5-kHz layers. The higher occurrence of peaks in 38.5- than in 12-kHz scattering layers was influenced by the greater portion of the 12-kHz echograms that were gated out near the surface.

During the day, catches of most groups of animals were largest below both the 38.5- and 12-kHz layers. Only euphausiids and pteropods peaked at scattering depths, and then only infrequently.

Poor correlations also were found between abundances and scattering between 100 to 275 m during day and night periods, but the total number of tows was low. Small *Stenobrachius leucopsarus* were common in all four tows in 12-kHz layers between 350 and 420 m. Euphausiids were also more abundant in this DSL than above it in three of the four tows.

CONCLUSIONS

1. The depth and migratory pattern of scattering layers observed on echograms was variable among diel periods.
2. Replicate samples at discrete depths indicated patchy distributions of fishes and *Sergestes similis*. Catches of *Euphausia pacifica* were less variable.
3. Sampling during single nocturnal periods suggested that the depth distribution of species and species groups may change within surface scattering layers.
4. Although catches of species often varied among depths, many species were caught over wide depth ranges and were not completely aggregated into high-density, thin layers.
5. Catches of fishes, shrimps, and euphausiids were sometimes largest at scattering-layer depths. Sometimes catches of animals were low at scattering-layer depths, however, and sometimes large catches were made where no dense scattering layer was recorded.
6. *Euphausia pacifica*, *Sergestes similis*, and *Stenobrachius leucopsarus* were the animals that were caught most often in largest numbers in scattering layers, especially in the upper 100 m at night.
7. Small *Stenobrachius leucopsarus* (with gas-filled swimbladders) were caught in all tows that sampled the DSL (350 to 420 m) during day or night periods.

ACKNOWLEDGMENTS

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A RECONNAISSANCE OF THE DEEP SCATTERING LAYERS IN THE EASTERN TROPICAL PACIFIC AND THE GULF OF CALIFORNIA

C. R. Dunlap
Hopkins Marine Station, Stanford University
Pacific Grove, California

ABSTRACT

Observations made during three cruises in the eastern tropical Pacific and the Gulf of California showed sonic scattering layers at approximately four discrete depths (50-250 m, 300 m, 400 m and 500 m). DSL's in the Gulf of California appear to be an integral extension of the eastern tropical Pacific scattering layers. Midday scattering layers do not indicate any obvious relationship to oxyclines and were commonly observed in oxygen concentrations less than 0.5 ml/1. Tucker midwater trawls taken in sonic-scattering layers indicated much more biomass than those taken outside the layers; myctophids, gonostomatids, sternoptychids, larval fishes, euphausiids, prawns, tunicates, siphonophores, and squid were most commonly associated with the layers. Evidence is presented that some layers may migrate in the evening to the depth of maximum chlorophyll *a*, presumably due to feeding behavior. Swimbladder measurements and resonant volume calculations for the myctophid, *Myctophum nitidulum* are included.

INTRODUCTION

Although investigators have observed the deep scattering layers (DSL) in the eastern tropical Pacific, there have been few ecological studies of the organisms in the DSL (Dietz, 1948; Kanwisher, et al., 1957; Barham, 1966; Beklemishev, 1967). Clearly, more information is needed on the diurnal migration of the organisms and their relation to variables such as light, temperature, and oxygen.

This investigation reports a portion of the results of a DSL study (Dunlap, 1968) made during Stanford Oceanographic Expeditions (S.O.E.) 16 and 21 in the Gulf of California and Expedition 17 in the eastern tropical Pacific.

METHODS

The majority of the DSL recordings (Figure 1) were obtained with a 30-kHz Simrad fathometer, model 540-4. An 11-kHz Simrad fathometer, model 513-1, provided limited comparative information.

Spurious secondary sea-floor echoes occasionally occurred when water depths were less than 2000 m. These were identified by analysis of the strength of the echo, movement of the echo during the dawn-to-dusk periods, and movement of the echo in relation to bottom depth changes on the cruise track.

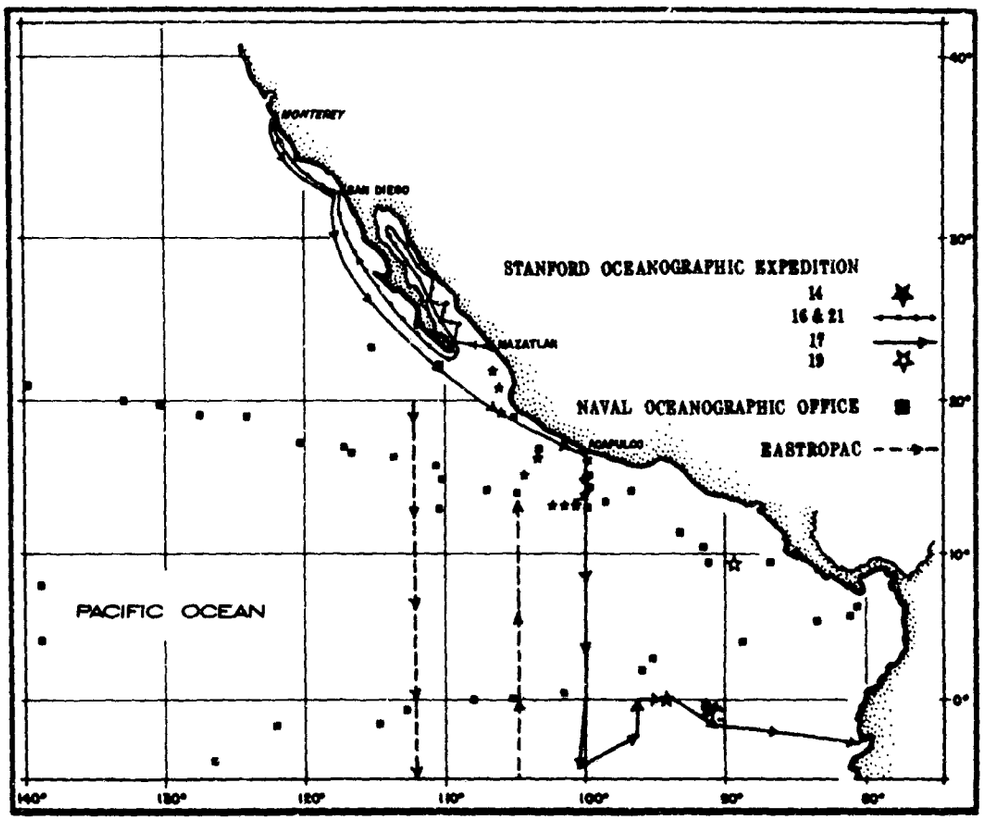

Figure 1. A geographical distribution of recent DSL observations in the eastern tropical Pacific

DSL fauna was sampled with a Tucker opening-closing micronekton net (Davies and Barham, 1969) equipped with a time-depth recorder. The depth of the net was determined by geometric triangulation. The trawl was towed at depth for one hour to minimize the effects of patchiness (Wiebe, 1968). Tow speed was 2 knots.

Daytime environmental variables (temperature, salinity and oxygen concentration) were examined by making hydrocasts to 1000 m. Bathythermograph records were taken at most stations. Oxygen concentration was determined by the Winkler technique (Carpenter, 1965), light intensity at the sea surface was observed with a pyrheliometer, and light penetration was measured with a photometer or Secchi disc.

The abundance of food (as phytoplankton) at night in the upper 100 m was sampled by a separate series of night hydrocasts. The phytoplankton cells were concentrated by membrane filtration and a Turner fluorometer was used to determine chlorophyll *a* by the method of Lorenzen (1965).

Swimbladder morphology of several midwater fishes was studied by measuring the major and minor axes of the swimbladder, and determining swimbladder volume directly by injecting water from a calibrated syringe into the swimbladder. Sonic resonance curves from the swimbladder volumes were then constructed according to Capen (1967).

RESULTS AND DISCUSSION

Day DSL Depths, Light and Oxygen Variables

Layers were present at almost all locations where observations were made. Longhurst (personal communication) got similar results from 30-kHz observations on an EASTROPAC program latitudinal transect (Figure 1).

Light appeared to be the major factor related to the day depths of the DSL in this study. The mean midday depths of the layers occurred mainly at (1) 50-250 m, (2) 300 m, (3) 400 m, and (4) 500 m. The combined results of a northward transect of the Gulf of California in October-November 1967, and a southward transect of the eastern tropical Pacific in January-February, 1968, are shown in Figure 2. It is apparent that the midday depth of the first layer deepens as the equator is approached. Surface incident-light intensity increased toward the equator (70 to 90 cal/cm^2/hr), and the penetration of the 1% light level also increased from 49 to 120 m. The continuity of the data in Figure 2 suggests that layers in the Gulf of California are probably an integral part of the DSL pattern of the eastern tropical Pacific.

These results confirm earlier reports of Dietz (1948) and Beklemishew (1967) that DSL's are found at greater depths as the equatorial region is approached. Light-intensity observations suggest that this increase in DSL depth might be due to increasing intensity. This is contrary to the findings of Moore (1958), who indicated that seasonal or other incident sunlight changes would not change the layer depths by more than 50 m.

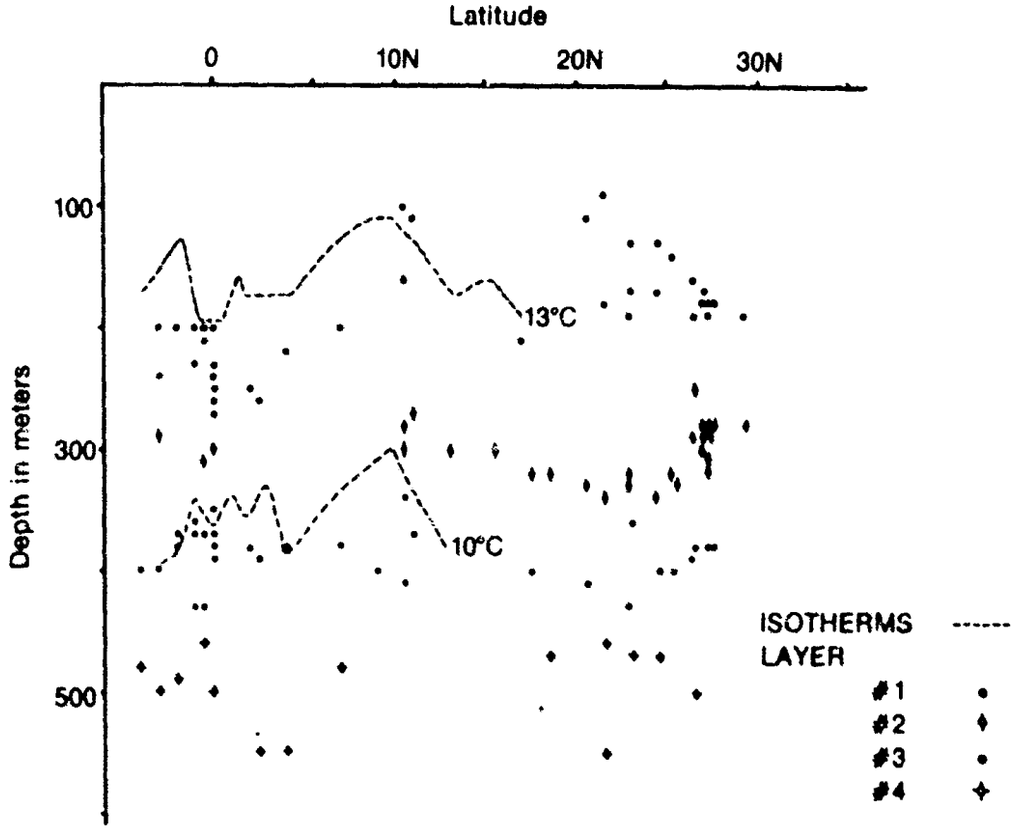

Figure 2. The mean day depth distribution of 30-kHz DSL's and isotherms at various latitudes, showing layer 1 deeper at the Equator

Oxygen concentration in the Gulf of California had no apparent effect on the 30-kHz layers during the day, contrary to previous reports by Bary (1966) and Kanwisher (1966). Except for the uppermost layer, all layers in the Gulf of California were typically found in oxygen concentrations of less than 0.5 ml/L O_2. Bary (1966) suggested that day layer depths in Saanich Inlet might be determined by an oxycline. In the Gulf of California the oxycline is above a similar oxygen minimum, but the DSL's are not restricted by it. Possibly the layers in Saanich Inlet (British Columbia) are oxygen controlled and there is a physiological difference between the causative organisms in these two different areas. Perhaps, with light-intensity data and current work using a range of frequencies (Pieper, 1969), the discrepancy will soon be resolved. Others have shown that organisms found at DSL depths can readily survive at extremely low oxygen conditions (Teal and Carey, 1967; Childress, 1969). Kinzer (1966) has also found DSL's in an oxygen minimum region in the Arabian Sea.

Figure 3 presents oxygen profiles and scattering layers for the eastern tropical Pacific at 100° W (data from S.O.E. 17). There seems to be no general relationship between oxyclines and the 30-kHz DSL. The amount of oxygen present between a depth of 100 and 300 m does increase proceeding south, but incident sunlight also increases and the 1% light depth gets deeper along the transect. In fact, equatorial scattering layers seemed to respond to changing light conditions independent of the oxygen distribution.

I conclude that light appears to be the dominant factor in the determination of the depths of the midday DSL. Any acoustical or biological DSL study should therefore include light measurements, if only Secchi disc readings. Although Secchi disc readings have been shown to have great limitations (Tyler, 1968), they may have real alue in broad geographical DSL studies (Dickson, personal communication).

Diurnal Vertical Migration Patterns

Three continuous 24-hour observations of deep scattering layers were made in the eastern tropical Pacific. The results of the first observation, made on January 28 and 29, 1968 at the equator (0°0'N, 100°0' W), are shown in Figure 4. The two major migrating layers were observed at mean day depths of 260 and 390 m. Another scattering layer appeared at about 500 m, but its evening migration took it to about 410 m for its night residence depth. Diffuse scattering was also found at 310 m, 230 m, and 190 m during the night, while their day positions were not clear. The DSL's reached their maximum day depths at approximately 0945, when sunlight (56 cal/cm^2/hr.) was about 66% of the maximum daytime value. The layers remained stationary at this depth until 1500 hours when the intensity was again about 55 cal/cm^2/hr.

The diurnal cycles of Figures 5 and 6 were observed in the Gulf of California in the late summer of 1969. The 1% light depth occurred at approximately 86 m for 24°N and 69 m for 27.5°N. Surface light intensities and rates of change were identical during the DSL migrations, and the layers were deepest at about 0800 local time at both latitudes in the Gulf. The pyrheliometer values at that time were 30 cal/cm^2/hr. The two stations had similar layers near 300 and 400 m. An interesting phenomenon occurred at lesser depths. At 27.5°N a layer was present at about 180 m. However, at 24°N, patches of scattering occurred above the 300-m layer, instead of a consistent diffuse scattering layer. This suggests a faunal change or a behavioral (schooling) change between the two stations. Beklemishev (1967) comments that in the tropical part of three oceans the 300-m layer consisted of significant sound scatterers, sometimes including tuna. These rose upward with the layer in the afternoon, remaining until sundown. The patchy echoes at 24°N followed a similar behavior pattern; however, many other phenomenon such as the schooling of smaller fish could also explain these echoes. Nonmigratory DSL's also occurred

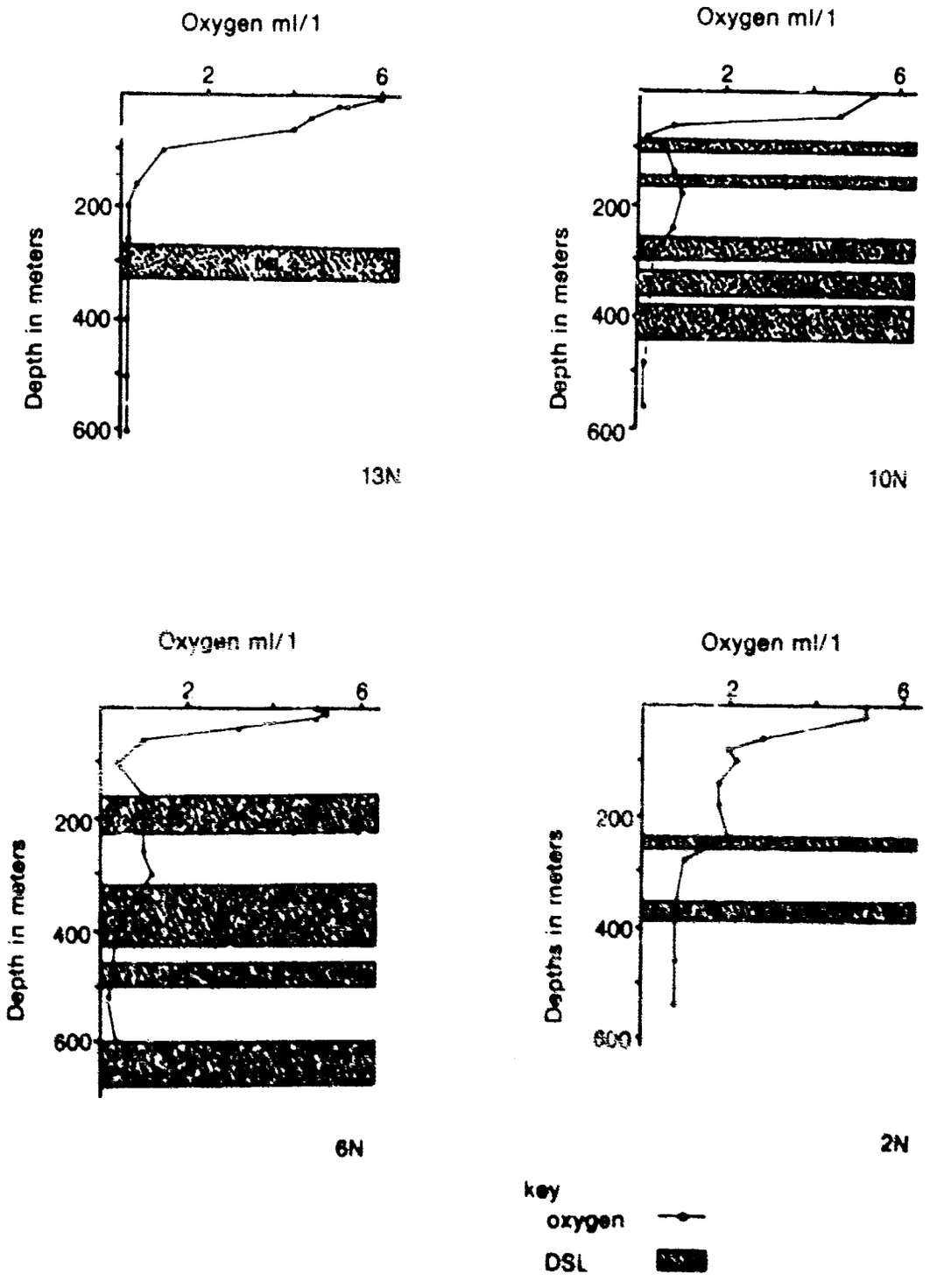

Figure 3. DSL's and oxyclines in the eastern tropical Pacific

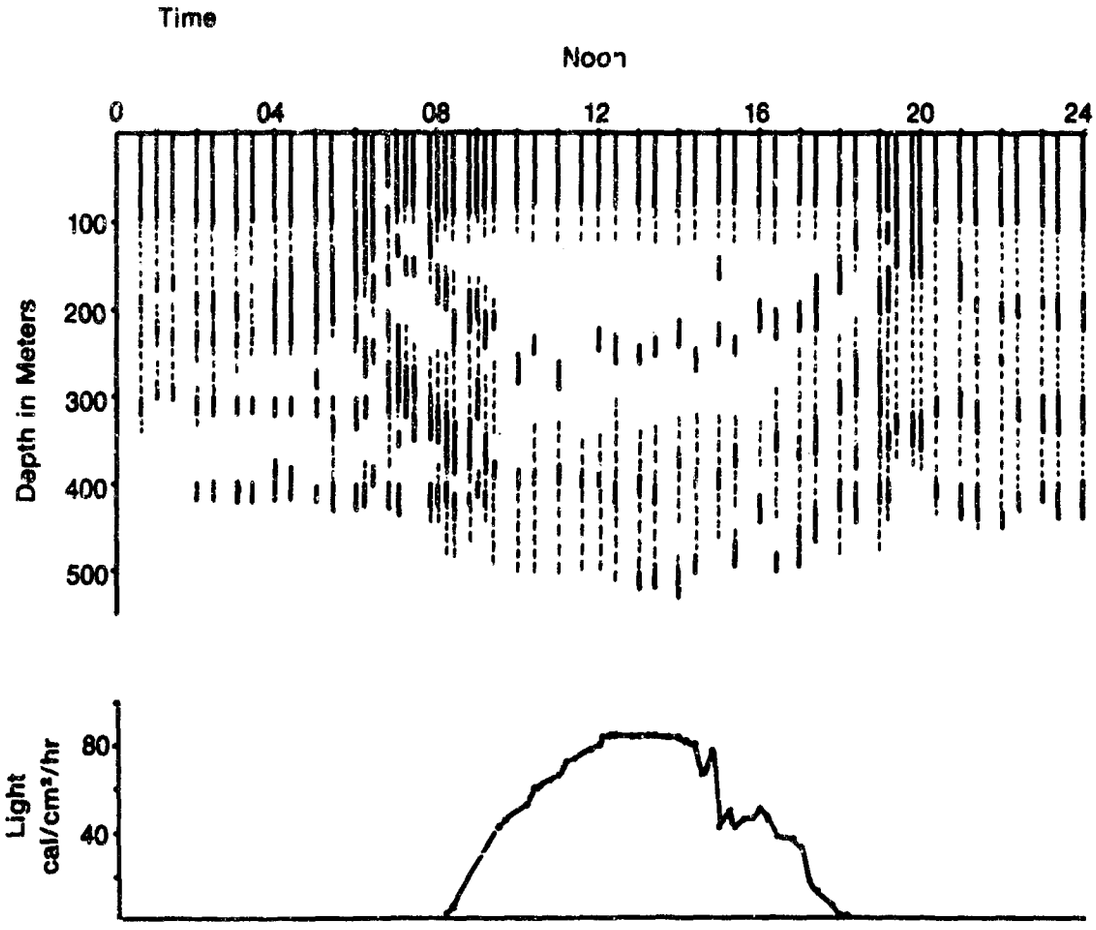

Figure 4. A 24-hour observation of the diurnal vertical migration of 30-kHz DSL's showing their relation to surface light intensity at the Equator. Observations were made in January 1968.

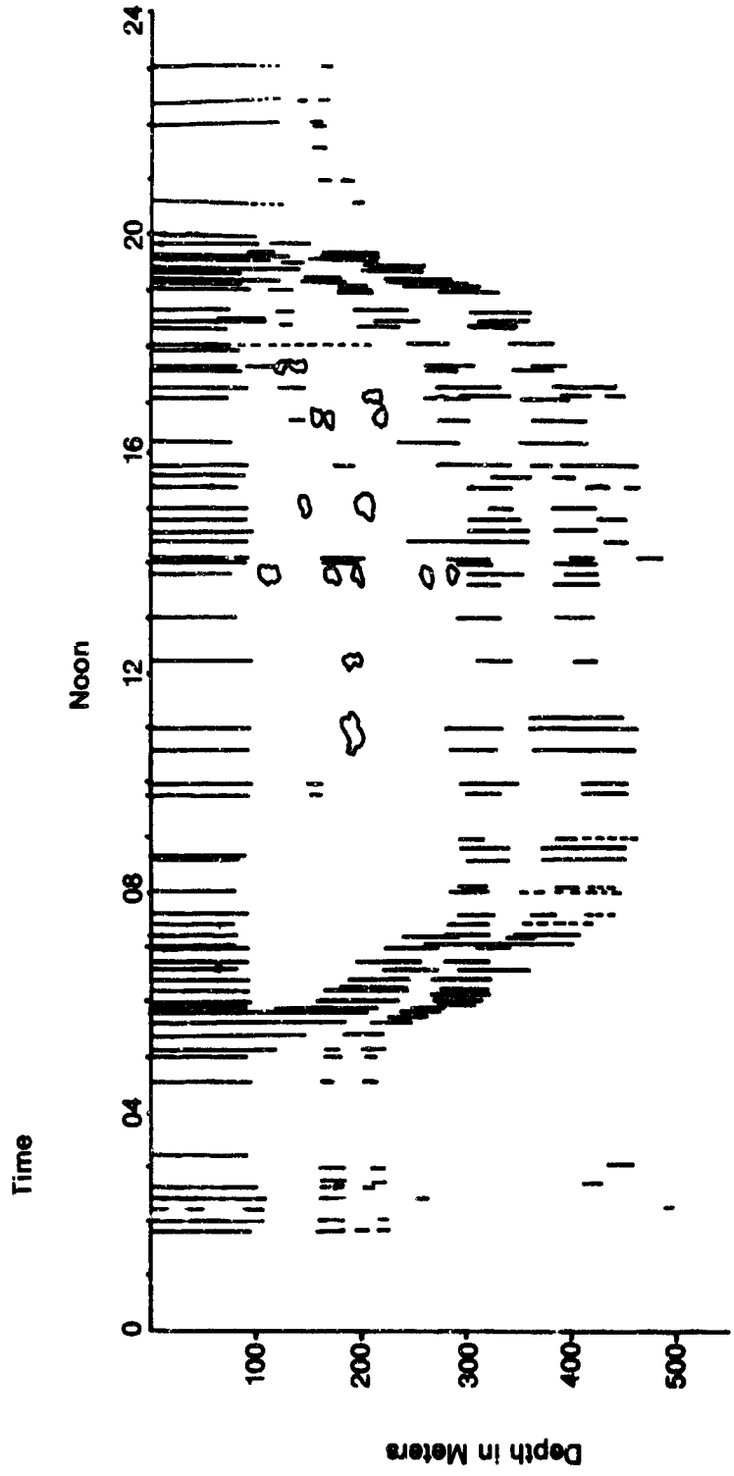

Figure 5. The diurnal 30-kHz DSL pattern (vertical migration) observed at the mouth of the Gulf of California, 28° N, during July 1969. A number of patchy echoes are indicated at a depth of about 200 m between 1030 and 1760 hrs local time.

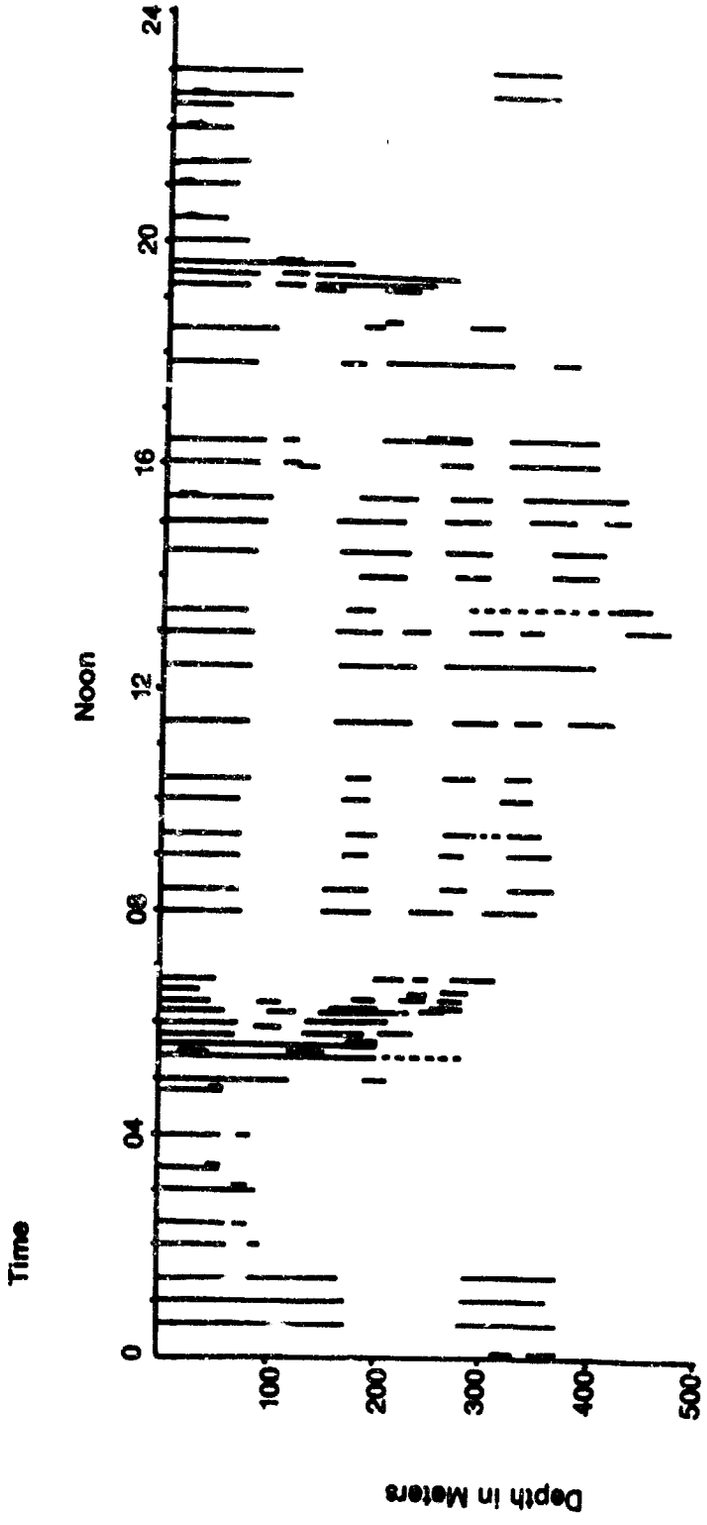

Figure 6. The diurnal 30-kHz DSL pattern (vertical migration) at 27.5° N, well inside the Gulf of California, during August 1969. The patchy echoes (Figure 7) are replaced by a normal diffuse scattering layer.

at both stations. Bradbury (personal communication) observed 30-kHz DSL migration patterns during S.O.E. 19 (Figure 1), and her results further support the presence of many nonmigratory DSL's in the eastern tropical Pacific.

Night Shallow-Scattering Layers

Table 1 summarizes the occurrence of shallow scattering layers at night in the Gulf of California in relation to the abundance of chlorophyll *a* (i.e. phytoplankton) and of oxygen, and the thermocline. The highest intensity of sound scattering was usually at the depth of maximum chlorophyll *a* which, in turn, was generally near the top of the thermocline. Since the thermocline was not unusually sharp (1°C/5 m), the occurrence of a nonbiological scattering phenomenon is not suggested, and I believe that the scattering is caused by feeding animals. A scattering layer was also observed at the maximum chlorophyll *a* or phytoplankton level by Levenson (1968). Longhurst (1967) found that the greatest zooplankton biomass migrating to the surface waters at night was at the depth of maximum chlorophyll *a*. Migrators probably come in to the surface waters at night because of greater food availability (Marshall, 1954). Factors such as the depth of the mixed layer and higher temperatures could limit this upward migration (Hersey and Backus, 1962; Paxton, 1967; Harder, 1968).

Midwater Trawl Results

Trawls in scattering layers yielded a higher biomass than trawls out of the layers. Tables 2 and 3 summarize the daytime trawls in and out of the DSL's of the Gulf of California and the eastern tropical Pacific. In these tables "small" invertebrates included all macroplankton less than 2.5 cm in length. Only the general results of the Tucker trawls are presented in this paper. Myctophids, gonostomatids, sternoptychids, larval fishes, euphausiids, prawns, tunicates, siphonophores, and squid were most commonly associated with the scattering layer. The trawl results suggest that not all individuals in monospecific populations (e.g., *Triphoturus mexicanus*, Gilbert) migrate to the surface at night. Thus, not all individuals are light-followers. This is contrary to the findings of a previous study of myctophid distribution off southern California (Paxton, 1967).

Resonant Properties

Myctophum nitidulum Garmen was examined for resonant properties (Figure 7), and it appears that with a frequency of 12 kHz and depths of less than 500 m, fish with standard lengths up to about 40 mm would resonate. The volume of gas in the swimbladder was greater on a calculated and direct measurement basis than for most Pacific myctophids (Capen, 1967). *Myctophum nitidulum* seemed to be similar to the Pacific hake in its possible resonant scattering range (Capen, 1967).

Conclusions reached in this study have been based on the relationship between the environment and the deep scattering layer in the eastern tropical Pacific. A more complete understanding of the subject awaits completion of the faunal analysis of the DSL of this region.

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Table 1. Gulf of California S.O.E. 16 Night Surface Scattering Intensities and Other Parameters

R/V *Te Vega* Station	Depth of Max Intensity Night Surface Scattering (m)	Depth of Max O_2 Concentration (m)	Depth of Max Chlorophyll *a* (m)	Acid Factor at Chlorophyll *a* Max	Position of Chlorophyll *a* Max in Relation to Thermocline
102	29-37	20-25	–	–	–
113	40 Secondary at 25 m	20	40	1.6	Top
119	30-50	20	40	1.6	Top
127	22-30	20	40	1.4	Top
132	25-37	30-40	–	–	–
139	30-58	30-40	40	1.8	Top
140	30-42	30-40	40	1.8	Top
148	40	10	40	1.9	Top
156	40 Secondary at 20-22 m	30	40	1.45	Top
164	–	30-40	40	1.65	Top
179	40 Secondary at 65 m	0-40	–	–	–
187	33	0-40	40	1.58	Top

Table 2. Gulf of California S.O.E. 16 Biomass Summary of Day Tucker Trawls

A. Selected Trawls Which Trawled Exclusively in the DSL

R/V *Te Vega* Station	Number of Large Invertebrates	Small Invertebrate Displacement Volume (ml)	Total Number of Fishes	Trawl Depth (m)	Layer Number	Time
35	28	25	146	355	3	1102/1202
121	18	50	12	175	1	0945/1045
135	21	22	72	290-345	2	1035/1135
145	33	40	1626	390	3	1250/1350
161	20	40	185	250-300	2	0950/1050
163	2	15	82	130-145	1	1405/1505
Average	20	34	354			

B. Selected Trawls Which Trawled Exclusively Out of the DSL

Station	Number of Large Invertebrates	Small Inverterbrate Displacement Volume (ml)	Total Number of Fishes	Trawl Depth (m)	Time
64	4	5	33	425-445	1500/1600
112	21	25	27	850	1335/1435
122	9	50	124	235	1200/1300
123	3	25	22	540-650	1420/1520
136	138	0	154	320-360	1237/1337
144	2	25	136	525-560	1029/1129
184	64	7	47	360-390	1520/1620
191	1	2	8	170-175	0604/0704
192	2	0	5	770-830	0845/1045
193	20	1	0	275	1235/1335
Average	26.4	14.0	55.6		

C. Summary of Data by Layers (from A)

Layer Number	Average Number of Large Invertebrates	Average Small Invertebrate Displacement Volume (ml)	Average Number of Fishes	Dominant Invertebrates	Dominant Fish
1	10	32	47	Squid	Larval Fishes
2	20	31	128	Squid/Euphausiid/Decapods	*Triphoturus mexicanus*
3	30	32	886	Squid/Euphausiid	*Triphoturus mexicanus*

Table 3. Eastern Tropical Pacific S.O.E. 17 Biomass Summary of Day Tucker Trawls

A. Selected Trawls Which Trawled Exclusively in the DSL

R/V *Te Vega* Station	Number of Large Invertebrates	Small Invertebrate Displacement Volume (ml)	Total Number of Fishes	Time	Trawl Depth (m)	Layer Number
17	3	8	122	1400/1500	385-481	3
31	0	43	2	1303/1403	200-270	1
32	12	62	219	1520/1620	355-410	2
42	0	743	51	1358/1458	390-400	2
47	65	166	36	1000/1100	250-400	2
49	23	43	200*	1505/1605	450-500	3
57	73	412	117	0935/1035	350-378	2
60**	7	43	15	1625/1655	140-160	1
66	19	430	99	1435/1535	300-350	2
Average	22	216	96			

B. Selected Trawls Which Trawled Exclusively Out of the DSL

8	8	45	33	1244/1344	235-277	
10	0	8	5	1155/1255	185-225	
15	3	43	9	0931/1031	200-246	
16	1	12	0	1139/1239	60-90	
40	6	64	1	0937/1037	210-230	
41	–	27	3	1122/1222	215-227	
48	18	39	9	1230/1330	185-335	
58	13	26	6	1135/1235	160-210	
69	11	210	24	0900/1000	290-310	
70	21	167	–	1040/1140	250-265	
Average	9	64	10			

C. Summary of Data by Layers (from A)

Layer Number	Mean Layer Depth (m)	Average Number of Large Invertebrates	Average Small Invertebrate Displacement Volume (ml)	Average Number of Fishes	Dominant Invertebrates	Dominant Fish
1	250	3	43	8	Tunicates, Siphonophores	Larval Leptocephalus
2	390	34	362	104	Euphausiids	Gonostomatids and Hatchet Fish
3	500	23	43	200	Sergestid Shrimp	Myctophids and Gonostomatids

*Estimated Number

**Data corrected to Standard Day Trawl

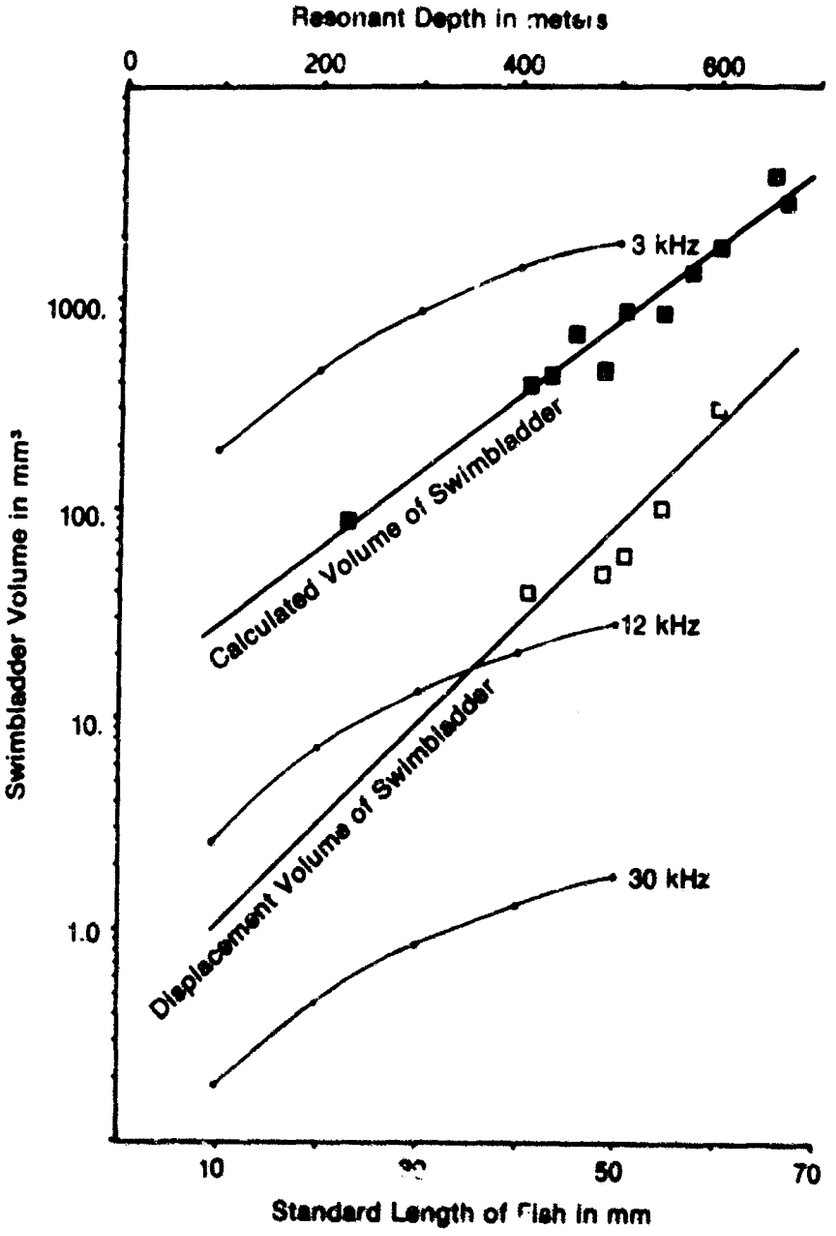

Figure 7. The results and possible resonance implications of a swimbladder analysis of the myctophid fish, *Myctophum nitidulum* for 3, 12, and 30 kHz.

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STUDIES ON THE FAUNA ASSOCIATED WITH THE DEEP SCATTERING LAYERS IN THE EQUATORIAL INDIAN OCEAN, CONDUCTED ON R/V *TE VEGA* DURING OCTOBER AND NOVEMBER 1964

M.G. Bradbury, D.P. Abbott, R.V. Bovbjerg, R.N. Mariscal, W.C. Fielding, R.T. Barber, V.B. Pearse, S.J. Proctor, J.C. Ogden, J.P. Wourms, L.R. Taylor, Jr., J.G. Christofferson, J.P. Christofferson, R.M. McPhearson, M.J. Wynne, and P.M. Stromborg, Jr.[1]

ABSTRACT

Acoustic studies show the daytime scattering pattern in the equatorial Indian Ocean to consist of a main deep scattering layer (DSL) (sometimes a double layer) with a top at 300 to 350 m and an intermediate layer (not always present) at about 200 to 250 m, as well as surface scattering. At night, a combined layer forms in the upper 150 to 250 m by merging of surface scattering with the ascended main DSL and deeper elements. A nomenclature for scattering features is suggested. Horizontal distributions from Africa to the Nicobar Islands are given for 161 species of midwater animals, including 16 siphonophores, 14 pteropods, 10 heteropods, 3 mysids, 7 euphausids, 19 shrimps, 8 tunicates, and 79 fishes. Vertical distributions are discussed for 56 genera and species that were taken frequently enough to suggest diel patterns. Of these, 13 were taken primarily at main DSL depths and lower in daytime and in the combined layer (upper 100 to 150 m) at night, indicating that they are vertical migrators. The six species showing the strongest association with the main DSL were *Abylopsis tetragona* (a siphonophore), *Cymbulia* sp. (a pteropod), *Thysanopoda* sp. and *Nematobrachion* sp. (euphausiids), *Vinciguerria nimbaria* (a stomiatoid fish), and *Notolychnus valdiviae* (a myctophid fish). Partial migrators of the genus *Argyropelecus* (stomiatoid fishes) were also strongly associated with the main DSL, but not with the combined layer.

[1]M.G. Bradbury, San Francisco State College, San Francisco, California; D.P. Abbott, Hopkins Marine Station, Pacific Grove, California; R.V. Bovbjerg, State University of Iowa, Iowa City, Iowa; R.N. Mariscal, Florida State University, Tallahassee, Florida; W.C. Fielding, Community Hospital of Monterey Peninsula, Carmel, California; R.T. Barber, Duke University Marine Laboratory, Beaufort, North Carolina; V.B. Pearse, Hopkins Marine Station, Pacific Grove, California; S.J. Proctor, Vancouver Public Aquarium, Vancouver, B. C., Canada; J.C. Ogden, Smithsonian Tropical Research Institute, Balboa, Canal Zone; J.P. Wourms, McGill University, Montreal, Quebec, Canada; L.R. Taylor, Jr., Scripps Institution of Oceanography, La Jolla, California; J.G. Christofferson and J. P. Christofferson, Stanislaus State College, Turlock, California; R.M. McPhearson, University of Alabama, University, Alabama; M.J. Wynne, University of California, Berkeley, California; P.M. Stromborg, Jr., Northern Illinois University, DeKalb, Illinois.

INTRODUCTION

Cruise 5 of R/V *Te Vega*, operated by Stanford University under the auspices of the National Science Foundation,[2] departed from Mombasa, Kenya, on 5 October 1964 and terminated 12 December 1964 in Singapore (Fig. 1). A major objective of the scientific party aboard[3] was to gather information on the association of organisms occurring at the depths of the deep scattering layer (DSL) and at levels immediately above and below the DSL. Previous studies of the DSL (reviewed by Hersey and Backus, 1962) have stressed problems of recording and comparing echograms or have been concerned primarily with determining the species responsible for sonic scattering at DSL depths. In the present study, we have been concerned mainly with three topics: (1) the behavior of the DSL as interpreted from fathometer and sonar echograms; (2) the kinds of macroscopic organisms present in and near the DSL at various times of day and night, their numbers and their movements; and (3) the food habits of these organisms. Although the work covered only a 2-month period and was carried out within a restricted range of latitudes, the results obtained have yielded a picture of the DSL fauna somewhat broader than that obtained in most previous studies.

Acoustic and trawling operations were conducted in the area between Kenya and the northern tip of Sumatra over a cruise-track distance of about 4,300 nautical miles (Fig. 1). Three stops were made along this track for supplies and biological work on inshore communities. The trawling and DSL observation stations therefore fall into four series:

1. Mombasa, Kenya, to Port Victoria, Seychelles, across the southern portion of the Somali Basin; 1,400 nautical miles, traversed 5 to 14 October 1964.
2. Port Victoria, Seychelles, to Male Atoll, Maldive Islands, across the Somali Basin, the Carlsberg Ridge, and the southern portion of the Arabian Basin, terminating on the Mid-Indian Ridge; 1,500 nautical miles, traversed 27 October to 4 November 1964.
3. Male Atoll, Maldive Islands, to Colombo, Ceylon; 400 nautical miles, traversed 9 to 12 November 1964.
4. Colombo, Ceylon, to the northern tip of Sumatra across the southern portion of the Bay of Bengal; 1,100 nautical miles, traversed 19 to 26 November 1964.

The first and last stations were made on 7 October and 24 November, respectively; they were therefore about 7 weeks apart and are separated in space by a straight-line distance on the chart of about 3,000 nautical miles. All stations were made in open waters ranging in depth from 2,012 to 5,121 m. Proximity to land masses varied with the station, but no stations were made on island or continental shelves (insert, Fig. 1).

Weather conditions varied considerably during operations. The first leg of the cruise and the initial part of the second were made during the last of the southeast monsoon, with a heavy swell on the starboard bow and stiff breezes. As the ship neared the Maldive Islands, the winds declined to almost nothing, then shifted to westerlies. East of the Maldive Islands, we experienced our only serious storm. In the vicinity of Ceylon, the westerlies moderated until at the last station in the Bay of Bengal, we operated in a dead calm. The northeast monsoon began about 5 December, after all trawling operations had been completed.

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[2]Supported by National Science Foundation grant G17465.

[3]Chief Scientist: Prof. D.P. Abbott; Faculty: Prof. R.V. Bovbjerg, Prof. M.G. Bradbury; Faculty Assistant: R.N. Mariscal; Ship's Physician: Dr. W.C. Fielding; Graduate Students. R.T. Barber, V.B. Pearse, S.J. Proctor, J.C. Ogden, J.P. Wourms, L.R. Taylor, Jr., J.G. Christofferson, J.P. Christofferson, R.M. McPhearson, M.J. Wynne, P.M. Stromborg, Jr.

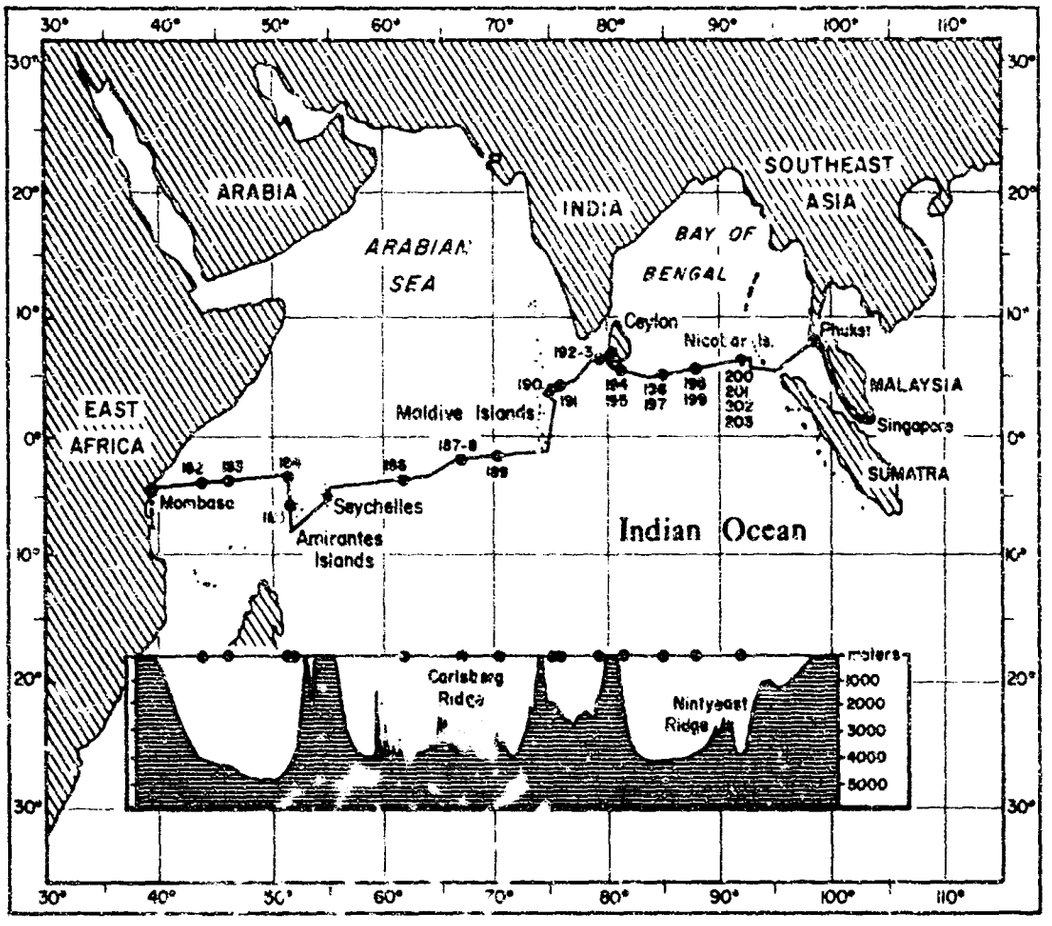

Figure 1. Map of the track of R/V *Te Vega* during Cruise 5, showing midwater trawling localities. Number shown along the cruise track are station numbers. Inset shows a section profile of the cruise track.

MATERIALS AND METHODS

Twenty-two DSL stations were completed at 14 localities (Table 1). Each trawling station (not locality) was assigned a *Te Vega* station number. Although the number of stations was limited by the regimen of the ship and by periods of unfavorable weather, an attempt was made to sample different geographic regions as well as to sample the DSL and layers adjacent to it around the clock (Fig. 2).

No complete hydrographic casts were made, but thermal conditions were recorded at each trawling station (Fig. 3). Surface temperatures, taken by bucket thermometer, showed little variation (25.5° to 27.0°C). Temperatures below the surface were measured with a 900-foot bathythermograph (GM Mfg. Co. Thermarine Recorder). The 10°C isotherm was recorded at roughly 300 m at all trawling stations. Between the surface and 300 m, thermal conditions were variable, but a thermocline was always present, varying in slope from gradual to abrupt, and in depth from 30 to 120 m. Incident illumination, recorded on deck periodically during trawling and monitoring of the DSL, was measured with a Norwood Director light meter.

Table 1. Summary of Data for Individual DSL Hauls

Station number	Locality	Date (1964)	Ship's time at midpoint of haul	Depth range fished most effectively (m)	Relation of effective fishing range to scattering layers
182	3°23′S, 43°44′E	7 Oct	1013	550-750	In and below DSL curtain
183	3°28′S, 46°10′E	8 Oct	0926	600-750	In and below DSL curtain
184	3°22′S, 51°15′E	10 Oct	0930	800-1250	Below DSL curtain
185	5°15′S, 51°27′E	11 Oct	0940	400-525	In main DSL
186	3°15′S, 61°28′E	29 Oct	1900	140-240	In combined layer
187	1°38′S, 66°28′E	31 Oct	1348	175-215	In surface curtain
188	1°38′S, 66°28′E	31 Oct	1513	275-525	In main DSL
189	1°07′S, 69°37′E	1 Nov	1829	275-375	In combined layer curtain & night condensation
190	4°27′N, 74°15′E	9 Nov	2245	265-500	In and below combined layer curtain and night condensation
191	4°25′N, 74°57′E	10 Nov	0643	250-400	In main DSL
192	6°43′N, 78°47′E	11 Nov	1814	70-80	In combined layer
193	6°43′N, 78°47′E	11 Nov	1950	450-600	Below combined layer curtain & night condensations
194	5°46′N, 81°13′E	20 Nov	0937	300-390	In main DSL
195	5°46′N, 81°13′E	20 Nov	1108	150-240	In surface curtain and clear layer above main DSL
196	5°06′N, 84°51′E	21 Nov	2026	75-85	In combined layer
197	5°06′N, 84°51′E	21 Nov	2224	75-85	In combined layer
198	5°44′N, 88°24′E	23 Nov	0327	75-120	In combined layer
199	5°44′N, 88°24′E	23 Nov	0535	75-90	In surface layer
200	6°00′N, 92°01′E	24 Nov	1047	80-85	In surface layer
201	6°05′N, 92°06′E	24 Nov	1228	275-280	In intermediate layer and surface curtain
202	6°05′N, 92°06′E	24 Nov	1358	400-475	In main DSL
203	6°05′N, 92°06′E	24 Nov	1537	750-850	Below main DSL and DSL curtain

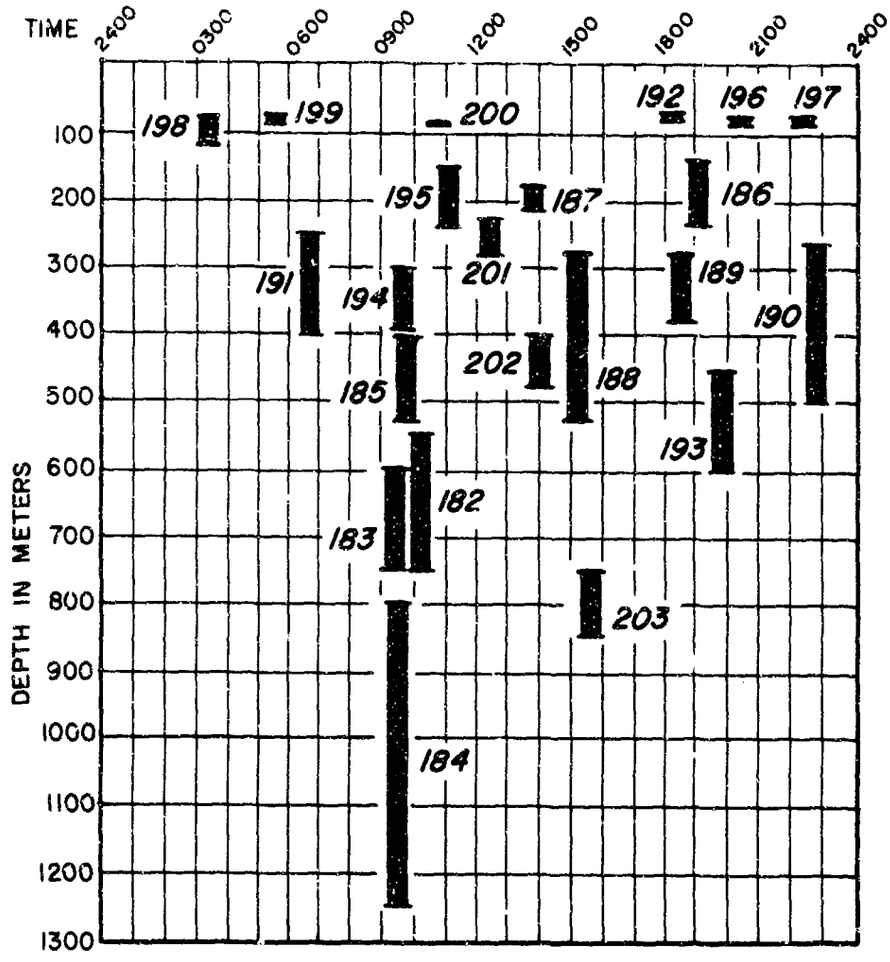

Figure 2. Distribution of midwater hauls with respect to time of day. Black bars represent individual hauls; length and vertical position of each bar indicate the depths the trawl was estimated to have fished most effectively.

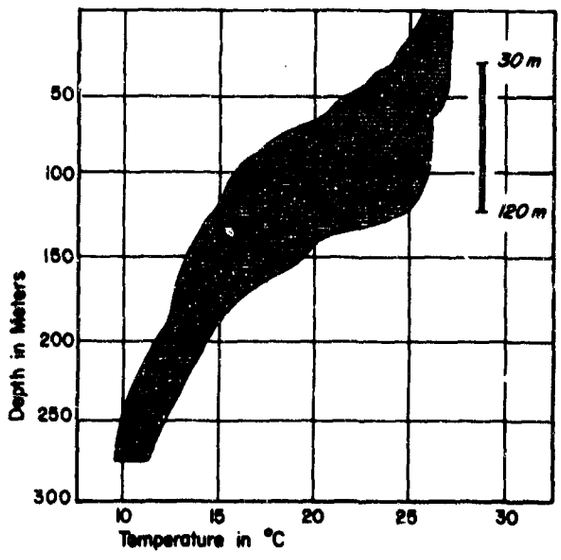

Figure 3. Composite bathythermograph tracings; the perimeter of the shaded area encompasses all tracings made during midwater trawling stations. Vertical bar from 30 to 120 m indicates region of the thermocline.

All samples of organisms reported in this paper were taken in a Tucker trawl. The mouth of the net was 10 by 10 feet, framed above and below by bars of 3-inch galvanized iron pipe and along each side by a braided nylon rope that connected the upper and lower bars. The net was 26 feet long, tapered evenly from mouth to cod end, and consisted of four sections of knotless nylon netting whose mesh sizes decreased from mouth to cod end as follows: an 8-foot section nearest the mouth with square mesh size 3/8 inch (stretched mesh 3/4 inch); a second section 9 feet long with square mesh size 1/4 inch (stretched mesh 1/2 inch); a third section 4 1/2 feet long with square mesh size 1/16 inch (stretched mesh 1/8 inch); a cod-end section 4 1/2 feet long of 1/16 inch square mesh Ace netting (stretched mesh 1/8 inch). The cod end terminated in a canvas collar into which fitted a stainless steel bucket 8 1/2 inches in diameter and 10 inches deep. The upper bar of the mouth frame was connected by a bridle and swivel to a tow cable of 3/8-inch wire rope that passed over a meter block suspended from an A-frame about 12 feet above the sea surface.

From stations 182 to 185 inclusive (between Mombasa and the Seychelles), the trawl was used as described above. For all subsequent stations, the trawl was modified in two ways. First, four 15-lb bronze homogeneous depressors, evenly spaced, were attached to the lower bar of the mouth frame to improve diving performance. Second, the cod-end section was lined inside with a cone of nylon gauze 20 meshes per inch. This lining not only aided in retaining organisms which formerly passed through the 1/16-inch square mesh of the outer net, but it reduced turbulence in the cod-end bucket so the trapped plankton and smaller nekton arrived at the surface in much better condition than they had before the net was modified.

On most stations, the trawl was lowered with the ship running slow ahead and the winch either running free or rapidly powering out the towing wire to avoid fishing above the desired depths as much as possible. On some occasions, when the ship was driven by a following sea and wind, the net was lowered with the propeller dead. In either case, following braking of the winch, the trawl was towed at 1 to 1.5 knots for 30 minutes, then recovered with the engines either stopped or on slow ahead. We assumed that the trawl continued to fish to some extent during recovery.

The depth of the net at all stages of a haul (Figs. 4 to 6) was estimated by calculations based on amount of wire paid out and the wire angle as measured by a Scripps inclinometer. The error introduced by the catenary of the wire was probably greatest during the period when the wire was being paid out and for the first few minutes after the winch was braked. (See Backus and Hersey, 1956, and Barham, 1957, Figures 9 and 10, for analyses of similar situations.) Depth-time recorders on board were all malfunctional, so no independent check on the accuracy of depths calculated from wire angles was available. However, the pull exerted by the large trawl and the action of the four depressors put such a heavy strain on the towing wire that we have assumed that once the wire angle became stabilized after braking the winch, the catenary of the towing wire, while unknown, was not enough to introduce a significant error into our depth calculations, considering the relatively short lengths of wire paid out. Times required for stabilization of wire angles for different lengths of wire out are shown in Figure 7. For hauls at depths to 150 m, wire angles stabilized within 2 to 5 min after the winch was braked; for hauls at depths of 200 to 500 m, wire angles usually stabilized within 10 min after the winch was braked. During some hauls (e.g., Stations 190 and 195), and with ship's speed maintained the while, wire was taken in *after* the wire angle was stabilized; the strain on the wire increased on such occasions, and wire angles appear to reliably indicate net depth. Also, the calculated path of the net during recovery, with the ship moving ahead at 1 to 1.5 knots, is considered to be reliable for all hauls. The curves shown in Figures 4 to 6 represent our best estimates of the path of the trawl for each haul. At a few stations, which were made in rough water and with a

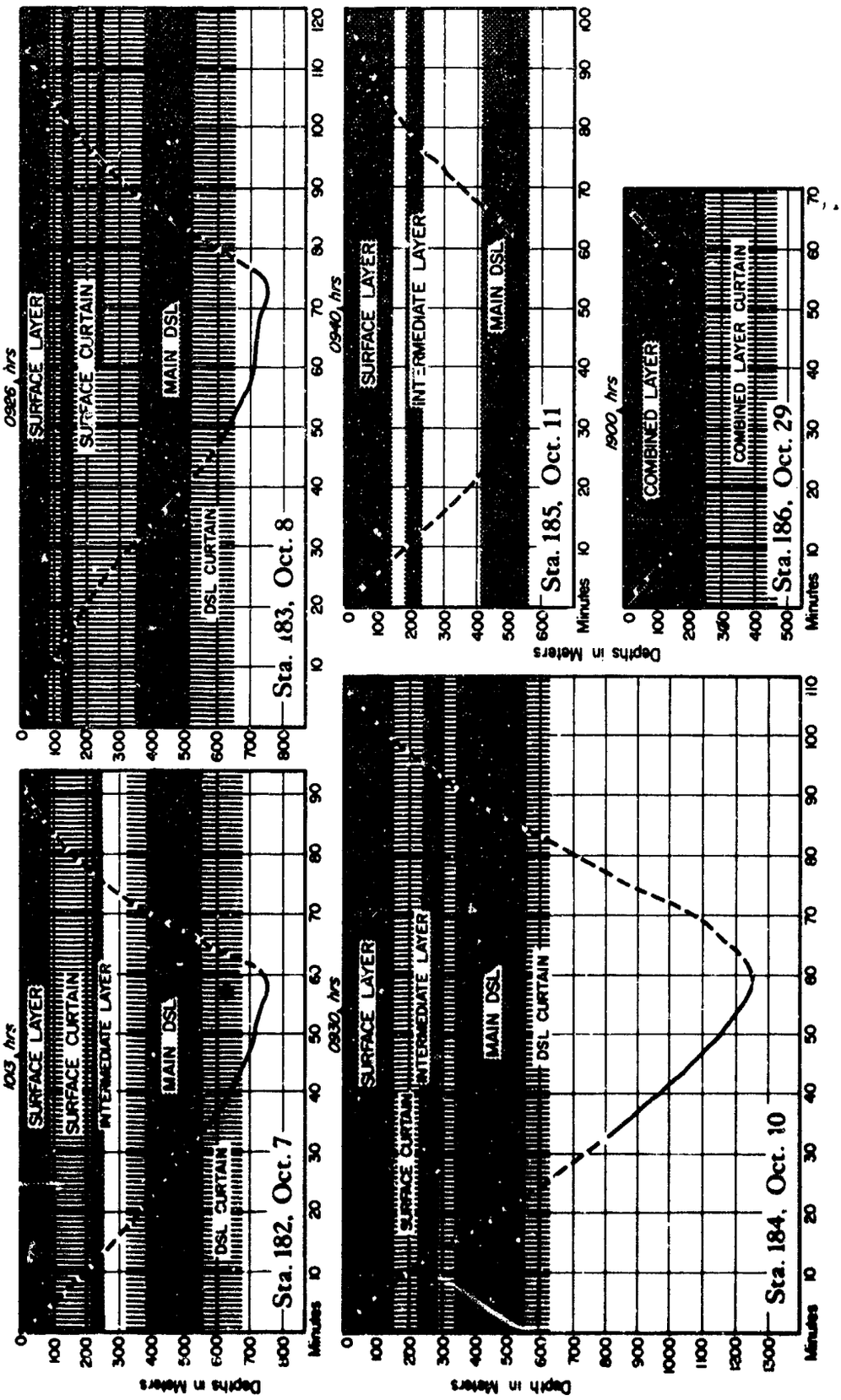

Figure 4. Profiles of Stations 182 to 186. For each profile, the heavy line indicates the estimated path of the trawl; the solid portion of the line indicates the portion of the haul during which the net was estimated to be fishing most effectively. Stipple pattern indicates heavy scattering; vertical bars indicate light scattering.

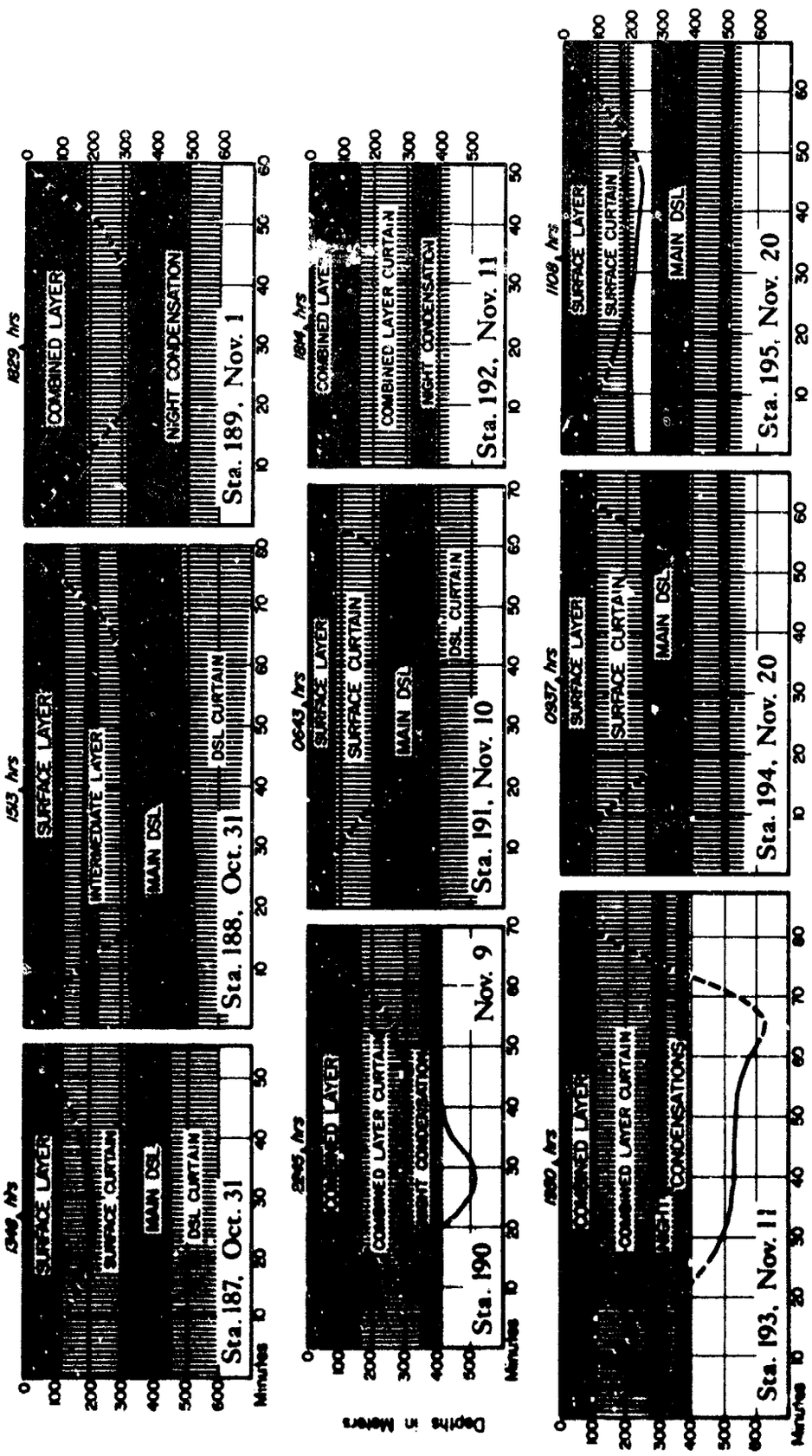

Figure 5. Profiles of Stations 187 to 195. For each profile, the heavy line indicates the estimated path of the trawl; the solid portion of the line indicates the portion of the haul during which the net was estimated to be fishing most effectively. Stipple pattern indicates heavy scattering; vertical bars indicate light scattering.

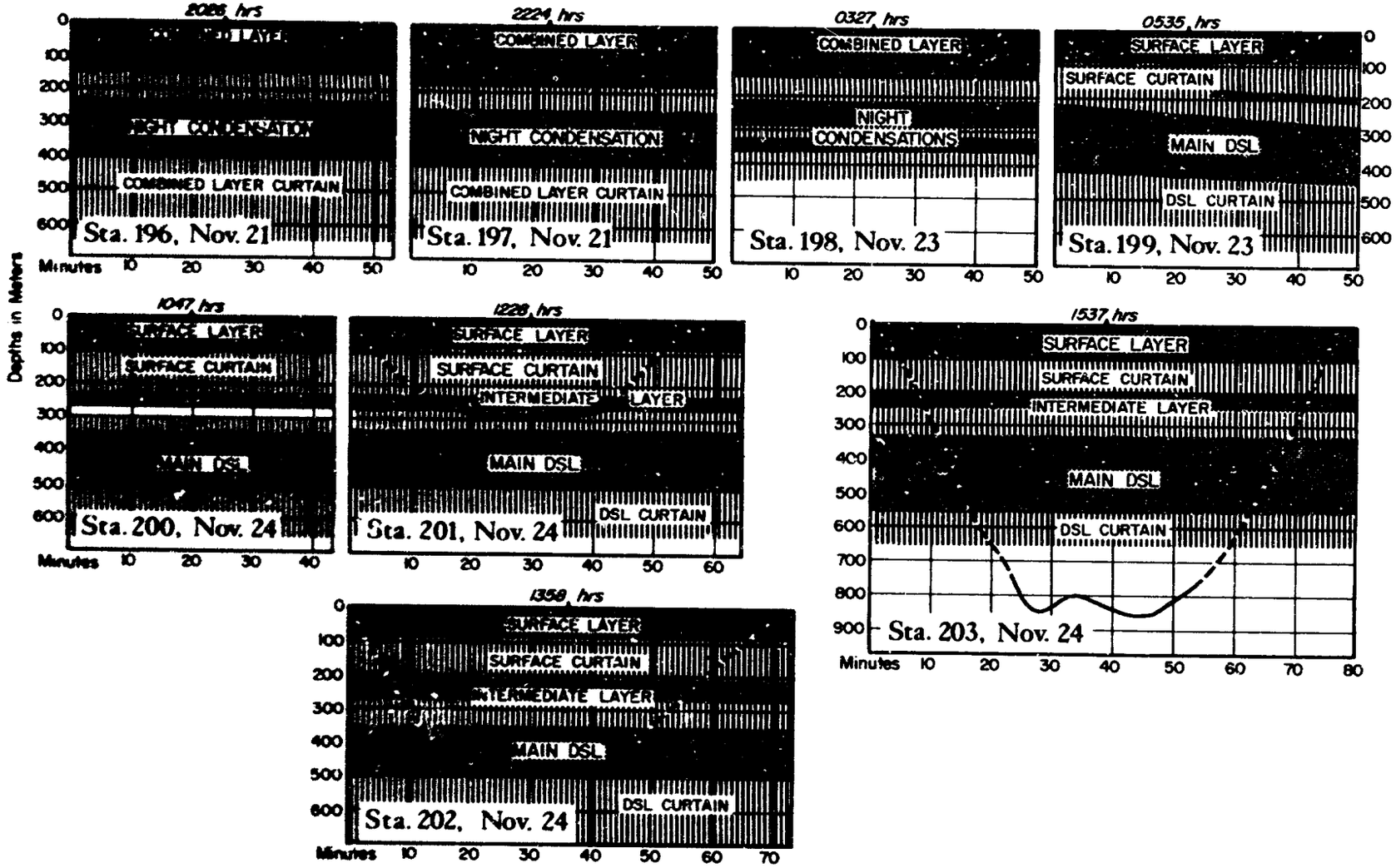

Figure 6. Profiles of Stations 196 to 203. For each profile, the heavy line indicates the estimated path of the trawl; the solid portion of the line indicates the portion of the haul during which the net was estimated to be fishing most effectively. Stipple pattern indicates heavy scattering; vertical bars indicate light scattering.

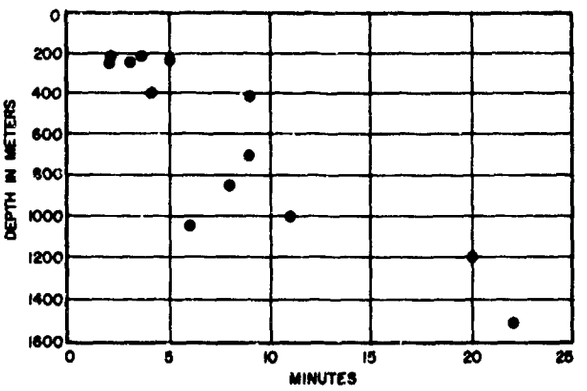

Figure 7. Time required to stabilize the wire angle for various lengths of wire paid out (omitting cases in which the wire was taken in or the ship's speed altered before the wire angle stabilized, or in which the wire angle never stabilized)

following wind and sea (e.g., stations 191, 198), the inclinometer was difficult to read and wire angles did not stabilize satisfactorily; under those conditions, adjustments in the ship's speed were made during the haul in an attempt to maintain wire angles within the range desired. The calculated depth curves for these stations show a wavy line, which appears to indicate marked changes in the depth of the net during the main trawling period; actual variation in net depth is probably less than that indicated.

On recovery, after the bucket was retrieved from the cod end, the net was flushed with sea water and picked over for organisms caught in the mesh; organisms recovered in this fashion were included in the rest of the catch. The catch was rough-sorted and preserved immediately thereafter. Members of the scientific party, each responsible for a different taxon, made tentative identifications and counts of each species taken and examined gut contents of selected specimens. Those responsible for particular groups were Proctor (siphonophores), Fielding (chaetognaths), Buchsbaum (molluscs), Ogden (amphipods), McPhearson (penaeids), Taylor (carideans), Jeanne Christofferson (euphausiids), Jay Christofferson (mysids and stomatopod larvae), Barber (tunicates), Stromborg, Wourms, and Bradbury (fishes). After the expedition, it was possible to recheck the identifications of the following groups: siphonophores, molluscs, penaeids, carideans, mysids, tunicates, and most fishes.

The following references proved the most useful. Siphonophores: Bigelow, 1911; Totton, 1954; Totton and Bargmann, 1965. Molluscs: Stubbings, 1938; Teach, 1946, 1948, 1949; Thore, 1949. Euphausiids: Einarsson, 1945; Tattersall, 1939. Mysids: Sars, 1885; Tattersall, 1939; Tattersall and Tattersall, 1951. Stomatopods: Townsley, 1953. Penaeids: Alcock, 1905; Boone, 1931; Dana, 1852; Hall, 1962; Hansen, 1896; Ramadan, 1938; Wood-Mason and Alcock, 1891. Carideans: Barnard, 1950; Borradaile, 1916; Calman, 1939; Chace, Jr., 1936; DeMan, 1920; Kemp, 1939; Holthuis, 1955. Tunicates: Thompson, 1948. Fishes: Bauchot-Boutin, 1953; Beebe and Crane, 1937; Bertelsen, 1951; Bertin, 1937; Bolin, 1959; Cohen, 1964; D'Ancona, 1928; D'Ancona and Cavinato, 1965; Fraser-Brunner, 1949; Gibbs, 1964a, 1964b; Grey, 1960, 1964; Lea, 1913; Marshall, 1966; Morrow, 1964a, 1964b; Morrow and Gibbs, 1964; Parr, 1960; Rofen, 1966a, 1966b; Roule and Bertin, 1929; Schultz, 1961; Walters, 1964. We

were assisted in the identifications by a number of specialists (see Acknowledgments). Some specimens have been retained by the specialists, but most have been deposited in the Smithsonian Oceanographic Sorting Center, Washington, D.C.

Recordings of the DSL were made with two instruments. The most generally useful was a Simrad Sonar, Model 540-4 (Simonsen Radio A.S., Oslo), powered through a 24-V Constavolt battery eliminator model 6024. Pulse power was 1,000 W with a frequency of 30 kHz. The instrument was used on echo-location (depth-sounding) setting and was set to record echos from the upper 1,500 m. Best recordings were obtained with a pulse length of 11 msec (dial setting of 3) and a sensitivity setting between 6 and 10, with best results between 6 and 7. Signal-to-noise ratio was unfavorable while underway with the main engine, so all recordings were taken with the ship's propeller stopped.

Subsidiary recordings were taken, often simultaneously with a Simrad Echo-Sounder Type 513-1. Power was supplied by the ship's generators, raised from 115 to 220 V by a Simrad Transformer Type 517-33. Pulse power was 800 W, with a frequency of 1 kHz. Best recordings were obtained with a pulse length of 8 msec (dial setting of 3) and a sensitivity setting of about 6. The Simrad Echo-Sounder, when used to record only the acoustical phenomena in the uppermost 500 m, provided a finer resolution of the upper DSL than did the Simrad Sonar, but it proved the less useful instrument for our purposes for two reasons: first, slight fluctuations in the strength and frequency of the ship's generator output or marked fluctuations in power usage aboard caused some artificial variations in recordings of the DSL; second, at several critical depths, a bottom echo from a previous pulse was recorded on the tape at DSL levels, obscuring the recorded DSL.

THE PATTERN OF THE DSL

Data on the sonic scattering layers were collected as follows.

Echograms were taken before and during each DSL trawling station to establish the position and structure of the sound scattering layers .

On five different days, 28 October to 2 November, 15 minutes of tracings were made at 3-hour intervals to assess the variability of the scattering pattern at specified hours of the day and night. During each period of recording, water and air temperature, sea conditions, wind force, and incident light were also recorded.

The DSL was recorded continuously for 37 hours from the evening of 24 November through the early morning of 26 November except for short periods when the tape was replenished. During the day, incident light was measured at 15-min intervals.

Isolated recordings of the DSL were made on a variety of other occasions.

The high read-out rate of the Simrad Sonar (about 2 m per hour) resulted in detailed resolution of scattering-layer changes per unit of time, which allowed careful analysis of these changes but made it impractical to publish photographs of complete echograms. Therefore, echograms were converted to diagrams (i.e., Figs. 4 to 6, 8, and 9) by greatly compressing the time axis of the echogram tape and reducing the various light and dark portions of the scattering recording to two or three categories represented respectively by light lines, medium lines, and dark stippling on the diagrams. Conversion from tape record to diagram involved interpretation and simplification but was done with consistency and care, so that the diagrams reflect fairly accurately the real differences in layers shown on the echograms.

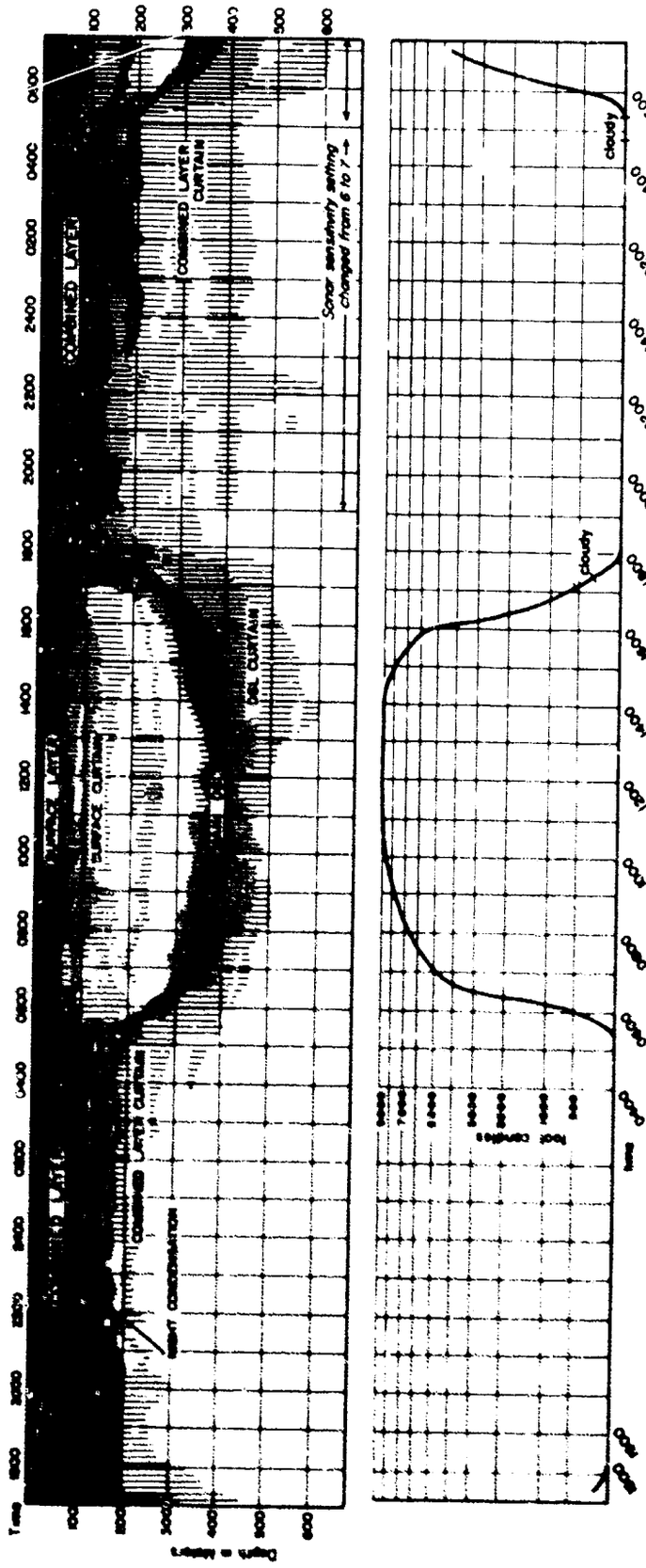

Figure 8. Above: diagram of scattering layers prepared from a 37-hour-long echogram recorded in the Bay of Bengal at 06°10'N, 93°07'E, beginning 1700 hours November 24 and ending 0715 hours November 26. Stippled patterns indicate heavy scattering, medium and light vertical lines indicate medium and light scattering respectively (see Figs. 10 and 11 for photographs of the actual echogram). Light scattering between the surface curtain and main DSL, centered at 250 m during the day, corresponds in position to the intermediate layer seen as heavy scattering on numerous other echograms (Figs. 4 to 6). Below: curve showing intensities of incident light for the period the echogram was being recorded.

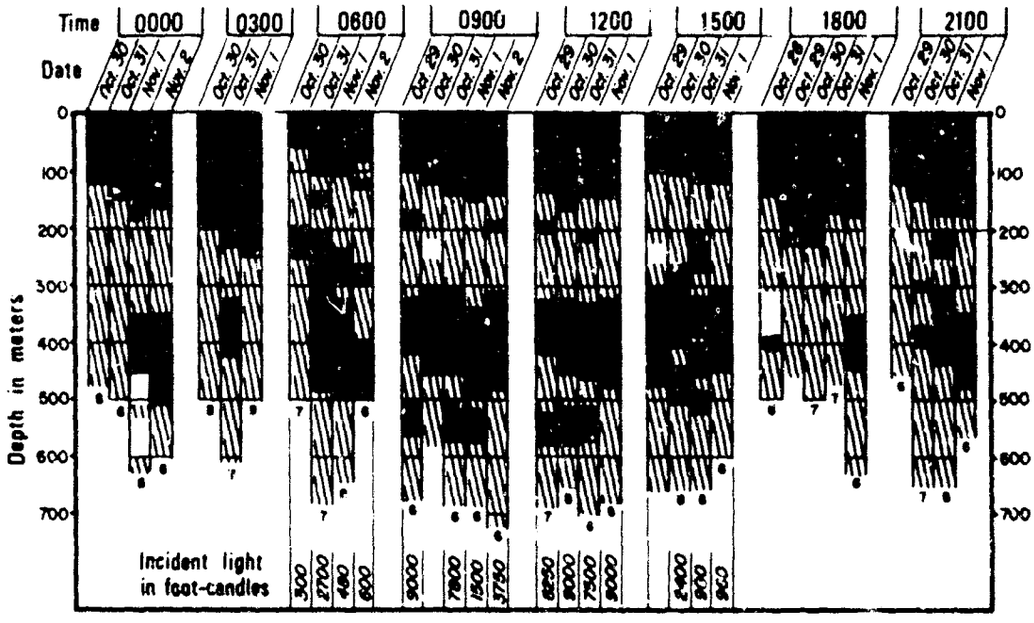

Figure 9. Diagrams showing variation in scattering layers recorded at specific hours between 28 October and 2 November between the Seychelles and Maldive Islands. Numbers below columns show sonar sensitivity settings.

General Features of DSL Patterns

Although echograms taken at the same time of day on consecutive days usually showed variation in thickness, vertical position, and number of bands, there were features that occurred regularly, or at least very frequently. For our comparative purposes it was convenient to designate each of these features by a distinctive term; Figures 4 to 6 and 8 show bands labeled with the terms we used. Definition of the terms are given as follows.

Main DSL. A layer of heavy scattering at least 50 m thick (e.g., Fig. 3) but generally thicker (e.g., Fig. 5, Sta. 187, 188, 191, etc.), represented on echograms by a dark band, which during the main part of the day lay with its top about 300 to 350 m below the surface. Sometimes the main DSL was very thick and subdivided into two bands, the lower band centered at or below 500 m (e.g., Fig. 6, Sta. 194 and 195; Fig. 9 shows that this split in the main DSL occurred frequently between 29 October and 2 November).

DSL curtain. A region of lightly recorded scattering that appeared on echograms as a fringe below the main DSL. The width of this band varied directly with the sensitivity setting of the sonar, but in general, the DSL curtain was not detectable more than 200 m below the bottom of the main DSL, tending to thicken in late afternoon because its lower margin did not ascend through as many meters as did the main DSL.

Surface layer. A layer of heavy scattering that occupied the top 60 to 150 m in daytime. We do not know whether the surface scattering resulted from the outgoing signal or whether there were actually sound scatterers present near the surface whose recording merged with that of the outgoing signal on the echogram.

Surface curtain. A layer of lightly recorded scattering extending from the surface layer to the main DSL. This layer often showed some heavy scattering within it (see Intermediate Layer) or clear layers from which no scattering was recorded (e.g., Fig. 4, Sta. 182; Fig. 5, Sta. 195; Fig. 6, Sta. 200; Fig. 8).

Intermediate layer. Any daytime layers that registered as relatively heavy scattering within the surface curtain (numerous echograms shown in Figs. 4 to 6).

Combined layer. A nighttime surface layer that occupied the top 150 to 250 m and that appeared on echograms to represent the band of the main DSL merged with the surface layer.

Combined layer curtain. A layer of lightly recorded scattering extending as a fringe below the combined layer. The combined layer curtain was continuous with the DSL curtain.

Night condensation. One or more layers of heavy scattering often recorded at night from below the combined layer but within the combined layer curtain. These night condensations sometimes persisted throughout the night, and on cloudy days they sometimes appeared at sunset.

The only bands consistently present on echograms were the main DSL, the surface layer, and the combined layer, and the main DSL showed variation in width and vertical position at any given hour from day to day. The most notable feature of the scattering layers was the 350-m migration of the main DSL downward from the surface at dawn and its return to the surface at sunset. Each migration was completed within 1.5 to 2 hours and was recorded on the sonar tape as a solid band or as several poorly separated bands moving gradually up or down. The main DSL remained at lower depths during the daylight hours. The intermediate layer, when present, underwent a similar migration at dawn and sunset. It is likely that the vertical movements of scattering layers are influenced by light intensities and by rates of change of light intensities, as Clarke and Backus (1964) were able to show for scattering layers in the north Atlantic.

The combined layer persisted throughout the night, and often, between 2400 and 0300 hours, a part of it appeared to descend 50 m, where it remained until sunrise.

Comparisons With Other DSL Studies

The generalized equatorial Indian Ocean DSL pattern is similar in its daytime DSL pattern to patterns recorded in the equatorial and North Pacific (Dietz, 1948), the southeastern Pacific (Hersey and Backus, 1962), the Mediterranean (Frassetto and Della Croce, 1965) and the eastern central Pacific (Barham, 1966). In the echograms reproduced in these publications, the daytime depth of the center of the main DSL is between 350 and 400 m, which is approximately the daytime depth of the main DSL in Fig. 8. In view of the differences in latitude and light regime between all these areas, the similarity of daytime depth of the main DSL is striking.

However, Hersey and Backus (1962) report that in the North Atlantic, the DSL band appears as two layers, one centered at 250 m and the other at 500 m. This generalized pattern is based on the examination of about 150 separate recordings. The echogram of Moore (1950, his Fig. 1a) from the North Atlantic shows a very similar pattern, with an intermediate layer at 250 m and a main layer between 500 and 600 m. These data indicate that the main scattering layer is consistently about 100 m deeper in the North Atlantic than it is in the equatorial Indian Ocean, but in both oceans there is usually an intermediate layer at 250 m. The DSL's recorded by Dietz (1948) and Barham (1966) in the Pacific conspicuously lack the intermediate layer that is present at 250 m in the Indian Ocean, the North Atlantic, and the Pacific off the coast of Chile (Hersey and Backus, 1962, their Fig. 6).

Barham (1966) noted that an echogram, which was being recorded on Scripps Research Vessel T-441 as it accompanied the diving saucer *Soucoupe* during Dive 3 off Baja California, showed an intermediate layer splitting off from the main layer; shortly thereafter, the intermediate layer disappeared from the echogram. Barham, who was in the diving saucer while the echogram was being recorded, saw scattering organisms in what corresponded to the intermediate

layer as it was splitting off from the downward-migrating main layer (his Fig. 2). About 45 min later, he saw no organisms at the depth where the intermediate layer would have been, that is, at 220 to 240 m.

In the Indian Ocean, the intermediate layer becomes most distinct in the middle of the day, from 0900 to 1300 hours. Hersey and Backus (1962, their Fig. 6) show a heavy intermediate layer present throughout daylight hours. The 250-m intermediate layer appears to be a most variable component of the scattering layers.

Continuous 37-Hour Recording

The 37-hour length of fathometer tape is diagramed in Figure 8, in which the time axis is reduced to about .0032 that of the actual tape length. The figure illustrates how the size, number, and vertical position of individual bands varied within short periods of time, and also how a change of one unit in the sensitivity setting of the sonar could introduce bands that were not previously recorded. Photographs of portions of the 37-hour echogram are shown in Figures 10 and 11.

Light-intensity readings taken at 15-min intervals during most of the period of continuous sonar recording are shown below the echogram in Figure 8. Note that with the first daylight, the main DSL began its migration downward, reaching its lowest depth at the time of greatest light intensity. As the light intensity dropped in the late afternoon, the main DSL approached the surface.

Variation in Scattering Layers

Figure 9 illustrates variation in scattering layers recorded at particular times of day on different days from 28 October to 2 November. During each 15-min DSL observation, records were also made of the amount of incident light, the barometric pressure, air and water temperatures, wave height, wind force, and percent of cloud cover. The variability in layering that was recorded did not show any clear correlation with variations in any of these factors.

The amount of light at a particular time of day did not appear to have any consistent effect on the type and depth of the scattering layers that formed. For example, the light conditions at 0600 hours were similar on 30 October, 1 November, and 2 November (Fig. 9); incident light in foot-candles (ft-c) registered 300, 480, and 600 ft-c, respectively. However, the pattern for 1 November does not resemble that for 30 October nearly as much as it resembles the pattern for 31 October, when the incident light registered 2,700 ft-c at 0600 hours, or approximately 5.5 times that measured for 1 November. At 0900 hours on 29 October and 31 October, the incident light readings were similar (9,000 and 7,800 ft-c, respectively), yet the echogram for 29 October includes an intermediate layer, whereas that for 31 October does not. The main DSL was split into two bands at 1200 hours on 30 October, but not on 1 November, although the illumination was the same on the two days. Interpretation of these findings would require knowledge of the light conditions for the hour or two immediately preceding each observation, but such data were not recorded.

HORIZONTAL DISTRIBUTION OF ANIMALS

Horizontal distributions of animals taken during the cruise are very incomplete because only 14 localities were sampled along a cruise track of 4,300 nautical miles. However, our data show some agreement with the works of others. For example, the stomiatoid fish *Diplophos taenia* is known only from the western Indian Ocean (Grey, 1960), and we collected this form at three

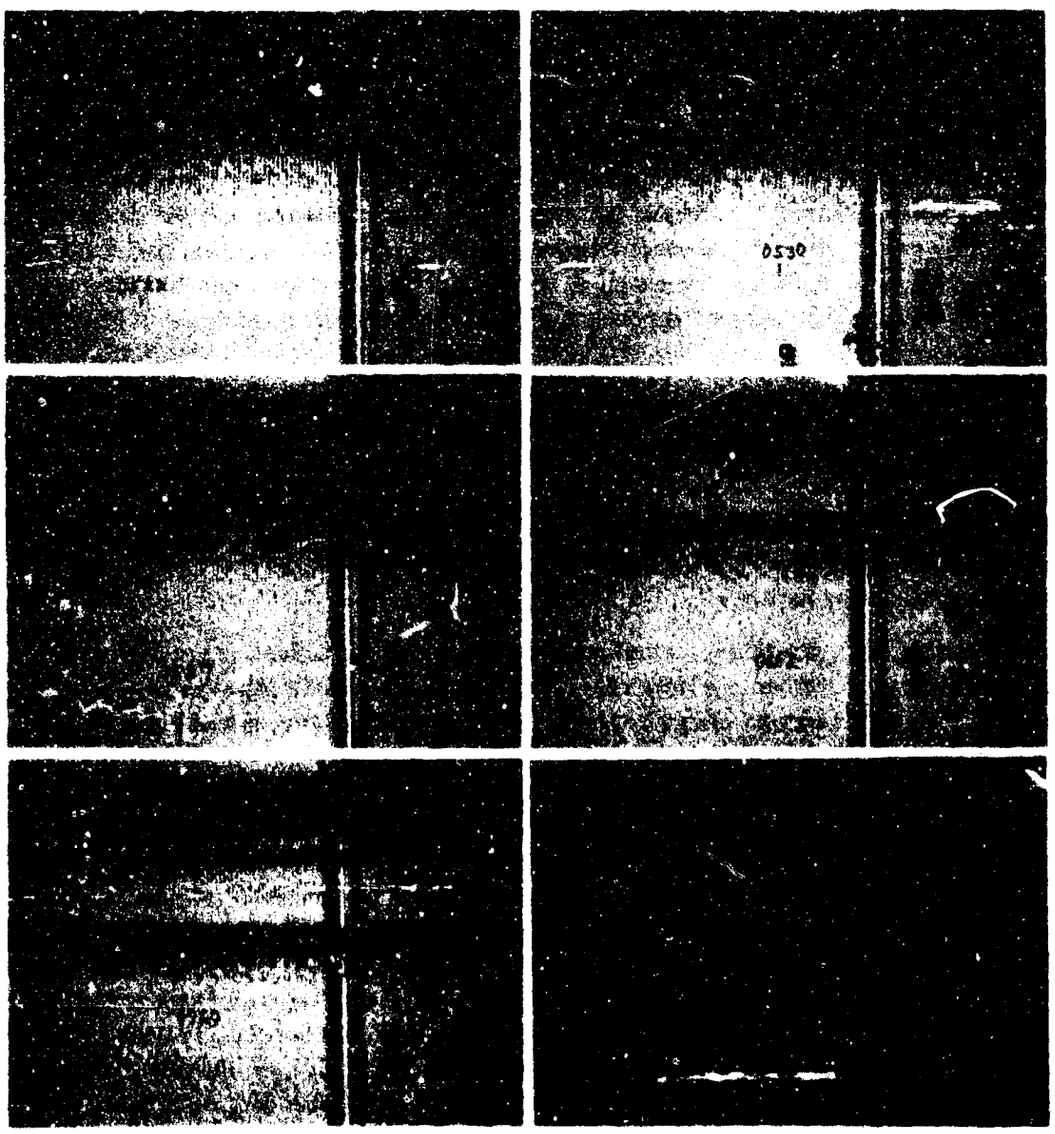

Figure 10. Photographs of selected portions of the 37-hour echogram. a-e; descending main DSL on 25 November. f; main DSL at daytime depth on 25 November. Times covered by photographs are as follows: a, 0521 through 0525; b, 0528 through 0532; c, 0535 through 0539; d, 0650 through 0654; e, 0718 through 0722; f, 1359 through 1403.

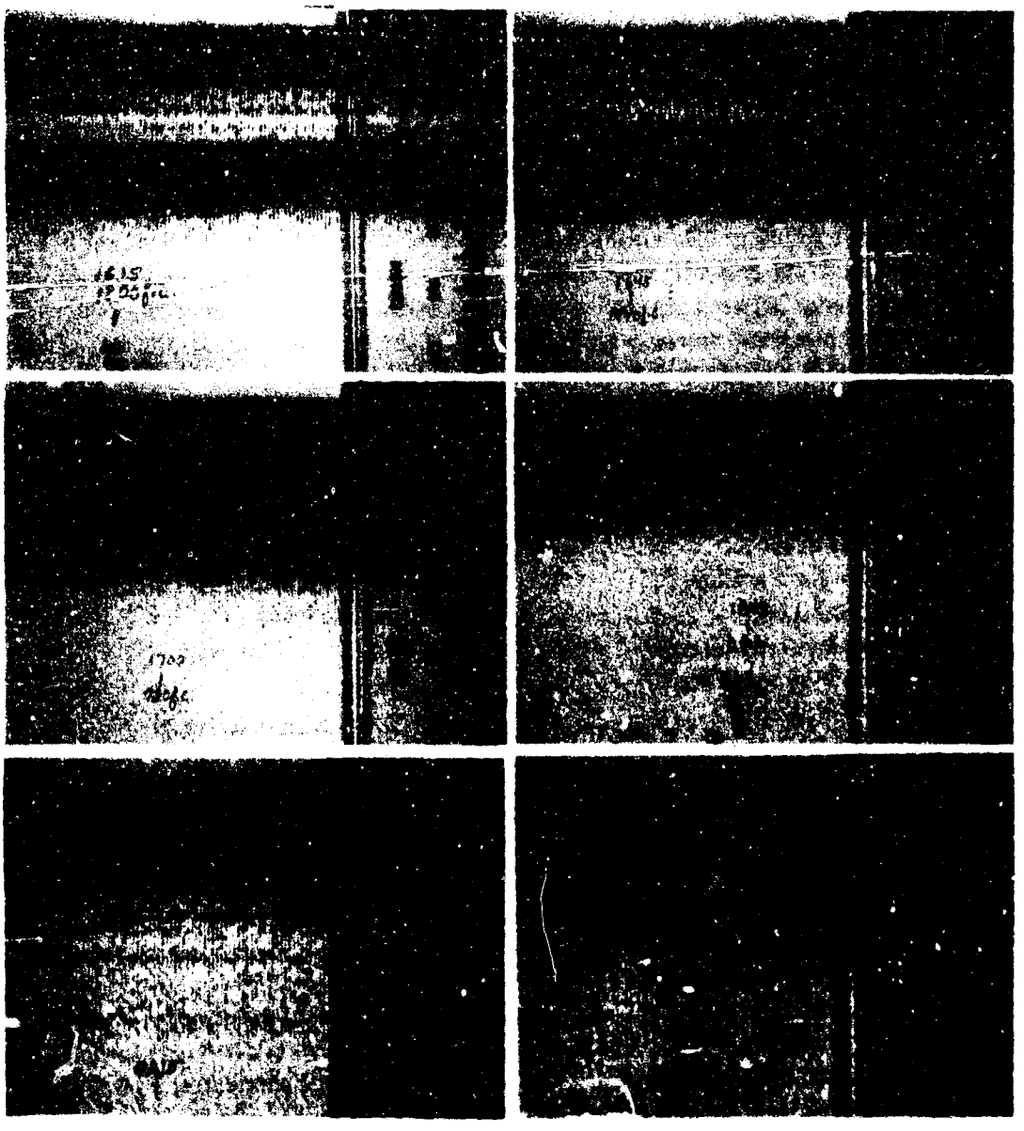

Figure 11. Photographs of selected portions of the 37-hour echogram. a-c, ascending main DSL on 25 November, d-f; combined layer on 25 and 26 November (e shows a night condensation). Times covered by photographs are as follows: a, 1614 through 1618; b, 1644 through 1648; c, 1659 through 1703; d, 1801 through 1805; e, 2214 through 2218; f, 0229 through 0233.

localities west of the Maldive Islands but never east of them (Fig. 1). The myctophid fishes *Benthosema suborbitale* and *Centrobranchus nigro-ocellatus* are apparently restricted in the Indian Ocean to latitudes south of the equator, while *Benthosema fibulatum* has a northerly distribution in the Indian Ocean (Nafpaktitis and Nafpaktitis, 1969), and our data agree with these findings. Gibbs and Hurwitz (1967) have reaffirmed that two species of *Chauliodus* occur in the Indian Ocean, *Chauliodus pammelas* to the north in the Arabian Sea and Bay of Bengal and extending just south of Ceylon, and *Chauliodus sloani* in more southerly portions of the Indian Ocean, its horizontal range overlapping that of *Chauliodus pammelas* somewhat. Thus, during the southerly leg of our cruise (southwest of the Maldive Islands), we took only *Chauliodus sloani*, as might be expected, and we took *Chauliodus pammelas* on the northern leg.

The literature concerning the horizontal distributions of midwater animals in the Indian Ocean suggested we would find a faunal break between the locality of Sta. 189 and that of Sta. 190 (Fig. 1). Because our cruise track extended in a direction from southwest to northeast, the geographical difference between Sta. 189 and Sta. 190 would reflect simultaneously both a north-south faunal break and an east-west faunal break. Sampling regimes from the two sections of the cruise were only roughly comparable, as follows.

Southwest Cruise track, seven localities (Sta. 182-189)	Northwest Cruise track, seven localities (Sta. 190-203)
5 localities for 5 deepwater daytime hauls	3 localities for 4 deepwater daytime hauls
2 localities for 2 shallow nighttime hauls	3 localities for 4 shallow nighttime hauls
(1 shallow daytime haul was also made at one of the above localities)	1 locality for a deepwater nighttime haul
	(4 shallow daytime hauls and 1 additional deepwater nighttime haul were also made at the above localities)

Of the 161 species of invertebrates and fishes eventually identified (Table 2), only 73 were taken in both the southwestern and northeastern equatorial Indian Ocean; these forms include 11 siphonophores, 7 pteropods, 2 heteropods, 2 mysids, 7 euphausiids, 8 decapod crustaceans, 7 tunicates, and 29 fishes. There were 52 species collected only in the southwestern equatorial Indian Ocean (Sta. 182-189), including 2 siphonophores, 4 pteropods, 5 heteropods, 4 cephalopods, 6 decapod crustaceans, and 31 fishes. There were 36 species collected only in the northeastern equatorial Indian Ocean (Sta. 190-203), including 3 siphonophores, 3 pteropods, 3 heteropods, 1 cephalopod, 1 mysid, 5 decapod crustaceans, 1 tunicate, and 19 fishes.

Examples of fishes we collected in both the southwestern and northeastern equatorial Indian Ocean that were already known to have distributions that broadly span the entire equatorial Indian Ocean are *Danaphos oculatus* (Grey, 1960) *Vinciguerria nimbaria* and *Valenciennellus tripunctulatus* (Grey, 1964), *Chauliodus sloani* (Morrow, 1964b), *Stomias affinis* and *Stomias nebulosus* (Morrow, 1964c), *Argyropelecus lychnus* (Schultz, 1961) and some of the lantern fishes, for example, *Notolychnus valdiviae*, *Diaphus elucens*, *Diaphus luetkeni*, *Diaphus splendidus*,

Table 2. Species with Numbers of Individuals Taken at Each Station

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
SIPHONOPHORA		All siphonophores from this trawl were lost																				
Physonectae																						
Agalma okeni Eschscholtz	–		–	–	–	–	–	x*	–	–	x	x	x	–	x	x	x	–	–	x	x	–
Agalma sp.	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–
Halistemma rubrum (Vogt)	–		–	–	–	–	–	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–
Unidentified physonects	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x
Calycophorae																						
Abyla trigona Quoy & Gaimard	2		–	4	4	5	2	–	–	–	1	–	–	–	–	–	1	–	–	–	1	–
Abylopsis tetragona (Otto)	14		19	48	54	1	23	3	8	10	394	11	3	9	103	176	227	1	1	–	32	11
Ceratocymba dentata (Bigelow)	–		–	–	2	1	–	–	–	–	–	1	–	–	1	2	–	–	–	–	–	–
Ceratocymba leuckarti (Huxley)	–		–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
Ceratocymba sagittata (Quoy & Gaimard)	–		–	–	–	–	–	–	–	1	–	–	–	–	–	3	–	–	–	1	–	–
Chelophyes appendiculata (Eschscholtz)	–		5	6	–	2	–	4	–	–	3	–	–	–	–	–	–	4	8	10	–	4
Chelophyes contorta (Lens & van Riemsdijk)	–		–	–	–	76	–	–	–	–	–	–	–	1	–	1	9	5	–	7	–	7
Chuniphyes multidentata Lens & van Riemsdijk	1		3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diphyes bojani (Eschscholtz)	–		–	–	–	49	1	–	–	–	–	–	–	–	–	1	–	–	9	9	6	–
Diphyes dispar Chamisso & Eysenhardt	–		–	–	1	–	–	–	–	–	3	–	2	13	1	9	6	7	5	–	1	–
Eudoxoides mitra (Huxley)	–		1	–	–	14	–	–	–	–	2	–	–	3	–	1	3	–	1	1	–	3
Hippopodius hippopus (Forskål)	–		x	–	x	x	x	x	–	–	x	–	–	x	x	–	x	–	–	x	x	x
Vogtia spinosa Keferstein & Ehlers	–		x	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified calycophorans	–		3	–	–	4	1	–	–	–	3	1	–	–	7	7	–	–	–	1	–	–
MOLLUSCA																						
Gastropoda, Pteropoda																						
Cavolinia globulosa (Rang)	2	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–	3	–	–	–	–	–
Cavolinia inflexa (Rang)	9	2	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cavolinia longirostris (Lesueur)	–	–	–	4	–	1	2	–	23	1	1	–	–	12	7	22	1	–	–	3	1	–
Cavolinia uncinata (Rang)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Cavolinia sp.	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Creseis (probably *acicula* or *virgula*)	–	1	–	–	–	1	–	–	–	3	–	–	2	8	1	9	–	–	–	–	–	–
Cuvierina columnella (Rang)	2	–	2	–	–	–	2	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–

x = nectophores present; siphonophore individuals could not be counted.

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Number	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Diacria q. *quadridentata* (Lesueur)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	72	14	12	11	3
Diacria q. *costata* Pfeffer	20	15	8	3	–	3	5	–	1	–	2	1	–	5	4	4	–	3	–	–	–	–
Diacria quadridentata juvenilus (*Claudova pygmaea* Boas)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–
Diacria trispinosa major (Boas)	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ruelio cuspidata (Bosc)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–
Ruelio pyramidata (Linné) (or possibly *balantium* (Rang))	3	15	3	–	6	–	25	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ruelio sp.	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	3	–	–	1	–	–	–
Styliola subula Quoy & Gaimard	–	–	–	–	–	–	9	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Limacina (more than one species?)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	1	–	–	–	–	–
Cymbulia sp.	20	*	1	33	10	–	100	20	3	28	59	9	4	90	190	284	30	1	1	–	–	2
Peracle (more than one species?)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	6	–	1	–	–	–	–
Gastropoda, Snails																						
Columbellidae, sp.	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
Tomtes "*limacina*" larvae	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–
Natacidae, sp.	–	–	–	–	–	5	4	1M	–	–	–	–	–	6	1	3M	4	5M	–	–	–	–
Natacidae	–	–	–	–	–	1	–	–	–	–	–	3	–	5	–	1M	–	–	1	–	–	–
Unidentified snails	–	–	–	–	–	–	–	–	–	–	1	3	–	2	–	–	–	1M	1	–	–	–
Gastropoda, Heteropoda																						
Oxygyrus keraudrenii (Lesueur)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–
Atlanta (more than one species)	–	–	–	–	–	10	5	2	5	2	–	–	1	12	–	70	21	111	26	7	1	18
Carinaria placenta (Lesson)	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–
Carinaria cithara Benson	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Carinaria cristata (Linné)	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Carinaria sp.	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pterosoma planum Lesson	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Pterotrachea coronata Forskål	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pterotrachea minuta Bonnevie	–	–	–	–	–	1	1	1	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Pterotrachea scutata Gegenbaur	1	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pterotrachea sp.	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified heteropods	–	–	–	–	–	–	1	3	–	–	–	–	1	3	3	1	–	1	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Cephalopoda, Decapoda																						
Chiroteuthidae, juvenile	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cranchia scabra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Unidentified cranchiids	–	–	–	–	–	–	1	–	–	–	2	1	–	2	1	–	–	2	–	–	–	–
Pterygioteuthis sp.	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calliteuthis sp., juvenile	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified histioteuthid juvenile	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Chiroteuthis sp., juvenile	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified squid, adult	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Unidentified squids, juveniles	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Cephalopoda, Octopoda																						
Amphitretus pelagicus Hoyle, adult	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphitretus pelagicus Hoyle, juveniles	–	–	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphitretidae, sp.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Unident. larval & juvenile cephalopods	–	–	3	–	–	9	2	2	–	–	4	–	–	2	1	6	2	1	–	2	–	–
CRUSTACEA																						
Amphipoda																						
Scina	2	–	3	1	2	–	–	–	1	–	5	–	–	–	1	–	–	–	–	–	–	–
Cyphocaris	–	–	1	1	–	–	2	–	1	1	–	1	–	–	–	–	–	–	–	2	6	2
Paraphronima	–	–	1	–	5	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Phronima	10	1	3	4	3	9	9	3	1	1	1	1	–	–	7	4	–	10	5	3	2	–
Anchylomera	–	–	15	–	6	25	3	8	70	2	2	2	–	–	–	–	30	48	2	6	6	12
Hyperiona?	–	–	–	–	–	–	–	–	–	–	1	3	–	–	–	–	–	–	–	–	–	–
Phronina	–	–	1	–	3	3	2	2	–	1	1	–	1	–	1	1	–	4	1	7	–	1
Oxycephalus	–	–	–	2	1	–	–	–	–	–	1	–	–	–	2	1	–	–	1	1	–	–
Oxycephalidae	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	4	3	–	–	–	–
Cranocephalus	–	–	1	–	1	3	–	1	–	–	–	–	–	–	3	2	–	–	–	1	–	–
Rhabdosoma	2	1	1	–	1	1	3	1	–	–	–	–	–	–	2	4	64	57	1	1	–	4
Hyperiidae	–	–	–	–	–	–	–	2	3	–	–	1	2	–	–	3	–	–	–	–	–	–
Platyscelidae	–	–	–	6	2	10	8	8	1	5	2	1	1	–	6	1	12	25	7	3	4	8

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Pilidia	–	–	–	–	2	4	5	5	–	–	3	–	–	–	–	–	5	–	–	–	–	1
Gammaridae	1	–	–	1	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified amphipods	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
Mysidacea																						
Mysidia gracilis Dana	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	81	–	–	–	–	–
Mysidia shoemakeri Milne-Edwards	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	5	2	–	–	–	–
Gastrophasmis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Isopoda																						
Lyidotanella larvae	2	1	1	5	–	1	–	–	–	–	3	1	–	–	–	–	5	1	5	3	2	4
Odonandrocyclus larvae	–	–	–	3	–	–	–	–	–	–	–	–	1	–	–	–	4	–	–	1	–	–
Pseudotanella larvae	–	1	1	3	x	–	–	–	–	–	=	1	5	–	1	–	13	–	1	3	–	–
Tanella larvae	1	–	4	23	–	–	–	–	–	3	6	10	9	37	3	3	45	1	–	2	1	1
Euphausiacea																						
Thysanopoda sp.	44	26	47	72	66	1	219	50	131	33	142	128	254	3	132	490	601	17	–	–	56	37
Thysanoessa sp.	36	–	–	5	56	11	11	8	5	1	13	10	4	–	–	–	4	1	–	–	–	–
Stylocheiron, species a	–	6	1	6	–	117	9	37	89	5	179	70	26	47	61	247	275	40	173	37	8	13
Stylocheiron species L	2	–	6	–	10	–	–	5	–	–	3	5	1	–	3	7	–	–	–	–	–	–
Nematoscelis sp.	–	–	20	–	2	–	–	–	47	6	–	6	20	–	1	3	3	–	–	–	–	15
Nematobrachion sp.	–	–	–	–	19	–	3	2	1	3	2	5	3	–	–	4	2	13	–	–	4	1
Euphausia sp.	–	2	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified euphausiids	21	31	22	3	40	15	106	54	121	121	107	135	214	12	127	269	274	2	37	14	16	45
Decapoda, Penaeidea																						
Hemipenaeus crassipes (Wood-Mason)	–	–	20	–	18	–	–	7	22	–	–	25	46	–	–	–	–	–	–	–	–	44
Sergestes robustus Smith	13	–	6	–	13	–	–	26	24	5	159	23	–	4	47	88	14	–	–	–	–	19
Sergestes sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acetes sp.	–	–	6	–	12	–	–	5	–	–	–	17	–	–	–	–	–	–	–	–	–	10
Eusicyonis carbonata (Olivier)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acetes bullosa (Dana)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Lucifer acuta (Dana)	–	–	4	2	3	1	–	22	1	5	–	–	6	57	15	–	62	136	403	29	49	27

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Number	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Decapoda, Caridea																						
Acanthephyra armiphorus Bate	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acanthephyra indica Bate	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Acanthephyra quadriplicata Kemp	–	–	6	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acanthephyra sividoi Kemp	–	–	–	–	6	–	–	5	2	5	–	6	–	–	–	–	–	–	–	–	–	–
Acanthephyra sanguinea Wood-Mason	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ophiopherus gracilirostris A. Milne-Edwards?	1	–	–	–	2	–	–	–	–	2	1	1	–	–	–	–	–	–	–	–	1	–
Ophiopherus typus H. Milne Edwards	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Systellaspis orientalis (Faxon)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hymenopbar gilesii Wood-Mason	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Notocrangon antiqui A. Milne-Edwards	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Pasiphaea sivadasani Bate	–	–	–	–	1	–	–	3	–	–	–	–	–	–	4	2	2	–	–	–	–	5
Thalassocaris lucida (Dana)	–	–	–	–	–	–	–	–	18	13	–	45	–	–	207	262	–	–	–	–	–	5
Unidentified decapod larvae	9	10	3	17	–	–	–	–	–	5	2	2	–	9	2	–	6	11	–	–	–	9
CHAETOGNATHA																						
Unidentified chaetognaths	5	56	156	87	186	106	78	22	340	1040	75	575	150	155	390	130	915	515	6	23	61	80
UROCHORDATA																						
Pyrosoma atlanticum Peron (colonies)	6	–	4	–	204	–	500	800	5	1	17	7	–	–	10	1	16	6	–	–	2	8
Doliolum gegenbauri (Uljanin)	–	–	–	–	–	–	–	–	2	1	1	–	600	114	–	–	28	13	–	–	–	–
Megalina hemigena (Quoy & Gaimard)	–	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	3	–	–	–	–	–
Cyclosalpa virgula (Vogt)	–	–	–	–	–	50	–	–	–	–	–	–	–	–	–	5	10	–	31	2	11	–
Pegea confoederata (Forskal)	–	–	–	–	–	50	2	11	6	2	–	1	–	–	–	–	13	31	–	3	–	–
Salpa zonaria (Pallas)	23	5	7	17	32	–	16	57	34	27	–	–	–	2	3	–	38	–	–	–	–	–
Salpa fusiformis Cuvier	–	–	–	–	12	–	200	100	1	–	–	–	–	–	12	13	24	–	–	–	–	–
Thalia democratica (Forskal)	–	–	1	–	3	1	2	–	4	–	–	–	1000	132	–	2	–	–	–	1	–	1
young (Pegea?)	–	–	–	–	–	–	1000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
FISHES																						
Argentinoidei																						
Bathylagus sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Opisthoproctus soleatus Vaillant	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Number	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Stenotrichid																						
Vinciguerria nimbaria (Jordan & Williams)	1	–	1	2	1	–	1	–	1	–	4	1	6	–	23	45	1	–	–	–	–	1
Diplophos taenia Gunther	1	–	–	–	3	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ichthyococcus ovatus (Cocco)	–	–	–	–	–	–	2	–	–	2	–	1	–	–	–	–	–	–	–	–	1	–
Gonostoma atlanticum Norman	1	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyclothone alba Brauer	45	84	92	74	–	–	24	–	12	67	–	131	30	–	–	–	–	–	–	–	2	44
Cyclothone pallida Brauer	24	7	47	–	–	–	–	–	–	–	–	–	18	–	–	–	–	–	–	–	–	39
Cyclothone pseudopallida Mukhacheva	13	6	5	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	10
Cyclothone undulata Garman	6	–	44	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
Danaphos oculatus (Garman)	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Polustomidion atlanticum (Kenrick)	–	–	–	1	–	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Gonostomatid larvae	–	–	–	–	–	–	6	–	–	–	2	–	–	–	–	7	7	–	–	–	–	–
Unidentifiable gonostomatids	9	2	–	–	1	–	–	1	–	2	–	2	–	–	7	–	–	–	–	–	–	1
Argyropelecus hemigymnus dolfeini Regan	–	–	–	1	1	–	1	2	1	3	–	–	1	–	–	–	–	–	–	–	2	–
Argyropelecus hemigymnus Cocco	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Argyropelecus affinis Garman	–	–	–	–	–	–	–	–	3	1	–	6	–	–	–	–	–	–	–	–	–	–
Unidentified Argyropelecus	–	2	–	3	–	–	1	–	–	3	–	–	1	–	–	–	–	–	–	–	–	–
Sternoptyx diaphana Hermann	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified sternoptychids	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1
Chauliodus danae Bruun & Schmidt	–	–	–	–	1	–	–	1	1	1[a]	–	–	–	–	–	2	3	–	–	–	–	–
Chauliodus guentheri Alcock	–	–	–	–	–	–	–	–	–	1	2	3[a]	4	–	–	–	–	–	–	–	–	–
Stomias nebulosus Alcock	4	2	4	–	5	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Stomias affinis Günther	2	–	–	–	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	–	–	–
Unidentifiable Stomias	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	4
Allocyttus fusiformis Peters	1	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astronesthes cyaneus (Brauer)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astronesthes indicus Brauer	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melanostomias valdiviae Brauer	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photonectes oligopus (Döderlein)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Bathophilus g. vent Parr	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Number	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Bathophilus sp. (probably *bifilis* Gibbs) *Stylephorus*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Alepocephalidae																						
Holtbyrnia sp.	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Myctophidae																						
Coccorella atrata (Alcock)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Scopelarchoides ?	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scopelosaurus sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hygophum (*proximum* Becker?)	1	–	–	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	–	–	–	–
Benthosema fibulatum (Gilbert & Cramer)	–	–	–	–	–	–	–	–	–	–	4	–	3	–	4	–	–	–	–	–	–	–
Benthosema suborbitale (Gilbert)	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diogenichthys panurgus Bolin	–	–	1	–	–	–	–	1	–	–	8	1	–	–	1	3	3	–	–	–	–	–
Myctophum lychnobium Bolin	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2	–	–	–	–	–	–	–
Myctophum spinosum (Steindachner)	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Myctophum nitidulum Garman	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–
Myctophum asperum Richardson	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–
Symbolophorus sp. (*evermanni* (Gilbert)?)	–	–	1	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Symbolophorus sp.	–	–	–	–	3	–	–	–	–	–	–	2	–	–	–	–	1	–	–	–	–	–
Centrobranchus nigro-ocellatus (Günther)	1		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus problematicus Parr	–	–	–	–	9	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–
Diaphus splendidus (Brauer)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	17	–	–	–	–	–	–	–
Diaphus garmani Gilbert	–	–	–	1	1	–	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–
Diaphus lucidus Goode & Bean	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus regani Tåning	–	–	–	–	–	–	–	–	2	1	7	1	–	–	2	2	–	–	–	–	–	1
Diaphus jenseni Tåning	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus elucens Brauer	1	1	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Diaphus termophilus Tåning	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus parri Tåning	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–
Diaphus (*gracilis* Tåning?)	–	4	–	–	1	–	–	–	–	4	8	1	5	–	6	–	–	–	–	–	–	–
Diaphus kendalli Fowler	–	–	–	–	–	–	1	–	2	1	–	3	–	–	–	–	–	–	–	–	1	–
Diaphus richardsoni Tåning	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Diaphus luetkeni Brauer	–	–	1	–	7	–	–	–	–	2	5	1	–	–	27	24	–	–	–	–	–	–
Diaphus glandulifer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Diaphus fragilis	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentifiable *Diaphus*	1	–	1	–	1	–	1	–	1	5	–	–	3	–	–	4	1	–	–	–	–	1
Lobianchia gemellari (Cocco)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Notolychnus valdiviae (Brauer)	–	–	1	5	11	–	16	–	–	–	7	7	3	–	39	80	–	–	–	–	–	6
Lampadena sp.	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus macropterus Brauer	–	–	–	–	–	–	1	–	–	–	5	–	–	–	2	–	–	–	–	–	–	9
Lampanyctus nigrescens Brauer	3	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus nobilis Tåning	–	–	4	–	–	–	–	–	1?	–	4	2	–	–	1	5	–	–	–	–	–	–
Lampanyctus niger Günther	1	1	–	–	–	–	–	3	–	–	–	1	–	–	–	–	–	–	–	–	–	4
Lampanyctus alatus Goode & Bean	4	–	3	–	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus australis Tåning	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentifiable *Lampanyctus*	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–
Lepidophanes pyrsobolus Alcock	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	5	–	–	–	–	–
Ceratoscopelus warmingi (Lütken)	–	–	–	–	–	–	–	–	1	–	1	–	–	–	5	7	3	–	–	–	–	–
Unidentifiable *myctophids*	1?	4	2	–	5	–	2	8	5	–	–	12	–	–	2	–	1	–	–	–	–	3
Gigantureoidei																						
Bathylagus ioides (Brauer)	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stephanoberycoidei																						
Poromitra megalops (Lütken)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Scopeloberyx robustus (Günther) "dwarf"	–	–	–	–	3	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Scopelogadus m. mizolepis (Günther)	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	–	–	–	–	–	–	2
Beryciidei																						
Diretmus argenteus Johnson	–	–	2	3	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Percoidei																						
Howella brodiei Ogilby	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Ceratioidei																						
Cryptopsaras couesi Gill	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Gadoidei																						
Bregmaceros macclellandi Thompson	–	–	–	–	–	–	–	–	–	–	4	3	–	–	–	–	–	–	–	–	–	–
Bregmaceros rarisquamosus Munro	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Eustomias sp. (probably *bifilis* Gibbs) *Stylephorus*	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Alepocephaloidei																						
Holtbyrnia sp.	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Myctophoidei																						
Coccorella atrata (Alcock)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Scopelarchoides ?	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scopelosaurus sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hygophum (*proximum* Becker?)	1	–	–	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	–	–	–	–
Benthosema fibulatum (Gilbert & Cramer)	–	–	–	–	–	–	–	–	–	–	4	–	3	–	4	–	–	–	–	–	–	–
Benthosema suborbitale (Gilbert)	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diogenichthys panurgus Bolin	–	–	1	–	–	–	–	1	–	–	8	1	–	–	1	3	3	–	–	–	–	–
Myctophum lychnobium Bolin	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2	–	–	–	–	–	–	–
Myctophum spinosum (Steindachner)	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Myctophum nitidulum Garman	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–
Myctophum asperum Richardson	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–
Symbolophorus sp. (*evermanni* (Gilbert)?)	–	–	1	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Symbolophorus sp.	–	–	–	–	3	–	–	–	–	–	–	2	–	–	–	–	1	–	–	–	–	–
Centrobranchus nigro-ocellatus (Günther)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus problematicus Parr	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus splendidus (Brauer)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1?	–	–	–	–	–	–	–
Diaphus garmani Gilbert	–	–	–	1	1	–	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–
Diaphus lucidus Goode & Bean	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus regani Tåning	–	–	–	–	–	–	–	–	2	1	7	1	–	–	2	2	–	–	–	–	–	1
Diaphus fraseri Tåning	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus dicrus Bruun	1	1	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Diaphus termophilus Tåning	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diaphus parri Tåning	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–
Diaphus (*mollis* Tåning?)	–	4	–	–	1	–	–	–	–	4	8	1	5	–	6	–	–	–	–	–	–	–
Diaphus howelli Fowler	–	–	–	–	–	–	1	–	2	1	–	3	–	–	–	–	–	–	–	–	1	–
Diaphus richardsoni Tåning	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Diaphus hubbsi Bruner	–	–	1	–	7	–	–	–	–	2	5	1	–	–	27	24	–	–	–	–	–	–
Diaphus glandulifer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Diaphus fragilis	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentifiable *Diaphus*	1	–	1	–	1	–	1	–	1	5	–	–	3	–	–	4	1	–	–	–	–	1
Loblanchia gemellari (Cocco)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Notolychnus valdiviae (Brauer)	–	–	1	5	11	–	16	–	–	–	7	7	3	–	39	80	–	–	–	–	–	6
Lampadena sp.	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus macropterus Brauer	–	–	–	–	–	–	1	–	–	–	5	–	–	–	2	–	–	–	–	–	–	9
Lampanyctus nigricans Brauer	3	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus nobilis Tåning	–	–	4	–	–	–	–	–	1?	–	4	2	–	–	1	5	–	–	–	–	–	–
Lampanyctus niger Günther	1	1	–	–	–	–	–	3	–	–	–	1	–	–	–	–	–	–	–	–	–	4
Lampanyctus alatus Goode & Bean	4	–	3	–	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lampanyctus australis Tåning	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentifiable *Lampanyctus*	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	1
Lepidophanes pyrsobolus Alcock	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	5	–	–	–	–	–
Ctenoscopelus warmingi (Lütken)	–	–	–	–	–	–	–	–	1	–	1	–	–	–	5	7	3	–	–	–	–	–
Unidentifiable *myctophids*	1?	4	2	–	5	–	2	8	5	–	–	12	–	–	2	–	1	–	–	–	–	3
Gigantactidae																						
Rhadinesomus bradleyi (Bruner)	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stephanoberycoidei																						
Pseudotrachipterus megalops (Lütken)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Stephanoberyx rubustus (Günther) "dwarf"	–	–	–	–	3	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Scopelogadus m. mizolepis (Günther)	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	–	–	–	–	–	–	2
Berycoidea																						
Diretmus argenteus Johnson	–	–	2	3	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Percoidei																						
Howella brodiei Ogilby	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Carangidae																						
Cryptopsaras couesi Gill	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Gadoidei																						
Bregmaceros macclellandi Thompson	–	–	–	–	–	–	–	–	–	–	4	3	–	–	–	–	–	–	–	–	–	–
Bregmaceros rarisquamosus Munro	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–

Table 2. Species with Numbers of Individuals Taken at Each Station (Continued)

Station Numbers	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
Angelichthini																						
Cyema atrum Günther	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Serrivomer rector Garman	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Nemichthys sp.	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Leptocephalus nebulella Roule	–	–	–	–	–	–	–	–	–	–	1?	–	–	–	–	–	–	–	–	1	1	–
Unidentified leptocephali	1	–	–	1	1	–	–	–	–	1	1	1	1	–	5	3	–	–	–	1	–	–
Nemichthyidae ?, leptocephali	–	–	–	–	–	–	–	–	–	–	1	2	–	–	1	–	–	–	1	–	1	–
Myctophid larvae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–
Scombroid larvae	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–
Flatfish larvae	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Other, larvae & juveniles	4	4	5	8	6	16	2	14	12	14	77	14	33	14	14	51	47	16	8	4	5	2

Lampanyctus niger, *Lampanyctus macropterus*, *Lepidophanes pyrsobolus*,[4] *Hygophum proximum*,[5] and *Diogenichthys panurgus* (Bolin, 1959; Fraser-Brunner, 1949). On the other hand, we took *Sternoptyx diaphana* (Schultz, 1961) only once and *Ceratoscopelus warmingi* (Bolin, 1959; Nafpaktitis and Nafpaktitis, 1969) only a few times in the northeast equatorial Indian Ocean. Since neither species is uncommon and both are circumglobal in distribution, it appears that our results do not reflect the actual distributions of all midwater fish species; presumably the same may be said of invertebrates.

In some cases, our horizontal distribution data may be explained by the differential depths of hauls. For example, the four members of the genus *Cyclothone* taken by us certainly occur at more localities than indicated by Table 2. Known depth distributions for the four species indicate that *Cyclothone alba* is the shallowest of the four in vertical distribution, followed by *C. pseudopallida*, then by *C. acclinidens*, with the deepest being *C. pallida* (personal communication, B. N. Kobayashi). Thus, nets that did not fish deeper than 250 to 300 m during the daytime did not catch *Cyclothone alba*, and nets generally had to reach about 400-m depths to catch the other three species. Although diel migrations are described for the genus *Cyclothone* (Grey, 1964), the four species we encountered were never taken in the upper 200 m, either day or night.

Lack of nighttime collections in the southwestern Indian Ocean (Fig. 2) probably accounts for the absence from hauls 182 to 189 of such a common lanternfish as *Ceratoscopelus warmingi*. The large proportion of deep daytime hauls in that area, however, probably accounts for our having netted more organisms with deep daytime distributions from the southwestern equatorial Indian Ocean than from the northeastern portion.

VERTICAL DISTRIBUTION, MIGRATION, AND RELATIONSHIP OF ANIMALS TO THE DSL[6]

Because neither closing nets nor depth recorders were employed in the sampling program during the cruise, results of analyses for vertical distributions are fairly crude estimates. Nevertheless, our methods did show diel changes in vertical distributions of some species that suggest relationship with the main DSL.

To make analyses of vertical distributions, a basic diagram was drawn up that showed a generalized main DSL and combined layer such as reproduced in Figures 12 to 16, with a vertical scale in meters that relates to the scattering pattern. For the sake of simplicity, all other scattering features are omitted. The effective fishing range for each haul (vertical stippled bars) was superimposed on the scattering pattern, but the top and/or bottom of each bar was adjusted to the generalized DSL pattern rather than to the depth scale, as follows. For hauls taken below the main DSL or combined layer (Sta. 182, 183, 184, 189, 190, 193, 203), the effective fishing range was adjusted upward or downward so that for each haul the distance between the top of the effective fishing range and the bottom of the main DSL or combined layer was the same as prevailed at the time the haul was actually taken. (See Table 1 or Fig. 2 for actual effective fishing

[4] Although we identified our material soon after the cruise was finished as *Lepidophanes pyrsobolus*, a recent paper by Nafpaktitis and Nafpaktitis (1969) shows that one more species of this genus occurs in the area we had sampled than we had considered; our material will have to be re-examined in the light of their work.

[5] Bolin (1959) indicated that *Hygophum reinhardti* is a name that should be used to designate an Atlantic population but did not name the Indian Ocean populations of this genus. The recent work of Nafpaktitis and Nafpaktitis (1969) indicates that our material may represent *Hygophum proximum* Becker.

[6] Only the following groups are included in this discussion: siphonophores, gastropods, euphausiids, penaeids, caridoeans, tunicates, and fishes.

ranges.) For hauls taken in the main DSL (Sta. 185, 188, 191, 194, 202), the effective fishing range was adjusted so that the top and bottom of the fishing range bore the same relationship to the top and bottom of the main DSL as actually prevailed at the time the haul was taken. For hauls taken between the bottom of the surface layer and the top of the main DSL (Sta. 187, 195, 201), the top and bottom of the effective fishing range were adjusted to conform to the actual distances from the bottom of the surface layer and the top of the main DSL, respectively, that prevailed at the time the hauls were made. For hauls taken in the daytime surface layer or nighttime combined layer (Sta. 192, 196, 197, 198, 199, 200), the bottom of the effective fishing range was adjusted to be the same distance above the bottom of the surface layer or combined layer as actually prevailed when the haul was made. Haul 186 required considerable adjustment to fit the generalized scattering diagram; it was clearly made in the combined layer (Fig. 4), but the combined layer extended downward unusually far that day (23 November). For the purposes of the generalized diagram, the effective fishing range was adjusted upward so its lower limit coincided with the bottom of the combined layer on the diagram.

With the diagram prepared as described above, a graph was prepared for every species, showing the number of specimens for every haul in which the species was taken. The results of graphing were best for species that were taken at one half or more of the localities and in relatively large numbers and suggested the following distribution patterns relative to the main DSL.

1. Species taken primarily at main DSL depths and below in the daytime, and in the combined layer at night.
2. Species taken primarily below the main DSL in daytime, and in the combined layer at night.
3. Species taken primarily at main DSL depths and below both day and night.
4. Species taken from below the main DSL in daytime and below the combined layer at night.
5. Species taken primarily above 200 m day and night.
6. Species taken primarily above 500 m day and night.

Species taken primarily at main DSL depths and below in the daytime, and in the combined layer at night. Figure 12a shows three species that were taken in large numbers during the cruise; *Abylopsis tetragona* (a siphonophore), *Cymbulia* sp. (a pteropod), and *Thysanopoda* sp. (a euphausiid). There is a dramatic difference between the number of these organisms taken from the combined layer at night and those taken in the surface layer in daytime, with many fewer taken in the surface layer in daytime. The largest numbers in the daytime catches were from the main DSL, although all three species were taken in hauls below the main DSL. No hauls were made below 500 m at night, so we have no information about the distribution of these forms below 500 m at night, but our data suggest that these three species have wide bathymetric ranges in daytime, from 300 m to about 1000 m, with their centers of distribution in the main DSL (except for *Cymbulia* sp., a total of 90 once being taken in a haul that fished above the main DSL). At night, their distribution is heavily centered above 100 m. The pattern indicates that these animals migrate toward the surface at night and return to depths during the daytime; they may be among the organisms chiefly responsible for sound scattering at main DSL and DSL curtain depths.

Although taken in fewer numbers, three additional species show a similar distribution pattern; these three are *Nematobrachion* sp. (a euphausiid), *Vinciguerria nimbaria* (a stomiatoid fish), and *Notolychnus valdiviae* (a myctophid fish), Figure 12b. Of these, none were taken from layers

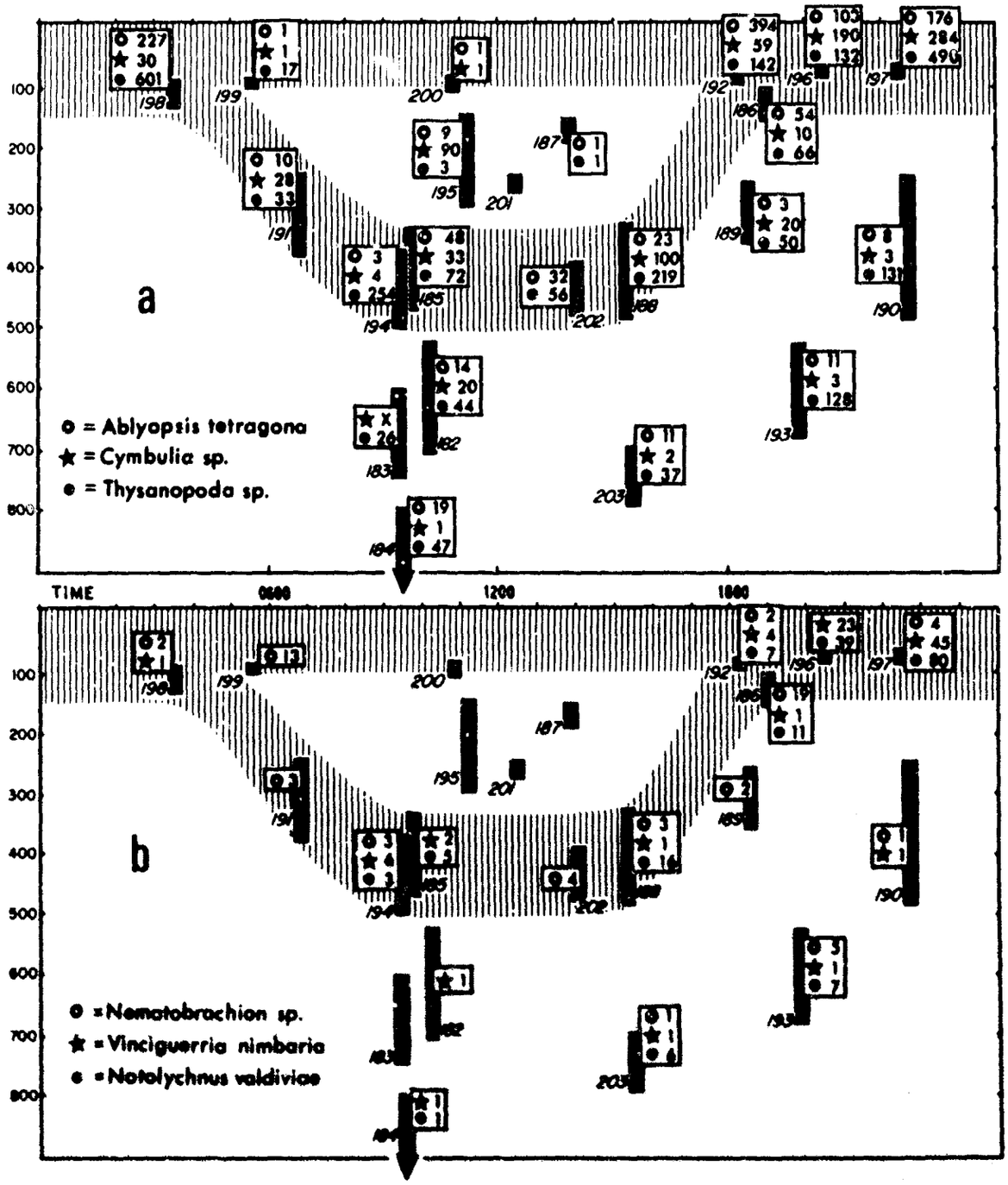

Figure 12. Six species taken primarily at main DSL depths and below in daytime and in the combined layer at night. Numbers of individuals are given beside symbols for each species.

above the main DSL in daytime, although all were taken above 100 m at night. None show special affinity for the main DSL, although all were taken in it in at least three of the five hauls made in the main DSL.

It is possible that at least some of the fishes can avoid slowly moving nets in lighted shallower waters in daytime. Pearcy and Laurs (1966) have analyzed vertical distributions of four dominant mesopelagic fish species in the eastern Pacific off Oregon. They found that the largest catches in daytime were made in the 150 to 500 m (intermediate) range, but at night the largest catches were made in the 0 to 150 m (surface) range. However, they found that the increase from day to night in fishes per unit volume in the surface range was always greater than the increase from night to day in the intermediate range. In other words, if migrations were really taking place and fishes were retiring to the intermediate range in daytime, one might expect that the numbers of fishes captured in the intermediate range in daytime would represent about the same increase over nighttime captures in the intermediate range as occurs in reverse at the surface, where the numbers of fishes captured in the surface range at night were greater than in daytime; in fact, results showed that fewer fishes were taken in the intermediate range in daytime than could probably be accounted for by the migration hypothesis. Pearcy and Laurs (1966) reasoned that the difference might result from net avoidance by fishes in the upper 500 m in daytime, and they estimated that diel differences in catches probably were in part the effect of net avoidance for three of the four species with which they worked. Their chief criterion for showing vertical migration, therefore, would be the diel differences in catches in the intermediate range while allowing for net avoidance rather than diel differences in the surface range. Our data for *Vinciguerria nimbaria* and *Notolychnus valdiviae* are meager and our localities were widely separated, but the two species of fishes were taken in larger numbers below 250 m in daytime than they were from below 250 m at night (Fig. 12b), suggesting they do in fact disappear from below 250 m at night by migrating up. The increase from day to night of numbers taken in the upper 250 m is so much greater than is the increase from night to day below 250 m that net avoidance may be involved.

During Cruise 6 of the R/V *Anton Brunn* in the Indian Ocean, collections of *Notolychnus valdiviae* at stations closest to the equator (Sta. 333B, 337A, and 342A) show that the species was present in hauls made from the surface to 250 to 400 m at night but not in deeper hauls made at the same localities on the same nights (Nafpaktitis and Nafpaktitis, 1969), showing some agreement with our data. Both *Vinciguerria nimbaria* and *Notolychnus valdiviae* have been previously thought to make diel vertical migrations (Marshall, 1960). In fact, like many other myctophids, *Notolychnus valdiviae* has been taken at the very surface at night by dip-netting (Beebe and Vander Pyl, 1944). However, *Vinciguerria nimbaria*, although frequently taken in the upper several hundred meters at night, is not taken at the very surface; moreover, smaller specimens, not adults, are generally recorded as being taken in upper layers at night (Marshall, 1960, p. 88), a generalization that is made for numerous stomiatoids (Morrow, 1964a). Thus, it will probably eventually be necessary to define vertical migration patterns for young stages separately from those for adults, as has been the case for some pelagic crustaceans such as *Euphausia pacifica* in Monterey Bay, California (Barham, 1957). Both *Vinciguerria nimbaria* and *Notolychnus valdiviae* have gas-filled swimbladders that would serve as scattering targets (Marshall, 1960), so both species may be implicated as contributing to scattering in the main DSL.

Additionally, although they were not taken frequently or in large numbers, there were one pteropod, two crustaceans, and four fishes with vertical distribution patterns that suggested that they, too, normally inhabit depths in or below the main DSL in daytime and migrate upwards at night. These are *Euclio pyramidata* (a pteropod), *Nematoscelis* sp. (a euphausiid), *Oplophorus gracilirostris* (a caridean), *Diaphus mollis* and *Benthosema fibulatum* (myctophid fishes), and

Chauliodus pammelas and *Chauliodus sloani* (stomiatoid fishes) (Table 2). We captured the pteropod *Euclio pyramidata* only in the western Indian Ocean, where it occurred in all three hauls below the main DSL in morning (182 to 184) and in the main DSL in afternoon (188); because no hauls were made in the upper 100 m at night in the western Indian Ocean, it is impossible to tell whether this form occurs there at night, but its presence in hauls 186 (above 240 m) and 189 (above 375 m) just after dark suggests that it moves near the surface at night. We took 11 specimens of *Benthosema fibulatum*, but as its range is restricted to the northern Indian Ocean north of about 4°N (Nafpaktitis and Nafpaktitis, 1969), we may say that we captured it at 3 out of a possible 7 localities, once in the main DSL in daytime and twice in the upper 100 m at night. Similarly, *Chauliodus pammelas* has a northerly distribution (Gibbs and Hurwitz, 1967) and was taken by us at 3 out of a possible 7 localities; of a total of 10 specimens,[7] 5 were taken in the main DSL, 2 in the upper 100 m at night, and 3 below 500 m at night. Species of *Chauliodus* are all thought to perform extensive diel vertical migrations, with the distributions of adults centered at greater depths than those of juveniles (Morrow, 1964b). They do not have swimbladders (Marshall, 1960), and it is doubtful that they are sound-scattering targets. Data for *Diaphus mollis* shows that the form was taken at 7 localities, 13 specimens from 3 hauls in and below the main DSL, 15 specimens from 3 hauls above 240 m at night, and 1 specimen in a haul below 450 m at night, indicating that it is a vertical migrator. Unfortunately, we did not check the swimbladder of this form, but it has apparently never been recorded as lacking a swimbladder and may be hypothesized as contributing to sound scattering.

Species taken primarily below the main DSL in daytime and in the combined layer at night. Vertical distributions for the following species are shown in Figure 13a and b: *Stylocheiron* sp. L (a euphausiid), *Sergestes robustus* (a penaeid), *Thalassocaris lucida* (a caridean), and the fishes *Diogenichthys panurgus*, *Diaphus regani*, and *Diaphus lutkeni* (all myctophids). These species almost never occurred in hauls through the main DSL save for haul 191, which was made shortly after sunrise while the main DSL was descending. Thus, while these species probably are migrators, they probably are not constituents of the main DSL. All six species were taken in largest numbers at night in the combined layer. The crustaceans were all taken in larger numbers between 265 and 600 m at night than they were in daytime, suggesting that either they avoid the net at these intermediate depths in daytime, or their daytime center of distribution is below these intermediate depths in daytime. Data for the fishes are equivocal, as samples are few and small.

The vertical distributions of three other species resemble the above distributions. These species are *Parapandalus zurstrassemi* (a caridean), *Stomias nebulosus* (a stomiatoid fish), and *Lampanyctus nobilis* (a myctophid fish) (Table 2). *Stomias nebulosus* was taken once above 240 m (haul 186) and once above 375 m (haul 189) at night but not in the upper 100 m at night, a finding that agrees with the known distribution, for, although small specimens of other species of *Stomias* frequently have been taken in surface waters at night, *Stomias nebulosus* has not (Marshall, 1960). The species, like others of its family, lacks a swimbladder, so perhaps may be discounted as a sound-scattering target.

[7] The total may have been slightly higher, because the record for one station is incomplete for this species.

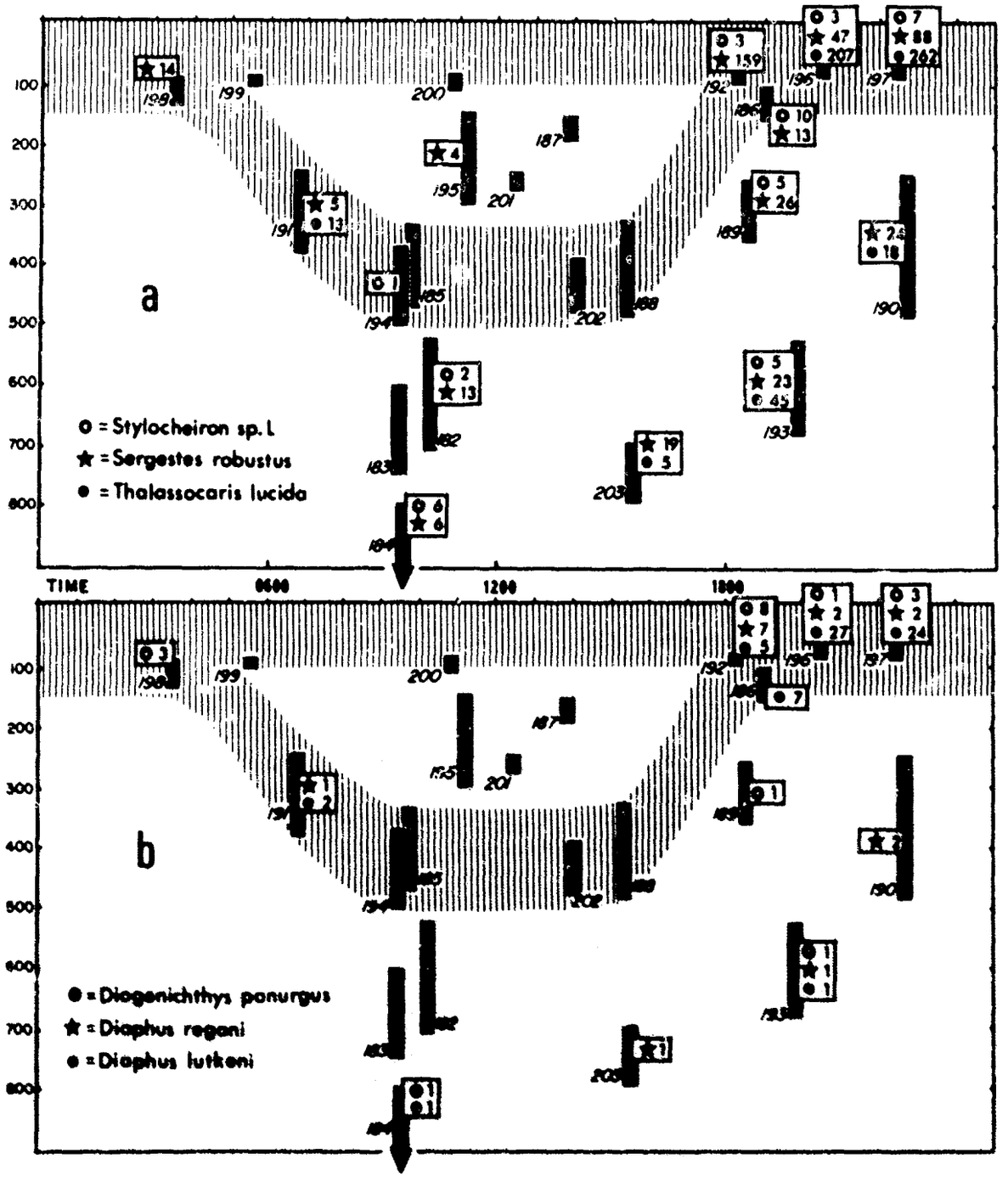

Figure 13. Six species taken primarily below the main DSL in daytime and in the combined layer at night. Numbers of individuals are given beside symbols for each species.

Species taken primarily at main DSL depths and below both night and day. The vertical distributions of two stomiatoid fishes that were nearly always taken below 275 m, day and night, are shown in Figure 14a. Of the two, *Cyclothone alba* had the greater depth range, occurring in all hauls in which the net fished below 300 m except haul 189. Species of *Cyclothone* have been known to undergo vertical migrations, but Grey (1964, p. 187) writes, "The vertical distribution of these fishes is complicated, as some undergo daily vertical migrations during at least part of their lives, they inhabit shallower depths in cold seas than in tropical and temperate waters, and older specimens live in deeper water." Our data do not show a pattern of migration. Depth distributions of species of *Cyclothone* are known to be stratified in some localities (Grey, 1964; B. N. Kobayashi, personal communication), with the pale-colored *C. alba* having a shallow distribution; of the species of *Cyclothone* we captured, *C. alba* had the shallowest range and was the only species of *Cyclothone* to occur in the main DSL. Swimbladders are present in adults of *Cyclothone*, although regressed in size from the premetamorphosis size (Marshall, 1960). Because so many specimens of *Cyclothone alba* were taken during Cruise 5 at depths from which no sound scattering was recorded, it is doubtful that this form contributes to strong sound scattering in the main DSL even though a substantial portion of the population occurs there in daytime.

Members of the stomiatoid genus *Argyropelecus* have been called partial migrators by Marshall (1960, p. 88), meaning that nighttime populations are centered higher than daytime populations, but the nighttime distribution does not reach much above 150 m. Our data for *Argyropelecus lychnus sladeni* agree with those observations. However, although previous records indicate that the species has been taken below 600 m in the Indian Ocean (Schultz, 1961), none of our specimens were taken below that depth. In fact, of a total of 23 specimens belonging to at least three species of *Argyropelecus* (Table 2), 21 were taken in the main DSL. All of the 13 taken at night were captured between 150 and 600 m. These forms have gas-filled swimbladders (Marshall, 1960) and are probably sound scatterers.

Like *Argyropelecus*, two other stomiatoids, *Valenciennellus tripunctulatus* and *Ichthyococcus ovatus*, and the myctophid *Diaphus kendalli* were taken only in the main DSL in daytime, although the data for these forms are extremely meagre (Table 2). *Diaphus kendalli* may be one of the exceptions to the generalization that most myctophids make extensive vertical migrations to the surface at night, for we never took this form in the hauls in shallow depths at night in which myctophids were normally relatively numerous.

Species taken from below the main DSL in daytime and below the combined layer at night. In general, hauls at depths below scattering features were not as productive as hauls in shallower depths, so that distribution patterns of the animals there are not so easily discernible. Six species were taken by us in sufficient numbers to suggest patterns; these were *Hemipenaeus crassipes* and *Aristeus* sp. (penaeids), *Lampanyctus niger* (a myctophid fish), and *Cyclothone pallida*, *C. pseudopallida*, and *C. acclinidens* (stomiatoid fishes). Vertical distributions for the two penaeids (Fig. 14b) show their daytime distributions to be well below the main DSL. Nighttime hauls show these forms present from below 100 m to 500 or 600 m, suggesting that they migrate up at night but stop short of the upper 100 m. Previous authors have suggested that vertical migrators that cease their upward migration below the surface mixed layer are stopped by the thermocline (Marshall, 1960), a possible explanation for our data, because the region of the thermocline during Cruise 5 was 30 to 120 m (Fig. 3). The myctophid *Lampanyctus niger* may fall into this category (Table 2), as may the migrators mentioned previously as not having occurred in the upper 100 m, such as *Stomias nebelosus*, *Argyropelecus* spp., *Diaphus kendalli*, etc.

Three species of *Cyclothone*, *C. pallida*, *C. pseudopallida*, and *C. acclinidens* (Table 2), were regularly taken below the main DSL in daytime except for *C. pallida*, which was once taken in

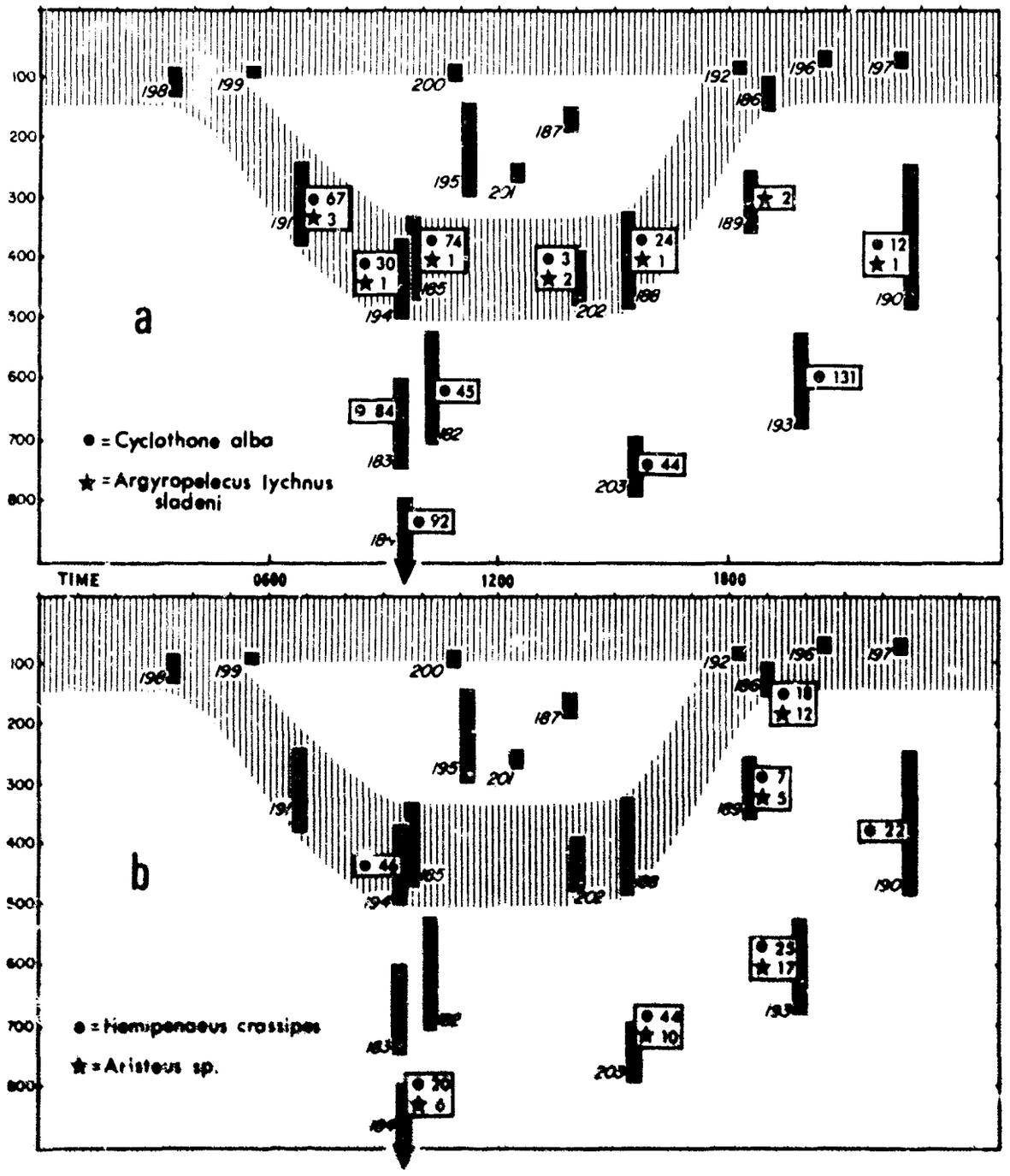

Figure 14. (a) Two species taken primarily at main DSL depths and below both night and day. (b) two species taken from below the main DSL in daytime and below the combined layer at night. Numbers of individuals are given beside symbols for each species.

the main DSL (haul 194). Their absence from depths above 600 m at night indicates that none of them make extensive vertical migrations in this range (it is possible, of course, that they perform migrations below these depths).

Species taken primarily above 200 m day and night. The vertical distributions for two crustaceans whose center of distribution was in surface layers day and night are shown in Figure 15; these are *Stylocheiron* sp. s (a euphausiid) and *Leucifer acestra* (a penaeid). Both were taken in the main DSL and below in daytime, but generally not in numbers as great as were taken nearer the surface. Heteropods of the genus *Atlanta* (our collections probably consisted of more than one species) had similar concentrations near the surface (data for *Atlanta* given in Table 2); their vertical distribution varied somewhat from those of the crustaceans in that they were absent (with one exception) from depths below the main DSL. The distributions for the crustaceans and heteropods indicate that they may be involved as agents of sound scattering at the surface and daytime intermediate layers but that they are probably not involved in the diel changes in the main DSL.

Species taken primarily above 500 m day and night. A pteropod and a number of siphonophores and tunicates were widely distributed throughout the upper 500 m day and night; none appeared to have any affinity for the main DSL, although they sometimes were captured in hauls through it. The siphonophore *Diphyes dispar* did not appear in hauls below about 150 m at night (Figure 16a). This fact suggested that it congregates near the surface at night. Another siphonophore, *Diphyes bojani*, and the tunicate *Cyclosalpa virgula* may have a similar distribution pattern (Figure 16a), but we took them in fewer hauls and the picture for them is unclear. Two other forms, the pteropod *Cavolinia longirostris* and the siphonophore *Agalma okeni* (Figure 16b), had distributions showing their tendency to leave the upper 100 m in daytime; that is, they

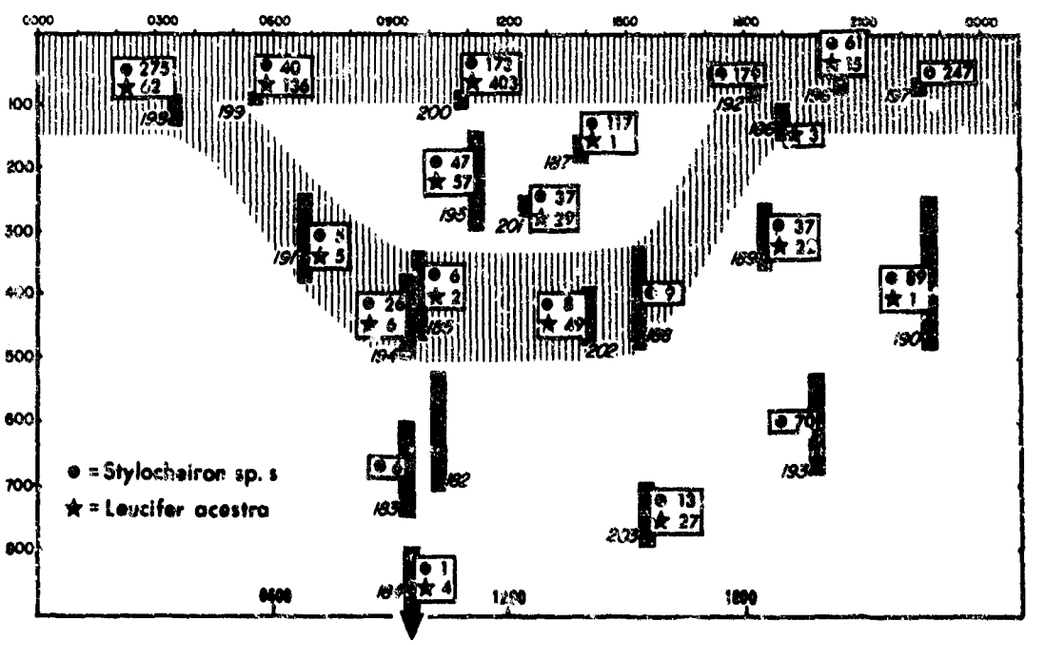

Figure 15. Two species taken primarily above 200 m day and night. Numbers of individuals are given beside symbols for each species.

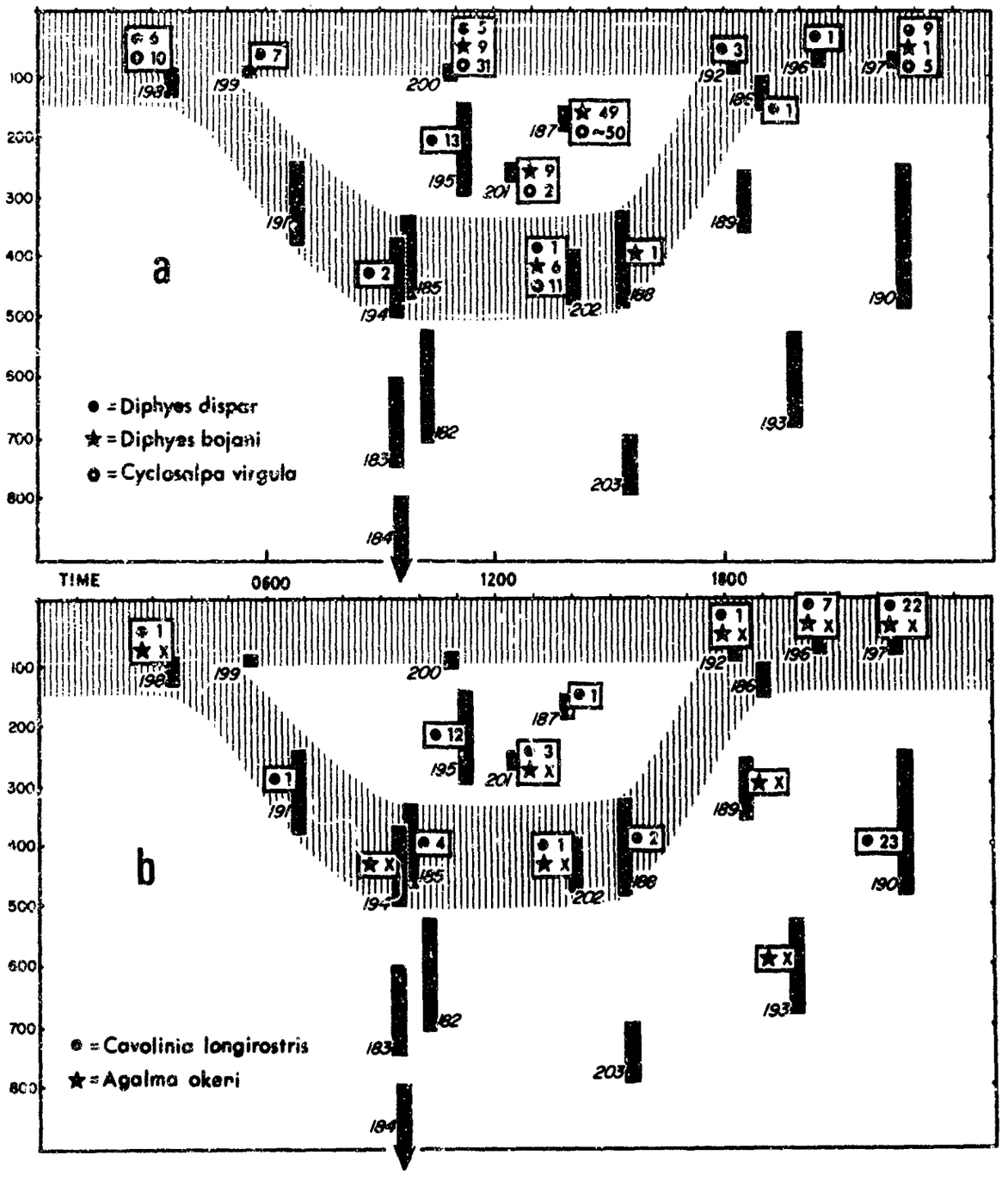

Figure 16. Five species taken primarily above 500 m day and night. Numbers of individuals are given beside symbols for each species except *Agalma okeni*, which is scored as present or absent in hauls by the presence or absence of the symbol X.

occurred in haul 198 (75 to 120 m) before daybreak but not in haul 199 (75 to 90 m) just after daybreak on the same day, and they occurred in hauls 201 and 202 (225 to 475 m) but not in haul 200 (80 to 85 m) earlier the same day.

Three tunicates were taken above 500 m night and day, but their distributions show no special patterns: they are *Salpa fusiformis, Pegea confoederata,* and *Dolioletta gegenbauri* (Table 2).

By this method of analysis, we are left with a number of invertebrates that occurred variously in moderate to large numbers from the surface to below 700 m, some of which were patchy in distribution but none of which show any particular affinities for any particular depths. These were the siphonophores *Abyla trigona, Hippopodius hippopus, Chelophyes appendiculata, Chelophyes contorta,* and *Eudoxoides mitra;* the pteropods *Diacria quadridentata* (two subspecies) and *Creseis* sp.; the euphausiid *Thysanoessa* sp.; and the tunicates *Thalia democratica, Iasis zonaria,* and *Pyrosoma atlanticum* (Table 2).

The pitfalls of plotting distributions and making inferences from them about dynamics of population movements probably are numerous, but the following example is especially instructive. Nafpaktitis and Nafpaktitis (1969) report that the myctophid fish *Ceratoscopelus warmingi* has a broad distribution from the Atlantic Ocean through the Indian Ocean, probably to the South Pacific; they write concerning collections from *Anton Brunn* Cruises 3 and 6 in the western Indian Ocean, "*C. warmingi* seems to be common in the Indian Ocean. The 386 specimens were taken almost uninterruptedly from about 12°N to 44°S." Yet during *Te Vega* Cruise 5, this species was taken only at four localities (Table 2), none of which were in the western Indian Ocean. Also, the species was taken only in nighttime hauls during *Te Vega* Cruise 5, with 16 of the 17 specimens taken in hauls from 0 to 120 m, but *Anton Brunn* Cruises 3 and 6 took the species in daytime in 15 hauls that sampled the upper 1000 m. (Of a total of 80 *Anton Brunn* hauls that captured *C. warmingi,* 15 were made during daylight hours and 38 during the night, while 27 could not be scored as either day or night hauls; the latter hauls were evidently made partly by day and partly by night in at least some cases.) Thus it is plain that our data are insufficient to show the relationship of *Ceratoscopelus warmingi* to the main DSL, even though other workers have found the fish to be common in the Indian Ocean and have taken it at various depths. The same is undoubtedly true for other species we attempted to treat, but the case of *C. warmingi* is especially provocative because schools of one of its congeners, *C. maderensis,* were recently identified with a deep scattering layer composed of discrete hyperbolic echo sequences off the continental slope of the northeastern United States (Backus et al., 1968).

To summarize, for the species for which we could discern migration patterns, there were six that appear to perform extensive migrations and one that is a partial migrator, any or all of which may be important sound scatterers in the main DSL in the equatorial Indian Ocean in October and November. Best evidence for association with the main DSL was obtained for *Ablyopsis tetragona* (a siphonophore), *Cymbulia* sp. (a pteropod), and *Thysanopoda* sp. (a euphausiid). Lesser evidence was obtained for *Nematobrachion* sp. (a euphausiid), *Vinciguerria nimbaria* (a stomiatoid fish), *Notolychnus valdiviae* (a myctophid fish), and the partial migrator *Argyropelecus lychnus sladeni* (a stomiatoid fish).

NOTES ON FOOD RELATIONSHIPS

Although time and facilities did not permit an extensive study of food relationships among organisms occurring in the vicinity of the DSL, qualitative examinations of stomach contents were made on selected species. For some of these species it was possible to examine specimens collected at several different times of day and night. Several prominent species were never taken

with recognizable food remains in the gut, a situation not uncommonly encountered among zooplankton (Raymont, 1963, p. 502). Our methods did not permit decisions as to whether this might be the result of regurgitation upon capture or preservation; rapid digestion and elimination; ingestion only of soft parts or soft-bodied organisms; feeding on organic matter in the form of fine detritus, organic aggregates, or dissolved organic matter (Riley, 1963); or other factors. Fragmentary as our data are, they are deemed worth tabulating in view of the lack of detailed information on the food habits of most zooplankters (Raymont, 1963).

In Table 3, the feeders (left hand margin) and the foods found in their stomachs (top) are arranged in such an order that the herbivores and microphagous feeders are grouped in the upper part of the table, omnivores fall near the middle, and carnivores are clustered in the lower part. A number of forms were noted in which the stomachs contained both microscopic and macroscopic foods. In some cases, both may have been selectively ingested. In other cases, such as the euphausiids *Stylocheiron* and *Thysanopoda*, the caridean shrimp *Acanthephyra*, and perhaps the penaeid prawns (see Hall, 1962), some of the microscopic forms reported in the gut may represent organisms that were present in the stomachs of ingested animals.

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SUMMARY

Twenty-two stations were occupied at 14 localities in the equatorial Indian Ocean between Mombasa, Kenya, and the Nicobar Islands to secure organisms from deep scattering layers (DSL) and vicinity by midwater trawling and to determine the behavior of the DSL by echogram analysis.

Prominent scattering features of the equatorial Indian Ocean are described and named. Main layers observed were (1) a daytime *surface layer* (outgoing signal plus any surface scattering) in the top 60 to 150 m; (2) a daytime *main DSL*, 50 m or more thick, sometimes recorded as a double layer, with a top at 300 to 350 m; (3) a daytime *intermediate layer*, not always present, centering at about 200 m; and (4) a nighttime *combined layer* in the upper 150 to 250 m,

Table 3. Gut Contents of Selected Animals

Pelagic animals analyzed for gut contents	Number containing food	Number examined	Unicellular Algae	Filamentous Algae	Flagellates	Dinoflagellates	Coccolithophores	Silicoflagellates	Diatoms	Foraminiferans	Radiolarians	Tintinnids	Planula Larvae	Echinoderm Larvae	Nemertean Larvae	Annelid Larvae	Gastropods	Pteropods	Crustacean parts	Crustacean Larvae	Crustacean Eggs	Ostracods	Copepods	Amphipods	Mysids	[illegible]	[illegible]	[illegible]	Tunicata	Fish Parts & Scales	Fish Larvae
TUNICATA																															
*Iasis zonaria**	1	1				X	X		X	X	X																				
Pegea confoederata	1	1	X				X		X	X																					
Pyrosoma, soft form	1	1				X	X		X																						
Pyrosoma, berry	2	2				X	X	X	X																						
Pyrosoma, large colony	1	1					X																								
Salpa sp.	1	1				X	X		X	X	X																				
Salpa fusiformis	1	1	X				X		X	X																					
MOLLUSCA																															
Cavolinia longirostris	4	4	X						X	X	X	X					X		X	X											
Euclio pyramidata	6	6	X			X	X	X	X	X		X																			
ARTHROPODA																															
Copepoda	8	40							X		X								X												
Stylocheiron (euphausiid)	6	10							X		X								X												
Thysanoessa (euphausiid)	2	6																	X				X								
Thysanopoda (euphausiid)	17	31	X	X	X	X			X	X	X	X							X				X	X							
Anchylomera (amphipod)	4	11																	X												
Cystosoma (amphipod)	2	3	X																X												
Phronima (amphipod)	4	5																	X												
Platyscelid (amphipod)	4	8																	X												
Rhabdosoma (amphipod)	1	12									X																				
Penaeidae																															
Hemipenaeus crassipes	6	6				X										X														X	
Sergestes robustus	5	12	X			X			X	X									X												
Aristeus	10	10									X	X	X						X				X	X							
Caridea																															
Acanthephyra sanguinea	6	7							X									X	X		X		X								
Species E	12	19													X	X	X		X			X					X				
CHAETOGNATHA																															
Sagitta ferox	2	?												X									X								
Sagitta hexaptera	2	?																			X		X								
Sagitta sp.	9	?															X		X	X			X				X			X	
COELENTERATA, Siphonophora																															
Unident. feeding polyp	1	1																									X				
Abylopsis tetragona	4	4																					X								
Agalma okeni	1	1																					X				X				
PISCES																															
Cyclothone	3	11																	X						X						
Ichthyococcus ovatus	2	2																											X		
Vinciguerria nimbaria	5	5															X					X	X	X							
Argyropelecus lychnus	8	4															X		X				X	X							
Myctophidae																															
Species 1	10	10																X	X		X		X	X			X	X	X		
Species 2	10	11																X	X			X	X	X	X		X	X	X		
Species 3	3	3															X		X				X	X					X		X
Species 4	2	2																	X				X						X		
Species 5	2	3																	X				X	X		X	X	X	X	X	
Species 6	2	8																	X			X		X				X			
Gadoidei																															
Bregmaceros macclellandi	1	1																	X												

*X = materials present in the gut

formed by merging of the surface layer with the main DSL. Scattering layers of the Indian Ocean are compared with those from other oceans.

Geographical distribution data are presented for the 161 species of animals that were identified; of these there were 16 siphonophores, 14 pteropods, 10 heteropods, 3 mysids, 7 euphausiids, 19 shrimps, 8 pelagic tunicates, and 79 fishes. Distribution of amphipod genera is given; chaetognaths, medusae, annelids, copepods, and other groups taken were generally not identified; collections of these as well as of the identified species are available for study.

Vertical distributions for 56 genera and species are discussed with special reference to migration patterns. Best evidence for association with the main DSL was obtained for the vertical migrators *Ablyopsis tetragona* (a siphonophore), *Cymbulia* sp. (a pteropod), and *Thysanopoda* sp. (a euphausiid), with lesser evidence for *Nematobrachion* sp. (a euphausiid), *Vinciguerria nimbaria* (a stomiatoid fish), and *Notolychnus valdiviae* (a myctophid fish), and the partial migrator *Argyropelecus lynchnus sladeni* (a stomiatoid fish).

A small amount of information on gut contents is presented for 39 species.

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COMPARISONS BETWEEN SURFACE-MEASURED SWIMBLADDER VOLUMES, DEPTH OF RESONANCE, AND 12-kHz ECHOGRAMS AT THE TIME OF CAPTURE OF SOUND-SCATTERING FISHES

Lloyd W. Shearer
U.S. Naval Oceanographic Office
Washington, D.C.

ABSTRACT

During January and February 1969 the Naval Oceanographic Office conducted biological and acoustic measurements of deep scattering layers in the tropical western Atlantic. Swimbladder volume determinations were made on 91 specimens of four species of mesopelagic physoclistous fishes. In *Myctophum nitidulum*, *Lepidophanes guntheri*, and *Sternoptyx diaphana*, there was very little correlation between estimated swimbladder volumes and those calculated from total lengths by either Haslett's or Andreeva and Chindonova's equations. For *Diaphus brachycephalus*, only a slight difference was apparent between swimbladder volumes calculated by Andreeva and Chindonova's equation and the regression equation derived from measurements made in this study.

Swimbladder volumes required for resonance at 12 kHz over a wide range of depths were calculated from the resonance frequency equations of Minnaert, Andreeva, Andreeva and Chindonova, and for a free gas bubble. Curves plotted for each equation make it possible to determine resonance depths for surface-measured volumes for both swimbladder behavior responses, viz active or passive. In the former case, volume is kept constant at all depths by the fish secreting or absorbing gas as required; in the latter, the volume simply expands or compresses according to Boyle's law.

If one assumes that the swimbladders of physoclistous fishes respond actively, only 36.6% of the *S. diaphana* specimens and none of the other fishes measured were capable of resonating at 12 kHz between their depth of capture and the surface (860 to 0 m). If, however, the swimbladder responds passively, then 100% of the *S. diaphana*, 93.7% of the *D. brachycephalus*, and 42.5% of the *L. guntheri* specimens were capable of resonating at this frequency at specific depths between their depth of capture and the surface.

BACKGROUND

Although a huge literature concerning the morphology, histology, and physiology of the swimbladder of fishes exists, very little data are available on such basic facts and figures as estimates of swimbladder size or volume.

Black (1948) estimated the swimbladder volume in the Mummichog *Fundulus heteroclitus* by allowing the extracted gas to displace its volume in a calibrated bulb filled with water.

Jones (1951) removed the head, tail, and viscera from perch *Perca flavescens*, placed the trunk with the attached swimbladder in a density bottle, and made weight determinations before and after the bladder was torn away from the trunk. The difference between the two weighings gave the weight of the water displaced by the swimbladder, from which the volume could be estimated.

Alexander (1959b) working with small specimens of a goby *Gobius flavescens* weighed them in a density bottle filled with distilled water. Next they were cut in half, which allowed the swimbladder gases to escape, and they were reweighed in the same bottle. The difference in grams between the two weighings equalled the total swimbladder volume in milliliters.

Marshall (1951 and 1960) removed the swimbladders of numerous preserved specimens of myctophids, gonostomatids, sternoptychids, and others and presented data on the major and minor axes of the organ as well as the standard lengths of the measured fish.

Capen (1967) presents similar data on both fresh and preserved specimens of similar groups of fishes but goes a step further by assuming that the shape of the swimbladder approximates that of a prolate spheriod; he presents calculated volumes for his physical measurements.

More refined methods for directly estimating swimbladder volumes are available which negate the need for either mutilating the fish and/or removing the swimbladder or its gases. Kanwisher and Ebeling (1957) determined the swimbladder volumes in numerous specimens of surface and mesopelagic marine fishes by placing them in a pressure chamber and noting the volume of water required to double the pressure in the chamber. Applying Boyle's Law, this volume equals the half-volume of the swimbladder at one atmosphere at the surface.

Alexander (1959a) subjected a number of anesthetized physostomes to changes of pressure and determined the corresponding changes in the swimbladder volume before and after the restraining influence of the swimbladder wall had been eliminated by the expression of some of the gases through the pneumatic duct. The remaining or "unconstrained" gas obeys Boyle's Law so that the total volume at test depth can be calculated from the known change in volume with pressure.

Brawn (1965) modified Alexander's method in order to estimate the swimbladder volume in a living physoclist, the Pollock *Pollachius virens*. Due to the absence of a pneumatic duct in physoclists it is impossible to expel gas by varying the pressure. In her method the swimbladder volume can be estimated from its change in volume with change in applied pressure only after the contained gases have been sufficiently compressed to remove the constraint of the swimbladder wall.

Rahn (1968) described a simple field method for estimating the swimbladder volume of male salmon. His apparatus seems to be identical with that of Kanwisher and Ebeling's in that it is fitted with a manometer and syringe rather than a compression-vacuum pump as in the case of Alexander's and Brawn's apparatus. Whereas in the latter two worker's methods the restraining influence of the swimbladder walls has to be eliminated in order to estimate the volume of swimbladder gases, Rahn's method assumes that any increase in volume by the injection of water results in a corresponding decrease in the swimbladder volume. The initial swimbladder volume in both the Brawn (1965) and Rahn (1968) methods can be calculated by the Boyle-Mariotte Law. Thus

$$V = \Delta v \frac{(P_B + \Delta p)}{\Delta p}. \qquad (1)$$

Brawn Method	Rahn Method
V = volume of unconstrained gas at 0 applied pressure	= initial swimbladder volume
Δv = change in volume which the swimbladder gas would have shown if it had not been compressed by the swimbladder walls between 0 and 42 cm Hg applied pressure	= know volume of water injected into the system

P_B = total pressure at 0 applied pressure = barometric pressure
Δp = the increase in pressure of 42 cm Hg = concomitant pressure increase above barometric pressure due to Δv

Several workers have attempted to estimate swimbladder volumes as a function of one or another measurable parameter of the fish. Jones (1951) was first to suggest that if the swimbladder functions as a hydrostatic organ if should occupy about 7% of the volume of a freshwater teleost but slightly less, about 5% of that of a marine teleost. Haslett (1962) constructed a "standard fish structure" based on 6 specimens of the whiting *Gadus merlangus*, from which he derived the following approximation as the mean volume of a [the] fish:

$$\text{Volume}_{\text{fish}} = 8.3 \times 10^{-3} L^3 \text{ cm}^3, \quad (2)$$

where L equals the total length of the fish in centimeters. Using the same "standard fish structure," he found the mean volume of the swimbladder to be 4.1% of the total volume of the fish, or

$$\text{Volume}_{\text{swimbladder}} = 3.4 \times 10^{-4} L^3 \text{ cm}^3. \quad (3)$$

Andreeva and Chindonova (1964) citing Haslett (1962) state that the volume of the fish may be determined in the first approximation from the length L (although it was not stated, it is assumed that the unit of total length is centimeters) in the following manner:

$$\text{Volume}_{\text{fish}} = 0.01 L^3 \text{ [cm}^3\text{]}. \quad (4)$$

They further assume that the volume of the swimbladder is 5% of the total volume of the fish, therefore

$$\text{Volume}_{\text{swimbladder}} = 5 \times 10^{-4} L^3 \text{ [cm}^3\text{]}. \quad (5)$$

To emphasize that formula (5) is not infallible, they state that it can only be used for determination of the order of magnitude of volume of the swimbladder and does not pretend to give a precise determination of the size of the swimbladder for a particular fish.

Currently, there are two schools of thought regarding the swimbladder's response to changing hydrostatic pressures as a physoclist migrates vertically. One, the active response theory, is that the fish remains neutrally buoyant at all depths by either secreting or absorbing gas as required to maintain constant swimbladder volume. This implies that as the fish ascends with the approach of sunset, it must constantly absorb gas, and conversely as it descends with the approach of sunrise, gas must be rapidly secreted to fill the diminishing swimbladder. Herney et al. (1962) attributed a shift in the resonance scattering frequency (at peaks above 5 kHz) during vertical migration of scattering layers which varied as the one-half power of the pressure to actively responding swimbladders.

The passive response theory states that the fish in only neutrally buoyant at some near-surface level. This implies that the fish responds passively to changing hydrostatic pressures during its vertical migration. It begins to swim downward with the approach of sunrise, and as the depth increases, its swimbladder volume decreases, its density increases, and it becomes heavier as it continues its downward motion until its maximum daytime depth is reached where, presumably, its level is maintained by minimum swimming activity. To ascend, it merely has to start an

upward swimming motion and as the pressure decreases, the swimbladder and consequently the total volume increase, the fish becomes less dense, and it continues swimming upward until it reaches its nighttime activity level. Hersey et al. (1962) attributed a shift in resonant scattering frequency which varies as the 5/6 power of the hydrostatic pressure to swimbladders which respond passively.

MATERIALS AND METHODS

During January-February 1969 the U.S. Naval Oceanographic Office conducted investigations of deep-scattering layers in the tropical western Atlantic. Specimens of a lanternfish *Myctophum nitidulum* were dipnetted in the nighttime at four oceanographic stations located at 08°00′N, 48°00′W; 0°52′S, 35°09′W; 8°00′S, 30°00′W; and 8°00′S, 25°00′W. Specimens of two lanternfish *Lepidophanes güntheri* and *Diaphus brachycephalus*, and a hatchetfish *Sternoptyx diaphana* were captured in a 10-foot Isaacs-Kidd Midwater Trawl (IKMT) within 10 miles of one or more of the above stations as well as at another location at 2°12′N, 44°00′W. During each net haul a continuous echogram depicting the depth of scattering layers was recorded on a Gifft GDR-19-T depth recorder. Due to malfunctioning of the electronic components of the four-chambered cod-end sampler, only two discrete samples were obtained (Aron et al., 1964). Since all of the specimens taken in net hauls were dead or at best moribund, they were retained in plastic buckets of surface seawater and swimbladder measurements were made as soon as possible.

Estimations of swimbladder volumes were made according to the method of Kanwisher and Ebeling (1959), using a modified version of their apparatus. Apparatus modifications included the replacement of the manometer with a pressure gauge (Alfred Ebeling, personal communication) and the attachment of a vernier scale to the plunger of the syringe.

In the final data analysis, all fish that did not sink when the pressure was doubled were eliminated. In this respect the data presented in this report may be somewhat biased.

Correlation coefficients r between estimated swimbladder volumes and total lengths for each species were calculated by the method of least squares. Both Haslett's (1962) and Andreeva and Chindonova's (1964) functions appear basically to be regression equations closely related to Monastyrsky's logarithmic method for calculating growth in fishes:

$$\log L = \log c + n \log S, \tag{6}$$

where L = body lengths, S = scale length, c and n are constants, the intercept and slope, respectively, of the straight line of the equation (see Lagler, 1952, p. 122). Since variations of formula (6) are often used by fishery researchers to determine the regression of one or more diagnostic characteristics of a species, such as the snout-to-anus length, greatest body depth, eye diameter, head or fin lengths on body length, etc., it was suspected that the same type of linear relationship existed between the growth of organs and the body length. Therefore, the regression equation used for each species in this study is of the following form:

$$\text{Log } V_{SB} = \log a + b \log L, \tag{7}$$

where

V_{SB} = volume of the swimbladder in mm^3,
L = total length of the fish in cm,
a = a constant, the intercept of the equation, and
b = a constant, the slope or regression coefficient of the equation.

Equation (7) can be further simplified to

$$V_{SB} = aL^b. \tag{8}$$

Since the convenient unit for swimbladder volumes in this study is mm^3, equations (3) and (5) had to be converted to the following to be compatible:

$$\text{Volume}_{SB} = 0.34L^3 \text{ mm}^3 \tag{9}$$

and

$$\text{Volume}_{SB} = 0.50L^3 \text{ mm}^3. \tag{10}$$

Swimbladder volumes (actually equivalent spherical volumes) required to resonate at 12 kHz over a wide range of depths (0 to 1500 m) were calculated from the resonance frequency equations of Minnaert (1933), as $f_r = 1/(2\pi r)(3\gamma P/\rho)^{1/2}$, Andreeva (1964) as $\omega_0 = 1/R\,(3\gamma P + 4\mu_1/\rho)^{1/2}$, Andreeva and Chindonova (1964) as $f_r = 1.5\sqrt{H + 30}/\sqrt[3]{\text{swimbladder vol.}}$, and for a free gas bubble $f_r = (D + 10)^{1/2}/r$, which is an approximation of Minnaert's formula for entrained air bubbles in water. Two volumes for each depth were plotted from Andreeva's equation to include the lower and upper limits for (μ_1) the real part of the complex shear modulus of the body tissues surrounding the swimbladder, expressed as

$$\mu = \mu_1 (1 + i\mu_2), \tag{11}$$

where $\mu_1 = 10^6$ to 10^7 dynes/cm^2 and $\mu_2 = 0.2$ to 0.3.

Curves for each of the above equations for both swimbladder behavior responses, viz., active and passive, were plotted on log-log paper with surface volumes in cubic millimeters as the abscissa and (Depth + 10) in meters as the ordinate. In the active case volume is kept constant at all depths by the fish secreting or absorbing gas as required, and the depth at which the swimbladder resonates at 12 kHz can be read directly from the abscissa. In the passive case the volume simply expands or compresses according to Boyle's Law. When plotted, Boyle's Law is a straight line which slopes at −45°. Thus by placing a 45° triangle at the known surface volume, the depth at which the swimbladder resonates at 12 kHz and its volume at that depth are the coordinates of the point at which the hypotenuse of the 45° triangle crosses the curve of interest.

RESULTS AND DISCUSSIONS

Preliminary substitutions of measured lengths or swimbladder volumes in either Haslett's or Andreeva and Chindonova's equations resulted in wide discrepancies between measured and calculated values. The same discrepancies resulted when other workers' data were treated likewise. For instance, in Capen's data only 4 of the 46 calculated swimbladder volumes were in close agreement (within 0.68 to 13.91 mm^3) with those calculated from either equation. This gives credence to Andreeva and Chindonova's statement that their equation does not pretend to give precise determination of the size of the swimbladder for a particular fish and should only be used for determination of the order of magnitude of the volume of the swimbladder.

The regression equation and the correlation coefficient between the total lengths and the estimated swimbladder volumes for *M. nitidulum* are presented in Figure 1. The correlation coefficients between estimated swimbladder volumes and the above-mentioned equations for this species are presented in Figures 2 and 3. The same statistics for *L. güntheri*, *D. brachycephalus*, and *S. diaphana* can be found in Figures 4 through 12 and are summarized in Table 1. This table gives the coefficients for the regression equation for each species and for Andreeva and Chindonova's (1964) and Haslett's (1962) equations.

From Table 1, one might assume that since the calculated correlation coefficients in 3 of the 4 species are larger than those obtained with equations (9) and (10), that it would be better to estimate swimbladder volumes from total lengths on regression equation (8). This assumption, however, may not be valid since, with the exception of r = 0.879 in the case of *S. diaphana*, the correlation coefficients are too low to be considered seriously.

One should use caution in attempting to interpret the significance of these r values and other presented statistics primarily because of the relatively small-sized samples investigated. Ideally in a study designed solely to determine the proper relationship between the swimbladder volume and a measurable parameter (be it the total or standard length, the greatest body depth, or the weight or volume of the fish to mention a few), thousands of specimens of a species, encompassing a wide range of the body sizes, age groups, and sexes should be thoroughly examined and measured in order to obtain a high degree of confidence in the overall results.

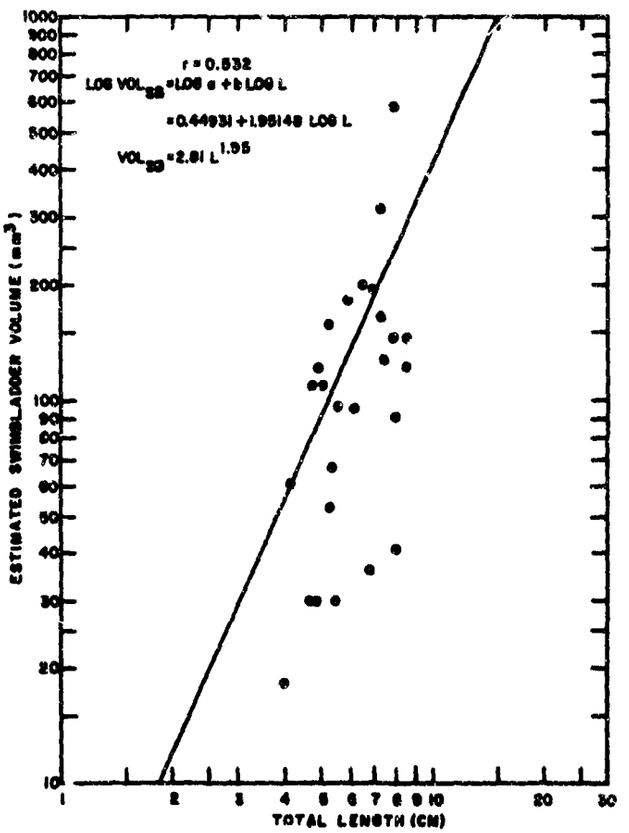

Figure 1. The regression of swimbladder volume on total length in *Myctophum nitidulum* dipnetted at the surface

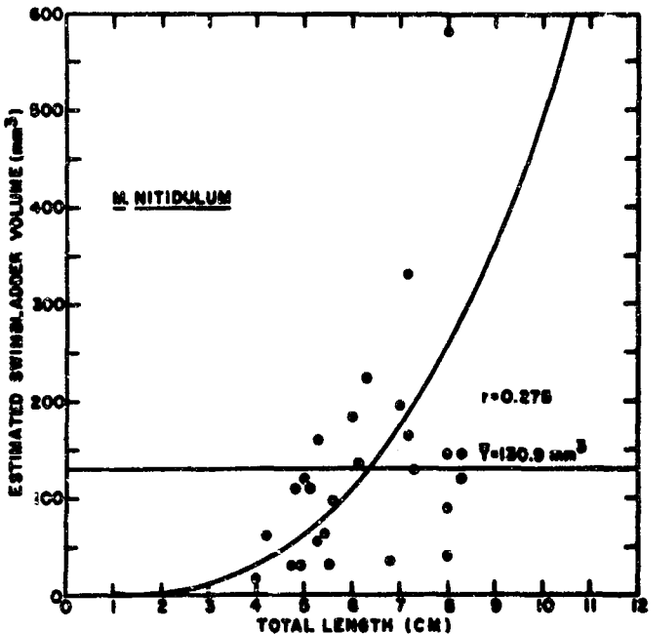

Figure 2. Correlation between estimated swimbladder volume in *Myctophum nitidulum* and Andreeva and Chindonova's (1964) equation: $V_{SB} = 0.50\,L^3$ mm^3.

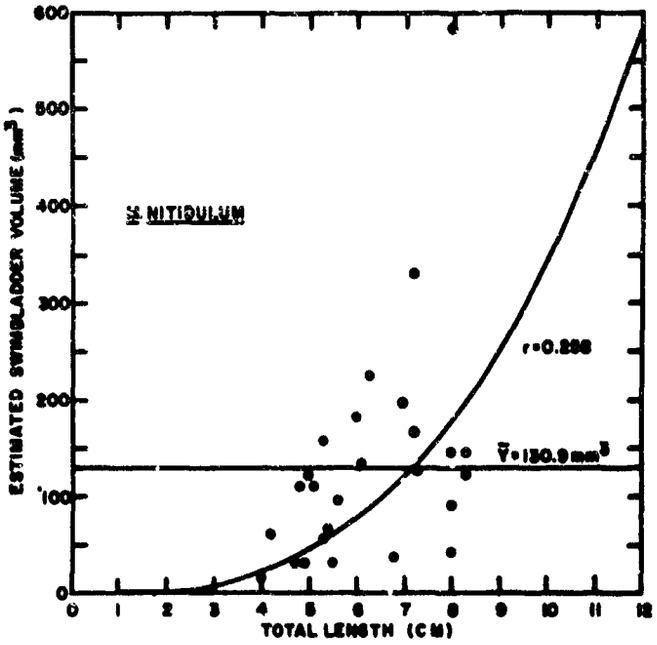

Figure 3. Correlation between the estimated swimbladder volume in *Myctophum nitidulum* and Haslett's (1962) equation: $V_{SB} = 0.34\,L^3$ mm^3

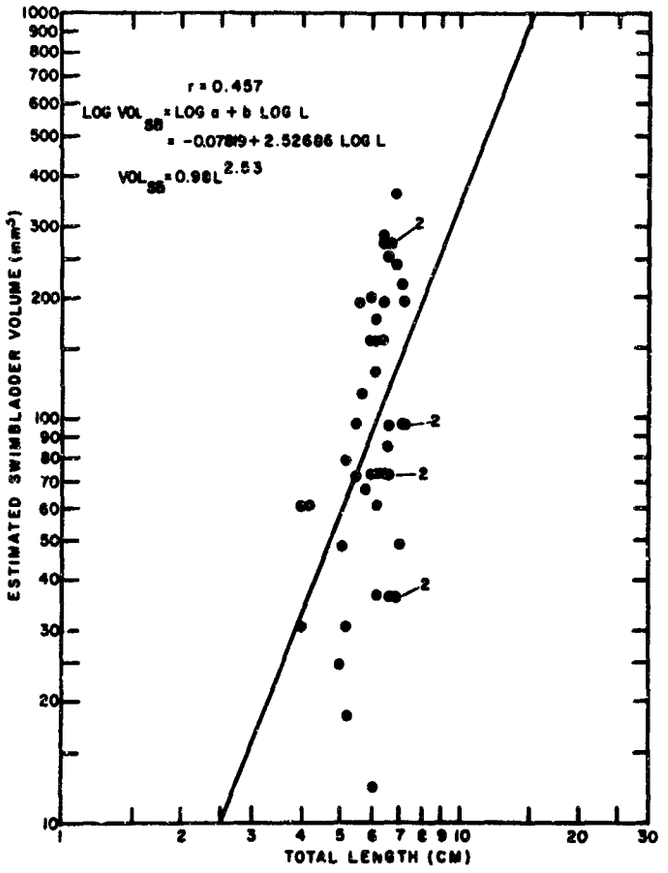

Figure 4. The regression of estimated swimbladder volume on the total length in *Lepidophanes guntheri* captured in a 10-foot iKMT at depths between 230 and 0 m

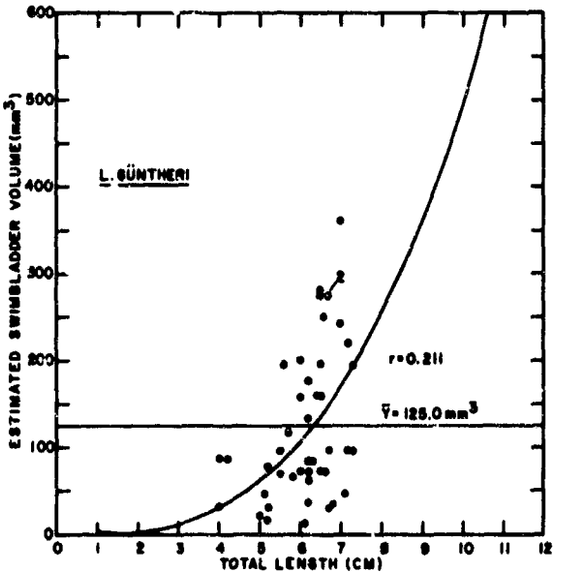

Figure 5. Correlation between estimated swimbladder volume in *Lepidophanes guntheri* and Andreeva and Chindonova's (1964) equation: $V_{SB} = 0.50\,L^3$ mm^3

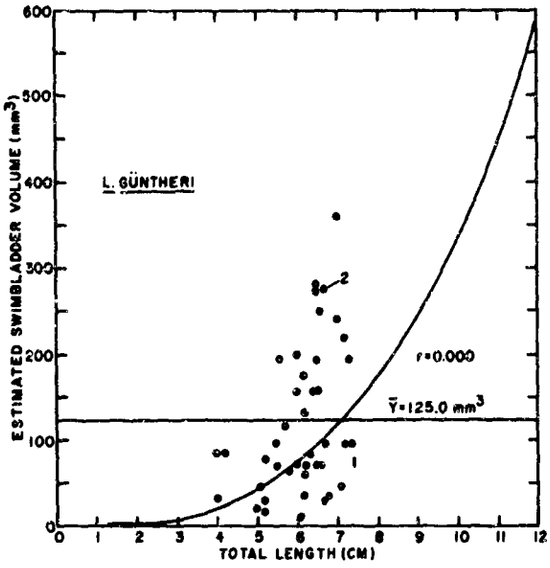

Figure 6. Correlation between the estimated swimbladder volume in *Lepidophanes güntheri* and Haslett's (1962) equation: $V_{SB} = 0.34\,L^3$ mm^3

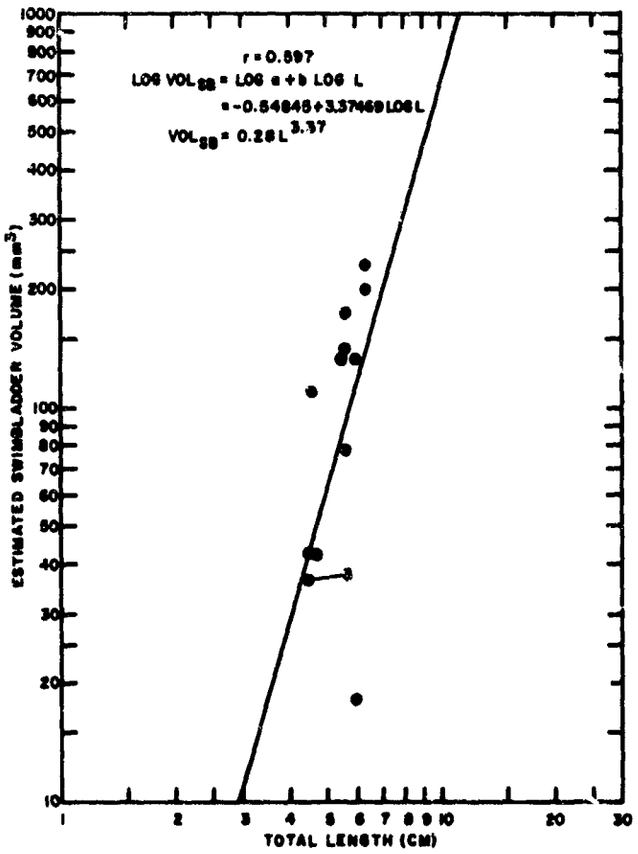

Figure 7. The regression of swimbladder volume on the total length in *Diaphus brachycephalus* captured in a 10-foot IKMT at depths between 230 and 0 m

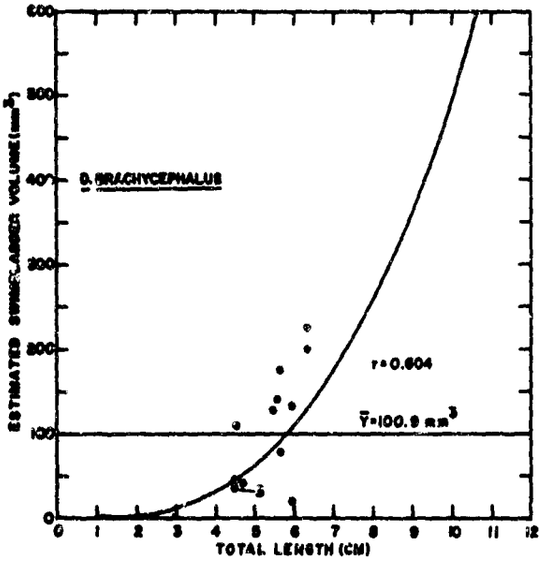

Figure 8. Correlation between the estimated swimbladder volume in *Diaphus brachycephalus* and Andreeva and Chindonova's (1964) equation: $V_{SB} = 0.50 L^3$ mm^3

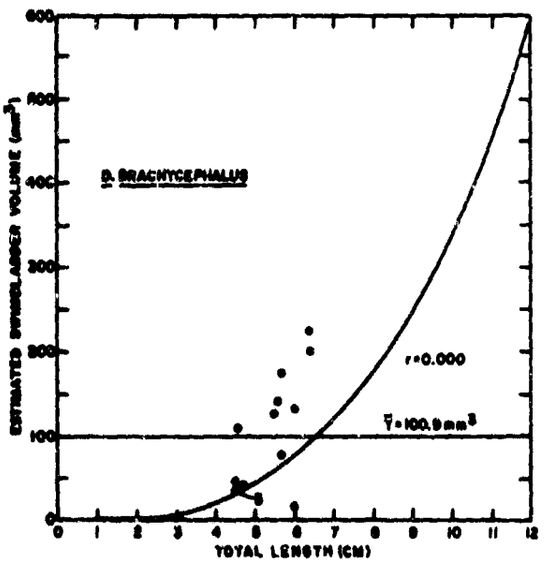

Figure 9. Correlation between the estimated swimbladder volume in *Diaphus brachycephalus* and Haslett's (1962) equation: $V_{SB} = 0.34 L^3$ mm^3

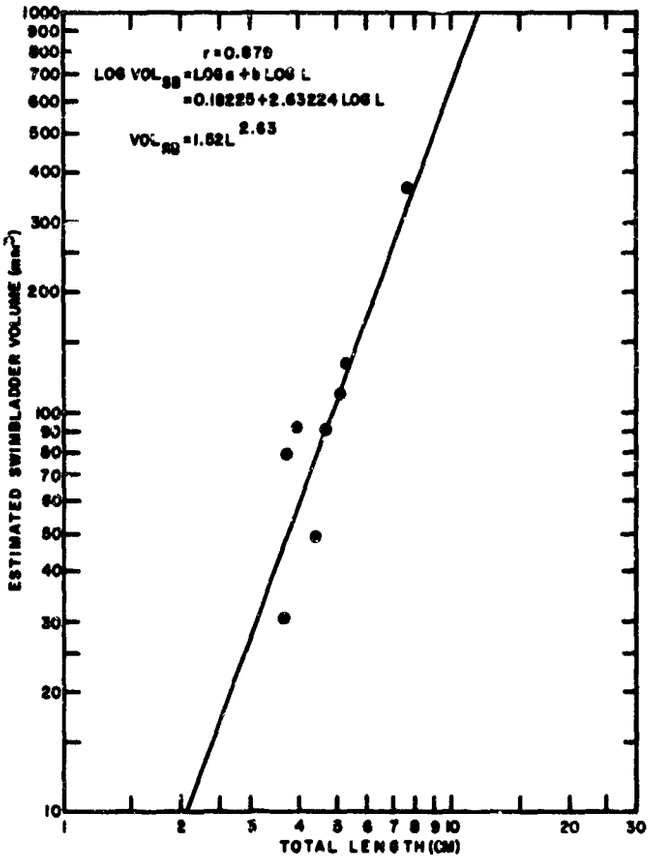

Figure 10. The regression of estimated swimbladder volume on total length in *Sternoptyx diaphana* captured in a 10-foot IKMT between 860 and 0 m

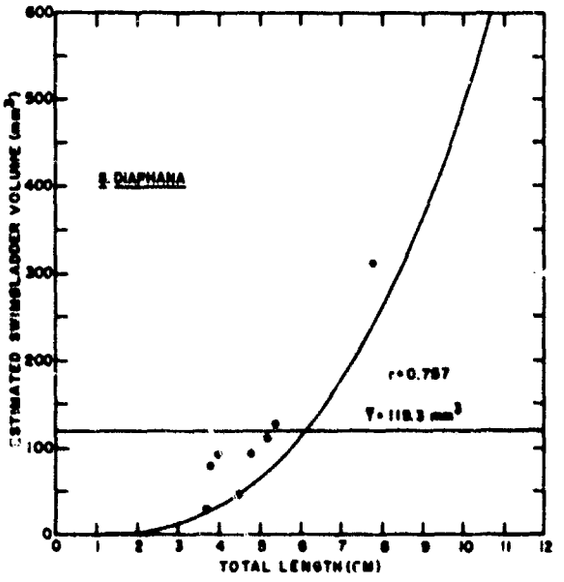

Figure 11. Correlation between estimated swimbladder volume in *Sternoptyx diaphana* and Andreeva and Chindonova's (1964) equation: $V_{SB} = 0.34\,L^3$ mm^3

Table 1. Summary of Correlation Coefficients

Species and numbers of specimens		Calculated Coefficients: Regression equation	Calculated Coefficients: r	Andreeva and Chindonova $V_{SB} = 0.50\,L^3$ mm^3 r	Haslett $V_{SB} = 0.34\,L^3$ mm^3 r
Myctophum nitidulum	(26)	$V_{SB} = 2.8\,L^{2.0}$ mm^3	0.532	0.275	0.258
Lepidophanes guntheri	(43)	$V_{SB} = 1.0\,L^{2.5}$ mm^3	0.457	0.211	0.000
Diaphus brachycephalus	(14)	$V_{SB} = 0.3\,L^{3.4}$ mm^3	0.597	0.604	0.000
Sternoptyx diaphana	(8)	$V_{SB} = 1.5\,L^{2.6}$ mm^3	0.879	0.757	0.406
All specimens	(91)	$V_{SB} = 2.5\,L^{2.1}$ mm^3	0.509	0.408	0.255

Swimbladder volumes required to resonate at 12 kHz between 0 and 1500 m based on the resonant frequency equations of Minnaert, Andreeva (1964), and Andreeva and Chindonova and volumes for a free gas bubble are given in Figure 13. Table 2 summarizes the data on the range of swimbladder sizes in each collection, their depths of resonance for each equation, the depths of various scattering layers at the time of capture for each collection, and the percentage of specimens resonating between their depth of capture and the surface, assuming either active or passive swimbladder response. Figure 14 graphically depicts the range of resonant depths for each collection, based on all equations, for the smallest, largest, and mean swimbladder volumes for each species.

If one assumes that volumes estimated by the Kanwisher and Ebeling method at atmospheric pressure are the maximum values possible, there should be very little difference in this volume at all depths in the case of actively responding swimbladders. However, if the swimbladder responds passively this volume would tend to obey Boyle's Law and would be practically halved in the first 10 m below the surface. This is apparent from the shallower and much narrower range of resonance depths for the smallest, largest, and mean volume for each collection (see Table 2 and Figure 14). Furthermore, it can be ascertained from Table 2 that a wide range of theoretical resonance depths are possible for a single specimen due to the idiosyncrasies of each of the available resonant frequency equations. This is more evident in the case of actively responding than in the case of passively responding swimbladders. Suffice it to say that more studies on this aspect alone are needed. The percentage of specimens in each collection resonating at 12 kHz was determined by ascertaining from Figure 13 what volume was required for each equation, for both responses, to resonate at the greatest depth of the trawl. Any specimen with volumes smaller than these would consequently resonate at lesser depths.

If one assumes that the swimbladder responds actively an average of 36.6% of all *S. diaphana* specimens and none of the other species were capable of resonating at 12 kHz between the greatest depth of the trawl and the surface. If, however, the swimbladder responds passively then 100% of all the *S. diaphana* and *D. brachycephalus* specimens and 75.6% of all *L. güntheri* specimens were capable of resonating at this frequency at specific depths between the greatest depth of the trawl and the surface (see Table 2).

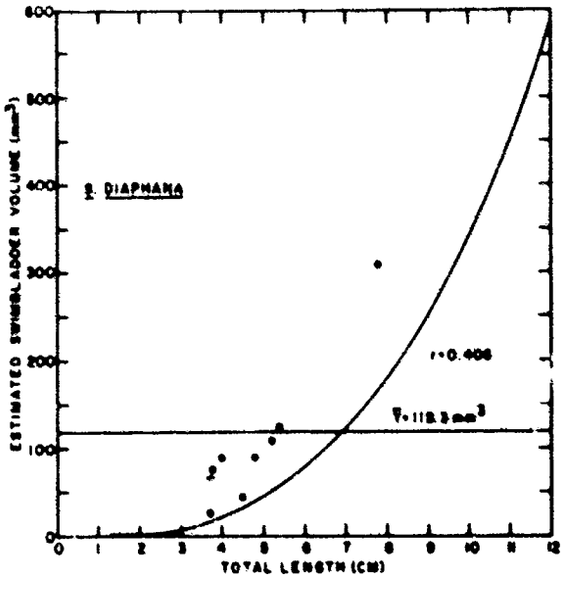

Figure 12. Correlation between the estimated swimbladder volume in *Sternoptyx diaphana* and Haslett's (1962) equation: $V_{SB} = 0.34\,L^3$ mm^3

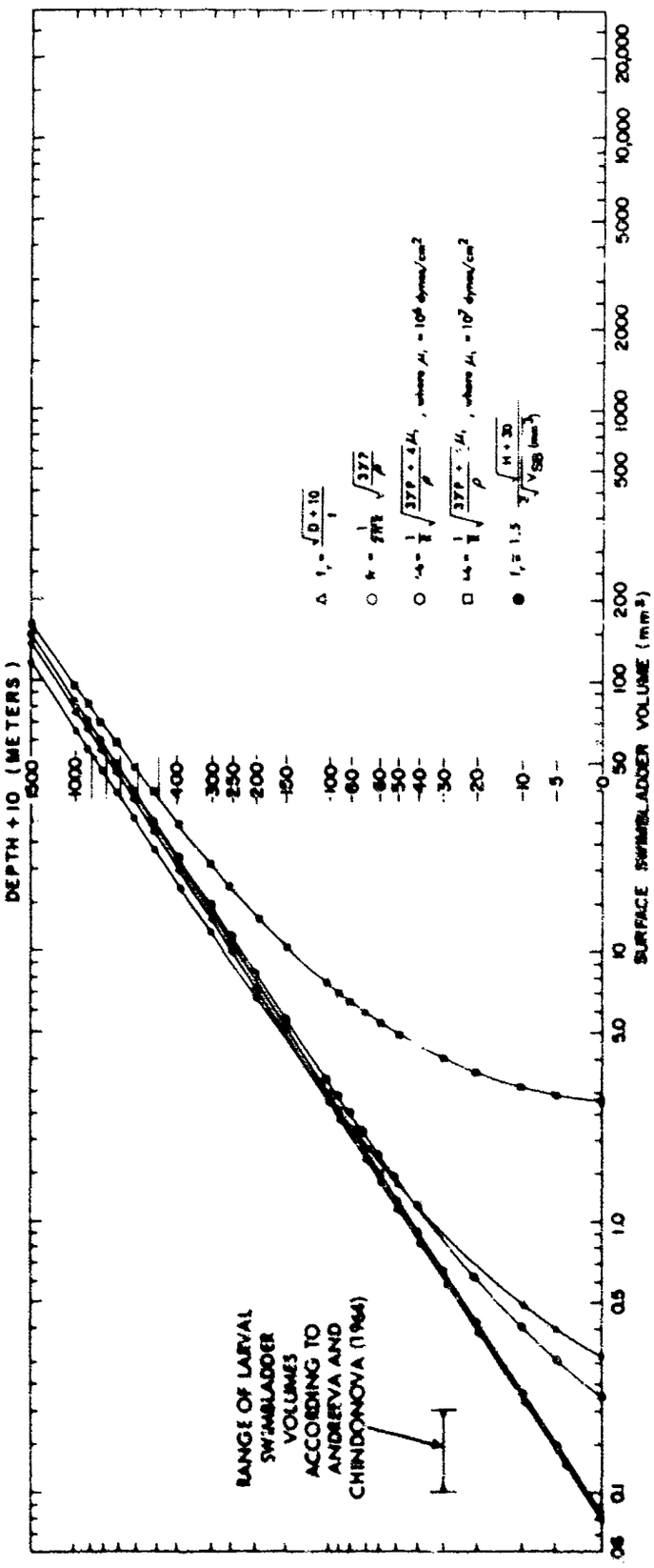

Figure 13. Swimbladder volumes required for resonance at 12 kHz between the surface and 1,500 m

Table 2. Active and Passive Resonance Depth Ranges at 12 kHz

Resonance Depth Range at 12 kHz (m)

Species and Number of Specimens Measured	Depth of Capture (m)	Period of Capture Day/Night	Range and Mean of Swimbladder Volumes (cm³), Measured at Atmospheric Pressure		Actively Responding Swimbladders (Constant Volume)					Passively Responding Swimbladders (Variable Volume)					Depth of Diff.'s (m) at Time of Capture as Recorded on the Girth GDR-19-T	Percentage of Sample Resonating at 12 kHz at Depth of Capture		Known Depth Distributions (m)
					$f_r = \sqrt{\frac{3p+10}{\rho}}$	$f_r = \frac{1}{2\pi}\sqrt{\frac{3P}{\rho}}$	$\omega_0 = \frac{1}{R}\sqrt{\frac{3P\rho+\sigma_1}{\rho}}$	$f_r = 1.5\sqrt{\frac{3p+10}{\sqrt[3]{V_{SB}}}}$		$f_r = \sqrt{\frac{3p+10}{\rho}}$	$f_r = \frac{1}{2\pi}\sqrt{\frac{3P}{\rho}}$	$\omega_0 = \frac{1}{R}\sqrt{\frac{3P\rho+\sigma_1}{\rho}}$		$f_r = 1.5\sqrt{\frac{3p+10}{\sqrt[3]{V_{SB}}}}$				
							$\sigma_1 = 10^6$	$\sigma_1 = 10^7$				$\sigma_1 = 10^6$	$\sigma_1 = 10^7$			Active	Passive	
Myctophum nitidulum (36)	0	N (Specimens)	18.40-541.40 M = 148.98	S[a] L[b] M[c]	375 3030 1430	360 3650 1350	350 3640 1340	370 3360 1260	415 4455 1630	80 550 190	80 340 185	70 330 180	35 285 135	80 375 200	0-200	0	0	Day [illegible] Night [illegible]
Lepidophanes guentheri (7)	100	N	30.60-275.40 M = 114.30	S L M	530 3325 1295	530 2330 1730	500 2220 1220	410 2130 1140	595 2680 1480	106 335 180	95 250 175	90 260 170	50 195 120	100 270 185	0-135,155-220, 510-552	0	40.0	Day 365-310[d] Night 200-55[e]
(8)	145-90	N	36.50-97.90 M = 60.40	S L M	440 1165 840	430 1150 880	430 1100 790	340 1010 710	510 1330 955	95 165 135	90 160 130	80 155 125	45 110 80	90 170 135	0-220	0	100.0	Day 365-310[d] Night 200-55[e]
(12)	140-0	N	99.00-362.00 M = 191.30	S L M	730 2000 1830	750 2670 1340	690 2640 1730	680 2570 1660	825 3215 2095	125 295 230	120 290 215	115 265 205	70 220 160	125 310 230	0-170,275-310, 345-375	0	25.0	Day 365-310[d] Night 200-55[e]
(9)	140-0	D/N	12.20-195.00 M = 68.00	S L M	300 1860 1023	270 1770 970	260 1760 970	180 1670 880	310 2130 1165	65 220 150	65 215 145	60 210 145	25 165 95	60 235 155	0-365, Thickest 0-145	0	88.8	Day 365-310[d] Night 200-55[e]
(3)	145-0	N	79.00-180.70 M = 130.60	S L M	1013 1830 1540	970 1590 1370	960 1720 1360	870 1630 1180	1135 2085 1550	150 220 180	145 215 175	140 205 170	95 160 120	155 230 190	0-165,400-475, 530-570	0	100.0	Day 365-310[d] Night 200-55[e]
(40)	330-0	N	97.00-381.50 M = 169.00	S L M	1165 2570 1690	1140 2260 1610	1100 2250 1600	1020 2170 1520	1330 2720 1930	165 260 210	160 255 205	155 245 200	110 145 150	170 275 215	0-510, Thickest 0-145	0	100.0	Day 365-310[d] Night 200-55[e]
(6)	175-0	N	36.90-140.30 M = 51.80	S L M	600 1265 750	570 1200 720	560 1190 710	490 1110 620	675 1440 850	110 175 125	105 170 120	100 165 115	60 120 75	110 180 125	0-140,180-220 (others in 400)	0	100.0	Day ? Night 120-90[e]
(8)	330-0	N	10.00-220.40 M = 148.50	S L M	375 2000 1470	360 1960 1480	518 1940 1390	370 1850 1310	415 2345 1685	80 255 190	80 250 185	70 245 180	35 180 135	80 250 200	0-200,210-250, 325-365	0	100.0	Day ? Night 120-90[e]
(3)	660-0	N	38.60-91.80 M = 67.30	S L M	530 1120 900	510 1060 860	500 1060 850	410 970 770	600 1270 1020	100 160 140	95 155 135	90 150 130	50 105 90	100 165 145	0-200	33.3	100.0	Day 88[d], 800 and below[e] Night 800-400[e]
(3)	660-0	D	99.00-367.20 M = 150.60	S L M	730 2030 1460	700 2040 1480	690 2680 1470	680 2650 1390	825 3250 1780	125 290 200	120 285 195	115 265 190	70 230 145	125 310 205	110-150,360-280, 380-420,500-510	66.0	100.0	Day 88[d], 800 and below[e] Night 800-400[e]

[a] Smallest swimbladder volume for each collection
[b] Largest swimbladder volume for each collection
[c] Mean swimbladder volume for each collection
[d] These data are taken from distributional records of species captured during our investigations using either the fixed multiple plankton sampler or the Isaacs-Kidd midwater trawl (1965 to present).
[e] These data are taken from Gostansian (1967).

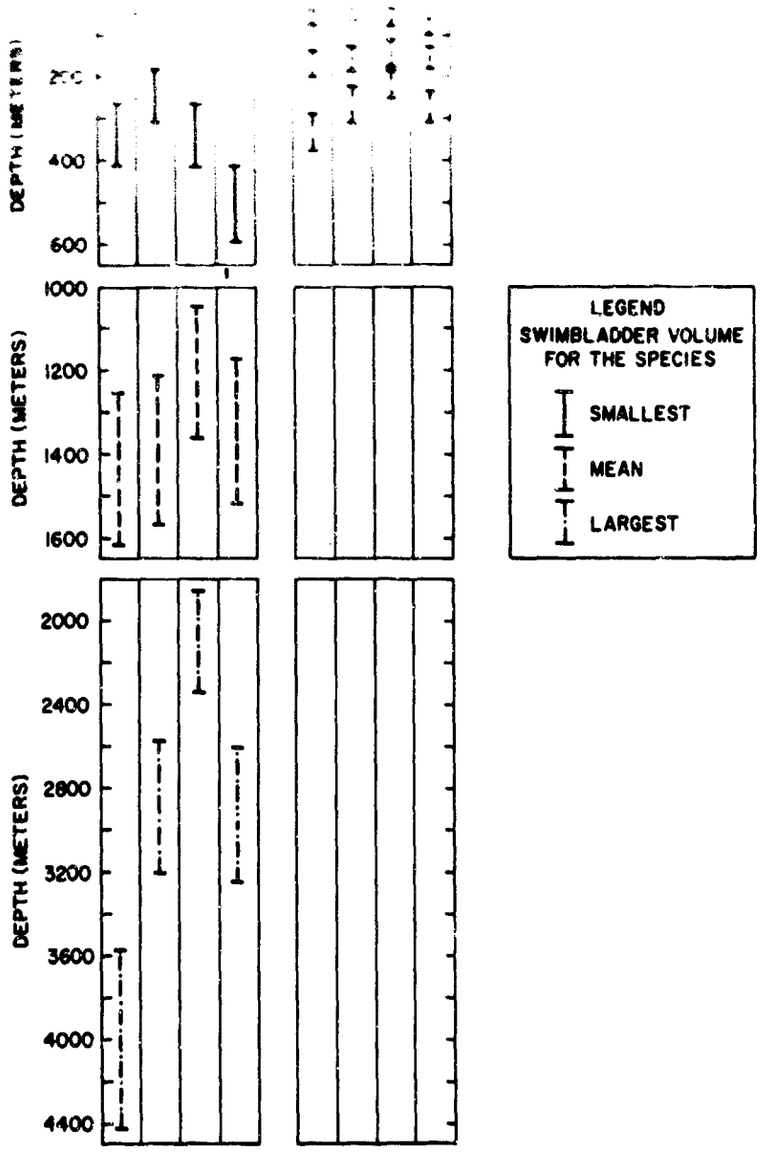

Figure 14. Active and passive resonance depth ranges at 12 kHz for the smallest, largest, and mean swimbladder volumes for each species, derived from the resonance frequency equations of Minnaert (1933), Andreeva (1964), Andreeva and Chindonova (1964), and for that of a free gas bubble

Least square straight lines fitted to the measured data, with one exception, also show poor agreement. Correlation coefficients derived in this study are low and inadequate for the prediction of swimbladder volumes from the measured length of the fish. Although regression equations derived from measured data appear to be superior to either equation (9) or (10) in 3 of the 4 species, some reservations should be made regarding their use. The most important fact is that when a statistical approach such as this is employed, the implication should be kept in mind that one variable is completely related to the other. This may not be strictly true in the relationships between swimbladder volume and the length of a specimen, since additional contributing factors undoubtedly play a part in this relationship. In this respect all future investigations will be oriented to gathering more data concerning the morphology and size of individual specimens, their age, and the rate of growth of organs as a function of the overall growth rate, whether or not the swimbladder becomes fat invested with age, and the sex and effects of gonadal development on the expansiveness of the swimbladder. All of these factors, as well as any other measurable parameters which might become apparent during future investigative programs, will be subjected to a multiple stepwise regression analysis designed to select the independent variable or variables most highly correlated and to reject those not correlated with the dependent variable—the swimbladder volume. Primary effort will be made to obtain larger numbers of specimens to insure a fairly representative sample of the total population of a particular species. In this study a fairly wide size range was used in determining the swimbladder volumes for each species, but it is questionable whether 43 specimens of *L. güntheri* and 26 specimens of *M. nitidulum*, and highly doubtful that 14 specimens of *D. brachycephalus* and only 8 of *S. diaphana* could be considered as fairly representative samples of the total populations of these species.

Formulas used at present for determining the depth of resonance for a given frequency, vary widely, especially at shallow depths. Use of approximations and those applicable to free bubbles (included here for comparison) should be avoided. It may very well be that Andreeva, with $\mu_1 = 10^6$, is the best of the curves shown in Figure 13. However, it is thought that a more accurate determination of μ_1 would be an ideal solution to the problem of determining resonance depth at any given frequency.

The family of curves developed from each of the resonant frequency equations simplifies the determination of the ranges of resonance depths at 12 kHz for any physoclistous fish, provided its surface measured swimbladder volume is known. If it is suspected that the physoclistous swimbladder responds actively the resonance depth can be read directly from the abscissa. If, however, one assumes that it responds passively, then a 45° triangle can be placed at the known surface volume, and both the depth at which the volume resonates at 12 kHz, and its volume at depth are the coordinates of the points at which the hypotenuse of the 45° triangle crosses each curve.

Based on the range of estimated swimbladder volumes obtained for each species in this study, it would appear that, with the exception of 36.6% of all the *S. diaphana* specimens that might have responded actively, only fish whose swimbladders could respond passively contributed to any of the scattering layers recorded at the time of capture.

determination of the resonance depth from the length alone.

In concluding I think that it would be apropos to quote a statement made 59 years ago by Professor R. W. Tower (1901). "The function of the swimbladder of fishes has attracted the attention of scientists for many centuries. The role that this structure plays in the life of the animal has been interpreted in almost as many ways as there have been investigations, and even now there is apparently much doubt as to the true functions of the swimbladder. Consequently, any additional data concerning this organ is of immediate scientific value."

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DISCUSSION

McCartney: I must say I enjoyed that paper very much. I have some data on gadoid fish which I did not use in my paper and which produces rather similar sorts of conclusions but on a limited number, perhaps 50 specimens. I would like to ask a question regarding the technique. You are catching fish near the surface and then making volume measurements?

Shearer: Only specimens of *Myctophum nitidulum* were taken at the surface; the other species were taken in the trawl at various depths. I should have also mentioned that all specimens taken in the trawl were dead and even the dipnetted *M. nitidulum* specimens were at best moribund when removed from the net and placed in a bucket of sea water.

McCartney: But the real point I have is that if these have migrated recently, there is a possibility that when you catch them, there is an excess internal pressure within the swimbladder.

Shearer: I suspected something like that. Actually the 91 specimens reported on were only those that sank when the pressure was doubled; those that didn't sink, which included more than half the *Sternoptyx* specimens, were eliminated. In doing this I hoped to obtain true values for the surface volumes uninfluenced by such factors as migration or retrieval from great depths.

McCartney: So the volumes are biased to those which would be low, in fact.

Shearer: Yes, somewhat. I don't know whether it's statistically legal, but the majority of all specimens of the four species would sink by doubling the pressure. In many of the *Sternoptyx diaphana* specimens the stomach was extruded from the mouth so that perhaps I was trying to compress the stomach too.

McCartney: What worries me about the technique is that the combined characteristics of the gas and the surrounding swimbladder, if stiff, may not follow Boyle's law to external pressure changes. I have a comment on your final statements about other parameters. If the swimbladder is a hydrostatic organ, one would presume that weight would be the best parameter on which to base regression lines.

Shearer: Yes, and perhaps volume as well.

McCartney: Weight or volume of fish. There are available, especially for commercial fish, regression lines of weight on length which would enable you to compare this.

Dunlap: It was interesting that you used *M. nitidulum* in the Atlantic, and I did it in the Pacific. Did the adults have seemingly completely gas-filled swimbladders? It would be very interesting to compare the same species from the Atlantic and the Pacific.

Shearer: Yes, there was gas present.

Shearer: Well, I made two assumptions. It might either act passively or actively, but I didn't come to any particular conclusion.

Alexander: I wonder whether the percentage figures you gave for 12-kHz resonance were intended to suggest passive response.

Shearer: The values were much higher in the passive condition than in the active.

Alexander: But you did not feel that you got any evidence here as to which is happening?

Shearer: No, and I don't think anyone has when you come right down to it.

Alexander: The other question I wanted to ask was whether you tried to get a swimbladder volume equation based on weight.

Shearer: No, it is hard to weigh fish at sea, and the only measurement that I could take accurately was their length. I also checked some of their volumes by the displacement method but that's also pretty difficult to do at sea.

D'Aoust: I want to say I enjoyed the paper too. I wonder if it's possible to get around this uncertainty about the accuracy of volume measurements strictly with compression. I am sure one could use the instrument by pulling on it as well.

Shearer: By what?

D'Aoust: By distention, such as Dr. Alexander has done, and get some sort of average. The combination of the behavior of the fish with a given amount of decrease and increase in pressure might be a way to get the type of regression you are after.

Shearer: Well, it looks like there is really a lot of work to be done. In fact, trying to determine which way the swimbladder responds to changing hydrostatic pressure seems like a lifetime job for an investigator.

Weston: I have a comment regarding your final remarks, which hint at some other parameters. These are really the observations of Harden-Jones of the Fisheries Laboratory at Lowestoft, but they were taken in some joint experiments. We were looking at pilchard in the Bristol Channel area that I was talking about yesterday. A lot of the female pilchard were gravid, and there was hardly any swimbladder left.

Shearer: I noticed that in looking at some of the specimens that we had. It appears as though ripe gonads, especially ovaries, so completely fill the cavity that they must exert a compression effect on the swimbladder.

Hansen: I wonder if the acousticians and the biologists would consider an experiment related to this topic of swimbladder function and the changes occurring within a swimbladder. In commercial fishery research, there are now available very small sonar tags, little capsules, which are placed on the fish and then tracked. What I am considering is what would happen if one could precalibrate such a capsule, surgically insert it alongside, but not within, a swimbladder and then observe a fish in migration and observe the changes in frequency which would probably be related to resonance of the swimbladder.

[illegible] hyperbaric [illegible] capsules"

[illegible] the size of a pill

[illegible] of the bladder, it would send your signal back?

Hansen: From the acoustical descriptions that we had yesterday, it should be possible that, rather than bouncing sound back, you are emitting sound which would be changing with swim-bladder functions like volume or pressure. This is an experiment I would like to suggest.

Shearer: Do you have the name of the manufacturer of those?

Hansen: Yes, and I will see you afterwards.

ACOUSTIC SCATTERING FROM ZOOPLANKTONIC ORGANISMS

Paul Beamish
Bedford Institute
Dartmouth, Nova Scotia, Canada

ABSTRACT

Sound scattering from a zooplanktonic organism, the euphausiid, was measured. Four-fifths of the acoustic scattering from euphausiids was found to be caused by the compressibility contrast. The remaining one-fifth is attributed to the density contrast. The backscattering cross section of a typical euphausiid was found to be 1.4×10^{-4} cm^2 at 102 kHz. Sounders with frequencies of about 12 kHz will produce a scattering cross section of the order 3×10^{-8} cm^2 for an average-sized euphausiid.

Acoustic scattering from zooplanktonic organisms occurs because of the acoustic impedance contrast between the animals and the surrounding water; that is, because some of the physical properties of the animals are different from the corresponding properties of the water. The impedance contrast in its basic form consists of a difference in compressibility, a difference in density, or a combination of both factors. The primary purpose of our studies at the University of British Columbia (Beamish, 1969 and 1971) was to determine the degree to which these factors contribute to plankton echoes. Four-fifths of the acoustic scattering from euphausiids was found to be caused by the compressibility contrast. The remaining one-fifth is attributed to the density contrast.

Furthermore, it was possible to measure backscattering cross sections; therefore, it becomes feasible to predict the scattering strengths of zooplanktonic organisms as a function of their size and of the frequency of the incident sound. The backscattering cross section of a typical euphausiid was found to be 1.4×10^{-4} cm^2 at 102 kHz. The scattering cross section is proportional to the fourth power of the incident frequency when the product of the wave number and the mean radius of the animal is small. Thus, the commonly used sounders with frequencies of about 12 kHz will produce, for an average-sized euphausiid, a scattering cross section of the order 3×10^{-8} cm^2. It is doubtful, therefore, that either the concentrations of these animals or the signal-to-noise ratios of commonly used 12-kHz sounders are high enough to permit the acoustic detection of euphausiids at this frequency.

More recent studies (Beamish and Mitchell, 1971) have revealed what may be an acceptable acoustic cross section of euphausiids for a baleen, plankton-feeding whale. Furthermore, it appears that these whales may have developed highly sophisticated plankton echolocation signals.

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DISCUSSION

Kinzer: I admire your discovery about this natural sound source in the baleen whale. Do you know how they produce a sound, the mechanism of sound production?

Beamish: No. We believe that these might be the first echolocation signals heard from baleen whales (mysticetes). Other people have been looking mostly in the audio region. There is quite a lot known about sounds and the related physiology of the toothed whales (odontocetes). To comment on your question, Ed Mitchell and I, working at the Blanford Whaling Station, are studying in detail the physiology of the middle ear and the transmission apparatus of mysticetes. Maybe we'll know more about these in the future. Let me say that it looks absolutely fascinating from a physics-acoustics point of view. I have an earbone (a tympanic bulla) of a fin whale in my briefcase, and we can look at that from an acoustic point of view. Maybe by this time next year we'll be able to tell you something about some of the acoustic properties in the transmission and reception areas.

McElroy: You discussed the quadripole factor and then essentially indicated later that it was probably not significant. I was wondering how you made that decision on the basis of a measurement made at what looked to me to be two different angles.

Beamish: I would like to show you some slides later on of a computer analysis that we did of an euphausiid composed of very many spheres. I was treating a single sphere on the blackboard. Our analysis showed us that, assuming the Born approximation, we could treat the animal as a series of spheres, and looking at the individual spheres themselves using our wave number as well as approximate compressibilities and densities, we computed that the coefficients of the quadripole terms were small compared to the coefficients of the dipolar terms. In this case we computed that the energy ratios (the upper to the outer hydrophone) would not change appreciably, and therefore not alter the results that the isotropic scattering had a great deal more effect than the dipolar or cosine type of scattering.

ON THE CONTRIBUTION OF EUPHAUSIIDS AND OTHER PLANKTON ORGANISMS TO DEEP SCATTERING LAYERS IN THE EASTERN NORTH ATLANTIC

Johannes Kinzer
Institut für Hydrobiologie und Fischereiwissenschaft
*Universität Hamburg, Germany**

ABSTRACT

In an area about 60 miles off the Portuguese coast, a series of 15 samples was collected with a large Lowestoft-High-Speed Plankton Sampler, equipped with a revolving bucket system and a depth and flow telemetering pinger. The oblique hauls covered the depths from below the deep scattering layer (DSL) to the surface. The sonic scattering, presumably caused by fishes, was recorded with an ELAC echo sounder at a frequency of 30 kHz. During the daytime the DSL was observed at a depth of 350 to 600 m. Similar to previous observations in the subtropical eastern North Atlantic, there was during daytime a pronounced maximum of biomass at the DSL depth, with euphausiids dominating in the upper portion and copepods prevailing in the lower part. Where large numbers of euphausiids (1.6/m^3) occurred, the plankton biomass of the upper DSL was up to 80% larger than at neighboring depths. The distribution of the more abundant euphausiid species is described. Below the DSL and between depths of 300 and 100 m, only low plankton volumes were observed. The few samples collected at night indicate that while the majority of euphausiids (mostly *Meganyctiphanes norvegica*) had already reached the surface layer, the copepods slowly descended to depths below the DSL. After sunrise the copepods reentered the DSL. The samples from off the Portuguese coast are compared to a series of hauls collected in the Norwegian Sea with a Longhurst-Hardy Plankton Recorder. Quite in contrast to the samples from the eastern subtropical Atlantic, no concentration of zooplankton has been observed at the depth of the DSL.

INTRODUCTION

There is evidence that the depth of deep scattering layers (DSL) is regulated by the vertical distribution of light (Boden and Kampa, 1967; Clarke and Backus, 1964; Dickson, 1969). Besides the direct effect of light by which the DSL follows the movement of isolumes during the daytime, plankton concentrations at the daytime level of the DSL also seem to attract fish. Except for a few investigations by Osterberg, Pearcy, and Curl (1964) and by Kinzer (1969), we unfortunately know practically nothing about the prey-predator relationship of organisms within the diurnal depth range of the DSL.

As a basis for food-web studies we still lack observations on the quantitative and qualitative composition of plankton and nekton with the DSL and its neighboring depths. Because of the specific transport mechanism, the euphausiids contribute greatly to a faster transport of nutrients

*New Address: Institut für Meereskunde an der Universität Kiel

from surface waters to scattering-layer depths (see review by Mauchline and Fisher 1969, p. 372-382). Particularly for catching the faster-moving euphausiids, a larger type of high-speed plankton sampler has been employed in our recent studies.

It is hoped that the design of more effective nekton samplers for stratified hauls from selected depths will stimulate more intensive studies on the food-web relationship of organisms within the DSL, which eventually will lead toward an understanding of the role of sonic scattering layers in the vertical transport of organic matter.

METHODS

Plankton Samplers

On cruise 15 of R/V *Meteor*, August 1968, in the eastern part of the Iberian Abyssal Plain off the Portuguese coast, a large Lowestoft High-Speed Plankton Sampler was used, with a mouth opening of 40 cm in diameter and a 400 μ Monyl net (Beverton and Tungate, 1967). The sampler was equipped with a revolving bucket system[1] actuated from the vessel through a single-conductor cable. The flowmeter of the depth and flow telemetering pinger[2] was mounted in the frontal opening of the sampler. Towing speed averaged 5 to 6 knots. Sampling was done in oblique hauls from a depth of 700 m to the surface, thereby covering the depth of approximately 100 m below the lower border of the DSL. Five samples were obtained in each haul: (1) 700 to 600 m (below the DSL), (2) 600 to 420 m (lower part of the DSL), (3) 420 to 300 m (upper part of the DSL), (4) 300 to 100 m (intermediate depth), and (5) 100 to 0 m (surface sample). Average sampling time for each of the five selected depth ranges was 15 min.

For sampling in the Norwegian Sea during a 7-day sampling station on cruise 130 of R/V *Anton Dohrn*, a Longhurst-Hardy plankton recorder (LHPR)[2] (Longhurst, Reith, Bower, and Seibert, 1966) was used, together with Bongo twin nets. Both nets were mounted in a steel frame, with one attached to the LHPR, the other equipped with a bucket. The nets had an opening 71 cm in diameter and were built according to the original design by McGowan and Brown (1966). Mesh size (in square aperture) of the net was 500 μ. Sampling was done in oblique hauls to a depth of about 600 m at a ship's speed of 2.5 knots. The gauze advance had been set at 0.5-min intervals. As the duration of each haul averaged 60 to 70 min and the LHPR was collecting both portions of the oblique haul, about 120 samples were obtained in each haul.

All samples were preserved in 40% formalin, buffered with hexamethylenetetramine. The samples collected with the LHPR were preserved in total on the gauze in 4% to 6% formalin. Rinsing the samples from the gauze into the bottles was done in the laboratory.

Echo Sounders

On cruise 15 of R/V *Meteor* an ELAC echo sounder was used, operating with a power output of 4.5 kw at a frequency of 30 kHz. The pulse length of the sounder was set at 30 msec. As the transducer has a sonic beam of only 2.7°, the depth of the DSL recorded in the echograms (Figs. 2 to 6) corresponds to its actual depth.

In the Norwegian Sea during cruise 130 of R/V *Anton Dohrn*, the DSL also was recorded at 30 kHz, but using an Atlas "Fishfinder" echo sounder.

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[1] Produced by Hydrobios, Kiel, F.R.G.

[2] Produced by Benthos, Inc., North Falmouth, Mass., U.S.A.

RESULTS

Eastern Subtropical Atlantic

During cruise 15 of R/V *Meteor*, a series of 15 samples was collected between 5 and 9 October 1968 in an area 160 to 50 miles off the Portuguese coast at an average sounded depth of 3000 m. The location of sampling is shown in Figure 1. As can be seen from Figures 2 to 6, the daytime depths of the two components of the scattering layer were between 320 and 600 m. The upper layer varied somewhat from day to day in its strength and vertical depth range, whereas the layer component of the DSL revealed little changes. Both layers performed the characteristic rise to the surface at dusk and descent to their daytime depth after sunrise. The echograms also show a considerable amount of scatterers remaining at their daytime depth during the night. In Figures 2 to 6 the biomass of each of the five samples from each haul is illustrated, together with the number of copepods and euphausiids per 100 m^3. For a comparison of the depth distribution of sonic scatterers (not identified) to the zooplankton sampled from each depth level, the route of the sampler is indicated in the echograms.

As to the quantitative distribution of zooplankton, the following data were obtained:

Stations 44 to 48, 5 October 1968 (Fig. 2)

During the daytime, both hauls (Sta. 44, 46) exhibited the maximum biomass at the depth of the upper DSL because of large numbers of adult euphausiids (0.8 to 0.9 ind./m^3). Also, the lower portion of the DSL was richer in biomass than in samples from above and below the DSL. After sunset (Sta. 47, 48), the depth of the DSL seemed depleted of zooplankton; and its main constituents, the euphausiids, were observed in the surface water (1.5/m^3).

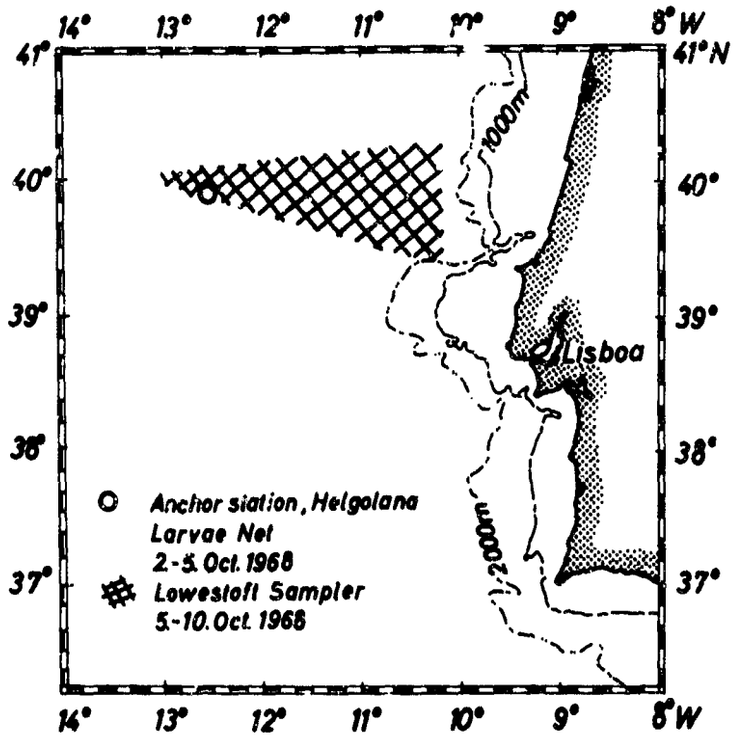


Figure 1. Location of plankton sampling in the eastern North Atlantic during cruise 15 of R/V *Meteor*

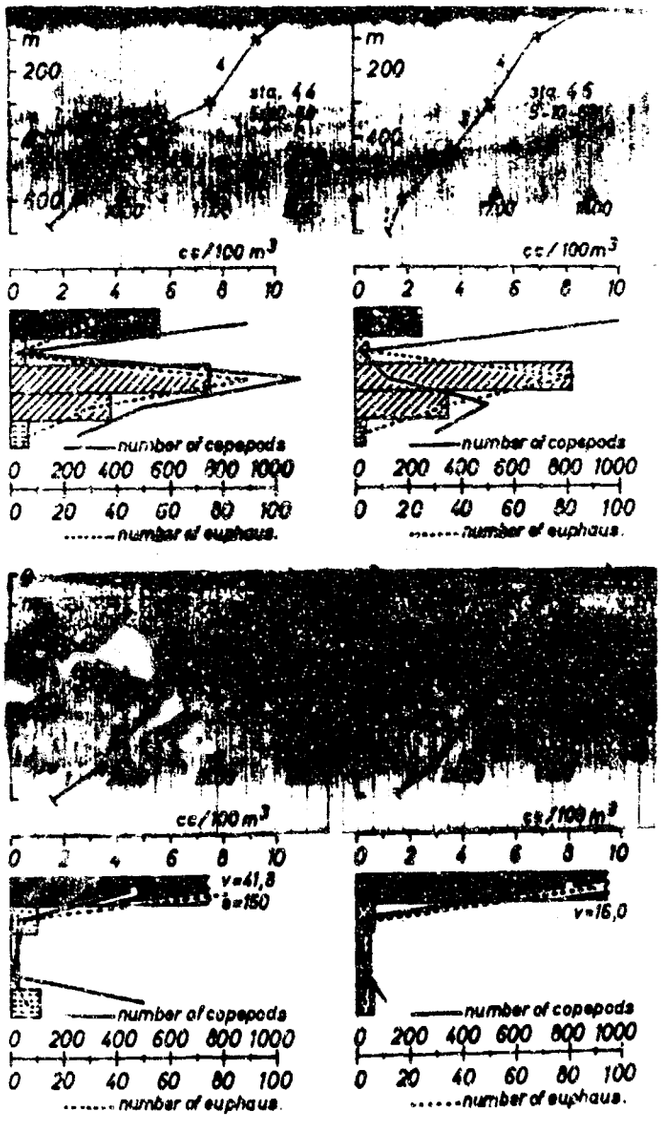


Figure 2. Towing paths of Lowestoft plankton sampler at stations 44, 46, 47, and 48 during 5 October, and the displacement volume collected at each depth level, together with number of copepods and adult euphausiids. (1. beneath DSL = 2. DSL 620-420 m = 3. DSL 420-300 m = 4. intermediate depth = 5. surface = v = volume, e = euphausiids.) Sound scattering was recorded at 30 kHz.

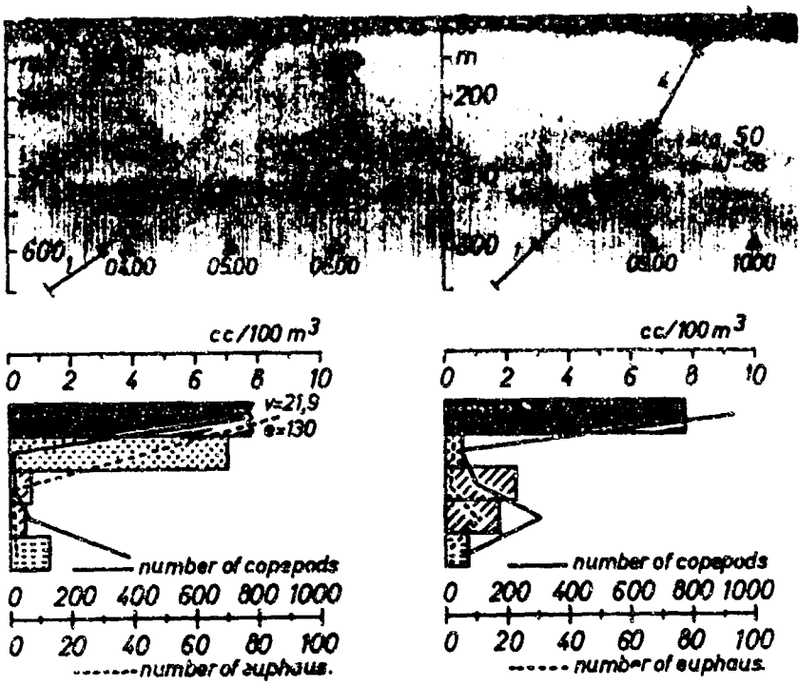


Figure 3. Towing paths of sampler, and plankton distribution at station 49 and 50 during 6 October (see Fig. 2 for explanation of histogram)

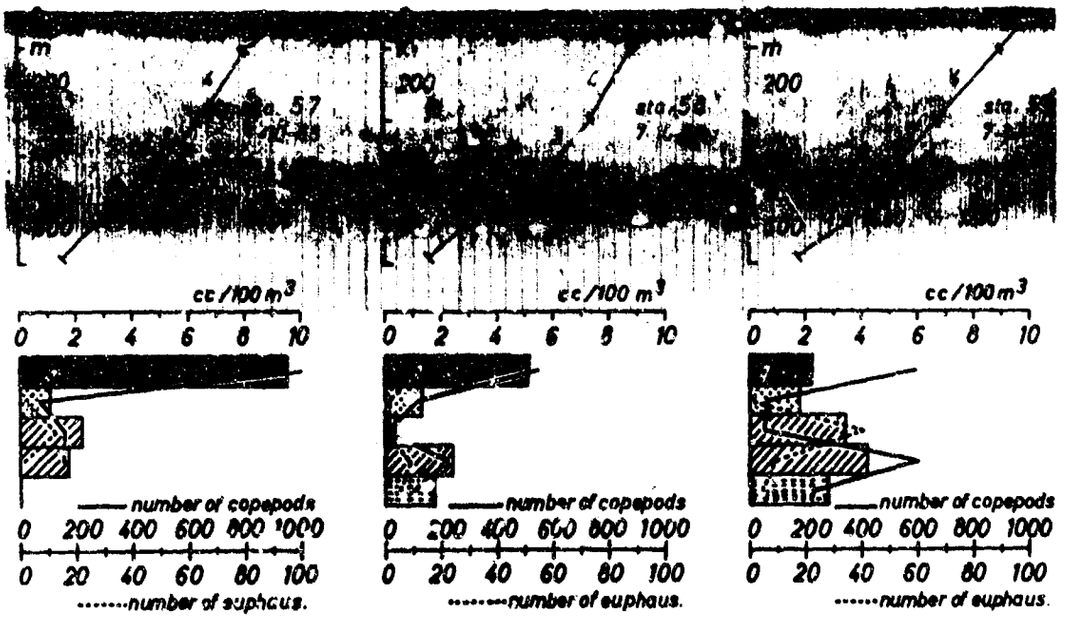


Figure 4. Towing paths of sampler, and plankton distribution at stations 57, 58 and 59 during 7 October (see Fig. 2 for explanation). At station 57 sampling failed at largest depth.

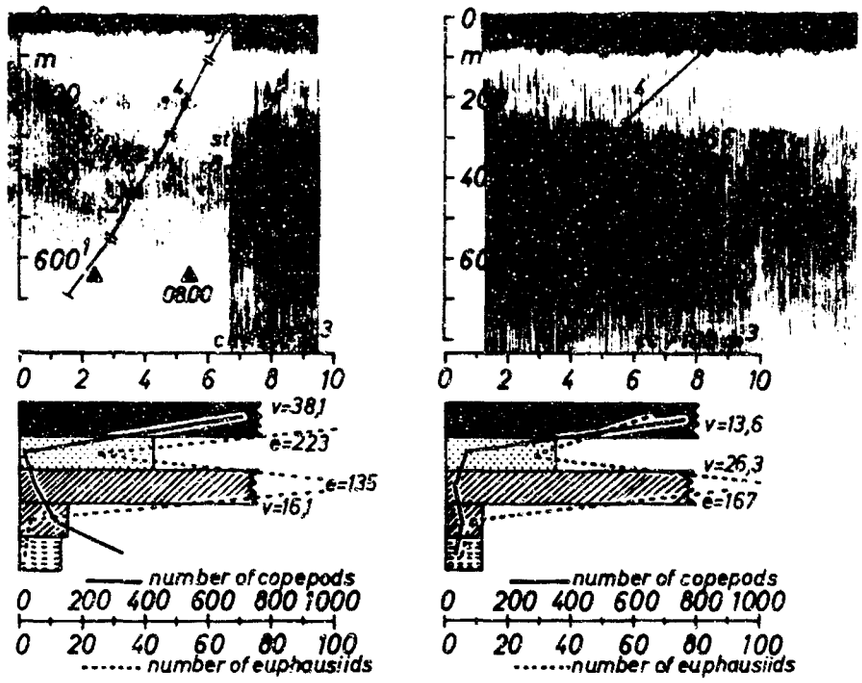


Figure 5. Towing paths of sampler, and plankton distribution at stations 65 and 66 during 8 October (see Fig. 2 for explanation). At station 66 the recording of sound scattering was disturbed.

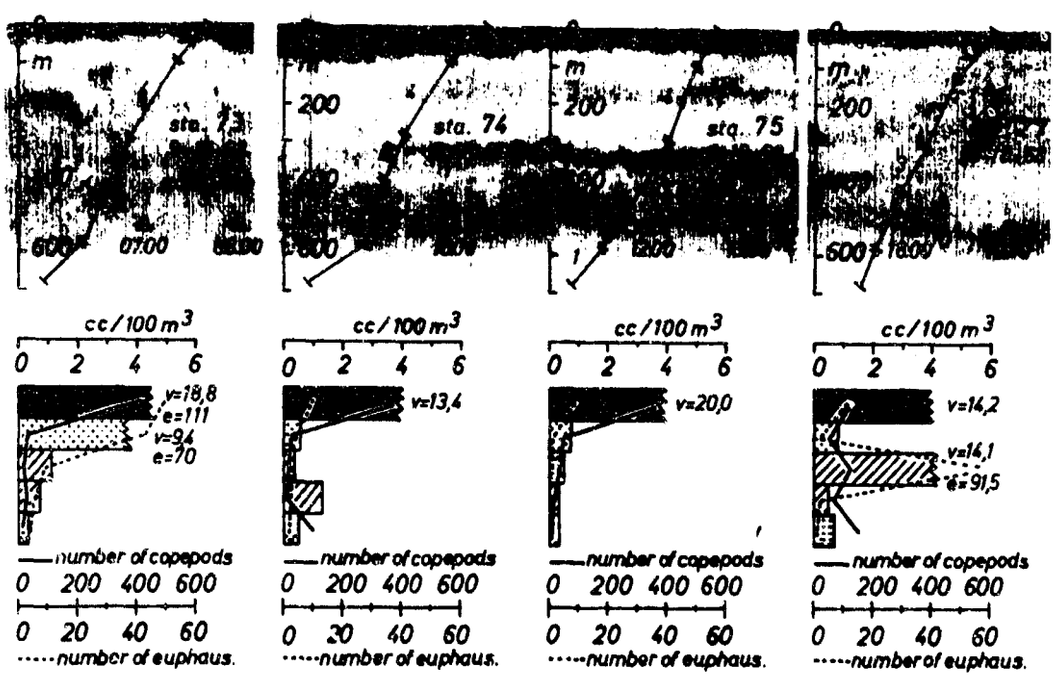


Figure 6. Towing paths of sampler, and plankton distribution at stations 73, 74, 75, and 77 during 9 October (see Fig. 2 for explanation).

As to the distribution of the copepods, the maximum observed at the upper depth level of the DSL (Sta. 44, 1100 hours) had descended continuously to the lowest depth of sampling (Sta. 47, 700 to 600 m). By midnight (Sta. 48) the mass of copepods apparently had continued their descent to a depth below 700 m.

Stations 49 and 50, 6 October 1968 (Fig. 3)

On the following day prior to sunrise, the largest number of euphausiids was observed descending from the surface (1.3 ind./m^3 in sample 5 and 0.3 ind./m^3 in sample 4). At about 0900 hours (Sta. 50), the biomass at both scattering-layer depths had reached its maximum again; whereas the bulk of copepods had ascended from below the scattering-layer depth into the lower DSL. During the day, only a few euphausiids were caught at all depths.

Stations 57 to 59, 7 October 1968 (Fig. 4)

Again only a few euphausiids were observed at all depths sampled during the daytime. The richest population of copepods was found at the depth of the lower DSL (60 ind./m^3 at Sta. 59); thus the maximum biomass was located at this depth. In the surface sample, an increasing number of pteropods was observed.

Stations 65 and 66, 8 October 1968 (Fig. 5)

A distinct maximum number of euphausiids (1.4 and 1.6 ind./m^3) occurred at the depth of the upper DSL. The catches indicated that the highest population was at the scattering-layer depth during the cruise. At that day another maximum concentration of euphausiids was found at the surface (2.2 ind./m^3), although the surface sample was collected two hours after sunrise. Even at depths from 320 to 100 m, both hauls appeared quite rich in biomass, partly because of the concentration of euphausiids.

Stations 73 to 77, 9 October 1968 (Fig. 6)

Differing from the echograms of the days before, an additional scattering layer was observed between about 150 and 200 m. Except for the extremely rich surface plankton in which the pteropod *Cavolinia inflexa* outnumbered even the copepods, the biomass was poor at all depths. Soon after sunrise (Sta. 73), part of the descending euphausiids were sampled between 320 and 100 m (0.7 ind./m^3). During the afternoon another distinct maximum in the distribution of euphausiids was observed at Station 77 at the depth of the upper DSL (0.9 ind./m^3).

Species Distribution of Euphausiids and Siphonophores

Copepods and euphausiids outnumbered all other plankton organisms at the scattering-layer depth. Of the chaetognaths, siphonophores, ostracods, and amphipods, surprisingly few specimens were caught.

As to the euphausiids, six species have been observed in the samples from the DSL and neighboring depths: *Meganyctiphanes norvegica*, *Euphausia krohnii*, *Nematobrachion boöpis*, *Nematoscelis megalops*, *Thysanoessa gregaria*, and *Stylocheiron elongatum*. In DSL samples containing rich numbers of euphausiids, *M. norvegica* outnumbered by far any other species, particularly at Stations 46, 65, and 66. Except for *M. norvegica*, it appears from the preliminary results, that *E. krohnii* and *N. boöpis* have been the prevailing species at depths of sonic scatterers. According to plankton samples collected at the same location (Fig. 1) in vertical hauls with the

Helgoland larvae net, which is equipped with a revolving bucket system, both species also appeared during the daytime in depths of 800 to 1,000 m—the maximum sampling depth.

Among the siphonophores, which in other areas may largely contribute to sound scattering (Barham, 1963), only nectophores of the *Calycophorae* were observed at scattering layer depths between 350 and 600 m. Where plankton was abundant within the DSL, the maximum in siphonophores also occurred. The prevailing species, particularly in the upper DSL, have been *Rosacea plicata* and *Vogtia glabra*, averaging 0.1 to 0.2 nectophores/m^3. Both species are mesopelagic or bathypelagic and are quite common in warmer seas (Leloup, 1955; Kinzer, 1965). Less abundant in our samples from the DSL have been *Vogtia spinosa* and *Lensia fowleri*.

Of the faster swimming micronekton, only small cephalopods, Caridean shrimps (*Acanthephyra* and *Systellaspis*), and young sternoptychids occasionally were caught with the Lowestoft sampler, all of them either at the depth of the lower DSL or below.

Norwegian Sea

From the samples collected with the LHPR in the Norwegian Sea at a position 62° 59′ N., 03° 44′ E, only a few preliminary data are yet available. Figures 7 to 12 show the zooplankton distribution on 8 and 9 August 1969 in six hauls from depths of 0 to 600 to 0 m. During the 7 days of sampling the migratory DSL was observed between 300 and 500 m in the daytime, ascending and descending in the typical diurnal cycle. From the few data already at hand, it seems,that the diurnal vertical migration of copepods, euphausiids, and pteropods was more or less restricted to the upper 150 m of the water column. A pronounced maximum in copepod distribution occurred just below the scattering-layer depth, possibly a result of hibernating stocks of *Calanus finmarchicus* (Hansen, 1960). Very few euphausiids were caught below 120 m. Even adult *M. norvegica*, a species well known for its large-range vertical migration (Mauchline and Fisher, 1969), were sampled only in the upper 120 m during the day.

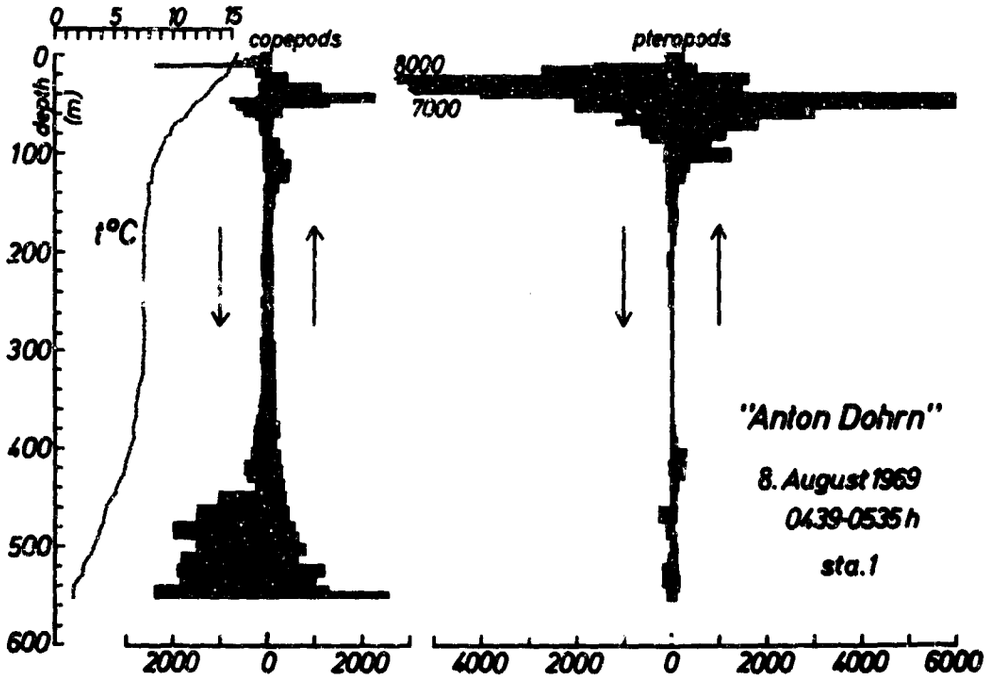
The scarcity of euphausiids in the samples from the lower layers may possibly be due to the sampling technique used. To maintain a position near an anchored radar buoy, the ship was steered in a half circle at 2.5 kts. Further, the sampling vehicle was towed with a heavy 16-mm cable, which resulted in a steep wire angle. Thus the net was actually moving in a small circle at reduced speed and the euphausiids could have effectively avoided the nets.

DISCUSSION

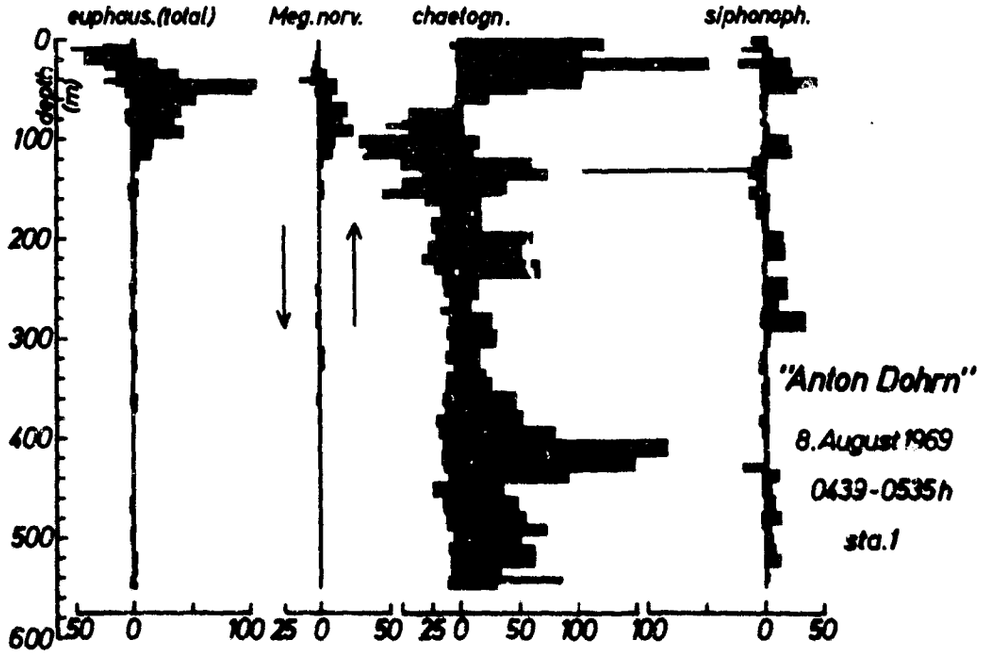
The plankton volumes observed off the Portuguese coast correspond well to the data collected during our prior cruises in the eastern North Atlantic (Kinzer, 1969). At daytime, the plankton volumes between 700 m and the surface were largest at the scattering-layer depth, mostly because of aggregations of euphausiids and copepods.

As can be seen from Figures 2 to 6, little positive correlation exists between the strength of scattering and the observed plankton distribution. At Sta. 66 (Fig. 5), unfortunately the recording of the echo sounder has been disturbed. In sample no. 3 of both Sta. 65 and 66, from the upper DSL, the largest concentrations of euphausiids had been observed; about 90% of them were adult *M. norvegica*, which possibly added to the backscattering of the 30-kHz sound pulses.

There have been pronounced variations in plankton volumes at all depths, particularly within the DSL. Besides the effect of inefficiency of sampling, these variations in biomass are probably a result of patchiness in zooplankton distribution or restricted grazing by fishes and other organisms on the plankton community. Patchiness of plankters should be largest among the euphausiids, particularly in *M. norvegica*, which—at least in surface waters—are known to swarm



(a)



(b)

Figure 7. Vertical distribution of the more abundant zooplankton groups as collected with the LHPR in the Norwegian Sea. The arrow indicates the descending and ascending profile of haul. Temperature distribution was recorded by the LHPR-system. The histograms show (a) the distribution of copepods and pteropods and (b) the distribution of adult euphausiids, *Meganyctiphanes norvegica*, chaetognaths, and siphonophores.

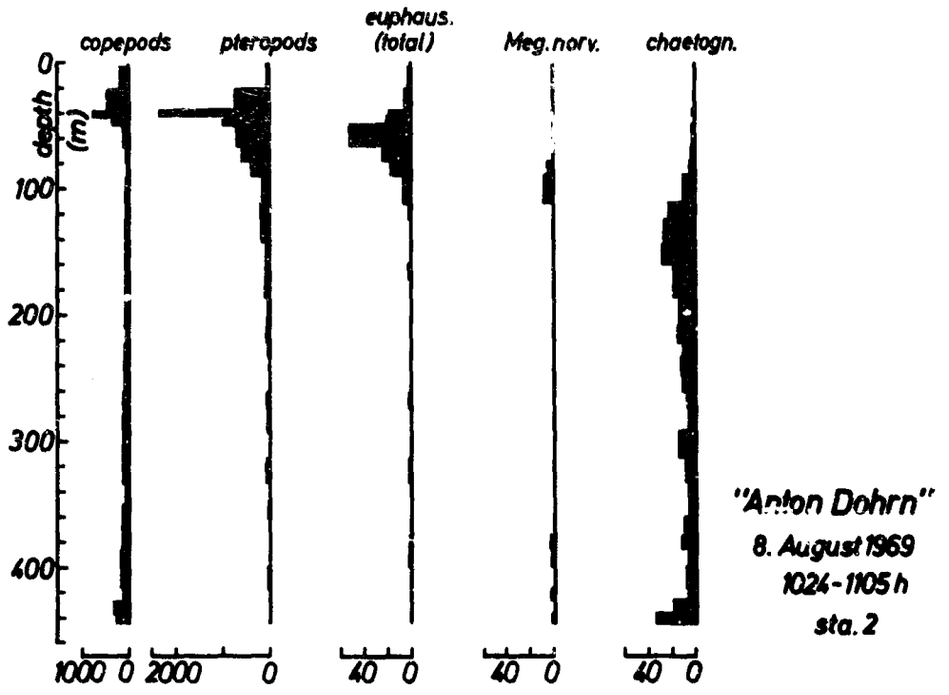


Figure 8. Vertical distribution of zooplankton from 0 to 440 m (descending profile) (see Fig. 7 for explanation)

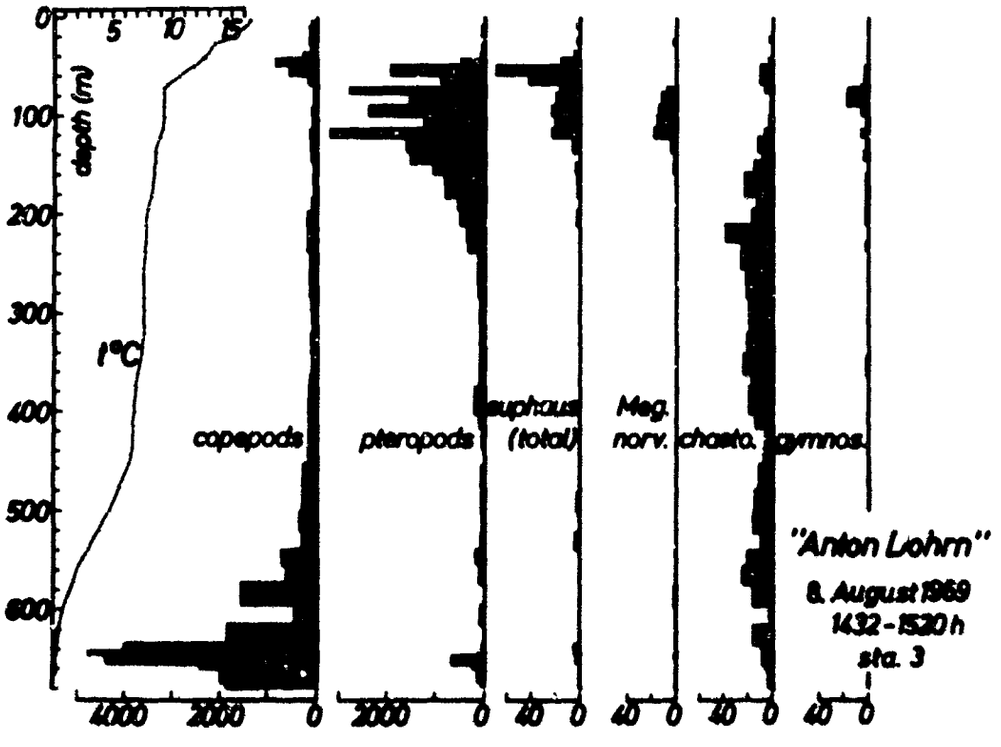


Figure 9. Vertical distribution of zooplankton from 0 to 680 m (see Fig. 7 for explanation)

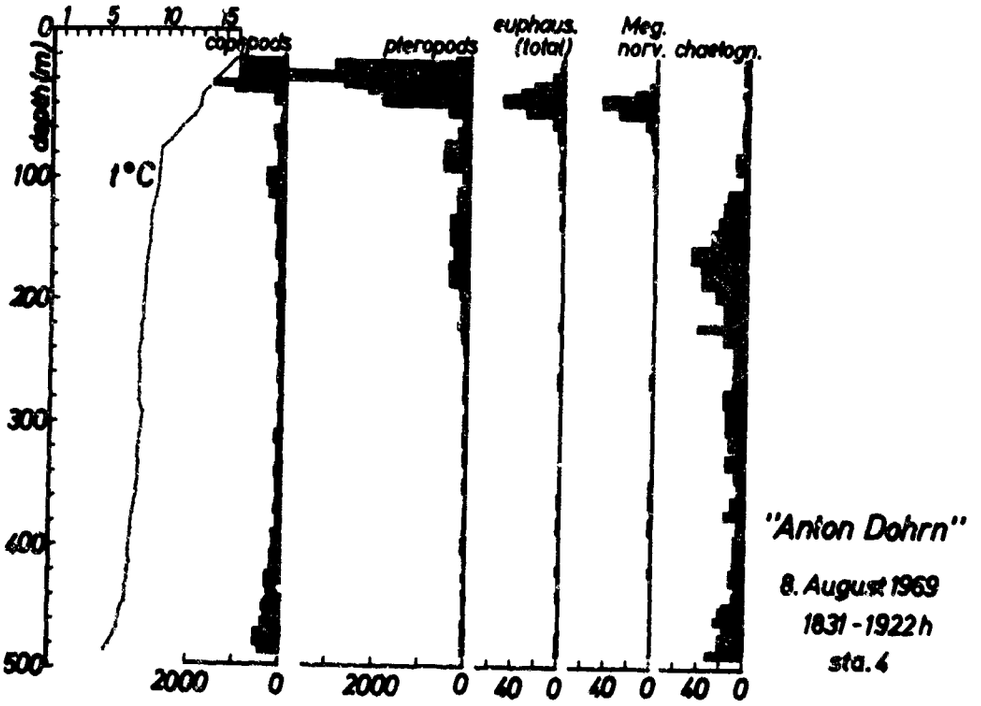


Figure 10. Vertical distribution of zooplankton from 0 to 480 m (see Fig. 7 for explanation)

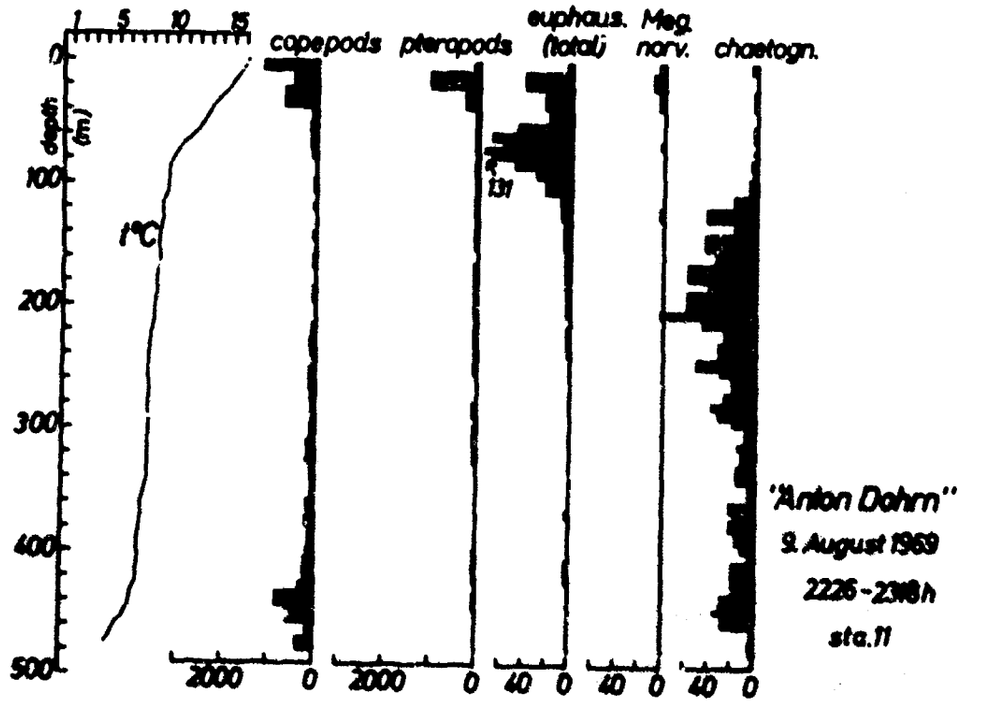


Figure 11. Vertical distribution of zooplankton from 0 to 480 m (see Fig. 7 for explanation)

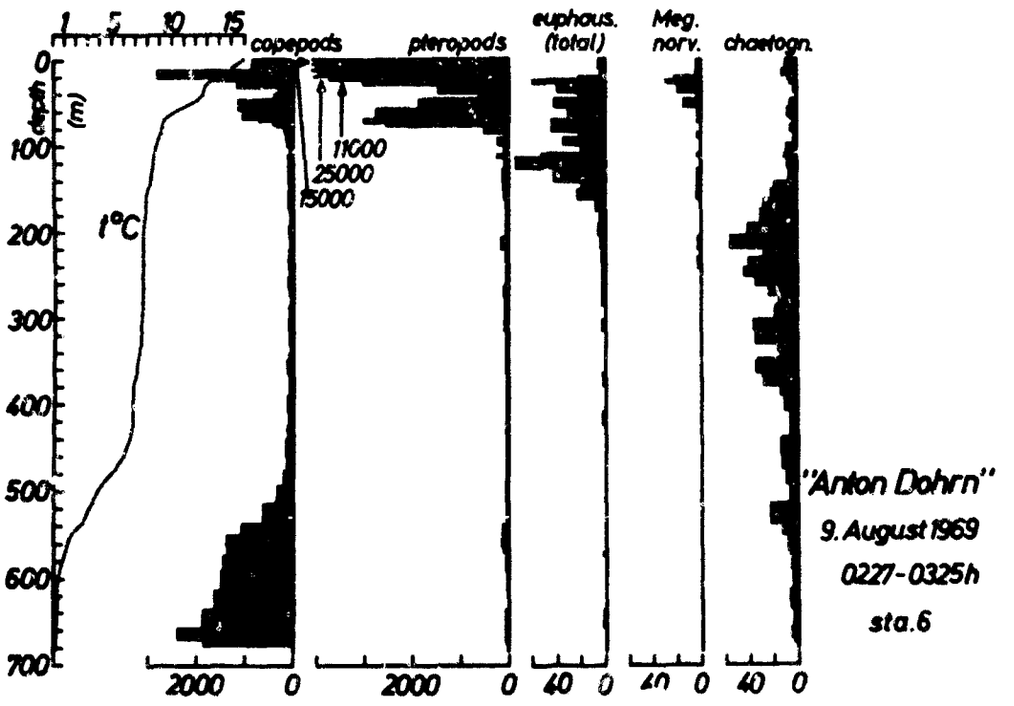


Figure 12. Vertical distribution of zooplankton from 0 to 680 m (see Fig. 7 for explanation)

(Aitken, 1960; Mauchline and Fisher, 1967). Unfortunately, we still lack data on the patchiness of plankton distribution within sonic-scattering layers.

Earlier, Hersey and Moore (1948) and Boden (1950) had suggested that euphausiids are important elements of deep scattering layers. Tucker (1951) gave evidence from stratified hauls about the depth distribution of euphausiids, indicating that during daytime these plankters concentrate in the upper DSL and ascend to the surface layer at night. Our observations from stratified sampling in the subtropical eastern North Atlantic have added further evidence. From the samples collected off the Portuguese coast, the dominance of euphausiids, particularly in the upper layer, again became obvious. Because of the 40-cm opening of the high-speed sampler, larger *M. norvegica* were also caught (total length about 34 mm) and at stations 65 and 66 were by far the dominant species.

At nighttime, adult euphausiids prevailed in the surface samples; and, with few exceptions, the depth of the DSL appeared depleted of euphausiids. According to Mauchline and Fisher (1969) all euphausiid species concerned migrate at least between the observed daytime depth of the DSL and the surface, except *Stylochetron elongatum* and possibly *Nematobrachion boöpis*, which are considered to be permanently mesopelagic.

During the Atlantic Seamount Cruise of R/V *Meteor* (March to July 1967), we found large concentrations of euphausiids within the DSL. Furthermore, we observed a seamount effect on the euphausiids. On a transect near Great Meteor Seamount (at 30° 00′ N, 28° 20′ W), euphausiids aggregated during the daytime in the upper part of the DSL between 350 and 500 m (Kinzer, 1969). Samples collected at night in the near vicinity of the Great Meteor Seamount from depths between 100 m and the surface contained large numbers of adult euphausiids; whereas at the same time only juvenile specimens of euphausiids were caught above the seamount.

The Great Meteor Seamount reaches from about a 4500-m depth to 270 m from the surface; thus the plateau of the seamount, which is about 30 miles in diameter, lies above the depth of the DSL during daytime. Off the seamount, euphausiids ascended to the surface at dusk, particularly adult *Euphausia hemigibba*, a species with a pronounced range of diurnal vertical migration. Because *E. hemigibba* was missing in samples from above the seamount, and only juvenile *Stylocheiron suhmii* and few *Nematoscelis* were observed, plankton samples collected during the night within the 400-m isobath have been strikingly poorer in volume than those collected off the seamount plateau. The same seamount effect was observed at Josephine Seamount, located at 36° 43′ N, 14° 18′ W.*

In the Norwegian Sea, quite in contrast to our observations from the lower latitudes in the eastern North Atlantic during this and previous studies (Kinzer, 1969), no aggregations of zooplankton were observed at the scattering-layer depth. The slow towing speed of the sampler at depth might have attributed to the small number of euphausiids caught at depths below 120 m; and the low temperature at the scattering-layer depth and below also might have had some effect on the restricted vertical distribution of euphausiids. According to Moore (1950) and Lewis (1954) who compared the depth distribution of euphausiids in various regions of the western North Atlantic and the Mediterranean Sea, the lower depth limit of several euphausiid species is markedly affected by temperature. Because only a small fraction of the LHPR samples from the Norwegian Sea has yet been analyzed, a discussion should be postponed until further data from the samples are available.

ACKNOWLEDGMENT

I acknowledge with thanks the kind assistance of Dr. R. Weigmann, Kiel, F.R.G., in the determination of euphausiid species.

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*Investigations of the effect of seamounts on the distribution of the surface plankton have recently been continued. The results will be published in "Meteor"-Forschungsergebnisse, Series D.

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DISCUSSION

Love: How big were the euphausiids and copepods?

Kinzer: The euphausiids, which as I pointed out, were up to 90 percent of *Meganyctiphanes norvegica*, average about 3 4 cm in size.

Love: And copepods?

Kinzer: Subtropical copepods averaged, I would say, 2 to 3 mm in our samples.

BIOLOGICAL ACOUSTIC SCATTERING OFF SOUTHERN CALIFORNIA, BAJA CALIFORNIA, AND GUADALUPE ISLAND

G.V. Pickwell, R.J. Vent, E.G. Barham, W.E. Batzler and I.E. Davies
Naval Undersea R&D Center
San Diego, California

ABSTRACT

On a two-ship joint operation in October 1968, observations were made of biological scattering conditions at three stations off southern California, Baja California, and Guadalupe Island, Mexico. Echograms obtained from a programmed Precision Depth Recorder (PDR) were correlated with simultaneously obtained, quantitative acoustic volume scattering data, both at 12 kHz, while direct observations from a submersible vehicle above, in, and below deep scattering layer (DSL) depths were correlated with near-simultaneous closing-net hauls.

In most cases volume scattering coefficients (i.e., 10 log m_v) with peaks in the -50 to -70 dB range agreed well with those subcomponents of the DSL most clearly recorded by the PDR. Direct observations from the submersible of presumed biological targets (species) were generally in good agreement with net collections from discrete depths within the DSL, although numbers of individuals collected were not always representative of numbers actually observed and counted.

Under the best circumstances data obtained by the four methods of observation within a time limit of 2 to 4 hours showed excellent agreement on depths of peak scattering and resident populations within those depths at the times of observation. The most prominent biological species observed and collected from migrating DSL's showing peak scattering coefficients were euphausiid shrimps and sergestid prawns, smaller lantern fishes (myctophids), and physonectid siphonophores (mostly *Nanomia bijuga*). Species most prominently seen and collected from deeper scattering layers registering peak scattering coefficients (either descended DSL's or nonmigratory components) included bristlemouths (*Cyclothone* spp.), larger myctophids, and some hatchetfishes as well as the migratory species already mentioned.

Unusually high peak scattering coefficients, on the order of -38 to -39 dB, recorded from one ship while hove-to, correlated exactly with the depths where clusters of large echo groups (LEG's) were recorded by the PDR of the nearby team ship while under way. Neither direct observations nor net collections were able to suggest the probable identification of these prominent targets.

INTRODUCTION

Many ships for many years have traversed the world ocean with echo sounders recording continuously, and whether by design or accident, a great deal of deep scattering layer (DSL) information has accumulated. For an even longer period scientists have trawled the middepths of the sea, collecting and describing the animal populations encountered. In the 25 years following World War II some of the scientific trawling has been connected with DSL research (Barham, 1956; Marshall, 1951; Tucker, 1951).

Techniques for adequately measuring acoustic scattering and volume reverberation in the oceanic water column have evolved largely during these past 25 years and have frequently been devoted to studies of the DSL (Batzler and Westerfield, 1953; Hersey, Backus, and Hellwig, 1962). With the advent of the bathyscaphe, *Trieste*, followed by the Cousteau "diving saucer," and thereafter an entire generation of research deep submersibles, it became possible for a number of scientists to directly observe the organisms of the DSL *in situ* (Barham, 1963 a and b; and 1966; Mizikos, 1968) and occasionally correlate these observations with simultaneous acoustic measurements or PDR recordings (Backus et al. 1968; Batzler and Barham, 1963 and 1965; Brown and Fessenden, 1969).

Seldom, however, have data been gathered of acoustic volume reverberation while scattering layer organisms were collected and precision echo-grams recorded. Rarer still are the opportunities to make such measurements and collections in conjunction with direct observations from a submersible vehicle.

In October 1968, such an opportunity became available to us and we subsequently made stations off Cabo Colnett, Baja California, Mexico (one dive, one net haul, acoustic measurements, echograms), Guadalupe Island, Mexico (net hauls, acoustic measurements, echograms, no dives due to weather), and in the San Diego Trough about 20 mi off San Diego, California (two dives, net hauls, acoustic measurements, echograms) (Figure 1).

METHODS

A converted search and rescue vessel, the USS *Marysville* (EPCER 857), long used as a research ship at this laboratory, provided the platform from which net hauls were made and echograms obtained. A Mark V Precision Depth Recorder (PDR), set at a long ping mode (20 to 30 msec), was slaved through a Gifft Precision Sonar Transceiver (Model ESRTR-4B) controlled by a Gifft Sonar Programmer (Model ESRPR-1). This permitted gating out the bottom return when it interfered with the trace obtained from the DSL. An EDO 12-kHz UQN transducer was mounted on the ship's sonar column and lowered to a depth of 4 fathoms (fm) below the sea surface when in operation (1 fm = 1.83 m).

The *M/V Search Tide*, an offshore oil-drilling vessel leased by Westinghouse Corp. as the tending vessel for the research submersible *Deepstar 4000*, provided the second platform for volume reverberation measurements. A 12 kHz directional source pointed vertically downward was suspended approximately 4 fm below the sea surface. Generally, each test consisted of 10 successive pings with a pulse duration of 25 or 50 msec. Return signals were recorded on a Honeywell Visicorder, a high speed, strip chart recorder.

A distance of 3 to 5 mi was maintained between the ships as a safety factor during simultaneous net hauls and submersible launchings and to avoid sonic interference during acoustic measurements. Coordination of operations was expedited by rapid communication between members of the two scientific teams using "handy talky" radios.

Collections of DSL organisms were made using a Tucker net (Davies and Barham, 1969; Tucker, 1951) towed at about 4 knots. This midwater trawl employs a clock-actuated release mechanism to open the 2-m^2 mouth of the net at a preset time and to close it after some designated interval. Thus, the net was open and fishing only at the desired depth within the DSL. The depth was monitored by a Benthos Model 1020 Depth Telemetering Pinger which read out on the PDR record, permitting a continuous appraisal of net depth. The depth of the net throughout the haul was further monitored by a Benthos D-T Recorder, Model 1170, which yielded a depth track record of the haul after retrieval of the net.

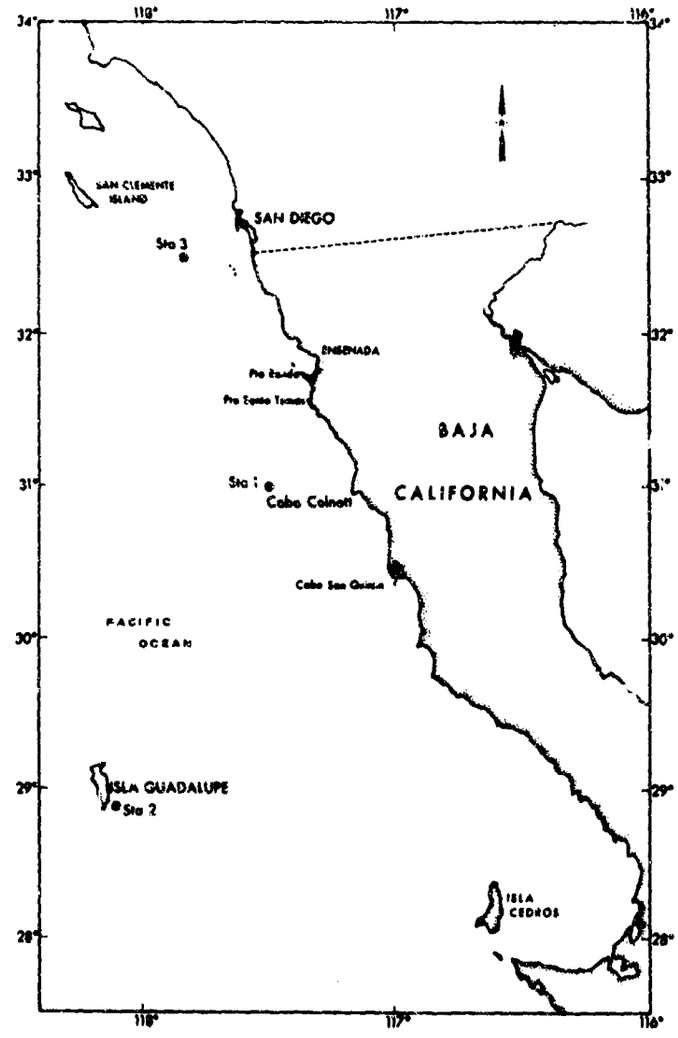

Figure 1. Station locations for the *USS Marysville–M/V Search Tide* joint operation, 14 to 18 October 1968

The Westinghouse research submersible *Deepstar 4000* is a 3-man vehicle capable of submerging to a depth of 4000 ft for periods up to 12 hours. It has provisions for a pilot and two scientists, one of whom may continuously observe through one of the two viewing ports. The vehicle can hover at any depth and has a forward speed of approximately 1.5 knots. Basic equipment includes a 16-mm movie camera with a 1000-W external movie light, and a 70-mm still camera equipped with strobe flash. The movie light was often employed to aid in direct visual observation. All observations and counts were recorded on magnetic tape. Typewritten transcripts were then made from the tapes from each dive.

RESULTS

Cabo Colnett

Station 1, approximately 60 mi off Cabo Colnett, Baja California, Mexico, was occupied briefly on 14 October 1968. *Deepstar* Dive 481 was made between 1530 and 1800 hours.

Scattering layers appeared on the echogram at 80 to 120 fm and 180 to 200 fm at approximately 1600 hours. Peak volume scattering coefficients of -62 dB (upper layer) and -57 dB (lower layer) were measured at 1600 hours (Figure 2). We use here the decibel form 10 log m_v of the scattering coefficient m_v. Its relation to the volume scattering strength S_v is $S_v = 10 \log (m_v/4\pi)$, a difference of 11 dB.

During the descent to 360 fm from 1530 to 1617 hours, *Deepstar* passed through concentrations of euphausiid shrimp between 140 and 190 fm (250 to 350 m), hatchetfishes between 164 and 190 fm (300 to 350 m), *Cyclothone* between 190 and 220 fm (350 to 400 m) and a sparse population of physonectid (float-bearing) siphonophores throughout the water column between 123 and 220 fm (225 to 400 m). During the ascent, from 1625 to 1800 hours, the populations of euphausiids and siphonophores shifted upward very little (Figure 3). A few sergestid prawns and lantern fish were seen between 190 and 230 fm (350 to 420 m) on both descent and ascent with no indication of upward displacement in the evening. However, net haul No. 1, fishing at 170 fm (310 m) in a nonmigratory layer from 2020 to 2050 hours collected a few large hatchetfish, myctophids (lantern fish), sergestid prawns, and several *Cyclothone* (Table 1).

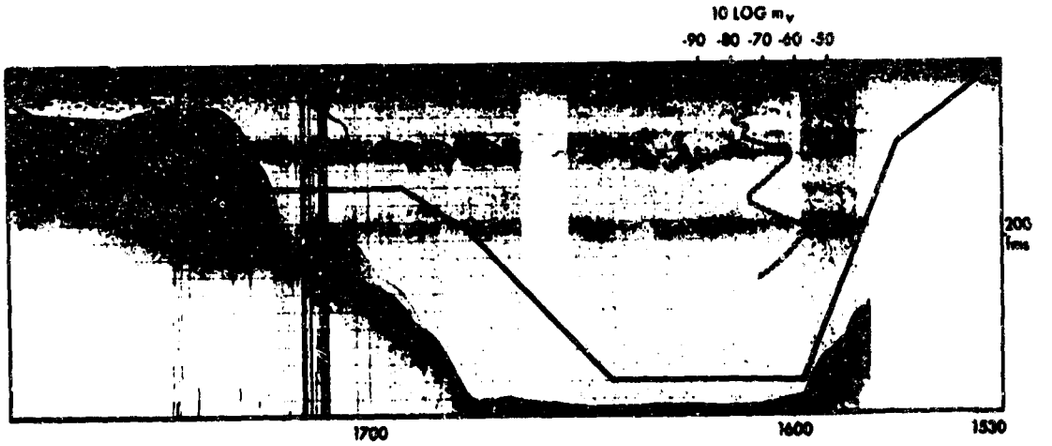

Figure 2. Station 1, off Cabo Colnett, Mexico, 14 October 1968, depth of water approximately 1110 fm (2000 m). *Deepstar* Dive 481 is represented by the solid line. On this dive and Dives 482 and 483, positions occupied by the submersible below or between components of the DSL were for the purpose of acoustic tests and not primarily for direct observation of scattering organisms. The 10 log m_v curve was obtained at a 50-msec pulse length. Note that the *Deepstar* dive track represents the depth of the submersible at a given time but does not indicate a horizontal traverse. Time on all echograms moves from right to left; length of each individual section in the horizontal lines, 3 min; depth between each horizontal line, 20 fm (36.6 m).

Guadalupe Island

Station 2, off the southeast corner of Guadalupe Island, Mexico, was occupied on the afternoon of 15 October 1968. At 1500 hours, a diffuse upper scattering layer appeared at 120 fm and a heavy layer at 150 to 200 fm (274 to 365 m) (Figure 4). Peak volume scattering coefficients of -62 dB (upper, diffuse layer) and -55 dB (both peaks of lower, heavy layer) were measured at 1515 hours.

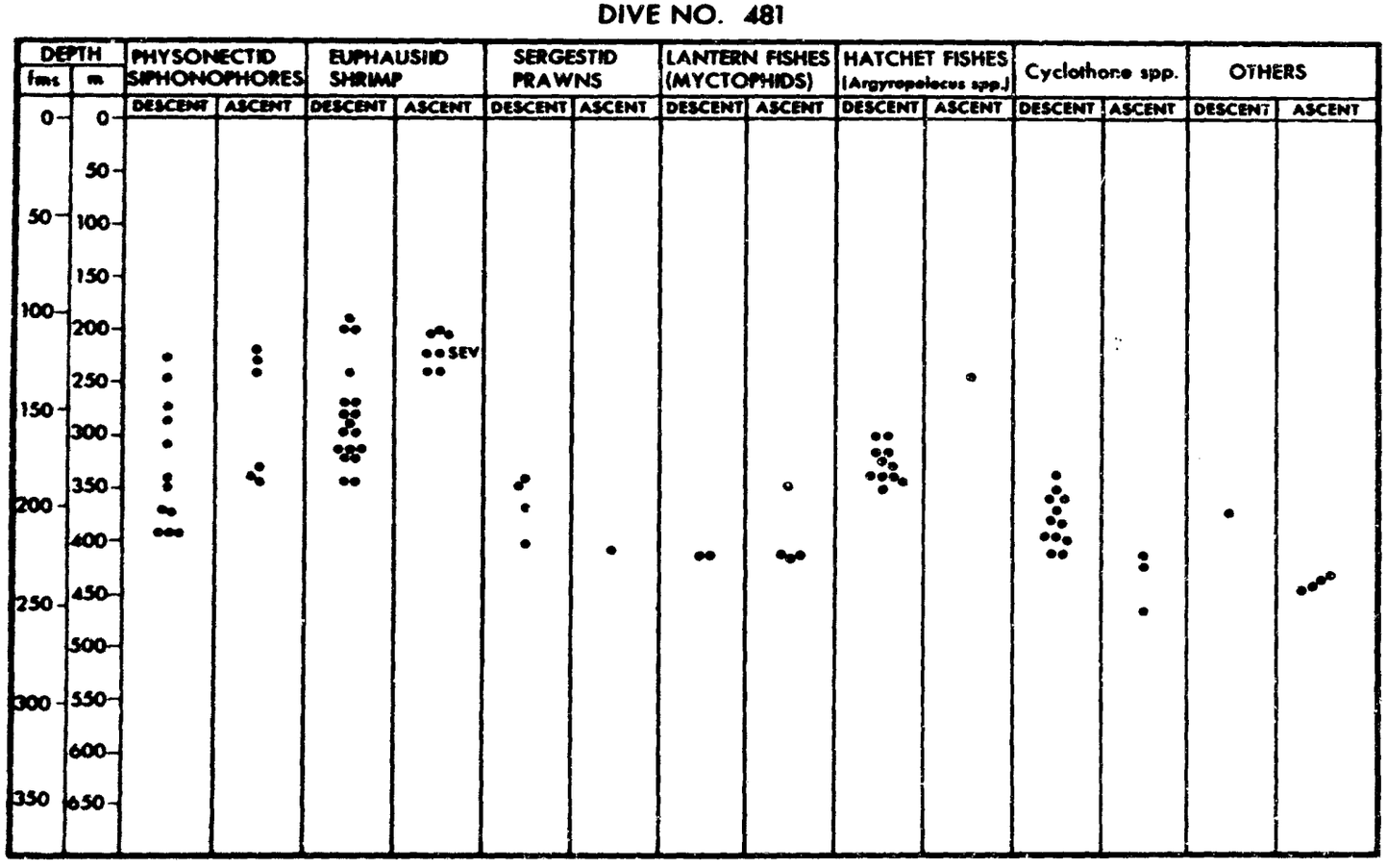

Figure 3. Organisms observed from *Deepstar* on Dive 481. In this figure and in Figs. 11 and 13 the terms "few," "sev" (several), and "many" were used when actual counts were not taken and are arbitrarily defined to represent sightings of 1 to 10, 10 to 20, and >20 organisms, respectively. Individual dots represent single sightings. In the "Others" column the descent sighting was a squid of undetermined species (approx. length 10 cm); the four ascent sightings were deep-sea smelt, *Bathylagus* sp.

Table 1. Tucker Net Hauls from Discrete Depths

Haul	Date	Station	Net Open	Net Closed	Depth of Haul†	Total Euphausiids	Total Sergestids	Total Physonectid Siphonophores	Total Lantern Fishes	Total Hatchet-fishes	Total *Cyclothone*	Other	Remarks
1	10-14-68	1	2020	††	170 fm (310 m)	present*	1 1		1	6	4	pteropods-4	Net preclosure
2	10-15-68	2	2005	2035	175-190 fm (320-348 m)	21	present*	present*	1	17	72	*Melamphaes*-2 mysids-2	Net preclosure
3	10-15-68	2	2210	2310	100-120 fm (183-220 m)	present*	present*	present*	3	1	present*	*Melamphaes*-1 mysids-8 squid-2	
4	10-16-68	2	0917	1017	153-167 fm (280-305 m)	627	6	3	9	14	17	mysids-4 *Vinciguerria*-4 pteropods-15	
5	10-16-68	2	1122	1222	200 fm (366 m)	273	97	present*	93	5	51	mysids-3 squid-2 *Vinciguerria*-11 pteropods-2	
6	10-17-68	3	1445	1615	190 fm (348 m)	>428	>1000	3	99	2	84	mysids-2 larval flatfish-5 pteropods-20 squid-3	
7	10-17-68	3	2010	2120	213 fm (390 m)	135	197	present*	55	2	44	mysids-7 squid-3 larval flatfish-2 juvenile rockfish-1	
8	10-17-68	3	2207	2307	115 fm (210 m)	present*		present*	29	7	5	squid-2 *Melamphaes*-1 juvenile rockfish-3 stomiads-2	
9	10-18-68	3	0753	0815	164 fm (300 m)	>119	66	present*	10	8	7	squid-2 pteropods-6 heteropod-1	Net preclosure

†(net open) ††(Uncertain) *"present" indicates insignificant number of smaller stages of the organism in question (generally less than 3), or only fragmented and incomplete specimens.

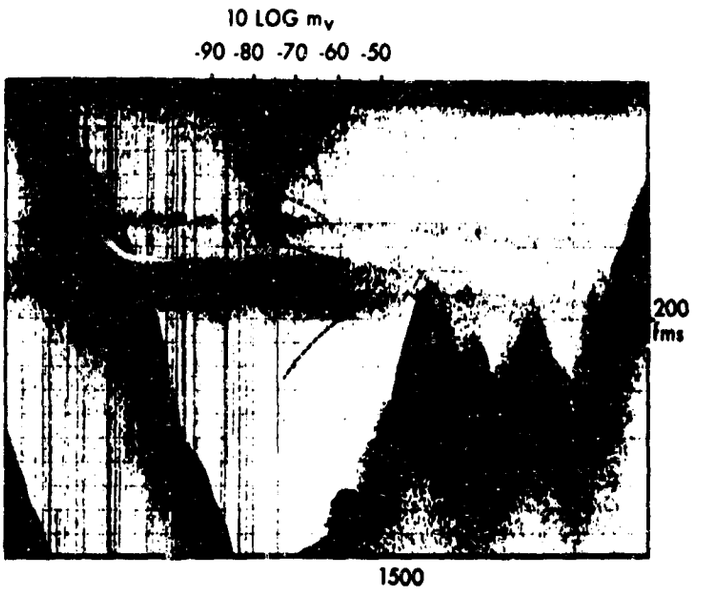

Figure 4. Station 2, 3 mi off the southeastern corner of Guadalupe Island, Mexico, 15 October 1968, depth of water approximately 1000 fm (1830 m); 10 log m_v curve obtained at 25-msec pulse length

The evening ascent of the DSL took place largely between 1800 and 1900 hours and revealed a nonmigratory component appearing at 170 to 190 fm (Figure 5). Net haul No. 2 (Table 1) through this layer from 2005 to 2035 hours produced comparatively large numbers of *Cyclothone* sp., hatchetfishes, and two *Melamphaes* sp. The latter fish, representatives of the suborder Anoplogastroidea, possess gas-filled swimbladders and are generally not taken at DSL depths in daytime hauls, but seem to migrate from greater depths at night.

Figure 5. Station 2, Guadalupe Island, 15 October 1968. Evening ascent of the DSL showing, particularly, a light, diffuse, partially migratory layer leveling out at approximately 120 to 130 fm, and a deeper nonmigratory component fading in at 180 fm.

At 2210 to 2310 hours, the Tucker net was fished through the upper of two partially migrating scattering layers at 100 and 120 fm (net haul No. 3, Table 1 (Figure 6). This haul produced parts of physonectid siphonophores, a few euphausiids and large mysid shrimp, a few *Cyclothone* sp., a hatchetfish, some lantern fish. and a *Melamphaes* sp.

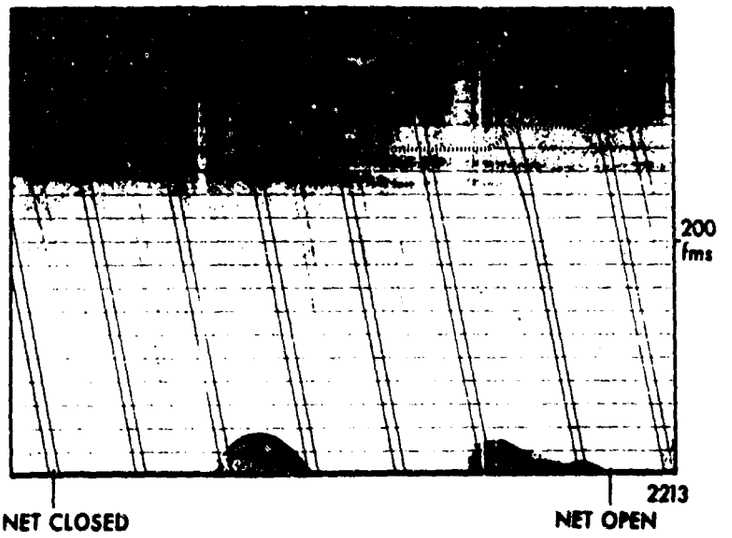

Figure 6. Station 2, 15 October 1968. Net haul No. 3 is represented by the horizontal dashed line at 100 and 120 fm. The diagonal lines represent the signals from the depth telemetering pinger attached to the net. The vertical distance between the line pairs is a function of depth.

The following morning, at the same location, net haul No. 4 was made through the broad, not yet fully descended DSL (Figure 7). This haul also produced parts of physonectid siphonophores, several sergestids, myrids, and euphausiids, some lantern fish, hatchetfish, *Cyclothone* and a few *Vinciguerria*, a gonostomatid fish well recognized as part of the vertically migrating fauna in this region, but lacking a swimbladder (Table 1). Volume scattering coefficients measured simultaneously registered peaks of -72 dB in the surface scattering from small echo groups (SEG's) and -57 to -59 dB for the broad DSL between 130 and 200 fm.

An hour later net haul No. 5 made through the fully descended DSL yielded some evidence of physonectid siphonophores, a few hatchetfish and *Vinciguerria*, but an abundance of euphausiid and sergestid shrimps, lantern fish and *Cyclothone* (Table 1). A peak volume scattering coefficient of -55 dB was measured at the same depth as the Tucker net just prior to the timed opening of the net (Figure 8).

San Diego Trough

Station 3, over the San Diego Trough approximately 20 mi offshore from San Diego, California, was occupied in the early afternoon of 17 October 1968. Net haul No. 6 was begun immediately in an effort to collect in the lowermost stratum of the slowly ascending DSL (Figure 9). *Deepstar* Dive 482 was launched shortly thereafter (Figures 9 and 10).

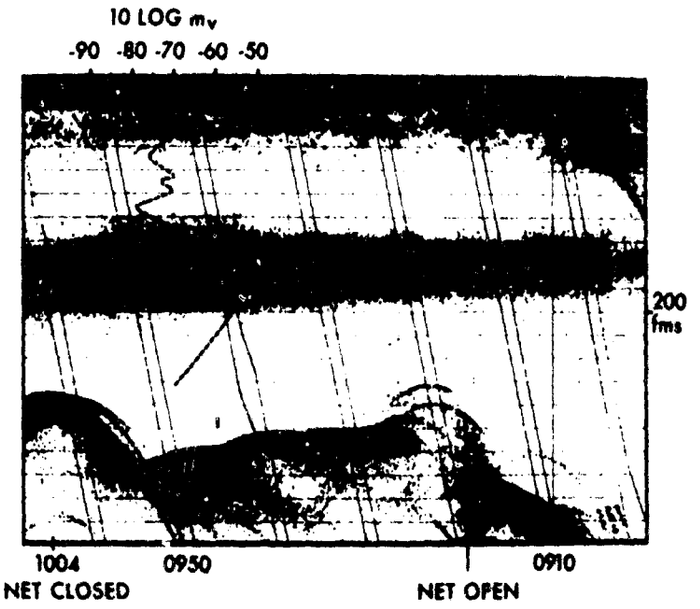

Figure 7. Station 2, 16 October 1968. Net haul No. 4 (horizontal dashed line). The 10 log m_v curve was obtained at a 25-msec pulse length.

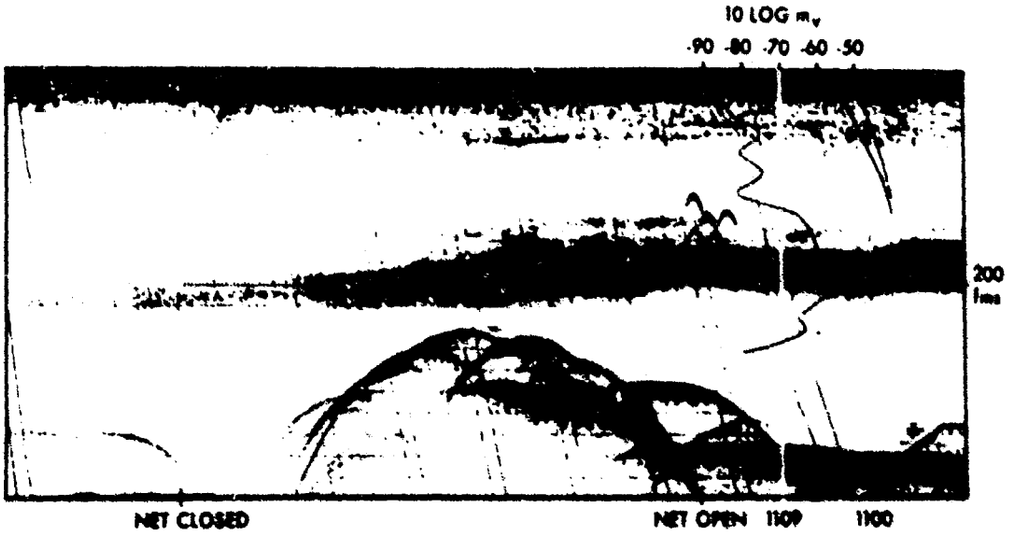

Figure 8. Station 2, 16 October 1968. Net haul No. 5 (horizontal dashed line). The 10 log m_v curve was obtained at a 25-msec pulse length.

Deepstar's descent, from 1459 - 1546 hours, disclosed concentrations of euphausiid shrimps at 110 to 148 fm (200 to 270 m), sergestid prawns at 164 fm (300 m), numerous physonectid siphonophores (mostly *Nanomia bijuga*) between 126 and 180 fm (230-330 m), lantern fishes

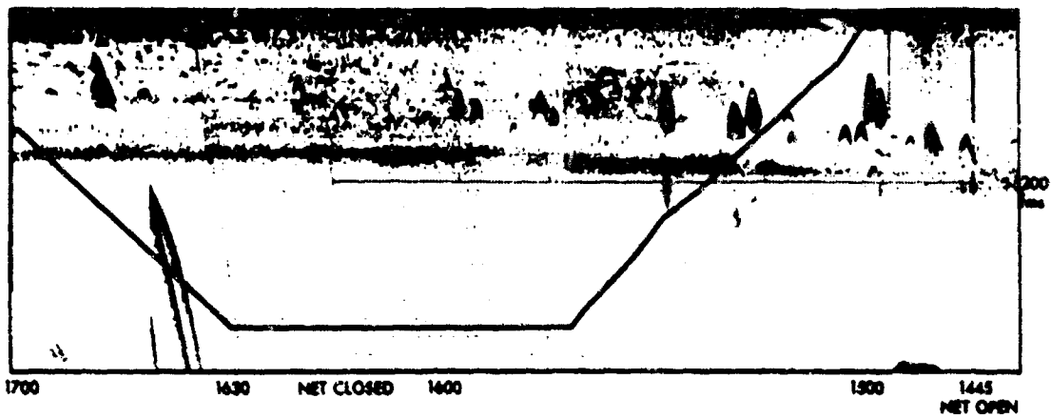

Figure 9. Station 3, San Diego Trough, 17 October 1968, depth of water approximately 650 fm (1190 m). Net haul No. 6 (horizontal dashed line at 190 fm). *Deepstar* Dive 482 (diagonal solid line to 350 fm) continued in Fig. 10. Large echo groups (LEG's) between 70 and 160 fm continue as observed from midmorning (Fig. 14).

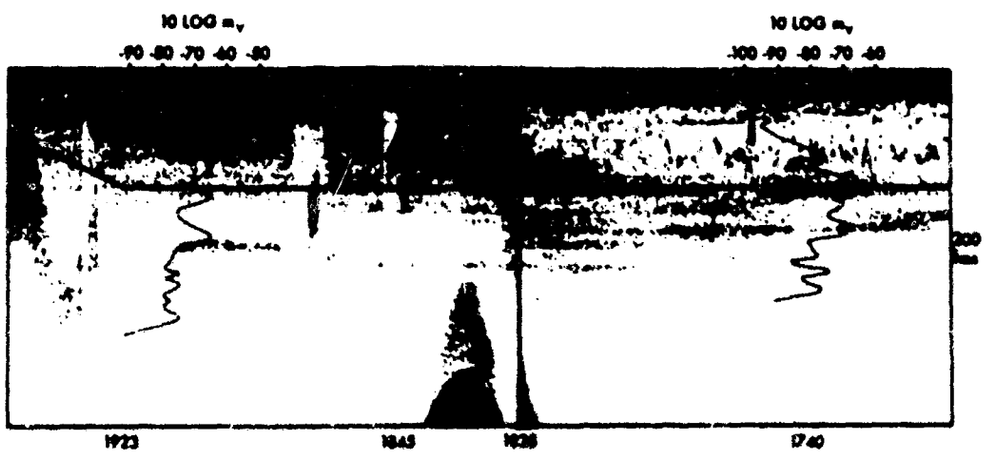

Figure 10. Station 3, 17 October 1968. *Deepstar* Dive 482 continues from Fig. 9 with *Deepstar* hovering at 170 fm for approximately 20 "light look" observations until final ascent at 1923 hours. Final, rapid evening migration of the DSL took place mostly between 1820 and 1900 hours and is largely obscured by bottom trace. The scattering coefficient curves (10 log m_v) were obtained at a 25-msec pulse length.

from 164 to 284 fm (520 m), but concentrated between 246 and 273 fm (450-500 m), and a concentration of deep-sea smelt (lacking swimbladders) at 273 to 317 fm (500-575 m). No hatchetfishes were sighted and only a few *Cyclothone* were seen, mostly in the vicinity of 190 fm (Figure 10). The net haul yielded several small physonectid siphonophores, many sergestid and euphausiid shrimps, many lantern fish and *Cyclothone*, and a few hatchetfishes and mysid shrimps (Table 1).

As *Deepstar* hovered at 134 fm, rotating slowly to permit periods of observation with the lights alternately on and off (termed "light looks") (Figure 10), volume scattering measurements from the surface at 1740 hours showed excellent agreement between peak coefficients and major recorded DSL features including a peak value of -67 dB near *Deepstar's* hovering depth. Deepest recorded peaks showed no echogram correlates, however.

At 1910 hours, volume scattering had shifted in the characteristic trend toward strong nighttime surface scattering with a range in values of -52 dB at 30 fm down to -65 dB for a nonmigratory scattering layer at 190 fm. Ascent observations from *Deepstar* disclosed significant upward shifts in the populations of euphausiids and sergestids, as well as the lantern fishes and siphonophores. There was, in addition, a minor implication of a partial migration by *Cyclothone* sp. (Figure 11).

Net hauls 7 and 8 (Table 1, but not figured) were evening hauls made through a nonmigratory DSL at 213 fm (haul No. 7) and a partially migratory scattering layer at 115 fm (haul No. 8). Haul No. 7 produced many euphausiid and sergestid shrimps, and many lantern fishes and *Cyclothone*. Haul No. 8 produced few euphausiids and no sergestids, but a moderately good catch of lantern fishes, a few *Cyclothone* and hatchetfish as well as two stomioids (deep-sea forms lacking gas-filled swimbladders) and one *Melamphaes*. Both hauls produced physonect siphonophore parts.

On station 3 during the morning of 18 October 1968, *Deepstar* executed Dive 483 from 0425 hours, with the migratory scattering layers ascended, until 0908 hours, after they again descended (Figure 12). Direct observations of vertical displacement of migratory species were thus reversed from those of Dive 482 (Figure 13).

Net haul No. 9 (Figure 12) suffered preclosure, but nevertheless yielded many euphausiid and sergestid shrimp, and some lantern fishes. *Cyclothone* and hatchetfish were also collected, but there was scant evidence of physonectid siphonophores, although many of the latter were seen during Dive 483 (Table 1).

Of special interest are the volume scattering coefficients recorded at midday on 17 October. Throughout the morning and afternoon large echo groups (LEG's) were recorded at varying depths between 80 and 160 fm above the DSL located at 180 to 220 fm. Peak scattering coefficients as high as -39 dB were recorded from these discrete targets (Figures 14 and 15), but no evidence of their species makeup was obtained either from *Deepstar* or net hauls.

DISCUSSION

In general agreement with previous studies, (Pickwell, Capen, and Sloan, 1968) nonmigratory or slightly migratory components of the DSL appeared to be chiefly hatchetfishes of the genus *Argyropelecus* and one or two species of *Cyclothone*, the so-called bristlemouths. Thus deep hauls at night produced specimens predominantly from these two groups, often with significant admixtures of lantern fishes (net hauls 1, 2, 7 in Table 1), but fewer numbers of other groups compared to daytime hauls at the same station and depth. Nighttime net hauls at intermediate depths through partially migratory components of the DSL (net hauls 3 and 8 in Table 1) produced less conclusive results, but in these hauls, lantern fishes tended to predominate.

Direct observations from *Deepstar* 4000, in the main, confirmed these findings. Dive 481 (Figure 3), abbreviated because of bad weather, gave only a slight indication of an upward displacement of the main species categories (ascent vs descent) often at a time when the upward DSL migration had already begun. Dives 482 and 483 (Figures 11 and 13), on the other hand, clearly demonstrated the migratory behavior of large numbers of euphausiid shrimp, sergestid prawns, physonectid siphonophores, and lantern fishes (myctophids). In the latter two groups, however, it was clear that migration did not include the entire species complex, suggesting, as pointed out previously in the case of siphonophores, (Pickwell, 1967 and 1970) that energetic considerations, possibly connected with gas-secreting ability, control the individual organism's inclination for vertical migration on any given evening. Dive 482 (Figure 11) showed some suggestion of weak upward displacement (25 to 30 fm) by *Cyclothone* at night. While the sparse

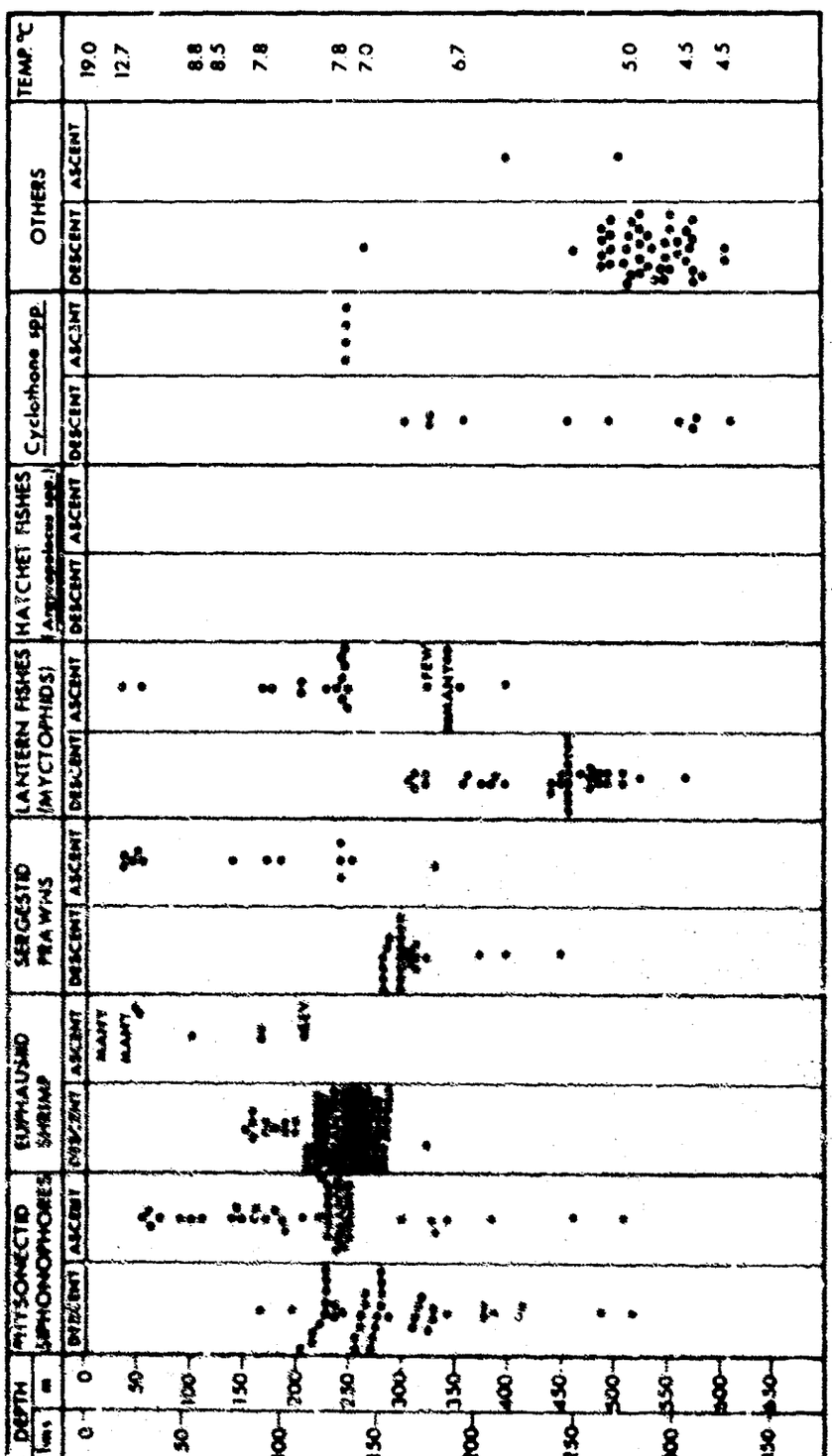

Figure 11. Organisms observed from *Deepstar* on Dive 482. Note that the DSL was migrating upward during this dive and the submersible hovered at 134 fm (for a period of approximately 2 hours during its ascent from below the DSL. Animals counted during this period are included in the "Ascent" columns. In the "Others" column the descent sightings included a small squid (approx. 6 to 10 cm) at 140 fm and another at 215 fm, then a cluster of sightings between 250 and 330 fm including 5 prawns, (possibly pasiphaeids), 24 deep-sea smelt (*Bathylagus stilbius*), 9 myctid shrimp (probably *Gnathophausia*), 2 stomiad fishes (*Stomias* sp) and 1 *Melamphaes* sp. The two ascent sightings in this column were both deep-sea smelt.

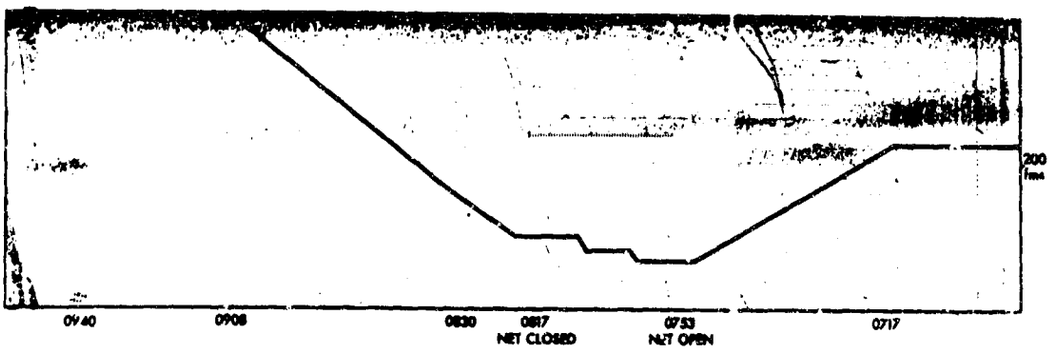

Figure 12. Station 3, 18 October 1968. *Deepstar* Dive 483 continues from launch at 0425 with the terminus of a stable 2-hour period hovering at 170 fm showing at 0717 hours. Net haul No. 9 at 164 fm suffered a preclosure so the net track is abbreviated.

sightings of hatchetfishes provided little information, the few observed on Dive 481 (Figure 3) again suggested the possibility of their slight upward migration. It is not unlikely that a negative phototropism on the part of the hatchetfishes, coupled with an absence of the lethargic state described particularly for some lantern fishes (Barham, 1970), enables these organisms to effectively avoid the lights of *Deepstar*.

A positive phototropism is thought likely in the case of some DSL species, however, further complicating the task of adequately quantifying the organisms observed. Thus, the numerous euphausiid shrimp sighted on Dives 482 and 483 (Figures 11 and 13) at 134 and 170 fm, respectively, were counted while *Deepstar* hovered motionless at those depths for periods of approximately 2 hours. Some 20 "light looks" of about 2 min duration alternated with equal periods of darkness (all observation lights out) were made each time while *Deepstar* slowly rotated about its axis. These were the only instances during the two-ship operation of such extended times spent at DSL depths (Figures 10 and 12). The periods of darkness were intentionally employed to circumvent possible attraction to the observation lights. Nevertheless, the possibility must be considered that some of the sightings constituted duplicate observations made on animals attracted to the vicinity of the lights and then held there by recurrent light periods.

Excellent agreement generally was found between major recorded components of the DSL and prominent peaks on the curve of 10 log m_v vs depth (Figures 2, 4, 7, 8, 10 and 14), as demonstrated in other studies where quantitative acoustic volume reverberation data were compared with simultaneously obtained echograms at the same sonic frequency (Batzler and Vent, 1967). In a number of cases, however, intriguing peaks of moderate prominence appeared on the volume scattering coefficient curve at intermediate depths where no scattering layers were recorded (Figures 7 and 8), and occasionally at depths below the DSL, again without echogram correlates (Figures 8 and 10). The converse did not seem to occur. That is, no echograms of prominent or even weakly recorded DSL's lacked acoustic analogs from volume reverberation data.

The distance of 3 to 5 mi maintained between the two ships as a safety feature during launch and recovery of the submersible, and in addition to avoid jamming acoustic equipment, might account for minor discrepancies of acoustically detected peaks lacking PDR-recorded traces. In addition, the series of peaks appearing as acoustic microstructure within the DSL on some scattering coefficient curves at 25 msec pulse length (Figures 7 and 10) suggests the intriguing

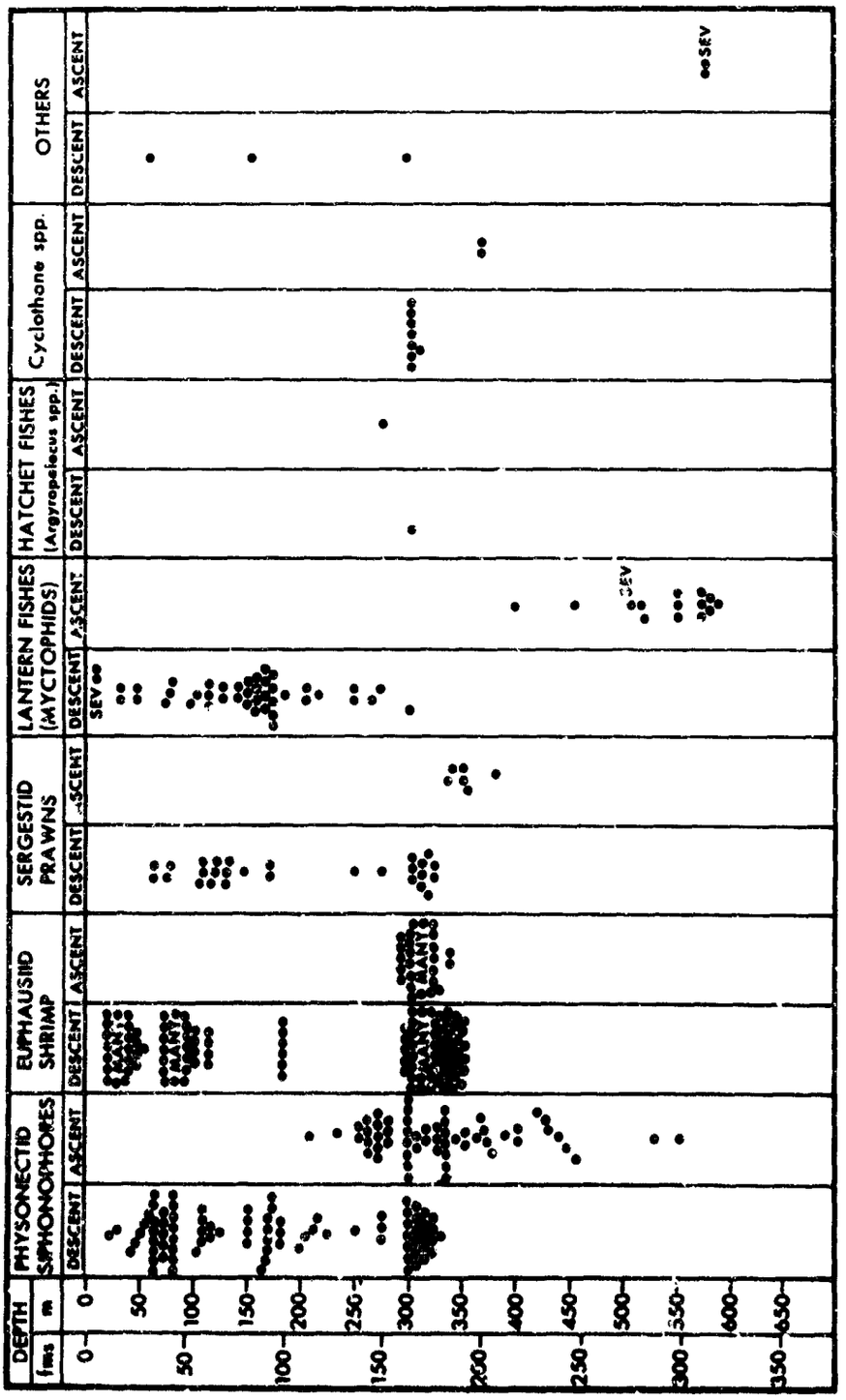

Figure 13. Organisms observed from *Deepstar* on Dive 483. Note that the DSL was migrating downward during much of the period that the submersible hovered at 170 fm (0500 to 0717). Animals counted during this period are included in the "Ascent" columns. In the "Others" column the descent sightings included a prawn (*Pasaphea* sp.), a 10-cm squid, and a stomiid fish, respectively. All ascent observations in this column were deep-sea smelt (*Bathylagus stilbius*).

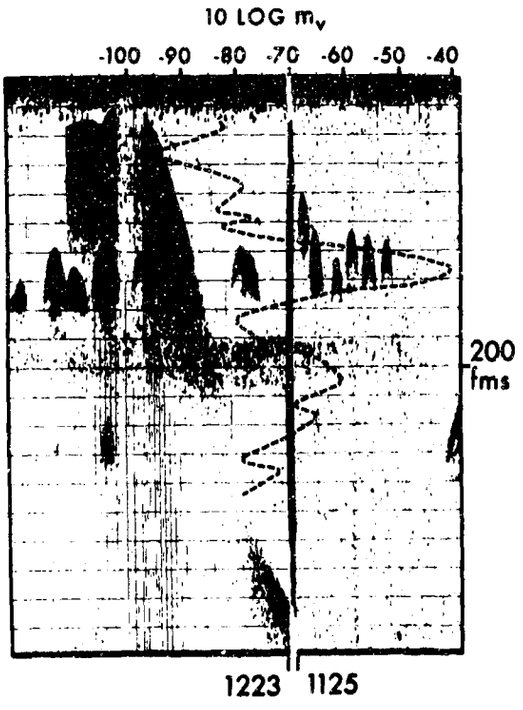

Figure 14. Station 3, 17 October 1968. Acoustic return from Large Echo Groups (LEG's). Compare with similar LEG's appearing throughout much of the same day on the same station in the echogram of Fig. 9. Volume scattering coefficient curve was obtained at a 25-msec pulse length.

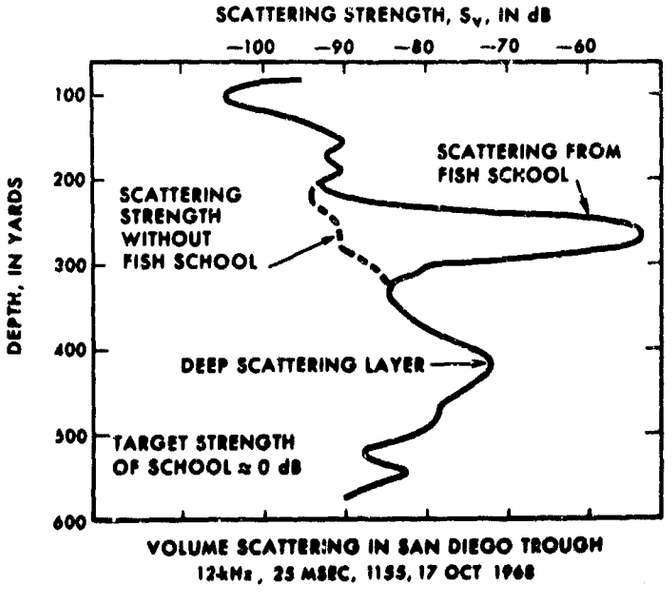

Figure 15. The same acoustic scattering return as that shown in the previous figure, but plotted as scattering strength, S_v. Note that the target strength of the presumed school or schools was approximately 0 dB at 1 yd.

possibility that the species groupings or age and year-class groupings of the organisms within the DSL may not be as heterogeneous as net hauls and submersible observations suggest. Stratification of the separately migratory groups that constitute various subcomponents of the DSL at night may operate to some degree even in the daytime, thus presenting vertical migration as a kind of accordion effect involving an alternate compaction (downward migration) and rarefaction (upward migration) of statistically discrete species complexes.

The numbers of organisms collected by the Tucker net, because of uncertainties regarding net attitude and total water filtered, are not quantified in terms of animals caught per unit volume of water (Table 1). Nevertheless, it seems clear that more than enough of those organisms possessing potentially resonant structures at 12 kHz were collected on most hauls to fulfill the condition of Batzler and Pickwell (1970), requiring only one resonant organism per 1000 m^3 of seawater to produce a better than average acoustic return in the vicinity of S_v = -65 dB. This still begs the interesting question regarding the contribution to measured and recorded acoustic scattering of nonresonant but abundant targets such as copious numbers of euphausiid shrimp and sergestid prawns (net hauls 4, 5, 6, 7, 9, Table 1). Nor do net hauls, submersible observations, or present acoustic measurements suggest the probable causative organisms responsible for the large echo groups and heavy acoustic returns shown in Figures 14 and 15. Shoals of anchovies, hake, or other densely schooling fishes are known to produce such acoustically hard targets, but probably only high-speed trawling gear can be expected to produce the identity of these rapidly swimming, highly maneuverable avoiders of our comparatively slow-moving midwater nets.

A marked disparity sometimes also occurs between net collections and direct visual observations. This was the case for the physonectid siphonophore, *Nanomia bijuga* on Station 3. Many of these delicate contributors to volume reverberation were seen on Dives 482 and 483 (Figures 11 and 13), but few were collected by the Tucker net (net hauls 6 to 9, Table 1). This was almost certainly due to the dragging speed which could not be reduced below about 4 knots, thereby contributing to the fragmentation and loss of these gelatinous coelenterates. Aboard other ships permitting net dragging speeds near 2 knots we have collected as many as 80 to 100 specimens in a single haul of the Tucker net in this same area.

Lastly, it is of interest to point out that the fadeout of DSL components during their final slow descent as seen, for instance, in Figure 8, is suggestive of resonant targets experiencing shrinkage of their gas bubbles in response to increasing hydrostatic pressure before resecretion of gas and reattainment of neutral buoyancy. That is, swimbladder partial or total collapse (nonresonant, nonbuoyant) and gas resecretion (resonant, neutrally buoyant) in organisms of a critical size relative to the sound frequency employed may be said to represent a condition of being "detuned" and subsequently "tuned" (in an analogy with tuned radio circuits) as the DSL fades out and then fades back in on the echogram. The time interval between fadeout and fadein as seen in Figure 12, that is, about 0800 to 0930 hours, seems realistic in terms of what is known of gas secretion rates in some fishes and siphonophores possessing structures resonant at 12 kHz at DSL depths (Enns, Douglas and Scholander, 1967; Pickwell, 1967 and 1970).

In this context note that confusion can arise in attempting to discriminate between true nonmigratory DSL's and migratory layers from deeper depths (i.e., greater than 200 fm in the regions discussed here) that fade in on the nighttime echo-sounder record at depths between 100 and 200 fm. We have yet to collect specimens of *Melamphaes* during the day above 200 fm, but during this cruise took several individuals at night above this depth (net hauls 2, 3, 8, Table 1) as well as other nonswimbladdered fishes such as stomioids (haul No. 8) that may also serve as indicators of deeper migratory populations.

This problem is difficult to resolve since standard echo-sounding equipment seldom records nonmigratory components with much intensity at night when other components have ascended.

Clearly, closing-net hauls at suitable times and depths can probably best solve this difficulty. Thus, our work suggests that at night at the depths of recorded nonmigratory or partially migratory scattering layers, deeper migratory species may appear and contribute to the resonant acoustic return. An example of such an organism in the present study was the anoplogastroid fish, *Melamphaes* sp.

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BIOLOGICAL CAUSES OF SCATTERING LAYERS IN THE ARCTIC OCEAN

W.J. Hansen and M.J. Dunbar
McGill University
Montreal, Canada

ABSTRACT

Two types of sonar-scattering layers are reported from the Beaufort Sea. In the present study, one is visible only at 100 kHz, the other at 12 and 100 kHz. The 100-kHz layer migrates vertically but only in part; part of it remains trapped on the interface between the Arctic surface water mass and the Arctic intermediate water mass, formed of Pacific water. It is concentrated at 50-m depth and is shown to correlate with an accumulation of the thecosomatous pteropod mollusc *Spiratella helicina*. The layer that was detected at both 12- and 100-kHz frequencies appears and behaves much like a classic deep scattering layer, except that the vertical migrations are modified to harmonize with the Arctic summer daylight pattern. It is found between 20 and 180 m and probably is caused by shoals of the polar cod *Arctogadus glacialis*.

INTRODUCTION

The results reported here are based on 3 years of observations from Ice Island T-3, a large tabular berg from the Ellesmere Ice Shelf circulating in the Beaufort Sea Gyral (Figure 1). The ice island carries a permanent, manned research station administered by the U.S. Naval Arctic Research Laboratory, Point Barrow, Alaska.

A scattering layer at about 100-m depth was reported first from the Arctic Ocean by Kenneth Hunkins (1965) of the Lamont-Doherty Geological Observatory. This observatory has been operating a 12-kHz Precision depth recorder almost continuously from T-3 for the past 6 years. An earlier study by Dietz and Shumway (1961) of echograms from nuclear submarine traverses of the Arctic showed no midwater sonar targets. Hunkins suggested that perhaps the submarines were moving within or below the scattering layers. However, there is strong evidence that Arctic sound-scattering layers are both seasonally and geographically restricted; thus, when the traverses took place, they may have missed the season, the location, or both (K. Hunkins, personal communication).

In 1966, the Marine Sciences Centre of McGill University, in cooperation with Lamont-Doherty Geological Observatory, undertook a study of the presumed biological causes of the Arctic deep scattering layer (DSL). During the first season of study, June to November 1966, no DSL was detected; the Ice Island was drifting westward about 400 miles north of the Alaskan coast at this time. In March 1967 a 100-kHz Ross Model 200A Fineline depth sounder was installed on T-3 by the Lamont-Doherty Geological Observatory. Immediately, a thin, shallow scattering layer was observed at approximately 50 m (Figure 2). This layer was not detected on a 12-kHz Precision depth recorder. It was found to conform with a water mass boundary sepa-

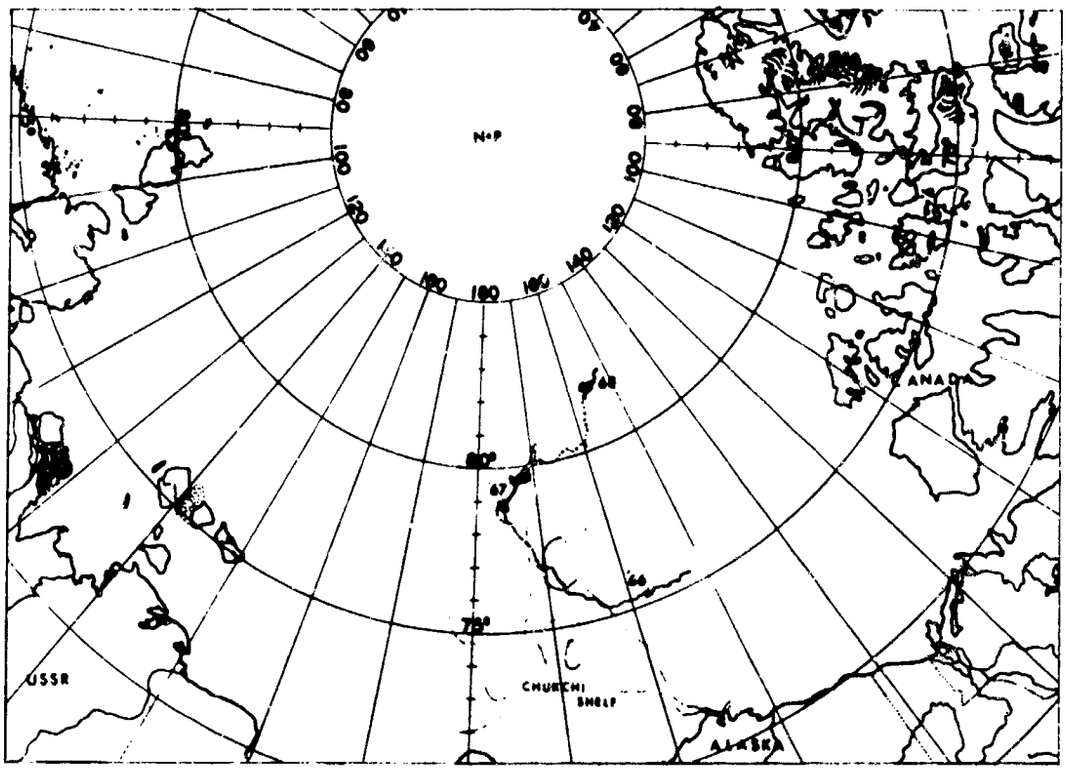

Figure 1. Drift course of Ice Island T-3, 1966-68. The solid line represents the course over which the sampling was made. Contours outline Chukchi Shelf.

Figure 2. Common appearance of the PSL (19 Oct. 1967, 0700 hours Greenwich Mean Time)

rating the upper Arctic water from the Arctic intermediate water, the latter being marked by a distinct Pacific water layer in the Canadian Basin of the Arctic Ocean (Figure 3).

At the interface, the temperature increases suddenly with depth, from -1.65° to -1.31°C in 10 m. Salinity behaves similarly, increasing from 30.4°/₀₀ to 31.3°/₀₀ over the same distance. This is an increase of 0.55 sigma-t. The scattering layer that occurred on this boundary was named the pycnocline scattering layer (PSL).

In late March 1968, a major DSL of the type and at the depths described by Hunkins (1965) appeared. It was detected between 20 and 180 m on both the Precision depth recorder (Figure 4) and the Ross recorder.

METHODS AND EQUIPMENT

Sonar

Two fathometers operated by Lamont-Doherty Geological Observatory were used. These were: (1) a 12-kHz Precision depth recorder with a standard Edo transducer, Gifft sonar transceiver, and spark-type rotating drum recorder; the time base advanced 1 cm/hr, and the pulse length was 80 msec; and (2) a Ross model 200A Fineline depth sounder and recorder with a 365-m (200 fm) range and 100-kHz frequency. The beam angle is 10° × 5°. The chart paper speed is variable from 6 to 24 in./hr, and the pulse duration is 0.4 or 1.5 msec. The instrument operates by switching through 90-m increments; thus, the whole thickness of the layer could not be viewed instantaneously. A reasonable facsimile of the full range of scatterer distribution could be obtained, however, by switching every minute, thus obtaining a narrow cross-sectional view in a 4-min period.

Hydrography

Routine hydrocasts were made during the study. Temperature was measured using a thermistor and Wheatstone bridge. Salinity samples were stored and then sent to the Bedford Institute, Dartmouth, Nova Scotia, for analysis.

Biological Sampling

Plankton

Mesh nets numbers 6 and 0 mounted on 0.5- and 1-m rings were used throughout the study. Both vertical and horizontal tows were made. Horizontal tows were made using the drift of the island during periods of high wind, when drift speeds up to 0.5 knot relative to the water beneath can occur. The actual relative drift rate and filtration-coefficient of the nets can be estimated only roughly, but the multiple-net horizontal tows gave excellent simultaneous collections from various depths. This method involves hanging the net rings on a heavily weighted cable, one above the other, so that the net will stream at the desired depth (Figure 5). Corrections of depth for wire angle were made in the field. It was found that with practice the nets could be attached or removed from a moving cable, so that the nets were set or hauled with a minimum of contamination from depths other than those under scrutiny.

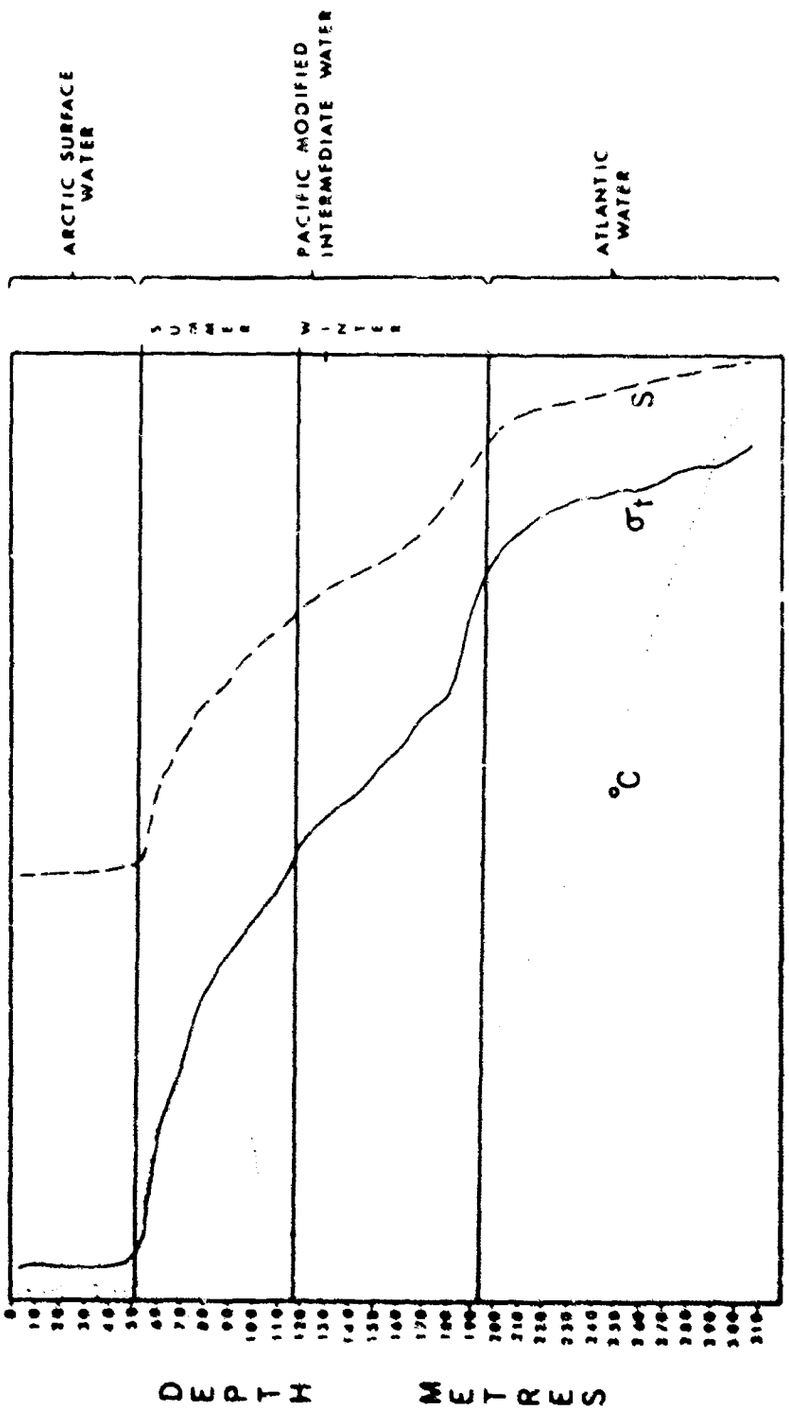

Figure 3. Curves of temperature, sigma-t, and salinity. Station 6-02; 3 May 1967

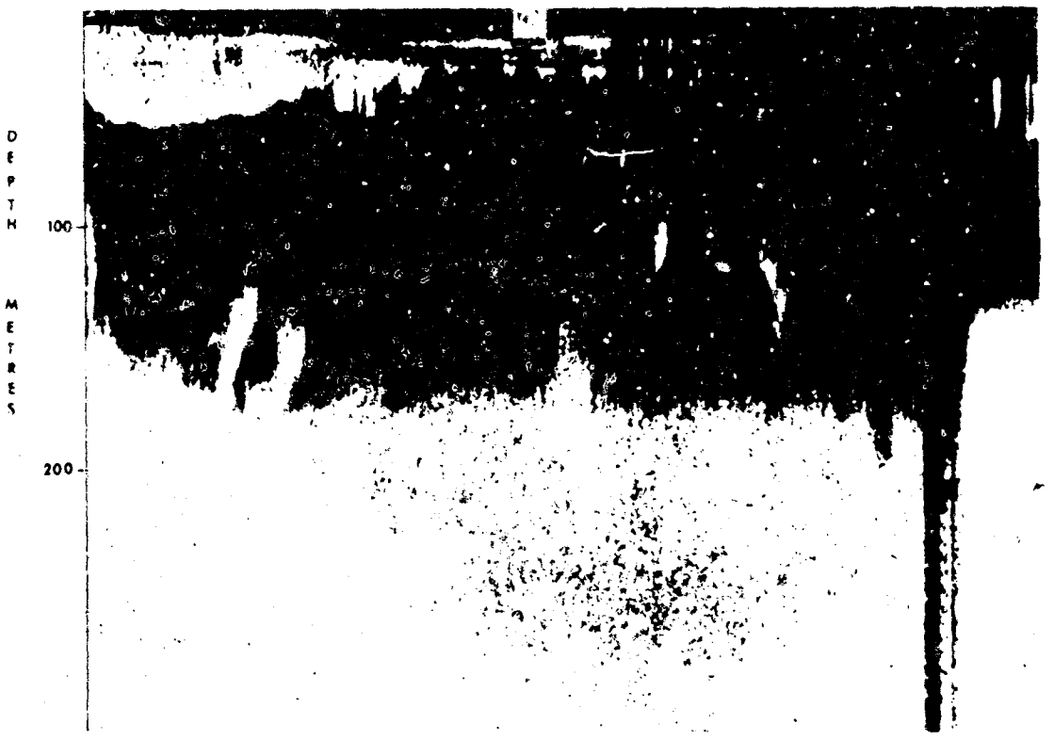

Figure 4. Typical appearance of the Arctic DSL on the PDR

Fishes

Attempts were made to capture fishes by hook and line, gill nets, and baited minnow traps; all were unsuccessful. Fishes were taken in the surface water of hydroholes in all years of the study by hand-held dip nets. It was observed that polar gadoids often follow any hanging object, such as cable, hose pipe, etc., that they encounter at depth up to the surface. Fishes almost invariably were taken in holes through which cables were hanging; one specimen was sucked into a pump hose at a depth of 12 m.

Pteropod Injector

To place potential sound scatterers in the water in a controlled manner beneath the Ross recorder transducer, a small device, the "pteropod injector," was constructed in the field from a sawn-off plastic hypodermic syringe. The device was assembled using a second piston in a reverse position so that a small toroidal space was left between the two pistons. A wire bridle passed through the plunger in such a way that a messenger would strike the plunger and eject the second piston with the contents of the toroidal space (Figure 6). Great care was necessary to remove the possibility of air bubbles being carried down into or on any part of the device. Normally the injector was held just beneath the surface of the hydrohole and agitated for a few minutes to shake free surface bubbles, though none actually were seen. Next, the outside was rubbed, underwater, with a cloth. The assembly, on a single strand of 12-gage copper wire, was lowered by hand through a bunched cloth underwater. The messenger likewise was cleaned of air bubbles.

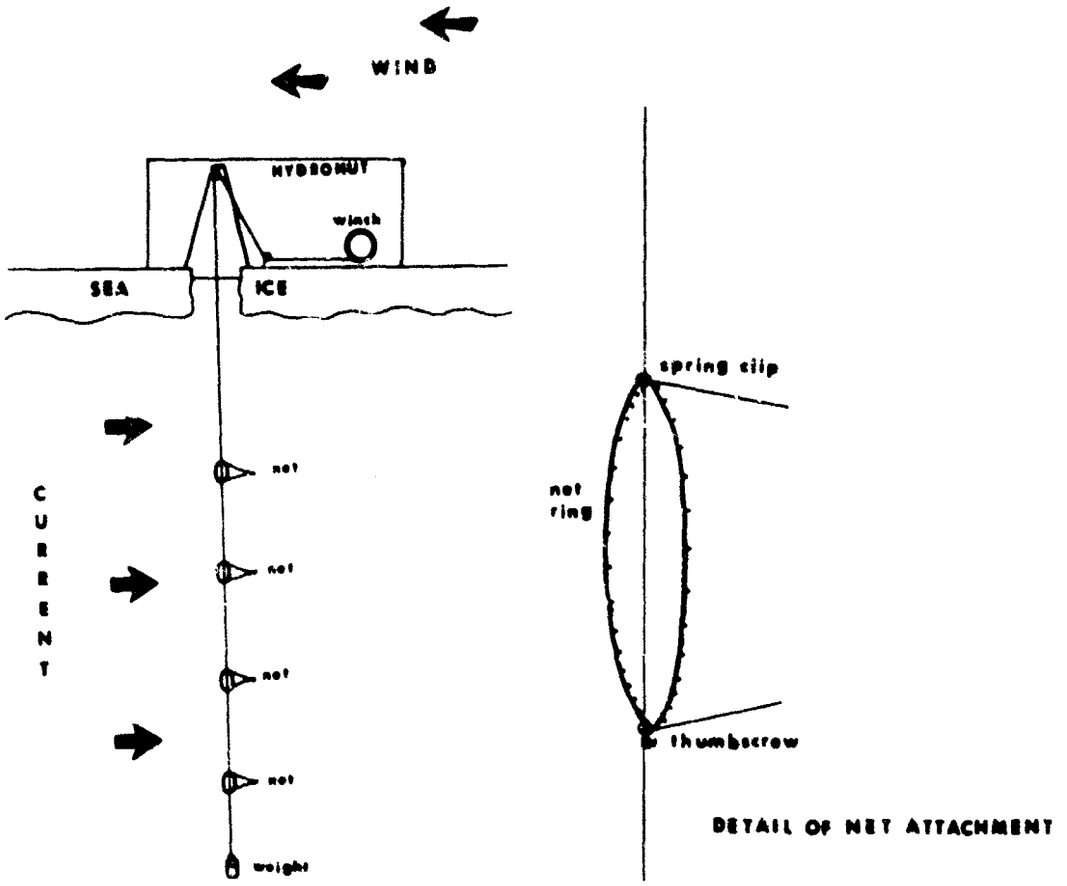

Figure 5. Technique used for the multiple-net horizontal tows. Nets may be removed from a moving cable by the spring clip.

THE PYCNOCLINE SCATTERING LAYER

Observations and Results

The appearance of this layer (Figure 2) on the Ross recorder is a thin, usually continuous, line approximately 1-m thick (N.B.: one pulse length). The thickness is often greater (Figure 7), however, especially during periods of high wind when internal waves become visible in the records. Occasionally, especially in midsummer and early fall, the layer becomes very thin and patchy, even disappearing completely for many days.

Initially it was thought that this scattering layer perhaps could be interpreted physically as an acoustic reflection from the density discontinuity. At the high frequencies (100 kHz) used, however, this is unlikely. Detailed examination of the records shows that diurnal splitting of the layer occurs; one fraction remains at the discontinuity and the other migrates either upward or downward from the discontinuity.

This is especially notable in the months bracketing the equinoxes, when greatest diurnal light variations occur. Figure 8 shows six sections of the chart record for 26 and 27 October 1967. At midday, a thin PSL is present with a few single targets visible. At 1500 hours, an ascending cloud of scatterers appears. At 2100 hours, two fractions of the layer are apparent, but the upper fraction tends to descend slowly. By midnight, however, a dense scattering layer has formed with fairly even distribution throughout the water column; a PSL is still visible. Then,

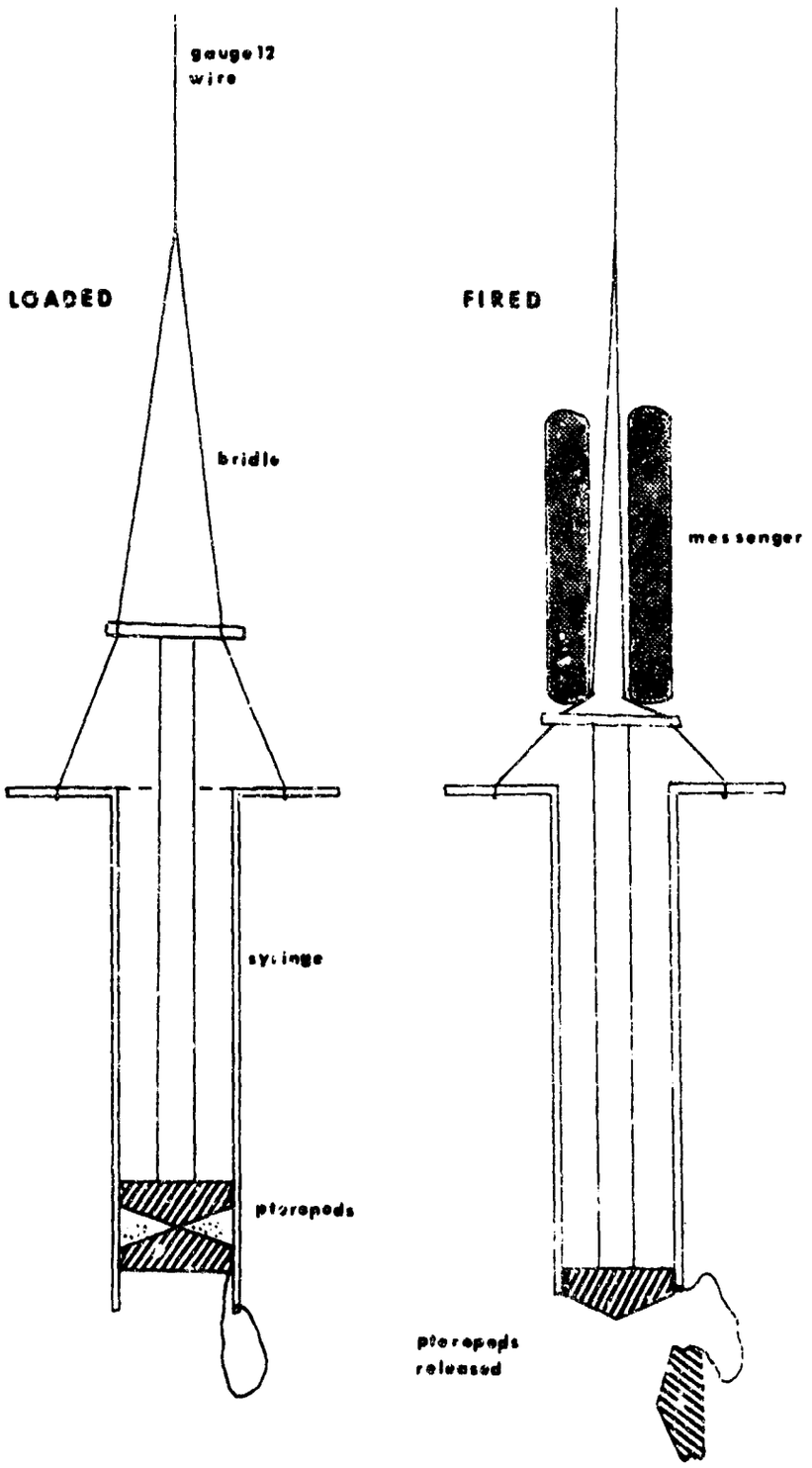

Figure 6. The pteropod injector Specimens of *Spiratella* are placed in the space between the two pistons

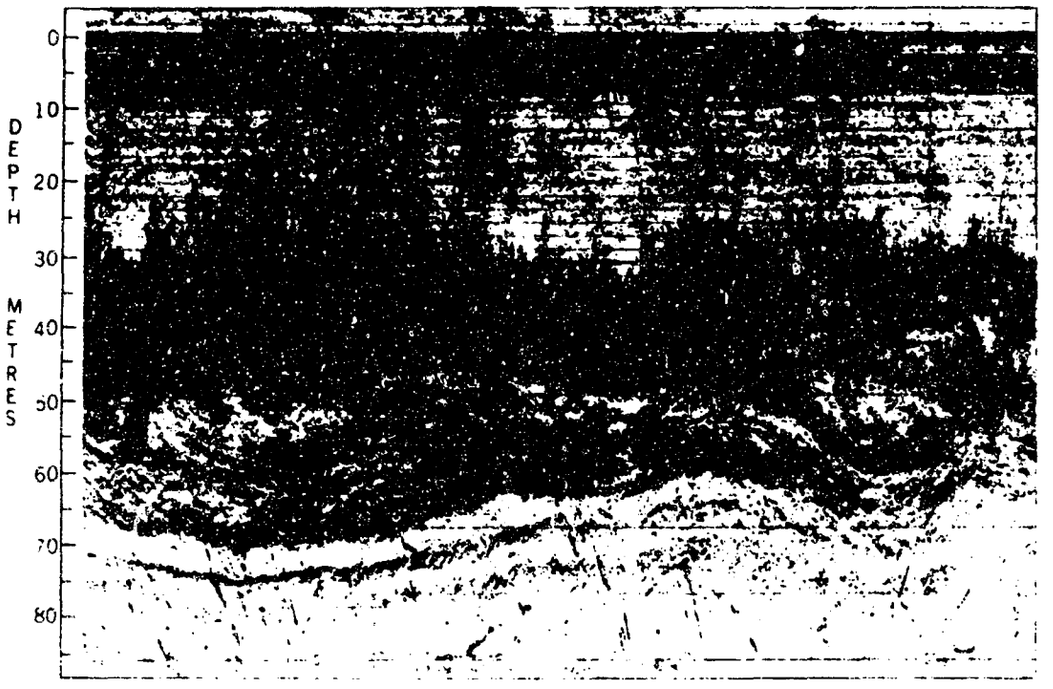

Figure 7. Very thick PSL. Turbulence possibly caused by the motion of Ice Island (23 Oct. 1967, 2300 hours Greenwich Mean Time).

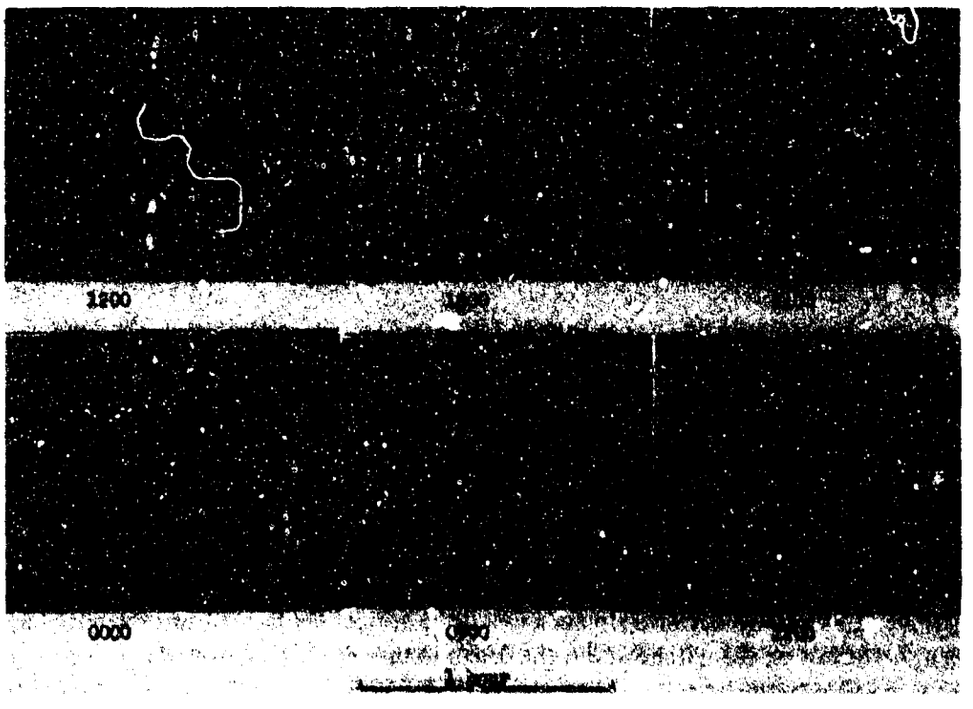

Figure 8. Six sections of the chart record for 26 and 27 October 1967

at about 0900 hours on the 27th, fairly rapid descent of the main scattering cloud occurs, leaving once more a PSL with a few single targets visible. The cycle repeated itself on subsequent days.

There is an interesting seasonal variation in the chart records. In winter, when continuous darkness prevails, the migrating fraction remains continuously above the PSL, (Figure 9a) as might be expected and as was predicted by Bogorov (1946). Interestingly, however, the same distribution seems to prevail during the summer (Figure 9b) rather than occurring at greater depths.

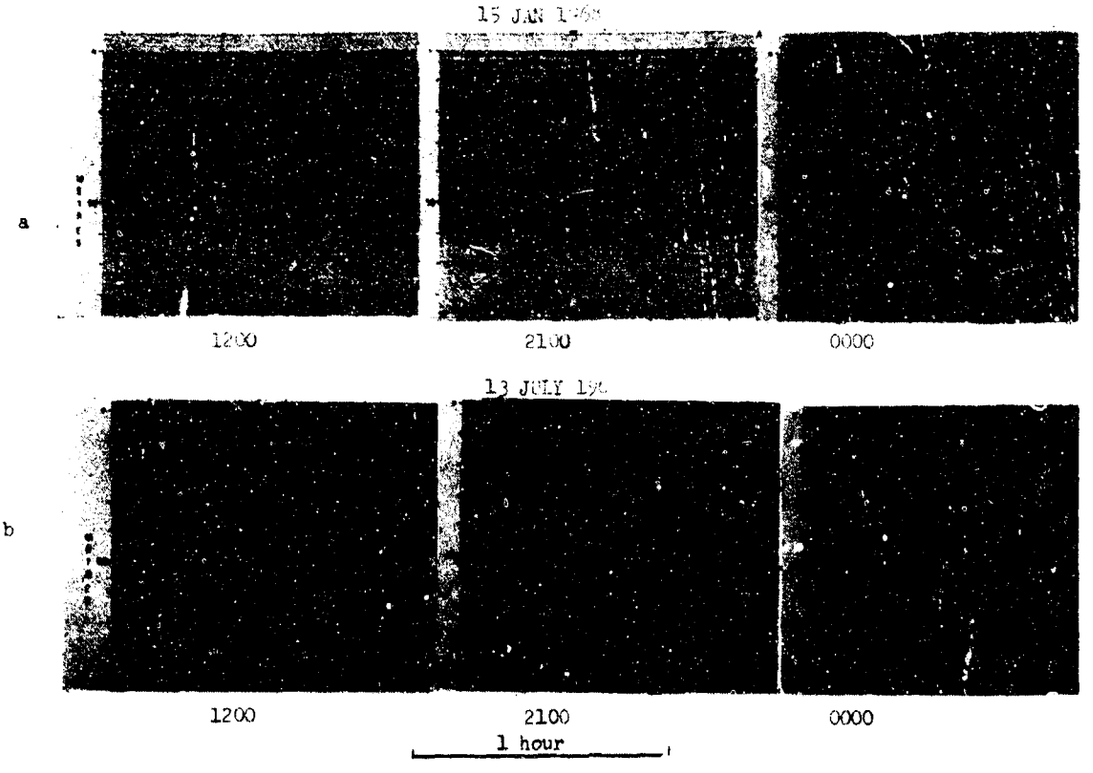

Figure 9. Sections of chart record in winter (a) and summer (b)

Analysis of the plankton offers evidence of the cause of this layer. The cosmopolitan thecosomatous pteropod *Spiratella helicina* (Figure 10) occurs in enormous numbers at the interface of the two water masses. These are little calcareous shelled planktonic snails. In our samples, they were very small individuals, usually less than 1 mm in diameter, in contrast to the large specimens of 10 to 15 mm normally taken in subarctic waters. This small size in itself is extremely interesting and requires further study. They are not juveniles; strings of eggs were observed within the body and exuding from the gonopores of many of the living specimens.

Because of the thinness of the layer and the general difficulty of hauling nets horizontally from the ice, it was not possible to stream a net at the correct depth with any accuracy. By placing a thermistor on the net, however, the discontinuity could be detected and the net held as close as possible to the layer depth. At Station 5, 79°57.9′ N, 17.4°24′ W, on 3 May 1967, a multiple-net horizontal tow was made with 0.5-m nets at 40, 45, 50, and 55 m. Internal waves of 6-m amplitude and approximately 10-min period were visible in the chart record at 50 m. The

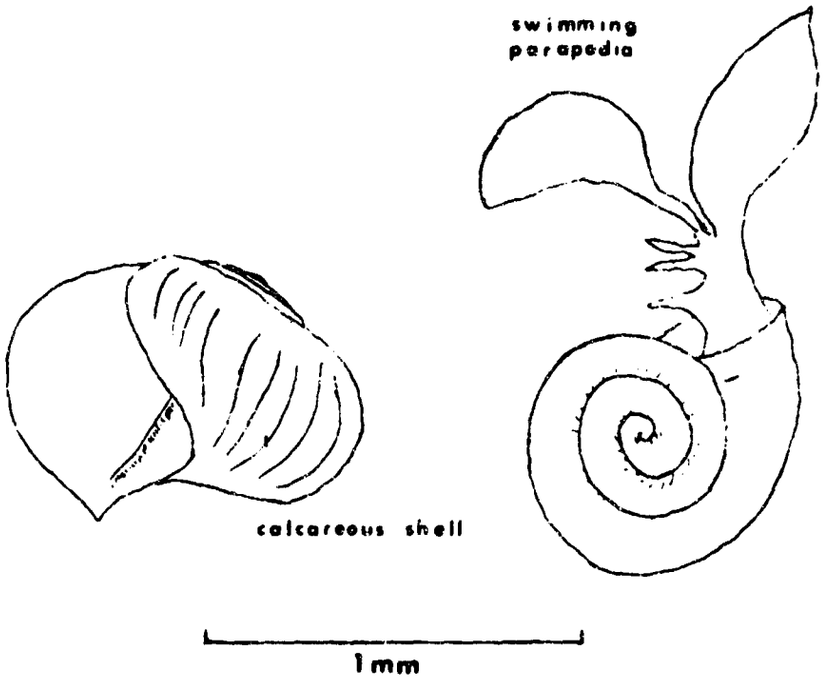

Figure 10. The thecosomatous pteropod *Spiratella helicina*. The specimens taken from the scattering layer are extremely small compared with those found further south.

layer at this time appeared to be about 8 m thick. The windspeed was a steady 20 to 25 knots, and the drift of the island an estimated 0.5 knot. Figure 11 is a histogram of pteropod distribution correlated with the depth-sounder record, demonstrating the correlation of pteropod numbers with the scattering layer. Other stations with horizontal net tows verify these distributions. A series of subtractive vertical tows was made using a 2-m increment for each tow. The net was triple washed and inspected visually to make sure no pteropods were missed. Counts were made immediately.

Station V.T. 4, 30 May 1967, showed a typical vertical distribution found by this method. Figure 12 is a histogram of pteropod distribution and numbers on a 2-m subtractive tow series, showing maximum concentration between 50 and 48 m. It is correlated with the chart record of that day.

The data presented here are excellent correlative evidence that *Spiratella* is the cause of the PSL.

Field tests with the Ross echo sounder were made, using small BB shot as test targets. Individual pellets, approximately 1.4-mm diameter, were detectable down to 30 m. An experiment was performed with the pteropod injector containing 80 live specimens of *Spiratella helicina*. Careful precautions were taken to eliminate air bubbles, and the injector was lowered to a depth of 60 m and allowed to hang for 4 min. The injector was then fired by messenger and, at the moment of impact, the injector was raised 10 m. On the chart record (Figure 13), a residual line of echo remained, slowly dispersing over a period of 1 min. The experiment was repeated three times with live specimens and once with a blank run (only water in the injector barrel). The results were identical on two out of three runs; on the third run, air bubbles, showing as rising streaks, occluded the record. The blank run showed no scattering. *Spiratella* has a hard calcareous

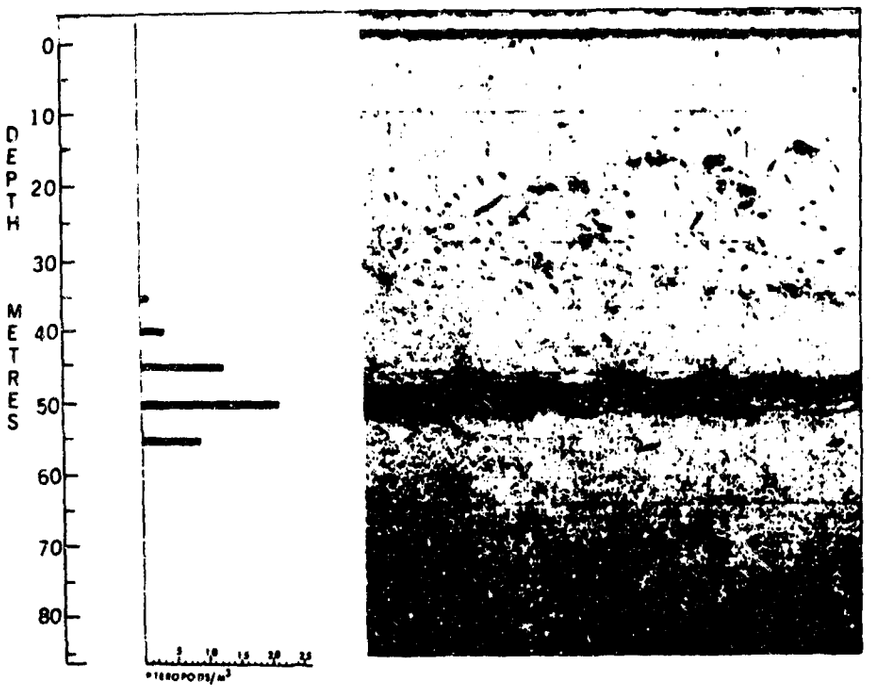

Figure 11. Histogram of pteropod numbers per cubic metre correlated with the depth-sounder record (sta. 5, 5 May 1967)

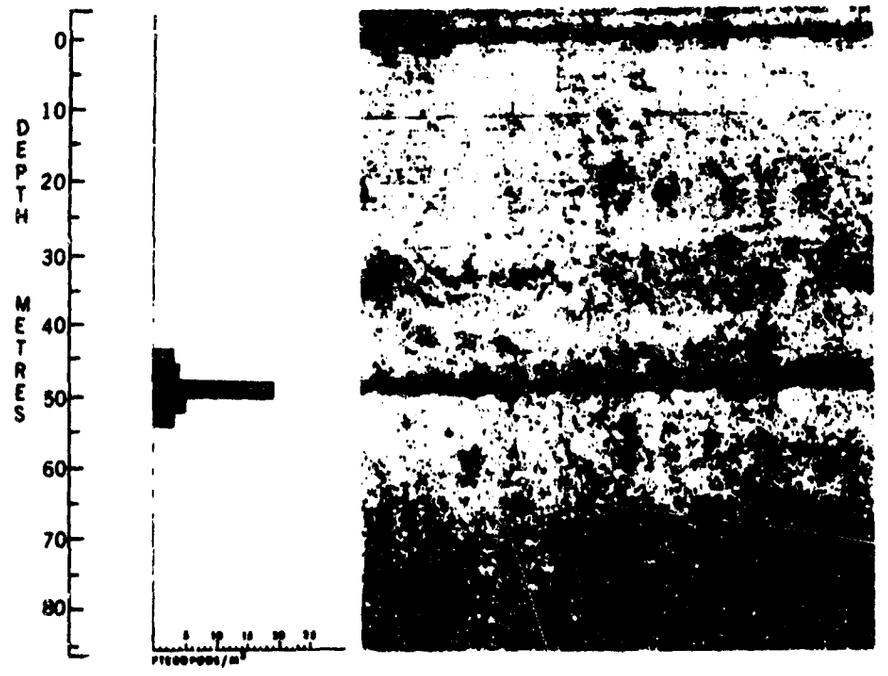

Figure 12. Histogram of pteropod numbers per cubic metre correlated with the depth-sounder recorder (from subtractive vertical tow, sta. V.T. 4, 30 May 1967)

Figure 13. Experiment with pteropod injector (sta. P.I. 2, 24 April 1968)

shell, which probably can be classified acoustically as a solid body; thus, if large numbers of *Spiratella* were present in a thin layer at 50-m depth, they would be expected to form a detectable scattering layer.

The behaviour of the organism as observed on the echo sounder deserves analysis. The sinking rates of the creatures in water from above and below the discontinuity were measured in the laboratory. The average sinking rate of 20 nonswimming specimens in water from 45 m (sigma-t 24.65) was 1.782 cm/sec. In water from 55 m (sigma-t 25.10), it was 1.521 cm/sec. One can postulate that less energy is required for *Spiratella* to maintain a constant depth by remaining at or below the PSL; the significance of this is doubtful, however, especially in such an actively swimming organism.

Harder (1968), reviewing plankton behaviour at water-mass boundaries, suggested that density interfaces act as concentrating levels for organic detritus and that many species feed at the interface. Other species may respond to physiological stress induced by salinity changes, which alter the osmotic pressure differential across the cell membranes.

Hunkins, Thorndike, and Mathieu (1969) examined the nepholometry of the Canadian Basin. They found no light-scattering layer indicative of a detrital accumulation at the interface depth. Thus, a feeding response seems unlikely to explain the behaviour.

There is a recurrent, though unresolved, suggestion in vertical migration studies (Lance, 1962; Loeb, 1893; Rose, 1925) that vertically migrating plankton organisms within a light field tend to some physiologically limited level of salinity (or temperature) as well as light intensity; once one constraint passes beyond a certain threshold, the sign of the migratory drive is changed. Thus, a stenohaline individual organism moving upward at sunset and passing into more brackish water will stop at the critical salinity level. As the light intensity drops lower, the triggering stimulus diminishes. In this condition, the physiological stress of the brackish water causes a reversal of

sign in the migration, and the organism tends to sink slowly toward the more saline water during the night. At dawn the increasing light tends to reverse the sign once more, and a second upward migration occurs toward the optimal halophotic level. Once the light intensity and the osmotic stress become too strong, however, a downward migration occurs, taking the organism back to optimum daylight depths.

In an ocean with a marked salinity boundary layer, there tends to be a segregation of individuals. Those of low tolerance to high salinity tend to remain on the boundary layer during downward migration at dawn. Those of low tolerance to brackish water tend to remain on the boundary layer during upward migration at sunset. The hardier or more euryhaline members of the population transcend the layer, albeit with some short delay, to accommodate the rapid change of osmotic balance.

This hypothesis would explain the general behaviour of the Arctic PSL as caused by pteropods whose salinity limits lie between 33.5°/₀₀ and 30.5°/₀₀ or so in this population (Harding, 1967). It does not explain the reason for the high position and nonmigratory behaviour of the summer and winter layer. The reason for this might be that, during these long, continuous light or dark periods, the primary trigger stimulus is absent; thus, the organism tends to remain at depths favourable in factors other than light, such as feeding.

THE DEEP SCATTERING LAYER

Observations and Results

Hunkins (1965) has described the Arctic DSL observed at 12 kHz as a "diffuse reverberation," similar in general appearance to the DSL in other oceans. The Arctic layer tends to be shallower (20 to 200 m) in distribution than elsewhere in the world and also to have an annual rather than a diurnal migration pattern, no doubt a result of the special Arctic daylight pattern. The layer has been recorded only during the summer months and only in the northern and northwestern part of the Beaufort Sea Gyral. Soundings elsewhere and at other times of the year were negative. Hunkins has shown that diurnal vertical migrations are, in fact, observable in this layer, especially about the time of the autumnal equinox. The layer usually is not present at the time of the vernal equinox.

Figure 14 is a continuous record of the development of the DSL in 1968, transcribed from the original daily chart records. The layer first appeared as isolated scattering groups, which developed into a thin, slightly discontinuous layer that was not particularly migratory. It later became thicker, and through mid-April, the layer showed definite diurnal migrations. As the summer progressed, the layer tended to split into two components and become a little patchy.

At the 100-kHz frequency, it was possible to observe only a 90-m vertical section of the water at any one time, but a good composite picture could be gained by switching through the depth ranges in sequence and placing the records in order one above the other. Figure 15 is such a composite of four chart records offering a complete section through the DSL as seen on the Ross recorder. The PSL is traversed freely by the DSL scatterers (Figure 16), and it does not appear in general to be a significant barrier.

Kanwisher and Volkmann (1955) found one scatterer per 8,500 m^3 off New England, and Johnson, Backus, Hersey, and Owen (1956) found one scatterer per 650 m^3 off Puerto Rico. In order to compare various features of the DSL with the findings of these workers, an index of scatterers per unit volume was calculated. The first step was to switch through the depth ranges of the 100-kHz instrument over a short period of time. The scatterer counts were then corrected by dividing the number of scatterers in each 10 m of the insonified cone by the volume of a 10-m deep segment and multiplying the result by 10^4 to place the decimal point in a convenient

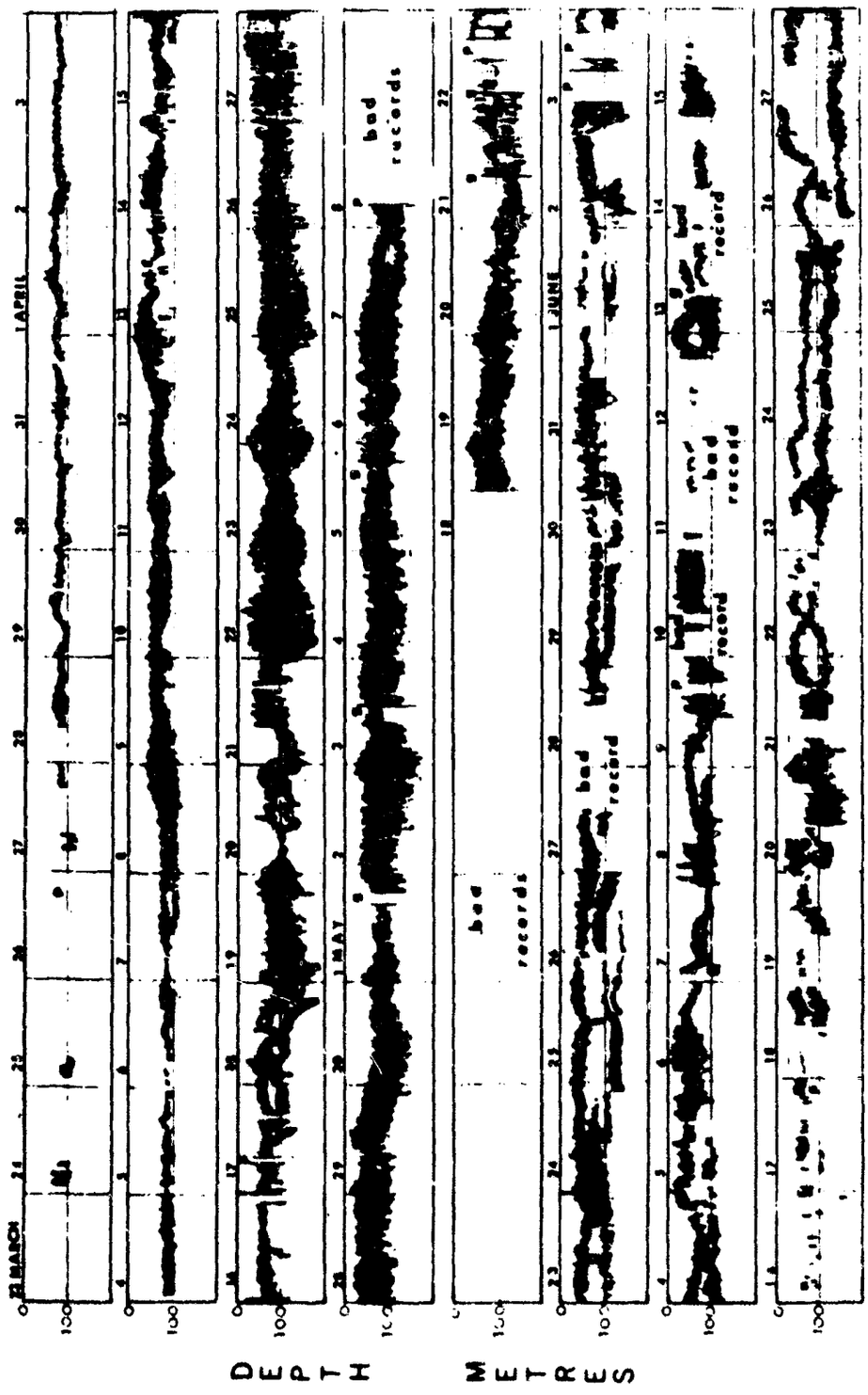

Figure 14. Continuous record of DSL sketched from daily records. P represents power failure and g, gain adjustment.

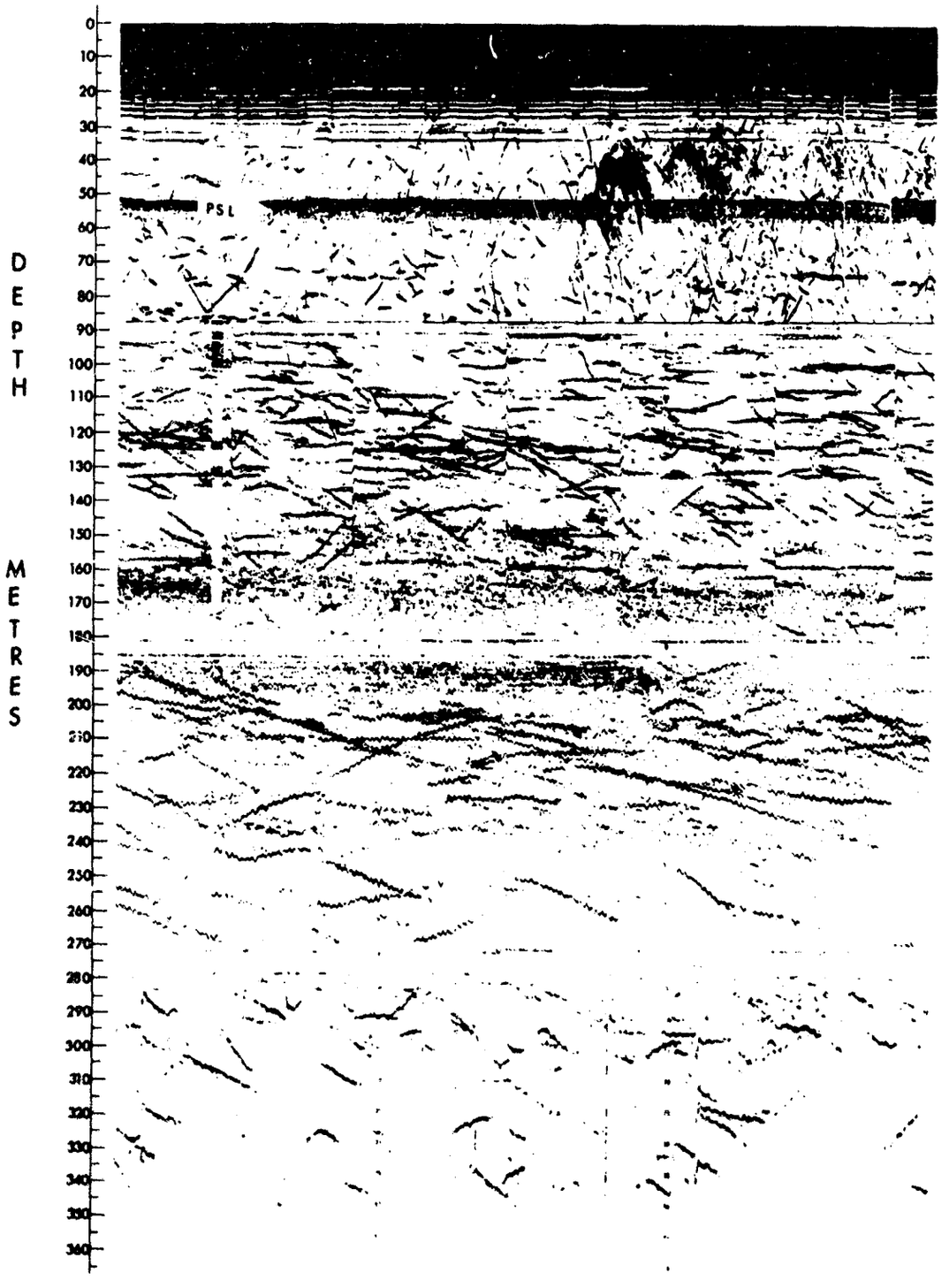

Figure 15. Composite record of the DSL from the Ross echo sounder

Figure 16. Scattering groups from the DSL traversing the PSL marked by the thin PSL (14 April 1968)

position. Figure 17 shows a histogram of the vertical distribution of the scatterers per 10,000 m^3. This gives a highest value of scatterers as approximately 1/5,000 m^3. Much higher concentrations can occur in the scattering groups, but because the echo traces tend to merge, no reliable count is possible.

Attempts to capture the organisms responsible for this layer were unsuccessful. In 2 different years only two larval polar gadoids were taken from horizontal plankton tows below the surface, at depths of 15 and 40 m respectively. One of them was taken when no scattering layer was present. Fishes *(Arctogadus glacialis)* frequently are captured, however, in the hydroholes cut through the sea ice.

The lack of positive evidence in the form of specimens taken at the layer depth is not surprising considering the impossibility of trawling from the surface of pack ice. It is obvious from the echograms that the scatterers are relatively large, scattering both 12- and 100-kHz sound. When the scatterers are viewed at 100 kHz as individual targets, they frequently are seen as fast-swimming hyperbolic traces; these traces are indicative of rapid relative motion between transducer and target. Furthermore, the organisms frequently move in dense shoals and are seen as scattering groups; they are therefore most probably nektonic fish, and the most likely species is *Arctogadus glacialis*, the polar cod (Figure 18).

The biology of *Arctogadus* is not well known. It is certainly the most frequently found species in the central Polar Sea. Walters (1961) identified and described 35 specimens of this species taken from Station Charlie in the winter of 1959-60. During this period, up to 500 specimens sometimes were taken from the hydroholes following seismic explosions at shallow depths below the ice. Andriashev (1957) took 11 specimens from the same general area as the

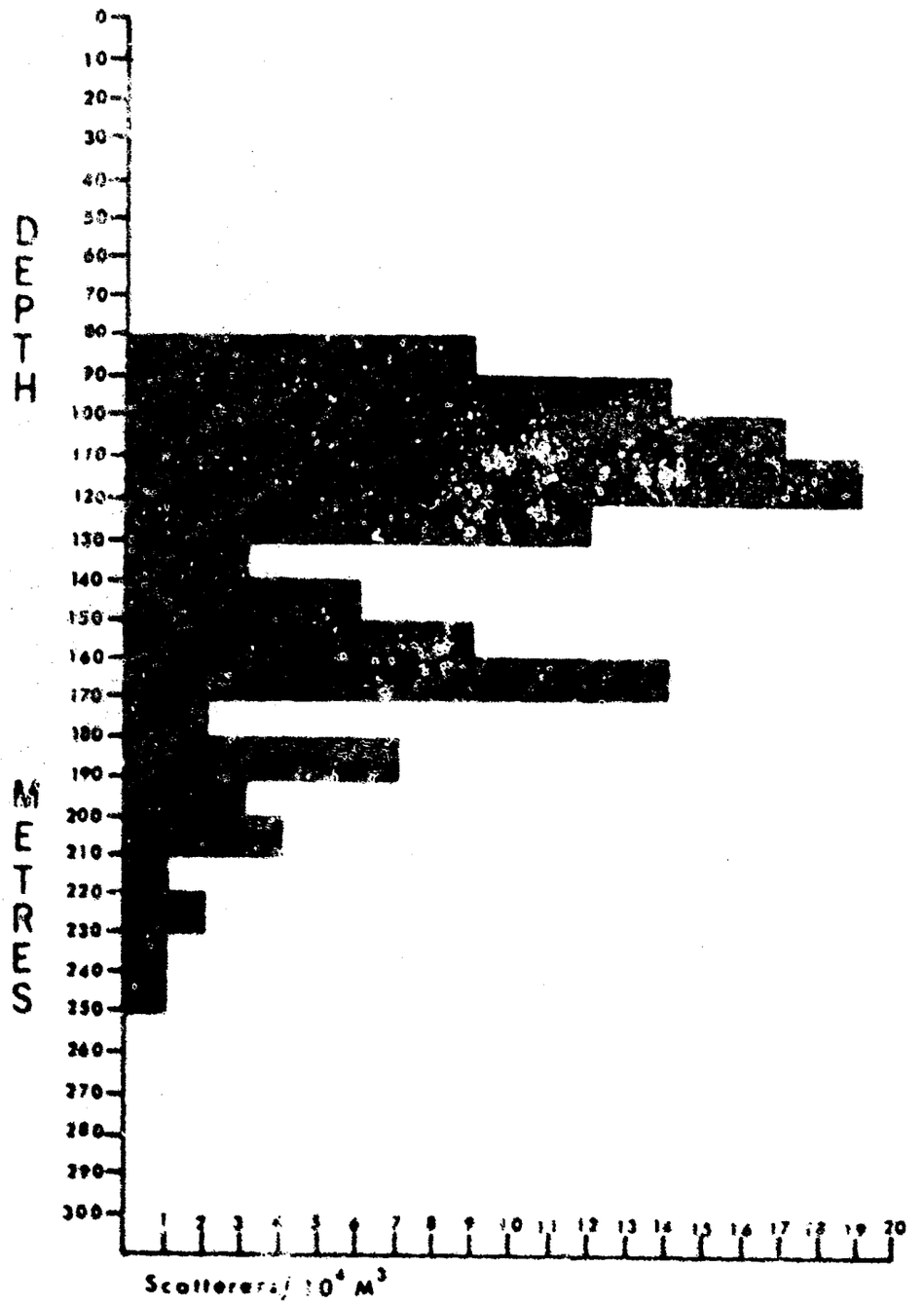

Figure 17. Histogram of scatterers per 10,000 m^3 made by counting a random section down a Rom depth-sounder chart and correcting to a unit volume from the transducer geometry

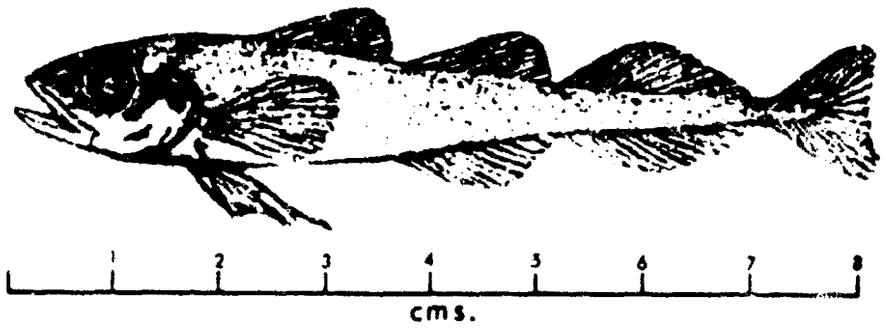

Figure 18. *Arctogadus glacialis* (drawn from a preserved specimen)

Station Charlie material, i.e., over the Chukchi Rise. In 1966 we took two specimens in this area; in April and May 1967, three were taken much farther north; and in May 1968, four were taken farther west.

Walters (1961) suggests that this species undertakes winter feeding migrations over the Chukchi Rise, moving in the winter in a generally southwest direction. Because the DSL has been detected only in summer and well north of the Chukchi Rise in the present work, it is possible that these fishes migrate back into the central Polar Sea from the Chukchi Rise by a northeasterly route during the summer.

Two specimens of the Arctic cod *Boreogadus saida* also have been taken in the course of this work. This species also must be a sound scatterer in the Polar Sea; however, its significance cannot be judged presently.

ACKNOWLEDGMENTS

We thank Dr. Max Brewer, Director, Naval Arctic Research Laboratory, Point Barrow, Alaska, for his support, facilities, and encouragement in the field. We acknowledge also the generous cooperation of Dr. Kenneth Hunkins and his associates at the Lamont-Doherty Geological Observatory, who made the echograms available to us and whose many helpful discussions and criticism are greatly appreciated.

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SONIC SCATTERING AND ITS PROBABLE CAUSES IN TWO AREAS OF PUGET SOUND

William A. Friedl
Naval Undersea Research and Development Center
San Diego, California

ABSTRACT

The composition and characteristics of sonic scattering in two areas of Puget Sound were investigated over a 2 1/2-year period using a 38.2-kHz Simrad echo sounder and three sizes of midwater trawls. In Port Orchard Narrows in the central basin (depths to 40 m), scattering during the day was irregular and often absent throughout the year; day hauls took no fish and essentially no macroplankton. Nocturnal conditions varied seasonally. During the winter, scattering was characterized by compact layers of individual targets at middepth. Samples in the layers were marked by catches of Pacific herring *(Clupea harengus pallasii)* and surf smelt *(Hypomesus pretiosus)*. At greater depths, increasing numbers of northern midshipmen *(Porichthys notatus)* and macroplankton, particularly the mysid, *Neomysis kadiakensis*, were taken. In the summer, while scattering was extensive, it was nebulous and largely lacked concentrations of individual targets. Samples were characterized by catches of *Porichthys* at all depths and by high concentrations of bay gobies *(Lepidogobius lepidus)* above 15 m. Macroplankton was dominated by *N. kadiakensis;* concentrations were greatest at middepths and exceeded winter values by more than an order of magnitude at all depths.

In Case Inlet in the southern Sound (depths to 120 m), scattering was of two general day/night patterns. In late winter, distinct layers of individual targets typically displayed marked diel depth changes at middepths, though daytime scattering above 30 m was observed in April. *Clupea* and the spiny dogfish *(Squalus acanthias)*, a predator upon *Clupea*, were taken at layer depths. Macroplankton was scarce in this period and concentrations generally increased with depth during the day. Euphausiids (mainly *Euphausia pacifica* and *Thysanoessa spinifera)* and the mysid, *Acanthomysis macropsis*, were taken near the surface at night and above the main layers during the day. *N. kadiakensis* dominated deeper hauls at night and daytime hauls below the layers. In the summer, layers were less well-defined and individual targets were more dispersed on the echographs. Persistent scattering was present in the upper 40 m both day and night; heavy scattering was observed during the day in August and September at lower depths. *Porichthys* dominated night catches, but no large fishes were taken during the day. Macroplankton concentrations were high during these months, dominated by ctenophores, fish larvae, and mysids *(N. kadiakensis* and *A. macropsis)*. Concentrations of mysids were marked at middepth at night and increased with depth during the day. Euphausiids were also abundant between 60 and 80 m in daytime hauls.

Behavioral patterns of herring, smelt, midshipmen, and mysids appear to influence the characteristics of sonic scattering observed at 38.2 kHz in central and southern Puget Sound. Better understanding of the distribution and behavior of organisms and their relationships to sonic scattering could result from the use of different trawls, designed to sample either macroplankton or fishes. The use of efficient trawls is particularly important during the winter when active fishes such as herring and smelt are apparent principal components of well-developed scattering layers in Puget Sound.

INTRODUCTION

Since the mid-1930's, commercial fishermen have utilized knowledge of sonic scattering in shallow water to increase their catch per unit effort (Balls, 1948; Cushing, Derold, Marr, and Kristjonsson, 1952; Tester, 1943). Reviews of the relationship of marine organisms to sonic scattering emphasize the differences between the scattering characteristic of the deep sea and that found over shoal bottoms inshore or near oceanic banks (Beklemishev, 1959; Boden, 1962; Hersey and Backus, 1962). In shallow water, sonic scattering is typically a manifestation of local aggregations of organisms. Such aggregations are often transitory; their nature and composition may change over horizontal distances of a few miles, and their characteristics and existence can vary greatly with seasons (Hersey and Backus, 1962). Until recently, however, an attitude akin to scientific benign neglect has limited extensive biological studies of scattering in shoal waters to some predominantly fisheries-oriented works in northern European waters in the early 1950's (Burd and Lee, 1951; Cushing, et al., 1952; Cushing and Richardson, 1956; Parrish and Craig, 1951).

In the last decade, extensive scattering was noted in Puget Sound by workers at the Bureau of Commercial Fisheries and at the University of Washington (U.S. Department of the Interior, 1966a, b; Cooney, 1967; Thorne, 1968). Sporadic hauls with various nets suggested that a variety of organisms (fishes, macroplankton, and ctenophores) were associated with sonic scattering in Puget Sound, but the seasonal and spatial variations in the nature and composition of the layers were not clear. The present study was initiated to investigate the biological aspects of sonic scattering in Puget Sound and to determine if any temporal or spatial patterns exist in the characteristics and composition of such layers. The work provided information and direction to subsequent, more detailed studies of sonic scattering in the Puget Sound system and helped relate that system to other shallow and deep water environments.

METHODS AND MATERIALS

The study was conducted in two areas of Puget Sound: Port Orchard Narrows, a constricted channel west of Bainbridge Island in central Puget Sound, and Case Inlet, one of several inlets in the southern sound (Figure 1). Water movement in these areas is irregular and modified locally by winds (English, 1961; Thorne, 1968); weak thermal stratification occurs in the areas during the summer (Cooney, 1967; T. Saunders English, *unpublished data).* In Port Orchard (Figure 2), samples were taken along a N-S track in the narrow channel south of Fletcher Bay; the maximum depth in the area is slightly over 40 m.

In the southern sound, samples were taken along a NW-SE track off Taylor Bay, near the mouth of Case Inlet (Figure 2). Maximum depths in the research area were slightly less than 120 m. Though moderately strong tidal currents sweep through Dana Passage and around Devils Head at the mouth of Case Inlet, surface circulation in the inlet is generally weak (Haight, 1948).

Between September 1965 and February 1968, 14 cruises were made to Port Orchard. Samples were taken at irregular intervals from January 1966 onward; the Department of Oceanography, University of Washington vessel R/V *Hoh* was used for all but the last cruise, when the College of Fisheries vessel R/V *Commando* was employed. Seven cruises were made to Case Inlet aboard the R/V *Hoh* between April 1966 and August 1967; samples were taken on each cruise.

Scattering observations were made with a Simrad EH-2a echo sounder operating at a frequency of 38.2 kHz. The hull-mounted transducer produced a primary sound cone 6° fore and aft by 20° abeam. The transmitter operated at 32 v (dc) with an output power of 60 watts and a

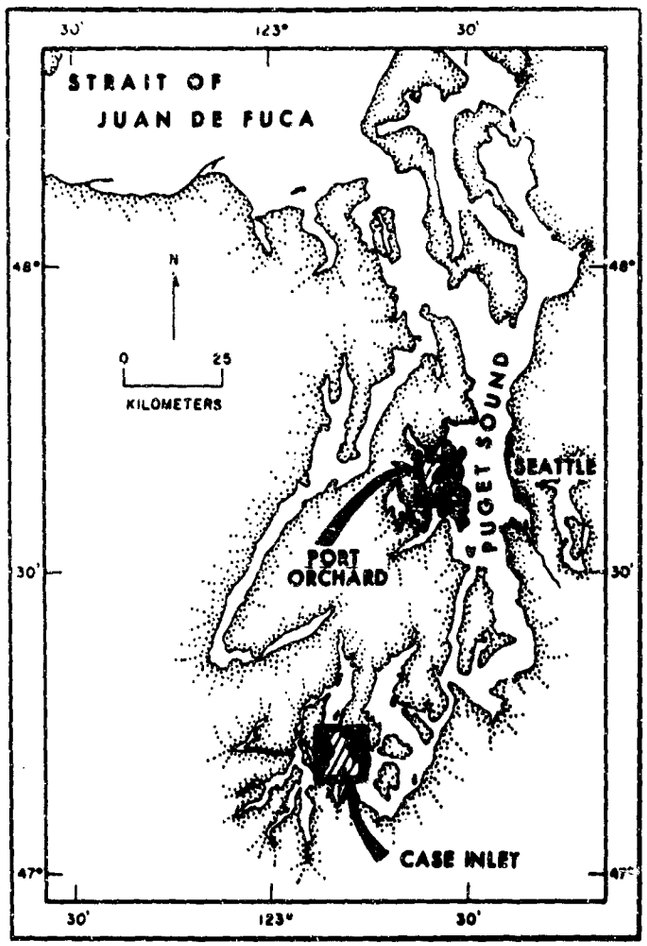

Figure 1. The relationship of the research areas to Puget Sound and adjacent waters

sounding rate of 96 pulses/min. Returning signals were recorded on dry paper moving 10.5 mm/min; the white line (maximum sensitivity) scale was used at all times. Most recordings were made from signals of 1-msec pulse length.

The majority of samples were taken with 6- and 10-foot Isaacs-Kidd midwater trawls (IKMT) (Aron, 1959; Isaacs and Kidd, 1953). A depressed 1-m ring trawl of 1/4-inch mesh knotless nylon was used for comparative purposes, principally in Port Orchard (Table 1). Speeds were measured at the surface with a Tsurumi-Seiki-Kosakusho Co. (TSK) flowmeter while the trawls were at depth. Speeds ranged from 1.5 to 2.7 m/sec for the IKMT and from 2.2 to 3.4 m/sec for the ring trawl (Table 1). The duration of hauls varied with season and location. Most hauls in Case Inlet and the majority of the 10-foot IKMT hauls in Port Orchard were at depth for 15 min; hauls with the smaller trawls in Port Orchard were generally at depth for 10 min. On summer cruises, when macroplankton was particularly abundant, shorter hauls were made.

Net depth was either measured by a Marine Advisers, Inc., bathykymograph time-depth recorder attached to the trawl bridle or was monitored on deck from signals transmitted through the towing cable by a pressure-activated sensing unit (designed and built by the Department of Oceanography, University of Washington) mounted above the trawl. Hauls were made above, in, and below the depths of principal scattering in each area. Paired hauls were taken at most depths in Port Orchard and at depths of significant scattering in Case Inlet.

Echographs were examined after each cruise, and the major patterns of sonic scattering were identified. Returns were classified as concentrated (a dense, dark trace) or as diffuse (a lighter,

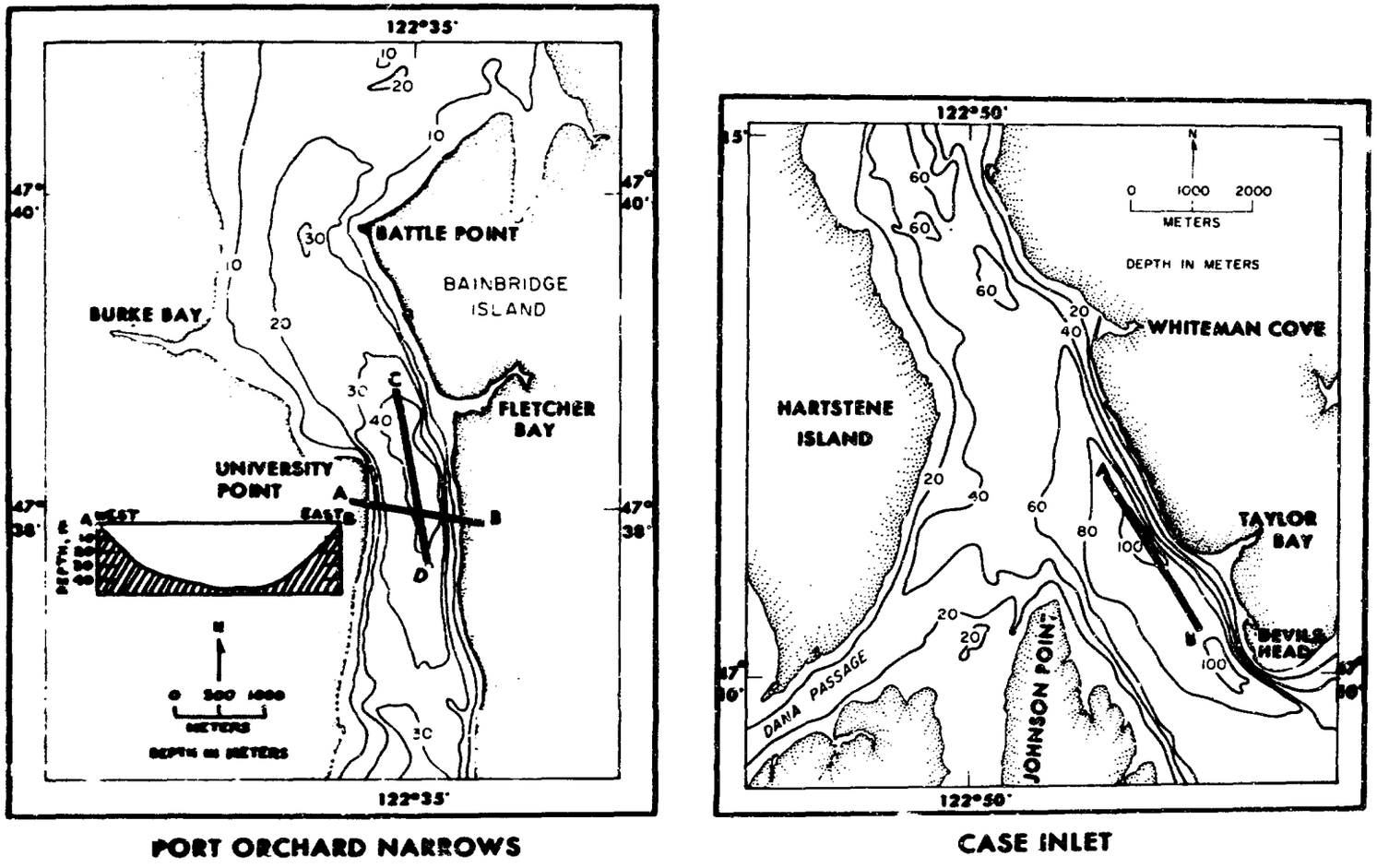

Figure 2. (Left) Bathymetry of the Port Orchard Narrows research area. A - B: Typical cross section. C - D: Midwater trawling track. (Right) Bathymetry of the Case Inlet research area and adjacent waters. A - B: Midwater trawling track.

TABLE 1. Dimensional and Deployment Data for the Trawls Used in this Study

Trawl	Area (m^2)		Hauls (day/night)		Speed (m/sec)	
	Mouth	Plankton	Port Orchard	Case Inlet	Average	Range
10-ft IKMT	7.68	1.75	18/53	12/16	1.90	1.5 – 2.3
6-ft IKMT	2.94	1.26	24/59	34/36	2.15	1.5 – 2.7
1-m Ring	0.78	0.78	4/25	0/2	2.52	2.2 – 3.4

Note: Mouth areas are based on the physical dimensions of the forward openings of the trawls. The cross-sectional area of each trawl effective in capturing larger zooplankton is listed under "Plankton." The effective area of the 10-foot IKMT was determined relative to that of the 6-foot IKMT after comparative hauls with both trawls in Port Orchard (details to be published elsewhere). The effective area of the 6-foot IKMT is from Barse and Semon (1963). Speed was measured at the surface with a TSK flowmeter while hauls were at depth (see text).

less defined record), and the distribution of scattering with depth in the sampling track was graphically summarized for each cruise. Cruise summaries were further grouped into winter (November through April) and summer (May through October) patterns for each area.

Fishes were identified to species (Clemens and Wilby, 1961) and measured to the nearest millimeter. Euphausiids, mysids, amphipods, and pasiphaeid decapods were identified to species. Other decapods, larval fishes, pteropods, isopods, and miscellaneous forms completed the categories enumerated. Concentrations of fishes and macroplankton were determined for each haul from information on ship speed, haul duration, and trawl mouth or effective area (Table 1). Distributions of organisms by 5-m depth intervals were graphically summarized for each area, and the results were compared with the seasonal patterns in sonic scattering.

RESULTS

Seasonal characteristics in both sonic scattering and trawl catches were identified for both Port Orchard and Case Inlet. These characteristics were basically identifiable as typical of winter or of summer conditions in each area.

Port Orchard

Sonic Scattering

In Port Orchard, scattering during the day was irregular throughout the year. In the winter, aggregations of targets often appeared, but these aggregations usually occurred in shallow water outside the normal sampling track. Day samples took no fishes and essentially no plankton. At night, however, scattering was observed throughout the year and was characterized by distinct compact layers of individual targets in midwater during the winter (Figure 3), and in the summer by nebulous, often extensive scattering that was largely lacking in concentrations of individual targets (Figure 4).

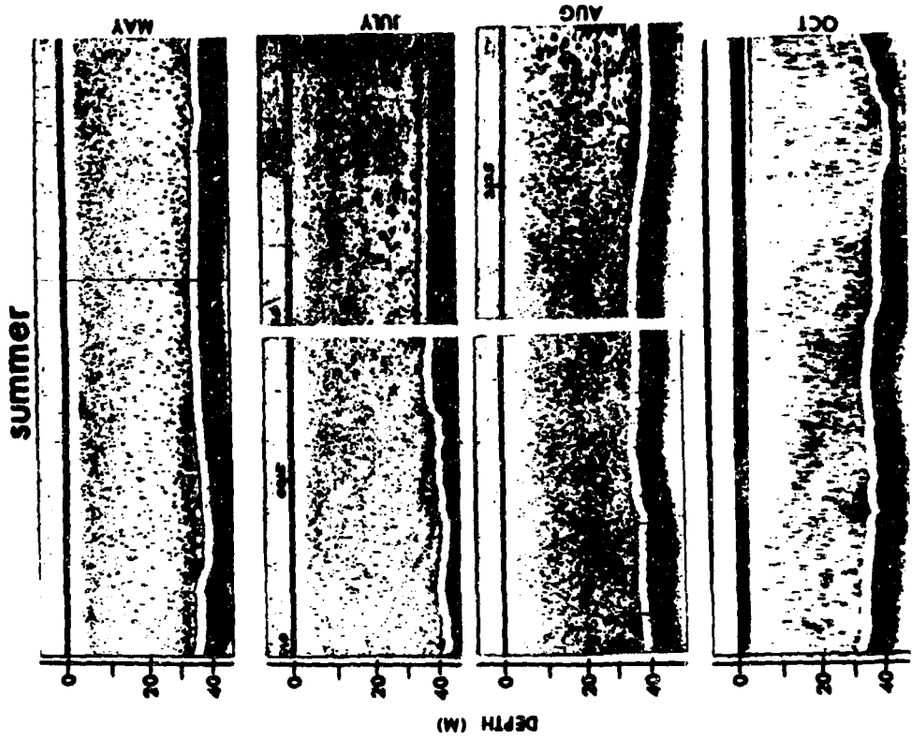

Figure 4. 38.2 kHz Simrad echosounder records of sonic scattering typical of the summer period (May - October) in Port Orchard Narrows. Vessel was drifting during recording of the right-hand July trace; speed 1-4 kt when other records were made. Pulse length 1 msec for May, July and August records; 3 msec for October trace.

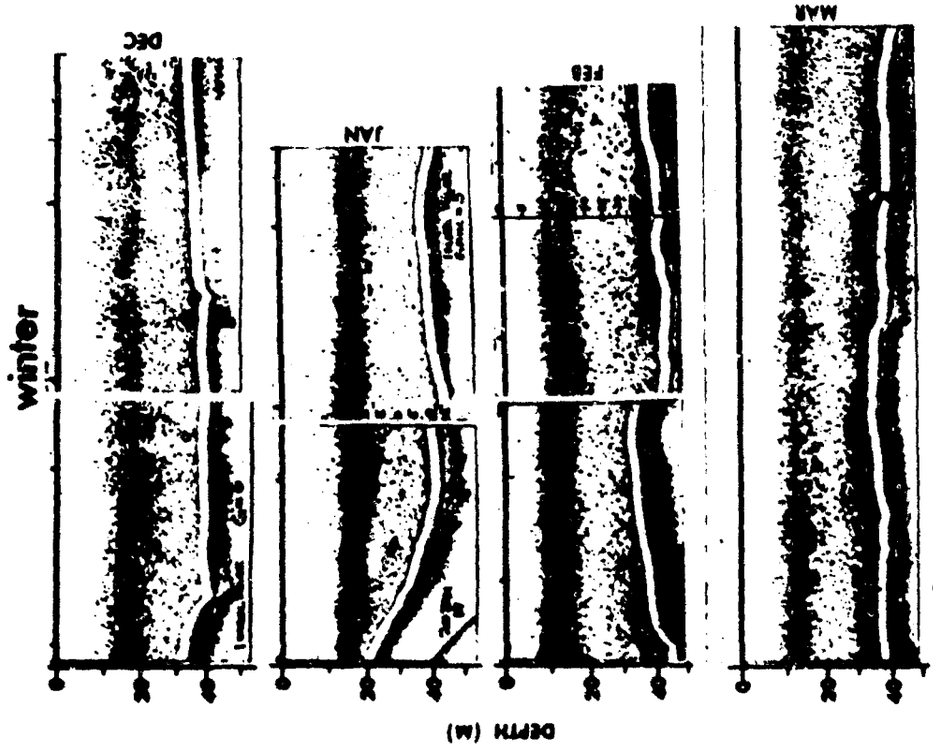

Figure 3. 38.2 kHz Simrad echosounder records of sonic scattering typical of the winter period (November - April) in Port Orchard Narrows. Vessel speed 1 - 4 kt. 1 msec pulse length.

Fishes, Winter

Trawl samples from Port Orchard also reflected seasonal differences. Eighteen species of fishes were taken in 12 nights of sampling in Port Orchard (Table 2); the northern midshipman *(Porichthys notatus)* and the bay goby *(Lepidogobius lepidus)* were taken on each cruise. In the winter, concentrations of fishes generally increased with depth, but the relationship of Pacific herring *(Clupea harengus pallasi)* and surf smelt *(Hypomesus pretiosus)* to the well-defined layers was marked (Figure 5). At middepths coincident with the layer, catches of herring and smelt ranged up to 2/1,000 m^3 for a single haul. Smelt were taken in greatest numbers in hauls

TABLE 2. Fishes Taken at Port Orchard Narrows and Case Inlet

Scientific Name	Common Name	Port Orchard			Case Inlet	
		Six	Ten	Ring	Six	Ten
Family Agonidae	Poachers					
Xeneretmus latifrons	Blacktip poacher	–	x	–	–	x
Family Batrachoididae	Toadfishes					
Porichthys notatus	Northern midshipman	x	x	x	x	x
Family Clupeidae	Herrings					
Clupea harengus pallasi	Pacific herring	–	x	–	x	x
Family Embiotocidae	Seaperches					
Cymatogaster aggregata	Shiner seaperch	x	x	–	x	–
Family Engraulidae	Anchovies					
Engraulis mordax	Northern anchovy	–	x	–	–	–
Family Gadidae	Codfishes and Hakes					
Gadus macrocephalus	Pacific cod	x	x	–	–	–
Merluccius productus	Pacific hake	x	–	–	–	x
Microgadus proximus	Pacific tomcod	x	–	–	x	x
Theragra chalcogrammus	Walleye pollack	–	x	–	x	x
Family Gobiidae	Gobies					
Lepidogobius lepidus	Bay goby	x	x	x	x	x
Family Osmeridae	Smelts					
Hypomesus pretiosus	Surf smelt	x	x	–	–	–
Family Pleuronectidae	Flounders					
Lepidopsetta bilineata	Rock sole	x	–	–	–	–
Parophrys vetulus	English sole	–	x	–	–	–
Platichthys stellatus	Starry flounder	x	x	–	–	x
Family Scorpaenidae	Rockfishes and scorpionfishes					
Sebastodes spp.		–	–	–	x	x
Family Squalidae	Dogfish sharks					
Squalus acanthias	Spiny dogfish	x	x	–	x	x
Family Stichaeidae	Pricklebacks					
Lumpenus sagitta	Pacific snakeblenny	–	x	–	–	–
Family Syngnathidae	Pipefishes and seahorses					
Syngnathus griseolineatus	Bay pipefish	–	–	x	x	–
Family Zoarcidae	Eelpouts					
Lycodopsis pacifica	Blackbelly eelpout	x	–	–	–	–

Note: All names according to recommendations of the American Fisheries Society, Committee on the Names of Fishes (1960). An x in a column following a common name indicates the area and trawl (6-foot IKMT, 10-foot IKMT or 1-m ring trawl) in which the particular species was taken.

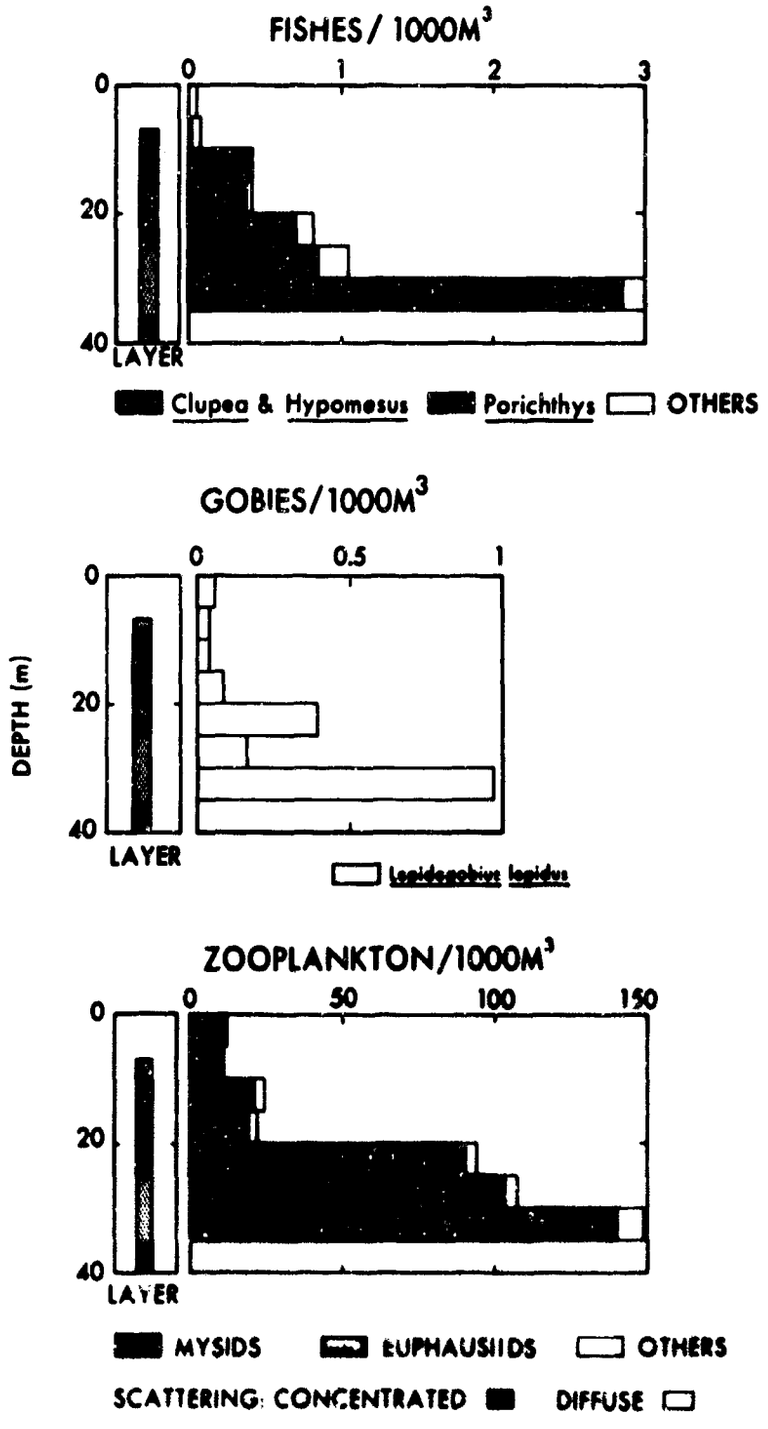

Figure 5. Nocturnal concentrations of organisms from all hauls made in Port Orchard Narrows during the period of winter scattering conditions (November - April). Concentrations determined from total catch and total volume of water filtered in each 5-m interval. Volumes based on ship speed and trawl mouth area for fishes (see text) or, for zooplankton, effective areas of the trawls (Table 1). The indicated scattering condition is a seasonal average made by 1-m increments from nightly summaries from cruises during the period (see text).

between 10 and 15 m, whereas herring concentrations were highest between 15 and 25 m. The midshipman was particularly abundant in hauls below the layers (Figure 6). Numbers exceeding 10/1,000 m^3 for single deep hauls were recorded on several occasions.

Concentrations of the bay goby were also found to increase with depth in the winter, with an intermediate maximum evident between 20 and 25 m (Figure 5). Though single haul concentrations as high as 12/1,000 m^3 were recorded, most winter hauls in Port Orchard took fewer than 1/1,000 m^3 at all depths. The *Lepidogobius* did not exceed 50 mm in length; the majority were between 35 and 45 mm long and thus were roughly equivalent to the wavelength of the pulses produced by the echo sounder.

Zooplankton, Winter

Low zooplankton concentrations were typical of winter samples from Port Orchard. Zooplankton concentrations generally increased with depth; mysids dominated the catch with euphausiids being of secondary importance (Figure 5). Single haul concentrations as high as 400 ind./1,000 m^3 were recorded in December, but average values were often about an order of magnitude below that maximum. The mysid *Neomysis kadiakensis* was the most abundant zooplankton species taken; it was taken on all cruises and was particularly common in winter hauls below 20 m. Hauls near the surface, above most of the scattering, regularly included the mysid *Acanthomysis macropsis* and the euphausiids *Euphausia pacifica* and *Thysanoessa raschii* during the winter sampling period.

Fishes, Summer

In the summer months, the distribution of organisms had changed along with the pattern of scattering. Although the concentration of fishes continued to exhibit a general increase with depth, the marked catches of *Clupea* and *Hypomesus* at middepth were absent. Instead, the northern midshipman dominated most catches and average concentrations of fishes were approximately twice winter values at comparable depths; the few *Clupea* taken were from hauls above 10 m (Figure 6). The summer distribution of the bay goby showed a marked maximum between 10 and 15 m (Figure 6). In that depth interval, concentrations as high as 17/1,000 m^3 were recorded for individual hauls in late summer; one haul in the interval, made in 20 m of water on the west side of the Narrows in July, indicated a *Lepidogobius* concentration of 16/1,000 m^3. The gobies taken in the summer months did not differ significantly in length from those taken in the winter samples.

Zooplankton, Summer

In the summer, average zooplankton concentrations exceeded winter values by more than an order of magnitude at all depths. Zooplankton samples were clearly dominated by the mysid *Neomysis kadiakensis* at all depths throughout the summer months (Figure 6). Zooplankton concentrations as high as 9,000 ind./1,000 m^3 were recorded for a single haul at middepth from midchannel; the single haul made on the west side of the Narrows in July took mysids in excess of 2,000/1,000 m^3 but few other crustaceans. Larval fishes, whose influence on sonic scattering has been noted in other shoal areas (Burd and Lee, 1951; Cushing, et al., 1952), were taken in increasing numbers in hauls from Port Orchard in July and August, though absolute numbers were considerably less than those recorded for *N. kadiakensis* in the same hauls. Tentaculate ctenophores were very abundant in May samples and made separation and identification of other zooplankton in the hauls nearly impossible. Hauls with the 6-foot IKMT in May averaged about 1 gal of ctenophores for each minute of hauling.

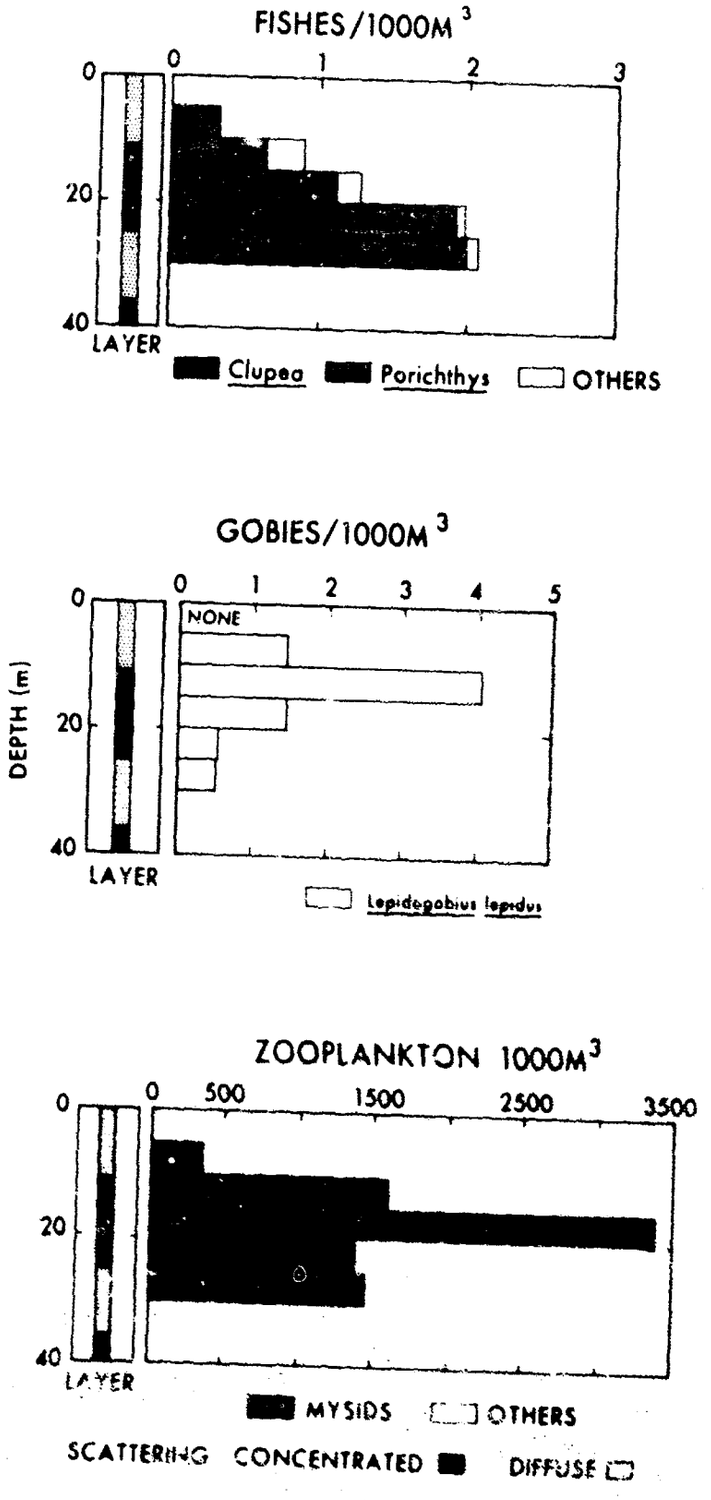

Figure 6. Nocturnal concentrations of organisms from all hauls made in Port Orchard Narrows during the period of summer scattering conditions (May - October). Volumes and scattering summaries determined as described for previous figure.

Case Inlet

Sonic Scattering

The sonic scattering observed in Case Inlet was of two general seasonal patterns. In late winter (January through April), well-defined layers of individual targets were common at mid-depths. Distinct diel differences in the depths of the layers were typical (Figure 7), though daytime scattering above 30 m was observed in April over a well-developed layer between 50 and 70 m. Scattering in the summer (May through September) was typically nebulous and diffuse; concentrated aggregations of individuals were rare (Figure 8). Diel differences in the depth of scattering were slight above 40 m, and near-surface scattering was sometimes heavier during the

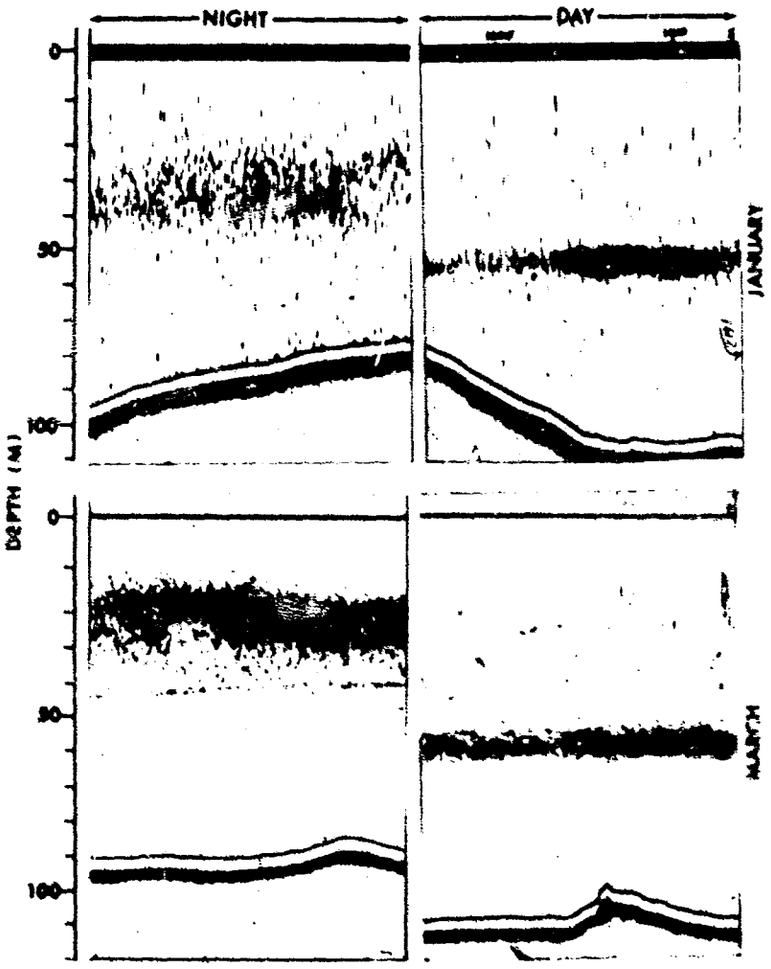

Figure 7. 38.2 kHz Simrad echosounder records of sonic scattering in the Case Inlet research area during the period of winter scattering conditions (January - April). Typical nocturnal traces on the left and day time traces on the right. Vessel speed 2 - 4 kt. A pulse length of 3 msec was used in January and of 1 msec in March. Faint line between 45 and 35 m in March night trace is an artifact on the recording paper. A pattern of interference from the fathometer on the bridge of the research vessel is evident in the traces, particularly the January day trace.

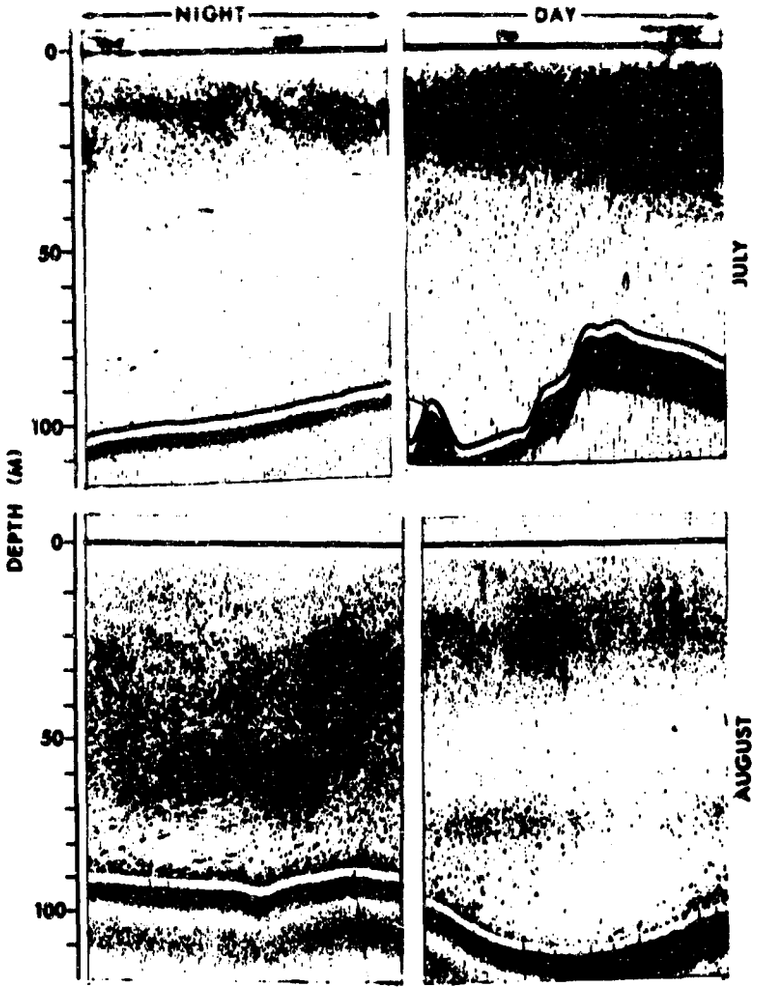

Figure 8. 38.2 kHz Simrad echosounder records of sonic scattering typical of the summer period (May - September) in the Case Inlet research area. Vessel speed 1 - 4 kt, 1 msec pulse length.

day than at night (Figure 8, July). In August and September, aggregations of individual targets appeared intermittently at depth during the day, suggesting the existence of layers, varying greatly in horizontal homogeneity, between 70 and 80 m (Figure 8, August).

Fishes, Winter

Diel and seasonal differences in the distribution and abundance of fishes and zooplankton with depth occurred in Case Inlet for each cruise. Twelve species of fishes were caught in Case Inlet (Table 2), though fewer than seven different species were caught on most cruises; the northern midshipman was caught on each cruise. Although the catch of fishes varied in number and composition from cruise to cruise, the average nocturnal concentrations of fishes were roughly comparable seasonally. In the winter, Pacific herring *(Clupea harengus pallasi)* and spiny dogfish (*Squalus acanthias*), a predator on *Clupea*, were taken both day and night in hauls generally coincident with well-developed scattering layers; the concentrations of *Porichthys*

typically increased with depth (Figure 9A). The category of "Others" in Figure 9A roughly reflects catches of dogfish above 50 m and catches of Pacific hake *(Merluccius productus)*, Pacific tomcod *(Microgadus proximus)*, and rockfishes *(Sebastodes* spp.*)* in deeper hauls during winter months. Single haul concentrations as high as 1/1,000 m^3 were recorded for *Porichthys* at night; maxima about 0.5/1,000 m^3 were calculated from single hauls for other species nocturnally and for winter concentrations of all fish species from hauls during the day.

Fishes, Summer

In the summer, nocturnal hauls in Case Inlet were marked by catches of *Porichthys* at most depths; no fishes were taken during the day (Figure 9B). A few herring were caught with the

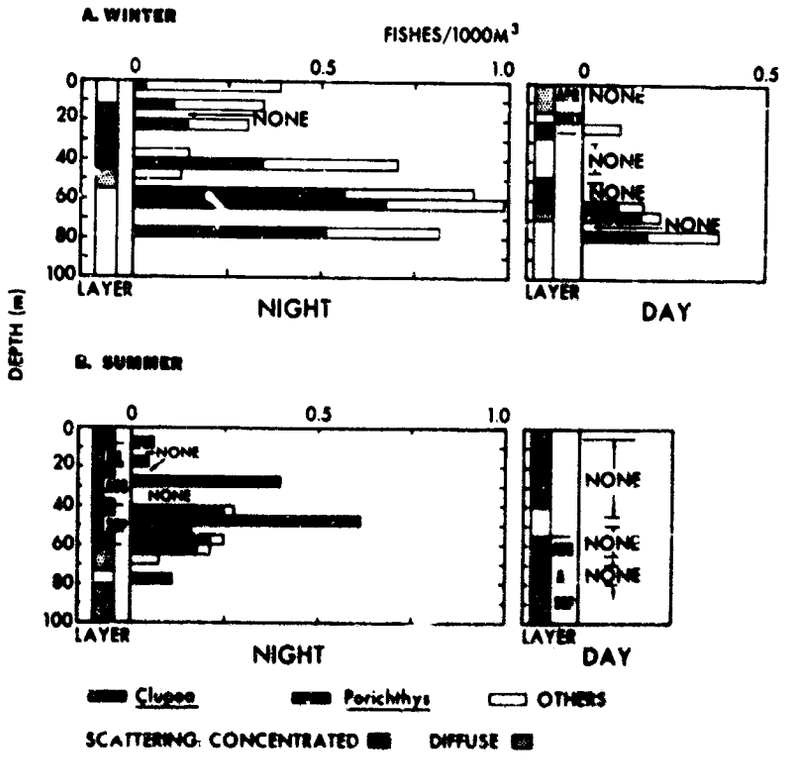

Figure 9. Concentrations of fishes from all hauls in Case Inlet. Nocturnal values on the left, day time values on the right. Concentrations determined from total catch and total volume of water filtered in each 5-m interval. A: Concentrations during period of winter scattering conditions (January - April). Indicated nocturnal scattering and day time scattering at depth are seasonal averages; near-surface day time scattering was recorded in April only (see text). B: Concentrations during period of summer scattering conditions (May - September). Nocturnal scattering was diffuse throughout most of the water-column. Depth intervals in which concentrated scattering was recorded in July, August or September are indicated. Day time scattering at depth occurred only in August and September. No fish were taken in day time hauls; intervals in which day time hauls were made are indicated.

6-foot IKMT at middepth in August, but maximum single-haul concentrations did not exceed 0.2/1,000 m^3; single-haul concentrations of *Porichthys* did not exceed 1/1,000 m^3. The midshipman exhibited a marked maximum concentration at middepths with seasonal average values just over 0.6/1,000 m^3 between 45 and 50 m (Figure 9B).

Zooplankton, Winter

Concentrations of zooplankton in Case Inlet were low in the winter and high in the summer. Diel differences in zooplankton distribution with depth occurred throughout the year. Mysids and euphausiids were the numerically dominant zooplankton in samples from Case Inlet; maximum euphausiid concentrations generally lay above peak mysid concentrations, particularly during the day. Maximum zooplankton concentrations in the winter did not exceed 200 ind./1,000 m^3 for a single haul. In winter collections at night, zooplankton concentrations generally decreased with increasing depth, particularly below 40 m. Hauls near the surface at night caught euphausiids, mainly *Euphausia pacifica* and *Thysanoessa spinifera*, and the mysid *Acanthomysis macropsis*. *Neomysis kadiakensis*, the most common zooplankton species taken at night, dominated hauls at and below middepth (Figure 10A). During the day, hauls above and at the depths of the well-developed scattering layers caught mainly euphausiids, principally *E. pacifica*, with *T. raschii* and *T. spinifera* of secondary importance; deeper hauls were marked by catches of *N. kadiakensis*, though *E. pacifica* remained relatively abundant (Figure 10A).

Zooplankton, Summer

In the summer months, zooplankton distribution had changed. Concentrations were highest at middepth at night and were over an order of magnitude greater than winter values at most depths; maximum concentrations, up to 7,700 ind./1,000 m^3, were found at middepth in August. Catches were dominated by the mysids *N. kadiakensis* and *A. macropsis* and were marked by the presence of larval fishes, particularly larval hake (Figure 10B). *A. macropsis* was relatively more abundant in shallower night hauls, whereas *N. kadiakensis* concentrations were highest in middepth and deeper samples (Figure 10B). Maximum zooplankton concentrations for daytime hauls in the summer (about 200 ind./1,000 m^3) occurred in the deeper samples in August and September. Extensive concentrations of ctenophores, at least equal in magnitude to those of Port Orchard, were encountered in Case Inlet in early summer. As a result, separation and enumeration of zooplankton from May samples was nearly impossible.

Biological Aspects Of Sonic Scattering Patterns

Coincident echo sounder observations and midwater trawl samples revealed generalized seasonal patterns in both Port Orchard Narrows and Case Inlet. In Figure 11, the sequential arrangement of typical monthly patterns of sonic scattering illustrates the seasonal and spatial variations observed during this study. Diel differences in the depth of scattering were often pronounced in Case Inlet. In Port Orchard, daytime scattering was irregularly distributed and often evident as aggregations in shallow water north of the sampling track. As a result, only nocturnal scattering conditions are presented for Port Orchard in the figure. Scattering varies month to month within seasons in each area. Seasonal transitions appear to be more rapid in Port Orchard than in Case Inlet. Observations from Port Orchard indicate less variation in scattering on successive months. Typical patterns for a given month are generally repeated annually. Well-defined compact layers of individual targets develop in the winter in each area. Associated with winter catches of Pacific herring at layer depths were surf smelt in Port Orchard and spiny dogfish in

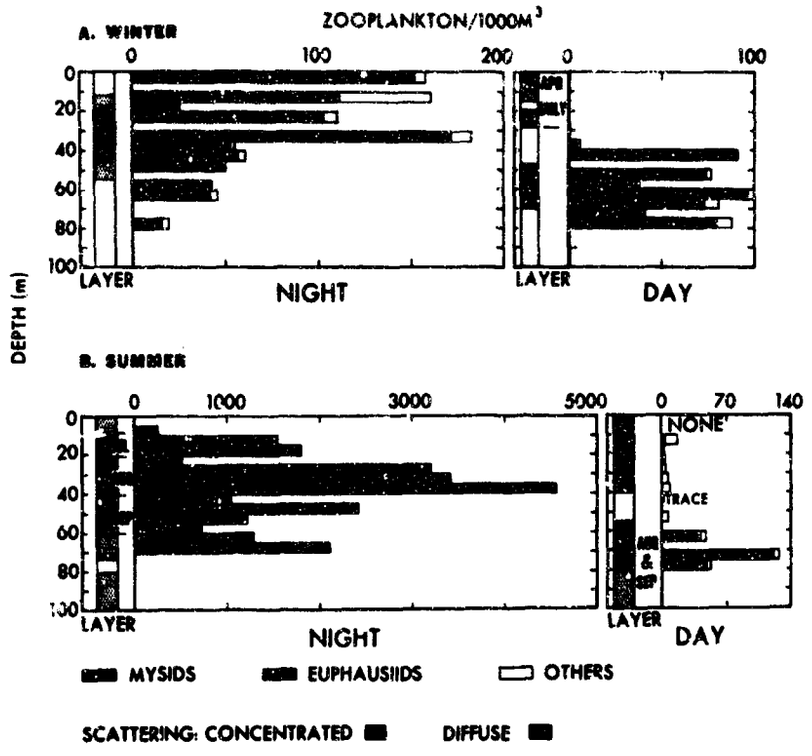

Figure 10. Concentrations of zooplankton from all hauls in Case Inlet. Nocturnal values on the left, day time values on the right. Concentrations determined from total catch and total volume of water filtered in each 5-m interval. Volume calculated is based on ship speed and effective areas of the trawls (Table 1). Scattering determined as described for previous figure. A: Concentrations during period of winter scattering conditions (January - April). B: Concentrations during period of summer scattering conditions (May - September). "Trace" concentration represents value too low to be accurately represented.

Case Inlet. Concentrations of the midshipman, *Porichthys*, increased with depth below the layers, as did concentrations of zooplankton and bay gobies in Port Orchard at night. In Case Inlet, however, zooplankton concentrations were generally highest at layer depths, both day and night.

In summer months, scattering was typically nebulous and generally more extensive, both horizontally and vertically, in both areas. Concentrations on individual targets were rare; heavy summer scattering, as indicated in Figure 11, lacked the characteristics of compact aggregations typical of the winter patterns. Catches of large numbers of tentaculate ctenophores were associated with the advent of typical summer scattering conditions in May in each area (Figure 11). Whereas heavy winter scattering was typically limited to middepth in the vicinity of the sampling tracks, summer scattering often was most concentrated shoreward of the tracks (Figure 11, Port Orchard, west side). *Porichthys* was taken at most depths in nocturnal summer hauls; concentrations increased with depth in Port Orchard but were maximum at middepths in Case Inlet. Zooplankton concentrations were high in summer months. Nocturnal middepth maxima of mysids and, in Port Orchard, gobies roughly corresponded to observed distributions

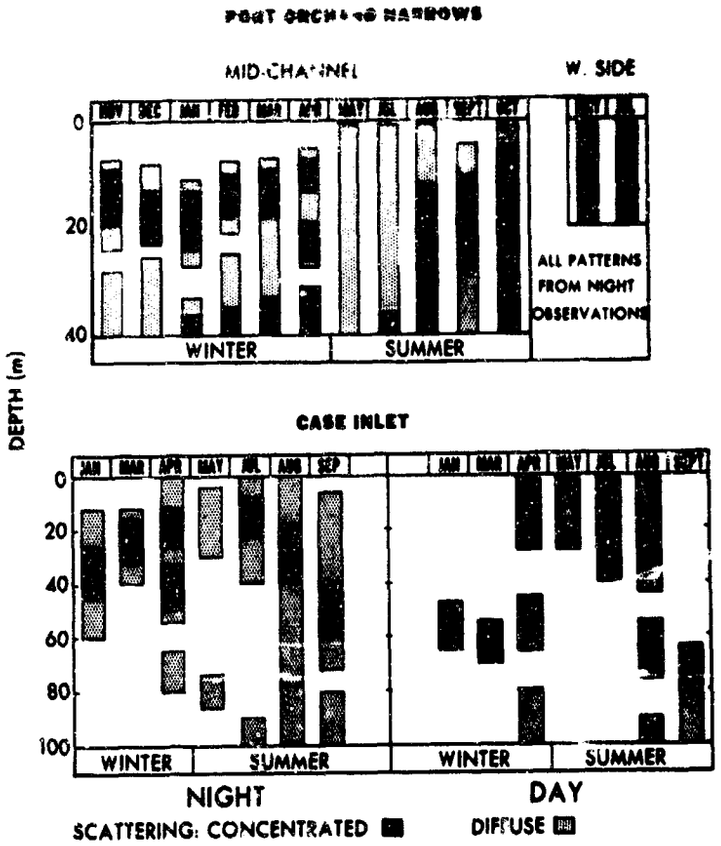

Figure 11. Patterns of sonic scattering typical of Port Orchard Narrows and Case Inlet arranged sequentially over an annual cycle. Patterns for months in which several nights of observations were available were made as generalizations of all traces for the month. Monthly patterns were generally repeated on successive years (see text).

of heavy, concentrated summer scattering in each area (Figure 11). Highest daytime zooplankton concentrations in Case Inlet were from hauls at depths of patchy, heavy scattering below 60 m in August and September (Figure 11). Larval fishes were taken in increasing numbers as summer progressed; no marked diel variations in numbers with depth were noted in Case Inlet. The larvae were essentially absent from hauls in the winter period.

DISCUSSION

Sonic scattering at 38.2 kHz is a regular feature of both Port Orchard Narrows and Case Inlet in Puget Sound. The distribution and abundance of certain fishes and zooplankton apparently influence the characteristics of the scattering; the characteristics change seasonally and the seasonal patterns are repeated annually. The basic conclusions of this study probably apply to many of the shallow, peripheral inlets of the Puget Sound system; though general conclusions for the system as a whole await more extensive investigations.

The relationship of certain fishes and zooplankton to sonic scattering in shallow water is a complex phenomenon; similar types of scattering may be caused by different types of organisms

(Taylor, MS, 1967; U.S. Department of the Interior, 1967a, b; 1968a, b) or by abiotic artifacts of the physical characteristics of the water column beneath the echo sounder (Lenz, 1965; Olsen, 1960; Tveite, 1969; Weston, 1958). In both the North Sea and Saanich Inlet, extensive investigations have related sonic scattering to aggregations of organisms. In the North Sea, studies in the 1950's indicated aggregations of small fishes (such as young pilchard, gobies, or small herring), zooplankton (especially euphausiids), or a combination of these types were generally associated with returns on echo sounders operating at frequencies between 10 and 30 kHz (Burd and Lee, 1951; Cushing, et al., 1952; Parrish and Craig, 1951, Weston, 1958). The nature and occurrence of the scattering usually changed over periods of weeks.

In Saanich Inlet (Vancouver Island, Canada), diffuse scattering above the sill depth (75 m) is generally associated with zooplankton, though some fishes may aggregate in the diffuse layers seasonally (Bary, Barraclough, and Herlinveaux, 1962; Barraclough and Herlinveaux, MS, 1965; Bary and Pieper, *in this symposium*). Group scattering at various depths and scattering detected at 12 kHz reflect aggregations of larger fishes, such as herring, dogfish, and hake (Bary, 1963, 1966a; Barraclough and Herlinveaux, MS, 1965; Herlinveaux, 1962). Although long-term continuity in the nature and structure of such scattering exists, detailed changes in the composition and depth of the layers can occur over periods of weeks, possibly reflecting changing ecological or oceanographic conditions within the environment (Bary, 1966b).

As in both the North Sea and Saanich Inlet systems, the characteristics and causes of sonic scattering in Puget Sound are related to seasonally changing distributions and abundances of fishes and zooplankton. In Puget Sound, Pacific herring begin to aggregate in shallow areas near spawning grounds during the month of November; most fish spawn between January and April (Chapman, Katz, and Erickson, 1941). The period during which aggregations of herring are likely to be found in shallow areas of the sound generally coincides with the season when typical winter patterns of scattering are encountered. Moreover, the diel distributions of Pacific herring observed by Tester (1943) near Saanich Inlet closely resemble those patterns typical of Case Inlet in winter months. The nocturnal pattern for Port Orchard in the winter does not differ greatly from the corresponding pattern described by Tester, but Port Orchard is apparently too shallow for normal development of daytime layers. Similar modification of herring behavior in shallow water was discussed by Balls (1951). It is likely that herring and, in Port Orchard, smelt that aggregate in shallow areas of Puget Sound during spawning periods are responsible for the scattering patterns typical of the winter in both Port Orchard Narrows and Case Inlet. Predators upon herring, such as dogfish and hake, may also be important to winter scattering, especially in Case Inlet; but, overall, the winter scattering pattern most accurately reflects changes in behavior and abundance of the herring.

Summer scattering patterns develop in May; their advent is accompanied by high numbers of ctenophores in the water column in both Port Orchard and Case Inlet. Typical summer patterns often resemble the "noisey" trace described by Cushing and Richardson (1956) and associated by them with fish larvae and euphausiids. Mysid populations increase during the period when summer scattering conditions prevail, and maximum numbers are attained in August. By the end of October, when summer conditions begin to change to winter scattering conditions, populations of mysids in both Port Orchard and Case Inlet have decreased sharply (Thorne, 1968). Small and larval fishes, often mentioned as potential causes of sound scattering in shallow areas (Barber and Haedrich, 1969; Burd and Lee, 1951; Cushing, et al., 1952; Cushing and Richardson, 1956; McCartney, Stubbs, and Tucker, 1965; Parrish and Craig, 1951; Trout, Lee, Richardson, and Harden Jones, 1952), are also abundant during the summer months in Port Orchard and Case Inlet. The absence of significant vertical migrations by fish larvae in Case Inlet may relate

to the persistence of scattering above 40 m in that area throughout the summer. Because the bay gobies, *Lepidogobius lepidus*, taken in Port Orchard Narrows are roughly as long as sound waves produced at 38.2 kHz, they might be particularly strong scattering agents (Hersey and Backus, 1962). Their relationship to the sonic scattering in Port Orchard, particularly in summer when their numbers are large, warrants further study.

Fishes in general were more dispersed throughout the water columns in both Port Orchard and Case Inlet during summer months; individual targets, not aggregations, were typical of summer traces (Figure 4, July). Though a few herring were taken in summer in each area, high numbers, characteristic of winter hauls, were absent. *Porichthys*, commonly taken in nocturnal summer samples, spawns in shallow water during the summer (Arora, 1948) and executes its greatest vertical migrations into midwater in Port Orchard during summer and early fall nights (Cooney, 1967). The diel vertical migration of *Porichthys* from the bottom during the day into midwater at night is more general and extensive in Port Orchard in summer months (Cooney, 1967). In Case Inlet, it is possible that *Porichthys* is associated with the bottom, shoreward of the sampling track, during the day and migrates horizontally from the bottom into the area from which samples were taken at night (R.T. Cooney, *personal communication*). Such horizontal migrations, if they occur, would largely explain the diel disparity of fishes in summer hauls in Case Inlet.

Summer midwater-trawl samples consisted of a greater variety and higher concentrations of organisms than did comparable winter hauls. The patterns of sonic scattering at 38.2 kHz during summer months appears to be indicative of the biological conditions of the period. The relationship of zooplankton to scattering at lower frequencies, 12 kHz for example, is often tenuous at best (Bary, 1966a). On echo sounders operating at intermediate frequencies, such as the Simrad used in this study, aggregations of zooplankton as well as those of small and larval fishes can be important sound scatterers (Cushing and Richardson, 1956). In winter months, when zooplankton concentrations are low, typical scattering patterns largely reflect the aggregations of fishes present in both Port Orchard and Case Inlet. In summer months, however, many more potential targets are present in each area. Some of the scattering doubtless results from targets such as *Porichthys*, larval fishes, and gobies; but the concentration and distribution of these forms do not fully explain scattering conditions. Zooplankton thus must also be considered. Physical conditions known for the research areas as well as the nature of the scattering observed in summer months tends to discount the importance of physical discontinuities as important causative agents of the observed summer scattering patterns. The larger zooplankton, such as the mysids and euphausiids common in the summer samples of this study, probably contribute significantly to the general summer patterns of scattering observed in Port Orchard and Case Inlet. The nebulous nature of sonic scattering in the summer period when zooplankton concentrations are high further suggests such a contribution. Studies such as those of Barv and Pieper (*this symposium*) and Cooney (*personal communication*) wherein intermediate and higher frequencies are employed simultaneously will further elucidate the exact nature of the relationships of large zooplankton to sonic scattering in inshore waters.

Gear-dependent factors influence the results and therefore the interpretations and conclusions of studies based on trawl samples. Selectivity of trawls and avoidance by organisms doubtless influenced the concentrations and distributions of organisms obtained in this study. Zooplankton, particularly larger forms such as mysids and euphausiids, may be quite adept at avoiding some sampling devices (see discussion in Clutter and Anraku, 1968). Despite the use of graded mesh nets on the 10-foot and 6-foot IKMT and the consequent dependence on estimates of effective areas for computing zooplankton concentrations (Table 1), concentrations of this study are comparable to those obtained by Thorne (1968) with plankton nets in the same areas.

The basic seasonal changes in zooplankton abundance are probably accurately represented by the trawls used in this study, and detailed determinations of precise values were beyond the scope of the work.

Though many aspects of gear dependency will be presented in another paper, some comments concerning the distribution and abundance of fishes indicated in this study are pertinent. Harrisson (1967) presents data indicating larger nets catch larger or more active species of mesopelagic fishes. In this study, more fish, larger fish, and generally more active fish were taken by the 10-foot IKMT, despite its generally slower fishing speeds (Table 1). Though total species taken by the 6-foot and 10-foot IKMT are comparable (Table 2), nearly all the herring and smelt and many of the gadids were taken by the larger trawl. The differential was larger than would be expected from considerations of trawl sizes alone. The larger trawl, which generally fished more slowly, may have produced fewer mechanical stimuli to warn active fishes of its approach (Chapman, 1964), or it may have herded herring in the vicinity of the trawl mouth (Blaxter, Parrish, and Dickson, 1964) better than the smaller trawl. Less active forms, such as *Porichthys* and *Squalus*, were taken roughly in proportion to the size of the nets and their speed of towing. The presence and distribution of fishes important to sonic scattering in the research areas would essentially have been missed if the 6-foot IKMT and the 1-m ring trawl had been used exclusively in this study. At best, however, even the information from the 10-foot IKMT only indicates the presence of fishes important as winter sonic scatterers in Case Inlet and Port Orchard. Recent work in Puget Sound with large trawls indicates that the concentrations of herring and smelt calculated in this study at depths of winter scattering layers are at least two orders of magnitude low (T. Saunders English, *unpublished data*).

Although trawls such as the 6-foot IKMT may adequately sample DSL organisms in the open sea, their ability to accurately sample and describe inshore scattering populations of active fishes appears limited. Distributional aspects of inshore fish populations may be reflected in IKMT samples. Inshore areas such as Puget Sounds however, possess well-developed sonic-scattering layers composed of fishes whose strength and cunning put them on, if not beyond, the very edge of the Isaacs-Kidd midwater trawl universe spoken of by others at this symposium. To use such trawls in these inshore areas and to expect the samples to reflect meaningful concentrations of important organisms is somewhat akin to trying to guess the number of beans in a jar one cannot see. Further studies of sonic scattering in the Puget Sound system clearly must include work with large trawls to further describe the distribution and abundance of the fishes related to the phenomenon.

SUMMARY

Cruises to investigate sonic scattering in the Port Orchard Narrows and Case Inlet areas of Puget Sound were conducted at irregular intervals over a 2 1/2-year period. Scattering observations were made with a 38.2-kHz Simrad echo sounder, and samples were taken with three sizes of midwater trawls. The following points generally summarize the work.

Sonic scattering at 38.2 kHz is a regular feature of both Port Orchard Narrows and Case Inlet, though a true diel pattern in the distribution of scattering was evident only in the scattering of the latter, deeper area.

The scattering has two main seasonal aspects. The pattern of winter seems to be associated with prespawning aggregations of herring in both areas and, in Port Orchard, with similarly inclined smelt. The summer pattern of scattering is more nebulous than that of the winter. It is associated with large numbers of zooplankton in the net hauls and with the generally dispersed character of the distribution of *Porichthys* throughout the water column. The mysid *Neomysis*

kodiakensis is particularly abundant in plankton samples. Ctenophores are abundant in the early summer and high numbers of gobies and larval fishes are typical in the latter part of the season.

The nets used in this work were adequate for survey purposes, indicating what was present in the two areas, and for capture of less active fishes, such as *Porichthys* or *Squalus*, in representative numbers. Concentrations of active fishes such as herring and smelt, however, are probably several orders of magnitude too low.

Puget Sound seems to resemble other inshore areas, such as the North Sea and the Strait of Georgia – Saanich Inlet system, in which the seasonal aspects of sonic scattering have been studied. It appears as if seasonal behavioral patterns of the various fishes in the system greatly influence the scattering conditions observed. During some seasons, high concentrations of zooplankton and small fishes also may influence scattering conditions.

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DISCUSSION

Aron: The College of Fisheries has done a lot of work in Port Orchard. Have you tried to compare your catches in the scattering layers to the trawl catches, knowing that a lot of the animals which they catch on the bottom during the day move up at night?

Friedl: Yes, my study actually was somewhat of a continuation of work done on the demersal fish population of Port Orchard by R.T. Cooney. He found some species demonstrated high day-night variability in beam trawl catches, and we suspected some of the fishes which lived on or near the bottom during the day might be joining the midwater community at night. The first midwater trawl samples taken to investigate this further in the Narrows were taken in association with Cooney's work. Forms such as *Gadis* and some flatfish seem to execute such migrations in Port Orchard; they are included in my category "Others" in the illustrations. In Case Inlet we often caught flatfish near the surface at night, a phenomenon others have reported, as you well know. I believe there is a portion of the population in these shallow areas that resides on the bottom during the day, as demersal fishes or epibenthic organisms, and comes into midwater at night. One would expect the numbers of such fishes to increase in deeper hauls. We generally tended to avoid taking hauls near the bottom with the Isaacs-Kidd trawls, although the ring net encountered the bottom a few times.

COMPARISON OF DIFFERENT INVESTIGATIVE TECHNIQUES FOR STUDYING THE DEEP SCATTERING LAYERS

William D. Clarke
Westinghouse Ocean Research Laboratory
San Diego, California

ABSTRACT

The use over the past five years of different investigative techniques to study the composition and vertical distribution of the deep scattering layers has allowed for new interpretations of the structure and behavior of this migrating community. The different approaches to be compared are (1) investigations with an instrumented midwater trawl, (2) acoustic investigations with a high-frequency focused side-looking sonar, and (3) observations from submersibles. Each of these techniques has permitted the gathering of different but complementary types of information on the organisms occurring in that migrating midwater community.

An instrumented midwater trawl (Figure 1) was used during a study of the light regime of organisms associated with sonic scattering layers in the Santa Barbara Basin off southern California (Clarke, 1966). The trawl was equipped with sensors to measure depth, ambient light (irradiance), temperature and the velocity of the trawl through the water. During operation of the trawl the signals from the sensors were FM-multiplexed to shipboard readout equipment (strip chart recorders and frequency counters) via a single-conductor towing cable. Thus the depth at which the trawl fished, the light level and temperature at that depth, as well as the speed of the trawl through the water could be monitored in real time during trawling operations.

The cod end of the midwater trawl was equipped with a multichambered sampling device, the chambers of which were arranged linearly. Each chamber could be closed on command from the ship while trawling at depth, thus permitting the taking of discrete samples of organisms at will from any portion of the water column. At the start of trawling operations, the doors of all of the chambers in the cod end sampler were in the open position, allowing organisms that entered the trawl to pass through. When the selected sampling depth was reached, the rearmost set of doors was closed and collection of the first sample began. After a predetermined length of time (usually 10 to 15 min), the second set of doors, just ahead of the rear set, was closed forming a chamber containing the first collection of organisms and at the same time starting the collection of the second sample in front of the newly closed doors. Again, after a predetermined length of time the third set of doors was closed. This process was repeated until all of the doors were closed yielding three discrete samples and one oblique sample (from last sampling depth to surface). A more complete description of the instrumented trawl and its operation is given by Bourbeau, Clarke and Aron (1966).

The trawling investigations of sonic scattering layers were conducted primarily in the Santa Barbara Basin (Figure 2), which is the northernmost of the submarine basins occurring on the

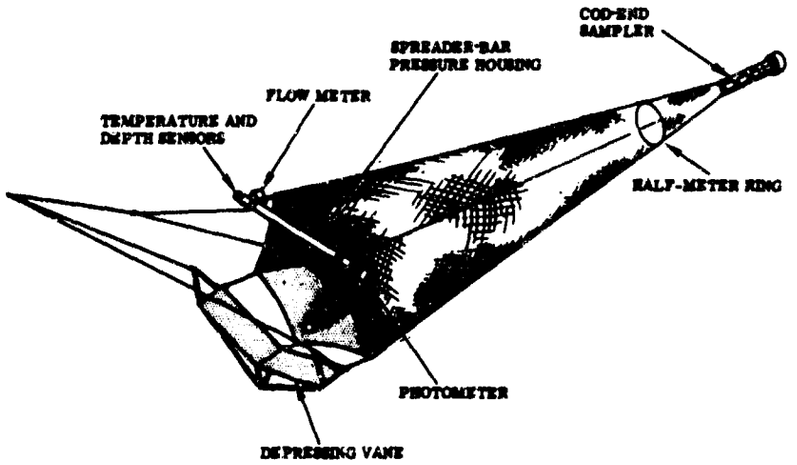

Figure 1. Instrumented midwater trawl

continental border and off southern California. The deepest part of this basin is 615 m. It communicates to the west with the open ocean over a still 475 m deep, thus there is a pool of bottom water 140 m deep that has restricted circulation. The characteristics of this bottom water are sufficiently different from the waters overlying them that they affect the distributions of some of the migrating organisms associated with the sonic scattering layers. The deeper hydrography and geology of the basin have been described by Emery (1954), and Ritterberg, Emery and Orr (1955). The physical oceanography of the region is dealt with by Reid (1965).

The instrumented trawl investigations were undertaken to learn more about the vertical distributions of organisms that might make up the sonic scattering layers, and the possible correlation of those organisms and the scattering layers with the distribution of submarine light. The diurnally migrating community in the Santa Barbara Basin contains a small number of species compared to the migrating communities of neighboring Santa Cruz Basin or of the open ocean. These few species are very abundant though (see Ebeling's contribution). A dimunition in the numbers of midwater organisms and in the intenaity of the sonic scattering layers occurs in the shoaler portions of the basin, particularly toward the eastern end. For that reason, the trawling studies were limited to the deepest part of the basin where the sonic scattering layers were strongest and the midwater organisms most prevalent.

The study extended over a year's period, and was supported by the Division of Biology and Medicine of the U.S. Atomic Energy Commission under contract AT(04-3)-584. Beginning in January 1965, and as nearly as possible thereafter on a monthly basis, cruises were scheduled to include the evening rise and morning descent of the sonic scattering layers during a continuous 24-hour period. Several sampling procedures were experimented with during the cruises to accomplish the following objectives: (1) to establish whether the same organisms were associated with the sonic scattering layers as the layers moved to and from the surface during the diurnal cycle, and (2) to learn more about the behavior of the migrating organisms relative to light level. Initially, sampling was conducted following a constant light level, or isolume (Figure 3), in, above, or below the 12-kHz sonic scattering layers. During periods of rapid change in the depth of penetration of solar light, trawling depth was changed so as to remain with the same light regime. This was done by using the photometer mounted on the trawl to monitor the light level and by adjusting the trawl depth to stay at the same light level. Isolume sampling with the trawl resulted in three discrete samples from the light level being followed and a fourth integrated collection from the isolume depth to the surface. This sort of sampling was conducted during migratory and nonmigratory periods of the sonic scattering layers.

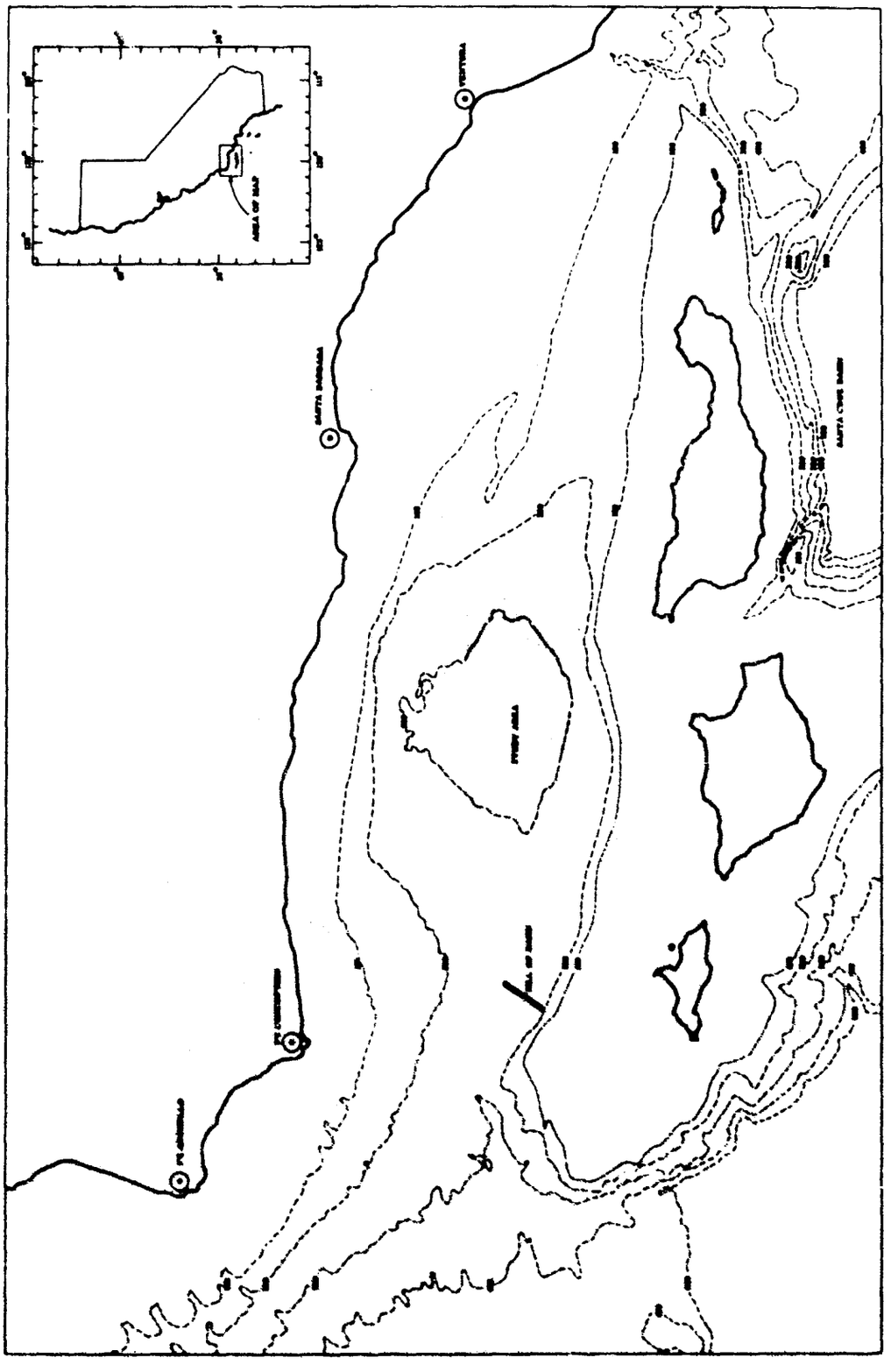

Figure 2. Chart of Santa Barbara Basin area (depths indicated in fathoms)

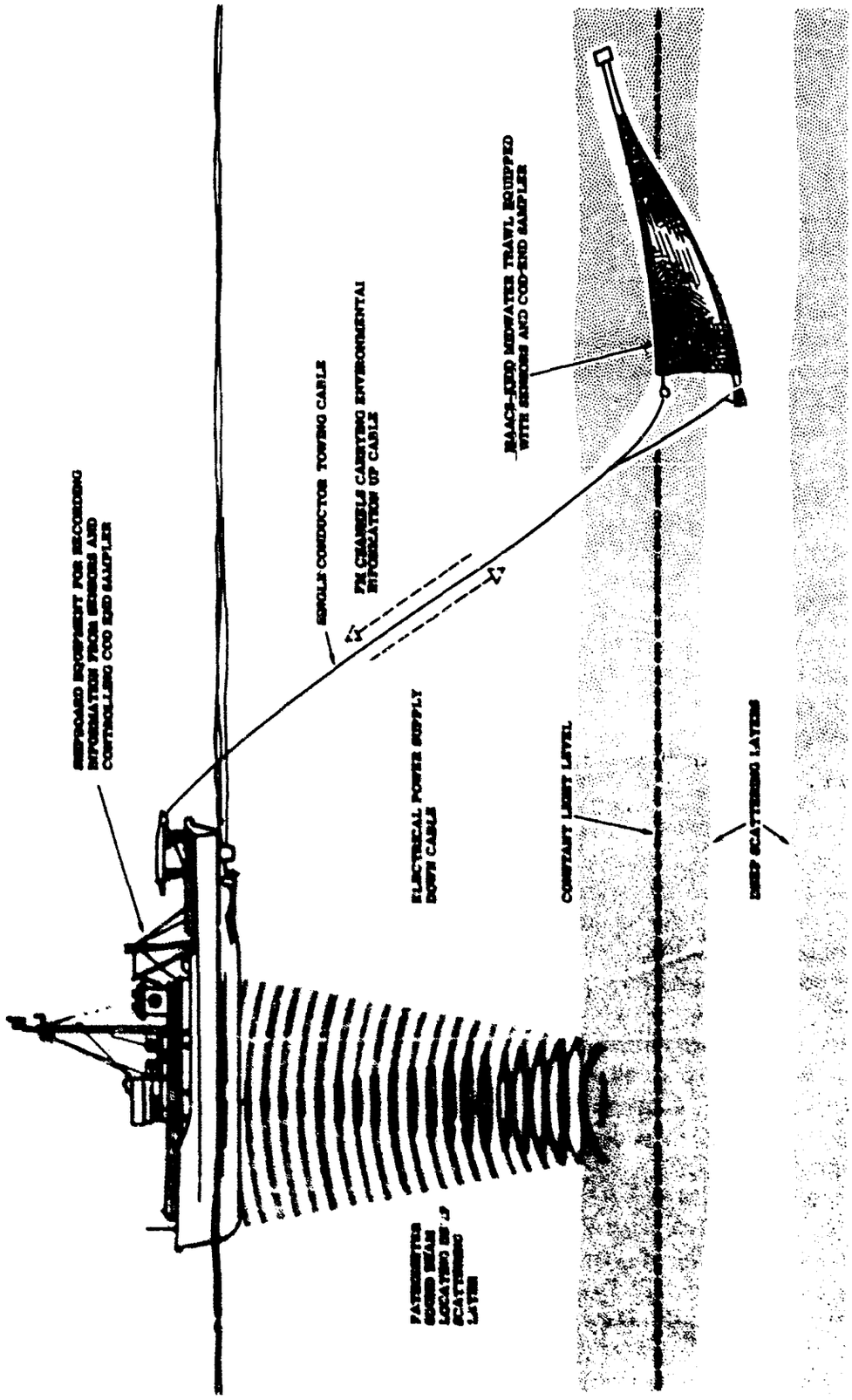

Figure 3. Method of isobuns trawling at sonic scattering depths

On later cruises, in addition to the isolume-following tows, oblique tows were made to obtain discrete samples of organisms from different strata of water between the maximum sampling depths selected for oblique tows and the surface. These types of tows were made initially when light conditions and the sonic scattering layers were fairly stable (i.e. at midday or midnight), so that the relative positions and vertical distributions of the migratory midwater organisms could be determined.

To make an oblique tow, the trawl was lowered to the maximum depth to be sampled; then the rear doors of the cod end sampler were closed and retrieval of the trawl was started immediately. Each of the three remaining doors in the cod end sampler was closed at a predetermined depth as the trawl was brought obliquely to the surface. Thus, discrete samples of organisms were obtained from four different strata of water. In most instances, each stratum of water was 70 to 80 m thick.

On several cruises, oblique tows were repeated one after the other as the light regime changed. This was done to look at changes in the distributions of migrating organisms relative to light conditions. Trawling was started before the migrations had begun, and the same strata of water were sampled repeatedly on successive oblique tows with the trawl throughout the migrational period. In this way, it was possible to observe changes in the composition of the organisms at given depths and to follow the main concentrations of specific organisms either upward or downward, depending on the part of the diurnal cycle being investigated.

Trawls were also made at the depths of the sonic scattering layers appearing on a 12-kHz echo-sounder record to determine the types of organism occurring in those layers and the intensity of the light associated with the layers. After the depth of the sound-scattering layer had been reached with the trawl, the light intensity was noted and the trawl was fished horizontally in the layer, taking three discrete samples of organisms at that depth and an oblique collection to the surface. These tows established what isolumes the scattering layers were following and what organisms were associated with those layers.

Tows following more than one isolume were made during the last cruises. The trawl was fished at the first selected isolume, taking a discrete sample of organisms at that light level. At the completion of that collection an oblique sample was taken from the depth of the first isolume to the depth of the second selected isolume. Once the depth of the second isolume was reached a discrete sample of organisms was taken at that light level and to complete the trawling operations an oblique collection was made from that depth to the surface. Thus a discrete sample was obtained from each of the two isolume levels and two oblique samples.

The most fruitful sampling program appeared to be a combination of oblique tows followed by isolume-following tows. The oblique tows established the depths of the different migrating organisms relative to the vertical distribution of light, and that information could be used for selecting a light level associated with a given organism to be sampled during migrational periods. The isolume sampling, in turn, gave a check on whether migrating organisms remained with the same light regime as has been demonstrated for sonic scattering layers (see Kampa's contribution).

The analysis of the biological collections was carried out primarily with the aim of establishing (1) the relationship of migrating organisms to changing submarine light distribution during the diurnal cycle and (2) the vertical depth ranges of the principal organisms making up the migrating community. Three organisms, as sampled by the 6-ft Isaacs-Kidd Midwater Trawl, emerged as the major constituents of the migrating community in the Santa Barbara Basin associated with the sonic scattering layers observed at 12 kHz. The euphausiid shrimp, the sergestid shrimp and the lanternfish dominated the trawl collections. The former two occurred in greatest abundance at the same depths that the 12-kHz sonic scattering layers were observed, while the lanternfish occurred in greatest abundance primarily below the scattering layers.

The three dominant migrating organisms, euphausiid shrimp, sergestid shrimp, and lanternfish, are distributed vertically, for the most part, the euphausiid shrimp forming the uppermost element. This layered structure was maintained throughout the migrational periods and during the midday period of quiescence when the sonic scattering layers and migratory organisms are at depth. Only at night, when the scattering layers reached the surface was there any significant breakdown of this structure. In a sense, the migrating community forms a layer cake, each layer consisting primarily of one particular organism. In the Santa Barbara Basin, the uppermost layer is dominated by euphausiid shrimp, the middle layer by sergestid shrimp and the lowermost layer by lanternfish. These three migrating organisms occurred in greatest numbers throughout the night and day in a constant low-level light regime which they followed as the depth of solar light penetration changed. The light levels these migratory organisms sought were determined from the irradiance measurements made by the photometer on the trawl during collection of the organisms. As would be expected from the layered structure, the light preferences are not the same for each species of organism. Thus the vertical stratification within the midwater migrating community results from the different light preferences of the organisms occurring in it. The euphausiid shrimp were present in greatest numbers at light levels lying between 1×10^{-3} to 1×10^{-4} $\mu W/cm^2$, whereas sergestid shrimp were most abundant at light levels between 1×10^{-5} to 1×10^{-6} $\mu W/cm^2$. The lanternfish were distributed at depths where light levels were for the most part below the sensitivity of the photometer on the trawl. Their preferred light levels would appear to be less than 1×10^{-6} $\mu W/cm^2$ (Clarke, 1966).

The three major organisms making up the midwater migrating community in the Santa Barbara Basin are luminescent forms. They have complex photophores which are primarily ventrally located and emit light downwards, fitting the requirements for the countershading hypotheses of silhouette elimination (Clarke, 1963). The following of a constant light level, as euphausiids, sergestids, and lanternfish do, would be expected if they are using luminescence to mask their ventral silhouette from predators in the downwelling light field. By way of contrast, three other major organisms found in the midwater trawl collections, two species of pasiphaeid shrimp and a deepwater smelt, *Bathylagus stilbius*, did not possess photophores, were not associated with a constant light level, and did not migrate diurnally as a layer.

Thus, findings of the instrumented trawl study demonstrated that three abundant organisms formed a multilayered migrating community in the Santa Barbara Basin at depths corresponding to the sonic scattering layers. The vertical depth distributions and thickness of the euphausiid and sergestid shrimp layers of this migrating community corresponded most closely with the depths and thickness of the sonic scattering layers observed at 12 kHz. The third element of the community, the lanternfish, occurred, for the most part, below the 12-kHz scattering layers. Significantly, the most prevalent species of lanternfish, *Stenobrachius leucopsarus*, has a fat-filled swimbladder which would make it a poor sound scatterer.

A word of caution as to interpretation; the euphausiid and sergestid shrimp caught so abundantly by the 6-ft Isaacs-Kidd Midwater Trawl may not be the sonic scatterers responsible for the layers on the 12-kHz echo-sounder. Barham (1963) has mustered convincing evidence that physonect siphonophores associated with the same migrating community may be the more important sonic scatterers. I believe, though, that the midwater crustaceans can also make significant contributions to sound scattering based on two lines of evidence: (1) the work of Smith (1954) demonstrating that shrimp are capable of scattering sound under experimental conditions and (2) the work of Enright (1963) which demonstrated on theoretical grounds that euphausiid shrimp should be capable of scattering sound since they are less compressible than sea water and have a density differing from sea water. Another objection that acousticians have raised in the past was that the populations of these crustaceans were not dense enough to scatter sound. The limited observations that I have made from submersibles both in the Atlantic

and Pacific convinces me that there are adequate numbers of euphausiid and sergestid shrimp at scattering layer depths to account for substantial amounts of sonic scattering, but these observations will be discussed later.

A peculiar aspect of the migrating midwater community in the Santa Barbara Basin is that its deepest elements, the sergestid shrimp and lanternfish, are limited in their downward migration by the pool of bottom water that lies below sill depth. This water contains little dissolved oxygen and appears to be unfavorable both to the sergestid shrimp and the lanternfish. Collections of organisms made below sill depth did not contain these two elements, and the photometer on the trawl did not register the characteristic luminescent flashes typical of the overlying water. By comparison, these same organisms migrated deeper in the neighboring Santa Cruz Basin where the dissolved oxygen content remains higher at greater depths than in the Santa Barbara Basin.

Finally, it is comforting to note that Dr. Ebeling (see Ebeling's contribution) and I arrived at essentially the same community structure for the Santa Barbara Basin, particularly in respect to the migrating midwater community. Our respective programs were independent of one another and we used different sampling regimes to make our biological collections, although we did use the same trawling gear. The important fact to emerge from both studies was that the migrating community in that area was dominated by euphausiid shrimp, sergestid shrimp, and lanternfish which were layered vertically from top to bottom in that order.

The second study to be discussed here was the assessment of a high-frequency side-looking sonar for use in the study of midwater organisms and in particular the sonic scattering layers. The particular unit used was an early model Westinghouse L-15 side-looking sonar which operated at frequencies of 150 and 160 kHz (Laing and Nelkin 1966). The investigations were conducted in the San Diego Trough off southern California in December 1966. The sonic scattering layer study using the side-looking sonar was conducted in conjunction with investigations of the scattering layers by personnel of the Naval Electronics Laboratory (NEL) using the submersible DEEPSTAR 4000.

The side-looking sonar was designed to operate in two different modes, a long-range unfocused mode and a short-range focused mode. The short-range focused mode was used for the midwater investigations of the sonic scattering layers. In this mode the two narrow-beam transducers of the side-looking sonar insonify a fan-shaped sector at right angles to the path of the towed body on which the transducers are mounted. Sound scattering is measured from 6 m out to 61 m to each side and downwards from the towed vehicle. Speed is adjusted so that each sound pulse insonifies a new section of water immediately in front of the last one insonified. Thus a 180 degree arc of water is continuously probed by sound as the side-looking sonar moves through the water. The technique is very similar in principles to that used in aerial photography.

The midwater records obtained by the side-looking sonar were most satisfactory in respect to obtaining information on the relative concentrations of sound scatterers above, in, and below the sonic scattering layers. One of the main advantages of this device is that it can profile through the water column, making all sound measurements at a fixed range so that sound scatterers from one part of the water column can be compared with those in another part of the water column. Hull-mounted sonars and echo-sounders cannot do this, and as ranges change with the migration of the sonic scattering layers, target strengths for the same organisms register differently. It is common experience with these surface units to have sonic scattering layers appear or disappear during vertical migrations.

The high-frequency side-looking sonar also has the advantage of being able to look at the finer structure of the sonic scattering layers, thus being able to obtain some measure of the

patchiness of sound scatterers in the horizontal plane and the numbers of scatterers per unit volume. Most of this sort of detail is not registered by hull-mounted sonars.

The results of the side-looking sonar investigations indicated that there was a definite stratification of sound scatterers in the water column. The most intense levels of sonic scattering registered by the side-looking sonar corresponded in depth with sonic scattering layers observed on a 12-kHz echo-sounder and with the vertical distribution of potential sound-scattering organisms observed by NEL scientists in the DEEPSTAR 4000. The changes in the relative densities of sonic scatterers are clearly seen in the side-looking sonar records. Figure 4 shows a record of the low concentrations of sound scatterers typically found below the scattering layers. Figure 5 shows large irregular sonic targets near the top of the sonic scattering layers which are probably aggregations of organisms. The interesting points emerging from the side-looking sonar records are that the sonic scattering layers are not uniformly distributed horizontally and in many instances are more like an irregular mosaic, consisting of schools of organisms separated by open volumes of water which contain few sound scatterers. Other parts of the layers are more continuous, and patchiness is less pronounced. Also, there are qualitative and quantitative differences in the side-looking sonar records from the top of the sonic scattering layers to the bottom. Thus, in comparing the results from the instrumented trawl study with those obtained by the side-looking sonar, the structure of the sonic scattering layers takes on a new dimension. The "three-layer cake" as discerned by the instrumented trawl appears to be more like a three-layer mosaic of tiles from which some of the tiles are missing. Patchiness seems to be a universal characteristic of marine populations, and the sonic scattering layers appear to be no exception. The vertical dimensions and structure of this migrating midwater community off southern California seem fairly well established from studies to date. From top to bottom, the sonic scattering layers and the migrating midwater community appear to be about 250 m thick. Each component, the euphausiid shrimp, the sergestid shrimp, and the lanternfish, appears to extend over a vertical distance of roughly 90 m; thus there is overlap in the distributions of these organisms as demonstrated by the instrumented trawl studies and verified by direct visual investigations using submersibles.

The final set of investigations on the midwater migrating communities were conducted from submersibles taking advantage of the ability to make direct visual observations of organisms in their environment. The submersibles used were PISCES, DEEPSTAR 4000, ALVIN, and DEEPSTAR 2000. The areas of investigation were Saanich Inlet on the eastern side of Vancouver Island, Canada, the DeSoto Submarine Canyon in the Gulf of Mexico, the Slope Water off New England, and Santa Cruz Basin and the San Diego Trough off southern California.

The first dives were made in January 1967 in Saanich Inlet using the submersible PISCES. Saanich Inlet is a deep fjordlike embayment on the eastern coast of Vancouver Island. The maximum depth is about 200 m, but despite this shallow depth, well-developed sonic scattering layers occur there (see Bary and Pieper's contribution). Observations of midwater organisms conducted from the submersible PISCES, in a series of four dives, indicated that the most prevalent animal at scattering layer depths was a euphausiid shrimp, *Euphausia pacifica*. This organism often occurred in association with amphipods and chaetognaths. The spatial arrangement of these different types of organisms was such that they tended to be mutually exclusive. Thus, when euphausiids were present in large numbers, the numbers of amphipods and chaetognaths were few. The whole scattering layer had a coarse graininess to it, consisting of large aggregations of the three organisms, the edges of each aggregation mixing with the next. On the whole, though, euphausiids were the most prevalent organisms in the midwater migrating community. It is encouraging to note that our visual estimates of euphausiid densities (up to 20 or 30 per cubic meter) matched very closely those calculated by Bary and Pieper from collections made with a high-speed plankton catcher (see Bary's and Pieper's contribution). There were

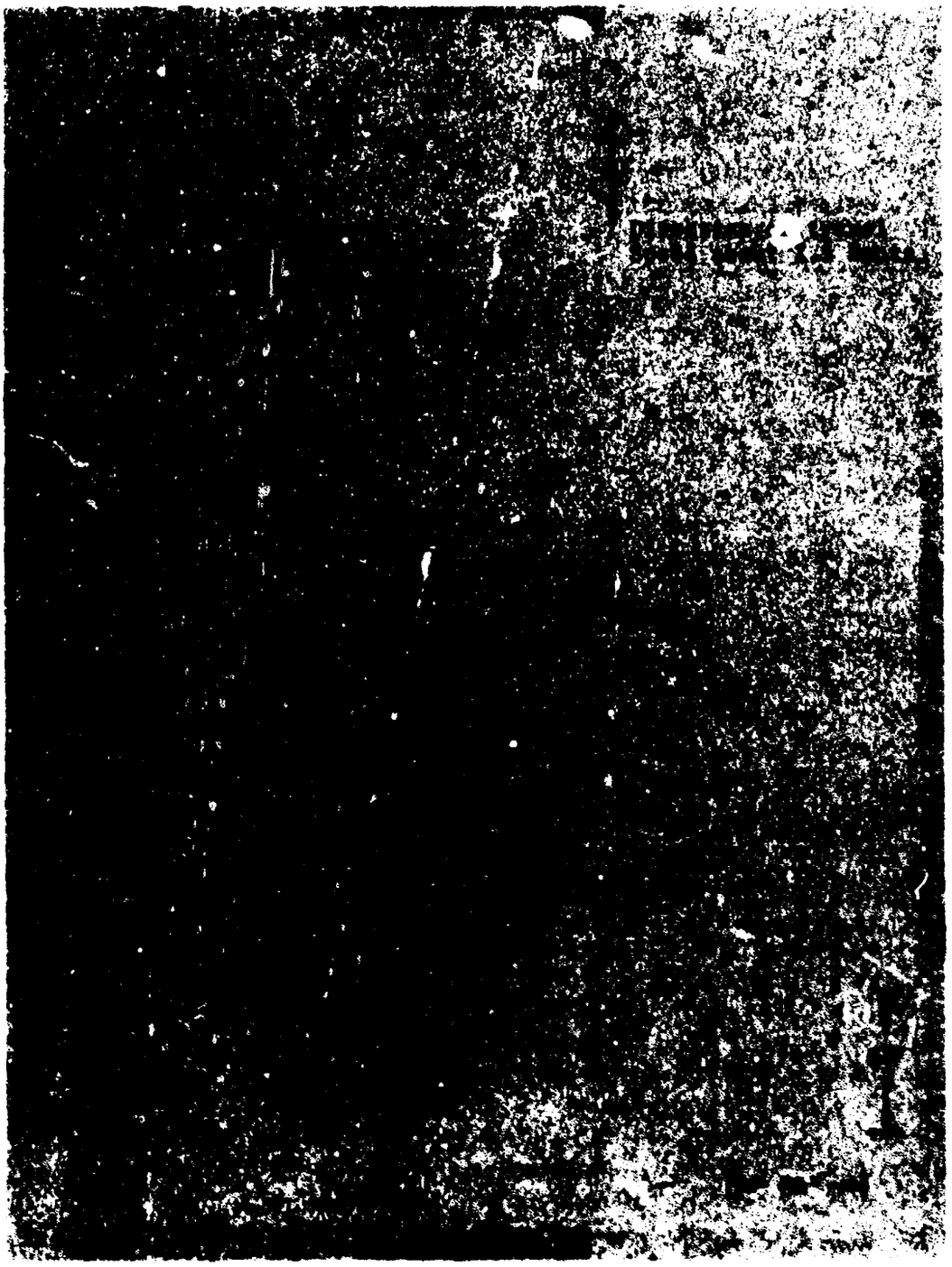

Figure 4. Low concentrations of sonic scatterers below the sonic scattering layers

Figure 5. Large irregular sonic targets near the top of the sonic scattering layers

also occasional voids at sonic scattering depths containing few organisms. Visual observations, in this instance, confirmed the patchiness of potential sound-scattering organisms in agreement with the information obtained from the side-looking sonar investigations.

The euphasiid-dominated sonic scattering layer in Saanich Inlet is quite different from those found in the open ocean. Sergestid shrimp and the lanternfish are very sparcely distributed below the euphausiids and we only sighted one or two specimens of those organisms per dive. The other peculiar feature of the area was extremely dense layers of copepods about 30 cm thick with concentrations up to one copepod per cubic centimeter.

The second set of dives was conducted in the DEEPSTAR 4000 in the Gulf of Mexico during May 1967. A total of five dives was made, three of which were in the DeSoto Submarine Canyon (Gaul and Clarke, 1968). The sonic scattering layers in that area were not very strong and the crustacean elements were poorly represented. We saw no euphausiid shrimp from the submersible and only a few sergestid shrimp. Lanternfish and hatchetfish, however, were very abundant. The behaviors of these two fish contrast markedly. The lanternfish definitely migrate, whereas the hatchetfish appear to remain stationary throughout the diurnal period. This non-migratory behavior in hatchetfish has been observed now at a number of widely separated localities. Another interesting aspect of behavior was noted at depth during these dives. Many of the fish and fair numbers of squid were found to be in an inactive or lethargic state (see Barham's contribution). These organisms could be approached very closely by the submersible, and it was not until the water was disturbed around them or the intense light field affected them that they would be alerted and swim off.

The submersible observations in the DeSoto Submarine Canyon area indicated that the typical three-layered migrating community found in most open ocean areas is poorly developed here. In fact, no euphausiid shrimp were seen at all. Sergestid shrimp were rare, but lanternfish appeared to be as numerous as off southern California.

The third set of submersible observations was conducted with ALVIN in the Slope Water off New England during October 1967. The dives were made to identify the organisms associated with a peculiar sound-scattering phenomenon known as Alexander's Acres. These strong tent-shaped sonic targets at scattering layer depths were found to be dense schools of the lanternfish *Ceratoscopelus maderensis*. During the daytime, the fish in these schools are very lethargic, but quickly become active and swim away when illuminated by the lights on the submersible. The distributions of these schools during daylight hours is described by Backus *et al.* (1968).

Other observations made during the dives revealed that the Slope Water contains the typical three-layered migrating community consisting of euphausiid shrimp, sergestid shrimp, and lanternfish. The peculiarity of the Slope Water midwater community is the more strongly schooled nature of the sergestid shrimp and lanternfish. The schools of those organisms were very dense and sharply defined while the space between schools contained few, if any, organisms. Again one gets the impression of a patchy mosaic consisting of isolated schools of organisms. The vertical stratification of this midwater community also differs in sharpness from top to bottom, the euphausiid shrimp being more clearly separated from the sergestid shrimp than the sergestid shrimp are from the lanternfish.

The fourth set of dives was made off southern California in the submersible DEEPSTAR 4000 during March 1969 and in DEEPSTAR 2000 during May and June 1970. The dives were made in the Santa Cruz Basin and San Diego Trough. The migrating community in these areas was found to correspond very closely in structure with that described for the Santa Barbara Basin during the instrumented trawl study. The only observation made during these dives that bears special mention is the occurrence of migratory organisms at daytime depths after the main layer had migrated upward during the evening. All of the animals observed at depth at those times were generally lethargic, usually hanging very still in the water. These occurrences were not

rare cases during the dives I made and they give one the impression that not all of the migratory organisms perform vertical migrations every day. Thus a given animal may remain at depth for one or possibly more diurnal cycles. This finding should be investigated more vigorously in future field work since it has important implications as to the behavior of the sonic scattering layers.

In summary, I am convinced it will take a combination of techniques to unravel the many questions concerning the behavior and structure of the sonic scattering layers. I hope the techniques compared here will stimulate others to explore new methods of investigation.

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DISCUSSION

Backus: The business about vertical migrators not making daily vertical migrations but three-times-a-week migrations or every-other-day migrations and so on seems to me an important point. Could you discuss the evidence for that in a little bit more detail? I haven't seen what I consider any good evidence for that yet.

W. Clarke: The Gulf waters were probably the best example of it. In dives in the Gulf of Mexico and also the San Diego Trough you would find animals at depth, lanternfish in particular, still sitting there when the rest of the layer had gone up, likewise with euphausiids. In the opening and closing cod-end sampler that we had on the Isaacs-Kidd midwater trawl, you could fish below the optimum isolume for the euphausiids and get euphausiids down there. Apparently they had stayed down. You could get lanternfish below their preferred light-level depth. Further evidence of this might be the fact that on an echosounder record you may see a layer made up of both migratory and non-migratory components.

Backus: I don't consider that good evidence at all because the echoes of the rising layer can be coming from totally different animals than the echoes from the nonrising ones. Nor do I consider

observations made from submersibles very good because of the difficulties of making identifications out of the submersibles. The net tow data I would take more seriously. I'm talking about individuals of the same age class, size class, some of them moving up and making the vertical migration and some of them staying there. I would consider neither the submersible nor the echosounder data that you cite very good. The net business I hear.

W. Clarke: Well, let's take the Santa Barbara area. We know what lanternfish are there, and during a recent series of dives you would see adult specimens of lanternfish at depth during the migration period just sitting there in the water, whereas either on the way down or on the way back up, you would pass the main layer and go through much higher concentrations of lanternfish. There were lanternfish left behind sitting down there. There were also sergestids left behind sitting down there.

Dunlap: With regard to *Triphoturus* in the Gulf of California, we found that of the ones that migrated up, there were still about 7 percent of the day hauls of the same species, and we could see no difference morphologically. Now I don't know about age classes and this type of thing, but Robeson at Hopkins has looked at it, and he couldn't see any difference between those and the ones that migrated up. So I would concur.

W. Clarke: One other brief observation in the Gulf of Mexico: We had squid commonly follow the submersible feeding actively on organisms around us, particularly on the lanternfish scattering layer. But then we dropped down through the layer, and there were deeper populations of squid which were completely dormant in the water too, the same species of squid, and they characteristically take a "J" position. In other words, they put the tentacles together, fold them back, and tuck them in underneath the head, and they just hang there motionlessly in the water. You really had to bounce them around or disturb them with the light before they would wake up and swim off. Here again was an example of an animal that was just sort of sitting there during the daytime.

Barham: I think that this is a working premise. Obviously, the way to prove the point is to go out there and tag those things. But we haven't gotten around to that yet, or will we in the near future. It's not particularly a new idea. If you go back to the works of Marshall, you'll find that he made a comment on this particular point many years ago. I think that at least it's an idea that we can begin to coordinate observations around.

Holm-Hansen: Two comments which impinge upon Backus' question. In some of our studies with migrations of dinoflagellates in a ten-meter deep tank at Scripps, I've been perplexed by the fact that you get about 90 percent of them migrating in a sharp band close to the surface in the daytime and close to the bottom at night; however, you always get about 5 or 10 percent left evenly distributed in the water column. Now this I interpret as reflecting perhaps different metabolic states depending on the particular stage of the life cycle of each individual dinoflagellate cell. In regard to copepods, I asked Gus Paffenhofer in our lab just a few months ago about how long these things could go without any food and he said about a month or two. He gave me some individuals (*Calanus sp.*) which we put in a nutrient-free medium. They remained perfectly viable and happy for about two weeks, and then one weekend they were flushed down the drain by mistake. At least these copepods can go a long time without food.

W. Clarke: For Richard Backus' sake, I did say I was speculating at the beginning of this little talk here.

Craddock: You don't really need to speculate, I don't think, even with respect to fishes. I'm sure that Basil Nafpaktitis would be up on his feet, but he just left, so I'll cite some of his data. In *Diaphus* many species start out when they are little and don't migrate; when they're intermediate in size, they apparently migrate; and then when they become gravid, they simply don't migrate. I think we're dealing with a broad spectrum here.

W. Clarke: I concur.

THE HORIZONTAL DIMENSIONS AND ABUNDANCE OF FISH SCHOOLS IN THE UPPER MIXED LAYER AS MEASURED BY SONAR

Paul E. Smith
Bureau of Commercial Fisheries
La Jolla, California

ABSTRACT

This paper reports progress in a study to develop an acoustic method to count, measure the horizontal dimensions, estimate the biomass, estimate the size composition, and identify the species of fish schools in the upper mixed layer from a moving ship. Several thousand fish schools were counted and measured in the California Current region in 1969 using a sonar at a frequency of 30 kHz, with a 10° conic beam (at -3 dB), at ranges from 200 to 450 m during daylight hours. Counts and measurements were made at ship's speed of 8 to 13 knots. In the 200,000-square-mile study area there exists a great variety of sonar propagation conditions due to upwelling, stratification, internal waves, and volume reverberation.

The counts of fish schools, after correction for known biases and area, indicate the presence of about 1 million schooled sonar targets in the 200,000-square-mile area adjacent to the coastline between San Francisco and Cape San Lazaro, Baja California, Mexico. Most fish schools are between 10 and 30 m diameter, normal to the ship. Less than 5% of the schools exceed 60 m diameter. Most schools occur in groups of schools near the axis of the California Current, in the gyral waters of the Los Angeles Bight, Sebastian Vizcaino Bay, and the Abreojos Bight, and nearshore along the entire coast. Occasionally groups of schools were located over 160 miles from the coast. Analyses of the concentrations of schools during the spawning period indicates that their location coincides with known spawning grounds.

INTRODUCTION

Echo sounding and sonar apparatus has played a significant role in exploratory fishing and tactics for setting fishing gear (Sund, 1935; Tester, 1943; Balls, 1948; Gerhardson, 1946; Smith, 1947; Smith and Ahlstrom, 1948; Devold, 1950). Echo sounding is now established as a useful technique for making direct estimates of the abundance of solitary fish in midwater (Cushing, 1968a and b). Aggregating schools and pods of fish (Breder, 1959) have proved more difficult to survey (ACMRR–FAO, 1967). A sea survey methodology has been described and tested by Truskanov and Scherbino (1964).[1]

The study of which this report is a part was begun in 1966 with the following sequence of objectives: (1) to count the number of fish aggregations and schools in the survey area, (2) to measure the size of aggregations and schools, (3) to estimate the biomass of aggregated and schooled fish, (4) to estimate the size composition of individuals within the aggregations and schools, and (5) to identify northern anchovy schools. Since the survey was intended to encompass 100,000 to 200,000 square miles in less than 2 months with a single ship, it was considered

[1] Included as Appendix II because the paper is widely cited but not readily available.

imperative that the data be collected with the ship under way at full speed and that the amount of direct sampling be kept to a minimum.

Preliminary work with acoustic apparatus (Simrad 580-10 scientific sonar and sounder system[1]) revealed several unevaluated barriers to quantitative research. Of prime importance was the fact that anchovy schools are known to occur from the surface, too shallow for sounders to detect them, to 200 m deep (E. Barham, Naval Underwater Warfare Center, San Diego, California, personal communication; visual observation), too deep for horizontally directed sonar to detect them. We had previously noted that the effective range and number of targets per unit area varied with time of day and mixed layer depth. Also, the schooled targets were often found to occur in groups where counts from a sweeping sonar beam were not reproducible on repeated crossings of the target area.

This report will describe an experiment designed to determine the feasibility of the use of sonar to count and measure the sizes of fish schools and then the application of the techniques to determine the numbers and sizes of anchovy schools in the California Cooperative Oceanic Fisheries Investigation (CalCOFI) survey area. The survey ship and acoustic system were described by McClendon (1968).

Design of the Acoustic Experiment

The first phase of the design survey was to determine the optimum settings for source level, receiver gain, pulse length, transducer bearing, transducer directivity, and range for two sonars at frequencies of 11 kHz and 30 kHz, ultimately to find the combination of instrument settings best able to provide repeatable counts of the number of schooled targets per unit area. This survey was made up of three 2-week cruises in the fall of 1968 with two weeks or more between cruises to allow data processing and further planning in response to the results. The work was planned for an area known for high temperature gradient (often 3° per 10 m) and internal wave activity. The site was near Catalina Island off southern California where anchovy schools are found in considerable numbers in autumn.

Data were taken from 42 surveys of a rectangular grid, 2 X 4 nautical miles. Each sonar transducer was fixed at 90° relative bearing. Pulse lengths for each sonar were set at 30 msec at full power (ca. 123 dB above 1 μbar at 1 m). The range scale for the 11-kHz sonar was 2500 m and for the 30-kHz sonar was 1250 m. The bottom varied from 500 to 2500 m on the grid. The 16° isotherm varied from 29 m to 10 m with an 18 to 19° surface temperature.

The actual counts of targets are found in Appendix I (Tables I, II, III, IV), and Figures 1 and 2 illustrate the counts of targets per fifth of the range. For the purposes of this experiment it was assumed that the numbers of targets in each range increment were actually equal over time and that differences could be ascribed to changes in sonar effectiveness with range. We found that the 11-kHz sonar—Figure 3—(22° beam angle between "3-dB down" points) exhibited a continual and drastic drop in the number of targets with range in these propagation conditions. For the ensuing California Current surveys of 1969 it was decided to use this sonar set on long pulse (30 msec), long range (2500 m), and full power as an easily analyzed index of fish school occurrences. We had no intention of deriving extrapolated estimates of the number of fish schools from the 11-kHz sonar in the survey area since the effective range fluctuated in an erratic manner, presumably with changes in propagation conditions.

[1]Use of a trade name does not imply endorsement by the Bureau of Commercial Fisheries.

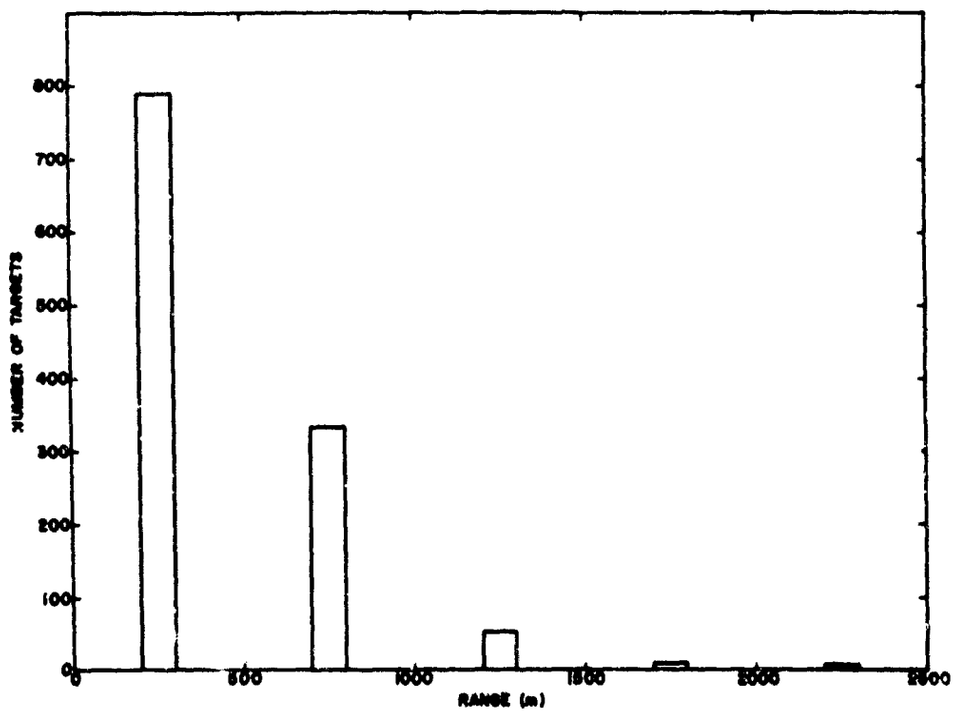

Figure 1. Actual numbers of targets per 500 m range off Catalina Island in October 1968 (see Appendix I, Tables III and IV), as detected by 11-kHz sonar

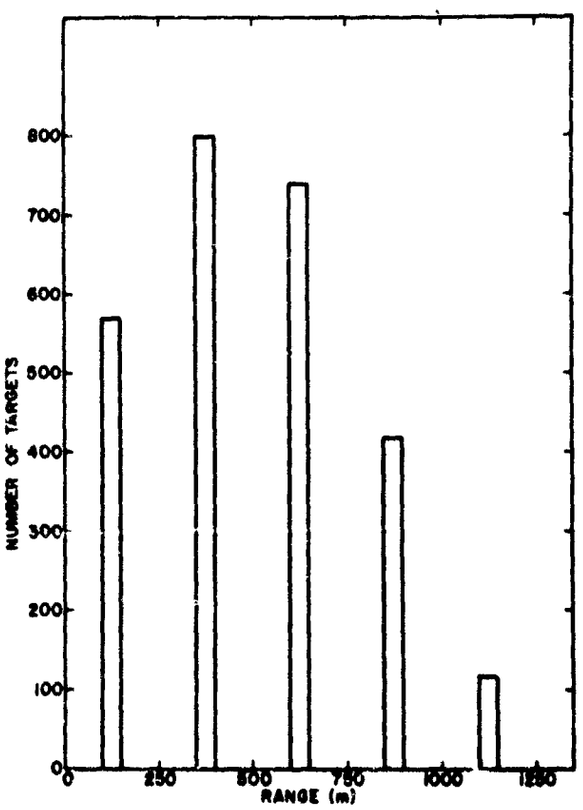

Figure 2. Actual numbers of targets per 250 m range off Catalina Island in October 1968 (see Appendix I, Tables I and II), as detected by 30-kHz sonar

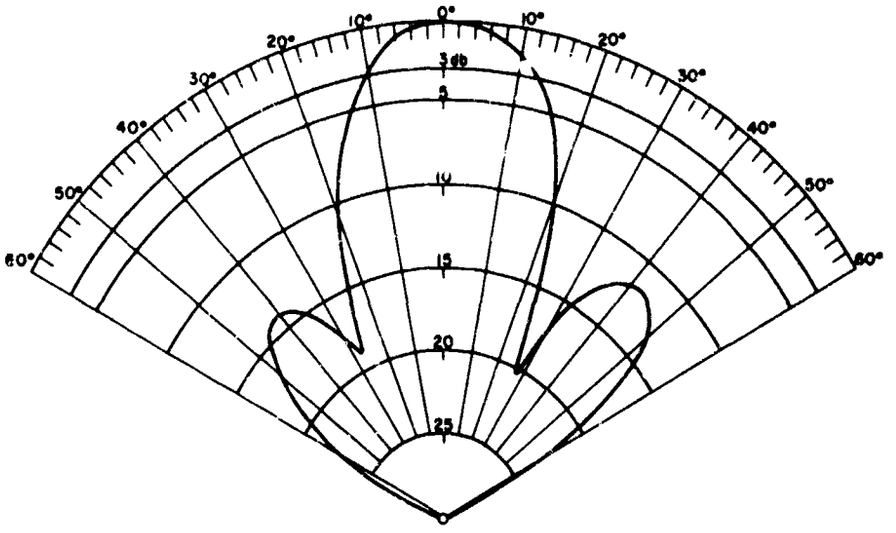

Figure 3. Horizontal beam-directivity diagram of the 11-kHz sonar transducer. (Courtesy of Simrad, Oslo.)

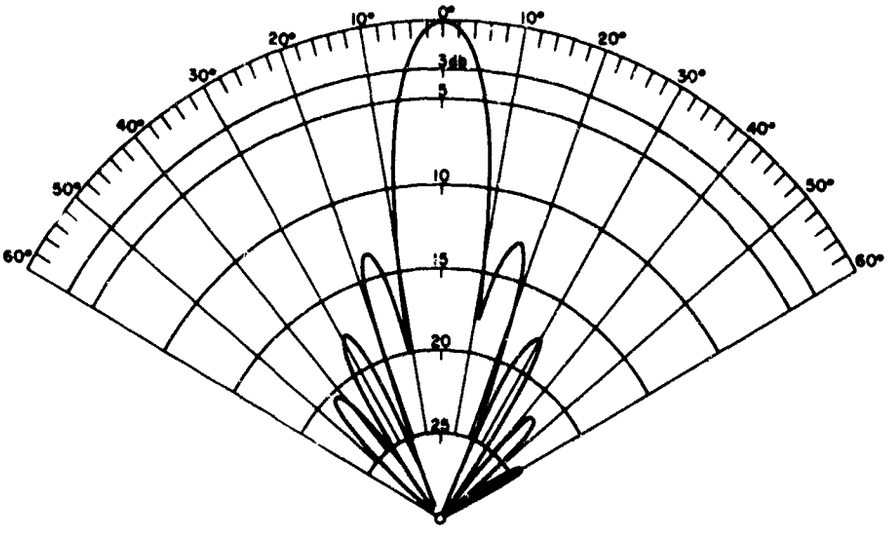

Figure 4. Horizontal beam-directivity diagram of the 30-kHz sonar transducer. (Courtesy of Simrad, Oslo.)

Three important features were observed for the 30-kHz sonar (10° beam angle at 3-dB down points—Figure 4) range-target number histogram (Figure 2): (1) the decline in numbers of targets at ranges greater than 750 m, (2) the decline in number of targets near the ship, and (3) the near-equality in the numbers of targets from 250 to 500 m and from 500 to 750 m. We interpreted the decline after 750 m to simple range-dependent loss in these sonar conditions. The lower number of targets near the ship was interpreted as arising from fish schools near the ship which were not detected due to receiver characteristics during and immediately after the transmission of the pulse and due in part to fish schools under the 10° beam angle in the near-ship portion of the range. For these reasons, we chose to record between the ranges of 200 to 450 m.

Figures 5 and 6 illustrate changes in the number of targets received with time of day. Since we anticipated a limit to the duration of manning the sonar on each cruise, we arbitrarily limited

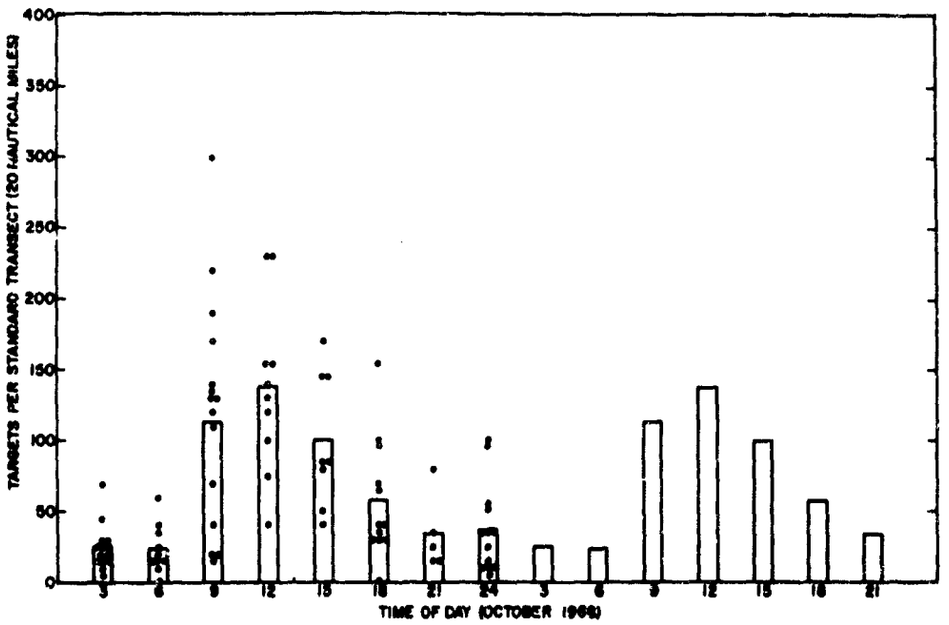

Figure 5. Variation in the number of targets per 20-mile transect with time of day with the 11-kHz sonar (see Appendix I, Tables III and IV). The daily cycle of the average number is repeated to emphasize the complete cycle. Each dot represents the count of a single 4-mile transect.

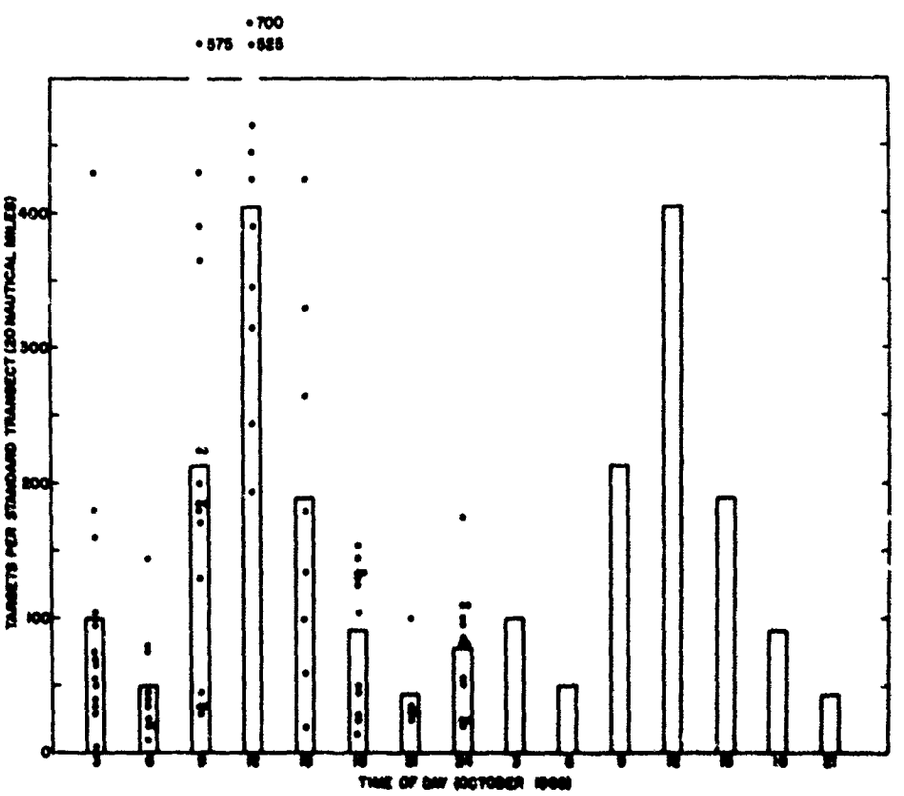

Figure 6. Variation in the number of targets per 20-mile transect with time of day with the 30-kHz sonar (see Appendix I, Tables I and II). The daily cycle of the average number is repeated to emphasize the complete cycle. Each dot represents the count of a single 4-mile transect.

the times of taking sonar observations to 0800 to 1600. This schedule was adopted because I did not think that we could correct target counts for differences due to time of day since it appeared to be complicated by cloud cover and moonlight, and probably day length, water clarity, and regional and species differences were also important.

Figures 7 and 8 illustrate the vertical and horizontal aspects of the configuration of the insonified area from which most targets were anticipated. Early trials of this system indicated that at right angles (normal to ship's track) fish school dimensions could be estimated to 2.5 m. During the Catalina trials, a series of targets was measured and the fish school dimensions parallel to the ship were estimated from the length of the targets on the recordings, the speed of the recording paper and ship speed and the assumed effective 10° beam angle (Figure 9). The apparent width of the fish school was calculated from the formula

$$W_t = csl, \tag{1}$$

where

W_t = the apparent width of the recorded fish school in meters

c = chart speed in seconds per millimeter

s = ship's speed in meters per second

l = measured width of target on chart in millimeters.

The effect of the beam angle was corrected for by subtracting the width of the sonar beam at the mid range of the school:

$$W = W_t - 2 \tan A\left(\frac{r_{max} + r_{min}}{2}\right), \tag{2}$$

where

W = the beam corrected estimate of fish school width

A = the half angle of the effective beam

r_{max} = range to the far side of the school in meters

r_{min} = range to the near side of the school in meters.

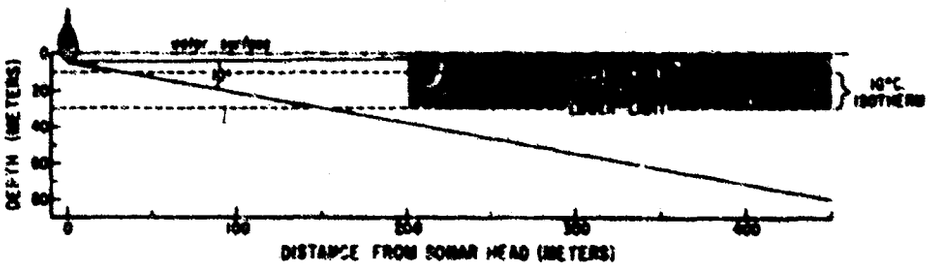

Figure 7. A depth-vs-distance plot (1:1) of the zone to be insonified and recorded in the 1969 CalCOFI cruises. The shaded portion is assumed to enclose the area from which schooled targets are most likely to be received. The dashed lines illustrate the range of depth of the 16° isotherm in 22 profiles taken hourly in October 1968: surface temperature was ca. 19°. Source depth was 4 m.

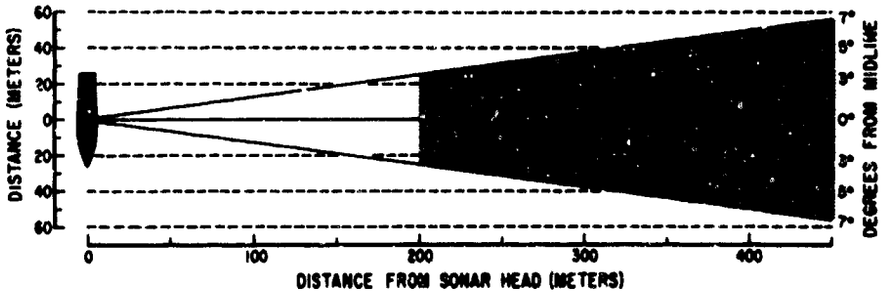

Figure 8. Plan view of the triangular isonified area for sonar mapping. The transducer is always pointed laterally rather than swept from side to side as in searching patterns. Effective beam angles from 6° to 14° are illustrated with a 1:1 scale. The shaded area represents the area from which target returns are recorded.

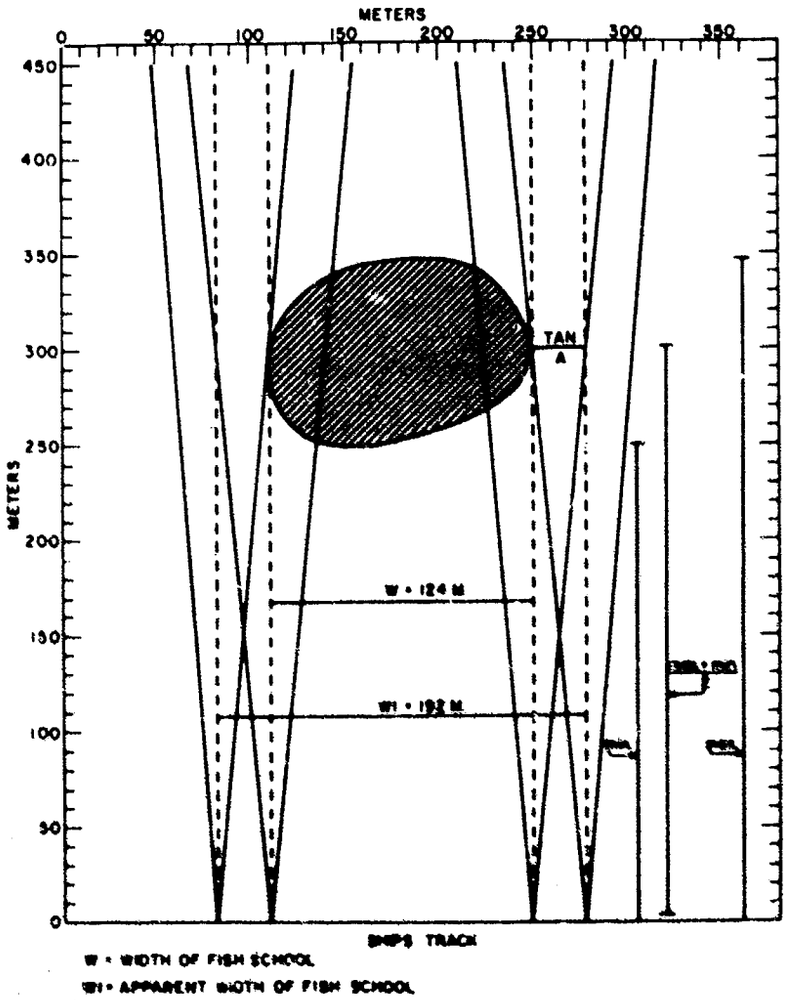

Figure 9. Geometry of the calculation of the axes of elliptical sonar targets. See formulas 1, 2, 3.

The school axis normal to the ship's track was calculated by the formula

$$d_i = r_{max} - r_{min} - p, \tag{3}$$

where

d_i = the axis normal to the ship in meters

and

p = pulse length in meters (1 msec = 1.5 m).

For the Catalina trials the frequency distribution of the measured axis normal to the ship (d_i) did not differ significantly from the frequency distribution of the measured axis parallel to the ship for 37 targets (χ^2 4d.f. = 8.44: not significant at the 95% level).

Areal Survey Results (CalCOFI Region)

Following the survey design above, 30-kHz sonar data were collected on ichthyoplankton and oceanography cruises in the CalCOFI area in January, February, April, May, June, and July 1969. Similar recordings, as yet unanalyzed, exist for the same area for October and December. On most surveys the 200,000-square-mile survey area was covered by two ships, only one of which, the David Starr Jordan, was equipped with sonar. During the May-June cruise the entire survey area was covered only by the sonar-equipped David Starr Jordan. The first estimate of the number of schooled sonar targets in the CalCOFI grid area is derived from this cruise. The horizontal size distribution is derived from the 2333 targets measured to date.

Horizontal Dimensions of Fish Schools

Fish schools were routinely measured in two dimensions: the axis of the target normal to the ship and the axis of the target parallel to the ship (Figure 9).

In Figure 10 the size frequency distribution of 2333 targets is illustrated. The open bars represent the actual number of fish schools which were entirely within the 250-m recorded strip. Since this biases the size frequency distribution toward the smaller targets, each count was corrected by the proportion of the width of the recorded strip which the target occupied. Thus, a 50-m-diameter target could be recorded in its entirety on only 200 m of the record strip and would have been undersampled relative to 10-m-diameter targets which could be recorded on 240 m of the strip. The shaded bars represent the size frequency of values which have been corrected for this "edge" effect in the following ways:

$$N_l' = N_l \left(\frac{250}{250 - D_l} \right), \tag{4}$$

where

N_l = the number of schools in size interval l

D_l = the diameter normal to ship's track representative of size interval l

N_l' = the number of schools in size interval l corrected for edge bias.

To compare the size frequency distribution of the axes of the schooled targets at right angles to the ship (D_i) to the size frequency of the axes of the schooled targets parallel to the ship (D_j),

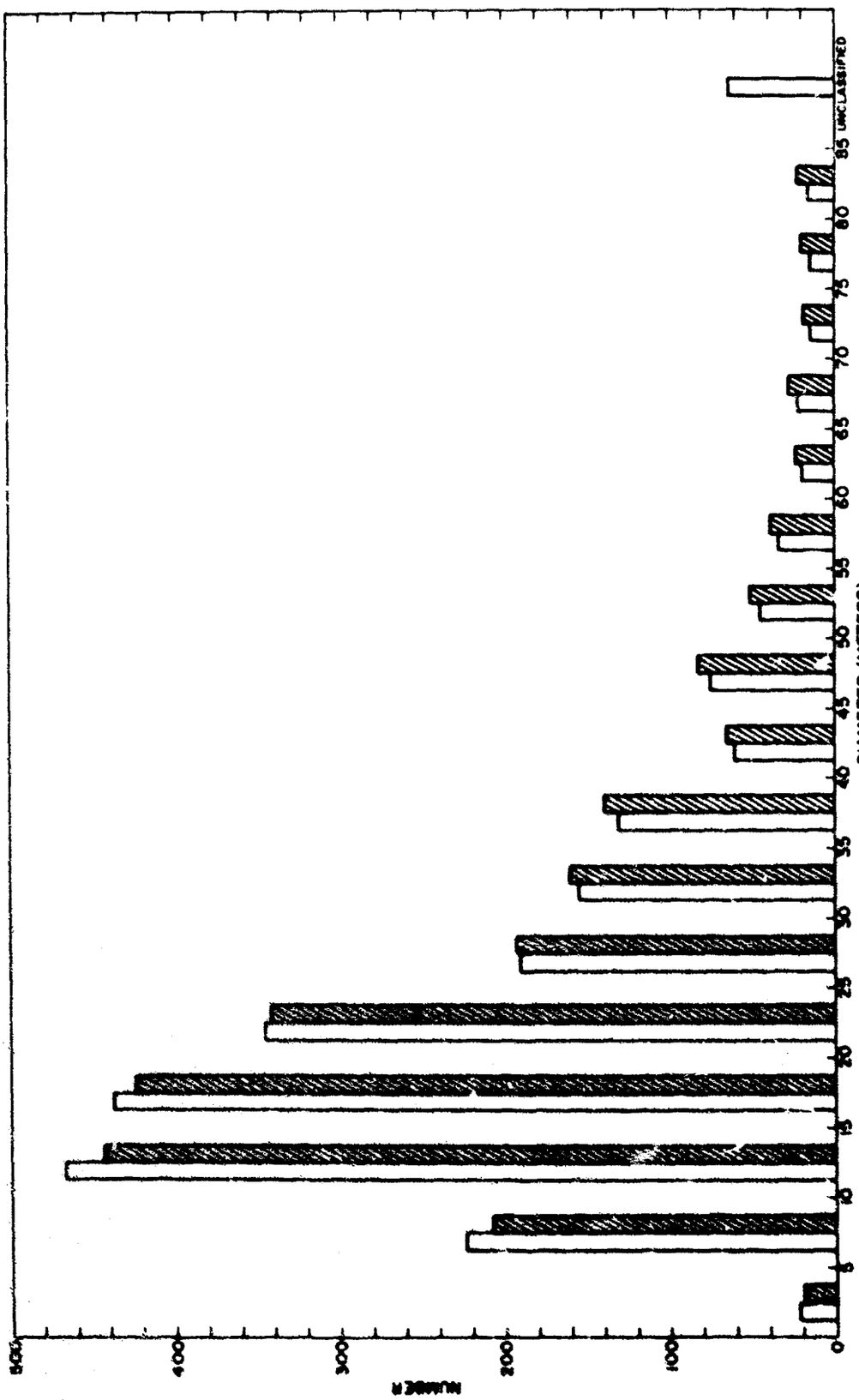

Figure 10. Distribution of the actual (clear bar) and edge-bias corrected (shaded bars) numbers of sonar targets for each 5 m diameter to 84 m in a plane normal (at right angles) to the ship. (See formula 4 for edge-bias correction formula.) The "unclassified" targets represent 63 targets larger than 84 m which were too infrequent in any interval to correct for edge bias precisely (see Table 1).

the frequencies of N_i were corrected to the original number of schools whose D_i axes were less than 85 m. Schools are too few in our samples, as yet, for this kind of comparison. This correction is

$$N_i'' = N_i' \left(\frac{\Sigma Ni}{\Sigma Ni'} \right), \tag{5}$$

where

N_i and N_i' are as above, and N_i'' is corrected proportionately so that the sum of N_i and the sum of N_i'' are approximately equal.

All numbers in Table 1 are rounded for simplicity after calculation of subsequent terms.

TABLE 1

Numbers and Areas of Sonar Targets Corrected for Edge Bias

Dimension (m)	N	N′	A	N′A	N″
0- 4	21	21	3	67	19
5- 9	224	230	38	8869	207
10- 14	467	491	113	55479	442
15- 19	438	470	227	106671	423
20- 24	345	378	380	143800	340
25- 29	190	213	573	121957	192
30- 34	155	178	804	142957	160
35- 39	131	154	1075	165320	139
40- 44	60	72	1385	99912	65
45- 49	75	92	1735	160247	83
50- 54	45	57	2124	120666	51
55- 59	33	43	2552	109078	39
60- 64	19	25	3019	76280	23
65- 69	22	30	3526	105962	27
70- 74	14	20	4072	80058	18
75- 79	15	22	4657	100938	20
80- 84	16	24	5281	125738	22
0- 84	2270	2520			2270
>84	63				

Figure 11 compares the distribution of sonar target dimension at right angles to the ship to the distribution of target dimensions parallel to the ship using the assumption that the effective beam angle is 10°. Since the proportions of both smaller targets and larger targets are overestimated, no single alternative beam angle will correct for this tendency. The assumption of a larger effective beam angle will correct the overestimate of the number of large schools (formula 2) but will emphasize the overestimate of the number of small schools relative to the right-angle axis. Similarly the assumption of an effective beam angle smaller than 10° will "correct" the

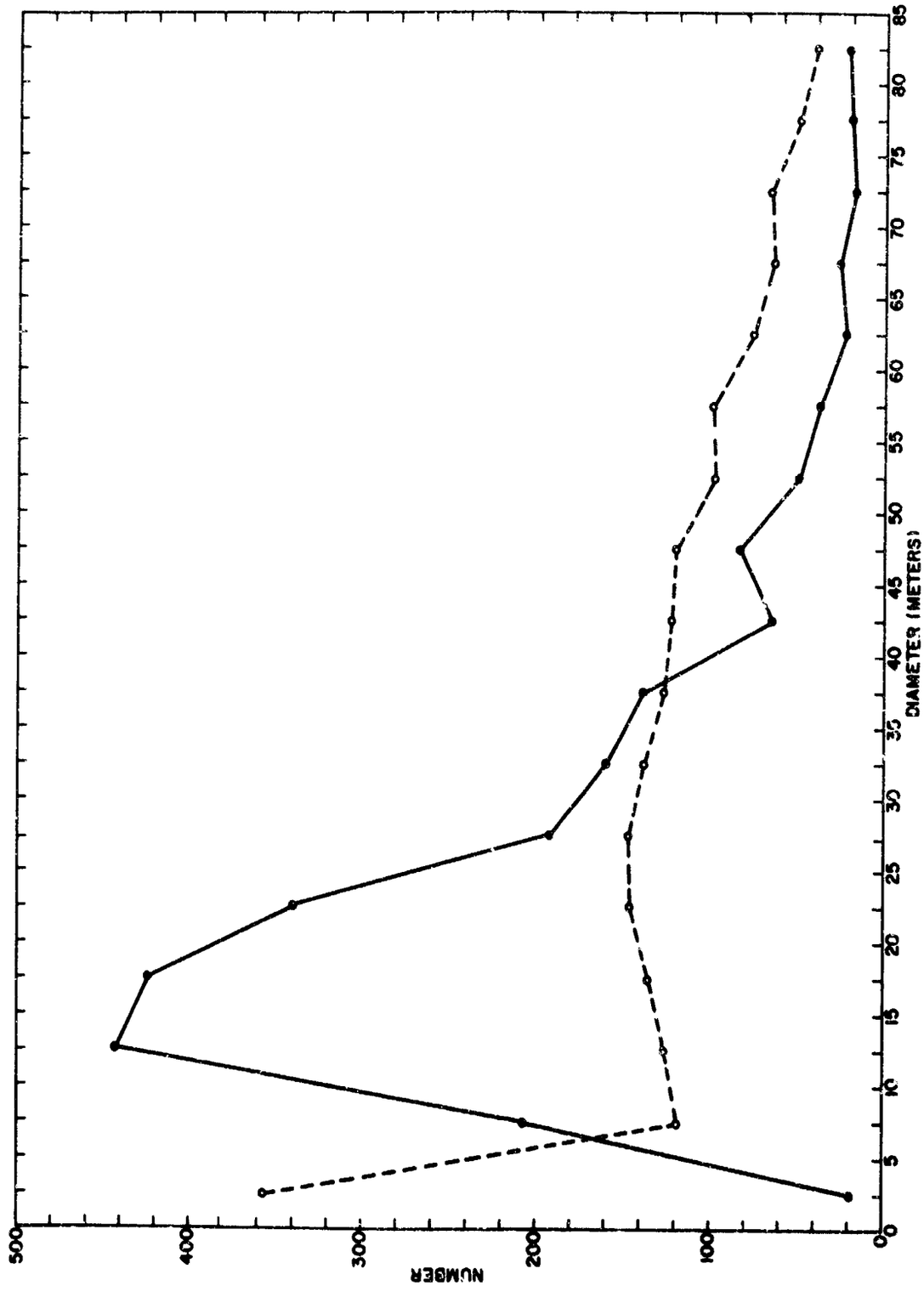

Figure 11. Comparison of the size frequency distribution of target dimension normal to the ship (solid line—see shaded bars, Fig. 10) to that (dashed line) of target dimension estimated by use of 10° effective beam angle

frequency of smaller schools but worsen the comparison in the number of larger schools. To solve this discrepancy the dimension of the schooled target parallel to the ship must be estimated from the beam directivity and axial target strength in the same manner that Cushing (1968b, p. 4) adjusted his echo sounding surveys (Figure 12).

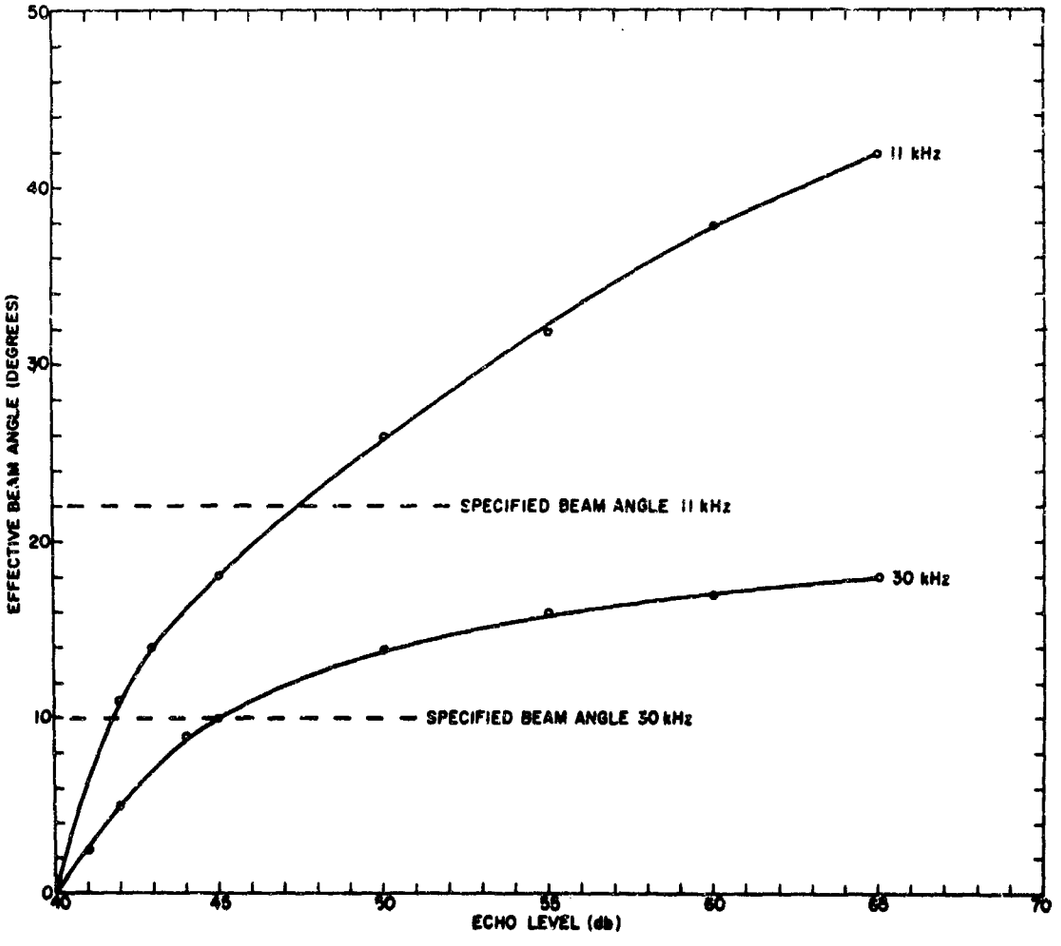

Figure 12. Comparison of relative echo level and effective beam angle for the directivity pattern in the horizontal plane of the 11- and 30-kHz sonar used in this study (see Cushing, p. 4, 1968b). Absolute target strength measurements have not yet been performed on these targets, but 40 dB is the lower threshold of the targets recorded and 60 dB is regarded as typical of large anchovy schools at midday.

It would be dangerous to imply that the small number of larger schools is unimportant. In Figure 10, 63 targets are judged to be too infrequent to correct precisely for edge bias. If the tonnage of fish is proportional to horizontal area (thickness is not evaluated), the biomass of these fish may be quite important collectively. Figure 13 illustrates the cumulative horizontal area of all the targets measured to date (Tables 1 and 2). In Table 1, N, N', and N'' are calculated as in formulas 4 and 5. The area typical of the size class is calculated from

$$A = \left(\frac{d_i}{2}\right)^2 \pi, \tag{6}$$

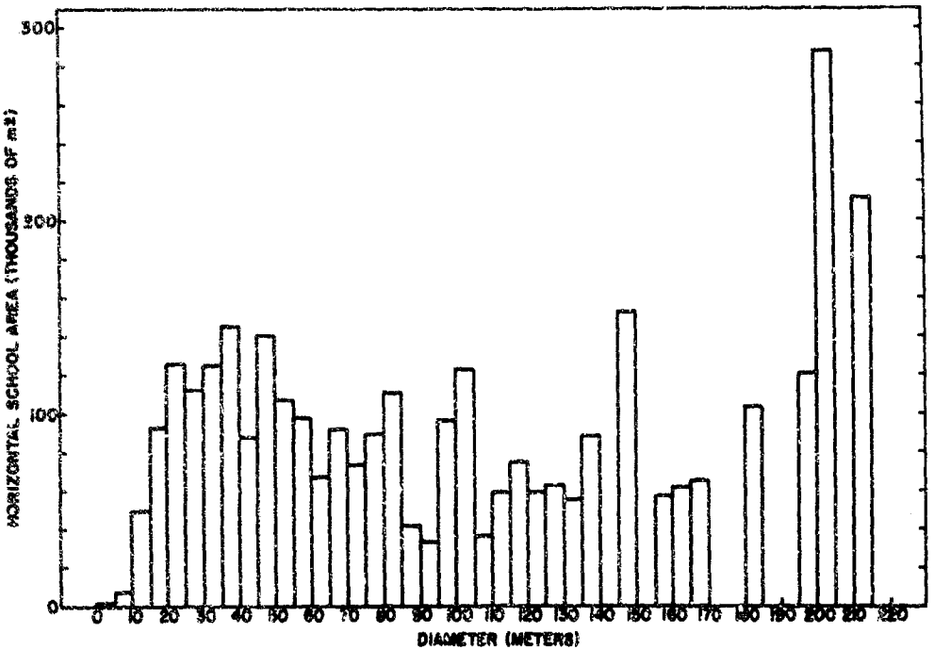

Figure 13. The relative importance of fish schools at different diameters corrected for edge bias. Each bar from 0 to 84 m is the sum of the number of schools found at each 5-m size class times an area representative of the size class (see Table 1 and formula 6). Schools greater than 84 m are adjusted here for comparison but are regarded as too infrequently encountered for precise correction (see Table 2).

where

A = the horizontal area of the schooled target

d_i = the midrange dimension of size class i in meters.

In Table 2 one can see that a single school recorded 197 m could be equal in area to the total of 345 22-m dimension schools. Targets indicated in Table 2 are considered to comprise an inadequate sample of large schools but are reported here to indicate important quantities of fish in large schools.

The Abundance of Fish Schools

We feel that a first estimate of the number of schooled sonar targets in such a large area is useful even though these are not good accompanying estimates of precision and accuracy. For this purpose, we have chosen the May-June 1969 survey when both halves of the 200,000-square-mile CalCOFI survey area were occupied in adjacent months (May 5-June 29). The usual CalCOFI lines (see Ahlstrom (1966) for details of pattern) are spaced at 40-mile intervals, run approximately normal to the coast, and are occupied alternately in shoreward and seaward directions. Biological, chemical, and physical oceanographic observations were taken at 20- to 40-mile intervals along these lines on arrival at stations without regard to time of day or oceanographic features. The sonar was operated only 8 hours per day and the recorded track width was only 250 m of the 74,080 m between track lines. The simplest estimate would be

$$N = \frac{T}{T_s} \frac{A}{A_s} \Sigma N_i', \qquad (7)$$

TABLE 2

Numbers and Areas of Large Rare Sonar Targets Adjusted for Edge Bias

Dimension (m)	N	N′	A	N′A
85- 89	5	8	5945	45588
90- 94	4	6	6648	42073
95- 99	9	15	7390	108674
100- 104	10	17	8171	138028
105- 109	3	5	8992	47161
110- 114	4	7	9852	71391
115- 119	4	8	10751	80837
120- 124	3	6	11690	68495
125- 129	3	6	12668	77242
130- 134	2	4	13685	57986
135- 139	3	7	14741	97859
140- 144	0	0	15837	0
145- 149	4	10	16972	164773
150- 154	0	0	18146	0
155- 159	1	3	19359	52041
160- 164	1	3	20612	58557
165- 169	1	3	21904	65976
170- 174	0	0	23235	0
175- 179	0	0	24606	0
180- 184	1	4	26016	95645
185- 189	0	0	27465	0
190- 194	0	0	28953	0
195- 199	1	5	30480	143776
200- 204	2	10	32047	333827
205- 209	0	0	33653	0
210- 214	1	7	35299	232230
>214				

where

T = 24 hours

T_s = the daily sampling period (8 hours)

A = 200,000 square miles

A_s = the area directly sampled (1/296 × 200,000 or ca. 696 sq mi)

N = the number of fish schools in the survey area

N_i' = number of fish schools converted for size-specific edge bias.

TABLE 3

Sonar Target Size Frequency Distribution Corrected for Edge Bias

May 1969

Diameter	N	N'	P	N''
0- 4	0	0	.000	0
5- 9	10	10	.019	9
10- 14	49	51	.097	45
15- 19	82	88	.168	77
20- 24	90	99	.189	87
25- 29	56	63	.120	55
30- 34	43	49	.093	43
35- 39	37	43	.082	38
40- 44	25	30	.057	26
45- 49	16	20	.038	18
50- 54	18	23	.044	20
55- 59	12	16	.030	14
60- 64	5	7	.013	6
65- 69	4	5	.010	4
70- 74	6	8	.015	7
75- 79	3	4	.008	4
80- 84	6	9	.017	8
0- 84	462	525	1.000	462
>84	24			

Tables 3 and 4 show the corrected size frequency distribution and proportions of targets at each interval. When all sizes are corrected for edge bias, the estimate within the area directly sampled is 1253 schools. When this estimate is applied to the whole area the number of schools is (from formula 7):

$$N = 3[296\ (1253)] = 1{,}112{,}664 \text{ schools.}$$

To get some idea of what proportion of these targets may be adult anchovy schools, I selected data (Ahlstrom, 1968) on the current estimate of anchovy spawning biomass (ca. 5×10^6 metric tons) and the mean size of anchovy schools as estimated from catch per purse seine set (data from Clarke Blunt, Marine Division, California Department of Fish and Game, Terminal Island, California);

Years	Sets	Metric tons	Mean tons/set	Range
1965-1967	2,985	50,230	17	0-113 T

TABLE 4

Sonar Target Size Frequency Distribution Corrected for Edge Bias

June 1969

Diameter	N	N'	P	N''
0- 4	5	5	0.008	4
5- 9	30	31	0.048	28
10- 14	109	114	0.175	101
15- 19	98	105	0.162	93
20- 24	73	80	0.123	71
25- 29	63	71	0.109	63
30- 34	52	60	0.092	53
35- 39	48	56	0.086	50
40- 44	23	28	0.043	25
45- 49	25	31	0.048	28
50- 54	18	23	0.035	20
55- 59	11	14	0.022	12
60- 64	9	12	0.018	11
65- 69	5	7	0.011	6
70- 74	3	4	0.006	4
75- 79	2	3	0.005	3
80- 84	4	6	0.009	5
0- 84	578	650	1.000	578
>84	15			

To use the tons per set as an index of average school size, one must be cautious about several biases. One is that a distribution with an arithmetic mean of 17 and a range from 0 to 113 is skewed; thus, it would be expected that the median and modal school size would be smaller than the mean. Also, the smaller schools may be undersampled by the fishery since mastmen and air spotters tend to ignore such schools. The figure for tons per set may also underestimate school size since an unknown number of fish escape from each haul. Also, large schools are often split because they exceed the capacity of the purse seine or the remaining capacity of the hold of the vessel. I would judge that the tons per set figure is as good as any alternative now available.

If one uses the northern anchovy spawning biomass of 5×10^6 metric tons and the mean school size of 17 metric tons, 300,000 of the 1,113,000 schools can be attributed to adult anchovy alone (27%). Other common schooled fish in the CalCOFI area include anchovy juveniles, jack mackerel juveniles, bonito, Pacific mackerel, and Pacific sardine.

Work is currently proceeding on target strength estimates of entrapped and wild fish schools. Suitable estimates of fish school target strength should allow estimates of the horizontal dimension of the school parallel to the ship's track. Also, correlation of target strength and school area with the biomass of fish schools as determined by commercial purse seines should allow refinement of survey biomass estimates. We are also looking at the frequency-dependent element of target strength to assist in judging the approximate size of individuals which make up the school.

The results of this survey lead me to believe that with suitable restraints on time of day and range, sonar equipment can yield useful estimates on the location, number, and size of fish schools in the upper mixed layer.

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DISCUSSION

McElroy: I was curious about the correction factor which you call the edge effect. Could you just specify a bit more what this is?

Smith: If you have a width such as 200 to 450 m and if, in your analysis, you exclude any target which apparently ends at the edge of that, then that school has been eliminated from comparison even though it has protruded into your sample width. As a result any target that is 50 m thick has a great chance of falling over an edge, so it would be undersampled then as a result. Merely by saying that the 250 m is only available to the extent of 200 m, you are restricting targets, and by that proportion the number of 50-m targets will be increased.

Collard: Would you recapitulate the number of fish per cubic meter?

Smith: We have a trap that is 3-½ m by 7 m and about 9 m deep, so it is fairly large. There are four alternative methods of judging how the fish were arrayed in this trap. I reject the random distribution model where there would be 112 anchovies per cubic meter. Now if you take the second model, a prolate spheroid mass (which I like because the fellow who dumped the fish in there said that that is the way they looked to him), there are 1312 fish per cubic meter. I personally like this concentration. If you like the model in which a sphere is inscribed in the trap, that is 1113. If you like the reduced sphere model, the number of fish is 3721 per cubic meter, and that is at the time when we only put in 25,000 per trap. If you put in 150,000 fish per trap, the equivalent values on those were 637, 7500, 6300, and 21,000 per cubic meter. This may include some fish in side aspect, and they have a large bladder. I think you can see why we have such a nice sharp target.

Friedl: We've seen these echo groups in some of the echograms taken in the California Current system, especially at sunset and sunrise. I know that you are working in shallow water near the surface, but could you inform us about the behavior of anchovies? Would this be a likely suspect, and could we expect these very high numbers that you speak of in these echo groups?

Smith: I don't think that anchovy should be excluded from any part of the upper 200 m or so of the California Current. No one has ever, to my satisfaction, demonstrated the existence of deep anchovy with trawls because the trawls are fished open to the surface. Any time that you drag a net in the presence of 5 million metric tons of fish, you are going to get some of those fish. So I do not believe any of the trawl identifications that have ever been put out. I would say that they should be anywhere they would like to be.

Barham: We have seen large concentrations of anchovies at about 200 m.

Smith: That is good. That is the best information we have on anchovies.

Aron: A group of five or six brothers flies airplanes out of Santa Barbara spotting schools of anchovies and sardines. I wonder if you have been able to compare, say, a ground truth by talking to them, determining what they estimate the size of typical schools to be versus what you are estimating on the basis of your Simrad.

Smith: We hired an air spotter from Santa Barbara three weeks ago. Due to an unfortunate circumstance we had a thin scattering layer at about 20 m. The fish were all deployed on that. The fishermen were catching fish on that, and the airplane spotter could not find the fish. We hunted for four different hours on three different days, and he was unable to find fish at the surface, which was where the airplane could find them. This is one of the reasons that I know

that we are likely to see more fish than the air spotter. The air spotter is important in other regards. That is, he sees fish that the fishermen can catch. We would more than likely see all the fish with a sounder and sonar.

McCartney: The corrections for beamwidth and size of the target have been done for echo sounding on single fish by Cushing, as I am sure you are aware, but other people may not be. You have to measure the target strength to do the correction, but it can be corrected. However, the target strength of a shoal as looked at on its edge may not be the same as looked at right full in the beam. I do not know how this might vary, but I think that in your case it would make it very difficult to correct, unlike the case of a single fish.

Smith: I am sorry that I did not point out more of the difficulties since I have a naturally optimistic nature. It is difficult to say anything about a shoal's target strength until we have a theoretical description of what the effect is of a target having physical size. You know that when you are working with a layer, you use one correction for range, and when you are working with a point source, you use another correction for range. The shoal, it seems to me, is intermediate between those points, and the target strength estimate may rest on how you make the range correction. You have to make a first-order approximation, which I think this one slide did with the 10° cone. I think that until we find the effective size of that cone, we cannot tell what proportion of the cone the school is at any given moment. So I am sure you are quite right. The complexity is good here. While the complexity affects my work, it does not affect this paper, which is restricted to horizontal dimensions and abundance—how many and how big. When we start saying how many fish are within these schools and how strong these schools are, then we are in another paper, I hope.

APPENDIX I

TABLES I TO IV

TABLE I.

Abundance of Sonar Targets by Range and Pulse Frequency Taken on Ribbon Rock Grid, Catalina Island, October 8-10, 1968.*

Grid	Inclusive Time	Velocity (knots)	0-250	251-500	501-750	751-1000	1001-1250	Total
October 8, 1968								
1								
Leg 1	0840-0902	10.9	12	8	5	1		26
Leg 3	0916-0936	12.0	2	19	18	5	1	45
2								
Leg 1	0948-1011	10.4	10	11	11	5		37
Leg 3	1023-1045	10.9	22	31	22	16	14	105
3								
Leg 1	1056-1118	10.9	22	19	25	15	4	85
Leg 3	1132-1155	10.4	15	19	20	6	3	63
4								
Leg 1	1627-1649	10.9	7	3				10
Leg 3	1702-1724	10.9	4	22	1			27
5								
Leg 1	2240-2302	10.9	1	2	1			4
Leg 3	2318-2340	10.9	5	4	4	3		16
October 9, 1968								
6								
Leg 1	0224-0246	10.9	30	20	20	14	2	86
Leg 3	0302-0326	10.0	22	5	2	2	1	32
7								
Leg 1	0341-0403	10.9	2	2	3	1		8
Leg 3	0417-0439	10.9		1				1
8								
Leg 1	0721-0742	11.4	1		3	2		6
Leg 3	0756-0816	12.6	3	5	1			9
9								
Leg 1	0829-0851	10.4	10	6	12	6	2	36
Leg 3	0904-0924	12.0	8	10	14	4	1	37

*Frequency, 30 kHz; Range, 0-1250 m; Gain, RCG.

TABLE I. (Continued)

Grid	Inclusive Time	Velocity (knots)	0-250	251-500	501-750	751-1000	1001-1250	Total
10								
Leg 1	0938-1001	10.4	8	7	12	5	2	34
Leg 3	1015-1035	12.0	4	10	14	8	9	45
11								
Leg 1	1047-1109	10.9	17	14	18	13	7	69
Leg 3	1124-1146	10.9	7	6	17	13	6	49
12								
Leg 1	1159-1221	10.9	25	32	39	27	17	140
Leg 3	1236-1258	10.9	6	11	16	6		39
13								
Leg 1	1311-1333	10.9	10	34	20	13	1	78
Leg 3	1347-1409	10.9	10	12	10	4		36
14								
Leg 1	1422-1444	10.9	12	29	26	12	6	85
Leg 3	1458-1520	10.9		5	10	5		20
15								
Leg 1	1534-1556	10.9		7	4	1		12
Leg 3	1610-1632	10.9			3	1		4
16								
Leg 1	1645-1706	11.4		4	1			5
Leg 3	1719-1740	11.4	9	12	6	2		29
17								
Leg 1	1754-1816	10.9	9	9	6	1		25
Leg 3	1829-1850	11.4	2	4	3			9
18								
Leg 1	1903-1925	10.9	1	2	3			6
Leg 3	2238-2259	11.4	2	3	2	4		11
19								
Leg 1	2313-2334	11.4	3	6	8			17
Leg 3	2349-2410	11.4	5	7	16	6	1	35
October 10, 1968								
20								
Leg 1	0024-0045	11.4	4	4	7	7		22
Leg 3	0059-0121	10.9	6	5	5	6		22
21								
Leg 1	0134-0155	11.4	1	3	5	4	1	14
Leg 3	0211-0234	10.4	1	9	4	6	1	21
22								
Leg 1	0247-0306	11.4		4	6	3		13
Leg 3	0322-0344	10.4	1	3	4	3		11

TABLE I. (Continued)

Grid	Inclusive Time	Velocity (knots)	0-250	251-500	501-750	751-1000	1001-1250	Total
23								
Leg 1	0359-0420	11.4	1	2	2	1	1	7
Leg 3	0434-0455	11.4		2	2			4
24								
Leg 1	0508-0529	11.4		6	4	4	1	15
Leg 3	0542-0603	11.4	1	5	3			9
25								
Leg 1	0616-0638	10.9	7	10	4	8		29
Leg 3	0650-0711	11.4	1	4	3			8
26								
Leg 1	0723-0745	10.9		3	2	2		7
Leg 3	0759-0819	12.0		2	4	1		7
Totals			329	463	451	246	81	1570

TABLE II.

Abundance of Sonar Targets by Range and Pulse Frequency Taken on Ribbon Rock Grid, Catalina Island, October 21 and 22, 1968.*

Grid	Inclusive Time	Velocity (knots)	0-250	251-500	501-750	751-1000	1001-1250	Total
October 21, 1968								
1 D								
Leg 1	2338-2359	11.4		3		2		5
Leg 3	0015-0037	10.9	7	1	2			10
October 22, 1968								
2 D								
Leg 1	0049-0110	11.4	1	2	5	7	1	16
Leg 3	0127-0150	10.4	2	2	6	5		15
3 D								
Leg 1	0204-0225	11.4	6	14	5	5	6	36
Leg 3	0242-0304	10.9	4	8	3	4		19
4 D								
Leg 1	0317-0338	11.4	1	3	2	3	1	10
Leg 3	0354-0416	10.9	1	3	1	1		6
5 D								
Leg 1	0430-0453	10.4	1	1	3			5
Leg 3	0507-0528	11.4	1	2	1			4
6 D								
Leg 1	0540-0603	10.4	1	3	2	1		7
Leg 3	0616-0636	12.0	1				1	2
7 D								
Leg 1	0648-0711	10.4	5	9	2			16
Leg 3	0726-0747	11.4	18	9	8	5		40
8 D								
Leg 1	0759-0822	10.4	14	27	32	5		78
Leg 3	0836-0857	11.4	18	24	23	18	3	86
9 D								
Leg 1	0912-0934	10.9	25	33	26	26	5	115
Leg 3	0950-1012	10.9	17	20	23	12	1	73
10 D								
Leg 1	1025-1047	10.9	15	29	26	20	3	93
Leg 3	1102-1125	10.4	15	25	29	16	4	89
11 D								
Leg 1	1456-1518	10.9	18	24	13	11		66
Leg 3	1533-1556	10.4	8	20	16	9		53
12 D								
Leg 1	1608-1629	11.4	2	9	11	5		27
Leg 3	1644-1706	10.9	7	9	3	2		21

*Frequency, 30 kHz; Range, 0-1250 m; Gain, RCG.

TABLE II. (Continued)

Grid	Inclusive Time	Velocity (knots)	0-250	251-500	501-750	751-1000	1001-1250	Total
13 D								
Leg 1	1718-1741	10.4	4	7	13	3		27
Leg 3	1755-1816	11.4	9	11	6			26
14 D								
Leg 1	1828-1845	12.0	10	10	4	5	2	31
Leg 3	1906-1927	11.4	1	1	1			3
15 D								
Leg 1	1938-2001	10.4	2	2	2			6
Leg 3	2016-2038	10.9	1	3	1	1		6
16 D								
Leg 1	2049-2110	11.4		3	1	1		5
Leg 3	2128-2150	10.9	11	3	6			20
17 D								
Leg 1	2202-2224	10.9	3	1	3			7
Leg 3	2240-2304	10.0	6	8	2		3	19
18 D								
Leg 1	2316-2338	10.9		1	1		3	5
Leg 3	2351-2415	10.0	5	5	4	3	3	20
Totals			240	335	286	170	36	1067

TABLE III.

The Abundance of Sonar Targets by Range and Pulse Frequency Taken on Ribbon Rock Grid, Catalina Island, October 8-10, 1968.*

Grid	Inclusive Time	Velocity (knots)	0-500	501-1000	1001-1500	1501-2000	2001-2500	Total
October 8, 1968								
1								
Leg 1	0840-0902	10.9	22	5				27
Leg 3	0916-0936	12.0	14	8	3	2	1	28
2								
Leg 1	0948-1011	10.4	31	6	1			38
Leg 3	1023-1045	10.9	19	10	2			31
3								
Leg 1	1056-1118	10.9	20	7	1			28
Leg 3	1132-1155	10.4	19	7				26
4								
Leg 1	1627-1649	10.9	14					14
Leg 3	1702-1724	10.9	7					7
5								
Leg 1	2240-2302	10.9	2					2
Leg 3	2318-2340	10.9	2	1				3
October 9, 1968								
6								
Leg 1	0224-0246	10.9	8	1				9
Leg 3	0302-0326	10.0	3					3
7								
Leg 1	0341-0403	10.9	3					3
Leg 3	0417-0439	10.9	1		1			2
8								
Leg 1	0721-0742	11.4	3	5				8
Leg 3	0756-0816	12.0	3					3
9								
Leg 1	0829-0851	10.9	14	8				22
Leg 3	0904-0924	12.0	4					4
10								
Leg 1	0938-1001	10.4	12	10	2			24
Leg 3	1015-1035	12.0	13	1				14
11								
Leg 1	1047-1109	10.9	19	5				24
Leg 3	1124-1146	10.9	5	10				15
12								
Leg 1	1159-1221	10.9	21	8	2			31
Leg 3	1236-1258	10.9	8					8

*Frequency, 11 kHz; Range, 5-2500 m; Gain, RCG.

TABLE III. (Continued)

Grid	Inclusive Time	Velocity (knots)	0-500	501-1000	1001-1500	1501-2000	2001-2500	Total
13								
Leg 1	1311-1333	10.9	18	2				20
Leg 3	1347-1409	10.9	6	4				10
14								
Leg 1	1422-1444	10.9	13	4				17
Leg 3	1458-1520	10.9	13	3				16
15								
Leg 1	1534-1556	10.9	15	2				17
Leg 3	1610-1632	10.9	5	3				8
16								
Leg 1	1645-1706	11.4	8					8
Leg 3	1719-1740	11.4	7	1				8
17								
Leg 1	1754-1816	10.9	6					6
Leg 3	1829-1850	11.4	3	3				6
18								
Leg 1	1903-1925	10.9						0
Leg 3	2238-2259	11.4	2					2
19								
Leg 1	2313-2334	11.4	1	4				5
Leg 3	2349-2410	11.4	2	5				7
October 10, 1968								
20								
Leg 1	0024-0045	11.4	1	6				7
Leg 3	0059-0121	10.9	6	11	2			19
21								
Leg 1	0134-0155	11.4	1	4				5
Leg 3	0211-0234	10.4	7	5	2			14
22								
Leg 1	0247-0308	11.4	2	1	1			4
Leg 3	0322-0344	10.9	3	3				6
23								
Leg 1	0359-0420	11.4	3	1	1			5
Leg 3	0434-0455	11.4	1	2	1			4
24								
Leg 1	0508-0529	11.4		2	1			3
Leg 3	0542-0603	11.4						0

TABLE III. (Continued)

Grid	Inclusive Time	Velocity (knots)	0-500	501-1000	1001-1500	1501-2000	2001-2500	Total
25								
Leg 1	0616-0638	10.9		1	2			3
Leg 3	0650-0711	11.4	1	1				2
26								
Leg 1	0723-0745	10.9	1	2	1			4
Leg 3	0759-0819	12.0						0
Totals			392	162	23	2	1	580

TABLE IV.

Abundance of Sonar Targets by Range and Pulse Frequency Taken on Ribbon Rock Grid, Catalina Island, October 21 and 22, 1968.*

Grid	Inclusive Time	Velocity (knots)	0-500	501-1000	1001-1500	1501-2000	2001-1500	Total
October 21, 1968								
1 D								
Leg 1	2338-2359	11.4		2				2
Leg 3	0015-0037	10.9			1			1
October 22, 1968								
2 D								
Leg 1	0049-0110	11.4	1	6				7
Leg 3	0127-0150	10.4	1	2				3
3 D								
Leg 1	0204-0225	11.4	3	2				5
Leg 3	0242-0304	10.9	1	2	1			4
4 D								
Leg 1	0317-0338	11.4	1	4	1			6
Leg 3	0354-0416	10.9		1				1
5 D								
Leg 1	0430-0453	10.4	1	3	1			5
Leg 3	0507-0528	11.4	3	3	2			8
6 D								
Leg 1	0540-0603	10.4	1	2				3
Leg 3	0616-0636	12.0	3	3	1			7
7 D								
Leg 1	0648-0711	10.4	10	2				12
Leg 3	0726-0747	11.4	20	6				26
8 D								
Leg 1	0759-0822	10.4	26	8				34
Leg 3	0836-0857	11.4	29	14	1			44
9 D								
Leg 1	0912-0934	10.9	36	22	2			60
Leg 3	0950-1012	10.9	21	3	2			26
10 D								
Leg 1	1025-1047	10.9	31	15				46
Leg 3	1102-1125	10.4	34	12				46
11 D								
Leg 1	1456-1518	10.9	27	7				34
Leg 3	1533-1556	10.4	20	9				29
12 D								
Leg 1	1608-1629	11.4	19	10				29
Leg 3	1644-1706	10.9	18	1				19

*Frequency, 11 kHz; Range, 0-2500; Gain, ROG.

TABLE IV. (Continued)

Grid	Inclusive Time	Velocity (knots)	0-500	501-1000	1001-1500	1501-2000	2001-2500	Total
13 D								
Leg 1	1718-1741	10.4	16	4				20
Leg 3	1755-1816	11.4	26	5				31
14 D								
Leg 1	1828-1848	12.0	12	1				13
Leg 3	1906-1927	11.4	5	1				6
15 D								
Leg 1	1938-2001	10.4	2	1				3
Leg 3	2016-2038	10.9	1	1	3			5
16 D								
Leg 1	2049-2110	11.4	1	2				3
Leg 3	2128-2150	10.9	9	5	2			16
17 D								
Leg 1	2202-2224	10.9	3	4				7
Leg 3	2240-2304	10.0	10	2	6	2		20
18 D								
Leg 1	2316-2338	10.9	1		4	3	2	10
Leg 3	2351-2415	10.0	5	5	1			11
Totals			397	170	28	5	2	602

APPENDIX II

SEMINAR

ON FISHERY BIOLOGY AND OCEANOGRAPHY FOR PARTICIPANTS FROM ASIA, AFRICA, THE PACIFIC AREA, THE MEDITERRANEAN REGION AND SOME EUROPEAN COUNTRIES

Moscow

August-September 1964

METHODS OF DIRECT CALCULATION OF FISH CONCENTRATIONS BY MEANS OF HYDROACOUSTIC APPARATUS

Dr. Truskanov M.D.
Dr. Scherbino M.N.

Every method is in the long run determined by a complex of means and facilities available at the disposal of the investigator. New technical means of research provide a possibility of working out the new methods. Hydroacoustic fish detection techniques is one of them. Presently, various countries of developed oceanic fisheries designed perfect hydrolocation gear of high discrimination providing a dependable means of fish detection at any depths open for fisheries.

Since 1958 the authors were engaged in designing a hydroacoustic method of determination of numerical strength of fish both in dense and dispersed concentrations.

In 1961 this method was formally adopted for assessment of stock condition of Atlanto-Scandian herring.

The hydroacoustic method of determination of numerical strength of fish is a method of direct calculation of the number of fish in the shoal and it is largely free from the defects of other methods of direct calculation of numerical strength which had been known before. Earlier methods of strength determination had one big disadvantage: for determining the abundance of any stock of commercially important fish, the data were used that only indirectly characterized the quantitative composition of a given stock.

Accuracy of such methods depends on a great number of factors which very often cannot be quantitatively assessed.

The hydroacoustic method of determination of fish abundance is a direct method allowing one to obtain information on the numerical strength of fish in the given area of the sea by means of hydrolocators and electronic apparatus.

Commercially important fishes are known to form concentrations of different density, the range of density being very large: from one specimen per hundreds of thousands of cubic meters of water to a score or two in one cubic meter.

Pelagic fishes as a rule form denser concentrations in comparison with bottom fishes. It was generally observed that the density of a fish concentration is inversely proportional to the size of the specimens it is composed of. It is also known that density of concentration of this or that species of commercially important fishes depends on the season; thus, spawning shoals are almost always denser than feeding shoals, etc.

When dense local concentrations are formed on the spawning or wintering grounds the same number of specimens may become more evenly distributed over a considerably great sea area during the feeding period.

In this connection all echograms can be divided into two categories:

a) echograms of dispersed concentrations enabling one to conduct visual calculation of the number of fish within the range of operation of the echo-sounder.

b) echograms of dense concentrations which do not permit one to conduct visual calculation of the number of fish within the range of operation of the echo-sounder, though in this case the echo traces also provide some information on the number of objects of dispersion, i.e. fish.

Numerous commercially important species assemble in certain areas of the sea during certain periods in their life time and their concentrations may be patterned accurately enough by means of hydrolocators, i.e. it becomes possible to assess the size of such concentrations.

The methods of determination of the size of fish concentrations, both dense and dispersed, are similar, but the methods of determination of density are different.

Solution of the problem of determination of the number of fish in the stock is based on the knowledge of two main factors: the size and density of a fish concentration.

I. Determination of the Size of Fish Concentrations

The size of fish concentrations, pattern of distribution, and absolute density value are assessed by means of direct echometric survey, its time and area being mainly determined by the life history of the investigated species. In this case it is desirable to take such period of time when all the population or its main part is concentrated within the smallest possible area (pre-spawning or spawning concentrations), or to choose a period when the stock is distributed over a wider area, but with more even density (feeding period).

In each case the character of echometric survey is governed by the following factors:

a) biology of species (character of concentrations, migratory paths, seasons and so on),

b) size of the ocean area to be investigated,

c) technical capacities of fish-finding hydroacoustic apparatus (echo sounders and hydrolocators).

At first one or more vessels carry out reconnaissance echo survey covering the area deliberately larger than the area occupied by the concentration. This is done in order to determine more precisely the locality of different parts of the concentration, its vertical distribution and character of separate individual shoals.

In case of dense concentrations hydrolocators and echo sounders are used, whereas only echo sounders are applied in case of dispersed concentrations. One of the vessels at the same time carries out hydro survey in the area of operations. After the mean sizes of shoals and their frequency of occurrence are determined (as well as reliable range of direction finding minimum size shoals) in case of dense concentrations, the required number of echometric tacks and after that the number of vessels required for survey are calculated.

The main survey is carried out synchronously by all vessels; all observed shoals with their actual sizes taken horizontally and vertically are registered by each vessel on a detailed chart board. In case of dispersed concentrations, the size of each shoal is determined by a grid of tacks covering the location of the shoal. Each tack is intermitted 5-10 minutes after the termination of the last recording of fish by the echo sounder. In case of dense concentrations the size of a shoal is determined by means of a hydrolocator (echo ranging type) showing the horizontal extension

of the shoal by different tack angles. In this case, the number of tacks is considerably reduced, as well as the number of vessels participating in the surveys. A special method was developed for the correction of errors observed in determination of the size of fish shoal by means of echo rangers and echo sounders, and a special adjustment table was prepared for quick determination of the actual size of each shoal.

The actual size of each shoal is determined by its horizontal and vertical extension and the total size of the concentration is estimated by summing up the sizes of individual shoals. Then the summary chart board of echo survey is prepared.

It must be noted that this survey requires a higher degree of navigation skill, as the latter may greatly effect the accuracy of this method.

In this way we determine the first main parameter of a concentration - its size.

II. Determination of the Density of Fish Concentration

The second main parameter, the density of a concentration, is determined by different methods depending on what sort of concentration (dispersed or dense) is subjected to echo survey.

1. Determination of the density and number of fish in dispersed concentrations

In case of dispersed concentrations the following method is used: the number of fish simultaneously observed within the echo range is read from an echogram. For this purpose, a chart of the direction of the transceiver system of the echo sounder is calculated first; then basing on the analysis of traces of separated individual specimens, the area of operation of the echo sounder is determined. The area of operation is similar in form to the direction chart of the transceiver system, but it shows in addition, what part of a space under the vessel's keel is controlled by the echo sounder. In this way, it is possible to determine the volume of water mass under the vessel's keel in which the number of individual specimens of the given concentration is registered after each sound impulse emission. Different types of echo sounders have different direction charts and, consequently, different areas of operations. The authors suggested a method of determination of the area of operation of any echo sounder from the data of its direction chart and from the data on reflecting capacity of an object subjected to echo-sounding. It must be born in mind that the area of operation of the echo sounders should be determined in advance by all vessels participating in the survey. These pre-calculated areas of operation of the echo sounders to be used for locating a concentration serve for determination of the vertical range of operation by the upper and lower edges of the surveyed concentration. The height of the layer where concentration found is obtained from the echogram. The speed of the vessel at the moment of echo tracing of fish and the period of echo sounding are also registered. Consequently, the volume of water explored by the echo sounder can also be determined. The echogram serves to calculate the number of fish registered by the echo sounder during the same period. After these data are obtained, the density is determined as the ratio of the number of fish to the value of water volume:

$$\rho = \frac{N}{v}$$

where

ρ = density; number of fish/m^3

N = number of fish

v = volume; m^3

Sometimes, it is more convenient to use an inverse ratio, i.e., the volume of water per one fish:

$$\frac{1}{\rho} = \frac{v}{N}$$

In surveys of disperse concentrations, it is advisable to choose such moments when all or main parts of the concentration is found off the bottom (at some stages of vertical migrations).

This is recommended because the rough ground may to some extent obscure the echo traces on the echogram produced by the fish at the bottom.

If the roughness of ground is great and the major part of specimens of a dispersed concentration keep close to the bottom, it is necessary to resort to some special measures, e.g. to use different types of echo sounder selectors of bottom traces: the "white line", "differential chain", "fish filter" types, etc. If the echo survey is taken during the period when fish keep in midwater, all specimens of fish are clearly traced by the echo sounders and may be easily read on the echogram. After the determination of distribution of density along the echo tacks is completed, the isolines of equal density are drawn on a chart board. The size of each part of the shoal between the isolines is calculated. The size and density being known, it is possible to calculate the number of fish in each part of the shoal, and then the number of fish in the whole concentration.

The size and age compositions of the concentrations are defined more precisely by means of experimental catches and analysis of echo traces.

2. Determination of density and numerical strength of dense concentrations

As the accuracy of determination of the number of fish in the size unit has a decisive importance in case of dense concentrations, three different methods of density determination were worked out which mutually supplement and define each other.

The first method of determination of the absolute density is based on a combined use of an automatic underwater camera and an echo sounder. By calculating the number of fish in one still photograph and having estimated in advance the volume of water where specimens are registered, one can calculate the density with sufficient degree of accuracy.

In practice, it is done as follows: the underwater camera is lowered into one and the same layer now and then occupied by shoals of different density which serve for measuring the amplitude of receiving the echo by means of echo sounder and electronic oscillograph.

From the data so obtained, the relation of the amplitude of the incoming echo received by the echo sounder amplifier, the density of stock is determined.

The second method is based on placing the transceiver system of the ship's echo sounder directly amid the concentration of fish which greatly improves the angular discrimination of the echo sounder, owing to the lesser number of objects within the operation range in comparison with the method of operation from the surface.

This allows to apply the method used for dispersed concentrations and to determine the density. An outboard echo sounder operates simultaneously with the ship's stationary echo sounder equipped with an electronic fish-tracer. Their indices are used for determining the relation of the amplitude of the incoming echo received by an amplifier to the density of the concentration.

The third method is based on density determination by means of the echo sounder, calibrated in advance with standard equi-models that had been selected on the basis of experimental data and the data derived from calculations.

In this case the degree of dispersion, the area of reflecting surface and the coefficient of fish reflection are taken into account. In density determinations, especially during the first echometric surveys, it is advisable to use the data obtained by all three above-mentioned methods. These data are used for calculating the relation of the value of the incoming signal to the density of fish concentration by means of the following formula:

$$Uinc = K\sqrt{\rho}$$

where

Uinc = amplitude of the incoming echo received by the echo sounder in μv

K = coefficient

ρ = density in specimens per m^3 – (Fig. 1).

Empirical coefficient K is obtained as a result of statistical treatment of experimental data; it characterizes the acoustic and electric properties of the echo sounder and the acoustic properties of the given fish concentration.

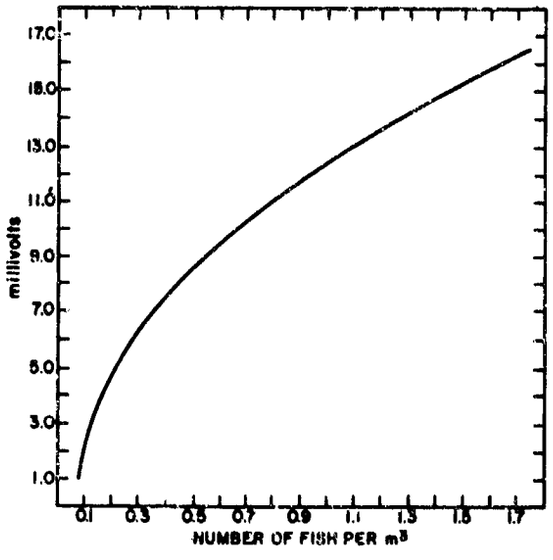

Figure 1. Graph shows the relation of echo trace to density of concentrations. Data were obtained during investigations in the North Atlantic area

In case of Atlanto-Scandian herring K = 12.65 (for HAG - 240 echo sounder). The above methods are used for determination of density in the course of echometric surveys. It is also possible to determine the relative density during the survey by means of the electronic fish-tracer of the echo sounder or by a special oscillograph switched to the echo sounder amplifier. By a simple calculation relative density is converted into the absolute density with the help of the above U_{inc}/ρ ratio.

The next stage is a precision treatment of the data obtained which is done along the following general line: horizontal and vertical sections of fish concentrations are plotted and the density values are entered after the corrections were made for navigation and instrumental errors. Then, zones of equal density are plotted and the size of each zone is calculated separately. Then the number of fish is determined first in each zone, then in the shoal and, finally, in the concentration as a whole. Size and age compositions of the concentrations are defined by control trawlings. Finally, the number of fish converted in weight units is determined.

This is a general outline of the sequence of operations of hydroacoustic method of calculation of stock abundance in dense and dispersed concentrations. Some results of its application are given below with a view to illustrate the advantages of this method.

RESULTS

Methods of determination of the numerical strength of dispersed concentrations were tested in different parts of the Barents Sea. Surveys were conducted on concentrations which as a result of vertical migrations were scattered in water thickness. Control hauls by the bottom trawl produced catches of a few specimens. As a result of echo surveys the numerical strength of separate local concentrations was defined.

Thus, the concentration in shallow waters near Murmansk numbered about 200,000 specimens of average size cod that kept in the near bottom layer, its density being in the order of 0.32×10^{-4} specimens/m^3.

Concentrations of big size cod on the Pinmarken Bank numbered about 308,000 specimens which were distributed with density 0.12×10^{-4} specimens/m^3. Cod concentrations of Rybachya Bank was composed of 102,000 specimens of even size cod with density 0.63×10^{-4} specimens/m^3. In 1962, an echo survey was carried out in the eastern coast area. The observed concentrations numbered about 73,000 small-sized cod and haddock specimens with mean density 0.78×10^{-4} specimens/m^3.

Small-scale operations were conducted during the echo surveying of wintering concentration of Atlanto-Scandian herring in the Norwegian Sea, north of the Faroes. This work was stared in 1958 and continued in 1961, 1962, and 1963.

Surveys were made by the leading vessel of BMRT type and about 7-10 control vessels of SRT type. The results of the survey are given in Table I.

CONCLUSION

In conclusion it is necessary to dwell in more detail on the possibilities and prospects of this method. While the other methods of direct determination of numerical strength are based on the theory of random sampling and are limited by the number of samples (possible number of

TABLE I

Index	1958	1961	1962	1963
Mean vertical size of the concentration in m	70	85	80	115
Total area occupied by the concentration in m^2	260×10^6	142×10^6	268×10^6	221×10^6
Total size of the concentration in m^3	18.5×10^9	12.1×10^9	21.4×10^9	20.9×10^9
Average density of concentration, specimens/m^3	1.0	0.75	0.68	0.77
Abundance of herring stocks in tons	6.03×10^6	2.50×10^6	2.80×10^6	3.00×10^6

Forecastings on abundance of stocks and fishing efficiency based on data of echometric surveys have fully come true.

experimental trawlings or purse seine hauls, etc.), the number of samples in hydroacoustic method amounts to a very high value (a few scores per minute), because every impulse of the echo sounder is, in a sense a sample by itself. While in determinations of the density of a concentration by means of experimental trawlings, the result may depend on a large number of factors, e.g. on the selection of the area of fishing on the design and catching capacity of fishing gears, etc., in our case there is a possibility to determine accurately enough the density and the limits of each concentration throughout the area occupied by the concentration. Basing on the result of this work, it seems possible to determine the numerical strength of any concentration with no less degree of accuracy than 10-15% if the number of vessels available is sufficient and if the echo survey is taken thoroughly enough.

As this method requires the synchronous survey, the time allocated to such survey should necessarily be kept to a minimum, because a re-distribution of concentrations may result in errors that cannot be taken into account. In practice, such survey is done within 1 or 2 days.

This method does not require too much effort except for a rather complicated process of treatment of the data obtained. Presently, the authors are working at the methods of automation of the process of collection and treatment of material.

The experiment echometric surveys in the conditions of the Barents and Norwegian Seas showed that this method can be successfully applied for determining the numerical strength of a number of pelagic and bottom fishes in different areas of commercial fisheries.

SONIC-SCATTERING STUDIES IN SAANICH INLET, BRITISH COLUMBIA: A PRELIMINARY REPORT

B. McK. Bary* and R.E. Pieper
Institute of Oceanography
University of British Columbia
Vancouver 8, British Columbia, Canada

ABSTRACT

The studies of sound scattering by marine organisms carried out by the Institute of Oceanography, University of British Columbia, have been directed towards the zooplanktonic community and to understanding the roles of fishes and zooplankton in scattering. The present study, begun in 1966, has been carried out in Saanich Inlet on the southeast coast of Vancouver Island, British Columbia. The frequency-dependent nature of the scattering has been studied with echo sounders operating at 11, 44, 107, and 197 kHz. The present paper deals with distributions of zooplankton and fishes relative to scattering recorded at 197 kHz. Both diffuse and fish scattering have been recorded from the near-surface and midwater depths in Saanich Inlet. The diffuse scattering near the surface is associated with larval fishes and copepods less than 0.5 cm long, whereas that at the midwater depth is correlated with high numbers of euphausiids. Deeper fish scattering is associated with juvenile and/or adult myctophids. Scattering layer migration also is discussed and correlated with zooplankton movement.

INTRODUCTION

The studies of sound scattering by marine organisms, carried out by the Institute of Oceanography, University of British Columbia, have been directed towards the zooplanktonic community and to understanding the roles of fishes and zooplankton in scattering. Several types of organisms have been suggested as possible scatterers besides fishes; these include euphausiids and other crustaceans (Boden, 1950; Moore, 1950), physonectid siphonophores (Barham, 1963, 1966), and squid (Lyman, 1948). Some investigators have found high concentrations of zooplankton from the depths where strong scattering is recorded. The crustacean *Euphausia pacifica*, for example, was reported to be the most significant planktonic component in a sonic-scattering layer recorded at 12 kHz by Boden and Kampa (1965).

Hersey and Backus (1962) suggest that fishes are the most likely scatterers in the deep scattering layer (DSL) recorded at frequencies around 12 kHz. They also find it highly improbable that, at this frequency, euphausiids would be the scattering agent in these layers. Bary (1966) compared the vertical distribution of both euphausiids and amphipods with the locations of a 12-kHz scattering layer in Saanich Inlet. Because he found no consistent relationship between the recorded scattering and the biomass or numbers of specimens, he concluded that zooplanktonic organisms of lengths up to 2 cm were not causing backscattering of sufficient intensity to be recorded at that frequency.

*Present address: Department of Oceanography, University College, Galway, Ireland

The use of echo sounders at frequencies greater than 30 kHz has been infrequent in studies of the relationship between acoustic scattering and the distributions of either fishes or zooplankton. Barraclough, LeBrasseur, and Kennedy (1969) concluded that shallow scattering layers recorded at 200 kHz in the Pacific probably resulted from zooplankton, primarily copepods, in concentrations up to 150/m^3. A 200-kHz sounder was also used by Northcote (1964) to record the distribution of *Chaoborus* larvae in a lake; but the existence of a gas bubble in the head of the organism makes its acoustical characteristics considerably different from the marine crustaceans of interest in our work.

The present study, begun in 1966, has been carried out in Saanich Inlet on the southeast coast of Vancouver Island, British Columbia. The inlet provides a favorable location for such studies because of the occurrence of large populations, usually separately stratified, of both fishes and euphausiids (mainly *E. pacifica*) at relatively shallow depths (Herlinveaux, 1962; Bary, 1966). Echo sounders operating at 11, 44, 107, and 197 kHz have been used to study the frequency-dependent nature of the scattering. A comprehensive report of the first part of this study will be published elsewhere. The present paper deals only with distributions of zooplankton and fishes relative to scattering recorded at 197 kHz.

MATERIALS AND METHODS

The echograms were recorded using three Ross Fineline[1] sounders and recorders at frequencies of 44, 107, and 197 kHz, plus a Gifft (GDRT) transceiver recorder, operating via the transducer of an 11-kHz Simrad (EH_4R) echo sounder.[2]

The primary biological sampler was the instrumented Catcher (Bary and Frazer, 1970) which collects discrete samples at depth. The filters used were either 2.5 or 16 mesh/cm (mesh opening 2.16 mm or 0.47 mm). Instrumentation on the sampler enabled information to be recorded (throughout all tows) on depth, temperature, the number of flowmeter revolutions and the rate of flow through the net. The volume of water filtered was calculated from the observed flowmeter counts. The signal from the depth unit was fed to the Ross echo sounder and transformed to provide a trace of the sampler depth simultaneously with the recording of scattering during the sampling operations. The depth unit on the sampler and the echo sounder were intercalibrated so that the trace of depth from the sampler is related directly to depth as shown by the echo sounder.

Biological collections also were obtained from a 6-foot Isaacs-Kidd midwater trawl (mouth area 2.9 m^2) and a ring net of 1-m diameter. Neither could be closed, and therefore collections from one depth may have been contaminated by specimens from a shallower depth. The depth-and-temperature instrument package was attached to these two samplers.

Biological samples were preserved on the ship in 5% formalin and later analyzed in the laboratory. Specimens over 0.5 cm long were counted and sorted into the following major groups: euphausiids, amphipods, decapods, chaetognaths, and siphonophores. Specimens of all groups less than 0.5 cm in length were classed as residue. Fishes and fish larvae were counted separately, measured, and examined for the presence of a swimbladder. After sorting, the zooplankton samples were drained and blotted, and the wet weight was determined. The number of organisms per cubic meter of water filtered for the Catcher collections have been determined (Figs. 1 and 2). Collections of fishes and fish larvae for all samples are presented in Figures 3 and 4 as the number of fishes per nautical mile of distance towed. The present study is concerned with only crustaceans, fishes, and fish larvae, these being the probable scatterers.

[1] Ross Laboratories, Inc., Seattle, Washington.
[2] Simonsen Radio A.S, Oslo.

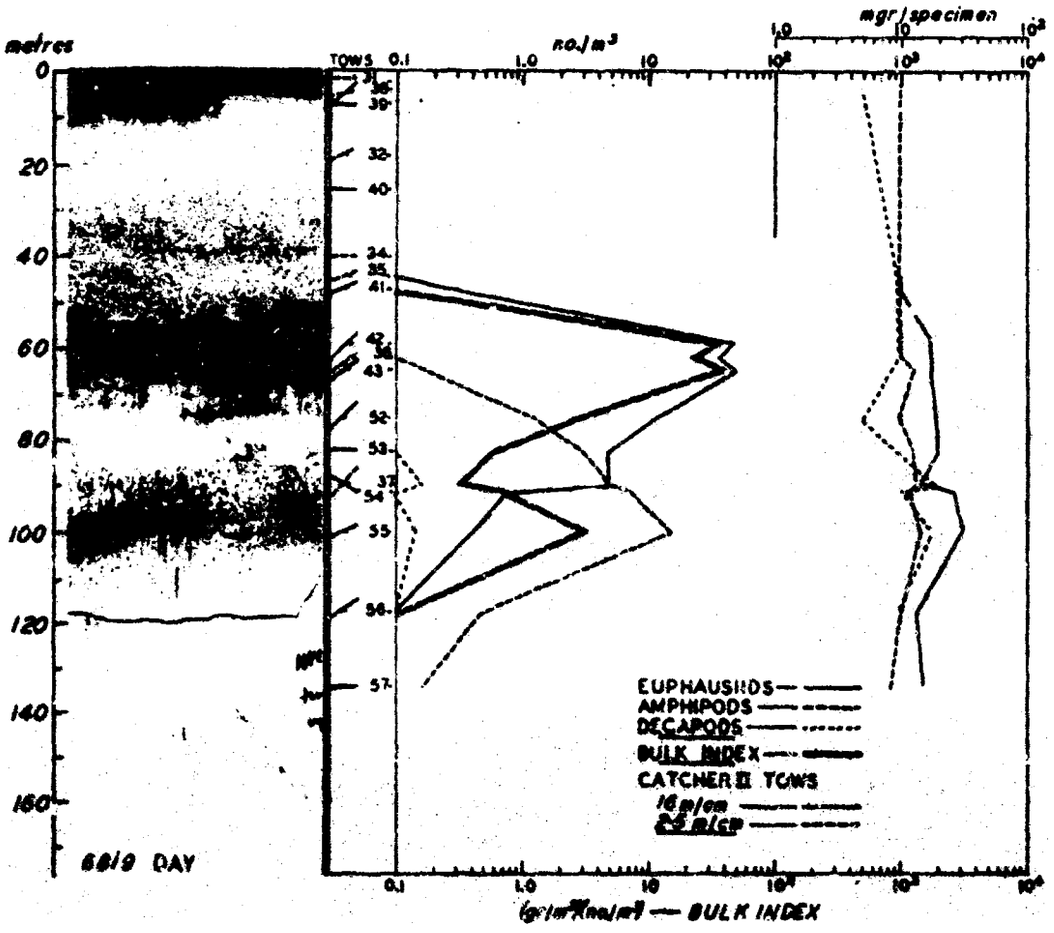

Figure 1. Zooplankton: Number per cubic meter, total bulk index, and mean wet weights per individual per sample; day series of tows made during March 30 to April 2, 1968 (cruise 68/9)

Numbers per cubic meter or per nautical mile and the mean wet weight of the organisms (Catcher only) for any given tow have been plotted against the location of the scattering recorded at the time of the tow. In Figures 1 to 4, the scattering shown in the panels is typical of that recorded during the series of tows included in the particular figure. A bulk index has been calculated by multiplying the number per cubic meter by the weight per cubic meter (Catcher only). This index has been devised to enable both size (weight) and abundance of zooplanktonic organisms to be considered with respect to their potential as scatterers.

RESULTS AND DISCUSSION

Results to date indicate that at the higher frequencies (197, 107, and sometimes 44 kHz), scattering is recorded from both fishes and zooplankton, whereas at the lower frequencies (11 kHz and sometimes 44 kHz), scattering is only from fishes. The Ross sounders have been operated with a narrow beam angle (5° by 10°) and a short pulse duration (0.1 msec) with an obvious increase in resolution. The result has been to minimize the overlapping and summing of single fish echoes. When summing and overlapping occur, they tend to produce a diffuse scattering that may mask, and can be confused with, the high-frequency "zooplanktonic" scattering.

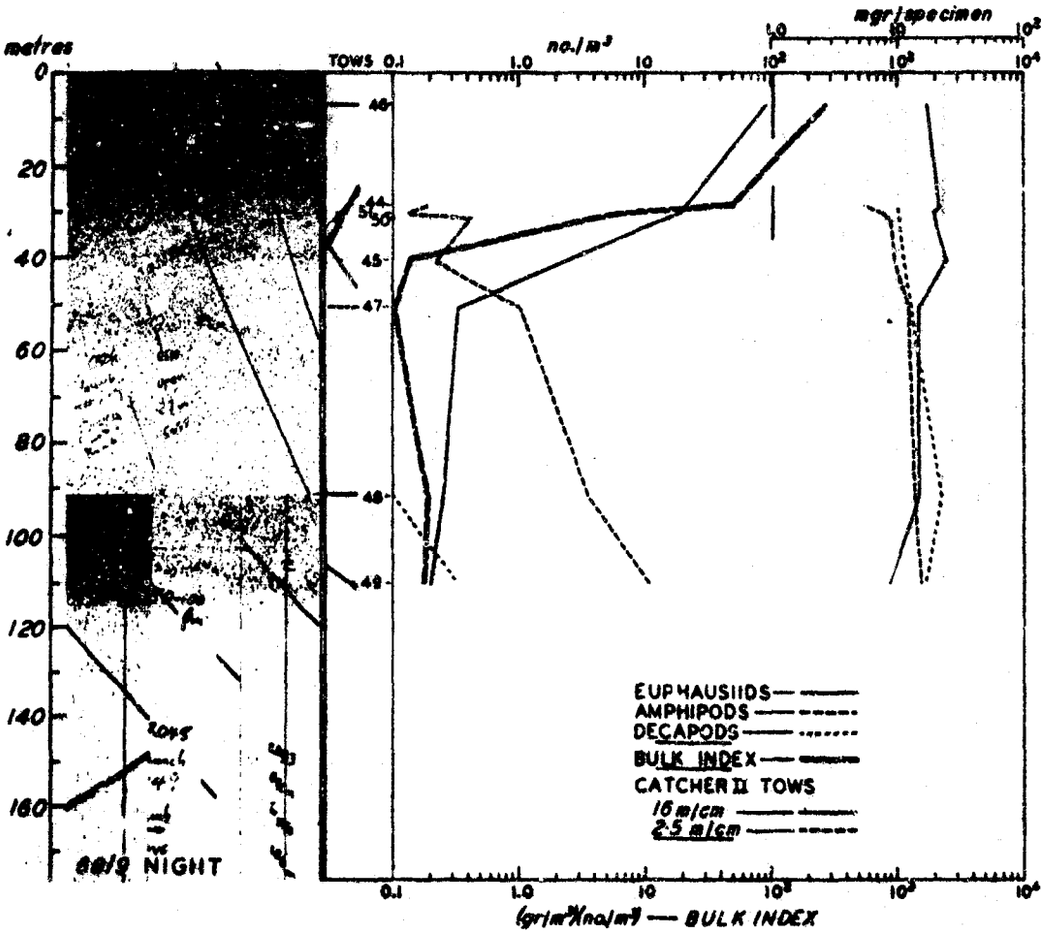

Figure 2. Zooplankton: Number per cubic meter, total bulk index, and mean wet weights per individual per sample; night series of tows made during March 30 to April 2, 1968 (cruise 68/9)

The high resolution obtained from the present sounders enables echoes of single fishes to be discerned within the diffuse scattering produced by the zooplanktonic organisms.

The distributions of zooplankton collected by the Catcher with respect to the 197-kHz scattering during the day are shown in Figure 1 and during the night in Figure 2. The distributions of fishes (all samples) and the zooplanktonic residue (collected by the Catcher using the filter of 16 mesh/cm) with respect to the scattering during the day are shown in Figure 3 and during the night in Figure 4. Table 1 lists the fish species collected from different depth ranges and indicates whether or not a swimbladder is present. The figures and table present data obtained during one 2-week cruise in March 1968 (cruise No. 68/9).

Figure 1 shows the distribution of euphausiids (mainly *E. pacifica*) to be maximal between 55 and 65 m (45/m^3), which corresponds with the scattering layer at that depth. The number of euphausiids per cubic meter falls off rapidly above and below this depth range. Similarly, scattering around 100 m appears to correspond with a maximum catch of amphipods (15/m^3) at that depth.

The night distribution of zooplankton (Fig. 2) is maximal at 0 to 30 m in concentrations of 50 to 250/m^3. This corresponds to a shift in the diffuse scattering from the day depth of 55 to

TABLE 1

Fishes caught in daytime tows at different depth ranges (cruise 68/9).

Fishes	Swimbladder	Number of fishes collected and their mean length in millimeters (in parentheses)					
		0-40 m	41-58 m	59-70 m	71-89 m	90-102 m	103-110 m
Clupea pallasii	Yes	3(10)			1(11)		
Myctophids (primarily *Stenobrachius leucopsarus*)	Yes	1(10)				29(46)	25(47)
Merluccius productus	Yes						1(83)
Theragra chalcogrammus	Yes	65(6)					
Sebastodes sp.	Yes	41(5)					
Leuroglossus stilbius	No	2(8)			1(8)	6(33)	47(37)
Hexagrammidae	No	1(8)					
Ophiodon elongatus	No	2(14)					
Gilbertidia sigalutes	No	5(17)	4(28)			1(30)	
Liparis fucensis	No	1(5)		2(5)			
Bathymaster signatus	No	14(10)					
Stichaeidae (4 sp.)	No	88(15)					
Pleuronectidae	No	2(9)					

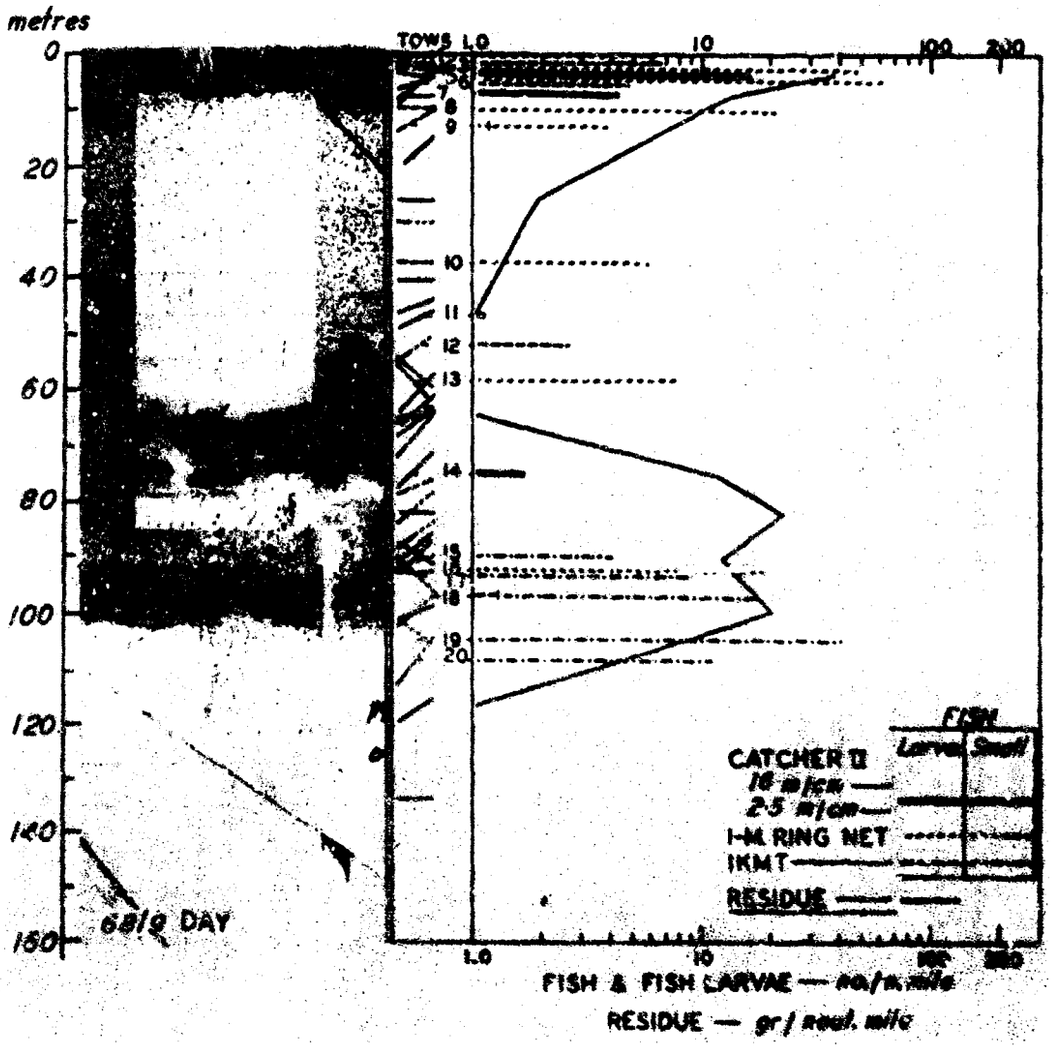

Figure 3. Fishes and fish larvae: Calculated number per nautical mile of tow for three samplers; day series of tows made during March 30 to April 2, 1968 (cruise 68/9)

65 m. The distribution of amphipods has spread upwards over a wider range of depths but is still maximal at 100 m (10/m^3).

Fishes and fish larvae caught during the day are plotted in Figure 3. High concentrations are found near the surface (up to 50/n. mi.) and around the 10 m scattering zone (40/n.mi.). Fishes between the surface and 40 m were predominantly *Theragra chalcogrammus* and *Sebastodes* sp. (both with swimbladders) and larval Stichaeidae (without swimbladders). These were all larval stages up to 2 cm in length (Table 1). Fishes collected from 90 to 102 m were predominantly juvenile and adult myctophids, primarily *Stenobrachius leucopsarus* (swimbladder present) and some juvenile *Leuroglossus stilbius* (swimbladder absent). Below 102 m, *L. stilbius* was present in highest numbers. *Stenobrachius leucopsarus* was also collected from this depth, though its occurrence possibly results from contamination. Fish larvae collected from 60 m (the zone of high-frequency scattering associated with high numbers of euphausiids) consisted only of *Liparis* sp., which have no swimbladders. Only two specimens were collected from this depth. This might be a result of contamination, because *Liparis* sp. were also collected in surface waters.

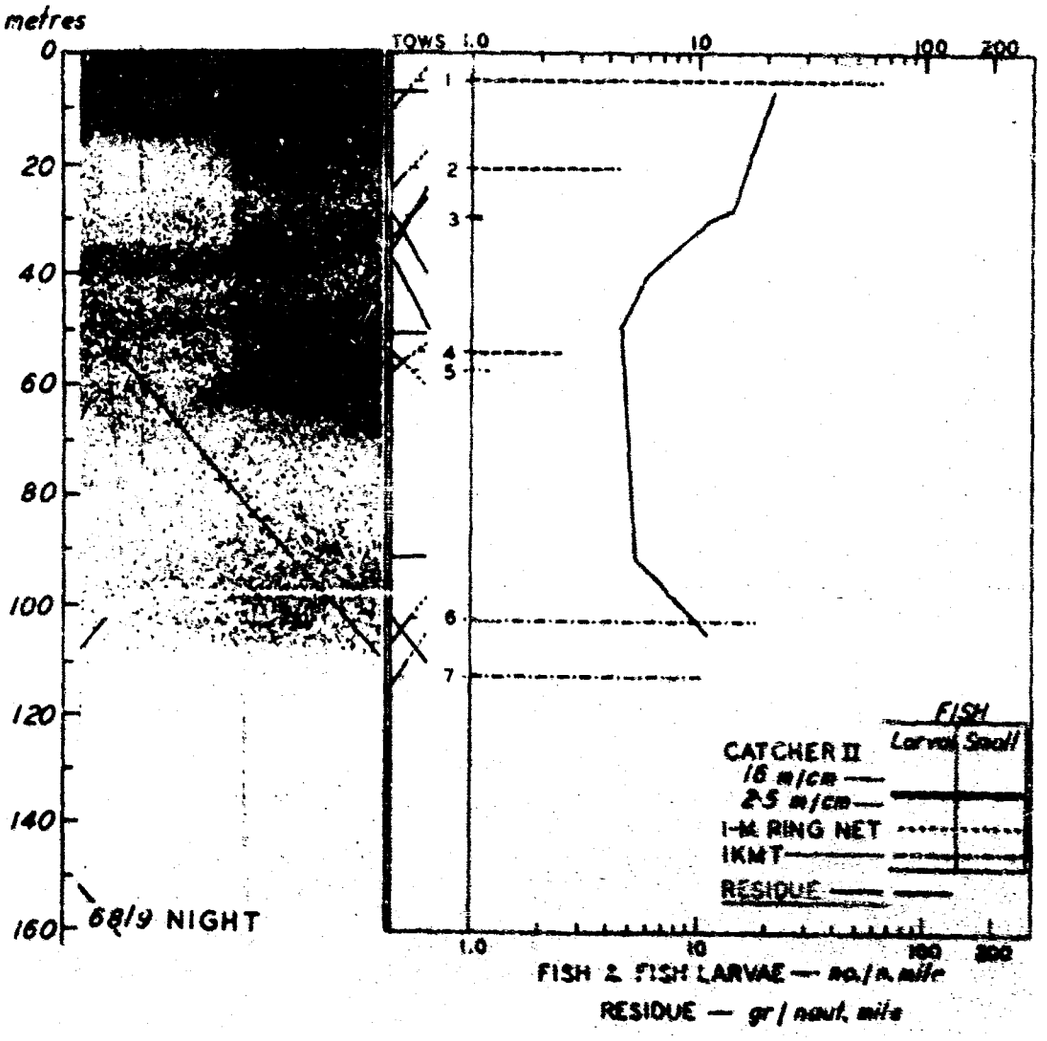

Figure 4. Fishes and fish larvae: Calculated number per nautical mile of tow for three samplers; night series of tows made during March 30 to April 2, 1968 (cruise 68/9)

The distribution of fishes and fish larvae at night (Figure 4) shows high concentrations between 100 and 120 m. The species collected were again primarily *S. leucopsarus* and *L. stilbius*. The former was predominant around 100 m, whereas *L. stilbius* was generally more abundant at a deeper depth.

Concentrations of zooplankton residue from the Catcher samples were large in both the day and night series near the surface (0 to 30 m) and at the depths of 70 to 110 m. The major component in the residue from both depth ranges were copepods less than 0.5 cm in length.

Physonectid siphonophores were not found in any samples from cruise 68/9. Physonectid pneumatophores and nectophores, present sparsely in collections from other cruises, could not be correlated with any particular scattering layer.

The results indicate that the scattering layer evident at 197 kHz during daylight is associated with high concentrations of euphausiids, which are probably the primary scatterers. Fish larvae (*Liparis* sp.) collected at this depth have no swimbladder and were less than 0.5 cm

long; thus, they probably do not contribute to the recorded scattering. Fishes and fish schools have appeared in this layer on other cruises, but were not prevalent during 68/9.

The scattering centered around 100 m is correlated with both fishes and amphipods. It is suggested that the darker, spotlike traces on the echograms at this depth are from fishes and/or fish larvae, whereas the more diffuse scattering may be from amphipods. Because myctophids, usually *Stenobrachius leucopsarus*, have also been suggested as the major source of scattering by others (Barham, 1966; Hersey and Backus, 1962; Taylor, 1968; Tucker, 1951), it is probable that these fishes are the source of fish scattering at this depth.

Scattering near the surface during the day may be caused by the presence of fish larvae (many with swimbladders) or from large numbers of copepods (as suggested by Barraclough et al., 1969). The near-surface scattering at night could result from these organisms and from fishes; the major portion of the scattering, however, probably results from the very high numbers of euphausiids that have migrated into the upper levels.

SONIC-SCATTERING: PART TWO (WORK IN PROGRESS)

In part one of this study the scattering was recorded graphically by means of the four echo-sounder systems. Although the graphical records are adequate to show scattering-layer depths, they do not enable measurements of backscattering intensities. Variations in scattering intensities are recognized only as darker or lighter marks on the recording paper, and the dynamic range of even wet papers is not wide. Furthermore, attenuation of underwater sound varies with frequency and other factors. The result is that records are uncalibrated and are useful only for broad, qualitative comparisons of the scattering at the four frequencies.

The second part of the study has been in progress for one year. In this part, qualitative studies are being continued and have been extended to include quantitative features of zooplanktonic scattering. The complete echo-sounding system has been calibrated. The sounders have also been modified to obtain the returning acoustic signal before it has been altered to suit the requirements of the graphic recorder. The signal reflected from the scattering layers is recorded on magnetic tape for analysis in the laboratory. The total reflected acoustic energy (intensity) will be obtained from these tapes by integrating the recorded signal over the thickness of the layer. These intensities will then be corrected mathematically for differences dependent on frequency, pulse duration, and beam angle among the sounders. The scattering intensities at the four frequencies are to be compared and correlated with the distributions and abundance of organisms.

Variations in scattering intensity on a daily and seasonal basis will be studied with respect to changes in the composition of the zooplanktonic population at scattering-layer depths. These variations may result from changes in species composition, in the numbers of one or more species, or in the size distribution of species. The sensitive equipment now being used for the recording of scattering should enable even minor fluctuations in one or more of these factors to be observed.

SUMMARY

Both diffuse and fish scattering have been recorded from the near-surface and midwater depths in Saanich Inlet using a Ross echo sounder of 197 kHz.

Diffuse scattering near the surface during the day is associated with collections of larval fish, and copepods less than 0.5 cm long.

Deeper fish scattering is associated with juvenile and/or adult myctophids, primarily *Stenobrachius leucopsarus*.

A midwater diffuse scattering layer recorded during the day is correlated with high numbers of euphausiids (mainly *Euphausia pacifica*) and few, if any, fish or fish larvae.

At night *E. pacifica* migrates to the surface. The midwater diffuse scattering layer recorded during the day also migrates to the surface waters and is correlated with the euphausiid distribution as well as with concentrations of fish larvae and copepods.

Deep, weak, diffuse scattering, both day and night, is probably from moderate numbers of amphipods; but at times, scattering from this depth cannot be separated from the fish scattering.

ACKNOWLEDGMENT

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DISCUSSION

Raymont: I accept the fact that you are recording euphausiids. The last figure showed that you apparently had some fish schools. These are presumably very small fish, are they not? If so, what are they?

Pieper: I really can't tell you what they are at the moment. I don't think that we have done enough work in the area to be able to tell. One bit of information that I can give you is that during one cruise in Saanich, Ed Barraclough collected fishes with an otter trawl concurrent with our biological sampling. He caught up to 2000 pounds of hake at a depth below our high-frequency scattering layer. At this deeper depth, scattering was recorded on all four echo sounders. Also, on another cruise, unfortunately not the same one, I saw large schools swimming in and out of the high-frequency scattering layers and thought maybe they were hake. We were able to dip net and jig some hake near the surface shortly after sunset. I cut them open and found that the stomachs were full of euphausiids. Now how good an indication this is you can determine. But we really haven't done enough work with the bigger nets in trying to catch the bigger fish to be able to tell what is there.

Friedl: This is a point of information. Some similar work using a 100-kHz Ross echo sounder is being conducted by the University of Washington in Puget Sound. It is interesting that you had variability from inlet to inlet. Within the Puget Sound system there seems to be month-to-month, or even week-to-week, variability in returns presumably caused mainly by euphausiids, and from year to year the numbers taken at a given location may vary by orders of magnitude. Apparently, yearly local variations in primary productivity, river runoff and the like can greatly influence the local populations of euphausiids in restricted areas such as Saanich Inlet or Puget Sound.

Pieper: We recognize that Saanich Inlet is very wierd. As I mentioned briefly the other night, a recent study at the University of British Columbia (Gilfillan, Ph.D. thesis, 1970) indicates that the euphausiids in Saanich are probably a resident species. They appear to "like" the water that's in Saanich better than the water you might find in the Strait of Georgia, in Juan de Fuca Strait, or out in the open Pacific. It appears that the Saanich population is a semistable one. It is true that the numbers vary over the period of a year, but during the last three years we've been there, it is semipredictable; it doesn't seem to vary all that much. It appears also that we are not getting too large an influence due to outside euphausiids coming in. The sergestids, pasiphaeids, lanternfish, and probably the smelts that are caught in Saanich appear not to breed there but to come in only during certain periods; they are probably oceanic forms that have moved in. Again, Saanich is rather wierd. It is nice to work in, but we definitely have to get out of there to make some general remarks about the animal life.

Love: I would like to ask Dr. Raymont why he assumed that they should be small fish.

Raymont: I thought we were talking about schools here, and these are single fish, presumably.

Pieper: At times we see single fish, as represented in these echograms; at times we see schools of fish; at times we see huge echoes that can completely overwhelm a scattering picture, and this will vary from time to time. I think that when hake are there you see large schools. The one that was represented here was not a large school compared to some of the other ones we have seen. We really do not have enough information on the distribution of fishes; scattering, and therefore fish distribution can be quite variable between cruises.

Love: The reason I asked is because Dr. McCartney and I were talking at lunchtime, and it is our opinion that a number of people, whenever they get an echo on an echo sounder or sonar, feel that it has to be a resonant scatterer. Those fish would have to be very small to resonate at 200 kHz.

Pieper: That is right.

Love: And you can get quite a nice echo at 200 kHz from a large fish. We would like to emphasize that once more.

Pieper: Going along with your point there in a way is the fact that the fish echoes at the lower frequencies, especially the 42 kHz compared to the 200 kHz, are much, much stronger when we record "planktonic" scattering at equal intensities. Involved in this is the fact that the euphausiids are a much better reflector at the higher frequencies. In order to get the same type of record of the high-frequency scattering at 200 kHz, we don't have to look at the fish quite as well.

Love: Even at 42 you would have a hard time getting resonance.

Pieper: Right. We are still high.

Aron: I have a comment on Puget Sound. At one time I worked there, and we did a fair amount of midwater trawling throughout the Sound. You can find tremendous variability which is clearly associated with things such as tidal changes or seasonal flushing. In a place like Holmes Harbor, for example, you could follow the actual flushing of the harbor just by watching the euphausiid populations; you could see the stuff go out. If you look particularly at the work that Cliff Barnes has done for many years on Puget Sound surveys, you can get some appreciation of the causes of variability in the biological data when you look at the tremendous variability in the physical and chemical data. I do not know anything about the oceanography of Saanich, but I think it is probably not too different than places in the Sound.

DISCUSSION
Thursday Evening, 2 April

Hersey: For the past three days a delightful community of ocean scientists have been addressing a very broad problem of interest to themselves. It is also a problem, in the long view, of great importance to nations, to the interests of groups within nations, and, of course, not only to the individuals who are here but also to a very, very large number of people who are concerned with the exploitation of the sea for the benefit of mankind.

One of the most useful and effective ways we have of sensing the natural phenomena of the undersea is by the use of underwater sound. Probably far and away the most fascinating, and in many ways the most rewarding and useful aspect of the undersea, is the use of it by the animal kingdom, which is the concern of the marine biologist. So we have two scientific communities, the biologists and, broadly speaking, the physicists, who are interested in physical oceanography, especially that part of it which we call underwater acoustics. A very special group selected from these two communities have been communicating with each other in a very complex way over the past three days to examine the manner in which underwater acoustics can reveal some of the phenomena of life in the sea as well as the ways in which the complex world of the animal kingdom in the undersea affects man's efforts to make use of underwater acoustics to find his way around in various pursuits in the sea. I think that this is what we are concerned with.

For the benefit of our guests who have not been aware in detail of the way we have addressed this part of our world, I would like to review a little. You see a comparatively small conference of people gathered here tonight. A few had to leave this afternoon. I doubt very much whether more than one or two people left before the end of our proceedings this afternoon. This, I think, represents an intensity of interest in the subject. I am afraid if we examined the usual pattern of scientific meetings we would find that altogether too many of us are concerned with doing a good job of presenting our own findings. We are very apt to slip into a scientific meeting within six or eight hours before we are due to appear on the program. I suspect that more like six or eight minutes after we have completed our presentation, we are very apt to be headed for the airport, scheduled for our next concern.

The meeting of the last three days has not been that kind of meeting at all. Virtually all of us arrived here Monday evening or early Tuesday morning, and we have taken part in listening to the findings of our colleagues, discussing them, poking holes in them in some instances, supporting them in others with corroborative evidence, and going through a program in which we have examined first of all, the biological concerns of the undersea, the acoustical phenomena that have been observed over a period of years that possibly are a reflection of biological activity and, finally, during this past day, how much we as scientists are able to conclude about the true nature of the association of these two concerns. So far as the world of practical affairs is concerned, these are of great importance in the realm of food production, in the area of fisheries. We can use underwater sound, as we and many nations in the world have done, to improve fish catching and the knowledge of husbandry of the fisheries resources of the world. This obviously will be a valuable aid to all nations and to all people.

As regards the concern of the navies of the world, we know that in times of stress when we have to keep track of what is going on under the sea, an important element of the background against which we have to compete is the biological activity of the undersea and the effect that this has on the performance of various naval systems.

In this particular conference we have not attempted, nor shall we tonight attempt, to address any of the problems of practical application. We are concerned here with the scientific background, and this leads me to the third important concern. And this is an important concern more to the individuals, not only those who are scientists interested in the natural order, in understanding it, and in being able to explain it, but also to the very large number of people who, either as scientists or as intelligent laymen, are interested and curious about the natural order and the mechanisms by which it operates. All of these are important concerns and have been part of what has made this conference the success that I feel it has been.

Tonight we are going to attempt, however effectively this may be done, to review the highlights of what has been presented over the last three days. This will be done in two stages. Our conference leader, Mr. Brooke Farquhar, will first present an overall review of the conference. He will be followed by the chairmen of the individual sessions of the conference who will review in a general sense the findings that have been presented against the background of what has previously been understood in this field. I am confident that the chairmen of these sessions, who have a considerable background and experience with this field, will be able to lead those of you who are not familiar with this field through the broad outlines of its past so that by the end of the evening you will understand what we now know about the interaction between underwater acoustics and the biology of the undersea and the major problems which we will have to address in the immediate future. The members of the conference are invited to participate with the conference chairmen in discussions of the various issues that will be addressed, but more particularly, our guests are invited to ask about the presentations as a stimulus to this discussion. Without further delay, I should like to introduce Mr. Brooke Farquhar of the U.S. Naval Oceanographic Office, who has been our conference chairman.

Farquhar: Thank you very much, Dr. Hersey. In reflecting earlier today on our get-together here at Airlie House and on the general history of the scattering problem, I was reminded of the jet airliner that left Kennedy Airport for a flight across the Atlantic. After being airborne for some time, the pilot turned the public address system on, welcomed the passengers aboard, told them to relax and stated that dinner would be served shortly. Then he said, "I'm afraid that I have some bad news for you, but I also have some good news. I'll give you the bad news first: We are completely lost. But the good news is that we are making extremely good time." It seems clear to me that we have shown in the past three days that we are not nearly as lost as we once were and that we are also making some pretty good time. No one expects to find all the answers from one of these conferences, but we have found some; we have some ideas about some others, and we have also defined some problem areas. One of the charms of this conference has been that the acousticians and the biologists have come together to look at the problem. The exchanges on the floor and after the formal sessions have been gratifying to see. It is true, too, that the participants have come from diverse activities and their interests represent a very broad spectrum of scientific effort.

It is perhaps obvious to those of us in this community, perhaps not so obvious to those outside of it, that there remains no doubt that the deep scattering layer phenomenon is caused by an assemblage of marine organisms in the volume of the ocean. In addition to contributing to backscattering of sound energy, they may also cause significant attenuation of sound in certain areas. We have seen, too, that these assemblages of animals sort themselves out in different ways which

are dependent upon various environmental influences and how they relate with each other in definable terms. The ten-foot or the six-foot [illegible] water travel universe has been mentioned several times in connection with biological sampling efforts, but it is abundantly clear that there are also acoustic universes which result from the choice of frequency used in a measurement.

Scattering strength measurements above, below, and at resonance have clearly shown the significance of scattering strength enhancement and the importance of gas-filled structures in producing certain frequency characteristics of scattering. Strikingly enough, gas-filled structures, particularly those carried by fishes and siphonophores, are in fact extremely abundant in the mesopelagic zone of the ocean, where the scattering is centered. Trawling data from various regions of the world ocean consistently show agreement between the depth of occurrence of some of these forms and certain scattering layers. Where we see non-migratory layers, we often find fishes and other animals which do not display a migratory behavior.

There are refinements and new developments and techniques for measuring the amount of backscattered energy from a piece of ocean and for more sophisticated analyses of the data. I cite as an example the development of an airborne technique for acoustic measurements over broad areas of the ocean, and the computerized techniques for analysis that we have heard about. There is an indication that we can carry the acoustic measurements a step closer to a link-up with the biologists' net hauls by developing a hypothetical population density curve from acoustic measurements.

We have seen further that what a fish does or does not do to regulate the gas in its swimbladder may play a significant role in determining the sorts of resonance profiles that we might expect to see acoustically. The discussions generated during the conference about this subject suggest to me that we have defined a problem area where further study into the physiological and energy mechanisms of the swimbladder and of vertical migrations will contribute significantly to our understanding of the complex acoustic features that we observe.

Finally, when we look at the levels of acoustic backscattering over broad reaches of the ocean, we see patterns of variability that are clearly evident, and the points of latitude or longitude where changes in levels are pronounced invariably are associated with observable changes in the environment. For example, we have seen that the Gulf Stream is a definite boundary across which changes in scattering characteristics may occur. Perhaps the most striking comparison that we have seen is that when the distributional or zoogeographic characteristics of fishes are examined—and I mean those fishes which are the most likely resonant scatterers—then there is a basis for setting off limits to their patterns of occurrence. When we examine these regional patterns, we see that the boundaries agree very well with the regions of pronounced changes in acoustic scattering level.

To provide you now with a closer look at some of the points that I have touched on, we will hear now from our respective session chairmen. It is a great pleasure to introduce Dr. Richard Backus of the Woods Hole Oceanographic Institution, chairman of the session dealing with biological considerations.

Backus: It is very stylish nowadays to say that we do not know anything about this, that, or the next thing, but I think we know a good deal about this particular subject. Properly, we have been playing in this no-man's land between what is pretty securely known and what we really do not know very much about at all. I will try to flirt along this ragged boundary for a couple of minutes and say a bit about the things we talked about in the biological session.

First of all, regarding light, it is characteristic of the sound scatterers that are organized into layers in the upper thousand meters of the ocean to make a diurnal vertical migration, coming

up toward the surface at night and going back into the depths by day. Not all scattering layers do this, but it is characteristic. This diurnal migration is obviously light-cued and moreover, within more or less but not quite homogeneous geographical provinces in the ocean one sees variations in the depths to layers of scatterers that are subtly attuned to small differences in the transparency of the water; that is, where the light penetrates deeper, so will a layer of scatterers lie somewhat deeper, and where light penetrates less well, so will the scatterers not lie so deep. Minor perturbations of given layers and the correlation of these with other physical factors in the ocean have not been nearly so successful. So it is clear that light is responded to very critically by these sound scatterers, but exactly how light levels—light changes— are sensed and responded to is not at all clear. I think that this is one of the boundary areas between what is known and what is not known. It is not certain that animals migrating upward in the evening, for instance, always stay at a constant light level or whether they wait until they have seen a particular change and then move on up for a bit, then wait until they see a certain change and move on. Perhaps various patterns are adhered to. It is clear, however, that this vertical migration is restricted to that part of the ocean into which daylight penetrates. Below about a thousand meters in the ocean no marine organism can sense the difference between night and day. Therefore these diurnal vertical responses to changes in light are limited to animals living in the upper thousand meters.

Another important factor in the so-called photo-environment of the upper thousand meters is not ambient light but the light that marine organisms themselves produce, so-called bioluminescence or living light. It is surely of significance, but it is not understood why so many animals in the environment are light producers. Moreover, it seems that the animals that comprise these layers of sound scatterers are very often light producers. Perhaps this is simply because the incidence of light production is so high, but there may be a bit more to it than that.

To go on now from light to swimbladders, a very important part of the sound scattering community is the marine animal that encloses a bubble of gas. That is straightforward enough. They scatter sound so well because they do enclose bubbles of gas, and because a bubble of gas differs both in density and compressibility from the surrounding water, it is a sound scatterer. The swimbladders of midwater fishes, a consideration of the structure or the distribution of these structures among midwater animals, and the functioning of this structure are very important matters in this sound scattering layer business. The swimbladder in a midwater fish is a hydrostatic organ. The tissue of a midwater fish is heavier than the surrounding sea water; so to become essentially weightless in the water, the midwater fish encloses a bubble of gas. A bubble of gas is a rather difficult thing to manage for an animal that moves up and down from several hundred meters to the surface and back each day because as the animal moves up, the compressing weight of the sea water above the animal is relieved; the gas bubble wants to expand. As the animal swims down, of course, the weight of water on the animal increases, and the bubble of gas is contracted so that the buoyancy of the animal is continually changing. If the animal wants to be buoyant at all levels, it obviously must add gas to or subtract gas from this bubble.

Two very thoughtful papers looked at the energetics of this business. The fish need not, of course, remain buoyant. It can be buoyant at some level in the water column and swim to maintain itself at other levels. So there are two strategies that a migrating fish can choose between: It can choose to secrete gas into or take gas out of its swimbladder as necessary, and of course this is an energy consuming process, or it can be neutrally buoyant and stay at one level in the ocean without using energy and be heavy at other levels and swim to stay afloat. Of course swimming is an energy consuming process. It seems likely, and indeed it is suggested by some acoustic evidence gained from watching the behavior of bubbles in migrating fishes acoustically,

that both games are played. One would like to observe these games in other ways and to see exactly how they are played. Unfortunately it is not really possible at the moment to make a clear choice between which strategy is more economical energy-wise because it has not yet been possible to make the necessary measurements on the animals actually involved. These little midwater fishes are fragile animals that have so far defied the aquarist's art in keeping them alive long enough to make these measurements. Most of the observations necessary to these considerations have been extrapolations of measurements made in fishes of other sorts, and fishes are a very variable group of animals.

Another point that was well made during the session was the tremendous increase in our knowledge of the behavior of midwater animals through direct observation, something that all of us are familiar with from reading the books of Beebe and a couple of others when we were younger. Many more of us now get a chance to enter directly into this environment that we studied indirectly before. This is really an exciting thing, and one sees problems that he had no way of imagining until he actually went down there.

Another thing that I want to call attention to without actually discussing any results has to do with the study of one spot in the ocean; that is, going back repeatedly to one spot time and again, year after year, and season after season, looking at its array of sound scatterers by towing nets, and looking at the distribution of the relevant animals. From this it has been possible to say a good deal about the animals actually involved in the sound scattering layers, but more important is the point that here a good deal of energy is focused on understanding one spot in the ocean over a long period of time.

Deep scattering layers are very important as stirrers of energy downward into the ocean by their vertical migrations. Although it is not generally agreed upon why animals undertake these elaborate migrations, it is apparent that many of them feed in the upper part of the ocean and carry this food downward into the ocean. All of us depend upon the sun and the fixation of the sun's energy by plants for our energy. This is true of all things that live in the ocean. The photosynthetic process is limited to the upper 100 meters or so of the ocean where enough light penetrates to let this process go on. The principal plants of the ocean are microscopic ones which are fed upon by tiny animals. These tiny animals are fed upon by larger animals, and so on, up this familiar chain-or because it's more complicated than a chain, a web-to the largest animals of the ocean.

Another sort of food chain in the ocean was discussed in two papers in the biological session. Though ultimately traceable to the sun through the plants of the upper part of the ocean, it does work in a somewhat different way than the well understood chain that I have just mentioned. That is, finely divided particulate organic material, the remains of dead plants and animals, and even more wondrously to me, dissolved organic material--that is, the dissolved remains of once living things--it appears is somehow utilized in the deep waters of the ocean by microscopic organisms. These organisms are fed upon by larger organisms, to be fed upon by still larger ones, etc. It appears that this does indeed happen, but the nature of these very small organisms which utilize the fine particulate and dissolved organic material and the nature of the process by which these are used by other animals are still not known. This to me is one of the most fascinating problems yet to be investigated in the deep ocean.

Finally, dividing up this open ocean realm, which looks to the uninitiated perhaps as a watery place where one gallon or acre looks very much like the next, is an exciting game that received some attention during this meeting. That is, all parts of the deep ocean are not alike, and how to usefully divide them geographically or ecologically into their constituent animal communities is another thing that we discussed.

Farquhar The chairman for the acoustics session is Mr Robert S Winokur of the Naval Oceanographic Office

Winokur It was suggested during the biology session, and I think quite clearly, that the ocean can be divided into oceanographic provinces. It was brought out further during the acoustic session that these oceanographic provinces and their boundaries bear a very distinct relationship to some observed and predicted geographic variations in biological scattering. By the variety of papers presented and the diverse locations in which reported research investigations were conducted, we have seen from the results reported that a significant amount of acoustic information providing extended geographic coverage is beginning to be amassed; however, much laboratory and field work remains to be done to fully understand scattering strength patterns. Experimental scattering strength measurements have been made in the North Atlantic Ocean toward the Norwegian Sea, across the Atlantic to the Azores, and in the western North Atlantic. Recent measurements have extended the geographic coverage to include the Mediterranean Sea, the South Atlantic Ocean along the coast of South America, and the eastern Pacific Ocean. The experimental measurements have been conducted using a variety of measurement techniques at a number of different frequencies. Measurement techniques include the use of explosive sound sources in conjunction with shipboard and airborne methods to provide data on the scattering strength of the water column, downward looking echosounders operated at a number of discrete frequencies, and upward-looking directional transducers located on the sea floor and trained toward the scattering layer. All of these techniques have their advantages and disadvantages, but all provide new and needed information on the acoustic properties of scattering layers.

With the use of various measurement systems and techniques available for a wide range of frequencies, from about 1 to 200 kHz, sound scattering and reflection from individual fish or fish schools is always observed over this broad frequency range. Resonant scattering has been clearly observed and identified within the range of frequencies from 1 to 20 kHz, particularly with the use of broadband explosive sound sources. Although measurements have been made over this very broad range of frequencies, the acoustic results presented during this Symposium do suggest that additional frequency coverage is needed; particularly at the lower frequencies below 1 kHz, and even at the higher frequencies to fill in gaps between the frequency limitations inherent in the variety of transducers and systems used to make measurements.

It was clearly brought out during the Symposium that an acoustic effect resulting from the presence of marine organisms is backscattering or reverberation; however, there is another effect, particularly in shallow water, that may be important in one-way propagation. Definite diurnal and seasonal propagation effects resulting from the presence of swimbladder-bearing fishes have been observed during shallow water studies. A number of definite propagation loss patterns have been associated with attenuation effects due to the presence of fish in shallow water.

The observation that Dr. Backus made about the need for an intensive study of an area to understand its biological characteristics applies equally well to the acoustic aspect of the problem. There is a very definite need for this kind of study, but the study should be multidisciplinary in character so that we can understand not only the biology of sound scattering layers but, equally as important, the acoustic characteristics associated with these layers.

The acoustic scattering data presented showed that very definite diurnal variations exist. Time variations of the order of hours are observed during sunrise and sunset. Some of the biological data suggest very definite seasonal acoustic variations should also be observed. However, we do need to devote our energies to studying these seasonal dependencies.

It was inferred from the acoustic results that the biological population required to produce some of the scattering strengths observed is not great. The densities of potential scatterers required to produce observed scattering strengths varied from the order of 10^{-3} fish per cubic meter to

about 10^{-1}, or that only one fish per million cubic meters may be sufficient to produce some of the observed scattering levels.

In addition to field measurements, some laboratory experiments have been made to understand and define further the resonant frequencies of some fishes, both shallow water and deep water species. There is certainly a need for this kind of work to be continued, so that the resonant frequencies associated with the fish being caught in scattering layers can be accurately defined. These experiments could also provide us with experimental evidence to define the exact mechanism or physiological process taking place within the fish when it is migrating. In addition, acoustic results gained with use of broadband sources will help to understand further the problem of tracing layers and layer migrations. I believe information of this type will provide further evidence for the kind of physiological process that occurs within the fish as it ascends and descends during the day.

The use of a single source does not provide information on all of the scattering layers present. For example the use of a 12-kHz echosounder provides evidence that there are 12-kHz scattering layers. Obviously, other discrete frequency measurements have provided ample evidence of the presence of sound scattering layers at the source frequencies; however, I suggest the use of broadband systems which would enable the investigator to determine the acoustic characteristics of scattering layers over a broad frequency range and at the same time delineate the distribution of these layers to permit the biologist to sample them. Certainly I think that we should get away from relying on the 12-kHz echosounder as the means for locating scattering layers. I recognize its convenience and the convenience of a number of other fisheries and standard commercial echosounders, but I believe there is a need to employ other systems, whether they be discrete frequency or broadband.

I have asked some of the authors to provide me with figures from their papers to further amplify the above remarks in order to summarize the acoustic session. If there are any questions, I am sure the authors can provide the answers at the end of the session.

Figure 1 shows the measurement geometry for the collection of scattering data at sea using explosive sound sources. An explosive source is shown being used with an omnidirectional hydrophone. This type of measurement provides the scattering strength of the water column or the integrated scattering strength. By using a directional downward-looking receiver with the explosive source as shown it is possible to determine the depth of the sound scattering layers and the scattering strength as a function of depth. An upward-looking transducer used in some investigations can be located on the bottom in shallow water or at some mid-water depth in deeper water and permits an acoustic description of the scattering near the surface that is sometimes lacking in other measurements.

Figure 2 shows another technique that has been utilized for acoustic measurements, the use of an aircraft and sonobuoys. The obvious utility of an aircraft is in providing rapid geographic coverage and in being able to collect quasi-synoptic data, or with a number of aircraft, synoptic data.

Figure 3 is a representation of the broadband scattering strength over the frequency range from 0.8 to 20 kHz that is typical of data collected with explosive sources. There is a sharp resonant peak for these data at 5 to 6.3 kHz, and a possible indication of one at 20 kHz. There is a rapid increase in scattering strength with increasing frequency in the lower frequencies; in one instance there is a reverse trend at the lower frequencies, suggesting the need for data at lower frequencies to determine the exact dependence. Some of the experimental laboratory measurements made on fish reported during this Symposium, reveal resonances at 200-300 Hz, which would suggest a possible low-frequency resonant peak. Data of the type shown are providing us with an understanding of some of the frequency effects over this frequency range in certain geographic areas.

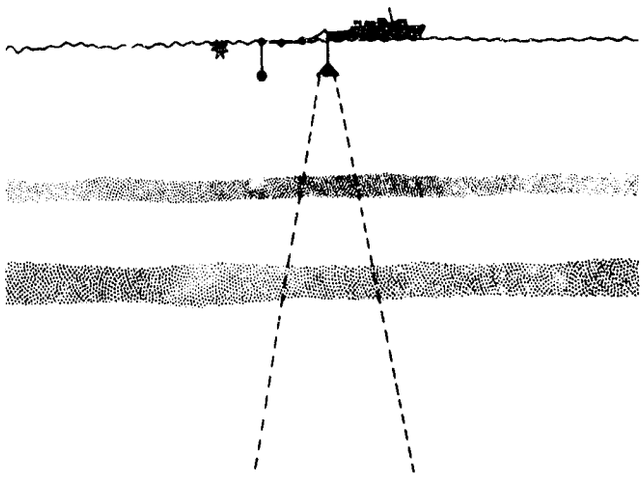

Figure 1

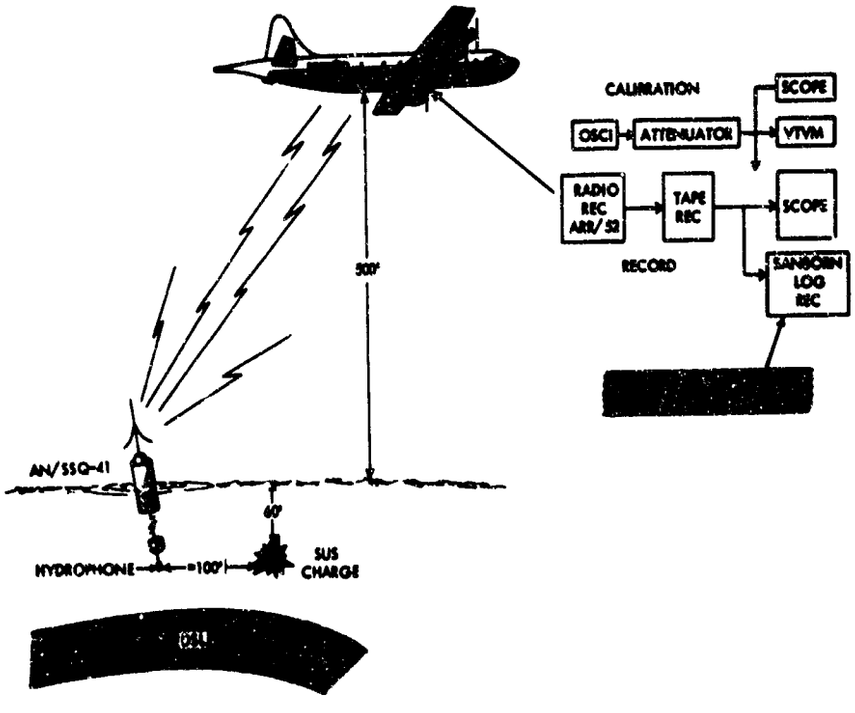

Figure 2

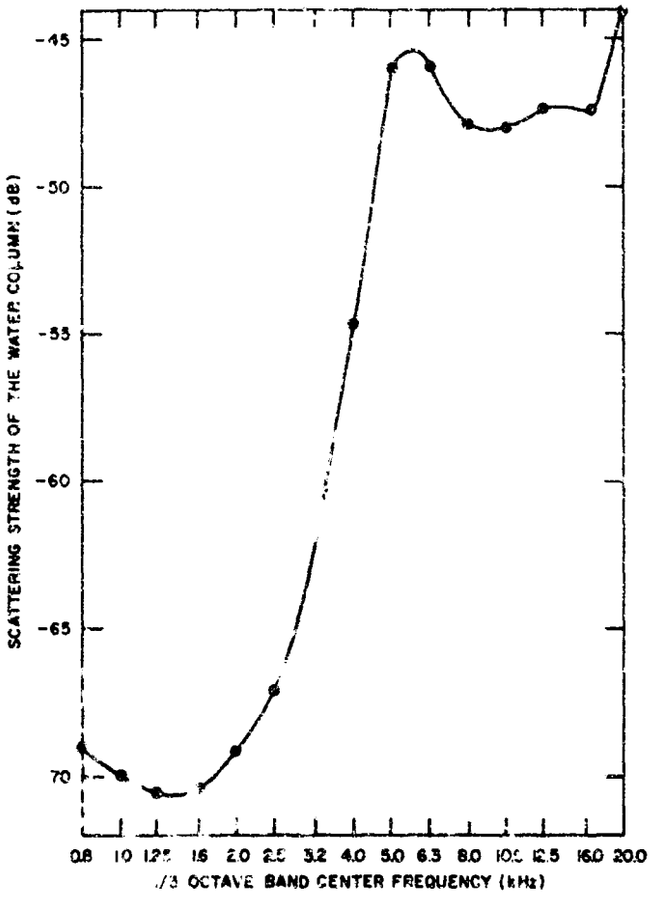

Figure 3

The data in Figure 4 illustrate the utility of airborne reverberation measurements. The data shown were collected during a single day. The contoured acoustic values indicate that scattering strengths can change very rapidly over relatively short distances. These data were collected near the Gulf Stream, and it was brought out quite well in the discussions that reverberation is quite variable in this region and not very well understood around the boundary and in the Gulf Stream. The contours also show a varying frequency dependence, as the patterns change with frequency.

Figure 5 presents integrated scattering strength data from the North Pacific Ocean. They show, for the Pacific Ocean, a pattern similar to the North Atlantic Ocean, where an increase in scattering strength with latitude is observed (Figure 6). In this case the diurnal variation is not as great as in the North Atlantic as was shown by Bob Chapman in his paper, but this may result from the way the data were collected, since it was not possible to collect day-night data at the same location.

Figure 6 in a sense delineates acoustic provinces, or suggestions of acoustic provinces. The darker lines are oceanographic boundaries. The data along the longitude between Puerto Rico and Nova Scotia indicate that the scattering strength is increasing, and an oceanographic boundary is seen to coincide with a sharp change in scattering strength near Bermuda. A decrease in scattering is seen toward the Azores, and suggests, related to the biological evidence presented earlier, that there are definite interrelationships between water masses, changes in species composition and variations in acoustic characteristics.

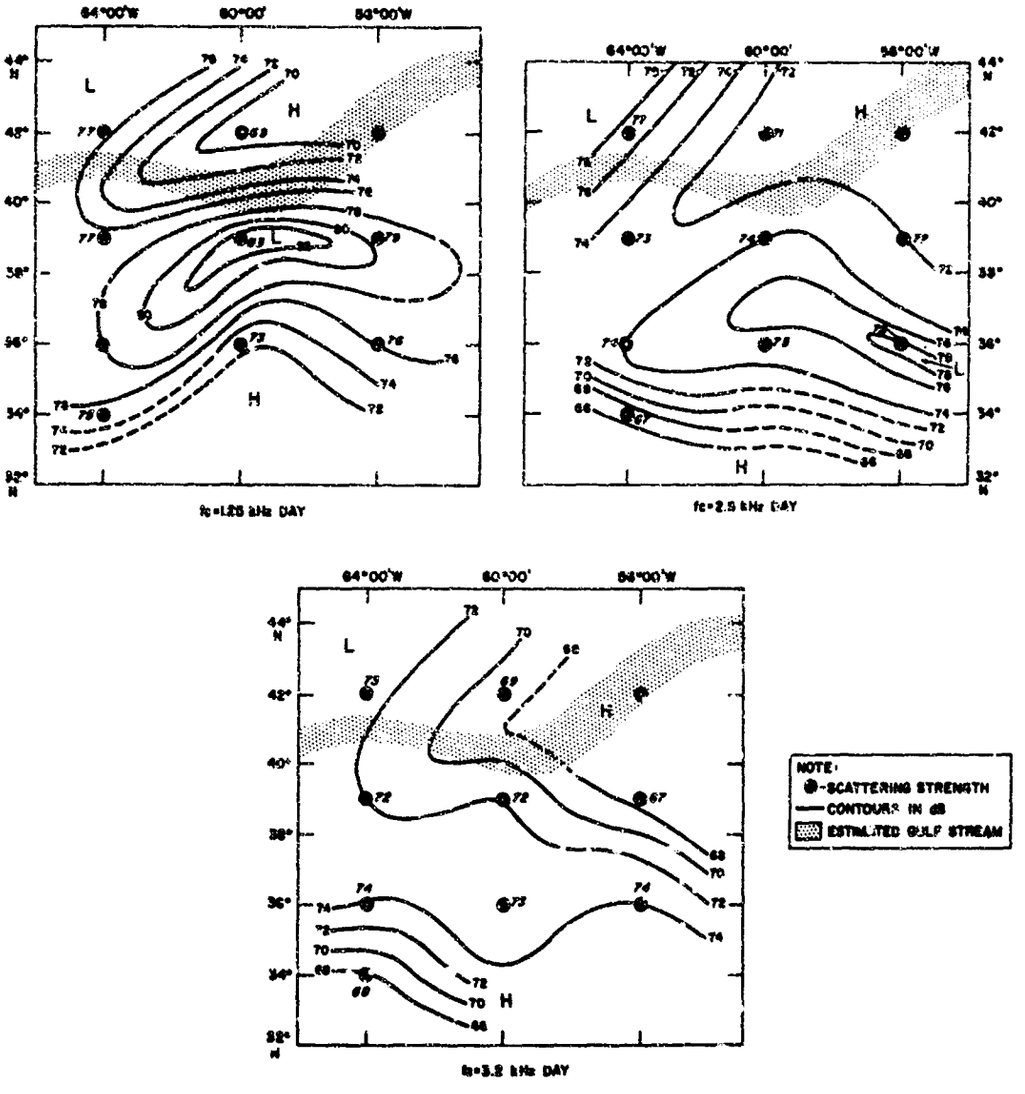

Figure 4

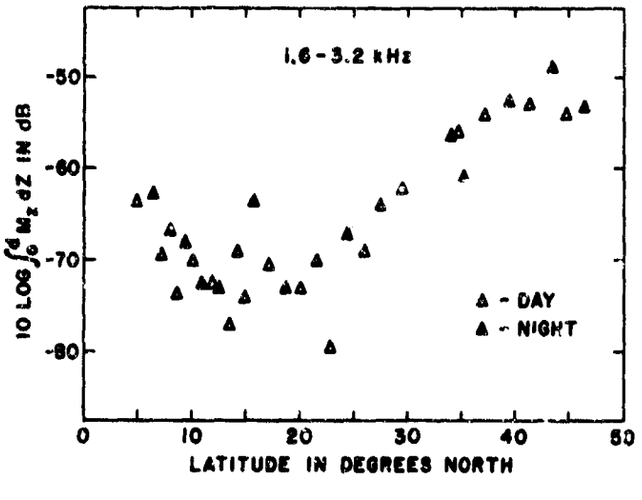

Figure 5

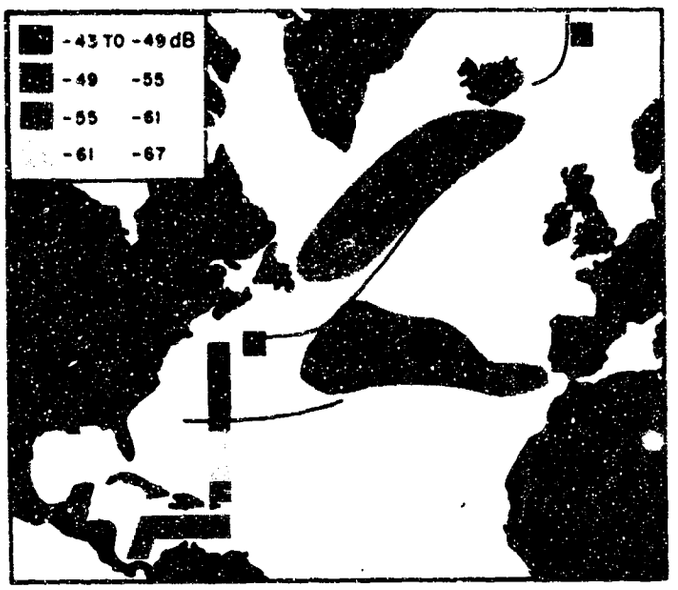

Figure 6

Figure 7 shows the results of measurements made with broadband explosive sources, but using a directional receiver. They point out the need and advantage of using a variety of echosounders or broadband sources to define scattering layer profiles. The profiles shown are from the Pacific near the mouth of the Columbia River. In the octave band from 1.6 to 3.2 kHz there is a rather deep scattering layer at 1000 meters, whereas at the higher frequencies (6.4 to 12.8 kHz band), that scattering layer has disappeared. Towards the south, the deeper low-frequency scattering layer is still observed and there is an indication of a higher frequency layer forming. Continuing farther south, the low-frequency layer has disappeared, and now a high frequency layer is observed. With a 12-kHz echosounder these frequency-dependent depth variations obviously would have been missed completely.

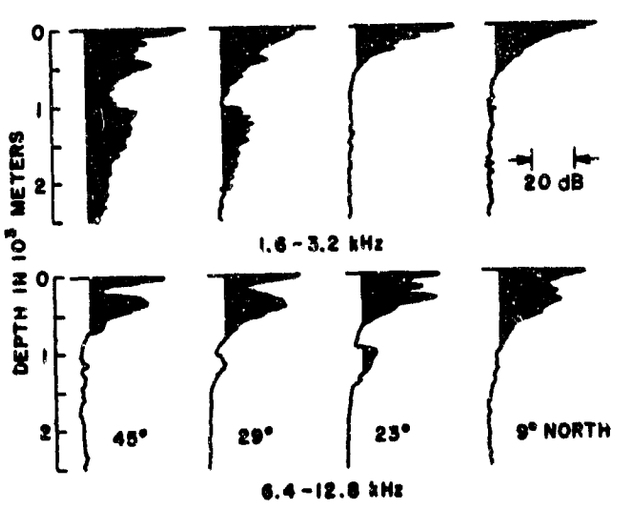

Figure 7

The experimental data shown in Figure 8 are the results of detailed laboratory studies involving measurements of live fish. The curves show the resonant frequency for a live anchovy, and for the swimbladder alone when removed from the anchovy. The resonant frequency is seen at about 1.3 kHz. The data also indicate the effect of the fish tissue surrounding the swimbladder and the damping resulting from the presence of this fish tissue. It can be seen that with the bladder removed the resonant effect is much sharper and the scattering is significantly greater than from the fish itself. Other experimental results presented during the Symposium have shown resonant frequencies as low as 200 Hz on some of the larger fishes that were tested.

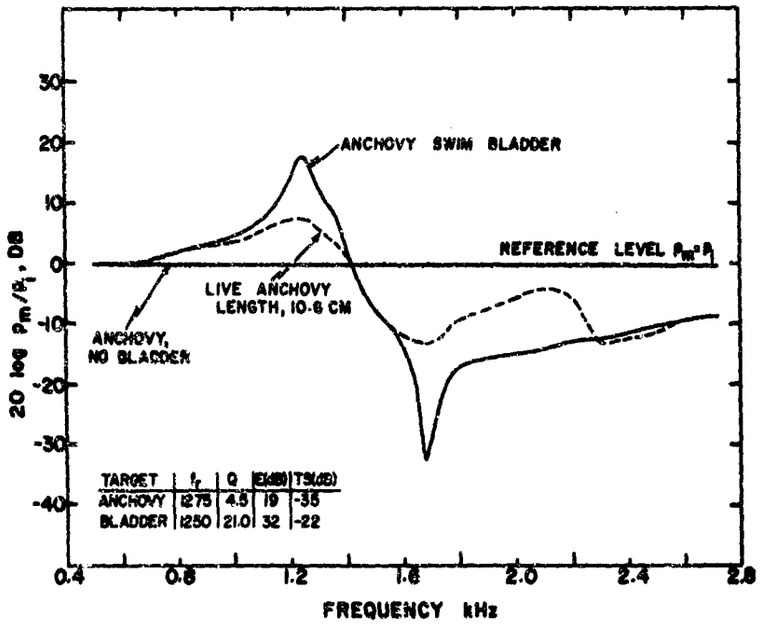

Figure 8

Figure 9 shows the pressure effect which is related to scattering from swimbladder-bearing fish. It shows the theoretically predicted result that as the pressure increases, the resonant frequency of the fish increases. It is measurements such as these, as well as at-sea experimental data, which I believe can provide insight into understanding swimbladder physiology.

During the Symposium we discussed not only resonant scattering but also the reflection of sound from the fish. The curve in Figure 10 shows a computed resonant peak and curves determined from empirical equations that enable one to predict the target strength of fish both for their side and dorsal aspect. The curve shows that for a given frequency as the size of the fish increases, its ability to reflect sound is increasing. In addition, the curves show that the side-aspect target strength of an individual fish is greater than its dorsal-aspect target strength.

Figure 11 illustrates the effect that fish populations can have on propagation loss. A number of propagation loss/attenuation time patterns have been identified as a result of measurements made in shallow water, showing that fish attenuation effects are somewhat complex. The apparent presence of swimbladder-bearing fish results in a number of interesting acoustic patterns. In the upper trace there is an abrupt increase in the propagation loss at sunset and then a recovery and a leveling off. Again at sunrise we see an abrupt increase and then leveling off again. Another pattern observed was the "bowl" pattern, where there is a gradual change in the propagation

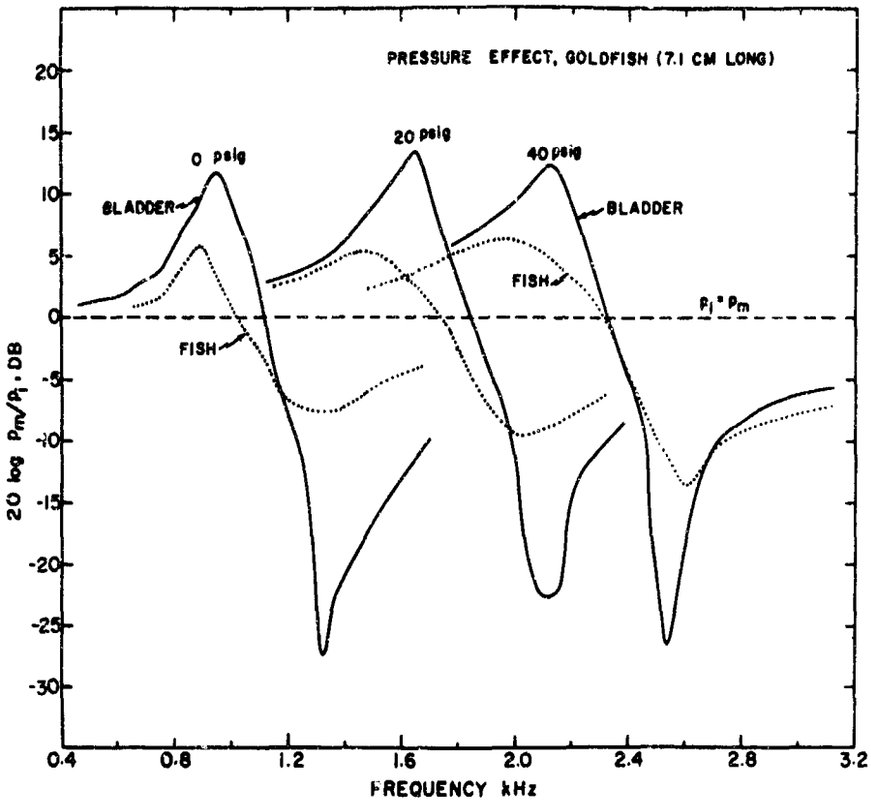

Figure 9

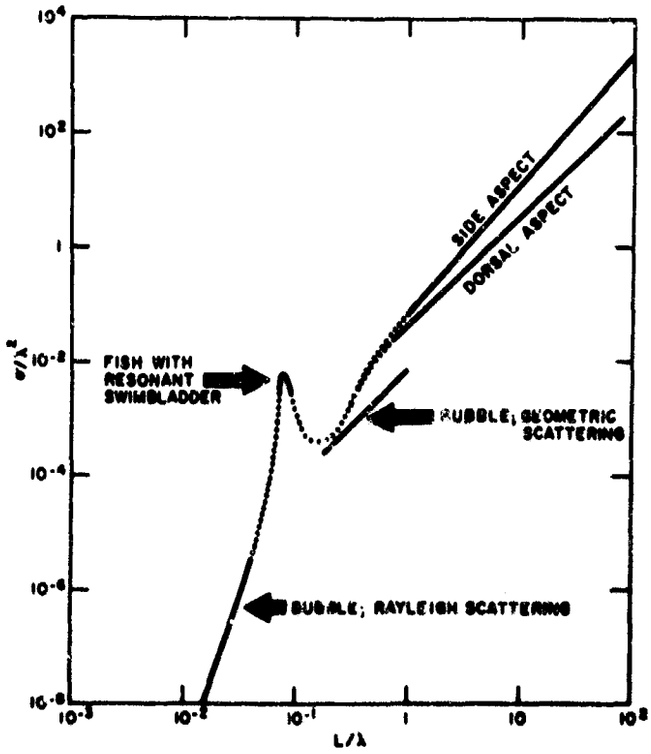

Figure 10

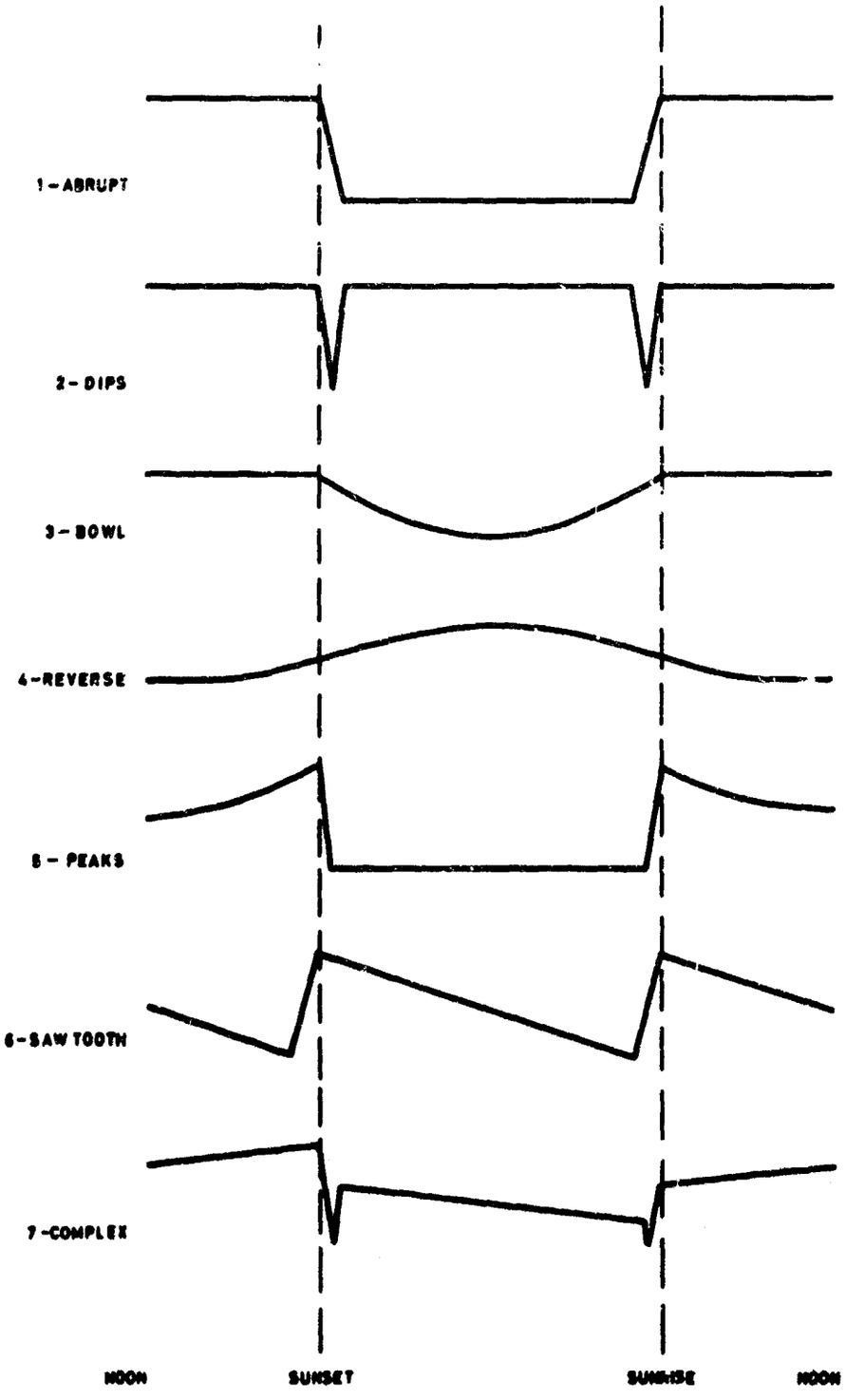
1 – ABRUPT
2 – DIPS
3 – BOWL
4 – REVERSE
5 – PEAKS
6 – SAW TOOTH
7 – COMPLEX
NOON
SUNSET
SUNRISE
NOON

Figure 11

loss as it increases, and then decreases toward sunrise. A reverse trend to this previous one has also been observed. Another trend is a gradual decrease in the propagation loss and then an abrupt change, leveling off, and then an abrupt change. There are also sawtooth and somewhat complicated patterns. The results of these measurements suggest that our understanding of propagation in shallow water is perhaps not as complete as we thought in that we are neglecting the presence of marine organisms, and that we should perhaps seriously consider them in the development of shallow water propagation models.

Farquhar: For today's joint session we had as co-chairmen Dr. Eric G. Barham and Mr. William E. Batzler from the Naval Undersea Center.

Barham: We have certainly come a very long way in the last fifteen years. I am speaking for the biologists now. Shortly after World War II the knowledge that we had of biological scatterers could not have been based on more than 200 net hauls that were specifically designed to sample these strata. Very few at all correlated with even the crudest kinds of echosounder records that we got in those days. Now we see the biologists coming to grips with the terrible problem that they have in sampling this vast environment. There is a terrible sampling problem over the amazing array of animal sizes and their ability to avoid nets. We have seen some really beautiful systems that are now in use. There has been a tendency along this line to particulate out. I think that there are almost as many nets as there are biologists, really. Perhaps this is for the good.

From the acoustic side of the question, I think it is very rewarding that acousticians are interested in the causes of the signals that they have been measuring for a number of years. I do not really think that was prevalent fifteen years ago. I think it was a phenomenon that acousticians studied for its own sake. I think that now there is a general sensitivity and feeling of interest on the part of acousticians that these are fascinating animals and we should learn more of them. This is one of the most rewarding things, that we do have a community, we do have a mutuality of interests. We see a breakdown on the part of our loyalties to traditional disciplines. We see an approach toward problem solving that cuts across these hide-bound lines that we so frequently have had drawn for us. That to me is the most joyful part of this very happy occasion.

We certainly had other very important things pointed out to us in today's session. One of the most revealing is the fact that there is an area in the ocean, perhaps the most accessible area, the shallow waters above the thermocline, that we have pretty much darn well avoided and that is chuck full of extremely strong targets. This is an area that we should pay a little more attention to.

I would like to introduce my co-chairman, Mr. William Batzler.

Batzler: When I tell you that I've been interested in the deep scattering layer for twenty-five years, maybe I should have tottered up here. I certainly am not very proud or very happy about that fact because I think this symposium has told me better than anything I have experienced if I did not know it before, that it is long past the time that I should have gotten on the ball. But I must say this. As interested as I have been in the deep scattering layer, I have been shunted off onto other things. I blame myself. I have not sold the importance of it. But sometimes I have not had it sold for me when I think it should have been. I have very strong feelings that the acousticians have not in the past cooperated or recognized the need for cooperation with the biologists. We have had demonstrated in the last several days that there are other disciplines that could be very helpful to us if we were not so blind and would see that other people are doing things that would be of help to us. I cannot help remark that when I came to NEL after World

War II, there was still a lot of reverberation data around, and most of these data were on 35 millimeter film. I know many people who have thicker and thicker eyeglasses because they read that data, not with a viewer that magnified it but by brute force. We have done many other things by brute force. We are still doing some of them by brute force, and I think we are impressed in this meeting with what Eric and other people have mentioned: There are better and faster ways of doing some of these things. I think there again we are impressed with the fact that we better get on the ball. I think that this is one of the important things that has come out of the meeting. We have seen what other people have been able to do. We have seen what real-time analysis on board ship is able to do. This has been very worthwhile for us.

I will mention just one other point which has also been touched on. The interest in the deep scattering layer is certainly worldwide, and this is evidence enough that it is not only interesting but it is important. It is not only worldwide, but it seems as though the disciplines involved are many and varied and are quite important to use.

A final word, and I guess it is emphasis. I think that many of us are still not cooperating the way we should. Acousticians are not being given the chance to cooperate with the biologists. They are not taking advantage of the opportunities. I have some examples right next door, and I hope we can do something about this.

Barham: I have gently criticized the acousticians in all good faith, and I think that I would like to criticize the biologists just a little. I think that in the beginning there was a natural tendency for what we call the friends of the euphausiids, the friends of the myctophids, or the friends of the physonects to enter into the identification of causative organisms. In other words, we tended again to follow our loyalties very closely to certain groups of organisms, and I think this is being overcome. This is good, because we are dealing with complex populations, and we must consider them as populations instead of taxa of particular major groups.

I would also say one more thing. I think that deep submergence vehicles or *in situ* observations are coming of age. They exemplify another sampling technique. More and more we will put these vehicles to exceedingly good use in this fascinating subject.

Hersey: I have been listening and waiting for one aspect of our meeting to emerge. I do not know how much of this I imagined, how much of it I have heard. Maybe some others will have a chance to help me. You biologists may want to turn off at this point because this will be an acoustician talking. I'm going to draw a graph, and you may not all agree with my graph. The abscissa of my graph will be the logarithm of the frequency expressed in Hertz. One Hertz there, and 10 Hertz here. Now you have heard nothing at all in the last few days about one hundred Hertz here, and still not much action at a thousand Hertz here, and now this should begin to be somewhat familiar; ten thousand Hertz there, and a hundred thousand Hertz there. I think that by this time it will be evident that this frequency range, a thousand to a hundred thousand Hertz encompasses everything we have discussed in the acoustics spectrum over the last three days. I would put a million Hertz here if the blackboard were not so small, and ten-million, etc. Now what do we know, just thinking in these dimensions, about the way sound behaves at sea?

Before I can proceed I must confess I feel very guilty at this point that we have not really provided an appropriate introduction to the subject for our guests this evening. I do not mean to embarrass anyone by pointing out this fact, but our guest who represents Germany tells me that we did not really help him very much to understand what we were going to be talking about this evening. So let me go back a little and say that all our remarks this evening are addressed to

exploring the ocean by means of emitting a pulse of sound into the water and then listening in one way or another to the echoes that come back. An outstanding characteristic of this experiment is that one does hear echoes that apparently come from the region between the surface and about 1000 meters. Most of what we hear is in that depth range, but not entirely confined to it. Furthermore, most of the echoes we have studied in any organized way are found in the acoustic spectrum between roughly 50 Hertz and what is just off the blackboard, roughly 200,000 Hertz. So our knowledge in the kinds of things we have been talking about in the last few days lies between these extremes. A very large part of our concern with the oceans and with the world lies to the right of a vertical line at 1000 Hertz. However, there are some other suggestions.

The geophysicists who explore for oil have been interested and perspicacious enough, to notice that when they send sound pulses through the water, in the frequency decade 10 to 100 Hertz, they get echoes back from something within the water. They have published one or two papers about this experience. On that basis we know a little about that part of the spectrum. There are echoes coming back from something in the water in the general region of 30, 40, or 50 Hz. I have not heard a thing about that in the last few days. But this is an area where positive indications have been obtained in the past, mostly schools of small fish.

Brian McCartney and others at this symposium have reported on measurements of resonance in scatterers in the region between 1 and 6 kilohertz, addressing the important problem of tracing commercial fishes, that is, fish that are large enough to be of interest to catch. We are making little inroads into the part of the spectrum from 1 to, say, 6 or 7 kHz, and we have had one instrument emerge in the last several years which operates in the general region of 3 or 4 kHz. We have heard very little about the instrument, but nevertheless, it does reveal some scatterers. The Norwegians have produced a very successful echosounder which has been alluded to here indirectly. Paul Smith reported on the Simrad equipment of the fisheries people. Then very, very close to the 11 kHz region – I can't really distinguish it on the blackboard – is our own equipment built originally by the Edo Corporation and used by everybody with various modifications, various recorders attached to it, so that we have done a great deal of looking at the oceans in that narrow window. I am very much heartened to see that a fair bit of work has been done in a thin line at 30 kHz, another one in the general area of 38-40 kHz, 100 kHz, and then this line that I cannot draw, out here at 200 kHz. When we look at this whole broad region, we have done something in the way of looking at our world over this frequency span. Now the significance of this, which is not lost on any of us, is that the frequency of the sound, inversely related to the wave length, is related vaguely to the scales of size in the animal kingdom or the natural order that we are capable of examining. We have mainly looked up here at the small animals, fascinating groups whose world controls that of the larger animals in many ways. But nevertheless a great deal of concern for us, both in fisheries, defense problems and elsewhere will be down in this region below 1 or 2 kilohertz. Since this had not been reviewed in this manner in the course of the symposium, I felt that it was well worthwhile to just back off and think about what faces us in the future. There are some exciting problems remaining certainly in this higher part of the spectrum, but a terrific challenge also faces us here below 2 kilohertz. Lest it not be said at all, the part of the blackboard that does not exist did not have one single report about 500 kHz or 1000 kHz or 10,000 kHz, and yet we should be lead on by the possibility of rewarding discovery there.

When we first started looking at the echoes that came from sound scatterers in the seas, a number of biologists were fresh from research of the 1930's in which it had been demonstrated that the small crustaceans performed some sort of diurnal migration. In fact, it had been pretty well worked out. I cannot speak professionally about this, but it was known that copepods

migrated. It was also known that euphausiids migrated. When we were aware of the diurnal migration of the deep scattering layer, I think a very quick reaction was, "No, this just couldn't have been copepods. They're just too small." But it could have been euphausiids. We examined that hypothesis, I am afraid not very thoroughly, certainly not compared with some of the beautiful things that have been reported in the last few days. But nevertheless, we did examine them. Now after twenty or twenty-five years of aging in the wood and also twenty to twenty-five years of having bright people being trained and becoming interested in this problem, we have appreciated that the thing to do was to examine what we could do at these higher frequencies. It was then that we discovered that we could find the euphausiids.

One of the handsomer experiments that has been reported here goes a little bit like this. It is the easiest thing in the world to get an echo from an assemblage of something or other in the sea, that will return this echo time after time after time as a ship proceeds over the surface of the sea. This repeated echo formed what we called scattering that appeared to come from more or less uniform depths wherever we observed it; so we call it a layer. To go to that depth and identify what is there, what is returning the echo, has turned out to be an extremely difficult thing to do experimentally, observationally. One of our younger scientists reported to us today that he had done the rather obvious (obvious now, obvious since about three o'clock this afternoon) experiment of introducing into the water the kind of material that he hypothesized might have been the cause of a scattering layer. He demonstrated that when you introduced that material in the water, it did indeed return the same kind of an echo that he had been observing. I suggest that for those of you who are particularly interested in even smaller scales of size in the marine animal community and even the organic community, including plants, you may find a great deal of use in looking at even higher frequencies. For those of you who are interested in aggregates of animals and the larger animals, you may find a great deal of utility in looking at experiments at lower frequencies.

I am very, very gratified and I think it has been a very rewarding experience, to see the increasing quality of all observations in this community. We have become interested in measuring, assigning numbers to, and appreciating the significance of the numbers. This field had to start out by identifying effect, and this we did. Perhaps we did it too often. But gradually we have measured what the effect was, and we have related it to a model of the physical or biological world. I think we are off to a very exciting future in learning about this aspect of the undersea.

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Editor

G. Brooke Farquhar
U.S. Naval Oceanographic Office

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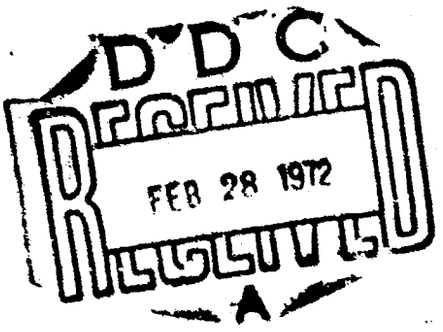

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