

ECOLOGY OF CERIANTHARIA (COELENTERATA, ANTHOZOA) OF THE NORTHWEST ATLANTIC FROM CAPE HATTERAS TO NOVA SCOTIA

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ABSTRACT

Ceriantharia, tube dwelling anthozoans, were collected in grab samples and documented by direct observations and photographs from research submersibles on the continental shelf and slope off the northeast United States coast (Cape Hatteras to Nova Scotia). Two species [*Cerianthus borealis* Verrill and *Ceriantheopsis americanus* (Agassiz)] were identified from grab samples and four species, probably including *C. borealis*, were observed from submersibles.

Ceriantharia distribution in relation to latitude, depth, temperature, and sediments was examined. They occurred throughout the study area, abundantly at depths of 0 to 500 m and less abundantly from 900 to 2,400 m. Ceriantharia habitats displayed an extreme range in bottom water temperature (summer maximum minus winter minimum) of from 8° to 16°C, and had every sediment type, except 100% gravel and coarse shifting sand. Geographic and bathymetric zonation is attributed primarily to temperature and secondarily to food supply and substrate type.

Ceriantharia distribution patterns, in submarine canyon heads at depths of <400 m, were determined from photographic transects run with submersibles; observed patchiness may be related to local differences in food supply, sediments, and microtopography.

The motile megafauna associated with Ceriantharia "forest" areas and the infauna and epifauna inhabiting ceriantharian tubes were evidence to show that tubes may enhance local species diversity and abundance in featureless soft-bottom areas by 1) attracting motile species seeking cover and 2), acting as a stable, elevated substrate for tubicolous and suspension feeding macrofauna.

The possibility of exploitation of energy reserves beneath the northwest Atlantic outer continental shelf and slope has prompted many new studies and the reexamination of past investigations for baseline information on the region's seafloor communities. Research submersible studies of potential oil lease tracts identified "indicator species" for assessing environmental changes owing to drilling activities. We considered Ceriantharia suitable for this purpose because they were abundant, passive suspension feeders, and nonmobile. Literature searches revealed that very little has been published on the Ceriantharia species occurring from Cape Hatteras to Nova Scotia. This is surprising in light of the group's significant contribution to the benthic biomass of the region (Wigley and Theroux 1981) and the important functional role [the effect a species has on the distribution and abundance of other residents (Sutherland 1978)] Ceriantharia may have in structuring communities inhabiting featureless soft-bottom substrate (O'Connor et al. 1977).

Woods Hole Laboratory, Northeast Fisheries Center (NEFC), National Marine Fisheries Service (NMFS), personnel have reported on the general composition and distribution of invertebrate fauna of the New England and Mid-Atlantic Bight continental shelf and slope (e.g., Wigley and Theroux 1981; Theroux and Wigley 1984³; Cooper et al., in press). Data on Ceriantharia were collected during ecological studies pertaining to various kinds of demersal fishes and benthic invertebrates: 1) a grab sample survey (Fig. 1) done from 1955 to 1969 (Shepard and Theroux 1983⁴), and 2) observations, photographs, and limited sample collections from research submersible studies. Dredge and trawl data were available (Shepard and Theroux fn. 4), but not analyzed since deep burrowing Ceriantharia (some-

³Theroux, R. B., and R. L. Wigley. 1984. Quantitative composition and distribution of macrobenthic invertebrate fauna of the New England Region. Unpubl. Manusc. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

⁴Shepard, A. N., and R. B. Theroux. 1983. Distribution of Cerianthids (Coelenterata, Anthozoa, Ceriantharia) on the U.S. East Coast Continental Margin, 1955-1969: Collection data and environmental measurements. Lab Ref. Doc. 83-12, 24 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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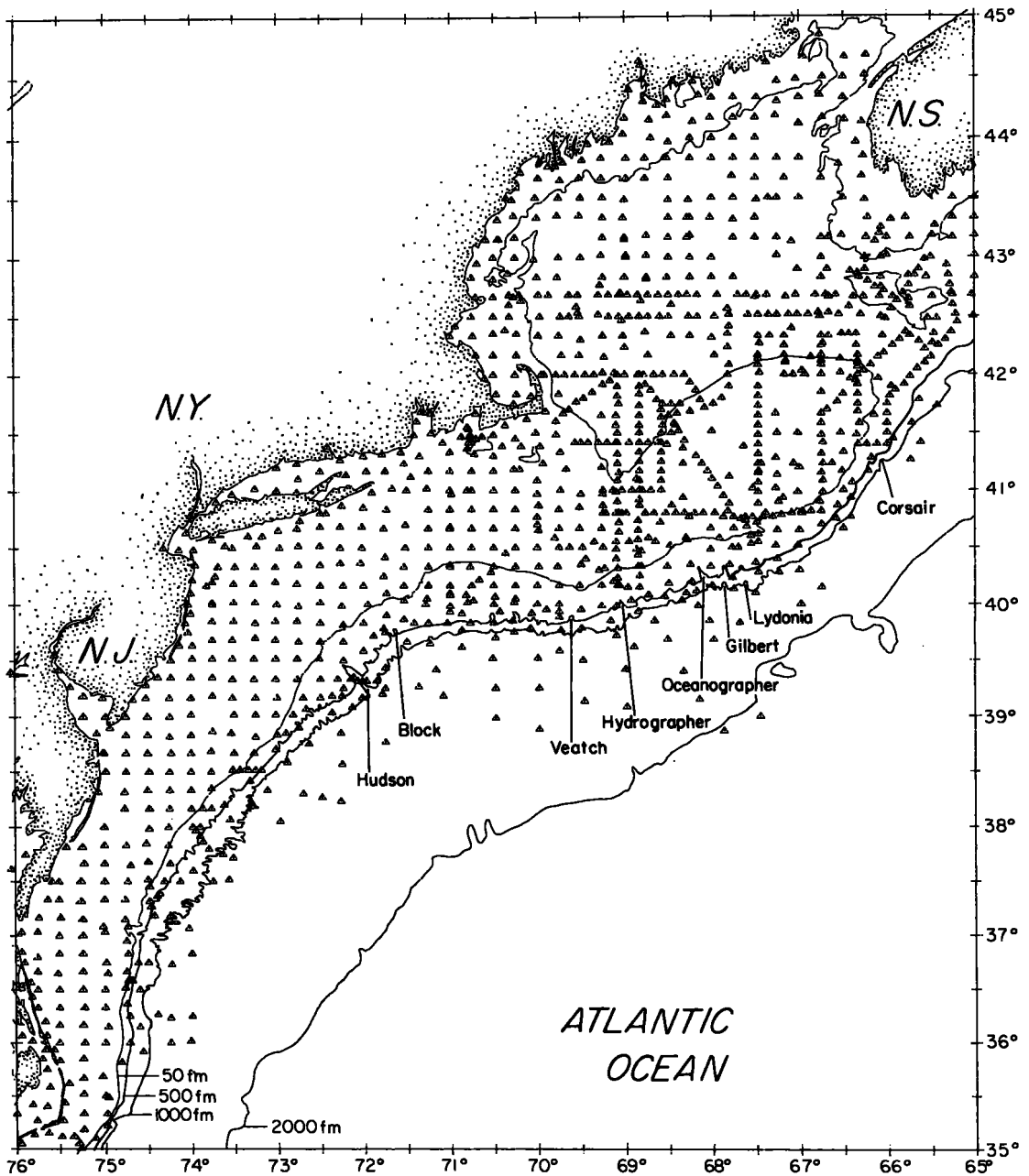


FIGURE 1.—Chart of the northwest Atlantic from lat. 35° to 45°N (Cape Hatteras to Nova Scotia) showing stations where grab samples of macrobenthic invertebrates were obtained, and the location of submarine canyons visited with research submersibles (1 fm = 1.83 m).

times more than 1 m; Sebens⁵) may be poorly sampled by dragged collection gear.

⁵K. P. Sebens, Maritime Studies Center, Northeastern University, Nahant, MA 01908, pers. commun. February 1985.

The objectives of this study are to describe 1) the Ceriantharia species encountered, 2) their general distribution in relation to latitude, depth, temperature, and sediments, 3) their local distribution pat-

terns, and 4) how they interact with other benthic species.

CERIANTHARIA

Ceriantharians represent a small, incompletely described order of Anthozoa. Species identification is difficult, and many species probably remain undescribed since twice as many larval forms as adults are known (Hartog 1977; Hartog⁶). Two northwest Atlantic species have been identified; *Cerianthus borealis* Verrill (1873) (see also Parker 1900; Kingsley 1904; Widersten 1976) and *Ceriantheopsis americanus* (Agassiz 1859) (see also Verrill 1864; McMurrich 1890; Parker 1900; Carlgren 1912; Field 1949; Widersten 1976). Two other unidentified species have been found on the continental slope (Grassle et al. 1975; Hecker et al. 1980; Valentine et al. 1980; Sebens in press). Table 1 summarizes the geographic and bathymetric ranges of the above four species.

Ceriantharia live in permanent semirigid tubes composed of a type of cnidae peculiar to the Order (called ptychocysts by Mariscal et al. 1977), mucus, and adhering substrate debris (Emig et al. 1972). The feltlike tube is usually deep purple in coloration and distinct enough to be used alone as evidence of Ceriantharia presence. New England bottom trawl fishermen are familiar with nets fouled with ceriantharian tubes (Rogers 1979). In contrast to other burrowing anemones which have a single whorl of tentacles, Ceriantharia have two distinct whorls (marginal and oral tentacles) which remain outside

the tube during feeding and rapidly retract into the tube when disturbed.

Ceriantharia are protandric hermaphrodites; gametes are produced in the mesenteries and fertilization is external. The larvae are pelagic and duration of the planktonic stage is variable (Carlgren 1912; Hyman 1940; Robson 1966; TRIGOM-PARC 1974). Adults are capable of oral disc regeneration by budding (Hyman 1940; Frey 1970). Asexual reproduction has been described for at least one species, *Aracnanthus oligopodus* (Cerfontaine 1909).

Ceriantharia are carnivorous passive suspension or impingement feeders (Emig et al. 1972; Caracciola and Steimle 1983). Digestion may begin in the tentacles, and larger particles are primarily taken up in the endoderm of sterile septa (Tiffon and Daireaux 1974). Fish species inhabiting the region, including cod, haddock, flounder, scup, and skate are known predators of whole juvenile Ceriantharia (Bowman and Michaels⁷) and may graze the tentacles of adults (TRIGOM-PARC 1974). Off the U.S. west coast, a nudibranch, *Dendronotus iris* Cooper, preys on adult Ceriantharia (Wobber 1970).

Previous documentation of Ceriantharia in the northwest Atlantic has come from grab samples (Sanders 1956; Wigley 1968; Pearce 1972; Pearce et al. 1976; Pearce et al. 1981; Reid et al. 1981; Wigley and Theroux 1981; Caracciola and Steimle 1983) and submersibles (Grassle et al. 1975; Rowe et al. 1975; Hecker et al. 1980; Valentine et al. 1980). However, no studies in the region report exclusively on ceriantharian ecology.

⁶J. C. den Hartog, Curator of Coelenterata, Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300 RA Leiden, Netherlands, pers. commun. March 1983.

⁷Bowman, R., and W. Michaels. 1983. Unpubl. data. Food Habits Program, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

TABLE 1.—Morphologic descriptions and geographic and bathymetric ranges of previously described Ceriantharia species inhabiting the study area.

Species	General morphologic description	Geographic range	Bathymetric range (m)
<i>Ceriantheopsis americanus</i>	see Verrill 1864	Cape Cod to Florida ¹	² 0- ³ 70
<i>Cerianthus borealis</i>	see Verrill 1873	Arctic to Cape Hatteras ¹	10- ⁴ 500
Unidentified species I ⁵	small (<5 cm contracted), dark brown tentacles, tube flush to seafloor. ⁵	Continental slope off New England	^{5,6,7} >1,000
Cerianthid A ⁸	larger than unidentified species I, uniformly dark tentacles, tube flush to seafloor ⁵	Continental slope off New England	^{5,8,7,8} >1,500

¹Parker 1900.

²Field 1949.

³Pearce et al. 1981.

⁴Miner 1950, p. 196.

⁵Sebens in press.

⁶Grassle et al. 1975.

⁷Hecker et al. 1980.

⁸Valentine et al. 1980.

METHODS

Grab sample methodology (gear description, sample processing, data reduction, bathymetry, temperature, and sediments) is reported in Wigley and Theroux (1981). A chi-square (χ^2) test, employing contingency tables (Richmond 1964), was used to assess ceriantharian occurrence at grab sample stations (relation to latitude, depth, bottom water temperature, and sediment type).

Table 2 lists the submersibles used and sampling gear employed by each. Quantitative data were obtained with externally mounted 35 mm camera-strobe systems. Qualitative ecological and behavioral information was acquired with 35 mm hand-held cameras, audio tapes, and video tapes made with a hand-held or externally mounted video camera. In situ faunal and sediment collections were made with the submersibles' manipulator arms. Only those dives performed to assess the distribution of megabenthos and associated habitat types were analyzed.

The externally mounted 35 mm camera systems used on *Nekton Gamma*, *Johnson-Sea-Link*, and *Alvin* were quantitatively calibrated, assessing 3.6 m², 7.0 m², and 15.0 m² of ocean floor per photographic frame, respectively (Bland et al. 1976; Cooper and Uzmann 1981^a).

Photographs were read on either a light table with a hand-held magnifying glass or motorized microfilm reader with a 36 × 36 cm screen and 15× magnification lens. Each photograph was time-annotated, thus allowing correlation with depth,

^aCooper, R. A., and J. R. Uzmann. 1981. Georges Bank and Submarine Canyon living resources and habitat baselines in oil and gas drilling areas. Northeast Monitoring Program Annual Report for FY 80. Unpubl. manusc., 34 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

TABLE 2.—Submersible, cruise year, and gear used for data collection. PC8 = *Perry Model C8*, NG = *Nekton Gamma*, AL = *Alvin*, and JSL = *Johnson-Sea-Link*.

Submersible/ year	Audio tapes	Video tapes	35 mm photographs		In situ collections of fauna/ substrate
			Hand-held	External	
PC8/1971	X	X			
NG/1973	X	X	X		
NG/1974	X	X	X		
NG/1979	X	X		X	
AL/1975	X	X		X	X
AL/1976	X	X			X
AL/1978	X	X			X
AL/1980	X	X		X	X
JSL/1980	X	X		X	X
JSL/1981	X	X		X	X

temperature, slope angle, substrate-habitat type, and current speed and direction documented on hand-held audio recorders during the dives.

RESULTS

Species Identification

Ceriantharia occurred at 229 of the 1,295 grab sample stations; 990 anemones were caught at 139 stations, whole tubes only at 29 stations, and tube fragments at 61 stations (Fig. 2). Two species, *Ceriantheopsis americanus* and *Cerianthus borealis*, were identified from grab samples (at four stations), the remaining anemones were identified only as Ceriantharia. The mean blotted wet weight of the 990 anemones was 5.0 g (95% C.L. = ±3.6); however, more than 90% weighed less than the mean.

Ceriantharia occurred at 82% of the submersible dive sites (Appendix Tables 1, 2) and at every major geographic feature visited (Fig. 2, Table 3). Submersible samples have not yet yielded anemones suitable for identification to the species level. Figure 3 shows three of the four species (Cerianthids A, B, C, and D) photographed from submersibles, and Table 3 classifies the species by morphological features apparent in photographs.

The minimum gross Ceriantharia size (height above seafloor or width of exposed tentacle crown and/or tube) visible in photographs was about 5 cm. It was not unusual to see large Cerianthid B or C tubes 20 cm above the seafloor. Based on laboratory examination of 61 anemones and a few specimens which were photographed in situ and then collected with the manipulator arm, a gross size of 5 cm corresponds to an anemone wet weight of about 16 g (3 times the mean weight of anemones captured with grab samplers).

Relation to Latitude

Ceriantharia occurrence at grab sample stations was not independent of latitude (χ^2 , $P < 0.05$). Occurrence was highest in three areas: off Chesapeake Bay (lat. 37° to 38°N); south of Cape Cod in the zone also including the southern half of Georges Bank (lat. 40° to 41°N); and on the shelf off Nova Scotia (lat. 44° to 45°N) (Fig. 4).

From submersibles, Cerianthid B was the only species seen on Georges Bank, or north of 41°N [Wilkinson Basin (Gulf of Maine) and Corsair Canyon]; Cerianthids A, C, and D were all seen in canyons or on the slope south of Georges Bank (Table 3).

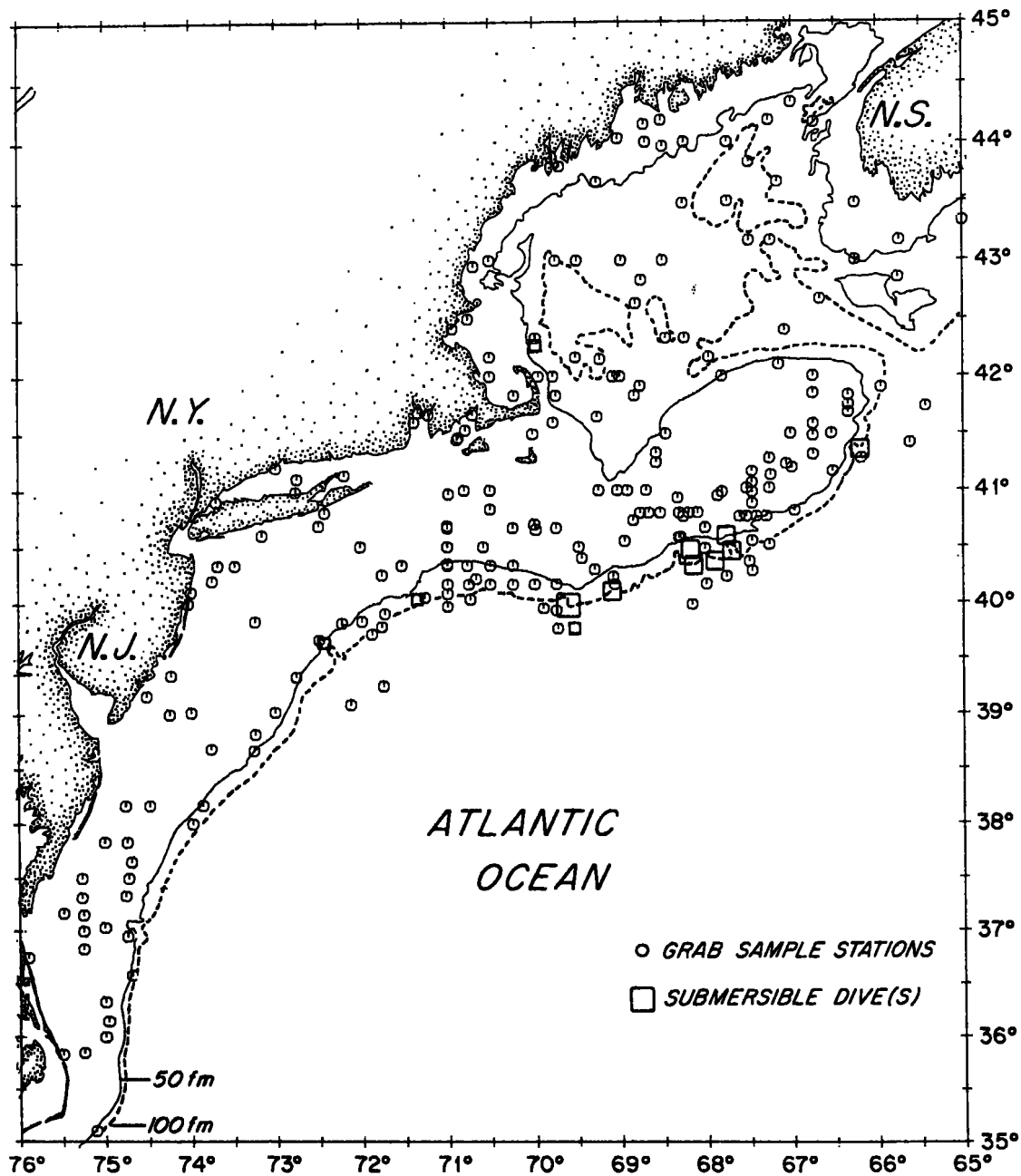


FIGURE 2.—Chart showing the submersible dive(s) sites and grab sample stations containing Ceriantaria. Symbols for submersible dive(s) sites often circumscribe more than one dive, since at this scale some dives were too close together to distinguish with separate symbols (1 fm = 1.83 m).

Relation to Bathymetry

In grab samples, Ceriantaria were found at depths from 6 to 2,329 m, but occurrence was not independent of depth (χ^2 , $P < 0.05$). Occurrence

was highest from 0 to 100 m, and no Ceriantaria were caught from 501 to 900 m (Fig. 4).

Submersible dive depth range was 80 to 1,930 m (Appendix Tables 1, 2). Ceriantids B, C, and D were seen within the 80-400 m range, no species were

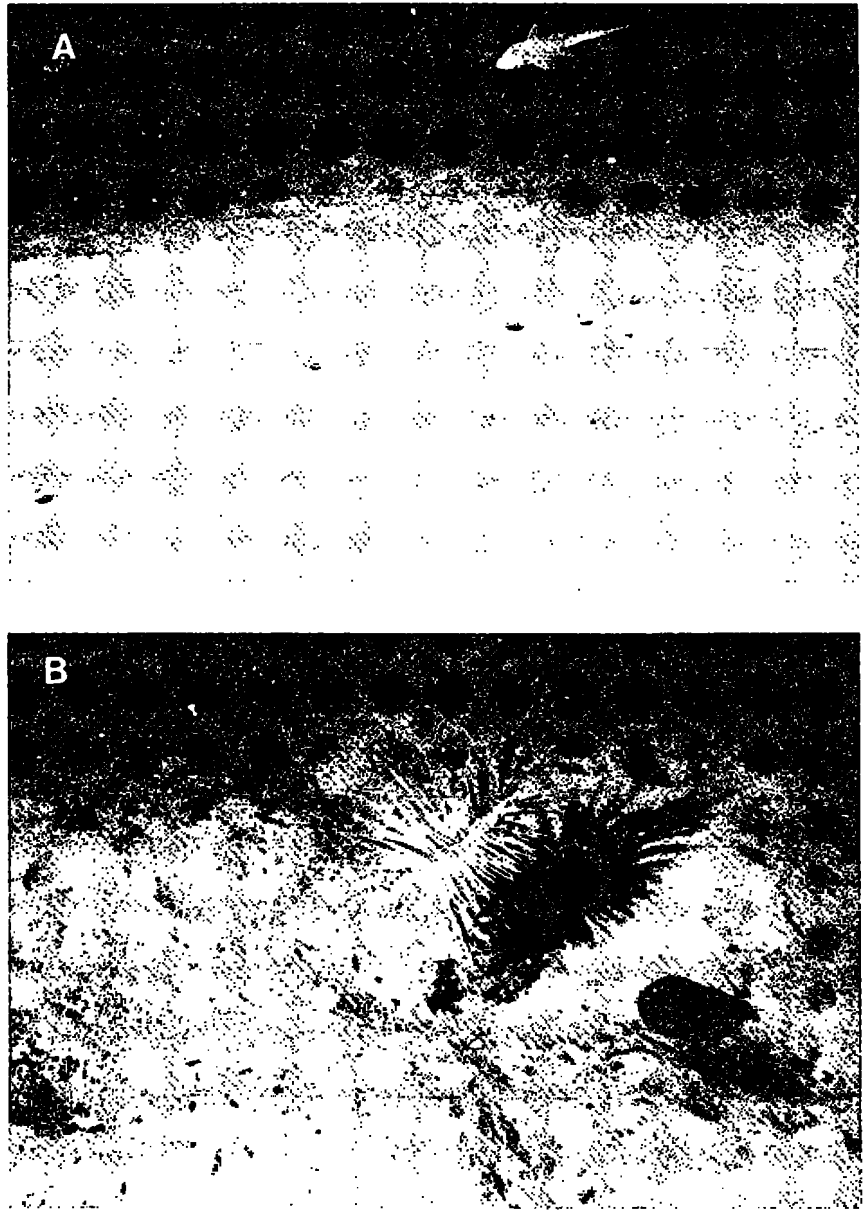


FIGURE 3.—A, B, C, - black and white prints of 35 mm Ektachrome transparencies from a hand-held camera; D - from externally mounted 35 mm brow camera. A. *Alvin* dive 838, axis of Oceanographer Canyon, 1,740 m: Cerianthid A (dark anemones); white brittle stars, *Ophiomusium* sp.; sea urchins, *Echinus affinis*; and a grenadier (Macrouridae) on a calcareous silt-sand substrate. B. *Nekton Gamma* 1974 dive 30, head of Lydonia Canyon, 300 m: Cerianthid B with a blackbelly rosefish, *Helicolenus dac-*



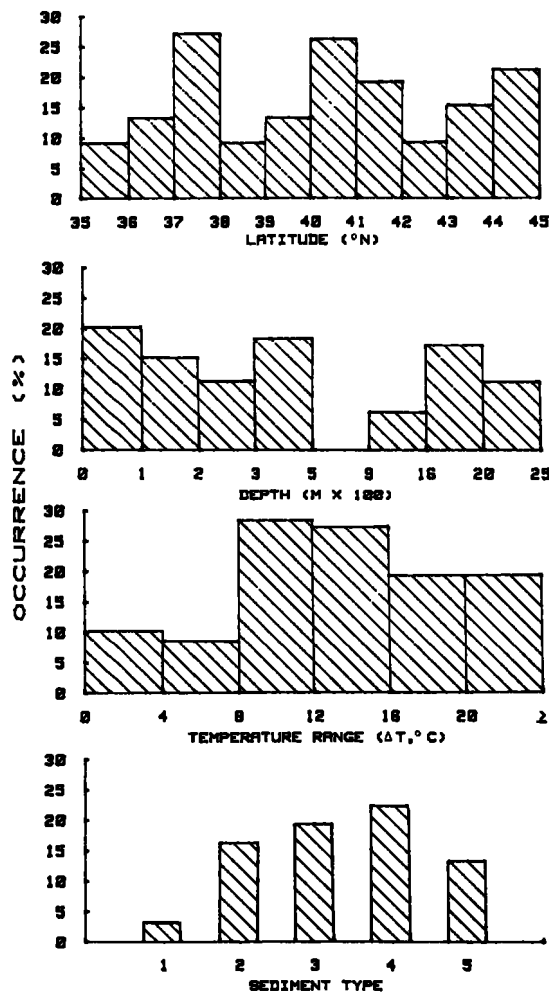
tylopterus, at its tube base, on silt-clay substrate. C. *Nekton Gamma* 1974 dive 30, 300 m: Cerianthid B with a portunid crab, *Bathynectes* sp., at its tube base on silt-clay substrate. D. *Nekton Gamma* 1979 dive 3, head of Block Canyon, 150 m: Cerianthid C with tube epifauna (sponges and colonial white anemones), and redfish, *Sebastes* sp., just visible near center of the photograph on a silt-clay substrate, current direction was from left to right.

TABLE 3.—Morphological features, apparent in photographs taken from submersibles, used to distinguish between four *Ceriantharia* species seen, and the geographic areas and bathymetric ranges in which they were found (cf. Fig. 3, Appendix Tables 1 and 2).

Species	Tube height in relation to seafloor		Characteristics of marginal tentacles			Geo-graphic areas ¹	Depth range (m x 100)
	Above	Flush	Length	Arrangement	Coloration		
A		X	unequal	multiplanar ²	dark red, black	6,8	16-19
B	X		unequal	multiplanar	pale purple, pink, tan, or brown	1-8, 10	1-4
C	X		equal	parabolic ²	white with purple marks	4,9	2-4
D		X	unequal	multiplanar	greenish yellow	10	2-3

¹ 1 - Wilkinson Basin, Gulf of Maine; 2 - Georges Bank; 3 - Corsair Canyon; 4 - Lydonia Canyon; 5 - Gilbert Canyon; 6 - Oceanographer Canyon; 7 - Hydrographer Canyon; 8 - Veatch Canyon; 9 - Block Canyon; 10 - Hudson Canyon.

² Used by Meyer (1980) to characterize feeding nets of other passive suspension feeders.



observed at depths from 400 to 1,600 m, and *Cerianthid* A was seen at depths from 1,600 to 1,930 m (Table 3).

Relation to Bottom Water Temperature

Temperature observations were sparse for grab sample stations, so, the extreme range of temperature (ΔT), a commonly used measure of climatic variability (MacArthur 1975), was used to compare temperature with *Ceriantharia* distribution; ΔT equals the difference between extreme annual recorded temperatures (summer high minus winter low), obtained from various published sources, and measurements, made by the NEFC. Site ranges were grouped for plotting: 0° to 3.9°C, 4° to 7.9°C, 8° to 11.9°C, 12° to 15.9°C, 16° to 19.9°C, and >19.9°C. Temperature range changed significantly with latitude and depth. Largest ΔT 's generally dominated shelf waters south of lat. 41°N, and in-shore waters (Fig. 5).

Ceriantharia occurrence at grab sample stations was not independent of temperature range (χ^2 , $P < 0.05$); occurrence was highest on the continental shelf where ΔT was from 8° to 15.9°C (Fig. 4).

All submersible dives were performed in July or August. Bottom water temperatures (external

FIGURE 4.—*Ceriantharia* occurrence (% of grab sample stations) in relation to latitude, depth, temperature range (ΔT = summer high minus winter low), and sediment type. Depth stratum size was determined by pooling, from shallow to deep, adjacent 100 m depth intervals until enough observations were available for a chi-square test. Sediment type codes are 1 - gravel; 2 - gravel/sand, silt, mud or clay; 3 - sand; 4 - silt/sand; 5 - silt/clay.

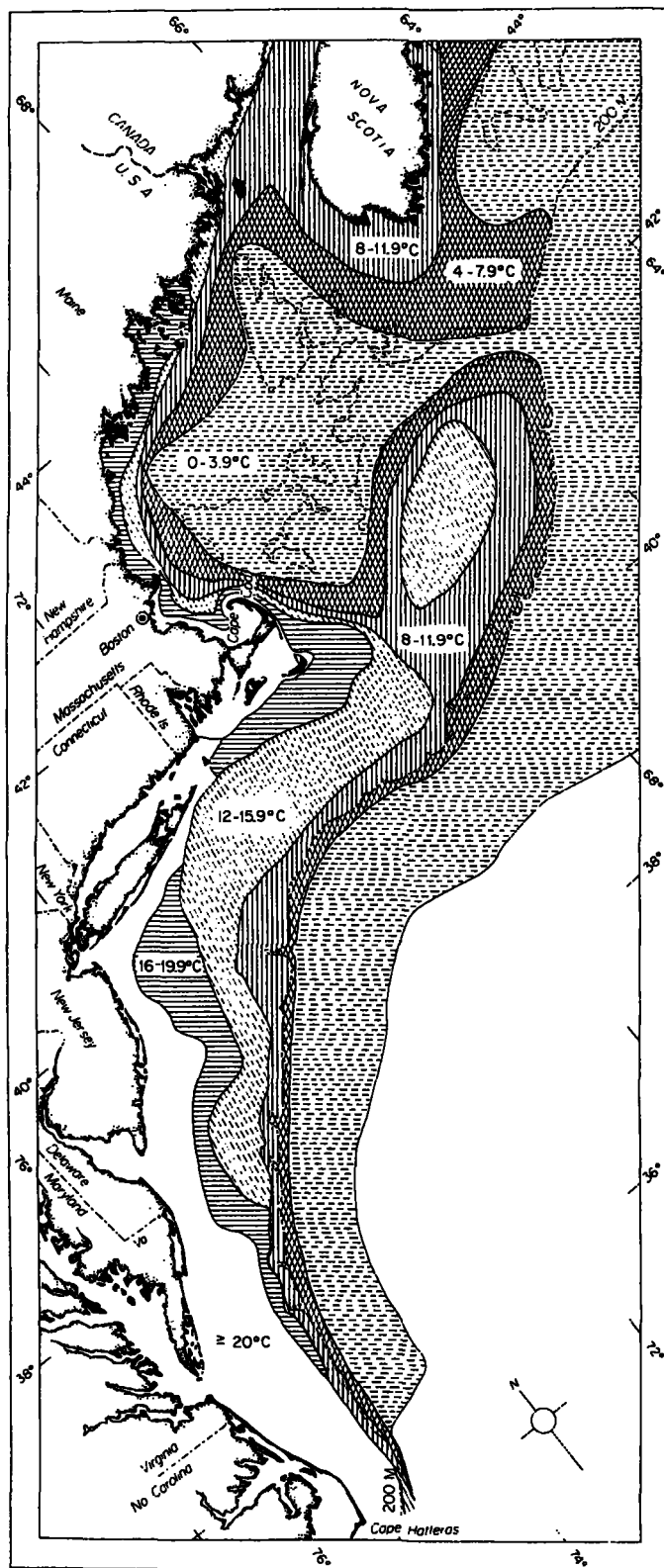


FIGURE 5.—Distribution of extreme range in bottom water temperature (summer maximum minus winter minimum) in the Middle Atlantic Bight (from Wigley and Theroux 1981) and New England region (Theroux and Wigley, text footnote 3).

thermometer observations) decreased with depth; temperatures ranged from 5° to 13°C at depths <500 m and declined gradually from 5°C at 500 m to 3.5°C at 1,900 m (Appendix Tables 1, 2). Depth-temperature profiles of three *Alvin* dives (Fig. 6) indicate depths of 500 to 600 m were a transition zone; deeper bottom water temperatures decreased little with depth, in comparison to shallower temperatures. Cerianthids B, C, and D were seen at temperatures of 5.3° to 13.0°C, and Cerianthid A was observed only in colder, deeper water, in the narrow range of 3.5° to 3.9°C (Appendix Tables 1, 2).

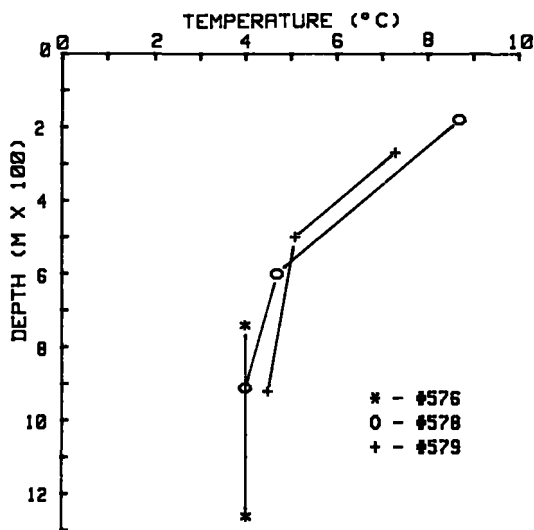


FIGURE 6.—Depth-temperature profiles constructed from observations (of external thermometers) made on the bottom during three *Alvin* dives in Veatch Canyon. Temperature stabilized at about 500-600 m.

Relation to Sediments

Ceriantharia occurrence at grab sample stations was not independent of sediment type (χ^2 , $P < 0.05$); they rarely inhabited 100% gravel sediments (Fig. 4). However, when stations with 100% gravel sediments were not included, occurrence was independent of sediment type (χ^2 , $P > 0.05$). Although occurrence in silt-clay sediments was lower than in other unconsolidated sediments (Fig. 4), this may be a result of the large proportion of silt-clay sediment stations at depths >500 m, where Ceriantharia were scarcer; if only silt-clay sediments from shallower than 500 m are analyzed, occurrence is more than 20%.

Photographic transect profiles of submersible

dives (Appendix Table 2, depths <400 m) provided information on Ceriantharia abundance with respect to substrate, depth, temperature, transect direction, and distance (Figure 7 shows one profile). Based on the number of sightings in various substrata (Appendix Tables 1, 2) and the transect profiles, about 70% of the Ceriantharia inhabited silt-sand and silt-clay sediments. However, they also commonly occurred in rarer gravelly substrata (less than about 50% gravel cover on sand or clay; only about 20% of the total seafloor viewed). They were not seen in coarse sand sediments (usually rippled and/or in dune formations).

The clay substrate observed from submersibles was actually a semiconsolidated mud (Cooper et al. in press); the term clay was used to differentiate it from sand substrates, but clay may only be a minor constituent.

Spatial Pattern

Ceriantharia density and biomass estimates from grab sample data were determined for comparison to other studies (e.g., Sanders 1956; Pearce et al. 1981; Reid et al. 1981; Caracciola and Steimle 1983). However, because no replicate sampling was done at over 90% of the stations, density and biomass were not analyzed further. For stations with anemones or whole tubes, mean density was 35.7 m^{-2} ($N = 168$, 95% C.L. = ± 12.1 , range = 1.7 to 1,370 m^{-2}). Mean station biomass (anemone blotted wet weight) was 48.6 $g m^{-2}$ ($N = 139$, 95% C.L. = ± 35.4).

On the quantitative submersible dives, Ceriantharia density ranged from 0 to 0.414 $m^{-2} dive^{-1}$ (Appendix Table 2). The maximum density in one photographic frame was 6.6 m^{-2} . The photographic transect profiles (Fig. 7) showed Ceriantharia populations shallower than 400 m were spatially aggregated. No quantitative information was available for the Cerianthid A populations seen in the axes of Oceanographer and Veatch Canyons.

The largest aggregation encountered (head of Lydonia Canyon, Fig. 7) was over 0.5 km wide and composed mostly of Cerianthid B, with some Cerianthid C individuals. The dives were run over a permanent station marker (37 khz pinger) positioned on a 14-15 m high knoll. Substrate atop the knoll was gravel-sand, near the base and surrounding the knoll was silt-sand. Approximately half of the Ceriantharia aggregation occupied the gravel-sand sediments. Ceriantharia were the dominant megafauna in the area, other common megafauna were galatheid crabs, *Munida iris* Milne-Edwards, and

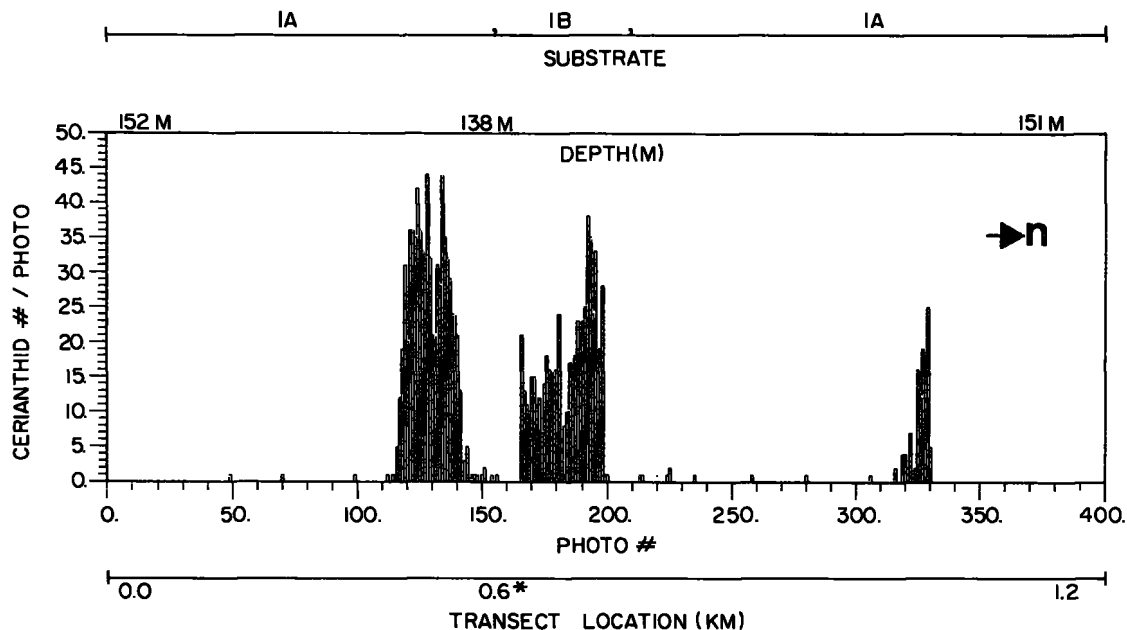


FIGURE 7.—One example, from 1980 *Johnson-Sea-Link* dives 15 and 16 in Lydonia Canyon, of the photograph-by-photograph transect profiles of Ceriantharia abundance constructed for quantitative submersible dives during which Ceriantharia density exceeded $0.1 \text{ m}^{-2} \text{ dive}^{-1}$, at depths of less than 400 m. Substrate codes: 1 - sand base, 1A - silt veneer, 1B - greater than 5% gravel cover. A permanent station marker (37 khz pinger) was located at 0.6 km into the transect, as denoted by the asterisk.

asteroids on gravel-sand, and shell-less hermit crabs, *Catapagurus* sp., on silt-sand. Galatheids were also observed on silt-sand sediments, often near ceriantharian tubes. A qualitative observation made on several submersible dives was that Ceriantharia "forests" (aggregations) were often associated with rises in seafloor topography.

Functional Role

Figure 8 (data from 1979 *Nekton Gamma* dive #3 in Block Canyon) shows Cerianthid C frequency of occurrence and number of associated species (diversity) plotted by photographic frame. The substrate throughout the dive was a low-relief silt-clay, and

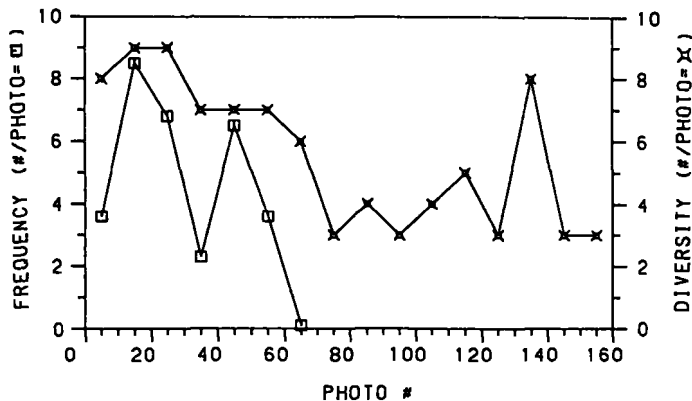


FIGURE 8.—Cerianthid C abundance and diversity (number of species) of associated fauna along a 1.0 km photographic transect from 1979 *Nekton Gamma* dive #3. Each data point represents the sum of 5 adjacent photographic frames: species diversity increased significantly in areas with Ceriantharia (Mann-Whitney test, $P < 0.01$).

the depth and temperature ranges were 137 to 183 m, and 13.0° to 10.7°C. Mean number of species was significantly higher in photographs with Ceriantharia (Mann-Whitney test, $P < 0.01$): Three groups of epifauna (hydroids, sponges, and small white anemones; Fig. 3D) were attached to Ceriantharia tubes only and not found on the surrounding substrate. Also, blackbelly rosefish, *Helicolenus dactylopterus* (De La Roche) (Fig. 3B), and redfish, *Sebastes* sp. (Fig. 3D), abundances were higher in the Cerianthid C patch (0.40/frame and 0.18/frame, respectively) than in the adjacent area (0.03/frame and 0.00/frame); about half of the fish were nestled at tube bases.

At other dive locations, motile megafaunal species often seen nestled near tubes included portunid crabs (*Bathymectes* sp.) (Fig. 3C); jonah crabs, *Cancer* sp.; pandalid shrimps, *Pandalus* sp.; American lobsters, *Homarus americanus* Milne-Edwards; hakes, *Urophycis* spp.; and greeneyes *Chlorophthalmus agassizii* Bonaparte.

Two Cerianthid B tubes (50 m apart) and adjacent sediments were collected with the grab sampler of the submersible *Johnson-Sea-Link*, in the head of Oceanographer Canyon at a depth of 293 m. The tubes were separated from the adjacent sediments immediately after the submersible surfaced. The volume of each tube was less than the volume of adjacent sediments (80% fine sand, <0.5 mm; 10% coarse sand; 10% silt) (Appendix Table 3). After preservation and staining, the macrofauna (>0.5 mm) were identified for each sample (Appendix Table 3): Polychaetes were dominant and the three most abundant polychaete species inhabiting the Ceriantharia tubes were absent or scarce in the adjacent sediments; *Polycirrus eximius* (Leily) (a tentacle feeder which sweeps the water and substratum for food), *Marpysa* sp. (a jawed omnivore), and a filter-feeder, *Potamilla neglecta* (Sars) (Fauchald 1977; Fauchald and Jumars 1979).

DISCUSSION

Collection Gear

Gear differences largely account for the differences in Ceriantharia size and density estimates from grab samples versus photographs. Due to limitations in resolution, photographs provide valid data only on larger epifauna (Emery et al. 1965; Barham et al. 1967; Wigley and Emery 1967). However, since the estimated depth of penetration of a 0.1 m² Smith-McIntyre grab sampler, the gear used most frequently in this study, is only 3 to 5 cm in

unconsolidated substrates (Smith and McIntyre 1954), and large ceriantharian tubes often extend much deeper than 5 cm below the seafloor (Sebens fn. 5), making them difficult to dislodge, if the primary objective is to sample large individuals and document the associations between tubes and other fauna, then photographs and direct observations are more useful than grab samples.

Species Identification

Ceriantheopsis americanus and *Cerianthus borealis*, identified from grab samples, occurred within the geographic and bathymetric ranges noted previously for these species (Table 1). Unfortunately, many Ceriantharia samples were discarded, and none of the available samples from depths greater than 500 m contained anemones for taxonomic identification.

The morphological features used to distinguish between the four species seen from submersibles (Table 3) may not individually be reliable; tentacle coloration may vary noticeably within a species (Arai 1971; Uchida 1979). However, taken together, we feel the features were consistent enough to indicate we saw four species of adult Ceriantharia: *C. borealis* (probably Cerianthid B), two unidentified species (Cerianthids C and D) from depths shallower than about 500 m, and another unidentified species (Cerianthid A) living deeper down the continental slope.

The conclusion that Cerianthid B is *C. borealis* is based on the similarities between our descriptions of Cerianthid B morphology and distribution (Table 3), and information from other studies on *C. borealis* (Table 1; Gosner 1979). The only other previously identified inhabitant of the study area, *C. americanus*, was probably not encountered on our submersible dives; the deepest record found for *C. americanus* was about 70 m (Pearce et al. 1981), whereas our shallowest submersible dive was to a depth of 80 m.

Sebens (in press) described two unidentified Ceriantharia species which occur at depths >1,000 m in the Northwest Atlantic: Unidentified Species II (seen at depths >1,500 m) resembles Cerianthid A (Table 3, Fig. 3A), Cerianthid A in Valentine et al. (1980), and a photograph of unidentified Ceriantharia taken by Grassle et al. (1975) at depths of 1,550 to 1,830 m just south of New England. The distinction Sebens (in press) makes between Unidentified Species I (seen at depths of >1,000 m) and Unidentified Species II (Cerianthid A) is that Species II is smaller (Table 1). Grassle et al. (1975) and

Hecker et al. (1980) also reported seeing small unidentified Ceriantharia at about 1,300 and 1,000 m, respectively. We saw (from submersibles) no Ceriantharia from 1,000 to 1,600 m for comparison.

In addition to the six documented species above, other Ceriantharia sighted in or near the region include two possible species photographed by Hecker⁹: one at depths of 1,800 to 2,800 m (from Lydonia Canyon to Cape Lookout, NC), which resembles a stout black Cerianthid B, and another resembling Cerianthid A (except its tube extends above the seafloor) at depths of 500 to 1,000 m off Cape Hatteras. Rowe and Menzies (1969) photographed Ceriantharia on the continental slope (at depths of 400 to 3,000 m) south of Cape Hatteras (about lat. 34°N) which they guessed to be *Ceriantheomorpha brasiliensis* Carlgren. However, they presented no photographs for comparison and collected no voucher specimens. The *C. brasiliensis* specimens identified by Carlgren (1931) were from Brazil, South America, and its resemblance to other slope species is uncertain. Submersible dive time devoted to in situ documentation and collection of specimens is obviously needed in order to identify the deep-water species¹⁰.

Relation to Latitude

North of Cape Cod and Georges Bank (lat. 42° to 44°N) the continental shelf is dominated by the Gulf of Maine, a feature unlike the rest of the shelf in the region because of its topographic irregularity and because it reaches depths of more than 100 m closer to shore. The lack of tidal mixing below 100 m over much of the gulf, and the fact that the principal source of its bottom water is thermally stable continental slope water introduced through the Northeast Channel, results in water temperature stratification which keeps the gulf bottom water temperatures virtually constant throughout the year (TRIGOM-PARC 1974; Rowe et al. 1975; Ingham et al. 1982, p. 43). The narrow extreme range of bottom water temperature (ΔT) dominant from lat. 42° to 43°N (Fig. 5) may account for low Ceriantharia occurrence at grab sample stations there (Fig. 4), while peaks in occurrence are evident at lat. 40° to 41°N (shelf just south of Cape Cod, including southern Georges Bank), and from 44° to 45°N (shelf off

Nova Scotia) may be associated with more favorable intermediate temperature ranges which prevail there (8° to 15.9°C). High Ceriantharia occurrence at grab sample stations between 37° to 38°N is in part due to high occurrence at stations in the lower half of Chesapeake Bay; occurrence was 56% at nine Bay Stations and 23% at 52 shelf/slope stations. However, our data is too sparse and inconclusive to make a bay versus non-bay comparison, or explain the high occurrence at shelf stations in this area.

According to Gosner (1971), the continental margin from Cape Hatteras to Nova Scotia is divided into two faunal provinces with respect to benthic invertebrates: a Boreal (cold-temperate) province north of Cape Cod, and a Virginian (warm-temperate) province of Cape Cod, MA. Theroux (in press) considers the situation to be more complex and to depend on the species considered, but agrees that Cape Cod and Georges Bank are the beginning of a rapid transition from cold to warm temperate fauna, and suggests that the transition is associated with Georges Bank and Nantucket Shoals thermal fronts (Fig. 5; Ingham et al. 1982, p. 40-41).

Using Gosner's (1971) faunal province descriptions, our submersible data indicate that, in addition to *C. americanus*, at least two other warm-temperate species inhabit the northwest Atlantic continental shelf (Cerianthids C and D). The only cold-temperate shelf species, Cerianthid B (probably *C. borealis*) ranges south to Cape Hatteras (Tables 1, 3). The last species we saw (Cerianthid A) is bathyal.

Relation to Bathymetry

Bathymetric zonation of benthic fauna has been previously described for the continental shelf-slope region of the northwest Atlantic (Wigley and Emery 1967; Rowe and Menzies 1969; Sanders and Hessler 1969; Rowe 1972; Grassle et al. 1975; Haedrich et al. 1975, 1980; Hecker et al. 1980; Valentine et al. 1980; Wigley and Theroux 1981). Rowe et al. (1982) cautioned, "'zones' that previous investigations have described apparently are a function both of the animal groups studied and distribution of samples with depth". Thus, our discussion of Ceriantharia zonation is limited to depths <2,000 m, since below that depth there were no submersible data to support the grab sample data.

Ceriantharia distribution, as determined from the grab sample data (Fig. 4), our submersible observations (Table 3), and data from other investigations (Table 1) imply boundaries (defined here as depths characterized by distinct changes in the benthic com-

⁹B. Hecker, Lamont-Doherty Geological Observatory, Columbia University, Palisades, NY 10964, pers. commun. October 1984.

¹⁰For all photographed, but unidentified slope species, we know of only one voucher specimen (of Unidentified Species I), presently located at the Harvard Museum of Comparative Zoology, Cambridge, MA.

munity's species composition) to Ceriantharia distribution exist at about 500, 900, and 1,600 m.

Our submersible data indicate that shelf species were confined to depths of less than about 400 m, and the bathyal species (Cerianthid A) was seen between 1,600 and 2,000 m. Published reports indicate another unidentified species lives deeper than about 1,000 m (Grassle et al. 1975; Hecker et al. 1980; Sebens in press). Similar depth zonation of slope fauna inhabiting the study area have been reported for isopods (Menzies et al. 1973), demersal fishes (Musick¹¹), and megafauna captured in trawls (Haedrich et al. 1980). Some environmental factors, suggested as causes for observed distributions, are temperature, sedimentation rates, and substrate types (summarized by Haedrich et al. 1975, 1980).

The depth interval between about 400 and 600 m on the continental slope south of New England is a temperature transition zone; shallower bottom waters experience larger seasonal temperature variations than stable deeper waters (Sanders and Hessler 1969; Haedrich et al. 1975). Depth-temperature profiles (Fig. 6) made on *Alvin* dives in Veatch Canyon showed larger depth related temperature variations also occurred shallower than 500 to 600 m. The shelf species (Cerianthids B, C, and D) may not be able to tolerate and/or thrive in the cold stable conditions below 500 m.

The Cerianthid A population, we saw deeper than 1,600 m in the axis of Oceanographer Canyon, inhabited sediments high in biogenic carbonates; canyon axes may act as settling basins for suspended matter being funneled down canyon (Valentine et al. 1980). Rowe and Menzies (1969) attributed increases in suspension-feeder concentration, in photographs from the upper slope (200-800 m) and at the slope base (3,000 m) off North Carolina, to increased detritus accumulation resulting from downslope movement and concentration by the prevailing bottom currents. Haedrich et al. (1980) stated, in reference to the depth zonation of megabenthic fauna on the slope off southern New England, that "zonation must result to some degree from varying strategies that promote success along a food resource gradient".

Haedrich et al. (1975) suggested boundaries to zones of larger epifauna, at about 400 and 1,000 m

on the continental slope south of New England, result from physical changes in the slope environment. MacIlvaine (1973, p. 30-70) reported on the physical environment in the same area (sediment type, suspended sediments, and slope gradient). The zone between 400 and 1,000 m consists largely of homogeneous silt-sand substrate, near-bottom suspended sediments at 520 m were 50 to 60 $\mu\text{g/L}$ (about 25% organics), and the slope gradient is about 1.4° . Deeper than about 1,000 m there are more variable sediment features (stiff clayey silt sediments which are smooth or hummocky, talus slopes, and rock outcrops), suspended sediments were 20 $\mu\text{g/L}$ (about 45% organics) at 1,000 m and 80 $\mu\text{g/L}$ (about 80% organics) at 1,670 m, and the slope gradient is steeper (7.6°).

Suspension feeders rely on current velocity and nutrient load for their food supply. Substrate variability deeper than 1,000 m may enhance Ceriantharia occurrence down to 2,000 m: Features such as hummocks may act as perches for suspension feeders, placing them up higher where current is swifter and their food supply is replenished more rapidly (Hughes 1975; Dyer 1980; Sebens 1984). Higher suspended sediments and percentage of organics may further enhance Ceriantharia occurrence below 1,600 m, as compared with 1,000 or 520 m. The lesser slope gradient between 400 and 1,000 m probably results in lower near bottom current velocities; near the shelf-slope break in Oceanographer Canyon, bottom currents are swifter at 105 to 300 m than at 650 m, due primarily to a difference in slope gradient (Valentine in press). Thus, increased slope gradient may enhance Ceriantharia occurrence below 1,000 m.

Other mechanisms may affect ceriantharian depth zonation such as the direct effects of pressure (Siebenallar and Somero 1978), or predators (Paine 1966; Rex 1976); however, data were not available to evaluate these factors.

Submarine canyons received particular attention during submersible dive activities because of the potential entrainment of discharges from oil exploration activities into productive canyon environments (Cooper and Uzman fn. 8). Bathymetric zonation of slope fauna may be altered and/or species abundance enhanced by submarine canyons (Rowe 1971; Haedrich et al. 1975). The conduitlike nature and substrate heterogeneity of canyons have both been implied as explanations for observed faunal enrichment in canyons as opposed to adjacent noncanyon slope areas (Rowe and Menzies 1969; Rowe 1971, 1972; Haedrich et al. 1975; Hecker et al. 1980; Valentine et al. 1980; Rowe et al. 1982). Although

¹¹Musick, J. A. 1976. Community structure of fishes on the continental slope and rise off the Middle Atlantic Coast of the U.S. Manuscript presented at Joint Oceanographic Assembly, Edinburgh, September. (Copies available from: J. A. Musick, Virginia Institute of Marine Science, Gloucester Point, VA 23062, USA).

we had no adjacent slope dives to compare with the canyon dives, Ceriantharia were common in canyons and have been suggested to be canyon "indicator" species (Rowe 1972). In the future, we hope a canyon-slope comparison of Ceriantharia species' diversity and abundance will be made.

Relation to Bottom Water Temperature

Wigley and Theroux (1981) found that total macrofaunal density in the Middle Atlantic Bight generally increased directly with increasing temperature range (ΔT). Ceriantharia occurrence at grab sample stations followed this trend until ΔT reached 15.9°C, after which it decreased (Fig. 4). Why an intermediate temperature range may be favorable to Ceriantharia is unknown. Wide ranges might entail harmful extremes of temperature, while narrower ones may be too constant at an unfavorable level, or larval stages may benefit from some degree of fluctuation for maximal development (Andrewartha and Birch 1954, p. 129-205). Information on how temperature affects ceriantharian metabolism, activity patterns, and development is lacking.

Marine organism distributions are largely controlled by temperature (Hutchins 1947; Crisp 1965; Gosner 1971). The most obvious effect of temperature on invertebrate distributions is exclusion of species from areas with unsuitable thermal regimes (Kinne 1970). Submersible data on ceriantharian geographic and bathymetric distribution demonstrate allopatric speciation which we believe is primarily a response to temperature.

Relation to Sediments

The presence of silt is characteristic of depositional areas which may be favorable to suspension feeders (Rowe and Menzies 1969). Wigley (1968) described Ceriantharia as common inhabitants of silty-sand sediments on Georges Bank. Through resuspension, surficial deposits are potential food for Ceriantharia (Rhoads 1974). In addition to low deposition, substrate instability may account for the scarcity of Ceriantharia in 100% gravel and rippled coarse sand substrate. Shifting substrates, such as the 100% gravel sediments at grab sample stations or the rippled sand dunes observed from submersibles, may harm suspension feeders through clogging of feeding apparatus, or the burial of larvae (Sanders 1956; Ross 1968; Rhoads and Young 1970; Rhoads 1974).

However, Ceriantharia were generally cosmopolitan with respect to substrate (Fig. 4; Appendix

Tables 1, 2). They are well adapted to withstand strong currents, sediment movement, and extreme deposition of fine material because their tubes provide firm anchorage (Frey 1970) and protection against clogging or burial (Pearce 1972). Pearce et al. (1976) found Ceriantharia were dominant macrofauna in fine carbon-rich sediments stressful to other benthic species, near New York Bight sewage sludge disposal sites.

Just as 100% gravel substrate is unfavorable for burrowing, a gravel veneer might also be expected to limit space available for burrowing. However, on submersible dives, Ceriantharia were frequently seen in gravel-covered areas (less than about 50% gravel cover). These deposits, probably Pleistocene ice-rafted glacial debris, are exposed in areas which usually experience higher currents than adjacent areas (Valentine et al. 1980; Valentine in press), a favorable consideration for suspension feeders.

Spatial Pattern

Local conditions of food supply, substrate, or microtopography, may enhance Ceriantharia aggregation (Fig. 7). Local differences in food supply may allow Ceriantharia to survive in aggregations. Grassle et al. (1975) observed that strongly clumped suspension-feeders were able to maintain aggregations because their food supply was continually renewed. Unusually high Ceriantharia abundances near a sewage sludge/dredge spoil disposal area may have occurred owing to the increased amounts of organic matter (Pearce et al. 1976).

Grassle et al. (1975) found Ceriantharia, similar to Cerianthid A, more randomly distributed on the continental slope, south of Cape Cod (depth of 1,465 to 1,830 m, homogeneous sandy silt-clay substrate). In comparison, substrata in canyon heads where aggregations were observed from submersibles are heterogeneous (Hecker et al. 1980; Valentine et al. 1980). Our grab samples showed the same contrast between heterogeneous substrata shallower than 500 m and homogeneous silt-sands and clays down-slope (Shepard and Theroux fn. 4). Since invertebrates are capable of substrate selectivity (Thorson 1966; Gray 1974), a variable substrate may be characterized by patchy inhabitant distributions (Hecker et al. 1980).

The Cerianthid B aggregation in Lydonia Canyon (Fig. 7), located on a knoll, may benefit from elevated positioning and swifter currents (Hughes 1975; Sebens 1984), thus aggregations may also form in response to local changes in surface elevation.

Functional Role

An increase in structural complexity of the substrate vertically and/or horizontally increases the number of microhabitats, and if the appropriate colonizers and mortality sources are present, within-habitat diversity will likely be increased (Steimle and Stone 1973; Abele 1974; Hughes 1975; Woodin 1976, 1978; Connell 1978; Suchanek 1979; Hulbert et al. 1982). *Ceriantharia* tubes may increase species diversity and abundance on featureless soft bottom areas by 1) attracting motile megafauna seeking refuge near tubes and 2) serving as a favorable substrate for epifauna and infauna, particularly suspension-feeders and tubicolous species.

By acting as a three-dimensional refuge, the tubes may ease predation pressure on smaller motile species (Ware 1972; Whoriskey 1983). Demersal fish and crustaceans similar to those we observed have been noted by others in association with *Ceriantharia* (Uzmann et al. 1977; Hecker et al. 1980; Valentine et al. 1980). The species most commonly observed near tubes, *Helicolenus dactylopterus*, *Sebastes* sp., and *Bathymectes* sp., characteristically exhibit thigmotactic behavior.

Associations similar to the ones we found between suspension feeders and *Ceriantharia* tubes in Block Canyon (Figs. 3D, 8), and polychaetes and tubes from Oceanographer Canyon (Appendix Table 3), have been recorded for *Ceriantharia* and polychaetes (Kingsley 1904; O'Connor et al. 1977), phoronids (Ponder 1971; Emig et al. 1972; Hartog 1977), and bivalves (Ponder 1971). These associations have been alternately referred to as commensalism or inquilinism; we prefer the latter definition as it highlights the role of the ceriantharian tube. Emig et al. (1972) speculated that *Cerianthus manua* Carlgren tentacles may act as baffles, causing waterborne food particles to settle out, and become available to suspension feeders (*Phoronis australis* Haswell) inhabiting the *C. manua* tubes, in which case the term commensalism may be more appropriate. However, Emig et al. also stated that increased food supply is probably a secondary benefit to the phoronids and that the suitability of the tube as a settlement surface for larvae motivates the association. O'Connor et al. (1977) studied a *Pachycerianthus multiplicatus* Carlgren population inhabiting deposit substrates (85% silt-clay, 15% sand) off Ireland and suggested tubes were prime settlement surface for the larvae of inquiline filter-feeding polychaetes, *Myxicola infundibulum* (Renier). The associates (sponges, hydroids, and colonial anemones) of *Ceriantharia* tubes in Block Canyon are generally nonmotile so

they probably had to arrive on the tubes as larvae. More unstable substrate surrounding the tubes may be less suitable as a settlement surface for larvae of suspension feeders (Rhoads and Young 1970, 1971; Rhoads 1974).

The vertical aspect of *Ceriantharia* tubes may enhance diversity and abundance by 1) allowing vertical stratification of trophic types (MacArthur and Levins 1964; Hughes 1975; Schoener 1975; Ausich and Bottjer 1982), and 2) affording inhabitants, such as the filter feeder *Potamilla neglecta*, elevated feeding stations where clogging by resuspended sediments is less likely, and current velocities tend to be greater (Dyer 1980), thus the food supply is more rapidly renewed (Hughes 1975; Sebens 1984).

The stable nature of the tubes may serve species behaviorally inclined to attach themselves to firm substrate. The three species of polychaetes, *Polycirrus eximius*, *Marphysa* sp., and *Potamilla neglecta*, most abundant on ceriantharian tubes caught in Oceanographer Canyon, but rarely found in the adjacent sediments (Appendix Table 3), usually attach their tubes to solid surfaces such as stones, algae, or hydroids (Gosner 1971; Fauchald and Jumars 1979).

Infaunal species may also gain relief from predation pressure by inhabiting ceriantharian tubes. The feltlike tubes are generally more consolidated than the sediments surrounding them, thus more difficult to graze. Ponder (1971) viewed protection as the principal benefit to a leptonid bivalve, *Montacutona ceriantha* Ponder, inquiline with *Cerianthus* sp. in Japanese waters. Protection may be enhanced for tubicolous infauna since their retraction may be stimulated by a similar response to disturbance by the host ceriantharian (Emig et al. 1972).

Ceriantharia tubes may serve as a preferential food source for some infauna. O'Connor et al. (1977) noted sipunculids, *Golfingia elongata* (Keferstein), inquiline with *Pachycerianthus multiplicatus* had tube remains in their guts. Scavengers, such as *Marphysa sanguinea* may benefit from the inquilinism for this reason.

Ceriantharia may also negatively affect the infauna in sediments adjacent to the tubes; large motile species, attracted to the tubes for shelter, might selectively graze near tubes. We hope to investigate *Ceriantharia* "forest" communities more thoroughly on future submersible cruises: Substrate collections taken away from tubes will further define their functional role. We believe *Ceriantharia* influence the ecology of the northwest Atlantic continental shelf and slope more than has been revealed from data collected by conventional surface tech-

niques alone; methods inadequate for collecting deep-burrowing adults, and providing information on behavioral and spatial relationships between Ceriantharia and other community residents.

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We dedicate this effort to the memory of John Lamont, whose talents, patience, and humor made our daily burdens easier to bear.

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APPENDIX TABLE 1.—Summary of statistics for submersible dives during which only qualitative data were collected. Substrate definitions: 1 = sand base; 1a = silt-sand; 1b = gravel sand; 1c = shell-sand; 2 = rocky cover; 2a = cobbles; 2b = boulders; 2/1 or 3 = rocks on sand or clay base; 3 = clay base; 3a = silt-clay; 3b = gravel-clay. Substrates and temperatures listed are those in which *Ceriantharia* were seen, for dives without *Ceriantharia* all substrates and temperatures recorded on the dive are listed. *Ceriantharia* species: 0 = absent; A, B, C, or D = species recorded on video tapes; + = *Ceriantharia* seen but species not identified.

Year/submersible dive(s) ¹	Geographic name	Lat. N	Long. W	Horizontal distance travelled (km)	Dive depth range (m x 100)	<i>Ceriantharia</i> depth range (m x 100)	Temp (°C)	Substrate	<i>Cerian- thid</i> species
1971 PC8 9/26 (1,2)	Wilkinson Basin	42°17'	69°58'	1.8	1.2-2.2	1.2-1.6	6.1	1a,1b,3a	B
1973 NG 4	Veatch Canyon	40°00'	69°38'	1.8	1.5	1.5	11.1	1a,3a	+
7	Veatch Canyon	39°59'	69°37'	2.0	1.9-3.0	2.4-3.0	7.2-9.2	3a	+
11	Veatch Canyon	39°57'	69°33'	2.0	1.6	1.6	9.4-10.0	1a	+
12	Veatch Canyon	39°56'	69°33'	2.0	1.7	1.7	10.6	1a	+
13	Veatch Canyon	39°55'	69°33'	2.0	2.5	2.5	7.2-7.8	1a,1c	+
14	Veatch Canyon	40°00'	69°37'	2.0	1.8	—	8.3-9.2	1a,3a	0
1974 NG 1, 2, 4-6	Veatch Canyon	40°00'	69°37'	1.0 km ²	1.7-2.6	2.1	8.3-11.1	1a	+
9	Hydrographer Canyon	40°12'	69°05'	1.3	1.5-2.5	1.6-2.4	8.9-10.8	1a	+
10	Hydrographer Canyon	40°08'	69°02'	1.2	2.0-3.0	2.8-3.0	9.2-11.1	1a	+
12	Hydrographer Canyon	40°09'	69°06'	0.7	1.5-2.7	1.6-1.7	8.3-11.1	1a,2/1	+
13	Hydrographer Canyon	40°04'	69°05'	1.3	1.9-2.1	1.9-2.1	10.8-11.1	1a	+
14	Oceanographer Canyon	40°30'	68°10'	3.0	1.7-2.4	?	?	1a,2a/1,3a	+
15	Oceanographer Canyon	40°28'	68°10'	3.0	1.3-2.7	1.3-2.7	9.4-11.0	1a,1c,3a	B
16	Oceanographer Canyon	40°29'	68°15'	1.7	1.6-2.2	1.6	9.7-11.9	1a,2a/1	+
17	Oceanographer Canyon	40°29'	68°09'	2.2	1.7	1.7	11.1	3a,3b	B
18	Oceanographer Canyon	40°27'	68°07'	1.5	1.9-3.0	2.7	8.2-9.7	1a	B
19	Oceanographer Canyon	40°23'	68°08'	2.0	1.9-3.0	2.4	9.7-10.4	3a	B
20	Oceanographer Canyon	40°20'	68°05'	2.6	1.9-3.0	2.1-2.9	8.1-12.8	1a	B
23	Corsair Canyon	41°21'	66°11'	3.0	1.5-3.0	1.8-3.0	6.4-9.7	1a,2a/3,3a,3b	B
24	Corsair Canyon	41°24'	66°14'	4.0	1.1-2.4	1.5	9.4	1b,2a/1	B
25	Corsair Canyon	41°23'	66°10'	1.0	2.2-3.0	2.4-2.7	5.8-9.2	1b	B
26	Corsair Canyon	41°20'	66°06'	3.2	1.5-3.0	2.6-2.9	6.9-7.2	1a,1b	B
27	Lydonia Canyon	40°32'	67°42'	1.5	1.5-3.0	1.6-3.0	7.2-11.4	1a,1c	B
28	Lydonia Canyon	40°32'	67°44'	2.2	1.4-3.0	1.4-2.7	8.3-10.8	1a,1c	B
29	Lydonia Canyon	40°31'	67°40'	1.7	1.4-2.9	2.4-2.7	8.9	1a	B
30	Lydonia Canyon	40°28'	67°41'	1.4	1.7-3.0	2.6-2.9	8.6-10.8	3a,3b	+
31	Lydonia Canyon	40°23'	67°41'	2.1	1.5-2.9	1.5-2.7	7.5-12.8	1a,1b,1c	B
32	Lydonia Canyon	40°24'	67°38'	1.3	1.8-2.2	—	9.2-9.7	1a	0
33	Gilbert Canyon	40°22'	67°49'	2.0	2.0-3.0	2.1-2.7	9.2-10.8	1a	B
34	Gilbert Canyon	40°22'	67°55'	2.4	1.5-3.0	2.4-2.6	9.4-12.2	1a	B
35	Oceanographer Canyon	40°20'	68°12'	2.1	1.8-3.0	1.8	7.2-12.2	1a	B
36	Veatch Canyon	39°59'	69°39'	1.8	1.6-2.3	—	10.0-14.1	1a,2/3,3a	0
37	Veatch Canyon	39°59'	69°38'	1.8	1.8	—	11.4	1a	0
38	Veatch Canyon	39°59'	69°37'	1.8	1.7-2.5	2.5	7.8-10.6	3a	+
1976 AL 667	Veatch Canyon	39°59'	69°35'	3.3	1.3-6.7	1.4-4.0	?	3a	+
668	Veatch Canyon	39°51'	69°33'	?	9.1-14.4	—	4.0	3a	0
669	Veatch Canyon	39°47'	69°32'	?	14.0-19.3	18.4-19.3	3.5	3a	A
670	Veatch Canyon	39°52'	69°34'	?	8.0-15.1	—	4.0	3a	0
671	Veatch Canyon	39°58'	69°37'	3.2	1.9-6.8	2.9	10.5	3a	+
672	Veatch Canyon	40°01'	69°37'	7.4	1.4-2.2	1.6-2.2	9.0	3a	B

APPENDIX TABLE 1.—Continued.

Year/submersible dive(s) ¹	Geographic name	Lat. N	Long. W	Horizontal distance travelled (km)	Dive depth range (m × 100)	Ceriantharia depth range (m × 100)	Temp (°C)	Substrate	Cerianthid species
1978 AL 835	Oceanographer Canyon	40°24'	68°10'	3.3	1.5-7.0	1.5-3.0	7.1-10.8	1a,1b,3a	+
836	Oceanographer Canyon	40°17'	68°07'	0.7	10.0-12.9	—	?	3a	0
837	Oceanographer Canyon	40°28'	68°10'	3.1	1.3-3.5	1.3-2.9	?	3a	+
838	Oceanographer Canyon	40°12'	68°05'	6.1	14.5-18.7	16-18.7	3.7-3.9	1a	A
839	Oceanographer Canyon	40°26'	68°07'	3.1	1.4-5.2	1.4-3.0	7.8-10.7	1a,1b,2a/3,3b	+
840	Oceanographer Canyon	40°21'	68°09'	0.4	9.0-9.5	—	?	3a	0

¹Submersible abbreviations: PCB = *Perry Model C8*, NG = *Nekton Gamma*, AL = *Alvin*.

APPENDIX TABLE 2.—Summary of statistics for submersible dives during which quantitative data were collected. Vessel information: AL = *Alvin* (15 m² photo⁻¹); NG = *Nekton Gamma* (3.6 m² photo⁻¹); JSL = *Johnson-Sea-Link* (7 m² photo⁻¹). Substrate definitions: 1 = sand base; 1a = silt-sand; 1b = gravel-sand; 1c = shell-sand; 2 = rocky cover; 2a = cobbles; 2b = boulders; 2/1 or 3 = rocks on sand or clay base; 3 = clay base; 3a = silt-clay; 3b = gravel-clay. Substrates and temperatures listed are those in which Ceriantharia were seen, for dives without Ceriantharia all substrates and temperatures recorded on the dive are listed. Cerianthid species: 0 = absent, A, B, C, or D = species (cf. Table 3). Densities are mean # m⁻²; * = Ceriantharia present but less than 0.01 m⁻²).

Year/submersible dive(s)	Geographic name	Lat. N	Long. W	Areal coverage (m ²)	Dive depth range (m × 100)	Ceriantharia depth range (m × 100)	Temp (°C)	Substrate	Ceriantharia		
									Species	Density (# m ⁻²)	95% C.L.
1975 AL 576	Veatch Canyon	39°54'	69°36'	4,170	7.4-12.6	—	4.0	3a	—	0	—
577	Veatch Canyon	39°59'	69°35'	6,840	2.1-4.6	2.7-4.0	5.3-7.6	3a	B	*	—
578	Veatch Canyon	39°56'	69°35'	5,355	1.8-9.1	2.0-3.6	5.5-9.2	3a	B	0.025	± 0.012
579	Veatch Canyon	39°55'	69°37'	5,010	2.7-9.2	2.7-3.8	5.5-7.3	3a	B	0.037	± 0.013
1979 NG 1	Oceanographer Canyon	40°29'	68°11'	572	1.6-2.3	1.6-2.0	11.0	1a,1b,2b/1	B	0.086	± 0.039
2	Oceanographer Canyon	40°28'	68°08'	418	1.7-1.8	1.7-1.8	—	3b	B	*	—
3,4	Block Canyon	40°02'	71°20'	756	1.4-2.4	1.4-1.8	9.1-13.0	3a	C	0.414	± 0.124
12	Hudson Canyon	39°30'	71°22'	868	1.5-3.0	1.5-2.9	—	3a	—	0	—
14	Hudson Canyon	39°38'	71°25'	378	1.6-3.0	3.0	—	3a	B,D	*	—
1980 AL 1034	Oceanographer Canyon	40°29'	68°10'	11,070	2.1-3.9	2.7-3.4	9.4	1a,3a,2a/3	B	0.016	± 0.008
1035	Oceanographer Canyon	40°18'	68°07'	8,580	7.3-13.2	—	5.8	3a	—	0	—
1036	Oceanographer Canyon	40°25'	68°09'	10,005	2.1-6.2	3.1	9.8-11.2	3a	B	*	—
1980 JSL 3,4	Georges Bank	40°43'	67°28'	5,992	0.9	0.9	9.6	1a	B	*	—
7,8	Georges Bank	40°37'	67°45'	6,230	0.8	0.8	9.2-9.5	1a	B	*	—
12,14	Lydonia Canyon	40°28'	67°42'	3,759	1.5-3.0	1.7-2.9	10.3-11.9	3a,1a	B,C	0.102	± 0.034
15,16	Lydonia Canyon	40°32'	67°43'	5,138	1.2-1.9	1.2-1.9	11.6-11.9	1a,1b	B,C	0.357	± 0.077
1981 JSL 2	Georges Bank	40°43'	67°28'	2,765	0.9	0.9	8.3	1a	B	*	—
3,4,5	Georges Bank	40°37'	67°45'	5,110	0.8	0.8	8.1	1a	B	*	—
8,9	Lydonia Canyon	40°32'	67°43'	5,551	1.2-1.7	1.3-1.6	9.9-10.8	1a,1b	B,C	0.377	± 0.062
12,13	Lydonia Canyon	40°28'	67°42'	4,655	1.4-2.6	1.7-2.5	9.6-9.9	3a,1a	B,C	0.030	± 0.012
16	Oceanographer Canyon	40°30'	68°09'	3,150	1.4-1.5	1.4-1.5	9.9-10.3	3a,1a,1c	B	0.029	± 0.008
19,20	Oceanographer Canyon	40°26'	68°09'	5,593	2.0-4.6	2.1-3.4	9.4-10.4	3a,3b,1a	B	*	—

APPENDIX TABLE 3.—Macrofauna (>0.5 mm) inhabiting two Cerianthid B tubes, and adjacent sediments (silt-sand), collected by a grab sampler (290 cm², 5-10 cm penetration depth) from the *Johnson-Sea-Link's* manipulator arm, at a depth of 293 m in Oceanographer Canyon. A tube and the adjacent sediments were collected together, put in the same sample container, and separated as soon as the submersible was aboard ship.

Tube (200 cc)	No.	Sediments (800 cc)	No.	Tube (1200 cc)	No.	Sediments (1,600 cc)	No.
Sample #1				Sample #2			
Annelida		Annelida		Annelida		Annelida	
Oligochaeta	2	Oligochaeta	7	Polychaeta		Oligochaeta	15
Polychaeta		Polychaeta		<i>Polycirrus eximius</i>	25	Polychaeta	
<i>Polycirrus eximius</i>	14	<i>Prionospio cirrifera</i>	11	<i>Marphysa</i> sp.	16	<i>Aricidea catherinae</i>	49
<i>Marphysa</i> sp.	8	<i>Aricidea catherinae</i>	7	<i>Potamilla neglecta</i>	11	<i>Prionospio cirrifera</i>	28
<i>Potamilla neglecta</i>	6	<i>Goniada maculata</i>	3	<i>Podarke obscura</i>	9	<i>P. juv.</i>	14
<i>Prionospio cirrifera</i>	5	<i>Exogone hebes</i>	2	<i>Exogone verugera</i>	5	<i>Tharyx annulosus</i>	13
<i>Ninoe gayheadi</i>	2	<i>E. verugera</i>	2	<i>E. hebes</i>	3	<i>Goniada maculata</i>	10
<i>Aricidea catherinae</i>	1	<i>Ninoe gayheadi</i>	2	<i>Aricidea catherinae</i>	1	<i>Ophalina accuminata</i>	7
<i>A. cerrutii</i>	1	<i>Ophalina accuminata</i>	2	Terebellidae	1	<i>Prionospio</i>	
<i>Exogone hebes</i>	1	<i>Aglaophamus igalis</i>	1	<i>Tharyx acutus</i>	1	<i>steenstrupi</i>	5
<i>E. verugera</i>	1	<i>Ampharete arctica</i>	1	<i>Typosyllis alternata</i>	1	<i>Dodecacaria</i> sp.	3
<i>Glyceria capitata</i>	1	<i>Cirratulus cirratus</i>	1	Arthropoda		<i>Exogone hebes</i>	3
<i>Lumbrineris</i> sp.	1	<i>Micronephthys minuta</i>	1	Crustacea		<i>E. verugera</i>	3
<i>Schistomerengos caeca</i>	1	<i>Neopodarke woodsholea</i>	1	<i>Photis dentata</i>	4	Nephtyidae juv.	3
<i>Tharyx annulosus</i>	1	<i>Nereis zonata</i>	1	Copepoda	1	<i>Paraonis gracilis</i>	3
Arthropoda		<i>Polycirrus eximius</i>	1	Crab zoea	1	<i>Anobothorus gracilis</i>	2
Crustacea		<i>Prionospio cirrifera</i>	1	Total	79	<i>Schistomerengos</i>	
Tanaidacea	38	<i>Protodorvillea</i>				sp.	2
<i>Photis dentata</i>	2	<i>gaspeensis</i>	1			<i>Tharyx acutus</i>	2
<i>Caprella linearis</i>	1	<i>Typosyllis</i> sp.	1			<i>T. sp.</i>	2
<i>Janira alta</i>	1	Arthropoda				<i>Aglaophamus</i>	
Total	87	Crustacea				<i>circinata</i>	1
		Copepoda	6			<i>Drilonereis longa</i>	1
		Tanaidacea	3			<i>Eunice pennata</i>	1
		Hyperiidea	1			<i>Haploscoloplos</i> sp.	1
		Total	56			<i>Lumbrineris fragilis</i>	1
						<i>Neopodarke</i>	
						<i>woodsholea</i>	1
						<i>Nereis zonata</i>	1
						<i>Protodorvillea</i>	
						<i>gaspeensis</i>	1
						<i>Spio</i> sp.	1
						Arthropoda	
						Crustacea	
						<i>Diastylis</i> sp.	1
						<i>Janira alta</i>	1
						<i>Pagurus annulipes</i>	1
						Total	176