ENVIRONMENTAL SUMMARY OF THE U.S. ATLANTIC CONTINENTAL SLOPE AND RISE, 28-42°N

VOLUME II

BIOLOGY
HUMAN ACTIVITIES
FUTURE STUDIES
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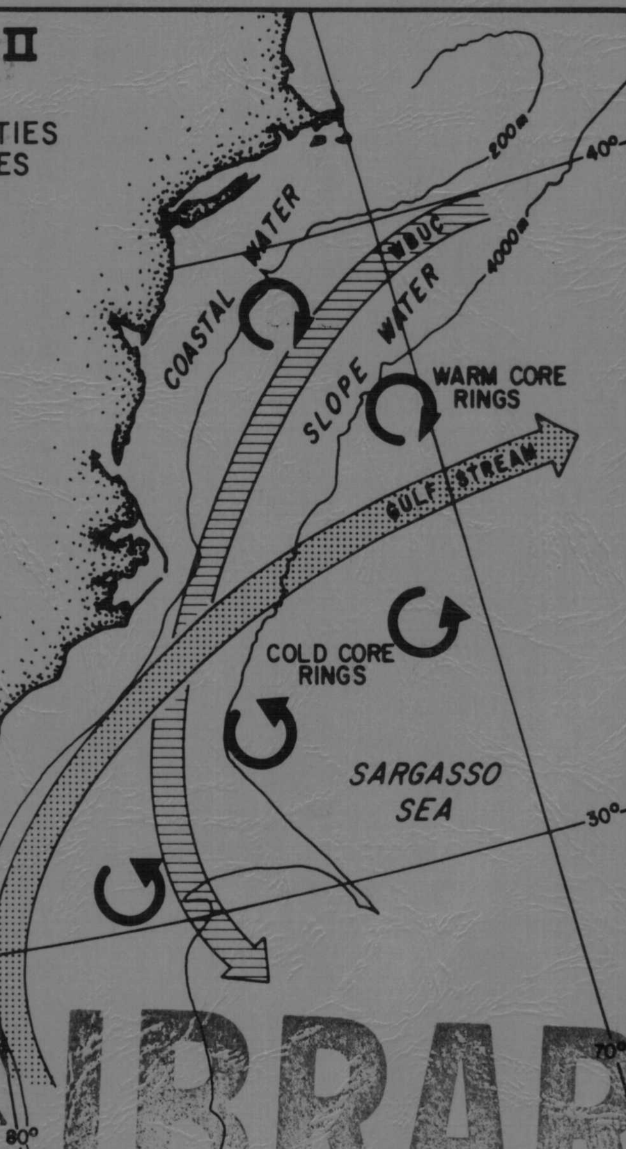

MARINE GEOSCIENCE APPLICATIONS, INC.

ENVIRONMENTAL SUMMARY OF THE U.S. ATLANTIC CONTINENTAL SLOPE AND RISE, 28-42°N

Volume II
Biology
Human Activities
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BIOLOGY

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BIOGEOGRAPHIC CONTEXT

The ACSAR study area lies across the western extremities of two biogeographic regions--the North Atlantic Temperate Region and the North Atlantic Subtropical Region. The Gulf Stream divides the study area into northeastern and southwestern pieces as it turns east from Cape Hatteras; it is the northern edge of this current that forms the boundary between temperate and subtropical regions in this part of the North Atlantic. Nowhere else in the Atlantic is there a stronger biotic contrast than at this boundary, thus preventing description of the ACSAR area as a homogenous region.

Biogeographic regions can be divided into biogeographic provinces. The northeastern part of the study area lies in the temperate province called "Slope Water", the southwestern part in the subtropical province called "Northern Sargasso Sea" (Backus et al., 1977). Although the Gulf Stream is considered to be a part of the Northern Sargasso Sea, it is biotically distinct (Jahn and Backus, 1976).

The Gulf Stream system occupies the western part of the southwestern, subtropical part of the study area. Thus, in the latter place there is an west-east biotic gradient related to water mass that is parallel to but independent of the biotic gradient related to the change in water depth from 200 to 4000 m. Off Cape Hatteras, the study area is narrowest (i.e., the 200 and 4000-m isobaths are closest) and it is occupied from edge to edge by the Gulf Stream.

The northern edge of the Gulf Stream is the southern limit for certain cold water animals and the northern limit for certain warm water ones. For other animals the Gulf Stream's edge is no boundary at all--they live equally well to the north in the temperate Slope Water and to the south in the subtropical Northern Sargasso Sea.

The tropical Caribbean biota carried by the Florida Current is quickly diluted by the lateral incorporation of subtropical plants and animals from the adjacent Northern Sargasso Sea as the volume transport doubles en route to Cape Hatteras. Although the dispersion and mortality of this tropical biota are rapid, individual organisms of Caribbean origin are found well to the northeast of Cape Hatteras.

Because of the hydrographic complexity, the distribution of plants and animals in the ASCAR area is complicated. For pelagic organisms, it is made even the more so by Gulf Stream rings (Chapter 3). The effect of cold-core rings is to translate temperate pelagic organisms south across the Stream into a subtropical environment; warm-core rings have an opposite effect. In both cases, tropical plants and animals are detached from the Gulf Stream and left behind. For various reasons, the subtropical biota carried north into the Slope Water by warm-core rings survives better than the temperate biota carried into the Northern Sargasso Sea by cold-core rings. Thus, the former is more often encountered in samples than the latter.

For pelagic organisms the effects of water mass on distribution are of paramount importance, while the comparative effects of the change in water depth from 200 to 4000 m across the study area are trivial. For benthic animals, however, almost the reverse is true: water depth is more important than the nature of the overlying water. Although benthic animals in the transition zone (250 to 300 m to about 1000 m) off New England may be affected by Gulf Stream rings (Grassle et al., 1979), most changes are independent of water masses. Changes with depth below the transition zone are more likely to result from changes in the amount of food reaching the bottom (Sanders and Hessler, 1969; Rex, 1981; Rowe et al., 1982).

MICROBIOLOGY

Microbiology in its broadest sense encompasses the biology of all those organisms too small to be seen by the naked eye, including the microalgae, the cyanobacteria (blue-green algae), the fungi, the protozoans, the bacteria and the viruses. The present report will be limited to a survey of our current knowledge of marine bacteria and protozoans (including the cyanobacteria) in the ACSAR area.

BACTERIA

The bacteria are unified by their cellular architecture; all possess the properties of procaryotic cells. Their enormous diversity is expressed physiologically. The principal forms of energy-yielding metabolism, aerobic respiration, photosynthesis and fermentation all exist in bacteria as well as in various groups of eucaryotic microorganisms. In addition, there are types of energy-yielding metabolism which are unique to bacteria, including variations of photosynthesis, anaerobic respiration, a large number of unique fermentations and the oxidation of reduced inorganic compounds. It is the existence of this physiological diversity among bacteria that makes assessing the ecological role of these organisms as a whole an extremely difficult, if not impossible, task. In attempting to assess the role of bacteria in the oceans, microbial ecologists are following two basic approaches, the study of specific groups of bacteria or bacterial processes and the study of bacterial populations and activities as a whole.

Techniques Used in the Study of Marine Bacteria

Bacterial Concentration and Biomass (Standing Crop)

Historically, bacteria were enumerated in seawater using culture techniques such as direct plating or serial dilutions. These techniques drastically underestimate the total number of bacteria present in seawater. Bacteria are extremely diverse physiologically, with the result that no single medium can be expected to promote the growth of all or even a major function of the bacterial types present in a given sample of sea-water. Conversely, culture techniques can be a powerful tool in studying single species of bacteria. In such instances it is often possible to design selective enrichment media that will promote the growth of specific bacteria (Jannasch and Jones, 1959).

Recent developments in techniques now make it possible to accurately count bacteria directly in seawater. The most important breakthrough came with the development and widespread use of epifluorescent microscopy. While this technique is very accurate for enumerating bacteria, it cannot distinguish the bacteria that are metabolically active from those that are dormant or near death. See Daley and Hobbie (1975), Watson et al. (1977), Porter and Feig (1980) and

Coleman (1980) for a description of this technique. Immunofluorescent techniques have recently been developed that enable the counting of specific species of bacteria in seawater. Ward and Perry (1980) have successfully used this technique to count marine ammonia oxidizing bacteria within the water column.

Bacterial biomass in seawater has been estimated by the measurement of cell volumes (Watson et al., 1977); the measurement of lipopolysaccharide, a unique component of the cell walls of gram-negative bacteria (Watson et al., 1977), the measurement of ATP (Holm-Hansen and Booth, 1966; Hodson et al., 1976), and the measurement of muramic acid, another compound unique to the cell walls of bacteria (Moriarty et al., 1979). In order to convert the quantities of the various compounds described above into biomass it is necessary, in each case, to apply a conversion factor to change them to estimates of cell carbon.

Bacterial Activity and Growth

Demonstration of Percent of Total Population that is Metabolically Active

Only a small fraction of the standing crop of bacteria can be cultured by traditional methods, suggesting that a large portion of the standing crop may either be metabolically inactive or non-viable. Several techniques have been developed in an attempt to document the active percentage of the standing stock. These include a technique combining autoradiography and epifluorescence microscopy (Meyer-Reil, 1978); incubation of natural bacterial populations with an organic substrate (yeast extract) in the presence of nalidixic acid (Kogure et al., 1979); reduction of tetrazolium salts via respiratory electron transport in conjunction with epifluorescence counting techniques to estimate the portion of natural populations of bacteria that were actively respiring (Zimmerman et al., 1978); the adenylate energy charge ratio (Chapman et al., 1971; Wiebe and Bancroft, 1975); and estimations of the activity of respirating electron transport systems in bacteria (Packard, 1969; Christensen et al., 1980; Christensen and Packard, 1979).

Use of Radioactive Isotopes to Measure Bacterial Processes in Natural Populations

The use of radioactive compounds employing radioisotopes, the most common of which are ^{14}C, ^{3}H, ^{35}S and ^{15}N, during the last 40 years has revolutionized the study of individual microbial processes. These techniques have also been widely employed in the study of natural populations of bacteria where they are typically used either to estimate the rate of incorporation of various labeled compounds into cell material or to measure the rates of mineralization of various compounds. See Hobbie and Rublee (1977) for a review of the use of radioisotopes by heterotrophic bacteria in aquatic ecosystems.

Measurement of Bacterial Growth in Natural Populations

Recently a number of investigators have been using the rates of incorporation of ^{3}H-labeled precursors of RNA and DNA, mainly thymidine and adenine, to estimate growth in natural populations of bacteria (Karl, 1979; Hollibaugh et al., 1980; Karl, 1981, 1982; Karl et al., 1981; Fuhrman and Azam, 1982; Kirchman et al., 1982). Considerable controversy currently exists concerning the numerous assumptions inherent in the technique. See Karl (1982) for an evaluation of the current status of this technique. Several investigators (Hagstrom et al., 1979; Newell and Christian, 1981) have attempted to use the frequency of dividing cells as an indicator of bacterial growth rates in natural populations.

In summary, the techniques listed above each have their advantages and disadvantages. Applied individually they almost certainly lead to unsatisfactory results. However, a great deal of meaningful information can be obtained from studies that incorporate a number of these techniques to examine specific ecological problems.

The vast majority of the recent literature in marine bacteriology concerns studies that have been conducted on inshore waters. A considerable number of bacteriological studies were conducted by Waksman and his collaborators off the coast of New England during the 1930s. (See Zobell (1946) for a summary of this early work.) Their work was largely confined to the continental shelf and dealt with the enumeration of bacteria and correlating the presence and activity of bacteria with decomposition and the availability of organic matter, both in the water column and in sediments. The number of bacteriological studies that have specifically examined processes in the Slope Waters off the eastern coast of the United States are relatively limited. They will be reviewed in two sections; one dealing with water column studies and the other with the study of deep-sea bacteriology. In addition a brief section is included on the Cyanobacteria. Planktonic members of this group have recently been shown to be important primary producers in both tropical and temperate waters. Even though these microorganisms perform oxygenic photosynthesis it was thought best to include them here because they are a group of bacteria which have been most successfully delt with using the techniques of microbiology.

Water Column

Hobbie and co-workers (1972) studied the distribution and activity of microorganisms at two stations within the ACSAR area. Station 1 (36°25'N, 74°43'W) was in Slope Water and station 2 (35°00'N, 73°00'W) was in the extreme western Sargasso Sea. Hydrographic data for the two stations are shown in Table 6.1. Bacterial numbers were determined by light microscopy using phase contrast optics. Phytoplankton were enumerated by light microscopy on fixed samples. Total microbial biomass was determined from ATP measurements. Estimates of metabolic activity were made from ETS activity (Electron Transport System), oxygen uptake, CO_2 uptake and from the uptake of specific radiolabeled organic compounds. In addition, total particle counts and volumes were determined by an electronic particle counter, and particulate organic carbon, chlorophyll and DNA were measured.

The major conclusion from their data set was that the bacteria were not present in sufficient number to contribute a significant fraction of the living biomass or to contribute significantly to the respiratory processes measured. They also concluded that bacteria and not phytoplankton were responsible for heterotrophic uptake of the dissolved organic substrates tested. Their results also indicated that the activity measured by the uptake of labeled organic substrates represented a small fraction of the total respiration as measured by respirometry and ATP and ETS activity. This led them to conclude that most of the observed respiration was non-bacterial or if bacterial must involve substrates they did not test. The organism responsible for the observed rates of respiration could not be identified. The actual bacterial cell counts at the two stations (Table 6.2.) were low as a result of counting by phase contrast microscopy. If the acridine orange technique using epifluorescence microscopy had been available, the major conclusion drawn by the authors, as stated above, might have been different.

Sta. 1, 17 Nov				Sta. 2, 19 Nov			
Thermo-metric depth (m)	Temp (°C)	S (‰)	O_2 (mg liter^{-1})	Thermo-metric depth (m)	Temp (°C)	S (‰)	O_2 (mg liter^{-1})
surf.	19.48	34.71	10.04	surf.	22.39	36.42	9.47
13	19.60	34.70	9.94	10	22.43	36.40	9.51
20	19.86	34.99	10.02	18	22.48	36.44	9.48
50	18.81	35.18	9.08	32	22.48	36.41	9.46
110	14.18	35.32	7.86	127	22.30	36.51	9.26
151	11.87	35.44	6.08	142	20.65	36.66	8.63
200	12.70	35.40	6.90	175	19.33	36.62	8.73
308	9.67	35.20	6.15	311	18.37	36.53	8.47
342	7.93	35.06	7.44	400	17.92	36.48	8.94
455	7.16	35.02	8.47	477	17.77	36.46	9.16
629	5.72	34.99	9.72	607	16.97	36.30	8.51
656	5.58	34.97	10.34	685	14.98	35.92	7.50

Table 6.1. Hydrographic data at two stations in the western North Atlantic at which living mass and metabolism of microorganisms were studied in 1969) (from Hobbie et al., 1972).

Depth (m)	Bacteria No./ml of concentrate*		Motile cells present	No. phytoplankton with Chl/ml (concentrate)	Dominant aggregate type†
	free cells	attached cells			
			Station 1		
40	1.70×10^5	$<10^3$	—	1.7×10^4	floc
100	7.00×10^3	$<10^3$	—	4.0×10^3	floc
200	1.60×10^4	$<10^3$	—	2.0×10^3	floc
500	3.60×10^4	$<10^3$	—	7.0×10^2	floc
700	‡		—	‡	floc and plate
			Station 2		
6	2.00×10^4	$<10^3$	—	1.6×10^3	floc and plate
100	2.50×10^5	$<10^3$	—	7.0×10^2	floc and plate
200	4.00×10^4	$<10^3$	+	‡	plate
500	1.50×10^4	$<10^3$	—	‡	plate
700	3.50×10^4	$<10^3$	+	‡	plate

* All values were calculated using 10,000× concentration of particles. These values are the same as raw seawater counts/ml when divided by 10^4; 100 fields were counted at 1,000× magnification under phase contrast.
† *See text* for description of the two types of aggregates.
‡ None seen.

Table 6.2. Microscopic observations at sea of freshly concentrated particulate material (from Hobbie et al., 1972).

Ferguson and Palumbo (1979) in a study of the distribution of suspended bacteria in neritic waters south of Long Island included one Slope Water station (39°40'N, 71°55'W). The bacterial profile showed concentrations approaching 10^6 cells ml^{-1} in the mixed layer, dropping to about 10^5 cells ml^{-1} below the thermocline and remaining relatively constant throughout the water column (Figure 6.1.).

Burney et al. (1981) examined the effect of small scale nannoplankton and bacterioplankton distributions on concentrations of dissolved carbohydrates in the western Sargasso Sea. Water samples were collected from two isotherms at drogue buoy stations, one of which was in the study area (Station 1, 32°41'N, 74°31.6'W). The writers concluded that the combined activities of the plankton smaller than 20 µm regulated the dissolved carbohydrate concentration in the Sargasso Sea.

Packard and Williams (1981) compared the rates of respiratory oxygen consumption and electron transport activity (ETS) in surface water of the North Atlantic. Two of their stations (40°14'N, 67° 13'W and 40°12'N, 67°12'W) were in the ACSAR area. Respiration rates in Slope Water, 5.6 g O_2 day^{-1} m^{-2}, were slower than those measured in the Gulf of Maine. They concluded that oxygen consumption and ETS activity are related and that water column respiration exceeded primary production in July.

Cuhel et al (1983) studied microbial growth and macromolecular synthesis at three stations in the northwestern Atlantic Ocean. Station locations, physical, chemical and standing crop data are shown in Table 6.3. Results indicate the utility of using inorganic nutrient uptake and subcellular incorporation patterns to measure growth and metabolism in natural microbial populations. They also stress the necessity of making time-course rather than end point incubations as evidenced by the marked deviation from linearity at many of their incubations.

Bacteria Associated with Particles ("Marine Snow")

The relative roles of free-living bacteria and bacteria associated with particles have been debated for some time. "Marine snow" seems to be present in the marine water column almost everywhere. The number and source of particles is variable with the result that the degree of colonization by bacteria also varies. Field observations indicate that some flocculent aggregates are produced by zooplankton (Silver and Alldredge, 1981). They include feeding structures formed by larvaceans, pteropods, salps, veligers and polychaetes.

Jannasch (1973) reported that bacteria were absent from particles collected from surface waters near the ACSAR area (29°33'N, 67°35'W). He suggested that the absence of bacteria might be due to a recent origin or labile state of the particulate material.

Wiebe and Pomeroy (1972) studied the association of microorganisms with aggregates and detritus. In the open ocean they observed two types of particles, flat, plate-like flakes and flocculent particles. The flakes seldom contained recognizable bacteria or other microorganisms, whereas, the flocs contained low numbers of bacteria. They concluded that the notion that bacteria coat particles in the ocean is generally not valid.

Hodson et al. (1981) in a study including five stations within ACSAR study area, observed that the per cell uptake of dissolved ATP by attached bacteria was one to two orders of magnitude faster than uptake by free living bacteria. They suggested that the increased uptake of the former could be accounted for by their larger cell volumes.

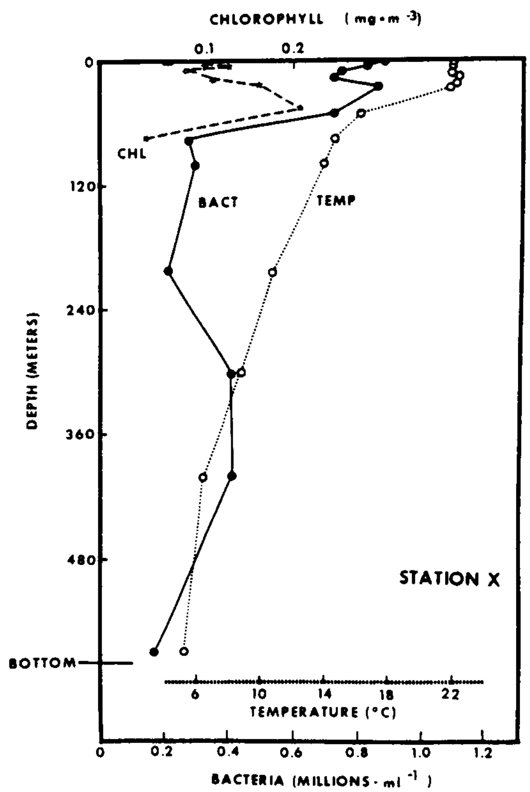


Figure 6.1. Depth profile of bacterial cell numbers and chlorophyll concentrations at station X which is seaward of shelf break. From Ferguson and Palumbo (1979).

Parameter	Continental shelf 27 Jul 80	Continental slope 21 Jul 80	Continental slope 1 Nov 81	Sargasso Sea 23 Jul 80
N lat, W long	40°07.91′, 68°41.2′	37°49.4′,64°41.9′		37°29.3′, 63°54.1′
Water column depth, m	175	2,300		4,900
Depth sampled, m	150	250		250
Sample temp, °C	11.5	11.3	10.5	18.4
Salinity, ‰	35.636	35.092	ND	37.011
Phosphate, μM	3.55	1.52	1.20	0.18
Nitrate + nitrite, μM	14.12	23.23	21.95	2.62
Ammonium, μM	12.66	0.83	0.33	0.62
Particulates				
Org C, $\mu g \cdot liter^{-1}$	35.1	31.3	61.8	23.5
Org N, $\mu g \cdot liter^{-1}$	3.7	2.1	6.1	1.6
C:N, wt	9.5	14.9	10.2	14.7
Carbohydrate, $\mu g \cdot liter^{-1}$	5.7	1.4	ND	3.7
Protein, $\mu g \cdot liter^{-1}$	4.8	3.7	5.2	4.0
Bacteria, $cells \cdot ml^{-1}$	3.34×10^5	ND	ND	1.63×10^5

Table 6.3. Physical, chemical, and standing crop data for R/V OCEANUS cruise 84 and 107 (ND-not determined) (from Cuhel et al., 1983).

Deep-Sea Populations

During the last decade there has been a renewed interest in the microbiology of the deep sea. Many of these studies have been conducted in the study area by Jannasch and co-workers at the Woods Hole Oceanographic Institution and by Colwell's group at the University of Maryland.

Three approaches have been used to examine deep sea microorganisms and their activities in the deep sea: 1) study of decompressed samples; 2) in situ studies; 3) laboratory studies of undecompressed samples. The first approach initiated by ZoBell and co-workers in the 1940's, entails studies enumerating, isolating, and studying the physiology of bacteria present in deep sea water and sediments and in the gut flora of deep sea animals. These studies use traditional microbiological techniques on decompressed samples to examine the effects of such properties as temperature and pressure. Results have been summarized in reviews by ZoBell (1970) and Morita (1976).

Two reports by Colwell and co-workers include stations (Tabor et al., 1981; Ohwada et al., 1980) in the ACSAR area. Tabor et al. isolated bacteria from deep-ocean bottom water and described isolates that passed through 0.45 um filters, showing that a significant relationship existed between decreased cell size and increased survival of bacteria isolated from the deep sea. In the study of Ohwada et al. (1980), the gut bacterial flora of animals collected from 570 to 2446 m were enumerated and characterized. Figure 6.2 gives the locations where samples were collected, Table 6.4 describes the animals examined, Table 6.5 gives the number of aerobic, heterotrophic bacteria found, and Table 6.6 shows the viability and growth of bacterial isolates at elevated pressures. The following conclusions were drawn from this study: 1) The number of culturable aerobic, heterotrophic bacteria was low in the animals that were collected from the greatest depths. 2) Vibrio spp. were the predominant isolates in ten of fifteen samples with Photobacterium and yeasts being predominant in the remainder. 3) Pseudomonas, Achromobacter and Flavobacterium comprised minor components of the gut flora of deep sea fish. 4) Strains of bacteria isolated from fish intestines were more barotolerant than those isolated from stomach.

Much of the interest in the study deep-sea bacteria stemmed from the accidental sinking of the research submersible ALVIN in 1968. A packaged lunch was found to be well preserved after ten months at 1540 m (Jannasch et al., 1971). The food stuffs rapidly decomposed when brought to the surface and incubated at 4°C, indicating that pressure had been responsible for slowing microbial degradation. See Jannasch and Wirsen (1977) and Jannasch (1979) for overviews of this work.

In Situ Studies

Jannasch's first approach (Jannasch and Wirsen, 1973; Wirsen and Jannasch, 1976) was to use ALVIN-deployed pressure containers containing serum stoppered bottles. The bottles, containing a variety of substrates, were deployed at Deep Ocean Stations (DOS 1-3) in the North Atlantic at depths between 1830 and 3640 m. The pressure chamber was opened and the bottles inoculated and incubated for periods up to one year. These early experiments showed that the solid organic substrates (agar, starch, gelatin) placed on the sea floor in open containers showed almost no sign of disintegration (except for animal feeding marks) after exposure of one year. The microorganisms collected and incubated on the deep sea floor exhibited extremely slow metabolic rates, confirming the conclusion that the deep sea is extremely inefficient at recycling organic wastes.

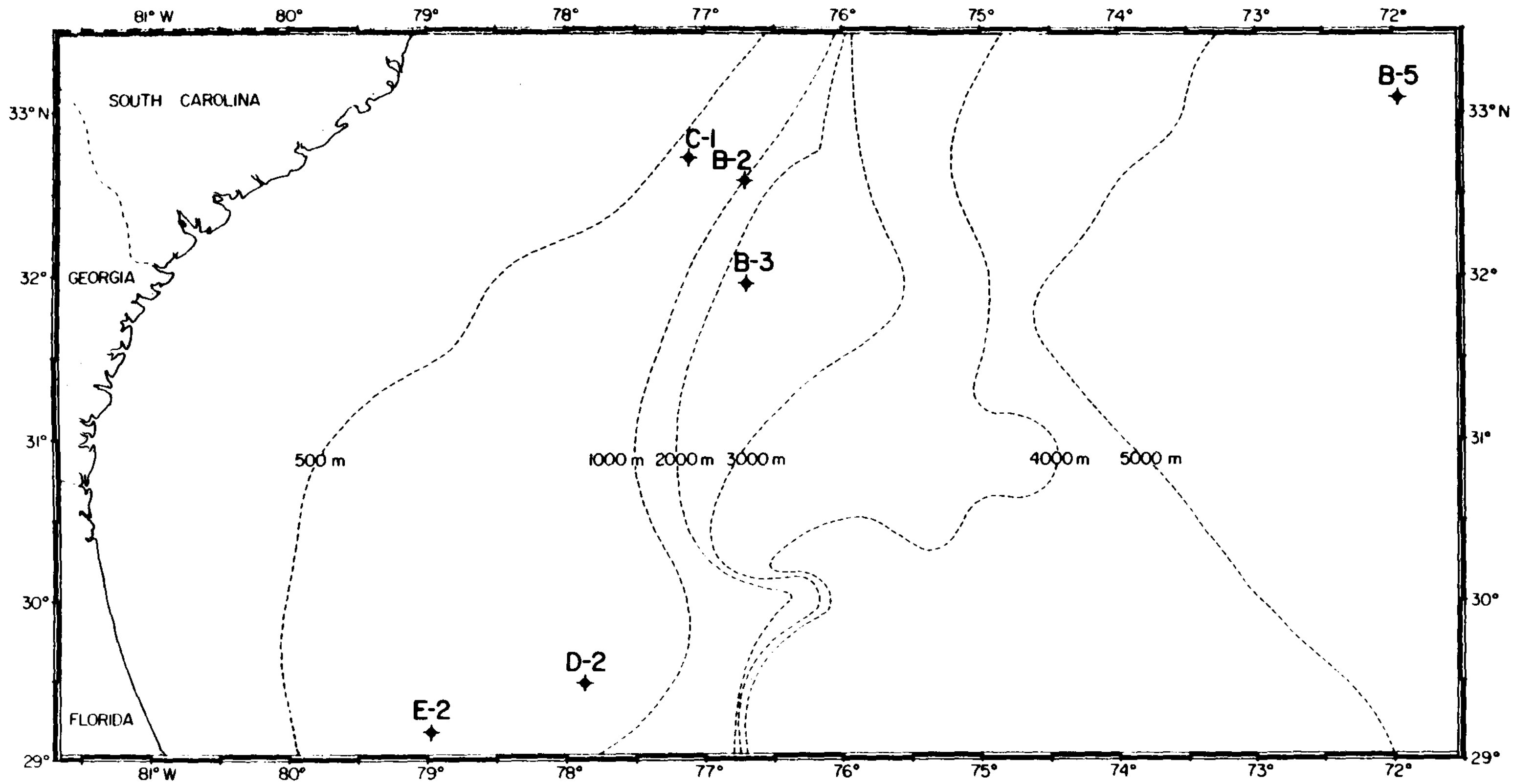


Figure 6.2. Location of stations and bathymetry of the area sampled during cruises of the R/V JAMES M GILLISS. Stations E-2 (828 m) D-2 (855 m), B-2 (1,393 m), B-3 (2,446 m), and B-5 (5,524 m) were sampled in November 1976. Stations C-1 (570 m), B-2, and B-3 were sampled in June 1977.

Specimen no.	Species name	Type	Sampling station	Specimen size		Gut wt (g)		
				Length (cm)	Wt (g)	Whole gut	Stomach	Intestine
UM 1	*Nematocarcinus cursor*	Shrimp	E-2	2.2	—	0.2		
UM 2	*Nezumia aequalis*	Fish	E-2	20.0	—	1.2		
UM 3	*Bathypterois bigelowi*	Fish	E-2	16.0	—	0.8		
UM 4	*Hoplostethus mediterraneus*	Fish	D-2	13.0	51.0	3.0		
UM 5	*Laemonema barbatulum*	Fish	D-2	9.0	7.5	0.4		
UM 6	*Bathypterois bigelowi*	Fish	D-2	16.0	31.0	1.2		
UM 7	*Synaphobranchus kaupi*	Fish	D-2	28.0	27.7	3.2		
UM 8	*Coryphaenoides armatus*	Fish	B-3	28.5	63.5	4.8		
UM 9	*Coryphaenoides armatus*	Fish	B-3	32.0	84.0	5.0		
UM 10	*Nezumia aequalis*	Fish	B-2	20.0	15.0	1.0		
UM 11	*Lycodes* sp.	Fish	B-2	21.0	31.5	1.7		
UM 12	*Laemonema barbatulum*	Fish	B-2	8.5	2.9	0.2		
UM 13	*Nezumia aequalis*	Fish	B-2	24.0	25.0	0.9		
UM 14	*Lycodes* sp.	Fish	B-2	24.5	42.5	2.7		
UM 15	*Acanthephyra parparea*	Shrimp	B-5	1.9	3.0	0.2		
UM 16	Not identified	Shrimp	B-5	1.9	2.5	0.2		
UM 17	*Plesiopenaeus edwardsianus*	Shrimp	B-5	2.0	2.5	0.1		
UM 22	*Halosauropsis macrochir*	Fish	B-3	60.0	160.0		4.0	4.0
UM 23	*Coryphaenoides armatus*	Fish	B-3	39.0	321.0		3.1	6.0
UM 24	*Antimora rostrata*	Fish	B-3	29.0	150.0		4.0	5.1
UM 25	*Synaphobranchus kaupi*	Fish	B-2	28.0	21.0		1.2	0.8
UM 26	*Ilyophis brunneus*	Fish	B-2	39.0	56.0		4.4	1.6
UM 27	*Laemonema barbatulum*	Fish	C-1	10.5	8.7		0.9	0.6

Table 6.4. Description of the 23 animals and the stomach and intestine, or whole gut, samples studied by Ohwada et al. (1980).

Specimen no.	Collection depth (station)	Initial concn (total viable count, CFU/g)[a]		
		Whole gut	Stomach	Intestine
UM 27	C-1	5.2×10^7	5.8×10^6	7.2×10^7
UM 1	E-2	5.0×10^4	—	—
UM 2	E-2	1.9×10^8	—	—
UM 3	E-2	2.3×10^6	—	—
UM 4	D-2	1.8×10^7	—	—
UM 5	D-2	4.0×10^5	—	—
UM 6	D-2	3.3×10^7 (2.5×10^7)[b]	—	—
UM 7	D-2	2.2×10^7	—	—
UM 10	B-2	1.2×10^5 (1.0×10^5)	—	—
UM 11	B-2	1.5×10^7	—	—
UM 12	B-2	4.4×10^4 (3.5×10^4)	—	—
UM 13	B-2	2.1×10^6 (1.7×10^5)	—	—
UM 14	B-2	6.7×10^6 (4.8×10^5)	—	—
UM 25	B-2	4.7×10^5	7.8×10^5	8.3×10^3
UM 26	B-2	9.2×10^2	2.3×10^2 (2.2×10^2)	2.8×10^3[c]
UM 8	B-3	5.2×10^6	—	—
UM 9	B-3	1.0×10^6	—	—
UM 22	B-3	2.5×10^2	2.3×10^2	2.5×10^2
UM 23	B-3	2.2×10^2	3.3×10^2	1.6×10^2
UM 24	B-3	2.2×10^2	2.0×10^2	2.5×10^2

[a] Stomach and intestine were not separated in the case of UM 1 through UM 17. The total viable counts of gut suspensions of UM 22 through UM 27 represent the total counts of stomach plus intestine, expressed as CFU per gram.

[b] Number in parentheses indicates the number of luminous bacteria observed.

[c] No luminous bacterial colonies were observed on *Photobacterium* agar, but a significant number of strains isolated from plates inoculated with suspensions of UM 26 intestine were identified as *Photobacterium* spp.

Table 6.5. Number of viable, aerobic, heterotrophic bacteria found in suspensions of gut, or separated stomach and intestine, of fish and shrimp specimens. (From Ohwada et al. (1980).

Culture no.	Identification[a]	Source[b]	Pressure (atm)[c]				
			100	250	450	600	750
900	A	UM 22, intestine	3+	2+	1+	NC	NC
890	Ps	UM 22, stomach	3+	1+	1+	NC	3−
891	Fl	UM 22, stomach	2+	1−	3−	3−	3−
892	V	UM 22, stomach	3+	2+	1+	NC	2−
893	Ps	UM 22, stomach	3+	2+	1+	NC	3−
894	Ph	UM 22, stomach	3+	1+	1+	1+	3−
896	V	UM 22, stomach	2+	1−	3−	3−	4−
887	Fl	UM 23, stomach	3+	2+	1+	1+	2−
888	Fl	UM 23, stomach	3+	2+	2+	NC	3−
889	Fl	UM 23, stomach	3+	1+	1+	NC	3−
902	Ps	UM 24, stomach	3+	2+	1+	NC	3−
904	A	UM 24, stomach	3+	2+	1+	NC	2−
905	Ps	UM 24, stomach	3+	2+	1+	NC	2−
844	Ph	UM 26, stomach	3+	2+	1+	NC	NC
845	Ph	UM 26, stomach	3+	2+	1+	NC	NC
846	Ph	UM 26, stomach	3+	2+	1+	1+	NC
847	Ph	UM 26, stomach	3+	2+	2+	1+	1−
848	Ph	UM 26, stomach	3+	2+	1+	1+	1+
849	Ph	UM 26, intestine	3+	1+	NC	1−	3−
850	Ph	UM 26, intestine	3+	1+	1+	NC	1−
851	Ph	UM 26, intestine	3+	2+	2+	1+	1−
801	V	UM 27, intestine	3+	2+	2+	1−	4−
802	V	UM 27, intestine	3+	2+	1+	NC	3−
803	V	UM 27, intestine	3+	2+	NC	NC	3−
804	V	UM 27, intestine	3+	2+	2+	3−	3−
805	V	UM 27, intestine	3+	2+	2+	2−	3−
806	V	UM 27, intestine	3+	2+	NC	2−	3−
807	V	UM 27, intestine	3+	2+	NC	3−	3−
808	V	UM 27, intestine	3+	2+	1+	3−	3−
809	V	UM 27, intestine	3+	2+	1+	NC	3−
810	V	UM 27, intestine	3+	2+	1+	3−	3−
811	V	UM 27, intestine	3+	2+	1+	3−	3−
813	V	UM 27, intestine	3+	2+	1−	1−	3−
820	V	UM 27, intestine	3+	2+	NC	NC	3−
821	V	UM 27, stomach	3+	2+	1−	2−	3−
822	V	UM 27, stomach	3+	2+	NC	2−	3−
823	V	UM 27, stomach	3+	2+	NC	2−	3−
824	V	UM 27, stomach	3+	2+	NC	2−	3−
825	V	UM 27, stomach	3+	2+	1+	2−	3−
826	V	UM 27, stomach	3+	2+	NC	2−	3−
827	V	UM 27, stomach	3+	2+	NC	2−	3−
828	V	UM 27, stomach	3+	2+	1−	3−	3−
829	V	UM 27, stomach	3+	2+	NC	2−	3−
830	V	UM 27, stomach	3+	2+	NC	2−	3−
831	V	UM 27, stomach	3+	2+	NC	2−	3−
833	V	UM 27, stomach	3+	2+	NC	2−	3−
101	O	Amphipod, gut, phenon 20	3+	2+	1+	2−	2−
102	O	Amphipod, gut, phenon 20	3+	2+	1+	NC	1−
103	O	Amphipod, gut, phenon 20	3+	2+	1+	1+	2−
105	O	Amphipod, gut, phenon 20	3+	2+	1+	2−	3−
327	O	Amphipod, gut, phenon 20	3+	3+	2+	NC	1−
344	O	Amphipod, gut phenon 20	3+	3+	2+	NC	1−
347	O	Amphipod, gut, phenon 20	3+	3+	3+	NC	1−
104	Ps	Amphipod, gut, phenon 26	3+	2+	1+	2−	3−
161	Al	Amphipod, surface, phenon 30	3+	2+	1+	NC	2−
162	Al	Amphipod, surface, phenon 30	3+	2+	1+	NC	2−
Pseudomonas fluorescens		Chesapeake Bay	3+	2+	NC	3−	3−
Bacillus megaterium		Chesapeake Bay	2+	1+	1−	3−	3−
P. maltophilia		Chesapeake Bay	2+	1+	3−	3−	3−
Chromobacterium sp.		Chesapeake Bay	1+	NC	3−	3−	3−

[a] O, *Oceanospirillum* spp.; Al, *Alteromonas* spp.; other abbreviations for genera are given in the legend for Fig. 2.

[b] Amphipod strains were included in a numerical taxonomy study (to be published elsewhere). Isolates clustering within the same phenon were concluded to be related.

[c] Increase or decrease in number of bacteria, measured as CFU and presented as the number rounded to the nearest order of magnitude: 1+ = one order of magnitude increase; 2+ = two orders of magnitude increase; NC = no change, i.e., less than one order of magnitude increase or decrease; 1− = one order of magnitude decrease in viable count; etc. Strains 888 and 344 were tested in duplicate, and no significant difference in number, in the case of duplicate samples, was observed at any of the pressures tested.

Table 6.6. Viability and growth at elevated pressure of isolates comprising the gut flora of deep-sea benthic fish and amphipods, and of reference strains included for purposes of comparison. (From Ohwada et al. (1980).

In a study designed to examine the role of chemoautotrophic bacteria, Tuttle and Jannasch (1976) examined the utilization of thiosulfate on a mooring at 5300 m located at 34°02'N, 69°59'W, just outside the ACSAR area. These experiments demonstrated the potential for microbial thiosulfate utilization at elevated pressure and low temperature in seawater by both natural populations as well as by previously isolated pure cultures of thiosulfate-oxidizing bacteria.

Jannasch's second approach to *in situ* studies was to develop a "free vehicle" that would not require submersible deployment (Jannasch and Wirsen, 1980). The experiment described by Jannasch and Wirsen (1980) (station DOS-2, 38°18'N, 69°36'W at 3580 m) showed the amount of acetate metabolites after decompression at 1 atmosphere and 3°C was 2 1/2 times that metabolized *in situ* (Table 6.7), confirming earlier observations that the combination of low temperature and high pressure greatly reduced rates of mineralization.

Laboratory Studies with Undecompressed Samples and Cultures

The *in situ* experimental methods described above have drawbacks. Most importantly, rate measurements are not possible, only end-point determinations can be made. To circumvent these problems Jannasch and Wirsen (1973) designed and built samplers and incubation chambers that would retain both *in situ* pressures and temperature. Colwell's group (Tabor and Colwell, 1978; Tabor et al., 1981) also developed similar devices. One of Jannasch's and Wirsen's early time-course measurements is shown in Figure 6.3 (Jannasch, 1979). The incorporation and turnover of casamino acids by a mixed microbial population showed an increase upon decompression. They observed that the degree of pressure sensitivity depended upon the type of substrate used.

In a recent, more comprehensive study, Jannasch and Wirsen (1982) compared microbial activities in undecompressed and decompressed deep-seawater samples. The collection sites were largely within ACSAR study area (Figure 6.4). Results show that rates of incorporation and CO_2 production as well as total substrate utilization are generally lower at pressure than at 1 atmosphere control. Rates also are different for each of the four substrates used. With one exception (a water sample collected at 4500 m and incorporrated with glucose), the transformation of all the substrates showed an increased lag period at pressure when compared to the 1 atmosphere control.

Marine bacteria show several responses to pressure. Barotolerant bacteria will tolerate elevated pressures but always grow better at 1 atmosphere. Barophilic bacteria grow optimally at pressures above 1 atmosphere and obligately barophilic bacteria will only grow at elevated pressures. Until recently, studies of barophilic bacteria (Yayanos et al., 1979, 1981; ZoBell and Morita, 1957) have been limited to strains that would survive decompression. Jannasch and co-workers (Jannasch, 1979; Jannasch et al., 1982) have developed an isolation chamber that permits isolation in pure culture of strains of bacteria in the absence of decompression. Using this chamber they have isolated 15 pure cultures of bacteria, 11 of the strains were barotolerant and four were barophilic.

Early in the study of microbial transformations in the deep sea, Jannasch and co-workers (Jannasch and Wirsen, 1973; Wirsen and Jannasch, 1976) noted that solid substrates incubated *in situ*, that were not screened to exclude larger organisms, showed feeding marks from small invertebrates. From these and other experiments, it became clear that a considerable part of the

A (North Atlantic, 38°18'N, 69°36'W, depth 3 580 meters) and B (Outer Ridge of Puerto Rico Trench, 20°39'N, 65°07'W, depth 5 330 meters). Under A' results are recorded obtained from sediment taken at A, but injected with substrate and incubated in the laboratory at 1 atm and 3 °C.

	Sediment sections (cm)	*Point of injection (cm)*	*Volume of section (cm^3)*	*Acetate injected* (μmol/section)	*Period of incubation* (hrs)	*Acetate incorporated* (μmol/cm^3/day)	*Acetate respired* (μmol/cm^3/day)
	0-5 1/2	4 1/2	111.5	2.47×10^{-1}	69	2.64×10^{-4}	5.84×10^{-5}
A	5 1/2-8 1/2	6 1/2	60.7	2.47×10^{-1}	69	6.26×10^{-5}	4.52×10^{-5}
	8 1/2-12	9 1/2	71.0	2.47×10^{-1}	69	2.95×10^{-5}	2.92×10^{-5}
	0-3	2	60.7	2.47×10^{-1}	69	5.74×10^{-4}	1.86×10^{-4}
A'	3-6	4	60.7	2.47×10^{-1}	69	1.91×10^{-4}	1.02×10^{-4}
	6-9	7	60.7	2.47×10^{-1}	69	7.38×10^{-5}	5.13×10^{-5}
	0-4	3	81.0	6.76×10^{-2}	124	1.37×10^{-5}	3.76×10^{-6}
B	4-7	5	60.7	6.76×10^{-2}	124	1.18×10^{-5}	3.32×10^{-6}
	7-10	8	60.7	6.76×10^{-2}	124	1.03×10^{-5}	2.71×10^{-6}

Table 6.7. Metabolic conversion of Na-^{14}C-acetate in the upper sediment layers at two locations: A (North Atlantic, 38°18'N, 69°36'W, depth 3580 meters) and B (outer Ridge of Puerto Rico Trench, 20°39'N, 65°07'W, depth 5330 meters). Under A results are recorded obtained from sediment taken at A, but injected with substrate and incubated in the laboratory at 1 atm and 3°C. From Jannasch and Wirsen (1980).

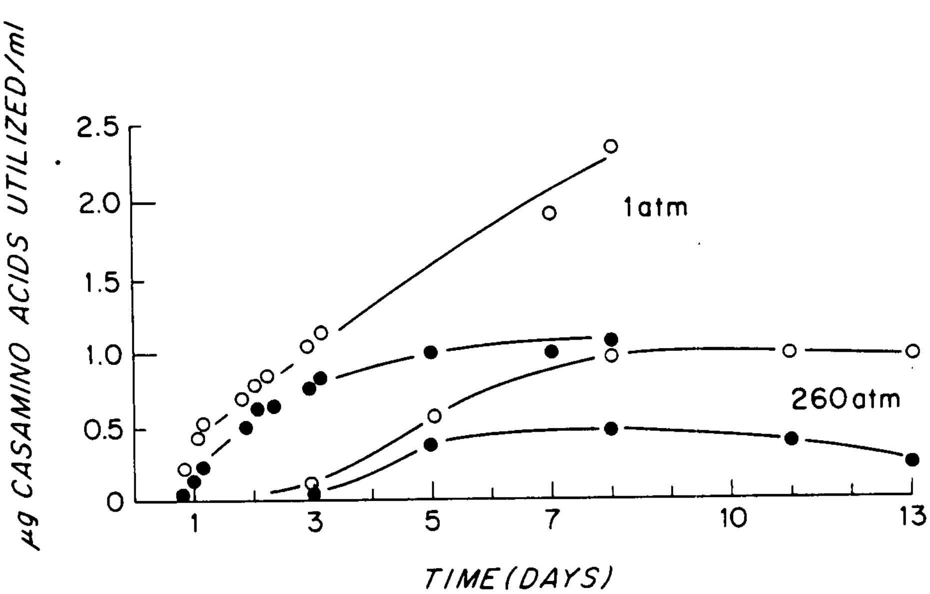


Figure 6.3. Incorporation (●●) and respiration (-o-) of ^{14}C from labeled casamino acids in a sea-water sample retrieved from 2700 m before and after decompression. From Jannasch (1979).

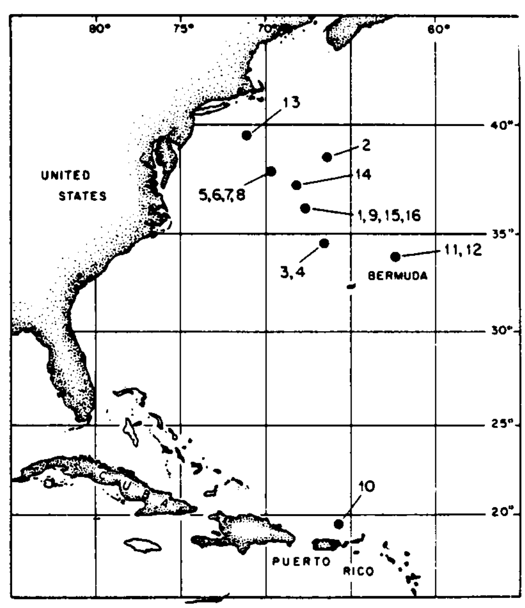


Figure 6.4. Area of sampling and sample numbers. From Jannasch and Wirsen (1980).

turnover of organic matter in the deep sea takes place in the guts of animals. The guts of animals such as arthropods, mollusks, echinoderms and fishes provide environments which are high in nutrients and favorable to bacterial growth. Barophiles have been successfully isolated from animal guts (Yayanos et al., 1979, 1981; Deming et al., 1981; Jannasch et al., 1982). In fact, the only obligate barophile currently in culture was isolated from an amphipod gut (Yayanos et al., 1979, 1981; Yayanos and Dietz, 1983).

In summary, advances in the study of deep sea microbiology in the last decade have shown that microbial activity is strongly influenced by the conditions characteristic of the deep sea. They are, in descending order of importance, low nutrient levels, except in localized areas such as invertebrate guts and where large pieces of organic input from surface waters (e.g., fish carcasses) are decomposing, low temperatures (typically between 2° and 3°C) and hydrostatic pressure. With respect to pressure, Jannasch and co-workers (Jannasch et al., 1982) believe that most of the free living bacteria in the deep sea are barotolerant and may represent bacteria that are introduced to the deep sea as the result of particle flux from the surface. Barophilic bacteria can also be isolated from the deep sea and may represent a class of bacteria that are indigenous to the area.

CYANOBACTERIA

Introduction

The cyanobacteria (blue-green algae) are a morphologically diverse group of bacteria that make their living by performing oxygenic photosynthesis in a wide variety of habitats. They are often important components of freshwater planktonic communities, where as many as 24 genera and over 100 species are known to be capable of forming extensive water blooms (Whitton, 1973; Fogg et al., 1973). In marked contrast to their freshwater counterparts, marine planktonic cyanobacteria are restricted to two principal general, *Trichodesmium* and *Synechococcus*. The organisms in the genus *Trichodesmium* are gas vacuolated oscillatorian forms which are common in tropical oceans where they form extensive blooms (Fogg et al., 1973). Their filaments aggregate into bundles which float to the surface and are seen easily with the naked eye.

The second genus, *Synechococcus*, while well documented in freshwater planktonic communities, was not known to be an important marine phytoplankter until members of this genus were observed in large numbers by Waterbury et al. (1979) using epifluorescence microscopy and by Johnson and Sieburth (1979) using transmission electron microscopy.

In addition to these two principal genera a number of others are known from the planktonic marine environment (Marshall, 1981). Two that have been studied recently are *Richelia* (Sournia, 1970; Mague et al., 1974) and *Dichothrix* (Carpenter, 1972).

Trichodesmium

Morphology

There are four described species of *Trichodesmium* (Sournia, 1968) that differ principally in the widths of their trichomes. These trichomes (or filaments) associate in two characteristic types of macroscopic aggregates; parallel bundles of trichomes or tufts in which the trichomes radiate to form a sphere. The two aggregate forms do not correlate with particular species, in fact, either form may contain more than one species.

Physiology and Nitrogen Fixation

Since Trichodesmium has never been cultured, knowledge of its physiology has been inferred from numerous in situ observations and shipboard analyses (Carpenter, 1983).

Like other cyanobacteria, Trichodesmium, contains chlorophyll a as its principal photosynthetic pigment. Phycoerythrin is its major light harvesting pigment with absorption maxima at 495, 547, and 562 nm (Shimura and Fujita, 1975). Trichodesmium contains carotenoids that are similar to those of other blue-green algae. They include ß carotene, echinenone and mixoxanthophyll (Shimura and Fujita, 1975).

Gaseous nitrogen must be reduced to ammonia prior to incorporation into nitrogenous cell components. This process, called nitrogen fixation, is limited to procaryotes including many, but not all cyanobacteria. Rates of nitrogen fixation by Trichodesmium have been measured using both the acetylene reduction assay by ^{15}N incorporation. Carpenter and Price (1976) hypothesized that N_2 fixation occurred in the center of Trichodesmium colonies, a claim that has been substantiated by experiments of Bryceson and Fay (1981) and Paerl and Bland (1982). Trichodesmium itself and not associated bacteria appears responsible for its reported nitrogen fixation (Stal and Krumbein, 1981). Rates of N_2 fixation reported for Trichodesmium are given in Table 6.8. Rates of N_2 fixation under bloom conditions (e.g., Saino and Hattori, 1978) are similar to rates reported in cultured heterocystous cyanobacteria (Fogg et al., 1973). In general, the rates of N_2 fixation by Trichodesmium are quite low under non-bloom conditions (Carpenter, 1983a).

Field studies indicate that maximum rates of photosynthesis are achieved by Trichodesmium between 20 and 30°C (Aruga et al., 1975). Field observations indicate that blooms do not begin until the water temperature reaches between approximately 20°C (Marumo and Nagasawa, 1976; Carpenter, 1983). Temperature appears to be extremely important in predicting where and when Trichodesmium will occur. This cyanobacterium has a narrow temperature range at which active growth can occur, with 20°C the apparent minimum and 30°C the maximum temperature.

Distribution and Concentration

Data on the distribution and concentration of Trichodesmium are excerpted from a recent review by Carpenter (1983a).

Summer: Hulburt (1962) reported 1.4×10^5 trichomes m^{-3} in August between Cape Cod and Bermuda. Carpenter and McCarthy (1975) observed a mean population of 1.0×10^3 trichomes m^{-3} in the Western Sargasso in late summer. Carpenter (1983a) concludes that concentrations of 10^3 trichomes would be typical of the open North Atlantic during the summer. Higher concentrations have been reported outside of the Sargasso during the summer. Dunstan and Hosford (1977) observed 2×10^6 trichomes m^{-3} near the coast of Georgia.

Autumn: Carpenter (1983a) concludes "the northern limit of the active population in the autumn is 45°N, with about 10^3 trichomes m^{-3} occurring south of this to 40°N where the population averages 10^4 trichomes m^{-3}." During the fall inshore concentrations of 10^5 trichomes m^{-3} have been reported (Dustan and Hosford, 1977; Marshall, 1971).

Table 6.8. Nitrogen-fixing rates (from Carpenter, 1983a).

Reference	Location	No. of Stations	pg N trichome hr^{-1}
Goering et al., 1966	Tropical Atlantic	6	7.8
Mague et al., 1977	Central N. Pacific	1	28.5
Carpenter and Price, 1977	Caribbean Sea	12	7.7
Carpenter and Price, 1977	Western Sargasso	16	3.3
McCarthy and Carpenter, 1979	Central N. Atlantic	5	1.9
Saino and Hattori, 1979	E. China Sea		
	T. erythraeum bloom	1	33.0
	T. thiebautii bloom	1	81.0
Capone (unpublished)	St. Croix, W.I. (mean 23 samples)	1	1.47
Bryceson, 1980	Tanzania, Indian Ocean (mean 5 samples)	1	14.8
Saino, 1977	S. China Sea	1	14.9
	Kuroshio (NiiShima I.)	1*	6.5
	Kuroshio (Shikoku I.)	1**	6.5

* 20 measurements in 4 profiles.
**24 measurements in 6 profiles.

Winter: Trichodesmium is not found in the Sargasso Sea when the surface temperature is 18°C (Dugdale et al., 1966). Dunstan and Hosford (1977) calculated a mean concentration of 1.5 x 10^5 trichomes m^{-3} off the Georgia coast. Carpenter (1983a) concludes that the northern limit of active populations in the winter is 30°N for the open Atlantic Ocean. In the western Atlantic Dunstan's and Hosford's (1977) data indicate that Trichodesmium extends to 35°N in the Gulf Stream in the winter.

Although data on the concentration and seasonal distribution of Trichodesmium in the study area are not extensive, Trichodesmium probably follows a seasonal pattern that is strongly influenced by water temperature. Trichodesmium may be present at low concentration in waters slightly colder than 20°C but most probably does not begin active growth until the water temperature exceeds 20°C. In the ACSAR area it is present in the Gulf Stream throughout the year, and in the Northern Sargasso Sea during the period when the water column is well stratified. Blooms may also occur in the Slope Waters north of the Gulf Stream during the summer months during periods of calm weather.

Primary Production

Estimates of primary production by Trichodesmium have been complicated by the extreme fragileness of this organism, with the result that cellular carbon doubling times vary widely. For example, Mague et al. (1977) recorded doubling times of 43 days in the central north Pacific Ocean, McCarthy and Carpenter (1979) reported mean doubling times of 180 days in the North Atlantic Ocean, and Carpenter and McCarthy (1975) observed similar carbon doubling times of 40 to 110 days in the western Sargasso Sea. Based on known doubling times for selected freshwater species and personal observations on cultures of Trichodesmium these numbers are probably an order of magnitude too slow. Future studies will probably show that Trichodesmium is capable of dividing once per day and will show that it is both a major primary producer and important nitrogen fixer in the central oceanic gyres.

The study of Carpenter and Price (1977) contains the most extensive data set on Trichodesmium within the ACSAR study area and is summarized below. A number of their stations were in or very near the study area (see Figure 6.5). Table 6.9 gives the concentrations of Trichodesmium at these stations. Tables 6.10 and 6.11 summarize nitrogen fixation by Trichodesmium at these stations. Note that in August the two stations in the Slope Water both have considerably higher concentrations of Trichodesmium and higher rates of N_2-fixation than the Sargasso Sea stations. Rates of primary production were not measured at any of the stations in the study area.

Synechococcus

Recent reports have shown that small unicelluar cyanobacteria are widely distributed and present in large numbers within the euphotic zone of the world's oceans (Waterbury et al., 1979; Johnson and Sieburth, 1979). Preliminary studies have also indicated that these cyanobacteria contribute significantly to primary productivity (Li et al., 1983 and Waterbury et al., 1980). The following summary is from unpublished data from J. B. Waterbury, S. W. Watson and F. Valois, Woods Hole Oceanographic Institution.

Morphology

Approximately 50 strains of Synechococcus have been cultured from the open ocean. They are small unicellular cyanobacteria (0.6 x 1.2 μm) with a typical synechococcoid ultrastructure.

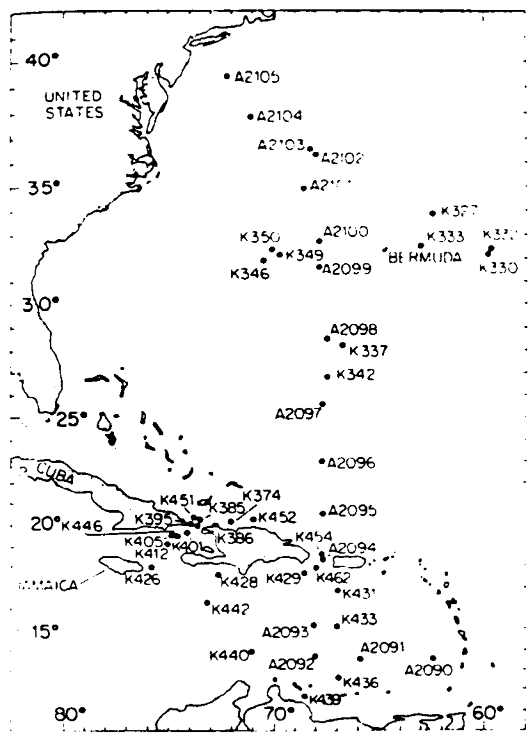


Figure 6.5. Stations sampled on three cruises (A-RV Atlantis II; K-RV Knorr). From Carpenter and Price, 1977.

Table 6.9. *Oscillatoria* cell concentrations x 10^6 m^{-3}. From Carpenter and Price (1977).

Depth (m)	K346	K349	K350	A2101	A2104	A2103	A2105
0	5.4	5.2	5.5	1.29	0.737	12.0	1.74
15	-	-	-	2.10	1.71	14.0	22.2
25	4.1	2.2	2.2	0.098	2.40	6.29	11.0
50	2.5	7.3	1.4	0.049	0.75	2.82	0.45
75	2.0	2.2	1.9	0.429	0.67	0.91	0.17
100	1.5	2.7	2.6	0.216	0.44	0.54	0.12
125	2.8	2.8	0.97	0.389	0.52	-	-
150	0.8	0.57	0.32	0.125	0.90	-	-
175	-	0.53	0.48	0.186	-	-	-
200	-	-	-	-	-	-	-

Table 6.10. N_2 fixation by *Oscillatoria* spp. as Pg N_2 $cell^{-1}$ hr^{-1}; from Carpenter and Price (1977).

Depth (m)	K346	K349	K350	A2102	A2103	A2105
0	0.035	0.017	0.069	0.013	0.014	0.017
12	0.004	0.004	0.008	0.012	0.01	0.026
20	0.001	0.022	0.001	0.006	0.023	0.038
30	0.004	0.009	0.008	--	0.014	0.001
50	0.005	0.003	0.009	0.002	-	-
75	-	-	-	-	-	-

Table 6.11. N_2 fixation by *Oscillatoria* sp. as µg N_2 m^{-2} hr^{-1}. From Carpenter and Price (1977).

Station	N_2 Fixation
K346	0.550
K349	0.170
K350	0.159
A2102	0.62
A2103	5.60
A2105	5.47

Physiology

All strains so far cultured contain chlorophyll a as their primary photosynthetic pigment and use phycoerythrin as their major light harvesting pigment. All the strains so far examined are obligate photoautotrophs, are incapable of nitrogen fixation and have high growth requirements for sodium chloride, magnesium and calcium.

Concentration and Distribution

Synechococcus is widely distributed in the world's oceans in surface waters between 5° and 30°C. It is present in the tropical oceans throughout the year at concentrations varying from 10^3 to 10^4 cells ml^{-1}, and seasonally distributed in the temperature oceans ranging from a few cells ml^{-1} in the winter months when the water temperature falls below 5°C to near 10^5 cells ml^{-1} during the summer months. Synechococcus appears to be excluded from waters below 5°C. Figure 6.6 shows a typical vertical distribution of Synechococcus in the study area just north of the Gulf Stream. Synechococcus counts were taken monthly throughout an annual cycle and are shown in Figure 6.7; within the ACSAR study area, Synechococcus concentrations varied between 10^3 and 10^5 cells ml^{-1} during the annual cycle.

Primary Production

Preliminary data indicated that Synechococcus is an important primary producer. In the Sargasso Sea it is responsible for 15 to 25 percent of the total primary productivity. In Slope Water, Synechococcus is responsible for 5 to 15 percent of the primary productivity and in inshore waters these unicellular cyanobacteria contribute about 5 to 7 percent of the total primary productivity.

PROTOZOA

Protozoa, singled-celled, eucaryotic organisms, constitute a highly diverse group of species. Taxonomically these organisms have received much attention but little agreement in recent years (Levine et al., 1980; Laval-Peuto, 1982). The groups pertinent to this discussion fall into two phyla by the most recent classification (Levine et al., 1980).

- Phylum: Sarcomastigophora
    - Subphylum: Mastigophora
        - Class: Phytomastigophorea (heterotrophic flagellates)
        - Class: Zoomastigophorea (heterotrophic flagellates)
    - Subphylum: Sarcodina
        - Superclass: Rhizopoda (naked amoebae and foraminifera)
        - Superclass: Actinopoda (radiolaria and acantharia)
- Phylum: Ciliophora (ciliates)

Within these groups there are approximately 5,100 species of flagellates, 11,300 species of extant sarcodines (4,600 of which are foraminifera), and 4,700 species of ciliates (Levine et al., 1980). Mercifully, many of these species are not marine.

Numerically there is a great deal of variability in the abundance of these protozoan groups. Heterotrophic microflagellates are present in the most oligotrophic waters at densities of hundreds to thousands per cm^3, while shell-bearing sarcodines may occur at densities less than 1 per m^3 (a difference of 9 orders of magnitude). These differences in standing stocks reflect trophic and

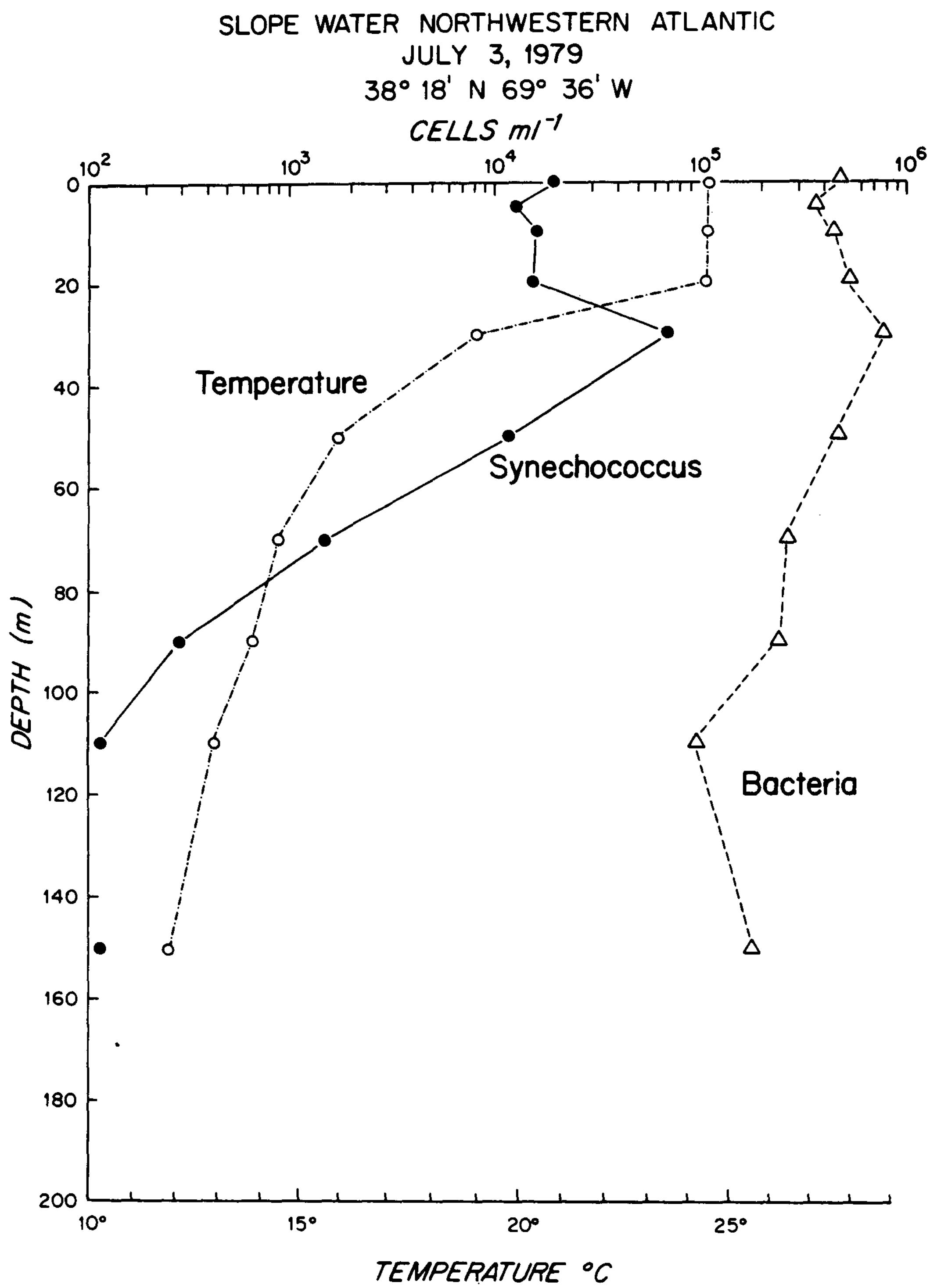


Figure 6.6. Vertical distribution of temperature, _Synechococcus_, and bacteria at a Slope Water station. (Waterbury, unpublished data).

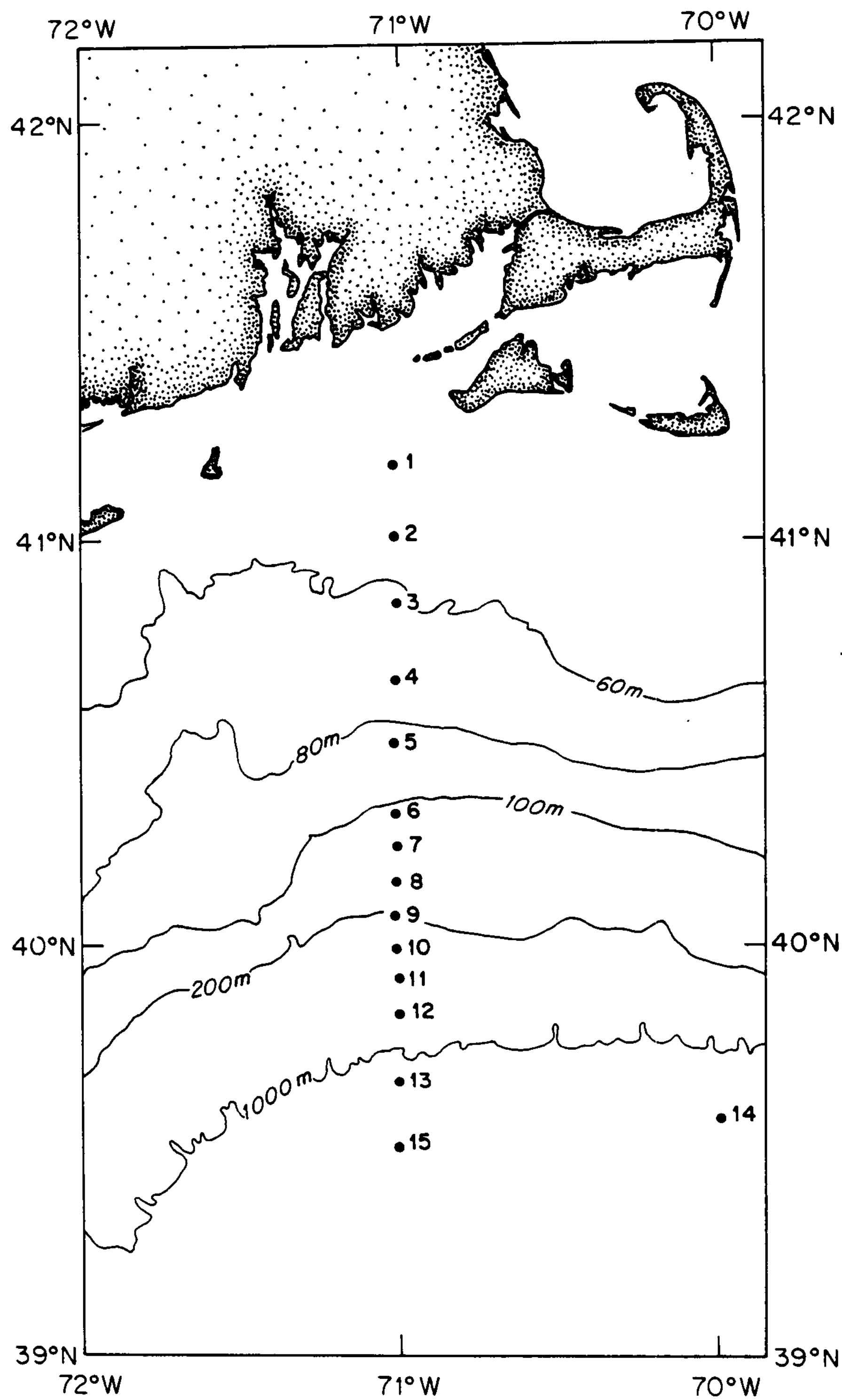


Figure 6.7a. Position of Slope Water and Shelf Water stations where surface temperature and Synechococcus samples were collected during a year long study (1981/82).

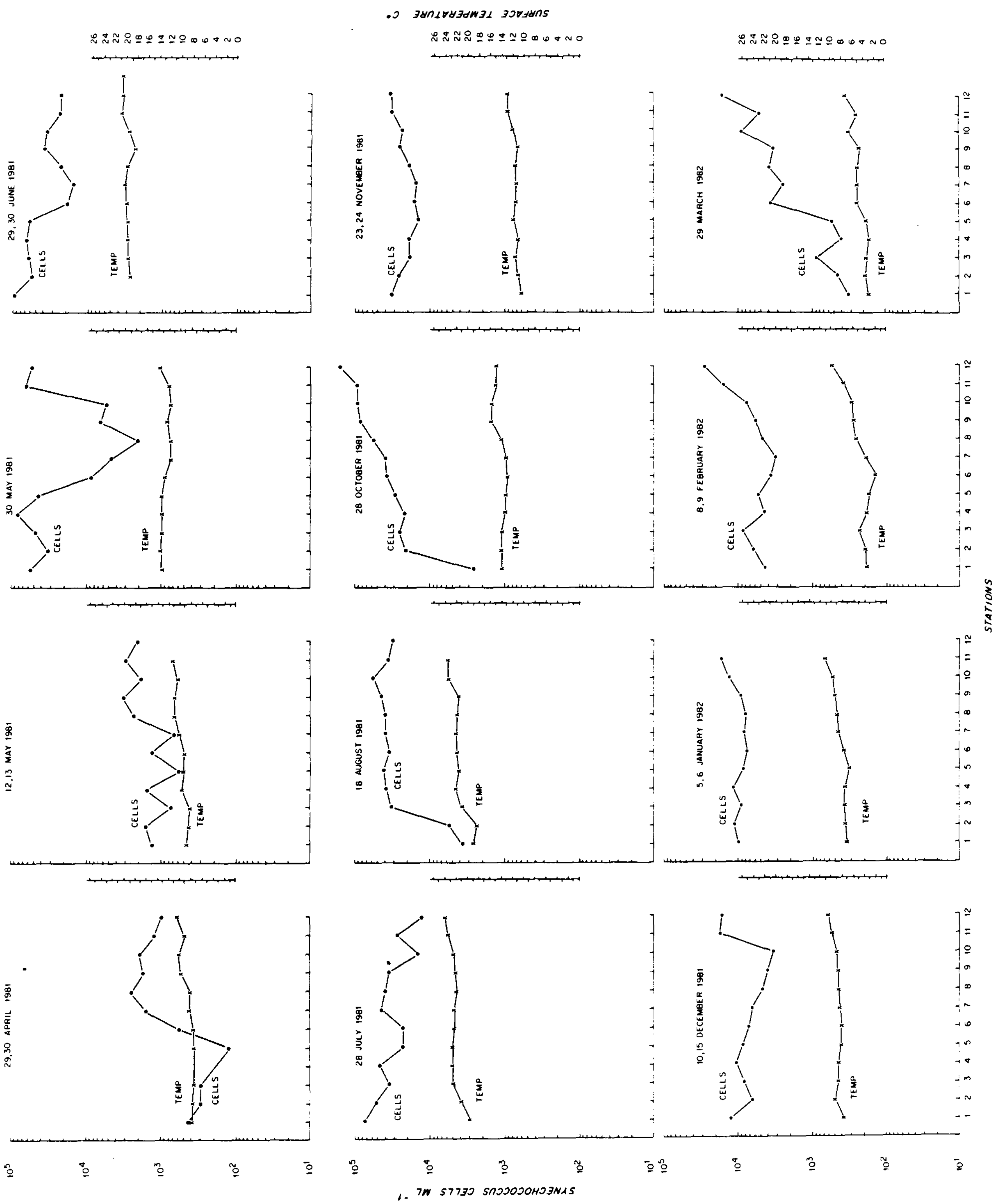


Figure 6.7b. Surface water temperature and abundance of Synechococcus along the transect. (Waterbury and Wiebe, unpublished data).

morphological differences between the groups. For example, bacterivorous (bacteria-eating) flagellates as small as 2 µm are common in the plankton, whereas omnivorous or carnivorous planktonic foraminifera can attain a few cm in diameter and colonial radiolaria can form colonies reaching more than 3 m in length (Swanberg, 1979) (a difference of six orders of magnitude). This represents a range from pico- to macro- (or even mega-) sized plankton by recent convention (Sieburth et al., 1978). However, the majority of protozoan species occur in the size range from 2 to 200 µm.

Recent studies have indicated that most of the respiration of the plankton is performed by organisms less than 30 µm in size (Williams et al., 1981a) and protozoa are the dominant heterotrophs in this size fraction (Beers and Stewart, 1969). Furthermore, the weight-specific filtration and ingestion rates for protozoa are as great as or greater than those for larger zooplankton (Conover, 1982). As a result several investigators have incorporated these formerly overlooked organisms into oceanic food webs (Pomeroy, 1974; Sieburth et al., 1978; Williams, 1981b; Sorokin, 1981; Azam et al., 1983).

Protozoan distributions and abundances are less well characterized for the oceanic realm than for littoral and neritic systems. This is due in part to the accessibility of the coastal environment, and in part to sampling techniques which have been used in the open ocean but which are inappropriate for the collection of many protozoan taxa. The protozoology of the deep-sea benthos is an area of a particularly acute lack of knowledge due to the problematic nature of sampling, fixation and examination. Work in the Pacific (Burnett, 1977, 1979, 1981) has indicated large populations of microbiota (16,500-26,900 cells/cm^2), but similar studies have not been carried out in the Atlantic. For this reason discussion of benthic protozoa will be omitted from this review.

This review deals first with the organisms which comprise the protozooplankton, the methods used for collection and enmmeration, and the resulting available information on distribution and abundance. Trophic interactions among the protozooplankton and with other plankton are then discussed.

Distributions and Standing Stocks of Protozooplankton

Assessing standing stocks of protozoa is difficult. Most protozooplankton cannot be sampled by conventional plankton collection techniques (plankton nets). Furthermore, because their size range overlaps that of the phytoplankton, biomass measurements used for other zooplankton (displacement volume, wet weight, dry weight, carbon) cannot be used directly on natural assemblages of protozooplankton, and population counts must be converted to biomass estimates using cell volume measurements based on microscopic examination. For these reasons most zooplankton studies have not enumerated the protozoa. Beers and Stewart (1969), however indicated a numerical and volumetric dominance of protozoa for organisms less than 35 µm in size.

Flagellates

Heterotrophic flagellates are now known to be a ubiquitous component of plankton communities (Davis, 1982; Fenchel, 1982c). Their importance has been overlooked until recently due to an inability to obtain accurate counts and to distinguish photosynthetic from non-photosynthetic cells. No distinction was made in most of the older literature between autotrophic and heterotrophic flagellates, and heterotrophic cells were generally included in the phytoplankton counts. Removing the heterotrophic component of these populations has been complicated by the fact that many phytoplankton taxa contain non-photosynthetic representatives (Sieburth, 1979). Taxa with non-photosynthetic species which appear often in the plankton include the chrysomonads, cryptomonads, euglenids and dinoflagellates. Many of the known species of dinoflagellates are non-photosynthetic (Kofoid and Swezy, 1921; Morey-Gaines, in press), and most oceanic species are thought to be non-photosynthetic.

In addition to the problem of non-photosynthetic flagellates within phytoplankton taxa, classical techniques for counting phytoplankton (Utermohl, 1958) underestimate populations of small (2-20 μm) flagellates by orders of magnitude (Booth et al., 1982; Davis and Sieburth, 1982). These two problems have been partially alleviated by the use of improved counting techniques, including microscopic examination of live samples (Sorokin, 1977), scanning electron microscopy (Booth et al., 1982), and epifluorescence microscopy (Davis and Sieburth, 1982; Haas, 1982; Caron, 1983; Sherr and Sherr, 1983).

Few studies have been conducted on the distribution of heterotrophic microflagellates and still fewer studies within the ACSAR area. Davis (1982) and Davis et al. (in prep.) enumerated heterotrophic nanoplankton (2-20 μm cells, presumably heterotrophic flagellates) by epifluorescence microscopy at stations throughout the North Atlantic, including several stations within the study area. Those studies indicate average population densities for the Slope Water, Gulf Stream, and Sargasso Sea of 0.7×10^3, 0.7×10^3 and 0.8×10^3 cells/ml, respectively, for subsurface samples in the mixed layer. The density of cells in the surface microlayer of the Slope Water is approximately twice as large. Nearshore waters contain densities up to an order of magnitude greater than oceanic densities. Flagellates are by far the most numerous protozoa in the plankton, with densities often rivaling or even dominating the number of phytoflagellates (Davis, 1982; Davis et al., in prep.).

Taxonomic characterization of the species from stations within the study area were not performed, but Davis (1982) has characterized the culturable species of bacterivorous flagellates occurring in Narragansett Bay, and for a transect across the North Atlantic at 24°30'N (Table 6.12). This latter species lists provide an indication of the taxonomic diversity of this group. In addition to heterotrophic species within several phytoplankton taxa, a number of true zooflagellate species were cultured. These isolates were dominated numerically by kinetoplastids, with the genus Bodo contributing the most species.

Taxonomic studies of this sort are dependent on the ability to culture all of the flagellates present in the samples. This is not yet possible, as evidenced by the large number of morphological forms observable in water samples which do not appear in culture, and by the fact that population estimates based on Most Probable Number cultural estimation are only a small fraction (approximately 0.1% for oceanic samples) of the direct microscopic counts. This is probably due in part to an inability to grow fastidious oceanic species under laboratory conditions, and in part to predation among protozoa in these cultures.

Vertical distributions of heterotrophic nanoplankton have been performed in the study area by D.A. Caron (unpubl.) (Fig. 6.8). Population densities tend to decrease with depth, and populations in the mixed layer tend to

Station:	1	2	3	4	5	6	7	8	9	10
Order Kinetoplastida										
Bodo celer Klebs	x									
parvulis Griessmann, 1914			x	x	x		(*)	(*)	x	
designis Skuja, 1948		x	x		x	x*	x	x*	x	
variabilis (Stokes) Lemmermann								(*)		
curvifilis Griessmann, 1914										x
Cryptobia maris n.sp.	x		x	x		x*	x		x	x
Rhynchomonas nasuta Klebs, 1892				x		x	x	x*		
Order Chrysomonodida										
Paraphysomonas imperforata Lucas, 1967			x					x	x	x
Pseudobodo tremulans Griessmann 1914							(*)	(*)		
Bicoeca vacillans Stolč							x			
Oikomonas trichonanis n.sp.							(*)	x		
Order Prasinomonadida										
Amastigonemis minuta n.g. n.sp.	x	x	x	x	x	x	x*	x*	x	x

*species present on marine snow cultures from this station

Table 6.12. Horizontal distribution of cultivable bacterivorous microflagellates from oceanic stations, Atlantis II, Cruise 109:3, August 1981.

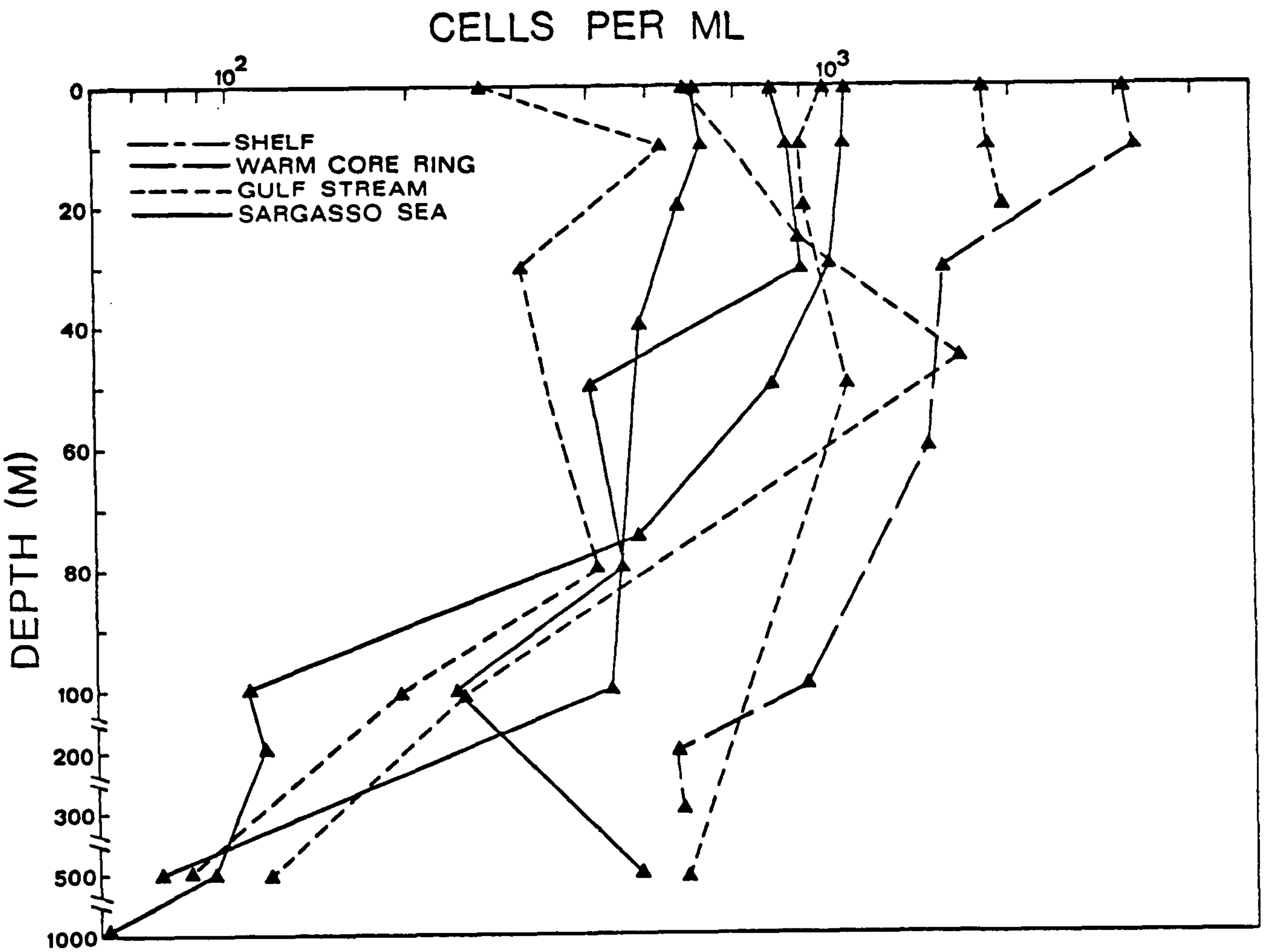


Figure 6.8. Vertical distributions of heterotrophic nanoplankton in the North Atlantic as shown by epifluorescence microscopy (from Davis et al., in prep.) (Caron, unpubl.).

decrease with distance from shore. Where subsurface peaks in bacteria and phytoplankton occur, heterotrophic flagellates often mirror these profiles. Davis et al. (in prep.) have noted a positive correlation between direct counts of bacteria and heterotrophic nanoplankton in the North Atlantic.

While Figure 6.8 depicts the gross distribution of heterotrophic flagellates in the study site, the microscale distributions of these organisms are much less predictable. Many species attach to surfaces (Fenchel, 1982a), and thus detrital material and other organisms represent microenvironments of elevated population densities. In addition, population numbers appear to undergo significant diel fluctuations (Burney et al., 1981; Davis et al., in prep.) due to rapid growth rates of the flagellates (U_{max} = 0.15–0.25; Fenchel, 1982b) and grazing by flagellate predators. Burney et al. (1981) noted a change in the heterotrophic nanoplankton concentration in the Western Sargasso Sea from 420 to 1200 cells/ml over a diel cycle. These results suggest that flagellates are highly dynamic populations.

Sarcodines

The planktonic sarcodines are composed of four major groups; foraminifera, radiolaria, acantharia, and naked amoebae. The first three possess a rigid skeleton or test which can withstand plankton net collection. For this reason distributional information for these groups is most complete. The paleoecological importance of fossilizable sarcodines as stratigraphic tools in sediment cores has been the main impetus behind studies designed to document the spatial (horizontal and vertical) and seasonal distributions of living species in the ocean. Plankton nets towed in the upper 200 m have generally been used for determining horizontal distributions of shell-bearing sarcodines, while the use of multiple opening-and-closing plankton net assemblies (Be, 1962; Wiebe et al., 1976) has been instrumental for mapping the vertical distributions of these species. While the collection procedure has not been particularly troublesome for shell-bearing sarcodines, dissolution during preservation (Be and Anderson, 1976; Bottazzi et al., 1971) and separation of these organisms from other zooplankton (Be, 1959) have caused problems for distribution and taxonomic studies.

Identification of the foraminifera, radiolaria and acantharia is based largely on the shell or skeleton structure (see Laval-Peuto, (1982) for review of the taxonomy of all three groups). The foraminifera possess a multichambered calcium carbonate test. Some radiolaria construct silica skeletons, but some species form no skeleton at all. These latter species are undoubtedly lost from plankton nets and are an unknown factor in the distributional data on radiolaria. The acantharia produce a skeleton composed of strontium sulfate.

The non-testate or naked amoebae comprise a poorly studied group of protozooplankton. These forms are traditionally thought of as benthic organisms, but their presence in the plankton has been recently substantiated. Identification is based on morphology and motility of live specimens, complicating work on this group. Also, the fragility of these protozoa warrant special collection and concentration procedures (Hinga et al., 1979).

Foraminifera-The foraminifera are perhaps the most intensively studied group of proto- zooplankton due to their importance in paleoecological work. While lacking fine-scale resolution, available data show a transition from low abundance to moderate abundance corresponding with changes in the water masses (Sargasso Sea to Slope Water) (Fig. 6.9). There are approximately 30 species of extant planktonic foraminifera (Be, 1967), and these appear to have distinct temperature and salinity optima. Due to the wide temperature minima and maxima many North Atlantic species have distributions which overlap the ACSAR study area. Boreal species extend into cold Slope Water (Fig. 6.10), while tropical and subtropical species occur in the Gulf Stream and Western Sargasso Sea (Fig. 6.11). Eighteen of the 20 species collected by Be and Tolderlund (1971) had distribution ranges which overlapped the study site.

Cifelli (1962, 1965) performed transects from the Shelf to the Sargasso Sea in all seasons. He consistently found the highest concentrations of foraminifera in the Slope Water, and these samples were generally dominated by Globigerina species. Species diversity increased towards the Sargasso Sea, but density of foraminifera decreased. Species diversity and density decreased dramatically on the shelf. Maximum densities in the Slope Water during spring and fall.

The above-mentioned distributions were based on plankton tows from 0 to 200 m (Cifelli, 1962, 1965) and 0 to 10 m (Be and Tolderlund, 1971). Vertical distribution was not investigated, but Fairbanks et al. (1980) showed that the vertical distributions of 13 species of foraminifera were not uniform within the mixed layer (Fig. 6.12) for 3 stations in (Slope Water). Highest densities in that study were also found in the Slope Water. Vertical distribution of planktonic foraminifera appears to follow the deep chlorophyll maximun (DCM) (Fairbanks and Wiebe, 1980)). Since DCMs are generally located at pycnoclines, Fairbanks and Wiebe proposed that the association of foraminifera with DCMs may be one reason why the vertical distributions of these protozoa have been related to the density of seawater.

Short term changes in the standing crop of foraminifera have received little attention. Diel changes in the vertical distribution of planktonic foraminifera have been suggested by Be (1960). However, Boltovskoy (1973) was unable to observe a significant difference between day and night tows, and the question of vertical migration by these organisms remains unresolved. Short term changes (days) can be expected on a regular or irregular basis due to the reproductive cycle inherent in some species of foraminifera. Hastigerina pelagica undergoes gametogenesis on a lunar cycle, resulting in a monthly cycle in its abundance in surface waters (Spindler et al., 1978). Another species, Globigerinoides sacculifer initiates gametogenesis at a specific time of day, but shows no synchrony as to which day gametogenesis occurs (Be et al., 1983). These aspects of behavior may cause large fluctuations in the standing crop of planktonic foraminifera whose meaning cannot be explained on the basis of hydrographic data alone.

Radiolaria-The radiolaria are another paleoecologically important group of planktonic protozoa. Life histories for these organisms are largely unknown, and species are much more numerous than the foraminifera. The radiolaria contain the largest protozoan structures alive, with some colonial radiolaria forming a gelatinous matrix up to 3 m long (Swanberg, 1979). Like foraminifera, densities of radiolaria generally range from less than 1 m^{-3} to more than 100 m^{-3}. Cifelli and Sachs (1966) compared numerical abundances of foraminifera and radiolaria along a transect which included stations within the ACSAR study area. Foraminifera generally outnumbered radiolaria, but

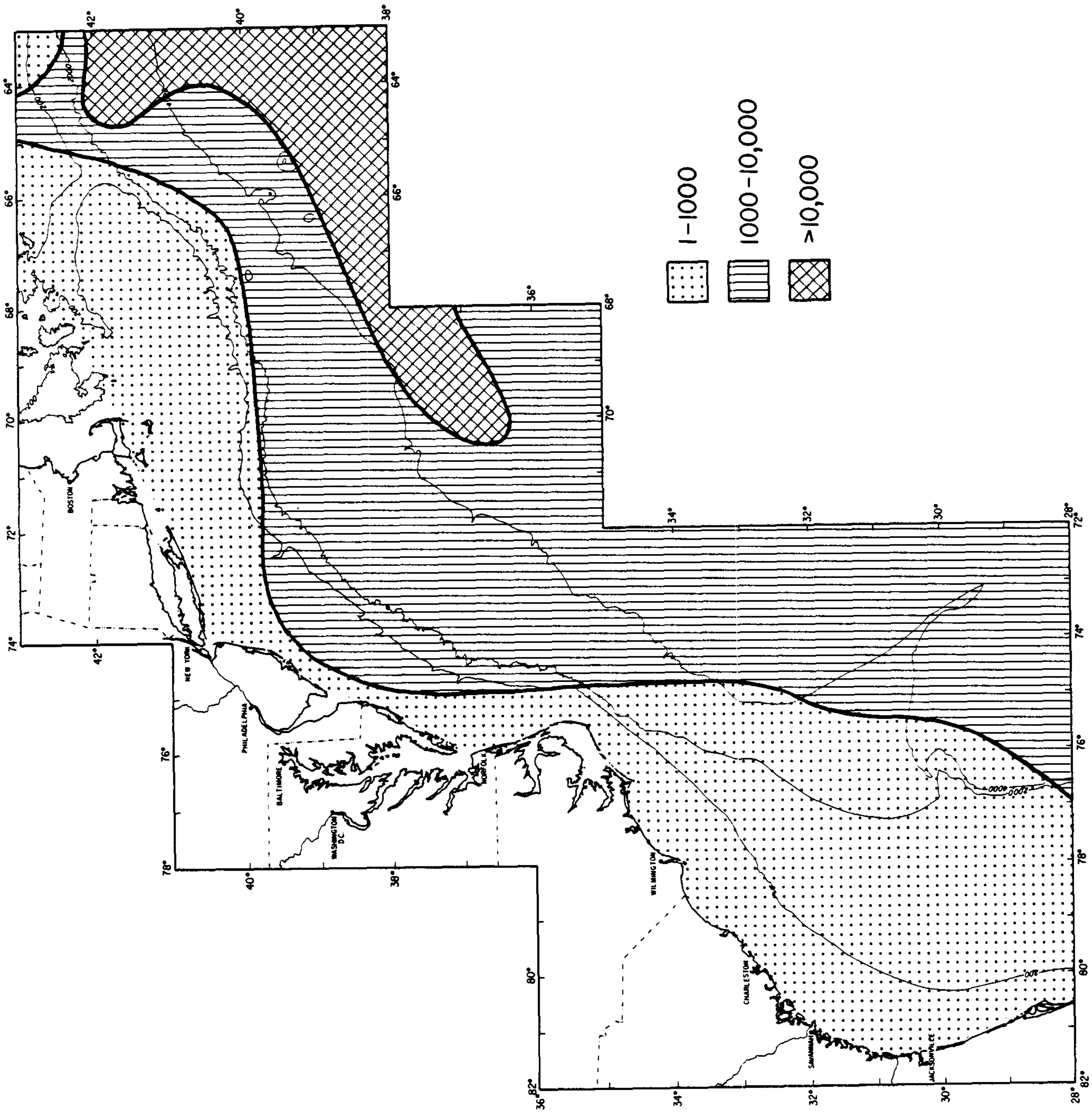


Figure 6.9. Absolute abundance of total planktonic foraminifera in surface waters (0-10 meters of water). From Bé and Tolderlund (1971).

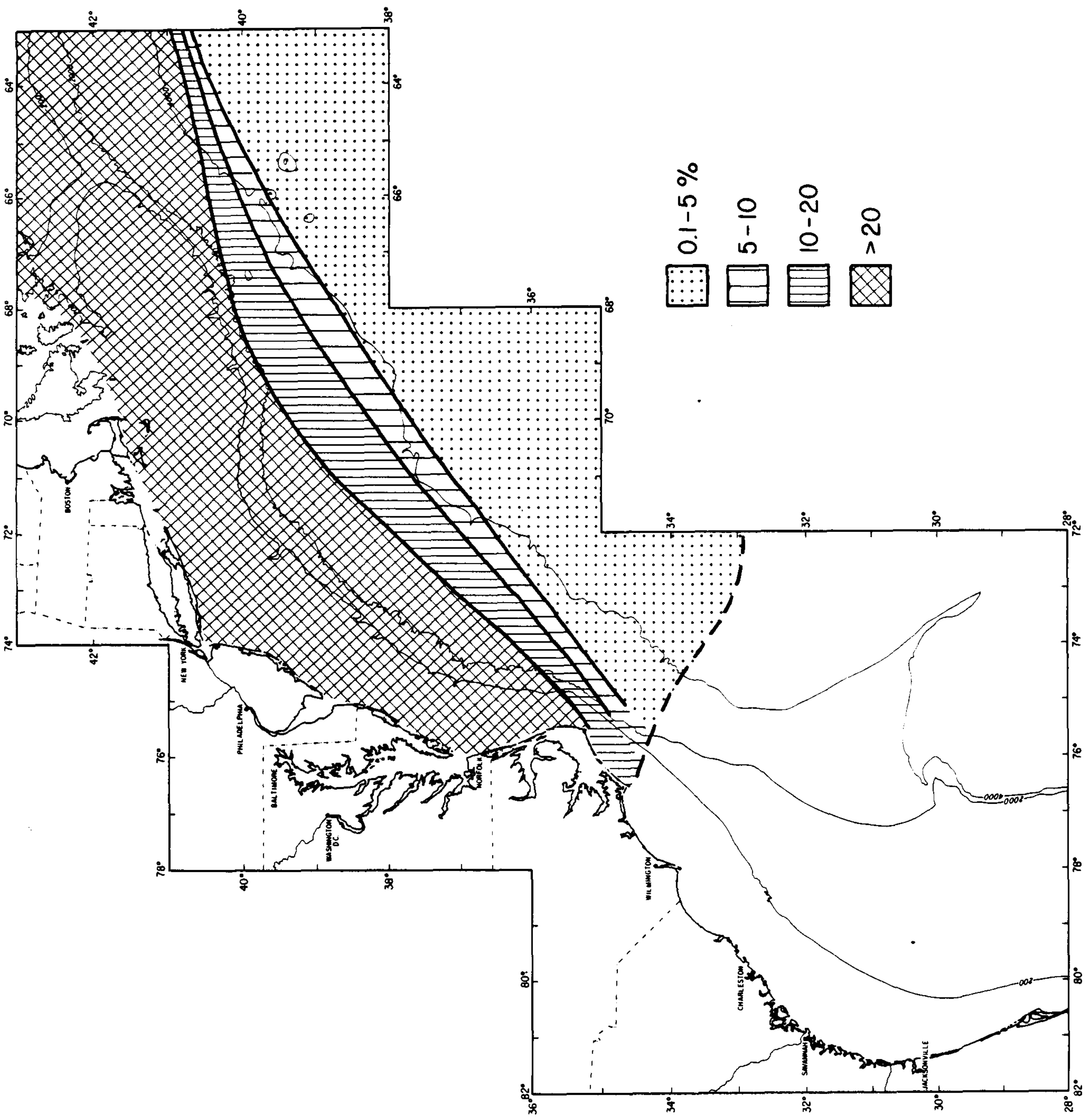


Figure 6.10. Distribution of relative abundance of Globigerina quinqueloba Natland in surface waters (0-10 meters of water). From Bé and Tolderlund 1971.

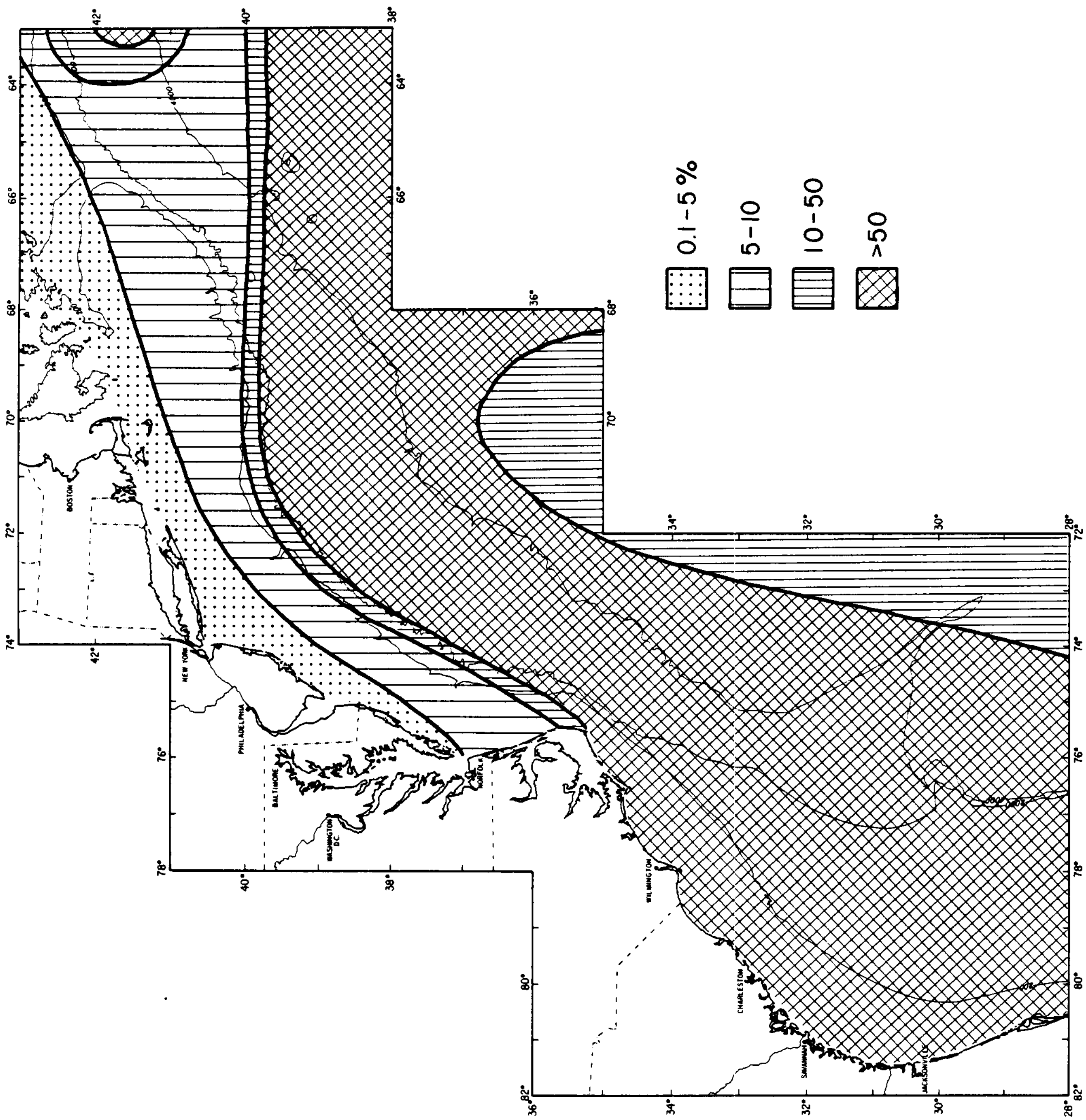


Figure 6.11. Globigerinoides ruber distribution in surface waters. From Bé and Tolderlund (1971).

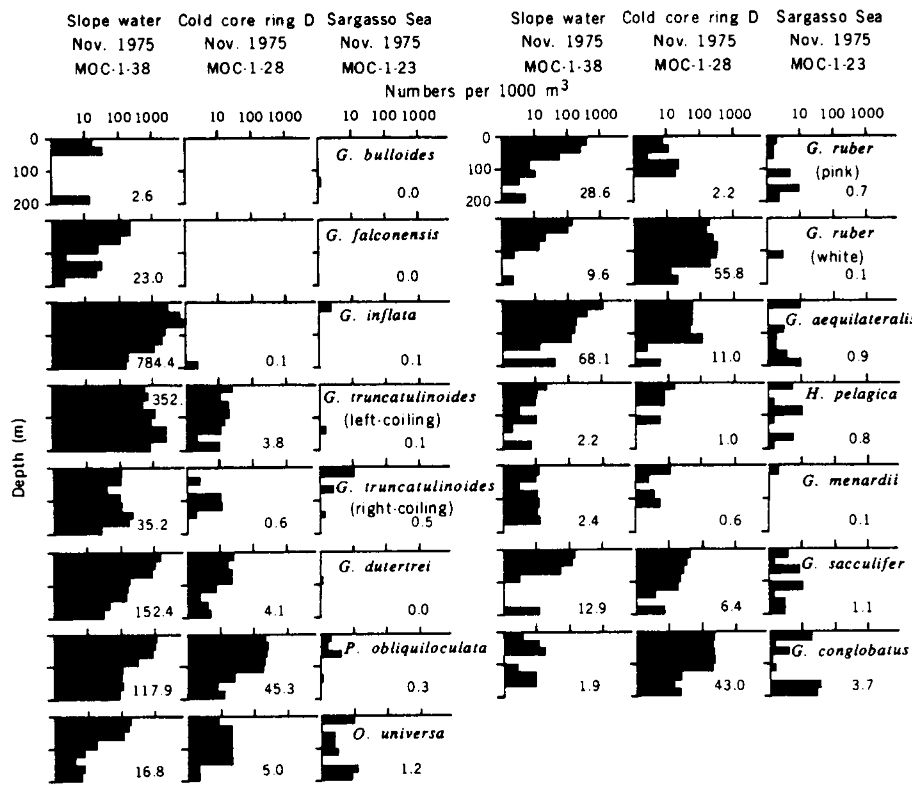


Figure 6.12. Slope water, ring, and Sargasso Sea planktonic foraminifera distributions during daylight (numbers per 1000 m^3) during the November 1975 KNORR cruise 53. Values within each profile are integrated number of forams per square meter in the upper 2000 m. Data are plotted for the following foraminifera: Globigerina bulloides, G. ruber, Globigerinella aequilateralis, Puileniatina obliquiloculata, Globoquadrina dutertrei, Orbulina universa, Globigerinoides sacculifer, Globorotalia menardii and hastigerina pelagica. From Fairbanks et al. (1980).

radiolaria were dominant at warm-water stations (Fig. 6.13). In most cases, radiolaria and foraminifera had coincident peaks in abundance. Thus, one group does not appear to prosper at the expense of the other.

Information on the vertical distribution of these protozoa does not yet exist to the extent that it does for foraminifera. However, Beers and Stewart (1969) noted that radiolaria are generally more abundant than foraminifera in deep waters of the Pacific while the converse is true in surface waters.

Extensive work has been performed on the colonial radiolaria collected by Swanberg (1979) throughout the North Atlantic. Colonial radiolaria were observed at 89% of the stations over a 4-yr period, although negative data are not conclusive because of the nature of the collecting method. Densities of radiolaria ranged from 0.04 to 540 colonies m^{-3}.

Acantharia-The acantharia have been less intensively studied than the other shell- bearing sarcodines, probably owing to dissolution problems in preserved samples. Still, the abundance of this group is at least as great as other sarcodines (Table 6.13); from a number of stations, some within the study area (Table 6.14). Densities range from 0 to 169 acantharia m^{-3}, and averages were approximately 25, 24 and 39 m^{-3} for the Slope Water, Gulf Stream, and Northern Sargasso Sea, respectively (Bottazzi et al., 1971). A summary of three studies including stations within or near the study site is given in Table 6.14. In general, species diversity and abundance of acantharia are greater in warmer waters, a similar trend observed for radiolaria. Nonetheless, species in the Slope and Sargasso Sea samples are not observed in the southerly stations, indicating an endemic fauna for this region.

Amoebae-Distributional information concerning the naked amoebae in the open ocean is rare. Considerable work has been done for inshore waters since the first major work on marine amoebae by Schaeffer (1926) (see Bovee and Sawyer (1979) and Sawyer and Griffin (1982), and references therein), but Davis et al. (1978) remains the only study from oceanic waters. That study included stations bordering the ACSAR area on the north and south. Highest densities were observed in the surface microlayer (up to 100 l^{-1}), while subsurface samples averaged about 1 amoeba l^{-1}. These densities are generally greater than for other sarcodines. When corrected for sample dilution, surface microlayer samples reached densities exceeding 10^3 amoebae l^{-1}. Seven families and 11 genera of amoebae were isolated during that study; three genera (Acantha- moeba, Clydonella, and Platyamoeba) accounted for more than half of these iso- lates and only one genus (Clydonella) was isolated from all three study sites.

The high density of amoebae associated with the surface microlayer is probably an indication of the particle-associated nature of these sarcodines. Amoebae are usually associated with particles in cultures (Davis et al., 1978), and high densities have also been observed on marine snow samples from the open ocean (Caron et al., 1982b).

Ciliates

The phylum Ciliophora contains a highly diverse fauna. However, only a relatively few species are known to be truly planktonic. Most pelagic marine ciliates are from the order Oligotrichida, which contains the familiar tintinnids, and the less well-known non-loricate oligotrichs.

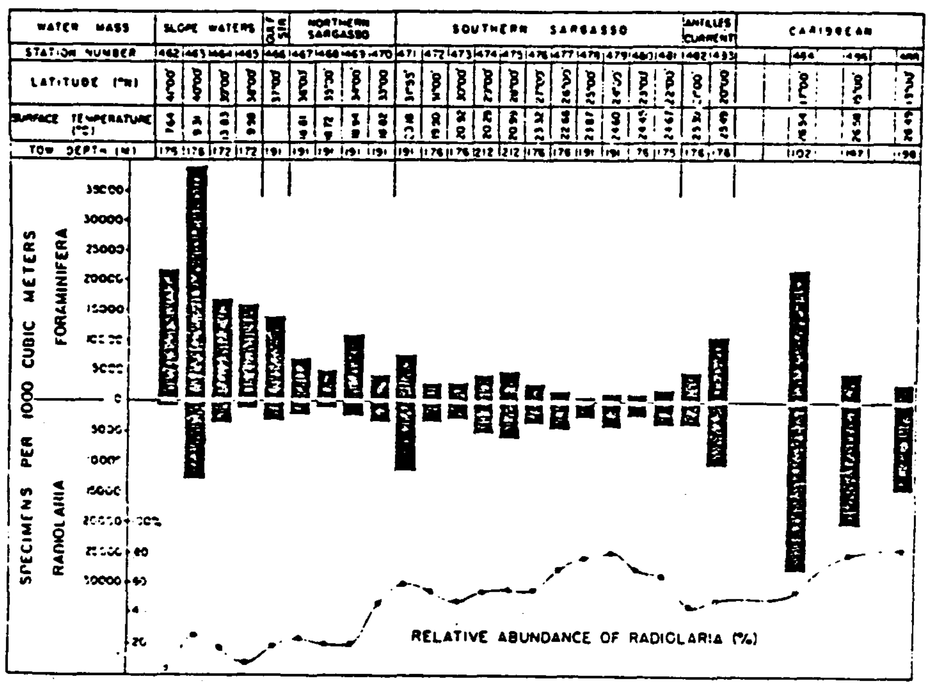


Figure 6.13. Abundance of planktonic foraminifera and radiolaria in the western North Atlantic and Caribbean along 65°00'W Long. From Cifelli and Sachs (1966).

Sta. No.	Acan-tharia	Foram-inifera	Radio-laria
Slope water			
462	2	22	<1
463	97	39	13
464	0	16	4
465	0	16	1
Gulf Stream			
466	44	14	3
Northern Sargasso			
467	40	7	2
468	14	5	1
469	4	11	2
470	6	5	3
Southern Sargasso			
471	120	8	11
472	0	4	3
473	14	4	3
474	79	5	5
475	89	5	6
476	36	3	4
477	13	2	5
478	30	1	3
479	12	2	5
480	19	2	2
481	22	2	4
Gulf Stream			
1	4	2.4	
Northern Sargasso			
89	169	7.6	
90	0	1.6	
Southern Sargasso			
3	6	1.2	
4	1	0.9	
6	1	0.5	
7	15	0.5	
8	6	0.4	
9	87	1.3	
10	18	0.5	
87	1	0.4	
88	17	0.4	

Table 6.13. Abundances (in specimens m^{-3} filtered) of Acantharia, Foram- inifera, and Radiolaria in plankton tows. From Bottazzi et al. (1971).

Table 6.14. Summary of Bottazzi and Vannucci (1964, 1965a, 1965b) data for acantharian abundances in Northern/Western Sargasso Sea, Gulf Stream, and Slope Water stations. Densities are No. m^{-3}.

Water Mass	Source of Data Base					
	1964		1965a		1965b	
	No. of Species	Density	No. of Species	Density	No. of Species	Density
Slope Water	4	negl.	7	24	51	3
Gulf Stream	28	89	10	44	-	-
Sargasso Sea	-	-	5	16	63	372

The tintinnids are a large group of ciliates characterized by the presence of a preservable lorica. Over 1000 species of tintinnids have been described, based primarily on the lorica structure (see Loeblich and Tappan, 1968). However, a great deal of phenotypic variation is possible for loricae (Laval-Peuto, 1981), raising doubts as to the validity of its use as a diagnostic feature. Tintinnid importance (relative to non-loricate species) has been overemphasized in plankton communities because non-loricate forms preserve poorly. Examination of live unconcentrated samples may be the only method which provides representative counts (Dale and Burkill, 1982; Sorokin, 1981).

Distribution patterns of oceanic tintinnid populations in the ACSAR area are poorly known. Most investigations have been conducted in nearshore environments. For example Gold and Morales (1975) reported 34 species of tintinnids from New York Bight over a 1 yr period. Microplankton studies conducted in the Pacific have shown that ciliates represent a large percentage of the total number of organisms in the size class less than 103 µm (Beers and Stewart, 1969), and generally constitute larger populations and greater biovolume than the sarcodines. In general, densities of ciliates tend to be intermediate between flagellate and sarcodine densities.

These and similar studies have indicated that non-tintinnid oligotrichs are a large portion of the total ciliate numbers. These ciliates can constitute 71% of the microplankton biomass, while tintinnids comprise 5.5% (Laval-Peuto, 1982). At present, however, our knowledge concerning the distribution of non-loricate pelagic ciliates is very poor (Borror, 1980), and the taxonomy is outdated and insufficient (Laval-Peuto, 1982).

Of much less importance than the oligotrichs are a few taxonomically diverse ciliate species which occur primarily in coastal waters but have been found in the oceanic environment. These include the free-living species Uronema sp. (order Scuticociliatida) (Hamiliton and Preslan, 1969) and Mesodimium rubrum (order Haptorida) (see review by F. Taylor et al., 1971), and the ectocommensal species Ephelota gemmipara (order Suctorida) (Sieburth et al., 1976), and Myoschiston centropagidarum (Hirche, 1974) and Zoothamnium sp. (Herman and Mihursky, 1964; Sieburth et al., 1976), both from the order Peritrichida. One peritrich species, Zoothamnium pelagicum, has been described as a truly planktonic species (Laval, 1968).

Aside from these occasional observations, few non-oligotrich ciliates occur in the open ocean. While this apparent absence may be due in part to improper fixation or culture techniques used in past studies, a more likely explanation is the inadequacy of food densities needed to support growth of bacterivorous ciliates in this environment. An exception appears to be "marine snow" detrital aggregates which support large populations of non-oligotrich ciliates.

Trophic Relations

As a group, the protozoa exhibit all major modes of heterotrophic existence (osmotrophy, bacterivory, herbivory, carnivory), and many species utilize more than one mode at once. In addition, many protozoa (particularly sarcodines) harbor symbiotic algae which also contribute to their nutrition. A brief discussion is given below concerning the major roles of protozoa as participants in planktonic food webs.

Flagellates

The once-popular belief that heterotrophic flagellates are largely osmotrophic is slowly being discarded as information appears which documents a phagotrophic existence for these protozoa. While osmotrophic nutrition may take place in benthic environments it is doubtful that flagellates can compete successfully with bacteria for low concentrations of dissolved organic material in oceanic waters.

Recent work has shown that heterotrophic microflagellates (less than 20 um) are significant bacterioplankton consumers (Davis, 1982; Fenchel, 1982b; Haas and Webb, 1979). This literature has been reviewed by Sieburth (in press). Measured feeding rates of flagellates vary from approximately 25 to 250 bacteria/flagellates/hr (Davis, 1982; Fenchel, 1982b). Davis (1982) was able to show that significant feeding rates were still observable at bacterial concentrations approaching in-situ concentrations. Microflagellates apparently compromise the ability to grow rapidly with an ability to survive periods of insufficient bacterial food. Microflagellates lower their metabolic rate, autophagocytize cellular organelles and form rapid-swimming swarmers in response to low bacterial density. These results, together with distributional information for these protozoa in the plankton have led to the conclusion that flagellates may be the major consumers of bacteria in the plankton. Correlations between the number of bacteria and the number of heterotrophic nanoplankton tend to strengthen this hypothesis and suggest an important role for bacterivorous flagellates as a mechanism whereby bacterial biomass becomes available to larger zooplankton (Azam et al., 1983).

In addition to bacteria, microflagellates are also capable of consuming chroococcoid cyanobacteria (Johnson et al, 1982) and eucaryotic algae (Haas, 1982). However little more than anecdotal information exists on the ability of microflagellates to ingest algae, and more work is required to determine the magnitude of this predation.

Larger flagellates (e.g. dinoflagellates) have a well-documented ability to feed and grow on microalgae. Gold (1970) cultured a heterotrophic dinoflagellate using phytoflagellates as food. Kimor (1981) gave evidence for phagocytosis in a number of marine dinoflagellate species. However, as is the case with microflagellates, the importance of this predation is unknown due to the scant information that is presently available.

Finally, symbioses have been described between heterotrophic dinoflagellates and various photosynthetic organisms (see F. Taylor (1982) for review). In the case of chroococcoid cyanobacteria invaginations of the cell wall may form special chambers which contain the cyanobacteria. Phagocytosis has not been observed, and the physiological relationship is not clear. For other phototrophs, the degree of integration with the host varies.

Sarcodines

The planktonic sarcodines display a spectrum of trophic modes from bacterivory to carnivory. The naked amoebae are probably the primary bacterivorous sarcodines in the plankton. Due to their low abundance in the water column relative to microflagellates, and to their manner of feeding (particle-associated), these protozoa are probably not important consumers of bacterioplankton. However, amoebae may play a role in the grazing of bacteria at interfaces. Davis et al. (1978) showed that highest concentrations of amoebae in the North Atlantic occurred at the air/water interface, and densities of protozoa in the neuston appeared to be positively correlated with densities of bacterioneuston. In culture, amoebae are usually found associated with particulate material. These observations suggest a potentially important role as surface-associated bacterivores.

Little pertinent information is available concerning the diet of acantharia, but radiolaria and foraminifera are known to accept a variety of organisms as food. Their prey includes algae, as well as a wide variety of zooplankters (Anderson and Be, 1976; Anderson et al., 1979; Be et al., 1977; Caron and Be, submitted; Swanberg, 1979). An electron microscopic examination of SCUBA-collected foraminifera showed an omnivorous diet for most species. One species, Hastigerina pelagica, is thought to be exclusively carnivorous (Anderson and Be, 1976). Planktonic foraminifera create a spider web-like rhizopodial network to ensnare and immobilize prey. Caron and Be (submitted) have developed a model based on this method of prey capture to predict the feeding rates of the planktonic foraminifera on zooplankton prey. Development of feeding models describing predation by foraminifera indicates that the role of these protozoa as consumers is beginning to become clear.

Radiolaria also consume a significant amount of animal tissue. Swanberg (1979) found copepods, appendicularians, mollusc larvae, hydromedusae and tintinnids as prey in colonial radiolaria. These observations suggest a role similar to planktonic foraminifera.

Many shell-bearing sarcodines possess symbiotic algae which contribute to their nutrition. These symbioses have been reviewed by Anderson (1980) for radiolaria, and by Be et al. (1977), Lee (1980), and F. Taylor (1982) for planktonic foraminifera. Acantharian symbionts have not been as intensively studied, presumably due to dissolution problems of these sarcodines during preservation (Bottazzi et al., 1971). However, F. Taylor (1982) has noted that 70% of the acantharia observed in the upper 50 m in waters off Puerto Rico possess zooxanthellae.

Swanberg (1979) concluded that primary production by the symbiotic algae of colonial radiolaria was an insignificant fraction of the total primary productivity of the water. However, symbiont-derived nutrition may have a profound effect upon survival and growth of the sarcodine host. Caron et al. (1982a) noted a survival time for the planktonic foraminifer Globigerinoides sacculifer in excess of 70 days in the absence of particulate food. Symbiont-derived nutrition was presumably responsible for this prolonged survival time. Be et al. (1982) showed in this same species that zooxanthellae influenced growth of the host and played a role in controlling the initiation of gametogenesis.

The occurrence of a large number of symbioses and an ability to capture and digest relatively large zooplankton make the shell-bearing sarcodines an ecologically unique group of protozooplankton.

Ciliates

The major role for ciliates in oceanic plankton communities appears to be as consumers of phytoplankton and other small protozoa. Fenchel (1980a,b) has concluded that bacterial populations in open waters are not sufficient to support feeding and growth of bacterivorous ciliates. This is consistent with field observations which showed that culturable bacterivorous ciliates were absent or in very low abundance (less than 10 l^{-1}) throughout most of the

North Atlantic (Caron, unpubl.). Tintinnid ciliates have been cultured on phytoflagellates in the laboratory (Gold, 1970), and the suitability of a number of phytoplankton species as food for ciliates has been tested (Repak, 1983; Stoecker, 1981), confirming that herbivory is a major mode of nutrition for these protozoa.

A considerable amount of work has been performed to investigate the magnitude of ciliates grazing on coastal phytoplankton both in-situ and in cultures (Capriulo, 1982; Heinbokel, 1978; Heinbokel and Beers, 1979). Most of this work has been performed with tintinnid ciliates. These studies have indicated that ciliates can have a significant effect on phytoplankton communities in coastal waters. Extrapolation of these results to oceanic waters is difficult, and the quantitative effect of ciliates grazing on phytoplankton in the open ocean remains largely unknown.

Unlike sarcodines, relatively few algae-ciliate associations have been described (F. Taylor, 1982), and these are largely coastal phenomena. Thus, the numerical importance of symbiont-bearing ciliates in the open ocean is probably negligible.

Protozoa as Food

Protozoa are eaten by larger zooplankton, and in some case may contribute significantly to the diets of zooplankton. The latter case is particularly true where the number of primary producers is low, such as in the deep-ocean (Hardy, 1974) or during the heterotrophic phase of plankton succession (Sorokin, 1977).

Bacterivorous microflagellates play a key a role in plankton communities by serving as a trophic link between bacteria and larger zooplankton. Heterotrophic flagellates are directly available to fine filter-feeding zooplankton. Kopylov et al. (1981) measured ingestion rates of heterotrophic microflagellates by species from several phyla and concluded that microflagellates were ingested, but at in-situ densities of microflagellates they constituted only a supplemental food source. Microflagellates were not directly available to large particle grazers, but attachment of flagellates to particles made them available to coarse filter-feeders.

Ciliates have also been investigated as a food source for larger zooplankton (Berk et al., 1977; Robertson, 1983). These studies have shown that while ciliates can constitute an important food source for copepods in neritic waters, they probably serve to supplement the diet of copepods in open water.

Sarcodines appear to be less palatable to zooplankton than flagellates and ciliates. Predators for planktonic foraminifera and acantharians are not well known, although foraminiferan tests have been found in the stomachs of salps. Swanberg (1979) has observed that colonial radiolaria appear to be distasteful to fish and are avoided after an initial mouthing. Primary consumers of colonial radiolaria appear to be planktonic amphipods, although a few copepods species and turbellarians may also eat them.

Protozoa and Nutrient Regeneration

Two recent reviews (Stout, 1980; G. Taylor, 1982) deal with the role of protozoa in the regeneration of nutrients. Although some disagreement exists as to the importance of these organisms in regeneration processes, evidence continues to increase that small (less than 20 um) protozoa have a significant role in regenerating major nutrients in the planktonic ecosystem. Glibert (1982) has shown that organisms passing a 10 μm filter were responsible for most of the NH_4^+ remineralization in and around the study site. Burney et al. (1979,1981) noted significant correlations over a diel cycle between carbohydrate concentrations and the microbial plankton less than 20 um, indicating an active role by these organisms in controlling the concentrations of these materials. They suggested that protozooplankton less than 20 μm may affect carbohydrate concentrations via their grazing activity.

Protozoa have been shown to increase the rate of decomposition of detrital material (Fenchel, 1977; Sherr et al., 1982), and the breakdown of zooplankton fecal material by acting as bacterial consumers and by physical disruption of feces (Gowing and Silver, 1982; Honjo and Roman, 1978; Pomeroy and Diebel, 1980).

Microenvironments and Protozoa

Recent work has established the importance of large aggregations of microorganisms as sites of intense protozoan activity in the plankton. This work has been primarily concerned with fragile, macroscopic detrital aggregates (marine snow). Marine snow has been shown to contain large populations of microorganisms (Caron et al, 1982b), with many protozoan species found on the aggregates which are absent from the surrounding water (Silver et al., 1982). Densities of culturable bacterivorous protozoa are up to 10^4 times as large on marine snow as in the surrounding water (Table 6.15). This raises questions as to the true habitat of some bacterivorous protozoa in the open ocean. In particular, the distribution of bacterivorous ciliates in the open ocean might be explained by the occurrence of these highly enriched aggregates in environments where the surrounding water contains too few bacteria to support ciliate growth (Caron et al., 1982c). Small particles may also have protozoa attached to them (Pomeroy and Johannes, 1968), and Goldman (in press) has proposed that microaggregates, like macroaggregates, may be important sites of high microbial activity and rapid nutrient cycling.

In addition to marine snow, a number of other aggregations exist which constitute important microenvironments for protozoan growth in plankton communities and whose distribution encompasses the study site. These include large algal aggregations such as *Rhizosolenia* mats (Carpenter et al., 1977), *Thalassiosira partheneia* colonies (Elbrachter and Boje, 1978; Caron, unpubl.) and *Oscillatoria* (*Trichodesmium*) bundles. *Rhizosolenia* mats contain large populations of protozoa throughout the matrix of the aggregate (Caron et al., 1982b), while *T. partheneia* colonies form hollow cylindrical colonies with protozoa living in the hollow center. High ciliate densities also occur sporadically on colonial radiolaria where they appear to cause breakup of the colonies (Swanberg, 1979). The presence of microenvironments of intense microbial activity in the plankton provide oases for the growth of protozoa which otherwise would not be able to survive on the dilute concentration of prey organisms in the surrounding water, and thus may be important in explaining the distribution of some protozoan species in oceanic plankton communities.

SAMPLE LOCATION AND COLLECTION DATES	NUMBER OF SAMPLES	POPULATION	PARAMETER RANGE	AVERAGE	CONCENTRATION FACTOR (SNOW:CONTROL)
SARGASSO (8/21/81-8/31/81)	16	FLAGELLATES	3-2400	743	3,229
		CILIATES	UN-23	2.6	>3,919
		AMOEBAE	UN-23	2.9	260
SARGASSO (2/19/82-2/24/82)	41	FLAGELLATES	85.9-859	329	701
		CILIATES	UN	-	-
		AMOEBAE	UN-3.72	0.53	177
GULF STREAM (2/28/82-3/2/82)	23	FLAGELLATES	390.3-1800	1000	1,970
		CILIATES	UN-57.0	19.59	10,590
		AMOEBAE	8.59-85.9	44.84	11,200
GULF STREAM (5/27/82-6/1/82)	29	FLAGELLATES	174-23,000	1693	4,460
		CILIATES	0.34-94.2	8.02	10,690
		AMOEBAE	0.34-174	81.3	5,910
WARM CORE RING (5/19/82-5/21/82)	8	FLAGELLATES	92.2-350	188.9	205
		CILIATES	UN-3.4	1.28	1,700
		AMOEBAE	UN-3.4	1.28	196
GEORGIA SHELF (2/27/82)	1	FLAGELLATES	-	173	100
		CILIATES	-	-	-
		AMOEBAE	-	8.59	954

Table 6.15. MPN of Protozoa (No. m^{-1}) on marine snow. Caron (unpubl.).

PHYTOPLANKTON

The following discussion reviews the state of knowledge of primary producers, their standing crop, species composition and distribution, and rates of primary productivity within the ACSAR region. Regional and seasonal horizontal and vertical distribution patterns are assessed, along with the common techniques for measurement and identification. The physical and environmental parameters which appear to influence the distribution patterns are also discussed. Little discussion will be made of nutrient distribution patterns, except where such data directly influences the distribution patterns of the primary producers.

STANDING STOCKS

Kinds of Measurements

Many methods have been used to assess the total phytoplankton in the sea, but each is subject to a number of sources of variability or error. The most widely used method for the estimation of phytoplankton biomass is the quantification of chlorophyll a; other methods include determinations of particulate carbon or nitrogen, adenosine triphosphate (ATP), or deoxyribonucleic acid (DNA) (Eppley, 1968; Holm-Hansen and Booth, 1966; Holm-Hansen et al., 1968; Sutcliffe et al., 1970). The latter methods provide poorer estimates of phytoplankton than chlorophyll determinations because they are based on measurements that are not unique properties of algal cells. Additionally, a large proportion (>75%, according to estimates of Wangersky, 1965; Gordon, 1970; and Chester and Stoner, 1974) of particulate matter may be detrital. Inasmuch as bacteria, as well as phytoplankton and microzooplankton, may frequently aggregate upon dead organic particles (Johannes, 1965; Barsdate et al., 1974; Fenchel and Harrison, 1976; Sherr et al., 1982; Goldman, in press), separate measurements of organisms and inert organics are often impossible. A technique for analyzing proteinaceous nitrogen associated with phytoplankton (Packard and Dortch, 1975) has been used in an attempt to circumvent some of these difficulties, but, to date, the determination of chlorophyll remains the most widely used method, and the technique that has provided the largest data base.

In recent years, chlorophyll distribution patterns have been tracked by remote sensors. Satellite imagery, in contrast to discrete shipboard measurements, has the tremendous advantage of being able to cover large areas of the sea synoptically, and to repeat this coverage at frequent intervals. Constraints also exist with this technology, however. Only a few biologically meaningful parameters may be measurable, and, only very near-surface phenomena can be monitored (Esaias, 1980; Esaias, 1981). Satellite imagery has been used extensively in the Gulf Stream Warm Core Ring program for both temperature and chlorophyll distributions, particularly as a tool for defining the location, size, shape, and orientation of the warm-core rings in near real time (Brown et al., 1982). Much of the chlorophyll imagery from the Rings study is yet to be published (Smith and Baker, pers. comm.); the reliability of satellite chlorophyll data depends on calibration with contemporaneous chlorophyll assays aboard ship. Unfortunately, the current Coastal Zone Color Scanner (CZCS), aboard satellite Nimbus-7, which is the instrument providing the bulk of the oceanographic data, will last at best only a few more years (Esaias, 1981), and a replacement facility is uncertain.

Regional and Seasonal Distributional Patterns

A large mass of data on the distribution of phytoplankton based on the distribution of plant pigments now exists. General seasonal phytoplankton dynamics were described for temperate waters as early as 1946 by G. Riley. Briefly, low-standing stocks of phytoplankton are usually observed during late fall and winter, followed by sporadic increases during early spring. As water column stratification becomes established in the spring, phytoplankton growth proceeds rapidly, and more or less continuously, until nutrients in the upper waters become depleted. Phytoplankton stocks then decline to a more modest level, maintained by nutrient regeneration processes and occasional mixing events, and remain at this level through the summer. Early fall may bring an autumn bloom, fueled with nutrients from below as an increase in vertical mixing is brought on by storm events or cooling.

Within this very general seasonal framework, many differences exist with regard to the large-scale phytoplankton distribution patterns observed between Slope Water and those in the northern Sargasso Sea or ring waters. These differences include the maximum phytoplankton standing stock reached on an annual basis and the seasonal rate of change in standing stocks both in the surface and with depth. For example, data from a variety of sources indicate the formation of a late spring to fall deep chlorophyll maximum in both regions, but a seasonal difference in the depth at which it occurs (Cox et al., 1982).

In Figures 6.14 and 6.15 vertical distribution profiles of chlorophyll are shown for the northern Sargasso Sea and Slope Waters. These data, compiled by Cox et al. (1982) are based on published and unpublished data from Wiebe et al. (1976), Ortner (1977), Ketchum and Ryther (1965), as well as data collected by them on R/V Knorr cruises 62, 65, and 75, and R/V Endeavor cruise 11. The most notable features of these profiles are that first, in Slope Water, phytoplankton standing stocks attain higher levels (>3.0 mg m^3 chlorophyll) in surface waters (<100 m) than in the northern Sargasso Sea, where maximum levels rarely exceed 0.5 mg m^3 chlorophyll. In addition, total standing stock in Slope Water remains fairly high after the spring bloom period, in contrast to standing stocks in the Sargasso, which decline rapidly after the spring bloom and formation of the deep chlorophyll maximum. Finally, the intensity of the deep chlorophyll maximum is greater although longevity is shorter in Slope Water relative to the northern Sargasso (Cox et al., 1982). As shown in Figure 6.16, the maximum depth of the deep chlorophyll maximum in Slope Water is approximately 75 m, occurring in September, while in the Sargasso Sea the maximum depth is approximately 85 m, occurring during July (Fairbanks and Wiebe, 1980).

There is some evidence that the maximum chlorophyll concentration within the deep chlorophyll maximum is strongly influenced by grazing pressure (Jamart et al., 1977; Ortner et al., 1980); therefore, regional and seasonal differences in zooplankton biomass and composition between Slope Water and the Sargasso Sea could help to explain the observed regional differences in depth profiles of chlorophyll (Figs. 6.14 and 6.15; Cox et al., 1982; see also the zooplankton section). For example, differences in the degree to which zooplankton could aggregate in the chlorophyll maximum layer in one region or the other would clearly impact the observed chlorophyll concentrations. Such aggregations of macrozooplankton and microzooplankton are more common at the deep chlorophyll maximum in the Sargasso than in Slope Water.

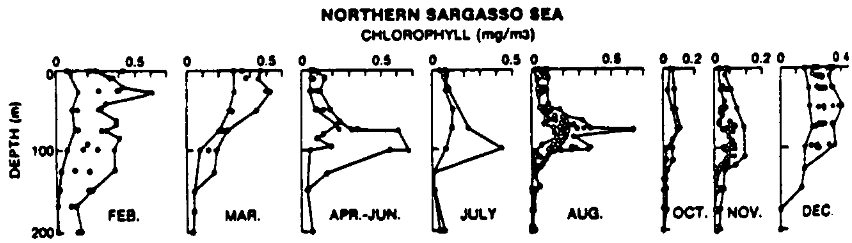


Figure 6.14. Composite vertical profiles of chlorophyll a from the northern Sargasso Sea. Solid lines represent arbitrary limits for high and low values from all the station data plotted and are not reflective of the values from any individual profile. Solid dots represent the maximum value for individual profiles, so the number of such dots in each composite plot is equal to the number of profiles used in its construction. In some cases, lower depth points are only represented by a single sttion, in which case the points are connected by a single line. Sources of data are listed in the text.

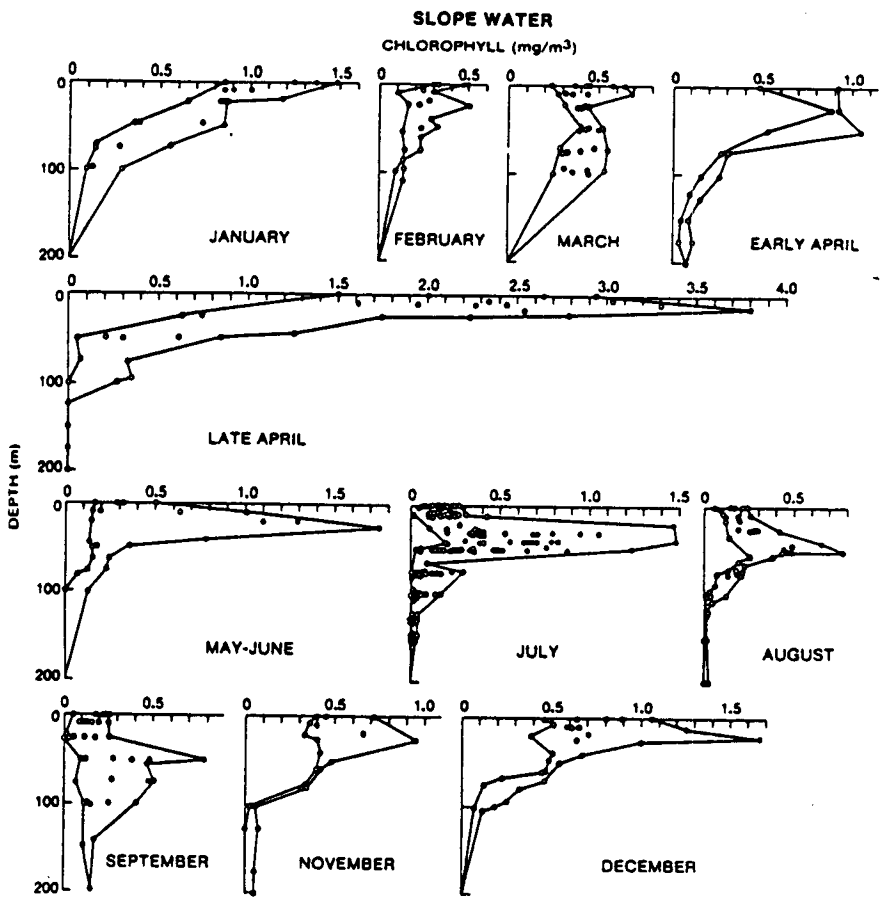


Figure 6.15. Composite vertical profiles of chlorophyll a from the slope water. Sources of data are listed in the text.

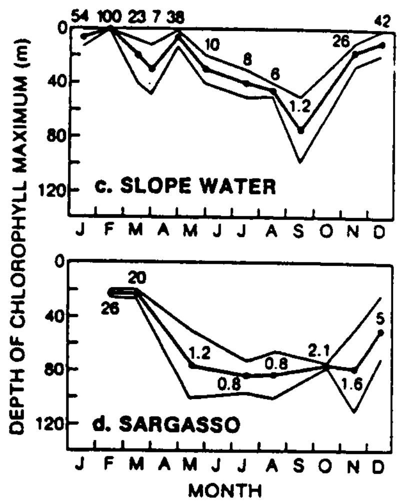


Figure 6.16. Seasonal record of the range and median values for depth of the chlorophyll a values from Figures 6.14 and 6.15. The numbers that appear next to the circles are the percent of light values for that depth. From Cox et al., 1982.

Variability in Distribution of Phytoplankton

From the discussion above, as well as the data shown in Figures 6.14 and 6.15, there are certain general seasonal patterns as well as regional differences in phytoplankton biomass in Slope Water and in the northern Sargasso Sea. Yet, also apparent from Figures 6.14 and 6.15, there can be tremendous variability in phytoplankton biomass in both regions. This variability can be observed on both large and small scales.

One source of large-scale variability in phytoplankton biomass within the ACSAR region is the sharp boundary zone separating coastal and shelf water from Slope Water (Fournier et al., 1977; 1979). Such fronts may become regions of localized aggregations of phytoplankton biomass in surface waters, particularly during spring bloom periods, and may be sites of enhanced production as well (Uda, 1959; Fournier et al., 1979). Typically high concentrations of phytoplankton biomass develop in the surface waters on the stratified side of the frontal boundary (Slope Water) during the spring bloom, but nutrients may subsequently become depleted. In nearby shelf water, waters remain unstratified due to high tidal currents. Although these currents may provide high nutrient levels by rapid vertical mixing, they also may limit the time during which phytoplankton are at light levels of sufficient intensity to cause high production (Pingree et al., 1975; Herman and Denman, 1979). In the front itself there are intermittent periods of thermal stability and nutrient renewal from tidal- or wind-mixing (Fournier et al., 1979), resulting in enhanced production. Such appears to have been the case along a frontal boundary 100-200 miles south of Nova Scotia during spring 1977 (Herman and Denman, 1979). They measured chlorophyll concentrations of 1-2 mg m^{-3} in the surface coastal waters, 2-3 mg m^{-3} in Slope Water, and highest values, ranging from 4-7 mg m^{-3} in the front itself. In another set of observations off Nova Scotia, made during the winter, chlorophyll concentrations averaged 1.3 mg m^{-3} in shelf water, increased sharply to 4.5 mg m^{-3} along a 6.5° temperature increase, and dropped to ~1.0 mg m^{-3} in Slope Water (Fournier et al., 1979). No peak in biomass has been observed near the shelf break in late fall (Fournier et al., 1977). The available data thus serve to demonstrate that the shelf-break front may be a well-defined feature at least several months of the year (Fournier et al., 1979; Herman and Denman, 1979), and may significantly impact production as well.

The formation, development, and/or presence of Gulf Stream rings may also have a significant influence on the biomass distribution within Slope Water and the Sargasso Sea. Biomass changes measured during an intensive study of warm core ring 82-B are discussed in the zooplankton section of this volume. Seasonal variation in chlorophyll a concentrations for warm core ring 82-B have not yet been published. Based on preliminary data, it appears that highest values were observed near ring center, compared with the ring periphery, although considerable variability in chlorophyll concentrations was found for any one month (Hitchcock, pers. comm.). Streamers or intrusions could have contributed to this variability. Given the fact that warm-core rings can occupy approximately 40% of surface Slope Water at various times, their impact on overall Slope Water biomass budget can be very significant. Likewise, cold-core rings, occupying 10-15% of the northern Sargasso Sea at any time, may also have a strong influence on meso-scale biomass structure.

Patchiness, independent of ring structure, also deserves comment. Phytoplankton patches on the order of 10 - 100 km may develop partly as a result of turbulent diffusion (Steele, 1976), but the environmental influences mediating patchiness development are not fully understood. Therriault and Platt (1981) have provided evidence for one near-shore ecosystem off Nova Scotia that during periods of low turbulent mixing, patchiness was induced by local differences in phytoplankton production efficiency, whereas, during periods of high turbulent mixing, spatial variations in phytoplankton distribution could become more homogeneous. This supports the notion that small-scale structure develops according to physiological dynamics until overriden by physical processes (Platt and Denman, 1980). Thus, when wind stress is low, spatial variation in production and biomass may be ascribed to differences in physiological state of the phytoplankton, but when wind stress is high enough for surface layer mixing, it dominates other sources of variability (Therriault and Platt, 1981).

SPECIES COMPOSITION AND DISTRIBUTION

Kinds of Measurements

One technique is that of the Continuous Plankton Recorder (Hardy, 1939), which allows an assessment of the degree of "green-ness" of the material filtered onto the silks; however, it does not allow direct enumeration of the species (Robinson, 1970). A more commonly used technique is that of direct counts. This technique has been used in Atlantic continental shelf waters by Hulburt (1967), Marshall (1969, 1971, 1976, 1982a,b, 1984), and Hulburt and MacKenzie (1971), among others. In this technique water samples preserved with buffered formalin are settled and centifuged and examined under a light microscope. Marshall (1976) has also supplemented the microscopic examinations with examinations by electron microscopy to facilitate species identification.

Regional and Seasonal Phytoplankton Composition

The most extensive studies on the composition of phytoplankton within the ACSAR region have been conducted by Marshall (1971, 1976, 1984). He has summarized data from a variety of literature sources as well as from collections made during 42 cruises from 1964 to 1981 covering sampling areas from the Gulf of Maine and southeast of Nova Scotia to the Florida Straits. A total of 609 species of phytoplankton were identified (but later updated to over 900), which included 277 diatoms, 247 pyrrhophyceans, 54 coccolithophores, 9 silicoflagellates, 6 cyanophyceans, and 16 representatives of the Chlorophyta, Euglenophyta, Crytophyceae, and Xanthophyceae (Marshall, 1976). Species lists for the major groups, compiled by Marshall (1971), are presented in Tables 6.16-6.19. Of the species identified in the Marshall (1971) study, 76% occurred in only one of the three regions studied, the Continental Shelf, the Gulf Stream, or the Sargasso Sea.

In terms of relative abundance, the concentration of diatoms decreases seaward, whereas the concentration of coccolithophores increases significantly in pelagic waters, and waters above 23° (Marshall, 1976). Dinoflagellate concentrations do not reach levels observed for diatoms, although isolated blooms may occur. Two other studies of phytoplankton composition in waters of the continental shelf (Fawley et al., 1980; Kalenak and Marshall, 1981) have also listed in decreasing order of abundance diatoms, dinoflagellates, and coccolithophores. In these latter two studies representatives of the blue-green algae, silicoflagellates, and an unidentified ultraplankton component were also noted. In Figures 6.17-6.19 are shown the seasonal distribution of total diatoms, dinoflagellates, and coccolithophores, as recently compiled by Marshall (1984). Highest concentrations of total phytoplankton were frequently observed adjacent to the lower New York Bay, the Delaware Bay, and the Chesapeake Bay, as well as in the Gulf of Maine, Georges Bank, and along the shelf margin.

	Shelf Waters				Gulf Stream				Sargasso Sea			
	W	S	S	F	W	S	S	F	W	S	S	F
Actinoptychus sp.	X	–	–	–	X	–	–	–	–	–	–	–
Amphiprora sp.	–	–	–	X	–	X	–	–	–	X	–	X
Amphora sp.	X	X	–	–	X	–	–	–	–	–	–	–
Amphora proteoides	–	–	–	B	–	–	–	X	–	–	–	–
Asterionella japonica	X	X	X	X	X	–	X	–	–	–	–	X
Asterolampra marylandica	–	–	–	–	–	–	–	–	–	–	X	–
Asteromphalus sp.	–	–	–	–	–	–	–	X	–	–	–	–
Bacteriastrum comosum	–	–	–	–	X	–	–	–	–	–	–	–
Bacteriastrum delicatulum	X	B	–	X	X	B	–	–	X	–	–	–
Bacteriastrum elongatum	–	–	–	X	–	–	–	X	–	–	–	–
Biddulphia sp.	X	X	–	–	X	X	–	X	–	X	–	–
Biddulphia alternans	–	–	–	X	–	–	–	–	–	–	–	–
Biddulphia longicruris	–	–	–	X	–	–	–	–	–	–	–	–
Biddulphia sinensis	X	–	–	–	–	–	–	–	–	–	–	–
Cerataulina bergonii	X	X	–	X	X	B	X	–	X	–	–	–
Chaetoceros sp.	–	–	–	X	–	–	–	–	–	–	–	–
Chaetoceros affinis	–	B	X	–	X	–	X	X	–	–	–	–
Chaetoceros atlanticus	–	–	–	–	–	–	–	X	–	–	–	–
Chaetoceros brevis	–	–	–	–	X	–	–	–	–	–	–	–
Chaetoceros coarctatus	–	–	–	X	–	–	–	X	–	–	–	–
Chaetoceros compressus	X	X	–	X	X	–	–	–	–	–	–	–
Chaetoceros constrictus	–	–	–	–	X	–	–	–	–	–	–	–
Chaetoceros curvisetus	–	–	–	X	X	–	–	–	–	–	–	–
Chaetoceros danicus	X	–	X	–	X	–	X	–	–	–	–	–
Chaetoceros decipiens	B	A	X	B	A	A	A	A	X	–	–	–
Chaetoceros didymus	–	–	X	–	–	–	X	X	–	–	–	–
Chaetoceros gracilis	–	–	X	–	–	–	X	–	–	–	–	–
Chaetoceros pendulus	X	X	–	–	X	–	–	X	–	–	–	–
Chaetoceros peruvianus	–	X	–	–	X	–	–	X	–	–	–	–
Chaetoceros pseudocurvisetus	–	–	–	–	–	X	–	–	–	–	–	–
Chaetoceros radicans	–	–	X	–	–	–	X	–	–	–	–	–
Chaetoceros socialis	–	X	–	–	–	–	–	–	–	–	–	–
Climacodium biconcavum	–	–	–	–	X	–	–	–	–	–	–	–
Climacodium frauenfeldianum	–	–	–	X	X	–	–	X	–	–	–	–
Cocconeis sp.	–	–	–	X	–	–	–	–	–	–	–	–
Corethron hystrix	X	X	–	–	–	–	–	–	–	–	–	–
Coscinodiscus sp.	X	–	–	–	–	–	–	X	–	–	–	X
Coscinodiscus centralis	–	–	–	–	–	–	–	–	–	X	–	–
Coscinodiscus excentricus	–	–	–	X	X	–	–	–	–	–	–	–
Coscinodiscus granii	X	–	–	–	X	–	–	–	–	–	–	–
Coscinodiscus lineatus	X	B	–	X	A	B	X	B	–	–	–	–
Coscinodiscus marginatus	–	–	–	–	–	–	–	–	–	X	–	X
Coscinodiscus nitidus	X	–	–	X	X	–	X	X	–	–	–	–
Coscinodiscus perforatus	X	B	–	–	X	X	–	–	–	X	–	–
Coscinodiscus radiatus	–	X	–	–	X	X	–	–	–	–	–	–
Diatoma elongatum	–	–	–	B	–	–	–	–	–	–	–	–
Diatoma hiemale	X	–	–	–	X	–	–	–	–	–	–	–
Diploneis sp.	X	B	X	–	X	–	X	–	–	–	–	–
Diploneis bombus	–	X	X	–	–	–	–	–	–	–	–	–
Ditylum brightwellii	X	–	X	–	X	–	X	–	–	X	–	X
Eucampia cornuta	–	–	–	X	–	–	–	–	–	–	–	–
Eucampia zodiacus	X	B	–	–	X	X	–	–	–	X	–	–
Fragilaria sp.	X	X	–	–	–	X	–	–	–	–	–	–
Fragilaria crotonensis	X	X	–	–	X	–	–	X	–	–	–	–
Gomphonema sp.	X	–	–	–	X	–	–	–	–	–	–	–
Grammatophora marina	X	X	–	X	–	–	–	X	–	–	–	–
Guinardia flaccida	–	–	–	–	–	X	–	–	–	–	–	–
Gyrosigma sp.	–	–	–	–	–	–	–	–	–	X	–	–
Hemiaulus hauckii	B	B	X	–	X	–	X	X	–	–	A	–
Hemiaulus membranaceus	–	X	–	X	X	X	–	X	–	–	–	–
Hemiaulus sinensis	–	X	–	–	–	X	–	–	–	–	–	–
Lauderia annulata	X	X	–	–	X	–	–	–	–	–	–	–
Leptocylindrus danicus	X	X	–	X	X	–	–	X	–	–	–	X
Licmophora abbreviata	–	X	–	–	–	–	–	–	–	–	–	–
Licmophora paradoxa	X	–	–	–	X	–	–	–	–	–	–	–
Mastogloia sp.	–	X	–	–	–	–	–	–	–	–	–	–
Melosira hummii	–	–	–	X	–	–	–	–	–	–	–	–
Melosira sulcata	X	X	X	X	X	–	X	X	–	X	–	X
Navicula sp.	B	B	B	B	X	X	X	X	B	B	–	B
Nitzschia sp.	X	X	X	X	–	–	X	X	–	X	–	X
Nitzschia closterium	–	–	–	X	X	–	X	–	–	–	–	X
Nitzschia longissima	X	–	–	–	X	–	–	–	–	–	–	–
Nitzschia seriata	A	A	–	–	A	–	–	–	X	–	–	–
Plagiogramma vanheurckii	–	X	X	–	–	–	X	–	–	–	–	–
Planktoniella sol	–	X	–	–	–	X	–	X	–	–	–	–
Pleurosigma sp.	X	–	–	X	–	–	–	X	–	–	–	X
Pleurosigma angulatum	X	–	–	–	X	–	–	–	–	–	–	–
Pleurosigma elongatum	–	X	–	–	–	–	–	–	–	–	–	–
Pleurosigma formosum	–	X	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata	A	A	A	A	A	A	B	A	X	X	A	X
Rhizosolenia calcar-avis	X	X	–	B	A	B	B	B	X	X	X	–
Rhizosolenia castracanei	–	–	–	X	–	–	–	–	–	X	–	–
Rhizosolenia delicatula	–	X	–	–	X	–	–	X	–	–	–	–
Rhizosolenia fragilissima	–	–	X	–	–	–	X	–	–	–	–	X
Rhizosolenia hebetata semispina	–	–	–	–	–	–	X	–	–	–	–	X
Rhizosolenia imbricata	–	X	–	–	–	–	X	–	–	–	–	X
Rhizosolenia robusta	–	X	–	X	–	–	–	X	–	–	–	–
Rhizosolenia setigera	X	X	–	X	X	–	–	X	–	X	–	X
Rhizosolenia stolterfothii	A	A	–	X	B	–	–	X	X	–	–	X
Rhizosolenia styliformis	–	X	X	–	–	–	X	–	–	X	–	–
Skeletonema costatum	A	X	B	A	A	–	A	A	–	X	–	–
Stephanopyxis sp.	–	–	–	–	–	X	–	–	–	X	–	–
Stephanopyxis palmeriana	–	–	–	X	–	–	–	–	–	–	–	–
Striatella unipunctata	–	X	–	–	–	–	–	–	–	–	–	–
Surirella sp.	–	X	–	X	–	–	–	–	–	–	–	–
Synedra ulna	X	–	–	–	X	–	–	–	–	–	–	–
Thalassionema nitzschioides	–	B	X	B	–	B	–	X	–	X	–	X
Thalassiothrix delicatula	–	–	–	–	–	–	–	X	–	–	–	–
Thalassiothrix frauenfeldii	–	X	–	B	–	X	–	X	–	–	–	–
Thalassiothrix mediterranea	–	B	–	–	–	–	–	X	X	–	–	X

Table 6.16.

Seasonal appearance of diatoms recorded for the Shelf Waters, Gulf Stream, and Sargasso Sea. (The more abundant species are indicated by: A, dominant species for two or more years; B, dominant species during one season. X indicates presence.) From Marshall, 1971.

	Shelf Waters				Gulf Stream				Sargasso Sea			
	W	S	S	F	W	S	S	F	W	S	S	F
Amphidinium sp.	X	X	X	A	–	X	X	–	X	X	–	–
Ceratium sp.	–	–	X	–	–	–	–	–	–	–	–	–
Ceratium extensum	–	–	–	–	–	–	–	X	–	–	–	–
Ceratium furca	X	X	X	X	X	X	B	–	–	–	–	–
Ceratium fusus	X	X	–	X	–	X	–	X	–	–	–	–
Ceratium lineatum	–	–	–	X	–	–	–	X	–	–	–	–
Ceratium longipes	–	–	–	–	–	–	–	X	–	–	–	–
Ceratium pentagonum	–	–	X	–	–	–	B	–	–	–	X	–
Ceratium tripos	X	X	X	X	–	X	X	X	–	–	X	X
Chroomonas sp.	X	–	–	–	X	–	–	–	–	–	–	–
Cochlodinium pellucidum	–	–	–	–	–	X	–	–	–	–	–	–
Dinophysis sp.	–	–	–	X	–	–	–	X	–	X	–	–
Dinophysis schuetti	–	–	–	–	–	X	–	X	–	–	–	–
Exuviaella sp.	X	B	B	B	X	B	X	X	X	X	X	X
Exuviaella compressa	–	–	–	–	–	–	–	X	–	–	–	–
Exuviaella perforata	–	–	–	–	–	X	–	–	–	–	–	–
Gonyaulax sp.	–	–	–	X	–	X	–	X	–	–	–	X
Gymnodinium sp.	X	X	X	B	X	X	X	–	X	X	–	X
Gymnodinium costatum	–	–	–	X	–	–	–	–	–	–	–	–
Gymnodinium rhomboides	–	–	–	X	–	–	–	X	–	–	–	–
Gymnodinium simplex	–	–	–	X	–	–	–	X	–	–	–	–
Gyrodinium sp.	–	–	–	X	X	–	–	–	–	–	–	–
Noctiluca scintillans	X	–	–	–	X	–	–	–	–	–	–	–
Oxytoxum sp.	–	–	–	X	–	X	–	–	–	–	–	–
Oxytoxum gladiolus	–	–	–	X	–	–	–	–	–	–	X	–
Oxytoxum milneri	–	–	–	–	–	X	–	X	–	–	–	–
Oxytoxum reticulatum	–	–	–	–	–	X	–	–	–	–	–	–
Oxytoxum scolopax	–	–	–	X	–	–	–	X	–	X	–	–
Oxytoxum sphaeroideum	–	–	–	X	–	–	–	X	–	–	–	–
Oxytoxum variabile	–	–	X	–	–	–	X	–	–	–	X	–
Peridinium sp.	X	B	–	X	X	X	–	–	–	–	–	–
Peridinium breve	–	–	–	–	–	X	–	–	–	–	–	–
Peridinium depressum	X	–	–	–	X	X	–	–	–	–	–	X
Podolampas bipes	–	–	–	–	–	–	–	X	–	–	–	–
Podolampas elegans	–	–	–	X	–	–	–	X	–	–	X	X
Podolampas palmipes	–	–	–	X	–	X	–	X	–	–	–	X
Prorocentrum sp.	X	X	X	B	X	X	X	–	–	–	X	X
Prorocentrum micans	–	–	–	–	–	–	–	X	–	–	X	X
Prorocentrum minimum	–	–	X	–	–	–	X	–	–	–	–	–
Prorocentrum rostratum	–	–	–	–	–	–	X	–	–	–	X	–
Prorocentrum scutellum	–	–	–	–	–	X	–	–	–	–	–	–
Pyrodinium bahamense	X	–	–	–	X	–	–	–	–	–	–	–

Table 6.17. Seasonal appearance of Pyrrhophyceans recorded for the Shelf Waters, Gulf Stream, and Sargasso Sea. (The more abundant species are indicated by: A, dominant species for two or more years; B, dominant species during one season. X indicates presence.) From Marshall, 1971.

	Shelf Waters				Gulf Stream				Sargasso Sea			
	W	S	S	F	W	S	S	F	W	S	S	F
Acanthoica sp.	–	–	–	–	–	–	–	X	–	–	–	–
Acanthoica acanthifera	–	X	–	–	–	–	X	–	–	X	X	–
Acanthoica acanthos	–	–	X	–	–	–	X	–	–	–	–	–
Acanthoica ornata	–	–	–	–	–	–	–	X	–	–	–	–
Acanthoica quattrospina	–	–	–	–	–	–	–	X	–	–	–	–
Anoplosolenia brasiliensis	–	–	–	–	–	–	–	X	–	–	–	–
Anthosphaera sp.	–	–	–	–	–	–	–	–	–	–	X	–
Anthosphaera quadricornu	–	–	–	–	–	–	–	X	–	–	–	–
Calcioconus vitreus	–	–	–	–	–	–	X	–	–	X	X	X
Calciosolenia granii	–	–	–	–	–	–	–	–	–	X	–	X
Calciosolenia murrayi	–	–	X	A	–	–	X	X	–	X	–	–
Calyptrosphaera sp.	–	–	–	–	–	–	–	–	–	X	–	–
Calyptrosphaera globosa	–	–	–	–	–	–	–	X	–	–	–	–
Calyptrosphaera oblonga	–	–	–	–	–	X	–	X	–	–	–	–
Coccolithus huxleyi	A	A	A	A	A	B	A	A	B	B	X	A
Coccolithus pelagicus	–	–	X	X	–	X	X	X	–	X	X	X
Cricosphaera carterae	–	–	X	–	–	–	X	–	–	–	–	–
Cyclococcolithus fragilis	–	–	X	–	–	–	X	X	–	–	–	–
Cyclococcolithus leptoporus	–	–	–	X	–	B	–	–	–	–	–	X
Discosphaera tubifera	–	–	B	X	–	X	B	B	–	X	A	B
Gephyrocapsa oceanica	–	–	–	X	–	X	X	A	–	X	–	X
Halopappus adriaticus	–	–	X	–	–	–	X	–	–	–	–	–
Heimiella excentrica	–	–	–	–	–	–	X	–	–	–	–	–
Lohmannosphaera adriatica	–	–	–	–	–	X	X	X	–	–	–	–
Lohmannosphaera paucoscyphos	–	–	–	–	–	–	X	–	–	–	–	X
Michaelsarsia asymmetrica	–	–	–	–	–	–	–	–	–	X	–	X
Michaelsarsia elegans	–	–	X	–	–	–	X	–	–	X	X	–
Pontosphaera nigra	–	–	–	–	–	–	X	–	–	–	–	X
Pontosphaera syracusana	–	–	–	–	–	–	–	X	–	–	–	X
Rhabdosphaera clavigera	–	–	–	–	–	X	–	–	–	–	–	–
Rhabdosphaera hispida	–	–	–	–	–	–	–	X	–	–	–	–
Rhabdosphaera stylifera	–	–	X	–	–	X	X	X	–	–	–	X
Scyphosphaera apsteinii	–	–	–	–	–	–	–	X	–	X	–	X
Syracosphaera brandtii	–	–	–	–	–	–	X	–	–	–	–	–
Syracosphaera brasiliensis	–	–	–	X	–	–	–	X	–	–	–	–
Syracosphaera mediterranea	A	X	X	X	X	A	X	A	X	X	–	A
Syracosphaera molischii	–	–	–	X	X	X	–	–	–	–	–	–
Syracosphaera pirus	–	–	–	–	–	X	–	–	–	–	–	–
Syracosphaera pulchra	A	B	X	X	X	X	X	A	X	X	X	A
Syracosphaera radiata	–	–	–	–	–	–	X	–	–	–	–	–
Thoracosphaera heimii	X	–	–	–	X	–	X	–	–	X	–	X
Umbellosphaera irregularis	–	–	X	–	–	–	X	–	–	–	–	X
Umbellicosphaera mirabilis	–	–	–	–	–	–	X	X	–	X	X	X

Table 6.18. Seasonal appearance of Coccolithophores recorded for the Shelf Waters, Gulf Stream, and Sargasso Sea. (The more abundant species are indicated by: A, dominant species for two or more years; B, dominant species during one season. X indicates presence.) From Marshall, 1971.

	Shelf Waters				Gulf Stream				Sargasso Sea			
	W	S	S	F	W	S	S	F	W	S	S	F
Dictyocha fibula	X	X	X	X	X	X	X	X	–	–	X	X
Dictyocha staurodon	–	–	–	–	–	–	–	X	–	–	–	–
Distephanus speculum	–	–	–	–	–	X	–	–	–	–	–	–
Mesocena polymorpha	–	–	–	–	–	X	–	X	–	–	–	–

Table 6.19. Seasonal appearance of Silicoflagellates recorded for the Shelf Waters, Gulf Stream, and Sargasso Sea. (The more abundant species are indicated by: A, dominant species for two or more years; B, dominant species during one season. X indicates presence.) From Marshall, 1971.

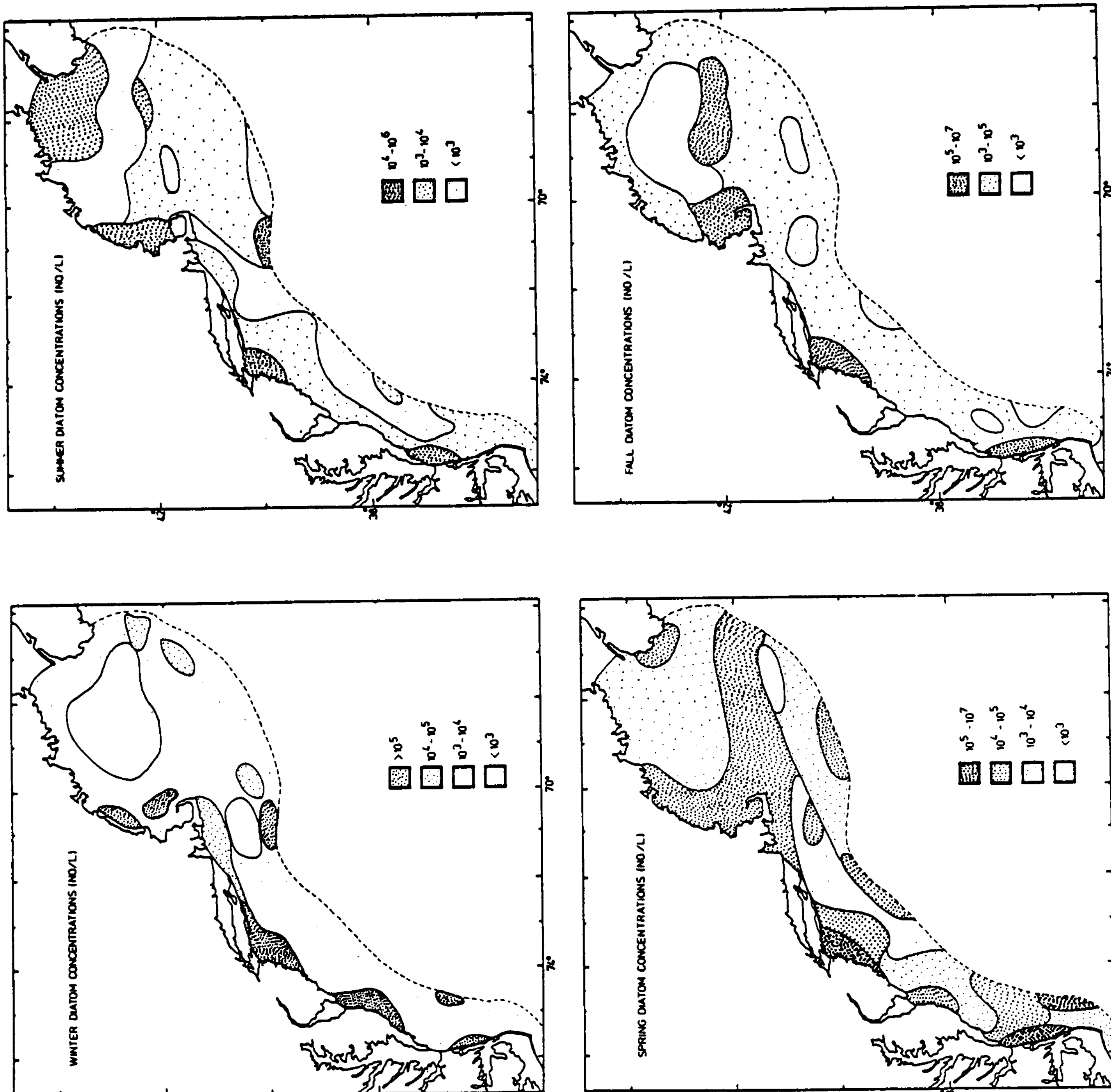


Figure 6.17. Seasonal distribution of diatoms in surface waters off the northeastern U.S. From Marshall, 1984.

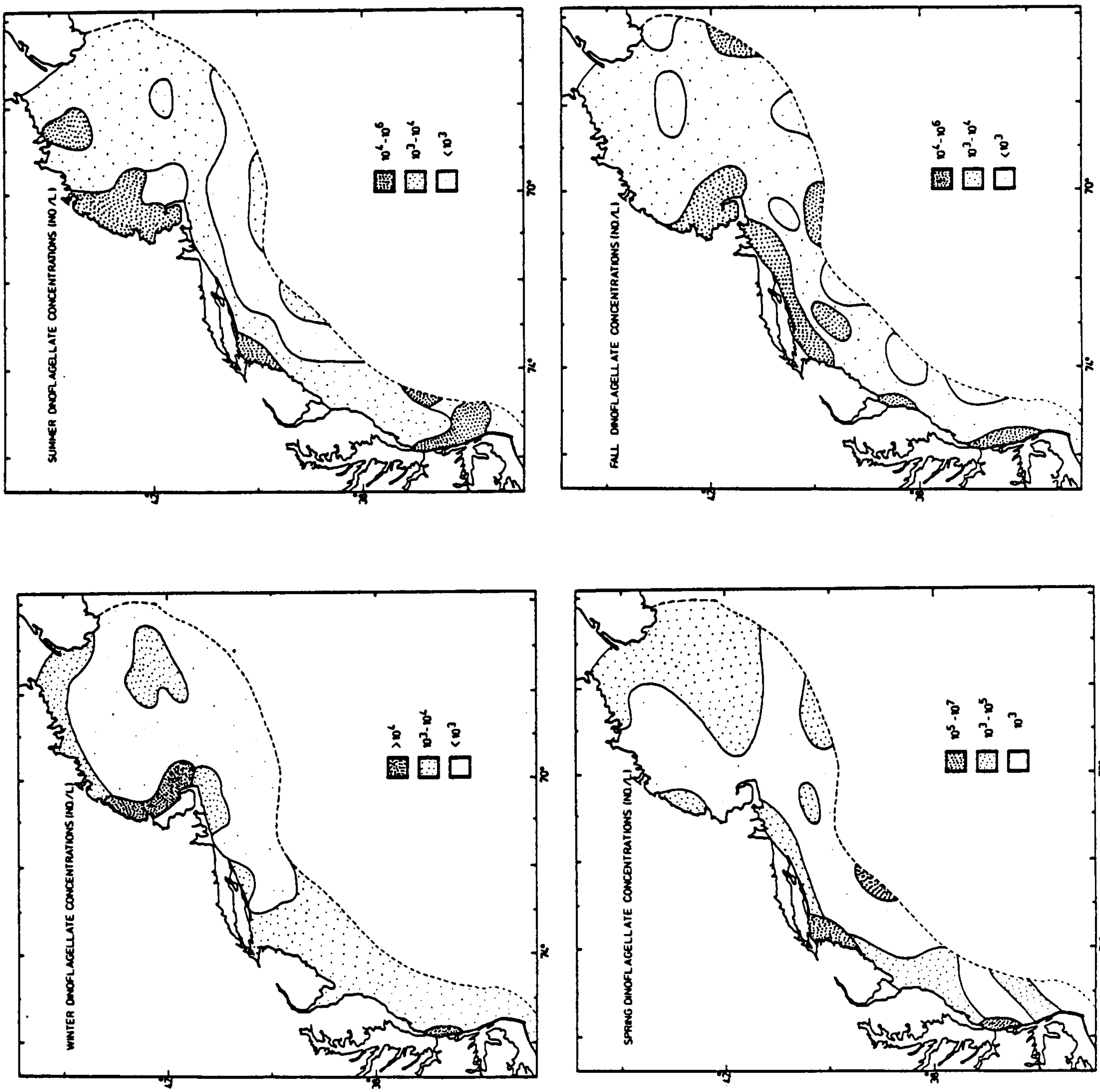


Figure 6.18. Seasonal distribution of dinoflagellates in surface waters off the northeastern U.S. From Marshall, 1984.

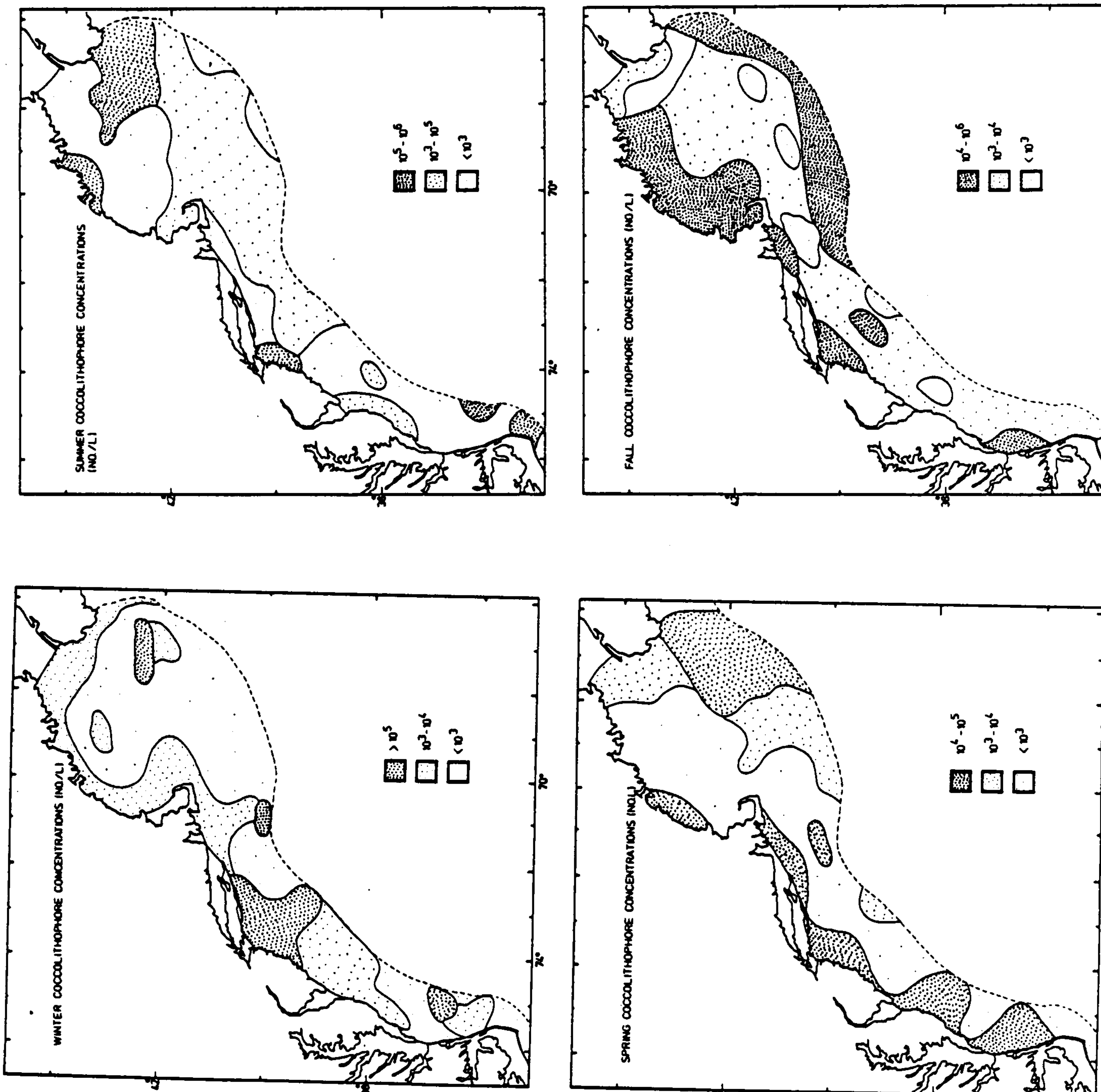


Figure 6.19. Seasonal distribution of coccolithophores in surface waters off the northeastern U.S. From Marshall, 1984.

Recently, another class of phytoplankton, the Cyanobacteria, have been found to have a cosmopolitan distribution, and contribute significantly to primary productivity (Waterbury et al., 1979; Li et al, 1983). Because of their prokaryotic nature, however, a discussion of their distribution and abundance is included with the microbiology section of this volume.

Temporal and Spatial Variability

Several other studies on phytoplankton species composition and distribution have been conducted in the ACSAR region, but were more localized in scope. Hulburt and MacKenzie (1971) assessed the distribution of phytoplankton of the Continental Shelf of the southern United States during the winter of 1968. Marshall (1982a) assessed the phytoplankton abundance and distribution in southeastern shelf waters of the United States. In contrast to several of the earlier studies, this study observed a large unidentified ultraplankton component in almost all collections, as well as a fair amount of patchiness in species dominance. Species identifications of phytoplankton in and around Gulf Stream warm-core rings have also been made, but as yet, remain unpublished.

Phytoplankton composition in the northern Sargasso Sea, Slope Water, and in Gulf Stream cold-core rings was also described by Ortner et al. (1979) in relation to the physical and chemical properties of the water masses. They observed that although the physical and chemical properties of the cold-core rings frequently appeared intermediate between Slope Water and northern Sargasso Sea conditions, at no time did species composition appear intermediate. Rather, phytoplankton composition in northern Sargasso Sea samples was more similar to that in Slope Water samples than that in the rings. Diatoms appeared to be greatly reduced in numbers in the cold-core ring relative to the Slope Water or northern Sargasso, while several dinoflagellate and coccolithophore species had higher abundances in the rings. Factors such as differential grazing pressure, nutrient flux, and physical mixing processes were hypothesized to be important in controlling these distributional patterns (Ortner et al., 1979).

In summary, the studies cited above have all indicated that a characteristic pattern of abundance as well as species composition exist for Shelf Waters, the Gulf Stream, and the Sargasso Sea, with considerable localized distributional patterns or patchiness. Clearly, the boundaries between regions are variable, and mixing will occur, particularly from the meanderings of the Gulf Stream. The capacity of species to change or to tolerate new environmental conditions will determine their success in a new water mass (Marshall, 1971; Hulburt, 1983).

RATES OF PRIMARY PRODUCTIVITY

Measurement Techniques

The ability to make accurate measurements of primary production in natural waters has major importance to marine phytoplankton ecologists. Yet, the magnitude of these rates and the reliability of the measurements currently employed are widely debated (Eppley, 1980).

The standard technique that is used for measuring production rates generally involves confinement of a natural water sample in a container with an added isotopic tracer (such as $^{14}CO_2$, $^{15}NH_4^+$, $^{15}NO_3^-$), and then assaying the quantity of tracer incorporated into the particulate material (Steemann Nielsen, 1952; Dugdale and Goering, 1967) at the end of the incubation period. A critical assumption upon which the utility of these techniques is based, but one which has recently come under considerable scrutiny, is that the measured activity in the assay chamber is identical to that in the undisturbed natural environment from which the sample was collected. In recent years numerous problems with long-term bottle incubation techniques have been addressed, including changes in species composition during confinement (Venrick et al., 1977), contamination or effects due to size of the incubation vessel itself (Gieskes et al., 1979; Carpenter and Lively, 1980; Fitzwater et al., 1982), and non-linearity in uptake responses, both as a result of, and independent of, nutrient depletion effects (Conway et al., 1976; Glibert and Goldman, 1981; Goldman et al., 1981; Wheeler et al., 1982). Hence, there is considerable uncertainity as to the reliability of much of the older data in the literature (Eppley, 1981). The currently funded program, Plankton Rate Processes in Oligotrophic Oceans (PRPOOS), may provide data which will shed light on this current debate. Generally it is assumed that the magnitude of the analytical problems in estimating production is greater in nutrient depleted open ocean waters than in more productive coastal regimes.

Regional and Seasonal Primary Productivity Patterns

There have been numerous reviews over the past several decades of the extensive literature on seasonal cycles of production in the major oceanic regions (c.f. Ryther, 1963; Cushing, 1975; Eppley, 1981). In general, seasonal patterns of production can be explained in terms of stratification of the water column and the rate of nutrient input. The spring bloom, typical of most areas, occurs when seasonal stratification begins to set in, thereby reducing the depth to which surface phytoplankton are mixed. Net phytoplankton growth occurs then because the mixing depth is shallower than the 'critical depth', the depth at which integrated water column photosynthesis equals respiration. When nutrients become depleted in the surface waters, growth rates and standing stocks decline. Development of a subsurface chlorophyll maximum may be noted following spring blooms (Figs. 6.14 and 6.15). A fall bloom may also be seen, if there is renewed nutrient input to the surface, or if grazing pressure becomes relaxed (Eppley, 1981).

Unfortunately few data sets exist for offshore waters where seasonal cycles of production have been assessed over the course of several years. Rather, most productivity measurements have been made as part of oceanographic cruises to specific areas at irregular times. In the Sargasso Sea, however, there has been one study (Menzel and Ryther, 1960; 1961) in which productivity rates were determined on a biweekly basis for two and a half years. This data set, shown in Figure 6.20, shows not only a clear seasonal pattern in productivity rates, with the maximum occurring between January and April, but also major yearly differences in the amplitudes of the maximum and minimum productivity. These year-to-year differences were at least partially attributed to climatic differences, in that the winter of 1957-1958 was severe enough to completely destroy the thermocline by March, but the subsequent winters were milder, and slight thermal gradients persisted all year (Ryther, 1963).

Malone et al. (1983; see also references cited therein) have recently reviewed seasonal as well as small-scale variations in the distribution and growth of phytoplankton on the continental shelf and adjacent Slope Waters. They observed that whereas phytoplankton biomass (as chlorophyll) is at a maximum during March-April and a minimum during July, production per unit biomass increases from a November-January minimum to a July maximum. Approximately 39% of the annual production for the region as a whole occurs during the spring diatom bloom period (February-April), and 54% during the period of water column stratification (May-October).

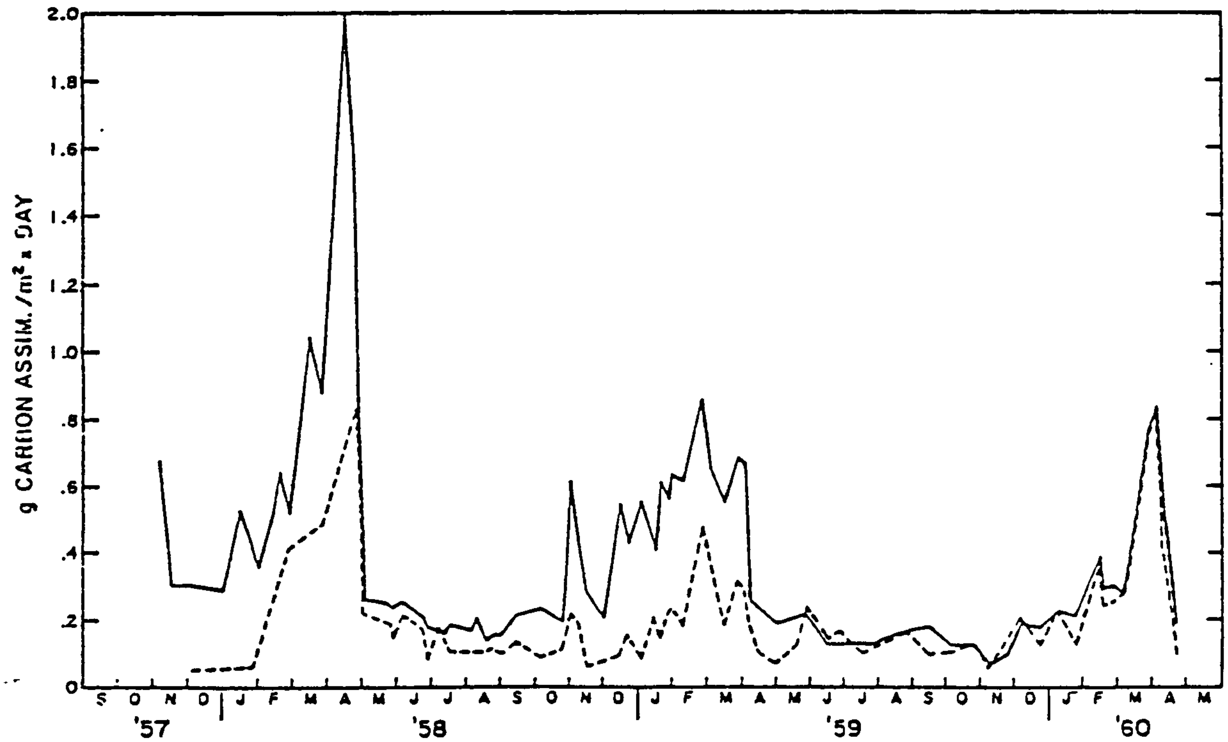


Figure 6.20. Gross (solid line) and net (broken line) primary production at station 'S' 1957-1960. (From Menzel and Ryther, 1961).

Within this broad perspective, biomass availability and productivity can be influenced by physical factors such as wind events and the shelf-break front (Malone et al., 1983). High phytoplankton growth rates and significant biomass accumulation occur during both spring and summer on the shelf side of the front. However, during the diatom bloom period, most of the biomass accumulates in surface waters due to stratification which sets in between storm events. In the summer, in contrast, most of the biomass accumulates below the pycnocline (Malone et al., 1983).

Factors Regulating the Rate of Primary Productivity

Important factors known to regulate the rate of marine primary productivity are light, temperature, availability of essential nutrients, and degree of vertical mixing. Each of these is briefly reviewed below.

Light alone rarely limits the rate of primary productivity in oceanic waters; it has been suggested that if light alone were limiting, then our estimates of primary productivity would be five to ten times those typically reported (Ryther, 1959; Vishniac, 1971). During winter inshore, however, productivity may be limited by light availability (Fournier et al., 1979). Additionally, phytoplankton growth rates during the spring diatom bloom on the continental shelf are likely light - limited as accumulation of biomass is high (Malone et al., 1983). The strategies by which phytoplankton adapt to different light levels has been the subject of many investigations, and have been reviewed by Falkowski (1980) and Harris (1978, 1980).

Temperature may be extremely important in controlling both the rate of primary productivity as well as seasonal succession of species. Eppley (1972), in reviewing the wealth of published data on algal growth rates, established that there was an upper limit to phytoplankton growth which could be described by the equation:

$$\mu_{max} = 0.851(1.066)^{t}$$

where μ_{max} is the specific growth rate in doublings/day, and t is the temperature of growth in degrees celcius (<40°C).

This is an extremely useful expression, but it should be born in mind that other factors may prohibit certain species from attaining their maximal growth rate at a given temperature, and not all species will necessarily reach the same growth rate even when their optimal temperatures are similar (Goldman and Ryther, 1976). Harrison and Platt (1980) have observed that for natural assemblages collected from shallow, coastal waters, a linear fit of temperature and assimilation number appears to be statistically acceptable. In several recent studies, however, it has been observed that high productivity and/or growth rates may be attained in near-freezing waters. Malone (1976) observed, for natural phytoplankton assemblages from the New York Bight, that maximal photosynthesis (normalized to unit biomass) was similar at 4° and 24°, but significantly less at intermediate temperatures. This phenomenon was attributed to time periods of relative temperature stability: at the warmest and coolest temperatures, cells have the opportunity to adapt to the temperature regime and flourish, whereas, during rapid warming or cooling, adaptation is more difficult. Hitchcock and Smayda (1977) have also observed large winter blooms at <2°C. Glibert and Goldman (1982) also noted that maximal photosynthetic rates are not significantly different for summer and winter phytoplankton assemblages off Woods Hole.

The nutritional requirements of phytoplankton for macro-nutrients (nitrogen and phosphorus) and micro-nutrients (vitamins and trace metals) have been well reviewed in the past several years (McCarthy, 1980; 1981; Nalewajko and Lean, 1980; Swift, 1980; Huntsman and Sunda, 1980; Bonin and Maestrini, 1981; Maestrini and Bonin, 1981).

Vitamins and vitamin-like substances have been identified as essential for phytoplankton growth, but there is little evidence that their availability limits marine primary productivity. There is more evidence that trace metals may limit productivity, and may also be toxic to phytoplankton in their excess. It is now clear from several studies that it is the activity of the free metal ion which determines the availability or toxicity of the metal (Sunda and Guillard, 1976; Anderson and Morel, 1978). The free ion activity is, in turn, a function of the organic chelator concentration and pH.

Of the major elements required by phytoplankton, however, nitrogen is usually considered to be the nutrient limiting primary productivity. The role of NH_4^+ and NO_3^- in the physiological ecology of phytoplankton has received considerable attention during the past decade. Nevertheless, the degree to which nitrogen may be limiting phytoplankton growth in oligotrophic oceanic waters is still not well understood, in part because current analytical techniques restrict our ability to collect data on the temporal and spatial scales necessary to make meaningful interpretations of in situ rates of nitrogen utilization (McCarthy, 1980; Goldman and Glibert, 1983). Goldman et al. (1979), using chemical composition data concluded that growth rates of natural oligotrophic phytoplankton were near maximal and not nutrient limited, and Glibert and McCarthy (in press), using a variety of indices of nutritional status, have demonstrated only mild, if any, nitrogen limitation for phytoplankton assemblages in the Sargasso Sea during summer. Resolution of the uncertainity regarding the degree of nitrogen limitation typical for oceanic phytoplankton would further our understanding of the role nitrogen plays in regulating marine primary productivity. Clearly one of the major recent advances in our understanding of the marine nitrogen cycle is the recognition that a small nutrient pool turning over rapidly (NH_4^+) can be as important to phytoplankton uptake as a large nutrient pool with a longer renewal time (NO_3^-).

On a more global scale, we clearly lack sufficient data to state whether nitrogen fluxes to and from the oceanic region are balanced (McCarthy and Carpenter, 1983). Deficiencies are most pronounced in estimating riverine discharge and vertical flux of NO_3^- (McCarthy and Carpenter 1983). With regard to the latter, the problem of estimation is confounded by the fact that a variety of physical processes may contribute to vertical nutrient flux on variable time and space scales. Additionally, given current analytical methodology, we are often poorly equipped to measure the small concentration changes with the necessary spatial resolution. In this regard, greater collaboration between physical and biological oceanographers will be required to elucidate the impact of vertical motion on phytoplankton production.

Thus, in a very broad sense the regional and seasonal distribution of biomass and associated rates of production are reasonably well known. An improved understanding of the spatial and temporal variability of the system will be possible when some of the current analytical constraints are overcome.

MACROZOOPLANKTON

Zooplankton are aquatic animals ranging from the smallest protozoans to the largest shrimps and jellyfish. Although many are able swim sizeable distances at moderate speeds and thus can perform diel vertical migrations of hundreds of meters, their large-scale horizontal distributions are determined by the ocean currents and the suitability of the physical, chemical, and biological components of the hydrographic regimes they encounter. Thus, they are distinguishable from the larger nektonic marine animals, which have control over their horizontal as well as their vertical distributions.

This review of the zooplankton of the ACSAR study area will focus first on their ecological structure in terms of standing crop or biomass and species composition, and second, on ecosystem function in terms of secondary production and related physiological and biochemical aspects of their biology.

STANDING CROP

Kinds Of Measurements

There are four commonly used techniques to measure zooplankton biomass: displacement volume, wet weight, dry weight, and carbon. Additionally, ash free dry weight and the caloric content of the zooplankton are occasionally measured. Laurence (1976) for example gives caloric values for some North Atlantic calanoid copepods several of which may occur in the present survey area. Wiebe et al. (1975), using samples from a variety of oceanic areas and hydrographic regimes including the present study area, established predictive relationships among the former four biomass measures. Use of the interconversion equations, however, requires that volume of water filtered by the net has been measured, usually by a flow meter. In early studies of plankton biomass in the ACSAR area (i.e. Bigelow and Sears, 1939; Clarke, 1940), biomass as displacement volume was measured in terms of perminutes of towing time; flowmeters were not used. These values can not be compared unless towing time can be converted to volume filtered, which in many parts of the study area it can not. There is additionally the problem that biomass data from different investigators may not yield directly comparable results. The problem is most serious for displacement volume and wet weight (see discussion in Wiebe et al. 1975). There is also the incompatibility of data sets introduced when different investigators use different mesh sizes (see example below) and thus collect zooplankton with different size frequency spectra.

Horizontal Distribution

Patterns From Conventional Data

Compared to the middle Atlantic continental shelf region, the zooplankton of the Slope Water, Gulf Stream, and northern Sargasso Sea have been poorly sampled until recently. Previous to the current work described below, the only long-term studies of zooplankton of the region were by Clarke (1940) and Grice and Hart (1962). Both studies were based on samples taken at stations on the continental shelf, in the Slope Water, and in the Sargasso Sea on a line from Montauk Point, Long Island, N.Y., to Bermuda. Clarke's samples were principally collected with ring nets equipped with scrim netting (about 800 um mesh) and with stramin netting (about 1500 um mesh); they were taken in the upper 50 to 275 m on 10 cruises spaced irregularly throughout the years 1937 to 1939. Grice and Hart used ring nets equipped with 230 um mesh and towed obliquely to between 100 and 200 m, on five quaterly cruises, taken over a 15-month period (1959-1960). Such shallow sampling provided a biased estimate of the seasonal pattern of upper water column zooplankton.

Bé, et al. (1971) provided the most recent comprehensive summary of the zooplankton biomass in the upper 300 m for the entire North Atlantic Ocean. A sizeable number of samples were collected within the Slope Water/Sargasso Sea portion of the ACSAR area, but they were not singled out for detailed discussion.

Seasonal Cycle of Zooplankton Biomass

Beginning in 1972, studies of the zooplankton populations in Gulf Stream rings (see chapter 3 for description of the physical structure of these mesoscale eddies), the Sargasso Sea, and the Slope Water have been carried out by P. Wiebe and associates at Woods Hole Oceanographic Institution. For the first three years 1m diameter ring nets and opening/closing Bongo Nets (McGowan and Brown, 1966) equipped with flowmeters were used to sample to depths of 800 m. With the development of the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) in 1974 (Wiebe et al., 1976), higher resolution stratified sampling of the region commenced. In 1981 and 1982, the zooplankton group at Woods Hole conducted two concurrent programs in the northern portion of the study area. The first was a 19-month time series study of the life history and population dynamics of Slope Water populations. During this investigation, great effort was made to sample unadulterated Slope Water i.e. water not directly influenced by warm-core rings or the Gulf Stream. The second was a time-series study of the warm-core rings themselves and the zooplankton work was only a small part of total multidisciplinary effort (Warm-Core Rings Executive Committee, 1982).

The picture of the seasonal cycle of biomass in the Northern Sargasso Sea outside the influence of cold-core rings is incomplete; because sampling has been spread out over a number of years, it must be presented as a composite picture rather than as a time-series for any one year. Values integrated from 800 to 1000 m appear to show a pattern considered typical of subtropical regions of a spring high and a late fall and winter low (Fig. 6.21). A similar pattern emerges if data from depth specific tows integrated from 200 m to the surface are used. However, only the April data are substantially higher than other months and there are no data for key months of May, June, and July. Thus, in the northern Sargasso Sea evidence for a coherent seasonal cycle of zooplankton biomass in the upper 1000 m is skimpy at best. Similar conclusions are reached for the Slope Water where extreme variability obscures any underlying seasonal pattern and ontogenetic vertical migrations (migrations associated with the reproductive cycle of the animal i.e. eggs, larvae, and young live at or near the surface and adults live at depth) appear responsible for the apparent seasonal pattern in surface waters.

Using Slope Water time-series data, there appears to be a seasonal enhancement of biomass during the spring within the upper 200 m, but very little evidence for this trend within the upper 1000 m as a whole (Fig. 6.22). Biomass of zooplankton in the upper 200 m of the water column, however, shows fairly pronounced changes although not neccessarily on a seasonal basis (Figure 6.23). While data are not available for a definitive explanation for these differences, ontogenetic shifts in the vertical distribution of dominant copepod species such as Calanus finmarchicus, which come to the surface to spawn in the spring and whose progeny subsequently return to subsurface depths a month or two later, are likely to be responsible in part for the variations in the upper 200 m.

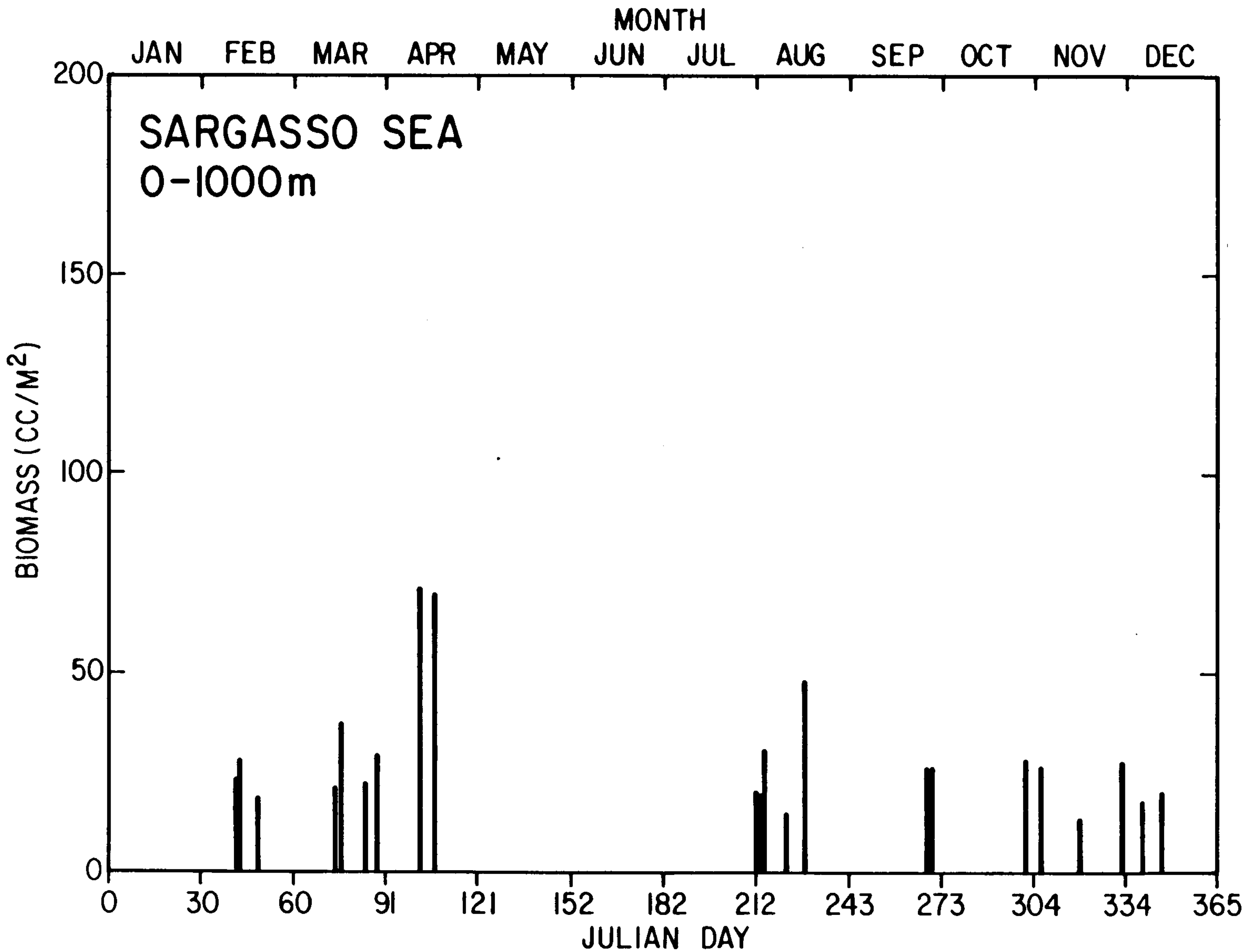


Figure 6.21. Seasonal cycle of zooplankton biomass (displacement volume) in the upper 1000 m of the Sargasso Sea based on tows taken between 1972 and 1982.

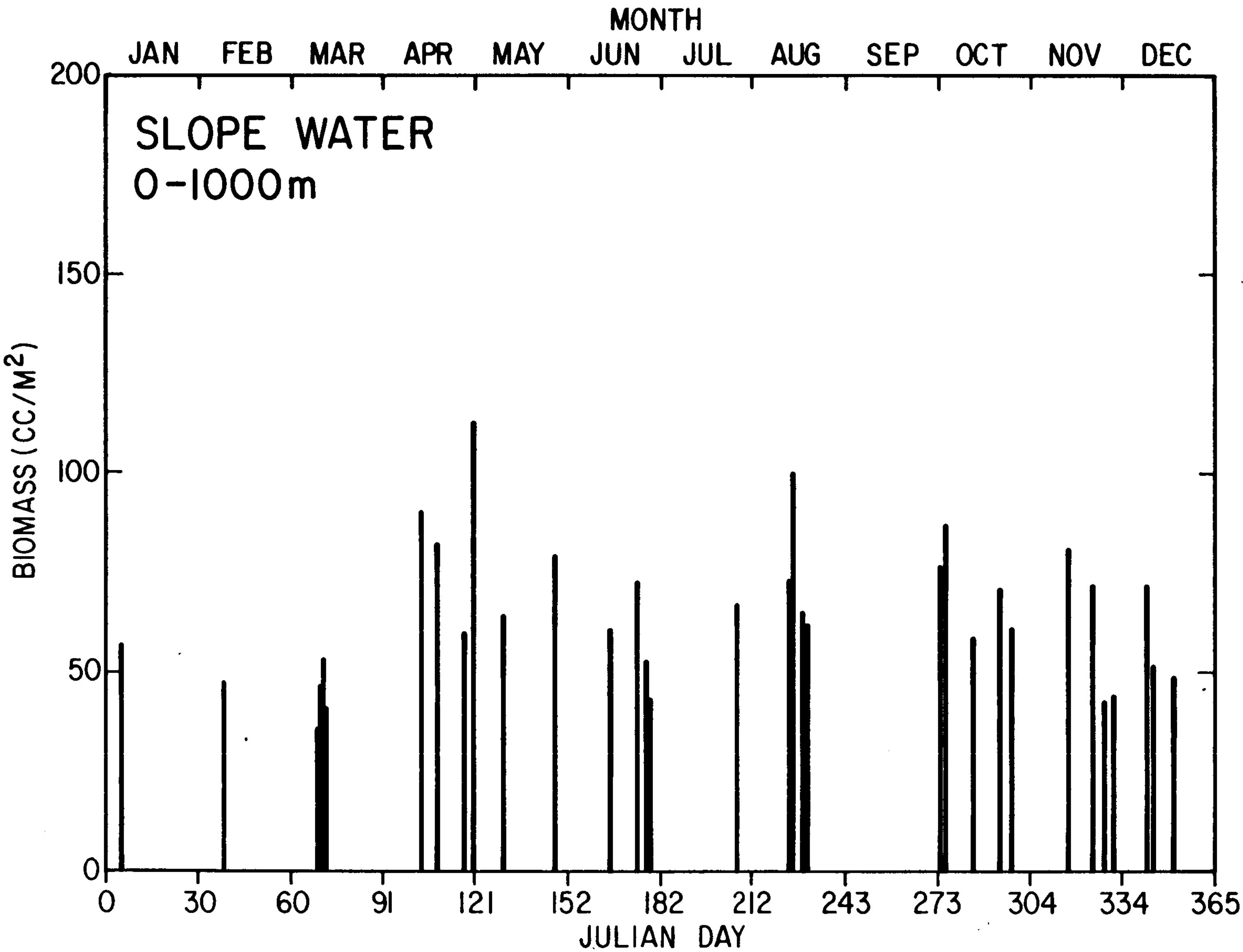


Figure 6.22. Seasonal cycle of zooplankton biomass (displacement volume) in the upper 1000 m from "hydrographically pure" Slope Water based on tows taken between 1972 and 1982.

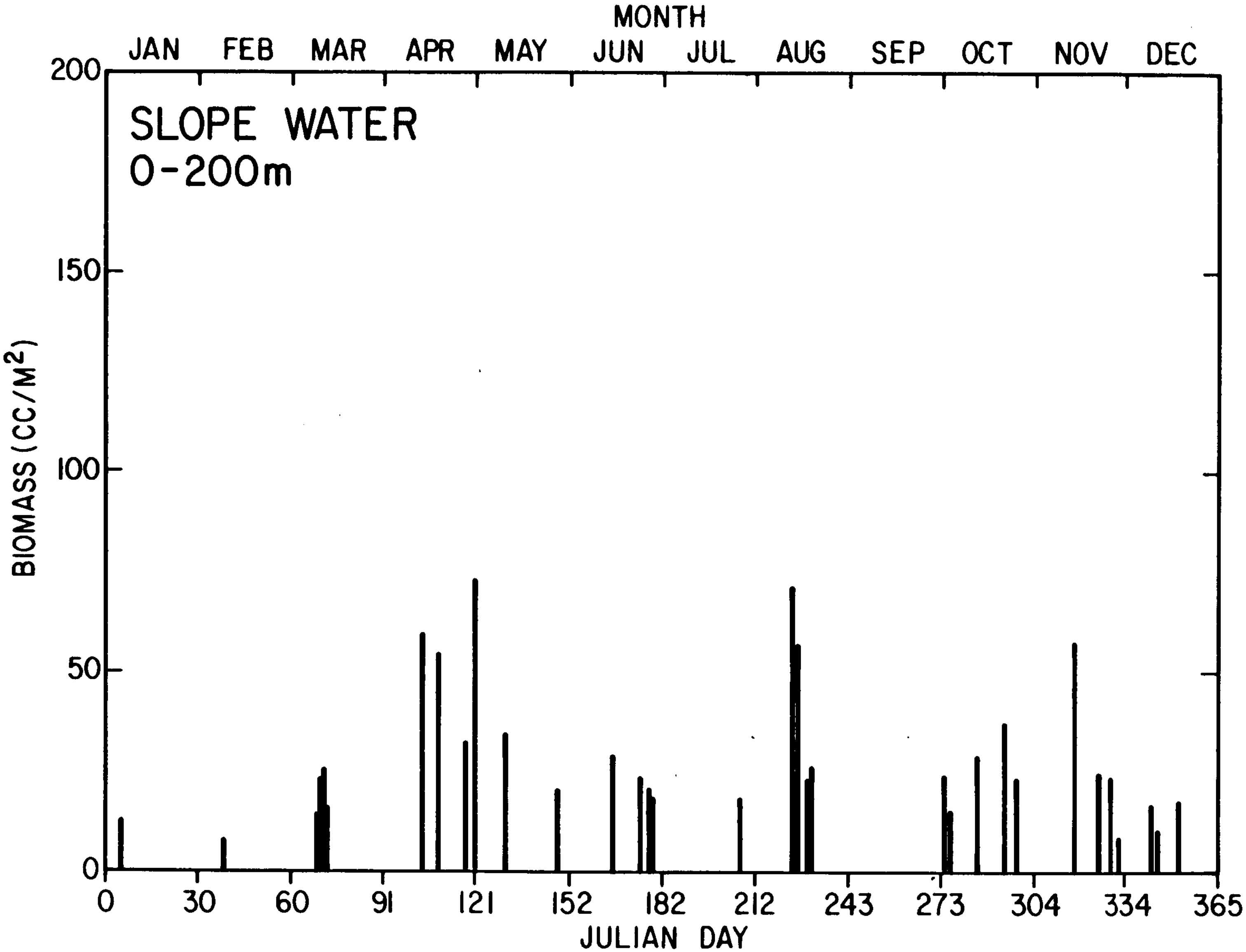


Figure 6.23. Seasonal cycle of zooplankton biomass (displacement volume) in the upper 200 m of the Slope water based on tows taken between 1972 and 1982.

Within the upper 200 m the largest variation observed in this data set between maximum and minimum values is a factor of about eight whereas Clarke (1940) and Grice and Hart (1962) reported variations factors up to 40. Much of the difference can be explained by differences in mesh sizes and tow depths of the nets, but both investigations, without doubt unknowingly, sampled portions of warm-core rings with lower biomass rather than Slope Water.

Clark (1940) and Grice and Hart (1962) found about four-times more zooplankton biomass in the Slope Water than in the Sargasso Sea within the depths they sampled. If Wiebe and coworkers data for the upper 1000 m are compared, the difference is only a factor of 2 or 3. Clark's physical data indicate that some of his samples were taken in cold-core rings rather than in Sargasso Sea water. His high values may have come from these collections thus increasing his estimate of the spread for the Sargasso Sea.

Effect Of Interaction With Shelf Water, Including Seasonal Dependence

In addition to the bias introduced into the seasonal cycle of Slope Water zooplankton by the inadvertent sampling of warm-core rings or Gulf Stream meanders, bias can be caused by the sampling of Slope Water overridden by shelf water. Nutrient rich shelf water can extend out over the Slope Water either as a result of cold-water bulge formation or as part of the entrainment field frequently associated with the presence of warm-core rings. In the former case shelf water can penetrate into the Slope Water as much as 80 km (Wright, 1976; Halliwell and Mooers, 1979; Mooers et al., 1979) whereas in the latter, shelf water can be drawn out and then entrained along the northern edge of the Gulf Stream. Because shelf water is relatively fresh (<34 $^{\circ}/_{\circ\circ}$, it is difficult to mix vertically with the underlying Slope Water; high nutrients and shallow mixed layers appear to give rise to enhanced production throughout the year. It is not certain how shelf water intrusions affect seasonal estimates of zooplankton standing crop.

Effect Of Cold And Warm-Core Rings

The above discussion of seasonal cycles in biomass structure of the Slope Water and Sargasso Sea ignores the significant exchanges of water and biota between these two hydrographic regions as a result of the formation and presence of Gulf Stream rings. Cold-core rings occupy between 10 and 15 percent of the surface area of the northern Sargasso Sea at any given time and warm-core rings can cover as much as 40 percent of the Slope Water. They have, for a significant portion of their existence, a biomass structure and species composition distinctly different from the adjacent Sargasso Sea and Slope Water (Wiebe et al. 1976a; Jahn, 1976; Wiebe, 1976; Ortner 1977; Ortner, 1978; Wiebe and Boyd, 1978; Cox and Wiebe, 1979; The Ring Group, 1981; Wiebe, 1981; Wiebe, Barber and Boyd, in manuscript). By virtue of the distribution of rings, there is in the northwestern Atlantic Ocean, a mosaic pattern of expatriated communities interspersed throughout home-range communities. This pattern is continuously changing because of the horizontal movement of rings and because of hydrographic changes resulting from air-sea interactions and physical exchange processes with adjacent waters which foster change in ring biotic structure towards that of the surrounding water (Wiebe and Flierl, 1983). Thus, rings are responsible for major perturbations in the horizontal and vertical distribution of zooplankton biomass in the upper 800 to 1000 m of the water column.

In the case of cold-core rings, zooplankton biomass in the upper 1000 m is generally higher in the ring core than in the surrounding Sargasso Sea for at least a year after formation. For the five different rings reported by Ortner et al. (1978) and Wiebe et al. (1976), standing stock of zooplankton was from 1.3 to 1.8 times larger. Data from four additional rings support these findings (The Ring Group, 1981).

As much of the work on the biological structure of warm-core rings has occurred recently (Warm-Core Rings Executive Committee, 1982), most of the data have not been published. However, some preliminary information is available about the zooplankton biomass structure of warm-core rings (Wiebe, 1982, Wiebe, Barber, and Boyd, in manuscript). The data were collected on six cruises between September 1981 and October 1982, the four middle ones being to ring 82-B.

Ring 82-B was first sampled in March 1982 about 3 weeks after it was formed. The waters of the ring center were isothermal at 17.7°C from the surface to 330 m and the salinity was 36.6 °/₀₀, indicating winter-mixed northern Sargasso Sea water. By April, winter mixing had cooled the core waters to 15.6 C and had extended the depth of the mixed layer to 440 m. During both of these sampling periods, the total integrated zooplankton biomass per m^2 in the ring center was significantly lower than in adjacent hydrographic regimes giving rise to a negative relationship between biomass and the depth of the 10 C isotherm (Fig. 6.24). Between March and April, biomass increased in ring 82-B by about 50 percent and in the Slope Water by about a factor of three. It is important to point out that in April, a major spring bloom of phytoplankton was taking place in the Slope Water. In the ring core, production and biomass was also high but because the mixed layer was several hundred meters deep (i.e. seasonal stratification had not yet occurred in the ring) concentrations of phytoplankton were much lower than in the Slope Water.

Data for June indicate a major change. Between April and June, the ring surface waters had warmed sufficiently to form a shallow mixed layer and seasonal thermocline. Ship of opportunity observations in May showed sharp increases in phytoplankton biomass concentration in the ring. Levels were still high in June whereas in the Slope Water levels decreased. In June, zooplankton biomass was higher in the ring than in the Slope Water giving rise to a significant positive relationship between biomass and depth of the 10 C isotherm (Fig. 6.25).

During July, the ring underwent at least one interaction with the Gulf Stream during which it lost a considerable portion of its mass (Joyce et al., in press) At the beginning of the sampling period in August, Gulf Stream meander swept over part of the ring to depths of at least 75 to 100 m. The biomass in ring 82-B, while higher in August than in June, was non-significantly lower than in the Slope Water (Fig. 6.25). However, variability in the Slope Water was extreme with the jellyfish, Pelagia pelagia, dominating one Slope Water station and strongly affecting the estimates of the Slope Water zooplankton mean state. During this cruise, the Sargasso Sea and Gulf Stream were also sampled. Ring 82-B biomass was substantially higher than at either of these locations (Fig. 6.25).

In a comparison of the evolution of zooplankton standing crop in cold and warm-core rings, one fact stands out. Elevation of biomass in warm-core rings can take place much faster than the decline in biomass in cold-core rings to Sargasso Sea levels. This is probably a result of higher frequency of interactions that warm-core rings undergo with the Gulf Stream and continental shelf waters.

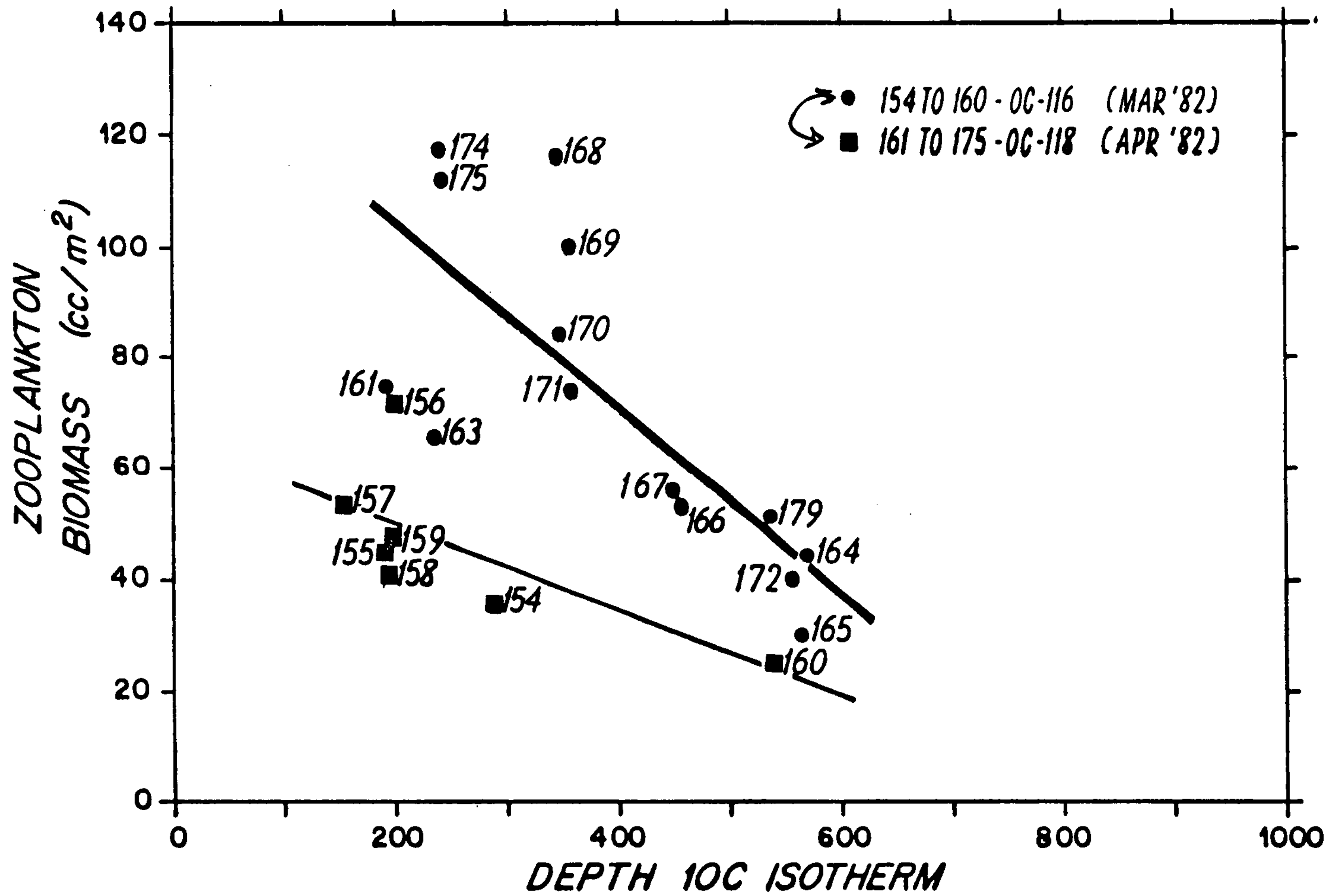


Figure 6.24. Relationship between zooplankton biomass (displacement volume) and the depth of the 15°C isotherm based on transect sampling from the center of warm core ring 82-B to the Slope Water in April and June 1982 (from Wiebe, Barber, and Boyd, in preparation).

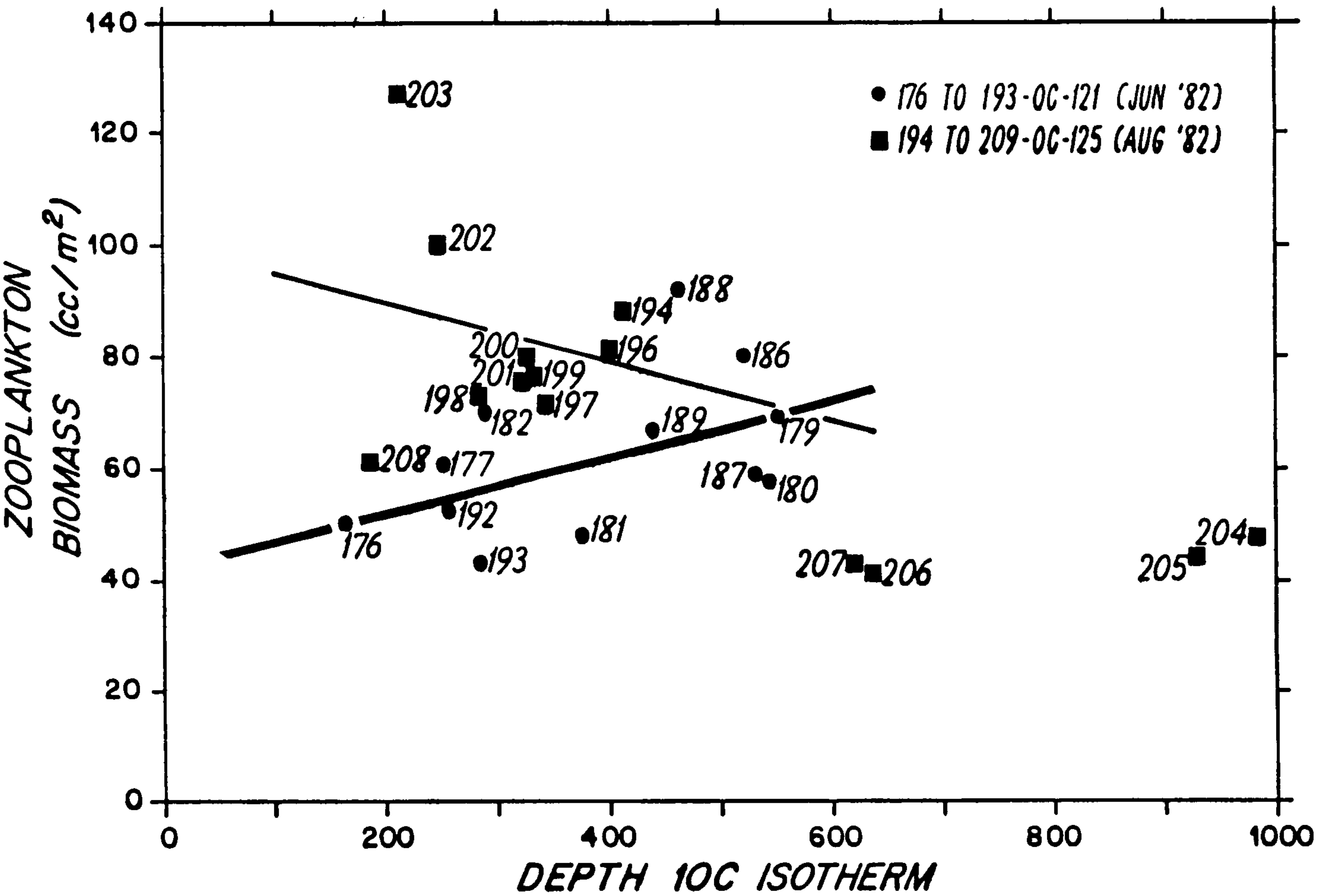


Figure 6.25. Relationship between zooplankton biomass (displacement volume) and the depth of the 15°C isotherm based on transect sampling from the center of warm core ring 82-B to the Slope Water in June and August 1982 (from Wiebe, Barber, and Boyd, in preparation). Tows 204 and 205 taken in the northern Sargasso Sea and 206 and 207 taken in the Gulf Stream were not used in the regression analysis for August.

Vertical Distribution

Typical Distribution

The literature contains only a few quantitative studies of the vertical distribution of zooplankton biomass in the study area portion of the northwestern Atlantic Ocean. Sampling below 300 m was rare until the mid-1970's when a fairly extensive sampling program in the upper 1000 m of this area was begun by Wiebe and co-workers using MOCNESS. There are currently five different MOCNESS systems designed for capture of different size ranges of zooplankton and micro-nekton. Each system is designated according to the size of the net mouth opening and in one case the number of nets it carries.

The distribution of biomass vertically throughout the upper 1000 m of the study area is not uniform with depth (Fig. 6.26 and 27). Because of the extreme variability in the Slope Water, it is difficult to describe quantitatively a typical biomass profile. However, zooplankton biomass is generally highest at night in the upper 100 to 200 m in both the Slope Water and Northern Sargasso Sea. Values typically range between 50 and 500 cc/1000 m^3 in the Slope Water and between 15 and 400 cc/1000 m^3 in the Sargasso Sea (Ortner et al., 1978; Wiebe, 1981; Wiebe, Barber and Boyd, in manuscript). In the Slope Water, there is often a substantial subsurface peak in biomass between 300 and 600 m (up to 200 cc/1000 m^3) which is not evident in the Sargasso Sea. Extreme deviations from the typical pattern occur in the Slope Water as a result of blooms of salps or jellyfish. Wiebe et al. (1979) documented a massive population explosion of the salp, *Salpa aspera*, over a substantial portion of the western Slope Water. This species dominated the zooplankton biomass in August 1975 and was still present in substantial numbers in November 1975. Vertical diel migrations during the August sampling period were from the upper 25 m of the column to depths of 600 to 800 m, and sometimes to below 1000 m.

Seasonal Changes In Zooplankton Biomass

A brief description of seasonal changes in vertical biomass structure in the Slope Water and northern Sargasso Sea is given below, but no systematic study of this subject has been published to date.

Effects Of Interaction With Shelf Water

There is very little published information that relates directly to the biomass structure of shelf water overriding the Slope Water, but samples were taken in 1981 and 1982 as part of the Warm-Core Rings Program. Once they are worked up, they should provide the data necessary to evaluate the effect of such intrusions.

Effects Of Cold And Warm-Core Rings

Highest biomass occurs near the center of a cold-core ring and usually declines on the flanks. However, in ring 'Bob' , within and below the region of intense circular currents, a zone of low biomass was evident at intermediate depths on both sampling occasions (Fig. 6.28). Because the Gulf Stream supports a lower standing crop of zooplankton than either the northern Sargasso Sea or the Slope Water for a portion of the year, this unusual feature may have been introduced at the time of ring formation, or it may have resulted from the strong interaction with the Gulf Stream at age 2 months (The Ring Group, 1981).

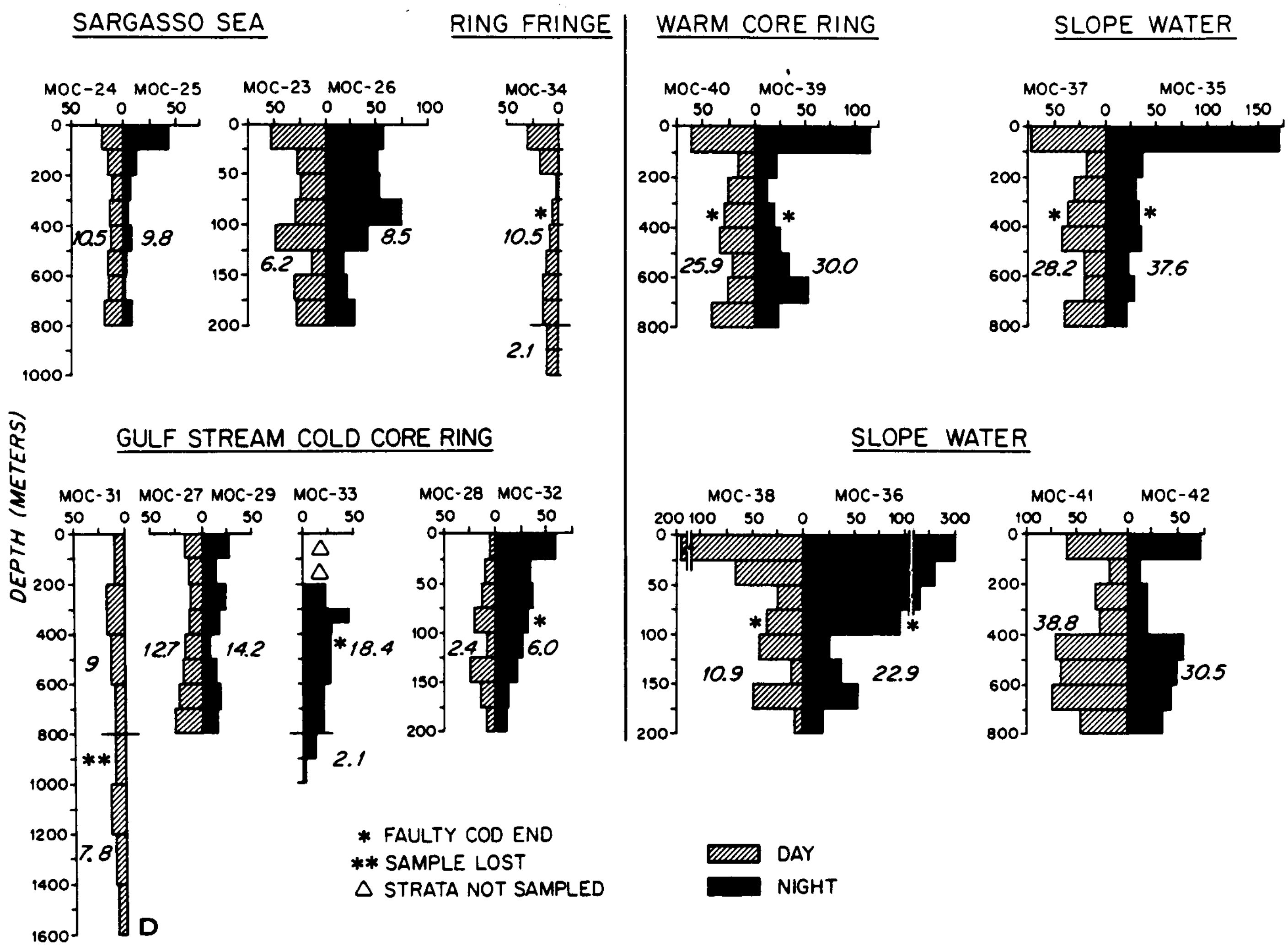


Figure 6.26. Slope Water ring and Sargasso Sea zooplankton biomass cm^3 $1000\ m^{-3}$ November 1975 KNORR cruise 53. Values associated with each profile are cubic centimeters per square meter for the water column sampled except for MOC-31, MOC-33 and MOC-34 where values have been calculated for above and below 800 m. Note that 0-200 m profiles have an expanded vertical depth scale. From Ortner et al., 1978.

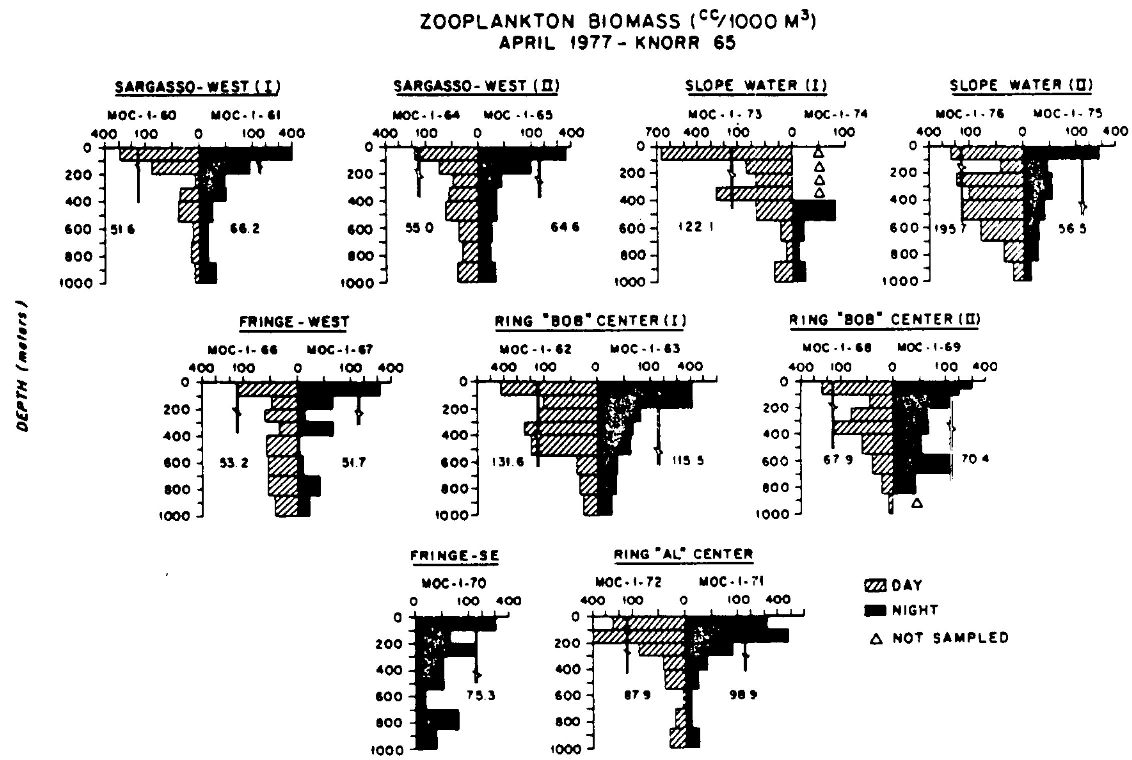
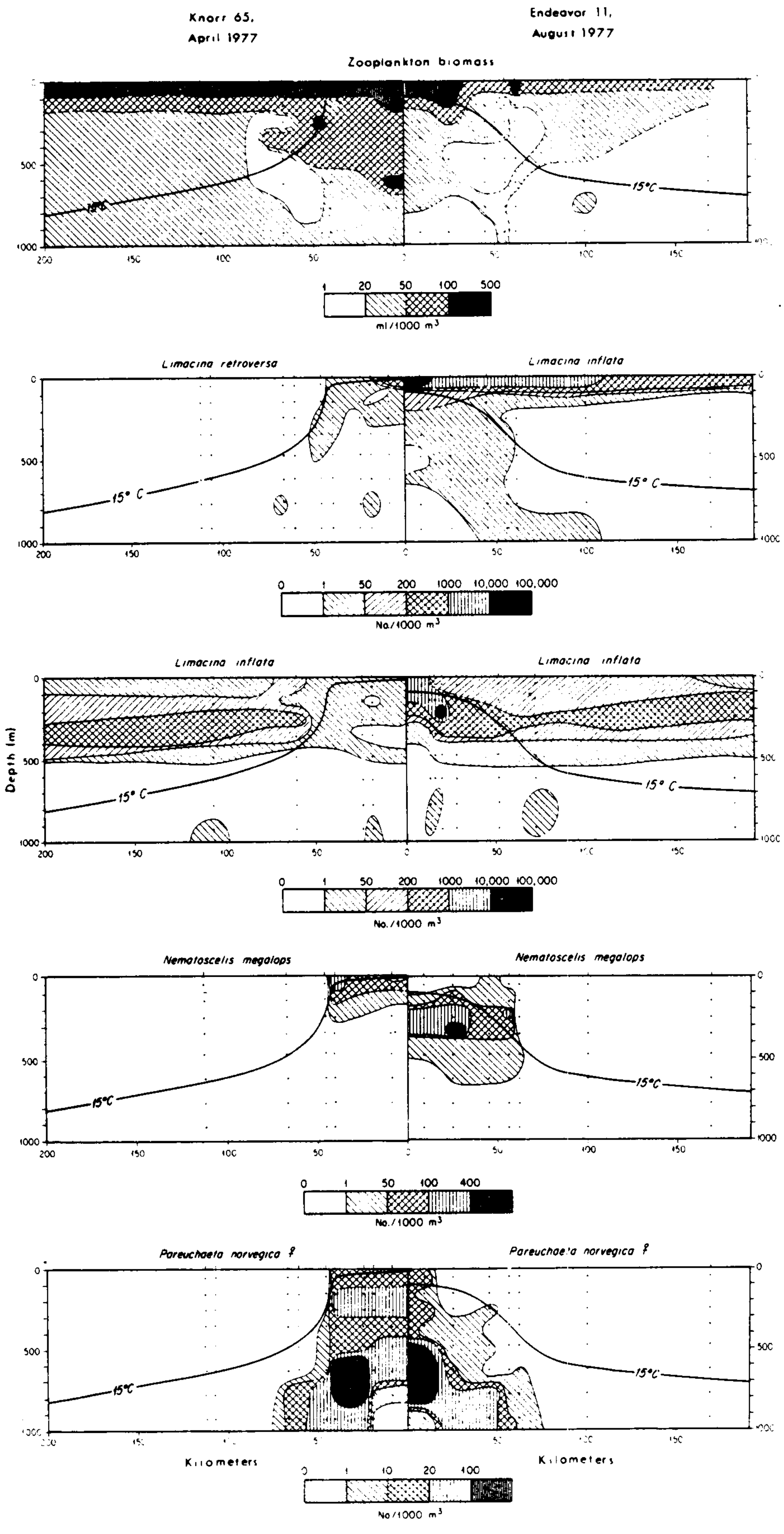


Figure 6.27. Vertical distribution of zooplankton biomass (measured as displacement volume) in the Sargasso Sea, Gulf Stream cold core rings "Bob" and "Al", and the Slope Water. The samples were obtained with a MOCNESS fished obliquely from 1000 m to the surface and equiped with 9 nets which were open and closed sequentially (see Wiebe et al., 1976b for details). The station denoted "Sargasso-West (II)" was actually taken in the Gulf Stream west of ring "Bob". The number appearing to the left or right of each profile is the integrated biomass in the upper 1000 m i.e. it's the biomass m^{-2} to 1000 m. From Wiebe, 1981.

Figure 6.28 Vertical sections of zooplankton biomass [measured as displacement volume (55)] and the abundance of warm-water (Limacian inflata) and cold-water (Nematoscelis megalops, and Pareucnaeta norvegica) zooplankton indicator species from the center of ring Bob out to 150+ km for April 1977 (left) and August 1977 (right). Collections were made with a MOCNESS; the solid dots denote the center of the oblique portion of the tow taken with one of eight nets. The ring extended out to about the 80-km mark as indicated by the depth of the 15°C isotherm; beyond was the Sargasso Sea. The cold-water pteropod Limacina retroversa already had disappeared from rign Bob by August. The left-right pair for L. inflata show daytime distributions. The vertical pair allows a day (above)-night (below) comparison for August and shows diel vertical migration. By August Nematoscelis and Pareuchaeta had become less abundant and lay deeper in the water column. From the Righ Group (1981).



Knorr 65, April 1977
Endeavor 11, August 1977
Zooplankton biomass
ml/1000 m³
Limacina retroversa
Limacina inflata
No./1000 m³
Limacina inflata
Limacina inflata
Depth (m)
Nematoscelis megalops
Nematoscelis megalops
Pareuchaeta norvegica ♀
Pareuchaeta norvegica ♀
15°C
Kilometers
Kilometers

Another feature in most cold-core rings is that an unusually large proportion of the biomass is found between depths of 200 and 1000 m compared to the Sargasso Sea. There are times when older rings have significantly less surface layer (0-200 m) biomass than the surrounding waters and the generally higher ring standing crop is due entirely to the larger subsurface biomass. This was the case of cold-core ring D which was sampled at ages 6 and 9 months (Ortner et al., 1978); the percent of 0-800 m biomass in the upper 200 m for the Sargasso Sea and ring D in August were 51% and 27%, and in November were 45% and 25%.

The relationship between the deep chlorophyll maximum (DCM) and epizooplankton biomass and abundance distributions in the Sargasso Sea, cold-core ring D and the Slope Water was examined by Ortner et al. (1980) during summer and fall 1975. Total zooplankton biomass was significantly enhanced in or adjacent to the seasonal thermocline in all three hydrographic regimes. The DCM in these regions was also predictably associated with the seasonal thermocline, thus giving rise to a significant correlation between zooplankton biomass and the DCM.

In addition to measuring total biomass, Ortner et al. (1980) counted a number of categories of functional zooplankton groups in the Clarke-Bumpus samples: large copepods >1 mm, medium copepods 0.5-1 mm, small copepods, copepodites, nauplii, large ostracods > 0.5 mm, euphausiids, coelenterates, chaetognaths, larvaceans, amphipods, polychaetes, mysids, decapods, molluscs, dinoflagellates, foraminifera, and tintinnids.

In August, the distribution patterns of particular zooplankton functional groups or taxa were consistent with those of zooplankton biomass in the three areas. In general, for the northern Sargasso Sea, medium copepods, larvaceans, the copepod development stages listed above, molluscs, chaetognaths, and tintinnids were concentrated in the 75-100 m depth interval, i.e. DCM depths. Other groups were concentrated near the surface or were too variable to be categorized. Variations to this pattern were evident in the Slope Water and ring D.

Fall mixing substantially changed the vertical temperature and salinity structure of the upper water column, largely erasing the DCM in the Slope Water and Ring D, but not in the Sargasso Sea. In the latter region, there was still a subsurface peak in biomass around the base of the seasonal thermocline and nearly all functional groups had distributions centered on the DCM which was still present. In ring D, although the DCM was not evident and subsurface peak in zooplankton biomass was very small, many of the functional groups had nocturnal peak abundances at the sharpened thermocline. In the Slope Water, zooplankton biomass was concentrated at or near the surface, yet some groups (for example, tintinnids, nauplii, and medium copepods) still showed enhanced numbers at the permanent thermocline.

For warm-core rings, the vertical biomass structure has been examined in more detail. Again, the focus is on ring 82-B. In April, when the ring was 2 months old, the median (50%) depth of biomass in the ring center was below 200 m whereas in the Slope Water it was about 50 m (Fig. 6.29). The transition between the distribution in the ring core and the Slope Water was abrupt and coincided with the changes in the vertical temperature and salinity structure. A similar pattern is evident in the daytime data except that cumulative percentage biomass depths were 50 to 100 m deeper.

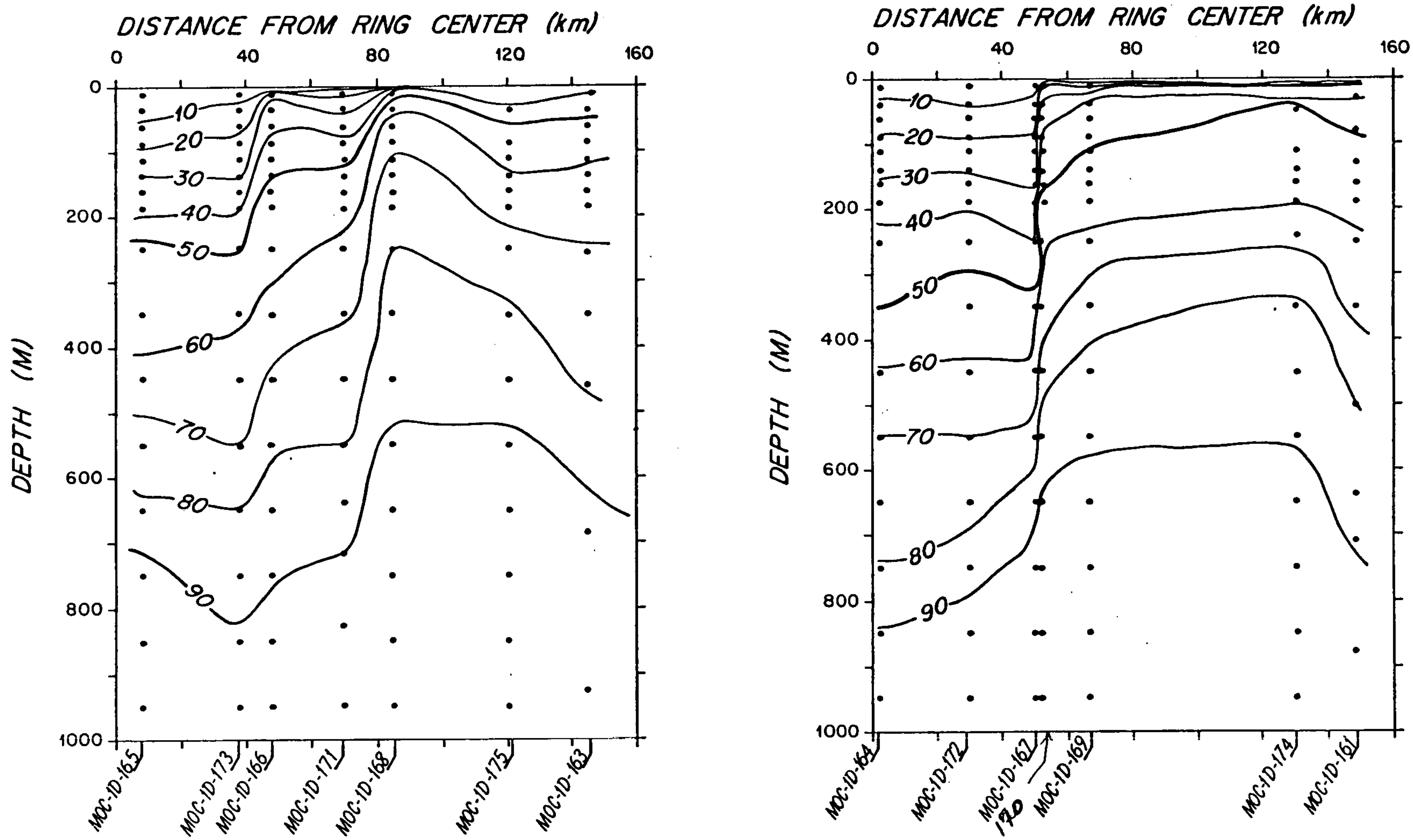


Figure 6.29. Cumulative percent of zooplankton biomass collected with MOCNESS night (left) and day (right) tows taken in the upper 1000 m plotted as a function of depth and jdistance from te center of ring 82-B in April 1982. From Wiebe, Barber, and Boyd, (in preparation).

The night and day sections for June (ring age 4 months) show a dramatic shift (Fig. 6.30). The median biomass depth shoaled to between 100 and 200 m in the ring core and deepened to between 200 and 300m in the Slope Water. The night data are more complete, but the trend is evident in the day data as well. The August data (ring age 6 months) show similar vertical distribution of biomass at night in both Slope Water and ring, and a fairly deep (>200 m) median depth of biomass (Fig. 6.31). Similar distributions were found in the Sargasso Sea and Gulf Stream during this cruise. Except for the anomolous catch at the day Slope Water station furthest from the ring, where the jellyfish Pelagia pelagia dominated, daytime distributions were deeper by 100 to 200 m.

Diel changes in vertical biomass distribution with distance from ring center can be observed more clearly if the median depths of the biomass versus tow position in the ring are plotted (Fig. 6.32). The April data show the contrast in vertical distribution between the ring center and the Slope Water described above. Generally the diel shift upward in median biomass depth is 100 m or less. In June, except for the very deep median biomass depth on the ring edge which gave rise to a high vertical day/night biomass shift, the day/night differences were 100 m or less. In August, median biomass depths were fairly uniform across the entire region except for the day/night pair where the day tow was dominated by P. pelagia (Fig. 6.32).

The evolution of biomass as a warm-core ring ages can be compared with that in cold-core rings and in the Sargasso Sea. As described above, the median depth of biomass in ring 82-B at night started out deep (400 m) in March and progressively shoaled through June (Fig. 6.33). In August there was a downward shift due in part to interactions with the Gulf Stream. Day biomass was distributed generally less than 100 m deeper than at night. The cold-core ring data show the opposite trend (Fig. 6.34). Young rings can start out with a relatively shallow median biomass which then proceeds to deepen with increasing age. The diel shift in biomass in cold-core rings is larger than in warm-core rings; the delta averages approximately 200 m.

Vertical distribution of biomass in Slope Water from the cold-core ring cruises is similar to that obtained on the warm-core ring cruises (Fig. 6.35). Median biomass depth is shallowest in April; diel shifts in biomass are similar and generally 100 m or less in magnitude. The distribution of biomass at night in the Sargasso Sea is no deeper and often shallower than in either the warm or cold-core rings or the Slope Water (Fig. 6.36). Furthermore, there is a stronger diel migration pattern in the Sargasso Sea, with daytime median biomass 150 to 250 m below the nightime level.

Several conclusions can now be drawn about the biomass structure of warm core rings. 1) The vertical distribution of zooplankton biomass was substantially deeper in the core of ring 82-B than in the adjacent Slope Water during the ring's first several months. In addition, biomass concentrations in this ring were significantly lower. 2) There was a dramatic upward shift in the median depth of zooplankton biomass which occurred after the spring bloom in both the Slope Water and the ring. However, ring 82-B lagged a month or two behind the Slope Water in both of these patterns. In the Slope Water, the shoaling and subsequent submergence is believed associated in part with ontogenetic migrations of species such as Calanus finmarchicus. Ontogenetic migrations did not seem a factor in the biomass shift in ring 82-B. 3) Generally, diel shifts in biomass were substantially lower in warm-core ring 82-B and the Slope Water than in cold-core rings and the Sargasso Sea. 4) The pattern of biomass evolution in warm-core rings appears to be distinctly different from that observed in cold-core rings, the Slope Water, and the Sargasso Sea.

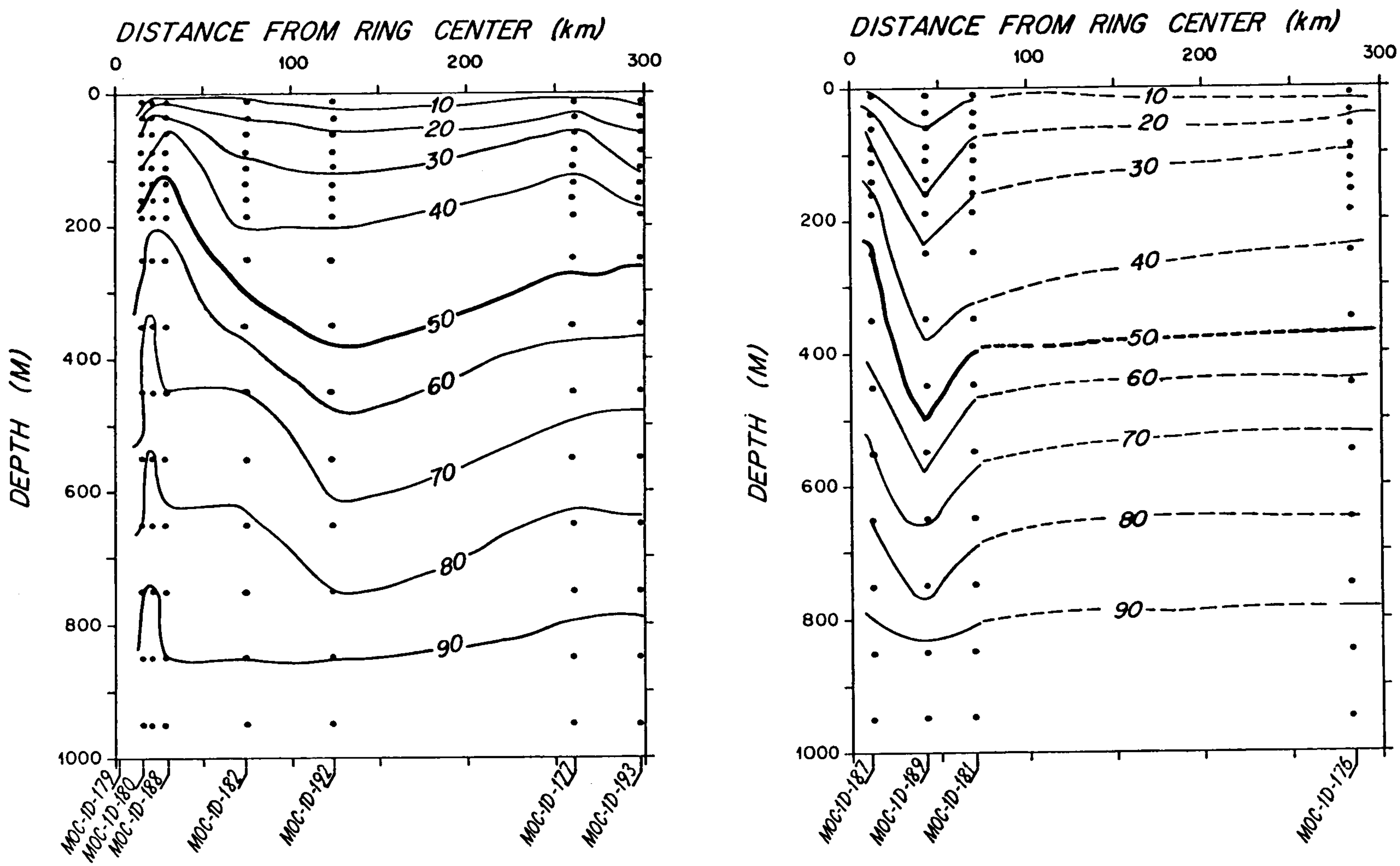


Figure 6.30. Cumulative percent of zooplankton biomass collected with MOCNESS night (left) and day (right) tows taken in the upper 1000 m plotted as a function of depth and distance from the center of ring 82-B in June 1982. From Wiebe, Barber, and Boyd (in preparation).

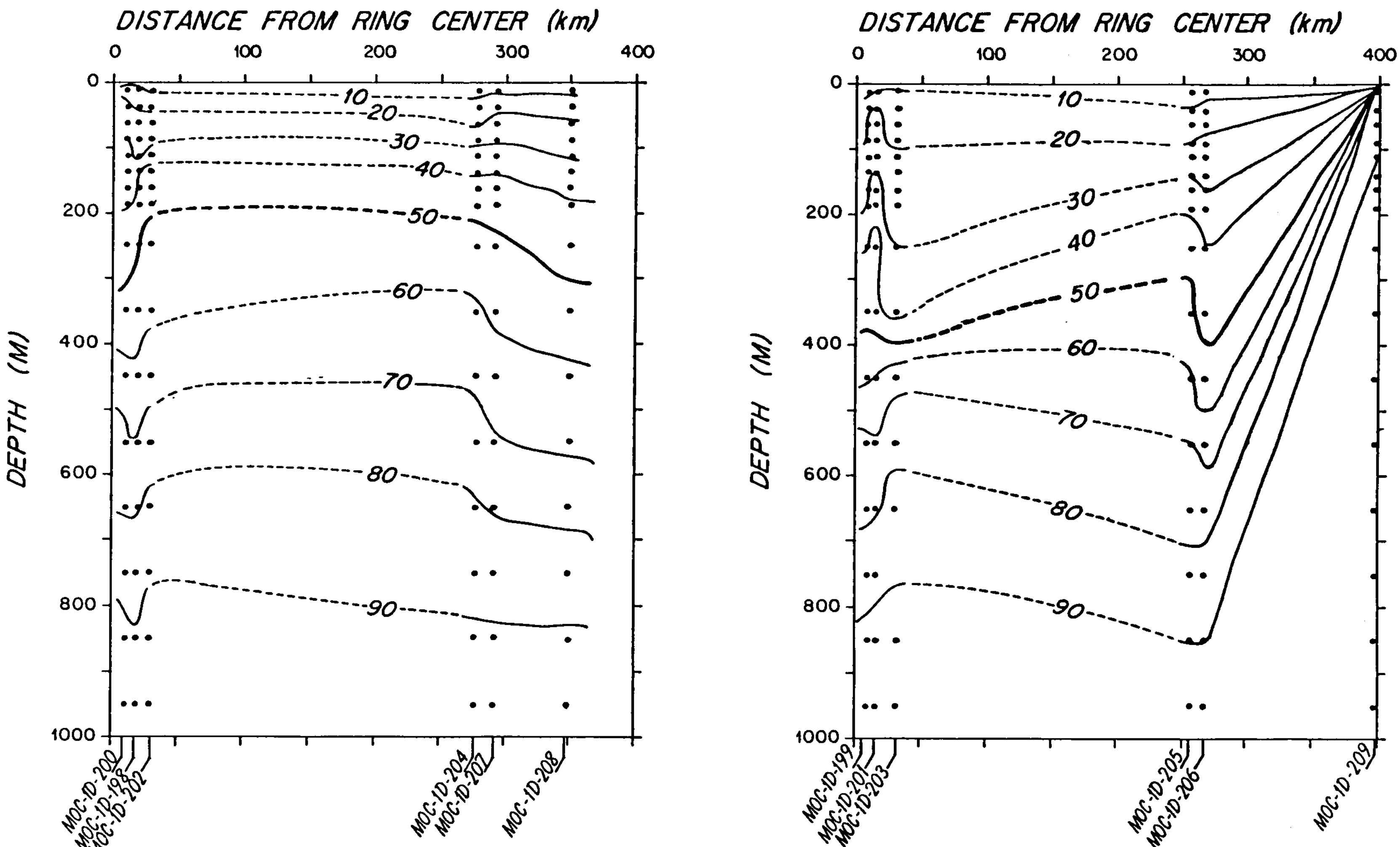
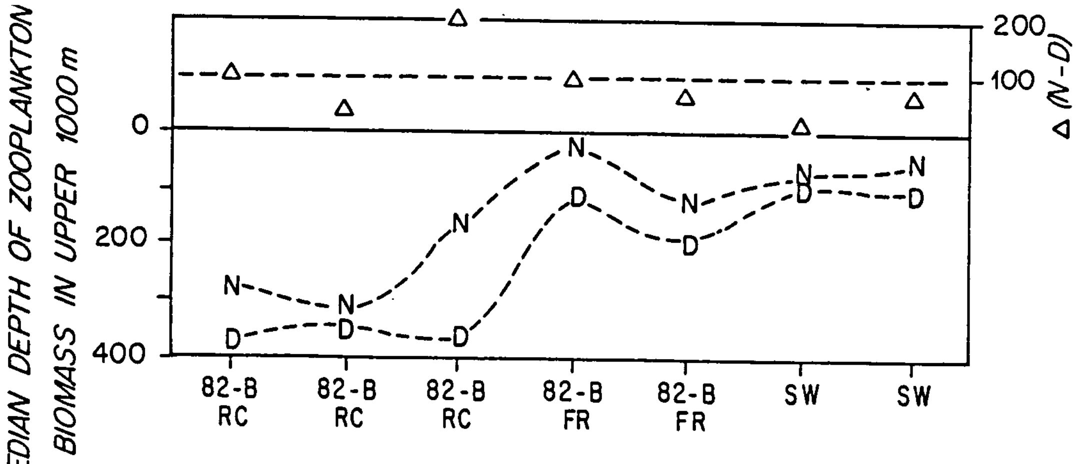


Figure 6.31. Cumulative percent of zooplankton biomass collected with MOCNESS night (left) and day (right) tows taken in the upper 1000 m plotted as a function of depth and distance from the center of ring 82-B in August 1982 (from Wiebe, Barber, and Boyd, in preparation). Note that tows 204 and 207 are from the Sargasso Sea and Gulf Stream respectively.

Figure 6.32 Day and night median depth of zooplankton biomass in the upper 1000 m and the difference between day and night medians plotted as a function of position from the center of righ 82-B in April June and August 1982 (from Wiebe, Barber, and Boyd, in preparation). N = night, D = day, RC = ring center, Fr = ring fringe, RE = ring edge, ENTRAINMENT = ring entrainment field, SW = Slope Water, GS = Gulf Stream, SS = Sargasso Sea.



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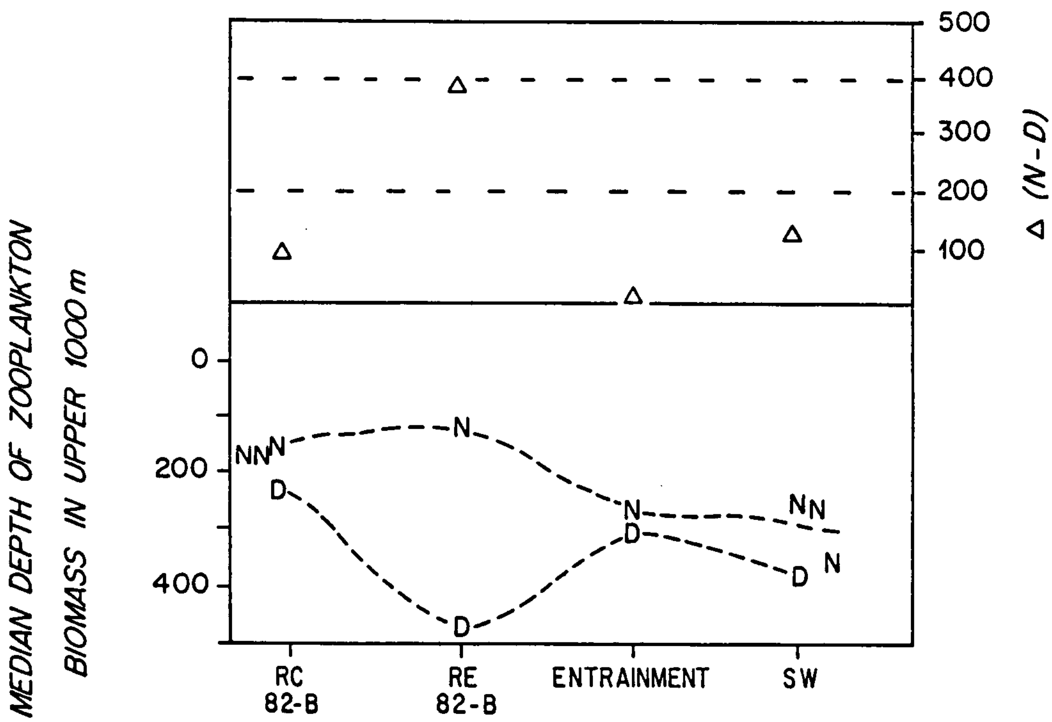

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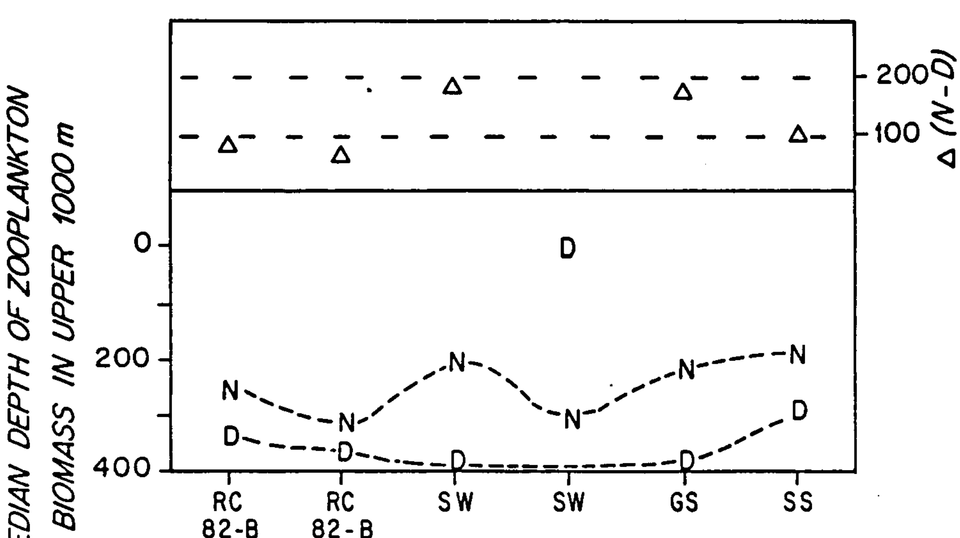

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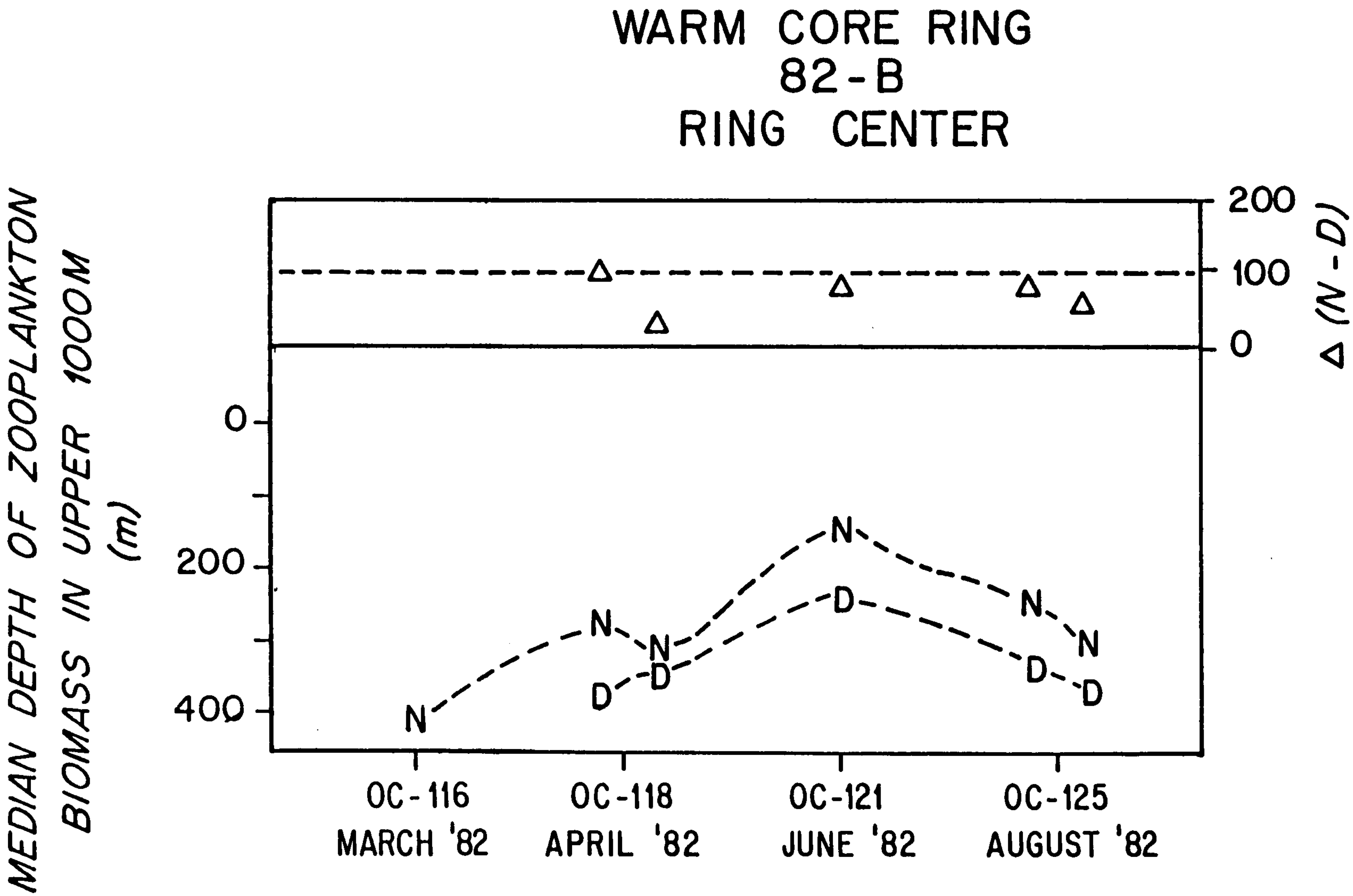


Figure 6.33. Ring 82-B center day and night median depth of zooplankton biomass in the upper 1000 m and the difference between day and night medians plotted for the four time-series cruises (from Wiebe, Barber, and Boyd, in preparation). N = night, D - day.

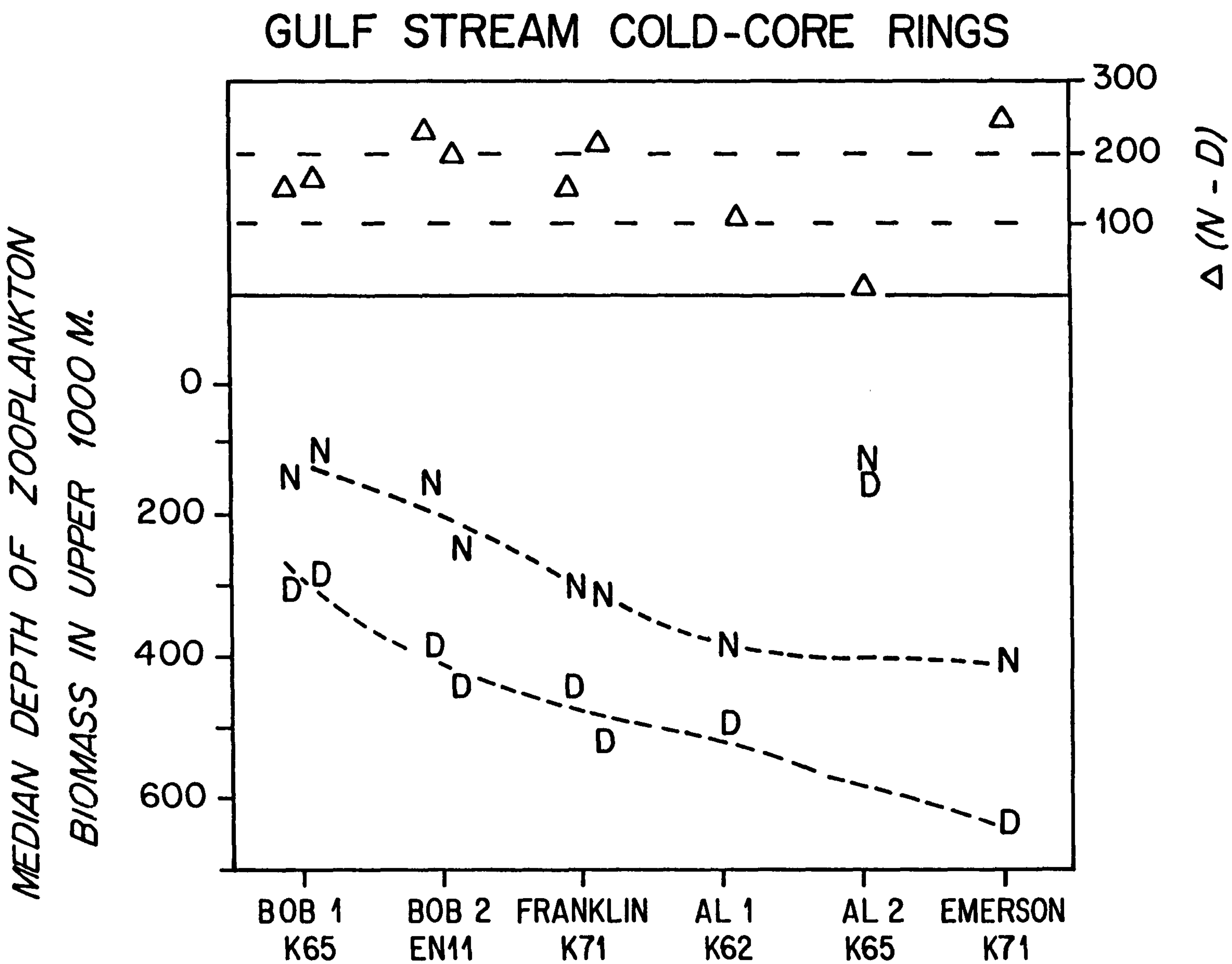


Figure 6.34. Cold-core ring Day and night median depth of zooplankton biomass in the upper 1000 m and the difference between day and night medians plotted for rings sampled in 1976 and 1977 (from Wiebe, Barber, and Boyd, in preparation). N = night, D = day.

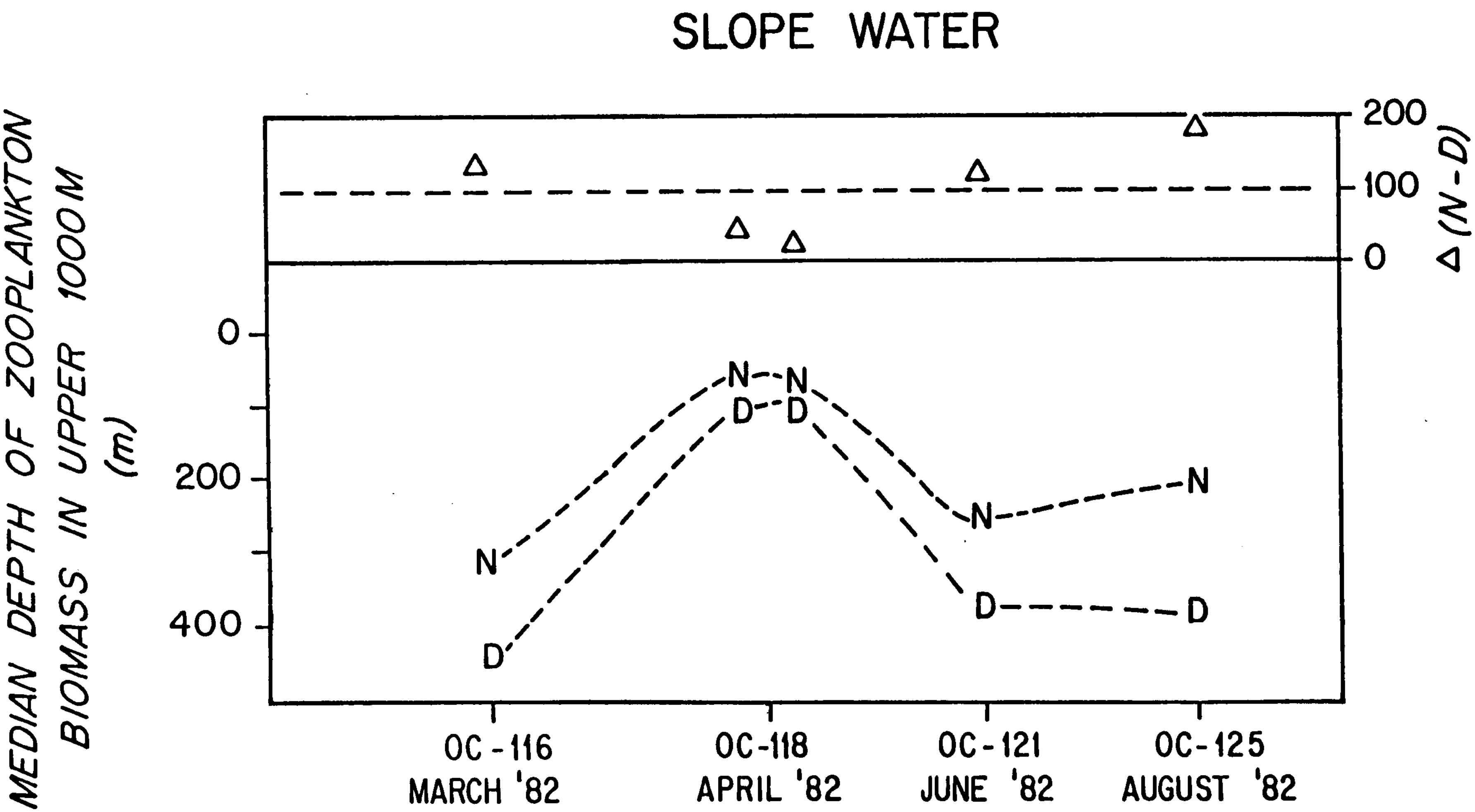


Figure 6.35. Slope Water day and night median depth of zooplankton biomass in the upper 1000 m and the difference between day and night medians plotted for the four time-series cruises of 1982 (from Wiebe, Barber, and Boyd, in preparation). N = night, D = day.

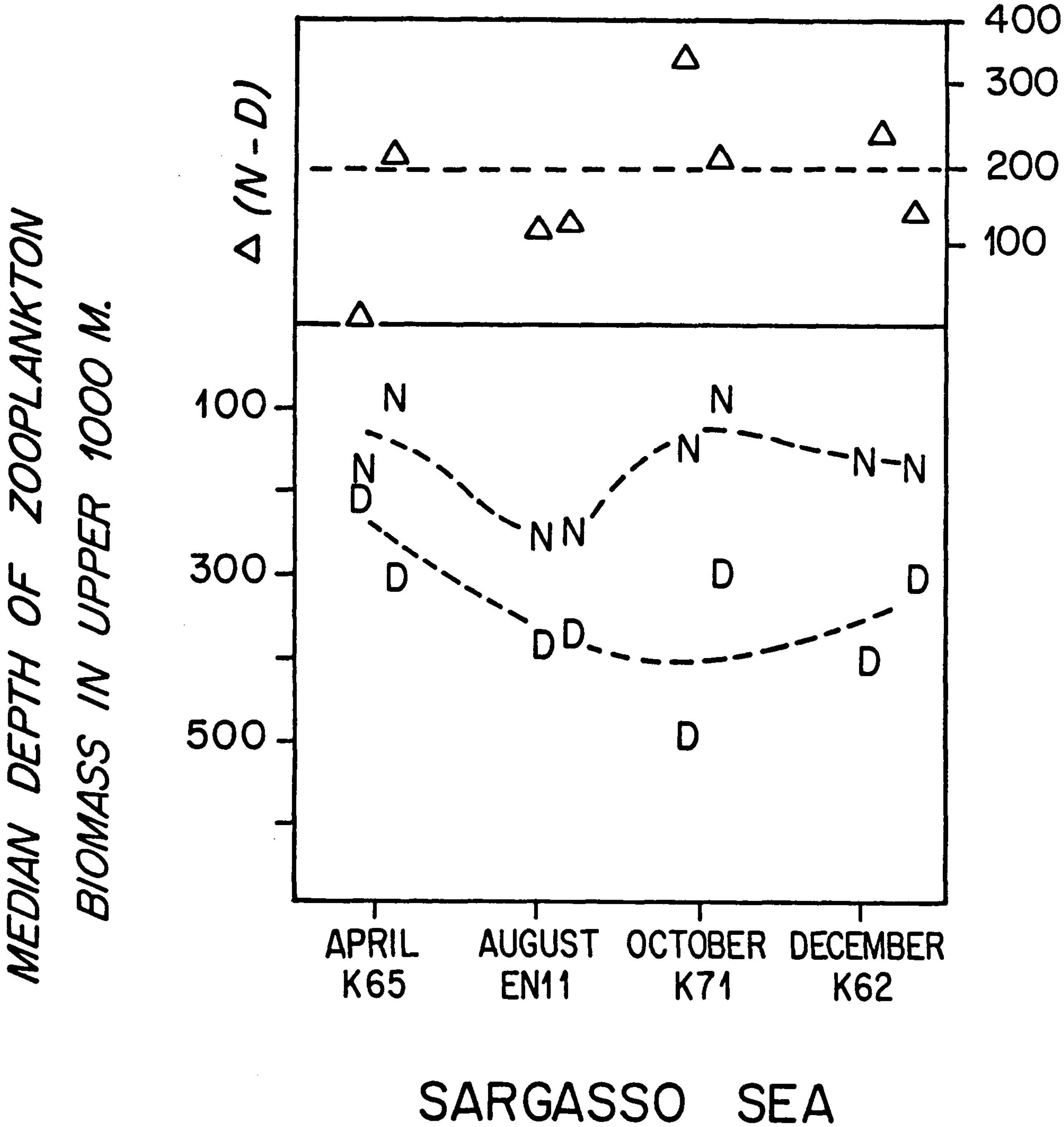


Figure 6.36. Sargasso Sea day and night median depth of zooplankton biomass in the upper 1000 m and the difference between day and night median plotted for the cruises of 1976 and 1977 (from Wiebe, Barber, and Boyd, in preparation). N = night, D = day.

SPECIES COMPOSITION

Measurement

Information about species composition of zooplankton in the ACSAR area comes exclusively from counts of individuals of particular species in samples collected principally with nets. Counts are usually made with the aid of a microscope. Errors associated with various counting techniques (Venrick, 1971; Longhurst and Seibert, 1967; McGowan, 1971; Cheney, 1982) account for a wide range in values. Patchiness of zooplankton may also cause large differences between successive tows taken at a single station (Wiebe, 1971; Haury and Wiebe, 1982).

Unlike sampling errors induced by patchiness, which is essentially unbiased, avoidance of towed nets by organisms is a major source of underestimation in zooplankton abundance measurements. This factor is perhaps the most important determinant of the accuracy of abundance estimates for some of the larger zooplankton species. However, field population size-frequency distributions probably are not materially affected by avoidance although abundance estimates clearly are; for most species of euphausiids and many copepods, chaetognaths, and pteropods there was no evidence of differential day/night avoidance (Wiebe et al., 1982).

Principal Groups and Relation to Biogeographic Provinces

A general discussion of the biogeographic patterns in the ACSAR area has been given above. Only the previous work of Grice and Hart (1962) includes counts of the vast majority of species which occurred in their samples thereby enabling a comparison of the relative importance of major taxonomic groups of the zooplankton. Dominant taxa include copepods, amphipods, chaetognaths, euphausiids, thecosomes, ctenophores, cnidaria, and thaliacia. Species of gelatinous zooplankton are generally under-represented because many species are damaged beyond recognition in nets or disentegrate in the preserving fluid (Harbison et al., 1978). Chenoweth (1978) has summarized what is known about the zooplankton species composition in most of the study area up to the mid-1970's. This review will dwell mainly on work published recently.

Horizontal Distributions

Typical Seasonal Distributions

There is very little good seasonal data on the abundance, reproductive capacity or timing, size frequency distribution, and the rate of individual growth for the vast majority of the species in the survey area. Point source sampling off Miami by Stepien (1980) provides an update of studies of plankton of the Florida Current by Pierce (1951), Moore (1953), Moore et al (1953), Miller et al. (1953), Lewis (1954), Moore and Corwin (1956), Moore and O'Berry (1957), Pierce and Wass (1962), and Wormelle (1962). But Stepien's sampling, although providing some seasonal coverage, was designed to look at reversals in the deep flow of the Florida Current; seasonal fluctuations in abundance can not be readily determined from her data.

Wormuth (1981) and Cheney (1982) examined some of the samples taken with the 9-net MOCNESS-1 by Wiebe and coworkers (described above), which provide seasonal patterns in abundance. Wormuth studied the vertical distribution and seasonal variation of nine of the most abundant or most frequently occurring pteropods in the northwest Sargasso Sea using 14 tows to 1000 m and 5 tows to

200 m. Variability in abundance was so great that he found that none of the seasonal patterns was significant although five of the nine species had highest values in the spring and one had highest values in the summer.

Cheney (1982) identified 21 species of chaetognaths from 52 9-net MOCNESS-1 tows in the Slope Water (18 tows), Northern Sargasso Sea (18 tows), Gulf Stream (2 tows), and Gulf Stream rings (14 tows). Many tows were those used by Wormuth (1981). Three species (S. elegans, S. hispida, S. megalophthalma) were rarely collected and were not statistically analyzed for seasonal cycles. For the remaining 18 species, mean abundances in the above hydrographic regimes (Table 6.20) showed major differences between the Slope Water and northern Sargasso Sea for all but 2 of these species. The exceptions were S. enflata and K. pacifica. The latter was one of the least abundant of chaetognaths in the collections, while S. enflata was one of the most widespread and abundant. Seven species were most abundant in the Slope Water, while nine were most abundant in the northern Sargasso Sea. In the Gulf Stream collections, abundances of chaetognaths were between those observed in the Slope Water and northern Sargasso Sea, although species composition was more similar to the northern Sargasso Sea fauna (percent similarity 59-80%) than the Slope Water fauna (36-54%). The Gulf Stream is, however, a gradient region and similarity with other hydrographic regimes depends to a large extent on the placement of the tows within the gradient.

Cheney (1982) also examined seasonal pattern in integrated numbers (0-1000 m) of individuals of each species (Figure 6.37) Two species, S. hexaptera and S. serratodentata, showed significant seasonal fluctuations in the Slope Water. However, with 17 species such a result is probable at the 0.21 level, so Cheney concluded that there was no evidence for seasonal change in chaetognath numbers in the Slope Water. On the other hand, 7 of the 17 species had significant shifts in seasonal abundance in the Northern Sargasso Sea and the probability of this was <.00001, indicating that these shifts were indeed significant. Highest values occurred in April for 12 of 17 species; most species not showing such a peak were bathypelagic species. While Wormuth (1981) was forced by high variability in his pteropod data to conclude that seasonal fluctuations were non-significant in the northern Sargasso Sea, the fact that highs for five out of nine of his species came at the same time as the chaetognath highs suggests that real spring enhancement of abundance for some of the pteropods also took place.

Using the same samples as Cheney and Wormuth and earlier collections with meter nets and Bongo nets, Wiebe (in manuscript) found that the total number of adolescent and adult euphausiids in the upper 1000 m of the Slope Water and northern Sargasso Sea also reflect the differences in hydrography. Numbers of individuals are substantially higher and considerably more variable in the Slope Water than in the northern Sargasso Sea. Although the seasonal picture is incomplete, there appears to be a spring high and a late fall and winter low in the northern Sargasso Sea. The extreme variability in the Slope Water obscures any underlying seasonal pattern that may exist, but minima occur in late fall and winter. The few samples from the southern Sargasso Sea only permit the observation that euphausiid numbers overlap the northern Sargasso Sea at the low end of the scale. This is consistent with observations of biomass, numbers of individuals, and species composition at other trophic levels. For example, Backus et al. (1969) found midwater fish biomass and numbers of individuals were substantially lower in the southern Sargasso Sea than in the northern Sargasso Sea. Hulburt (1960) found a similar change in the numbers of phytoplankton cells and species composition from north to south. Lower primary production was measured in the southern Sargasso by Ryther and Menzel (1960). There are too few tows to examine seasonal cycles in the Gulf Stream.

Species	SW		NSS		GS		CCR		R	P
			Slope Water Species							
E. bathypelagica	1.8	(9)	0.05	(14)	0.74	(2)	0.02	(9)	36	***
E. fowleri	5.6	(9)	2.8	(14)	3.4	(2)	5.7	(9)	2.0	**
E. hamata	43.5	(14)	0.87	(14)	4.5	(2)	30.6	(14)	50	***
S. helenae	7.6	(17)	0.08	(18)	5.9	(2)	0	(14)	95	*
S. macrocephala	39.5	(8)	7.6	(14)	29.6	(2)	44.9	(9)	5.2	***
S. maxima	21.1	(8)	2.0	(14)	3.5	(2)	45.5	(9)	11	***
S. tasmanica	339	(17)	0.30	(18)	60.5	(2)	69.3	(14)	1130	***
			Northern Sargasso Sea Species							
K. subtilis	3.2	(15)	103	(16)	23.9	(2)	31.0	(14)	32	***
P. draco	4.9	(17)	160	(18)	75.1	(2)	29.6	(14)	33	***
S. bipunctata	3.7	(17)	42.9	(18)	14.6	(2)	33.6	(14)	12	***
S. decipiens	14.7	(16)	150	(18)	90.3	(2)	144	(14)	10	***
S. hexaptera	3.2	(17)	101	(18)	38.5	(2)	34.9	(14)	32	***
S. lyra	8.9	(15)	179	(18)	51.6	(2)	56.5	(14)	20	***
S. minima	66.0	(18)	110	(18)	21.7	(2)	46.5	(14)	1.7	***
S. planctonis	2.0	(8)	7.6	(14)	3.1	(2)	3.4	(9)	3.8	**
S. serratodentata	36.7	(17)	342	(18)	110	(2)	33.0	(14)	9.3	***
			"?" Species							
K. pacifica	13.5	(17)	24.8	(18)	25.1	(2)	1.9	(14)	1.8	NS
S. enflata	252	(17)	118	(18)	106	(2)	143	(14)	2.1	NS

Table 6.20 Mean chaetognath species abundance (No. m^{-2}) in the Slope Water (SW), Northern Sargasso Sea (NSS), Gulf Stream (GS) and cold core rings (CCR). The number of tows on which the average is based, is given in parentheses. R represents the ratio of SW to NSS or NSS to SW abundance, whichever is larger P is the probability of equal SW and NSS abundances as tested by the Mann-Whitney U test (***=p<0.001, **=p<0.01, *=<0.05, NS= not significant). (From Cheney, 1982).

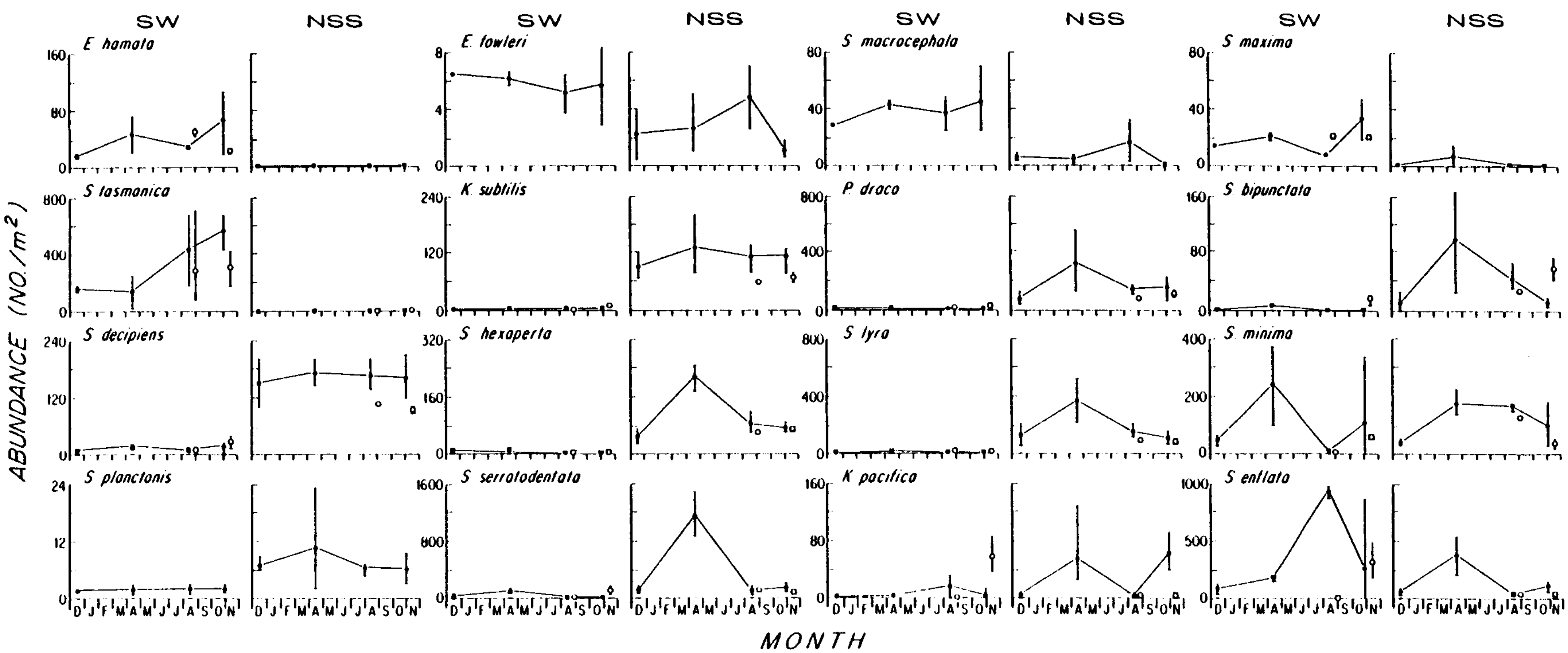


Figure 6.37. Seasonal abundance patterns of chaetognaths in the SW and NSS. Open circles represent 1975 cruises and closed circles represent 1976-77 cruises. Bars indicate the ranges of abundance. From Cheney (1982).

Thirty-three species of euphausiids have been recognized in the zooplankton collections taken by Wiebe and co-workers described above. Six species, Euphausia krohnii, Meganytiphanes norvegica, Nematoscelis megalops, Thysanoessa gregaria, T. longicaudata, and Thysanopoda acutifrons are temperate or arctic-boreal species (Mauchline and Fisher, 1968) and are generally restricted to the Slope Water and to cold-core rings (Wiebe et al, 1976a; Wiebe et al, 1976b; Wiebe, 1976; Wiebe and Boyd, 1978; Cox and Wiebe, 1978, Ring Group, 1981; Wiebe and Flierl, 1983). These species do not, however, have identical distributions. M. norvegica occurs in maximum numbers near the continental slope, sporadically in the more open waters of the Slope Water, and only incidentally in cold-core rings. T. acutifrons also occurs sporadically and is usually in low numbers in the Slope Water and in cold-core rings. This species shows strong evidence of submergence in the Slope Water as compared to its vertical distribution further to the north (Einnersson, 1948) and this trend is accentuated in rings. Submergence is also a factor in the distribution of T. longicaudata, but this species occurs more regularly and in higher numbers than the previous two species. Only E. krohnii, N. megalops, and T. gregaria typically occur in the upper 300 m and are the usual numerical dominants in the Slope Water and in young rings.

All of the other species have tropical or sub-tropical affinities. Species typical of the northern Sargasso sea are Bentheuphausia amblops, Euphausia americana, E. mutica, E. tenera*, E. hemigibba*, E. gibboides, Thysanoessa parva, N. atlantica, Nematobranchion boopis, N. flexipes, Stylocheiron abbreviatum*, S. carinatum*, S. longicorne, Thysanopoda pectinata, T. obtusifrons, T. monocantha, and T. tricuspidata. The four asterisked species are frequently dominant numerically and account for a majority of the variability at northern Sargasso Sea stations. These four species as well as E. americana, E. mutica, T. parva, and N. atlantica, regularly occur in low to moderate abundance in the Slope Water region under the influence of warm-core rings or meanders of the Gulf Stream, but rarely in the Slope Water itself (Cox and Wiebe, 1978). Some of these species, E. hemigibba, S. abbreviatum, S. carinatum, and T. obtusifrons, also occur in the southern Sargasso Sea at more than half the stations, but in proportionately lower numbers.

The remaining species, Euphausia brevis*, Nematoscelis microps*, N. tenella*, Nematobranchion sexspinosus, Stylocheiron affine*, S. elongatum*, S. maximum, S. suhmii,*, Thysanopoda aequalis*, and T. orientalis are characteristic of southern Sargasso Sea stations. The asterisked species account for a sizeable proportion of the variability at these stations. Some of these species (e.g., E. brevis, N. microps, S. affine, and S. elongatum) can, however, also dominate in the northern Sargasso Sea as well, and do occur in the Slope Water under the influence of rings or the Gulf Stream.

Of the six euphausiid species characteristic of the Slope Water, only two, E. krohnii and N. megalops, show strong evidence of seasonal variation in their numbers. E. krohnii has an abundance maximum between May and July, while N. megalops peaks between August and October. The abundances of the other four species are so variable that a seasonal periodicity is not readily visible. Fluctuations of tropical and sub-tropical euphausiids found in the Slope Water are also without a distinct seasonal influence.

Seasonal peaks in abundance are evident in nine species in the northern Sargasso Sea; E. brevis, E. hemigibba, E. tenera, N. microps, N. tenella, S. abbreviatum, S. carinatum, T. parva, and T. aequalis. Except for T. parva, the peaks all occur in the spring. *T. parva*, a bathypelagic form, peaks in the fall and strangely disappears from the zooplankton samples taken throughout all of the northwestern Atlantic between February and May (Wiebe and Flierl, 1983).

Effects Of Shelf Water Interactions

The effect of the entrainment of shelf water into the Slope Water on the species composition of the Slope Water zooplankton has not been studied in detail, although programs now funded to study warm-core rings and seasonal cycles in the Slope Water will certainly contribute towards filling this void. Cheney (1981) noted that the dominance of the boreal coastal chaetognath species, *Sagitta elegans*, in the Slope Water reported by Grice and Hart (1962) reflected entrainment of shelf water.

Effects Of Cold- And Warm-core Rings

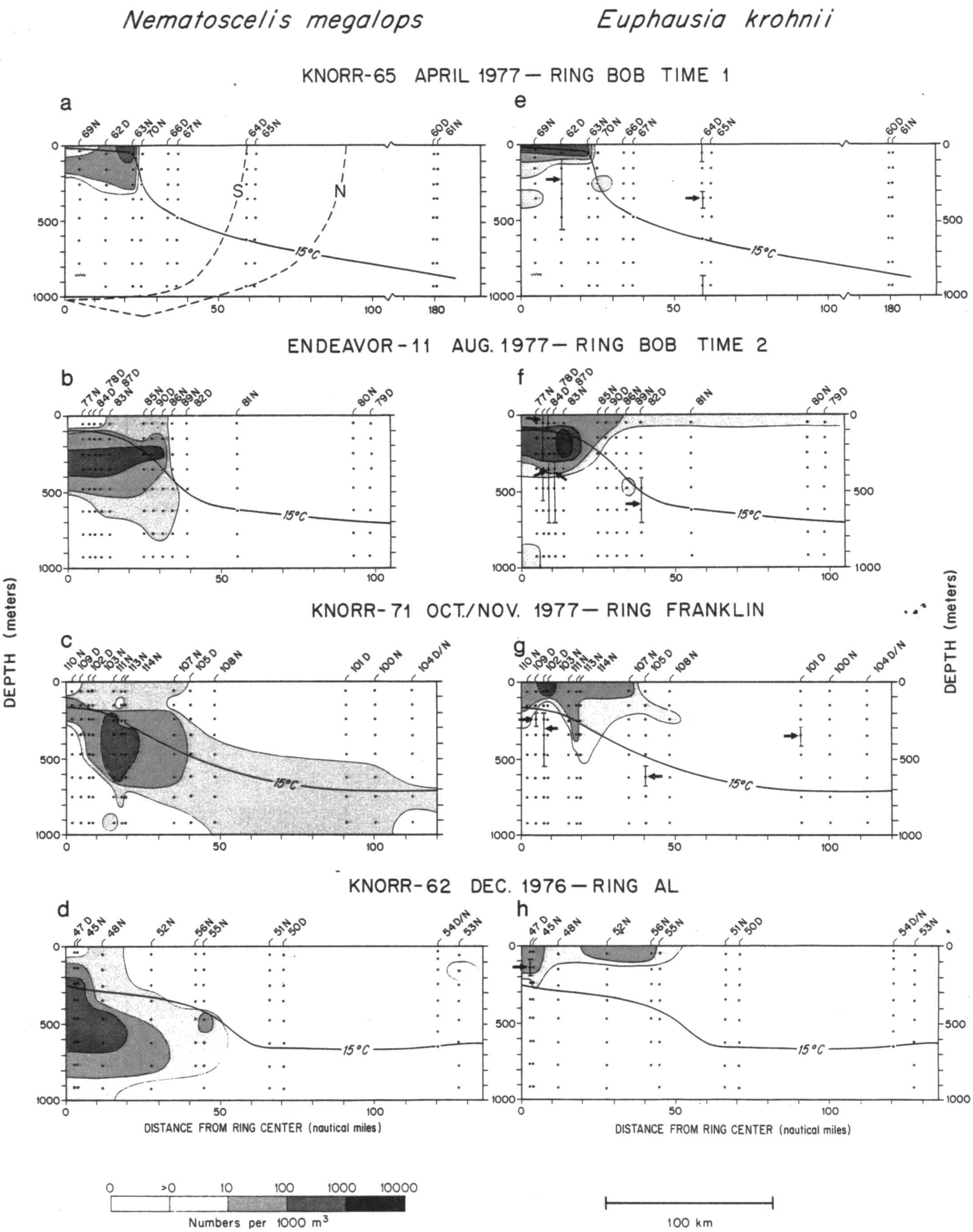
Rings are also sites of strongly contrasting species composition compared to surrounding waters. Because rings begin life containing water from the opposite side of the Gulf Stream, their patterns of zooplankton species distribution are strongly dependent upon their age or state of decay, the affinity of a species for a particular hydrographic regime, the vertical distribution of the species, and the particular composition of the Slope Water or Sargasso Sea Water population at the time of ring formation. This latter point is especially important both because the evolution of the species composition within a ring in terms of absolute abundance is strongly dependent on the starting composition and because absolute abundances vary strongly due to seasonal cycles which may be proceeding differently within or outside the ring or due to patchiness of species in the parent water mass (Cox and Wiebe, 1978; Ortner et al., 1979; Wiebe, 1976; Wiebe et al, 1976; Wiebe and Boyd, 1978; Wiebe and Flierl, 1983). This discussion focuses first on cold-core rings because they are presently best known.

Many of the published data are for the euphausiids. Wiebe et al. (1976) showed that in cold-core rings 3-11 months of age there was a gradual transformation in euphausiid species composition from one dominated by species characteristic of the Slope Water to one more similar to the adjacent Sargasso Sea waters. It also appeared that the decay rate of the Slope Water species assemblage was much more rapid than that of the physical properties characterizing a ring, especially below 200 m.

More extensive details of the changes in distribution and abundance of euphausiids in aging cold-core rings are presented by Wiebe and Flierl (1983). In a young ring such as Bob at age 2 months, species endemic to the Slope Water (for example *Nematoscelis megalops*, *Euphausia krohnii*, and *Thysanoessa longicaudata*) were mostly or wholly restricted to the ring center (Figs. 6.38 and 6.39); only a few individuals of *E. krohnii* were found 95 km from ring center in the outer portion of the Gulf Stream remnant. Species in other taxonomic groups such as the copepod *Pareuchaeta norvegica* and the pteropod *Limacina retroversa*, showed very similar patterns.

A number of euphausiids found in the Sargasso Sea during all seasons show the opposite pattern. Virtually none of the species of the *Stylocheiron* was present in the center of Bob (Fig. 6.40). Similarly, of the two abundant species of *Nematoscelis* with subtropical/tropical distributions, only a few individuals of *N. microps* were found in the ring (Wiebe and Flierl, 1983). In contrast, two of the three species of *Euphausia* which were present in the

Figure 6.38. Cold-core ring/Sargasso Sea vertical sections of abundance of the Slope Water species *Nematoscelis megalops* and *Euphausia krohnii*. Four cruises are illustrated for each species, two to ring "Bob", KNORR 65 and ENDEAVOR 11, one to ring "Franklin", KNORR 71, and one to ring "Al", KNORR 62. The solid line is the depth of the 15°C isotherm. For species which show strong diel vertical migration, night data are contoured, and day data are given as the range (I) with an arrow indicating the center of the distribution. the number/letter combinations along the top of each section are the MOCNESS tow numbers (D - day tow; N = night tow). The dashed lines in the top left section (*N. megalops*, KNORR 65) are the approximate north (N) and south (S) positions of the trapped region of a ring moving westward at 5 cm/sec. (From Wiebe and Flierl, 1983).



Nematoscelis megalops
Euphausia krohnii
KNORR-65 APRIL 1977 — RING BOB TIME 1
ENDEAVOR-11 AUG. 1977 — RING BOB TIME 2
KNORR-71 OCT./NOV. 1977 — RING FRANKLIN
KNORR-62 DEC. 1976 — RING AL
a
b
c
d
e
f
g
h
15°C
S
N
DEPTH (meters)
DISTANCE FROM RING CENTER (nautical miles)
0
>0
10
100
1000
10000
Numbers per 1000 m³
100 km

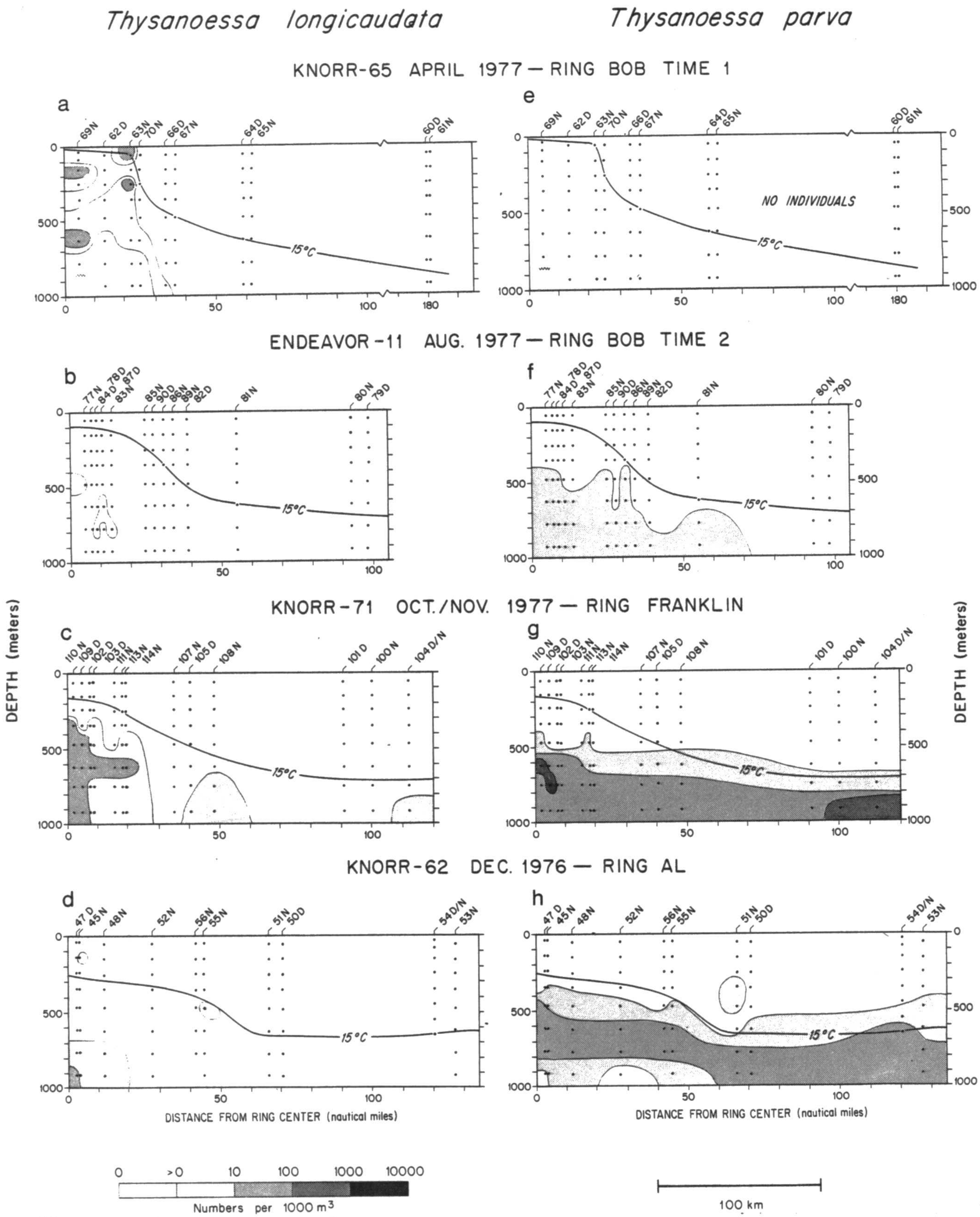


Figure 6.39. Same as Figure 6.38., but for the Slope Water species Thysanoessa longicaudata and the bathypelagic species Thysanoessa parva. (From Wiebe and Flierl, 1983).

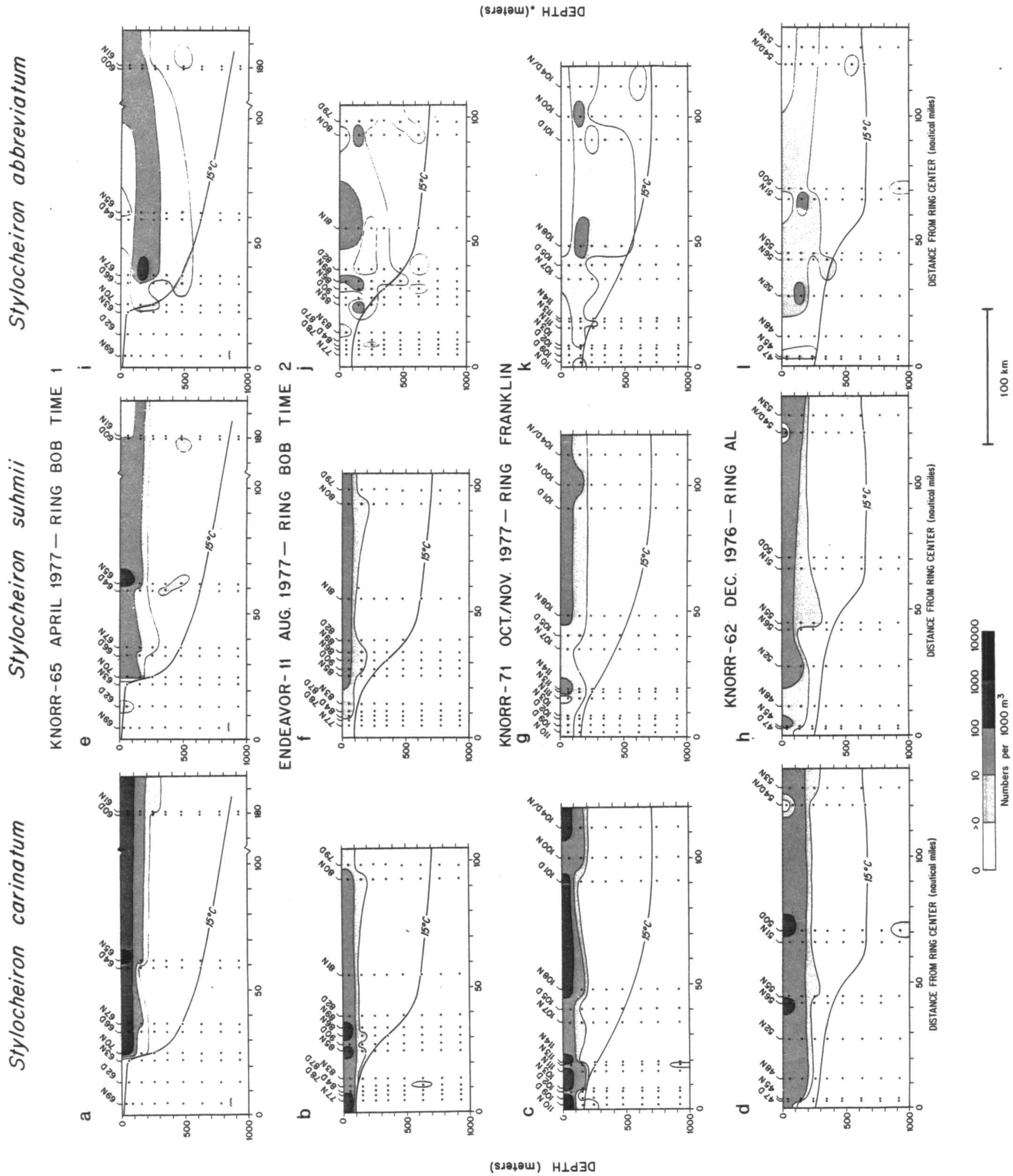


Figure 6.40. Same as Figure 6.38., but for the Sargasso Sea species Stylocheiron carinatum, S. suhmii, and S. abbreviatum. (From Wiebe and Flierl, 1983).

Sargasso Sea in reasonably large numbers were also present in ring Bob in moderate numbers (Fig. 6.41). The pteropod, Limacina inflata, showed a similar distribution pattern. Only E. brevis was totally absent from the ring center area. Another species, Thysanopoda aequalis, was present in low numbers within the ring, but not at the centermost station.

Ring Bob was sampled a second time when it was approximately 6-months old. Deeper dwelling non-migrators showed essentially no penetration of the ring core waters i.e. S. elongatum, S. affine, S. abbreviatum (Figs. 6.36 and 6.37). Of the surface forms, S. suhmii was present in the ring in low numbers except that it was absent at the centermost station and S. carinatum was distributed throughout the ring in numbers which exceeded those caught in the surrounding waters by a factor of ten (Fig. 6.36). Limacina inflata was the only other warm water species counted thus far to show significantly higher abundance in ring Bob at time 2 (6 months) than in the surrounding Sargasso Sea (Wiebe and FLierl, 1983). The abundance levels of the warm-water Euphausia and T. aequalis had not changed significantly (Fig. 6.41) and neither N. microps nor N. tenella had much success in invading the ring.

Thus even after a period of 6 months, there remained a substantial degree of segregation of warm- and cold-water populations. The euphausiid species abundance sections in the other two rings, Al and Franklin, complement the patterns observed in Bob (Figs. 6.38-6.41).

For the euphausiids, the pattern of cold-core ring evolution that emerges is the following: (1) Warm water species living permanently at or near the surface and those which perform diel migrations invade a ring more quickly than do species which live at subsurface depths of 150 to 600 m. However, even for these rapid invaders, there is often a tendency for population numbers to be lower within the ring compared to adjacent seas for ½ year or more. (2) Vertical migrators migrate to shallower depths in young rings and "non-migrators show a strong tendency to shoal. (3) Cold-water species persist within the ring core for extended periods. In some species, population numbers in middle-aged rings exceed levels at the time of formation (i.e., E. krohnii and N. megalops). Other species such as T. longicaudata can show rather drastic declines in numbers during this same period in rings like 'Bob'. (4) Cold-water species, such as N. megalops and T. longicaudata, which show submergence as a ring ages, appear to be dispersed out of a ring at depths of 400 to 1000 m. For the shallower dwelling species like E. krohnii, which can survive surface water modification, dispersal appears to take place near the surface. (5) The species compositional structure of the ring core remains distinctly different from the surrounding Sargasso Sea for 6 to 8 months after formation in spite of the exchanges of species into and out of the ring which appear to be taking place. These data corroborate the earlier findings of Wiebe et al. (1976).

The changing pattern of species abundance as cold-core rings age has been studied for three other groups of zooplankton: chaetognaths by Cheney (1982); amphipods by Hart and Wormuth (1982); copepods by Cowles (1982). One other group, the thecosomotus pteropods, has been sorted and counted by Wormuth, but except for the data on Limacina inflata and L. retroversa, his findings are still unpublished.

Cheney (1982) presented abundance patterns for 16 species of chaetognaths from the center of ring Bob to the Sargasso Sea during the second period of sampling of this ring (Fig. 6.42). Species classified as northern Sargasso Sea species by Cheney, based on the horizontal abundance patterns described above, all showed low abundance in the ring core and a monotonically increasing

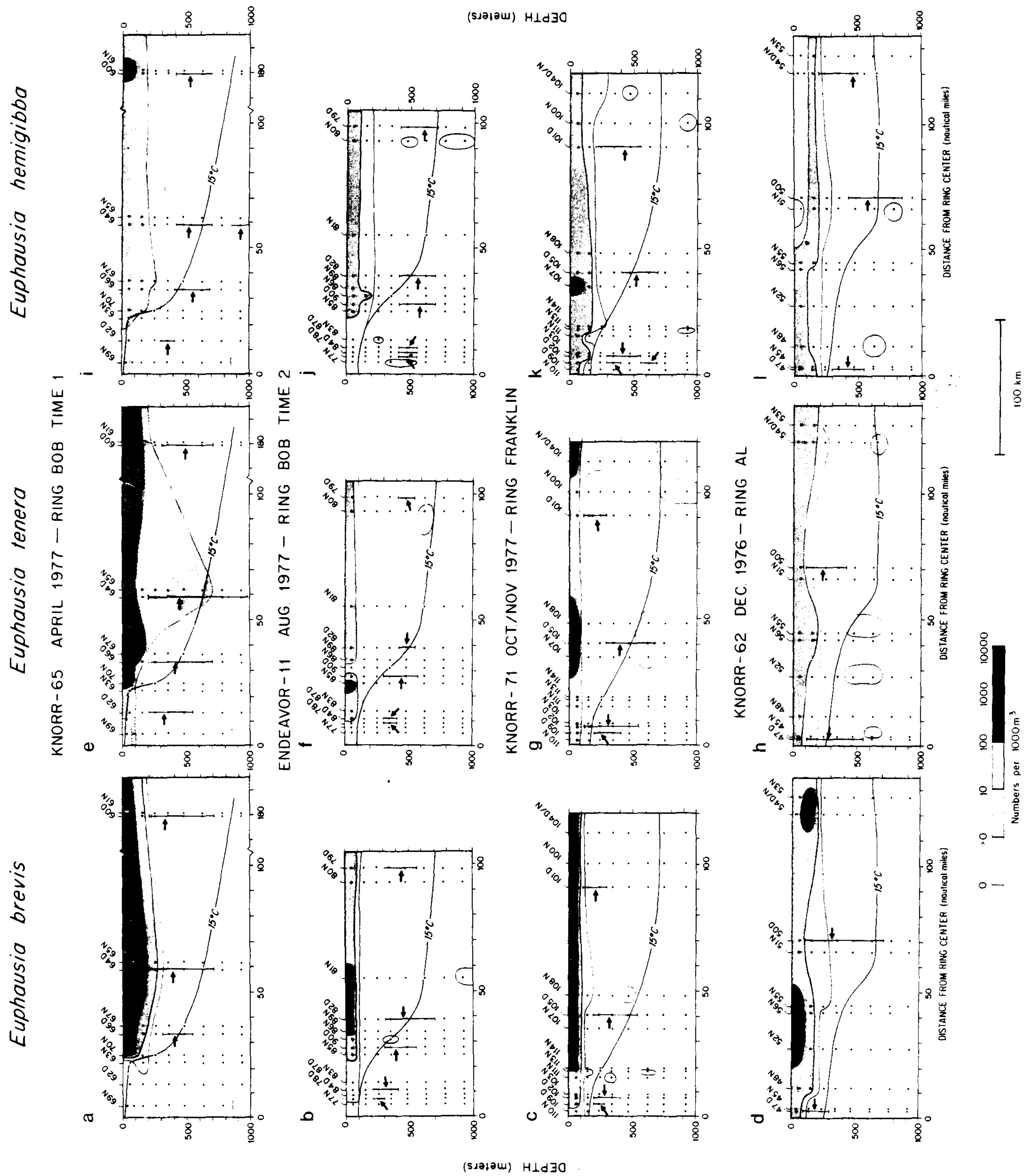


Figure 6.41. Same as Figure 6.38., but for the Sargasso Sea species Euphausia brevis, E. tenera, and E. hemigibba. (From Wiebe and Flierl, 1983).

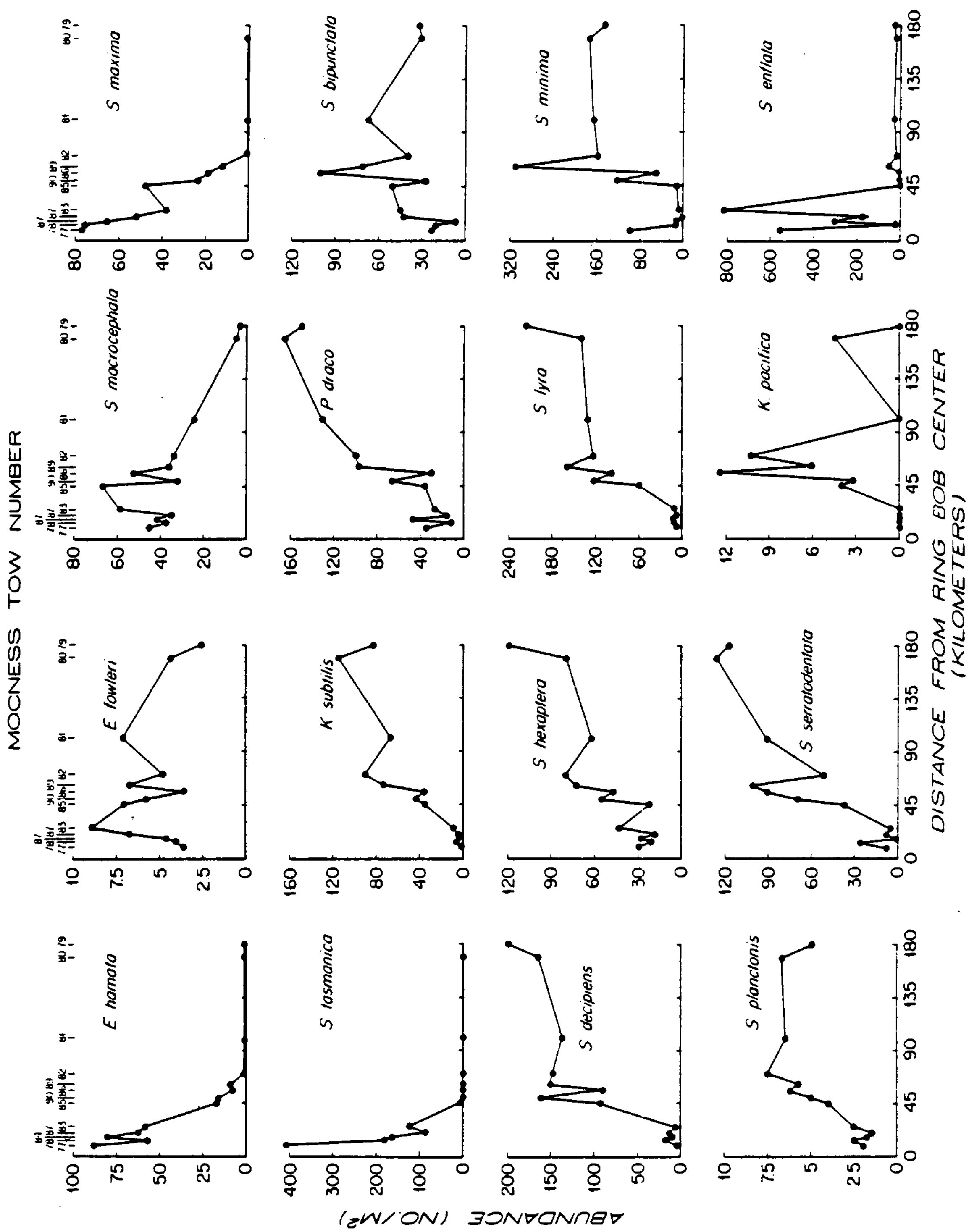


Figure 6.42. Spatial abundance patterns of chaetognaths in Ring Bob. (From Cheney, 1982).

abundance to the Sargasso Sea except for S. bipunctata. This species had a peak abundance in the ring fringe. Five of the seven species characteristic of the Slope Water showed the reverse pattern of higher abundance in the ring core and either lower abundance or absence in the Sargasso Sea. One Slope Water species, S. helenae, was absent from the ring entirely and another, S. bathypelagica was present in small numbers in only one tow from the ring core.

Cold-core ring D studied earlier by Wiebe and Boyd (1978) and Boyd et al. (1978) was also used by Cheney to examine temporal changes in chaetognath species composition in an older ring. This ring was sampled at 6- and 9-months of age. Except for S. macrocephala which maintained abundances in ring D equivalent to its Slope Water levels, Slope Water species either declined in abundance or disappeared during the period (Fig. 6-43). The expected opposite pattern was also observed for most of the Sargasso Sea species although none save S. decipiens reached abundance levels in ring D as high as generally observed in the Sargasso Sea. S. decipiens actually attained numbers considerably above the level normally found in the Sargasso Sea and Cheney suggested that it was opportunistically exploiting the hybrid ecological conditions present in the ring. Similar observations were made by Wiebe and Flierl (1983) with regard to S. carinatum and the Ring Group (1981) with regard to Limacina inflata. There are also midwater fish species which appear to exploit conditions in middle aged rings (Backus and Craddock, 1982 and below).

The data summarized by Cowles (1982) for the copepods Calanus finmarchicus, Rhincalanus nasutus, Pleuromamma robusta, and P. borealis which are characteristic Slope Water species and P. gracilis and P. abdominalis which are important in the Sargasso Sea, show essentially the pattern described above. Ring Bob had a larger total copepod biomass and a larger proportion of cold-water species than ring D. Nevertheless, significant numbers of warm-water species were present in the near-surface portion (upper 200 to 400 m) of the core waters of both rings. Evolution of the pelagic amphipod species composition in these same rings was parallel to the above groups (Hart and Wormuth, 1982).

Although substantial information about the species composition of warm-core rings will soon be available, the only currently published data come from Cox and Wiebe (1978) who examined the potential role of warm-core rings as a source for the expatriated oceanic zooplankton species that occur on the middle-Atlantic Bight shelf. Abundance data for 31 euphausiid species at three Slope Water stations, two Gulf Stream stations, two warm-core ring stations, and a composite shelf station made up of data from Grice and Hart (1962) were presented. The species composition of warm-core rings was most similar to the Gulf Stream and to a station on the Slope Water under the influence of a warm-core ring (Table 6.21).

Vertical Distributions

Typical Seasonal Distributions

Very little published information relates specifically to the seasonal pattern of vertical distribution of zooplankton from the Slope Water or the northern Sargasso Sea, although this will change for the Slope Water when data from the extensive samples being analyzed by Wiebe and co-workers are reported. The works of Deevey (1971) and Deevey and Brooks (1971, 1977) provide seasonal data for a number of zooplankton taxa, but are not reviewed here because the sampling had limited vertical resolution and the collection site was 15-30 km off Bermuda. The works of Wormuth (1981), Cheney (1982), and Wiebe and Flierl

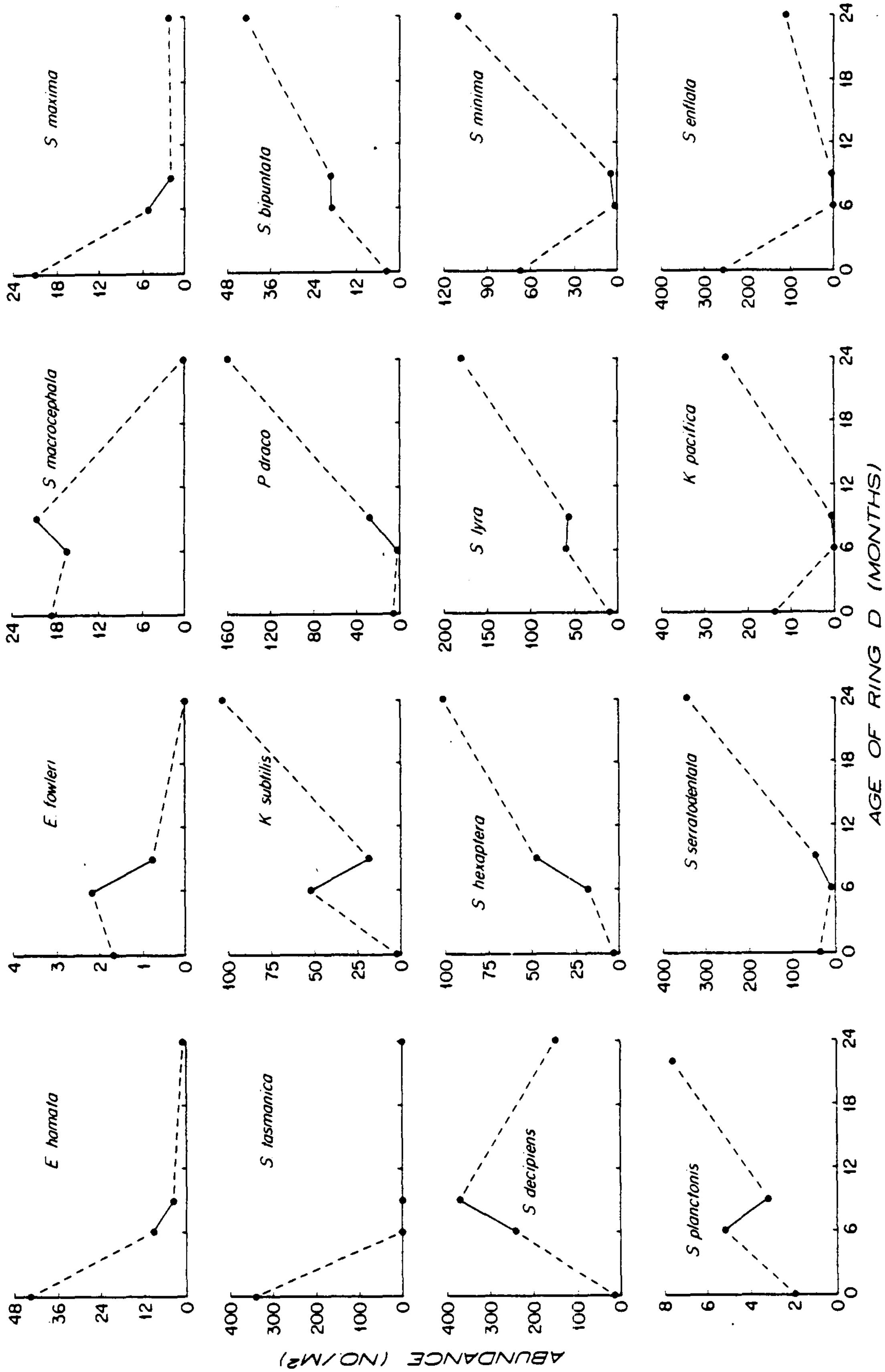


Figure 6.43. Temporal abundance patterns of chaetognaths in Ring D. (From Cheney, 1982).

Composite[c] Shelf Station	MOC–20 (Slope) Water	SL–6 (Slope) Water	MOC–39 (Slope) Water	GS–4 (Gulf Stream)	GS–3 (Gulf Stream)	WFO 4, 5 (Warm Core) Ring	
5.9	4.6	39	45	46	51	49	WSO–1 (Warm Core Ring)
13.8	13	19	34	65	42		WFO–4, 5
0.82	0.28	29	45	67			GS–3
0.80	0.07	25	36				GS–4
5.9	3.4	26					MOC–39
30.8	29						SL–6
17.3							MOC–20

[a]Whittaker & Fairbanks (1958).
[b]MOC–20 was taken at a position well removed from the Gulf Stream and warm core rings, as judged by analysis of concurrent satellite imagery. Designation of water types at each station was based on temperature and salinity profiles.
[c]Stations A, B, C, and D of Grice & Hart (1962) for March, December, July, and September were averaged to obtain overall % composition of adult euphausiids over the Shelf region. A total of 16 tows are included in the composite of the four station locations; percentages appear in Table 2.

Table 6.21. Percent similarity analysis (a) of 30 species of euphausiids from 800 m zooplankton tows in the western Slope Water and Gulf Stream (b), including representative Shelf samples for comparison (c). (From Cox and Wiebe, 1978).

(1983), provide some insight into the changes that are to be expected for the pteropods, chaetognaths, and euphausiids living in the Northern Sargasso Sea, although the seasonal coverage is sparse at best.

The most exhaustive analyses of vertical structure for both the Slope Water and the northern Sargasso Sea have been done by Cheney (1982) for the chaetognaths from 52 9-net MOCNESS-1 tows. Based on their average vertical distribution in these two hydrographic regimes, 9 species were considered epipelagic (0-200 m) - K. pacifica, P. draco, S. bipunctata, S. enflata, S. helenae, S. hexaptera, S. minima, S. serratodentata, and S. tasmanica, 4 species were mesopelagic (200-1000 m) - K. subtilis, S. decipiens, S. lyra, and S. planctonis, and 5 were bathypelagic (> 1000 m) - E. bathypelagica, E. flowleri, E. hamata, S. macrocephala, and S. maxima (Fig. 6.44). For all epipelagic species, the fraction of the population below 100 m was larger in the northern Sargasso Sea than in the Slope Water. Most mesopelagic species showed no shift in vertical distribution between these two regimes. In contrast, of the bathypelagic species only the population center of abundance of E. bathypelagica did not shift upward 100 to 500 m in the Slope Water.

None of these species showed evidence of significant diel vertical migration, although it would not have been discernable in the upper 100 m because of the coarseness of the sampling. Ontogenetic migrations were, however, quite evident in the seven mesopelagic and bathypelagic species for which size frequency data were obtained (Fig. 6.45). The typical migration resulted in small individuals predominating near-surface and large individuals predominating at the bottom (e.g. S. lyra, E. hamata, S. decipiens, and S. macrocephala). Cheney (1982) pointed out that spatial or temporal variation in ontogenetic shifts in vertical distribution coupled with the decreases in abundance with increasing size could give rise to shifts in the overall vertical distribution of a species which would be unrelated to changes in the physical environment, although they could appear to be. He did not, however, present data to show seasonal shifts in vertical distribution nor did he relate ontogenetic migrations to the seasons.

The Northern Sargasso Sea vertical distributions of the nine pteropods described by Wormuth (1981) show three distinct patterns (Figures 6.46 to 6.48). Three species, Creseis acicula (Fig. 6.46), C. virgula concia, and Limacina trochiformis, were epipelagic non-migrators; their centers of distribution (day, night, and year-round) were within the upper 100 m. A mesopelagic non-migrator, Clio cuspidata, lived below 300 m; its center of distribution was quite variable, ranging typically between 450 and 800 m (Fig. 6.47). There were four strong vertical migrators, C. pyramidata (Fig. 6.48), L. inflata, L. lesueuri, and Styliola subula, which typically were at depths of 200 to 500 m during the day and in the upper 50 to 100 m at night. L. bulimoides was a much weaker diel migrator moving from 120 to 160 m during the day to above 50 m at night.

There was very little evidence for large changes in vertical distribution seasonally, although the December 'daytime' tows were taken so close to dusk and the time of upward movement of the diel migrators that they give the appearance of a fall shoaling. The seasonal picture for the vertical distribution of euphausiids in the northern Sargasso Sea can be derived from Figures 6.38-6.41, from profiles given by Wiebe et al. (1976), and from some unpublished data of Wiebe (Fig. 6.49).

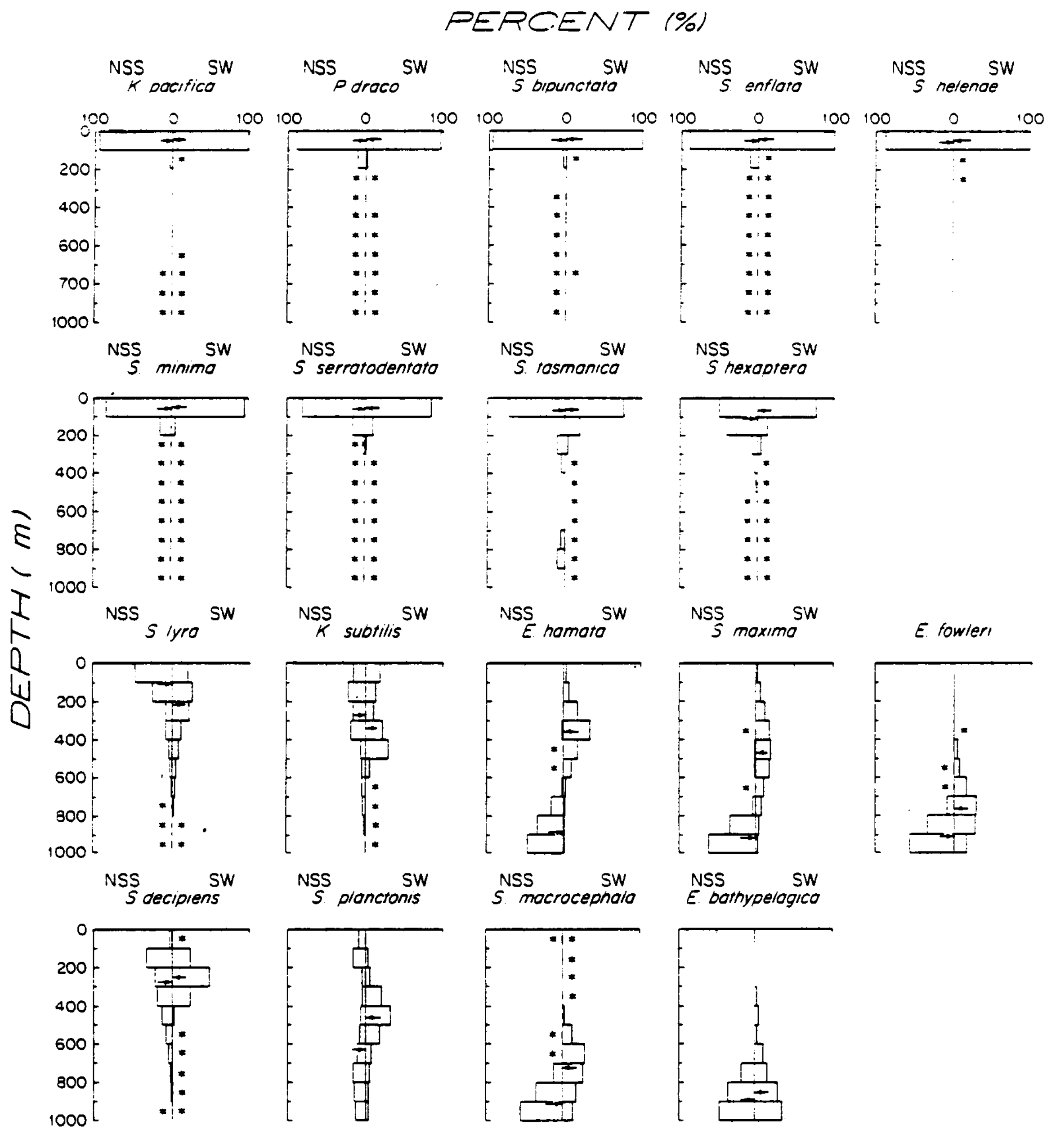


Figure 6.44. Average vertical distributions of chaetognaths in the upper 1000 m of the Slope Water and Northern Sargasso Sea. Arrows indicate median depths calculated from the average vertical distributions. Depth intervals labeled with asterisks contained less than 1% of the population (after Cheney, 1982).

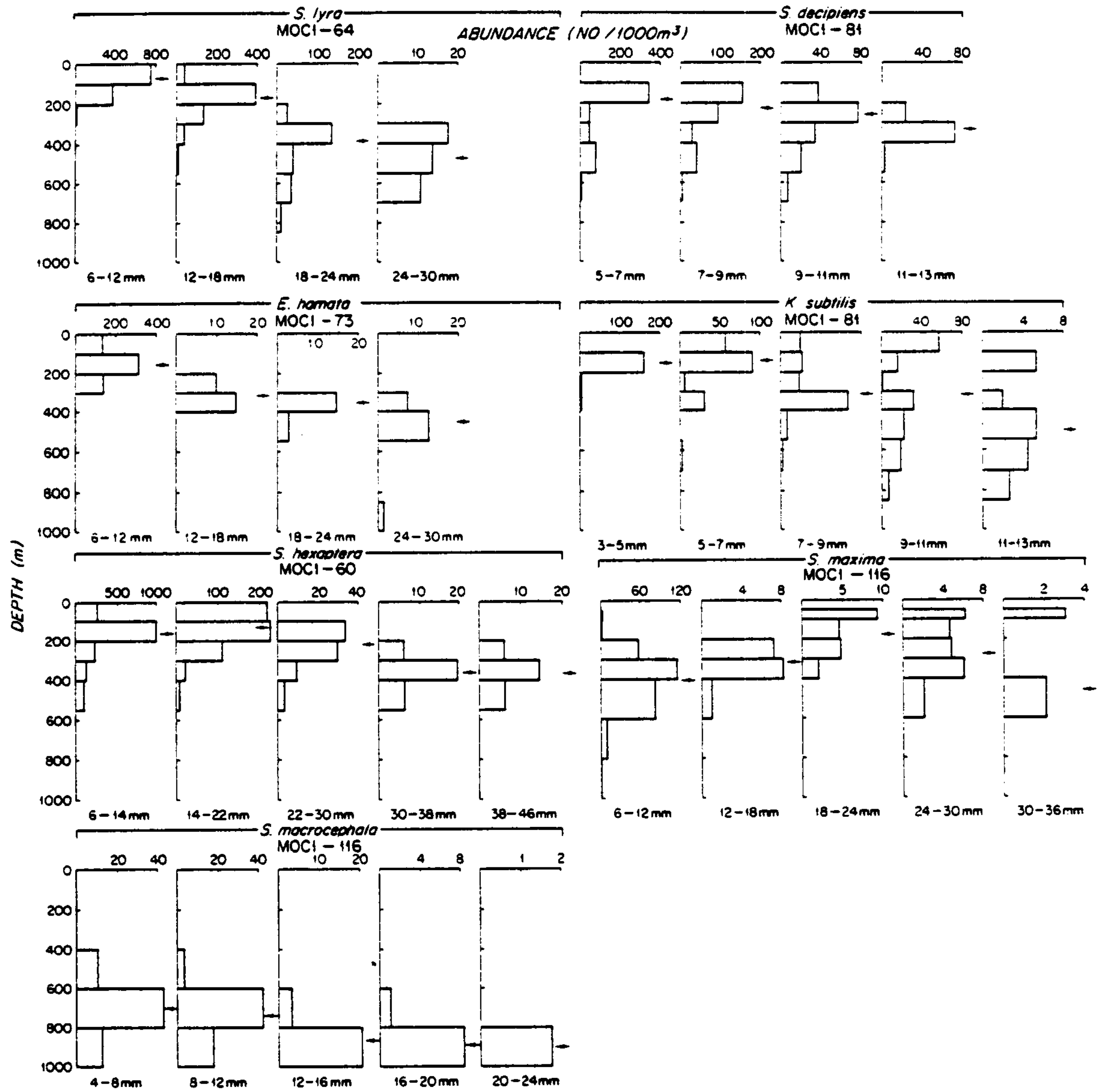


Figure 6.45. Ontogenetic migrations of seven chaetognaths. Arrows indicate median depths for each length class (after Cheney, 1982).

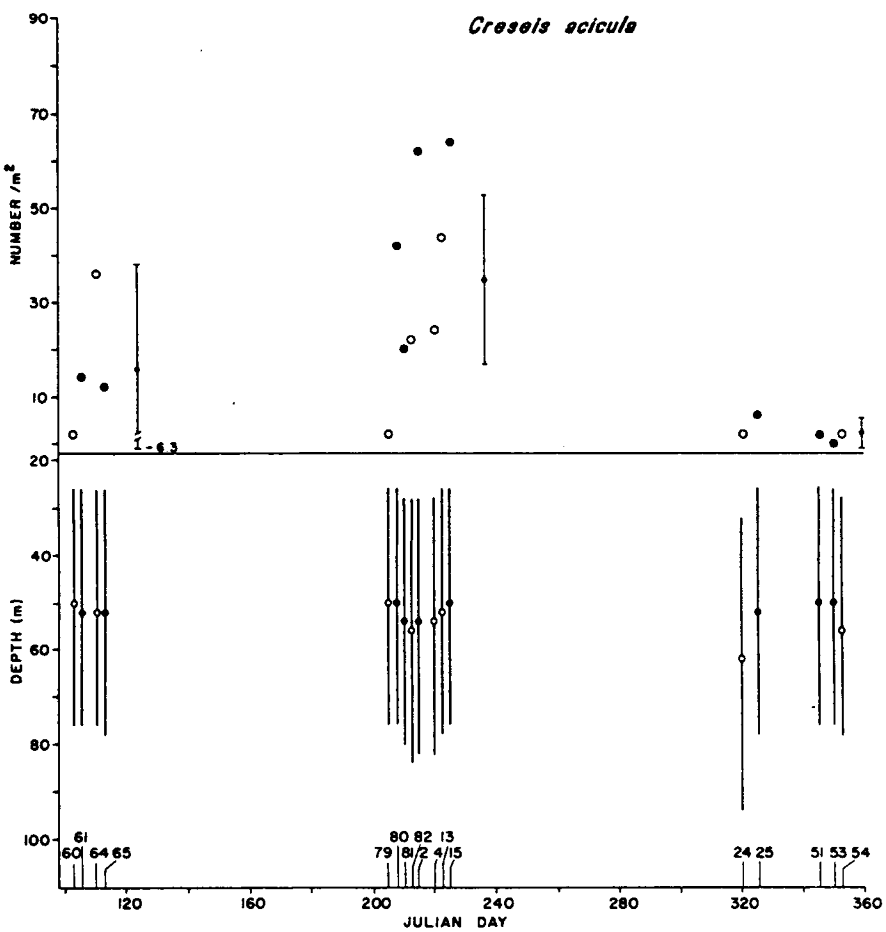


Figure 6.46. Numbers per square meter and vertical distributions at different Julain dates for C. acicula. Open circles represent day tows, closed circles night tows. Vertical lines show means (dots) and 95% confidence intervals (ends of lines) for each time period. (Bottom) The top of each line represents the depth of the 25th the dot the 50th, and the bottom of the line the 75th percentile of the population. The numbers above the x-axis are the tow numbers (offsets <5 days have been made for clarity). From Wormuth (1981).

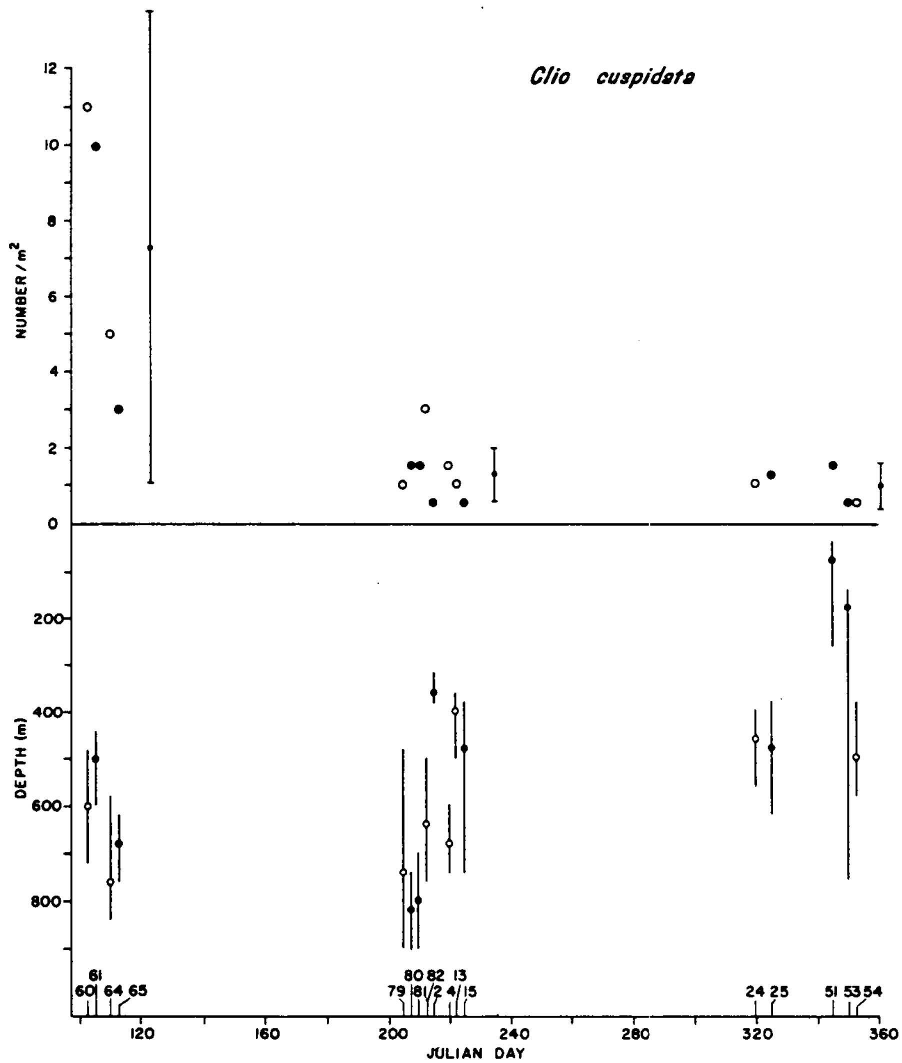


Figure 6.47. Numbers per square meter and vertical distributions at different Julain dates for C. cuspidata. Symbols and in Figure 6.46. Y axes are scaled separately for each species (from Wormuth, 1981).

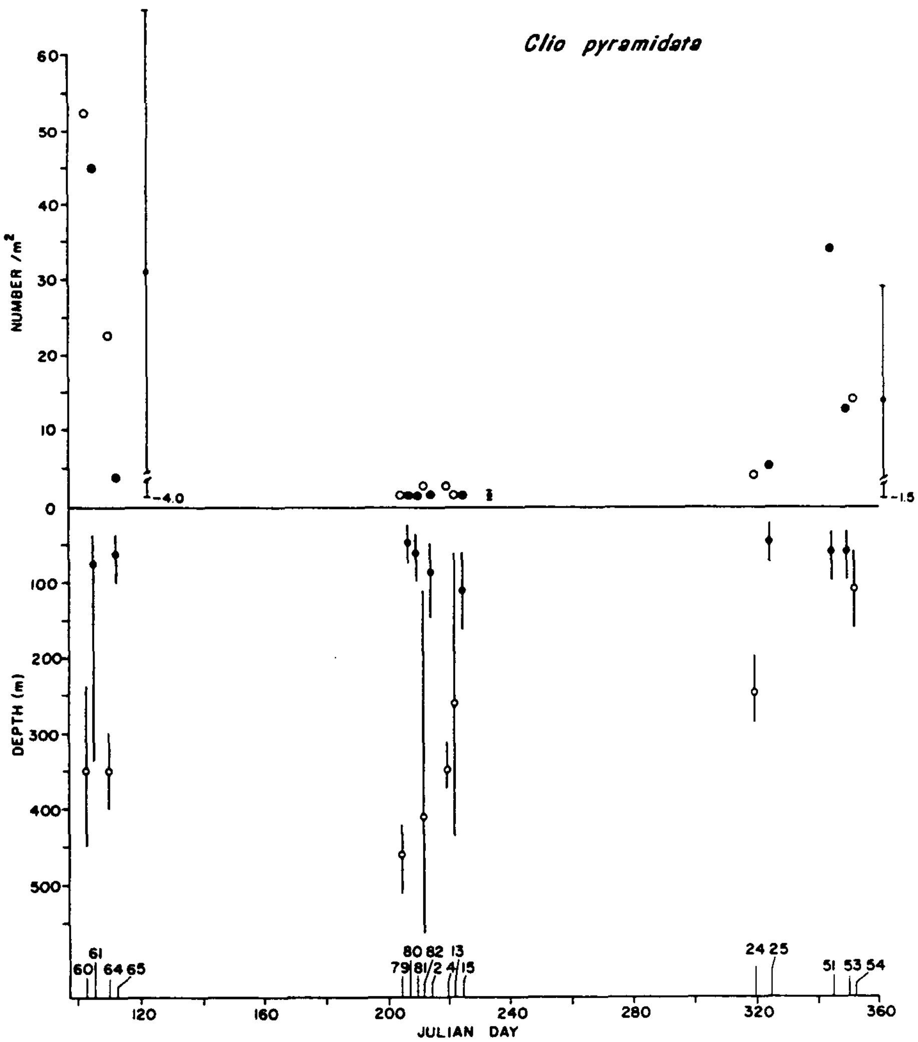


Figure 6.48. Numbers per square meter and vertical distributions at different Julain dates for C. pyramidata. Symbols and in Figure 6.46. Y axes are scaled separately for each species (from Wormuth, 1981).

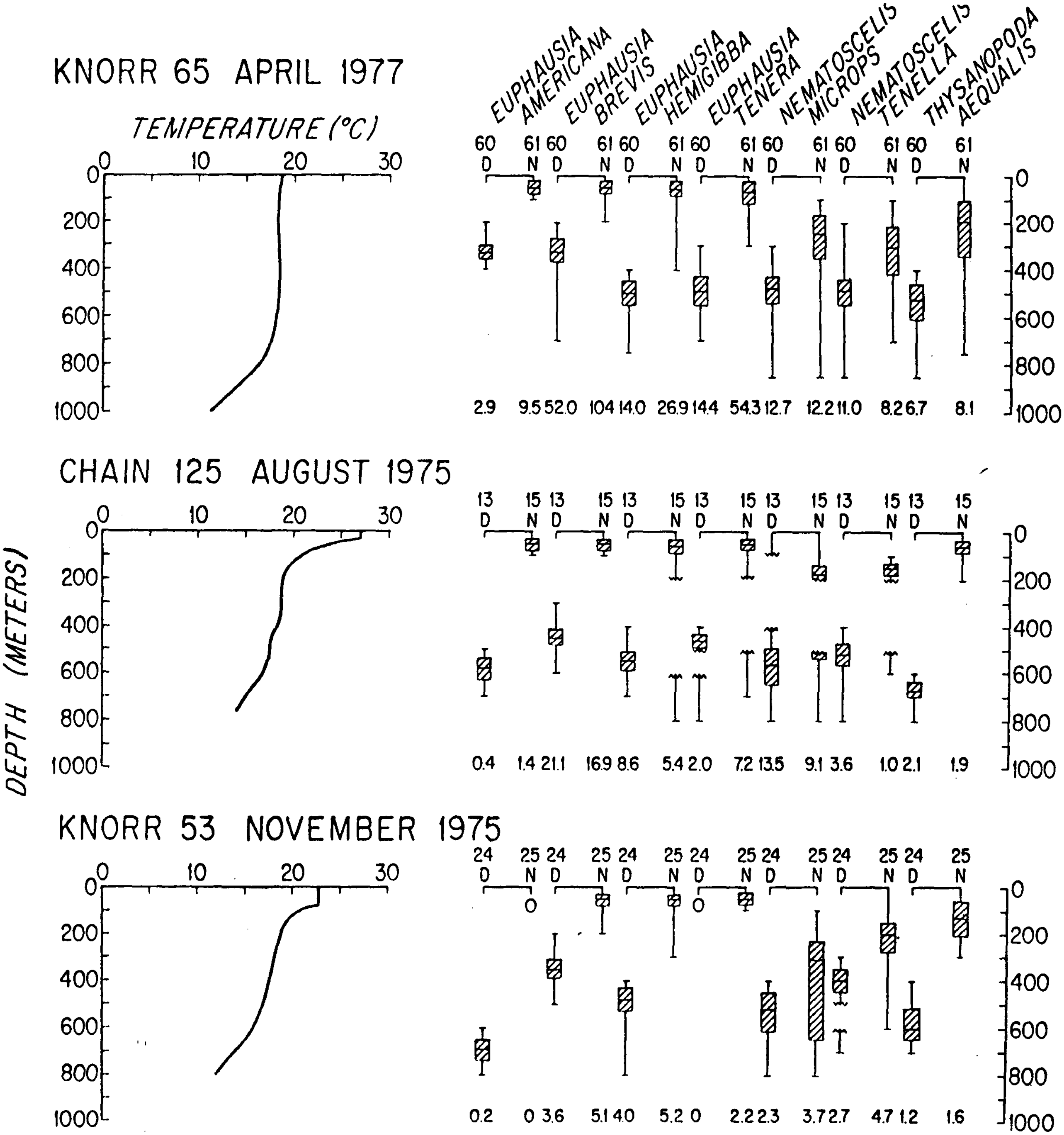


Figure 6.49. The day/night vertical distributions of adult euphausiids which are strong or moderate migrators in relation to vertical temperature structure. The species illustrated are typically found in the northern Sargasso Sea all year, and some are considered grazers (Nemoto, 1967). The profiles are given as cumulative percentages. The number at the top of each profile is the MOCNESS tow number; the D = day tow and N = night tow. The number at the base of each profile is the number per m^2 in the column of water sampled. For KNORR cruise No. 65 this was 0-1000 m; for CHAIN 125 and KNORR 53 it was 0-800 m (from Wiebe, unpublished data).

Effects Of Shelf Water Interactions

The effects of shelf water overflow on the vertical distribution of Slope Water zooplankton has not been studied in detail. Cheney (1982) showed that the shelf water chaetognath, Sagitta elegans, was most abundant in the upper 50 to 100 m of two tows taken in the entrainment field east of warm-core ring 'Q', but he did not indicate what affect the presence of shelf water had on the other species.

Effects Of Warm And Cold-core Rings

Only the effects of cold-core rings on the vertical distribution of zooplankton species in the regions has been studied in depth for the euphausiids (Wiebe and Boyd, 1978; Wiebe et al., 1982; Wiebe and Flierl, 1983) and chaetognaths (Cheney, 1982).

The warm-water euphausiids which penetrate cold-core rings exhibit a common reaction of shoaling. In the vicinity of a ring, it often involves truncation of the lower portion of the depth distribution by 100 to 300 m and for deep-dwelling species, elevation of the upper limit by about 100 m. The pattern is most pronounced in young rings such as Bob and less evident in the older rings Al and Franklin. For non-migrators living near the surface (Stylocheiron carinatum, S. suhmii) the shoaling is subtle (Fig. 6.40). These species typically range the upper 200 m in the Sargasso Sea, but become restricted to the upper 100 m in young rings. For deeper living non-migrators (S. affine, S. elongatum), shoaling is more dramatic. The day and night vertical distributions of migrators of Euphausia, Nematoscelis, and Thysanopoda (Fig. 6.41) show pronounced shoaling relative to the patterns of vertical distribution in the Sargasso Sea. In ring Bob at time 2 (6 months), Al, and Franklin (Fig. 6.39), the center of abundance of the bathypelagic species Thysanoessa parva was shoaler than in the Sargasso sea by at least 200 m. In addition, 0-1000 m abundance of this species was 1.4 to 2.6 times larger in the rings.

The Slope Water species, Nematoscelis megalops, is found south of the Gulf Stream only in association with cold-core rings. Data presented by Wiebe and Boyd (1978) and Wiebe et al. (1982) show that N. megalops typically lives in the upper 600 m with most individuals above 300 m both day and night. A similar pattern was observed in ring D at 6 months of age (August 1975), except a larger fraction of the population was present below 300 m and individuals occurred down to 800 m (Fig. 6.50). On the second cruise to ring D (November 1975), the distribution of this species had shifted significantly downward with the major portion occurring below 300 m. On the third cruise to ring D (June 1976), there were no N. megalops in the single night sample taken in the ring core. A similar pattern was evident in vertical distributions in rings Al, Bob, Emerson, and Franklin (Fig. 6.38). The older the ring, the deeper the distribution of this species. A similar observation can be made for the cold-water species, Thysanopoda acutifrons, but not for Euphausia krohnii or Thysanoessa longicaudata, although their abundance declined with ring age.

Changes in chaetognath vertical distribution in cold-core rings is inextricably related to the pattern of ontogenetic migration and changes in the size frequency distribution. Thus, in ring D, Cheney (1982) found that the five significant shifts in vertical distribution between August and November 1975 were for populations which became shallower (Fig. 6.51). All were species which Cheney had shown to have strong ontogenetic migrations; if individuals were smaller on average in November, then their vertical distribution should have been shallower if they were ontogenetically migrating. In support of this

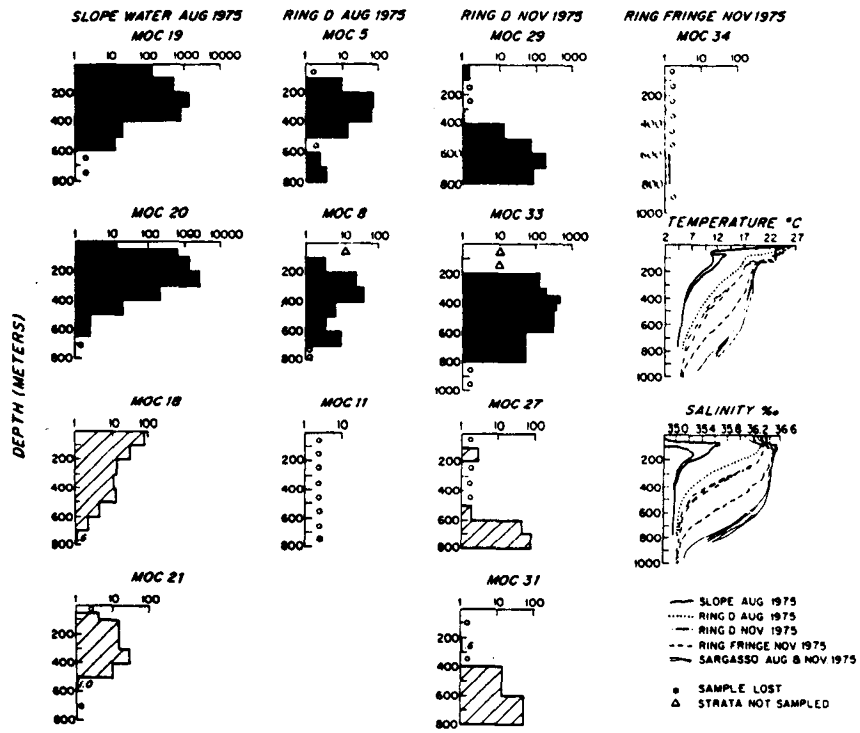


Figure 6.50. Vertical distribution of N. megalops in the Slope Water during August 1975 and in ring D during August and November 1975. Night samples are blacked; day samples are cross hatched. Also illustrated are the temperature and salinity profiles taken within each hydrographic area (Abundance in No. 1000 m^{-3}). From Wiebe and Boyd (1978).

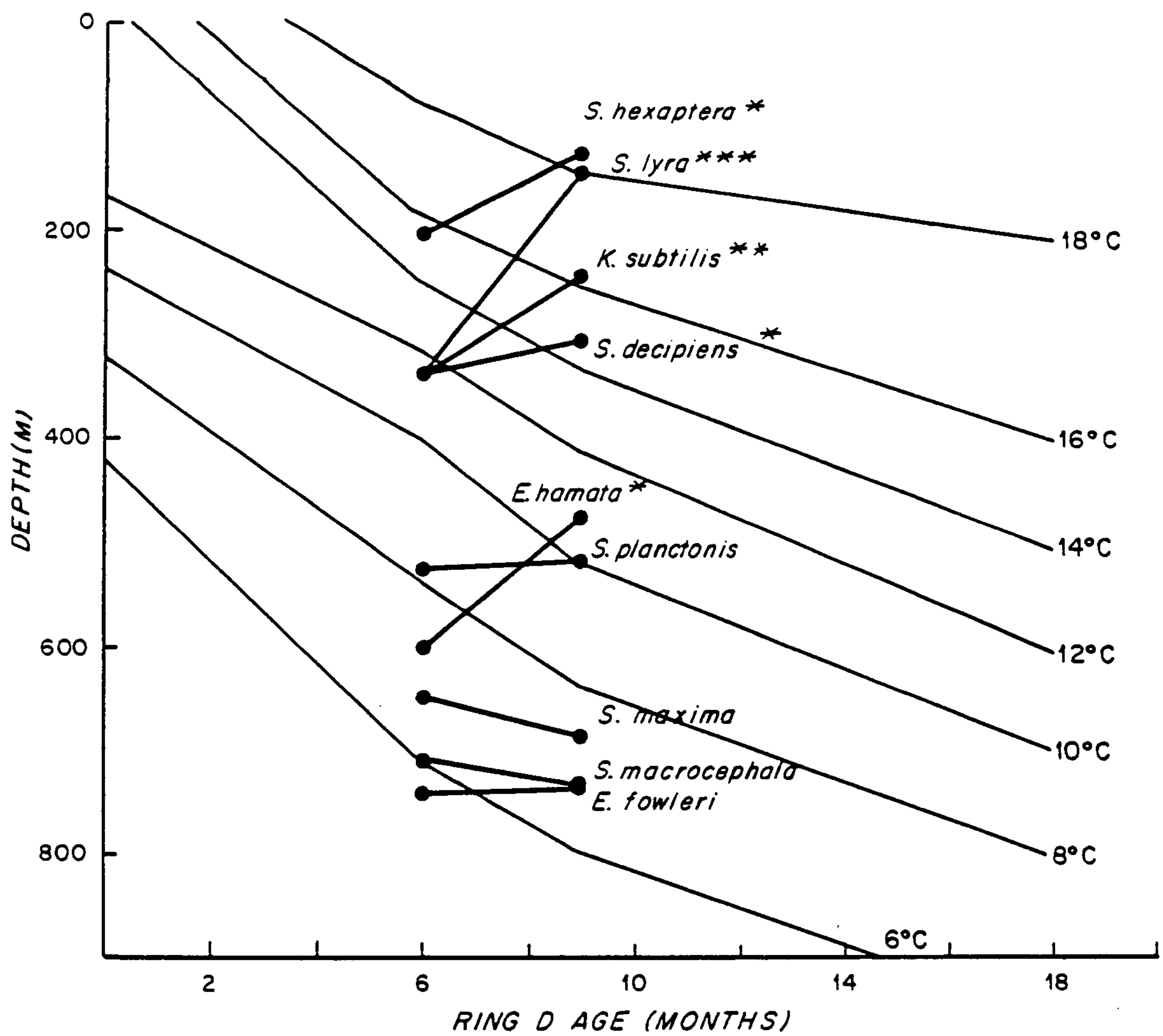


Figure 6.51. Relationship of isotherm depth with median depths for nine chaetognaths in ring D. Asterisks denote significant differences in median depth (*=<0.05, **p=<0.01. ***p=<0.001). From Cheney (1982).

hypothesis, individual size for the one species that was measured in all samples he examined, Sagitta lyra, showed that the average size of the population in November (11.8 mm) was about half that in August (22.0 mm).

On a section from the center of ring Bob at age 6 months to the Sargasso Sea, the vertical distribution of six chaetognath species deepened and the distribution of three shoaled (Fig. 6.52). There is presently no published information on the vertical distribution of zooplankton in warm-core rings.

Relation To Chemical And Physical Factors

The spatial and temporal patterns of plankton distributions summarized above are the result of physical and biological processes acting alone and in concert. Haury et al. (1978) reviewed major causative factors affecting plankton populations and the spatial and temporal scales upon which they might be expected to affect planktonic biotas. Although it seems self-evident that biological factors such as competition, predation, social interaction and reproduction should have a profound effect on plankton patterns, for the ACSAR area, there are few directly relevant data. Nor have there been many attempts to rigorously define the physical-chemical structure of the habitat of oceanic plankton in the area. The early work of Moore and co-workers (cited above) may have been severely compromised by fluctuations in vertical and horizontal distributions caused by (then unknown) flow reversals of the Florida Current (Stepien, 1980). This discussion will focus on the few recent reports which attempt to link changes in spatial pattern to the physical-chemical environment.

In the case of epipelagic and mesopelagic diel migrators, light is clearly one of the most important abiotic factors directly influencing vertical distributions. Vertical temperature structure also seems to play a crucial role in determining the vertical distribution of some zooplankton, but not others.

For example, vertical migration of warm water euphausiids of the genera Euphausia, Nematoscelis, and some Thysanopoda takes place regardless of season or vertical temperature structure. Vertical migration shown in Figure 6.49 took place when the upper 500 m of the Sargasso Sea was isothermal and the vertical extent of the populations and the depths inhabited during the daytime under isothermal conditions were generally similar to those observed under stratified conditions. Some species (N. microps, N. tenella, and T. aequalis) which appeared to cut short their migration into the surface waters as a result of the sharp thermocline, exhibited the same behavior when the thermocline was absent.

While temperature structure at or near the surface does not seem to affect the migration pattern of warm-water euphausiid species, abnormally colder water at depths does inhibit the daytime depth of migration. Thus, in the Slope Water and cold-core rings shoaling (100 to 300 m) occurs for both migrating and non-migrating species (Wiebe et al., 1976; Wiebe and Flierl, 1983).

Although vertical temperature structure would appear to be a major factor causing the shift in the vertical distribution of most if not all of these species, Wiebe and Flierl (1983) suggest it is not the only factor regulating these patterns. For one thing, when warm-water species are dispersed into a colder regime, temperature compensation is not perfect, i.e. species living at colder temperatures than is typical in their home range. Light penetration, at least for some species, appears to set an upper limit for shoaling. Stylocheiron elongatum individuals, for instance, do not occur at light levels higher

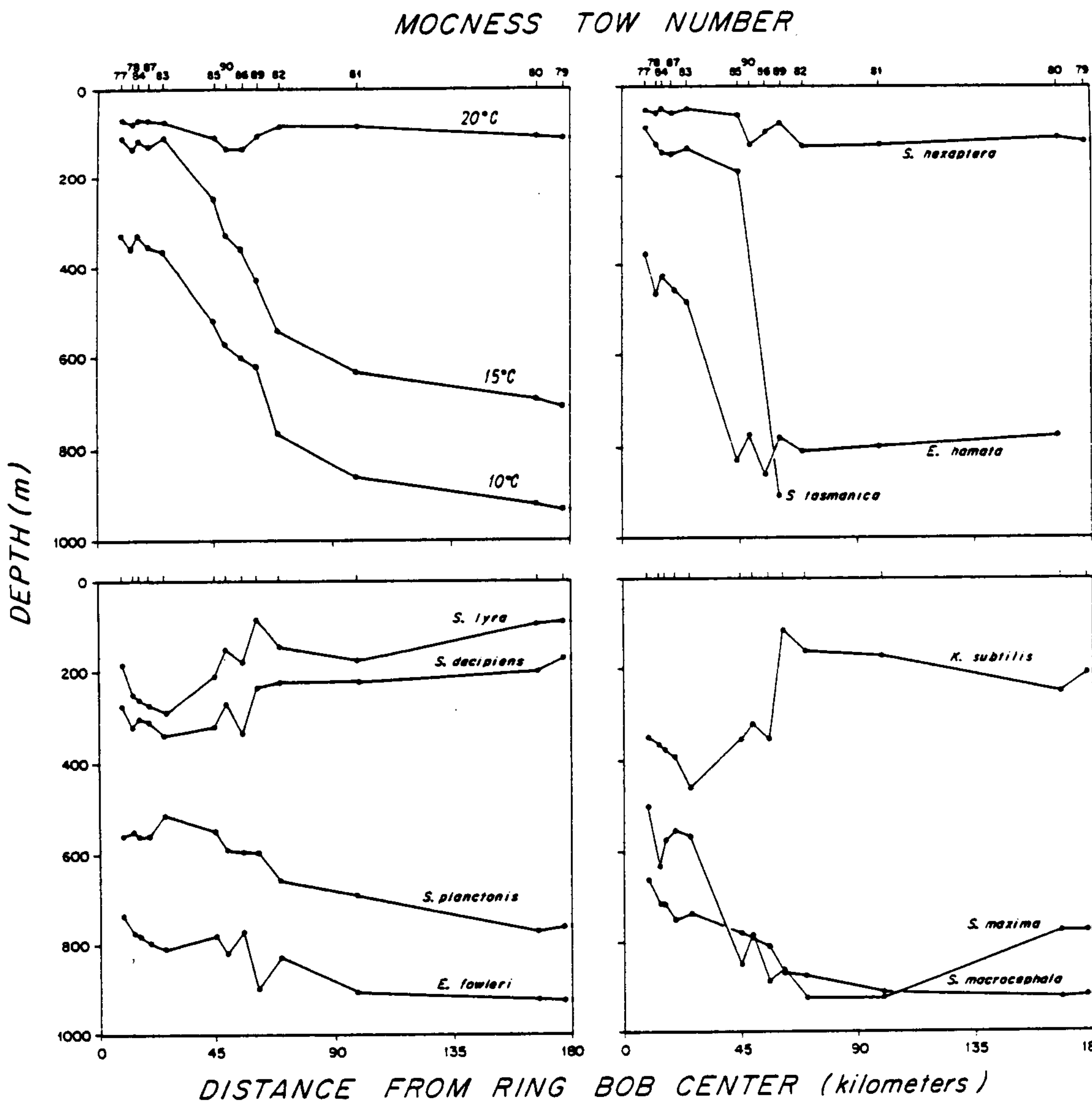


Figure 6.52. Isotherm depths and median depths of ten chaetognaths plotted as a function of distance from the center of Ring Bob. (from Cheney 1982).

than 10 μW/cm^2; optimal levels appears to be between 10^{-2} and 10^{-1} μW/cm^2 (Fig. 6.53). Optimal temperature appears to be 16-18°C, a range which frequently occurs in rings and in the Slope Water above the apparent upper limit for light. Thus individuals in these regions seem to be unable, because of light, to adjust their vertical distribution to find optimal temperatures. It remains to be determined whether temperature structure in combination with light levels sets limits on the day-time verti- cal distribution of warm-water diel migrating species of euphausiids listed above.

For some cold-water species vertical temperature structure appears to be a major determinant of their vertical distribution. For the non-migrator N. megalops, Wiebe and Boyd (1978), Wiebe et al. (1981), and Wiebe and Flierl (1983) found that the central 50 percent of the adult portion of the population generally stayed within about ± 2°C of the 10°C iosotherm in both the Slope Water and cold-core rings. In the Slope Water, this species is generally distributed above 300 m both day and night, while in aging rings, the center of the vertical distribution deepens coincidently with the sinking of isotherms and isohalines to below 300 m and deeper in an apparent attempt to stay in an 'optimal' temperature and salinity regime. Wiebe and Boyd argued that vertical temperature structure was the main factor to which N. megalops was responding in withdrawing from near surface layers. This change in vertical distribution as a ring ages appears to bring about changes in the physiology and biochemistry of this species which ultimately leads to local extinction. Data from Boyd et al. (1978) provide a picture of the ring population of N. megalops being physiologiclly stressed by the environmental changes associated with ring decay. In rings aged between 6 and 9 months, respiration rates of individuals declined from $\frac{1}{5}$ to $\frac{1}{20}$ th of the rates determined for the Slope Water populations. Furthermore, in older rings, adult males disappeared, production of eggs and larvae appeared to cease, and growth rates of individuals were markedly reduced relative to Slope Water individuals (Boyd et al., 1978). The conclusion was that as a ring decays, N. megalops tends to live deeper in the water column, away from the relatively food rich surface layers. Food levels are reduced to a point inadequate for growth and reproduction. In spite of a drastic lowering of the metabolic rate, body energy stores are used. Thus in older rings, individuals of this species appear to be in a state of starvation, and this probably is a major factor for demise of the ring population.

Cheney (1982) found that mixed layer depth played a major role in determining the vertical distribution of a majority of the epipelagic chaetognaths species. Krohnitta pacifica, Sagitta bipunctata, S. enflata, S. lyra, S. minima, and S. serratodentata, all appear limited primarily to the surface mixed layer. Cheney presumed that colder temperatures in the pycnocline limited depth, but he emphasized the need for higher resolution data. The median depth of only one epiplelagic species, the cold-water form S. tasmanica, was strongly correlated with temperature. As surface waters warmed and deepened, the center of vertical distribution was also found to be deeper.

For selected mesopelagic and bathypelagic species and one epipelagic species, S. hexaptera, Cheney observed that differences in vertical distribution were largely a function of differences in population size structure and population abundance as noted above. The fact that there were significant changes in size structure from one hydrographic regime to another gave rise to spurious correlations between median depth and environmental variables such as temperature and salinity for some species. This appeared to be the case for S. lyra and K. subtilis. It was also possibly true for the bathypelagic species, S. macrocephala and E. hamata, although Cheney concluded that there was insufficient data to distinguish between control of vertical distribution

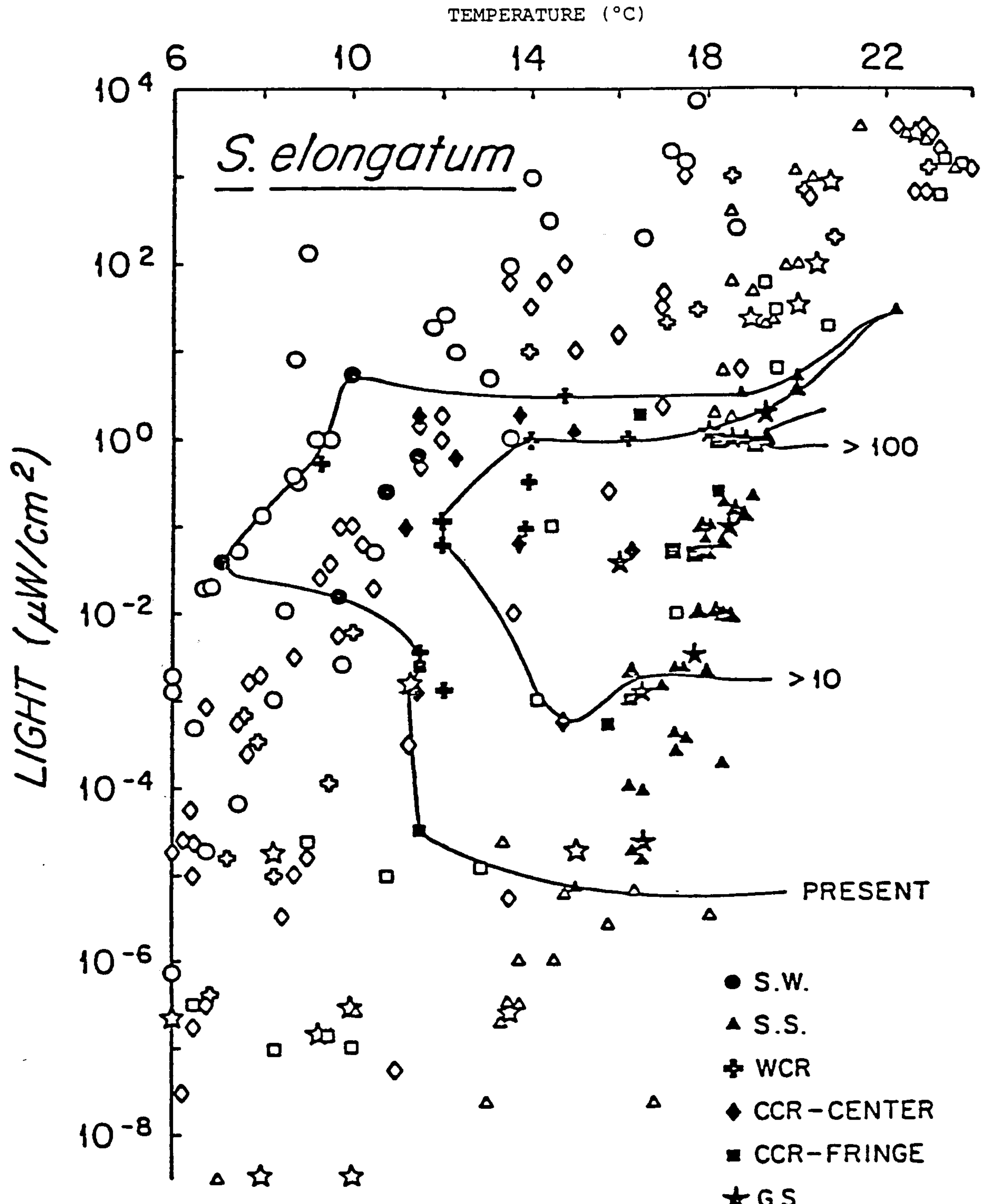


Figure 6.53. Abundance of Stylocheiron elongatum versus temperature and light for all MOCNESS taken during daytime in the Northwestern Atlantic. Open symbols represent samples taken in which no individuals of this species were present; blacked symbols represent positive occurrences. Small symbols represent fewer than 10 individuals present; medium sized symbols represent 10 to 99 individuals; large symbols represent 100 or greater individuals. The symbols are plotted at the mid-point of temperature and light for the depth strata sampled. The lines divide the observations into particular classes; for example, the line labelled ≥ 10 encloses all observations in which 10 or more individuals were found. Note that some of the samples within this area may contain fewer or no individuals.

by vertical temperature structure or population size structure for these species. Two species, S. decipiens and S. hexaptera, both ontogenetic migrators, showed no significant correlations to measured environmental variables nor were there significant shifts in vertical distribution between the Slope Water and the Sargasso Sea.

Light penetration did not appear to be a significant factor controlling the vertical distribution of any chaetognath species; there were no significant correlations between median depth of abundance and light at 100 m for any species.

While Cheney did not find salinity to be a major factor shaping the vertical distribution of the chaetognaths studied, he made one interesting observation. Epipelagic species which typically inhabited the surface Slope Water were severely reduced in numbers when low salinity water of shelf water origin was present in the Slope Water. This may reflect an intolerance to lower salinity water, but it is more likely due to physical displacement of them and their habitat.

Wormuth (1981) examined the relationship of temperature, salinity, and total zooplankton biomass to the abundance of each of the nine most abundant pteropods in his samples from the Sargasso Sea. Separate analyses were done for day and night tows to avoid complications caused by diel migration of some of the species. For the migrating species (Limacina inflata, L. bulimoides, L. lesueuri, and S. subula), none of the variables accounted for much of the population abundance variation during the day. In contrast, temperature was the dominant factor correlating with abundance changes for the migrators at night and for the non-migrators both day and night. Total zooplankton biomass was significant for only three species, Creseis acicula, C. virgula concia, and Clio pyramidata, and salinity was even less significant. Wormuth concluded that the depth distribution of these species showed no significant seasonal response to different thermal structures.

NEUSTON

The term "neuston" is generally defined as the plant and animal community that inhabits the narrow zone of the uppermost layer (perhaps 10 or 20 cm) of the ocean. Some authors have produced a complex of descriptive categories within the neuston. Hempel and Weikert (1972) group neuston components into three major ecological categories: (1) "euneuston": organisms with maximum abundance in the immediate vicinity of the surface where they stay day and night; (b) "facultative neuston": organisms which concentrate at the surface only at certain hours, mostly during darkness; (c)"pseudoneuston": maximum concentrations of these animals lie at deeper layers, but the range of their vertical distribution reaches the surface layer during certain hours. Zaitsev (1970) provides the following terms: (a) "pleuston": hydrobionts whose bodies are situated partly in the water and partly in the air (e.g. Portugese Man of War, Physali); (b) "epineuston": the aerial surface film organisms (e.g., the marine water strider, Halobates).

Interest in the marine neuston is quite recent and detailed information on the subject is therefore limited, including knowledge for the ACSAR area. The importance of the surface layer in the economy of the sea was first stressed by Zaitsev (1970), based largely on studies in the Black Sea. Neuston fauna is dominated by Crustacea and Cnidaria (Hempel and Weikert 1972; Morris, 1975) and within these groups copepods and siphonopnores are most dominant. The surface layer is also important to a wide variety of fishes (David, 1965;

Craddock, 1968). Zaitsev (1970) found evidence that this zone serves as an "incubator" for the reproductive stages of numerous fishes and crustaceans. Grant (1977, 1979) found a similar result for the neuston of the Middle Atlantic Bight and in addition found important qualitative differences between the neuston and subsurface zooplankton. In contrast studies over deep ocean depths in the northwest Atlantic (Morris, 1975) and the Gulf of Mexico (Berkowitz, 1976) have found the neuston layer to be impoverished compared with the subsurface.

STANDING CROP AND FAUNAL COMPOSITION

The general faunal composition of the neuston is affected by the diel vertical migration of animals (Craddock, 1968; Hempel and Weikert, 1972; Morris, 1975; Grant, 1979). There are very few enueustonts and the community is dominated by "facultative" animals from subsurface depths. Thus the majority of neuston animals have a maximum abundance during hours of darkness, therefore the faunal structure is temporally quite variable. Generalized patterns of diel variations for the various ecological groups composing the neuston are shown in Figure 6.54.

Neuston biomass in the North Atlantic reflects the general level of productivity in the underlying waters (Morris, 1975). Higher neuston biomasses occur in the more productive temperate and boreal coastal waters than in the subtropical and tropical waters of the open ocean. Thus the northeastern part of ACSAR likely has a higher neuston biomass than the southwestern areas (Gulf Stream and Sargasso Sea). Morris (1975) found that in autumn the waters of the Scotian Shelf and Slope Water have about four times the standing stock of neuston of the Gulf Stream or Sargasso Sea. Daytime neuston biomasses were found to fall within two ranges: (a) oligotrophic waters, such as the southeastern part of the report area (Sargasso Sea), where neuston wet weights generally average less than 25 mg m^{-3} and (b) eutrophic waters such as the temperate - boreal seas (northern part of the report area) where biomasses between 50 - 100 mg m^{-3} are found.

All regions show enhanced biomasses at night. Hempel and Weikert (1972) concluded that the magnitude of the nocturnal increase depended on several factors such as the abundance and composition of the subsurface zooplankton, hydrographic features of the water column, and depth to bottom. The deep ocean (>200 m) neuston at night is less enhanced by benthic migrants than that in shelf regions (Morris, 1975).

Seasonal Changes

Seasonal changes in the abundance of neuston is thought to reflect the changes in the subsurface waters, however this is not well understood.

No study has specifically examined the neuston of the ACSAR region. Since several biogeographic regions occur within the area, it is assumed that the neuston community shows complexity associated with these different regions and their interactions. Insight into parts of this community can be gained from neuston studies from adjacent waters.

Grant's (1977, 1979) study of the Middle Atlantic Bight had three stations beyond the 200 meter isobath, some of which were seasonally in Slope Water. Neuston collections showed a progressive change from a highly structured and predictable pattern in coastal waters to a relatively unpredictable faunal structure at the shelf edge, the latter dependent on incursions of offshore

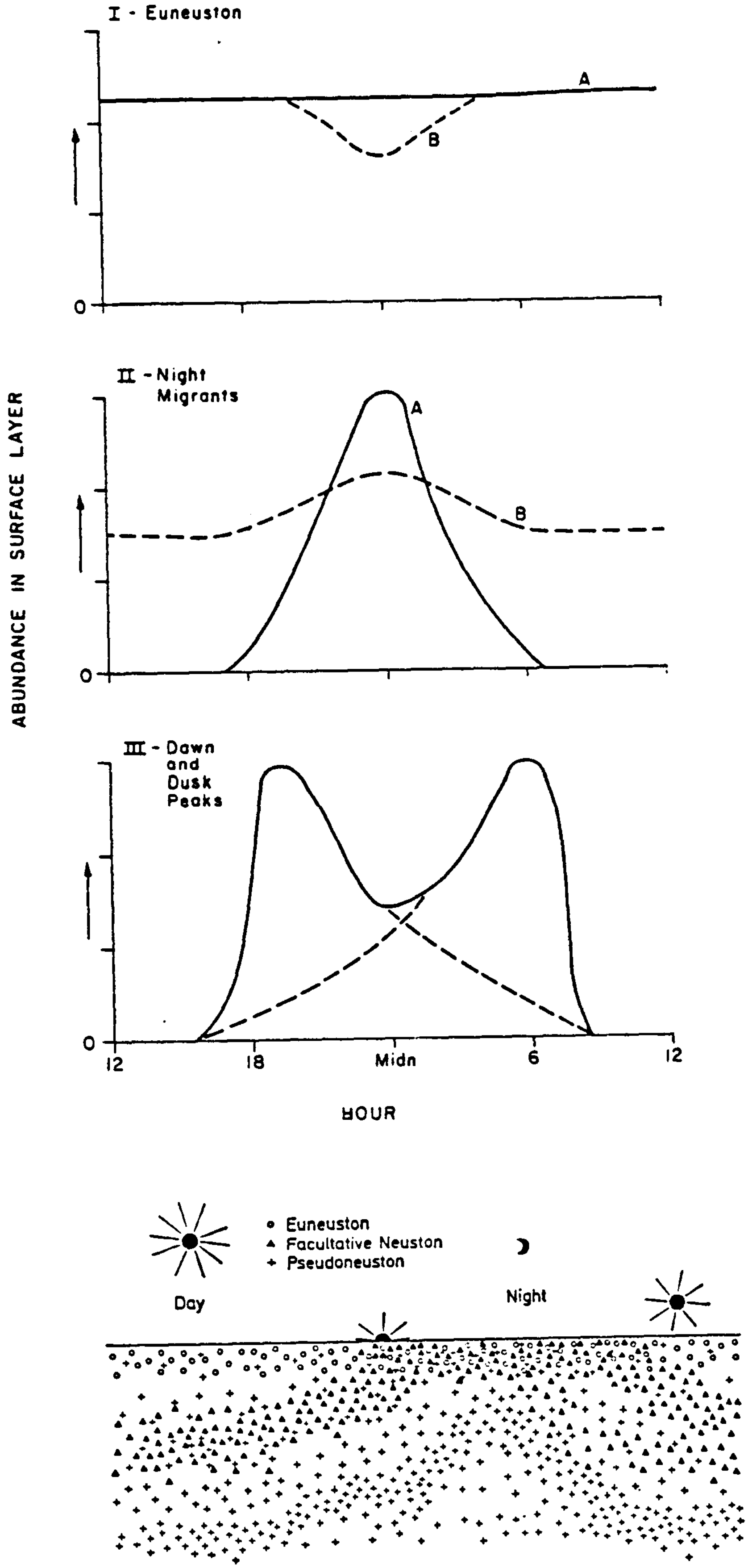


Figure 6.54. Generalized variations of diel concentrations of different neuston groups.

waters and the presence or recent passage of Gulf Stream warm-core rings. Copepods numerically dominated the neuston fauna at these deep stations in all seasons except spring when the salp Thalia democratica took over. Other important neustonts are amphipods (Parathemisto), euphausiids (Thysanoessa), and hake larvae (Urophycis). A list of seasonal numerical dominants is given (Table 6.22).

The National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration conducts seasonal ichthyoplankton and hydrographic (MARMAP) surveys which regularly tow neuston nets on the continental shelf with some stations in water deeper than 200 m. Although most of these data (1972-present) have not been examined, 16 spring and summer transects with deep shelf-edge stations were analyzed in the course of a seabird feeding ecology study (Powers and Backus, in review). Twelve deep stations were examined in a gross taxonomic fashion (e.g. copepods, fish eggs etc.) to determine dominant groups and particle size classes. All stations were dominated numerically by copepods, except one which was dominated by crab larvae. Other important neustons were amphipods, fish eggs, and euphausiids.

Smyth (1980) as part of the Middle Atlantic Bight study found crab larvae (Callinectes) in significantly greater abundance in neuston tows compared to subsurface collections. Megolopae of Callinectes were present at outer stations in winter and spring together with other decapod forms of southern origin.

Backus et al. (1977) made extensive neuston collections in the Slope Water south of Cape Cod and Georges Bank (300 - 2000 m). They found that many mesopelagic fishes occur regularly in the neuston of this region. Gonichthys cocco, by far the most common, has a strong affinity for the neuston layer (on one cruise 3,000 were caught neuston fishing while only 14 were caught mid-water trawling (Craddock, 1969). Subpolar/temperate, temperate, subtropical/tropical, and tropical species are represented, a species list is given (Table 6.23). While exploring primarily the mesopelagic fish fauna, their neuston tows also caught other fish of this zone. Dolphin (Coryphaena lippurus), butterfish (Peprilus triacanthus), flying fishes (Exocetidae), and filefishes (Alutera and Monocanthus) were most common (Craddock unpubl. data). A species list based on 270 summer tows is given (Table 6.24). It is interesting to note the regular presence of the commercially important species hake (Urophysis spp.), mackerel (Scomber sp.), and unidentified flatfish.

Neuston tows were made in early 1973 at 50 stations seaward of the 200 m curve between Cape Canaveral and Cape Fear (28° to 34°N) as part of two MARMAP cruises (Mathews and Pashuk, 1977). Ichthyoplankton catches in the offshore neuston were bigger and more widespread in May than in February-March (Powles and Stender, 1976). In winter, larvae of Mullidae Carangidae and Mugilidae were most numerous; a few larvae of other families (Sciaenidae, Clupeidae, Gadidae, Bothidae and Scombridae) were found, mostly north of 32°N. In May the most numerous catches were of Carangidae, Mugilidae, and Scombridaex, with some larval Pomatomidae. Significant differences between day and night hauls were found only with Serranidae, which were caught only at night on both cruises.

Neuston sampling along the shelf break south of New England was done by the U.S. Coast Guard in conjunction with MARMAP during all seasons between 1975 and 1982. The data are being worked up by Tossi and Benway (in preparation).

TABLE 6.22 Seasonally Dominant Zooplankters in the Deep Water Neuston of the Middle Atlantic Bight.

Fall	: *Parathemisto gaudichaudii* *Pleuromamma gracilis* *Centropages typicus* *Nannocalanus minor* Unidentified Fish eggs *Lestrigonus bengalensis* *Temora stylifera* *Thysanoessa* spp.	 *Idotea metallica* *Paracalanus* spp.
Winter	: *C. typicus* *Anomolocera ornata* *P. gaudichaudii* *Metridia lucens* *Urophycis* spp.	*Calanus finmarchicus* *P. gracilis* *N. minor* *Clausocalonus arcnicornis* *Euphausia* spp.
Spring	: *Thalia democratica* *C. typicus* *P. gaudichandii* *Sapphirina ovatolanceolata* *P. gracilis*	
Summer	: *Labidocera* spp. *T. stylifera* *L. bengalensis* *Undiaula vulgaris* *Penilia avirostris* *N. minor*	

TABLE 6.23 Mesopelagid Fishes Found in the Neuston of the ACSAR region.

<u>Gonichthys cocco</u> *
<u>Centrobranchus nigroocellatus</u> *
<u>Gompylus serpens</u>
<u>Diaphus dumerili</u>
<u>Hygophum hygomi</u>
<u>Myctophum puctatum</u>
<u>M. nitidulum</u>
<u>M. obtusirostre</u>
<u>M. asperum</u>
<u>M. affine</u>
<u>Symbolophorus veryani</u>

* common

TABLE 6.24 Fishes Found in the Neuston of the ACSAR region (excluding mesopelagics).

Bonito - *Sarda* sp.

Butterfish - *Prionotus triacanthus*

Dolphin - *Coryphaena hippurus*

Flatfishes (larval)

Filefishes - *Alutera* and *Monocanthus*

Flying Fishes - *Exocetidae*

Hakes - *Urophycis* spp.

Jacks - *Caranx* spp.

Lizardfishes - *Synodus* spp.

Mackerel - *Scomber* sp.

Mullet - *Mugil* sp.

Puffer - *Sphaeroides* sp.

Triggerfish - *Bolistes* spp.

Pilotfishes - *Naucrates* spp.

The Slope Water surveys of the Soviet Fishery Research Vessel Stvor in the fall of 1981 included 142 neuston tows, which have not been analyzed. In February, 1983, 50 neuston tows were made from the Canadian R/V Alfred Needler along the northern edge of the Gulf Stream between 31°N and Cape Hatteras. Chief Scientist was T.W. Rowell of the Department of Fish and Oceans, Halifax.

Three other well-known neustonts are present in the study area. Halobates micans, the marine water strider is an epineustont (Scheltema, 1967). Portugese Man of War (Physalia physalis) and Velella (the "by the wind sailor") are both siphonophore pleustonic animals (David, 1965). All three are found regularly in the subtropical waters south of Cape Hatteras and in the Gulf Stream but the seasonality of their occurrence there is not known. Appearances of these animals in the temperate northern part of the region occur mostly in summer or perhaps with Gulf Stream warm-core rings.

PLASTICS AND PETROLEUM WASTES

The presence of plastics and petroleum wastes are well-known components of the neuston (Backus, 1968; Morris, 1971). Colton et al. (1974) analyzed neuston tows taken during the first NMFS MARMAP survey in summer 1972 (which was widespread compared to subsequent years). Fish larvae from the same series of cruises have been identified and counted by NMFS but the data have not been published (Maurer, personal communication). Sixty-nine percent of neuston samples collected in coastal, slope, and Gulf Stream waters between Florida and Cape Cod contained various types of plastic particles. None, however, were found in coastal and Gulf Stream waters south of Cape Lookout, NC. While the greatest concentrations were in the coastal waters of southern New England and Long Island Plastics occurred regularly in lesser amounts in the off-shelf waters of the report area. The sources of these particles is believed to be disposed at sea by ships and water-borne wastes from U.S. east coast manufacturing plants. Plastics are currently not known to have serious deleterious effects on environments, but they are non-biodegradable and their concentrations in the study region are suspected to be increasing.

No study has examined the quality and distribution of neuston petroleum wastes but they are known to occur regularly in the report area at various depths mostly as a result of shipping traffic.

MESOPELAGIC FISHES

Mesopelagic fishes are a conspicuous element in the marine fauna everywhere seaward of the edges of the continental shelves. Although the mature stages of many species escape the small midwater trawls used to collect these fishes for scientific purposes, a number of species mature at lengths as short as 25 or 30 mm, and it can be said that as a whole the mesopelagic fish fauna consists of small species. (Many larger shallow species are discussed in Chapter 7; p. 7.)

These fishes inhabit the water column from the surface to a little beyond the limit of penetration of daylight--about 1000 m. Many species, if not most, make a pronounced light-controlled diel vertical migration, spending the night somewhere in the upper 100 m and the day 500 meters or more deeper. Most of the species are large-eyed, large-mouthed, sharp-toothed carnivores, eating such things as copepods, euphausiids, and other fishes smaller than themselves. Most species are bioluminescent. Many have gas-filled swimbladders and thus are effective sound-scatterers, responsible for the so-called "deep scattering layers" so often conspicuous on echo-sounder records.

These fishes have been collected mainly by nets with mouth areas of 3 to 8 m^2, but recently nets as large as 20 m^2 have been used routinely. More importantly, nets of recent design have allowed better resolution of depth of capture and better calculation of water volume filtered. For instance, the MOCNESS-10 and MOCNESS-20, scaled-up versions of the MOCNESS-1 (Wiebe et al., 1976), consist of sets of nets that can be opened and closed by command from the surface via an electrically conducting towing warp. Apparatus attached to the net frame measures and transmits temperature, salinity, depth, flow and net-frame angle to the towing ship's laboratory. The area of the projected net mouth is about 10 m^2 in the MOCNESS-10 and about 20 m^2 in the MOCNESS-20 when the nets are in the common fishing attitude.

These and the other mid-water trawls upon which mesopelagic fish studies are generally based, sample fishes down to a length of about 7 or 8 mm. Smaller fishes escape these trawls. This cut-off point approximately coincides with the length at which many of the fishes studied transform from larva to juvenile. Thus, studies of the sort reported here are based on the examination of juveniles and adults. Larval fishes of open waters are generally taken to comprise the so-called "ichthyoplankton". So far as the writer is aware, there are no studies of the ichthyoplankton of the ACSAR area.

ZOOGEOGRAPHIC BACKGROUND

The North Atlantic mesopelagial can be divided into six faunal regions - four ocean-spanning ones - the Atlantic Tropical, the North Atlantic Subtropical, the North Atlantic Temperate, and the Atlantic Subarctic Regions, plus two small, marginal regions, the Mauritanian Upwelling Region and the Gulf of Mexico. As explained earlier, the ACSAR area spans the western extremities of two of these regions. The northeastern part of the study area lies in the Slope Water, a province of the North Atlantic Temperate Region, while the southwestern part of the study area lies in the Northern Sargasso Sea, a province of the North Atlantic Subtropical Region. From a zoogeographical standpoint, the Florida Current and its continuation, the Gulf Stream, are considered special parts of the Northern Sargasso Sea. The first bounds the southwestern part of the study area at its western extremity, the second divides the study area into its two main parts--a northeastern temperate one and a southwestern subtropical one.

Mesopelagic fishes and other pelagic species of temperate and subpolar-temperate distribution find the southern limit of their western North Atlantic range at the Gulf Stream - Slope Water boundary, i.e., the boundary between the northeastern and southwestern parts of ACSAR. The same boundary sets the northern limit in the west for species of subtropical and tropical-subtropical distribution. Tropical and tropical-semisubtropical species originating in the Caribbean Sea, the westernmost province of the Atlantic Tropical Region, are swept north by the Florida Current and Gulf Stream. (Backus et al., 1977).

Not all species are limited by the Gulf Stream - Slope Water boundary, of course. Temperate-semisubtropical ones, for instance, normally live in Northern Sargasso Sea and Slope Water alike. However, species living on both sides of this important boundary may have different vertical distributions in the two domains.

A convenient way of locating oneself in the complex and highly variable environment of the Gulf Stream region is to observe the depth to 15° C. A depth of 200 m for 15° is generally considered to mark the northern edge of the Gulf Stream and, so, draw the boundary between Slope Water, where 15° is shallower, and the Gulf Stream and Northern Sargasso Sea, where 15° is deeper than 200 m. (The depth to 10° C has been similarly used.)

A further complication in the distribution of pelagic animals and plants in this corner of the North Atlantic is the formation, wandering, and dissipation of the large eddies known as Gulf Stream rings (Chapter 3). A biotic result of cold-core ring formation is the translation across the Gulf Stream of a temperate fauna and flora into a subtropical environment, while the opposite happens in the case of warm-core rings. In both cases, tropical plants and animals are detached from the Gulf Stream. Whatever their normal range, the local distribution of all species in the Gulf Stream region is altered by the formation, dissipation, and reincorporation with the Gulf Stream of both kinds of rings.

MESOPELAGIC FISH RESEARCH IN THE STUDY AREA

The principal studies of mesopelagic fishes in the ACSAR area are (chronologically) as follows:

Backus et al. (1969) contrasted the mesopelagic fish faunas of the Northern and Southern Sargasso Seas. Information relating to the former is pertinent to the southwestern, subtropical part of the study area.

Backus et al. (1970) described the distribution of mesopelagic fishes in the equatorial and western North Atlantic and gave zoogeographic information for both the Slope Water and Northern Sargasso Sea.

Jahn and Backus (1976) compared the mesopelagic fish faunas of Slope Water, Gulf Stream, and Northern Sargasso Sea.

Jahn, A. E. (1976) studied mesopelagic fishes in cold-core Gulf Stream rings and necessarily compares Slope Water and Northern Sargasso Sea.

Krueger et al. (1977) summarized what was learned in an investigation of mesopelagic fishes at Deepwater Dumpsite 106, located in the ACSAR area at 38° 50'N, 72° 15'W. During part of this study the dumpsite was under the influence of warm-core rings, part of the time occupied by more typical Slope Water.

Backus and Craddock (1977) and Backus et al. (1977) described faunal regions and provinces for the Atlantic Ocean and provided information about mesopelagic fishes in the Slope Water and Northern Sargasso Sea.

Backus and Craddock (1982) studied mesopelagic fishes in cold-core Gulf Stream rings and made comparisons of the fauna of the rings with those of Northern Sargasso Sea and Slope Water.

Other papers in preparation by Backus and Craddock contain information on mesopelagic fishes in the Florida Current and on fishes of the mesopelagic genus Cyclothone in the Gulf Stream region, but information from these incomplete works is not included here.

Because the study area is such a patchwork of environmentally distinct areas--Slope Water, Northern Sargasso Sea, Florida Current, and Gulf Stream--it has a very rich mesopelagic fish fauna. If a simple list were to be made of all the species that have been collected in the study area, it would number in the hundreds of species. Such a list, making no distinction between the very common and the very rare, would be of interest only for its length. Modern biological oceanography, instead, concentrates on describing areas of the ocean in terms of its most abundant and characteristic species.

Here we pay attention mainly to the ecologically important families Myctophidae, the lantern-fishes, and Gonostomatidae, sometimes called "pearl-sides". (We use Gonostomatidae in a broad sense to include Gonostomatidae, Photichthyidae, and Sternoptychidae.) Fishes in these families make up most (in numbers of individuals and in their displacement volume) of the mesopelagic fishes caught wherever in the world ocean the biologist's midwater trawl is towed. For instance, in an elaborate study of the upper 1000 m off the Canary Islands, Badcock (1970) found that myctophids and gonostomatids together made up about 80% of the midwater fish fauna as a whole, and this may be typical of mesopelagic communities in general.

The Mesopelagic Fish Fauna of the Slope Water

The best description of the mesopelagic fish fauna of the Slope Water is found in Backus and Craddock (1982). Table 6.25, which lists the 20 most abundant myctophid and gonostomatid fishes excluding Cyclothone species, comes from a set of 12 collections made where the 15° C isotherm was shallower than 100 m in Slope Water and in newly formed cold-core rings. Although these species show diverse patterns so far as their Atlantic-wide ranges go, the basically temperate character of the Slope Water fauna is well shown. The four most abundant species in the set (accounting for 76 percent of the specimens) are of subpolar-temperate (Benthosema glaciale, 51% of the total number of specimens in the set), temperate (Ceratoscopelus maderensis, 13%), and temperate-semisubtropical (Hygophum hygomii and Lobianchia dofleini, 13%) distribution. Of the remaining species in Table 6.25, most are broadly distributed in the tropical and subtropical Atlantic and probably reflect both the more or less continuous input of alien species into the Slope Water by the means of warm-core rings and the modification of the Slope Water as a habitat by the same mechanism. Indeed, four species--Diaphus dumerilii, Lampanyctus alatus, Lepidophanes guentheri, and Myctophum affine-- having otherwise tropical ranges, may actually reproduce in the Slope Water.

Jahn and Backus (1976) described the Slope Water mesopelagic fish fauna from two dozen collections in which the Slope Water criterion (in addition to a simple geographical one) was that the depth to 15° C was less than 200 m. The three most abundant species in their set--Lobianchia dofleini, Benthosema glaciale, and Ceratoscopelus maderensis--are among the top four in the Slope Water set of Backus and Craddock (1982). Most samples taken in the Slope Water (excluding warm-core rings) will show principal species much like Table 6.25, which can be taken as descriptive of the mesopelagic fish fauna in the northeastern, temperate part of the study area. The actual catch-rates shown can be expected to vary widely depending upon seasonal and other factors.

The Mesopelagic Fish Fauna of the Northern Sargasso Sea

The 20 most abundant species in the Northern Sargasso Sea are to be found in Table 6.26, based upon 12 stations made seaward of the Gulf Stream where 15° was deeper than 450 m (Backus and Craddock, 1982). This set shows a more equitable abundance among species than does the Slope Water set. The four most abundant species account for only 45 percent of the total, while 10 to 11 species are required to account for the 76 percent that the four most abundant species in the Slope Water set comprised of the total there.

Table 6.25 - Slope Water mesopelagic fishes, 20 most abundant
(from Backus and Craddock, 1982)

This table describes the mesopelagic fish fauna of the temperate, northeastern part of the study area with the exceptions noted in the text.

Rank*	Species	Number caught	Catch/ $10000m^3$	Sargasso Sea rank	Sargasso Sea rate
1.	*Benthosema glaciale*	1550	10.14	-	.03
2.	*Ceratoscopelus maderensis*	381	2.49	3	1.00
3.	*Hygophum hygomii*	209	1.37	5	.95
4.	*Lobianchia dofleini*	176	1.15	19	.24
5.	*Lampanyctus alatus*	92	.60	-	.14
6.	*Sternoptyx diaphana*	77	.50	12	.42
7.	*Lepidophanes guentheri*	64	.42	-	.20
8.	*Benthosema suborbitale*	55	.36	-	.14
9.	*Hygophum benoiti*	53	.35	14	.34
10.	*Notolychnus valdiviae*	47	.31	6	.73
11.	*Lampanyctus crocodilus*	41	.27	16	.32
12.	*Ceratoscopelus warmingii*	39	.26	1	2.38
13.	*Myctophum affine*	37	.24	-	.02
14.	*Gonostoma elongatum*	36	.24	11	.44
15.	*Notoscopelus resplendens*	34	.22	20	.24
16	*Bolinichthys indicus*	31	.20	4	.97
17	*Diaphus dumerilii*	31	.20	-	.02
18.	*Diogenichthys atlanticus*	31	.20	8	.55
19.	*Hygophum taaningi*	29	.19	-	.15
20.	*Lampanyctus cuprarius*	28	.18	10	.45

*With samples of the size taken ranks after 5 or 6 should not be regarded seriously according to Miller and Wiebe (McGowan 1971).

Table 6.26 - Northern Sargasso Sea mesopelagic fishes, 20 most abundant (from Backus and Craddock, 1982)

This table describes the mesopelagic fish fauna of the southwestern, subtropical part of the study area with the exceptions noted in the text.

Rank	Species	Number caught	Catch/ $10000m^3$	Slope rank	Water rate
1.	Ceratoscopelus warmingii	311	2.38	12	.26
2.	Argyropelecus hemigymnus	171	1.31	-	.16
3.	Ceratoscopelus maderensis	131	1.00	2	2.49
4.	Bolinichthys indicus	127	.97	16	.20
5.	Hygophum hygomii	125	.95	3	1.37
6.	Notolychnus valdiviae	96	.73	10	.31
7.	Lampanyctus pusillus	78	.60	-	.16
8.	Diogenichthys atlanticus	72	.55	18	.20
9.	Bonapartia pedaliota	66	.50		
10.	Lampanyctus cuprarius	59	.45	20	.18
11.	Gonostoma elongatum	58	.44	14	.24
12.	Sternoptyx diaphana	55	.42	6	.50
13.	Pollichthys mauli	52	.40		
14.	Hygophum benoiti	45	.34	9	.35
15.	Lepidophanes gaussi	43	.33	-	.01
16.	Lampanyctus crocodilus	42	.32	11	.27
17.	Vinciguerria attenuata	42	.32	-	.10
18.	Argyropelecus aculeatus	36	.28	-	.07
19.	Valenciennellus tripunctulatus	35	.27	-	.18
20.	Lobianchia dofleini	32	.24	-	1.15

The distribution patterns for the first ten fish on the list are, with one exception, those to be expected for a subtropical faunal province: tropical-subtropical (Ceratoscopelus warmingii and Bonopartia pedaliota, 23% of total specimens), tropical-subtropical-temperate (Argyropelecus hemigymnus and Notolychnus valdiviae, 16%), temperate-semisubtropical (Hygophum hygomii and Lampanyctus pusillus, 13%), subtropical (Bolinichthys indicus and Lampanyctus cuprarius, 12%), and tropical-subtropical-Slope Water (Diogenichthys atlanticus, 4%). A temperate species, Ceratoscopelus maderensis, 8%, is the exception. It occurs in the Sargasso Sea set by virtue of cold-core ring transport (Backus and Craddock, 1982). Close comparisons of catch rates of species between Table 6.25 and Table 6.27 should not be made, because the abundance of some species is a function of season, and samples were not distributed uniformly by season in the two sets.

Jahn and Backus (1976) described the midwater fish fauna of the Northern Sargasso Sea from 20 collections. The most abundant species in their set, Ceratoscopelus warmingii, is the same as that in the set of Backus and Craddock (1982) and their top four species fall within the top eight (Table 6.27). The fauna described in Table 6.27 applies to the southwestern, subtropical part of the study area except that the western extremity of that part, the western part of the Florida Current, can be expected to carry a more tropical mesopelagic fish fauna (see below).

The Mesopelagic Fish Fauna of the Gulf Stream and the Slope Water and Sargasso Sea Further Compared

The mesopelagic fish fauna of the Gulf Stream itself has not been thoroughly studied, although it is known to carry some vestiges of a tropical fauna. Jahn and Backus (1976) studied sets of mesopelagic fishes from Slope Water (200-m temp. <15°C), Gulf Stream (200-m temp. 15-17.5°C), and Northern Sargasso Sea (200-m temp. >17.5°C). A similarity measure showed the Slope Water set to be about equally distinct from the Gulf Stream and Northern Sargasso Sea sets (percentage of similarity 39 and 36 respectively), while the last two were somewhat similar (PS 57). A cluster analysis showed the Gulf Stream set to be intermediate between the distinct Slope Water and Northern Sargasso Sea sets, but suggested that the Gulf Stream fauna was not simply a mixture of the other two faunas.

The Northern Sargasso Sea Fauna as Modified by Cold-Core Gulf Stream Rings

The southwestern, subtropical part of the study area can be expected to have a fauna normal for the Northern Sargasso Sea (Table 6.26), except in those parts temporarily occupied by cold-core Gulf Stream rings. Because the cold-core rings entering this part of the study area are aged, the fauna that they carry is not much different from the normal one of the Northern Sargasso Sea. Table 6.27 shows the 20 most abundant species at 15 stations at various places in several cold-core rings, the depth to 15°C at these stations varying from 100-450 m. A cold-core ring in the southwestern, subtropical part of the study area would have a mesopelagic fish fauna intermediate between the faunas shown in Tables 6.26 and 6.27.

The Fauna of the Westernmost Slope Water as Modified by Warm-Core Gulf Stream Rings

The way in which the Slope Water mesopelagic fish fauna is modified by the presence of warm-core rings is being studied by R. H. Backus and colleagues at the WHOI. Presumably a newly formed warm-core ring has a mesopelagic fish

Table 6.27 - Mesopelagic fishes in cold-core Gulf Stream rings, 20 most abundant

The table compares the fauna in cold-core rings with that of Slope Water and Northern Sargasso Sea. See text.

Rank	Species	Number caught	Catch/ $10000m^3$	Slope Water rank	Slope Water rate	Sargasso Sea rank	Sargasso Sea rate
1.	Ceratoscopelus maderensis	1223	7.29	2	2.49	3	1.00
2.	Benthosema glaciale	933	5.56	1	10.14	-	.03
3.	Lampanyctus pusillus	272	1.62	-	.16	7	.60
4.	Argyropelecus hemigymnus	256	1.53	-	.16	2	1.31
5.	Ceratoscopelus warmingii	169	1.01	12	.26	1	2.38
6.	Bolinichthys indicus	164	.98	16	.20	4	.97
7.	Hygophum benoiti	161	.96	9	.35	14	.34
8.	Lampanyctus crocodilus	117	.70	11	.27	16	.32
9.	Notolychnus valdiviae	84	.50	10	.31	6	.73
10.	Vinciguerria attenuata	82	.49	-	.10	17	.32
11.	Lampanyctus photonotus	70	.42	-	.07	-	.23
12.	Lobianchia dofleini	62	.37	4	1.15	19	.24
13.	Lepidophanes guentheri	57	.34	7	.42	-	.20
14.	Argyropelecus aculeatus	52	.31	-	.07	17	.28
15.	Valenciennellus tripunctulatus	51	.30	-	.18	18	.27
16.	Diogenichthys atlanticus	47	.28	18	.20	8	.55
17.	Diaphus mollis	43	.26	-	.04	-	.16
18.	Gonostoma elongatum	36	.21	14	.24	11	.44
19.	Lampanyctus alatus	36	.21	5	.60	-	.14
20.	Benthosema suborbitale	30	.18	8	.18	-	.14

fauna at its center very much like the one of the Northern Sargasso Sea (Table 6.26). This fauna presumably becomes more and more like the fauna of the Slope Water (Table 6.25) with ring age. It is possible, if not probable, that the westernmost part of the Slope Water has a mesopelagic fish fauna somewhat different from the remainder of the Slope Water because of a continual replenishment of warm-water species and quasi-permanent modification of the habitat by warm-core rings. It can be assumed for the time being that the mesopelagic fish fauna of this part of the study area is somewhat intermediate between the faunas described in Tables 6.25 and 6.26.

The Tropical Component of the Mesopelagic Fish Fauna of the Florida Current

As explained above, the western portion of the southwestern, subtropical part of the study area is occupied by the Florida Current; the current is divisible into an eastern, subtropical filament and a western, tropical filament. The description of the Northern Sargasso Sea mesopelagic fish fauna in Table 6.26 approximately describes the fauna to be found in the subtropical filament of the Florida Current. The fauna of the western, tropical filament and the way in which it differs from the fauna of the eastern filament is the subject of a study in progress (Craddock and Backus, in preparation). In the meantime, the myctophid element of the western, tropical filament of the Florida Current can be approximated by the description of the myctophid fauna of the whole Atlantic Tropical Region given by Backus et al. (1977) (Table 6.28).

THE DISPLACEMENT VOLUME OF MESOPELAGIC FISHES IN THE STUDY AREA

There are relatively few good data on the displacement volume of mesopelagic fishes in the study area. Generally speaking the northeastern, temperate part supports a larger standing crop than the southwestern, subtropical part. Gulf Stream cold-core rings are intermediate in this regard, but there are no data as yet for Gulf Stream warm-core rings.

Fig. 6.55 shows the biomass (ml 10,000 m^3 for the water column 0-1000 m) of myctophids plus "gonostomatids" (excluding Gonostoma elongatum and Cyclothone spp.) for the several stations plotted against the depth to 15°C. The general inverse relation between biomass and depth to 15° is evident and shows the reduction in standing crop by several-fold that others have described in going from Slope Water to Northern Sargasso Sea (Grice and Hart, 1962 for epizooplankton, about 4:1; Jahn and Backus, 1976 for mesopelagic fishes with about 60 percent of the fishing effort above 200 m, about 4.5:1; Jahn, 1976 for mesopelagic fishes 0-1000 m, about 2:1; and Ortner et al., 1978, for zooplankton 0-750 m, 3.5:1).

Biomass data for the deep-living Cyclothone spp. (Fig. 6.56) suggest a relationship among the sets similar to that for myctophids-"gonostomatids", but the Slope Water Northern Sargasso Sea ratio appears to be less - 2 or 3:1, rather than 4 or 5:1.

THE NORTHERN EDGE OF THE GULF STREAM AS A FAUNAL BOUNDARY BETWEEN THE TWO PARTS OF THE STUDY AREA

The northern edge of the Gulf Stream forms a sharp southern limit to the normal range of many cold-water animals. The transgression of this boundary by such animals can be explained readily in terms of transport by cold-core rings. The reverse effect is not so clear; that is, the northern edge of the

Table 6.28- Ranking Myctophidae (lanternfishes) in the western Atlantic Tropical Region (adapted from Backus et al., 1977)

This table can be used to approximate the abundance ranks of the most abundant myctophid species in the western, tropical filament of the Florida Current, the westernmost extremity of the southwestern part of the study area of the present report.

Rank	Species
1	Lepidophanes guentheri
2	Diaphus dumerilii
3	Ceratoscopelus warmingii
4	Notolychnus valdiviae
5	Benthosema suborbitale
6	Lampanyctus alatus
7	Diogenichthys atlanticus
8	Diaphus luetkeni
9	Hygophum macrochir
10	Diaphus brachycephalus

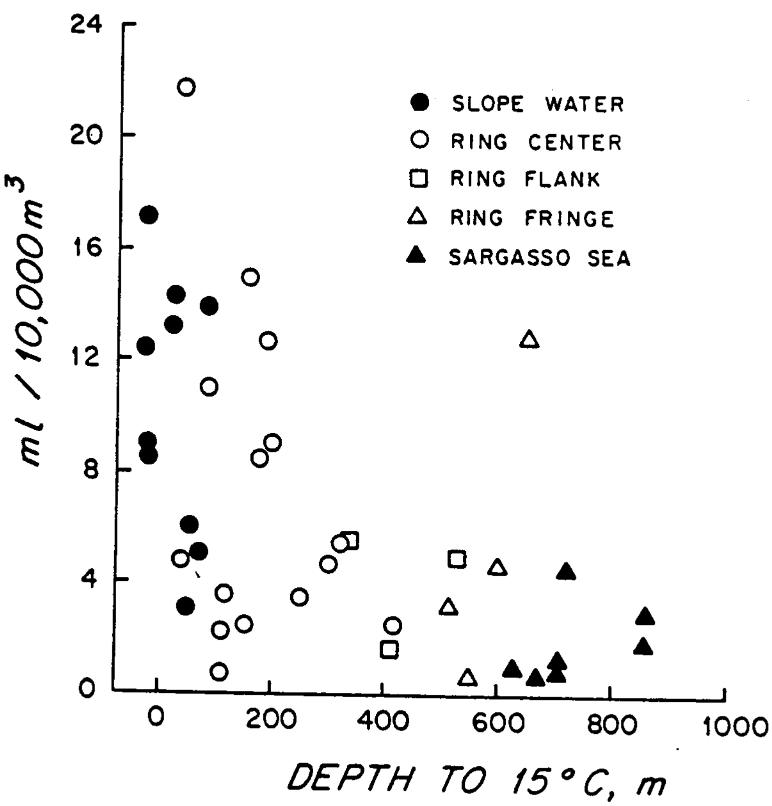


Figure 6.55. Myctophid-"gonostomatid" biomass as a function of depth to 15°C. The four points to the left of depth zerc represent stations at which the surface temperature was less than 15°. From Backus and Craddock (1982).

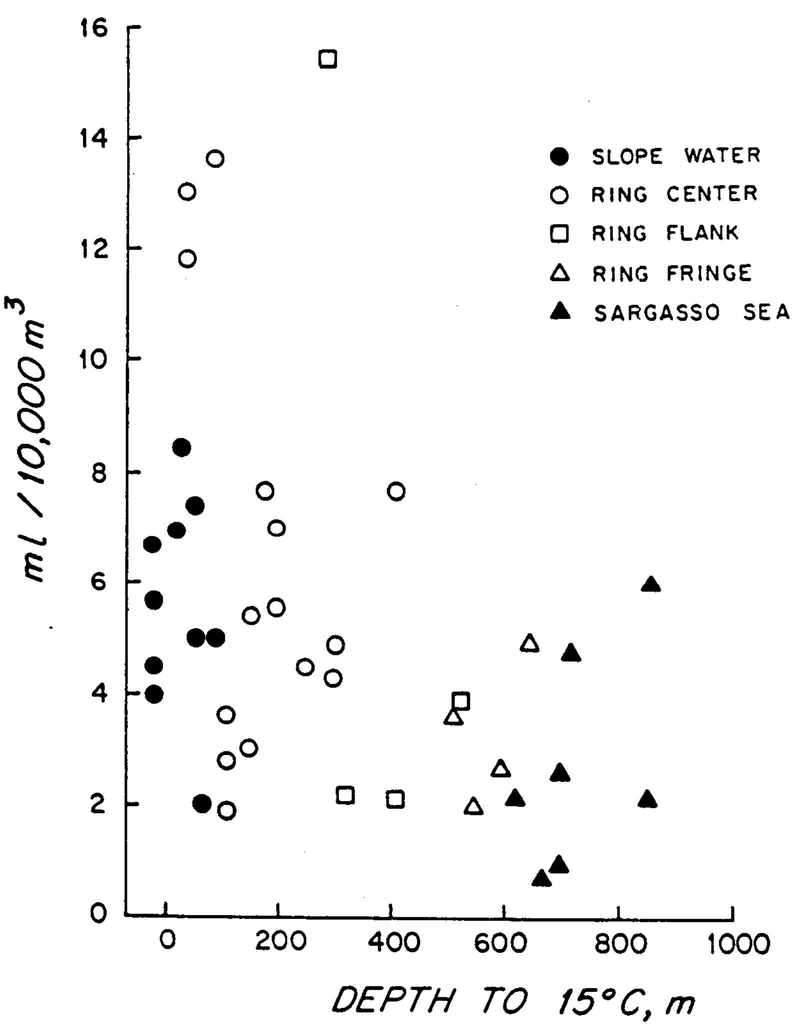


Figure 6.56. Cyclothone spp. biomass as a function of depth to 15°C. The four points to the left of depth zero represent stations at which the surface temperature was less than 15°. The four high points, from the center and flank of Ring "Bob", are considered exceptional. They may be within the normal range of variation for the Slope Water, although they exceed the Slope Water values observed on the Rings Cruises. From Backus and Craddock (1982).

Gulf Stream does not form so sharp a northern limit to the range of warm-water animals inhabiting the Northern Sargasso Sea, and it is far commoner to find midwater fishes of various warm-water distribution patterns in the Slope Water than it is to find fishes of cold-water distribution patterns in the Northern Sargasso Sea. This can probably be related (1) to differences in the effects that cold-core rings and warm-core rings have on the environments that they invade and (2) to differences between the pressures exerted by the two environments on foreign organisms.

According to the Ring Group (1981), the area of the Northern Sargasso Sea affected by cold-core rings is about 3×10^{12} m^2. On the other hand, the area of the Slope Water, into which warm-core rings intrude, is only about 0.5×10^{12} m^2 (Jahn, 1976). If mass is preserved by the formation of a warm-core ring for each cold-core ring formed, then the gross effect of warm-core rings on the Slope Water is about six times that of cold-core rings on the Northern Sargasso Sea. Thus, even if the midwater fish biomass of the Slope Water were three times that of the Northern Sargasso Sea, expatriates from the Sargasso Sea in the Slope Water would be twice as available as Slope Water expatriates in the Sargasso Sea, assuming equal survival and uniform dispersal.

But, a warm-core ring cannot be viewed simply as a vehicle by which plants and animals are carried into a foreign environment. If a warm-core ring has a volume of 3×10^{13} m^3 (Ring Group 1981) and eight rings per year enter the Slope Water (ibid.), whose volume is 0.5×10^{12} $m^2 \times 1000$ m or 0.5×10^{15} m^3 (Jahn, 1976), then about half of the Slope Water will be replaced each year by the rings were the rings to mix into the Slope Water completely. The common fate of a warm-core ring is to drift westward and coalesce with the Gulf Stream in the vicinity of Cape Hatteras after a lifetime of about seven months. There seem to be no estimates of how much of a ring, on the average, is mixed away in the Slope Water and how much of it is reabsorbed by the Gulf Stream. Thus, there is a large, virtually continual, input of Western North Atlantic Water from the Northern Sargasso Sea into the Slope Water, as well as the input of some water of tropical origin from the Gulf Stream itself, that significantly contributes to the Slope Water's character as a habitat for plants and animals. It is mainly this contribution that makes the Slope Water, particularly that part of it which is of concern in the present report, faunally distinct from the other provinces of the North Atlantic Temperate Region (Backus et al., 1977) and possibly a place where certain animals of otherwise warm-water distribution can reproduce as noted above.

CETACEA - WHALES AND PORPOISES

INTRODUCTION

There are no books or papers devoted precisely to the relative abundance of the cetaceans of the ACSAR area. However, there are systematic reports of sightings of cetaceans for parts of this area and for immediately adjacent ones. From these and from the more general literature for the western North Atlantic it is possible to state what cetacean species probably occur in the study area and to assign them, although less certainly, to one of four general abundance categories--abundant, common, uncommon, or rare. We refer to the temperate part of the study area from Cape Hatteras north and east to off Georges Bank as the "northeastern part" and to the subtropical part from Cape Hatteras south to off central Florida as the "southwestern part".

Specific sightings of cetaceans are provided for the shoreward or western part of the northeastern temperate half of the present study area by CETAP (1981, undated, and 1982) and by Powers et al. (1982). The area of coverage of the CETAP reports extend seaward to a depth of about 2000 m from Cape Hatteras to the northeast beyond the limit of ACSAR. The study by Powers et al. included a small amount of observing just seaward of the 200-m isobath and had latitudinal limits similar to the CETAP study. There has been less systematic observing in the southwestern, subtropical part of the present study area, i.e. south of Cape Hatteras. Some observations, mainly for the shoreward part of the area, are to be found in Schmidly (1981). Recent, useful general works for the western North Atlantic include Katona et al. (1975) and Leatherwood et al. (1976). General remarks are also based to some extent upon observations by the writer (R.H. Backus).

No values in terms of numbers of animals are attached to the four abundance categories used; they are merely relative within the area of concern. For some species, parts of the study area are probably among those parts of the North Atlantic where the species is most abundant. Thus, the apparently anomalous designation of "common" might be given for an endangered species, as it has been for the sperm whale, *Physeter catodon*. The systematic classification followed below is from Leatherwood et al. (1976).

The species fall into both of the main groups of cetaceans--the Mysticeti or baleen whales, mostly large, and the Odontoceti or toothed whales, which except for the large sperm whale are medium-sized to small. Several species of toothed whales in the 3 to 6 m class are sometimes called "blackfish". Small odontocoetes are generally called "dolphin" or "porpoise". We prefer the latter and use it here, because it is the term in general use with mariners, the people who most often see these animals, and avoids confusion with the fish called "dolphin".

The baleen whales are conspicuous migrants, moving through shoreward parts of the study area to its northern parts and beyond in summer to feed, then to its southernmost parts and beyond in winter to reproduce. Such a seasonal movement is also well known in the sperm whale, and probably is present in most cetaceans on some scale or another. These movements result in a seasonal change in the species present, particularly if the temperate and subtropical halves of the study area are considered separately.

Because the seasonal movements of cetaceans are only known in a general way and because the region of the report is so narrow in the onshore-offshore dimension, it is impossible to know with any precision the extent to which some cetaceans actually use the area. The baleen whales, which in the North Atlantic are mostly inhabitants of the continental shelves, are no doubt mostly confined to the shoreward, western side of the area.

Finally, it should be noted that six species that have been designated "endangered" are found within the study area. This designation is noted in the species accounts where it applies.

MYSTICETI - Baleen Whales

Balaenopteridae - Rorquals

Balaenoptera acutorostrata - minke whale. This small whale occurs in the temperate, northeastern part of the study area, principally in spring and summer and especially north of about 40°N. Here it is probably uncommon, for this is an inshore animal as a rule. The species withdraws to the south in fall, probably mainly but not completely beyond the southern limits of the study area. CETAP (1982) has provided some sightings in the north near the 2000-m isobath.

Balaenoptera physalus - fin whale (endangered). The fin whale is an uncommon to common species in the study area, both as a migrant and as a resident. Spring and summer numbers are greater than fall and winter ones, although the seasonal contrast is probably not so great in the study area as it is further shoreward over the continental shelf where the species is much more abundant. The fin whale occurs in small numbers more or less throughout the area in winter, but in summer is found mostly or wholly in the northeastern temperate part of the area. Two stocks may be involved--northern and southern ones with seasonally overlapping ranges.

A number of sightings have been made on the shoreward edge of the present study area by CETAP (1982) and by Powers et al. (1982), but like most baleen whales this is an animal of the continental shelf, and its numbers diminish rapidly with distance from the shelf edge.

Balaenoptera musculus - blue whale (endangered). This biggest of animals occurs in the northeasternmost part of the study area in unknown numbers, but undoubtedly should be classed as rare. It is possible that the species moves through the area as a migrant--south in fall, north in spring--but its wintering ground and migration paths are not known. There appear to be no sightings of record for the present study area, although CETAP (1982) reported two sightings just to the north.

Balaenoptera borealis - sei whale (endangered). This poorly known rorqual is probably rare to uncommon in the study area. Like other large whales it moves north and south with the seasons, but in our area it may live offshore more than the other baleen whales. Judging from CETAP (1982), it is commonest in the study area in spring and in its northeasternmost part. It may be resident in the southwesternmost part of the study area in winter.

Balaenoptera edeni - Bryde's whale. This whale is hard to identify and has often been confused with other rorquals; thus, its distribution is poorly known. It is mainly a nearshore species. If it occurs in the study area at all, it will be on the shoreward side of the southwestern, subtropical part. There appear to be no sightings of record here, but Schmidly (1981) reports a number of strandings on the shore just to the west. The species should be classified as rare in the study area.

Megaptera novaeangliae - humpback whale (endangered). This whale is probably rare to uncommon in the study area, for as a resident it mostly occurs in the shallower water to the west of our area. CETAP (1982) reported a few sightings near the 2000-m isobath in 40°-41°N. Some humpbacks probably move through the area on their annual north-south migrations. Schmidly (1981) summarizes a number of observations based on captures made years ago in the

Straits of Florida just to the south of the southern limit of the study area. These captures seem to have been of individuals making their northward migration in early spring, but some may have been of resident animals; therefore, there may be some wintering individuals on the southwest fringes of the study area..

Balaenidae - Right Whales

Eubalaena glacialis - right whale (endangered). This rare species moves north in summer, south in winter, like the other baleen whales. It mainly occurs shoreward of the northeasternmost part of the study area in spring. Its migration paths are very poorly known, but they too probably lie mainly shoreward of the study area. CETAP (1982) made a few sightings near the 2000-m isobath in the northeastermost part of the study area, but the CETAP data shows that numbers diminish rapidly seaward of the shelf edge. There may be some wintering animals on the shoreward edge of the southwestern, subtropical part of the study area. Schmidly (1981) reports sightings and strandings all along this coast from southern Florida to Cape Hatteras.

ODONTOCETI - Toothed Whales

Ziphiidae - Beaked Whales

Mesoplodon bidens, densirostris, europaeus, and mirus. These four species are everywhere rare, but might be encountered in the study area, judging from the distribution of their strandings. According to CETAP (1982) sightings, these whales are more often to be seen over the continental slope than over the continental shelf. The first species probably is found only in the northeasternmost part of the study area. Schmidly (1981) reports strandings of the last three species along the coast from Florida to Cape Hatteras.

Ziphius cavirostris - goose-beaked whale. This rare species might be encountered anywhere in the study area. The few CETAP sightings (CETAP, 1982) indicate that this is principally an offshore animal, more to be seen in the study area than over the continental shelf to the west. Schmidly (1981) reports a number of strandings in the Bahamas and along the coast from Florida to Cape Hatteras.

Hyperoodon ampullatus - bottlenosed whale. This little known whale is probably rare and confined to the northeastern part of the study area, where its numbers may increase in winter due to the southward movement of animals that summer to the north. CETAP (1982) reported two sightings that come from the study area.

Physeteridae - Sperm Whales

Physeter catodon - sperm whale (endangered). This largest of toothed whales is common in the study area, perhaps being most numerous on the traditional sperm-whaling grounds off Cape Hatteras in the westernmost Slope Water and Gulf Stream (Townsend, 1935). There is a withdrawal to the south in winter, and some animals may use the southwesternmost part of the study area as a wintering ground. CETAP (1982) reported numerous sightings that fall within the study area. Schmidly (1981) summarizes numerous captures from years ago. These cover the southwestern subtropical part of the study area and come at all times of year.

Kogia breviceps - pygmy sperm whale and Kogia simus - dwarf sperm whale. These are widely distributed, hard to distinguish, little seen offshore species. They may be uncommon to rare in the southwestern part of the study area, rare in the northeast. CETAP (1982) reports a single sighting in the study area. Schmidly (1981) reports numerous stranding for the coast west of the southwestern part of the study area. In these breviceps is commoner than simus.

Stenidae

Steno bredanensis - rough-toothed porpoise. This is a poorly known warm-water species not easy to identify, and it might be common in the southwestern subtropical part of the study area. Like other warm-water porpoises, it may come north of the Gulf Stream into the Slope Water in summer or with Gulf Stream warm-core rings. CETAP (1982) reported one such occurrence in about 39°N (latitude of Cape Henlopen). Schmidly (1981) reports two strandings to the west of the southwestern part of the study area.

Delphinidae - Porpoises

Peponocephala electra - melon-headed blackfish. It is possible that this poorly known and apparently rare animal is to be found in the southernmost part of the study area. There are no records of its occurrence there, but it is known from the Lesser Antilles (Schmidly, 1981).

Feresa attenuata - pygmy killer whale. This warm-water species, which is everywhere rare to uncommon, has been reported for the northeastern part of the study area (CETAP, 1982, one sighting). There appear to be no sightings of record in the southwestern part of the study area, but it is possible that the species is more abundant there than in the northeast. Schmidly (1981) records a few strandings in Florida just southwest of the southern limit of the study area. The species should be considered rare in our area.

Pseudorca crassidens - false killer whale. This blackfish, though poorly known, is probably common in the southwestern subtropical part of the study area. Schmidly (1981) reports some strandings just to the west. It may occur in the western part of the temperate Slope Water in summer or as a part of warm-core Gulf Stream rings. CETAP (1982) reported one sighting on the 2000-m isobath off Cape Hatteras.

Globicephala melaena - pothead whale. This blackfish is common to abundant in the temperate part of the study area, where its numbers may be higher in the shallower parts for most of the year. It is possible, however, that there is an offshore movement in winter. CETAP observations (made for Globicephala spp., but probably pertaining mainly to G. melaena) suggest that numbers are highest right on the shelf edge (CETAP, 1982).

Globicephala macrorhynchus - short-finned pilot whale. This blackfish replaces the preceding species in the southwestern subtropical part of the study area, where it is common. Schmidly (1981) reports sightings here and strandings to the west all along the coast from Cape Hatteras to the Straits of Florida.

Orcinus orca - killer whale. This whale is probably rare to uncommon in both parts of the study area. There were a few sightings by CETAP (1982) in the northeast, both inshore and near the 2000-m isobath, and a few by Schmidly (1981) to the west and south of the southwestern part.

Lagenorhynchus acutus - white-sided porpoise. This species occurs in the northern reaches of the temperate part of the study area--from about Hudson Canyon north. It is mainly a species of the continental shelf, but there appear to be onshore-offshore movements with the seasons such that it may be uncommon in the study area in winter although rare at other times. CETAP (1982) reported some sightings for the shoreward part of the study area. It is not known where the main part of the population of this species, which is common inshore, spends the winter.

Lagenorhynchus albirostris - white-snouted porpoise. This Lagenorhynchus is a colder-water species than the preceding one; its range is mostly north of the study area and so it is classed as rare to uncommon there. CETAP (1982) reports a few sightings for the study area.

Lagenodelphis hosei - Fraser's dolphin. This little known porpoise occurs in the Caribbean Sea (Caldwell et al., 1976), which makes it likely that it will be found sometime in the southernmost part of the study area. It should be classified as rare.

Tursiops truncatus - bottle-nosed porpoise. This species is common in the northeastern part of the study area, but uncommon in the southwestern subtropical part, where it is more of an inshore animal. There appears to be a pronounced north-south, summer-winter movement. CETAP (1982) and Powers et al. (1982) report numerous sightings of this animal for the temperate part of the study area, mainly along the inner slope and shelf edge. Schmidly (1981) reports some sightings and numerous strandings in the latitude of the southwestern subtropical part of the study area, but these are wholly within the 200-m isobath except at Cape Hatteras..

Grampus griseus - grampus. This small toothed whale or big porpoise is probably common to abundant throughout the study area. There appears to be a northward movement in spring and summer into the temperate part of the study area, the converse in fall and winter into the subtropical part, although the species is found in some numbers in both places in all seasons. CETAP (1982) data suggest that the species is most common on the shelf edge.

Stenella longirostris - spinner. This poorly known porpoise is probably uncommon in the southwesternmost part of the study area and rare or absent elsewhere. It may be one of those warm-water species that come north into the Slope Water in summer or with warm-core Gulf Stream rings. CETAP (1982) reported a few sightings in deep water, the northernmost of which was between 39° and 40°N.

Stenella clymene - short-snouted spinner. This little-known Stenella probably occurs in the southwestern part of the study area. There are a few stranding records outside the study area to the west (Schmidly, 1981). It probably should be classed as rare to uncommon.

Stenella plagiodon and S. frontalis-spotted porpoises. These porpoises, which are difficult to distinguish, are common to abundant in the subtropical part of the study area, and are often found north of the Gulf Stream in the westernmost part of the Slope Water, perhaps in summer or associated with warm-core rings. CETAP (1982) reported a number of sightings for the temperate northeastern half of the study area, particularly from its southwesternmost part. Schmidly (1981) gives some records for the shoreward edge of southwestern part of the study area.

Stenella coeruleoalba - striped porpoise. This porpoise is common to abundant in the study area, but its occurrence north of the Gulf Stream may be associated with summer or warm-core rings. CETAP (1982) reports numerous sightings (in the northeastern, temperate part of the study area).

Delphinus delphis - saddleback porpoise. This species is common to abundant shoreward of the study area, but, being an animal of the outer shelf, probably should be classed as uncommon to common in the study area itself. The numerous sightings reported by CETAP (1982) suggest that many individuals summer north of the study area, moving back into it in winter. Judging from Schmidly (1981) the species may be less abundant in the southwestern part of the study area than it is in the northeast.

A rank order of abundance of cetaceans in the ACSAR area for three size-classes (Table 6.29) tries to take into account numbers of animals and seasonal usage; that is, a few animals passing rapidly throught the area during migration would be low on the list, many animals resident throughout the year, high on the list. The boundary between size classes is not sharp. It should be emphasized that this is educated guesswork.

BENTHOS

THE FAUNA OF SOFT SEDIMENTS

Standing Crop

Kinds of measurements

Deep-sea fauna are generally divided into three classes (or four including microorganisms covered under the section on Microbiology) on the basis of size and taxonomic position. The largest size group is the megafauna defined as animals visible in photographs. Counts of these animals are made from photographic transects and trawls (Wigley and Emery, 1967; Grassle et al., 1975; Haedrich et al., 1980). The macrofauna are the animals retained by screens ranging from 250 to 500 μm. The two most commonly used screens for deep-sea studies of macrofauna are 300 and 420 μm. In a comparison of these two sieve sizes, Smith et al. (1978) estimated that up to 76 percent of the animals may be lost using the 420 μm sieve, however, excluding merofaunal groups, only 25 percent of the macrofauna are missed. Individuals belonging to meiofaunal groups such as foraminifera, copepods, nematodes, and podocopid ostracods are generally excluded from the macrofauna. The lower size limit for collections of meiofauna is generally 40-42 μm mesh screens; however, many studies of meiofauna have used 63 μm screens (Coull et al., 1977).

Quantitative estimates of macrofaunal abundance have been made with an anchor dredge (Sanders et al., 1965), but, box cores have generally been used for most recent quantitative deep-sea studies.

There is only one site sampled by several different investigators using somewhat different methods. Four sets of samples have been studied from Deep Water Dump Site 106 at 2200 to 2800 m depth south of New England. Rowe et al. found 1790 individuals per m^2 using 0.42 mm screens in 1975 at DWD 106 and a nearby site. Smith et al. (1978) obtained about $2095/m^2$ from a single grab

Table 6.29. Rank order of Cetacean Abundance in ACSAR area.

<u>Large cetaceans</u>

Physeter catodon
Balaenoptera physalus
Balaenoptera acutorostrata
Balaneoptera borealis
Megaptera novaeangliae
Eubalaena glacialis
Balaenoptera edeni
Balaenoptera musculus

<u>Medium-size cetaceans</u>

Globicephala melaena
Globicephala macrorhynchus
Pseudorca crassidens
Orcinus orca
Ziphius cavirostris
Hyperoodon ampullatus
Mesoplodon spp.

<u>Small cetaceans</u>

Tursiops truncatus
Grampus griseus
Delphinus delphis
Lagenorhychus acutus
Stenella coeruleoalba
Stenella plagiodon and frontalis
Stenella longirostris
Steno bredanensis
Lagenorhynchus albirostris
Stenella clymene
Kogia breviceps
Kogia simus
Feresa attenuata
Lagenodelphis hosei
Peponocephala electra

at DWD 106, (excluding nematodes, ostracods, and copepods) using 0.42 mm screens and 2810 m^{-2} using 0.297 mm screens. Smith's results are the same order of magnitude as those obtained by Rowe et al. (1982). Reish (1981) in 1976 found a minimum of 378 individuals m^{-2} and an average of about 700-800 m^{-2} using 0.5 mm sieves and box cores deployed by the submersible, ALVIN. The 0.42 mm and 0.5 mm sieves normally collect close to the same fraction of fauna and the differences are most likely the result of differing methods of processing. Pearce et al. (1979) found 47 m^{-2} in 1976 and 403 m^2 in 1974 using 0.5 mm screens and a Smith-McIntyre grab. The studies of Pearce et al. (1979) indicate that traditional shallow-water sampling techniques should not be used in the deep sea.

Meiofauna may be estimated by subcoring larger cores. These subcores should be taken on the seafloor to avoid disturbance of surface layers of sediment during recovery of the sample.

Biomass of macrofauna and megafauna in the ACSAR region has been estimated from wet weight (Haedrich et al., 1980; Haedrich and Rowe, 1977; Rowe et al., 1982) of formalin-preserved specimens with shells. These numbers have large errors because of the carbonate in large molluscs and echinoderms and are not very useful (Khripounoff et al., 1980; Mills et al., 1982). Smith (1978) and Smith et al. (1978) using estimates corrected for shell weight and 0.297 mm screens found the same order of magnitude of biomass that Rowe (1983) found using weights uncorrected for shells using 0.420 mm screens. These data only show trends and do not provide statistically reliable estimates of biomass from any particular site.

Distribution

Biomass and density vs depth-Changes in density of macrofauna with depth occurred along the Gay Head-Bermuda Transect (Fig. 6.57; Sanders et al., 1969). Densities at 300 m depth on the continental slope were up to 21,000/m^2 and densities at about 5000 m depth ranged from 33 to 92 per m^2 (Table 6.30). Changes with depth in numbers of individuals and biomass from box core samples are given in Fig. 6.58 (Rowe et al., 1982). The biomass reduction with depth is similar for macrofauna and megafauna (Haedrich and Rowe, 1977). Smith (1983) also found a reduction in biomass with depth. Off North Carolina meiofaunal densities per 10 cm^2 were 442.4 ± 196.7 at 400 m, 891.9 ± 350.1 at 900 m and 73.5 ± 46.0 at 4000 m depth.

Zonation of fish and megafauna are summarized in Grassle et al. (1975) and Haedrich et al. (1975). The density of fish on the slope is summarized in Figure 6.59. Biomass and density decrease with depth but the average size of fish may increase.

The most comprehensive sampling of deep-sea macrofauna was done in the 1960's by Sanders and Hessler (summarized in Sanders and Hessler, 1969) on a transect from Gay Head on Martha's Vineyard, Massachusetts to Bermuda. The macrofauna below 200 m depth are generally reduced in size (Sanders et al., 1965). Haedrich and Rowe (1977), Haedrich and Polloni (1976), Wenner and Musick (1977), and Wenner (1979) indicate an increase in average weight of individual fish from 500 m to 2500 m, however, Wigley et al. (1975) and Wenner (1978) found an inverse relationship between depth and size in decapod invertebrates.

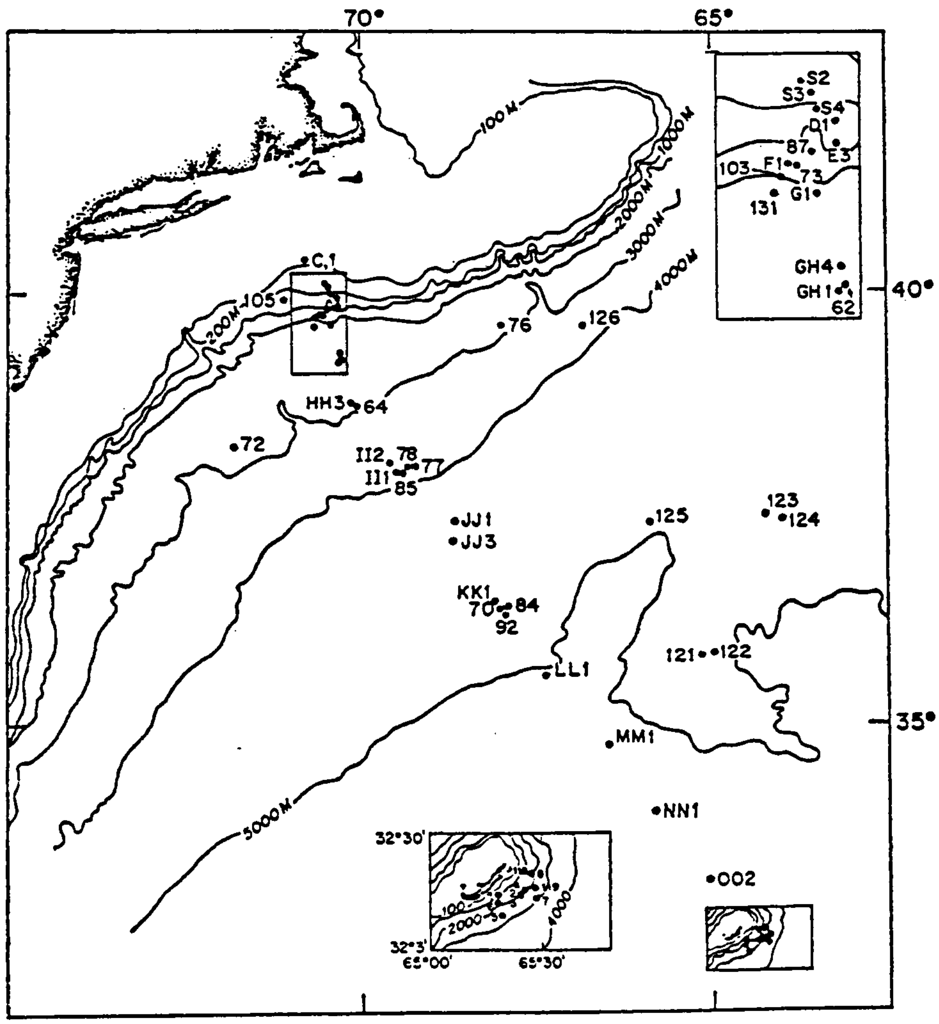


Figure 6.57. Depth contours and locations of sampling stations of the Gay Head-Bermuda transect. (Sanders and Hessler, 1969).

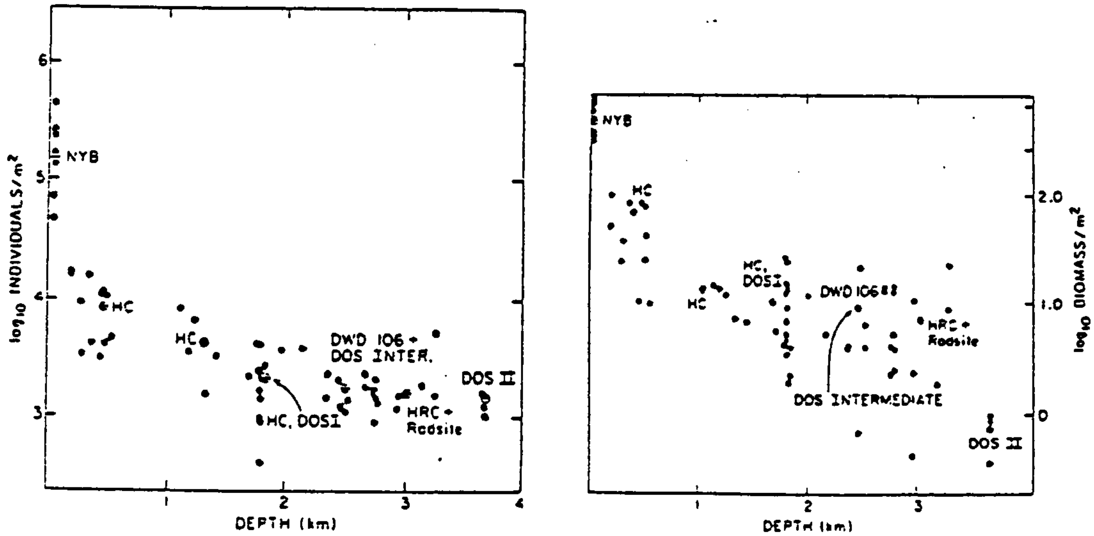


Figure 6.58. Numbers of animals and wet-weight biomass per square meter vs depth. (Rowe et al., 1982). Solid circles are individual samples and open circles are averages for areas defined in Table 6.30.

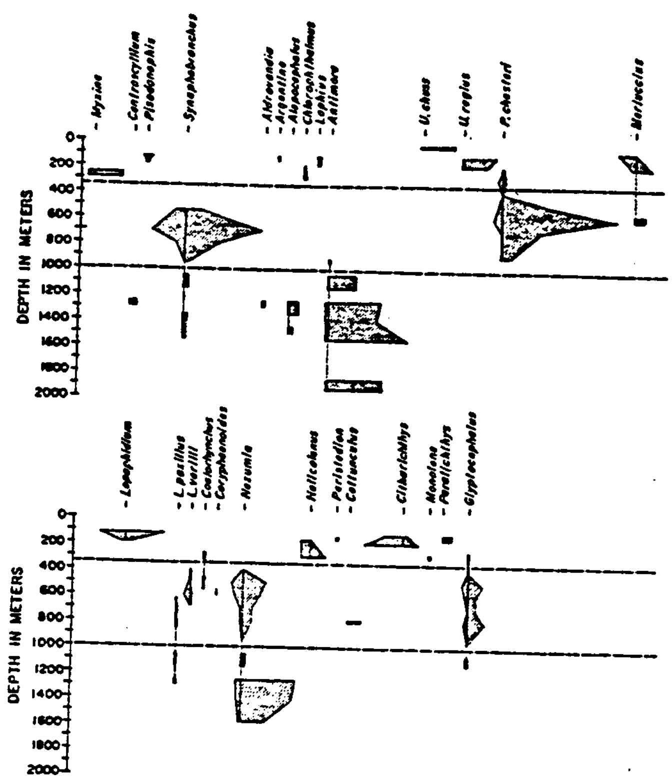


Figure 6.59. Depth range and relative abundance of fishes on the slope. The left-hand side of each kite diagram reflects relative number per hours, and the right-hand side relative weight per hour. Dashed horizontal lines indicate the approximate depth of the two faunal boundaries. From Haedrich et al. (1975).

Table 6.30 Depth, latitude, longitude, number of animals collected, and number of animals per square meter for transect stations in ACSAR area. From Sanders et al. (1965).

Station	Depth (m)	Latitude	Longitude	No. animals in sample	No. animals/ m^2
55	75	40°27.2.1'N	70°47.5'W	3791	13073
C 1	97	40°20.5'N	70°47'W	3082	5314
Sl. 2	200	40°01.8'	70°42'	6455	12910
Sl. 3	300	39°58.4'	70°40.3'	11907	21263
Sl. 4	400	39°56.5'	70°39.9'	4439	6081
D 1	487	39°54.5'	70°35'	5115	8669
E 3	832	39°50.5'	70°35'	3008	2979
F 1	1500	39°47'	70°45'	997	1719
G 1	2086	39°42'	70°39'	1120	2154
GH 1	2500	39°25.5'	70°35'	365	521
GH 4	2469	39°29'	70°34'	299	467
HH 3	2870	38°47'	70°08'	636	748
II 1	3742	37°59'	69°32'	*	*
II 2	3752	38°05'	69°36'	391	1003
JJ 1	4436	37°27'	68°41'	264	264
JJ 3	4540	37°13.1'	68°39.6'	101	158
KK 1	4850	36°23.5'	68°04.5'	113	92
LL 1	4977	35°35'	67°25'	67	55
MM 1	5001	34°45'	66°30'	27	33
NN 1	4950	33°56.5'	65°50.7'	51	38
OO 2	4667	33°07'	65°02.2'	58	126
Ber. 7	2500	32°15'	64°32.6'	91	120
Ber. 5	2000	32°11.3'	64°41.6'	89	189
Ber. 4	1700	32°17'	64°35'	217	271
Ber. 3	1700	32°16.6'	64°36.3'	126	274
Ber. 2	1700	32°36.3'	64°36.3'	189	215
Ber. 6	1500	32°14.3'	64°42'	208	178
Ber. 8	1000	32°21.2'	64°33'	326	729
Ber. 1	1000	32°16.5'	64°42.5'	243	528

*Sample excluded from quantitative analysis because of small size.

Horizontal Variation in Density

Little is known about variation in population density along isobaths since the same methods have never been used over the latitudinal range of Eastern North America. Most of the work on macrofauna has been done off the northeastern U.S. and the meiofauna studies have been off North Carolina. Regressions of density of meiofauna indicate a decline with depth despite horizontal location (Thiel, 1979). An unpublished study of fish from the slope and rise of the Middle Atlantic U.S. Coast, found similar results to those of Haedrich et al. (1980). Musick (1976) found the most rapid change in species composition of fish at 150-200 m, 400-600 m, 950 m, 1350-1525 m, 1930-2130 m and 2700 m. Boundaries between zones proposed by Haedrich et al. (1980) south of New England are at 270 m, 650 m, 1300 m, 2000 m, 2500 m, 3200 m, and 3800 m.

Species Distributions

Measurement-The best information on species distribution of macrofauna comes from epibenthic trawls (Hessler and Sanders, 1967). This device collects several thousand individuals at each lowering and has a closing door to prevent winnowing of the smaller and lighter individuals on the way to the surface. With this device it is possible for a single sample to exceed the total number of animals collected in the first hundred years of deep-sea dredging (Sanders, 1977). These large samples are necessary to provide complete growth series for accurate taxonomic and life history studies. Information on megafauna comes from otter trawls and photographs from submersibles or camera sleds. Species distributions of meiofauna have not been studied on the Atlantic Coast of North America.

Species in the Region-Over the last decade there have been a number of monographs describing the deep-sea fauna. The most important deep-sea group in terms of numbers of individuals and species is the polychaetes. Hartman (1965) and Hartman and Fauchald (1971) summarize results from anchor dredge and epibenthic sled samples mainly from the Gay Head-Bermuda transect. The number of species recognized increased and several families were revised in the second monograph (Hartman and Fauchald, 1971). The second volume (1971) has a list of 46 of the most abundant species from all samples studied. These polychaete species have a broad depth distribution, however, all but about three of these are very abundant only at depths less than 1500 m. *Myriochele* nr *heeri*, *Melinnata americana*, and *Paraonis uncinatus* are the only species on this list most common at depths below 1500 m. *Melinnata americana* was abundant (100+ per trawl) only in a series of replicate trawls from 4800 m depth. In an environ- ment where species seldom make up more than 5 percent of the fauna, it is very difficult to single out individual species as more or less important. When results of more quantitative box cores and more taxonomic studies of indi- vidual families are available from the Atlantic (such as the doctoral dis- sertation of Maciolek 1983), it should be possible to identify numerically dominant species within particular depth ranges. For example, *Aurospio dibranchiata* is clearly one of the more common polychaete species at depths from 1700 to 3600 m (Grassle, 1977; Rowe et al., 1982; Maciolek, 1981). According to Maciolek (1981), this species was identified as both *Prionospio cirrifera* and *Prionospio steenstrupi* in Hartman (1965) and *Laonice antarcticae* in Hartman and Fauchald (1971). This same species was called spionid (undescribed) by Grassle (1977) and spionid A by Rowe et al. (1982). A species of Glycera called Glycera mimica by Hartman (1965) and Grassle (1977) and Glycera capitata by Rowe et al. (1982) is also common at these depths. Grassle (1977) and Rowe et al. (1982) also found Poecilochaetus fulgoris and Pholoe minuta anoculata to be very abundant at 1700-1800 m.

A summary of bivalve distributions by Sanders and Allen is not yet complete. The bivalve systematic studies published thus far include Allen and Sanders (1966, 1969, 1973), Allen and Turner (1974), Allen and Morgan (1981), Sanders and Allen (1973, 1977). Some of the work is summarized in Allen (1979) but abundance of named species is not discussed. Two trawl samples from about 3800 m depth had four species whose percentage abundance was similar between the trawls (12-26 percent) and mean percentage abundance ranged from 15 to 23 percent. Grassle (1977) and Rowe et al. (1982) found that Nucula cancellata was among the most abundant species at 1700-1800 m depth south of New England. The same two studies also showed that the aplacophoran mollusc, Prochaetoderma sp. A, is very common at 1700-1800 m south of New England. Scaphopods are also common but taxonomic studies of this group are still in progress.

Gastropods are not very abundant in the deep sea but Rex (1972, 1974, 1977, 1981, 1983) has done an excellent job of summarizing the distribution and ecology of this group. Below shelf depths quantitative samples do not provide enough individuals for community and population studies. From anchor dredge samples ranging in size from 0.5 to 1.0 m^2, in area, Sanders et al. (1965) found less than one gastropod per m^2 from depths below 2000 m and no gastropods per m^2 in five samples below 4500 m depth. At depths below 1500 m, 2442 individuals were collected from large nonquantitative epibenthic sled samples. Of these 2442 animals, 904 are Cithna tenella occurring at depths below 3800 m. The next most common species was Mangilia bandella with 185 occurring from 2500 m to 3800 m. At depths between 478 m to 1102 m, there were 970 Alvania americana out of 3704 gastropods collected.

Ophiuroids are among the most abundant deep-sea benthic groups, however, they are represented by only a few species (Sanders, 1977). The main study in the Western Atlantic is the doctoral dissertation and subsequent publications by Schoener (1967, 1968, 1969a, b, 1972). Of the nearly 30,000 individuals considered by Schoener, 10,098 were of a single species, Ophiura ljungmani, from a single sample. There is some uncertainty about identification of juveniles of this species but approximately 90 percent of the juveniles are likely to have been correctly identified as O. ljungmani. Although this and other species have been shown to reproduce seasonally in the Eastern Atlantic, Ophiura ljungmani is the only deep-sea species in the Western Atlantic where there is good evidence for seasonal reproduction.

The taxonomic groups with highest species diversity in the deep sea are the peracarid crustacean orders amphipoda, cumacea, isopoda, and tanaidacea. The systematics have yet to be worked out for most of these groups despite extensive work on amphipods by Mills (1967, 1971, 1971/72), cumacea by Jones (1973, 1974) and Reyss (1974, 1978), isopoda by Chardy (1974, 1976), Hessler (1967, 1968, 1970a,b), Kensley (1982), Siebenaller and Hessler (1977, 1981), Thistle and Hessler (1976, 1977), Wilson (1976, 1980a, b, 1981), Wilson and Hessler (1974, 1980, 1981), and tanaids by Gardiner (1975).

Mills reviewed the number of species and distribution of amphipods on the Gay Head-Bermuda transect. Ampeliscid amphipods gradually drop out on the upper slope and phoxocephalids and lysianassids are important at all deep-sea depths. In four epibenthic sled samples from 1300 to 2900 m depth, the number of species ranged from 20 to 43 and a single sample from about 4700 m had 17 species.

The number of species of cumacea per epibenthic sled trawl at depths from 1300 to 2900 m were 15 to 32 (Jones and Sanders, 1972). At depths around 4700 m, two samples had 10 and 11 species. Of 100 species found on the Gay Head-Bermuda transet, 37 percent are new or undescribed. A single sample may have as many as 8 congeneric species of Campylaspis or 7 congeneric species of Leucon.

Samples from the same series of epibenthic sled hauls yielded 51 isopod species from 2900 m and 39 isopod species from 3800 m on the Gay Head-Bermuda transect (Hessler et al., 1979). Comparison with transects elsewhere in the Atlantic suggest that the North American Basin along the east coast of the United States has somewhat lower diversity of species.

In the tanaids, only the Neotanaidae have been studied (Gardiner, 1975). This difficult and highly diverse peracarid order is particularly in need of further study.

Other groups that have been studied from the Gay Head-Bermuda transect include the tunicates (Monniot and Monniot, 1968, 1970, 1975, 1976a, b, c, 1978; Monniot, 1971, 1979); sipunculids (Cutler, 1973,; Cutler and Duffy, 1972; Cutler and Doble, 1979); oligochaetes (Erseus, 1979a, b; 1982); echiurans (Datta-Gupta, 1981); pycnogonids (Child, 1982), crinoids (Clark, 1977); and Pogonophora (Southward, 1963, 1971, 1974; and Southward and Brattegard, 1968). From these studies the fauna of the North American Basin off the United States is much better known than other regions of the ocean. Despite the vast amount of work, much more taxonomic work is needed before the entire fauna from any single locality can be described.

A few taxonomic studies of western Atlantic meiofauna have been completed (Benson, 1975; Hope and Murphy, 1969a, b, 1970; Hope 1977; Humes, 1974; Bartsch, 1981, 1982) but ostracodes, nematodes, harpacticoid copepods, and mites are still poorly known. The Foraminifera have been comparatively well-studied by Buzas and Gibson (1969), Buzas and Culver (1970), Bulver and Buzas (1982), and Sen Gupta and Strickert (1982). Diversity of foraminiferan species increases at depths below 200 m.

Some deep-sea species are widely distributed and others are restricted or endemic to particular ocean basins. Endemism has been discussed by Jones and Sanders (1972) and Sanders (1977) in terms of the proportion of species known only from the North American Basin. Of the species of cumacea collected on the Gay Head-Bermuda transect, 49 percent are not found elsewhere. High endemism is likely to characterize most of the peracarid groups such as isopods, amphipods, and tanaids because they brood their young and do not have a planktonic stage of development. The ophiuroids and the bivalves tend to have the broadest distributions(Sanders 1977). Many of the megafaunal species, such as Hyalinoecia tubicola and Ophiomosium lymani, have much more restricted distributions than had previously been thought (Grassle et al., 1965). For most groups too few samples have been studied with uniform criteria to determine broad-scale zoogeographic distribution. In a well-studied group, the tunicates, endemism has been diminishing as more samples become available from additional areas (Monniot and Monniot, 1978).

Megafaunal Distributions

Megafaunal distribution with depth is given in Haedrich et al. (1980) and Grassle et al. (1976) Figure 6.60 illustrates the changes with depth. It is possible to identify depths of more rapid changes in one group or another but the boundary between zones is somewhat arbitrary. The most rapid transitions occur at depths shallower than 2000 m.

The methods of study and incompleteness of most of the taxonomy make comparisons along depth zones difficult. The fish on a transect off New England differ from those off Greenland at similar depths (Haedrich et al., 1980). Markle and Musick (1974) studied changes in fish species composition along the 900 m contour from approximately 36° to 40° N and found a shift from an association dominated by *Glyptocephalus cynoglossus* and *Phycis chesteri* to one dominated by *Synaphobranchus kaupi*. Several species were found only in the north and others were found only in the south. Although Haedrich et al. (1975) found a zonation similar to that of Rowe and Menzies (1969) and Musick (1976), a direct quantitative comparison of species distributions cannot be made from the published data.

Horizontal Variation in Macrofaunal Distribution

A portion of the deep-sea fauna is surprisingly homogeneous along depth contours. A station at 1400 m off New England shares 48 percent of its bivalves with a station off the west coast of Africa. About 30 percent of the bivalves are common to both sides of the Atlantic (Allen, 1974). Other groups such as peracarid Crustacea are much less similar with horizontal distance (Grassle et al., 1979; Jones and Sanders, 1972). The 49 percent endemism of cumacea from the Gay Head-Bermuda transect has already been mentioned. Tunicates have been studied from all of the Atlantic transects sampled from Woods Hole ships. The western Atlantic tunicates have greatest affinity with those species from off Labrador and the Eastern Atlantic. As with other groups, a few species are cosmopolitan and others have restricted distributions (Monniot and Monniot, 1978). Along the East Coast of the United States, Cape Hatteras may be a geographic boundary for upper slope fauna (Cutler and Doble, 1979). Along the Gay Head-Bermuda transect five samples from a depth range of 4800 and 4862 m and three samples from the depth range of 2862-2891 m showed high similarity even though the stations were 100 miles or more apart (Fig. 6.61). There are not enough samples taken with similar methods to define zoogeographic boundaries along depth zones. The zonation of macrofauna is described by Sanders and Hessler (1969), Sanders (1977), Grassle et al. (1975), and Rex (1981); some examples are shown in Figures 6.62-6.66 and Table 6.31. Names of common species are given in Rowe et al. (1982) (Table 6.32). Zonation within each major faunal group is a little different, suggesting that zones should not be thought of as discrete ecological entities.

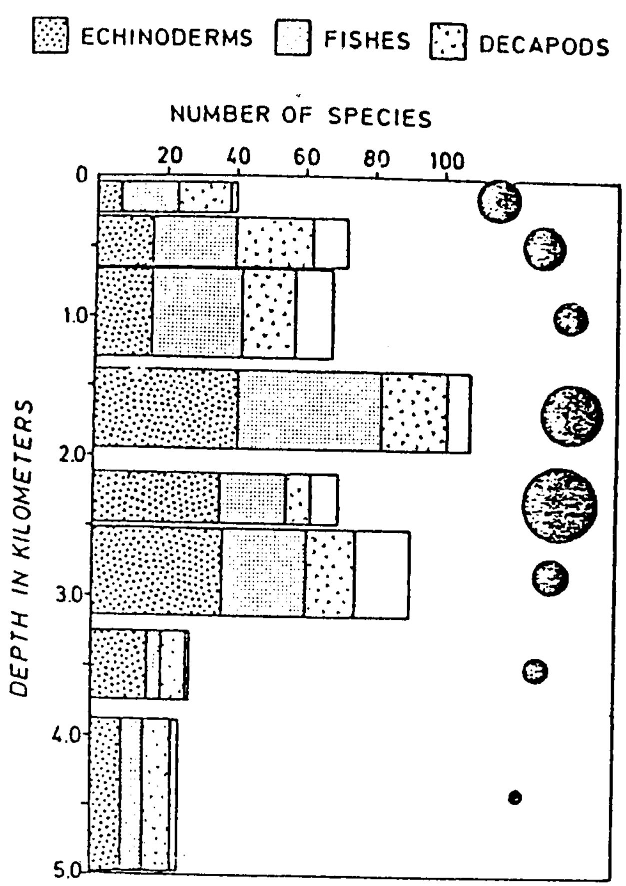


Figure 6.60.

Vertical extent of each of the 8 zones (regions of relatively little faunal change) summarized along depth axis; discontinuities are the faunal boundaries (regions of relatively rapid faunal change). Length of each bar indicates total number of megafaunal species subdivided into number of echinoderms, fishes, decapod crustaceans, and other groups (clear area). Filled circles to right represent megafaunal biomass. From Haedrich et al. (1980).

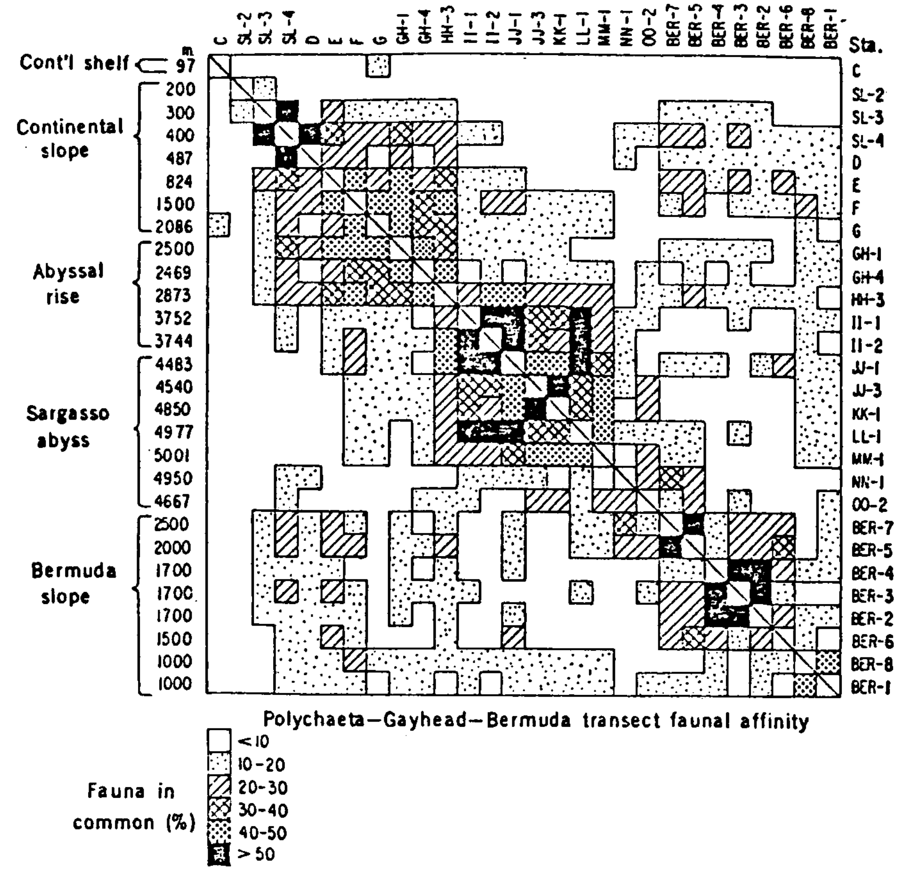


Figure 6.61.

Degree of polychaete faunal similarity among the stations (Sta.) of the Gay Head-Bermuda transect. From Sanders and Hessler (1969).

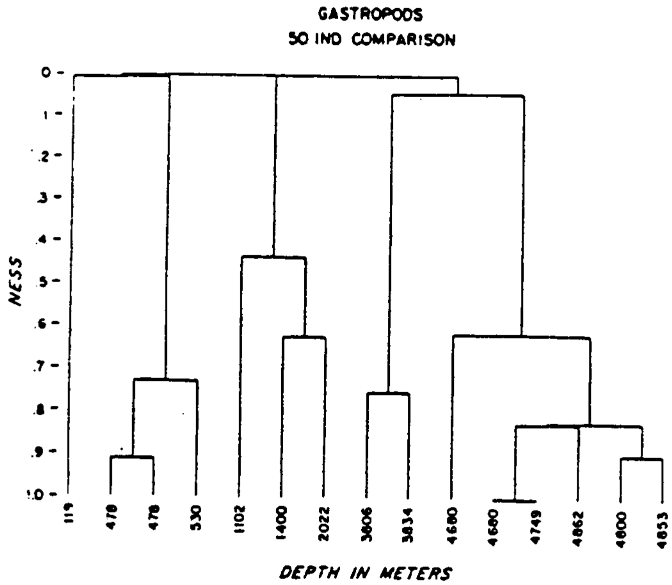


Figure 6.62. NESS clustering at m = 50 for epibenthic sled samples of gastropods taken at various depths on the Gay Head-Bermuda transect. From Grassle et al. (1979).

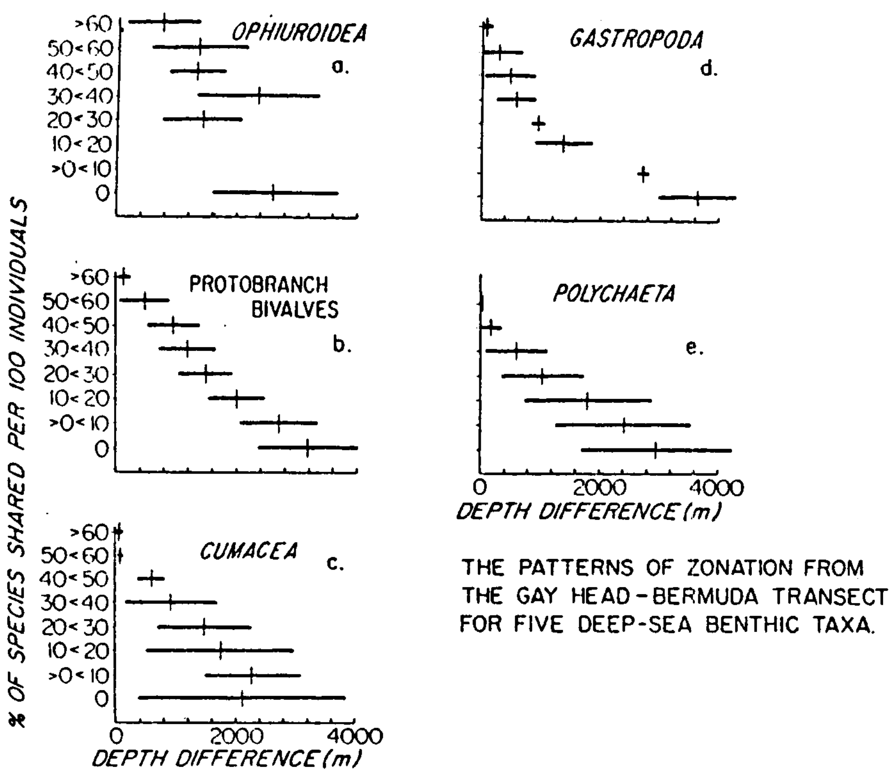


Figure 6.63. The patterns of zonation for five major deep-sea benthic taxa from the Gay Head-Bermuda transect. Mean depth differences and standard deviations are compared for station pair groupings on the basis of the percentage of species shared.

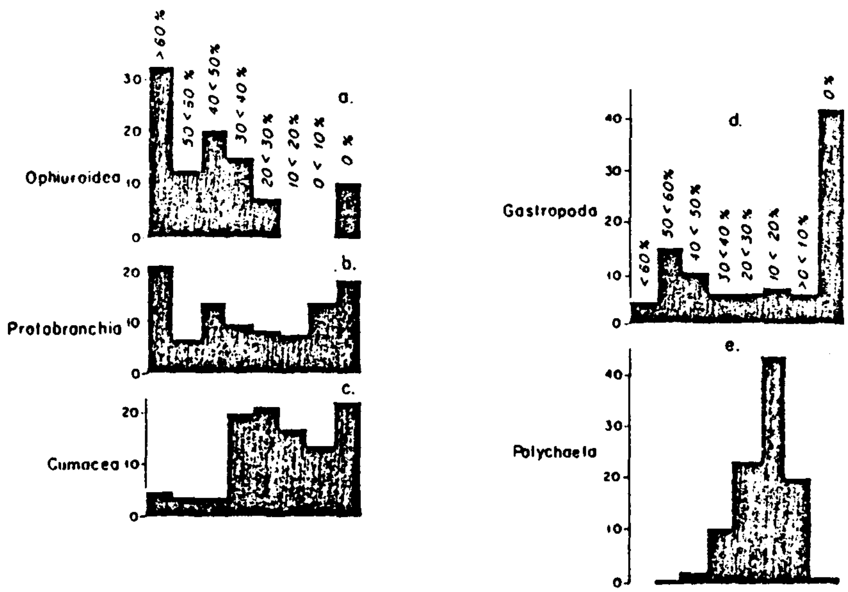


Figure 6.64. The proportional distributions of station pairs within each of the faunal similarity groupings for the Ophiuroidea, Protobranchia, Cumacea, Gastropoda, and Polychaeta.

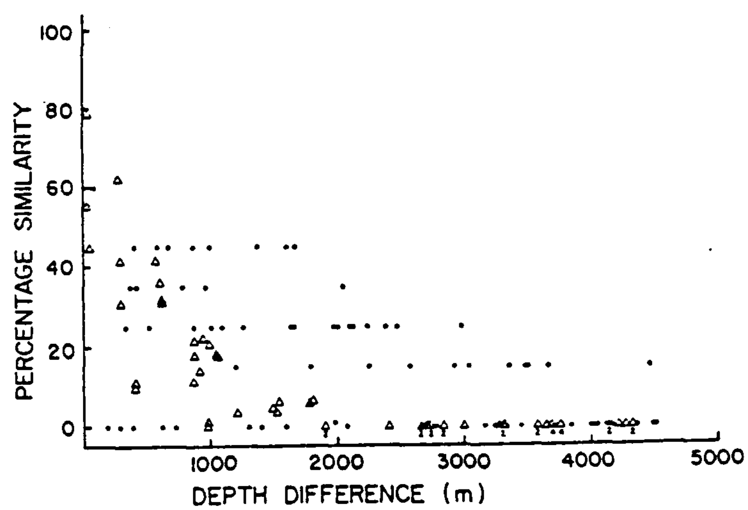


Figure 6.65. Percentage faunal similarity values for samples of polychaetes (solid circles) and gastropods (open triangles) plotted against difference in depth to selected reference stations. All samples are from the western North Atlantic. From Rex (1981).

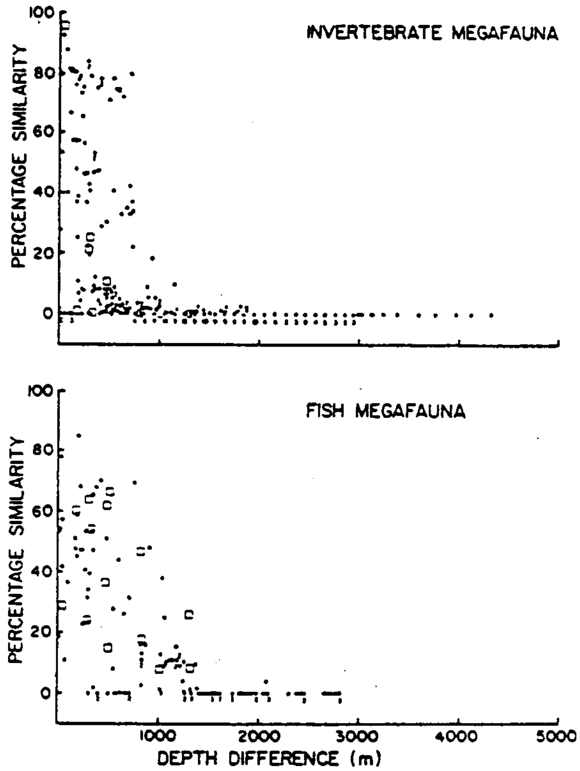


Figure 6.66. (top) Percentage faunal similarity values for samples of invertebrate megafauna plotted against difference in depth to selected reference stations. (bottom) Same comparisons for the fish megafauna. From Rex (1981).

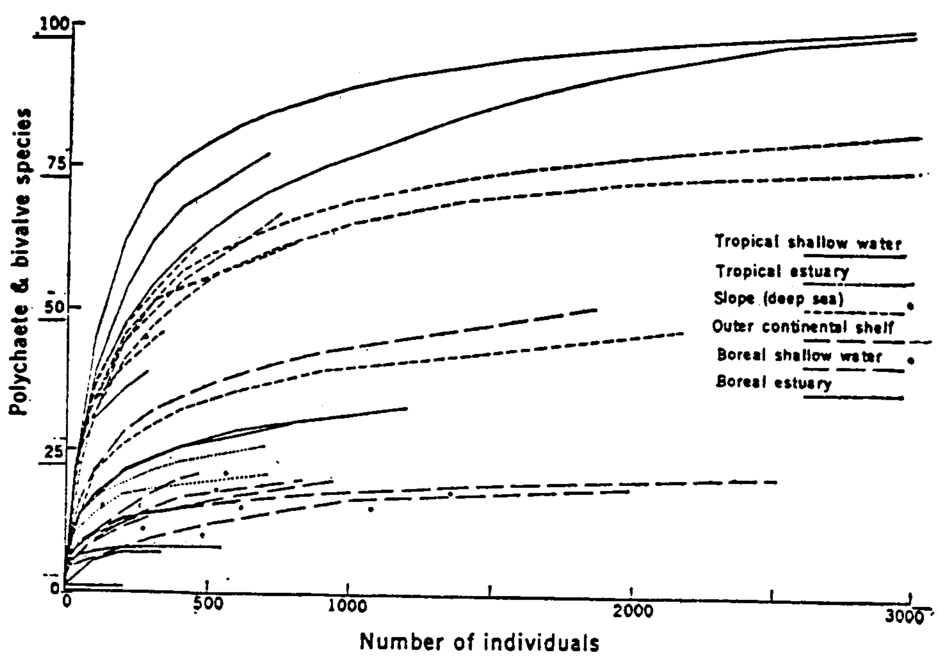


Figure 6.67. Diversity values for different benthic environments by the rare-faction method. The line represents the interpolated curves. From Sanders and Hessler (1969).

Table 6.31. NESS similarities and approximate 95 percent confidence limits between samples at 1102 m (Sta. C5087), 1400 m (A1273), and 3834 m (C5085).

	3834 m vs 1102 m	3834 m vs 1400 m	1120 m vs 1400 m
Ophiuroids	.55 ± .01	.40 ± .04	.82 ± .05
Polychaetes	.13 ± .02	.12 ± .02	.64 ± .01
Protobranch bivalves	.08 ± .01	.08 ± .01	.88 ± .03
Gastropods	.01 ± .01	.00 ± .01	.60 ± .04
Cumaceans	.01 ± .01	.02 ± .03	.36 ± .04

(From Grassle et al., 1979)

Table 6.32. Ten most abundant 'species' at various depth intervals (percentages in parenthesis). From Rowe et al. (1982).

32 m	203 to 570 m	1141 to 1437 m	1707 to 1815 m	2351 to 2673 m	2749 to 3264 m	3659 m
Tharyx acutus (29.8)	Oligochaete "A" (29.9)	Cossura longocirrata (16.1)	Nucula cancellata (10.3)	Glycera capitata (5.8)	Sipuncula spp. (8.2)	Scaphopod "Spp." (7.6)
Prionospio steenstrupi (23.5)	Cassura longocirrata (5.3)	Heteromastus filiformis (10.8)	Poccilochaetus fulgoris (8.9)	Oligochaeta "Spp." (5.6)	Spionid "A" (6.0)	Ophelina abranchiata (7.6)
Nucula proxima (13.5)	Tharyx acutus (4.6)	Axinulus ferruginosus (7.7)	Glycera capitata (5.7)	Prochaetoderma sp. (A) (5.4)	Oweniid "Spp." (5.5)	Ampharete "A" (6.5)
Cassura longocirrata (8.1)	Minuspio cirrifera (4.0)	Tharyx acutus (7.1)	Nemertean "Spp." (2.8)	Leptognathia C (4.2)	Glycera capitata (4.2)	Oweniid "Spp.: (3.3)
Mediomastus ambiseta (8.0)	Terebellides stroemi (3.2)	Axinulus sp. (6.5)	Harpiniopsis sp. (2.8)	Notomastus latericeus (4.0)	Ophiura "A" (3.6)	Sigambra tentanculata (3.3)
Asabellides oculata (6.4)	Paraonis geacilis (3.1)	Nucula granulosa (4.7)	Polycarpa delta (2.6)	Tharyx "B" (3.3)	Ehlersia anoculata (3.3)	Sipuncula "Spp." (3.3)
Euchone incolor (1.7)	Siphonodentalium sp. (2.7)	Ceratocephale loveni (4.7)	Aricidea neosuccia (2.6)	Ophiura ljungmani (3.3)	Typhlotanais "G: (2.4)	
Dorvillea caeca (1.2)	Chaetozone setosa (2.6)	Glycera capitata (4.5)	Prochaetoderma sp. (A) (2.6)	Spionid "A" (2.4)	Oligochaeta "Spp." (2.2)	
Thracia myopsis (1.1)	Nemertean "Spp." (2.3)	Paramphinome jeffreysi (2.8)	Spionid "A" (3.0)	Sipuncula "Spp." (2.6)	Cirratulid "Spp." (1.9)	
Aricidea jeffreysi (0.9)	Falcidens caudatus (2.9)	Falcidens caudatus (2.4)	Pholoe minuta (2.4)	Malletia estheriopsis (2.3)	Scaphopod "Spp." (1.7)	

There were 48 taxa among the 10 most abundant species in the seven sample sets.
*Next 14 "ranking" species at 2.2 percent with two specimens each.
"Spp." indicates more than one species is included.

Meiofauna

The vertical and horizontal distribution of meiofauna is unknown since, except for Foraminfera, few taxa are identified to species. The distribution of major groups off North Carolina at 400 and 4000 m are shown in Tables 6.33-6.34.

FAUNA OF HARD SURFACES

Aside from a few isolated submersible observations (Grassle et al., 1975) the main information on hard surfaces in the ASCAR region comes from the work of Hecker at Lamont-Doherty Geological Observatory (Hecker et al., 1980). The hard-surface epifauna is not as dense as in shallow water however, canyons can develop a lush epifauna (Hecker, 1982).

Hecker et al. (1983) found that canyons differ from the slope environments in that increased environmental heterogeneity results in faunal differences. In Baltimore Canyon there are three faunal zones: 800-1400m, 1300-1600 m, and 1600-2050 m. Ophiomusium lymani dominates the deeper zone but is relatively rare at depths less than 1600 m allowing the suspension/filter feeding species to dominate the middle depths. Densities are generally low in depths of 800-1400 m. The fauna at depths less than 800 m is extremely variable and relationships to substratum, depth, and geography are less obvious. Results from studies in Lydonia Canyon are similar (Hecker et al., 1983).

In contrast to the findings of Haedrich et al. (1980), Hecker et al. (1983) found that additional faunal groups (mainly associated with hard substrata) are located in canyons. The canyons sampled by Haedrich et al. (1980) (Alvin and Hudson Canyons) have limited exposure of hard substrata and trawls are not an effective means of sampling the high topographic relief that occurs. Continous observation from manned submersibles or towed photographic vehicles are needed to describe the highly patchy faunal assemblages that occur in canyons.

Extensive banks of coral are known from the Blake Plateau at depths between about 650 and 850 m (Stetson et al., 1962; Milliman et al., 1967; Stetson et al., 1969). The banks are made up principally of Dendrophyllia profunda. Lophelia prolifira is abundant on the crest of the banks and Bathypsammia, Caryophyllia, and Balanophyllia are dominant between the banks. Deep-water coral mounds have been reported from the southern Blake Plateau and the slopes of Little Bahama Bank, just south of ASCAR the study area (e.g., Neumann et al., 1977; Mullins et al., 1981). Dominant coral genera are Bathypsammia and Solenosmilia, but numerous other species also are present. These corals trap finer-grained sediment, ultimately resulting in growth of deep-water coral mounds which can host numerous other invertebrate fauna, including many mollusks, echinoderms, and crustaceans. To date there has been no detailed biological study of these mounds, although they compose one of the dominant communities on the Blake Plateau.

DIVERSITY

Using several methods of expressing diversity including number of species per sample, Sanders and Hessler (1969), Sanders (1968), and Hessler and Sanders (1967) described the relatively high diversity of species of the polychaete and bivalve fraction of the deep-water samples from the Gay Head-

Table 6.33. Numbers (10 cm^{-2}) of meiofauna off North Carolina at 400 m. The numbers 24301-24305 represent individual box cores and the single digits refer to the subsample from each box core (See Table 1 for how each subsample was processed). From Coull et al. (1977).

Taxon	24301					24302					24303						24305					x	of all meio-fauna
	6	7	1	9	3	8	4	6	1	7	8	1	3	6	7	2	4	4	7	1	8		
Foraminifera	101	152	39	126	136	136	39	110	51	136	136	87	140	75	89	136	136	238	523	136	136	136.1	30.8
Nematoda	264	145	353	520	184	231	238	94	352	45	51	79	59	173	334	227	257	175	76	196	137	199.5	45.1
Copepoda	103	30	46	234	27	66	39	17	55	21	9	24	9	37	138	20	43	43	16	11	7	47.4	10.7
Unidentified	23	10	52	60	35	85	4	12	31	8	10	3	47	24	26	0	42	4	0	1	0	22.7	5.1
Polychaeta	13	15	15	44	10	22	10	7	15	5	11	6	8	7	36	6	6	17	5	1	1	12.3	2.8
Turbellaria	17	8	0	2	0	0	8	9	2	0	0	5	7	3	5	3	10	17	4	1	1	4.9	1.1
Gastrotricha	19	9	0	23	0	0	13	5	4	6	10	0	0	2	7	8	22	2	11	3	1	6.9	1.6
Oligochaeta	3	3	0	0	1	3	3	1	0	3	1	1	1	0	0	0	1	5	2	0	0	1.3	0.3
Ostracoda	7	3	1	15	3	2	4	2	2	0	0	4	0	1	1	2	1	1	1	0	0	2.4	0.5
Tardigrada	1	1	1	18	0	13	2	2	2	0	2	3	0	4	9	1	3	1	0	1	1	3.1	0.7
Konorhyncha	4	0	0	6	0	2	0	1	1	2	1	0	0	0	2	0	2	0	0	1	0	1.0	0.2
Other groups	3	8	3	9	4	16	4	8	6	1	2	5	3	2	6	4	10	4	0	2	0	4.8	1.1
Total	558	384	510	1057	400	576	364	267	521	227	233	217	274	328	653	407	533	507	638	353	284		
x ± SD											442.4 ± 196.7												

[A]Forams not counted. Numbers given are estimates based on mean of all other samples.

Table 6.34. Numbers (10 cm^{-2}) of meiofauna off North Carolina at 4000 m.

Taxon	24326			24239				x	Percent
	1	4	2	3	5	6	9		
Foraminifera	101	32	131	1017	483	181	123	295.3	33.1
Nematoda	382	328	601	361	280	834	942	532.6	59.7
Copepoda	7	16	28	5	2	67	24	21.3	2.4
Unidentified	11	6	25	9	11	23	7	13.1	1.5
Polychaeta	6	11	26	7	9	23	18	14.3	1.6
Turbellaria	3	1	0	0	1	1	0	0.9	0.1
Gastrotricha	0	2	0	1	1	0	0	0.6	0.1
Oligochaeta	8	9	0	0	2	0	0	2.7	0.3
Ostracoda	7	16	1	5	10	2	1	6.0	0.7
Kinorhyncha	1	2	0	1	0	2	1	1.0	0.1
Other groups	0	11	6	2	2	5	2	4.0	0.4
Total	526	434	818	1408	801	1138	1118		
x ± SD				891.9 ± 350.1					

Bermuda transect (Fig. 6.67). Previous studies had indicated that deep-sea species diversity was low. An increase in the diversity of the entire fauna was observed on the continental slope in comparison to the continental shelf off North Carolina (Grassle 1967, 1972). The diversity of most groups increases to intermediate depths and declines in deeper water (Rex, 1981) (Fig. 6.68). From trawl data, megafaunal diversity also appears greatest at intermediate depths (Haedrich et al., 1975, 1980) (Fig. 6.60).

Several explanations have been made for the increase in diversity in the deep sea and the changes in diversity within the deep-sea environment. These are reviewed by Rex (1983). An intermediate disturbance argument (Connell, 1978) is increasingly favored (Grassle and Sanders, 1973; Grassle, 1977; Rowe et al., 1982; Rex, 1981, 1983). In greatly disturbed environments few species are able to recover rapidly enough to maintain themselves. In very infrequently disturbed environments competitive exclusion is likely to result in fewer species. A balance between these processes has been called a dynamic equilibrium (Huston, 1979; Rex, 1983). The spatial scale of disturbance is not discussed in most theoretical papers and this is particularly important in the deep sea. Grassle and Sanders (1973) and Jumars (1976) argue that deep-sea spatial heterogeneity results from small-scale biogenic disturbance.

On coral reefs, disturbance results from storms or breakage of coral from its own weight and the activities of boring animals. In rain forests, individual tree falls produce gaps in the forest and opportunities for settlement of species excluded by tree canopy. Richerson et al. (1970) call the spatial heterogeneity from disturbance a contemporaneous disequilibrium, Johnson has called it a temporal mosaic. In the deep sea the sources of disturbance are falls of organic material from the surface such as wood, algal remains or carcasses of animals falling from the surface, mud slumps, and the activities of large animals such as snails moving over the bottom or sessile animals such as glass sponges projecting above the bottom to accumulate fine sediments or increase microbial activity. Predation by large animals, such as rattail fishes or various echinoderms, may be regarded as another form of disturbance. Disturbance allows both for reduction in competition and adaptations to different kinds of disturbance. For example, the species increasing in the vicinity of wood sunk from the surface differ from those increasing as a result of deposition of particles around glass sponges or as a result of defaunated spaces left by the feeding activities of predators and scavengers.

Another hypothesis relates number of species to total area in an entire region. The theory stems from correlation between species numbers and island areas on land. This hypothesis was rejected by Rex (1981) because the species-area correlation does not hold in the deep sea. The relationship between species diversity and sediment texture (Gray, 1974) has also been rejected by Rex (1983).

A high proportion of the increased diversity in the deep sea may also relate to commensal or mutual interactions. These relationships are still very poorly understood.

Proportion of Planktonic Larvae and Reproduction

The general life histories of major deep-sea taxa are summarized by Grassle and Sanders (1969) and Sanders (1977). The peracarid Crustacea brood their young and have no planktotrophic dispersal. Most bivalves have a lecithotrophic larva which may indicate near bottom dispersal of larvae. The groups

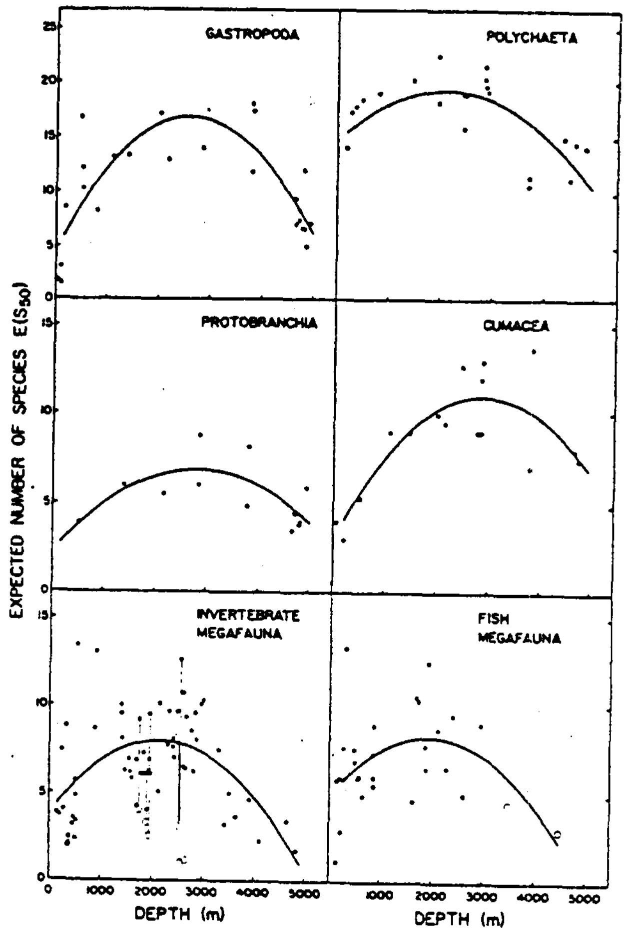


Figure 6.68. Depth gradients in species diversity for the Gastropoda (79,80), Protobranchia, Polychaeta, Cumacea, invertebrate megafauna, and fishes. All samples are from the western North Atlantic south of New England. From Rex (1981).

with planktotrophic development are the ophiuroids (Schoener, 1972) and gastropods (Rex and Waren, 1982). Shallow water studies indicate that planktonic feeding stages increase dispersal ability of a species, however, it is unknown whether this is true in the deep sea. Rex and Waren (1982) suggest that the predominately predatory gastropods with planktotrophic development have greater dispersal ability than other deep-sea species.

In the few species of bivalves observed from the Western Atlantic, there appears to be no seasonality of reproduction (Allen, 1979; Scheltema, 1972). Egg numbers in the protobranch bivalves range from two for the genus Microgloma to several hundred (Sanders and Allen, 1973), and within the genus Nucula, egg number declines with increasing depth (Scheltema, 1972). Some species of polychaetes are in reproductive condition at all times of the year (Scheltema, 1972).

The gastropod Benthonella tenella appears not to reproduce seasonally but some seasonal variations cannot be discounted (Rex et al., 1979). Recruitment appears to be variable and infrequent. Another gastropod, Alvania pelagica shows a lower proportion of energy devoted to reproduction and greater longevity than continental slope populations.

Crangonid, glyphocrangonid and nematocarcinid shrimp show asynchronous, year-round reproduction (Wenner, 1978, 1979). The only estimate of larval dispersal range is for the red crab, Geryon quinquedens, from upper slope depth. The larvae of this species are thought to disperse over distances of several hundred kilometers (Kelley et al., 1982).

Genetic Variation

Species of deep-sea megabenthic invertebrates show a higher genetic variability than shallow-water relatives (Murphy et al., 1976; Doyle, 1972; Schopf and Gooch, 1971). This result is supported by studies on genetic variation of deep-sea animals in the Pacific (Ayala and Valentine, 1978). Most of the work has been done with coarse mesh trawls collecting large mobile scavengers with good dispersal ability (Grassle and Grassle, 1978). Genetic variation in these species is likely to be maintained by selection for different genotypes within each local biotic environment within the range of each species.

Feeding Types and Proportion of Predators

The majority of deep-sea animals feed at the sediment-water interface by removing particles from the sediment surface. The proportion of motile vs sessile polychaetes increases on the Hudson Canyon Rise and at 3600 m on the Gay Head-Bermuda transect, and Rowe et al. (1982) attributed this to increased current activity. Filter feeding animals are rare.

The proportions of predatory gastropods (Rex, 1973, 1976) and predatory tunicates (Monniot and Monniot, 1978) increase with depth within the deep sea. Predatory bivalves never make up more than five percent of the bivalve individuals in the deep sea (Allen and Turner, 1974). Most Aplacophora or solenogasters are predators on foraminifera, hydrodids, crustacean eggs and possibly small worms and crustacea (A. Scheltema, 1981). The only other major macrofaunal invertebrate group with substantial numbers of predators is the polychaetes. A relatively high proportion of predators are found in association with large concentrations of wood. Predatory animals feed on the primary consumers in these circumstances (Turner, 1977). Many of the species classified as predators may also be scavengers or omnivores, so that food web interpretations are difficult even though relatively few species are involved.

Tietjen (1971) has studied changes in the feeding type of nematodes with depth. Deposit feeders increase and epigrowth feeders decrease in deeper water.

Most of the invertebrates big enough to be visible on the sediment surface (megafauna) are nonselective predators and/or scavengers (Haedrich et al., 1980). Nematocarcinid shrimp feed on the bottom after a more pelagic existence early in life (Wenner, 1979).

Fish spend varying amounts of time feeding on the bottom depending on jaw morphology and stage of development (McLellan, 1977; Haedrich et al., 1980; Sedberry and Musick, 1978). Some deep-ocean fish may show some preferred prey (Haedrich and Polloni, 1976); however, most are nonspecific in their feeding (Haedrich et al., 1980; Sedberry and Musick, 1978). Bottom-feeding fish are heavily parasitized from invertebrate intermediate hosts (Campbell, 1983, McLellan, 1976).

Growth and Colonization Rates

The only studies of deep-sea colonization rates of soft sediments in the Western Atlantic deep sea are those of Grassle (1977). Rates of colonization of disturbed deep-sea sediments are very low in comparison to shallow water. After two years on the bottom at about 1800 m depth, the populations were an order of magnitude lower in the trays than in the surrounding community, and few of the individuals had reached maturity. In other, similar experiments with relatively high concentrations of organic material in the sediments, more rapid colonization may occur (Grassle, unpubl.; Desbruyeres et al., 1980; and discussion in Hecker, 1982).

Rate of colonization of wood on the bottom is relatively high (Turner, 1973) and colonization of rock or artificial surfaces is very slow (Grassle, unpub.) Where there is extra food, a few groups such as polychaetes in the genera Ophryotrocha, Capitella or Prionospio may become abundant. This occurs in the vicinity of wood islands where the feces of animals living on the wood are spread over the surrounding sediments (Grassle, unpubl.).

Respiration Rates

Smith (1982) has measured whole community respiration along the Gay Head-Bermuda transect and finds a decline with depth and distance from land (Table 6.35). It is unknown whether this result is primarily the result of a decrease in microbial respiration or the respiration of the fauna. An approximate energy budget has been drawn by Rowe and Gardner (1979) (Fig. 6.69). Deep-sea scavenging fish also have lower rates of respiration than fish in shallow water (Smith, 1982).

Table 6.35. Sediment community respiration from 10 stations in the Western North Atlantic with associated environmental parameters[A] (from Smith, 1982).

Station	Sediment Community Respiration ml O m h	Depth (m)	Distance from Shore (km)	Annual Primary Productivity $g\ C\ m^{-2}\ y^{-1}$°C	Bottom Water Temp.	Dissolved Oxygen Bottom ml/l	Benthic Abundance/ m^2	Benthic Biomass mg wet wt/m^2	Sediment Organic Carbon mg/g/dry wt	Sediment Organic Nitrogen mg/g dry wt	Particulate Organic Carbon Flux $g\ m^{-2}\ y^{-1}$
DOS-1	0.50	1,850	176	120	4	7.05	3,218	9,450	10.0	1.1	--
DWD	0.46	2,200	172	100	3	6.34	22,988	556	12.1	1.5	6.3
ADS	0.35	2,750	259	160	3	6.52	8,764	8,764	13.3	1.6	2.3
HH	0.20	3,000	291	160	3	6.15	2,146	653	9.1	1.1	2.3
DOS-2	0.21	3,650	352	100	3	6.54	1,632	771	13.0	0.9	4.2
JJ	0.09	4,670	497	68	3	6.43	753	220	0.8	0.1	--
KK	0.04	4,830	612	68	3	6.04	285	180	6.9	0.7	--
NN	0.07	5,080	880	72	3	6.25	117	78	6.4	0.9	0.7
MM	0.02	5,200	806	72	3	6.15	259	142	6.4	0.9	0.7
77DE	1.31	1,345	148	85	4	5.65	--	--	15.6	--	5.4

[A]Adapted from Hinga et al., 1979; and Smith, 1978a.

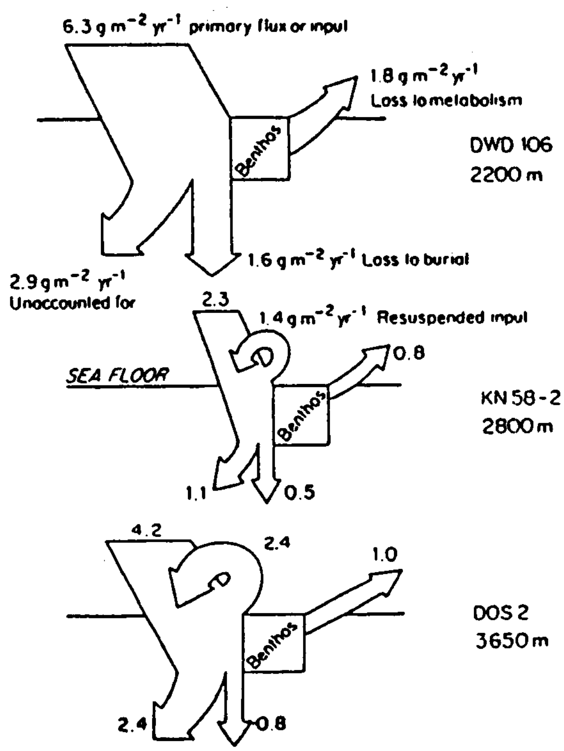


Figure 6.69. Organic carbon budget for the deep North Atlantic, in g cm^{-1} yr^{-1}. From Rowe and Gardner (1979).

SEABIRDS

INTRODUCTION

Our knowledge of pelagic distributions of seabirds in the western North Atlantic has been rapidly increasing over the past decade. Although much information is now published, there is a considerable amount of observation data scattered between unpublished reports, personal files of individuals, and current research. This report is an attempt to compile and synthesize as much of this information as possible into a quantitative evaluation of seabird distribution and abundance in the ACSAR region. The term "seabird" in this report refers to birds from the families: Procellariids (including albatrosses, shearwaters, petrels and storm-petrels), Pelecanifoms (including gannets, tropicbirds, frigatebirds and pelicans), and the Lari-Limicolae (including phalaropes, jaegers, skuas, gulls, terns and alcids).

Jespersen (1924) began the quantitative description of the pelagic distribution of seabirds in the western North Atlantic. Following him, other important contributions were made by Wynne-Edwards (1935), Baker (1947), Rankin and Duffey (1948), Moore (1941, 1951), Palmer (1962) and Butcher et al. (1968). Surveys in the last ten years include: Brown et al. (1975), Brown (1977), Rowlett (1973, 1980), Lee and Booth (1979), Lee and Rowlett (1979), Powers (1983) and Powers and Brown (in press). Additional seabird distribution data from the area of interest lies with the Manomet Bird Observatory (MBO), David Lee (N.C. State Museum, Raleigh, NC), Richard Rowlett (Ocean City, MD), and Peter Stangel and Christopher Haney (Zoology Dept., University of Georgia, Athen, GA).

Using these sources of information, the distribution of those seabirds found in the ACSAR study area are described in the section on Species Accounts. Since extensive reference was made to Brown (1977), Powers (1983), and Powers and Brown (in press) in these accounts, citations to these manuscripts were not made and were left as understood. One problem with seabird observation data is that different investigators have used different methods of measuring abundance, so that quantitative relationships between different sources of data cannot be addressed. Powers (1982) made a detailed comparison of the two most popular abundance estimators used in the North Atlantic: density (birds km^{-2}) and abundance (birds seen per 10-min). He found that the former method minimizes inflationary effects caused by a number of bird behaviorial and observer counting biases, which are not controlled in the latter method. Thus, I have also presented quantitative data on seasonal seabird densities throughout the ACSAR study area. These data provide a means to compare variability in abundance within a given species (not among different species) between different oceanographic habitats of the ACSAR study area. For waters north of Cape Hatteras (ca. 35 degrees N), seasonal densities of seabirds are given by year from 1978 to 1982. This provides an additional measure, annual variability in abundance, which is not available in any of the previously mentioned literature.

SPECIES ACCOUNTS

Fulmars

Northern fulmars are found throughout boreal, subarctic and arctic waters of the North Atlantic. In the western North Atlantic they occur as far south as Virginia in late winter and early spring (December to April). The majority of fulmars found south of the Grand Banks off Newfoundland concentrate on the north and east flanks of Georges Bank from December to April.

Shearwaters and Petrels

Five shearwaters seasonally occur in the western North Atlantic. Greater and sooty shearwaters breed in the southern hemisphere and spend the austral winter north of the equator. Greaters are principally found in boreal and subarctic waters of the western North Atlantic from May to December. The majority of the population resides on shelf waters from Georges Bank northeast to the Grand Banks, although spring (April-May) and fall (September-December) migrations occur through the ACSAR study area. The distribution of sooties is similar to that of greater's except that they have a clockwise migration in the North Atlantic; thus, the majority of the population is in the western part from April to July and by August it's in the eastern part, from which they return to the South Atlantic (Phillips, 1963). Cory's shearwaters breed on islands in the eastern North Atlantic and in the Mediterranean. Non-breeding birds are found throughout subtropical waters of the North Atlantic from June to November. In the western North Atlantic Cory's are most abundant on the shelf from Long Island to the Great South Channel. Of the smaller "black-and-white" shearwaters, many remain in boreal waters of the North Atlantic from April to November, although birds in the western part must pass through the ACSAR study area during their migrations to and from wintering areas off Brazil (Spencer, 1972). Audubon's are found principally in slope waters from June to at least October; they are probably the most common shearwater in the ACSAR study area during that time.

Black-capped petrels breed on islands and adjacent mainlands of the Caribbean (Wingate, 1964) and the closely allied and endangered Bermuda petrels which breed only on Bermuda (Murphy and Mowbray, 1951). The pelagic distributions of these species are not well known. Bermuda petrels have not been recorded away from Bermuda (Clapp et al., 1982), but black-capped petrels are regularly seen from April to November in slope and Sargasso waters south of 35°N (Morzer-Bruyns, 1967; Lee and Rowlett, 1979).

Storm-Petrels

Wilson's storm-petrels breed in the southern hemisphere and a large population spends the austral winter in the western North Atlantic from April to November. Their seasonal migrations pass through the ACSAR study area (Roberts, 1940). From April to May they are found in greatest abundance along the shelf-edge of the Middle Atlantic Bight and from June to August in the southwestern Gulf of Maine and on northern Georges Bank. Leach's storm-petrels breed from Massachusetts to Labrador in eastern North America. Their pelagic distribution is mainly centered around the larger colonies off Newfoundland. Leach's occur in the ACSAR study area from April to November. White-faced storm-petrels breed on islands in the eastern North Atlantic and in the South Atlantic (Cramp et al., 1977). Sight records of this species are scattered throughout the subtropical parts of the western North Atlantic from August to October.

Gannets

Northern gannets breed in eastern Canada and migrate to shelf waters off the eastern United States and Gulf of Mexico during the period from October to May. The center of their winter distribution occurs in the Middle Atlantic Bight. Large numbers of gannets aggregate around the large fleets of trawlers fishing in the canyons of the Bight, particularly in the vicinity of Hudson Canyon off New York and New Jersey.

Phalaropes

In the western North Atlantic red and red-necked phalaropes are seasonal migrants principally in shelf waters. Reds are the most abundant species in spring (April to May); neither species is abundant in fall (September to November). In spring the majority of red phalaropes migrate in a "corridor" between the 60 and 200-m isobaths from Cape Hatteras to Georges Bank. Small numbers of both species spend the winter in shelf waters from Chesapeake Bay south to Florida (Weston, 1953; Lee and Booth, 1979; Rowlett, 1980).

Jaegers and Skuas

Three Jaegers, all circumarctic breeders, occur in the western North Atlantic. Jaegers are migrants through the ACSAR study area in spring (April-May) and fall (September-November). Pomarine and parasitic jaegers are the more common species; long-tailed Jaegers are rarely sighted in the western North Atlantic south of Newfoundland.

Two skuas occur in the western North Atlantic. Great skua breeds from Iceland east to the British Isles. It is found throughout the year off the northeastern United States, but is most common from November to March in shelf waters. South polar skuas migrate into the western North Atlantic from the southern hemisphere. They probably occur as migrants in the ACSAR study area from May to October.

Gulls

Eight gulls, all of which breed in eastern North America, occur in shelf waters off the northeastern United States. These include: glaucous, Iceland, great black-backed, herrings, laughing, ring-billed, Bonaparte's and Sabine's gulls and black-legged kittiwakes. Great black-backed and herring gulls are the most common in the ASCAR study area. From November to April they concentrate around the commercial fishing fleets at the shelf-edge in the Middle Atlantic Bight and Georges Bank.

Terns

Seven terns potentially occur in the ACSAR study area. Common and arctic terns are spring (April-May) and fall (August-October) migrants from wintering areas in the southern hemisphere and breeding areas along the coast of the northeastern United States and Canada. Royal and sandwich terns are coastal inhabitants from Chesapeake Bay south to the Gulf of Mexico. Black terns breed in the interior parts of North America, but their fall migration is coastal south of Cape Hatteras where flocks may stray into the ACSAR study area. Sooty and bridled terns are pelagic during their nonbreeding season. Sooties breed off southern Florida, but autumn hurricanes will "blow" them into the ACSAR study area. Bridled terns, which breed on islands in the Caribbean, regularly occur from August to October in shelf-edge and slope waters of the ACSAR study area south of 36°N.

Alcids

Five alcids (raxorbill, common and thick-billed murre, dovekie, and Atlantic puffin) have pelagic ranges in the western North Atlantic. None of these species regularly occurs away from the shelf. Goerges Bank and the adjacent shoal waters to its west are the southern limit of any significant numbers of these species.

SEASONAL DISTRIBUTION

Since only Powers (in press) and Powers and Brown (in press) presented seabird densities (birds km^{-2}) for the ACSAR study area, quantitative evaluation is limited to those publications and to a compilation of unpublished MBO data from 1978-1982. The study area is divided into five regions: Georges Bank edge (GBe), Middle Atlantic Bight edge (MABe), Slope Water north of 35°N (SLn), over the Slope Water from 28°-35°N (SLs) and shelf water from 28°-38°N (SHs). The regions include depths from 100-500 m for GBe and MABe, 500-4000 m for SLn, <200 m for SHs, and >200 m for SLs. Data from 1978 were considered separately because of the extensive foreign fishing activity along the shelf break from Hudson to Lydonia canyons in that year.

The year was divided into winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug) and autumn (Sep-Nov). Observation effort from the MBO seabird data files for these seasons from 1978 through 1982 is summarized in Table 6.36 for the three regions (GBe, MABe and SLn) north of 35°N latitude. Since only six cruises were made south of 35°N, effort for shelf (SHs) and slope (SLs) waters from 28°-35°N was considered separately in Table 6.37. Mean densities of seabirds by species from 1979-1982 are summarized by region in Tables 6.38 - 6.41: GBe (Table 6.38), MABe (Table 6.39), SLn (Table 6.40), and SHs and SLs (Table 6.41). Mean densities of seabirds by species from 1978 only are given for GBe (Table 6.42), MABe (Table 6.43) and SLn (Table 6.44).

Winter

Total bird densities in winter (1979-1982) were lower than 10 birds km^{-2} for each region except MABe, where 132.7 birds km^{-2} was recorded (Table 6.39). North of 35°N, fulmars, gannets, great black-backed and herring gulls, black-legged kittiwakes and dovekies were most common. South of 35°N, no species was common and species richness (number of species) was greater on shelf waters (SHs) (13 species) than over slope waters (SLs) (7 species). Excluding herring gulls, which are ship-followers, no species density exceeded 0.1 bird km^{-2} in SLs.

The most important distribution feature during winter was the concentrations of gannets and great black-backed and herring gulls at the shelf break in the Middle Atlantic Bight (Table 6.38). These concentrations involved thousands of each species and they were all associated with large foreign fishing fleets in the Hudson Canyon area approximately 160 km southeast of New York City. Concentrations of these three species were also found with fishing fleets in the MABe region in 1978 (Table 6.42).

Region	Year	Winter	Spring	Summer	Autumn
Slope (SLn)	1978	6.0(7)	16.8(15)	180.2(187)	43.6(46)
	1979	76.7(70)	116.3(106)	359.6(335)	175.0(184)
	1980	17.6(19)	4.1(4)	63.1(47)	38.7(26)
	1981			7.5(6)	
	1982	2.8(2)	129.3(109)	236.4(185)	56.4(43)
Georges Bank edge (GBe)	1978	10.4(11)	43.2(46)	19.1(20)	23.0(25)
	1979	9.9(11)	3.4(4)	17.6(27)	48.7(61)
	1980	12.6(10)	2.0(2)	16.7(16)	12.4(9)
	1981		98.4(82)	70.9(56)	3.4(6)
	1982		37.0(29)	5.0(4)	12.7(12)
Middle Atlantic Bight edge (MABe)	1978	22.7(25)	22.7(21)	52.0(59)	16.8(20)
	1979	16.0(18)	75.8(79)	85.9(54)	34.7(40)
	1980		24.0(26)	55.1(40)	27.0(18)
	1981	12.5(10)	34.7(28)	42.3(34)	96.5(77)
	1982	18.5(14)	103.1(85)	72.5(61)	95.8(91)

Table 6.36 Seabird observation effort for each region north of 35°N by season and year from 1978 through 1982. Effort is measured by area (km^2) and number of transects (in parentheses).

Month/year	Region	
	SHs	SLs
Feb 1980	100	39
Mar 1983	158	14
Aug-Sep 1979	122	32
Sep 1981	64	
Sep 1982	34	

Table 6.37 Observation effort (no. of bird transects) on shelf waters (SHs) and slope waters (SLs) south from 28°-35°N off the southeastern United States, 1979-1983.

Species[1]	Season			
	Winter	Spring	Summer	Autumn
NOFU	0.7(±1.2)	6.8(±16.6)	< 0.1(±0.2)	0.4(±0.6)
COSH			0.2(±0.7)	0.2(±0.4)
GRSH	0.1(±0.2)	< 0.1(±0.1)	1.1(±1.8)	3.7(±6.4)
SOSH		0.1(±0.3)	0.1(±0.3)	
AUSH			< 0.1(±0.1)	
WISP		1.5(±2.7)	5.0(±7.1)	
LESP		< 0.1(±0.2)	0.6(±1.5)	
NOGA	0.1(±0.2)	0.1(±0.2)		0.3(±1.4)
REPH		34.4(±31.0)		0.5(±1.4)
POJA	< 0.1(±0.2)	0.1(±0.3)	< 0.1(±0.1)	0.1(±0.4)
PAJA			< 0.1(±0.1)	
UNSK	< 0.1(±0.2)			< 0.1(±0.1)
GLGU		< 0.1(±0.1)		
GBBG	0.3(±0.5)	1.4(±3.5)		0.3(±1.0)
HEGU	0.5(±0.7)	0.7(±1.3)		3.2(±8.1)
LAGU			< 0.1(±0.1)	
BLKI	1.8(±3.1)	3.7(±7.1)		0.6(±1.8)
DOVE	0.2(±0.5)			0.2(±0.4)
ATPU		0.1(±0.3)		
Total	9.6	48.9	7.0	9.5

[1]Key to species codes is given in Appendix 6.1.

Table 6.38 Mean bird densities (birds km^{-2}) by season on George Bank edge (GBe) water from 1979 through 1982.

Species[1]	Season			
	Winter	Spring	Summer	Autumn
NOFU	1.0(±3.5)	1.1(±6.4)	< 0.1(±0.1)	
COSH			0.3(±2.1)	0.6(±2.9)
GRSH			1.3(±7.7)	1.1(±4.6)
SOSH		< 0.1(±0.2)	0.1(±0.3)	
MASH			< 0.1(±0.1)	
AUSH			0.1(±0.2)	< 0.1(±0.1)
WISP		0.6(±4.4)	7.0(±19.3)	0.4(±1.0)
LESP		< 0.1(±0.1)	< 0.1(±0.1)	< 0.1(±0.1)
NOGA	28.9(±50.9)	19.0(±79.0)	< 0.1(±0.1)	< 0.1(±0.1)
REPH		34.4(±234.0)		0.2(±2.5)
RNPH		0.1(±0.1)		< 0.1(±0.1)
POJA				0.2(±0.7)
PAJA				< 0.1(±0.1)
UNSK	< 0.1(±0.2)	< 0.1(±0.1)		
GLGU		< 0.1(±0.1)		
ICGU		< 0.1(±0.1)		
GBBG	56.7(±115.5)	25.4(±92.9)	< 0.1(±0.2)	0.1(±0.6)
HEGU	44.4(±79.3)	37.1(±103.3)	< 0.1(±0.1)	1.4(±4.2)
RBGU				< 0.1(±0.1)
LAGU		< 0.1(±0.1)		
COTE			< 0.1(±0.1)	< 0.1(±0.1)
BLKI	1.2(±3.5)	0.5(±2.7)		0.1(±0.4)
RAZO		< 0.1(±0.1)		
DOVE	0.4(±1.3)	< 0.1(±0.1)		
ATPU	0.1(±0.2)	< 0.1(±0.1)		
Total	132.7	118.1	8.8	4.1

[1]Key to species codes is given in Appendix 6.1.

Table 6.39 Mean densities of birds (birds km^{-2}) by season on Middle Atlantic Bight edge (MABe) waters from 1979 through 1982.

	Season			
Species[1]	Winter	Spring	Summer	Autumn
NOFU		0.2(±0.6)	<0.1(±0.1)	<0.1(±0.1)
COSH		<0.1(±0.1)	0.2(±1.6)	0.1(±1.0)
GRSH		<0.1(±0.1)	0.6(±3.8)	0.1(±0.2)
SOSH			<0.1(±0.8)	
MASH		<0.1(±0.1)	<0.1(±0.1)	<0.1(±0.1)
AUSH			0.5(±3.4)	0.1(±0.2)
BCPE			<0.1(±0.1)	0.5(±3.8)
WISP		0.3(±1.8)	4.4(±15.1)	0.6(±1.0)
LESP		0.1(±0.3)	0.2(±0.9)	<0.1(±0.2)
WFSP			<0.1(±0.1)	
NOGA	<0.1(±0.1)	0.7(±3.7)		<0.1(±0.2)
REPH		1.5(±4.3)		<0.1(±0.1)
RNPH		0.2(±0.4)		
POJA		<0.1(±0.1)	<0.1(±0.1)	<0.1(±0.1)
PAJA		<0.1(±0.1)		
UNSK	<0.1(±0.1)	<0.1(±0.1)		
ICGU	<0.1(±0.1)			
GBBG	0.2(±0.8)	0.4(±0.5)	<0.1(±0.1)	0.1(±0.1)
HEGU	2.4(±5.6)	4.0(±19.3)	<0.1(±0.1)	1.0(±3.1)
RBGU				<0.1(±0.1)
LAGU				<0.1(±0.2)
BLKI	0.4(±2.4)	0.2(±0.9)		<0.1(±0.2)
ARTE			<0.1(±0.1)	
COTE			<0.1(±0.1)	<0.1(±0.1)
BRTE	<0.1(±0.1)		<0.1(±0.1)	
SOTE				<0.1(±0.1)
DOVE	1.8(±2.5)			
Total	4.8	7.6	5.9	2.4

[1]Key to species codes is given in Appendix 6.1.

Table 6.40 Mean bird densities (birds km^{-2}) by season in slope water (SLn) north of 35°N from 1979 through 1982.

Species	Winter		Spring		Autumn	
	SHs	SLs	SHs	SLs	SHs	SLs
NOFU	< 0.1(±0.1)		< 0.1(±0.1)			
COSH					1.2(±6.6)	0.8(±0.8)
MASH			0.1(±0.1)			
AUSH		0.1(±0.1)			0.4(±2.8)	0.6(±0.9)
BCPE		< 0.1(±0.1)				1.7(±2.8)
WISP			< 0.1(±0.1)		< 0.1(±0.1)	0.1(±0.1)
NOGA	0.5(±0.4)	0.1(±0.1)	0.7(±0.7)	0.2(±0.1)		
BRPE	< 0.1(±0.1)					
REPH	0.1(±0.1)					
RNPH	0.1(±0.1)		0.1(±0.1)		0.4(±4.3)	
UNPH	0.7(±0.6)		0.2(±0.3)			
POJA		< 0.1(±0.1)				
PAJA					< 0.1(±0.1)	
GLGU	< 0.1(±0.1)					
ICGU			< 0.1(±0.1)		< 0.1(±0.1)	
GBBG	< 0.1(±0.1)		< 0.1(±0.1)	< 0.1(±0.1)	< 0.1(±0.1)	
HEGU	3.6(±12.0)	1.8(±5.7)	0.7(±0.7)	0.4(±0.7)		
RBGU	< 0.1(±0.1)					
LAGU	0.7(±0.9)	< 0.1(±0.1)	< 0.1(±0.1)		0.7(±1.1)	
BOGU	0.6(±0.9)	< 0.1(±0.1)	0.2(±0.2)			
BLKI	< 0.1(±0.1)			< 0.1(±0.1)		
ROTE	0.1(±0.1)		< 0.1(±0.1)			
COTE			0.1(±0.1)		< 0.1(±0.1)	< 0.1(±0.1)
BRTE			< 0.1(±0.4)			0.2(±0.1)
SOTE			0.1(±0.4)			0.2(±0.1)
SATE			0.2(±0.4)			
BLTE			0.6(±3.4)			0.1(±0.1)
Total	7.7	2.0	2.9	0.6	2.7	3.6

[1]Key to species codes is given in Appendix 6.1.

Table 6.41 Mean bird densities (birds km^{-2}) by season on shelf (SHs) and slope (SLs) waters from 28°-35°N off the southeastern United States, 1979-1983.

Species[1]	Season			
	Winter	Spring	Summer	Autumn
NOFU	6.9(±12.1)	75.7(±456.0)	0.2(±0.7)	1.1(±3.0)
COSH			0.1(±0.4)	0.1(±0.5)
GRSH	0.9(±2.1)		4.2(±10.4)	10.9(±26.1)
SOSH		0.1(±0.2)	0.2(±0.6)	
AUSH				0.1(±0.2)
WISP		0.9(±2.8)	14.8(±20.6)	0.3(±1.2)
LESP			0.1(±0.3)	
NOGA		16.3(±62.3)		0.1(±0.5)
REPH		0.1(±0.7)		0.3(±1.3)
POJA		0.1(±0.4)		0.1(±0.3)
UNJA				0.2(±0.4)
UNSK				< 0.1(±0.2)
GBBG	0.9(±0.9)	53.6(±282.8)		0.3(±1.1)
HEGU	0.6(±1.3)	69.3(±356.1)		1.0(±3.7)
BLKI	3.6(±6.5)	0.6(±1.8)	0.1(±0.5)	
RAZO		< 0.1(±0.4)		
TBMU		0.3(±1.5)		
UNMU	0.6(±1.2)	0.6(±2.4)		
DOVE	2.4(±5.9)	0.3(±1.7)		
ATPU		< 0.1(±0.2)		
Total	16.2	217.9	19.7	14.2

[1] Key to species codes is given in Appendix 6.1.

Table 6.42 Mean bird densities (birds km^{-2}) by season on George Bank edge (GBe) waters in 1978. Foreign fishing activity was heavy in this area from March through June.

Species[1]	Season: Winter	Spring	Summer	Autumn
NOFU	0.2(±1.1)	0.5(±0.9)	<0.1(±0.2)	0.1(±0.5)
COSH			0.2(±0.5)	
GRSH		2.1(±6.4)	6.8(±30.9)	1.4(±2.9)
SOSH		0.8(±2.6)	0.2(±0.8)	
MASH			<0.1(±0.1)	
AUSH			<0.1(±0.1)	
WISP		52.2(±212.9)	18.1(±102.6)	
LESP			<0.1(±0.1)	
NOGA	3.8(±7.7)	2.4(±3.6)		0.1(±0.3)
REPH		5.8(±11.5)		
RNPH		<0.1(±0.1)	0.4(±3.5)	
POJA				0.6(±1.6)
PAJA				0.1(±0.4)
UNJA			<0.1(±0.1)	0.2(±1.0)
UNSK	0.1(±0.4)		<0.1(±0.1)	
GLGU	<0.1(±0.2)			
ICGU	<0.1(±0.2)			
GBBG	169.4(±753.8)	1.7(±3.6)		0.3(±0.8)
HEGU	55.3(±214.8)	1.3(±3.1)		3.1(±5.1)
LAGU			<0.1(±0.3)	
BLKI	24.0(±108.0)	<0.1(±0.2)		0.2(±0.7)
UNTE		0.5(±1.8)	<0.1(±0.1)	
UNMU		<0.1(±0.2)		
Total	252.6	67.4	25.9	6.1

[1]Key to species codes is given in Appendix 6.1.

Table 6.43 Mean bird densities (birds km^{-2}) by season on Middle Atlantic Bight edge (MABe) waters in 1978. Foreign fishing activity was heavy in this area from January through March and sporadic from May to July.

	Season			
Species[1]	Winter	Spring	Summer	Autumn
NOFU	5.1(±6.6)	16.2(±42.5)	$<$ 0.1(±0.1)	0.3(±0.9)
COSH			0.2(±1.6)	0.1(±0.3)
GRSH		1.1(±3.1)	0.6(±2.3)	3.1(±7.5)
SOSH		0.1(±0.2)	0.1(±0.4)	
AUSH			0.2(±0.9)	0.1(±0.2)
WISP		3.6(±5.3)	8.0(±23.2)	0.2(±0.8)
LESP			2.6(±5.3)	
NOGA	0.2(±0.6)	8.6(±29.6)		$<$ 0.1(±0.1)
REPH		1.6(±2.7)	0.1(±1.3)	0.1(±0.3)
POJA		0.1(±0.2)		0.1(±0.5)
UNJA				0.1(±0.3)
UNSK			$<$ 0.1(±0.1)	
GBBG	3.8(±4.1)	11.8(±36.5)		0.2(±0.8)
HEGU	14.4(±23.3)	3.1(±10.2)		0.7(±1.7)
BLKI	4.2(±10.3)	0.2(±0.5)		0.5(±1.7)
TBMU		0.2(±0.8)		
UNMU	0.4(±1.0)	0.4(±0.9)		
DOVE	4.5(±7.8)			
ATPU		0.1(±0.5)		
Total	32.6	47.1	11.9	5.6

[1]Key to species codes is given in Appendix 6.1.

Table 6.44 Mean bird densities (birds km^{-2}) on slope water (SLn) north of 35°N latitude during 1978. Foreign fishing activity was heavy over the continental shelf edge from January through June.

Spring

The greatest seasonal densities of seabirds were typically found in spring. North of 35°N total seabird densities were 48.9-118.1 birds km^{-2} along the shelf break (Tables 6.38-6.39), but only 7.6 birds km^{-2} in slope water (Table 6.40). The spring migration of arctic-bound red phalaropes occurs along the outer shelf off the northeastern United States between the 60 and 500-m isobaths. Local densities often exceeded 1000 birds km^{-2} on the shoreward edge of the shelf/slope front (Powers and Backus, 1981; Powers and Brown, in press). In the MABe region the concentrations of gannets and great black-backed and herring gulls with foreign fishing fleets continued until April when densities of these species declined substantially (Table 6.40). In 1978 foreign fleets were actively fishing the seaward edge of Georges Bank, which caused fulmars, gannets and great black-backed and herring gulls to concentrate there in that year (Table 6.42). These concentrations in 1978 even spilled over into slope water (SLn) within the 1000-m isobath (Table 6.43).

South of 35°N, the effort data were limited to March (Table 6.37), but again densities were relatively low (<3 birds km^{-2}) (Table 6.41). Although no species was found to be numerically dominant in March, the shearwater, storm-petrel and phalarope migrations north during spring must have passed through the SLs region during April and May. In addition, Audubon's shearwater and black-capped petrel are found in the SLs region during spring (Lee and Booth, 1979; P. Stangel, personal communication).

Summer

In summer north of 35°N total densities of seabirds were typically low (<10 bird km^{-2}). Wilson's storm-petrel was the most abundant species with densities of 4.4-7.0 birds km^{-2} (Tables 6.38-6.40). Audubon's, greater and Cory's shearwaters were commonly found in low numbers. Flocks of Audubon's shearwaters (<100 birds) were sometimes found along the northern edge of the Gulf Stream in the SLn region. No data were available for the areas south of 35°N at this time, but in August black-capped petrels were found in Gulf Stream water north of 35°N. This suggests a greater abundance in the SLs region to the south (cf, Lee and Booth, 1979; Powers, in press).

Foreign fishing activities along the shelf break are limited during summer to a few squid fleets. Their importance to attracting birds appeared to be limited to greater shearwaters. In 1978 the pattern of distribution and abundance of seabirds north of 35°N was similar to that observed in 1979-1982, except that densities of Wilson's storm-petrels were slightly greater in that year (Tables 6.41-6.43).

Autumn

In autumn, as in summer, total densities of seabirds were typically low (<10 birds km^{-2}) throughout the regions north of 35°N. Densities of greater shearwaters may have increased over summer estimates along the shelf-break regions (Tables 6.38-6.39), but not farther offshore in SLn (Table 6.40). The fall migration of red phalaropes is not comparable to that of spring along the shelf break. They apparently take a more direct route from the Canadian arctic (Orr et al., 1982) to suspected wintering areas off northwest Africa. Other than ship-following herring gulls, no other species is particularly common at this time.

In autumn south of 35°N total densities of seabirds were also low (2.7-3.6 birds km^{-2}), both on shelf (SHs) and slope (SLs) waters (Table 6.41). The most abundant species in slope water were Cory's and Audubon's shearwaters and black-capped petrels. This pattern was probably evident in summer as well. Audubon's shearwaters may be locally abundant along the edge of the Gulf Stream (cf, Lee and Booth, 1979). Bridled, sooty and black terns were also found in slope water from at least late August to probably October, but again they were not abundant (Table 6.41).

ECOLOGICAL CONSIDERATIONS

Seasonal total densities of seabirds over the continental slope off the northeastern and southeastern United States are relatively low compared to the shelf and shelf break areas off New England. Seasonal densities throughout North Atlantic Slope Water were always less than 10 birds km^{-2} in summer (Powers and Brown, in press). Foreign fishing fleets are an important factor in concentrating certain species of seabirds (usually fulmars, greater shearwaters, gannets, and great black-backed and herring gulls) along the shelf break, particularly in winter and spring from Hudson Canyon in the Middle Atlantic Bight east to Lydonia Canyon on Georges Bank. The large influx of red phalaropes at the shelf break in April and May is tied to oceanographic factors, not fishing activity (Powers and Backus, 1981).

A paucity of any significant concentrations of prey near the surface in Slope Water may explain the low densities of seabirds relative to shelf regimes further north. The isothermal layer above the thermocline is deep in shelf break areas during summer and fall and throughout the year in Slope Water. These nutrient-poor waters set this area apart from a boreal shelf system, which gets completely mixed in winter from storms and low air temperatures. Well-mixed waters are more productive because a supply of nutrients is maintained in near-surface waters. Thus an increased growth in phytoplankton stocks stimulates production in higher trophic levels because more energy is available for consumption at each successive link in the food chain. On a smaller scale, fronts are probably one of the most important factors controlling the distributions of seabirds in these deep-water areas. The shelf/slope front in spring and the northern edge of the Gulf Stream in summer and early fall may be mechanisms which provide local aggregations of prey at the surface for birds like phalaropes, shearwaters and storm-petrels.

Seabird distribution north of 35°N is relatively well understood at present, but data are limited to the south. Although seabird densities there are undoubtedly low, a better understanding of (1) the migration corridors of phalaropes, shearwaters and storm-petrels in spring and fall and (2) the relationship of seabird interactions with the shelf/slope front and the front associated with the edge of the Gulf Stream south of 35°N need further examination. Also it is not clear whether or not the endangered petrel, cahow (*Pterodroma cahow*), which breeds only in Bermuda, ranges over part of the area of interest (SLs). This species is not easily distinguished in the field from its close ally, the black-capped petrel.

Appendix 6.1. Key to species codes used in Tables 6.46-6.52, including common and scientific name.

Species Code	Common Name	Scientific Name
NOFU	Northern fulmar	Fulmarus glacialis
COSH	Cory's shearwater	Calonectris diomedea
GRSH	Greater shearwater	Puffinus gravis
SOSH	Sooty shearwater	P. griseus
MASH	Manx shearwater	P. puffinus
AUSH	Audubon's shearwater	P. LHERMINIERI
BCPE	Black-capped petrel	Pterodroma hasitata
WISP	Wilson's storm-petrel	Oceanites oceanicus
LESP	Leach's storm-petrel	Oceanodroma leucorhoa
WFSP	White-faced storm-petrel	Pelagodroma marina
BRPE	Brown pelican	Pelecanus occidentalis
NOGA	Northern gannet	Sula bassanus
BRBO	Brown booby	S. leucogaster
REPH	Red phalarope	Phalaropus fulicaria
RNPH	Red-necked phalarope	P. lobatus
POJA	Pomarine jaeger	Stercorarius pomarinus
PAJA	Parasitic jaeger	S. parasiticus
UNJA	Unidentified jaeger	S. sp.
UNSK	Unidentified skua	Catharacta sp.
GLGU	Glaucous gull	Larus hyperboreus
ICGU	Iceland gull	L. marinus
GBBG	Great black-backed gull	L. marinus
HEGU	Herring gull	L. argentatus
RBGU	Ring-billed gull	L. delawarensis
LAGU	Laughing gull	L. atricilla
BOGU	Bonaparte's gull	L. philadelphia
BLKI	Black-legged kittiwake	Rissa tridactyla
ARTE	Arctic tern	Stern paradisaea
COTE	Common tern	S. hirundo
SATE	Sandwich tern	S. sandvicensis
ROTE	Royal tern	S. maximus
SOTE	Sooty tern	S. fuscata
BRTE	Bridled tern	S. anaethetus
UNTE	Unidentified tern	S. sp.
BLTE	Black tern	Chlidonias niger
RAZO	Razorbill	Alca torda
TBMU	Thick-billed murre	Uria lomvia
UNMU	Unidentified murre	U. sp.
DOVE	Dovekie	Plautus alle
ATPU	Atlantic puffin	Fratercula arctica

CHAPTER SEVEN

HUMAN ACTIVITIES AND IMPACTS

A.G. Gaines, M.E. Silva, S.B. Peterson, and D.A. Ross

ENVIRONMENTAL, REGULATORY AND POLITICAL CONSIDERATIONS

The coastal waters of the eastern United States are among the most intensely used and managed of the world. Nevertheless, it is evident that the future will see even increasd exploitation of resources in this area and an increasing population of people seeking their livelihood and recreation in coastal related activities.

The ACSAR region is demarked roughly by the 50 mile and 200 mile offshore limits (Fig. 7.1). The 200 mile fisheries zone established by the Magnuson Fisheries Conservation and Management Act (MFCMA) approximates the outer limit of the ACSAR within U.S. jurisdiction. Portions of the Blake Outer Ridge, the Blake Spur and a small area near the seaward terminus of the Hudson Canyon lie outside the 200 mile limit (Fig. 7.1).

Constraints on human activities in the OCS are imposed by natural features of the area as well as by political and regulatory factors. The following section will summarize these constraints as a basis for more specific treatment later. Furthermore, impacts or potential impacts of human activities in the OCS depend on the nature of the undisturbed environment, against which the impact is measured or perceived. The distribution of physical and living environments, and of certain species of organisms as well as of economic activities and political jurisdictions are given in 125 maps prepared by NOAA (1980). This data atlas is a valuable resource for people interested in the ACSAR area and the adjacent continental shelf. An automated computer-based inventory, accessible by narrowly defined geographic grid, is presently being developed by NOAA (D. Basta, personal communication). The system contains updated information on topics covered in the atlas and should aid in manipulation of large quantities of data in support of decision-making.

GENERAL ENVIRONMENTAL FEATURES

Previous chapters of this report examine the physical, chemical, biological, and geological features of the ACSAR area, which provide a context for the human activities and opportunities as well as impacts considered in this chapter, and to which the reader is referred for this information. To recapitulate briefly, certain of these environmental features are as follows:

Physical Oceanography

In the oceanic environment physical processes are not only of direct importance on human activities, but also can control biological, chemical and geological aspects. A unique feature of ACSAR is that it contains the strongest currents in the world ocean: namely the Gulf Stream, the deep Western Boundary Undercurrent and currents associated with warm- and cold core rings. On the basis of surface circulation, the ACSAR area can be divided into two sections, separated by Cape Hatteras (Fig. 7.2). South of Cape Hatteras the Gulf Stream (also called the Florida Current) lies against the continental slope and extends to bottom depths. Landward of about 200m, the inshore waters (Fig. 7.2) characterized by strong seasonal fluctuations in temperature and water composition, and higher productivity and standing crop

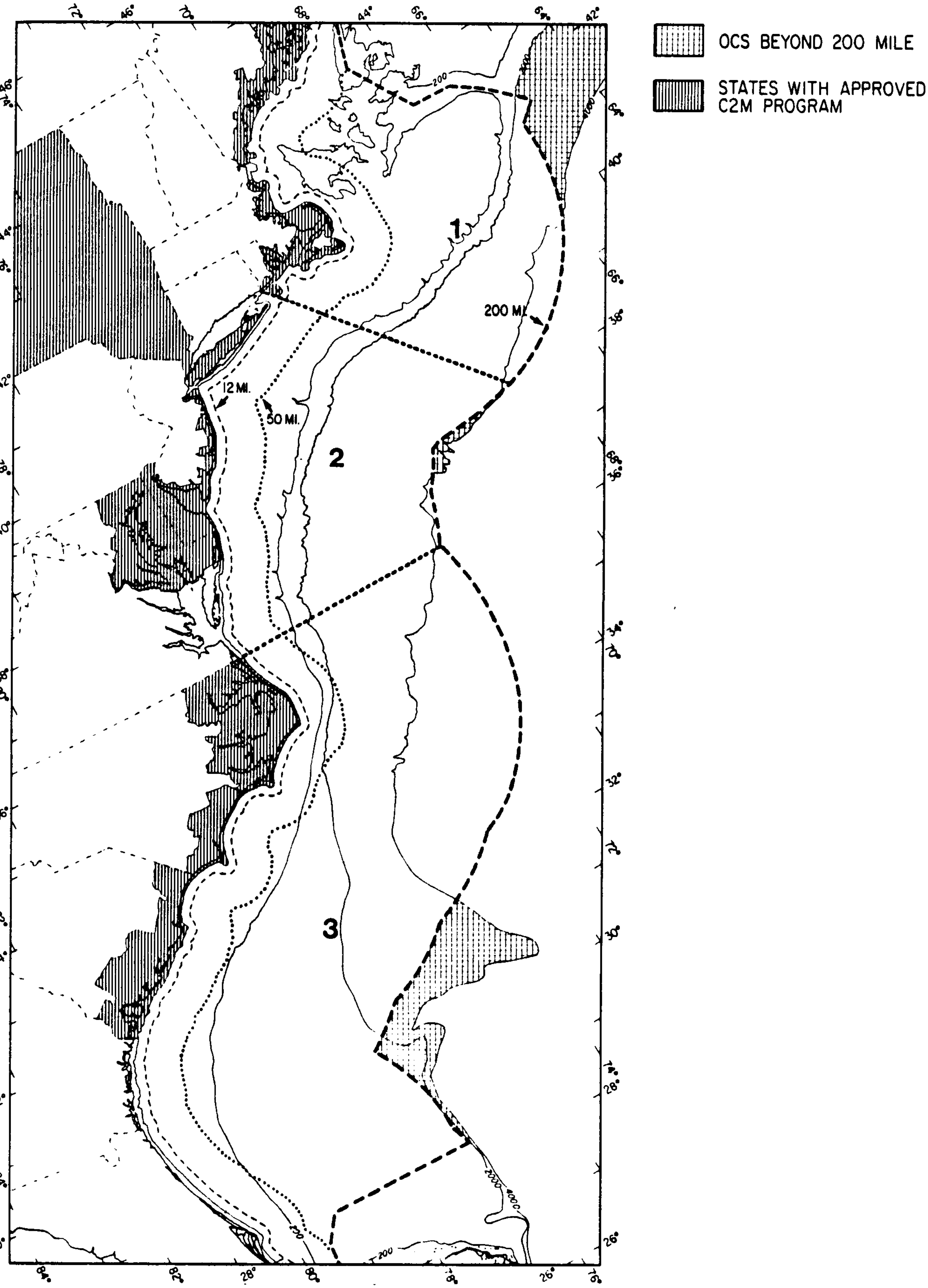


Figure 7.1. Bathymetry and certain jurisdictional delimitations of the ACSAR area. Numbers 1-3 indicate regional fisheries management council jurisdictions; heavy dashed line indicates boundary of the U.S. fishery conservation zone (modified from NOAA 1980).

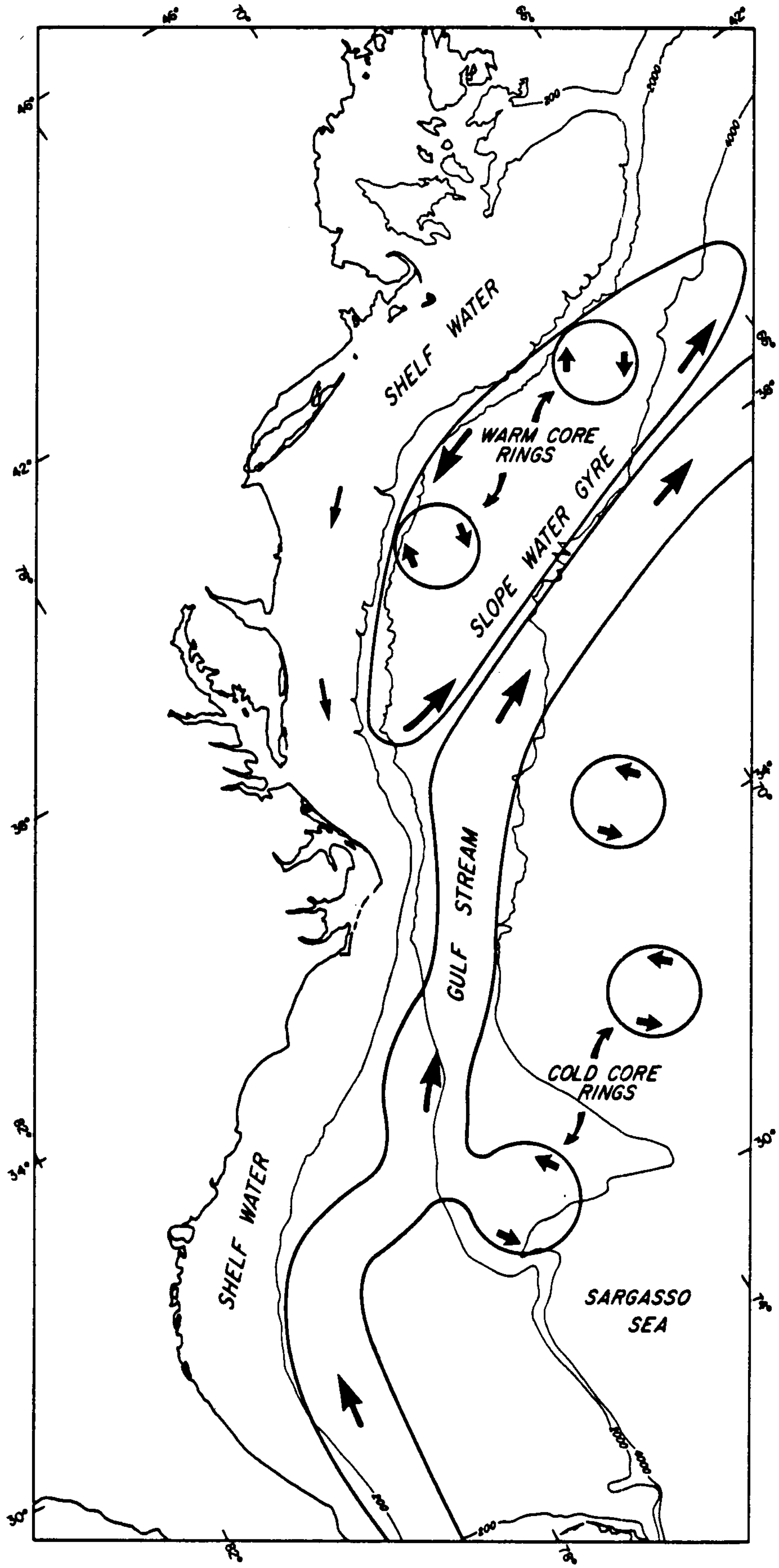


Figure 7.2. General oceanographic features of the ACSAR area (modified from NOAA 1980 and Csanady et al. 1979).

of water column biota. Seaward of the Gulf Stream, the water column of the Blake Plateau and Blake Outer Ridge area is dominated by Sargasso Sea water masses, with relatively constant temperature and salinity profiles. However, significant hydrographic variation in this region (temperature, current speed and direction, salinity, nutrient composition) results from the passage of cold core rings formed north of Cape Hatteras, which interact with and may be absorbed into the Gulf Stream between Cape Hatteras and about 30°N, several months after their formation (Richardson, 1980). Cold core rings may extend to bottom depths in the ACSAR. The deep environment in this southern area is also influenced by the second major strong current of the ACSAR, the southward moving Western Boundary Undercurrent (McCave, 1978). This deep current is characterized by flow of variable speed, sometimes exceeding 30 cms^{-1} (Hollister et al., 1978), with often relatively high turbidity from suspended sediment.

North of Cape Hatteras the picture is different. The Gulf Stream curves seaward over the Western Boundary Undercurrent (in a manner yet to be clarified by oceanographers), and displays meandering behavior along the seaward margin of the ACSAR area (U.S. Department of Commerce, 1980). Between the Gulf Stream and the continental shelf, an area occupied by slope water, surface circulation has been depicted as a counterclockwise gyre (Csanady, 1979; Fig. 7.2), with surface temperature-salinity characteristics between those of the seasonally varying shelf waters and the more constant Gulf Stream water. In this area warm core rings containing Sargasso Sea water spin off landward from Gulf Stream meanders and move southward along the continental slope and rise, embedded in the slope water gyre. The warm core rings typically have diameters of about 100 km and are surrounded by frontal regions characterized by current velocities in excess of 100 cms^{-1} (Csanady et al., 1979). In addition to these warm core rings, numerous smaller lenses of relatively fresh seawater have been identified at depths between 50 and 200 m. Small-scale frontal features are common and are assumed to be ultimately associated with transport of fresh water from continental runoff to the Sargasso Sea, as waters of different density slide over one another in a cross-frontal direction (Csanady et al., 1979). Mixing and advection processes of the region north of Cape Hatteras are characterized by great complexity, in response to storms, frontal features, rings, the interleaving processes and other mechanisms. In this area, the mean circulation does not provide a good basis for short-term predictions.

The salient feature of air-sea interactions and weather in the ACSAR area is the frequent occurrence of storms. These disturbances tend to be hidden in standard climatological averages, but their significance to human activities cannot be overlooked. Storms are of both tropical and extra-tropical origin, and have a time scale of 2 to 5 days, although the surface currents they produce can persist for up to two weeks.

Biology

Abundance of benthic invertebrate fauna both in biomass and density decrease with increasing water depth in the ACSAR (Fig. 7.3 and 7.4). Wigley's and Theroux's (1981) data suggest part of this relationship may be due to decreasing sediment size: finer sediments characteristic of deeper water contain lower abundance of organisms.

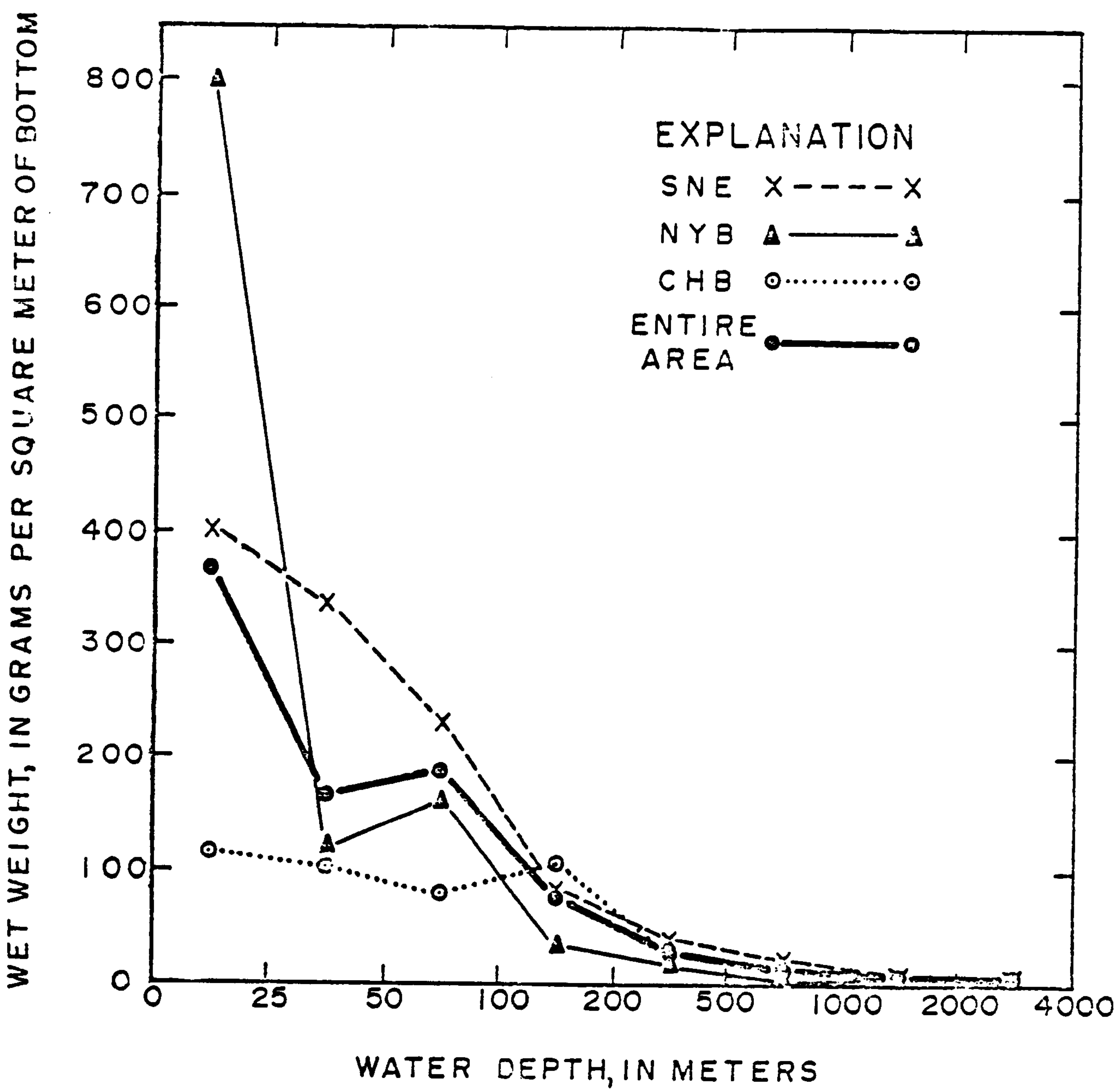


Figure 7.3. Relationship between biomass and water depth for the continental margin off southern New England (SNE), New York Bight (NYB), Chesapeake Bight (CHB), and the entire area off Cape Hatteras-Cape Cod (from Wigley and Theroux, 1981).

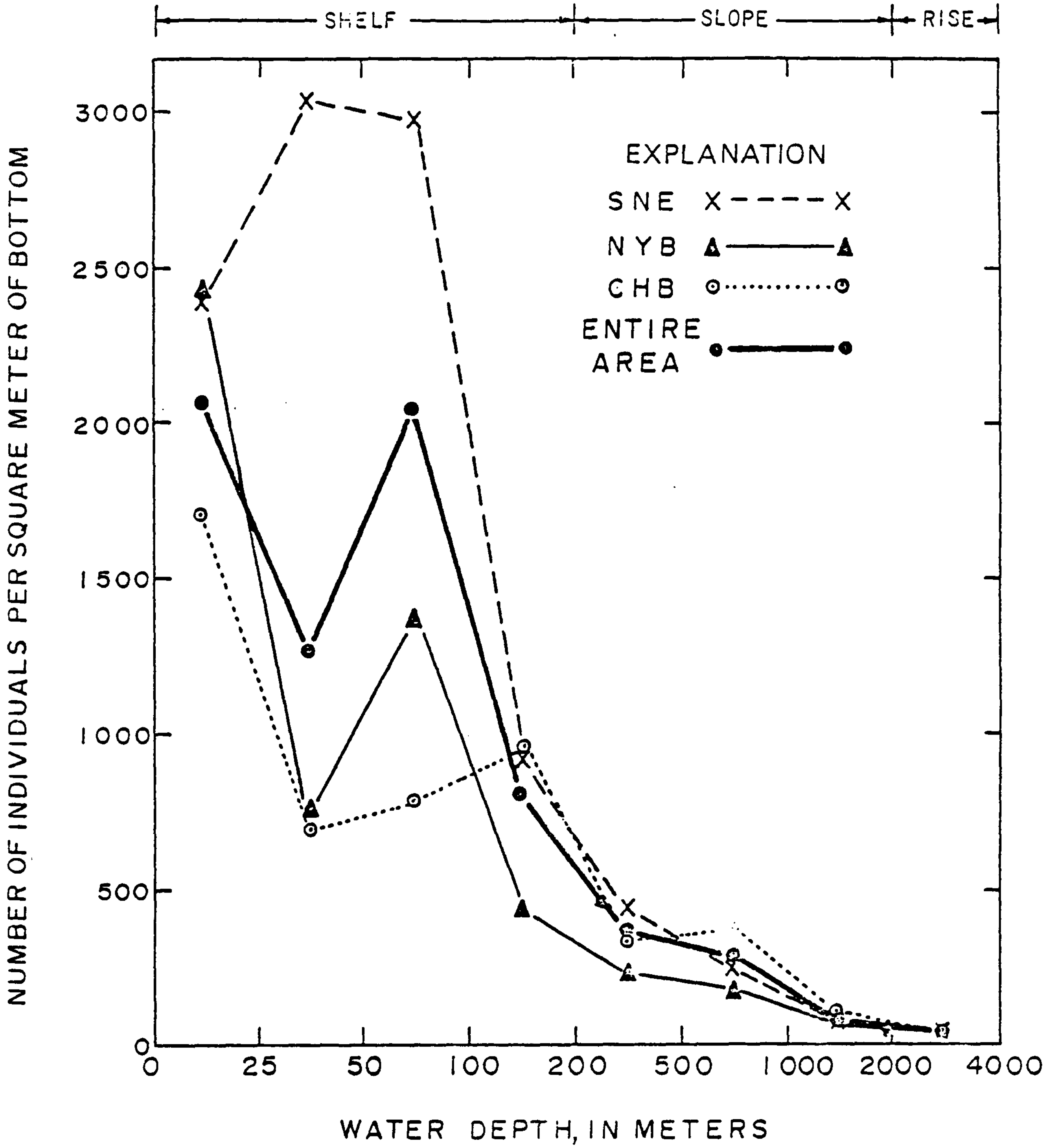


Figure 7.4. Relationship between number of individual animals and water depth for the continental margin between Cape Hatteras and Cape Cod (southern New England (SNE), New York Bight (NYB), Chesapeake Bight (CHB; from Wigley and Theroux, 1981).

For water column organisms, the Gulf Stream forms a sharp biogrographic boundary between the North Atlantic Temperate and North Atlantic Subtropical regions. This current also serves to transport tropical organisms northward, where they are diluted and dispersed as the entrainment process incorporates surrounding waters and their subtropical biota. Gulf Stream rings further complicate the picture as waters of Sargasso Sea or continental shelf origin are pinched off and transported elsewhere, along with associated flora and fauna.

Geology and Geohazards

The bathymetry of the continental slope of the ACSAR area is characterized by an average seaward gradient of 3-6°, but locally slopes can be vertical. North of Cape Hatteras there are numerous submarine canyons (Fig. 7.2) while these features are scarce or absent to the south.

The "mud line" occurs at 250-300 m, below which silt and clay size sediments predominate and carbonate content increases. Above this depth, detrital sediments predominate. Sediment thickness on the slope is at maximum 9 kilometers. Because of the existance of strong bottom currents at all depths in the ACSAR area, erosion is not limited to shallow water environments here.

While the dominent sedimentary process in the ACSAR area is gravity controlled downslope movement, the significance of this process as a geohazard is not clearly known. The potential impact of slumping is illustrated by the Grand Banks Slump of 1929 which occurred at the northern edge of the ACSAR area (Turekian, 1976), Although slumping events of this dramatic scale are unusual.

Sediment instability, or slumping, on the continental slope of the mid-Atlantic U.S. have recently been identified as a potential hazard to OSC activities such as oil drilling. As summarized by Robb et al. (1981), geohazard features of the mid-Altantic OCS could include "...observed slumps or slides, canyon or valley axes which may serve as conduits for downslope currents or transport of failed debris, areas of Quaternary sediment cover greater than 10 m thick, topographic slopes greater than 12°, filled valleys which have been intersected by present-day canyons, faults,..." and probable debris fields at canyon mouths. Disagreement seems to exist in the literature as to the magnitude or significance of geohazard risk resulting from these downslope movements. For example, the range in total area of slump features reported in the literature varies from as high as 2,000 km^2 to as little as 3 km^2. Robb et al. (1981) suggest slumping events in their study area have been of small scale and cover only about 1.3% if its 1400 km^2 area. They indicate geohazards should be addressed on a site-specific basis.

Chemistry

As for other spatial features, chemical distributions in the ACSAR area are at least as complicated as the distribution of water types. Even so, the regional concentrations are considerably better known than fluxes and processes. Nutrients are relatively depleted during summer months and elevated during the colder seasons. Maxima for phosphorus and nitrogen occur at about 300 m in slope waters and 1000 m offshore, below which concentrations are relatively constant.

Trace metal data quoted in the literature are not entirely reliable, because of contamination problems in analysis. Artificial radionuclides, introduced through nuclear weapons testing, deep-water dumping and accidents are present in the ACSAR area, as are naturally occurring radionuclides.

OUTLINE OF ENVIRONMENTAL REGULATIONS, TRENDS, AND CONCEPTS

National Trends in Environmental Regulations

Use of the OCS is directly affected by national trends in the focus, extent, and enforcement of regulations. Public concern over chemical contamination of the environment and destructive environmental effects surrounding practices of industry and government increased during the 1950's and 1960's and became embodied into federal legislation, policy, and infrastructure largely in the 1970's. The decade of the 1970s, for example, saw establishment of the Council on Environmental Quality and the Environmental Protection Agency; Coastal Zone Management legislation and plans; consolidation of diverse Federal ocean functions into the National Oceanic and Atmospheric Administration; as well as numerous laws designed to protect one aspect or another of the nations's air, waters, biota, and special environments and habitats.

The problems resulting from this intensive effort to stave off environmental damage are illustrated by the issue of ocean dumping (see review of Farrington et al., 1982; Lahey, 1981). In essence, the five federal statutes affecting disposal of society's waste materials protect the air by prohibiting incineration, protect the ocean by prohibiting ocean dumping, and protect ground and surface water by prohibiting landfill or deep-well injection. The overall effect has been to shift the burden of receiving society's wastes to the medium least regulated at the moment, or in the case of sludge disposal, leaving a city with no viable options.

In 1981, the National Advisory Committee on Oceans and Atmosphere (NACOA) prepared a special report to the President (NACOA, 1981) drawing attention to this difficulty and indicating that regulations on waste disposal should aviod the single purpose approach of the 1960s and 1970s; instead, regulations should identify the medium on which a given waste material would have least impact. Although this recommendation may have been influenced by pragmatism and current value judgements, it also is supported by recent scientific concepts pertaining to the flexibility of ecosystems in accommodating changes in the supply of materials or energy, the so-called "assimilative capacity".

Environmental Impact, Pollution and Assimilatory Capacity

The National Environmental Policy Act of 1969 established the requirement for an environmental impact statement to accompany any proposed federal actions "...significantly affecting the quality of the human environment". In one sense the terms, "environmental impact", "pollution", and "assimilative capacity" are similar or identical, in that each calls for a subjective identification of an "acceptable" amount of environmental change resulting from human activities. The term "environmental impact" carries no connotation of whether environmental changes associated with a given human activity are regarded as beneficial or otherwise; in comparison, the term "pollution" implies a deleterious change or that any change is deleterious. For the ocean, the newer term "assimilative capacity", defined as the amount of material that could be contained within a body of seawater without producing an unacceptable biological impact (U.S. Department of Commerce, 1979) carries with it the connotation that some level of environmental change is acceptable. The above definition of assimilative capacity also contains a functional basis for quantifying assimilative capacity, although determination of what is "unacceptable" still leaves wide margins of variability.

Assimilative capacity can in principle be assessed by successive additions of a pollutant to a water body; the impact becomes evident at an "endpoint". Like the other terms relating to the affect of human activity on the environment, value judgements are involved in the selection of the endpoint. For example, the endpoint selected by a committee assessing the impact of industrial wastes on plankton in the ocean selected death of all plankton in the wake of the discharging vessel as an endpoint. Another committee might have selected death of the most sensitive species as the endpoint, and very different conclusions regarding the assimilative capacity of the ocean site would have resulted. The concept of assimilative capacity accurately connotes the ability of organisms to endure a range of environmental conditions and of ecosystems to accept variations in the nature and rate of materials and energy flux. This ability to accomodate changes represents the value and the limit of the environment as a renewable resource for human use.

APPLICABLE DOMESTIC AND INTERNATIONAL REGULATIONS AND TREATIES

All of the ACSAR area considered here lies outside the 3-mile territorial sea and all but a small area near Cape Hatteras lies outside 50 miles (Fig 7.1). Most of the area is within the 200-mile fisheries zone established by the MFCMA and the 10 March 1983 Reagan Proclamation (establishing a 200 nautical mile Exclusive Economic Zone); a portion of the Blake Outer Ridge defined by the 4000m isobath falls beyond 200 miles (see Fig. 7.1). The ACSAR area considered here is free of international disputes, except a small area on Georges Bank for which sovereignty is contested by the U.S. and Canada, and which presently awaits a decision by the World Court. This ACSAR region could be affected by legislation concerning marine scientific research (H.R. 703), establishment of a U.S. exclusive economic zone (H.R. 2061) and the Presidential Proclaimation regarding a U.S. 200-mile exclusive economic zone. Domestic and international regulation of ocean dumping is reviewed by Park and O'Connor (1981); Pararas-Carayannis (1973) gives an historical synopsis of the River and Harbor Act of 1899 as well as other U.S. legislation up to 1972.

Domestic Laws and Regulations

At present, in excess of 35 domestic laws pertain to activities in the ACSAR (U.S. Department of Interior, 1981; Table 7.1). Coastal states having approved Coastal Zone Management Programs (Fig. 7.1) can exercise the power of Federal Consistency review, stipulated by the Coastal Zone Management Act (as amended). This gives states with approved CZM programs the power to review federal decisions (such as OCS lease sales or licensing) affecting their waters and legally challenge those which are inconsistent with state's coastal policies.

The Magnuson Fishery Conservation and Management Act of 1976 (MFCMA; P.L. 94-265) regulates foreign and domestic fishing within 200 miles of the U.S. coast. This law established regional fishery management councils: the New

England Fishery Management Council in Saugus, Mass., the Mid-Atlantic Fishery Management Council in Dover, Del., and the South Atlantic Fishery Management Council in Charleston, S. C. are important for ACSAR. These management councils develop fishery management plans which define an optimum yield for each species or species group and identify the tonnage needed to support the domestic fishery; any remainder is allocated to foreign fishing interests by the State Department following guidelines negotiated with the council(s).

The Magnuson Fishery Conservation and Management Act of 1976 provided that the management of highly migratory species (i.e., some species of tuna) should be left to international or regional organizations. Nonetheless, there have been many efforts to have bluefin tuna included in the category of coastal fish because they are found predominantly in coastal waters. All tunas, however, remain under the management and conservation of agreements forged by international fisheries commissions. However, "...PL.94-265 provides for the conservation and management of fishery resources of the U.S. by establishing a fishery conservation zone of 200 nautical miles within which the U.S. has exclusive management authority over all fishery resources except highly migratory species of tunas...." Although the Act exempts tunas from the expansion of U.S. jurisdiction over fisheries resources, it does define 'fishing' to include any 'activity which can reasonably be expected to result in the catching, taking or harvesting of fish.' Since billfish and sharks fall within the definition of 'fish', and the Act does not provide an The U.S. has not signed the treaty, and the Reagan adminstration remains opposed to it through 1983, although the recent Reagan Proclaimation adopts certain elements of the treaty for the U.S. The U.S. is, however, party to a Geneva Convention treaty negotiated in 1958. Until ratification of the LOS treaty the Geneva Convention remains technically the law of the sea. The Geneva Convention defines a territorial sea without stating the breadth of that sea; in the U.S., a 3-mile territorial sea has been adopted. The Convention also provides for a contiguous zone not to exceed 12 miles from the baseline. Rules for continental shelf exemption for incidental take, billfish and sharks taken incidental to the catch of tuna by foreign vessels can be regulated within the FCZ (NOAA, 1978)."

International Agreements and Treaties

Activities in the OCS area considered here are presently subject to several international treaties. The International Convention for the Prevention of Pollution of the Sea by Oil regulates and restricts the intentional discharge of oil and oily mixtures by ships. For tankers over 150 gross tons (GRT) the discharge of oil or oily mixtures within 92.6 km (57.5 miles) of the nearest land is prohibited. Ships other than tankers over 500 GRT can discharge only when as far as practical from the nearest land. The International Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matter ("the London Dumping Convention") regulates ocean dumping and as of 1979 was ratified or acceded to by 43 governments including the United States (Park and O'Connor, 1981). This agreement prohibits ocean dumping of organohalogens, mercury, cadmium and their compounds, persistent plastics, high-level radioactive wastes, and biological and chemical warfare agents.

Administrative Procedure, 5 USC 551-559, Including Provisions of the Freedom of Information Act, Privacy Act, and the Government in the Sunshine Act.
Clean Air Act
Crude Oil Windfall Profits Tax Act of 1980
Deepwater Port Act of 1974
Department of Energy Organization Act
Emergency Natural Gas Act of 1977
Emergency Petroleum Allocation Act of 1973
Endangered Species Act of 1973
Energy Policy and Conservation Act
Energy Reorganization Act of 1974
Energy Supply and Environmental Coordination Act of 1974
Environmental Quality Improvement Act of 1970
Federal Energy Administration Act of 1974
Federal Water Pollution Control Act (as amended; Clean Water Act)
Fish and Wildlife Act of 1956
Fish and Wildlife Coordination Act
Land and Water Conservation Fund Act of 1965
Marine Mammal Protection Act of 1972
Magnuson Fishery Conservation and Management Act of 1976
Marine Protection, Research and Sanctuaries Act of 1972 (Ocean Dumping Act)
Marine Resources and Engineering Development Act of 1966, including the Coastal Zone Management Act of 1972
Mining and Minerals Policy Act of 1970
National Advisory Committee on Oceans and Atmosphere Act of 1977
National Environmental Policy Act of 1969
National Historic Preservation Act
National Ocean Pollution Research and Development and Monitoring Planning Act of 1978
Natural Gas Act
Natural Gas Pipeline Safety Act of 1968
Natural Gas Policy Act of 1978
Occupational Safety and Health Act of 1970
Outer Continental Shelf Lands Act Amendments of 1978
Pipeline Safety Act of 1979
Ports and Waterways Safety Act
Submerged Lands Act
Withdrawal of Lands for Defense Purposes Act

Table 7.1. Domestic laws pertaining to activities in ACSAR area.

Several international fisheries agreements may need to be considered in OCS development. These include, for example, Northwest Atlantic Fisheries Organization (NAFO), the successor to the International Commission for Northwest Atlantic Fisheries, the International Commission for Conservation of Atlantic Tunas (ICCAT)and the Convention for the Conservation of Salmon in the North Atlantic Ocean (see U.S. DOI Compilation of Laws related to Mineral Resource activities on the OCS, Vols. I and II, 1981 for more detail).

The Law of the Sea (LOS) Convention as negotiated over the last decade may have to be considered for any activity outside U.S. territorial waters. Activity refer to the seabed and subsoil to a depth of 200 m or to where the depth of the superadjacent waters admit to exploitation of the natural resources. The Geneva Convention defines the freedoms of navigation, fishing, laying of submarine cables and piplines, and overflight. It also establishes a vague international system for the control of fishing and conservation of living resources of the high seas.

The new law of the sea conference, called UNCLOS III, defines the continental shelf of a coastal state (Article 76, Paragraph 1) as "the sea-bed and subsoil of the submarine areas that extend beyond its territorial sea throughout the natural prolongation of its land territory to the outer edge of the continental margin, or to a distance of 200 nautical miles from the base-lines from which the breadth of the territorial sea is measured where the outer edge of the continental margin does not extend up to that distance." If the continental margin extends beyond 200 nautical miles, various formulas, often confusing, can be applied to establish its outer limit. Furthermore, the coastal state can exercise sovereign rights over the continental shelf for the purpose of exploring and exploiting its natural resources; these rights are exclusive in the sense that if the coastal state does not explore the continental shelf or exploit its resources, no one may undertake these activities without the express consent of the coastal state. The term "natural resources" includes the mineral and other non-living resources of the seabed and subsoil together with sedentary species of living organisms--long ago defined as those immobile organisms on or under the seabed, or unable to move except in constant physical contact with the seabed or subsoil.

FISHERIES

CURRENT COMMERCIAL FISHING ACTIVITIES

Active commercial fishing in the deep water on and over the edge of the continental shelf includes tile fish, billfish, sharks and lobster. Other commercial fisheries for cod, haddock, silver hake, and redfish also exist, although none of these fisheries is done predominantly in the area. There are no commercial fisheries of record on the rise, although various trawl surveys were done in that area in the late 1960s and early 1970s by the U.S.S.R. and the German Democratic Republic (G.D.R.)

Since passage of the MFCMA in 1976, the fisheries off the U.S. east coast have been dominated by U.S. and Canadian fishermen. However, before that time, there were valuable commercial fisheries in deep water done by Bulgaria, Cuba, F.R.G., G.D.R., Japan, Poland, Romania, Spain and the U.S.S.R. Japan continues to fish in the slope area for squid, butterfish, mackerel and tuna, with a permit from the State Dept. for the first three fish. No permit is needed to fish for highly migratory species such as tuna.

Until recently, Poland and the U.S.S.R. also had permits to fish off the Atlantic coast for some of these species. Those permits were rescinded when the U.S. government disagreed with non-fishing policies of those governments; however, it is likely in the future that permits will be granted for squid, herring, whiting, mackerel, and other species within the U.S. 200-mile fishery conservation zone.

Catches in ICNAF areas 5Ze, 5Zw, and 6 by Canada of silver hake, red hake, herring, mackerel, butterfish, *Illex* and *Loligo* were reported in 1980-81, and the the European Economic Community (EEC) had catches of silver hake, butterfish, *Illex*, and Loligo in that area. Japanese and Polish fishermen caught butterfish, *Illex* and *Loligo* squid (NAFO 1981; Fig. 7.5).

Using data from the weighout files of NMFS for commercial landings from the New England, and to a lesser extent, the Middle Atlantic fishing ports, Lange *et al*. (1981) analyzed species composition of otter trawl catches by statistical areas, depth zones, and months. They identified 9 major and 29 minor fisheries in the offshore waters. Total catch in the Mid-Atlantic winter-summer fishery has increased since 1974, with a significant peak in 1976. The major summer species caught are summer flounder and tilefish. However, lobster, silver hake and industrial catches (principally menhaden) have predominated this fishery at various times in the past. Total catch in the Middle Atlantic spring-autumn fishery has also increased since 1974, although a significant decline occurred in 1978. The major component of this fishery was scup, with catches of butterfish and several flounder species.

Lange *et al*. (1981) also characterized Georges Bank/Southern New England groundfish fishery during the late 1970s as having large catches of cod, yellowtail flounder, winter flounder, and haddock. However, the deep-water Georges Bank fishery was not fished much by the U.S. commercial fleet in the years covered by their report, producing less than 0.1% of total catch. The deep-water fishery is potentially important to U.S. groundfish fishermen, but is not now fished because the costs of steaming to that area are higher than for those areas closer to port and the traditional species less abundant. The deep-water fishery has a great proportion of lobster and red crab than does the area fish predominantly by U.S. fishermen. Lobster was the primary catch between 1968 and 1978, while before that time cod, haddock, and silver hake were important. From 1977-79 43% of the catch from deep water was lobster; silver hake 20%; and redfish 19% (Lange *et al*., 1981).

The offshore fishing fleet has no small vessels participating in the deep-water fishery, and large boats' effort has fluctuated from 2 to 55 days per year. Medium ton class vessels are predominant in this fishery, and their average time fishing in the area has ranged from 7 to 67 days per year. Total catch from the deep-water areas averaged 105 mt per year from 1971 to 1981. Catches between 1965 and 1969 were greater, averaging 380 mt for U.S. commercial vessels. The increases in operating costs---especially fuel after 1973---probably explain the decline since the abundance of most species sought by U.S. fishermen have remained the same or increased since 1971 (Lange *et al*., 1981).

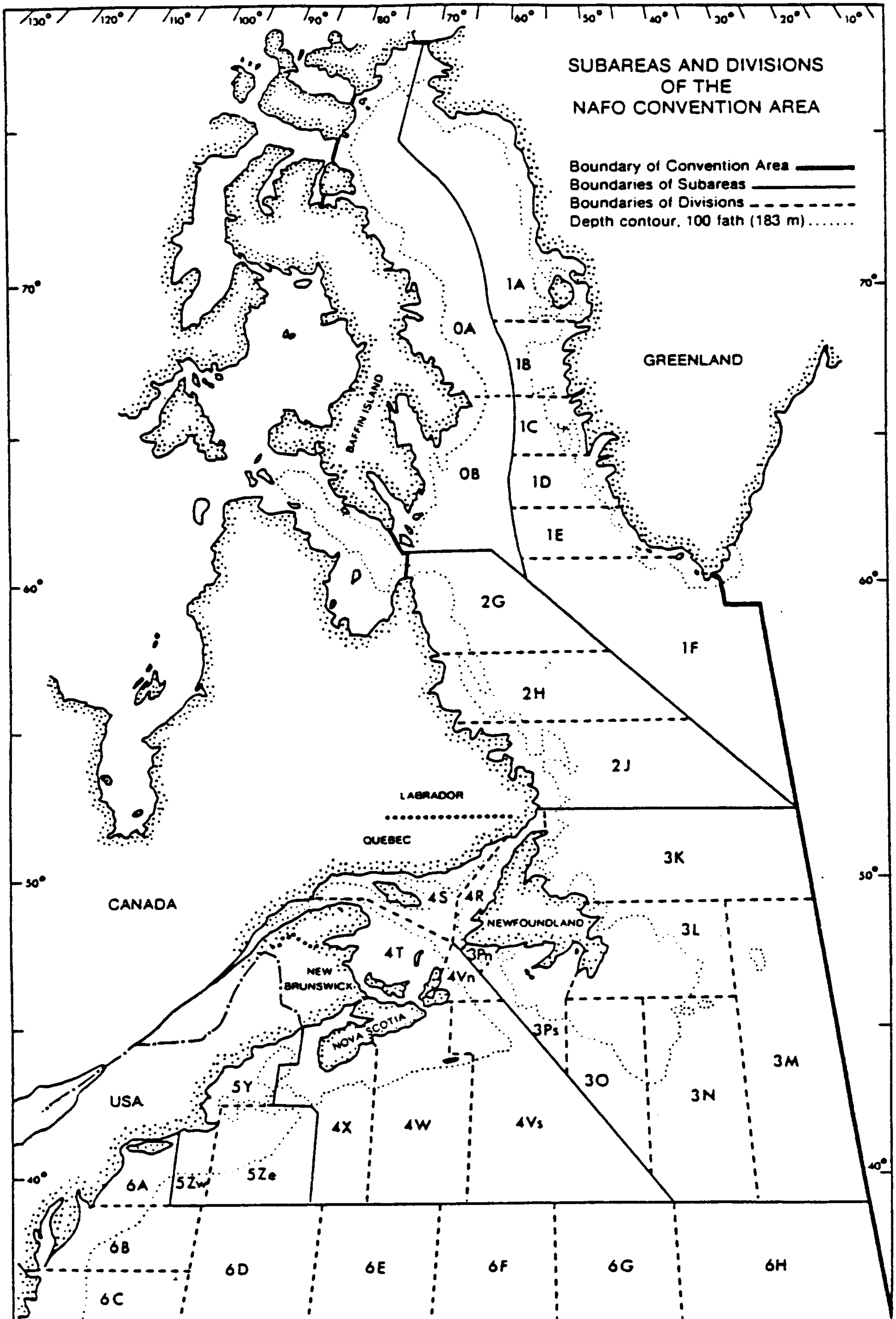


Figure 7.5. Subareas and divisions of the North Atlantic Fisheries Organization (NAFO) Convention area.

Fish distribution charts from the Spring and Fall surveys done by NMFS and foreign fishery scientists show potentially where the fish can be caught if the fishermen so desired. These charts, updated annually, show silver hake and mackerel in water deeper than 200 m along the slope in the spring in the area from 36 to 42 m. In the same series of Spring surveys, Loligo are present in the same depths and latitudes as are alewives, butterfish, lobster, red hake, redfish, scup, Illex, sea bass, and summer flounder. Fall surveys showed butterfish, lobster, silver hake, red fish, herring, Illex and Loligo squid in slope waters (NMFS 1960-80).

CURRENT RECREATIONAL FISHING

The 1978-79 Marine Recreational Fishery Statistics survey reports estimates of participation, catch and effort by recreational fishermen from Nov. 1978 to Oct. 1979. Data of several types were recorded, including total number of fish caught and brought ashore in whole form from which length/ weight samples were obtain, fish filleted, discarded dead, used for bait, and those caught and released alive. For the Mid-Atlantic offshore region, species include sea basses, bluefish, Atlantic Bonito, catfishes, Atlantic croaker, cunner, American eel, summer flounders, winter flounder, flounders, hakes, herrings, Atlantic mackerel, mackerels and tunas, white perch, yellow perch, porgies, scup, sea robins, spotted sea trout, sharks, dogfish, skates and rays, spot, striped bass, tautog, toadfishes, weakfish, and windowpane (Human Sciences Research Inc., 1979). The offshore fishery for many of these was curtailed by high fuel costs in the last decade. However, offshore fisheries do exist for cod and pollock because they can be taken year-round in the water deeper than 40 m in the area extending from Block Island, R.I. to Cape May, N.J. (Freeman and Walford, 1974). Current estimates are that about 90% of commercial sportfishing for groundfish is conducted within 20 miles of shore (Nicholson and Ruais, 1979), although the division of catch between the territorial seas (from 0 to 3 miles) of the coastal states and the Fishery Conservation Zone (3-200 miles) is not known.

Most recreational fishing is done within 20 miles of shore for two reasons. First, charter and party boats are licensed by the U.S. Coast Guard, and for many of those boats, the license restricts travel to within 20 miles of a harbor of safe refuge. The second reason is cost, both for fuel and time. Boats for hire prefer short fishing trips to reduce operating costs and to enable them to make several trips each day. Privately owned boats can find many sport fishing opportunities within 30 or 40 miles of shore with a few exceptions. These include substantial recreational fisheries for tilefish, whiting, mackerel, billfish, tuna, and shark which exist in offshore areas, but were curtailed when the price of fuel rose precipitously after 1974. Privately owned recreational fishing boats (i.e. those which do not take passengers for hire) are free to fish wherever and whenever they like.

STATUS OF SPECIES

The following pages include summaries by species or species group, including information on the location of the fishery, volume caught, potential catch, nationality of fishing country, whether the activity is commercial or recreational, gear or gears used, the value of the fishery, and a discussion of the fishery's potential in the deep waters off the continental shelf.

Billfish and Sharks

Fishing for billfishes and sharks in the Atlantic Ocean is mostly in waters varying in depth from 100 m to well over 1000 m (Fig. 7.6). The fishery is essentially a surface one, although canyons, seamounts, and other major geographical configurations are distinctive features in the area where the fishery is most intense. Sport fish include tunas, billfishes and sharks, and associated species---dolphin fish, wahoo, king mackerel, and great barracuda. Except possibly for some mid-water fishes or some of the squids, no other resource presently of equal commercial importance exists in the same area or at the same seasons as these pelagic fishes. Marine Mammals are rarely assocated with billfishes. Yellowfin tuna, albacore, bluefin tuna, bigeye tuna, skipjack tuna, blackfin tuna; sailfish, blue marlin, white marlin, longbill spearfish, swordfish, longfin mako, blue shark, shortfin mako shark, night shark, oceanic white tipshark, scalloped hammerhead shark, silky shark, thresher shark, tiger shark, bignose shark, porbeagle shark, spinner shark, bigeye thresher shark, great hammerhead shark, smooth hammerhead shark and Galapagos shark are all included in the commercial and recreational fisheries of the U.S. east coast (Department of Commerce, NOAA, 1978; Fig. 7.7).

The sport fishery for billfishes is seasonal, particlarly for the marlins. The fishery is most intense from April through October, but is heavily dependent on the weather rather than availability of billfishes since fishing is done a considerable distance from shore (South Atlantic Fishery Management Council, 1979). The only species for which maxiumum sustainable yield (MSY) estimates have been made are blue marlin, 4000 mt; white marlin, 1,900 mt; sailfish/spearfish, 960 mt.

Both commercial and recreational fisheries for pelagic sharks (i.e. sharks other than dogfish) are pursued with longlines, handlines, net trawls, and gill nets. The most intensive commercial fishery has been by foreign fleets; current commercial catches are low, but are likely to increase; in 1981 landings were valued at nearly $2 million. World landings of elasmobranch fishes in 1973 were 564,000 mt and rose to 587,000 mt in 1978. This is about 1/3 the tonnage of tuna caught per year and about 1/2 the tonnage of flat fish. Sharks are popular recreational fish, especially with charter boats because their greater abundance almost ensures that the recreational fishermen will catch something, even while fishing for swordfish, billfishes and tunas. U.S. commercial catch of large pelagic sharks in the waters off North Carolina to East Florida varied between 3 and 598 mt over the last decade, with an average of about 55 mt; the by-catch of sharks in the commercial swordfish fishery was estimated at 1020 mt for 1978; MSY estimates were 41,000 mt. Estimated catches by U.S. and Canadian fishermen of swordfish by longline have ranged as high as 5000 mt per year, although the average in the late 1970s has remained below 2000 mt; MSY in 1978 was estimated as 5800 mt. Swordfish are also caught commercially and recreationally by harpoon. Estimated recreational catch for large pelagic sharks is approximately 1872 mt. There has also been a substantial by-catch of shark, estimated to be over 2000 mt, in the Japanese longline fishery for swordfish during the last decade (Mid-Atlantic Fishery Managment Council, 1980).

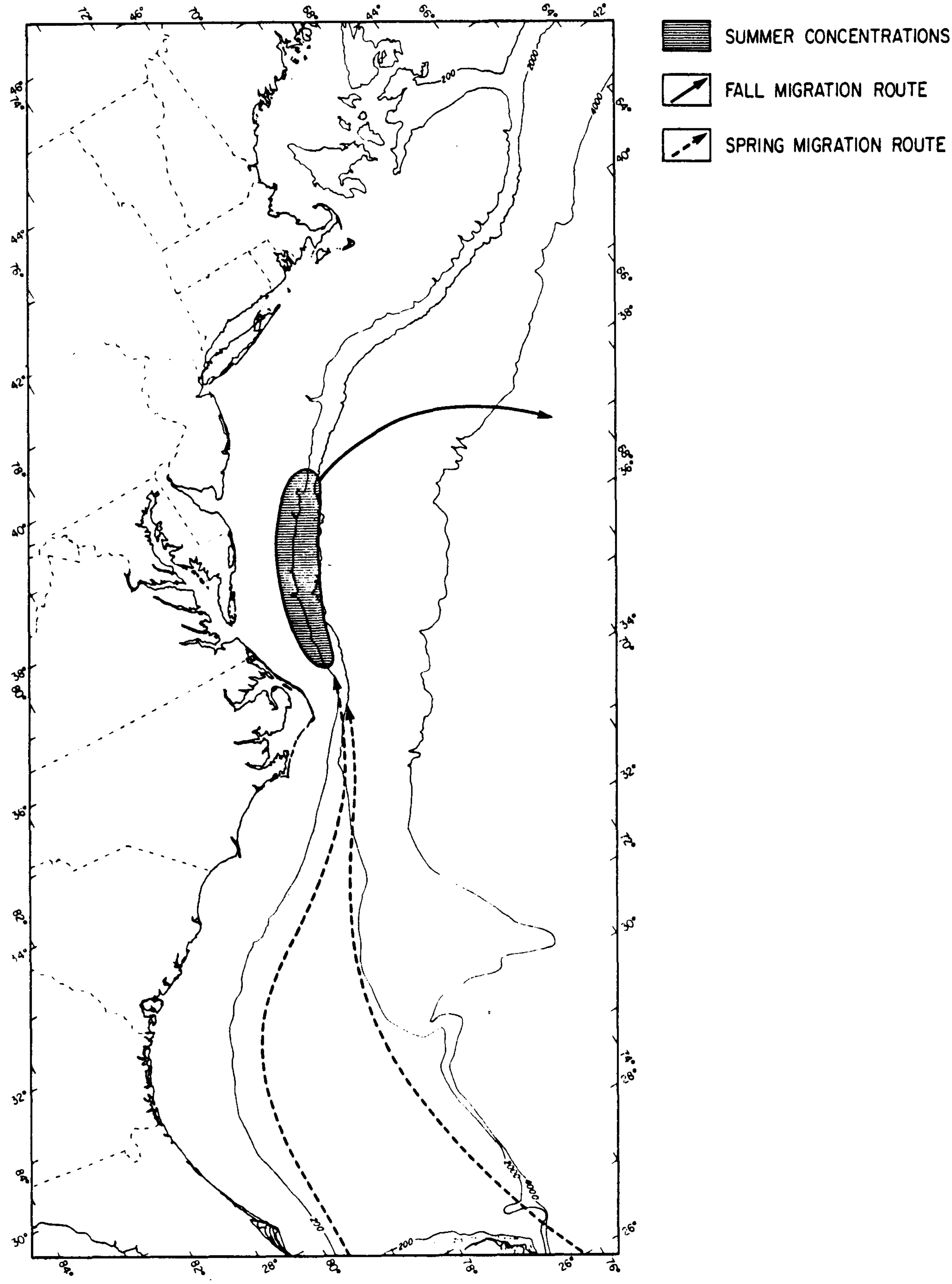


Figure 7.6. The distribution of white marlin (from NOAA 1981).

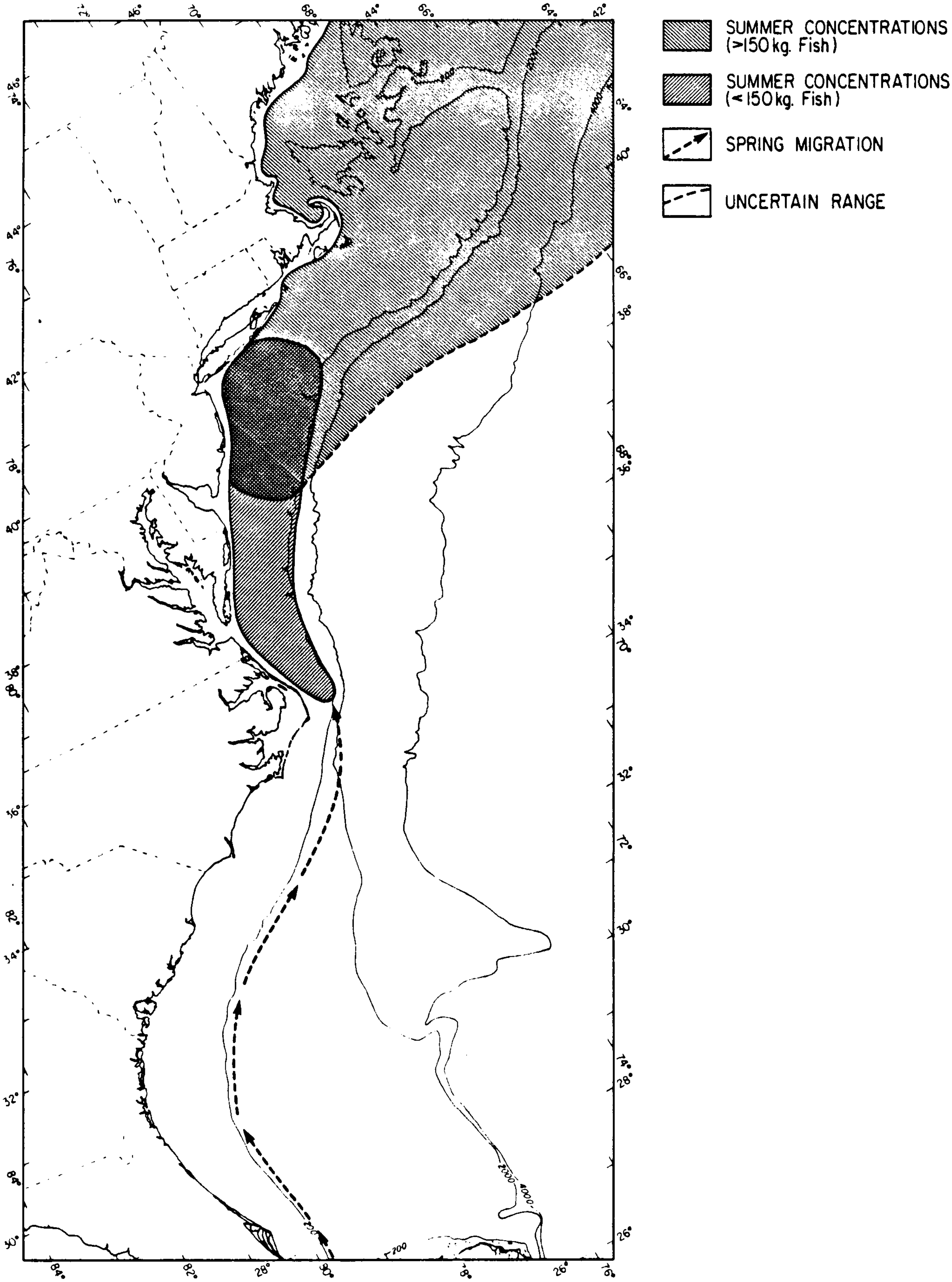


Figure 7.7. The distribution of blue fin tuna (from NOAA 1981).

The Fishery Conservation and Management Act of 1976 left management of highly migratory fish up to international organizations; although there have been many efforts to have bluefin tuna included in the category of coastal fish because they are found predominantly in coastal waters. As yet, tuna are managed under agreements forged by international fisheries commissions. (see page 13 for more detail).

Bluefish

Commercial and estimated recreational catches of bluefish (Pomatomus saltatrix) have undergone approximately a four-fold increase during 1960-78. Estimates of MSY range from 85,800 to 92,100 mt, and catches are about at MSY; 1975-78 catches averaged 88,200 mt (Anderson and Almeida, 1979). The value of commercial landings was $3.2 million and does not reflect the enormous recreational value of this fishery.

From Billingsgate Shoal off Cape Cod, Mass. to about Cape Lookout, N.C., angling for bluefish is particularly important. Recreational fishing in this area accounts for 83% by weight of all bluefish caught. Young of the year and yearlings are caught in the bays and sounds while older bluefish, some weighing as much as 30 lbs, are caught offshore. Some years, the fish do not appear inshore. Commercial fishing is done by trawling and seining, although in some states limitations on gear type are set to favor recreational fishing interests. There is no substantial (i.e. less than 2%) foreign catch of bluefish. There appear to be two major areas and seasons of spawning along the U.S. east coast: one offshore near the inner edge of the Gulf Stream from southern Florida to North Carolina in the Spring (chiefly in April and May), and other in the Middle Atlantic Bight (i.e. Cape Hatteras to Cape Cod) over the continental shelf in the summer (chiefly June through August) (Mid-Atlantic Fishery Management Council, 1980).

Tilefish

A domestic commercial longline fishery for tilefish (Lopholatilus chamaeleonticeps) has developed in the area between Cape Hatteras and Cape Cod (Fig. 7.8), with catches increasing from about 30 mt in 1968-69 to approximately 3800 mt in 1979. In 1981 the value of the catch was estimated at $7.5 million. The fish occur along the outer continentl shelf from Nova Scotia to Surinam in depth of 80 to 540 m. They are abundant in the southern New England-Middle Atlantic area where a commercial fishery has existed since 1915. In that area, the tilefish generally occur at depths of 80 - 440 m and at temperatures of 9 to 14.5 C. Fish have been observed from Norfolk to Lydonia Canyons; the limited area between appropriate isobaths south of the Hudson Canyon region limits large concentrations of tilefish. The fish have been observed in burrows as well as depressions near boulders and obstructions. Burrows are found in Pleistocene clay and generally located vertially with respect to the bottom although horizontal burrows have been observed in the walls of submarine canyons. The principle fishery is from ports in New York, New Jersey, Massachusetts, and Rhode Island. Both longlines and bottom trawls are used although the former dominate. Ireland, Japan, and Spain were the only foreign countries to report catches, although it is possible that some tilefish were caught by distant-water fleets during the 1960s and 70s but reported as "other finfish." Since 1977 they have been reported as by-catch in the distant water fleet fisheries for silver hake, red hake and squid.

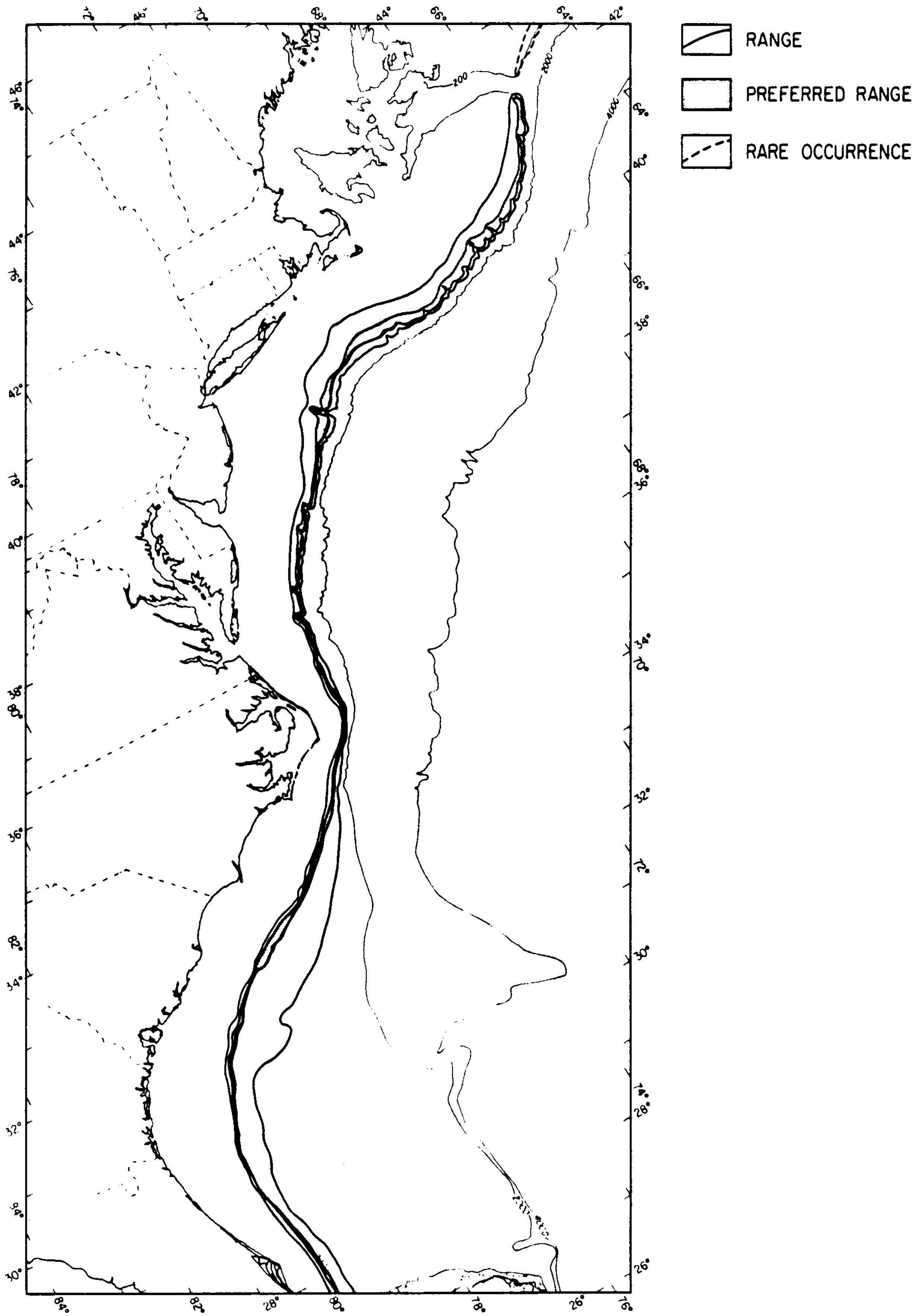


Figure 7.8. The distribution of tilefish (from NOAA 1981).

There is no allowable foreign catch for tilefish, and they are required to be discarded. The recreational fishery for tilefish developed in 1968 and party-, charter-, and private-boat activity was high during the early and mid-1970s. Since 1968, annual catches are estimated to have ranged from 5 to 340 mt. The recreational effort was greatly reduced by 1978 due to increase fuel costs and decreased size and availabiity of tilefish (Turner et al., 1981).

Squid

During late spring and summer, long-finned squid genera may be found in harbors and estuaries, particularly in southern New England. In the fall, concentrations appear in the southern New England and Hudson Canyon area (ICNAF 5Zw and 6A) in water less than 110 m deep. NMFS spring bottom trawl surveys show primary concentrations of Loligo in depths of 111-183 m and lesser concentration in other depth surveyed (27-110m and 184-366m). Size distribution correlates with depth in both spring and fall survey data, with the largest individuals usually taken at the greatest depths. MSY estimates are 40,000 mt for Illex and 44,000 mt for Loligo. The total allowable level of foreign fishing was 20,000 mt for Illex and 30,000 mt for Loligo (Mid-Atlantic Fishery Management Council 1978). In previous years, foreign catches of squid have been two to three times the amount now allocated, and continued requests from foreign nations for squid allocations are expected if a U.S. commercial fishery does not expand. U.S. expansion is limited by lack of domestic markets and severe competition in foreign markets. The 1981 value for squid caught in the Atlantic was $2.3 million. Although there is no "recreational" fishery for squid, squid are important as bait for many anglers.

The R.V. Lady Hammond (Canada), one of four vessels committed to a NAFO sampling program, was assigned to conduct intensive surveys within a small geographical area, in the vicinity of 63°W, in the region of the Slope Water-Gulf Stream-Sargasso Sea water masses and their interfaces. The table below summarizes data from the NAFO report (Amaratunga and Budden, 1982).

Hakes

Two representatives of the Genus Merluccius are found off the Atlantic coast; the silver hake, which favors the continental shelf waters (Fig 7.9), and the American hake, Merluccius albidus, a fish of the deeper continental slope. The ranges of both species overlap at the outer edge of the shelf and the commercial catch in that area may include both. The winter-spring distribution of silver hake (whiting) is along the outer continental shelf and slope and the summer-fall distribution is along the inner shelf and on the shoaler banks. The traditional locations of the commercial fisheies reflect the seasonal pattern of silver hake distribution. The U.S. fishing effort is conducted primarily in the summer and fall in depths less than 30 fathoms, and the value is estimated at $7.4 million. Any catches of American hake are likely to be recorded as silver hake since the two are caught together in the deep waters. The foreign fishing effort has traditionally been heaviest during the winter/spring along the outer edge of the shelf where wintering concentrations are found. The whiting fisheries were important to the foreign trawl fleets which caught approximately 80% of the 125,000 mt per year through the mid 1970s. Foreign countries involved in that fishery include Bulgaria, Cuba,

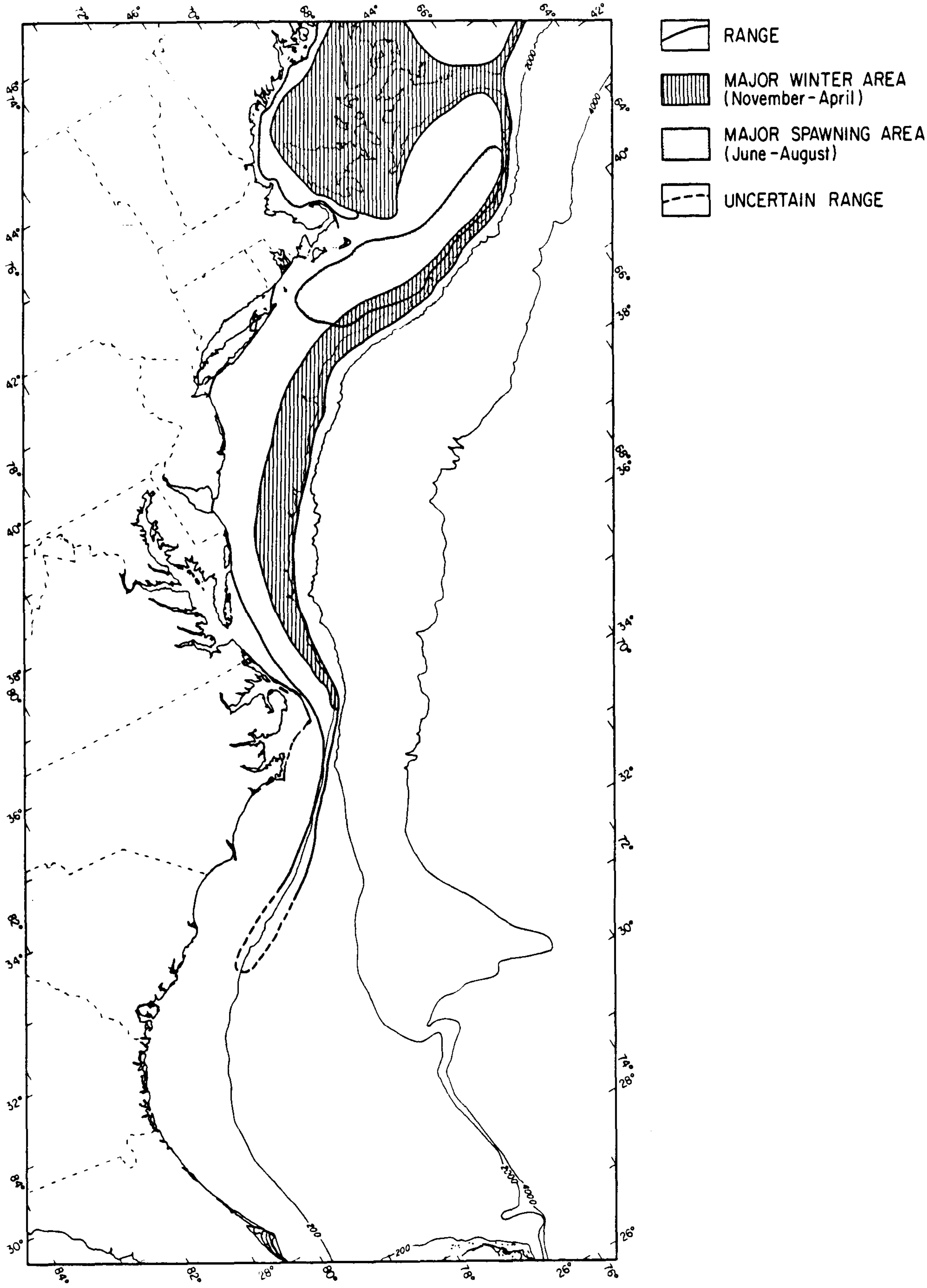


Figure 7.9. The distribution of silver hake (from NOAA 1981).

FRG, GDR, Japan, Poland, Romania, Spain and the USSR. In the 1973-75 period, 160,000 mt were taken from NAFO areas 5ZE and 5Zw/SA6. In 1976, 93,000 mt were taken and in 1977 115,000 mt were taken from those areas (Coombs, 1977). The recreational fishery is particularly important along the New York and New Jersey coasts where it supports a sizeable party and charter boat business. No offshore recreational fishery is recorded or anticipated for New England (New England Fishery Management Council 1978).

Total catches by New England and mid-Atlantic fishermen averaged about 16,800 tons during 1955-59, declined to 9,952 mt in 1960, and then increased steadily to 137,400 mt in 1966. Catches dropped sharply to 50,900 mt in 1967 and have since fluctuated between 19,200 and 67,000 mt. In the late 1970s catches averaged 27,200 mt. In 1978 the US commercial and recreational catches were estimated to be 11,405 and 4,000 mt respectively. The foreign catch that same year was 10,765 mt (Almeida and Anderson 1979). Markets for fresh or frozen whiting are limited; the largest existing domestic commercial market for whiting (frozen) has been extensive in the mid-Atlantic, Southeastern and southern parts of the U.S. Price are low and catches are highly variable from one year to the next (Coombs 1977).

The silver and American hake fishery in the mid-Atlantic area has a bycatch of mackerel, herring, squid, and red hake (Fig 7.10). There is potential bycatch of lobster for American fishermen in the offshore lobster pot fishery. During January-March, there are only a few lobster fishermen in the offshore area, but during April-June there is a substantial pot fishery along the edge of the continental shelf in waters greater than 150m (NMFS/NOAA, 1977).

Mackerel

There have been active commercial and recreational fisheries for mackerel (Figs. 7.11 and 7.12) in the U.S. for almost our entire historical period starting in the early 1600s. Peak U.S. catch was in 1884; recent U.S. harvest have been below 5000 mt for commercially caught fish and value was low at approximately $800,000. There was a major foreign harvest in the early 1970s, when foreign trawlers caught approx 400,000 mt per year. Catch fell to less than 100,000 mt in 1976. Markets for fresh or frozen mackerel are limited; the largest existing domestic commercial market for mackerel is for zoo food (Coombs, 1977). The geographical distribution of this fishery changes from year to year; thus it is difficult to predict the importance of the fishery in the ASCAR area.

Groundfish

Both cod and haddock (Figs. 7.13 and 7.14) are present in the deep waters off the edge of the continental shelf although the fishery there is limited. U.S. commercial fishery from deep water accounts for 0.1% of the catch, and thus may be valued at about half a million dollars. Since cod is available in the deep water year round, it may be attractive to a limited number of recreational fishermen, although any fishing in recreational boats would be severely restricted by weather.

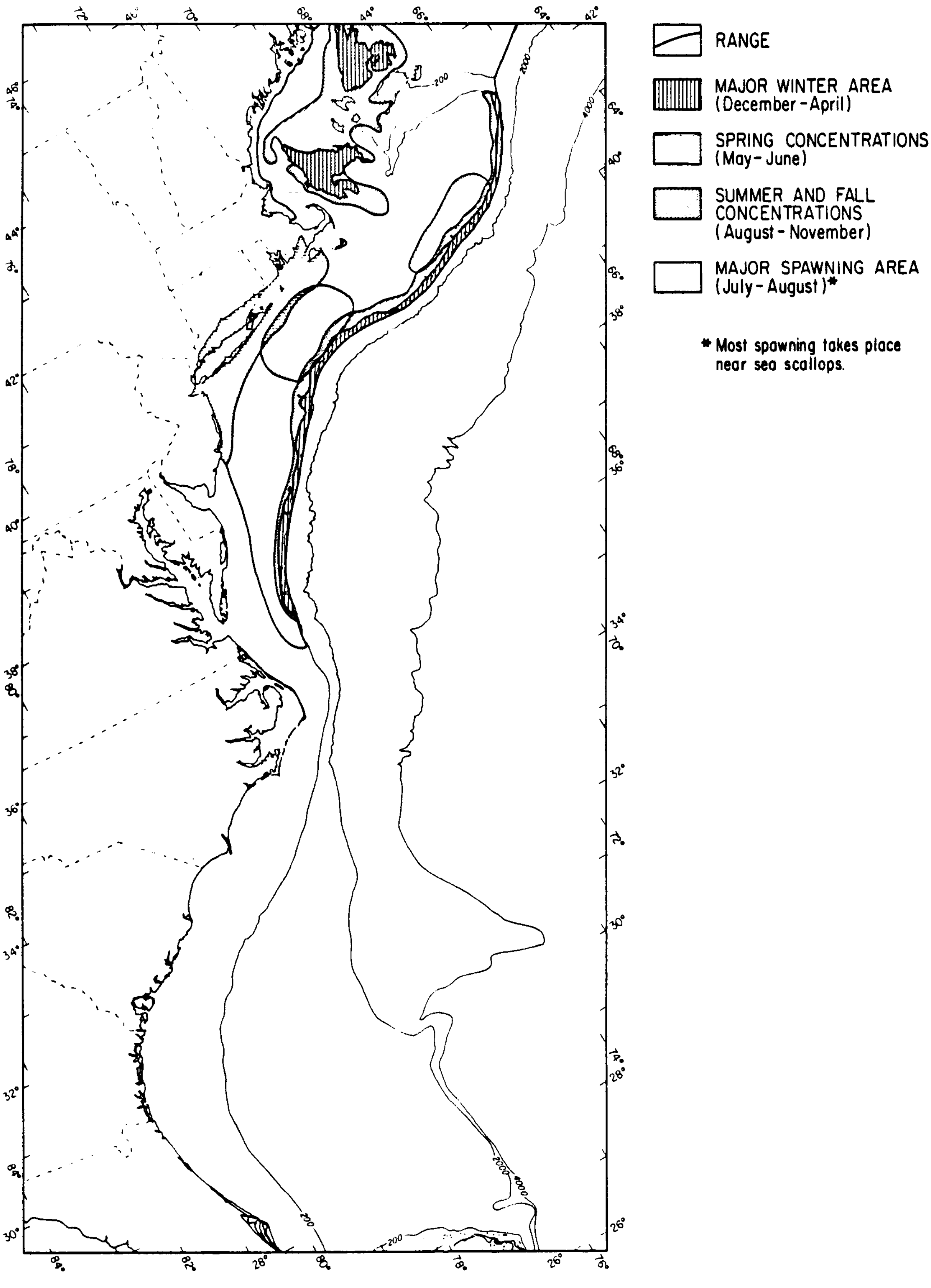


Figure 7.10. The distribution of red hake (from NOAA 1981).

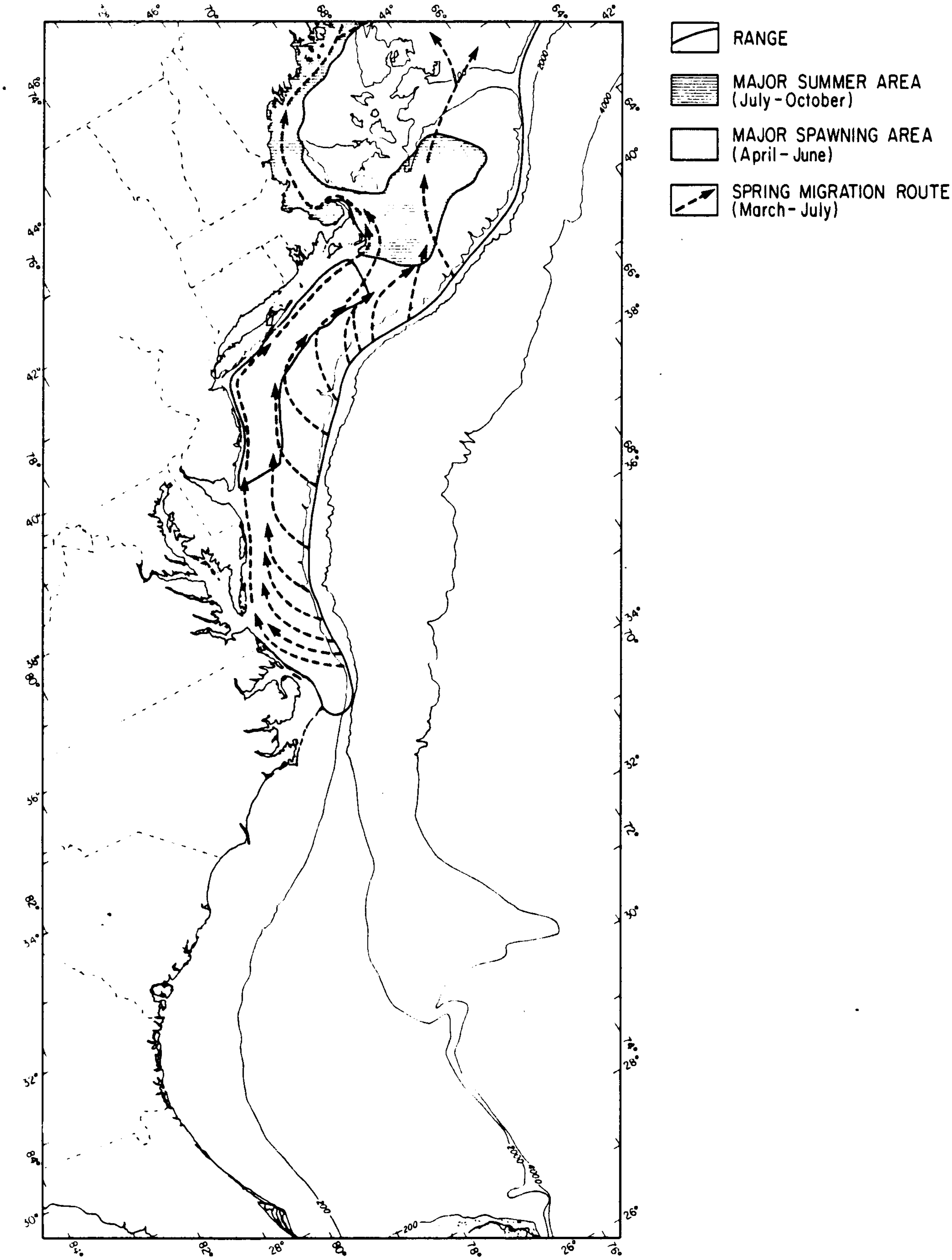


Figure 7.11. The distribution of Atlantic mackerel (summer and winter; from NOAA 1981).

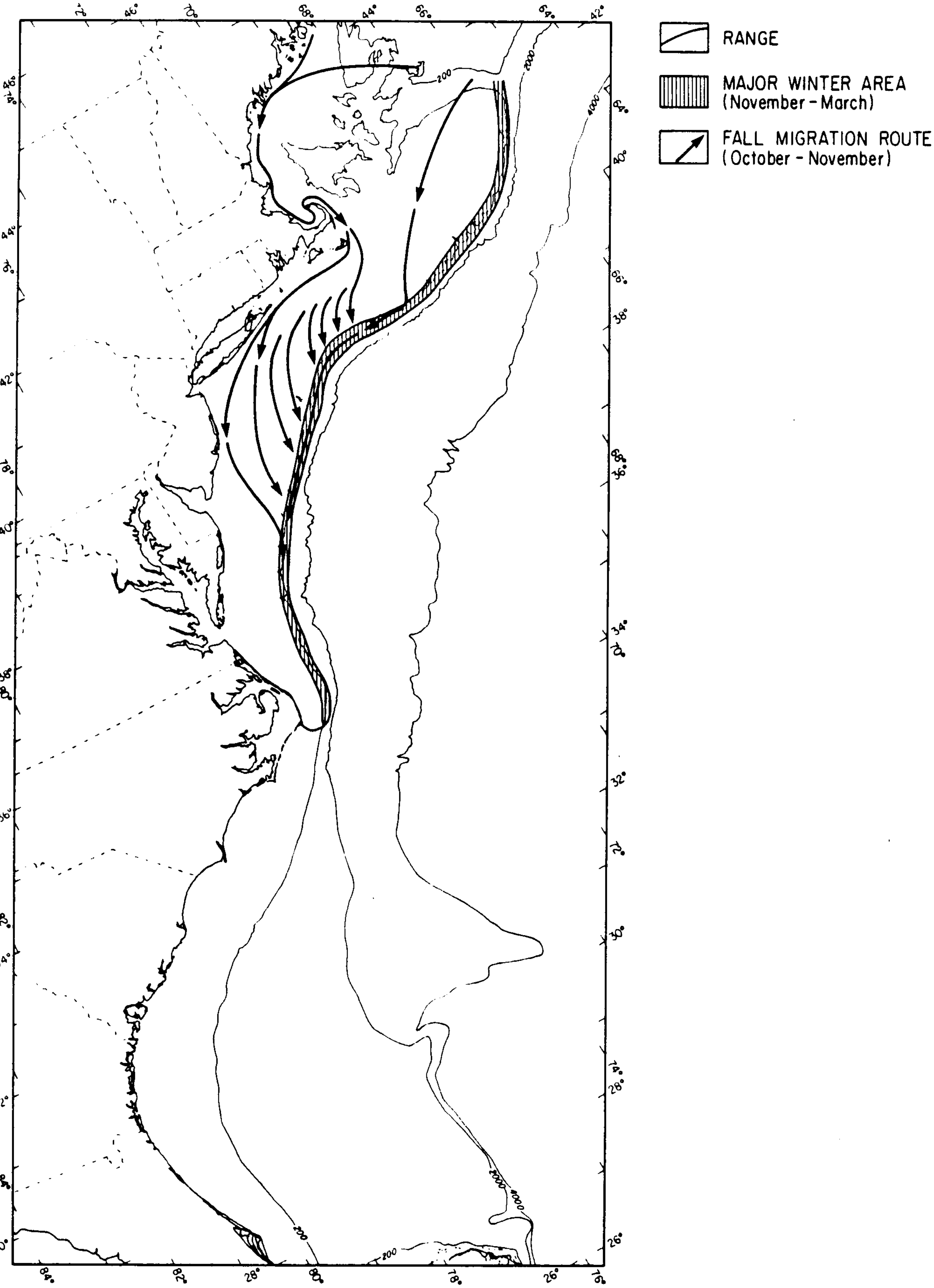


Figure 7.12. The distribution of Atlantic mackerel (fall and winter; from NOAA 1981).

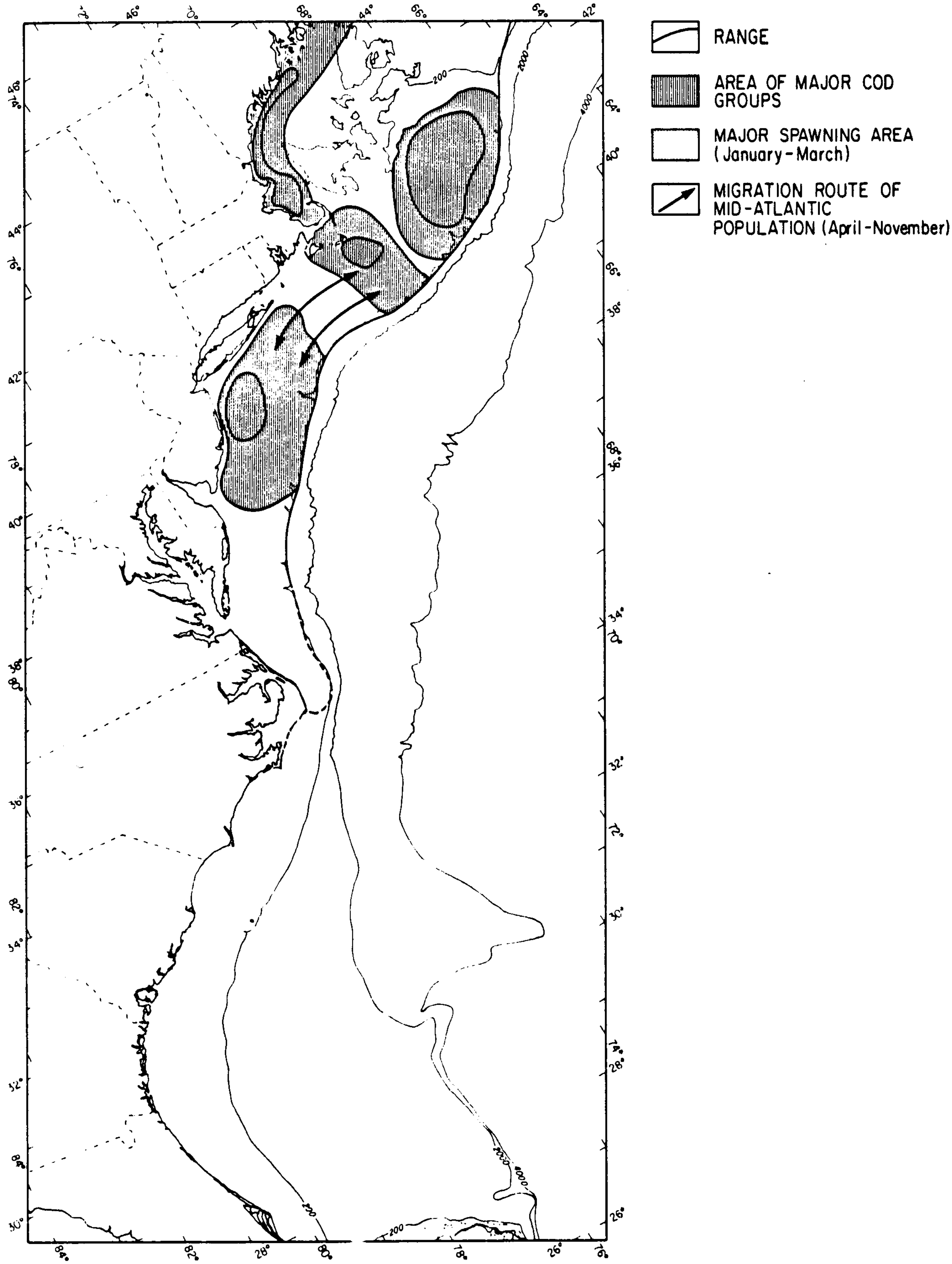


Figure 7.13. The distribution of Atlantic cod (from NOAA 1981).

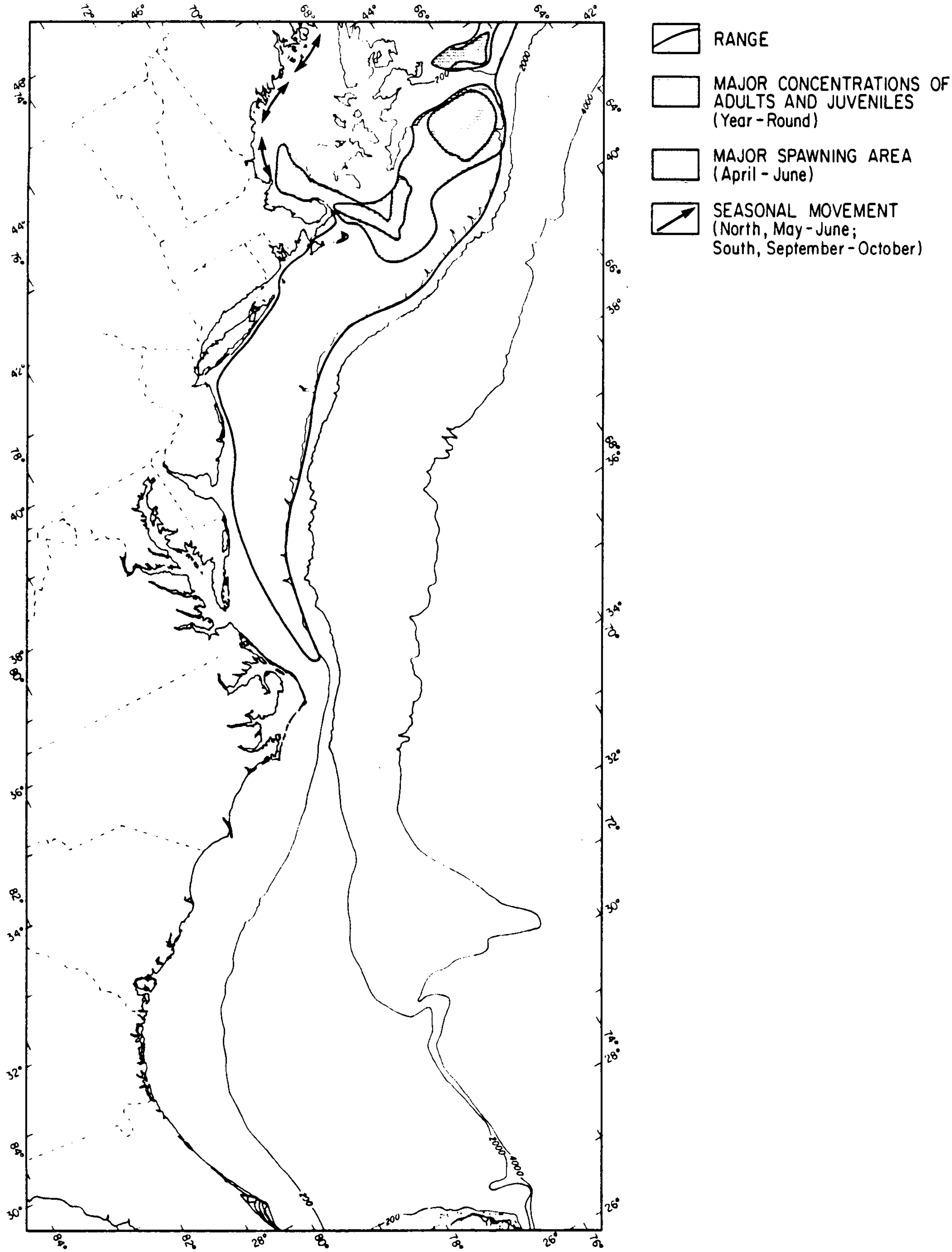


Figure 7.14. The distribution of haddock (from NOAA 1981).

Herring

Herring is worth over $7 million to the U.S. commercial fishing fleet, but less than 5% of that is caught outside the 3-mile limit (Fig. 7.15). There are stocks of herring on Georges Bank and in the deep water over the edge of the shelf, but these stocks are quite depleted relative to the mid-1960s---from several hundred thousand metric tons to a few thousand mt in the last two decades. See Sinderman (1979) for more detail on potential abundance. Although existing stocks are low, as is the demand for Atlantic herring, the potential exists for a substantial commercial fishery when the stocks recover. It is difficult to speculate who might be doing the fishery; in the past, eastern European nations caught 95% of the offshore herring. In the future, those stocks may be sought primarily by Canadian or U.S. fishermen. If the fishery is dominated by the U.S., then it is likely to be near shore rather than offshore because of fuel costs and travel time.

Lobster

American lobster (Homarus americanus) is widely distributed off the northeastern coast of the U.S., from Maine to North Carolina and from the intertidal zone out to 700m. In the U.S. there are two prinicpal areas of harvest: the inshore waters from Maine to New Jersey out to a depth of from 40 to 100 m; and the continental margin from Corsair Canyon to Cape Hatteras in depths of 100 to 600 m. (Fig. 7.16). The inshore areas account for the greater share of production (about 83% in 1978). There may be numerous local populations of lobster indigenous to offshore canyons, with maximum separation between populations in winter months. However, dispersion of lobster larvae in water currents and seasonal migratory movements of adults results in genetic homogeneity. Landings reached a high in 1979 of 16,863 MT, valued at $72.3 million. Maine is the leading lobster producing state with 55% of total landings, but all of that is from inshore waters. In Massachusetts, 42% of lobster landed was from the offshore trap and otter trawl fishery; 77% for R.I.; 48% for New York; 59% for New Jersey; 81% for Delaware; 91% for Maryland, and 100% for Virginia (NEFMC, 1982).

Red Crab

The canyon areas along the edge of the continental shelf have populations of red crab - in particular the area between Veatch and Atlantis Canyons (figure) - in quantities attractive to commercial otter trawl fishermen. The commercial fishery began in 1973, and six boats fished regularly from 1973 to 1976; however, marketing problems made the fishery unattractive for many fishermen, and by 1980 there were only two full time red crab fishing boats in the Northeast. Most of the commercial fishery is in the areas of Atlantis, Block and Hudson Canyons. The crab can be harvested with pots or traps in canyon areas less suitable for dragging, such as those between Atlantis and Block Canyons. The red crab range from 300 to 1000 m (Gerrior, 1981), and there are heavy concentrations in water deeper than 410 m. The most profitable (largest catch and highest price per pot) fishery is for red crab found in depths ranging from 535 to 620 m (Gerrior, 1981). Seasonal changes effect red crab distribution, with deeper water fishing in spring and winter. In 1979, 1,220 mt were landed worth $917,000.

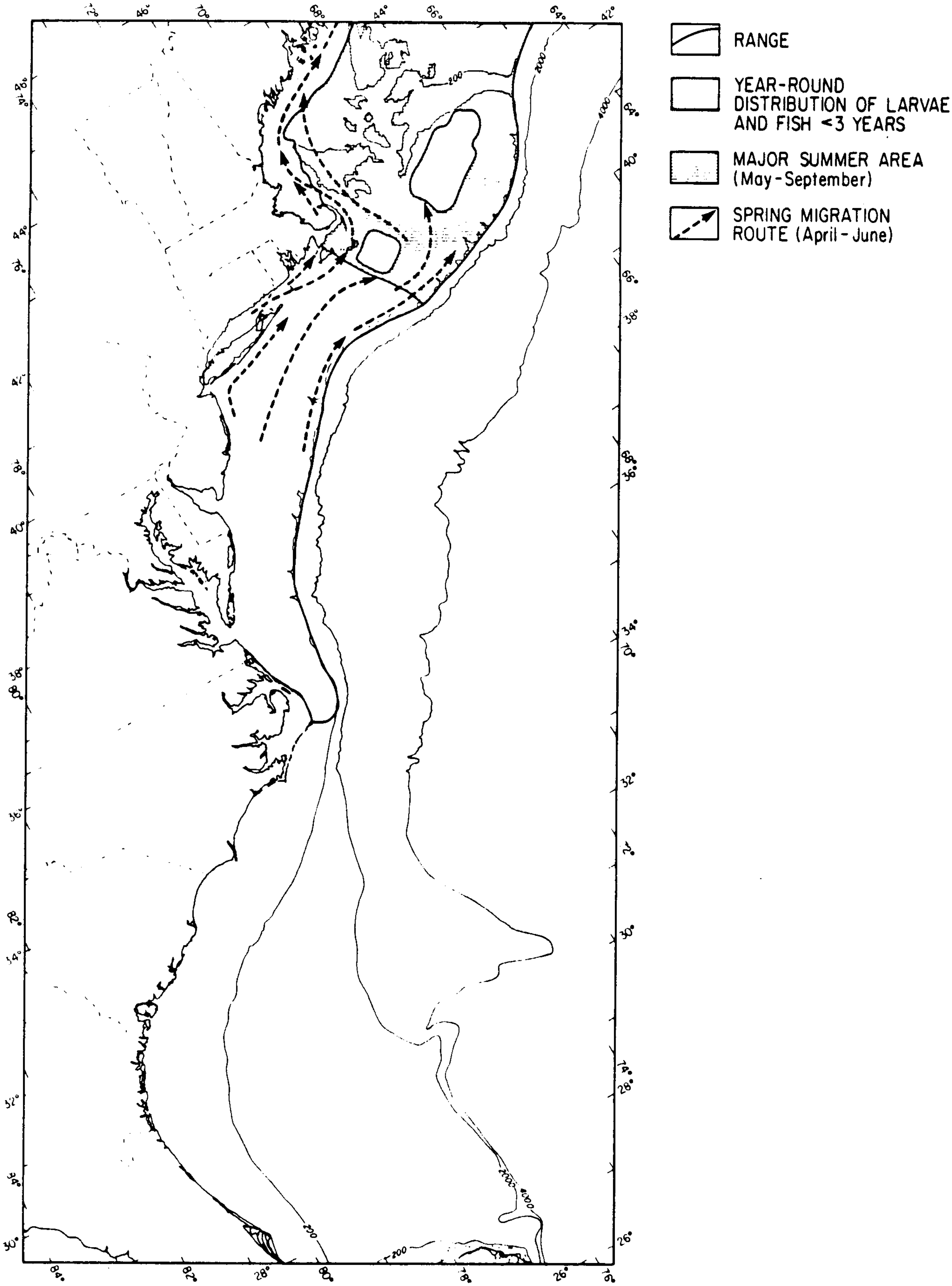


Figure 7.15. The distribution of herring (from NOAA 1981).

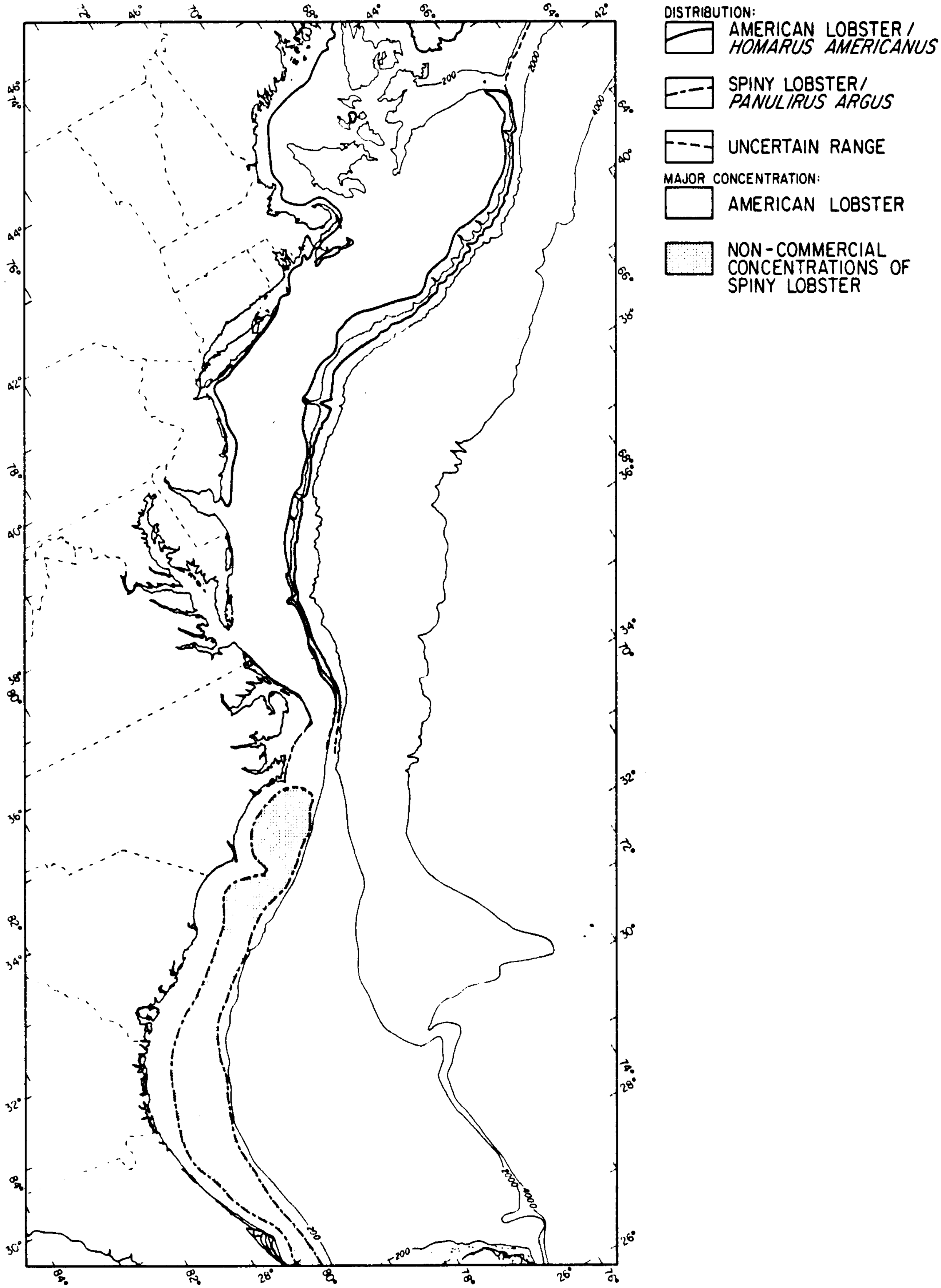


Figure 7.16. The distribution of lobsters (from NOAA 1981).

POTENTIAL COMMERCIAL AND RECREATIONAL FISHERIES

Existing commercial fisheries for those species found in deep water have been described in section A above. Landings by port are summarized for 1981 in Fig. 7.17, which depicts total landings as opposed to total catch or catch per area. Potential commercial fisheries depend upon the demand for the catch in U.S. and world markets, the cost of catching fish in the offshore waters, the advantage of catching the fish year-round rather than in the season most of them are available near shore, and the availability of species. For example, mackerel and whiting have the potential to be very valuable offshore fisheries when abundant and concentrated. Those same species are less valuable to the commercial fleet if dispersed in the offshore areas because the costs of catching them grow rapidly with distance from shore. Currently boats which fish offshore waters spend from $4000 to $8000 per 10 day trip on fuel. Quite a few of the species reported above are usually caught in near-shore waters because it is more practical for the U.S. fleet to catch them there. Foreign fleets have been kept out of nearshore waters because of potential conflicts with coastal fishermen. Thus foreign boats the most likely commercial boats to be fishing slope waters. But that fishery would be under permit from the U.S. as long as the foreign fishermen were within 200 miles of shore. See page 7 for the details of management of foreign nations seeking highly migratory species in U.S. FCZ. Species most likely to be sought for an intensive slope fishery by foreign boats include squid, mackerel, hakes, herring.

RECOMMENDED RESEARCH

Most of the data on commercial fisheries in the area is collected by the National Marine Fisheries Service in two ways: first, through Spring and Fall surveys taken in a standardized sampling procedure from Cape Hatteras to the Canadian border; second, by interviews with fishermen in the major fishing ports along the east coast. The second activity provides NMFS scientists with information on species caught, discards, regions fished, days fished, time spent fishing, number of tows, number of crew as well as basic information on the fishing boats themselves. This information was collected uniformly in New England from the early 1960s on, but only in the last three years has this kind of data been collected for ports from New York south. Before that time, catch information came from the individual states and was based on estimates of fishing using a non-standardized sampling procedure. Thus our ability to generalize about commercial fishing in the southern half of the area is constrained by lack of time series information.

Recreational fishing surveys have been done only twice in the last decade, and because of the expense, are not expected to be carried out any more frequently than once every five years. However, if offshore recreational fishing becomes more popular in the next decade, a simple survey of party- and charter-boat operators in the mid-Atlantic states would provide information on the extent and value of that fishery. Thus it may be important to have funding available to respond to currently unanticipated events.

Foreign fishing will continue to be monitored by NMFS and the Coast Guard within the 200-mile fishing limit. Any foreign fishery which develops outside that area will be of great concern to U.S. commercial fishing interests, but not subject to U.S. regulations. Currently NAFO, the Northwest Atlantic Fisheries Organization, would be the responsible international agency for sponsoring research in the Northwest Atlantic outside the 200-mile limit. Since the U.S. in not a member of NAFO, our influence on their research programs is not great.

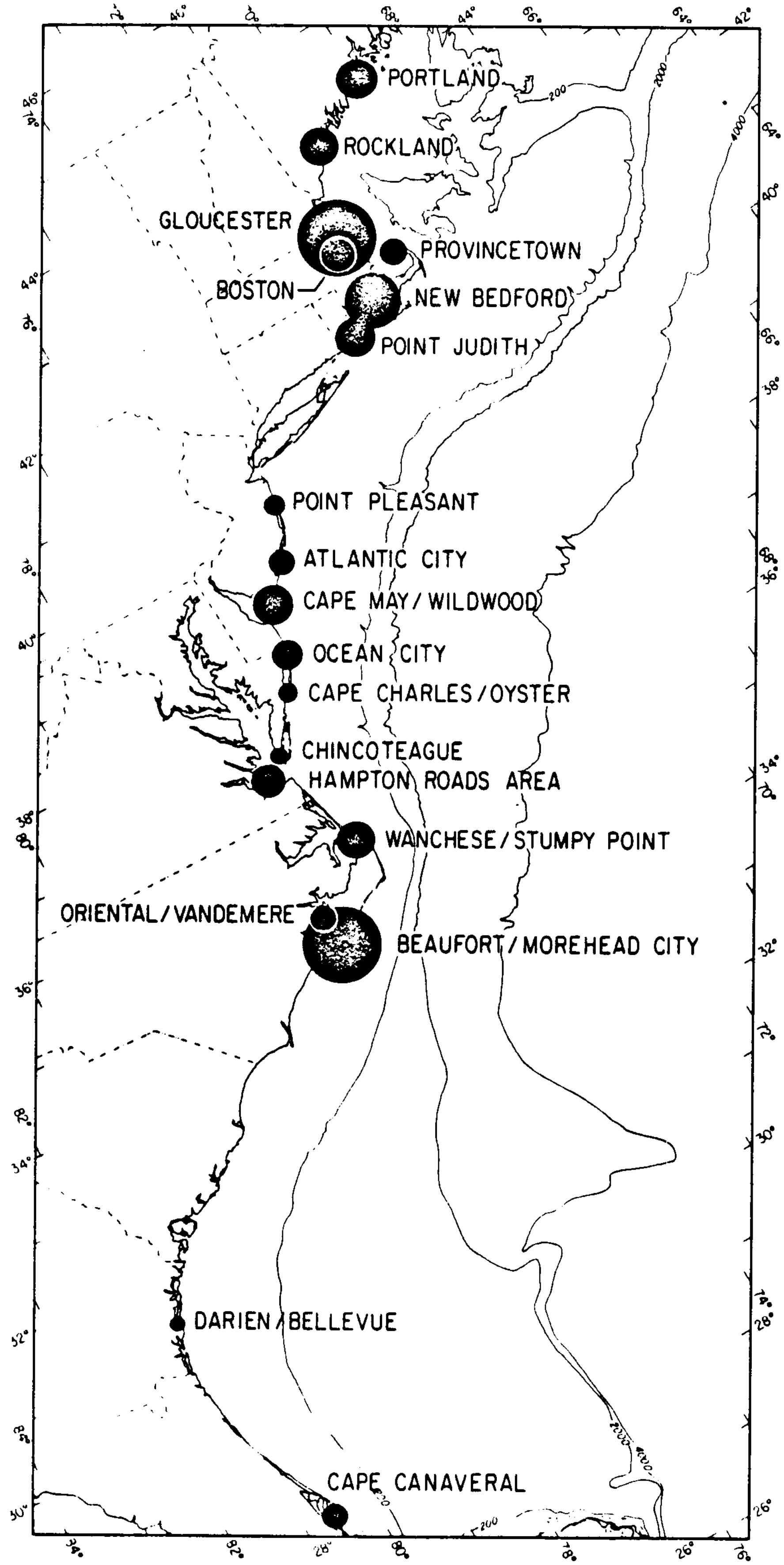


Figure 7.17. The relative commercial fish landing (weight) for 19 ports of the U.S. east coast (data from NMFS, 1982).

LEGAL STRUCTURE SURROUNDING EXPLOITATION

As with most human activities on the outer continental shelf and beyond, the extraction of oil and gas resources is heavily regulated. Although not a result of oil and gas potential in the study area, there are many laws and legal cases which bear on the future of oil and gas activities in this area, either directly or indirectly (and some which are only tangentially relevant). For a full listing of these laws, see Table 7.1.

A primary issue is which level of government has responsibility for the management of oil and gas resources in the ACSAR area. Currently this responsibility is vested in the Federal government (Breeden, 1976; Ball, 1982). This status can be traced back to the Supreme Court decision, U.S. v. California, in which the Supreme Court held that it was the Federal government, and only the Federal government, who had the constitutional authority to grant leases for the purpose of marine mineral extraction in waters off the coast of the United States. In response to this Court decision, the U.S. Congress passed two acts which modified the findings in the case. One was the Submerged Lands Act of 1953, which ceded the proprietary right over marine mineral resources to the States out to three nautical miles. The second, and more important for the purposes here, was the Outer Continental Shelf Lands Act of 1953 (OCSLA). It codified the right of the Federal government, through the Secretary of the Interior, to grant oil and gas leases in offshore areas greater than three nautical miles from shore.

Though amended in 1978 (Krueger and Singer, 1979; Vild, 1979; Jones, et al., 1979), the OCSLA as amended remains the primary statute for the development and regulation of oil and gas activities in the ACSAR area. Among other things, the OCSLA and its amendments (OCSLAA) prescribe the way in which leases are to be established and maintained, and the system of bids and royalties which will apply to leases. It requires that the Secretary of the Interior shall periodically prepare a five-year leasing program which will include a schedule of proposed lease offerings. The five-year plan (the current operable five-year plan is the 1982-1987; see U.S. DOI, BLM, 1982) is to indicate the size, timing, and location of leasing activities (U.S.C. 1344).

In terms of safety and environmental regulations, enforcement responsibilities are mandated, in addition to the Secretary of the Interior, to the Secretary of the Army (because of permitting duties of the Army Corps of Engineers) and the Secretary of the Department in which the Coast Guard is operating.

An important aspect of the OCSLA for the development of the oil and gas is the provisions of Section 19, added by the 1978 Amendments. These require that state governments likely to be affected by leasing activities be kept informed of those activities by the Secretary of the Interior. Further, the Secrerary must take into account any comments those states may have. Generally, it is felt that this will increase the ability of states to participate in OCS decisions (Vild, 1979). At the same time, however, it complicates the process of oil and gas leasing and development.

While the Federal government is responsible for leasing, the states, in addition to Section 19 of the OCSLA, have an important regulatory tool which gives them some control of oil and gas (and any other federally approved or licensed activity) in the study area. That tool is the "consistency" provision of the Coastal Zone Management Act of 1972 (Section 307 (c) (2)). Under this provision, any state with a Department of Commerce approved coastal zone management plan can block a federal activity (such as the leasing of oil and gas tracts) if that state determines that the activity, or some part thereof, is inconsistent with its coatal zone management plan (Brewer, 1976; Deller, 1980; Behr, 1979; Best, 1979; California v. Watt, 1982).

CURRENT AND PROJECTED ACTIVITY

Until very recently, there has been very little in the way of OCS oil and gas development between 28°N and 42°S in water depths of 200 to 4000 meters in the Northwest Atlantic. It is a frontier area in terms of oil and gas; therefore, not much is known regarding the area's potential. In fact there has been no development or production although there has been some exploration and some gas discoveries made. While uncertainty remains about future production levels, it seems certain that exploration activities will continue to occur. Under the DOI five-year plan for 1982-1987 (U.S. DOI, 1982), several lease offerings are scheduled. While earlier sales in the Northwest Atlantic have focused on the shallower waters of the continental shelf, recent and pending lease offerings (numbers 52, 76, 78, and 82 (82 is now known as the 1984 North Atlantic Lease Offering but has been postponed)) are generally moving off the shelf and down the slope into waters of more than 200 meters (see Figs. 7.18 to 7.21).

While exploration which has occurred has produced no significant finds of gas or oil in particular, there is some optimism about the future (Sumpter, 1979). On the slope, there is an ancient submerged reef structure that some feel could provide economically recoverable resources (Edgar and Bayer, 1979).

Since no commercial finds have occurred to date, any projections about future activity must be based on resource estimates. Estimates for the area will be discussed shortly but it is important first to consider resource estimates themselves. As Schanz (1978) observes, there are three commonly used methods for estimating undiscovered oil and gas resources: the volumetric approach which, based upon past geologic knowledge, estimates the total oil and gas that may exist in promising sedimentary rock formations; engineering projections, which suggest future production through use of mathematical formulae based on historical trends; and, econometric models, which also apply mathematical models (in this instance based upon past market/price trends) to suggest future supplies of oil and gas attendent to exploratory and development efforts prompted by changes in price.

The problem with each approach in making informed judgements about oil and gas activities is that they base future projections partly on past experience. "Insofar as the past does not adequately represent the future, their estimates are likely to be in error" (Schanz, 1978, p.18).

Since each of these estimating methods is based upon different assumptions and methodologies, the oil and gas resource estimates they produce are often in disagreement. This can lead to political conflicts about the advisability of pursuing various development strategies (Wildavsky and

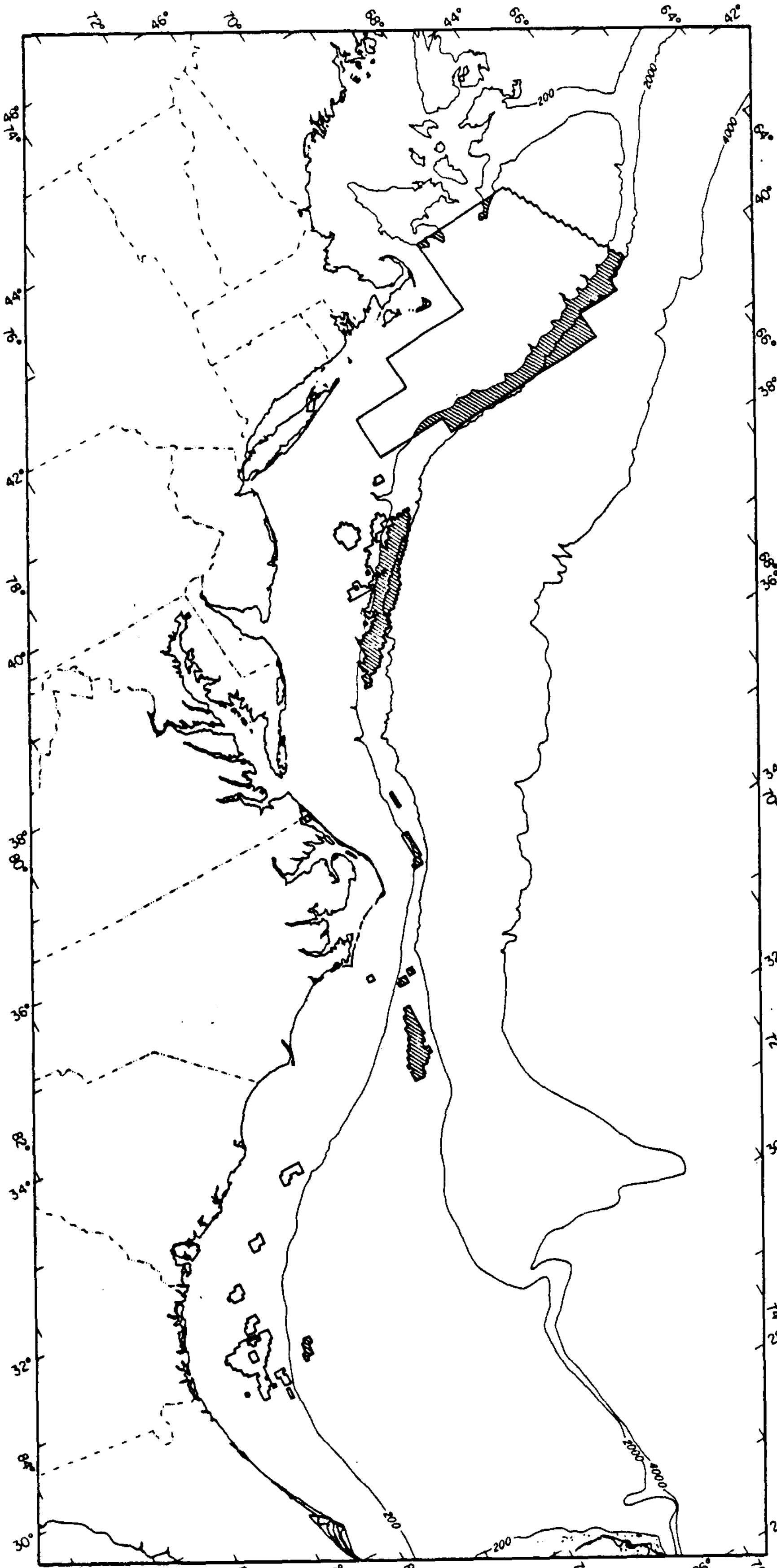


Figure 7.18. Oil and gas lease sites for the U.S. east coast and for the ACSAR area (shaded; from NOAA 1981).

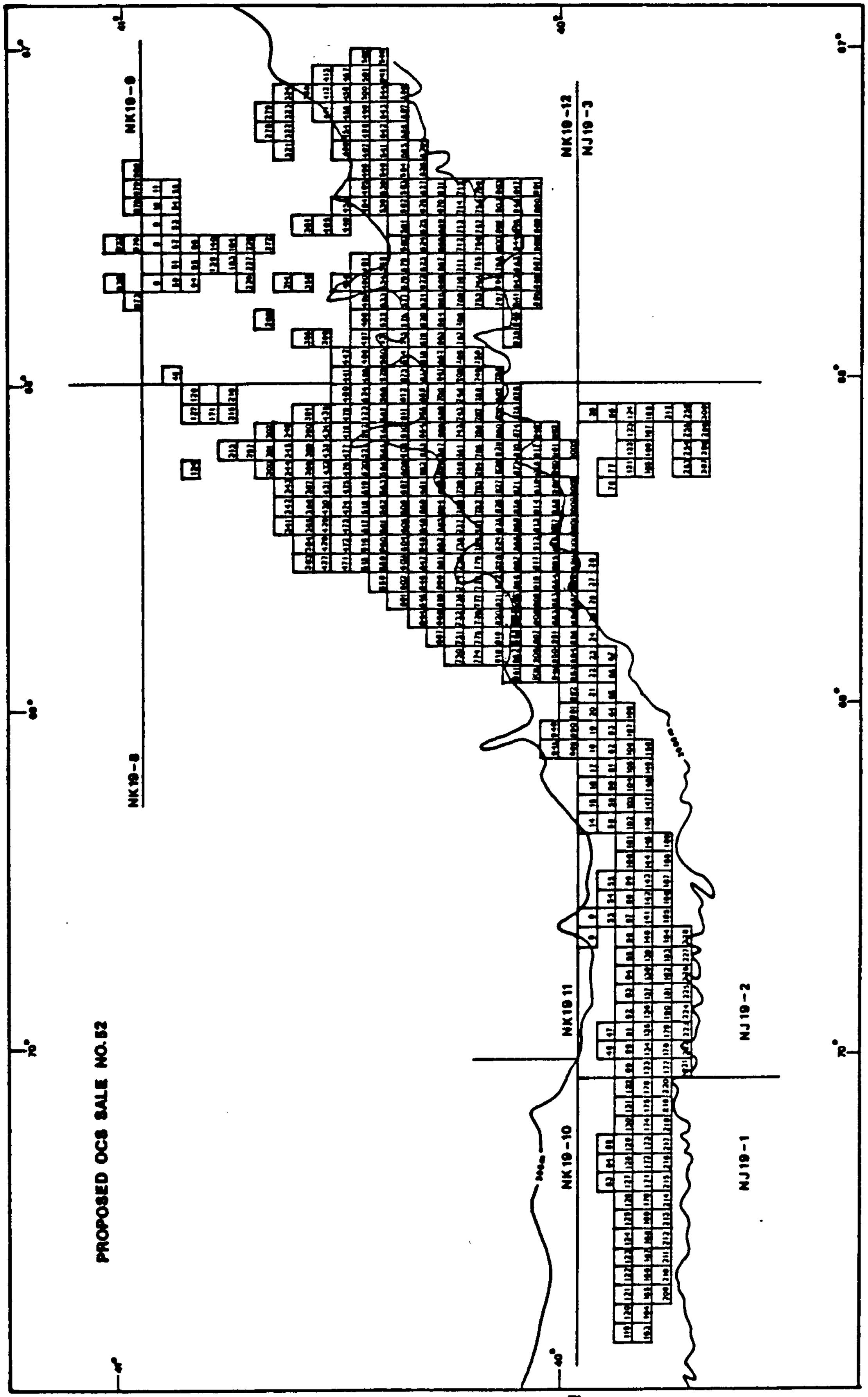


Figure 7.19. Proposed Lease Sale No. 52 (from BLM 1981).

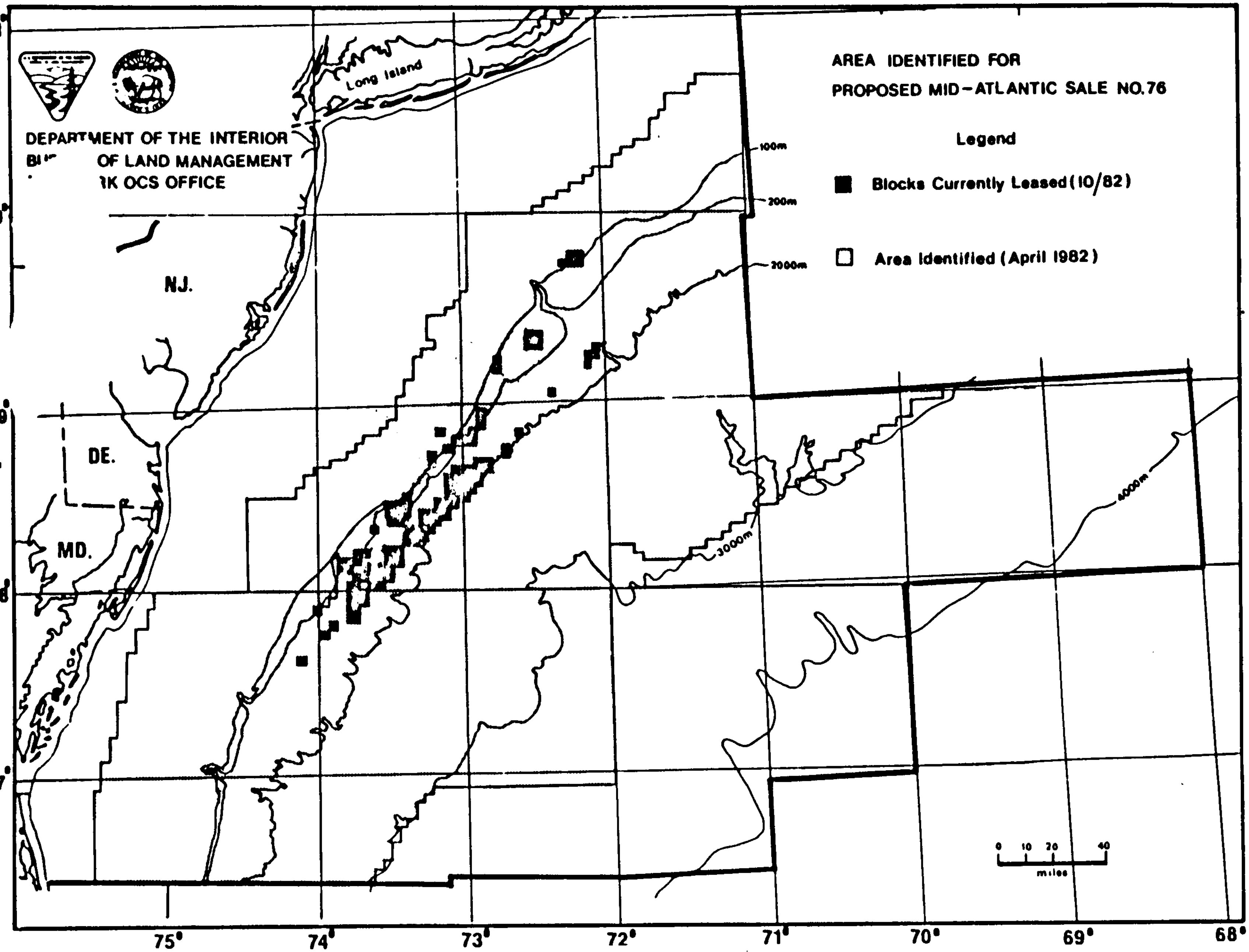


Figure 7.20. Proposed Lease Sale No. 76 (from Minerals Management Service 1982).

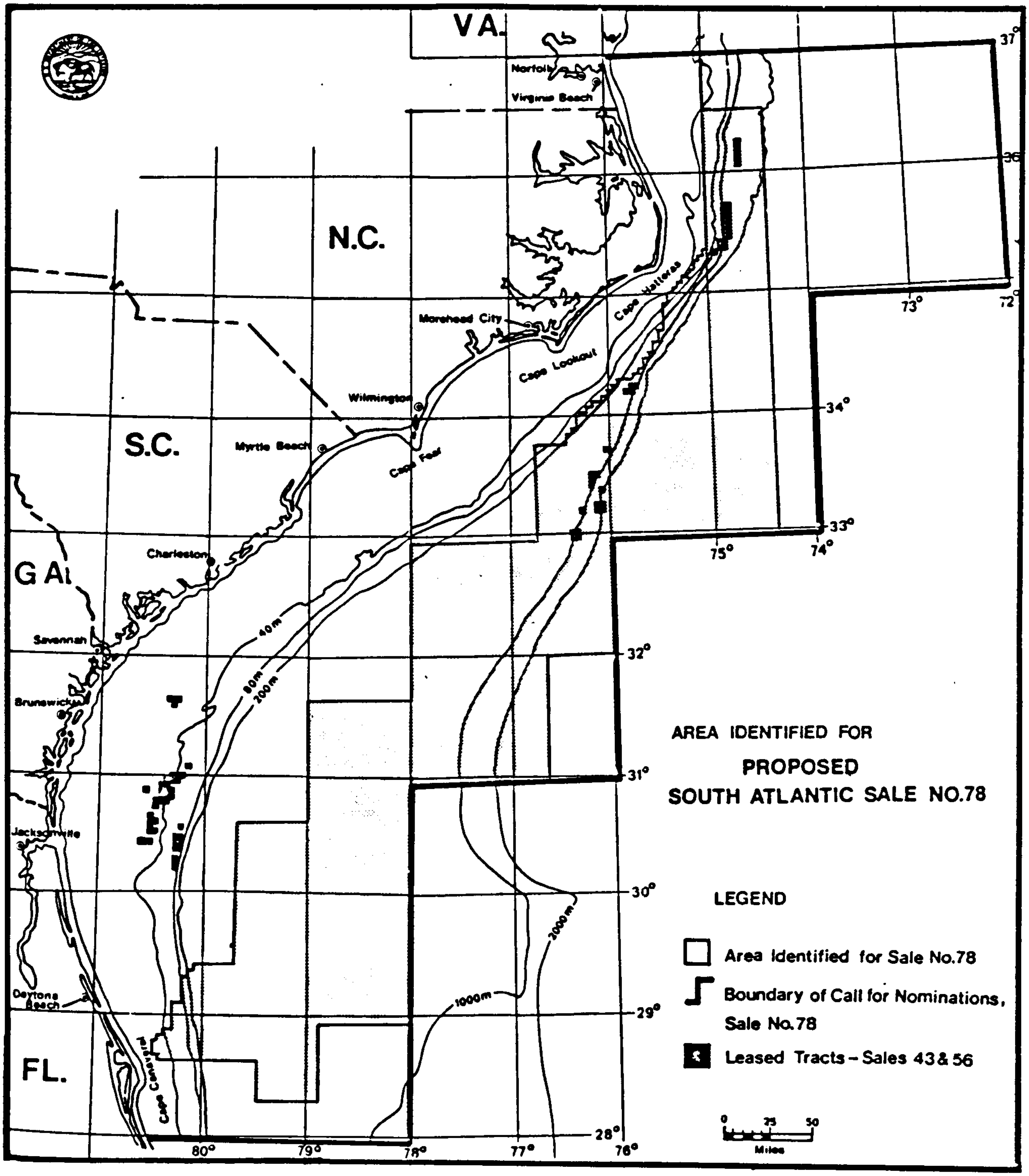


Figure 7.21. Proposed Lease Sale No. 78 (from Minerals Management Service 1982).

Tenenbaum, 1982). This could affect the future development, or at least the rate of exploration and development, of oil and gas resources in the area under consideration. As happened with Lease Sale No. 42 (Georges Bank), opponents of leasing used lower estimates (and the impression of estimates) to argue that the value of fishery resources outweighed the potential of oil and gas resources (Colgan, 1982). While it is too early to predict the conflicts which may arise from disagreements about oil and gas resources in the area, it is an issue which should be considered.

With these general comments and caveats about estimating oil and gas reserves, we can now turn to specific estimates for oil and gas in the northwest Atlantic. There are four lease areas in the ACSAR region which are thought to have oil and gas potential: the Blake Plateau, the South East Georgia Embayment, Baltimore Canyon, and Georges Bank (see Fig. 7.18). With the exception of the South East Georgia Embayment, the lease areas have large portions in waters deeper than 200 meters. Of these three, the Baltimore Canyon area is considered to have the greatest potential (Edgar and Bayer, 1979).

RESOURCE ESTIMATES

Blake Plateau

Under the new five-year leasing program (BLM, 1982), the Blake Plateau has been combined with other areas of the South Atlantic Planning area (i.e., South East Georgia Embayment) . Based on U.S. Geological Survey data, resource estimates for that part of this broader area which will be covered by Lease Sale No. 56 are:

	5%	Mean	95%
Oil (billions of barrels)	.8	1.4	2.1
Gas (trillions of cubic feet)	1.4	2.5	3.5

That is, if hydrocarbons are found, there is a 5% probability that there will be less than 0.8 bbl of oil and/or less than 1.4 tcf of gas; and a 95% probability that less than 2.1 bbl of oil and/or 3.5 tcf of gas will be found (BLM, 1981). The estimates as to the portion that may occur in the Blake Plateau are 300 million barrels of oil and 700 billion cubic feet of natural gas (USGS, 1982).

Baltimore Canyon

Currently there is no production or development in this area. As exploration continues, the efforts will move into deeper waters. Beginning with Lease Sale No. 59 and continuing with future offerings, the exploration effort (and development and production) will occur in waters of the continental slope. For Lease Sale No. 59, the U.S. Geological Survey provided estimates of oil and gas for this region. Using 5% and 95% confidence intervals, they estimated that the lease sale area may contain from 0.36 to 7.3 bbl of oil and from 1.9 to 28.5 tcf of oil (BLM, 1980). For Lease Sale No. 76, the mean estimates of recoverable resources, pending discovery, are 0.879 bbl of oil and 3.693 tcf of natural gas (U.S. DOI, 1982:7).

Georges Bank

At this time, no development or production activities are occuring in this area. With this area as well, the trend is into deeper waters. Some of the tracts which were to have been offered in Lease Offering No. 52 (the lease offering was cancelled in November of 1983 as a result of litigation and because the tracts involved could be included in what is to be the next North Atlantic offering (see below)) were in waters as deep as 2,800 meters. Estimates for the lease offering no. 52 area provided by the U.S. Geological Survey ranged from lows of 0.017 bbl for oil and 0.196 tcf for gas to highs of 6.35 bbl of oil and 13.49 tcf for gas. The conditional mean estimates were 1.73 bbl of oil and 5.25 tcf of gas (BLM, 1981). For the entire North Atlantic region, the risked resource estimates for water depths greater than 200 meters are 1 bbl of oil and 3.2 tcf of gas (USGS, 1981).

With the cancellation of lease offering 52, the next lease offering for the Georges Bank area is the proposed April 1984 North Atlantic lease offering (formerly referred to as Lease Offering No. 82) It is not known at this time when this offering will occur. The Secretary of the Interior announced in December of 1983 that it would be postponed until differences with the states could be worked out. When this offering does occur, some 25 million acres will be available for lease. Much of this area, however, is in waters shallower than 200 meters. The mean estimates for recoverable oil and gas in the entire lease offering are 210 million barrels and 4.9 trillion cubic feet respectively. (See Fig. 7.22)

Since, as noted above, resource estimates are based on historic evidence, the estimates for oil and gas will change as oil and gas exploration progresses on the Atlantic margin. If significant commercial discoveries are made, it is likely that the estimates will adjust upwards. Conversely, continued disappointment in exploration efforts would press the estimates down.

Thus any statement about the potential for oil and gas development on the Atlantic margin must be conditional. There are several ways to keep abreast of current developments. Oil and gas industry journals such as Oil and Gas Journal, Offshore Engineering, and Petroleum Engineering International regularly run short news items on wells started, finds, wells capped, leases abandoned, etc. The Outer Continental Shelf Oil and Gas Information Program prepares and periodically updates several documents which are useful in keeping track of oil and gas activities: the Atlantic Index, the North Atlantic Summary Report, the Mid-Atlantic Summary Report, and the South Atlantic Summary Report.

LIMITING FACTORS

Beyond the unknown resource quantities, there are two factors which may slow or prevent the development of oil and gas resources in the ACSAR area. One is technological, the other environmental. The technological limitation stems from the capability, or lack of capability, of the oil and gas industry to exploit resources in deep water. Currently, the industry can drill exploratory wells in waters up to 2400 meters. They expect to be able to extend this to 3000 meters within 5 years. But the problem is not with exploratory drilling, the limiting factor is the technology required for actual production in deepwater. The deepest production facility in the world is only 900 meters;

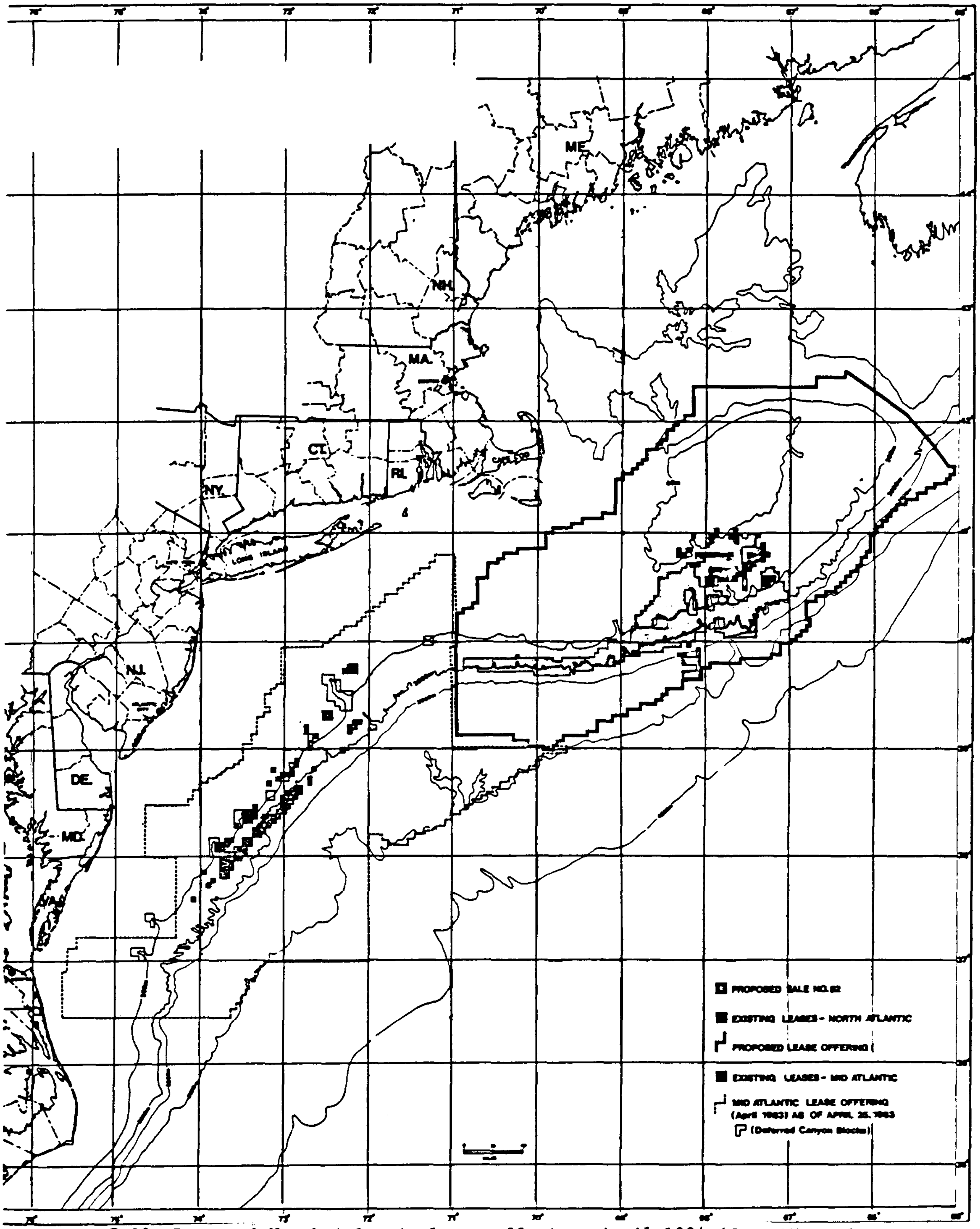


Figure 7.22. Proposed North Atlantic lease offering, April 1984 (from Minerals Management Service, 1982).

the industry hopes to be able to produce at 1800 meters within 10 years. The technological production problems are compounded by the transportation problems associated with deepwater oil and gas. If a major find were to occur, it is usually proposed that a pipeline be used to move the resource ashore. Yet current pipeline technology has only been applied in waters out to 600 meters. (U.S. DOI, 1981, p. 559). Thus, it will be some time before the industry has the facilities for developing oil and gas resources in much of the ACSAR area.

The environmental consideration relates largely to commercial fisheries. Specifically, a great number of political and jurisdical conflicts have developed over the issue of whether or not the production of OCS hydrocarbons will harm commercial fisheries. A major component of this controversy is the impact oil spills can have on fisheries stocks. Only recently has research begun into the probable impacts of oil spills on specific stocks within the ACSAR area (University of Rhode Island and Applied Science Associates, 1982, p. 8-9). The most recent work indicates that the impact of spills on specific stocks is related to the portion of the spawning cycle during which the spill occurs (University of Rhode Island and Applied Science Associates, 1982, p. 210-214).

OCS MINERAL DEVELOPMENT

In addition to oil and gas, there are other mineral resources on the Atlantic continental margin which have economic potential. The most publicized hard mineral resources with economic potential on the continental margin are sand and gravel, phosphorite, and Blake Plateau manganese nodules. Other minerals are known to exist, such as placer gold and platinum, but their distribution, depth, and grade are for the most part poorly defined (Manheim and Hess, 1981). There is also some speculation that large deposits of metals such as copper and nickel may underlie the continental shelf. Depending on economic, political, and technological factors these resources may be mined in the future (National Academy of Science, 1975), particularly as land-based supplies are exhausted or become non-exploitable because of environmental considerations (Manheim, 1979; Trondsen and Mead, 1977). A further factor which may induce mining for minerals in deeper waters of the continental margin (i.e., 200+ meters) is the fact that many people would like to see decreased U.S. dependence on foreign mineral sources (Manheim and Hess, 1981).

LEGAL STRUCTURE SURROUNDING OCS MINING

Mining of Atlantic continental margin hard mineral resources would be covered by the same regulatory scheme, mentioned earlier, as applies to OCS oil and gas. The primary legislation is the the Outer Continental Shelf Lands Act of 1953 as amended. Although national legislation has been adopted for the mining of manganese nodules (Deep Sea Bed Hard Minerals Resources Act) these would not pertain to any nodules which might be mined from the Blake Plateau; they would still be regulated by the OCSLA (Manheim and Hess, 1981; Anonymous, 1983; Bureau of Land Management; 1973).

As with oil and gas, hard minerals of the Atlantic coastal margin must be exploited according to the provisions of many other pieces of domestic legislation. The National Environmental Protection Act and the Coastal Zone Management Act of 1972 (as amended) are particularly relevent. The former because of its environmental impact state requirement; the latter because of its requirement (as interpreted in recent court cases---see above) that any activity conducted under a federal license or permit must be consistent with the coastal zone management programs of affected states.

Additionally, the techniques which would be used for ocean mining (National Academy of Sciences, 1975; Cruikshank, 1975), particularly dredging, would require permitting by the Army Corps of Engineers under provisions of the Rivers and Harbors Act of 1899, the Federal Water Pollution Control Act (amendments of 1972) and the Marine Protection, Research and Sanctuaries Act of 1972 (Pearce, 1979; Mazmanian and Nienaber, 1979).

While ocean minerals are to be mined under current provisions of the OCSLA, there is some growing opinion that this must be changed. Either the OCSLA must be amended or new legislation must be passed in order to address the special problems of marine hard minerals as compared with OCS oil and gas (Anonymous, 1983).

MANGANESE NODULES AND PAVEMENTS

In the ACSAR study area, the only manganese deposits with the potential for economic development are found on the Blake Plateau (Fig. 7.23). This resource appears in two forms: 1) pavement (layers of manganeses-bearing deposits of from 2 to 6+ centimeters thick, predominantly in water depths between 500-600 meters); and, 2) nodules (potato-like "rocks" found primarily in waters from about 675 to 1050 meters deep; see Fig. 7.23).

In the 14,000 km^2 area where manganese pavements and nodules have been identified, preliminary estimates indicate between 176 million and 528 million tons of pavement (based on high and low estimates of pavement thickness) and between 10 million and 100 million tons of dry nodules (based on high and low estimates of the fractional area of the bottom covered by nodules; Manheim, Popenae, et al., 1982). Although not as high in concentrations of economically valuable minerals as the prime nodules of the Clarion-Clipperton fracture zone in the Pacific, the Blake Plateau nodules do contain higher levels of platinum than nodules from other parts of the world's oceans. Nonetheless, the Blake Plateau nodules were considered submarginal until 1978. However, since that time, the ocean mining industry has indicated some interest in obtaining leases in this area (Manheim et al., 1982). One reason is that the manganese nodules of the Blake Plateau are found within 200 miles of U.S. shores. As a result, these resources have not been shrouded in the jurisdictional uncertainty associated with other manganese nodule resources located in international waters and the subject of controversy at the recently completed United Nations Conference on Law of the Sea. While it has been uncertain what the conclusion of the Law of the Sea negotiation might mean for exploitation of deep-water nodules, there has been global unanimity on permitting coastal nations to control and regulate exploitation of resources within 200 miles their shores, e.g., Blake Plateau nodules by the U.S. (Charles River Associates, Inc., 1979, p. 1-2)

An assesment of an hypothetical manganese nodule mining operation on the Blake Plateau was conducted by Charles River Associates, Inc. (1979). Based on their analysis, it would seem that the interest in Blake Plateau nodules is unwarranted in purely economic terms. Using different sets of assumptions for various development scenarios, they came to the conclusion that, "...a Blake Plateau manganese nodule project is likely to be a marginal investment, under the best of circumstances. In all other circumstances it is likely to be a submarginal investment (Charles River Associates, Inc., 1979, p. 5-1)

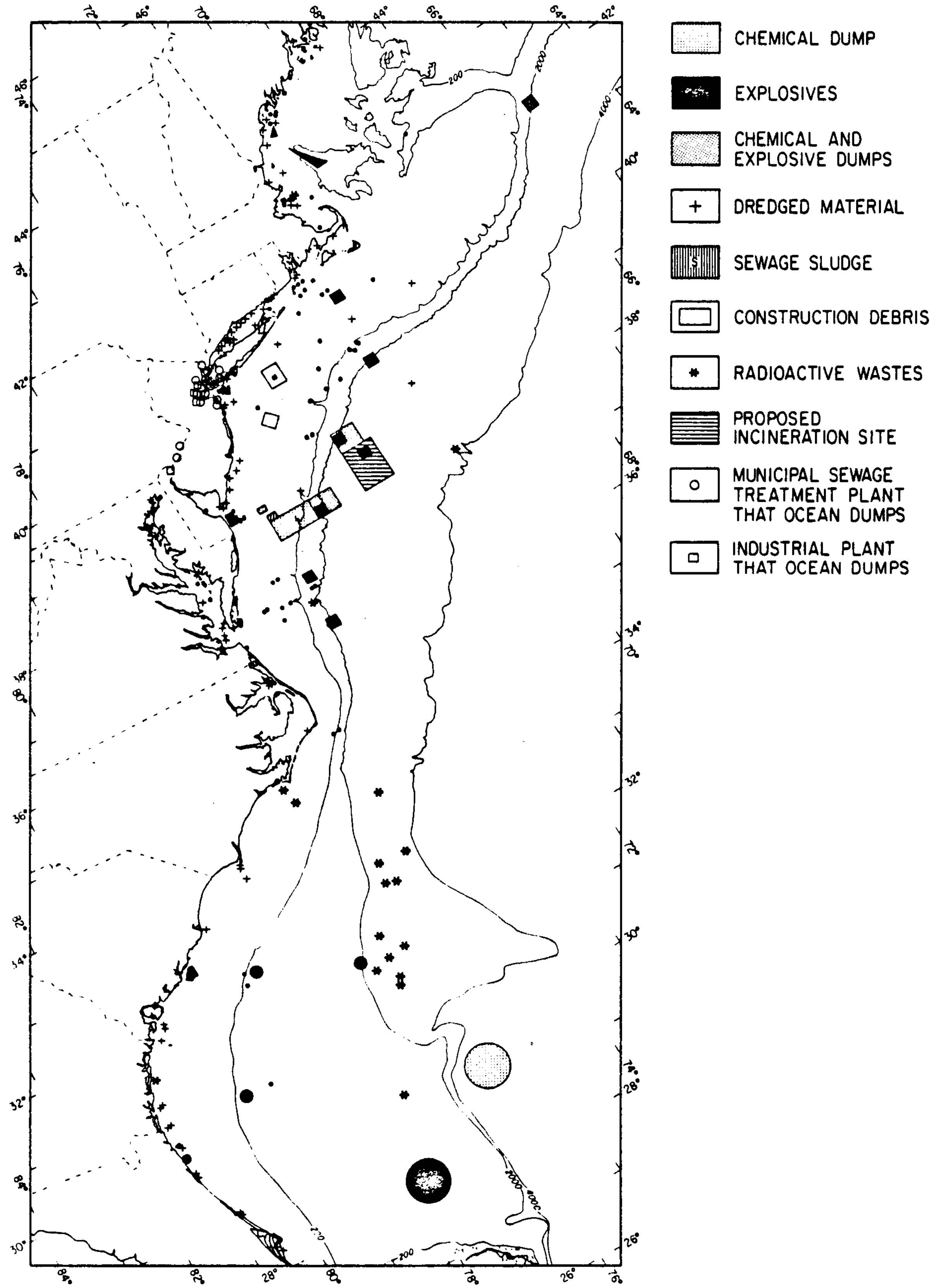


Figure 7.23. Active and inactive ocean disposal sites of the U.S. east coast (from NOAA, 1981).

SAND AND GRAVEL

There are many hard mineral resources with economic potential in the study area. Virtually none of these resources are now being exploited. Research, therefore, on the economic value of these resources has been speculative. Estimates of the amount of the resources available are given, but there is a gap in the literature in terms of what their dollar value might be. Also, little is said about the time frame in which to expect the economic development of these resources to occur.

Sand and gravel is one marine hard mineral resource which is now being exploited on the continental shelf. Although national land-based sand and gravel resources are considerable, there tend to be shortages in the major eastern metropolitan areas. This shortage is a result of the transportation costs involved with moving sand and gravel great distances. As a result, there will be a continued interest in marine sand and gravel resources of the Atlantic margin (National Academy of Sciences, 1975). However, no exploitation of this resource is now occuring in waters deeper than 200 meters on the Atlantic continental margin (Pearce, 1979; Manheim, 1979; Manheim and Hess, 1981; Cruikshank and Hess, 1979; Schlee, 1975) and very little future activity is likely to occur, given the distance from land and the vast sand and gravel deposits accessible on the adjacent shelf. Manheim (1979) identifies only one deposit in waters of the ACSAR area, located offshore from the South Carolina-Georgia border (see Fig. 7.24).

PLACER DEPOSITS

Placer deposits are minerals concentrated in a particular area as a result of river transport processes. Therefore, placers on the ocean bed can largely be expected to be limited to portions of the continental margin exposed during former low stands of sea level. During the late Quarternary glaciation, sea level was depressed a level approximately 130 m below its present level (Emery and Uchupi, 1972), which suggests placers should not be found beyond 200 m depth. In fact, there is little direct evidence to indicate the presence of placer deposits in the ACSAR study area. Deposits which have been identified on the Atlantic continental shelf are in waters of average depth from 20 m to 80-140 m (Milliman, 1972). These shallower deposits are commonly associated with drowned shoreline features.

Very little is known about the economic potential of the nearshore placer resources identified to date (Mannheim and Hess, 1981). However, using existing grab samples, the U.S. Geological Survey has begun estimating the economic potential of the Atlantic nearshore placer deposits. Preliminary findings indicate that economic deposits of placer minerals may occur in the Virginia offshore area. (Grosz and Ecowitz, 1983, p. 8)

Given the facts that placer deposits have only been identified in shallow waters and that little evaluation of these nearshore deposits has occurred, it seems unlikely that any exploitation of placer deposits will occur in the ACSAR study area for the forseeable future

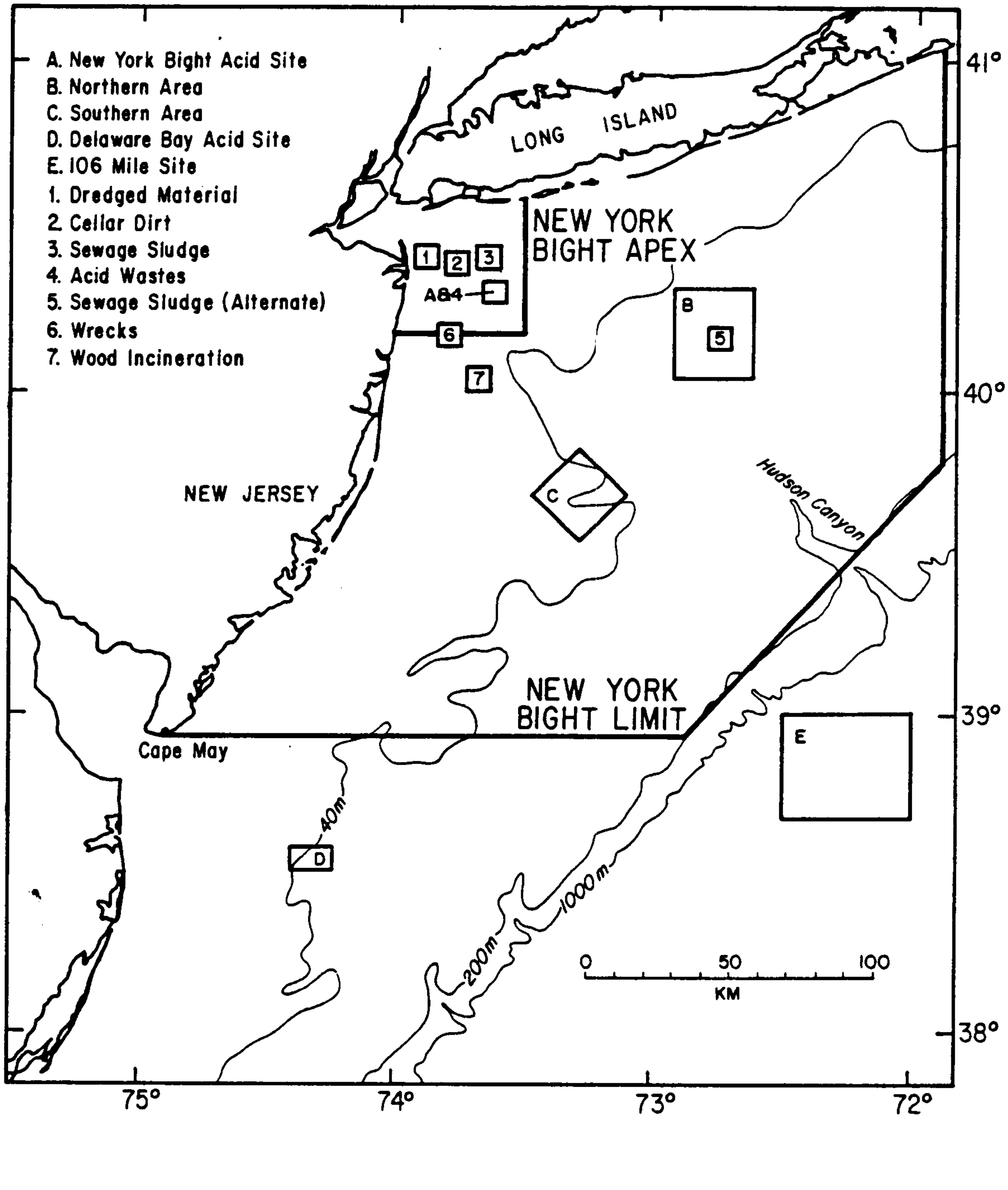


Figure 7.24. Active and inactive ocean disposal sites of the New York Bight area (modified from NOAA, 1979).

PHOSPHORITES AND CALCIUM CARBONATE

Phosphorite

Phosphorite has important agricultural applications as a source of phosphate for fertilizers. Although land-based sources of phosphorite have not been exhausted, environmental related conflicts have increased interest in marine deposits (Trondsen and Mead, 1977; National Academy of Sciences, 1975; Manheim and Herr, 1981). No current mining operation for phosphorite are reported in the ACSAR area. However, mining operations for offshore phosphorite resources, or plans for such activities, have been reported in southern California, Mexico, and New Zealand (Trondsen and Mead, 1977; Manheim and Hess, 1981). Similar activities on the Atlantic margin could be responsive to the same economic and political considerations as those reported elsewhere.

While actual mining of marine phosphorite resources is not a reality on the Atlantic margin, the general economic potential and concerns evaluated may be relevant to the study area (for examples of general studies on marine phosphorites or studies of problems associated with the resource in other geographical areas, see: Mero, 1959; Walter and Chougill, 1968; Manderson, 1972; Elkins and Spangler, 1968; Bowen, 1972; Overall, 1968; Sorenson and Mead, n.d.)

The only identified deposit of phosphorite with economic potential in the ACSAR area is found on the Blake Plateau (see Fig. 7.23). Present estimates are that there are 2 billion metric tons of phosphorite nodules in the area (Manheim, Pratt and McFarlin, 1980). The recovery of these resources will not be economically feasible for some time, depending on the environmental and regulatory factors. The dollar value of these resources is not now estimated.

Calcium Carbonate

Pure deposits of calcium carbonate (95% $CaCO_3$) occur in shallow waters off southern Florida and on the Blake Plateau (see Fig. 7.25). At present, this resource is not mined in the ACSAR waters; however the Marcona Corporation is mining this resource in very shallow U.S. waters (approximately 3 meters) off the Bahama Islands (Manheim, 1979; Anonymous, 1978).

OCEAN DUMPING

The literature on ocean dumping has grown rapidly in the past few years and will continue to do so at least for the next few years. Of special relevance here are the proceedings of the International Ocean Dumping Symposiums (IODS) dealing with industrial wastes (Ketchum et al., 1981), industrial and sewage wastes (Duedall et al., 1983), dredged materials (Kester et al., in press), radioactive wastes (Park et al., in press) energy wastes (Duedall et al., in prep.), deep-sea waste disposal (Kester et al., in prep.) and nearshore ocean dumping (Ketchum et al., in prep.). A recent special IODS symposium at the University of Rhode Island was held to further develop comprehensive and coordinated strategies for ocean disposal, to address the issue of safe disposal of wastes in the ocean. Studies on dumping in the New York

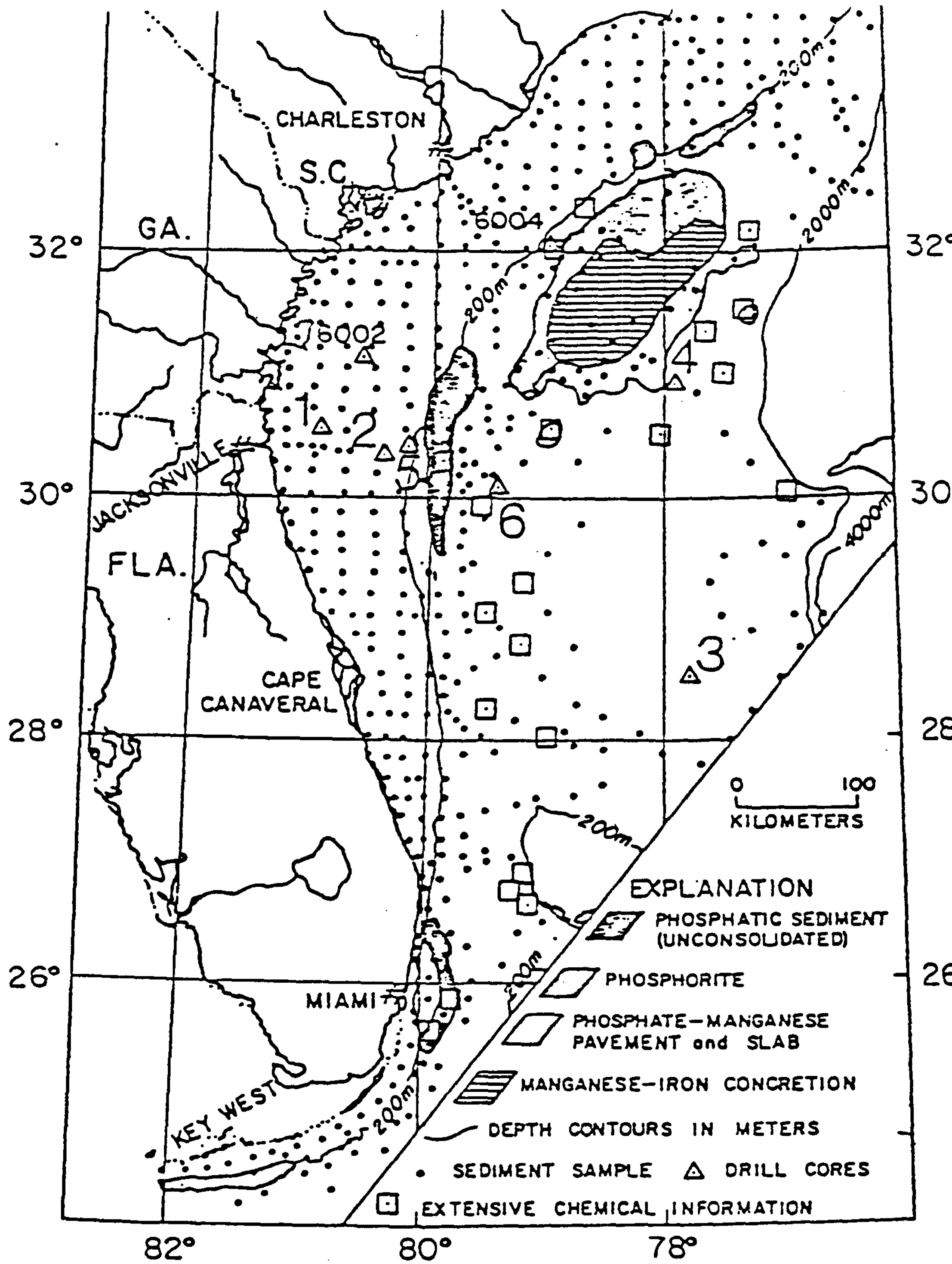


Figure 7.25. Phosphorite and manganese deposits of the Blake Plateau region (from Manheim et al., 1980).

Bight area, which borders the ACSAR, are collected in a recent volume edited by Mayer (1982). Champ and Park (1982) prepared a comprehensive bibliography on worldwide literature pertaining to ocean dumping. Implications of the concept of assimilative capacity to ocean dumping are discussed in the proceedings of a workshop held at Crystal Mountain, Washington (NOAA, 1979).

Waters of the U.S. East Coast are dotted with marked disposal sites (active, inactive, and proposed) for industrial chemicals and other wastes, explosives, dredged materials, sewage sludge, construction debris and radioactive wastes (Fig. 7.26, 7-27; U.S. Department of Commerce, 1980; OCS oil and gas lease sale EISs prepared by U.S. Department of the Interior). Many of these sites are located in the ACSAR area (Fig. 7.26). Since 1972, EPA has approved ocean dump sites, and publishes announcements in the Federal Register (U.S. Environmental Protection Agency, 1977). In 1977 about 87% by volume of all ocean dumping of waste materials, other than dredge spoils, took place at dump sites located in the New York Bight off the coasts of New York and New Jersey, inshore of the ACSAR area (Anderson and Dewling, in Ketchum et al., 1981; Fig 7.27). Before 1972 there was no uniform national regulation of ocean disposal and information on volumes and types of materials dumped before that time are sparce (U.S. Department of Commerce, 1979). Park and O'Connor (1981) indicate ocean dumping activity in the U.S. increased rapidly following World War II. Since regulation of ocean dumping under the Federal Water Pollution Control Act Amendment of 1972 ("Clean Water Act") and the Marine Protection, Research, and Sanctuaries Act (PL 92-532; "Ocean Dumping Act") many valuable data have accumulated on the volume, characteristics and impacts of wastes dumping. These acts established a national policy of strictly regulating ocean dumping by banning the dumping of chemical, biological, or radiological warfare agents and high-level radioactive wastes, and by authorizing a permit system for all other ocean dumping. EPA was authorized to administer and enforce the entire ocean dumping program and to issue dumping permits, except for dredged materials which falls under the perview of the U.S. Army Corps of Engineers.

DEEPWATER DUMPSITE 106 (DWD 106)

Perhaps the best studied deepwater disposal site is located 106 nautical miles from the entrance to New York Harbor, in the ACSAR area. Water depth ranges from 1,800 m to 2,700 m over the approximately 1,700 km^2 area of this site. DWD 106 has received industrial and municipal wastes since 1972 and is under investigation to determine the likely upper limit to its capacity to receive wastes without undesirable impacts, at least until more appropriate land-based option is available. Some of these studies address generic issues regarding the suitability of deep ocean sites to receive the residues of human activity and industry. The following synopsis is largely from Czanady et al. (in NOAA, 1979).

Deepwater dumpsite 106 is located in the slope water gyre (Fig. 7.2) between the Gulf Stream and continental shelf systems. The area is characterized by episodic passage of warm core rings, spun off from meanders of the Gulf Stream; these transient features contain areas of high current speed and are partly responsible for the highly dispersive nature of this site. Estimates of transport in the westward leg of the slope gyre itself are from 10-20 million m^3 s^{-1}. Current velocities are typically 10 cm s^{-1} in the top 200 m of the water column and less at greater depths. The current associated

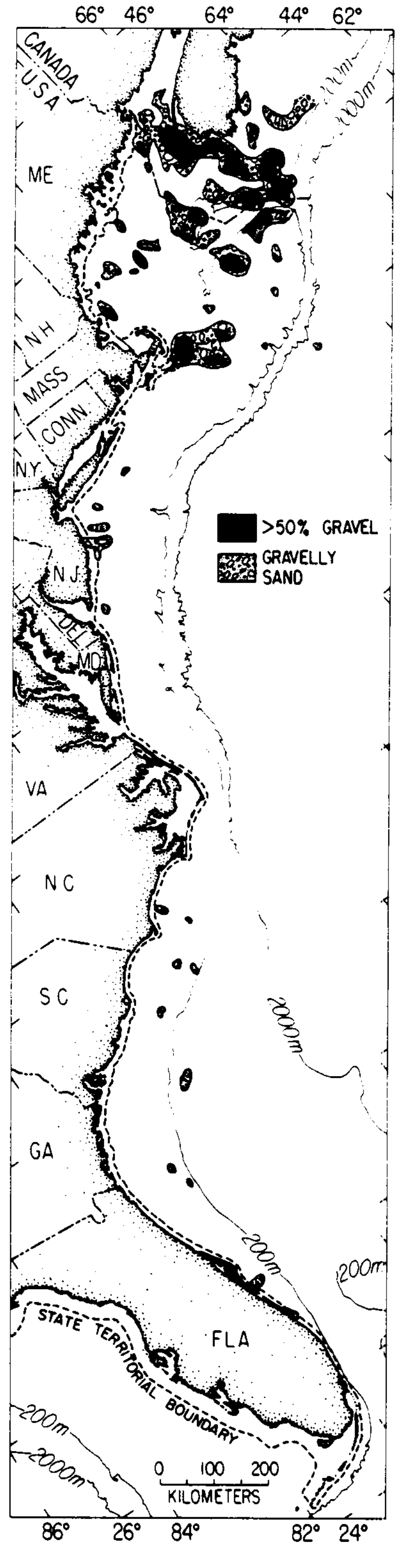


Figure 7.26. Sand and gravel deposits of the U.S. east coast continental margin (from Manheim, 1979).

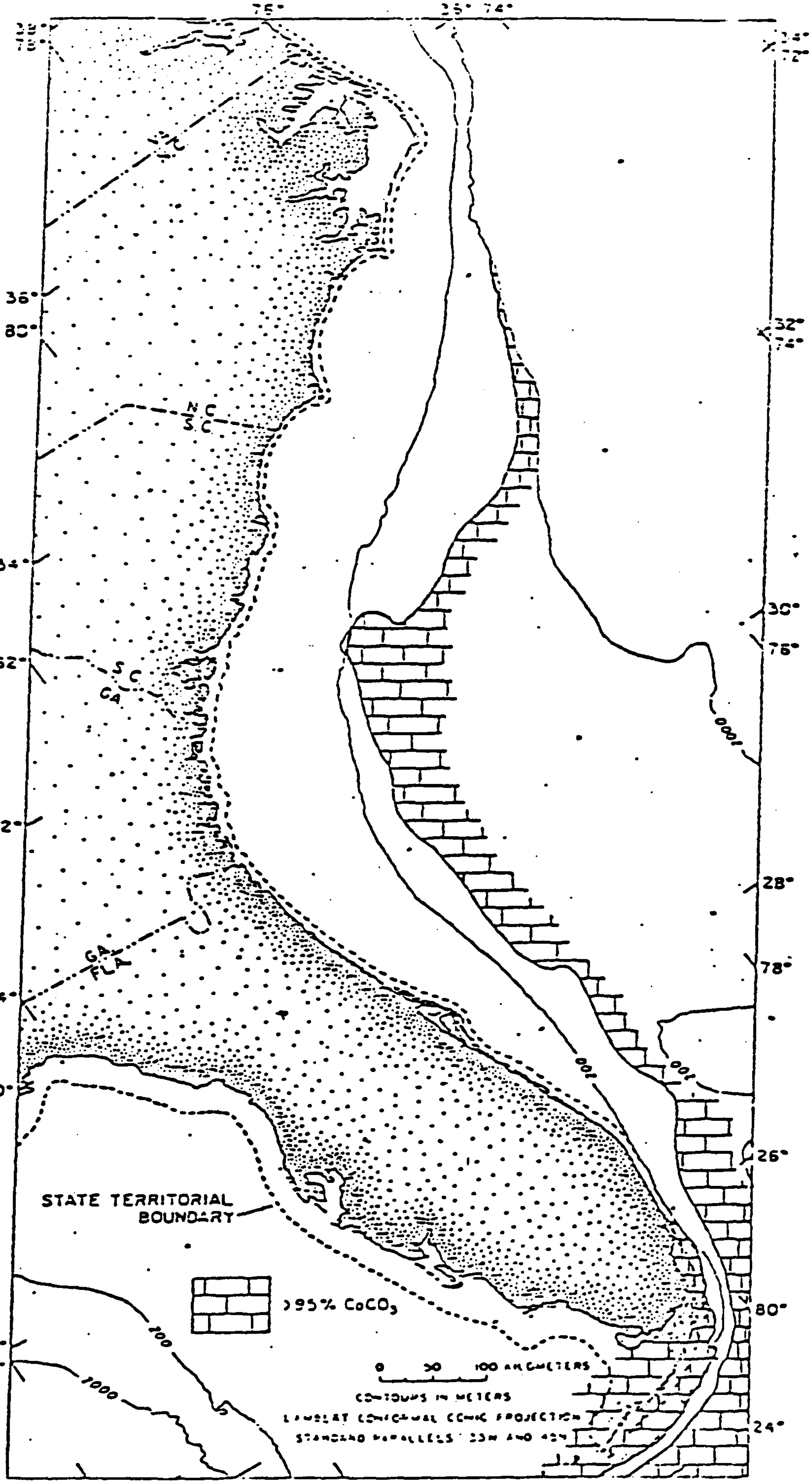


Figure 7.27. Carbonate deposits of the U.S. east coast continental margin

with the slope gyre is about 100 km wide. At Cape Hatteras the gyre turns abruptly toward the east, the bulk of it apparently moving under the Gulf Stream. Advection and mixing in the slope water from storm mixing, density flow, and rings are only some of the irregular processes contributing to the complex hydrography observed here. Nevertheless, westward flow predominates on the average; it has been estimated that water from DWD 106 takes about 2 months to reach the Cape Hatteras area.

In 1978, 800,000 m^3 of industrial wastes was dumped at DWD 106. Most of this came from three plants. The Dupont waste derived from titanium dioxide production was a strongly acid solution of iron chloride, containing chromium, vanadium, copper, zinc, nickel, lead, and traces of cadmium. At the dump site the acid is quickly neutralized by seawater and iron precipitates to form a flocculent particulate phase. The formation of these particles has important consequences regarding scavenging of heavy metals, availability of the waste materials to zooplankton and, potentially, the transport of wastes through the thermocline to the deep ocean.

The DuPont-Grasselli waste was an highly alkaline solution of sodium sulfate, containing some trace metals and such organic compounds such as methyl sulfate and phenol. Upon dumping in seawater, this alkaline material causes precipitation of magnesium in seawater as magnesium hydroxide. Though expected to redissolve in normal seawater, this precipitate has been observed to persist. Strong mixing enhances dissolving of the particles.

In 1978 American Cyanimid dumped about 120,000 m^3 of a complex, acidic solution containing 4% organic matter, derived from production of organophosphorus pesticides and chemicals associated with rubber production and the paper industry. No significant particulate phase is associated with dumping this material.

Wastes are carried to the dumpsite aboard approximately 4,000 m^3 barges or tankers and discharged from the moving vessel at a rate prescribed by EPA. This occurs over an approximately 45 km, U-shaped course, which causes an initial dilution by a factor of about 5,000. During the first hour or two the waste is distributed in the top 10 to 30 m during summer or in the top 150 to 200 m during winter. Very little, if any, of the waste penetrates into deep water, although particulates are known to sink slowly and accumulate on density surfaces (pycnoclines). Presumably, this material is dispersed by horizontal mixing and advection processes.

The possible impact of dumping practices at DWD 106 is a particularly complex topic: 1) the water column at this site is inhabited by constantly changing assemblages of organisms, as waters of shelf, slope and Sargasso Sea origin alternately occupy the location; 2) the toxic fraction of the wastes involved is not precisely defined, and the composition of wastes may vary among allotments (this, in turn, could cause variations in its physical state after dumping) and, 3) as in other instances where biological systems are involved, potential impacts are not limited to acute toxicity or abrupt death of adults of single species, but may involve long-term impacts to certain life cycle stages or often subtle changes in metabolism or the ability of a species or assemblage to persist over the long term. Methods used to assay marine organisms or biosystems for these kinds of effects are still primative, and extrapolation of laboratory results to the field remains an area where major advances are needed. These are only a few of the complexities associated with this issue; in view of the overwhelming difficulty associated with defining the biological impacts of deepwater dumping, one of the most compelling arguments for continuing to use deep sites is that other environments are likely to be biologically richer and socially and economically more valuable.

Bioassays of the American Cyanamid waste indicated a detrimental effect at concentrations known to exist at DWD 106; however, the phytoplankter used in these tests was not a dominant species in the area. Other assays involving DuPond-Grasselli wastes and using two species of zooplankton showed a slight lethal effect and decreased feeding rate.

Areas of needed research include better definition and understanding of large-scale circulation affecting deepwater dumpsites; mixing processes distributing the wastes; cross-frontal and cross-pycnocline transport mechanisms; the fate of dumped chemicals; many aspects of the biological response and impact of wastes; and physical, chemical, and biological mechanisms for concentration of waste components.

RADIOACTIVE DUMPING

The following synopsis is largely from testimony of Hurd (1982). Between 1946 and 1962 (when land disposal was introduced) the U.S. Atomic Energy Commission permitted ocean disposal of about 120,000 curies of low-level radioactive wastes, largely contained in 55 gallon steel drums, at about 30 locations,. This activity was phased out before 1970 when ocean dumping of radioactive materials was banned following recommendations of the newly created Council on Environmental Quality. This recommendation was later incorporated into the Ocean Dumping Act.

EPA studies on radioactive dumping focus on three sites which contain 95% of radioactive materials dumped by the U.S.: the Farallon Island site 50 miles off the coast of California, and two sites about 120 miles and 200 miles off the Maryland-Delaware coast, respectively (Fig. 7.26). EPA concludes from these studies "there is no evidence of harm to humans or the marine environment from past U.S. ocean dumping of radioactive wastes" and cite a General Accounting Office report reaching the same conclusion (U.S. General Accounting Office, 1982).

OTHER OCS USES, ACTIVITIES AND IMPACTS

Other uses and activities of the OCS encompass diverse aspects; they share in common that they have not attracted study by a large audience of academic researchers and as a result they are only briefly treated in the literature. In some cases, such as shipping, this may be because there is little associated controversy amenable to academic research. In other cases, such as military operations, what literature exists may not be freely open to the public. Nevertheless, some of these OCS uses, such as the examples cited above, probably involve economic consequences well in excess of those for fishing, mining, ocean dumping or other OCS activities considered at length in this report (see Pontecorvo et al., 1980).

SHIPPING

Shipping lanes for international transportation from ports along the U.S. east coast cross the ACSAR area at many places (Figs. 7.28-7.30). These shipping lanes connect 15 major U.S. ports with three principal passes leading to or through the Caribbean---the Straits of Florida, Mona Pass, and Anegada Pass (Fig. 7.29)---and four major world commodity (mainly oil) exchange regions---Northern Europe, the Mediterranean/North Africa, West Africa, and the Persian Gulf (via Cape Horn; Fig. 7.30). Domestic shipping lanes (Fig. 7.31) most strongly affect the ACSAR area south of Cape Hatteras, where traffic lanes converge toward the Straits of Florida.

The tanker traffic pattern among East Coast ports displays a size dependency. The smaller tankers (e.g., 6,000 to 50,000 deadweight tons) are most involved in domestic traffic among the large port cities of the northeast and in shipments to all East Coast ports from the Gulf of Mexico. Tankers of this size range also participate in international petroleum shipping originating in the Caribbean (Table 7.2). On the other hand, large tankers (greater than 50,000 deadweight tons) serve only Portland (up to 100,000 tons), New York, and Philadelphia and involve cargos mainly from the Persian Gulf, North Africa, and West Africa and to a limited extent, the Caribbean (Table 7.2).

NOAA (1980) charts the flow of total commodities into East Coast ports. As for petroleum, the ports of New York and Philadelphia lead the East Coast in commodity shipping. The rank of other ports depart widely; for example New Haven ranked third in petroleum imports but 13th for total commodities. The major ports for fish landings (see Fig. 7.17) differ even more widely. The major east coast fishing ports ranked by dollar landings or by quantity landed---New Bedford, Mass., Gloucester, Mass., Hampton Roads area, Va., Rockland, Me., Cape May-Wildwood, N.J., etc.---are not included in the top 15 ports for oil or commodities.

Conflicts of shipping with other OCS uses could include collision danger for surface objects, whether moored, fixed to the bottom or dynamically positioned. Pollution resulting from vessel discharges at sea and from shipwrecks poses other potential problems. The U.S. Coast Guard, Office of Marine Environment and Systems, Pollution Response Branch operates a computerized Pollution Incident Reporting Service (PIRS) which logs and classifies oil spills. This involves rigorous documentation of spills within about 10 miles of land, with less complete coverage offshore where reporting may be spotty. NOAA (in prep.) is analysing operational discharges of ships (Basta, personal communication), which, in combination with traffic patterns should provide spatial information on oil inputs to the ACSAR area originating from this source.

The best known tanker spill associated with the ACSAR area, the Argo Merchant spill, did not actually occur within ACSAR. Nevertheless, the slick was driven by prevailing winds and currents on a trajectory which probably took it into this area. During World War II, approximately 485,000 metric tons of oil was spilled within 50 miles of the U.S. Atlantic coast as a result of submarine attacks on shipping . Much of this oil, equivalent to 20 times the Argo Merchant spill, directly or indirectly became entrained into the Gulf Stream flow in the ACSAR area (Campbell, Kern and Horn, 1977). Most of these sinkings occurred during the first 6 months of 1942, with oil entering the marine environment at a rate of almost one Argo Merchant cargo per week. Nothing is known regarding the impact of this oil on the environment.

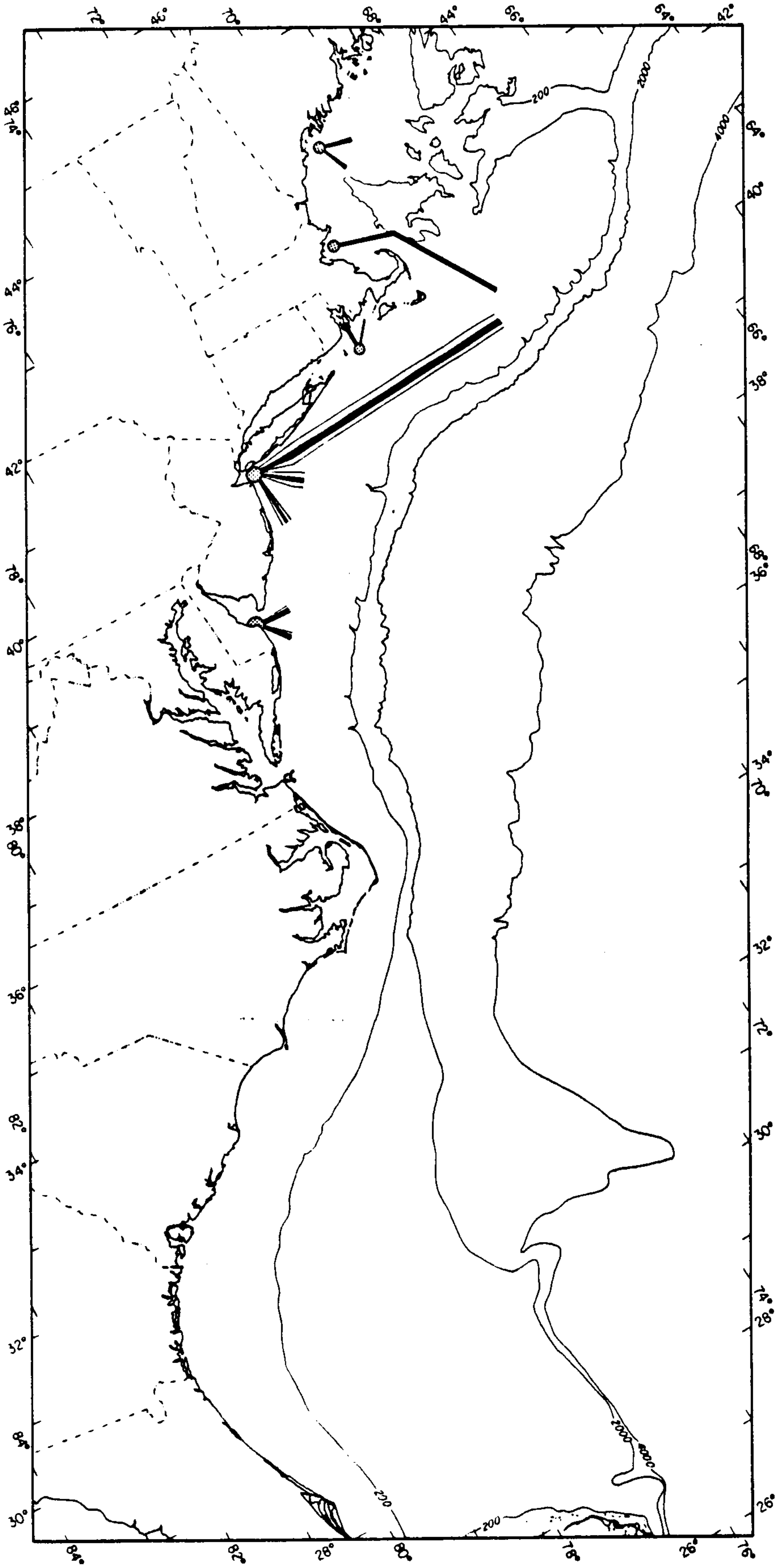


Figure 7.28. Traffic separation lanes for shipping at major U.S. east coast ports (modified from NOAA 1981).

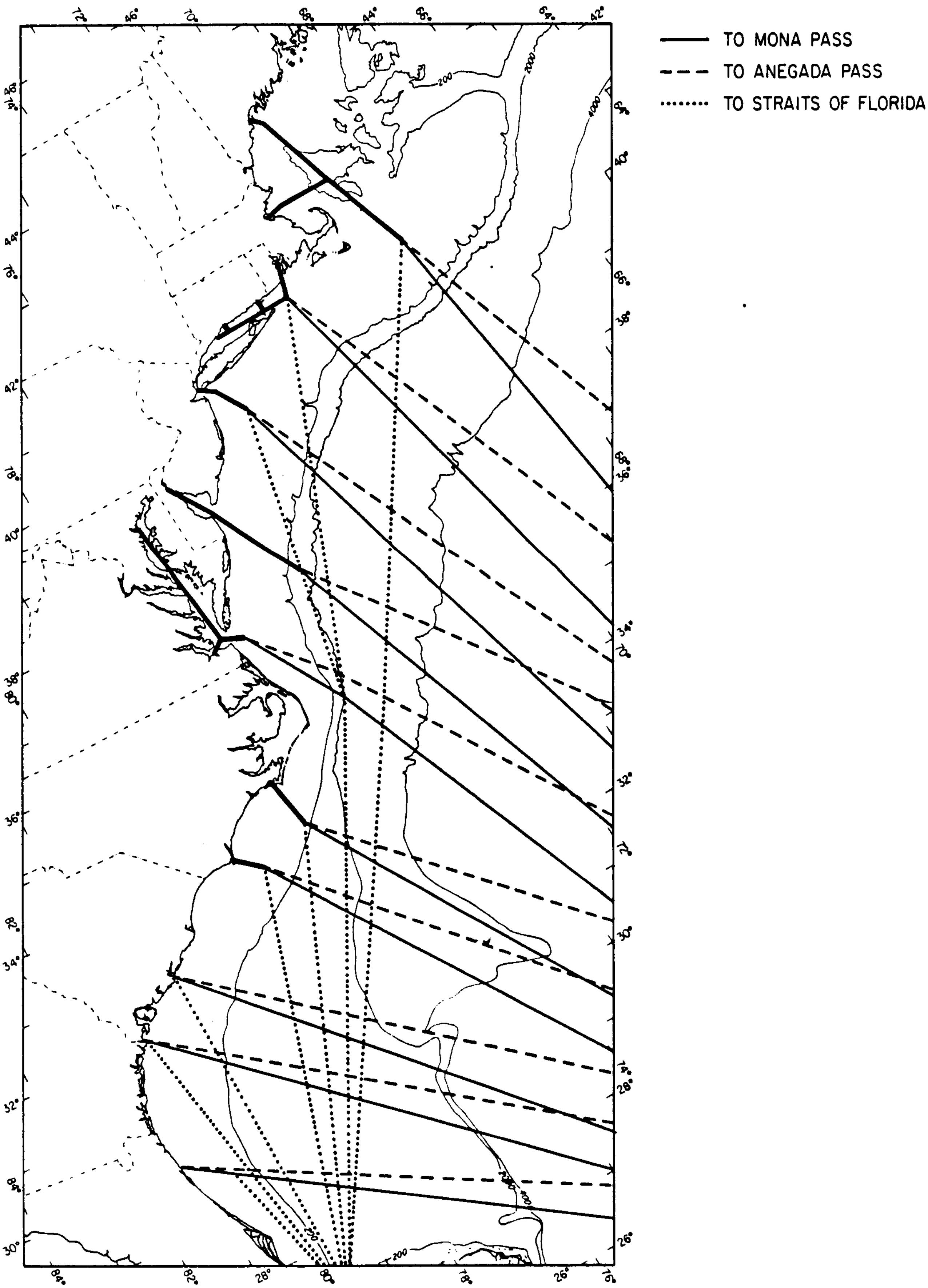


Figure 7.29. Major U.S. east coast-Caribbean shipping lanes (from D. Basta, personal communication).

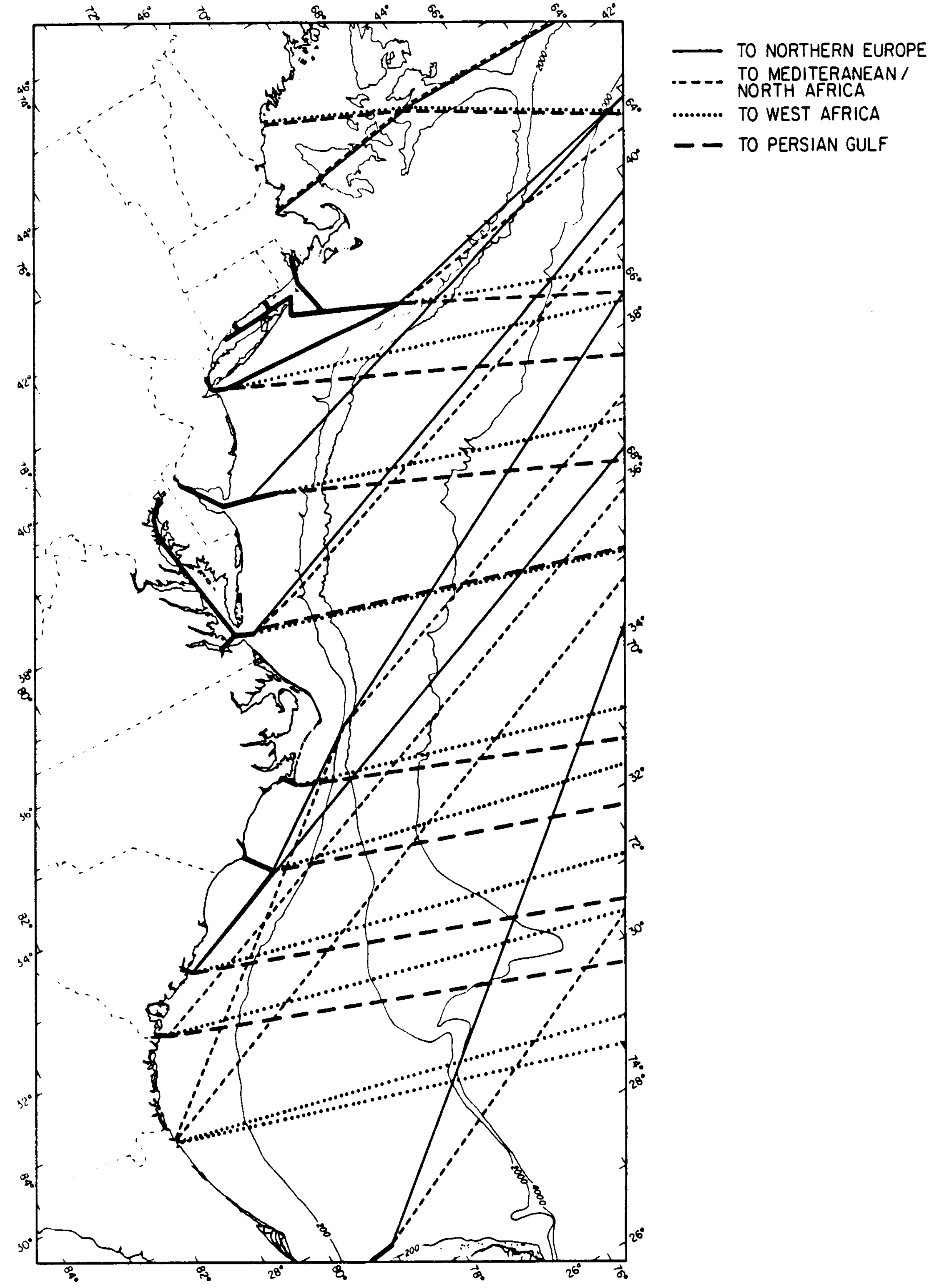


Figure 7.30. Major trans-Atlantic shipping lanes for the U.S. east coast (from D. Basta, personal communication).

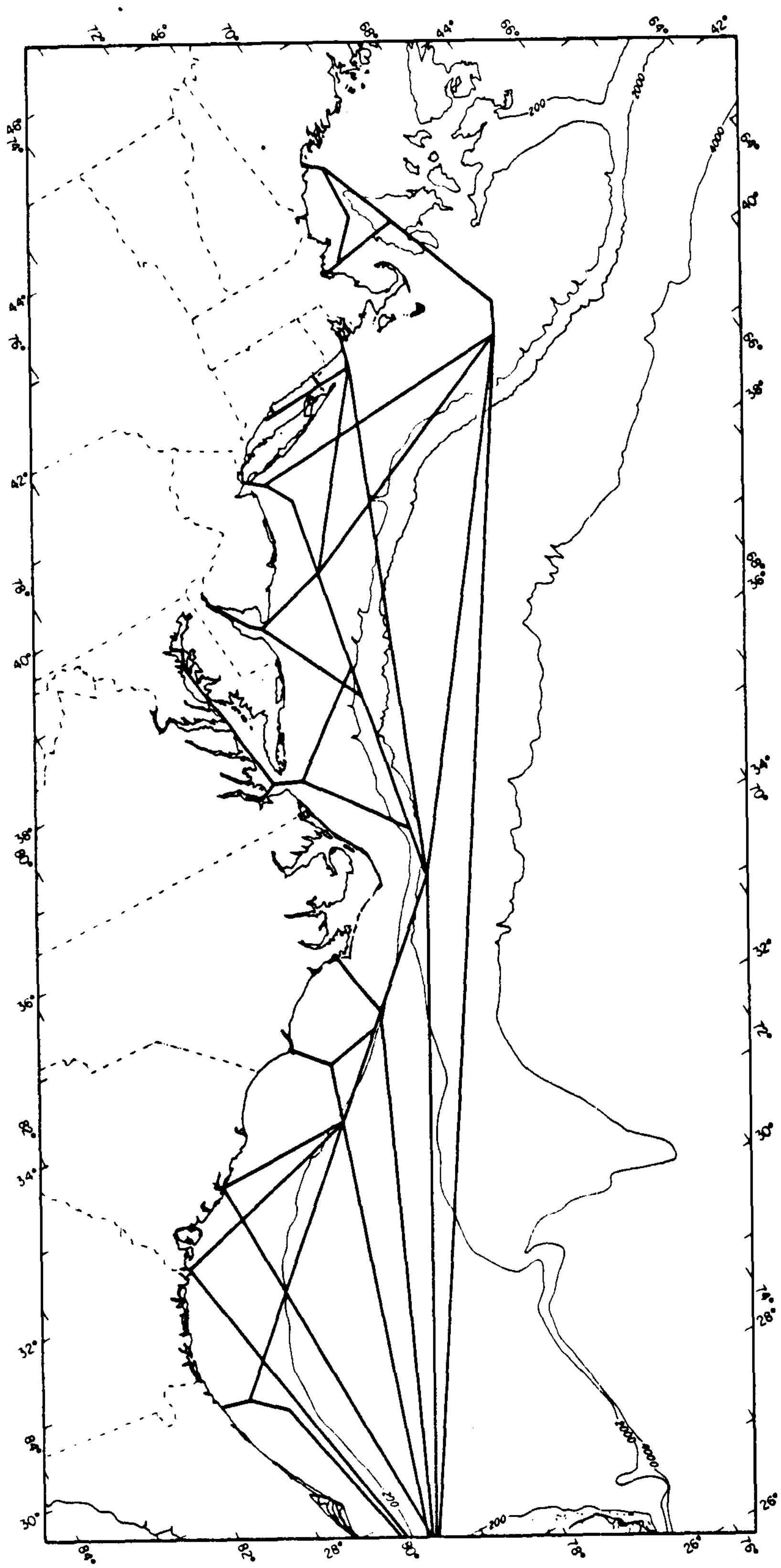


Figure 7.31. Principal domestic shipping lanes of the U.S. east coast (from D. Basta, personal communication).

Table 7.2 Number of port calls at U.S. east coast ports during 1979 by port, route, and tanker size

'ORT	FLORIDA STRAITS	MONA PASS	ANAGADA PASS	PERSIAN GULF	NORTH AFRICA	WEST AFRICA	NORTH EUROPE	BAHAMAS	BOSTON	NEW YORK	PHILA-DELPHIA	NORFOLK	WILM-INGTON	GULF OF MEXICO	SUM
'ORTLAND	1	36	1	0	2	0	1	4	14	13	49	0	0	67	188
OSTON	1	77	12	1	7	0	12	7	0	18	46	0	0	237	418
'ROVIDENCE	2	52	14	0	7	0	6	3	7	64	113	0	0	109	377
'EW HAVEN	0	31	12	0	6	2	5	0	0	94	100	0	0	171	421
EW YORK	21	276	134	1	55	27	42	75	0	0	166	0	0	681	1478
HILADELPHIA	8	106	24	5	23	1	7	20	0	11	0	0	0	261	466
ALTIMORE	2	64	9	3	10	5	2	5	0	31	2	0	2	100	235
ORFOLK	1	23	2	0	2	0	0	3	0	2	0	0	1	13	47
OREHEAD CITY	0	14	0	0	0	0	1	0	0	0	1	0	0	12	28
ILMINGTON	0	42	1	0	1	1	3	0	0	0	0	0	0	83	131
HARLESTON	1	36	2	1	0	0	0	0	0	0	3	1	0	111	155
AVANNAH	0	20	0	0	9	0	2	9	0	0	0	0	0	61	101
ACKSONVILLE	3	35	1	0	1	0	2	5	0	0	2	0	0	131	180
ORT EVERGLADES	0	8	0	0	0	0	0	2	0	0	1	0	0	71	82
IAMI	0	2	0	0	0	0	0	0	0	0	0	0	0	5	7

Table 7.2 Number of port calls at U.S. east coast ports during 1979 by port, route, and tanker size (continued)

PORT	FLORIDA STRAITS	MONA PASS	ANAGADA PASS	PERSIAN GULF	NORTH AFRICA	WEST AFRICA	NORTH EUROPE	BAHAMAS	BOSTON	NEW YORK	PHILA-DELPHIA	NORFOLK	WILM-INGTON	GULF OF MEXICO	SUM
PORTLAND	1	26	1	0	1	0	1	3	10	9	36	0	0	49	137
BOSTON	1	83	13	1	8	0	13	8	0	19	50	0	0	257	453
PROVIDENCE	1	31	8	0	4	0	4	2	4	38	68	0	0	66	226
NEW HAVEN	0	17	6	0	3	1	2	0	0	50	53	0	0	91	223
NEW YORK	19	246	119	1	49	24	37	67	0	0	148	0	0	606	1316
PHILADELPHIA	17	226	51	11	49	2	15	41	0	23	0	0	0	553	988
BALTIMORE	2	80	11	3	12	6	2	6	0	39	2	0	2	126	291
NORFOLK	18	310	23	4	22	0	5	36	0	31	0	0	10	167	626
MOREHEAD CITY	0	21	0	0	1	1	2	0	0	0	2	0	0	18	45
WILMINGTON	0	53	1	0	2	2	4	0	0	0	0	0	0	106	168
CHARLESTON	0	23	1	1	0	0	0	0	0	0	2	1	0	71	99
SAVANNAH	0	35	17	0	15	0	3	15	0	0	0	0	0	102	187
JACKSONVILLE	5	51	1	0	2	0	3	8	0	0	3	0	0	194	267
PORT EVERGLADES	0	35	0	0	1	0	1	7	0	0	5	0	0	309	358
MIAMI	0	17	0	0	0	0	0	4	0	0	0	0	0	40	61

Table 7.2 Number of port calls at U.S. east coast ports during 1979 by port, route, and tanker size (continued)

PORT	FLORIDA STRAITS	MONA PASS	ANAGADA PASS	PERSIAN GULF	NORTH AFRICA	WEST AFRICA	NORTH EUROPE	BAHAMAS	BOSTON	NEW YORK	PHILA-DELPHIA	NORFOLK	WILM-INGTON	GULF OF MEXICO	SUM
PORTLAND	0	0	0	0	79	0	0	0	0	0	0	0	0	0	79
BOSTON	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PROVIDENCE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NEW HAVEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NEW YORK	5	127	0	236	32	45	9	0	0	0	0	0	0	0	454
PHILADELPHIA	15	6	3	91	83	88	9	0	0	0	0	0	0	0	295
BALTIMORE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NORFOLK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOREHEAD CITY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WILMINGTON	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CHARLESTON	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAVANNAH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JACKSONVILLE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORT EVERGLADES	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIAMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

ANY TANKERS OF GREATER THAN 50,000 DWT ARE LIGHTERED BEFORE PROCEEDING INTO NEW YORK AND PHILADELPHIA

Table 7.2 Number of port calls at U.S. east coast ports during 1979 by port, route, and tanker size (continued)

PORT	FLORIDA STRAITS	MONA PASS	ANAGADA PASS	PERSIAN GULF	NORTH AFRICA	WEST AFRICA	NORTH EUROPE	BAHAMAS	BOSTON	NEW YORK	PHILA-DELPHIA	NORFOLK	WILM-INGTON	GULF OF MEXICO	SUM
PORTLAND	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BOSTON	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PROVIDENCE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NEW HAVEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NEW YORK	1	18	0	34	5	6	1	0	0	0	0	0	0	0	65
PHILADELPHIA	9	4	2	59	53	57	6	0	0	0	0	0	0	0	190
BALTIMORE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NORFOLK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOREHEAD CITY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WILMINGTON	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CHARLESTON	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAVANNAH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JACKSONVILLE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORT EVERGLADES	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIAMI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

ANY TANKERS OF GREATER THAN 50,000 DWT ARE LIGHTERED BEFORE PROCEEDING INTO NEW YORK AND PHILADELPHIA

A recent, unusual source of conflict between shipping and offshore oil exploitation arose when the State of New York Coastal Zone Management found Lease Sale No. 52 inconsistent with their coastal policies because of conflict with tanker traffic lanes.

DEEPWATER TERMINALS

Deepwater ports and offshore shipping terminals have been proposed mainly in connection with handling supertankers (Bragaw et al., 1975). According to Ross (1978) there are four reasons that deep-water terminals will be built: a) the U.S. importation of petroleum will remain high or increase in future years; b) supertankers have a clear economic advantage for moving petroleum; c) U.S. ports are not currently suitable for offloading supertankers at berth and to dredge them would incur vast spoil disposal problems, not to mention the expense itself; and, d) the principal alternative to constructing offshore terminals would be to offload crude oil in neighboring countries, such as the Bahamas or Canada, and transship it to the U.S. in smaller tankers. However, following some well publicized accidents involving sinkings of supertankers, as well as the reopening of the Suez canal, there is some indication that supertankers may no longer be regarded as preferable to smaller tankers.

The most common types of offshore terminals proposed include platforms or structures rigidly fixed to the bottom (conventional piers, sea islands, sea island piers) and anchored mooring systems (multiple buoy berths "MBB" and single-point mooring systems"SPM"). Over 100 SPMs have been installed around the world and they are now accepted within the oil industry. The American Bureau of Shipping (1975) issued rules for building and classing SPMs.

Bragaw et al. (1975) indicate a likely location for a deepwater terminal would be near the Delaware estuary, where about 90% of U.S. East Coast petroleum refinery capacity is sited. However, it would seem unlikely such a terminal in this area would be located in greater than 200m depth in the OCS. It is also unlikely that present large- or supertanker traffic patterns would be strongly changed in the ACSAR area. The port of Philadelphia already receives about 75% of large tanker traffic (Table 7.2).

CABLES AND PIPELINES

Nine telecommunications cables, all constructed by Bell System, cross the ACSAR (Fig 7.32). The site and U.S. landfall for a tenth cable has been proposed. An additional trans-Atlantic telecommunications cable, TAT-8, has been proposed but neither the U.S. nor European terminals have been selected (AT&T Longlines, 1980). The position of cables is plotted on NOS Chart 13003 by AT&T at a scale of 1:1,200,000. Warnings to fishermen printed on this chart suggest the cables lie on the bottom or are not deeply buried.

There are no existing pipelines in this ACSAR area. Their most likely application would be in association with offshore petroleum production, for which pipelines are often assumed to be preferable to tankers (see EIS for Lease Sale No. 52; Fig 7.33). In the past a sewer pipeline was proposed to conduct sewage and waste water across the continental shelf to an OCS outfall, but this was never constructed. The technology of offshore hydrocarbon pipelines (excluding cryogenic substances) appears to be fairly well advanced, at least for continental shelf waters. The American Petroleum Institute (1976)

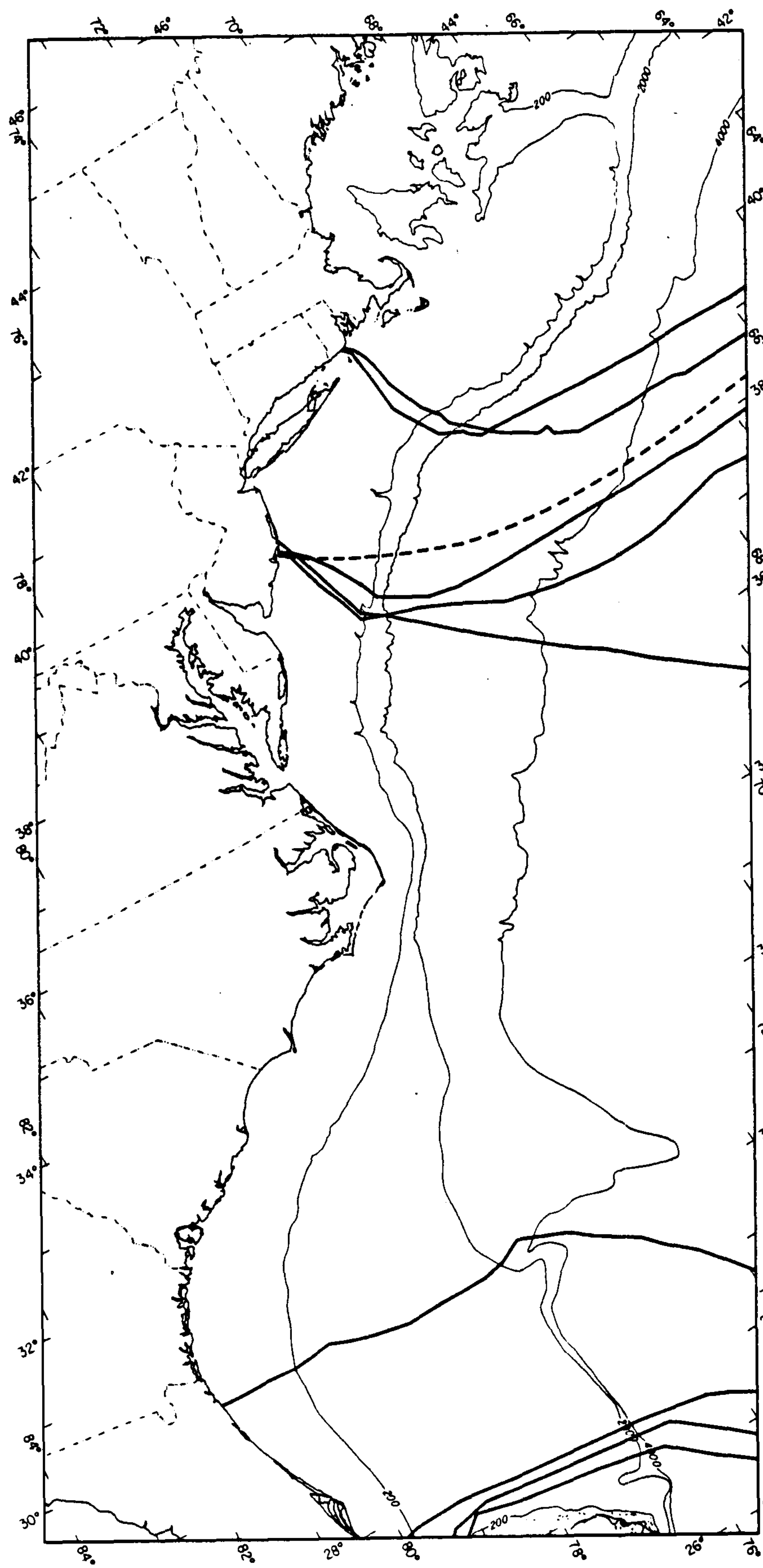


Figure 7.32. The location of telecommunication cables off the U.S. east coast. Dashed line indicates proposed cable (from AT&T Longlines, personal communication).

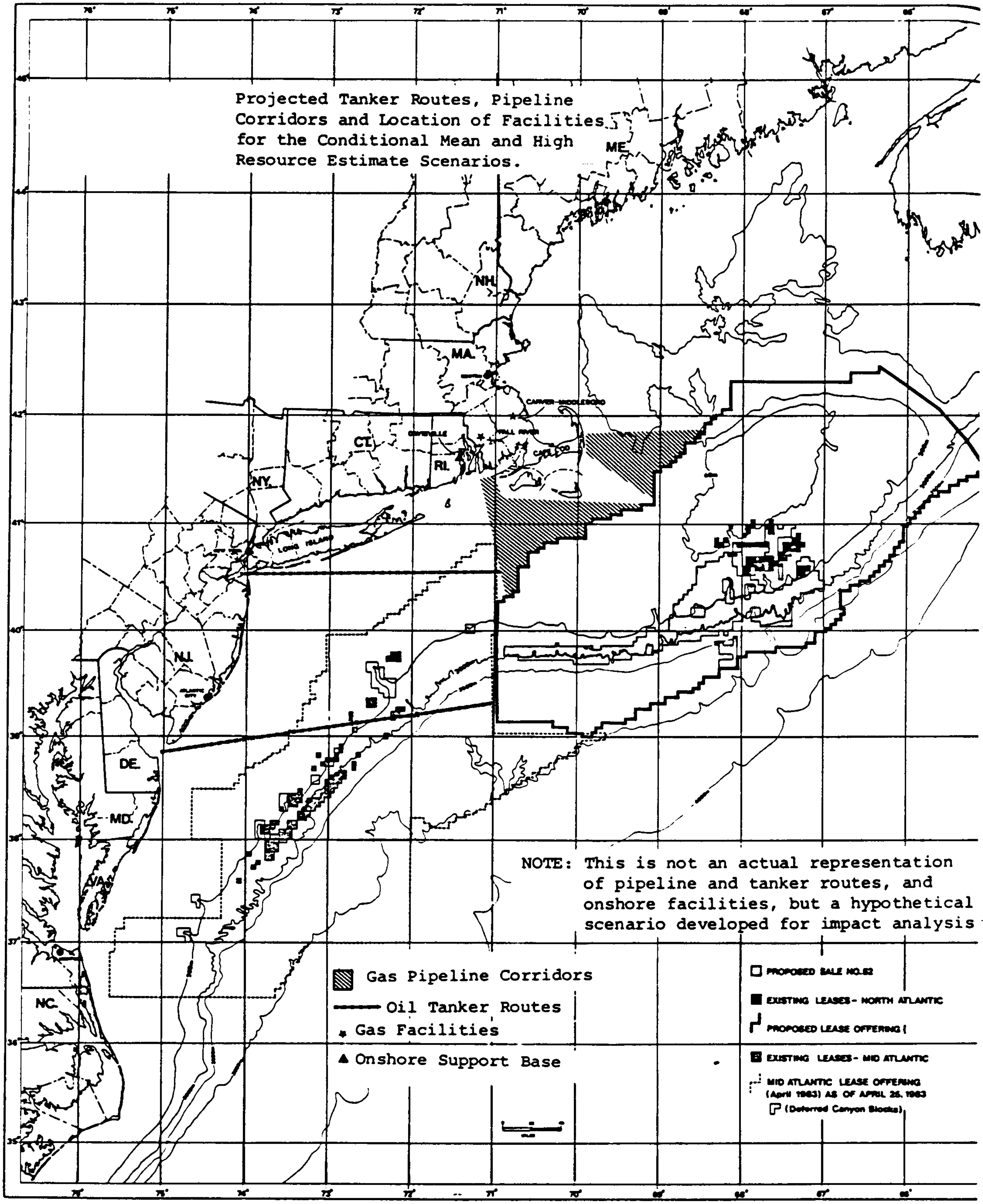


Figure 7.33. The location of pipelines proposed for Lease Sale No. 52.

and the Institute of Petroleum (1972) issued guidelines for their design, construction, operation and maintenance. One indication that pipelines in deep water are not yet feasible or not yet economical is that Norwegian oil produced in the North Sea is piped to Britain (where it is loaded aboard tankers) rather than across the Norwegian Trench (300 to 400 m deep) to Norway. A bibliography by Bowie and Wiegel (1977) compiles literature describing the design, construction, operation, and maintenance of pipelines up to 4 m in diameter in the ocean and rivers. A geographical index to marine pipeline locations is also included. A bibliography on offshore petroleum engineering by Chryssostomidis (1977) lists 51 general and specialized references on the topic of pipelines.

RESTRICTED ZONES AND OBSTRUCTIONS

Restricted zones in the ACSAR include a rocket impact area near Cape Kennedy and bombing areas off the coast of Georgia (Fig 7.34). Surface uses are not obstructed by reefs or shoals in the ACSAR area but seafloor uses may find conflict with submerged objects of human origin. Ocean dump sites have already been discussed (see Fig. 7.26) and need to be taken into account in other future use of the bottom. Shipwrecks are another potential obstruction to bottom activities in the OCS. Although their positions are less well known than for shallow waters, shipwrecks in the OCS have been plotted on the detailed maps accompanying the oil and gas lease sale environment impact statements. The Automated Wreck and Obstruction Information System (AWOIS), being developed by NOAA, is a computer-based file on shipwreck descriptions. The file can be searched by geographic coordinates. At present the coverage is best in shallow waters, but eventually AWOIS should be useful for OCS applications as well.

NON-POINT SOURCE ENVIRONMENTAL IMPACTS AND CONSEQUENCES

A discussion of human impacts on the environment is not complete without mentioning non-point source pollutants. These are largely substances that are dispersed by atmospheric circulation, such as radioactivity from nuclear weapons testing and the nuclear industry or chlorinated hydrocarbons and other organochlorine compounds, such as DDT and PCB's, manufactured for use as pesticides and in electrical components, respectively. In terms of radioactivity, surface waters of the Atlantic are known to contain measurable quantities of anthropogenic radionuclides such as tritium, cesium-137, strontium-90 and carbon-14. Except for carbon-14, these isotopes were dispersed in the atmosphere and deposited on the worlds' ocean surface largely by rain between 1954 and 1964; since then they have been mixed downward by natural processes and now occur to depth of at least 700 m in temperate areas of the North Atlantic (Broecker, 1974). Carbon-14 is taken up in the gaseous phase ($^{14}CO_2$) at the ocean surface in north temperate latitudes (Broecker, 1974).

Relatively few measurements are available of DDT, PCBs and other organochlorine chemicals for the ACSAR area, but available data indicate at least trace quantities of these substances even in deep water. A similar generalization can be made regarding some of the combustion products of petroleum hydrocarbons.

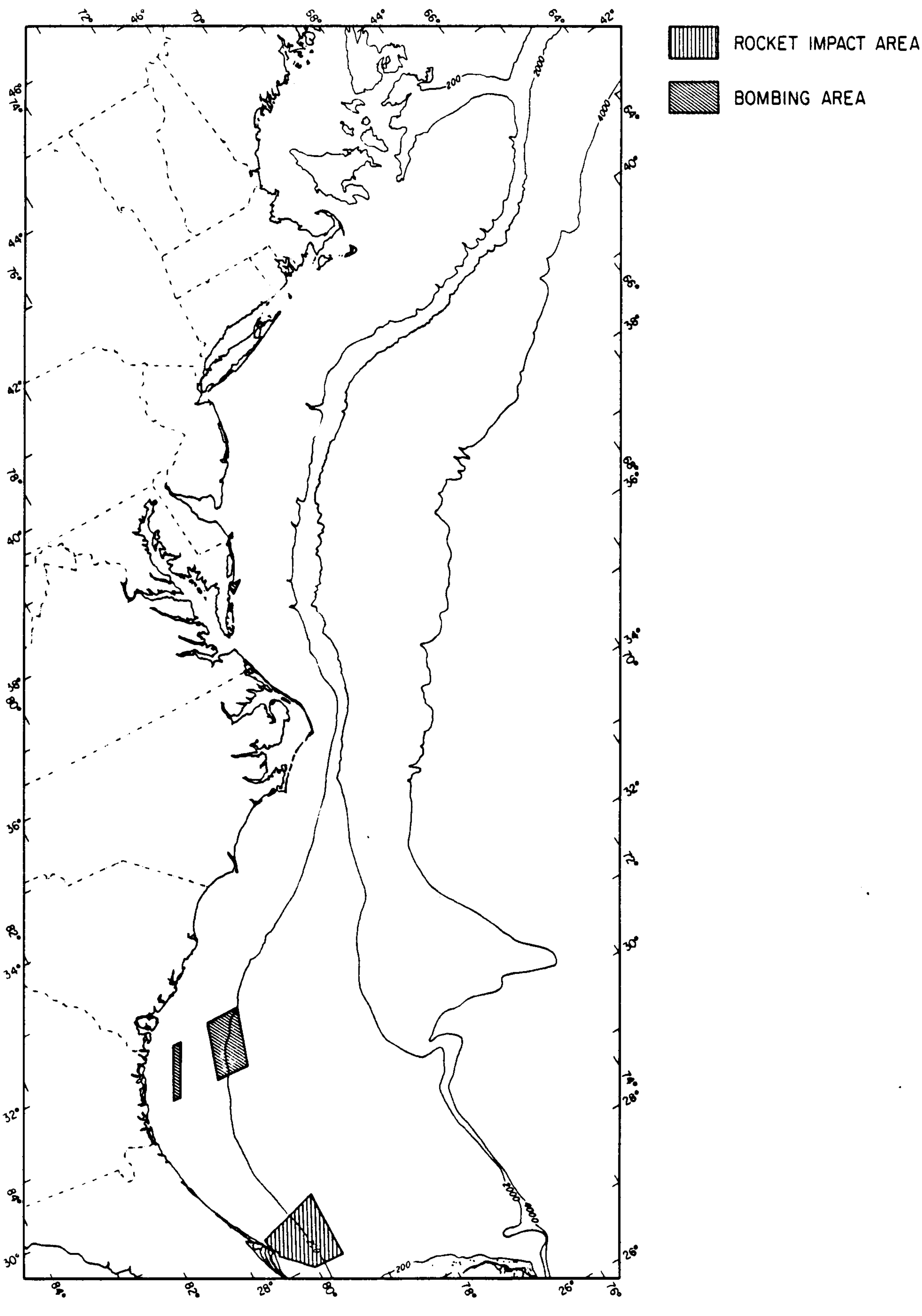


Figure 7.34. Rocket impact and bombing areas for the ACSAR area (modified from NOAA 1981).

MARINE MAMMALS, ENDANGERED SPECIES AND SPECIAL HABITATS

MARINE MAMMALS AND ENDANGERED SPECIES

In terms of human activity, two areas of wildlife management concern will be relevant to the economic development of resources in the study area. They are endangered species and marine mammals. As a result of federal legislation, the effects of human activity on these resources must be considered before development can go forward. The Endangered Species Act of 1973 (16 U.S.C. 1531-1543) has as its stated purpose, "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved" (Sec.2.b.). It further notes all federal departments and agencies shall seek to conserve threatened and endangered species (Sec.2.c.). The Marine Mammals Protection Act of 1972 (16 U.S.C. 1361-1407) has as its specific purpose to protect and encourage the development of marine mammal stocks, within the parameters of sound resource management, so as to maintain the health and stability of the marine ecosystem (Sec.2.(6)).

For the study area, endangered species can be considered to be encompassed by marine mammals. Further, the category of marine mammals can be reduced to cetacean species, i.e., whales and dolphins. Besides dolphins and whales, no other marine mammals or endangered species have been identified as being present on or in the waters of 200+ meters depth along the Atlantic margin of the U.S. (U.S.Department of Commerce, NOAA, and Council on Environmental Quality, 1980).

There are many sources, which identify and discuss the distribution of cetaceans along the Atlantic continental margin (CETAP, 1981; Katona, Winn and Steiner, 1977; Leatherwood, Caldwell, and Winn, 1976; Marcuzzi and Pilleri, 1971; Mitchell, 1973; Prescott, Kraus, and Gilbert, 1979; Rice, 1977). The most extensive study has been conducted by the Cetacean and Turtle Assessment Program (CETAP) of the University of Rhode Island. Unfortunately, the CETAP work only covers the Mid-Atlantic and North Atlantic portions of the study area (from 34° to 45° North) (CETAP, 1981; CETAP, 1982).

The EIS for Lease Sale No. 76 summarizes the cetaceans found in the western North Atlantic (see Table 7.3). Endangered species which have been sighted in 200+ meters of water include the sei, fin, humpback, right and sperm whales. It should be noted that though a specific cetacean may not have previously been sighted in the study area, this can not be taken to mean that the animal could not be present in the area (Moore, 1983).

Figs. 7.35 and 7.36 depict the geographical distribution of CETAP sightings. Their Type II cetaceans are species such as the baleens and *L. acutus*. Their Type III cetaceans are primarily odontocetes (CETAP, 1981).

While the above whales are the only endangered species which are present in significant numbers in the ACSAR area, this does not mean that they are the only ones which could be affected by human activity in the region. If a major oil spill were to occur from exploration or production activities, it is possible that that crude oil could foul the nearshore, shore, and estuarine ecosystems of the Atlantic coast. If this were to occur, turtles, other marine mammals, birds, and shore plants might be effected. Many of these are on the threatened or endangered species lists. (CETAP, 1981; CETAP, 1982; U.S. DOI, 1982a; U.S. DOI, 1982b; NOAA, 1980)

Table 7.3 Summary of cetacean species found in the Western North Atlantic Ocean.

Common Name		Distribution and Habitat	Population Estimate
+Minke whale	Balaenoptera acutorostrata	Sub-polar to tropical waters. Most common north of New York. A northward spring migration and southward fall migration has been noted. Most sitings are nearshore or within the 200 m contour. Eats fish (herring, capelin, etc.)	No estimates. Relatively common north of New York.
Brydre's whale	Balaenoptera edeni	Tropical and subtropical possibly straying as far north as Virginia. A nearshore species. Feeds on schooling fish (herring, mackerel, etc.).	No estimates. Of minimal importance in Mid-Atlantic.
+ *Sei whale	Balaenoptera borealis	Pelagic. Probably winters south of Cape Cod and summers from Cape Cod northward to southern Arctic. Feeds on copepods, krill, and small fish by skimming at or below the water's surface.	1,398 to 2,248 Uncommon in Mid-Atlantic
+*Fin whale	Balaenoptera physalus	Found between shore and the 2000 m contour. Present in all Mid-Atlantic areas throughout the year but concentrated from Cape Cod north in the summer and south in winter. Probably a nearshore northerly spring migration and an offshore southerly fall migration. Possibly breeds in Mid-Atlantic. Feeds on krill, planktonic crustaceans, and schooling fish (capelin, herring, etc.).	7,200. Most common large baleen whale.
*Blue whale	Balaenoptera musculus	Pelagic. Remaining individuals appear to be concentrated in waters from the Gulf of St. Lawrence north to Iceland. Limited north/south migrations probably occur, though little information is available. Feeds almost exclusively on krill.	Several hundred. Considered very rare in Mid-Atlantic area.
+*Humpback	Megaptera novaeangliae	Occurs in shallow coastal waters of the Mid-Atlantic during the spring. Present in the waters around Cape Cod from April to May. Fall migration to southern breeding grounds in the Caribbean may occur over deeper ocean waters. Feeds on euphasids and small fish.	2,000. Mid-Atlantic is a migratory area.
+*Right whale	Eubalaena glacialis	Found between shore and the 200 m contour. Present in the waters around Cape Cod from April and May. By June, most animals are north of Cape Cod in summer feeding grounds. The offshore southern migration occurs from mid-October to early January. Feeds exclusively on plankton by skimming at or below the water's surface.	A few hundred in entire North Atlantic (including Europe).

Table 7.3 Summary of cetacean species found in the Western North Atlantic Ocean. (continued)

dolphin	bredanensis	Found in warm temperate and tropical waters. Virginia is apparently the northern limit.	
+Bottlenose dolphin	Tursiops truncatus	Ranges from Florida through New England. Coastal in southen portion of range but north of North Carolina it begins to distribute offshore over the OCS. Probably winters south of Maryland. Eats fish and shrimp.	17,000
+Atlantic spotted dolphin	Stenella plagiodon	Warm temperate and tropical waters. Most abundant south of Cape Hatteras. Has been reported as far north as Massachusetts. Usually found from 5 miles offshore to the 200 m contour. Feeds primarily on squid, but also eats other fish.	No estimate.
+Striped dolphin	Stenella coeruleoalba	Relatively abundant along the continental slope from Georges Bank and Sable Island, south through the Caribbean and Gulf of Mexico.	No estimate.
+Saddleback dolphin (common dolphin)	Delphinus delohis	Pelagic, often found at the slope or beyond. Found along entire east coast. North of Cape Cod, the occurrence is apparently seasonal. Appears to follow schools of fish on which it preys.	30,000 Apparently common.
White-beaked dolphin	Lagenorhynchus albirostris	Generally an offshore species from Cape Cod northward. Cape Cod is apparently the southern boundary of its range where it is fairly common in April, May, and June. Feeds on squid, cod, herring, and capelin.	No estimate.
+Atlantic whitesided dolphin	Lagenorhynchus acutus	Ranges from nearshore to offshore. Generally from Cape Cod, or perhaps Hudson Canyon, northward.	No estimate.
+Whiteheaded grampus (Risso's) dolphin)	Grampus griseus	Pelagic, especially along continental slope. Found from Florida to Cape Cod and possibly Canada. Feeds on squid and fish.	No estimate.
False Killer whale	Pseudorca crassidens	Pelagic and nearshore. Ranges from Maryland south to Carribbean. Feeds on squid and large fish. Herds of up to at least 100 individuals reported.	No estimate.

Table 7.3 Summary of cetacean species found in the Western North Atlantic Ocean. (continued)

Common Name	Scientific Name	Distribution and Habitat	Population Estima
+Long fin pilot whale	Globicephala melaena	Pelagic (winter) and coastal (summer). Ranges from Greenland to Cape Hatteras. Feeds on squid.	No estimate. Frequently seen.
+Short fin pilot whale	Globicephala machrorhynchus	Pelagic and nearshore. Normal range is from Cape Hatteras south, although strays are reported from as far north as New Jersey. Feeds on squid and fish.	No estimate. Onl strays in norther waters.
Killer whale	Orcinus orca	Coastal and over the OCS ranging from Florida to the ice pack. Feeds on a wide variety of foods including squid, fish, turtles, seabirds, and mammals.	No estimate. More common in northern waters.
Harbor porpoise	Phocoena phocoena	Coastal and inshore. Normal southern limit of range is Long Island. Strays as far south as Cape Hatteras. Population concentrated north of Cape Cod. Eats mostly fish (herring, cod, mackerel) and squid.	No estimate. Very common north of Cape Cod and rare south of New Jerse
Beluga whale	Delphinapterus leucas	Shallow coastal waters and estuaries. Normal distribution is from the Gulf of St. Lawrence northward. Belugas from the St. Lawrence stock rarely stray to Cape Cod or Long Island during the warmer months.	Uncommon in New England waters.
+*Sperm whale	Physeter catodon	Pelagic. Common along the continental slope and seaward but rarely on the shelf. Ranges from the tropics to the Arctic but females, calves, and juveniles rarely migrate farther north than 40° to 42°N. There is a north-south migratory patterns but the Mid-Atlantic is always inhabited with sperm whales. Feeds on squid primarily along 1000 m contour.	North Atlantic population is estimated to be 22,000.
Pygmy sperm	Kogia breviceps	Seldom observed alive. Generally considered pelagic but the relatively high number of stranding incidents indicate it may be coastal also. Occurs from Canada to Florida. Feeds on squid, crab, shrimp.	No estimate.
Dwarf sperm whale	Kogia simus	Known only from strandings. Apparently a southern species - the northern-most record on the east coast is from Virginia. Little additional information known.	No estimate.

Table 7.3 Summary of cetacean species found in the Western North Atlantic Ocean. (continued)

Common Name	Scientific Name	Distribution and Habitat	Population Estimates
Goose-beaked whale	Ziphius cavirostris	Assumed to be a deepwater, pelagic species. Appears to be sparsely but widely distributed in non-polar latitudes. Most commonly stranded beaked whale on east coast.	No estimate.
North Atlantic bottlenosed whale	Hyperoodon ampullatus	Pelagic, usually found in water deeper than 1,450 m. Found from Rhode Island to the ice pack. Cape Cod is probably the southern extent of the wintering ground. Rare south of Canada. Feeds on squid.	No estimate.
True's beaked whale	Mesoplodon mirus	Possibly pelagic. Strandings occur from Nova Scotia to Florida. Little is known.	No estimate.
Antillean beaked whale	Mesoplodon europaeus	Possibly a deepwater species. Strandings are reported from Florida to New York. Little is known.	No estimate.
North Sea beaked whale	Mesoplodon bidens	Strandings reported from Nantucket and Newfoundland. Feeds on squid. Little is known.	No estimate.
Dense-beaked whale	Mesoplodon densirostris	Possibly most pelagic of the genus. Probably a warm-water species with northern limit at 45°N. Appears to be widely but sparsely distributed. Feeds on squid. Little is known.	No estimate.
LONG-SNOUTED DOLPHIN (SPINNER DOLPHIN)	STENELLA LONGIROSTRIS		

Source: BLM, FINAL EIS FOR LEASE SALE NO. 76, 1982

*Endangered Species

+ SIGHTINGS IN STUDY AREA REPORTED BY CETAP

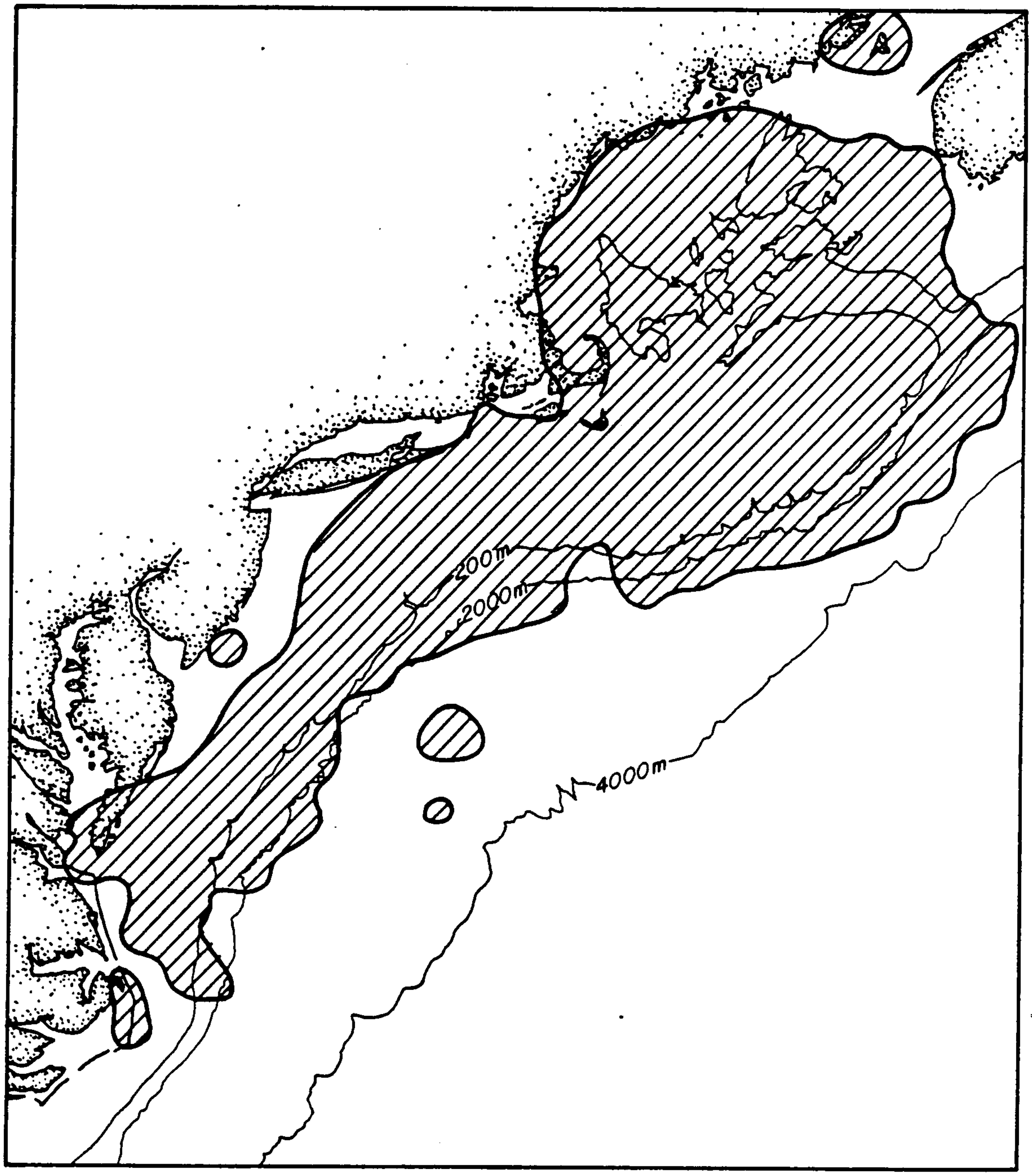


Figure 7.35. The distribution of baleen whales (from CETAP 1981).

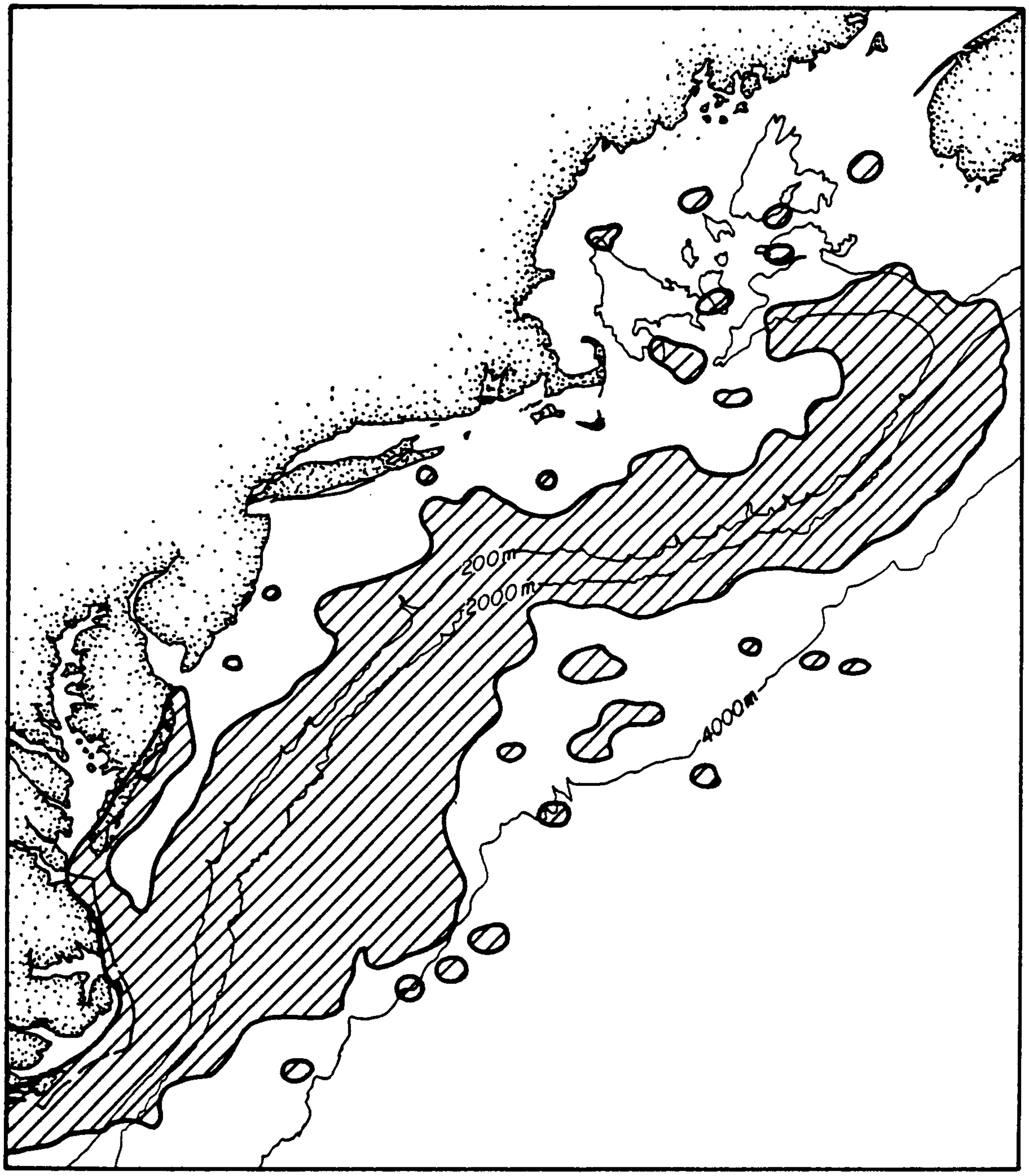


Figure 7.36. The distribution of Odontocete whales and dolphins (from CETAP 1981).

SPECIAL HABITATS

There are certain areas of the ocean bottom which, because of their unique characteristics as habitats for marine fauna, have been or may need to be considered in planning efforts for the management of the Atlantic continental margin. For the purposes here, two such habitats are considered--submarine canyons and colonies of deepwater corals.

Submarine Canyons

Recent actions by the states of New Jersey and Massachusetts (Hoyte, 1983) indicate the importance of submarine canyons in the overall planning for the study area. In both cases, the states, using the consistency provisions of the Coastal Zone Management Act, blocked lease sales for oil and gas by the Federal government because of the inclusion of canyon tracts in the lease sales. In each instance, the states wanted the tracts deleted because of the canyons' importance for fisheries (lobster for Massachusetts; tilefish for New Jersey).

Ongoing research by Lamont-Doherty Geological Observatory indicates the concerns of these two states may have some merit. Hecker et al. (1983), report the sightings of several species of either present or potential commerical value. Observations in Baltimore and Lydonia Canyons included sightings of lobster, shrimp (in association with coral colonies, e.g., *Paragorgia arborea*), several species of hake, flounder, tilefish and eels (Hecker et al., 1983, p. 348-363).

While presence of these and other commercial species has been established in the canyons and canyon heads, it would be premature to estimate the effect oil and gas development might have on these fish stocks. This area clearly needs additional research.

Deepwater Corals

Several deepwater coral species of the order *Scleractinia* (at least 14) have been identified in the study area (Cairns, 1981). Many occur as deep as 3,200 meters. Of the fourteen, thirteen are "ahermatypic", a term normally associated with non-reef-building species. Cairns (1981) reports that this is not always the case. There are some colonial deepwater ahermatypes which do create structures that are reeflike.

In addition to the scleractinia, approximately 75 other deepwater corals have been identified in or near the ACSAR area (See Table 7.4). The highest concentrations of these corals is to be found in waters between the 600 and 800 meter isobaths (Gulf of Mexico and South Atlantic Fishery Management Councils, 1982). Not much is known about the majority of deepwater corals. They are considered to be the most poorly understood corals in waters adjacent to the continental U.S. (Gulf of Mexico and South Atlantic Fishery Management Councils, 1982, p. 5-12).

Table 7.4 Deep Water Corals in the ACSAR Area.

	Gulf of Mexico	Straits of Florida	South Atlantic
Order STOLONIFERA			
Family Clavulariidae			
Clavularia modesta (Verrill)			X
Scleranthelia sp.		X	X
Order TELESTACEA			
Family Telestidae			
Telesto nelleae Bayer			X
Telestula sp.	X		X
Order ALCYONACEA			
Family Alcyoniidae			
Anthomastus agassizii Verrill			X
Anthomastus grandiflorus Verrill			X
Nidalia rigida Deichmann	X		
Bellonella sp.			X
Family Nephtheidae			
Pseudodrifa nigra Pourtales		X	X
Family Siponogorgiidae			
Siphonogorgia (=*Neospongodes*) *agassizi* (Deichmann)	X		
Order GORGONACEA			
Family Anthothelidae			
Anthothela grandiflora (Sars)			X
Anthothela tropicalis Bayer	X	X	X
Titanideum frauenfeldii (Kolliker)		X	X
Titanideum suberosum (E. & S.)			X
Family Paragorgiidae			
Paragorgia boschmai Bayer		X	
Paragorgia sp.		X	
Family Coralliidae			
**Corallium medea* Bayer		X	
**Corallium niobe* Bayer		X	
Family Acanthogorgiidae			
Acanthogorgia aspera Pourtales			X
Acanthogorgia schrammi (Duch. &			

Table 7.4 Deep Water Corals in the ACSAR Area. (continued)

	Gulf of Mexico	Straits of Florida	South Atlantic
Mich.)	X		
Family Paramuriceidae			
Paramuricea placomus (Linnaeus)			X
Paramuricea sp.	X	X	
Bebryce cinerea Deichmann		X	
Bebryce grandis Deichmann	X	X	
Bebryce parastellata Deichmann			X
Echinomuricea atlantica (Johnson)	X		
Muriceides sp.		X	
Placogorgia mirabilis Deichmann	X	X	
Placogorgia tenuis (Verrill)	X		
Placogorgia sp.		X	X
Caliacis nutans (Duch. & Mich.)	X	X	
Scleracis guadeloupensis (D. & M.)	X	X	
Swiftia casta (Verrill)	X	X	X
Swiftia koreni (Wright & Studer)		X	X
Swiftia pourtalesi Deichmann		X	
Swiftia exserterta (E. & S.)			X
Thesea nivea Deichmann		X	X
Thesea rugosa Deichmann	X		
Thesea solitaria (Pourtales)		X	
Trachymuricea kukenthali (Broch)	X		
Trachymuricea hirta (Pourtales)		X	
Villogorgia nigrescens Duch. & Mich.	X		
Family Plexauridae			
Eunicella albatrossi Stiasny			X
Eunicella modesta Verrill		X	X
Muriceopsis petila Bayer			X
Family Gorgoniidae			
Lophogorgia cardinalis Bayer			X
?Leptogorgia stheno (Bayer)	X	X	X
Family Ellisellidae			
Ellisella barbadensis (D. & M.)			X
Ellisella elongata (Pallas)	X	X	
Nicella guadalupensis (D. & M.)	X	X	
Riisea paniculata D. & M.	X		
Family Chrysogorgiidae			
Radicipes gracilis (Verrill)	X	X	X
*Chrysogorgia desbonni D. & M.		X	X
Chrysogorgia elegans Verrill	X		
Chrysogorgia fewkesi Verrill		X	X
Family Primnoidae			
*Callogorgia verticillata (Pallas)	X	X	
Callogorgia grimaldii Studer	X		
Plumarella aurea (Deichmann)		X	X
Plumarella goesi Aurivillus	X		
Plumarella pourtalesi (Verrill)	X	X	X

Table 7.4 Deep Water Corals in the ACSAR Area. (continued)

	Gulf of Mexico	Straits of Florida	South Atlantic
Thouarella aurea Deichmann		X	
Thouarella sp.		X	X
Calyptrophora trilepis (Pourtales)			X
**Narella pauciflora* Deichmann		X	
**Narella regularis* (D. & M.)		X	
**Narella versluysi* Hickson		X	
**Candidella imbricata* (Johnson)			X
Family Isididae			
**Keratoisis flexibilis* (Pourtales)	X	X	X
**Keratoisis ornata* Verrill		X	X
Acanella arbuscula Verrill	X		
**Acanella eburnea* (Pourtales)	X	X	X
**Lepidisis caryophyllia* Verrill		X	
?*Lepidisis longiflora* Verrill	X		
Chelidonisis aurantiaca Studer	X		
Primnoisis humilis Deichmann	X		
Order PENNATULACEA			
Family Kophobelemnidae			
Kophobelemnon sp.		X	X
Sclerobelemnon sp.		X	X
Family Anthoptilidae			
Anthoptilum murrayi Kolliker			X
Anthoptilum sp.	X		
Family Funiculinidae			
Funiculina quadranularis (Pallas)	X	X	X
Family Protoptilidae			
Protoptilum thompsoni Kolliker	X		
Family Scleroptilidae			
Scleroptilum sp.	X		X
Family Umbellulidae			
Umbellula guntheri Kolliker	X		
Umbellula lindahlii Kolliker	X		X
Umbellula eloisa Nutting	X		
Umbellula sp. 1 (sensu Giammona)	X		
Umbellula sp. 2 (sensu Giammona)	X		
Umbellula sp. 3 (sensu Giammona)	X		
Family Virgulariidae			
Virgularia sp.		X	
Acanthoptilum sp.	X	X	
Scytalium sp.		X	
Stylatula elegans (Deichmann)		X	X
Stylatula sp.	X	X	X
Family Pennatulidae			
Pennatula grandis Ehrenberg			X

Table 7.4 Deep Water Corals in the ACSAR Area. (continued)

	Gulf of Mexico	Straits of Florida	South Atlantic
Order SCLERACTINIA			
Family Pocillopridae			
Madracis myriaster (ME & H)	X	X	
Family Fungiidae			
Fungiacyathus pusillus (Pourtales)		X	
Fungiacyathus symmetricus (Pourtales)		X	
Fungiacyathus crispus (Pourtales)	X	X	
Family Oculinidae			
Madrepora oculata Linnaeus	X	X	X
Madrepora carolina (Pourtales)	X	X	X
Family Anthemiphylliidae			
Anthemiphyllia patera Pourtales			X
Family Caryophyllidae			
Caryophyllia polygona Pourtales		X	
Caryophyllia berteriana Duchassaing	X	X	
Caryophyllia cornuformis Pourtales	X	X	X
Caryophyllia ambrosia caribbeana Cairns	X	X	X
Caryophyllia parvula Cairns	X		
Concentrotheca laevigata (Pourtales)	X	X	X
Cyathoceras squiresi Cairns		X	X
Labyrinthocyathus facetus Cairns		X	X
Labyrinthocyathus langi Cairns		X	X
Oxysmilia rotundifolia (ME & H)	X		X
Trochocyathus rawsonii Pourtales	X	X	X
Tethocyathus cylindraceus (Pourtales)		X	
Tethocyathus variabilis Cairns		X	
Paracyathus pulchullus	X	X	X
Deltocyathus moseleyi Cairns			X
Deltocyathus calcar Pourtales	X	X	X
Deltocyathus italicus Michelotti	X	X	
Deltocyathus eccentricus Cairns	X	X	X
Deltocyathus pourtalesi Cairns		X	X
Stephanocyathus (*S.*) *diadema* (Moseley)	X	X	X
Stephanocyathus (*S.*) *paliferus* Cairns	X	X	X
Stephanocyathus (*S.*) *laevifundus* Cairns		X	X
Stephanocyathus (*O.*) *coronatus* (Poutales)	X	X	
Peponocyathus folliculus (Pourtales)		X	
Peponocyathus stimpsonii			

Table 7.4 Deep Water Corals in the ACSAR Area. (continued)

	Gulf of Mexico	Straits of Florida	South Atlantic
(Pourtales)	X	X	X
Desmophyllum cristagalli ME & Haime		X	X
Thalamophyllia gombergi Cairns		X	
Lophelia prolifera (Pallas)	X	X	X
Anomocora fecunda (Pourtales)	X		
Coenosmilia arbuscula Pourtales	X		
Dasmosmilia lymani (Pourtales)	X	X	X
Dasmosmilia variegata (Pourtales)	X	X	
Solenosmilia variabilis Duncan		X	X
Asterosmilia prolifera (Pourtales)	X	X	
Asterosmilia marchadi (Chevalier)			X
Phacelocyathus flos (Pourtales)	X		
Family Flabellidae			
Flabellum moseleyi Pourtales	X	X	X
Flabellum fragile Cairns	X	X	
Javania cailleti (D. & M.)	X	X	X
Polymyces fragilis (Pourtales)	X	X	X
Gardineria paradoxa (Pourtales)		X	
Family Guyniidae			
Guynia annulata Duncan	X		
Schizocyathus fissilis Pourtales	X		
Stenocyathus vermiformis (Pourtales)	X	X	X
Pourtalocyathus hispidus (Pourtales)		X	X
Family Dendrophylliidae			
Balanophyllia palifera Pourtales	X		
Dendrophyllia cornucopia Pourtales	X	X	
Dendrophyllia gaditana (Duncan)			X
Dendrophyllia alternata Pourtales	X	X	
Enallopsammia profunda (Pourtales)	X	X	X
Enallopsammia rostrata (Pourtales)			X
Thecopsammia socialis Pourtales		X	X
Bathypsammia tintinnabulim (Pourtales)	X	X	X
Bathypsammia fallosocialis Squires		X	X
Rhizopsammia manuelensis Chevalier	X	X	
Trochopsammia infundibulum Pourtales		X	

	Gulf of Mexico	Straits of Florida	South Atlantic
Order STYLASTERINA			
Family Stylasteridae			
Stylaster duchassaingi Pourtales		X	
Stylaster erubescens Pourtales	X	X	
*Stylaster filogranus Pourtales	X	?	
Stylaster gemmascens (Esper)			X
Allopora miniata Pourtales		X	
Cryptohelia peircei Pourtales		X	X
Stenohelia sp.			X
*Distichopora foliacea Pourtales		X	X
Distichopora sulcata Pourtales			X
Errina cochleata Pourtales		X	
Errina glabra Pourtales			X
Pliobothrus symmetricus Pourtales		X	
Order ANTIPATHARIA			
Antipathes americana D. & M.	X		
Antipathes hirta Gray		X	
Antipathes tanacetum (Pourtales)		X	X
Antipathes pennacea Pallas		X	
Antipathes tristis (Duchassaing)	X		
Antipathes picea Pourtales	X		
Parantipathes tetrasticha (Pourtales)		X	
Aphanipathes humilis (Pourtales)	X	X	
Aphanipathes thyroides (Pourtales)	X		
Aphanipathes felix (Pourtales)	X	X	
Aphanipathes abietina (Pourtales)	X		
*Leiopathes glaberrima (Esper)	X	X	
Bathypathes patula Brook	X		

Source: Appendix E, Fishery Management Plan: Final Environmental Impact Statement for Coral and Coral Reefs. Gulf of Mexico and South Atlantic Fishery Management Councils (Tampa, Florida and Charleston, South Carolina: 1982)

In addition to their habitat values, a very few deepwater corals also have a direct economic value. The skeletons of these species can be cut and polished for use in jewewlry manufacture. Within or bordering the ACSAR study area the following deepwater corals with economic potential have been identified: *Chrysogorgia desbonni*, *Candidella imbricata*, *Keratoisis flexibilis*, *Keratoisis ornata*, and *Distichpora foliacea* (see Table 7.4). As a result of distance from shore, deepwater corals are rather inconvenient to harvest. The use of deepwater submersibles, which is current practice in Hawaii for coral collection, could change this although submersibles have not been used for this purpose in the ACSAR area (Gulf of Mexico and South Atlantic Fishery Management Councils, 1982, p. 5-13). Any discussion of the economic potential of these resources must be speculative.

CHAPTER 8

SUGGESTIONS FOR FUTURE STUDIES

Despite the impressive number of research institutes and marine scientists that have studied and are studying the Atlantic continental slope and rise, and the very large number of scientific publications which have resulted from these studies, there are still areas which are poorly known and merit further study. In some areas, our knowledge is particularly sparse; for example, phytoplankton, neuston and radionuclides. Most subject areas are known in general terms, but require more detailed study particularly in terms of scale and rates. Some of these suggestions for future study relate to all six general topics covered in this report, others are specific to a single topic or subtopic.

GENERAL NEEDS

With few exceptions the oceanographic and environmental phenomena in the ACSAR area have been defined: we generally know what processes occur and where they occur. Three large areas, however, need to be addressed: meso- and micro-scale processes, fluxes, and more complete data utilization and interpretation.

Meso- and Micro-Scales

Two examples portray our state of knowledge in this realm: we know with relatively good accuracy the general bathymetry of the ACSAR area, but relatively little on horizontal scales finer than 100's to 1000's of meters. Similarly, finer scales in the distribution of plankton and neuston are not known. Many other examples could be given in which far more detailed study is required to define distributions and processes on finer scales. Such studies clearly represent a major path of future research.

Clearly it is impossible to examine the entire region in fine scale: what is critical is to define carefully those experiments which will help clarify general principles or important processes.

Furthermore, such studies require more sophisticated instrumentation than used in the past. Using again the example of bathymetry, meso- and micro-scales can be documented only by using accurate navigation, multi-beam echo-sounders and deep-towed vehicles. Deep-towed vehicles are only now becoming available to the scientific community; at present no research institute on the east coast has a multi-beamed echosounder, although one is being designed for the consortium of Lamont-Doherty, University of Rhode Island and the Woods Hole Oceanographic Institution. Similar documentation of other oceanographic phenomena would require a significant increase in stations, current meters, stations, etc. and/or greater sophistication in the measuring techniques.

Fluxes

The term "flux" refers to the rates of transport/transfer/reproduction of water, particles, chemical species or organisms. Where and when are various oceanographic components transported, and how? Specific examples will be given in a following section.

Data Utilization and Interpretation

In some instances, notably geology and meteorology, there exist large bodies of data which, if interpreted correctly, could aid immensely in our understanding of these systems. In some cases the data are in the hands of private companies (e.g., oil companies), but in others, the data are more accessible. For example, the data from the NOAA ocean buoys are available, but as of yet, not worked up. Similarly, the very large number of presently-available bottom samples (see Chapter 4) suggest that the need for (at least) more regional samples may be small. A final example is the apparent existence but present inavailability of fish landings from areas other than the northeast; integrating these data with the northeast figures would give us a more complete picture of the fishing industry off the eastern U.S.

Many other examples could be cited, but the main point to be remembered is that interpreting existing data sets can be much less expensive in terms of both time and money than acquiring new data sets through new field studies.

SPECIFIC STUDIES

Unfortunately, in many areas, available data are not sufficient to document thoroughly the required parameters. This is particularly true of documenting smaller scales or fluxes, as mentioned in the preceding paragraphs. Many of these are necessarily multi-disciplinary in approach. HEBBLE, PARFUX and Warm Core Rings are three recent projects in which marine scientists of various disciplines have worked cooperatively to investigate complex oceanographic problems.

Meteorology

Perhaps the greatest need in understanding offshore meteorology is obtaining a better picture of storms and their effect on air-sea interactions. As pointed out in Chapter 2, time-averaged data are not particularly valuable because of the large short-term fluctuations following passage of a storm. In this instance, better utilization of existing long-term weather buoy data would be valuable.

Physical Oceanography

Recent studies are pointing the way to better documentation of the physical environment in the ACSAR area. This includes increased current-meter moorings in the Gulf Stream, moorings on the slope and in canyons, and detailed studies in such diverse water masses as the Slope Water and in the Western Boundary Undercurrent. What is needed is a better documentation of processes at boundaries between water masses, reactions of oceanographic parameters to the passage of storms, and the relation between physical processes and the biological environment.

Geology

The most obvious need is the understanding of mesoand micro-scale morphology, which require bathymetric studies using far more sophisticated equipment and navigation than used previously. To understand downslope gravity movement, for instance, we need to delineate morphologic features on the scale of meters. Proposing sediment cores in relation to bottom morphology is particularly important, since zones of erosion and accumulation may lie directly adjacent to one another: a poor understanding of the morphology/shallow structure or poor navigation may result in sampling the wrong topographic features, with a corresponding wrong interpretation of the remote sensing records. Utilizing present seismic records with deep drilling logs, and integrating these data with finer-scale studies, could result in a better understanding of both the structural history and the neotectonics of the area.

Chemistry

In most instances, chemical studies in the ACSAR area have been purely descriptive. Few have focussed upon determining the processes governing distributions of various components, although proper documentation requires biological and sedimentological studies as well. Vertical flux of particulate matter, for example, has biological and geological implications as well as chemical. Similarly, remineralization rates are needed. These studies should be accompanied by a broad spectrum of ancillary measurements to characterize the sedimentary and biologic regimes. In sediment studies, for example, this would require defining redox conditions, major phase components (biogenic SiO_2, aluminosilicate, $CaCO_3$, organic carbon, leachable oxides of Fe and Mn), and mixing parameters using isotopes to elucidate benthic activity. Radionuclides have been studied less than other non-organic components, particularly with respect to influxes and removal rates.

In terms of hydrocarbons, there is a decided paucity of data for all types and molecular weight ranges in ACSAR. This includes dissolved, colloidal and particulate species, and is particularly true in terms of fluxes. Differentiating aeolian inputs of petroleum and pyrogenic hydrocarbons from exploration and production inputs may be particularly difficult, but needs to be undertaken.

Biology

In terms of phytoplankton, neuston and cetaceans, we know very little about the ACSAR area. The types of studies described for zooplankton in this report should be undertaken for other biologic components and in other oceanographic subenvironments. Problems such as patchiness, hydrographic variability, and net avoidance by large organisms are particularly important in interpreting data, and as such, should be studied in greater detail. Biological parameters should not be studied in isolation, but rather in concert with chemical, geological and physical oceanographic studies.

Biological sampling in the northwest Atlantic at depths greater than 1000 m is practically non-existent, either for plankton or fish. Clearly such studies are needed to understand the complete biological system in the ACSAR. Finally, there is a marked absence of coherent long-term time-series data with respect to population trends; such data should be integrated with flux/productivity studies in order to delineate the system.

Human Activities and Impact

Perhaps the most important aspect that needs further study is the impact of man and man's activities upon the ACSAR area. This includes sufficient understanding the environment to determine the impact of previous activities (such as old dump sites) and predict the effect of new activities (such as drilling, mineral exploration, waste disposal). Predicting where we can expect maximum human activity and identifying major hazards (e.g., storms, slumps, slides, faulting, etc.) and where they are likely to occur should facilitate this process. Many of these studies are presently in progress, and the next few years should see their results published and synthesized.

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