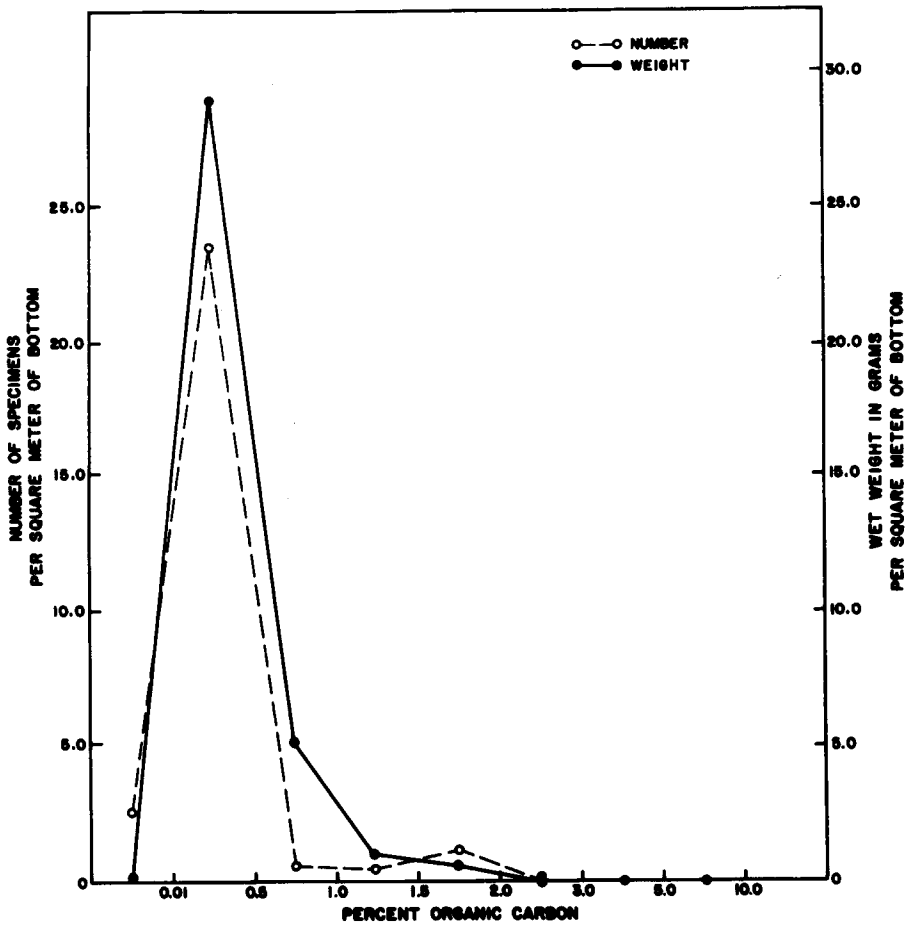


Figure 219
Density and biomass of Echinoidea in relation to sediment organic carbon.

occurred on the Southern New England Shelf, and a moderately high density (30/m^2) occurred in the Gulf of Maine. In the four remaining areas the density was moderate (14 to 17 individuals/m^2) and about equal.

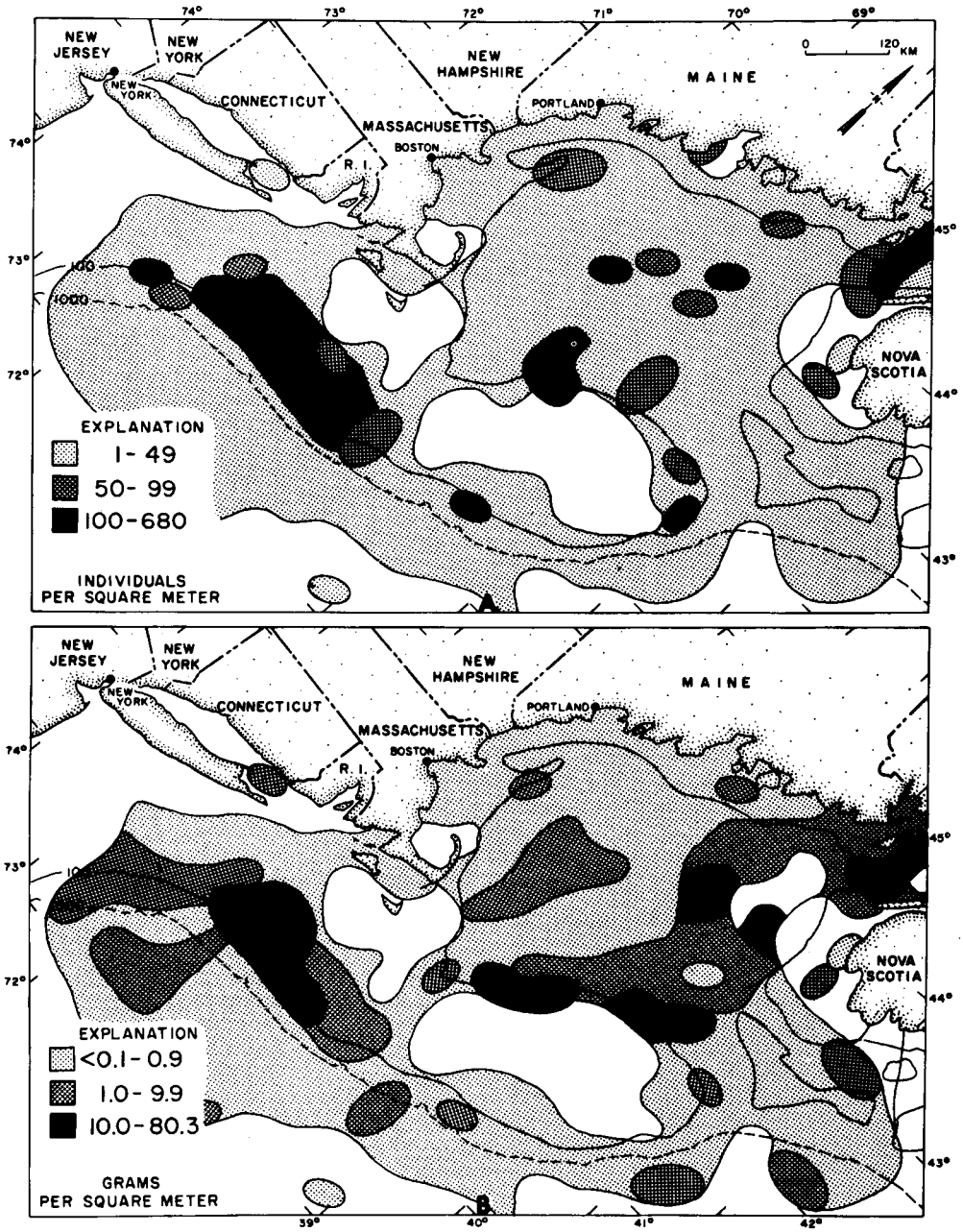
The biomass of ophiuroids, also, was relatively uniform from one area to another; total range was 0.8 to 5.4 g/m^2 (Table 8; Fig. 221). Relatively large biomasses (3.3 and 5.4 g/m^2) were encountered on the Southern New England Shelf and in the Gulf of Maine. Smallest (0.8 g/m^2) biomass was on Georges Slope. Although the average ophiuroid biomass on the Southern New England Slope was 2.6 g/m^2, an intermediate quantity, the proportion of the total fauna it made up was 13.5%, a much higher proportion than that for any other area (Table 9).

Frequency of occurrence of these organisms was moderately low (22 to 35%) in the samples from Georges Bank and, surprisingly, on the Southern New England Shelf. Ophiuroids were present in 55 to 64% of samples from all other areas (Table 10).

Bathymetric Distribution

Ophiuroids were taken at depths ranging from 13 to 3,820 m. Their density distribution revealed a pronounced zone of high abundance (35 to 87 individuals/m^2) at depths between 50 and 500 m (Fig. 222). Lower densities (0.8 to 6.2/m^2) prevailed in both deeper and shallower water. The lowest density occurred in the shallowest depth zone, 0 to 24 m.

The biomass of ophiuroids was more uniform among the various depth classes than was density; however, the same general trend was clearly evident (Table 13; Fig. 222). Biomass was relatively large (2.5 to 7.5 g/m^2) at depths between 50 and 500 m, and smaller in both deeper and shallower water.



OPHIUROIDEA

Figure 220
Geographic distribution of Ophiuroidea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

Occurrence of ophiuroids was low (9 to 10%) in samples from the inner continental shelf, at depths less than 50 m (Table 15). At depths of 50 to 500 m, where ophiuroids were most abundant, their occurrence in the samples was substantially higher, 40 to 72%. In water deeper than 500 m, ophiuroids were present in a slightly higher proportion of samples (44 to 76%). This indicates that these organisms were more uniformly distributed at a lower density in deepwater regions than they were in shallow water.

Relation to Sediments

Ophiuroids were rather plentiful in all types of bottom sediments, but trends in density and biomass in the

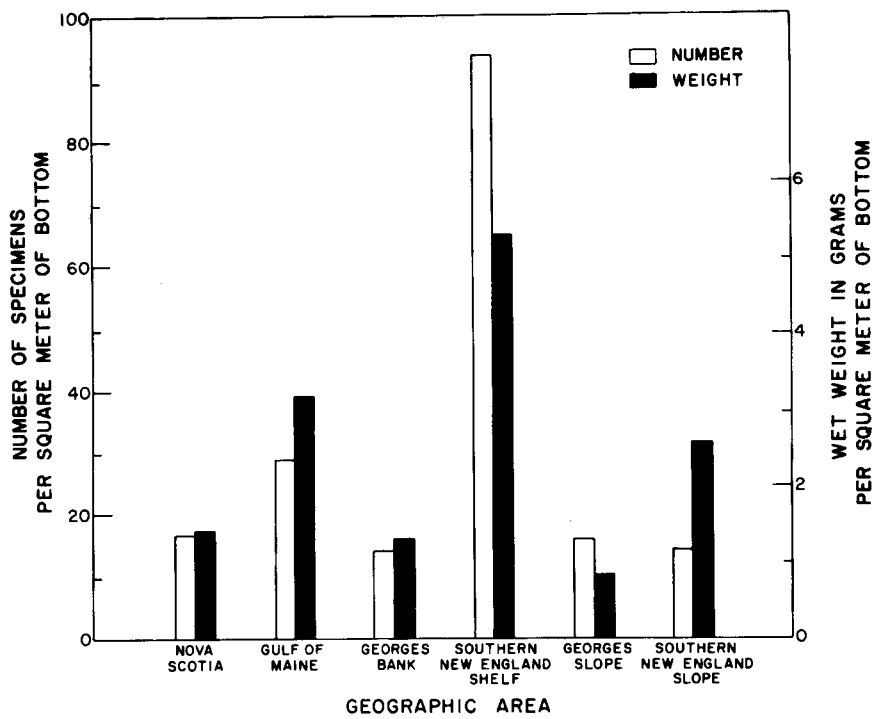


Figure 221
Density and biomass of Ophiuroidea in each of the six geographic areas.

different types were evident. Densities were low (16 to 26 individuals/m^2) in gravel, sand, and shell; intermediate (38 and 58/m^2) in till and silt-clay; and high (94/m^2) in sand-silt (Table 16; Fig. 223).

The trend of biomass in relation to sediment type was nearly the same as that revealed by density. Small biomasses of ophiuroids occurred in gravel, sand, and shell; intermediate quantities were found in silt-clay; and largest biomasses (5.3 and 5.8 g/m^2) occurred in till and sand-silt (Table 18; Fig. 223).

Occurrence of ophiuroids in the samples revealed a pattern similar to those of both density and biomass. They were present in a relatively small proportion (29–40%) of the samples from gravel, shell, and sand, and they were present in a substantially larger share (62–68%) of the samples in till, sand-silt, and silt-clay (Table 20).

Relation to Water Temperature

Ophiuroid density, biomass, and frequency of occurrence all conformed generally to the same trend of high abundance where the temperature range was less than 16°C, and low abundance

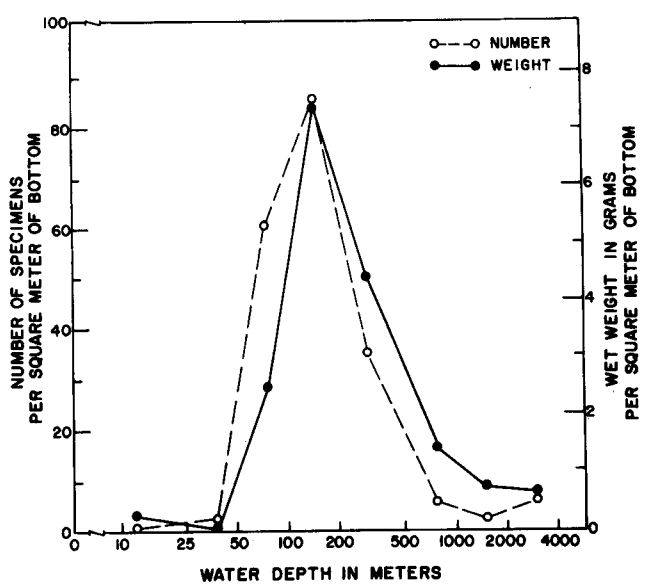


Figure 222
Density and biomass of Ophiuroidea in relation to water depth.

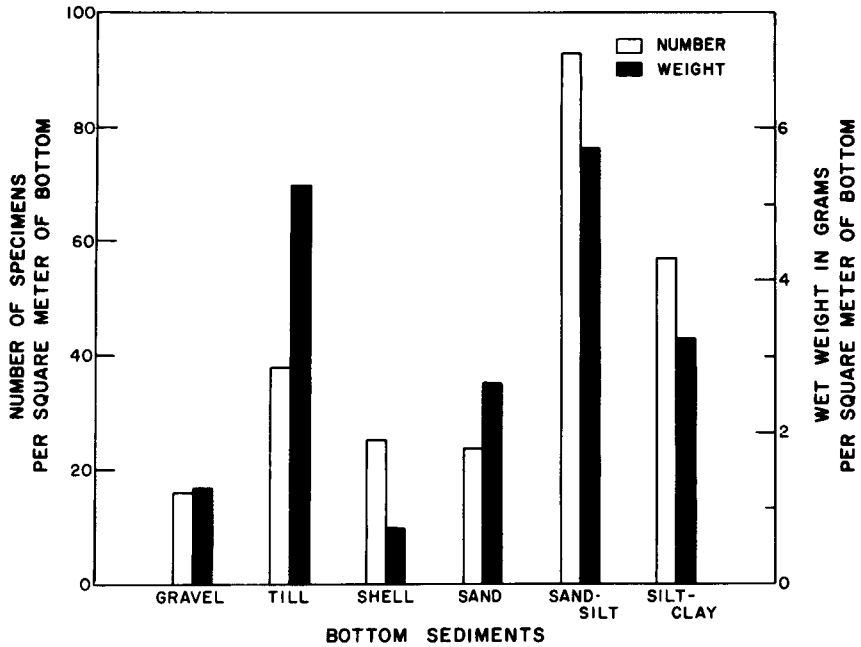


Figure 223
Density and biomass of Ophiuroidea in relation to bottom sediments.

where the range was greater than 16°C. Average density of ophiuroids increased from 25 to 74 individuals/m^2 as the range in temperature increased from less than 4°C to 12°–15.9°C, then dropped precipitously to less than 3/m^2 in the two broadest temperature range classes (Table 21; Fig. 224).

Biomass values were an order of magnitude lower than those of numerical density, but they revealed a general decline associated with an increased range in temperature (Table 23; Fig. 224). Where the temperature range was less than 12°C, the average biomass was about 3 to 6 g/m^2. Where the temperature range was greater than 16°C, the biomass averaged about 0.5 g or less/m^2.

Frequency of occurrence diminished rather consistently with increased range in water temperature (Table 25). Ophiuroids occurred in 64% of the samples in areas where the temperature range was less than 4°C and declined steadily to 11% in areas where the range in temperature was 20°C or more.

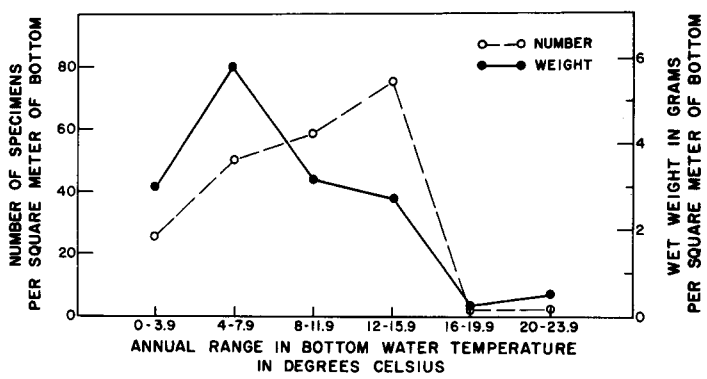


Figure 224
Density and biomass of Ophiuroidea in relation to the annual range of bottom water temperature.

Relation to Sediment Organic Carbon

Ophiuroids were numerically most abundant (72 to 81 individuals/m^2) where the organic carbon content was between 0.50 and 1.49% (Table 26; Fig. 225). Average density declined in both lesser and greater amounts of organic content, with the lowest density (5/m^2) occurring in the highest content class they occupied (2.00–2.99%).

Biomass showed a similar trend but at considerably lowered magnitude (Table 28; Fig. 225). Biomass was from 5 to 6 g/m^2 in areas of organic carbon content between 0.5 and 1.49% and fell off sharply to consider-

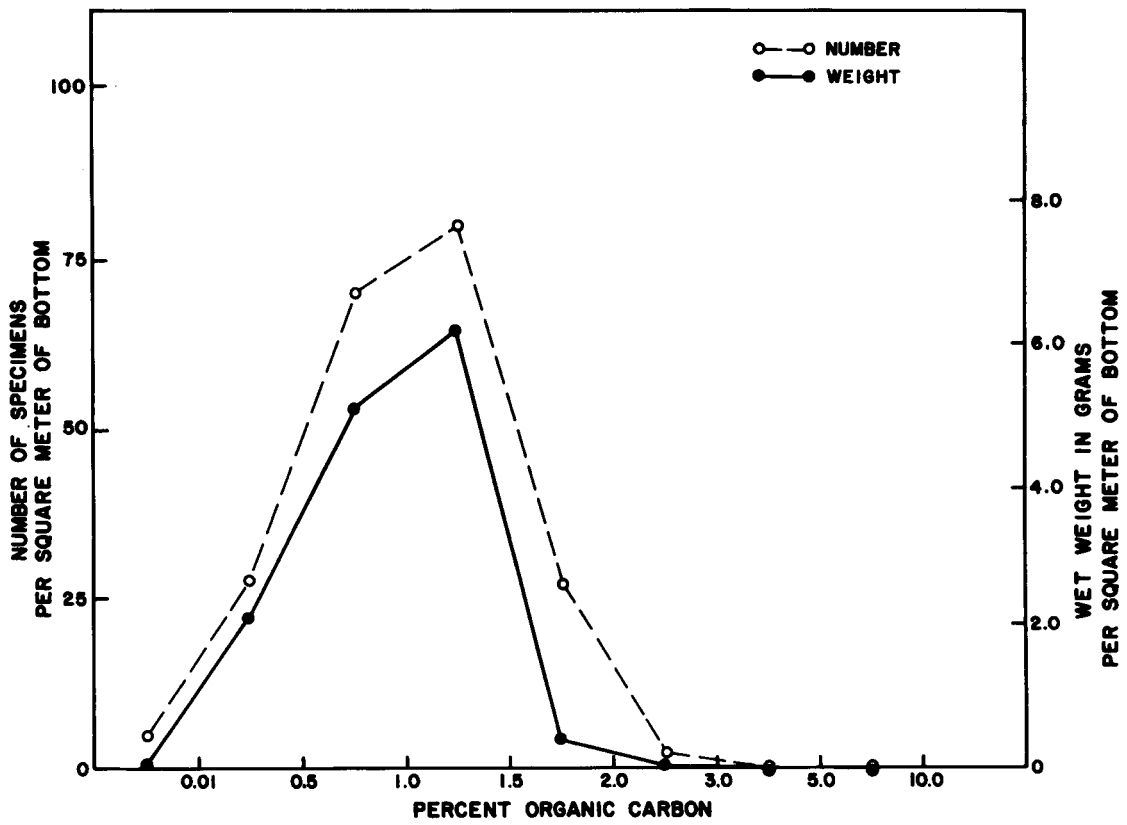


Figure 225
Density and biomass of Ophiuroidea in relation to sediment organic carbon.

ably lower levels (0.1–2 g/m^2) in classes on either side of these.

Occurrence of ophiuroids in the samples was moderate to moderately high (66–70%) in the two mid-range content classes and in the absence of measurable carbon, and moderately low (23 to 47%) in the other content classes they occupied (Table 30).

Asteroidea—Starfishes constituted a moderately small portion of the New England benthos. Their contribution to the total number of specimens was only 0.1%, but they provided 1.2% of the total biomass (Table 3).

Representatives of three orders of the Asteroidea were present in our samples: Phanerozonia, Spinulosa, and Forcipulata. All three orders contained species that were common in the samples.

Starfishes exhibited considerable variation in color, both inter- and intraspecifically. The most brightly colored species encountered was *Porania insignis*, which commonly was a deep, rich claret color with patches of whitish and yellowish papillae. Other specimens of the same species and other species within the same genus were much paler, even a drab brownish-gray. Other colorful genera encountered were *Hippasterias* and *Solaster*. Many of the more common genera, such as *Asterias*, *Astropecten*, and *Ctenodiscus*, were predominantly tan, brown, or olive.

Sizes ranged from juvenile specimens of various species that were 2 to 3 mm in radius to large specimens of *Asterias* and *Solaster* with radii of over 18 cm. Specimens with radii over 8 cm were uncommon.

Average weight of individual specimens was 1.4 g, which was large compared with other taxonomic groups.

The majority of starfishes in this region are carnivores, particularly the selective, predatory type of carnivore. Deposit feeding and filter feeding are adaptations of only a few species, some of which are locally abundant. Bivalve mollusks appear to be the principal food of New England starfishes, although a variety of small invertebrate species, as well as dead fish, are consumed. A few species of starfishes are serious predators of oysters, clams, mussels, and other commercially valuable mollusks.

Asteroids occurred in 144 samples (13% of the total). Their density averaged 1.5/m^2 and their biomass averaged 2.1 g/m^2 (Table 5).

Geographic Distribution

Starfishes had a moderately broad areal distribution in the study area (Fig. 226). They occurred in an especially large proportion of the samples from offshore Southern New England and the southern part of Georges Bank but were noticeably absent or sparse in the central Gulf of Maine, central Georges Bank, off New Jersey and along most of the continental rise.

Asteroid density was generally low throughout the New England region, averaging only 1 to 19/m^2. The slightly higher densities of 10 to 19/m^2 occurred only in the coastal and near-coastal zones. Biomass of starfishes was relatively high compared with their numerical abundance, and although they averaged less than 10 g/m^2 over most of their range, there was a substantial number of localities where the average biomass was between 10 and 105 g/m^2. The rather high biomass (10 to 50 g/m^2) along the outer margin of the continental shelf off Southern New England corresponds to the distribution of sand in that area (see Fig. 7).

Differences in starfish density among the six standard geographic areas was moderate—extremes of mean density were 0.2 and 2.5/m^2 (Table 6; Fig. 227). Densities of starfishes were generally higher in the continental shelf areas than they were on the continental slope. Indications of a north–south trend were revealed by a low density in the Nova Scotian shelf area, intermediate values in the Gulf of Maine and Georges Bank region, and relatively high density in Southern New England.

Biomass distribution was similar to density. There were only two geographic areas in which the biomass was unusually small (0.02 and 0.05 g/m^2), the two slope areas (Table 8; Fig. 227). Relatively high biomasses (1.0 to 4.5 g/m^2) occurred in the continental shelf areas.

Disparity in the average size of starfishes from the different areas was substantial. For example, in the Nova Scotia area the average weight of individuals specimens was 1 g, whereas in the slope areas, they averaged only 0.1 g each.

The frequency of occurrence of starfishes was low (6 to 19%) in all geographic areas (Table 10).

Bathymetric Distribution

Asteroids occurred at depths ranging from 13 to 2,329 m, and at a mean depth of 184 m. They occurred in substantially higher densities (1.8 to 2.5/m^2) at depths between 25 and 200 m than at other depths (Table 11; Fig. 228). In very shallow water (less than 25 m) and in depths beyond the continental shelf their density was 0.1 to 0.7/m^2. Densities were generally lowest in the deepest water. The maximum density of 167/m^2 was encountered at a depth of 49 m.

Starfish biomass varied considerably from one depth class to another, but the distributional pattern was similar to that described above for density (Table 13; Fig. 228). The average biomass on the continental shelf was 3 to 4 g/m^2 (except in the 25–49 m depth class where the biomass was unusually small). In depths below 200 m, the biomass averaged 0.04 g or less per square meter but was slightly higher on the lower continental slope and continental rise than on the middle and upper continental slope.

The proportions of samples in the various depth classes that contained starfishes ranged from 5 to 20% (Table 15). Their frequency of occurrence was slightly higher between 50 and 200 m than at other depths.

Relation to Bottom Sediments

Starfishes were taken in all sediment types except shell, and there were marked differences in quantity between samples from fine-texture sediments compared with those from coarse sediments (Table 16; Fig. 229). Largest quantities were from fine-grain sediments.

Average density in the coarse substrates (till and gravel) was 0.2 and 0.8/m^2, respectively. In the finer substrates (sand, sand-silt, and silt-clay) asteroids averaged 1.3 to 1.8/m^2.

Asteroid biomass was 0.5 g or less per square meter in the coarse sediments and 2.0 to 3.6 g/m^2 in the fine-grain sediments.

Starfishes occurred in a markedly higher proportion (14 to 16%) of samples from sediments composed of fine particles than of samples composed of gravel and till (8 and 9%) (Table 20).

Relation to Bottom Temperature

Asteroids were found in moderate to low amounts in all temperature range classes (Table 21; Fig. 230), but they were more abundant where the temperature range was moderate rather than extreme.

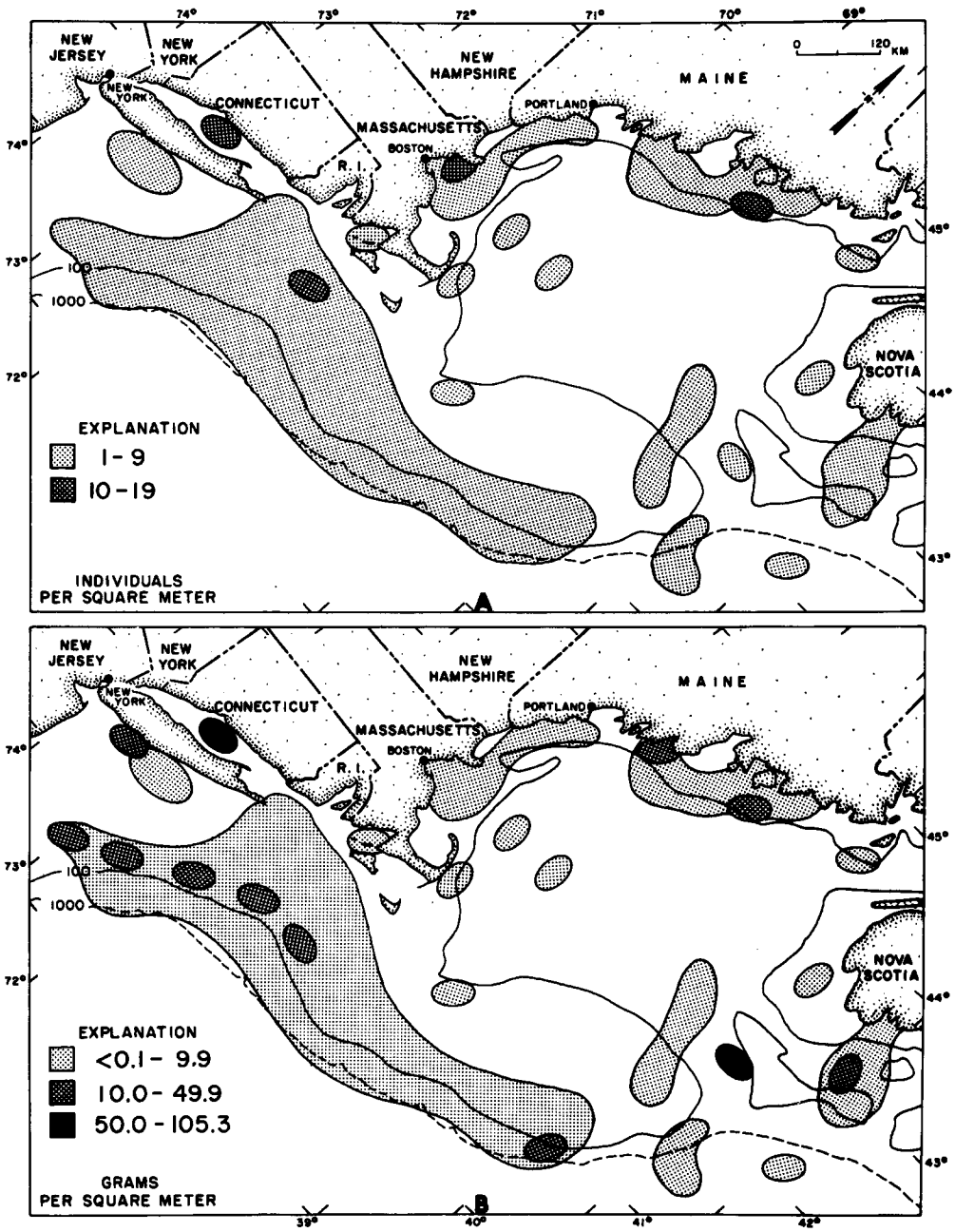
Average densities (0.4 to 0.9/m^2) of starfishes in the extreme temperature range classes (0°–3.0° and 16°–23.9°C) were considerably below those found in the mid-ranges (4°–15.9°C) where values of 1.2 to 2.7/m^2 occurred. In terms of total faunal density, asteroids provided only 0.2% or less of the total number of specimens in each of the six temperature range classes (Table 22).

The average biomass of starfishes in the intermediate temperature range classes was quite stable, varying only from 2.8 to 3.6 g/m^2; the two extreme classes, however, yielded only 0.1 to 0.5 g/m^2, respectively (Table 23; Fig. 230). Starfishes in the various temperature range classes represented from 0.1 to 4% of the total faunal biomass (Table 24).

The proportion of samples that contained asteroids was lowest (6–4%) in the two extreme temperature range classes and the highest (21%) in the 8°–11.9°C temperature range class (Table 25).

Relation to Sediment Organic Carbon

Asteroids were present in only four of the eight organic



ASTEROIDEA

Figure 226
Geographic distribution of Asteroidea: A–number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

carbon content classes. The four classes in which they occurred ranged from 0.01 to 1.99%. Average density was fairly low but relatively uniform in the three classes between 0.01 and 1.49% carbon content, ranging from 1.6 to 1.0 individuals/m^2 (Table 26; Fig. 231). The 1.50 to 1.99% class, however, contained only 0.4 individuals/m^2.

The distribution of biomass was parallel to that of density, highest (5.5 g/m^2) in the 1.00–1.49% carbon content class and dropping off significantly in higher and lower adjacent content classes where values were uniformly low, ranging from 1.03 to 1.42 g/m^2 (Table 28; Fig. 231).

Frequency of occurrence of asteroids in the samples in the organic carbon content classes ranged from 14 to

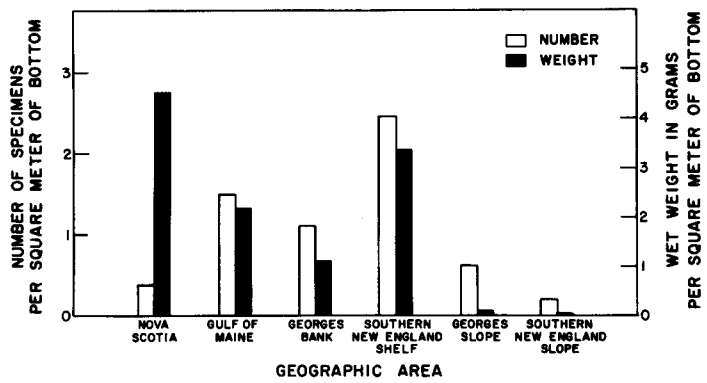


Figure 227
Density and biomass of Asteroidea in each of the six geographic areas.

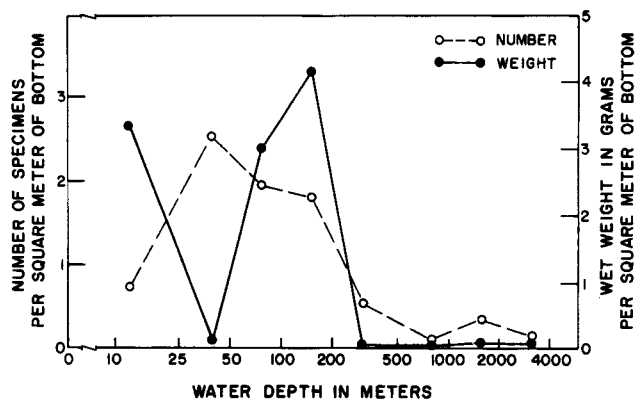


Figure 228
Density and biomass of Asteroidea in relation to water depth.

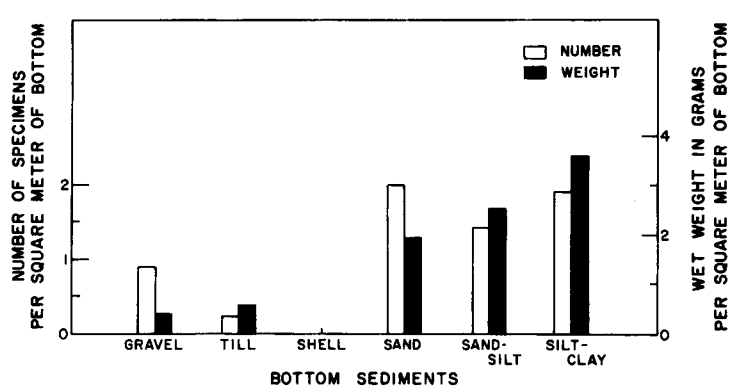


Figure 229
Density and biomass of Asteroidea in relation to bottom sediments.

17% in the three classes between 0.01 and 1.49%, and was 7% in the 1.50 to 1.99% content class (Table 30).

Hemichordata

Representatives of the phylum Hemichordata are all from one class (Enteropneusta, acorn worms) and one genus (*Balanoglossus*). A total of 101 specimens, weighing 18.7 g, were collected at 4 stations (0.4% of total); average density (0.1 individuals/m^2) and biomass (0.02 g/m^2) were very low (Table 5).

Geographic Distribution
The geographic distribution of acorn worms was restricted to the Southern New England Shelf (3 stations) and Southern New England Slope (1 station). Mean densities were 0.3 individual/m^2 or less and mean biomass 0.06 g/m^2 or less (Tables 6 and 8; Fig. 232). Frequency of occurrence of hemichordates in the samples was a very low 1% (Table 10).

Bathymetric Distribution
Acorn worms occurred in three depth range classes: 50–99 m, 100–199 m, and 500–599 m, where their mean density ranged from <0.1 to 0.5 individual/m^2 and their mean biomass was 0.01 g/m^2 in the two deepwater ranges and 0.05 g/m^2 in the mid-shelf range (Tables 11, 13; Fig. 233). Five percent of the samples in the 500–999 m depth range yielded specimens, whereas the occurrence in the other two was from <1 to 1% (Table 15). The depth range of our samples was from 79 to 567 m.

Relation to Bottom Sediments
Acorn worms were found in low abundance in sand, sand-silt, and silt-clay substrates. Mean density ranged from <0.1 to 0.2 individual/m^2 and mean biomass from <0.01 to 0.04 g/m^2 (Tables 16, 18; Fig. 234). Frequency of occurrence in the samples was <1 to only 1% (Table 20).

Relation to Bottom Temperature
Hemichordates were restricted to areas where the annual range in water temperature was less than 16°C. Mean density and biomass were very low (<0.1/m^2 and <0.01 g/m^2) in the lowest temperature range class; mean densities of 0.2/m^2 occurred in each of the two

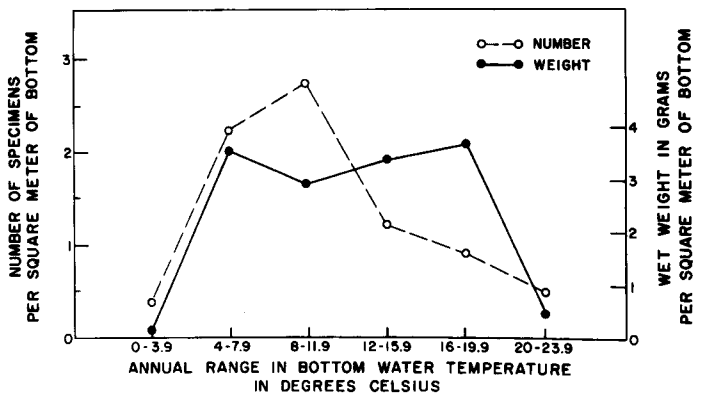


Figure 230
Density and biomass of Asteroidea in relation to the annual range of bottom water temperature.

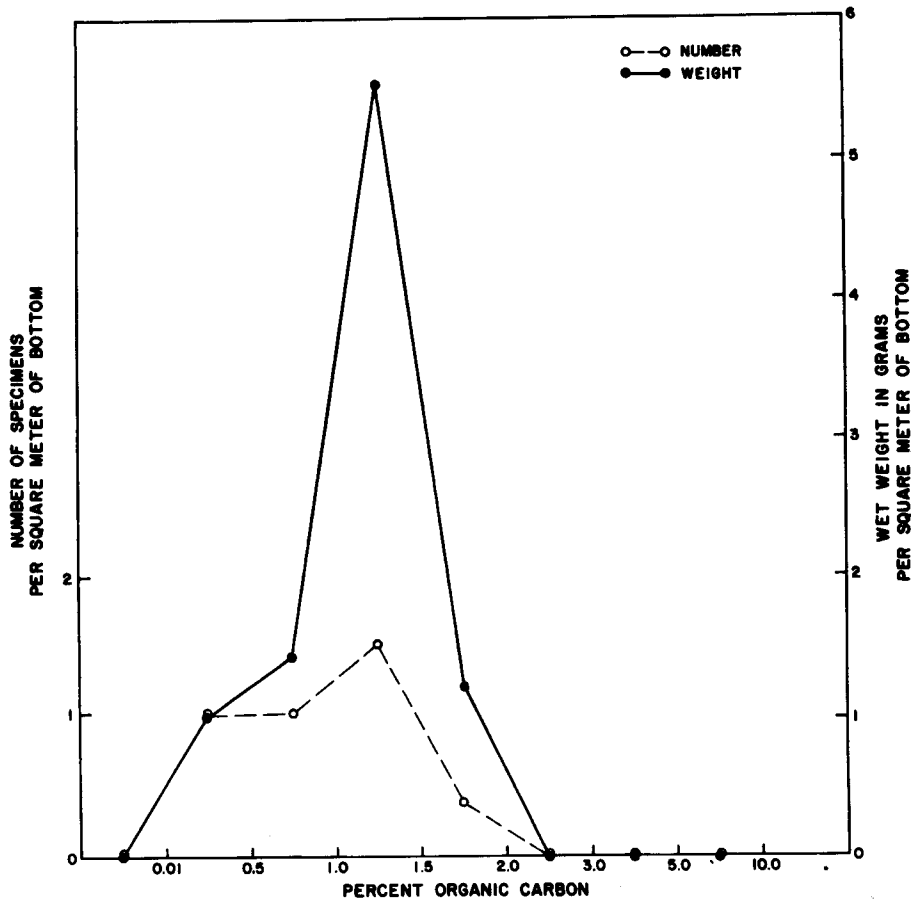


Figure 231
Density and biomass of Asteroidea in relation to sediment organic carbon.

range classes between 8 and 15.9°C. Mean biomass ranged from 0.03 to 0.04 g/m^2 (Tables 21, 22; Fig. 235). Frequency of occurrence was in the <1 to 1% range in the three range classes (Table 25).

Relation to Sediment Organic Carbon

Distribution of hemichordates was limited to the three organic carbon content classes between 0.01 and 1.49%. Mean densities were between 0.1 and 0.2 individual/m^2

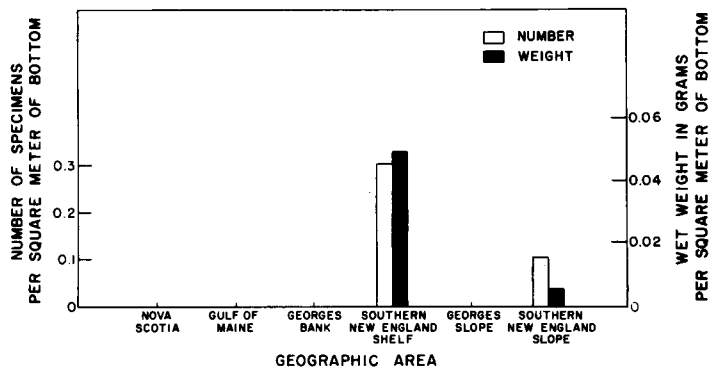


Figure 232
Density and biomass of Hemichordata in each of the six geographic areas.

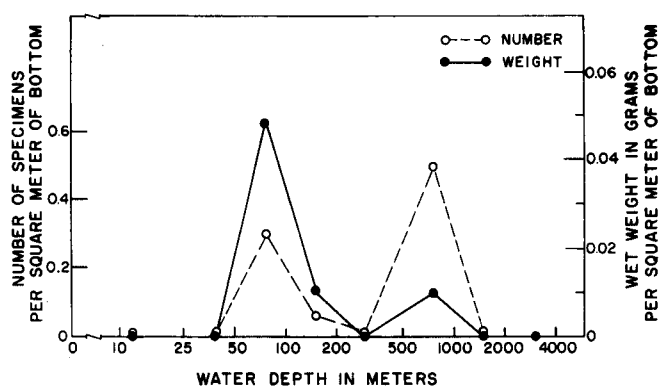


Figure 233
Density and biomass of Hemichordata in relation to water depth.

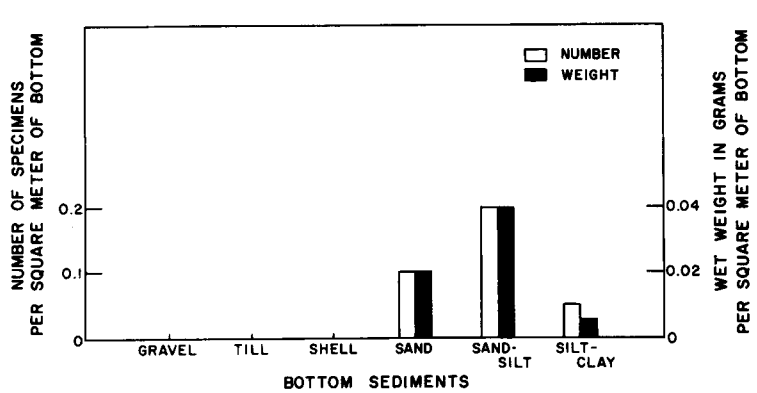


Figure 234
Density and biomass of Hemichordata in relation to bottom sediments.

and mean biomass between <0.01 and 0.03 g/m^2 (Tables 26, 28; Fig. 236). Only 1% of the samples in the three carbon content classes contained specimens of acorn worms (Table 30).

Chordata

Ascidiacea—Ascidians were moderately common in the New England benthos and constituted 1.1% of the total number of specimens and 2.2% of the total biomass (Table 3).

The size of solitary tunicates in our collections ranged from 4 mm to more than 20 cm. Although colonial forms are known to attain lengths greater than 50 cm in this region, the specimens in our samples were smaller (12 cm or less in length) than the largest solitary forms.

Interspecific variation in color of New England tunicates was rather broad, and in some groups the intraspecific variation was also considerable. The majority of species were dull olive, tan, or brown. A rather large number covered their tests with sand grains or silt that very effectively camouflaged them. A few groups contained beautifully colored species. Their coloration consisted of a blending of cream and light yellow with various shades of orange and red.

In order to control their rapid colonization on hard substrates and fouling of man-made structures, such as ship bottoms, pipes, buoys, and similar structures, the maritime industry incurs high economic costs. Ascidians occurred in 181 samples (17% of the total). Their density averaged 16.3/m^2 and their biomass averaged 4.1 g/m^2 (Table 5).

Geographic Distribution
Ascidians were distributed over large portions of the study area (Fig. 237), but their occurrence was patchy, with density changing abruptly from one locality to another. They were most common in the coastal areas and on the offshore banks and were sparse or absent from the following areas: the deeper part of the western Gulf of Maine, north-central Georges Bank, and parts of the continental shelf off Connecticut, New York, and New Jer-

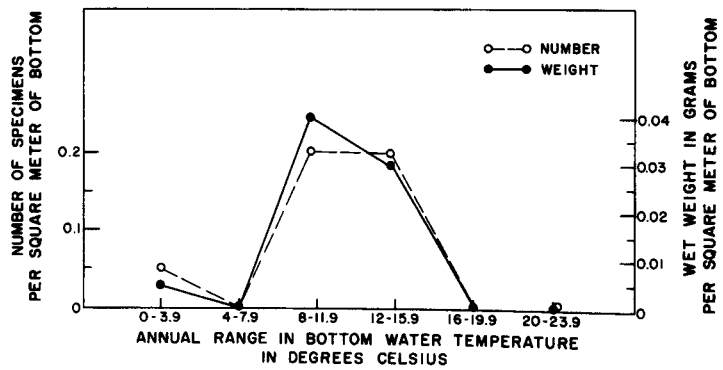


Figure 235
Density and biomass of Hemichordata in relation to the annual range of bottom water temperature.

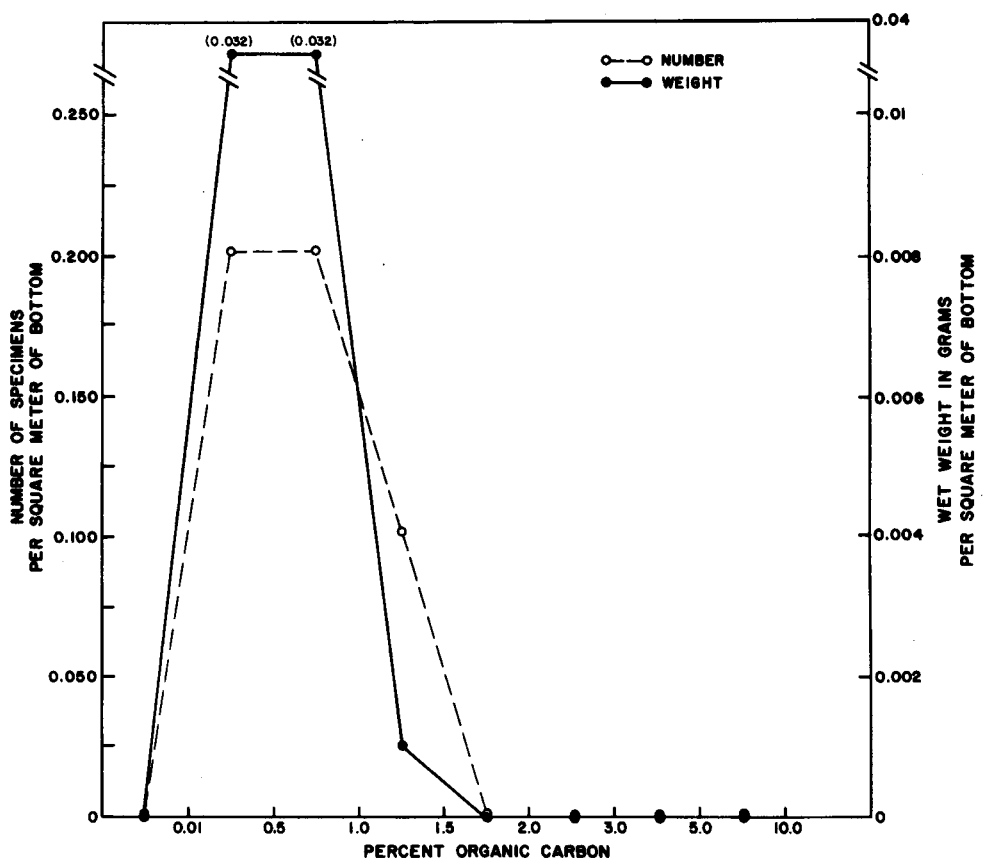
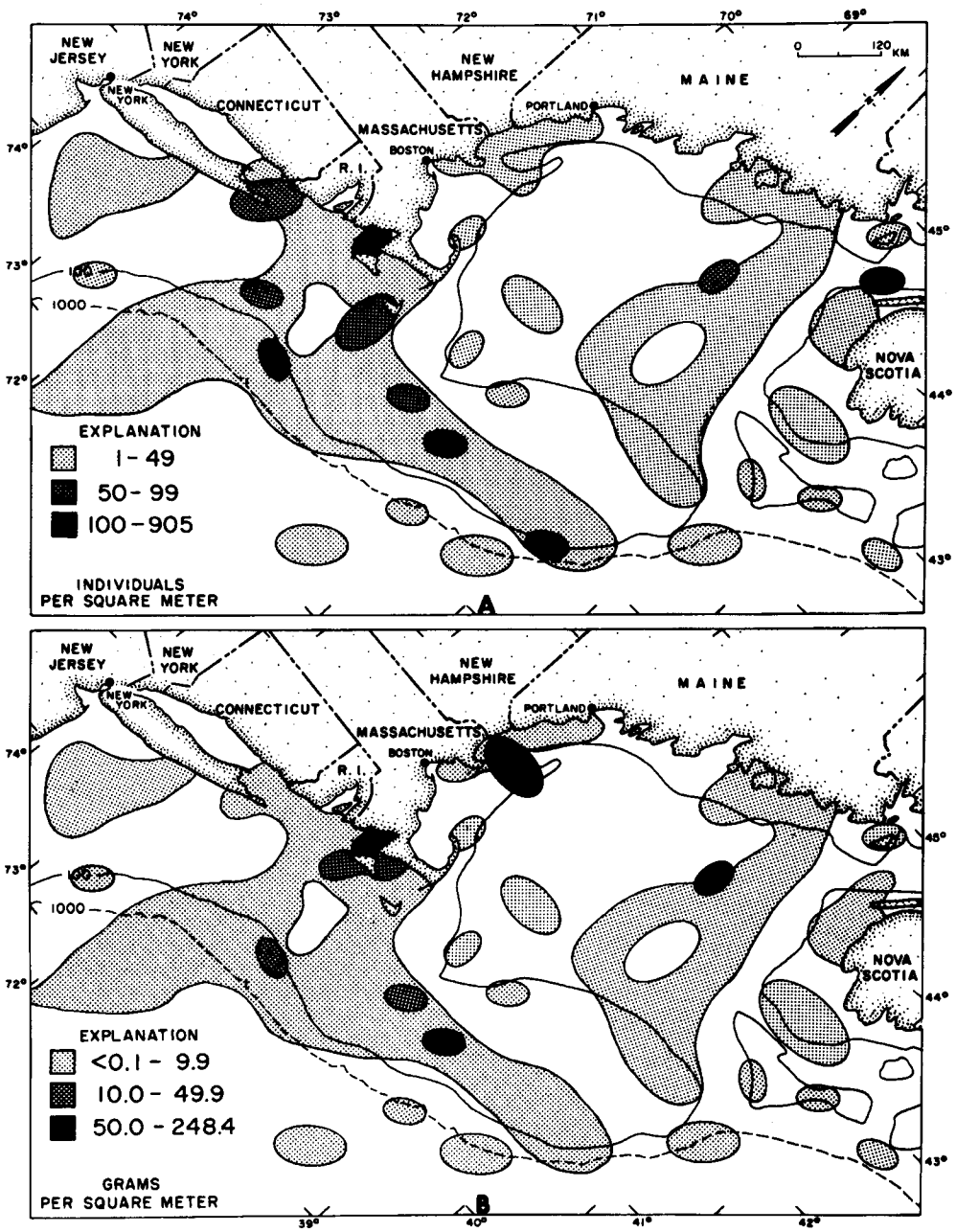


Figure 236
Density and biomass of Hemichordata in relation to sediment organic carbon.

sey. Densities throughout most of their range averaged less than 50 individuals/m^2. In a few localities, however, their density averaged between 100 and 900/m^2. Their biomass was moderate (less than 10 g/m^2) over most of their range and large quantities (50 to 288/m^2) were encountered in several different areas.

The average density of ascidians was moderately high (34 and 27 individuals/m^2) in only two of the six stan-



ASCIDIACEA

Figure 237
Geographic distribution of Ascidiacea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

dard geographic areas, Georges Bank and the Southern New England Shelf (Table 6; Fig. 238). In these two areas the biomass also was large (5.1 and 8.4 g/m^2) (Table 8; Fig. 238). In the four other areas their average density was low (2.8 or less/m^2), and the biomass was relatively small (0.1 to 2.6 g/m^2). Biomass was especially small (0.11 and 0.17 g/m^2) in the two slope areas.

Ascidians occurred in a moderately small proportion of samples (12 to 23%) and were present in approximately the same proportion of samples from all areas (Table 10).

Bathymetric Distribution

Ascidians occurred at water depths ranging from 13 to 3,080 m, (Table 11; Fig. 239). Relatively high densities

(6 to 32 individuals/m^2) were encountered on the continental shelf; low densities (0.1 to 2.7/m^2) occurred on the continental slope and continental rise.

Biomass of ascidians, also, was larger on the continental shelf than in deep water beyond the shelf (Table 13; Fig. 239). Average biomass at water depths less than 200 m ranged between 1.0 and 8.9 g/m^2, whereas at depths greater than 200 m the biomass averaged less than 0.7 g/m^2.

Ascidians were present in the samples from nearly all depth classes at about the same low range of 5 to 24% (Table 15).

Relation to Sediments

Ascidians occurred in all six types of bottom sediments; however, their density and biomass varied substantially from one type to another (Table 16; Fig. 240). Densities were relatively high (29 and 22/m^2) on gravel and sand bottoms, and intermediate (11/m^2) in sand-silt. Densities were low (5.1 or less/m^2) in till, shell, and silt-clay.

Biomass of ascidians followed the same trend as density, but the differences were less pronounced (Table 18; Fig. 240). Average biomass was largest (9.7 to 4.4 g/m^2) on gravel and sand, intermediate in sand-silt, and small (<2 g/m^2) in the remaining sediment types.

Frequency of occurrence in the samples was moderately low (11 to 32%) in all types of bottom sediments (Table 20). In the majority of sediment categories, the small differences in occurrence rate are correlated directly with ascidian density and biomass. Shell and till values, which are based on a small number of samples, are incongruous.

Relation to Water Temperature

Although the trends of ascidian density and biomass relative to the annual range in bottom water temperature were not consistent, generally the quantities were larger where the temperature range was moderate, and smaller at both temperature extremes (Tables 21, 23; Fig. 241). In areas where the temperature range was moderate, from 8° to 19.9°C, the average density of ascidians ranged from 6 to 59/m^2 and the biomass ranged from 7 to 14 g/m^2. Where water temperature ranges were extreme, less than 8°C and more than 20°C, the average density was low (2–4/m^2) and the biomass was small (0.5–4.1 g/m^2). Two temperature range classes (8°–11.9°C and 16°–19.9°C) contained significantly greater quantities than did the other classes.

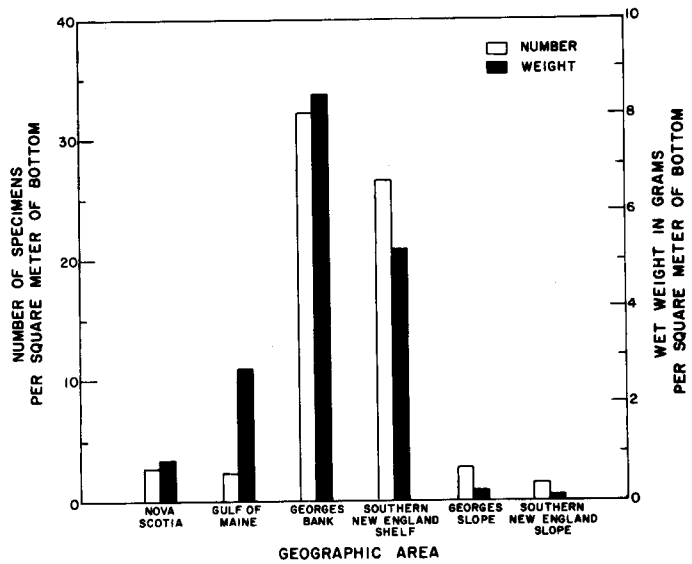


Figure 238
Density and biomass of Ascidiacea in each of the six geographic areas.

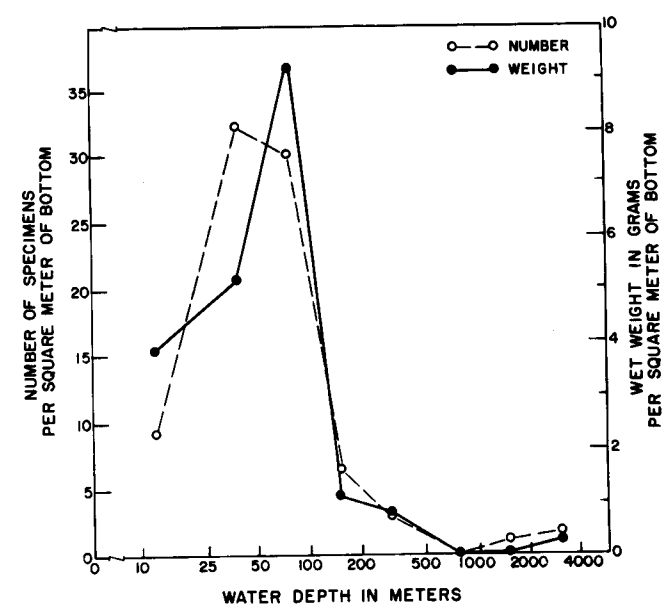


Figure 239
Density and biomass of Ascidiacea in relation to water depth.

Frequency of occurrence of ascidians was moderately low in all temperature range classes. Their occurrence rate, however, was somewhat high (17 to 24%) where the temperature range was moderate, and lower (11 to 12%) where the temperature range was very small and very large (Table 25).

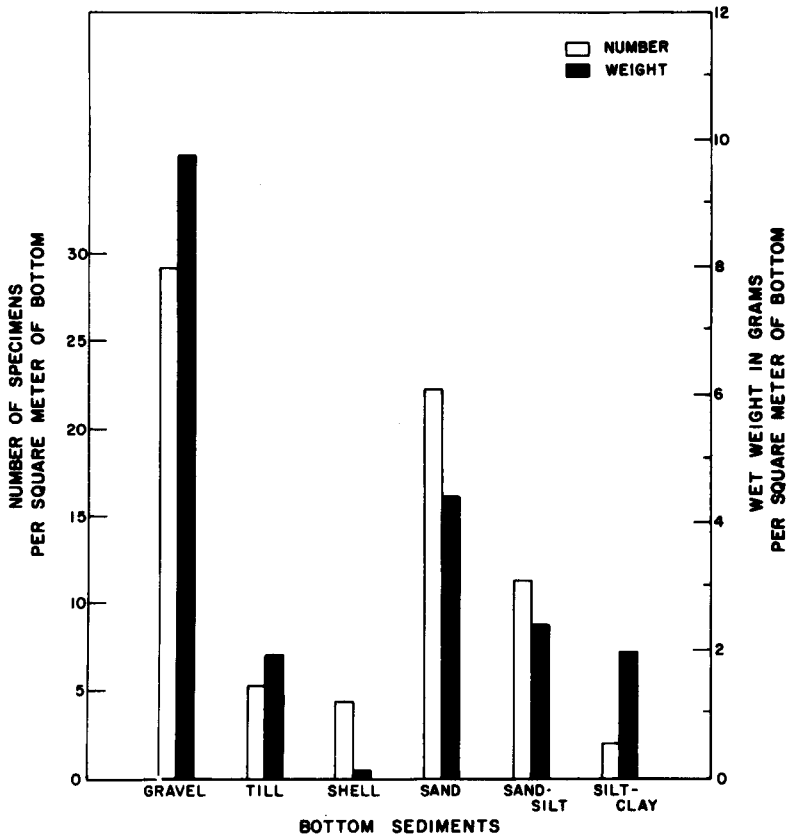


Figure 240
Density and biomass of Ascidiacea in relation to bottom sediments.

Relation to Sediment Organic Carbon

A general trend of diminishing density and biomass with increasing sediment organic carbon content was exhibited by New England region ascidians (Tables 26, 28; Fig. 242), and they were restricted to the low to mid-range carbon content classes between 0.01 and 2.99%. Mean density ranged from 21 to 4.4 individuals/m^2, and mean biomass from 4.4 to 0.2 g/m^2.

Frequency of occurrence in samples was low and paralleled the trend of density and biomass, ranging from 23% to 8% as carbon content increased (Table 30).

Dominant Components of the Macrobenthos

This section identifies and defines the dominant faunal constituents of the New England region macrobenthos and their relationship to each of the abiotic parameters considered in the treatment of each taxonomic group in the preceding sections. "Dominance," as used in this report, refers to the taxonomic group that mathematically contributed the highest number of individuals or greatest total accumulated wet weight. Results are expressed in both measures of abundance because of the marked differences that existed between them.

In spite of individual disparity in rank order within each measure of abundance, members of four taxonomic groups, collectively, made up the bulk of the macrobenthic invertebrate fauna of the New England region. The four major taxonomic components are 1) Annelida; 2) Mollusca, comprising Bivalvia, the chief component, as well as Gastropoda, Scaphopoda, Polyplacophora, and Cephalopoda; 3) Crustacea, with Amphipoda the chief component of this group, followed by Cumacea, Isopoda, Decapoda, Cirripedia, Mysidacea, Tanaidacea, Ostracoda, and Copepoda in progressively smaller proportions; and 4) Echinodermata composed of Ophiuroidea, Echinoidea, Holothuroidea, Asteroidea, and Crinoidea in diminishing proportions. Table 3 lists the contributions of each of the above taxa to the total density and biomass of the New England macrobenthic fauna.

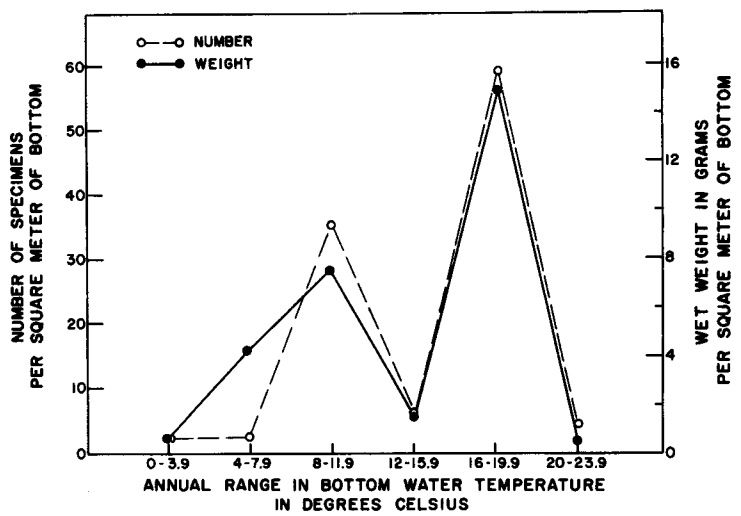


Figure 241
Density and biomass of Ascidiacea in relation to the annual range of bottom water temperature.

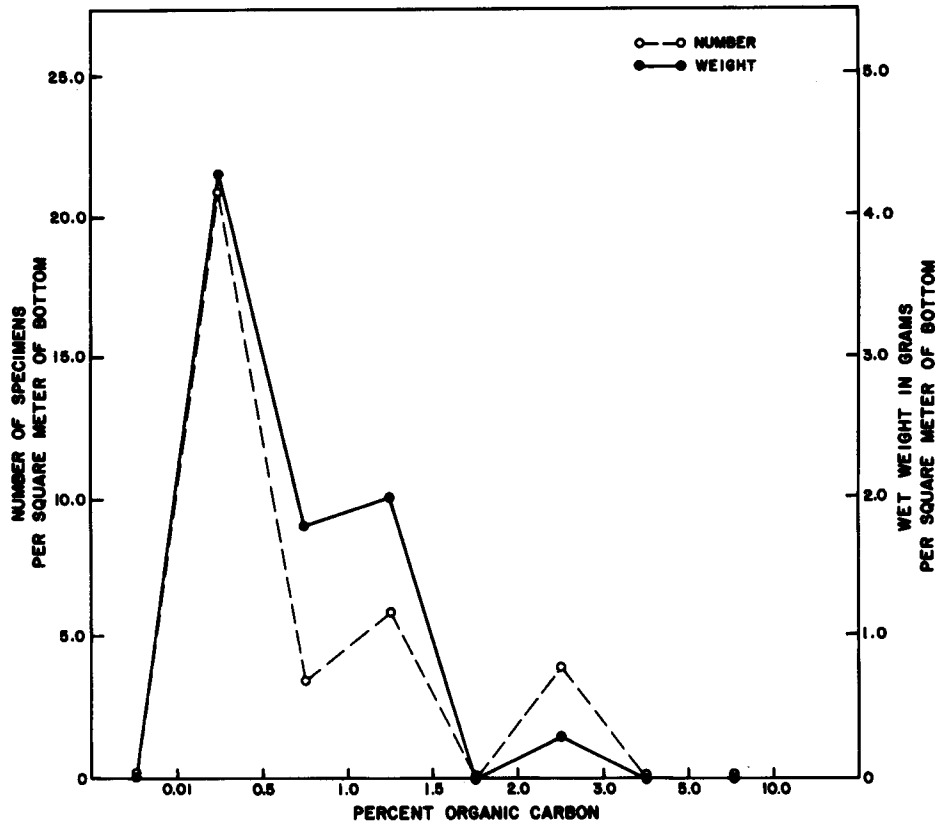


Figure 242
Density and biomass of Ascidiacea in relation to sediment organic carbon.

Frequency of Occurrence

Among the four dominant taxa, Annelida was the most ubiquitous in distribution, occurring in 96% of all stations sampled (Table 5). Next in order were members of Mollusca, which occurred in 88% of all samples, followed by Crustacea in 85% of the samples; echinoderms ranked fourth with a 72% occurrence rate.

For comparative purposes, some nondominant taxa showed intermediate frequencies; among these were Coelenterata, which occurred in 42% of the samples, and Nemertea and Sipunculida with frequencies of 34% and 23%, respectively. Ascidiacea, Bryozoa, Aschelminthes, Porifera, Brachiopoda, Pogonophora, Turbellaria, and Hemichordata were encountered with diminishing frequencies ranging from 17% to <1%.

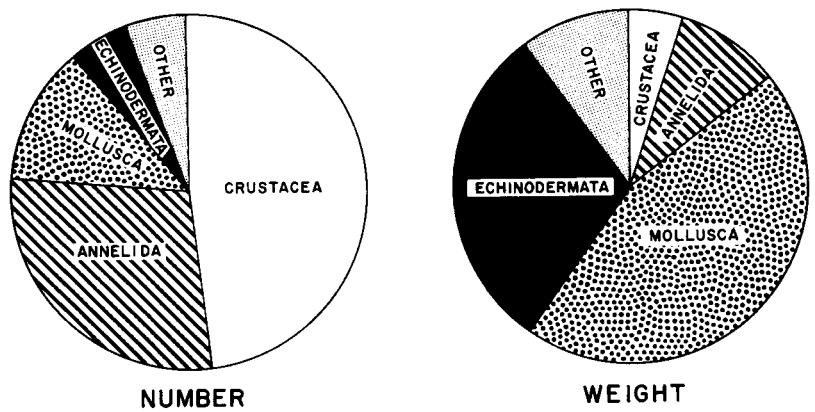


Figure 243
Percentage composition of the dominant components of the macrobenthic invertebrate fauna expressed in terms of number of individuals and wet weight of the total fauna.

Percentage Composition

The four dominant macrobenthic components collectively contributed more than 90% of the total number of individuals, and 90% of the accumulated wet weight of the macrobenthos sampled within the New England region. The relative contribution and ranking of the four, however, differed markedly between the two measures of abundance (Fig. 243).

Crustacea, with Amphipoda providing the single largest amount of individuals, was the highest ranking taxonomic component in terms of density, accounting for nearly one half (48%) of all individuals within the region. Annelida ranked second, providing slightly more than 28% of the total number of individuals encountered; Mollusca and Echinodermata followed, contributing somewhat more than 12% and 5% of the total number of individuals, respectively.

The biomass ranking was nearly the reverse of that for density. Mollusca, with Bivalvia predominating, ranked first in biomass versus third in density, contributing 46% of the total weight. Echinodermata ranked second versus fourth; Annelida ranked third versus second; and Crustacea, first in density, ranked fourth in biomass.

The differences in rank order between the two measures of abundance are attributable to size differences within the various taxonomic groups.

Geographic Distribution

The geographic distribution of density and biomass of each of the four dominant components of the macrobenthos of the New England region is depicted in Figures 69, 99, 146, and 202. Within the subareas of the region, the rank order of the four dominant taxa varied in terms of density and biomass (Figs. 13B, 14B; Tables 6, 8). In the Nova Scotia subarea, Annelida ranked first in density (648/m^2) but third in biomass (19 g/m^2); Crustacea was second in density (329/m^2) but fourth in biomass (17 g/m^2); Mollusca, third in density (77/m^2), was first in biomass (54 g/m^2); while Echinodermata fourth in density (24/m^2), was second in terms of biomass (39 g/m^2).

In the Gulf of Maine, mollusks (306/m^2) replaced annelids (29/m^2) as the dominant taxon in terms of density, the latter occupying second place, whereas mollusks were second (32 g/m^2) and annelids third (16 g/m^2), in biomass. Crustaceans (150/m^2) and echinoderms (43/m^2) ranked third and fourth, respectively, in density but were fourth (2 g/m^2) and first (56 g/m^2), respectively, in biomass.

On Georges Bank, the crustaceans (1052/m^2)were nearly twice as abundant as the annelids (546/m^2), almost nine times denser than echinoderms (121/m^2), and 22 times denser than mollusks (47/m^2). In terms of biomass, however, the echinoderms (120 g/m^2) outweighed mollusks (80 g/m^2) by 1.5 times, and crustaceans (10 g/m^2) and annelids (8 g/m^2) by 12 and 15 times, respectively.

In the Southern New England Shelf subarea, density was dominated by crustaceans (1385/m^2), followed by annelids (531/m^2), mollusks (244/m^2) and echinoderms (123/m^2) in terms of density. Mollusk biomass (171 g/m^2) was dominant in this subarea followed by significantly smaller amounts of echinoderm (36 g/m^2), annelid (30 g/m^2), and crustacean (17 g/m^2) biomass.

The two continental slope subareas contained lower densities and biomasses of all components than the shelf subareas. The mean densities and biomass on Georges Slope for the major taxa were as follows: Crustacea, 138/m^2 and 0.6 g/m^2; Mollusca, 83/m^2 and 2.7 g/m^2; Annelida, 80/m^2 and 4.9 g/m^2; and Echinodermata, 19/m^2 and 3.9 g/m^2. Southern New England Slope values were Annelida, 149/m^2 and 4.3 g/m^2; Mollusca, 58/m^2 and 1.2 g/m^2; Arthropoda, 22/m^2 and 0.1 g/m^2; Echinodermata, 19/m^2 and 10 g/m^2.

Selected Genera and Species—This section deals with the geographic distribution of 24 selected genera and species of macrobenthic invertebrates. These particular forms were selected because of their common occurrence, regional ubiquity, or distinctive distribution. Figures 244 to 249 depict the distributions of the selected forms.

Phylum Annelida

Aphrodita hastata (Moore) (Fig. 244). Commonly known as the sea mouse, this polychaete bristle worm of the family Aphroditidae may attain lengths up to 150 mm (6 inch); smaller individuals are often found in haddock, cod and red hake stomachs. It commonly inhabits mud bottoms, or mixed bottoms with a high mud content.

Scalibregma inflatum (Rathke) (Fig. 244). This medium-sized (1–5 cm) polychaete is a member of the family Scalibregmidae. An important food of many demersal fish, this species inhabits silty sand substrates.

Sternaspis scutata (Renier) (Fig. 244). This moderately small (1 cm), burrowing polychaete is stout in appearance and is a member of the family Sternaspidae; it is found in the diet of winter flounder. It commonly inhabits silty sediments.

Phylum Mollusca

Arctica islandica (Linnaeus) (Fig. 244). This rather large (18–15 cm) commercially harvested bivalve, known as the ocean quahog, mahogany quahog, or black clam, belongs to the family Arcticidae. It is a very slow-growing species that occurs very abundantly in some localities on the continental shelf. Small to medium-sized individuals are preyed upon by cod and several species of starfish. It usually inhabits muddy sand bottoms.

Astarte undata Gould (Fig. 245), the common wavy astarte of the family Astartidae, is a medium-sized (2.5–3.8 cm) bivalve. In the New England region, it is most prevalent at mid-shelf depths (50–99 m) in sand and till substrates. Although juvenile specimens are occasionally found in fish stomachs, it is not a major prey item of demersal fishes.

Cerastoderma pinnulatum (Conrad) (Fig. 245), the northern dwarf cockle, is a common, moderately small (1 cm) bivalve belonging to the family Cardiidae. This species is infrequently found in fish stomachs. It prefers sandy substrates but does occupy, in lower abundance, other types of sediments.

Cyclocardia borealis (Conrad) (Fig. 245), the northern cyclocardia, is a medium-sized (3–5 cm) bivalve of the family Carditidae. Broadly distributed throughout the region, it prefers sand and till substrates but does occur in other sediments as well. It is not common in fish diets.

Modiolus modiolus (Linnaeus) (Fig. 245), the northern horse mussel, is the largest (5–15 cm) and most common mussel of the offshore New England region; it is a member of the family Mytilidae. It is found on the periphery of the Gulf of Maine and on Georges Bank, and extends onto the Southern New England Shelf. It prefers sand and sand-shell substrates.

Placopecten magellanicus (Gmelin) (Fig. 246), the sea scallop, is one of the most valuable commercial shellfish resources of the U.S. East Coast, especially in the New England region. It is a large bivalve (12–20 cm) of the family Pectinidae, found most abundantly on coarse sandy bottoms. In addition to harvest by man, juveniles of this species are found in the diets of some demersal fishes, principally haddock, and ocean pout.

Buccinum spp. (Fig. 246) is represented in our samples by four species in the family Buccinidae. The species represented are *B. elatius, B. gouldi, B. hydrophanum,* and *B. undatum.* Among the four species, the moderately large (5–10 cm) *B. undatum,* the waved whelk, is overwhelmingly the most common form. They are typically found at mid- to lower-shelf depths in sand and coarser grained sediments.

Neptunea decemcostata (Say) (Fig. 246), the wrinkled whelk, is a moderately large (7–11 cm) gastropod belonging to the family Buccinidae. This species typically inhabits hard bottoms ranging from coarse sand to gravels at mid- to lower-shelf depths.

Phylum Arthropoda

Ampelisca agassizi (Judd) (Fig. 246), this gammaridean amphipod of the family Ampeliscidae is a medium-sized (4–7 mm) tube dweller. It is the most abundant and common species of amphipod in the southwestern half of the study area; in some localities it is exceptionally abundant. It prefers a sandy substratum. This species is a very common prey in the diet of many demersal fish.

Leptocheirus pinguis (Stimpson) (Fig. 247), a species of gammaridean amphipod, family Aoridae, is a moder-

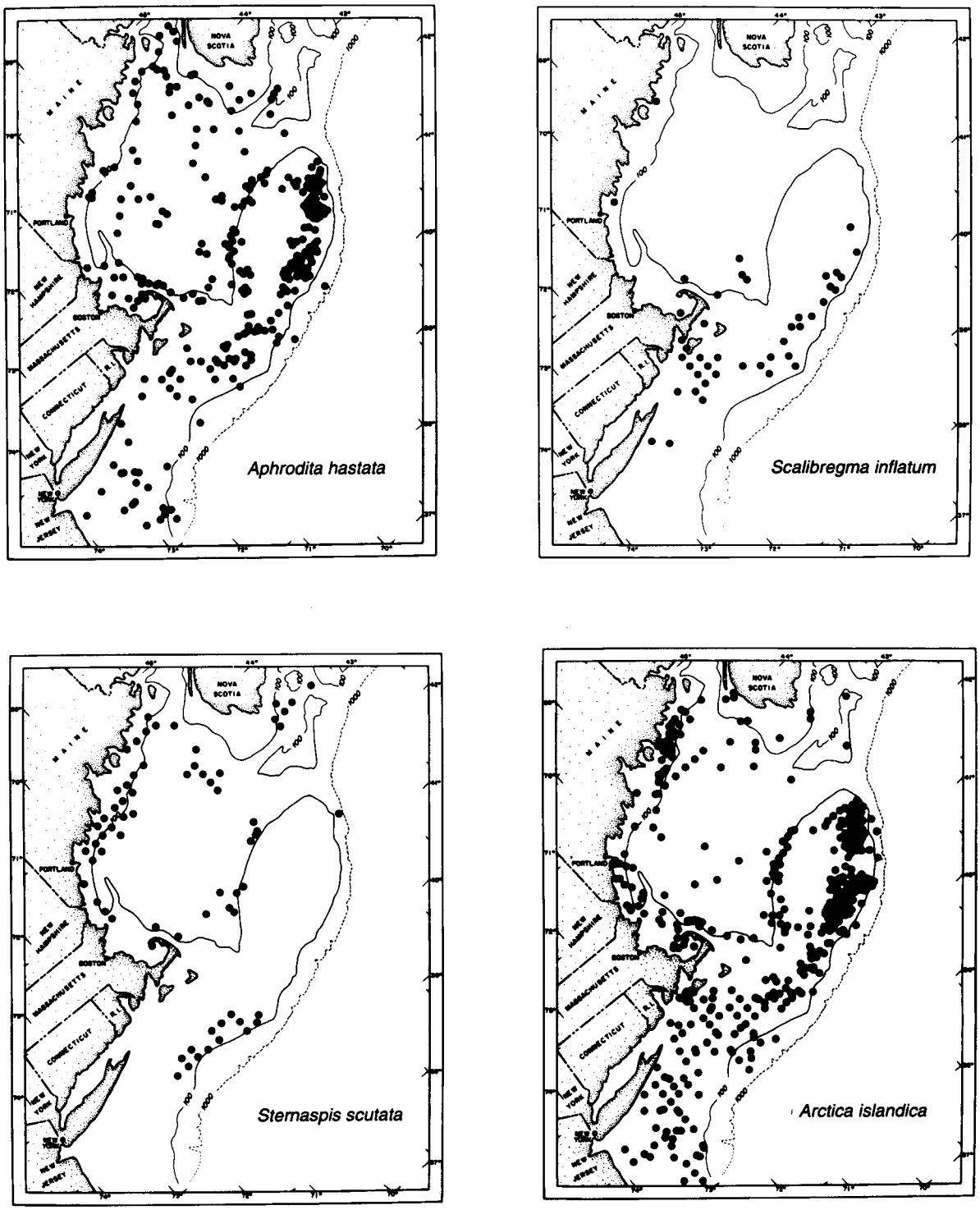


Figure 244
Geographic distribution of three selected species of Annelida, and one species of Bivalvia.

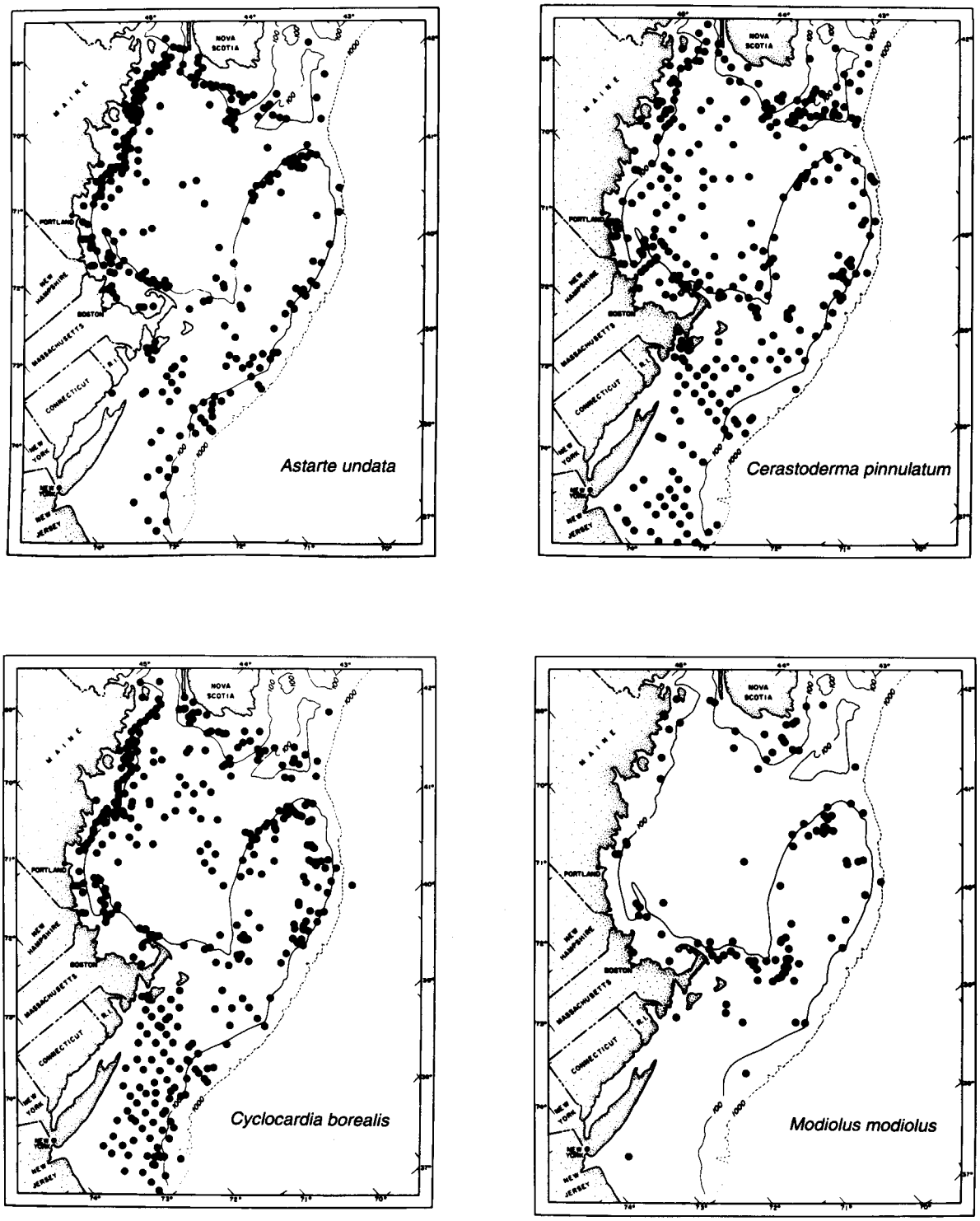


Figure 245
Geographic distribution of four selected species of Bivalvia.

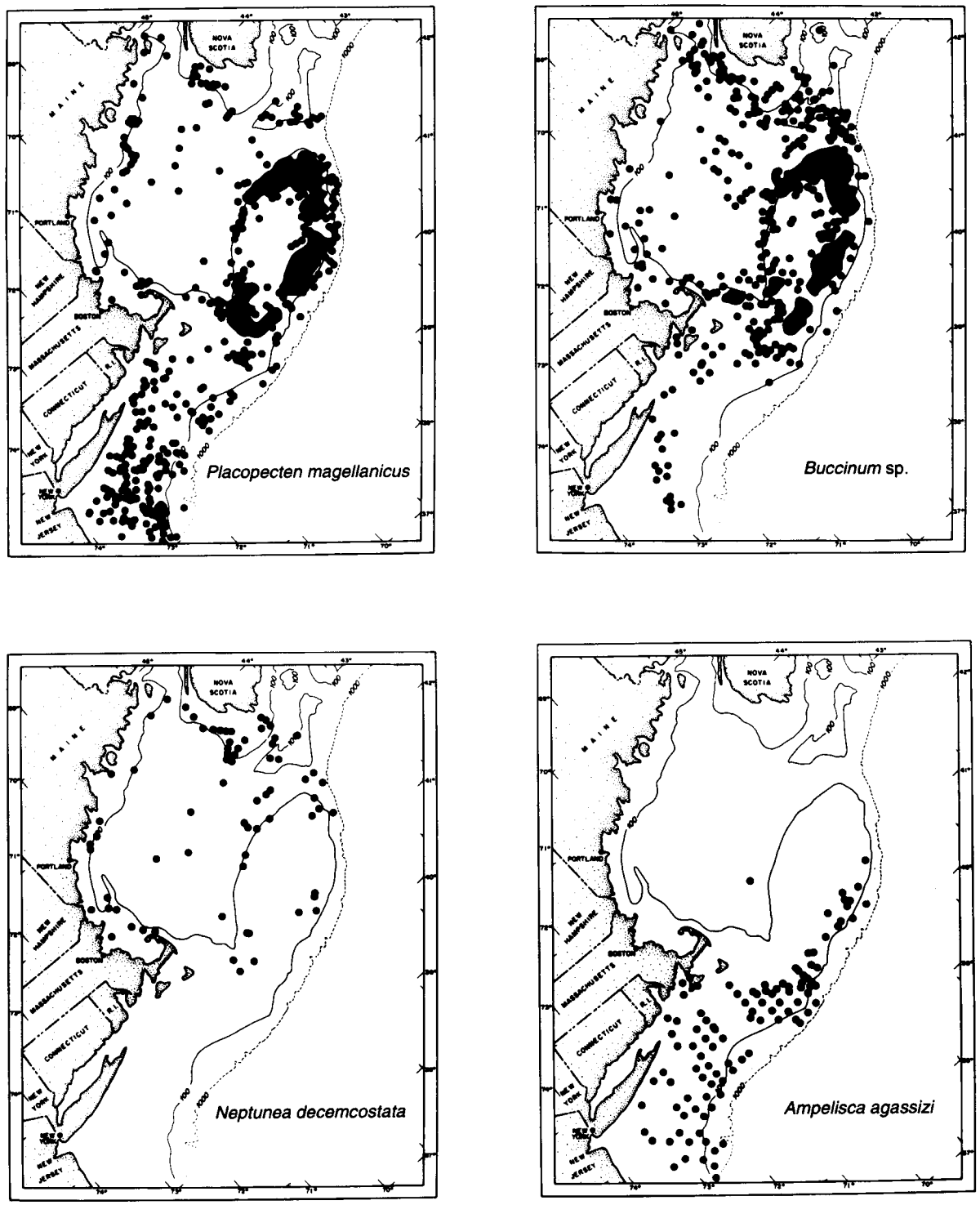


Figure 246
Geographic distribution of one selected species of Bivalvia, one genus and one species of Gastropoda, and one species of Amphipoda.

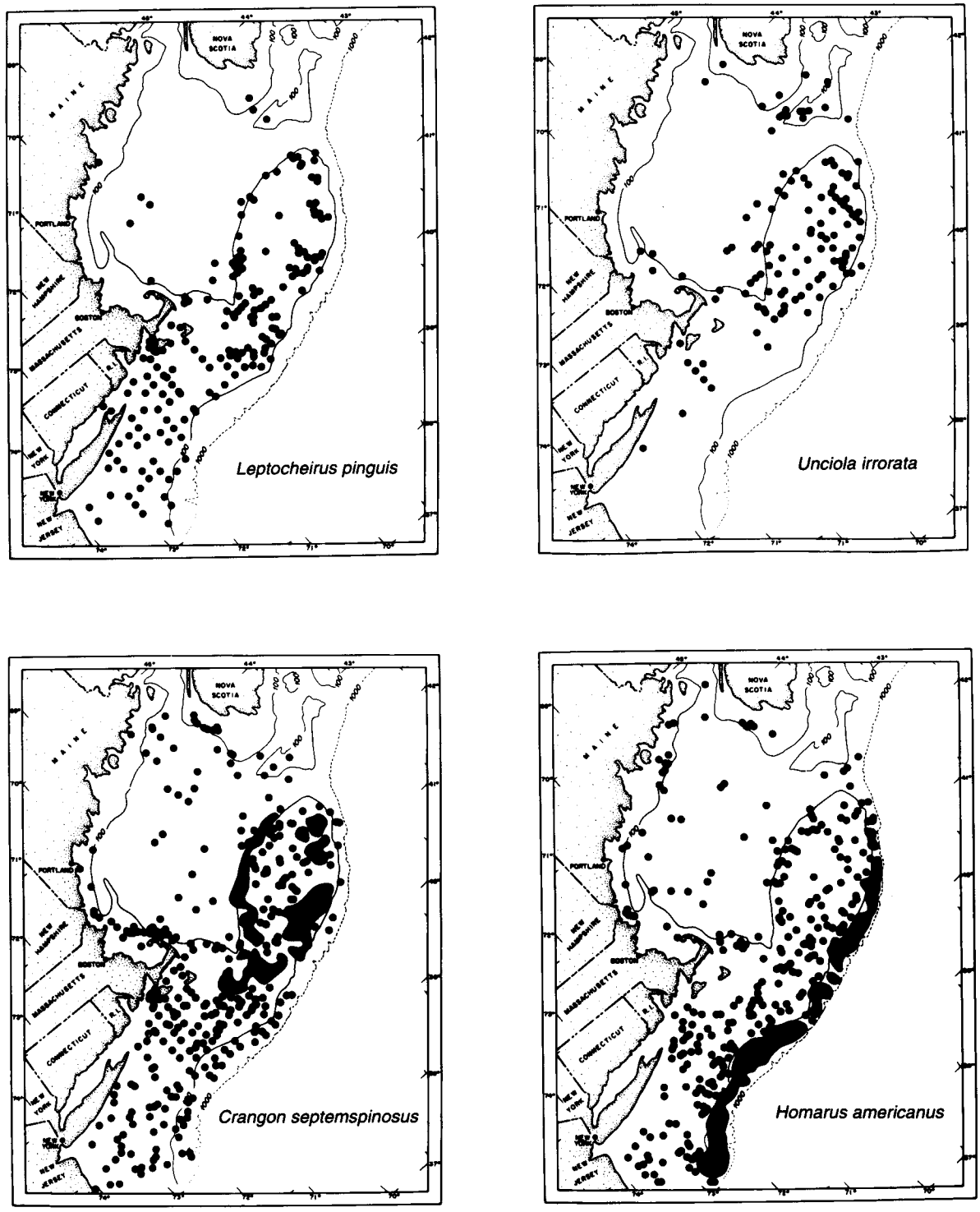


Figure 247
Geographic distribution of two selected species of Amphipoda, and two of Decapoda.

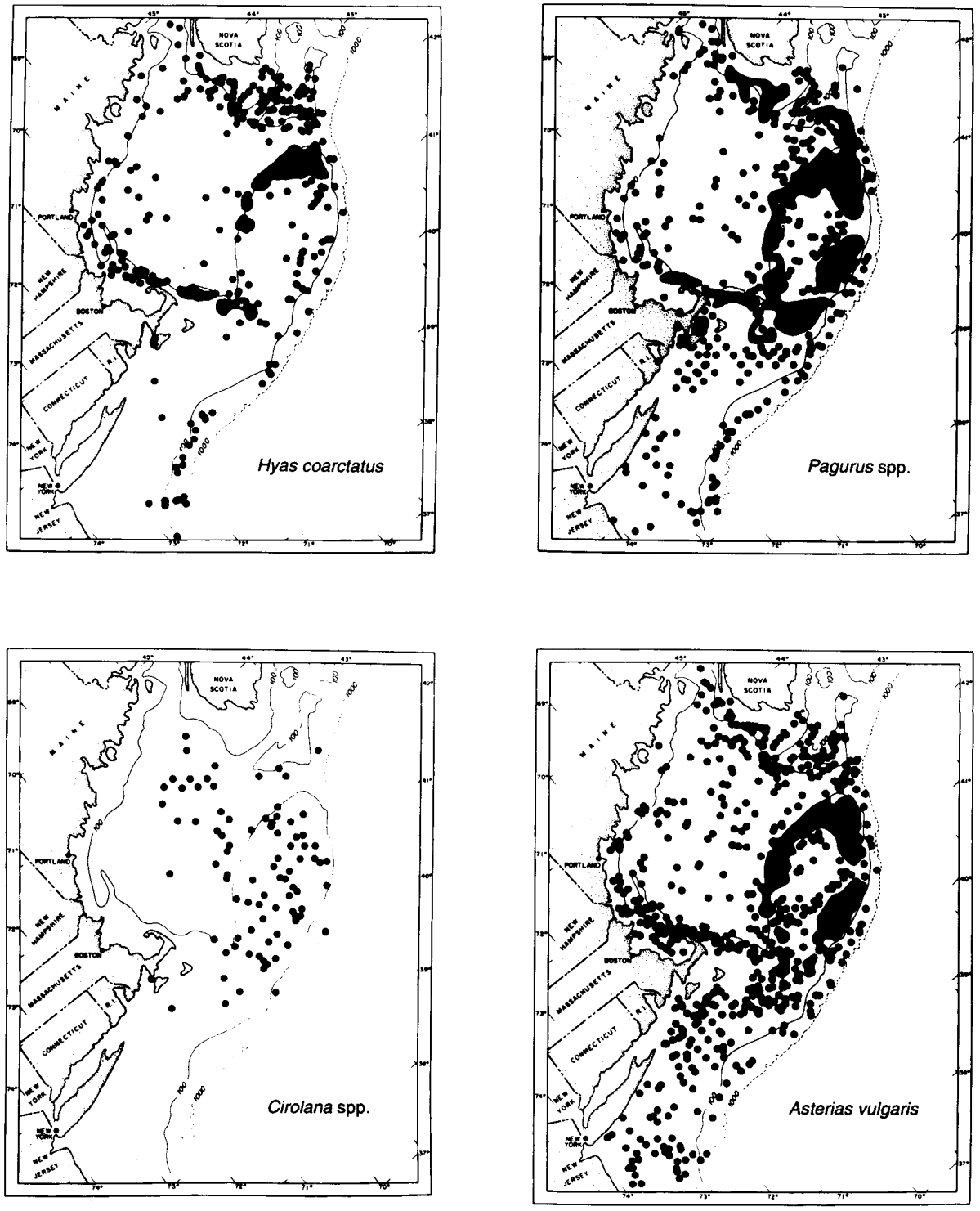


Figure 248
Geographic distribution of one species and one genus of Decapoda, one genus of Isopoda, and one species of Asteroidea.

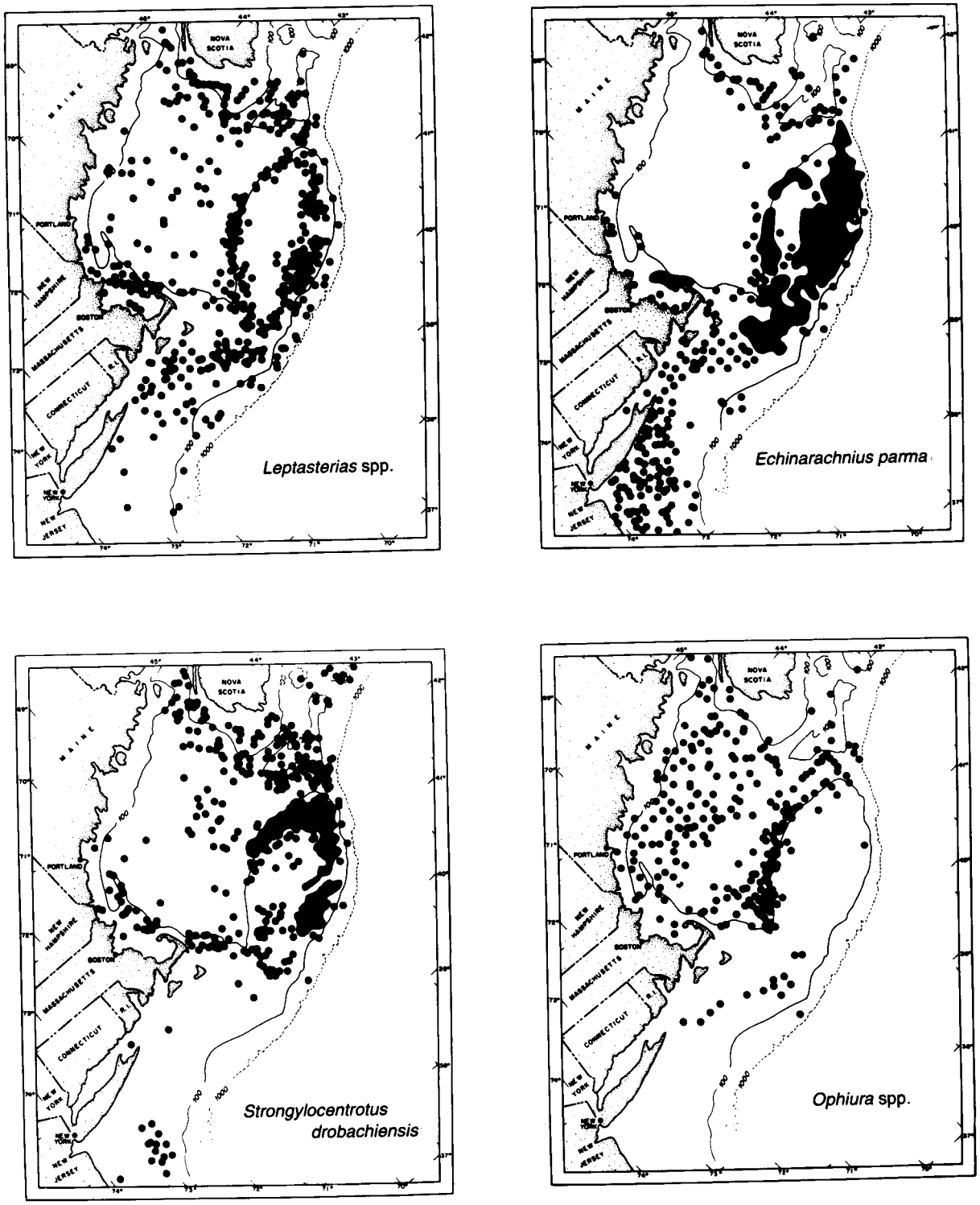


Figure 249
Geographic distribution of one genus of Asteroidea, two species of Echinoidea, and one genus of Ophiuroidea.

ately large (10–17 mm) and abundant tube-dwelling inhabitant of continental shelf sandy substrates. It is very important in demersal fish diets.

Unciola irrorata (Say) (Fig. 247), another moderate-sized (10–13 mm) tube-dwelling gammaridean amphipod of the family Aoridae, is abundant in the sands of Georges Bank and is also very important in demersal fish diets.

Crangon septemspinosa Say (Fig. 247), the sevenspined bay shrimp, a moderately small (5–8 cm) caridean shrimp of the family Crangonidae. It is typically found in sandy sediments of the region in both inshore and continental shelf waters, and in certain localities is very abundant. This shrimp is a very important prey to nearly all demersal fishes.

Homarus americanus H. Milne-Edwards (Fig. 247), the American lobster, is, together with the sea scallop, one of the most commercially valuable invertebrate resources of the northwest Atlantic. It is widely distributed throughout the New England region from inshore bays and sounds to the offshore canyons bisecting the edge of the continental shelf. Size of mature lobsters ranges from around 25 cm average length, for individuals captured for market by the inshore fishery, to very large (sometimes in excess of 80 cm), for specimens in the offshore stock; minimum legal size for capture is currently 8.13 cm (3.25 inch). Lobsters are scavengers and inhabit a variety of substrates.

Hyas coarctatus Leach (Fig. 248), the arctic lyre crab, is a moderately small (to 31 mm) spider crab in the family Majidae. This species is common throughout the New England region on muddy and pebbly bottoms. Small individuals have been reported to occur occasionally in the diet of long-horned sculpin.

Pagurus spp. (Fig. 248) comprise seven species of pagurid hermit crabs resident in the New England region. The species of the genus *Pagurus* in the family Paguridae represented in this study include *P. acadianus, P. annulipes, P. arcuatus, P. longicarpus, P. politus, P. pollicaris,* and *P. pubescens.* The represented species range from small to medium in size (9–31 mm, carapace length), are ubiquitous throughout the region in nearly all substrate types, and are preyed upon by bottom fishes. The most common and broadly distributed species is *P. acadianus.*

Cirolana spp. (Fig. 248), comprise three species of the isopod crustacean family Cirolanidae resident in the study area (*C. concharum, C. impressa,* and *C. polita*) along with several others identified only to the generic level. These moderately small (16–23 mm) crustaceans are fairly common on muddy and sandy bottoms in the Gulf of Maine and on Georges Bank. They are prey to a variety of demersal fishes.

Phylum Echinodermata

Asterias vulgaris Verril (Fig. 248), the northern starfish or purple star, is one of the most common starfishes inhabiting the offshore waters of the New England region and is a member of the family Asteriidae. This is a large species commonly between 15 cm and 30 cm (6–12 inch) in diameter; some specimens up to 42.5 cm (17 inch) have been reported from the northern limits of its range. It is normally found on sandy bottoms where it is a very important predator of bivalve mollusks. Juvenile specimens are occasionally encountered in fish stomachs.

Leptasterias spp. (Fig. 249), which represent several species of the genus *Leptasterias,* also of the family Asteriidae, are common inhabitants of the New England Region on sandy bottoms. These brightly, but variably, colored species are of moderate size (5–10 cm) and in some localities are very abundant. Small specimens are occasionally preyed upon by some species of groundfish.

Echinarachnius parma (Lamarck) (Fig. 249), the northern sand dollar, is the most abundant urchin (class Echinoidea, family Scutellidae) of the New England region; it is so abundant in some localities of Georges Bank that the bottom resembles a mosaic pavement. As its common name implies, it is a sand dweller. Sand dollars of the region are typically 7.5 cm in diameter. They are a common prey of flounders, haddock and cod.

Strongylocentrotus droebachiensis (Müller) (Fig. 249), another ubiquitous echinoid (family Strongylocentrotidea), the green sea urchin, is a hard bottom dweller for whose popular roe a commercial fishery, inactive since the 1930's and 1940's, is reemerging in northeastern U.S. and Canadian waters. Size ranges from 5 cm to nearly 9 cm. Haddock and American plaice prey on this spiny morsel.

Ophiura spp. (Fig. 249) comprise three species and some undetermined specimens of this genus of brittle stars (family Ophiolepididae) inhabiting the New England region; included are *O. ljungmani, O. robusta, O. sarsi,* and unidentified species. Members of this group are widely distributed and occur in most sediment types. Size of the central disc ranges from 10 to 38 mm. They are common in the diets of haddock and American plaice.

Bathymetric Distribution

In the New England region density and biomass of the major taxa generally decreased with increasing water depth (Tables 11, 13; Figs. 15, 16). Crustacea was the dominant component of the fauna, in terms of density, in shallow and continental shelf depths, ranging from 1,351 to 169 individuals/m^2. Substantially lower densities occurred in waters deeper than 200 m. Annelida had the next highest densities in shallow waters (719/m^2) and at continental shelf depths (519–437/m^2). Moderate numbers (241–107/m^2) occurred at conti-

nental slope depths, and low densities (9–30/m^2) were encountered at lower slope and upper rise depths. Mollusca showed a similar pattern of density distribution with depth; density was greatest (570/m^2) in shallow water, moderate (136–205/m^2) at shelf depths, and moderately low in deeper waters. However, mollusks were numerically dominant at the deeper depths. Echinoderm density was greatest (133/m^2) at mid-shelf depths between 25 m and 49 m, moderate (87–95/m^2) in deeper shelf water, and decreased with increasing depth beyond 200 m. Moderately low densities (47/m^2) occurred in shallow (0–24 m) water.

Mollusca was the dominant faunal component of biomass at nearly all depths. Greatest biomass (258 g/m^2) occurred in shallow water (0–24 m) with values moderately high (132–21 g/m^2) at shelf depths and diminishing rapidly at depths below 200 m. Echinoderm biomass was greatest (167–106 g/m^2) in waters of 49 m and less, decreased to 34 g/m^2 at outer shelf depths, but dominated at depths beyond 200 m (1.7–19 g/m^2). Annelida biomass was highest (27 g/m^2) in shallow (0–24 m) water and nearly equal (25 g/m^2) in water depths between 50 m and 99 m. Values ranged between 15 g/m^2 and 16 g/m^2 at other continental shelf depths but decreased rapidly with increasing depth beyond 200 m. Crustacea, although numerically dominant, ranked fourth in biomass at nearly all depths except the shallowest one (0–24 m) where a value of 37 g/m^2 placed them third. Biomass of crustaceans ranged from 2 to 16 g/m^2 at continental shelf depths (25–199 m), with a rapid decrease from 4 g/m^2 at 200–499 m to approximately 0.1 g/m^2 in slope and rise waters.

Relation to Bottom Sediments

Numerical abundance of the four dominant faunal components in relation to the six major sediment types encountered in the New England region did not exhibit any trend as dramatic as that for depth (Tables 16, 18; Fig. 17). Annelids seemed to prefer sand (558/m^2), gravel (505/m^2), and shell (443/m^2) bottoms but were moderately abundant in till, sand-silt, and silt-clay bottoms as well. Mollusks were generally more abundant in silt-clay (354/m^2), shell (229/m^2), and sand-silt (276/m^2) but were found in somewhat lower abundance in other sediments also. Crustacea were most abundant in sand (1,336/m^2), gravel (710/m^2), and sand-silt (275/m^2) and were found in diminishing amounts in shell (124/m^2), till (59/m^2), and silt-clay (34/m^2). Sand-silt (104/m^2) and sand (95/m^2) contained the most echinoderms, followed by till and silt-clay (67/m^2 and 65/m^2, respectively), then shell (28/m^2) and gravel (23/m^2).

Density rank order in the various sediments listed by decreasing particle size was as follows: gravel: Crustacea, Annelida, Mollusca, Echinodermata; till: Annelida, Mollusca, Echinodermata, Crustacea; shell: Annelida, Mollusca, Crustacea, Echinodermata; sand: Crustacea, Annelida, Mollusca, Echinodermata; sand-silt: Annelida, Mollusca and Crustacea equal, Echinodermata; silt-clay: Mollusca, Annelida, Echinodermata, Crustacea.

The distribution of the biomass of the major taxa among the various sediment types was fairly even. The annelids showed the greatest uniformity with the smallest biomass (11 g/m^2) in till and largest (26 g/m^2) in sand-silt. Biomass ranged from 15 to 16 g/m^2 in the four other types. Mollusks showed some variability, with shell bottoms containing the largest biomass (168 g/m^2) and till the smallest (6 g/m^2). Molluscan biomass in gravel was 94 g/m^2, in sand 121 g/m^2, in sand-silt 74 g/m^2, and in silt-clay 18 g/m^2. Crustacean biomass was 20 g/m^2 in gravel and 12 g/m^2 in sand; 7 g/m^2 and 6 g/m^2 in sand-silt and shell, respectively, and 2 g/m^2 and 0.6 g/m^2 in till and silt-clay ,respectively. Echinoderm biomass was greatest in sand (88 g/m^2), 43 g/m^2 in silt-clay, and 37 g/m^2 in sand-silt. Median amounts occurred in till (15 g/m^2) and lower amounts in gravel (6 g/m^2) and shell (3 g/m^2). Biomass rank order in bottom sediments was as follows: gravel: Mollusca, Crustacea, Annelida, Echinodermata; till: Echinodermata, Annelida, Mollusca, Crustacea; shell: Mollusca, Annelida, Crustacea, Echinodermata; sand: Mollusca, Echinodermata, Annelida, Crustacea; sand-silt: Mollusca, Echinodermata, Annelida, Crustacea; and silt-clay: Echinodermata, Mollusca, Annelida, Crustacea.

Relation to Water Temperature

Among the four dominant taxa there were no clear-cut trends discernible with regard to the annual range in bottom water temperature (Tables 21, 23; Fig. 18). Where ranges of temperatures were between 8 and 19.9°C, Crustacea was the numerically dominant taxon, with densities ranging from 768 to 1,475 individuals per m^2, whereas annelids dominated in areas exhibiting rather stable annual temperature regimes, between 0 and 7.9°C (212–513 individuals per m^2), and in areas experiencing the broadest temperature range of 20–23.9°C, where mean densities of 1,698 individuals per m^2 were found. Densities of Mollusca and Echinodermata were fairly consistent at moderate levels (84–345/m^2 for Mollusca and 21–171/m^2 for Echinodermata) throughout the temperature range spectrum. Mollusca, however, did make a strong showing (1,242 individuals/m^2) where the range in annual temperature was broadest.

Rank order of dominance for the major taxa in the six annual temperature range classes in terms of density was as follows: 0–3.9°C: Annelida, Crustacea, Echi-

nodermata, Mollusca; 4–7.9°C: Annelida, Crustacea, Mollusca, Echinodermata; 8–11.9°C: Crustacea, Annelida, Mollusca, Echinodermata; 12–15.9°C: Crustacea, Mollusca, Annelida, Echinodermata; 16–19.9°C: Crustacea, Annelida, Mollusca, Echinodermata; 20–23.9°C: Annelida, Mollusca, Crustacea, Echinodermata.

The relationship of the dominant taxa biomasses to annual range of bottom water temperature was similar to that of density in that no definite trends were evident. However, a marked change in dominance ranking prevailed, wherein the density dominants (crustaceans and annelids) were replaced by echinoderms and mollusks as the leading contributors to biomass in nearly all temperature range regimes. Echinodermata dominated biomass in four of the six temperature range classes, including the narrowest and broadest ranges; their mean biomass ranged from 12 to 263 g/m^2. Mollusk biomass, second to that of echinoderms in most temperature ranges, was clearly dominant where temperature ranges of 8–11.9°C and 16–19.9°C prevailed; their mean biomass was 129 g/m^2 in the former and 340 g/m^2 in the latter. The contributions of the other two dominant taxa, annelids and especially crustaceans, due to their small size, were clearly subordinate in all temperature regimes. Annelid biomass ranged from 10 to 40 g/m^2, and crustacean biomass from 1 to 25 g/m^2.

Rank order of dominance for the major taxa in the six annual temperature range classes in terms of biomass was as follows: 0–3.9°C: Echinodermata, Annelida, Mollusca, Crustacea; 4–7.9°C: Echinodermata, Mollusca, Annelida, Crustacea; 8–11.9°C: Mollusca, Echinodermata, Annelida, Crustacea; 12–15.9°C: Echinodermata, Mollusca, Annelida, Crustacea; 16–19.9°C: Mollusca, Echinodermata, Annelida, Crustacea; 20–23.9°C: Echinodermata, Mollusca, Annelida, Crustacea.

Relation to Sediment Organic Carbon

As mentioned above (see section "Total Macrobenthos") there was no clear-cut correlation between sediment organic carbon content and faunal abundance except in a few exceptional cases (Tables 26, 28; Fig. 26).

The numerical abundance of the dominant taxa varied widely in relation to organic carbon content for all except Echinodermata. This taxon ranked fourth in all organic carbon content classes except two (0.00% and 1.00–1.49%) where it ranked third, slightly ahead of Crustacea. Density of echinoderms was moderately low, ranging from only 3–91 individuals per m^2. Crustacean density varied widely among the various carbon content classes, ranging from 21 to 1,357/m^2. Greatest abundances occurred in carbon content levels of 0.01–0.49% (1,066/m^2) and 3.00–4.99% (1,357/m^2), with moderately low to fairly high densities occurring in carbon content levels between these two. Lowest densities (21–22/m^2) prevailed in areas where no measurable carbon existed as well as in areas where the greatest amounts of carbon were measured. Mollusca, was one exception, showing a positive correlation of generally increasing density with increasing carbon, ranging from 69/m^2 in areas devoid of carbon to 1,120/m^2 where carbon was between 3.0% and 4.9%. No mollusks occurred where carbon content exceeded 5%. Annelida were present in all organic carbon content classes. Their density was significantly lower at both extremes of the carbon content spectrum (between 11/m^2 and 81/m^2) compared with their abundance (196–504/m^2) in areas containing low (0.01–0.49%) to moderate (2.0–2.99%) amounts of carbon.

Rank order of the numerical abundance of the dominant taxa with regard to organic carbon content was as follows: 0%: Mollusca, Annelida, Echinodermata, Crustacea; 0.01–0.49%: Crustacea, Annelida, Mollusca, Echinodermata; 0.50–0.99%: Annelida, Crustacea, Mollusca; Echinodermata; 1.00–1.49%: Mollusca, Annelida, Echinodermata, Crustacea; 1.50–1.99%: Mollusca, Annelida, Crustacea, Echinodermata; 2.00–2.99%: Crustacea, Mollusca, Annelida, Echinodermata; 3.00–4.99%: Crustacea, Mollusca, Annelida, Echinodermata; 5.00%+: Crustacea, Annelida; no Mollusca or Echinodermata were found in this class.

Similar to numerical abundance, biomasses of dominant taxa showed no clear-cut correlation to the organic carbon content of the bottom sediments. Most notable was the considerable echinoderm biomass in all but the highest carbon content classes, compared with its low numerical density. Highest mean biomasses (105 g/m^2 and 562 g/m^2) occurred in areas with moderately high carbon contents (between 2% and 4.99%), and lowest (6 g/m^2) occurred in areas devoid of measurable organic carbon. Moderate biomasses, ranging from 23 to 44 g/m^2, occurred in areas with low to intermediate carbon content levels (0.01–1.99%). Mollusca, also absent where the highest measures of organic carbon occurred, nevertheless showed a preference for some organic carbon content, with highest biomasses (812 g/m^2 and 227 g/m^2) occurring in the two carbon content classes between 2.0 and 4.99%. However, moderately high biomass (132 g/m^2) was also found where carbon levels were only between 0.01 and 0.49%. Lowest biomass (only 0.8 g/m^2) occurred in sediments devoid of carbon. Moderate levels of biomass (25–13 g/m^2) occurred in organic carbon levels that ranged from 0.50 to 1.99%. The mean biomass of Annelida was fairly consistent at moderate levels ranging between 11 g/m^2 and 27 g/m^2 in areas of organic carbon content ranging between 0.01 and 4.99%. Lowest mean biomass of annelids (0.11 g/m^2) occurred in the highest carbon content class (5+%) and intermediate amounts (7 g/m^2) were found where measurable

carbon was absent in the sediments. Crustacean mean biomass ranged from a low of 0.11 g/m^2 in areas of highest organic carbon content to a high of 19 g/m^2 where organic carbon was between 2% and 2.99%. Moderately low biomasses (between 1 g/m^2 and 9 g/m^2) occurred in the other carbon content classes. Areas devoid of organic content also contained low mean biomass (0.31 g/m^2).

Rank order of the mean biomass of the dominant taxa in terms of organic carbon content was as follows: 0%: Annelida, Echinodermata, Mollusca, Crustacea; 0.01–0.49%: Mollusca, Echinodermata, Annelida, Crustacea; 0.50–0.99%: Mollusca, Echinodermata, Annelida, Crustacea; 1.00–1.49%: Echinodermata, Mollusca, Annelida, Crustacea; 1.50–1.99%: Echinodermata, Annelida, Mollusca, Crustacea; 2.00–2.99%: Mollusca, Echinodermata, Annelida, Crustacea; 3.00–4.99%: Echinodermata, Mollusca, Annelida, Crustacea; 5.00%+: Annelida and Crustacea were equal, whereas Mollusca and Echinodermata were absent in this class.

Acknowledgments

The authors are grateful to the many persons who provided assistance in the various phases of this study. We are especially indebted to Herbert W. Graham, Robert L. Edwards, and K. O. Emery for their assistance and support in the planning and organization of the study. Northeast Fisheries Center personnel who assisted with the collection and processing of biological samples included Bruce R. Burns, Gilbert L. Chase, Philip H. Chase Jr., Evan B. Haynes, Henry W. Jensen, Lewis M. Lawday, Arthur S. Merrill, Harriet E. Murray, Clifford D. Newell, Timothy Robbins, Carol Schwamb, and Ruth Stoddard Byron.

Appreciation is due the personnel of the NEFC ADP unit for assistance in processing the voluminous numerical database generated by the study; Edward M. Handy, Katherine Payne, Philip H. Chase Jr., Margaret E. Cory, Johnny Blevins, and Francis W. Tinker, for assisting with coding, data entry, programming, plotting, and data processing. Drafting assistance was provided by Frank A. Bailey, Herbert A. Ashmore, and John R. Lamont.

Scientists from the U. S. Geological Survey and Woods Hole Oceanographic Institution marine geology group who provided sedimentological information or participated in shipboard work were K. O. Emery, John C. Hathaway, Jobst Hülsemann, Frank Manheim, Robert H. Meade, Richard M. Pratt, David Ross, John S. Schlee, James V. A. Trumbull, and Elazar Uchupi.

Those who generously provided taxonomic assistance were Edward L. Bousfield, John C. McCain, Edward B. Cutler, Lion F. Gardner, Porter M. Kier, Peter Kinner, Louis S. Kornicker, John M. Kraeuter, Don Maurer, Arthur S. Merrill, Roy Oleröd, David L. Pawson, Frank Perron, Marian H. Pettibone, Thomas Phelan, Harold H. Plough, Johanna Reinhart, Howard L. Sanders, Thomas J. M. Schopf, Eve C. Southward, J. H. Stock, Lowell P. Thomas, Ruth D. Turner, Bertn Widersten, Austin B. Williams, Lev A. Zenkevitch, and Victor A. Zullo.

We also wish to thank Marvin Grosslein, Kenneth Sherman, Robert Reid, and Frank Steimle for their critical review of the manuscript and their many helpful suggestions to improve it.

It is our pleasure to acknowledge the wholehearted cooperation of the officers and crews of the research vessels *Albatross III* (Capt. Emerson Hiller), *Albatross IV* (Capt. Walter E. Beatteay), *Delaware* (Capt. John J. Walsh), *Asterias* (Capt. Arthur D. Colburn Jr.), and *Gosnold* (Capt. Harry Seibert).

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