2. HABITAT CHARACTERIZATION OF THE NORTHEAST U.S. SHELF ECOSYSTEM

The Northeast U.S. Shelf Ecosystem includes a broad range of habitats with varying physical and biological properties. From the cold waters of the Gulf of Maine (GOM) south to the more tempered climate of the Mid-Atlantic Bight (MAB), oceanographic and biological processes interact to form a network of expansively to narrowly distributed habitat types. This chapter provides a portion of the background information needed to evaluate the effects of fishing on benthic habitats in the region by: 1) reviewing habitat functions and associations; 2) describing four regional systems and their associated physical and benthic biological features; 3) covering the habitat aspects of coastal and estuarine features; and 4) describing benthic invertebrate communities in New England and the MAB, and their distribution in relation to depth and sediment type.

HABITAT FUNCTIONS AND ASSOCIATIONS

From a biological perspective, habitats provide living things with the basic life requirements of nourishment and shelter. Habitats may also provide a broader range of benefits to the ecosystem, such as the way seagrasses physically stabilize the substrate and help recirculate oxygen and nutrients. This section, however, focuses on how benthic marine habitats provide food and shelter for federally managed species in the Northeast Region.

The spatial and temporal variation of prey abundance influences the survival, recruitment, development, and spatial distribution of organisms at every trophic level above primary producers. For example, the abundance and distribution of planktonic organisms greatly influence the growth, survival, and distribution of fish larvae. In addition, the migratory behavior of juvenile and adult fish is directly related to seasonal patterns of prey abundance and changes in environmental conditions, especially water temperature. Prey supply is particularly critical for the starvation-prone, early-life-history stages of fish.

The availability of food for planktivores is highly influenced by oceanographic properties. The seasonal warming of surface waters in temperate latitudes produces vertical stratification of the water column which isolates sunlit surface waters from deeper, nutrient-rich water, leading to reduced primary productivity. In certain areas, upwelling, induced by wind, storms, and tidal mixing, inject nutrients back into the photic zone, stimulating primary production. Changes in primary production from upwelling and other oceanographic processes affect the amount of organic matter available for other organisms higher up in the food web, and thus influence their abundance and distribution. Some of the organic matter produced in the photic zone sinks to the bottom and provides food for benthic organisms. In shallower water, benthic macroalgae and microalgae also contribute to primary production. Recent research on benthic primary productivity indicates that benthic microalgae may contribute more to primary production than has been originally estimated (Cahoon 1999).

Benthic organisms provide an important food source for many fish species. Bottom-dwelling sand lances are eaten by many fish, and benthic invertebrates are the main source of nutrition for many demersal fish. Temporal and spatial variations in benthic community structure affect the distribution and abundance of bottom-feeding fish. Likewise, the abundance and species composition of benthic communities are affected by a number of environmental factors, including temperature, sediment type, and the availability of organic matter.

A number of recent studies have focused on the habitat associations of juvenile demersal fish. In shallow, coastal waters of the Northeast Region, effects of physical habitat factors and prey availability on the abundance and distribution of young-of-the-year flounder (various species) have been investigated in nearshore and estuarine habitats in Connecticut, New Jersey, and North Carolina (Rountree and Able 1992; Howell *et al.* 1999; Walsh *et al.* 1999; Manderson *et al.* 2000; Phelan *et al.* 2001; Stoner *et al.* 2001). There are few comparable studies of more open, continental shelf environments. In the Northeast Region, Steves *et al.* (1999) identified depth, bottom temperature, and time of year as primary factors delineating settlement and nursery habitats for juvenile silver hake and yellowtail flounder in the MAB. Also, in a series of publications, Auster *et al.* (1991, 1995, 1997) correlated the spatial distributions of juvenile benthic fish (*e.g.,* silver hake) with changes in microhabitat type on sand bottom at various open shelf locations in Southern New England.

In addition to providing food sources, another important functional value of benthic habitat is the shelter and refuge from predators provided by structure. Three-dimensional structure is provided by physical features such as boulders, gravel and cobble, sand waves and ripples, and mounts, burrows and depressions created by organisms. Structure is also provided by emergent epifauna such as sponges, bryozoans, anemones, mussels, tunicates, and corals.

The importance of benthic habitat complexity was discussed by Auster (1998) and Auster and Langton (1999). They developed a conceptual model that compared fishing gear effects across a gradient of habitat types. Based on this model, habitat value increases with increased structural complexity, from the lowest value in flat sand and mud to the highest value in piled boulders. The importance of habitat complexity to federally managed species is a key issue in the Northeast Region. Whether, and to what degree, the removal of emergent epifauna from gravel and rocky bottom habitats affects the survival of juvenile Atlantic cod and other species is of particular concern. Field studies (in the northeastern United States and eastern

Canadian waters, and other locations), laboratory experiments, and modeling studies have addressed the issue of removal of emergent epifauna. Because of the importance of this issue in the Northeast Region, this research is summarized below.

The first field study linking survival of juvenile Atlantic cod and haddock to habitat type on Georges Bank was by Lough *et al.* (1989). Using submersibles, they observed that recently settled age-0 juvenile Atlantic cod (and haddock), <10 cm long, were primarily found in pebble-gravel habitat at 70-100 m depths on eastern Georges Bank. They hypothesized that the gravel enhanced survival through predator avoidance; coloration of the fish mimicked that of the substrate, and from the submersible the fish were very difficult to detect against the gravel background. The authors considered increased prey abundance to be another, but less likely, explanation for the concentration of these fish on gravel. Presence of emergent epifauna, and any effects of epifauna on survival of the juveniles, were not noted.

Gregory and Anderson (1997), using submersibles in 18-150 m depths in Placentia Bay, Newfoundland, similarly found that the youngest Atlantic cod observed (age 1, 10-12 cm long) were primarily associated with low-relief gravel substrate; their mottled color appeared to provide camouflage in the gravel. Older juveniles (ages 2-4) were most abundant in higher relief areas with coarser substrate (*e.g.,* submarine cliffs). No selection by juvenile Atlantic cod for substrates with macroalgae cover was seen, and emergent epifauna was not mentioned.

In the first study suggesting an added value of emergent epifauna on Georges Bank gravel, Valentine and Lough (1991) observed from submersibles that attached epifauna was much more abundant in areas of eastern Georges Bank that had not been fished (due to the presence of large boulders). They felt the increased bottom complexity provided by the epifauna might be an important component of fisheries habitat, but both trawled and untrawled gravel habitats were considered important for survival of juvenile Atlantic cod.

Other field studies on the relationship between juvenile Atlantic cod abundance and habitat complexity have been in shallower inshore waters, and results may not be directly applicable to conditions on offshore banks like Georges Bank. In 2-12 m depths off the Newfoundland coast, Keats *et al.* (1987) found [in contrast to Gregory and Anderson (1997), above] juvenile Atlantic cod to be much more abundant in macroalgae beds than in adjacent areas which had been grazed bare by sea urchins. This was true of 1-yr-old fish (7.8-12.5 cm) as well as older, larger (12.6-23.5 cm) juveniles. The larger fish fed on fauna associated with the macroalgae, so enhanced food supply was a probable benefit of the increased complexity. The smallest 1-yr-olds fed on plankton, and it was unlikely their growth was affected by presence of macroalgae.

Tupper and Boutilier (1995a) examined four habitat types (sand, seagrass, cobble, and rock reef) in St. Margaret's Bay, Nova Scotia, and reported that Atlantic cod settlement was equal in all habitats, but survival and juvenile densities were higher in the more complex habitats. Growth rate was highest in seagrass beds, but predator (larger Atlantic cod) efficiency was lowest, and juvenile survival highest, on rock reef and cobble. The authors considered the different habitats to provide a tradeoff between enhanced foraging success and increased predation risk. In another study in St. Margaret's Bay, Tupper and Boutilier (1995b) found that Atlantic cod settling on a rocky reef inhabited crevices in the reef, and defended territories around the crevices. Fish that settled earlier and at larger sizes grew more quickly and had larger territories. Size at settlement and timing of settlement were thus considered important in determining competitive success of individuals.

Habitat associations of juvenile Atlantic cod were also examined by Gotceitas *et al.* (1997) using SCUBA divers in Trinity Bay, and beach seines in Trinity, Notre Dame, and Bonavista Bays, Newfoundland. In both types of surveys, almost all age-0 Atlantic cod were found in eelgrass beds as opposed to less structurally complex areas, and eelgrass was suggested to be an important habitat for these fish. Older juveniles were more abundant on mud, sand, and rocky bottoms than in eelgrass.

A seining study by Linehan *et al.* (2001) in Bonavista Bay, Newfoundland, found age-0 Atlantic cod (<10 cm long) to be more abundant in vegetated (eelgrass) than in unvegetated habitats, both day and night. However, potential predators of juvenile Atlantic cod were also most abundant in eelgrass. Tethering experiments with age-0 Atlantic cod at six sites in 0.7-20 m depths indicated that predation increased with depth, being about three times higher at deeper sites. At shallow sites, predation was generally higher in unvegetated sites than in eelgrass.

Habitat use of age-0 and -1 Atlantic cod in state waters off eastern Massachusetts is discussed by Howe *et al.* (2000), based on analysis of 22 yr (1978-1999) of data from spring and fall trawl surveys by the Massachusetts Division of Marine Fisheries. Results showed the survey area is important for Atlantic cod settlement, with at least two pulses of newly settled fish found in most years. Spatial distribution patterns of young Atlantic cod were clear, stable, and strongly related to depth. In spring, just-settled Atlantic cod were most abundant in depths <27 m; in fall these age-0 Atlantic cod were found in 9-55 m depths, but were concentrated in 27-55 m. Age-1 Atlantic cod were more abundant in deeper waters (18-55 m in spring, 37-55 m in fall). Habitat complexity per se was not the primary focus of this analysis, and some of the most complex (*e.g.,* rocky) habitats could not be sampled by the survey. However, the greater abundance of just-settled fish in shallower waters was thought to be linked to the higher complexity of these habitats. It was postulated that high densities of age-0 fish indicated areas of high productivity and preferred habitat. Given the abundance of juvenile Atlantic cod in these surveys, eastern Massachusetts waters were recommended as a coastal "Habitat Area of Particular Concern" for the GOM Atlantic cod stock.

Kaiser *et al.* (1999) analyzed beam trawl catch data from a number of stations in the English Channel and reported that small gadoid species were present in deeper (>30 m), structurally complex habitats with rocks, soft corals, bryozoans, hydroids, and sponges, and were absent in shallow water habitats which were inhabited by several species of flounder. Most of the structure-forming benthic species that were present in deeper water were also present in shallow water, but at reduced abundances, and the total biomass of sessile epibenthic species was higher in shallow water. These results suggest that depth and the amount of cover provided by certain types of emergent epifauna (*e.g.,* sponges) were the most important factors affecting habitat utilization by gadoid (and flounder) species.

Information on the effects of habitat complexity on juvenile Atlantic cod survival is also available from several laboratory studies. Gotceitas and Brown (1993) compared substrate preferences of juvenile Atlantic cod (6-12 cm) for sand, gravel-pebble, and cobble, before and after introduction of a larger Atlantic cod. Before the predator was introduced, small Atlantic cod preferred sand or gravel-pebble over cobble. In the presence of the predator, they chose cobble if available, and the cobble reduced predation. The experiment did not test effects of emergent epifauna on substrate choices or survival. Gotceitas *et al.* (1995) conducted a similar study, but with 3.5-8 cm Atlantic cod in a tank with one of two combinations of three substrates: 1) sand, gravel, and 30-cm long strips of plastic to simulate kelp (*Laminaria* sp.); or 2) sand, cobble, and "kelp." Based on the authors' earlier study, cobble was considered to provide a "safe" habitat that reduced predation. Responses to introduction of two kinds of larger Atlantic cod were tested: fish that actively attempted to eat the smaller Atlantic cod, versus "passive" predators that showed no interest in the smaller fish. In the presence of passive predators, small Atlantic cod preferred sand substrates and avoided kelp. When exposed to an active predator, they hid in cobble if available or kelp if there was no cobble. Both cobble and kelp significantly reduced predation, and small Atlantic cod appeared able to modify their behavior based on the varying risk presented by different predators.

Fraser *et al.* (1996) tested responses of age-0 (5.2-8.2 cm) and age-1 (10.2-13.5 cm) Atlantic cod to predators (3-yr old Atlantic cod), using the same tanks as Gotceitas *et al.* (1995), but with only two substrate choices: sand versus gravel, and sand versus cobble. With no predator present, age-0 or -1 Atlantic cod by themselves preferred sand to gravel or cobble, but if both age-0 and -1 fish were in the tank, the smaller fish tended to avoid the larger ones and to increase use of gravel/cobble. When a predator was introduced, both age-0 and -1 Atlantic cod hid in cobble if available; in the sand/gravel trials, they attempted to flee from the predator. In the predator's presence, the avoidance of age-1 Atlantic cod by age-0 Atlantic cod disappeared; overall, however, there was some indication of habitat segregation between age-0 and age-1 Atlantic cod.

Gotceitas *et al.* (1997) again used the same experimental system to compare use of sand, gravel, and cobble substrates, as well as three densities of eelgrass, by age-0 Atlantic cod (3.5-10 cm) in the presence and absence of a predator (age-3 Atlantic cod). With no predator, the small Atlantic cod preferred sand and gravel to cobble. When a predator was introduced and cobble was present, age-0 fish hid in the cobble or in dense eelgrass (720 stems/m^2) if present. With no cobble, they hid in all three densities of eelgrass. Age-0 Atlantic cod survival (time to capture and number of fish avoiding capture) was highest in cobble or eelgrass 1000 stems/m^2. In other combinations, time to capture increased with both presence and density of vegetation.

Borg *et al.* (1997) conducted a laboratory study of habitat choice by two size groups of juvenile Atlantic cod (7-13 and 17-28 cm TL) on sandy bottoms with different vegetation types. Four habitats, typical of shallow soft bottom on the west coast of Sweden, were tested in six combinations. During daylight, fish preferred vegetation to bare sand, while at night -- when juvenile Atlantic cod feed in open, sandy areas -- no significant choice was made. Both size classes preferred *Fucus* kelp, the most complex habitat that was tested.

Lindholm *et al.* (1999) tested effects of five habitat types, representing a gradient of complexity, on survival of age-0 Atlantic cod (7-10 cm) in the presence of age-3 conspecifics. Substrates were sand, cobble, sparse short sponge, dense short sponge, and tall sponge. Sponge presence significantly reduced predation compared to that on sand, with density of sponges being more important than sponge height. Increasing habitat complexity reduced the distance from which a predator could react to the prey. The authors concluded that alteration of seafloor habitat by fishing could lower survival of juvenile Atlantic cod. (There was no significant increase in survival in epifauna compared to bare cobble, however.)

In a mesocosm experiment, Isakkson *et al.* (1994) compared the foraging efficiency of Atlantic cod on three different prey species on bare sand and eel grass with varying percent cover of filamentous algae. Foraging efficiency of Atlantic cod on sand shrimp (*Crangon crangon*) and green crabs was greatest in unvegetated substrate. Survival of these two prey species was significantly enhanced by the addition of moderate amounts of algal cover to sand substrates. Shore shrimp (*Palaemon adspersus*) were equally susceptible to predation in all habitat types.

The effects of habitat complexity on post-settlement survival of juvenile Atlantic cod have been examined via modeling (Lindholm *et al.* 2001). Data from the Lindholm *et al.* (1999) laboratory study described above were used to assign maximum values for juvenile mortality in the least complex habitats, and in the most complex habitats. Twelve runs of a dynamic monthly model were made, with the first run (month) representing settlement of the Atlantic cod. Results indicated that reduction of habitat complexity by fishing had significant negative effects on survival of juvenile Atlantic cod, and that preservation of complexity through use of marine protected areas could reduce these negative effects.

Elsewhere and for other species, Charton and Ruzafa (1998) correlated increased habitat complexity (numbers of rocky boulders) in the Mediterranean with higher numbers and abundances of reef fish. There is evidence provided by laboratory experiments that habitat complexity can benefit fish that inhabit open, sandy habitats by providing refuge from bottom currents in the troughs between sand ripples (Gerstner 1998; Gerstner and Webb 1998).

In some situations, other habitat characteristics may be equally or more important than complexity. As discussed above, Lough *et al.* (1989) hypothesized that gravel substrate enhanced survival of juvenile Atlantic cod because the coloration of these juveniles mimicked the substrate. In a similar example, American plaice adults are thought to use gravel-sand sediments as a coloration refuge (Scott 1982). It is apparent that in identifying habitat value, a broad range of characteristics associated with habitat structure and function, which may vary by species and life stage, must be considered. Evaluations cannot be limited to individual aspects such as substrate type. Unfortunately, the amount of information available for individual parameters is limited, especially quantitative information necessary for multivariate analyses. Further development of multivariate relationships between biological, chemical, and physical habitat features will increase our understanding of the marine environment and advance the evidence of direct links between habitat conditions and fishery productivity.

REGIONAL SYSTEMS

The Northeast U.S. Shelf Ecosystem (Figure 2.1) has been described as including the area from the GOM south to Cape Hatteras, extending from the coast seaward to the edge of the continental shelf, including the slope sea offshore to the Gulf Stream (Sherman *et al.* 1996). The continental slope includes the area east of the shelf, out to a depth of 2000 m. Four distinct subregions comprise the Northeast Region: the GOM, Georges Bank, the MAB, and the continental slope. Occasionally, another subregion, Southern New England, is described; however, we incorporated discussions of any distinctive features of this area into the sections describing Georges Bank and the MAB.

The GOM is an enclosed coastal sea, characterized by relatively cold waters and deep basins, with a patchwork of various sediment types. Georges Bank is a relatively shallow coastal plateau that slopes gently from north to south and has steep submarine canyons on its eastern and southeastern edge. It is characterized by highly productive, well-mixed waters and strong currents. The MAB is comprised of the sandy, relatively flat, gently sloping continental shelf from Southern New England to Cape Hatteras, NC. The continental slope begins at the continental shelf break and continues eastward with increasing depth until it becomes the continental rise. It is fairly homogenous, with exceptions at the shelf break, some of the canyons, the Hudson Shelf Valley, and in areas of glacially rafted hard bottom.

Pertinent physical and biological characteristics of each of these subregions are described subsequently in this section. The first portion of each description summarizes oceanographic and geologic features, and the second portion summarizes biological features. Source references used to describe the general physical features of these subregions are not cited in the following text, but include Backus 1987; Schmitz *et al*. 1987; Tucholke 1987; Wiebe *et al*. 1987; Cook 1988; Reid and Steimle 1988; Stumpf and Biggs 1988; Abernathy 1989; Townsend 1992; Mountain *et al*. 1994; Beardsley *et al*. 1996; Brooks 1996; Sherman *et al*. 1996; Dorsey 1998; Kelley 1998; NEFMC 1998; and Steimle *et al*. 1999b. In some cases, recent or specific research results are cited in the text. References used in the biological summaries are also cited in the text.

Gulf of Maine

Physical Features

Although not obvious in appearance, the GOM is actually an enclosed coastal sea, bounded on the east by Browns Bank, on the north by the Nova Scotian (Scotian) Shelf, on the west by the New England states, and on the south by Cape Cod and Georges Bank (Figure 2.2). The GOM was glacially derived, and is characterized by a system of deep basins, moraines, and rocky protrusions with limited access to the open ocean. This geomorphology influences complex oceanographic processes that result in a rich biological community.

The GOM is topographically unlike any other part of the continental border along the U.S. Atlantic coast. The GOM's geologic features, when coupled with the vertical variation in water properties, result in a great diversity of habitat types. It contains 21 distinct basins separated by ridges, banks, and swells. The three largest basins are Wilkinson, Georges, and Jordan (Figure 2.2). Depths in the basins exceed 250 m, with a maximum depth of 350 m in Georges Basin, just north of Georges Bank. The Northeast Channel between Georges Bank and Browns Bank leads into Georges Basin, and is one of the primary avenues for exchange of water between the GOM and the North Atlantic Ocean.

High points within the Gulf include irregular ridges such as Cashes Ledge which peaks at 9 m below the surface, as well as lower flat-topped banks and gentle swells. Some of these rises are remnants of the continental shelf that was left after most of it was removed by the glaciers. Other rises are glacial moraines, and a few such as Cashes Ledge are outcroppings of bedrock. Very fine sediment particles created and eroded by the glaciers have collected in thick deposits over much of the GOM, particularly in its deep basins (Figure 2.3). These mud deposits blanket and obscure the irregularities of the underlying bedrock, forming topographically smooth terrains. Some shallower basins are covered with mud as well, including some in coastal waters. In the rises between the basins, other materials are usually at the surface. Unsorted glacial till covers some morainal areas, as on Sewell Ridge to the north of Georges Basin and on Truxton Swell to the south of Jordan Basin. Sand predominates on some high areas, and gravel, sometimes with boulders, predominates on others.

Coastal sediments exhibit a high degree of smallscale variability. Bedrock is the predominant substrate along the western edge of the GOM north of Cape Cod in a narrow band out to a depth of about 60 m. Rocky areas become less common with increasing depth, but some rock outcrops poke through the mud covering the deeper seafloor. Mud is the second-most common substrate on the inner continental shelf. Mud predominates in coastal valleys and basins that often abruptly border rocky substrates. Many of these basins extend without interruption into deeper water. Gravel, often mixed with shell, is common adjacent to bedrock outcrops and in fractures in the rock. Large expanses of gravel are not common, but do occur near reworked glacial moraines and in areas where the seafloor has been scoured by bottom currents. Gravel is most abundant at depths of 20-40 m, except in eastern Maine where a gravel-covered plain exists to depths of at least 100 m. Bottom currents are stronger in eastern Maine where the mean tidal range exceeds 5 m. Sandy areas are relatively rare along the inner shelf of the western GOM, but are more common south of Casco Bay, especially offshore of sandy beaches.

An intense seasonal cycle of winter cooling and turnover, springtime freshwater runoff, and summer warming influences oceanographic and biologic processes in the GOM. The Gulf has a general counterclockwise nontidal surface current that flows around its coastal margin (Figure 2.4). This current is primarily driven by fresh, cold Scotian Shelf water that enters over the Scotian Shelf and through the Northeast Channel, and freshwater river runoff, which is particularly important in the spring. Dense, relatively warm, and saline slope water entering through the bottom of the Northeast Channel from the continental slope also influences gyre formation. Counter-clockwise gyres generally form in Jordan, Wilkinson, and Georges Basins, and in the Northeast Channel as well. These surface gyres are more pronounced in spring and summer; with winter, they weaken and become more influenced by the wind.

Stratification of surface waters during spring and summer seals off a mid-depth layer of water that preserves winter salinity and temperatures. This cold layer of water is called "Maine Intermediate Water" (MIW), and is located between the more saline Maine Bottom Water (MBW) and the warmer, stratified Maine Surface Water (MSW). The stratified MSW is most pronounced in the deep portions of the western GOM. Tidal mixing of shallow areas prevents thermal stratification and results in thermal fronts between the stratified areas and cooler mixed areas. Typically, mixed areas include Georges Bank, the southwest Scotian Shelf, eastern Maine coastal waters, and the narrow coastal band surrounding the remainder of the Gulf.

The Northeast Channel provides an exit for cold MIW and outgoing MSW, while it allows warmer, more saline slope water to move in along the bottom and spill into the deeper basins. The influx of water occurs in pulses, and appears to be seasonal, with lower flow in late winter and a maximum in early summer.

GOM circulation and water properties can vary significantly from year to year. Notable episodic events include shelf-slope interactions such as the entrainment of shelf water by Gulf Stream rings (see the "Continental Slope/Physical Features" section), and strong winds that can create currents as high as 1.1 m/s over Georges Bank. Warm-core Gulf Stream rings can also influence upwelling and nutrient exchange on the Scotian Shelf, and affect the water masses entering the GOM. Annual and seasonal inflow variations also affect water circulation.

Internal waves are episodic and can greatly affect the biological properties of certain habitats. Internal waves can shift water layers vertically, so that habitats normally surrounded by cold MIW are temporarily bathed in warm, organic-rich surface water. On Cashes Ledge, it is thought that deeper nutrient rich water is driven into the photic zone, providing for increased productivity. Localized areas of upwelling interaction occur in numerous places throughout the Gulf.

Benthic Biological Features

Based on 303 benthic grab samples collected in the GOM during 1956-1965, Theroux and Wigley (1998) reported that, in terms of numbers, the most common groups of benthic invertebrates in the GOM were annelid worms (35%), bivalve mollusks (33%), and amphipod crustaceans (14%). Biomass was dominated by bivalve mollusks (24%), sea cucumbers (22%), sand dollars (18%), annelids (12%), and sea anemones (9%). Watling (1998) used numerical classification techniques to separate benthic invertebrate samples into seven bottom assem-blages. Distribution was determined from both quantita-tive soft-bottom sampling and qualitative hard-bottom sampling. These assemblages are identified in Table 2.1, and their distribution is indicated in Figure 2.5. This classification system considers predominant taxa, substrate types, and seawater properties. (See the last section of this chapter for more information on benthic invertebrate communities in New England.)

An in-depth review of GOM habitat types has been prepared by Brown (1993). Although still preliminary, this classification system is a promising approach. It builds on a number of other schemes, including Cowardin *et al.* (1979), and tailors them to Maine's marine and estuarine environments. A significant factor that is included in this system, but has been neglected in others, is the amount of "energy" in a habitat. Energy could be a reflection of wind, waves, or currents present. This is a particularly important consideration in a review of fishing gear effects since it indicates the natural disturbance regime of a habitat. The amount and type of natural disturbance are in turn an indication of the habitat's resistance to, and recoverability from, disturbance by fishing gear. Although this work appears to be complete in its description of habitat types, unfortunately, the distributions of many of the habitats are unknown.

Demersal fish assemblages for the GOM and Georges Bank were part of broadscale geographic investigations conducted by Gabriel (1992) and Mahon *et al.* (1998). Both of these studies and a more limited study by Overholtz and Tyler (1985) found assemblages that were consistent over space and time in this region. In her analysis, Gabriel (1992) found that the most persistent feature over time in assemblage structure from Nova Scotia to Cape Hatteras was the boundary separating assemblages between the GOM and Georges Bank, which occurred at approximately the 100-m isobath on northern Georges Bank. Overholtz and Tyler (1985) identified five assemblages for this region (Table 2.2). The GOM deep assemblage included a number of species found in other assemblages, with the exception of American plaice and witch flounder, which were unique to this assemblage. Gabriel's approach did not allow species to co-occur in assemblages, and classified these two species as unique to the deepwater GOM - Georges Bank assemblage. Results of these two studies are compared in Table 2.2. Auster *et al.* (2001) went a step further and related species clusters on Stellwagen Bank to different substrate types in an attempt to use fish distribution as a proxy for seafloor habitat distribution. They found significant associations for 12 of 20 species, including American plaice (fine substrate) and haddock (coarse substrate). Species clusters and associated substrate types are given in Table 2.3.

Georges Bank

Physical Features

Georges Bank is a shallow (3-150 m depth), elongate (161-km wide by 322-km long) extension of the continental shelf that was formed by the Wisconsinian glacial episode. It is characterized by a steep slope on its northern edge and a broad, flat, gently sloping southern flank. The Great South Channel lies to the west. Natural processes continue to erode and rework the sediments on Georges Bank. It is anticipated that erosion and reworking of sediments will reduce the amount of sand available to the sand sheets, and cause an overall coarsening of the bottom sediments (Valentine and Lough 1991).

Glacial retreat during the late Pleistocene deposited the bottom sediments currently observed on the eastern section of Georges Bank, and the sediments have been continuously reworked and redistributed by the action of rising sea level, and by tidal, storm, and other currents (Figure 2.6). The strong, erosive currents affect the character of the biological community. Bottom topography on eastern Georges Bank is characterized by linear ridges in the western shoal areas; a relatively smooth, gently dipping seafloor on the deeper, easternmost part; a highly energetic peak in the north with sand ridges up to 30 m high and extensive gravel pavement; and steeper and smoother topography incised by submarine canyons on the southeastern margin (see the "Continental Slope" section for more on canyons). The interaction of several environmental factors, including availability and type of sediment, current speed and direction, and bottom topography, has formed seven sedimentary provinces on eastern Georges Bank (Valentine and Lough 1991) which are described in Table 2.4 and depicted in Figure 2.6. The gravel-sand mixture is usually a transition zone between coarse gravel and finer sediments.

The central region of the bank is shallow, and the bottom is characterized by shoals and troughs, with sand dunes superimposed upon them. The two most prominent elevations on the ridge and trough area are Cultivator and Georges Shoals. This shoal and trough area is a region of strong currents. The dunes migrate at variable rates, and the ridges may also move. In an area that lies between the central part and Northeast Peak, Almeida *et al.* (2000) identified high-energy areas between 35 and 65 m deep where sand is transported on a daily basis by tidal currents, and a low-energy area >65 m deep that is affected only by storm currents.

The area west of the Great South Channel, known as Nantucket Shoals (Figure 2.2), is similar in nature to the central region of the bank. Currents in these areas are strongest where water depth is shallower than 50 m. This type of traveling dune-and-swale morphology is also found in the MAB, and further described in that section of this document. The Great South Channel separates the main part of Georges Bank from Nantucket Shoals. Sediments in this region include gravel pavement and mounds, some scattered boulders, sand with storm generated ripples, and scattered shell and mussel beds. Tidal and storm currents range from moderate to strong, depending upon location and storm activity (pers. comm.; Page C. Valentine, U.S. Geological Survey, Woods Hole, MA).

Oceanographic frontal systems separate water masses of the GOM and Georges Bank from oceanic waters south of the bank. These water masses differ in temperature, salinity, nutrient concentration, and planktonic communities, which influence productivity and may influence fish abundance and distribution. Currents on Georges Bank include a weak, persistent clockwise gyre around the bank, a strong semidiurnal tidal flow predominantly northwest and southeast, and very strong, intermittent storm-induced currents, which all can occur simultaneously (Figure 2.4). Tidal currents over the shallow top of Georges Bank can be very strong, and keep the waters over the bank well mixed vertically. This results in a tidal front that separates the cool waters of the well-mixed shallows of the central bank from the warmer, seasonally stratified shelf waters on the seaward and shoreward sides of the bank. The clockwise gyre is instrumental in distribution of the planktonic community, including larval fish. For example, Lough and Potter (1993) describe passive drift of Atlantic cod and haddock eggs and larvae in a southwest residual pattern around Georges Bank. Larval concentrations are found at varying depths along the southern edge between 60 and 100m.

Benthic Biological Features

Amphipod crustaceans (49%) and annelid worms (28%) numerically dominated the contents of 211 sediment samples collected on Georges Bank during 1956-1965 (Theroux and Wigley 1998). Biomass was dominated by sand dollars (50%) and bivalve mollusks (33%). Theroux and Grosslein (1987) utilized the same database to identify four invertebrate assemblages: Western Basin, Northeast Peak, central Georges Bank, and southern Georges Bank. (See the last section of this chapter for more information on benthic invertebrate communities in New England.) They noted that it is impossible to define discrete boundaries between assemblages because of the considerable intergrading that occurs between adjacent assemblages; however, the assemblages are distinguishable. Their assemblages are associated with those identified by Valentine and Lough (1991) in Table 2.4.

The Western Basin assemblage (Theroux and Grosslein 1987) is found in the upper Great South Channel region at the northwestern corner of the bank, in comparatively deep water (150-200 m) with relatively slow currents and fine bottom sediments of silt, clay, and muddy sand. The fauna is comprised mainly of small burrowing detritivores and deposit feeders, and carnivorous scavengers. Representative organisms include bivalve mollusks (*Thyasira flexuosa, [En]ucula tenuis,* and *Musculus discors*), annelids (*Nephtys incisa, Paramphinome pulchella, Onuphis opalina,* and *Sternaspis scutata*), the brittle star *Ophiura sarsi*, the amphipod *Haploops tubicola*, and the red deepsea crab (*[Chaceon] quinquedens*). Valentine and Lough (1991) did not identify a comparable assemblage; however, this assemblage is geographically located adjacent to Assemblage 5 as described by Watling (1998) (Table 2.1; Figure 2.5)

The Northeast Peak assemblage is found along the Northern Edge and Northeast Peak, which varies in depth and current strength, and includes coarse sediment consisting mainly of gravel and coarse sand with interspersed boulders, cobbles, and pebbles. The fauna tends to be sessile (coelenterates, brachiopods, barnacles, and tubiferous annelids) or free-living (brittle stars, crustaceans, and polychaetes), with a characteristic absence of burrowing forms. Representative organisms include amphipods (*Acanthonotozoma serratum* and *Tiron spiniferum*), the isopod *Rocinela americana*, the barnacle *Balanus hameri*, annelids (*Harmothoe imbricata, Eunice pennata, Nothria conchylega,* and *Glycera capitata*), the sea scallop *Placopecten magellanicus*, brittle stars (*Ophiacantha bidentata* and *Ophiopholis aculeata*), and soft corals (*Primnoa resedaeformis* and *Paragorgia arborea*).

The Central Georges Bank assemblage occupies the greatest area, including the central and northern portions of the bank in depths <100 m. Medium-grained shifting sands predominate this dynamic area of strong currents. Organisms tend to be small to moderately large with burrowing or motile habits. Sand dollars (*Echinarachnius parma*) are most characteristic of this assemblage. Other representative species include mysids (*Neomysis americana* and *Mysidopsis bigelowi*), the isopod *Chiridotea tuftsi*, the cumacean *Leptocuma minor*, the amphipod *Protohaustorius wigleyi*, annelids (*Sthenelais limicola, Goniadella gracilis,* and *Scalibregma inflatum*), gastropods (*[Euspira] heros* and *Nassarius trivittatus*), the starfish *Asterias vulgaris*, the shrimp *Crangon septemspinosa*, and the crab *Cancer irroratus*.

The Southern Georges Bank assemblage is found on the southern and southwestern flanks at depths from 80 to 200 m, where fine-grained sands and moderate currents predominate. Many southern species exist here at the northern limits of their range. The dominant fauna includes amphipods, copepods, euphausiids, and the starfish genus *Astropecten*. Representative organisms include amphipods (*Ampelisca compressa, Erichthonius rubricornis,* and *Synchelidium americanum*), the cumacean *Diastylis quadrispinosa,* annelids (*Aglaophamus circinata, Nephtys squamosa,* and *Apistobranchus tullbergi*), crabs (*Euprognatha rastellifera* and *Catapagurus sharreri*) and the shrimp *Munida iris*.

Along with high levels of primary productivity, Georges Bank has been historically characterized by high levels of fish production. Several studies have attempted to identify demersal fish assemblages over large spatial scales. Overholtz and Tyler (1985) found five depth-related demersal fish assemblages for Georges Bank and the GOM that were persistent temporally and spatially (Table 2.2). Depth and salinity were identified as major physical influences explaining assemblage structure. Gabriel (1992) identified six assemblages which are compared with the results of Overholtz and Tyler (1985) in Table 2.2. Mahon *et al.* (1998) found similar results.

Mid-Atlantic Bight

Physical Features

The MAB includes the shelf and slope waters from Georges Bank south to Cape Hatteras, and east to the Gulf Stream (Figure 2.1). Like the rest of the continental shelf, the topography of the MAB was shaped largely by sea - level fluctuations caused by past ice ages. The shelf's basic morphology and sediments derive from the retreat of the last ice sheet, and the subsequent rise in sea level. Since that time, currents and waves have modified this basic structure.

Shelf and slope waters of the MAB have a slow southwestward flow that is occasionally interrupted by warm-core rings or meanders from the Gulf Stream. On average, shelf water moves parallel to bathymetry isobars at speeds of 5-10 cm/s at the surface and 2 cm/s or less at the bottom. Storm events can cause much more energetic variations in flow. Tidal currents on the inner shelf have a higher flow rate of 20 cm/s that increases to 100 cm/s near inlets.

Slope water tends to be warmer than shelf water because of its proximity to the Gulf Stream, and tends to be more saline. The abrupt gradient where these two water masses meet is called the shelf-slope front. This front is usually located at the edge of the shelf and touches bottom at about 75-100 m depth of water, and then slopes up to the east toward the surface. It reaches surface waters approximately 25-55 km further offshore. The position of the front is highly variable, and can be influenced by many physical factors. Vertical structure of temperature and salinity within the front can develop complex patterns because of the interleaving of shelf and slope waters; *e.g.,* cold shelf waters can protrude offshore, or warmer slope water can intrude up onto the shelf.

The seasonal effects of warming and cooling increase in shallower, nearshore waters. Stratification of the water column occurs over the shelf and the top layer of slope water during the spring-summer and is usually established by early June. Fall mixing results in homogenous shelf and upper slope waters by October in most years. A permanent thermocline exists in slope waters from 200 to 600 m deep. Temperatures decrease at the rate of about 0.02°C/m, and remain relatively constant except for occasional incursions of Gulf Stream eddies or meanders. Below 600 m, temperature declines, and usually averages about 2.2°C at 4000 m. A warm, mixed layer approximately 40-m thick resides above the permanent thermocline.

The "cold pool" is an annual phenomenon particularly important to the MAB. It stretches from the GOM along the outer edge of Georges Bank and then southwest to Cape Hatteras. It becomes identifiable with the onset of thermal stratification in the spring and lasts into early fall until normal seasonal mixing occurs. It usually exists along the bottom between the 40- and 100-m isobaths, and extends up into the water column for about 35 m, and to the bottom of the seasonal thermocline. The cold pool usually represents about 30% of the volume of shelf water. Minimum temperatures for the cold pool occur in early spring and summer, and range from 1.1 to 4.7°C.

The shelf slopes gently from shore out to between 100 and 200 km offshore where it transforms to the slope (100-200 m of water depth) at the shelf break. In both the Mid-Atlantic and on Georges Bank, numerous canyons incise the slope, and some cut up onto the shelf itself (see the subsequent "Continental Slope" section). The primary morphological features of the shelf include shelf valleys and channels, shoal massifs, scarps, and sand ridges and swales (Figures 2.7 and 2.8).

Most of these structures are relic except for some sand ridges and smaller sand-formed features. Shelf valleys and slope canyons were formed by rivers of glacier outwash that deposited sediments on the outer shelf edge as they entered the ocean. Most valleys cut about 10 m into the shelf, with the exception of the Hudson Shelf Valley that is about 35 m deep. The valleys were partially filled as the glacier melted and retreated across the shelf. The glacier also left behind a lengthy scarp near the shelf break from Chesapeake Bay north to the eastern end of Long Island (Figures 2.7 and 2.8). Shoal retreat massifs were produced by extensive deposition at a cape or estuary mouth. Massifs were also formed as estuaries retreated across the shelf.

The sediment type covering most of the shelf in the MAB is sand, with some relatively small, localized areas of sand-shell and sand-gravel. On the slope, silty sand, silt, and clay predominate.

Some sand ridges (Figure 2.7) are more modern in origin than the shelf's glaciated morphology. Their formation is not well understood; however, they appear to develop from the sediments that erode from the shore face. They maintain their shape, so it is assumed that they are in equilibrium with modern current and storm regimes. They are usually grouped, with heights of about 10 m, lengths of 10-50 km, and spacing of about 2 km. Ridges are usually oriented at a slight angle towards shore, running in length from northeast to southwest. The seaward face usually has the steepest slope. Sand ridges are often covered with smaller similar forms such as sand waves, megaripples, and ripples. Swales occur between sand ridges. Since ridges are higher than the adjacent swales, they are exposed to more energy from water currents, and experience more sediment mobility than swales. Ridges tend to contain less fine sand, silt, and clay, while relatively sheltered swales contain more of the finer particles. Swales have greater benthic macrofaunal density, species richness, and biomass due, in part, to the increased abundance of detrital food and the physically less rigorous conditions.

Sand waves are usually found in patches of 5-10 with heights of about 2 m, lengths of about 50-100 m, and spacing of about 1-2 km. Sand waves are primarily found on the inner shelf, and often observed on sides of sand ridges. Sand waves may remain intact over several seasons. Megaripples occur on sand waves or separately on the inner or central shelf. During the winter storm season, these megaripples may cover as much as 15% of the inner shelf. They tend to form in large patches and usually have lengths of about 3-5 m with heights of about 0.5-1 m. Megaripples tend to survive for less than a season. They can form during a storm and reshape the upper 50-100 cm of the sediments within a few hours. Ripples are also found everywhere on the shelf, and appear or disappear within hours or days, depending upon storms and currents. Ripples usually have lengths of about 1-150 cm and heights of a few centimeters.

Sediments are uniformly distributed over the shelf in this region (see Figure 2.3). A sheet of sand and gravel varying in thickness from 0 to10 m covers most of the shelf. The mean bottom flow from the constant southwesterly current is not fast enough to move sand, so sediment transport must be episodic. Net sediment movement is in the same southwesterly direction as the current. The sands are mostly medium-to-coarse grains, with finer sand in the Hudson Shelf Valley and on the outer shelf. Mud is rare over most of the shelf, but is common in the Hudson Shelf Valley. Occasionally, relic estuarine mud deposits are re-exposed in the swales between sand ridges. Fine sediment content increases rapidly at the shelf break, which is sometimes called the "mud line," and sediments are 70-100% fines on the slope.

The northern portion of the MAB is sometimes referred to as Southern New England. Most of this area was discussed under Georges Bank; however, one other formation of this region deserves note. The "Mud Patch" is located just southwest of Nantucket Shoals and southeast of Long Island and Rhode Island (Figure 2.3). Tidal currents in this area slow significantly, which allows silts and clays to settle out. The mud is mixed with sand, and is occasionally resuspended by large storms. This habitat is an anomaly of the outer continental shelf.

Artificial reefs are another significant Mid-Atlantic habitat, formed much more recently on the geologic time scale than other regional habitat types. These localized areas of hard structure have been formed by shipwrecks, lost cargoes, disposed solid materials, shoreline jetties and groins, submerged pipelines, cables, and other materials (Steimle and Zetlin 2000). While some of materials have been deposited specifically for use as fish habitat, most have an alternative primary purpose; however, they have all become an integral part of the coastal and shelf ecosystem. It is expected that the increase in these materials has had an effect on living marine resources and fisheries, but these effects are not well known. In general, reefs are important for attachment sites, shelter, and food for many species, and fish predators such as tunas may be attracted by prey aggregations, or may be behaviorally attracted to the reef structure. The overview by Steimle and Zetlin (2000) used NOAA hydrographic surveys to plot rocks, wrecks, obstructions, and artificial reefs, which together were considered a fairly complete list of nonbiogenic reef habitat in the Mid-Atlantic estuarine and coastal areas (Figure 2.9).

Benthic Biological Features

Wigley and Theroux (1981) reported on the faunal composition of 563 bottom grab samples collected in the MAB during 1956-1965. Amphipod crustaceans and bivalve mollusks accounted for most of the individuals (41% and 22%, respectively), whereas mollusks dominated the biomass (70%). Three broad faunal zones related to water depth and sediment type were identified by Pratt (1973). The "sand fauna" zone was defined for sandy sediments (1% or less silt) that are at least occasionally disturbed by waves, from shore out to the 50-m depth (Figure 2.10). The "silty sand fauna" zone occurred immediately offshore from the sand fauna zone, in stable sands containing a small amount of silt and organic material. Silts and clays become predominant at the shelf break, line the Hudson Shelf Valley, and support the "silt-clay fauna." (See the "Regional Benthic Invertebrate Communities/Mid-Atlantic Bight" section of this chapter for more information on benthic invertebrate communities in the MAB and their relation to depth and sediment type).

Building on Pratt's work, the Mid-Atlantic shelf was further divided by Boesch (1979) into seven bathymetric/ morphologic subdivisions based on faunal assemblages (Table 2.5). Sediments in the region studied (Hudson Shelf Valley south to Chesapeake Bay) were dominated by sand with little finer materials. Ridges and swales are important morphological features in this area. Sediments are coarser on the ridges, and the swales have greater benthic macrofaunal density, species richness, and biomass. Faunal species composition differed between these features, and Boesch (1979) incorporated this variation in his subdivisions (Table 2.5). Much overlap of species distributions was found between depth zones, so the faunal assemblages represented more of a continuum than distinct zones.

Demersal fish assemblages were described at a broad geographic scale for the continental shelf and slope from Cape Chidley, Labrador, to Cape Hatteras, North Carolina (Mahon *et al.* 1998), and from Nova Scotia to Cape Hatteras (Gabriel 1992). Factors influencing species distribution included latitude and depth. Results of these studies were similar to an earlier study confined to the MAB continental shelf (Colvocoresses and Musick 1984). In this latter study, there were clear variations in species abundances, yet the authors demonstrated consistent patterns of community composition and distribution among demersal fishes of the Mid-Atlantic shelf. This is especially true for five strongly recurring species associations that varied slightly from spring to fall (Table 2.6). The boundaries between fish assemblages generally followed isotherms and isobaths. The assemblages were largely similar between the spring and fall collections, with the most notable change being a northward and shoreward shift in the temperate group in the spring.

Steimle and Zetlin (2000) described representative epibenthic/epibiotic, motile epibenthic, and fish species associated with sparsely scattered reef habitats that consist mainly of manmade structures (Table 2.7).

Continental Slope

Physical Features

The continental slope extends from the continental shelf break, at depths between 60-200 m, eastward to a depth of 2000 m. The width of the slope varies from 10-50 km, with an average gradient of 3-6°; however, local gradients can be nearly vertical. The base of the slope is defined by a marked decrease in seafloor gradient where the continental rise begins.

The morphology of the present continental slope appears largely to be a result of sedimentary processes that occurred during the Pleistocene, including, 1) slope upbuilding and progradation by deltaic sedimentation principally during sea-level low stands; 2) canyon cutting by sediment mass movements during and following sea-level low stands; and 3) sediment slumping.

The slope is cut by at least 70 large canyons between Georges Bank and Cape Hatteras (Figure 2.11), and by numerous smaller canyons and gullies, many of which may feed into the larger canyon systems. The New England Seamount Chain, including Bear, Mytilus, and Balanus Seamounts, occurs on the slope southeast of Georges Bank. A smaller chain (Caryn, Knauss, etc.) occurs in the vicinity in deeper water.

A "mud line" occurs on the slope at a depth of 250-300 m, below which fine silt and clay-size particles predominate (Figure 2.3). Localized coarse sediments and rock outcrops are found in and near canyon walls, and occasional boulders occur on the slope because of glacial rafting. Sand pockets may also be formed because of downslope movements.

Gravity-induced, downslope movement is the dominant sedimentary process on the slope, and includes slumps, slides, debris flows, and turbidity currents, in the order from thick cohesive movement to relatively nonviscous flow. Slumps may involve localized, short, downslope movements by blocks of sediment. However, turbidity currents can transport sediments thousands of kilometers.

Submarine canyons are not spaced evenly along the slope, but tend to decrease in areas of increasing slope gradient. Canyons are typically "v" shaped in cross section, and often have steep walls and outcroppings of bedrock and clay. The canyons are continuous from the canyon heads to the base of the continental slope. Some canyons end at the base of the slope, but others continue as channels onto the continental rise. Larger and more deeply incised canyons are generally significantly older than smaller ones, and there is evidence that some older canyons have experienced several episodes of filling and re-excavation. Many, if not all, submarine canyons may first form by mass-wasting processes on the continental slope, although there is evidence that some canyons were formed because of fluvial drainage (*e.g.,* Hudson Canyon).

Canyons can alter the physical processes in the surrounding slope waters. Fluctuations in the velocities of the surface and internal tides can be large near the heads of the canyons, leading to enhanced mixing and sediment transport in the area. Shepard *et al.* (1979) concluded that the strong turbidity currents initiated in study canyons were responsible for enough sediment erosion and transport to maintain and modify those canyons. Since surface and internal tides are ubiquitous over the continental shelf and slope, it can be anticipated that these fluctuations are important for sedimentation processes in other canyons as well. In Lydonia Canyon, Butman *et al.* (1982) found that the dominant source of low-frequency current variability was related to passage of warm-core Gulf Stream rings rather than the atmospheric events that predominate on the shelf.

The water masses of the Atlantic continental slope and rise are essentially the same as those of the North American Basin [defined in Wright and Worthington (1970)]. Worthington (1976) divided the water column of the slope into three vertical layers: deepwater (colder than 4°C), the thermocline (4-17°C), and surface water (warmer than 17°C). In the North American Basin, deepwater accounts for two-thirds of all water, the thermocline for about one-quarter, and surface water the remainder. In the slope water north of Cape Hatteras, the only warm water occurs in the Gulf Stream and in seasonally influenced summer waters.

The principal cold water mass in the region is the North Atlantic Deep Water. North Atlantic Deep Water is comprised of a mixture of five sources: Antarctic Bottom Water, Labrador Sea Water, Mediterranean Water, Denmark Strait Overflow Water, and Iceland-Scotland Overflow Water. The thermocline represents a straightforward water mass compared with either the deepwater or the surface water. Nearly 90% of all thermocline water comes from the water mass called the Western North Atlantic Water. This water mass is slightly less saline northeast of Cape Hatteras due to the influx of southward flowing Labrador Coastal Water. Seasonal variability in slope waters occurs only in the upper 200 m of the water column.

In the winter months, cold temperatures and storm activity create a well-mixed layer down to about 100-150 m, but summer warming creates a seasonal thermocline overlain by a surface layer of low-density water. The seasonal thermocline, in combination with reduced storm activity in the summer, inhibits vertical mixing and reduces the upward transfer of nutrients into the photic zone.

Two currents found on the slope, the Gulf Stream and Western Boundary Undercurrent, together represent one of the strongest low-frequency horizontal flow systems in the world. Both currents have an important influence on slope waters. Warm- and cold-core rings that spin off the Gulf Stream are a persistent and ubiquitous feature of the Northwest Atlantic Ocean. The Western Boundary Undercurrent flows to the southwest along the lower slope and continental rise in a stream about 50 km wide. This boundary current is associated with the spread of North Atlantic Deep Water, and forms part of the generally westward flow found in slope water. North of Cape Hatteras, it crosses under the Gulf Stream in a manner not yet completely understood.

Shelf and slope waters of the Northeast Region are intermittently affected by the Gulf Stream. The Gulf Stream begins in the Gulf of Mexico and flows northeastward at an approximate rate of 1 m/s (2 knots), transporting warm waters north along the eastern coast of the United States, and then east towards the British Isles. Conditions and flow of the Gulf Stream are highly variable on time scales ranging from days to seasons. Intrusions from the Gulf Stream constitute the principal source of variability in slope waters off the Northeast Continental Shelf.

The location of the Gulf Stream's shoreward, western boundary is variable because of meanders and eddies. Gulf Stream eddies are formed when extended meanders enclose a parcel of seawater and pinch off. These eddies can be cyclonic, meaning they rotate counterclockwise and have a cold core formed by enclosed slope water (cold-core ring), or anticyclonic, meaning they rotate clockwise and have a warm core of Sargasso Sea water (warm-core ring). The rings are shaped like a funnel, wider at the top and narrower at the bottom, and can have depths of over 2000 m. They range in approximate size from 150 to 230 km in diameter. There are 35% more rings and meanders near Georges Bank than in the Mid-Atlantic region. A net transfer of water on and off the shelf may result from the interaction of rings and shelf waters. These warm- or cold-core rings maintain their identity for several months until they are reabsorbed by the Gulf Stream. The rings and the Gulf Stream itself have a great influence over oceanographic conditions all along the continental shelf.

Benthic Biological Features

Polychaete annelids represent the most important slope faunal group in terms of numbers of individuals and species (Wiebe *et al.* 1987). Ophiuroids (brittle stars) are considered to be among the most abundant slope organisms, but this group is comprised of relatively few species. The taxonomic group with the highest species diversity is the peracarid crustaceans (which include amphipods, cumaceans, and isopods). Some species of the slope are widely distributed, while others appear to be restricted to particular ocean basins. The ophiuroids and bivalve mollusks appear to have the broadest distributions, while the peracarid crustaceans appear to be highly restricted because they brood their young, and lack a planktonic stage of development. In general, gastropods do not appear to be very abundant; however, past studies are inconclusive since they have not collected enough individuals for largescale community and population studies. (See the "Regional Benthic Invertebrate Communities" section of this chapter for more information on benthic invertebrate communities on the continental slope.)

In general, slope-inhabiting benthic organisms are strongly zoned by depth and/or water temperature, although these patterns are modified by the presence of topography, including canyons, channels, and current zonations (Hecker 1990). Moreover, at depths of <800 m, the fauna is extremely variable and the relationships between faunal distribution and substrate, depth, and geography are less obvious (Wiebe *et al.* 1987). The fauna occupying hard surface sediments is not as dense as in comparable shallow water habitats (Wiebe *et al.* 1987), but there is an increase in species diversity from the shelf to the intermediate depths of the slope. Diversity then declines again in the deeper waters of the continental rise and plain. Hecker (1990) identified four megafaunal zones on the slope of Georges Bank and Southern New England (Table 2.8).

One group of organisms of interest because of the additional structure they can provide for habitat and their potential long life span are the alcyonarian soft corals. Soft corals can be bush or treelike in shape; species found in this form attach to hard substrates such as rock outcrops or gravel. These species can range in size from a few millimeters to several meters, and the trunk diameter of large specimens can exceed 10 cm. Other alcyonarians found in this region include sea pens and sea pansies (Order Pennatulacea), which are found in a wider range of substrate types. In their survey of Northeast U.S. Continental Shelf macrobenthic invertebrates, Theroux and Wigley (1998) found alcyonarians (including the soft corals *Alcyonium* sp., *Acanella* sp., *Paragorgia arborea,* and *Primnoa reseda*, and the sea pens) in limited numbers in waters deeper than 50 m, and mostly at depths from 200 to 500 m. Alcyonarians were present in each of the geographic areas identified in the study (Nova Scotia, GOM, Southern New England Shelf, Georges Slope, and Southern New England Slope) except Georges Bank. However, *Paragorgia* and *Primnoa* have been reported in the Northeast Peak region of Georges Bank (Theroux and Grosslein 1987). Alcyonarians were most abundant by weight in the GOM, and by number on the Southern New England Slope (Theroux and Wigley 1998). In this study, alcyonarians other than sea pens were collected only from gravel and rocky outcrops. Theroux and Wigley (1998) also found stony corals (*Astrangia danae* and *Flabellum* sp.) in the Northeast Region, but they were uncommon. In similar work on the Mid-Atlantic shelf, the only alcyonarians encountered were sea pens (Wigley and Theroux 1981). The stony coral *Astrangia danae* was also found, but its distribution and abundance were not discussed, and are assumed to be minimal.

As opposed to most slope environments, canyons may develop a lush epifauna. Hecker *et al.* (1983) found faunal differences between the canyons and slope environments. Hecker and Blechschmidt (1979) suggested that faunal differences were due at least in part to increased environmental heterogeneity in the canyons, including greater substrate variability and nutrient enrichment. Hecker *et al.* (1983) found highly patchy faunal assemblages in the canyons, and also found additional faunal groups located in the canyons, particularly on hard substrates, that do not appear to occur in other slope environments. Canyons are also thought to serve as nursery areas for a number of species (Cooper *et al.* 1987; Hecker 2001). The canyon habitats in Table 2.9 were classified by Cooper *et al.* (1987).

Most finfish identified as slope inhabitants on a broad spatial scale (Colvocoresses and Musick 1984; Overholtz and Tyler 1985; Gabriel 1992) (Tables 2.2 and 2.6) are associated with canyon features as well (Cooper *et al.* 1987) (Table 2.9). Finfish identified by broad studies that were not included in Cooper *et al.* (1987) include offshore hake, fawn cusk-eel, longfin hake, witch flounder, and armored searobin. Canyon species (Cooper *et al.* 1987) that were not discussed in the broadscale studies include squirrel hake, conger eel, and tilefish. Cusk and ocean pout were identified by Cooper *et al.* (1987) as canyon species, but classified in other habitats by the broadscale studies.

Coastal and Estuarine Features

Coastal and estuarine features such as salt marshes, mud flats, rocky intertidal zones, sand beaches, and submerged aquatic vegetation are critical to inshore and offshore habitats and fishery resources of the Northeast. For example, coastal areas and estuaries are important for nutrient recycling and primary production, and certain features serve as nursery areas for juvenile stages of economically important species. Salt marshes are found extensively throughout the region. Tidal and subtidal mud and sand flats are general saltmarsh features and also occur in other estuarine areas. Salt marshes provide nursery and spawning habitat for many fish and invertebrate species. Saltmarsh vegetation can also be a large source of organic material that is important to the biological and chemical processes of the estuarine and marine environment.

Rocky intertidal zones are high-energy, periodically submerged environments found in the northern portion of the Northeast system. Sessile invertebrates and some fish inhabit rocky intertidal zones. A variety of algae, kelp, and rockweed are also important habitat features of rocky shores. Fishery resources may depend on particular habitat features of the rocky intertidal zone that provide important levels of refuge and food.

Sandy beaches are most extensive along the Northeast coast. Different zones of the beach present suitable habitat conditions for a variety of marine and terrestrial organisms. For example, the intertidal zone presents suitable habitat conditions for many invertebrates, and transient fish find suitable conditions for foraging during high tide. Several invertebrate and fish species are adapted for living in the high-energy subtidal zone adjacent to sandy beaches.

REGIONAL BENTHIC INVERTEBRATE COMMUNITIES

New England

Theroux and Wigley (1998) reported the results of an extensive, 10-yr benthic sampling program in New England. A total of 1,076 bottom grab samples were collected during spring, summer, and fall during 1956-1965 on the continental shelf and slope in Southern New England, Georges Bank, and the GOM. Twenty-eight percent of the samples (303) were collected in the GOM, 20% (211) on Georges Bank, 32% (344) in Southern New England, and 12% (133) on the slope in Southern New England and on Georges Bank. Results were summarized according to major taxonomic groups, principal species, depth ranges, sediment types, ranges of bottom water temperatures, and the sediment organic carbon content. Results presented here are for major taxa by depth range and sediment type. Detailed information for the individual subregions is not presented in this document. Distribution and abundance information for the Mid-Atlantic region is compiled in an earlier publication (Wigley and Theroux 1981) and is summarized in the next section of this chapter.

The density and biomass of all taxa exhibited similar patterns (Figure 2.12). Both were generally higher in coastal GOM waters, on the southern and eastern areas of Georges Bank (including the Northeast Peak), on most of the Southern New England shelf, and south of Long Island. Density and biomass were lower in deeper water of the GOM, on the north-central part of Georges Bank, on the western side of the Great South Channel, on the continental slope and rise, and in portions of Southern New England. Very high biomass was reported in Rhode Island coastal waters, in Cape Cod Bay, and at the southern end of the Great South Channel. Total biomass (mean wet weight per square meter) was about twice as high on the Southern New England shelf and on Georges Bank as in the GOM and over 10 times higher than on the continental slope. Echinoderms and mollusks dominated the biomass in the GOM, on Georges Bank, and in Southern New England. Crustaceans and annelids dominated the density in Southern New England and on Georges Bank; annelids and mollusks dominated in the GOM.

Depth Influence

Analysis of faunal composition by major taxonomic groups in eight different depth ranges reveals a pronounced decline in density at the shelf break, particularly between 100-200 m (Figure 2.13). Density declined very little between 25 and 100 m, and by 60% between 100 and 200 m. Density continued to decline at successively greater depths, but very slowly per meter increase in depth. The relative changes in biomass on the shelf were more pronounced (Figure 2.14). Biomass declined by 50% between 25-100 m and by 55% between 100-200 m.

On the shelf (down to 100 m), crustaceans (mostly amphipods) were numerically the most abundant taxon, with annelids accounting for 20-29% of the organisms; in just the 0-24 m depth range, mollusks accounted for 23%. Bivalve mollusks made up over half the biomass in the 0-24 and 50-99 m depth ranges, and 33% in the 25-49 m range. Echinoderms (sand dollars and sea urchins) dominated the biomass in the intermediate depth range (25-49 m) on the shelf. Between 100 and 499 m, annelids were the most numerous taxon, but echinoderms dominated the biomass. Mollusks accounted for 36-46%, and annelids for 12-39%, of the organisms in deeper water (500-4000 m), with a diminishing proportion of annelids and an increasing proportion of "other" organisms. Biomass on the shelf rise was composed of a variety of taxa.

Sediment Influence

Theroux and Wigley (1998) classified sediments sampled in the New England region into six categories: gravel, glacial till, shell, sand, sand-silt, and silt-clay. Four of these sediment types were well sampled (148-455 samples); shell and till sediments were poorly sampled (6-22 samples) and will not be included in the discussion that follows, even though the data are included in Figure 2.15. Total numbers and biomass were highest in sand and lowest in silt-clay, with intermediate values in gravel and sand-silt. Amphipods dominated numerically in gravel (42%) and sand (56%), but annelids were also numerous (25-33%). Annelids, crustaceans, and mollusks made up nearly equal proportions, by number, of the sand-silt samples, and mollusks and annelids dominated, by number, the silt-clay samples. Mollusks accounted for 50% of the biomass in gravel; the remainder was composed primarily of annelids, crustaceans (mostly barnacles and crabs), sea anemones, sponges, and tunicates. Bivalve mollusks accounted for about half (48%) of the biomass in sand, but echinoids were also important (33%). Bivalve mollusks were also the dominant taxon in biomass in sand-silt (42%), but less so in silt-clay (20%) where 50% of the biomass was composed of echinoderms, mostly sea cucumbers. Annelids made up 15% and 19% of the biomass in sand-silt and silt-clay sediments, respectively.

Important Fauna

Theroux and Wigley (1998) described the geographic distribution of 24 genera and species of benthic invertebrates in New England that were selected because of their common occurrence, regional ubiquity, or distinctive distribution patterns. Information summarizing the importance of these genera and species as prey for fish and their sediment associations is given in Table 2.10.

Mid-Atlantic Bight

Wigley and Theroux (1981) reported the results of an extensive 10-yr benthic sampling program in the MAB, an area extending from Cape Cod to Cape Hatteras and including Southern New England (which was also included in the more recent report by Theroux and Wigley (1998) for New England). A total of 667 bottom grab samples were collected during spring, summer, and fall, primarily between 1962 and 1965, on the continental shelf, slope, and rise. A nearly equal number of samples were collected in each of three subregions: Southern New England (Cape Cod to Montauk Point, Long Island), the New York Bight (Montauk Point to Cape May, New Jersey), and the Chesapeake Bight (Cape May to Cape Hatteras). Results were summarized according to major taxonomic groups, depth ranges, sediment types, ranges of bottom water temperatures, and the sediment organic carbon content. Results presented here are for major taxa by depth range and sediment type. Detailed information for the individual subregions is not presented in this document.

Over the entire MAB, arthropods (mostly amphipods) numerically made up 46% of the benthic fauna, followed by mollusks (25%, mostly bivalves) and annelids (21%). Biomass was dominated by mollusks (71%).

Among subregions, there was some variation in the densities of the major taxa; the proportion of amphipods diminished from north to south, while the proportion of mollusks increased. There was no variation in biomass, though; mollusks dominated the biomass in all three subregions.

From a geographic perspective, total density generally declined from shallow inshore areas to deeper areas on the slope, and from north to south. There were some small areas of low and high density on the mid-shelf in the southern half of the region, and there was a large area of high density in Southern New England and south of Long Island (Figure 2.16). Biomass (mostly mollusks) was more variable, with areas of high and low biomass scattered throughout the region (Figure 2.17).

Depth Influence

Total density was about the same in the shallowest depth interval (0-24 m) as it was at 50-99 m, and then declined by 61% between 50 and 200 m, and continued to decline, although not as rapidly (per unit change in depth) in deeper water (Figure 2.18). Mollusks (mostly bivalves) were numerically more abundant in the shallowest depth range (0-24 m), and amphipods in the next two deeper shelf depth ranges (25-49 and 50-99 m). The density of amphipods declined dramatically in the deeper water (100-199 m), as did annelids but less so, while the density of mollusks remained the same and that of echinoderms (brittle stars) increased. On a percentage basis, annelids, mollusks, and echinoderms made up nearly equal proportions, by number, of the benthic fauna between 100 and 200 m. Annelids were the most numerous taxon between 200 and 500 m, as were mollusks in deeper water.

Total biomass (mean grams per square meter) was lower in all depth ranges in the MAB than in New England, and declined by about 78% between shallow water (0-24 m) and the 100-199 m depth interval (Figure 2.18). The rate of decline generally diminished in deeper water. The high biomass in the 0-24 m depth range was due to the prevalence of bivalve mollusks, which were not nearly as abundant in deeper shelf waters, but still accounted for 58-65% of the biomass in depths <100 m. A variety of echinoderms (sand dollars, sea cucumbers, brittle stars, and starfish) accounted for 45% of the biomass between 100 and 200 m, where bivalve mollusks still made up 21% and sea anemones 19%. Sand dollars, sea cucumbers, and brittle stars (with annelids) still dominated the biomass between 200 and 500 m, and annelids were the taxon which accounted for most of the biomass between 500 and 1000 m. Echinoderms and echiurid worms dominated the biomass of the sparse fauna of the continental rise.

Sediment Influence

Sediments in the MAB were classified into eight categories: gravel, sand-gravel, shell, sand-shell, sand, silty sand, silt, and clay. Figure 2.19 was derived for this document from data given in Wigley and Theroux (1981), and excludes the results for two poorly sampled sediment types: gravel and shell. Sample sizes for the other six groups ranged from 18 (sand-gravel) to 285 (sand). Total density was highest in sand-gravel and sand-shell, moderately high in sand and silty sand, and low in silt and clay. Total biomass was highest in silty sand, moderate in sand-gravel and sand, and low in sand-shell, silt, and clay.

Amphipods dominated the sand-gravel and sand sediment types numerically, while mollusks were the most numerous taxon in the other four substrates. Almost all of the mollusks in sand-gravel, sand-shell, and sand were bivalves, but gastropods were also important in silty sand. Annelids, hydroids, and bryozoans were numerically important components of the sand-gravel fauna. Annelids were also common in sand, silty sand, sand-gravel, silt, and clay substrates. Bivalve mollusks dominated the biomass in all six substrates. Other taxa with abundant biomass were barnacles in sand-gravel, and sand dollars in sand-shell and sand.

Important Fauna

Wigley and Theroux (1981) described the geographic distribution of 24 genera and species of benthic invertebrates in the MAB that were selected because of their common occurrence or distinctive distribution patterns. Ten of them were also described in the New England region (see earlier): they are the annelids *Sternaspis scutata* and *Scalibregma inflatum,* the mollusks *Arctica islandica, Cerastoderma pinnulatum,* and *Cyclocardia borealis,* the arthropods *Leptocheirus pinguis, Cirolana* spp., *Crangon septemspinosa,* and *Pagurus* spp., and the echinoderm *Echinarachnius parma*. Information summarizing the habitat associations of the other 14 genera and species is given in Table 2.11.

Table 2.1. Gulf of Maine benthic assemblages as identified by Watling (1998). (Geographical distribution of assemblages is shown in Figure 2.4.)

Benthic Assemblage	Benthic Community Description
1	Comprises all sandy offshore banks, most prominently Jeffreys Ledge, Fippennies Ledge, and Platts Bank; depth on top of banks ~70 m; substrate usually coarse sand with some gravel; fauna characteristically sand dwellers with an abundant interstitial component
2	Comprises the rocky offshore ledges, such as Cashes Ledge, Sigsbee Ridge, and Three Dory Ridge; substrate either rock ridge outcrop or very large boulders, often with covering of very fine sediment; fauna predominantly sponges, tunicates, bryozoans, hydroids, and other hard-bottom dwellers; overlying water usually cold MIW
3	Probably extends all along coast of GOM in water depths <60 m; bottom waters warm in summer and cold in winter; fauna rich and diverse, primarily polychaetes and crustaceans, probably consists of several (sub-) assemblages due to heterogeneity of substrate and water conditions near shore and at mouths of bays
4	Extends over soft bottom at depths of 60-140 m, well within the cold MIW; bottom sediments primarily fine muds; fauna dominated by polychaetes, shrimp, and cerianthid anemones
5	Mixed assemblage comprising elements from the coldwater fauna as well as a few deeper water species with broader temperature tolerances; overlying water often a mixture of MIW and MBW, but generally colder than 7°C most of year; fauna sparse, diversity low, dominated by a few polychaetes, with brittle stars, sea pens, shrimp, and cerianthids also present
6	Comprises fauna of deep basins; bottom sediments generally very fine muds, but may have a gravel component in offshore morainal regions; overlying water usually 7-8°C, with little variation; fauna shows some bathyal affinities but densities are not high, dominated by brittle stars and sea pens, and sporadically by a tube-making amphipod
7	True upper slope fauna that extends into the Northeast Channel; water temperatures are always >8°C and salinities are at least 35 ppt; sediments may be either fine muds or a mixture of mud and gravel

Table 2.2. Comparison of two studies of demersal fish assemblages of Georges Bank and Gulf of Maine. (Species associated with the comparable habitats of both studies are listed opposite each other in bold type.)

Overholtz and Tyler (1985)		**Gabriel (1992)**	
Assemblage	**Species**	**Species**	**Assemblage**
Slope and Canyon	**Offshore hake** **Blackbelly rosefish** **Gulf Stream flounder** Fourspot flounder, goosefish, silver hake, white hake, red hake	**Offshore hake** **Blackbelly rosefish** **Gulf Stream flounder** Fawn cusk-eel, longfin hake, armored sea robin	Deepwater
Intermediate	**Silver hake** **Red hake** **Goosefish** Atlantic cod, haddock, ocean pout, yellowtail flounder, winter skate, little skate, sea raven, longhorn sculpin	**Silver hake** **Red hake** **Goosefish** Northern shortfin squid, spiny dogfish, cusk	Combination of Deepwater Gulf of Maine - Georges Bank and Gulf of Maine - Georges Bank Transition
Shallow	**Atlantic cod** **Haddock** **Pollock** Silver hake White hake Red hake Goosefish Ocean pout **Yellowtail flounder** **Windowpane** **Winter flounder** **Winter skate** **Little skate** **Longhorn sculpin** Summer flounder Sea raven, sand lance	**Atlantic cod** **Haddock** **Pollock** **Yellowtail flounder** **Windowpane** **Winter flounder** **Winter skate** **Little skate** **Longhorn sculpin**	Gulf of Maine - Georges Bank Transition Zone (*see below also*) Shallow Water Georges Bank-Southern New England
Gulf of Maine-Deep	**White hake** **American plaice** **Witch flounder** **Thorny skate** Silver hake, Atlantic cod, haddock, cusk, Atlantic wolffish	**White hake** **American plaice** **Witch flounder** **Thorny skate** Redfish	Deepwater Gulf of Maine - Georges Bank
Northeast Peak	**Atlantic cod** **Haddock** **Pollock** Ocean pout, winter flounder, white hake, thorny skate, longhorn sculpin	**Atlantic cod** **Haddock** **Pollock**	Gulf of Maine - Georges Bank Transition Zone (*see above also*)

Table 2.3. Substrate associations with five finfish aggregations on Stellwagen Bank, Gulf of Maine. (Numerical data are mean number of fish per research vessel survey tow for 10 dominant species in each aggregation (Auster et al 2001).)

SUBSTRATE TYPE					
Coarse		**Wide Range**		**Fine**	
Species	**Mean**	**Species**	**Mean**	**Species**	**Mean**
Northern sand lance	1172.0	American plaice	63.3	American plaice	152.0
Atlantic herring	72.2	Northern sand lance	53.0	Acadian redfish	31.3
Spiny dogfish	38.4	Atlantic herring	28.5	Silver hake	29.5
Atlantic cod	37.4	Silver hake	22.4	Atlantic herring	28.0
Longhorn sculpin	29.7	Acadian redfish	16.0	Red hake	26.1
American plaice	28.0	Atlantic cod	14.0	Witch flounder	23.8
Haddock	25.7	Longhorn sculpin	9.5	Atlantic cod	13.1
Yellowtail flounder	20.2	Haddock	9.1	Haddock	12.7
Silver hake	7.5	Pollock	7.9	Longhorn sculpin	12.5
Ocean pout	9.0	Red hake	6.2	Daubed shanney	11.4
No. tows = 83		**No. tows = 159**		**No. tows = 66**	
Haddock	13.1			Silver hake	275.0
Atlantic cod	7.3			American plaice	97.1
American plaice	5.3			Atlantic mackerel	42.0
Silver hake	3.3			Pollock	41.1
Longhorn sculpin	2.0			Alewife	37.2
Yellowtail flounder	1.9			Atlantic herring	32.0
Spiny dogfish	1.6			Atlantic cod	18.1
Acadian redfish	1.6			Longhorn sculpin	16.8
Ocean pout	1.3			Red hake	15.2
Alewife	1.1			Haddock	13.2
No. tows = 60				**No. tows = 20**	

Table 2.4. Sedimentary provinces and associated benthic landscapes of Georges Bank. (Provinces as defined by Valentine *et al.* (1993) and Valentine and Lough (1991) with additional information from Page C. Valentine (pers. comm., U.S. Geological Survey, Woods Hole, MA). Benthic assemblages as assigned by Theroux and Grosslein (1987). See text for further discussion on benthic assemblages.)

Sedimentary Province (province no.)	**Depth Range (m)**	**Description**	**Benthic Assemblage**
Northern Edge / Northeast Peak (1)	40-200	Dominated by gravel with portions of sand, common boulder areas, and tightly packed pebbles; bryozoa, hydrozoa, anemones, and calcareous worm tubes are abundant in areas of boulders; strong tidal and storm currents	Northeast Peak
Northern Slope and Northeast Channel (2)	200-240	Variable sediment type (gravel, gravel-sand, and sand) and scattered bedforms; this is a transition zone between the northern edge and southern slope; strong tidal and storm currents	Northeast Peak
North /Central Shelf (3)	60-120	Highly variable sediment types (ranging from gravel to sand) with rippled sand, large bedforms, and patchy gravel lag deposits; minimal epifauna on gravel due to sand movement; epifauna in sand areas includes amphipods, sand dollars, and burrowing anemones	Central Georges
Central and Southwestern Shelf - shoal ridges (4)	10-80	Dominated by sand (fine and medium grain) with large sand ridges, dunes, waves, and ripples; small bedforms in southern part; minimal epifauna on gravel due to sand movement; epifauna in sand areas includes amphipods, sand dollars, and burrowing anemones	Central Georges
Central and Southwestern Shelf - shoal troughs (5)	40-60	Gravel (including gravel lag) and gravel-sand between large sand ridges; patchy large bedforms, strong currents; minimal epifauna on gravel due to sand movement; epifauna in sand areas includes amphipods, sand dollars, and burrowing anemones	Central Georges
Southeastern Shelf (6)	80-200	Rippled gravel-sand (medium- and fine-grained sand) with patchy large bedforms and gravel lag; weaker currents; ripples are formed by intermittent storm currents; epifauna includes sponges attached to shell fragments and amphipods	Southern Georges
Southeastern Slope (7)	400-2000	Dominated by silt and clay with portions of sand (medium and fine), with rippled sand on shallow slopes and smooth silt-sand deeper	None

Table 2.5. Mid-Atlantic habitat types (as described by Pratt (1973) and Boesch (1979)), with characteristic macrofauna (as identified in Boesch (1979))

Habitat Type [after Boesch (1979)]	**Description**		
	Depth (m)	**Characterization (Pratt (1973) faunal zone)**	**Characteristic Benthic Macrofauna**
Inner shelf	0-30	Coarse sands with finer sands off MD and VA (sand zone)	Polychaetes: *Polygordius, Goniadella,* and *Spiophanes*
Central shelf	30-50	(sand zone)	Polychaetes: *Spiophanes* and *Goniadella* Amphipod: *Pseudunciola*
Central and inner shelf swales	0-50	Occurs in swales between sand ridges (sand zone)	Polychaetes: *Spiophanes, Lumbrineris,* and *Polygordius*
Outer shelf	50-100	(silty sand zone)	Amphipods: *Ampelisca vadorum* and *Erichthonius* Polychaetes: *Spiophanes*
Outer shelf swales	50-100	Occurs in swales between sand ridges (silty sand zone)	Amphipods: *Ampelisca agassizi, Unciola,* and *Erichthonius*
Shelf break	100-200	(silt-clay zone)	Not given
Continental slope	>200	(none)	Not given

Table 2.6. Major recurrent demersal finfish assemblages of the Mid-Atlantic Bight during spring and fall (as determined by Colvocoresses and Musick (1984))

Season	**Species Assemblage**				
	Boreal	**Warm Temperate**	**Inner Shelf**	**Outer Shelf**	**Slope**
Spring	Atlantic cod Little skate Sea raven Goosefish Winter flounder Longhorn sculpin Ocean pout Silver hake Red hake White hake Spiny dogfish	Black sea bass Summer flounder Butterfish Scup Spotted hake Northern searobin	Windowpane	Fourspot flounder	Shortnose greeneye Offshore hake Blackbelly rosefish White hake
Fall	White hake Silver hake Red hake Goosefish Longhorn sculpin Winter flounder Yellowtail flounder Witch flounder Little skate Spiny dogfish	Black sea bass Summer flounder Butterfish Scup Spotted hake Northern searobin Smooth dogfish	Windowpane	Fourspot flounder Fawn cusk eel Gulf Stream flounder	Shortnose greeneye Offshore hake Blackbelly rosefish White hake Witch flounder

Table 2.7. Mid-Atlantic reef types, location, and representative flora and fauna (as described in Steimle and Zetlin (2000))

Location (Type)	Representative Flora and Fauna		
	Epibenthic/Epibiotic	**Motile Epibenthic Invertebrates**	**Fish**
Estuarine (oyster reefs, blue mussel beds, other hard surfaces, semi-hard clay, and *Spartina* peat reefs)	Eastern oyster, barnacles, ribbed mussel, blue mussel, algae, sponges, tube worms, anemones, hydroids, bryozoans, common Atlantic slipper snail, jingleshell (*Anomia* sp.), northern stone coral, sea whips, tunicates, caprellid amphipods, and wood borers	Xanthid crabs, blue crab, Atlantic rock crabs, portly spider crab, juvenile American lobster, and sea stars	Gobies, spot, striped bass, black sea bass, white perch, oyster toadfish, scup, black drum, Atlantic croaker, spot, sheepshead porgy, pinfish, juvenile and adult tautog, pinfish, northern puffer, cunner, sculpins, juvenile and adult Atlantic cod, rock gunnel, conger eel, American eel, red hake, ocean pout, white hake, and juvenile pollock
Coastal (exposed rock/soft marl, harder rock, wrecks and artificial reefs, kelp, and other materials)	Boring mollusks (piddocks), red algae, sponges, anemones, hydroids, northern stone coral, soft coral, sea whips, barnacles, blue mussel, northern horse mussel, bryozoans, skeleton and tubiculous amphipods, polychaetes, jingle shell, and sea stars	American lobster, Jonah crab, Atlantic rock crab, portly spider crab, sea stars, urchins, and squid egg clusters	Black sea bass, pinfish, scup, cunner, red hake, gray triggerfish, black grouper, smooth dogfish, summer flounder, scad, bluefish, amberjack, Atlantic cod, tautog, ocean pout, conger eel, sea raven, rock gunnel, and radiated shanny
Shelf (rocks and boulders, wrecks and artificial reefs, and other solid substrates)	Boring mollusks (piddocks), red algae, sponges, anemones, hydroids, stone coral, soft coral, sea whips, barnacles, blue mussel, northern horse mussel, bryozoans, amphipods, and polychaetes	American lobster, Jonah crabs, Atlantic rock crab, portly spider crabs, sea stars, urchins, and squid egg clusters (with addition of some deepwater taxa at shelf edge)	Black sea bass, scup, tautog, cunner, gag, sheepshead, porgy, round herring, sardines, amberjack, Atlantic spadefish, gray triggerfish, mackerels, small tunas, spottail pinfish, tautog, Atlantic cod, ocean pout, red hake, conger eel, cunner, sea raven, rock gunnel, pollock, and white hake
Outer shelf (reefs and clay burrows including "pueblo village community")			Tilefish, white hake, and conger eel

Table 2.8. Faunal zones of the continental slope of Georges Bank and Southern New England (from Hecker (1990))

Zone	Approximate Depth (m)	Gradient	Current	Fauna
Upper slope	300-700	Low	Strong	Dense filter feeders: Scleratinians (*Dasmosmilia lymani, Flabellum alabastrum*), and quill worm (*Hyalinoecia* sp.)
Upper middle slope	500-1300	High	Moderate	Sparse scavengers: red deepsea crab (*Chaceon quinqueidens*), northern cutthroat eel, common grenadier (*Nezumia*), alcyonarians (*Acanella arbuscula* and *Eunephthya florida*) in areas of hard substrate
Lower middle slope/transition	1200-1700	High	Moderate	Sparse suspension feeders: cerianthids and sea pen (*Distichoptilum gracile*)
Lower slope	>1600	Low	Strong	Dense suspension and deposit feeders: ophiurid (*Ophiomusium lymani*), cerianthids, and sea pens

Table 2.9. Habitat types for the canyons of Georges Bank, including characteristic fauna. (Faunal characterization is from Cooper *et al.* (1987) and is for depths <230 m only.)

Habitat Type	Geologic Description	Canyon Locations	Most Commonly Observed Fauna
I	Sand or semiconsolidated silt substrate (claylike consistency) with <5% overlay of gravel. Relatively featureless except for conical sediment mounds	Walls and axis	Cerianthid, pandalid shrimp, white colonial anemone, Jonah crab, starfishes, portunid crab, greeneye, brittle stars, mosaic worm, red hake, fourspot flounder, shellless hermit crab, silver hake, and Gulf Stream flounder
II	Sand or semiconsolidated silt substrate (claylike consistency) with >5% overlay of gravel. Relatively featureless	Walls	Cerianthids, galatheid crab, squirrel hake, white colonial anemone, Jonah crab, silver hake, sea stars, ocean pout, brittle stars, shell-less hermit crab, and greeneye
III	Sand or semiconsolidated silt (claylike consistency) overlain by siltstone outcrops and talus up to boulder size. Featured bottom with erosion by animals and scouring	Walls	White colonial anemone, pandalid shrimp, cleaner shrimp, rock anemone, white hake, sea stars, ocean pout, conger eel, brittle stars, Jonah crab, American lobster, blackbelly rosefish, galatheid crab, mosaic worm, and tilefish
IV	Consolidated silt substrate, heavily burrowed/excavated. Slope generally >5º and <50º. Termed "pueblo village" habitat	Walls	Sea stars, blackbelly rosefish, Jonah crab, American lobster, white hake, cusk, ocean pout, cleaner shrimp, conger eel, tilefish, galatheid crab, and shell-less hermit crab
V	Sand dune substrate	Axis	Sea stars, white hake, Jonah crab, and goosefish

Table 2.10 Habitat associations, and importance as prey for fish, of 24 select genera and species of benthic invertebrates in New England. (Source: Theroux and Wigley (1998).)

Phylum	Genus/Species	Description
Annelida	*Aphrodita hastata*	Polychaete often found in Atlantic cod, haddock, and red hake stomachs; commonly inhabits mud bottoms, or mixed bottoms with high mud content
	Scalibregma inflatum	Polychaete that is an important food source for many demersal fish; inhabits silty sand substrates
	Sternaspis scutata	Burrowing polychaete eaten by winter flounder; commonly inhabits silty sediments
Mollusca	*Arctica islandica* (ocean quahog)	Small- to medium-sized individuals preyed upon by Atlantic cod; usually inhabits muddy sand bottoms, very abundant in some localities on the continental shelf such as the southern part of Georges Bank
	Astarte undata (wavy astarte)	Most abundant at mid-shelf depths (50-99 m) in sand and till substrates; not a major prey item of demersal fishes
	Cerastoderma pinnulatum (northern dwarf cockle)	Infrequently found in fish stomachs; prefers sandy substrates, but is also found in other types of substrate
	Cyclocardia borealis (northern cyclocardia)	Broadly distributed throughout the region, prefers sand and till substrates; not common in fish diets
	Modiolus modiolus (northern horsemussel)	Largest and most common mussel offshore of New England, prefers sand and sand-shell substrates
	Placopecten magellanicus (sea scallop)	Most abundant on coarse sandy bottoms; juveniles eaten by some demersal fishes, principally haddock and ocean pout
	Buccinum spp.	Four species of whelk of which *B. undatum* (waved whelk) is by far the most common, typically found at mid- to lower shelf depths in sand and coarser-grained sediments
	Neptunea [lyrata] decemcostata (wrinkle whelk)	Typically inhabits hard bottoms ranging from coarse sand to gravels at mid- to lower shelf depths
Arthropoda	*Ampelisca agassizi*	Tube-dwelling amphipod, the most abundant species of amphipod in the southwestern half of the region, preferring a sandy substratum; a common prey item in the diet of many demersal fish
	Leptocheirus pinguis	Another tube-dwelling amphipod abundant on sandy shelf substrates; very important prey species for demersal fish
	Unciola irrorata	Another tube-dwelling amphipod important in sands of Georges Bank; an important prey species for demersal fish
	Crangon septemspinosa (sevenspine bay shrimp)	Found in sandy sediments in inshore and shelf waters, very abundant in certain localities; an important prey item for nearly all demersal fishes
	Homarus americanus (American lobster)	Widely distributed from inshore bays to offshore canyons, inhabits a variety of substrates
	Hyas coarctatus (Arctic lyre crab)	Common throughout the region on muddy and pebbly bottoms
	Pagurus spp. (hermit crabs)	Seven species ubiquitous throughout the region in nearly all substrate types; preyed upon by demersal fishes
	Cirolana spp. (isopods)	At least three species, common on muddy and sandy bottoms in the GOM and on Georges Bank
Echinodermata	*Asterias vulgaris* (northern or purple starfish)	One of the most common species of starfish in the region, normally found on sandy bottoms; juveniles occasionally found in fish stomachs
	Leptasterias spp.	Several species of starfish that are common inhabitants on sandy bottoms, very abundant in certain locations; small specimens occasionally preyed upon by some species of demersal fish
	Echinarachnius parma (northern sand dollar)	Most abundant member of the urchin family in the New England region, especially in some locations on Georges Bank, lives on sand; a common prey item for flounders, haddock, and Atlantic cod
	Strongylocentrus droebachiensis (green sea urchin)	Another ubiquitous echinoid, a hard-bottom dweller; preyed upon by haddock and American plaice
	Ophiura spp. (brittle stars)	At least three species, widely distributed and occur in most sediment types; common in diets of haddock and American plaice

Table 2.11 Habitat associations of 14 of 24 (see Table 2.10 for information on the other 10) select genera and species of benthic invertebrates in the Mid-Atlantic Bight. (Source: Wigley and Theroux (1981).)

Phylum	Genus/Species	Description
Annelida	*Hyalinoecia tubicola*	Tube-dwelling polychaete that inhabits the shelf break at depths >200 m
Pogonophora	*Siboglinum ekmani*	Tube-dwelling species found in deep water on the continental slope and rise
Mollusca	*Thyasira* spp. (cleftclams)	Five species of small bivalves most commonly found in offshore waters and in fine-grained bottom sediments
	Lucinoma blakean[um] (Blake lucine)	Bivalve most common in outer continental shelf waters
	Ensis directus (razor clam)	Sand-dwelling species found in shallow inshore waters and on the continental shelf
	Polinices spp. (moon snails)	Two species found on sandy sediments on the continental shelf
	Alvania spp. (alvanias)	At least two species of small gastropods usually associated with silt-clay bottom sediments, found on the continental shelf and slope in Southern New England and on the slope further south
Arthropoda	*Ampelisca* spp.	Six species of tube-dwelling amphipods found inshore and on the shelf, very abundant in some localities
	Phoxocephalus holbolli	Amphipod that characteristically inhabits fine sand sediments on the continental shelf
	Trichophoxus epistomus	Widely distributed burrowing amphipod that inhabits sand and silty sand sediments on the shelf
	Cancer spp. (rock crabs)	Two species that inhabit a variety of bottom sediments throughout the Mid-Atlantic shelf
Echinodermata	*Echinocardium cordatum* (sea potato)	Burrowing heart urchin that usually inhabits sand sediments in moderately shallow water, found only in the southern part of the region
	Astropecten spp.	Two species of burrowing sea stars that are common in silty sand bottom sediments on the northern half of the Mid-Atlantic shelf
	Amphilimna olivacea	Brittle star that inhabits moderately deep water in Southern New England along the outer continental shelf and upper slope

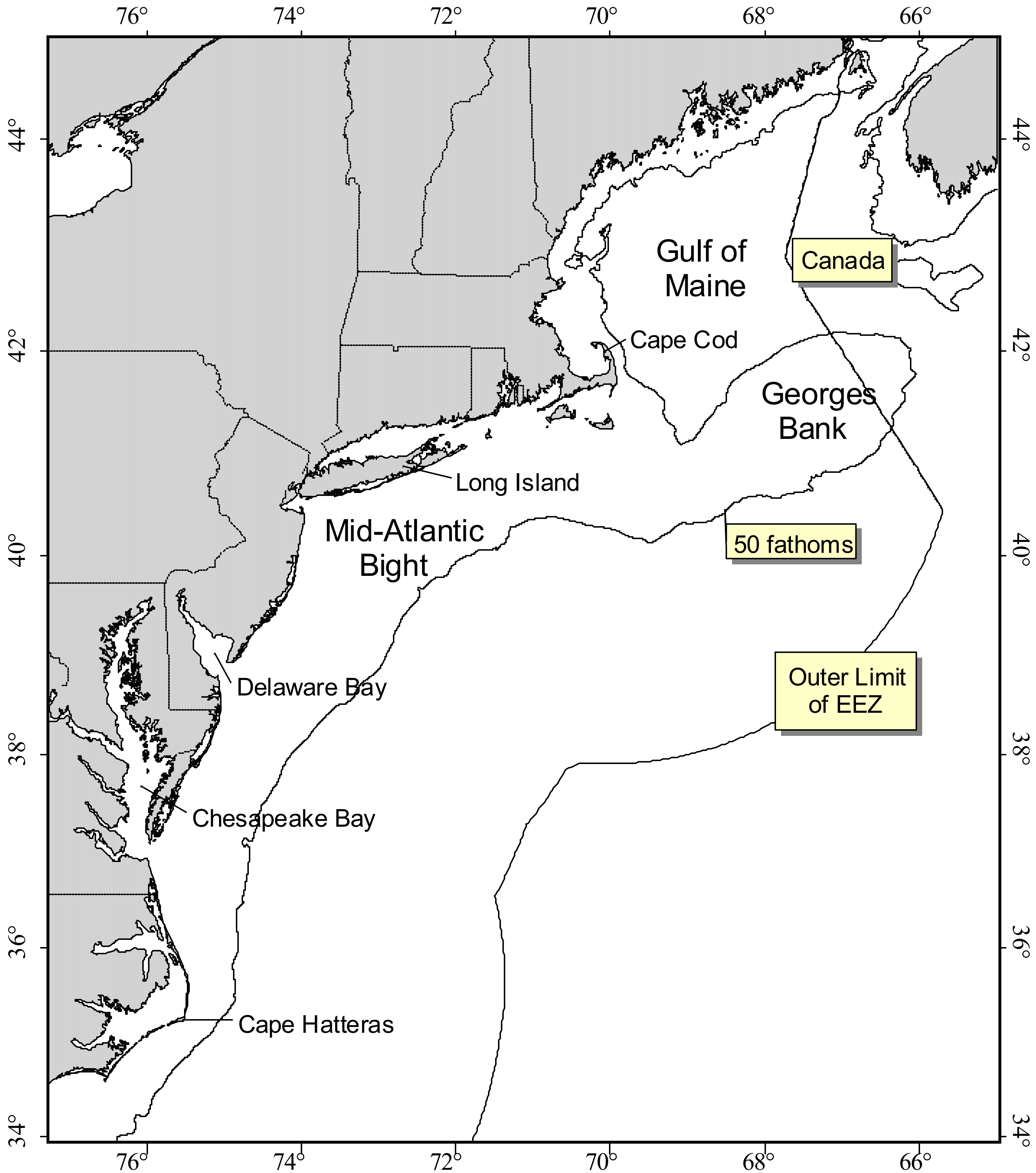


Figure 2.1. Northeast U.S. Shelf Ecosystem, showing the boundaries of the continental shelf (50-fathom line), the EEZ (200-mi limit), and the three principal systems (Gulf of Maine, Georges Bank, and Mid-Atlantic Bight).

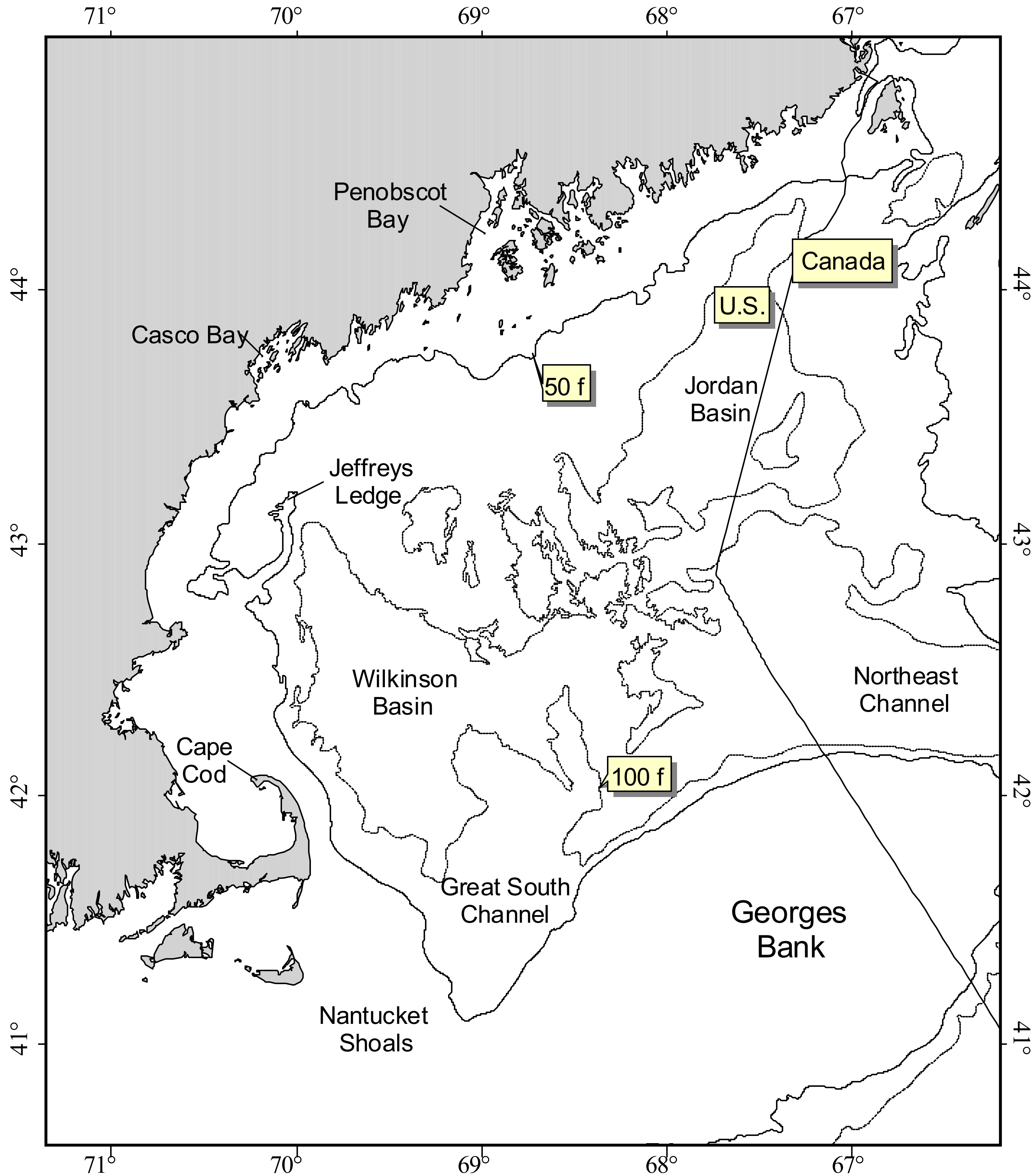


Figure 2.2. Gulf of Maine, showing the boundaries of the continental shelf (50-fathom line), the boundary between the U.S. and Canadian EEZs, and the principal physiographic features.

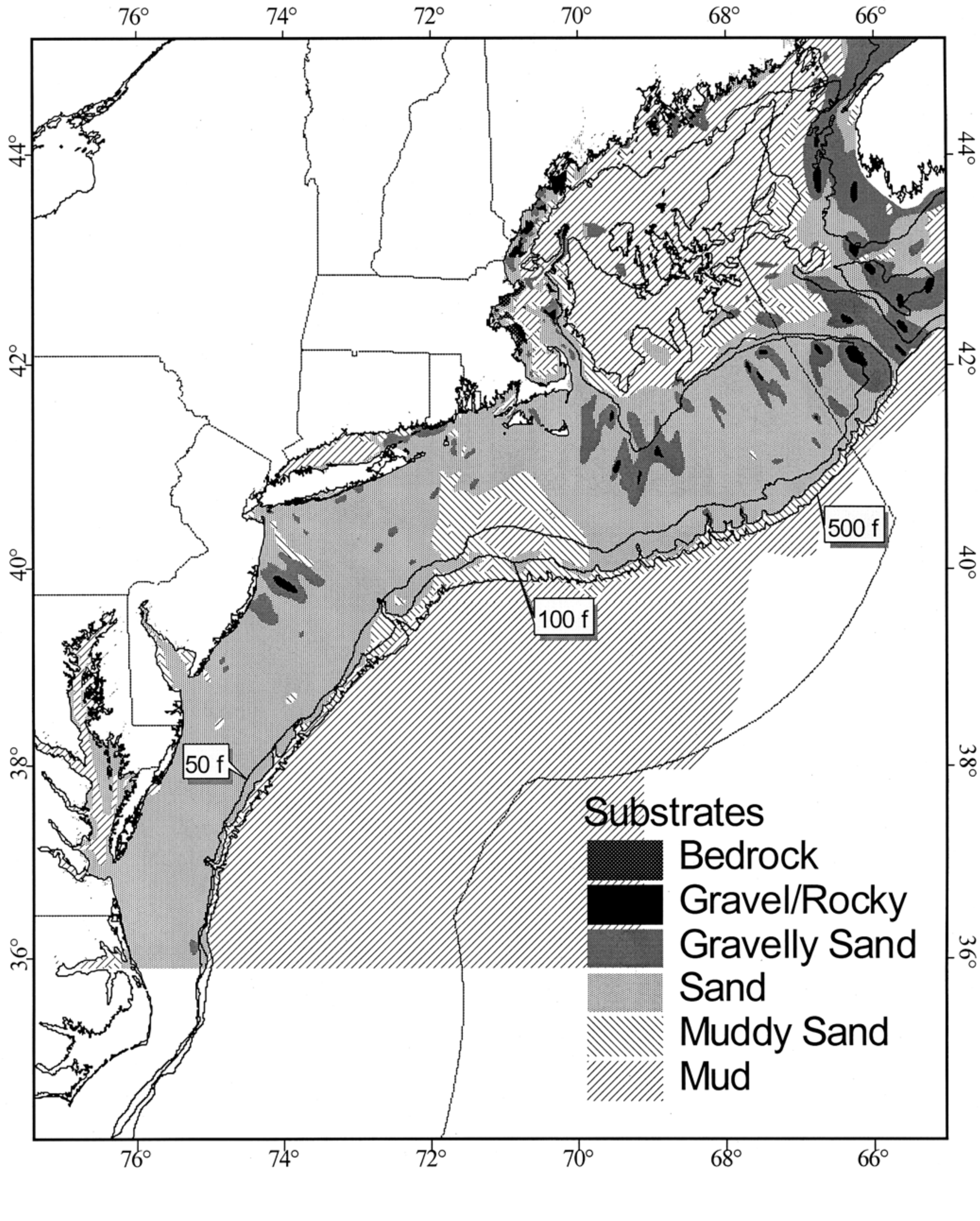


Figure 2.3. Northeast Region sediments. (Modified from Poppe, Schlee, Butman, *et al.* (1989), and Poppe, Schlee, and Knebel (1989).)

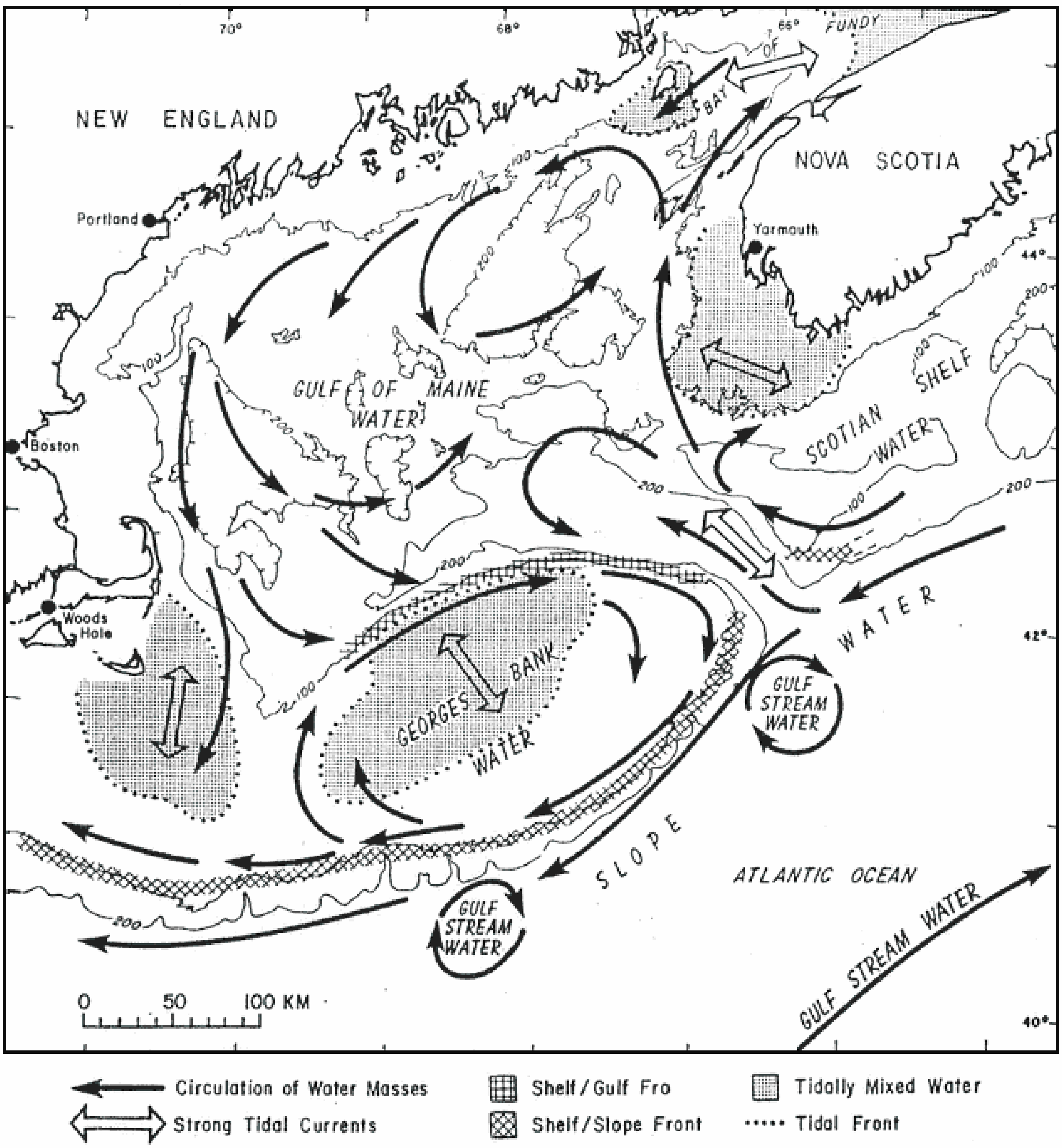


Figure 2.4. Water mass circulation patterns in the Georges Bank - Gulf of Maine region. (Depth in meters. Source: Valentine and Lough (1991).)

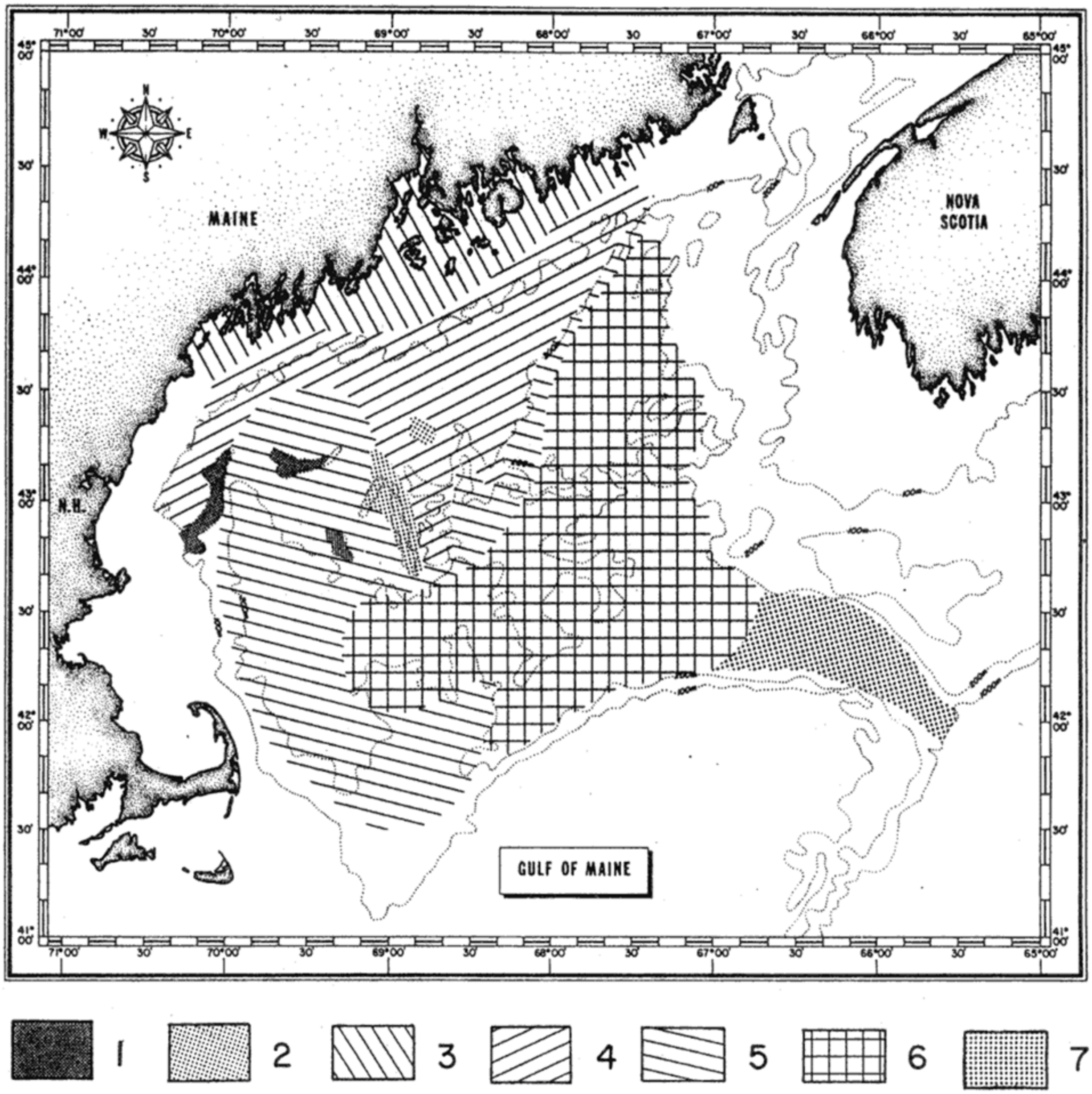


Figure 2.5. Distribution of the seven major benthic assemblages in the Gulf of Maine. (1 = sandy offshore banks; 2 = rocky offshore ledges; 3 = shallow (<50 m) temperate bottoms with mixed substrate; 4 = boreal muddy bottom, overlain by Maine Intermediate Water, 50-160 m (approximate); 5 = cold deep water, species with broad tolerances, muddy bottom; 6 = deep basin warm water, muddy bottom; and 7 = upper slope water, mixed sediment. Source: Watling (1998).)

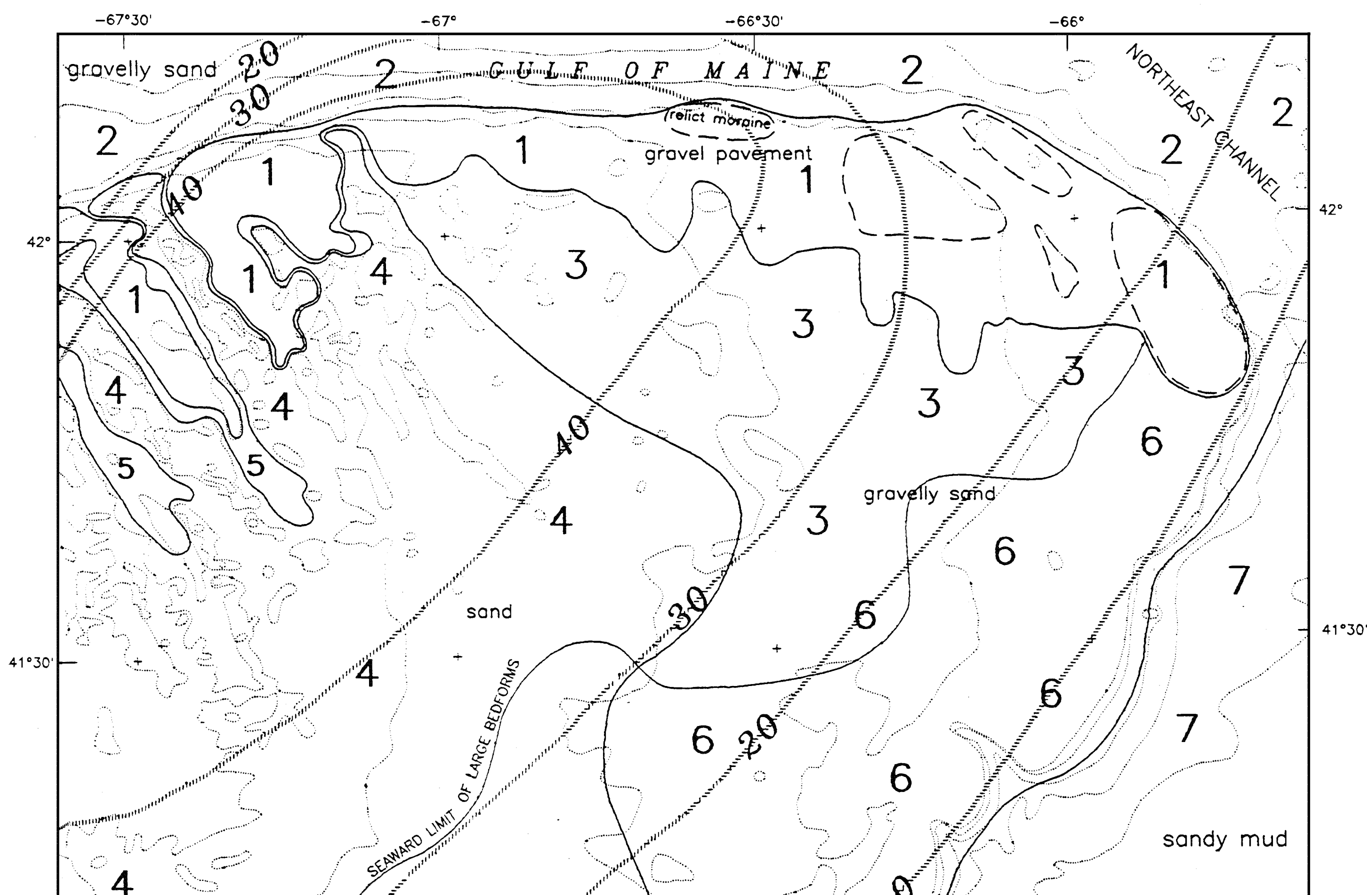


Figure 2.6. Sedimentary provinces of eastern Georges Bank. (Numbered 1-7. Based on criteria of seafloor morphology, texture, sediment movement and bedforms, and mean tidal bottom current speed (shown as hatched-line contours ranging between 10 and 40 cm/s). Relict moraines (bouldery seafloor) are enclosed by dashed lines. See Table 2.4 for descriptions of provinces. Source: Valentine and Lough (1991).)

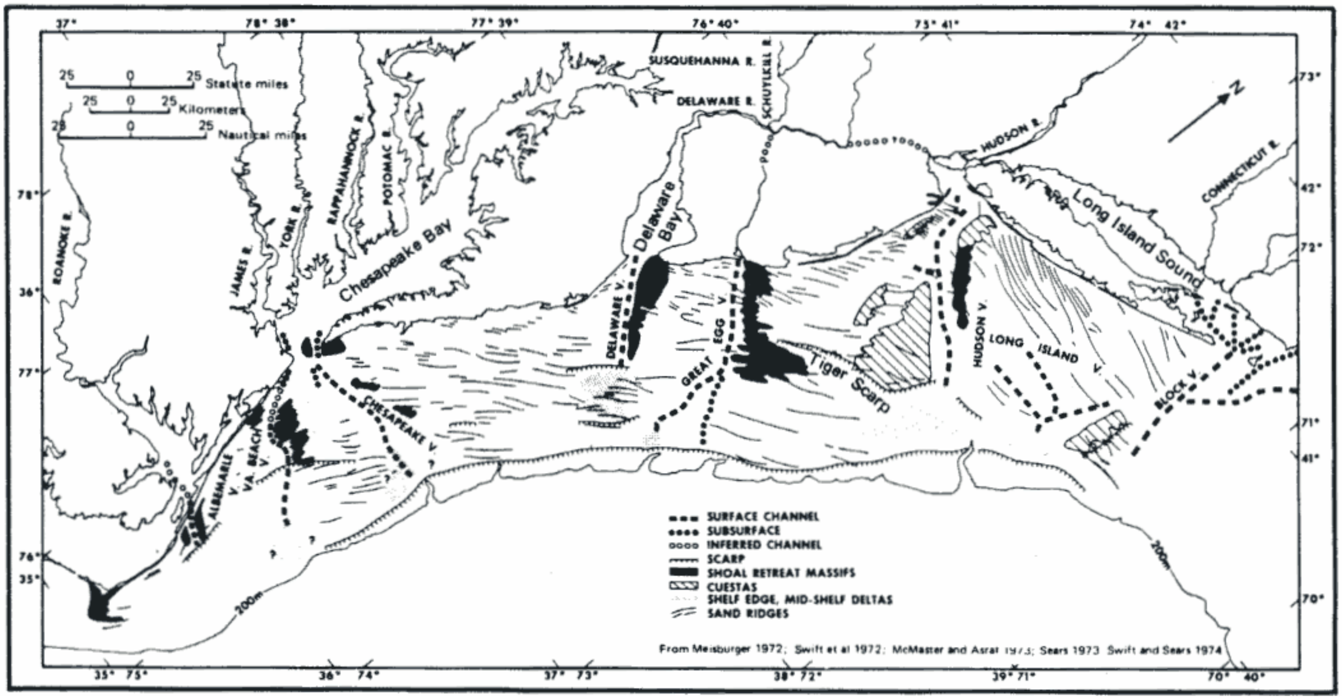


Figure 2.7. Mid-Atlantic Bight submarine morphology. (Source: Stumpf and Biggs (1988).)

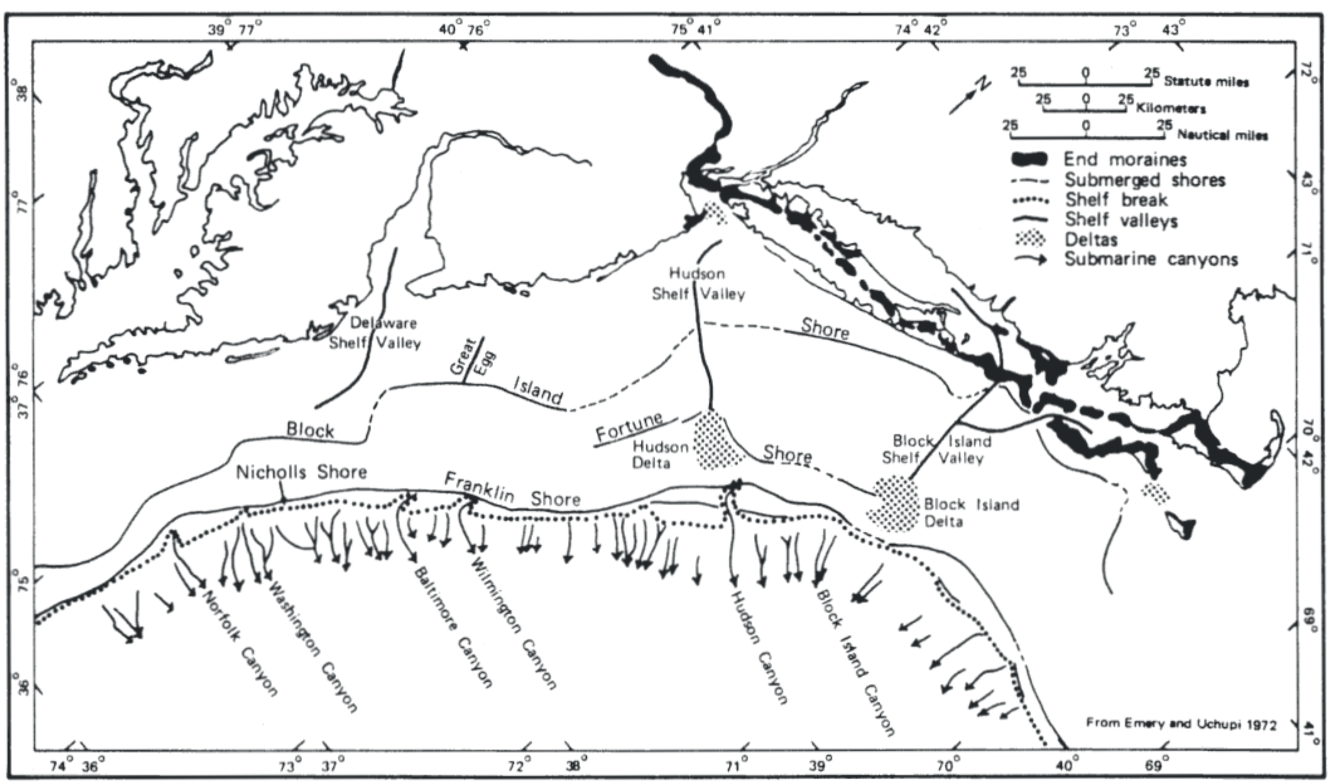


Figure 2.8. Major features of the Mid-Atlantic and Southern New England continental shelf. (Source: Stumpf and Biggs (1988).)

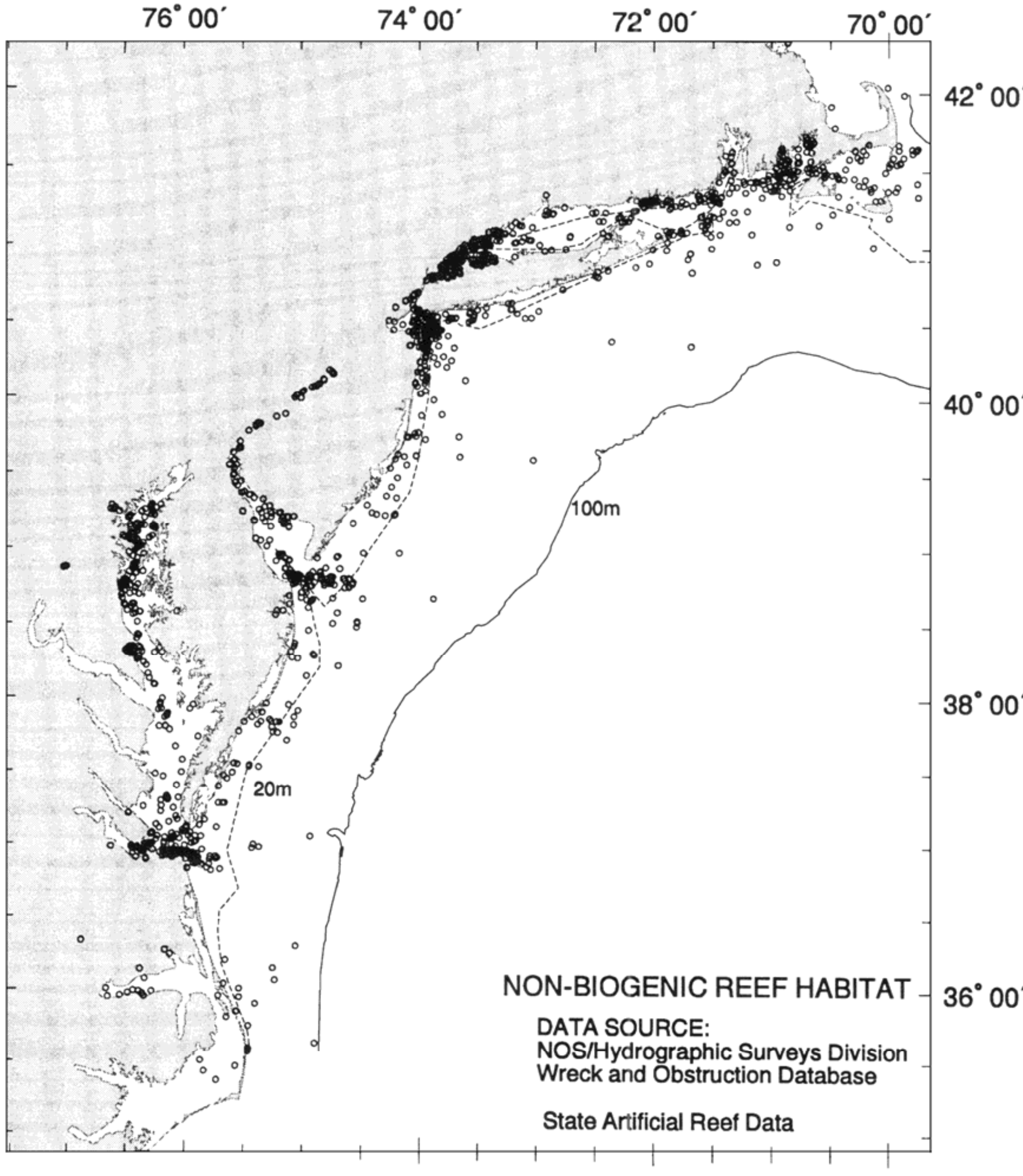


Figure 2.9. Summary of all reef habitats (except biogenic, such as mussel or oyster beds) in the Mid-Atlantic Bight. (Source: Steimle and Zetlin (2000).)

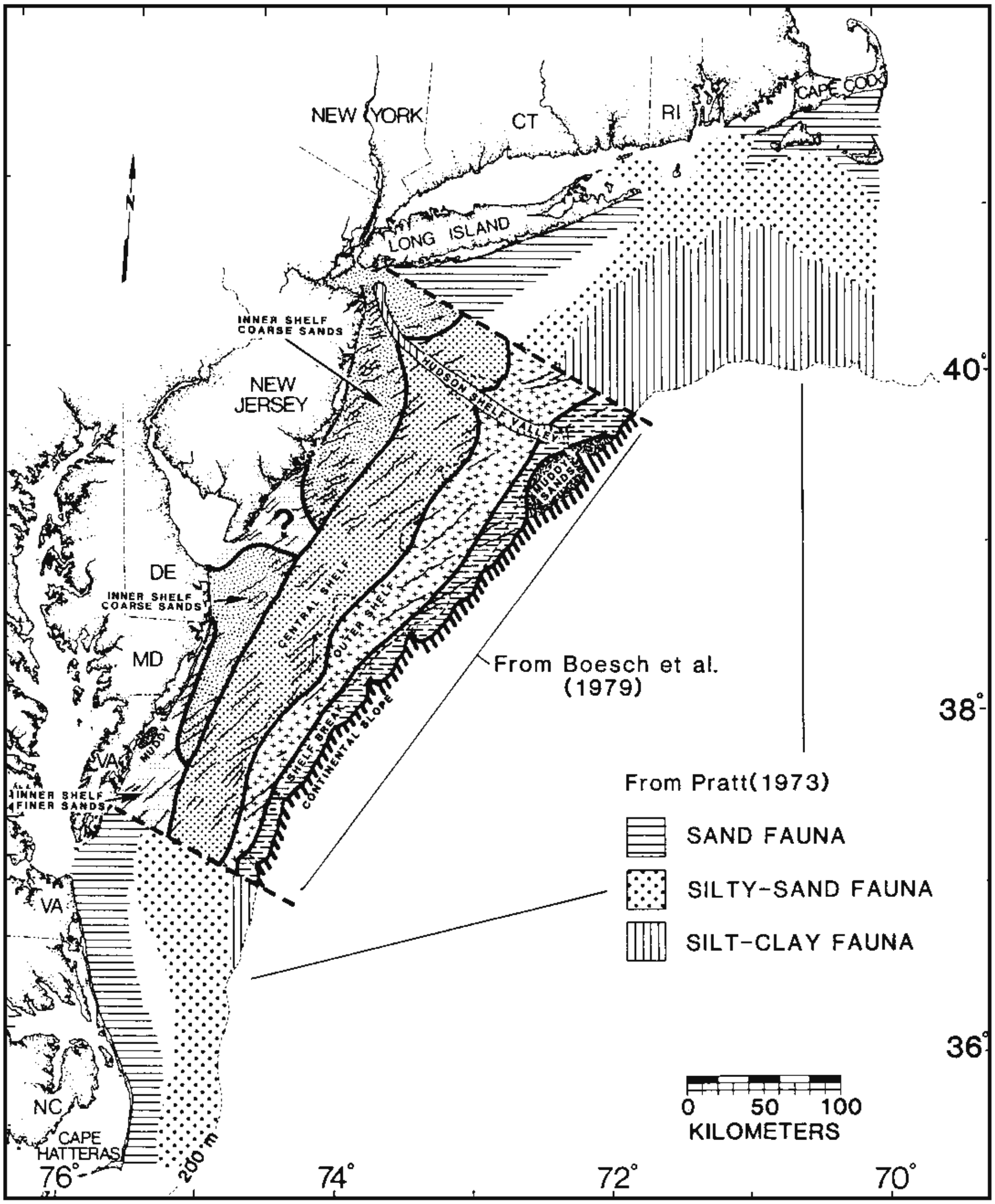


Figure 2.10. Schematic representation of major macrofaunal zones on the Mid-Atlantic shelf. (Approximate location of ridge fields indicated. Source: Reid and Steimle (1988).)

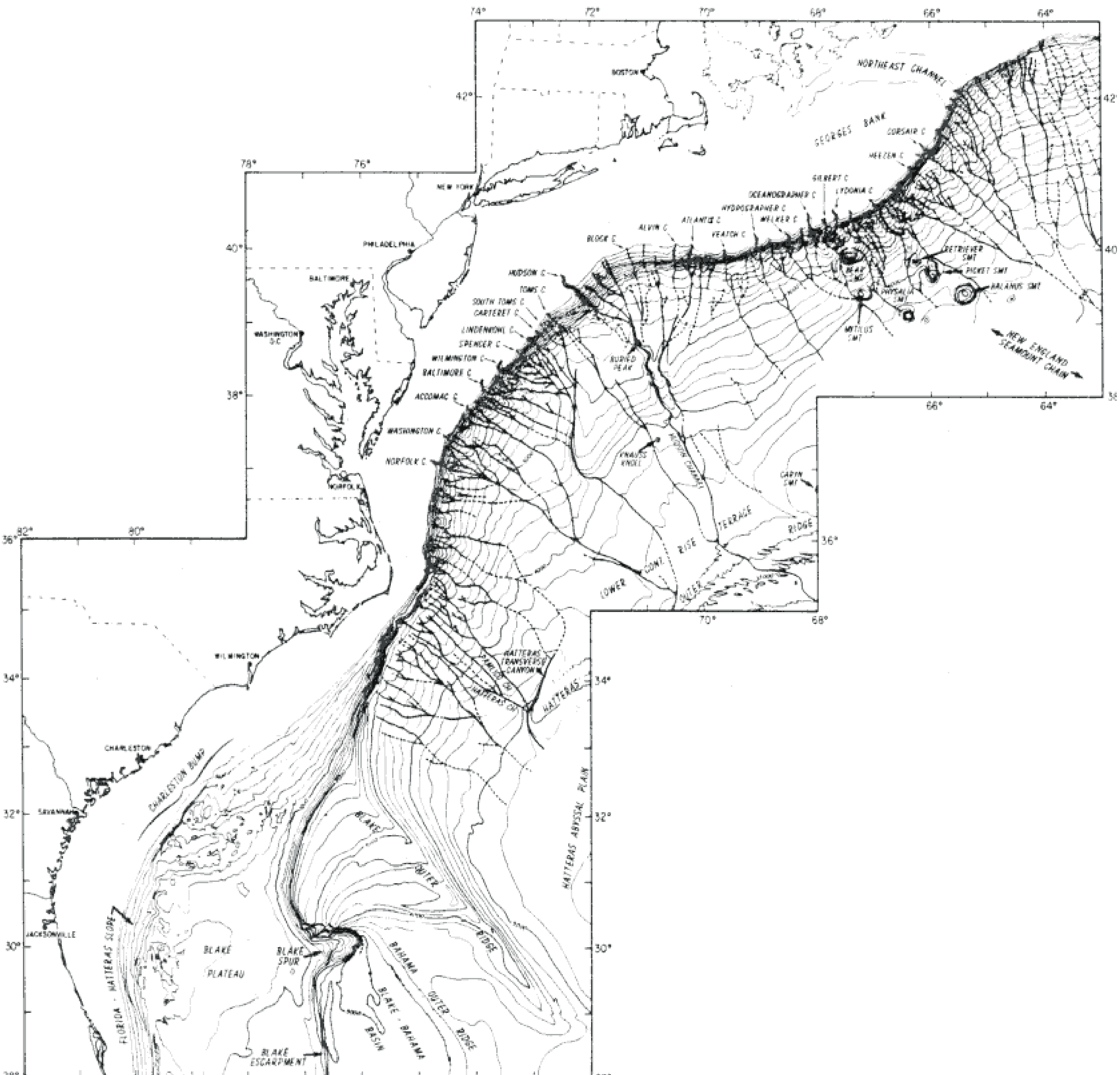
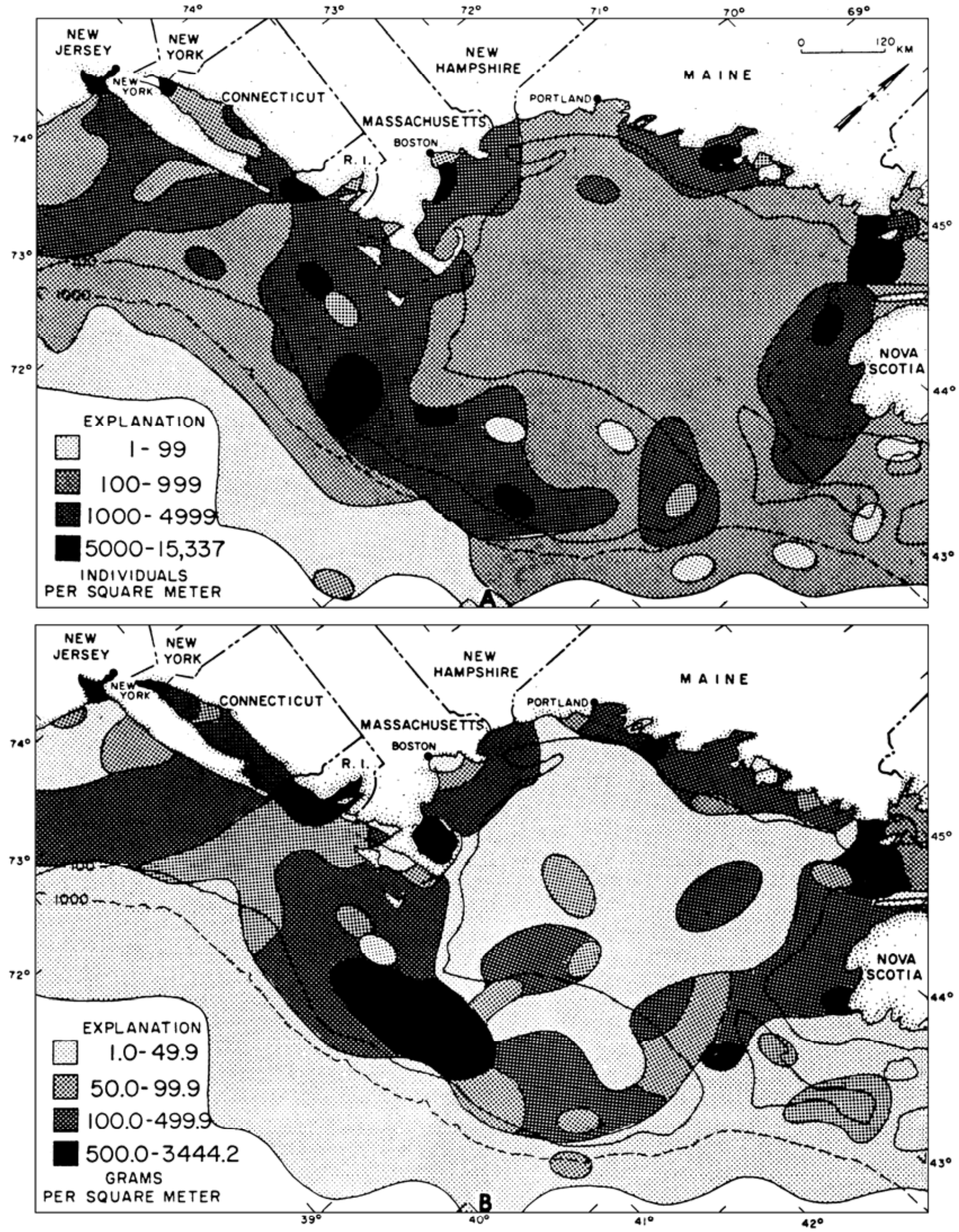


Figure 2.11. Bathymetry of the U.S. Atlantic continental margin. (Contour interval is 200 m below 1000 m of water depth, and 100 m above 1000 m of water depth. Axes of principal canyons and channels are shown by solid lines (dashed where uncertain or approximate). Source: Tucholke (1987).)



ALL TAXA COMBINED

Figure 2.12. Geographic distribution of the density (top) and biomass (bottom) of all taxonomic groups of benthic invertebrates in the New England region, 1956-1965. (Source: Theroux and Wigley (1998).)

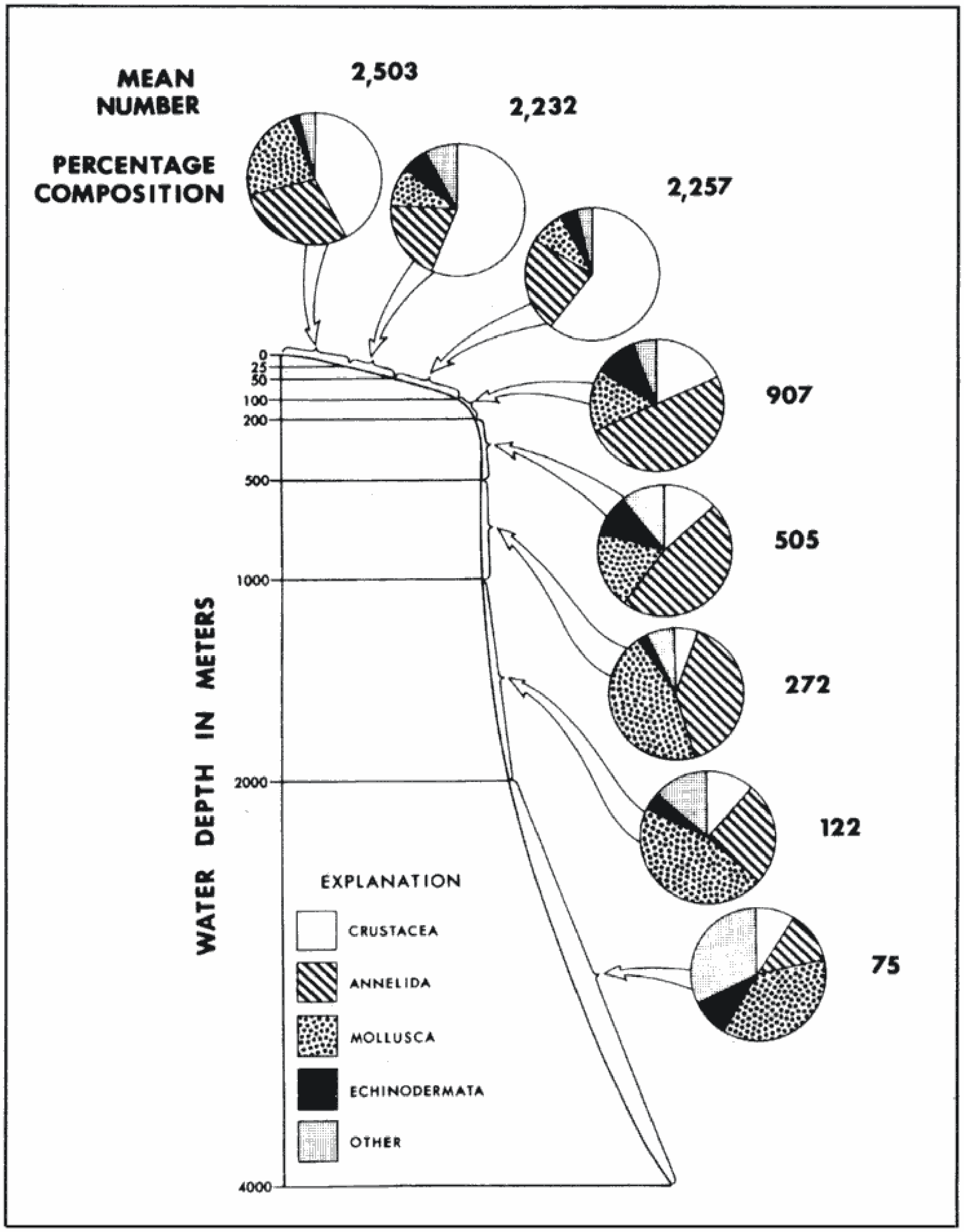


Figure 2.13. Percentage composition (by number of individuals) and density (as mean number of individuals per square meter of bottom area) of the major taxonomic groups of New England benthic invertebrate fauna in relation to water depth. (Source: Theroux and Wigley (1998).)

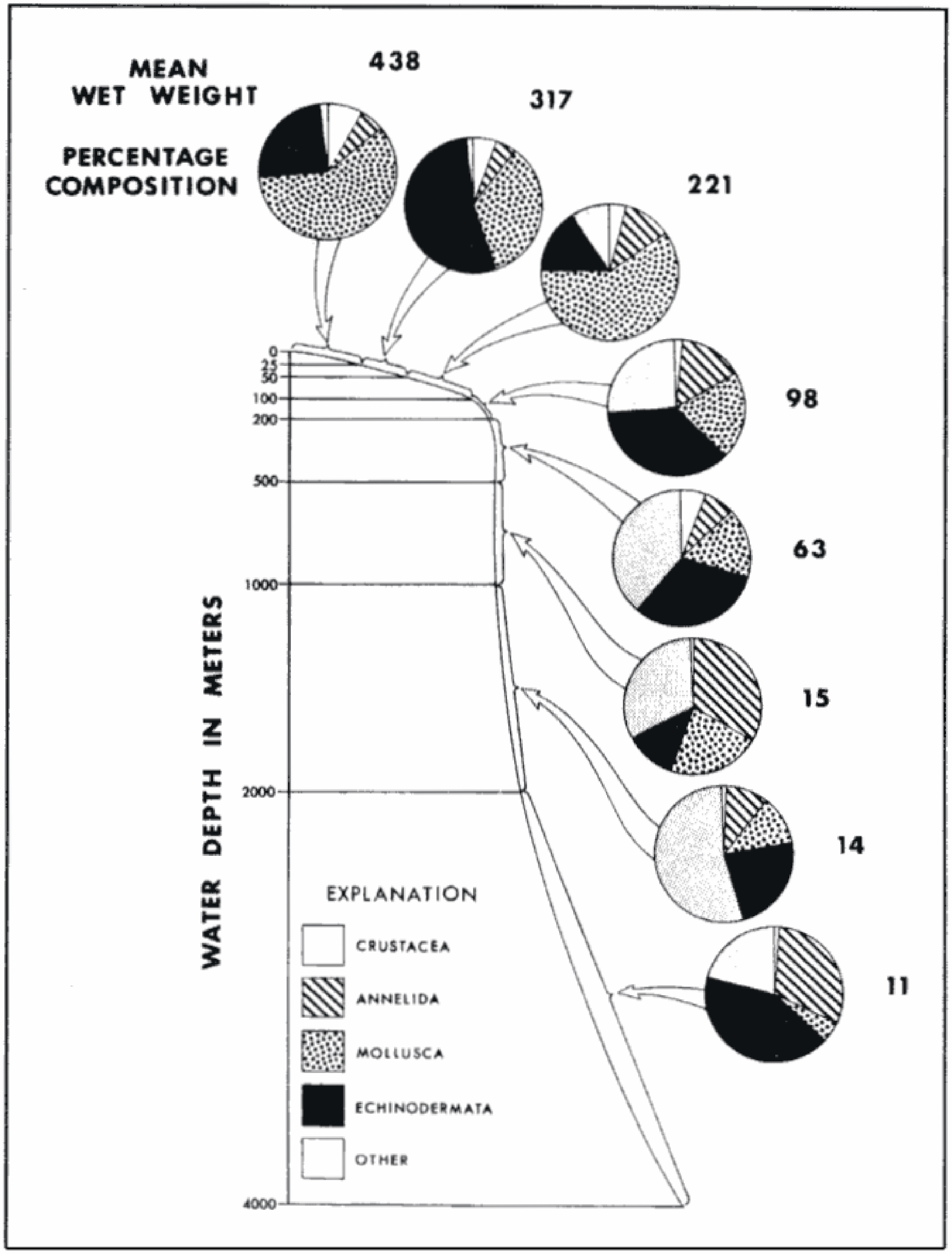


Figure 2.14. Percentage composition (by wet weight) and biomass (as mean wet weight in grams of individuals per square meter of bottom area) of the major taxonomic groups of New England benthic invertebrate fauna in relation to water depth. (Source: Theroux and Wigley (1998).)

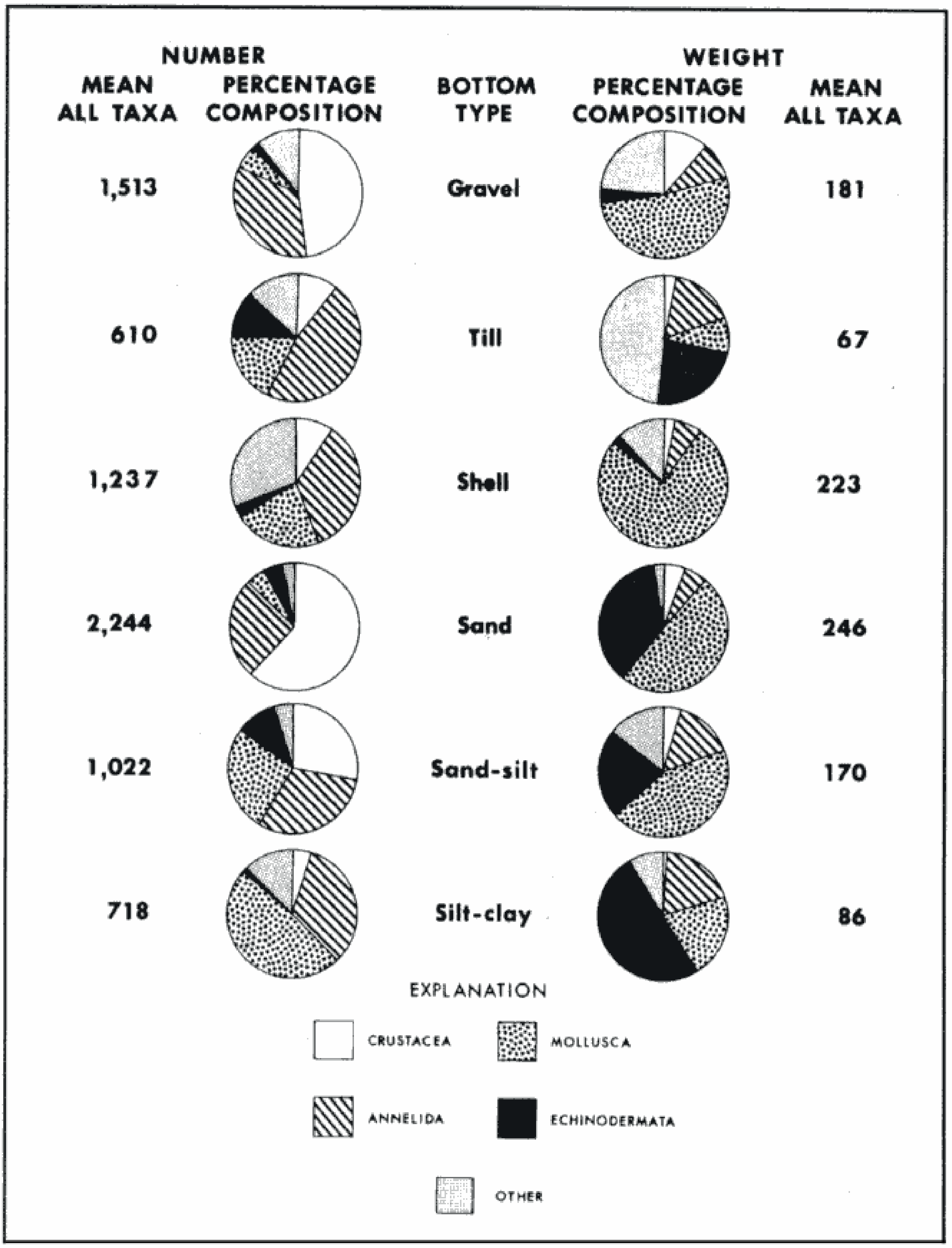


Figure 2.15. Percentage composition (by number of individuals and by wet weight) and density and biomass (as mean number and wet weight (in grams), respectively, of individuals per square meter of bottom area) of the major taxonomic groups of New England benthic invertebrate fauna in relation to bottom type. (Source: Theroux and Wigley (1998).)

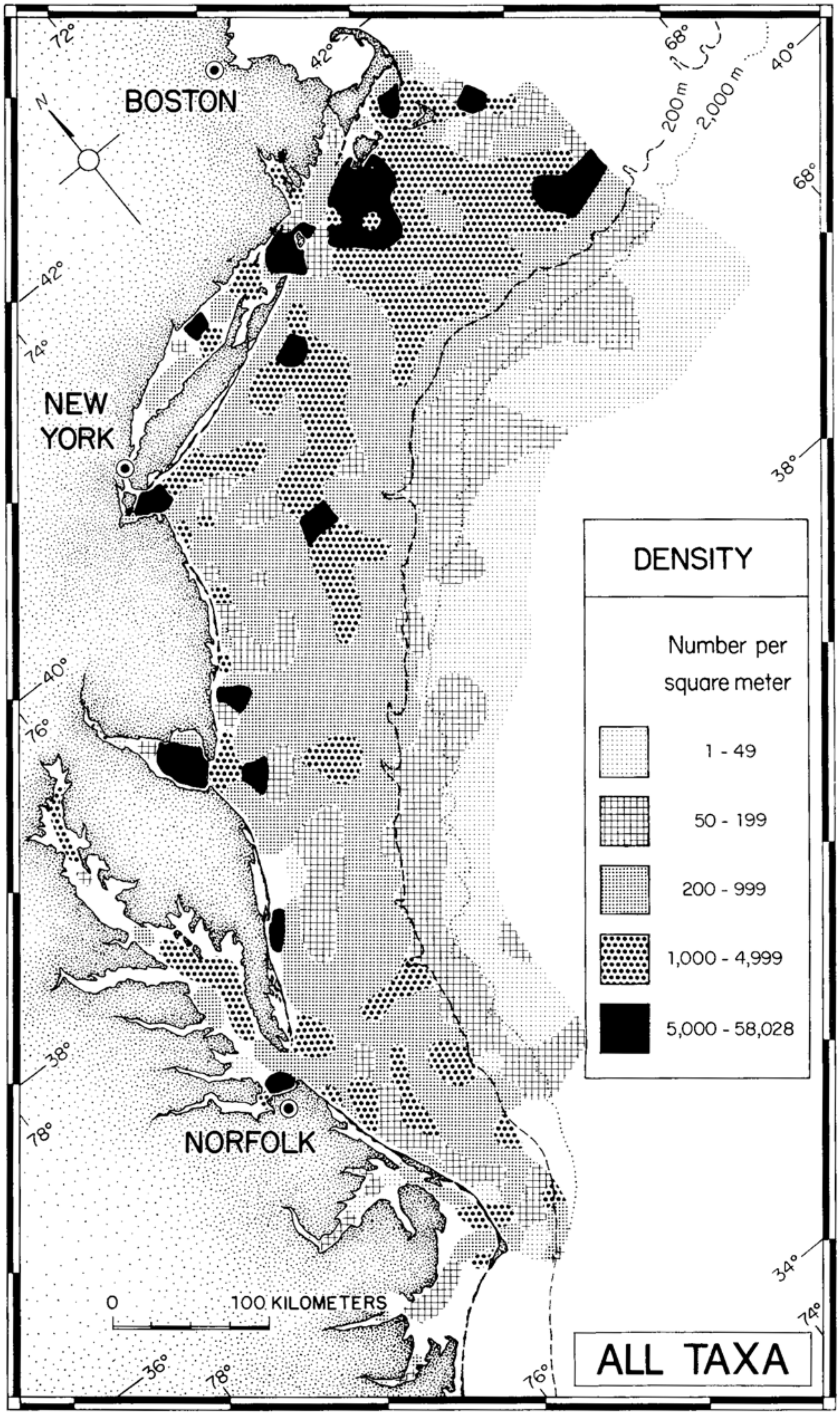


Figure 2.16. Geographic distribution of the density (as mean number of individuals per square meter) of all taxonomic groups of benthic invertebrates in the Mid-Atlantic region, 1956-1965. (Source: Wigley and Theroux (1981).)

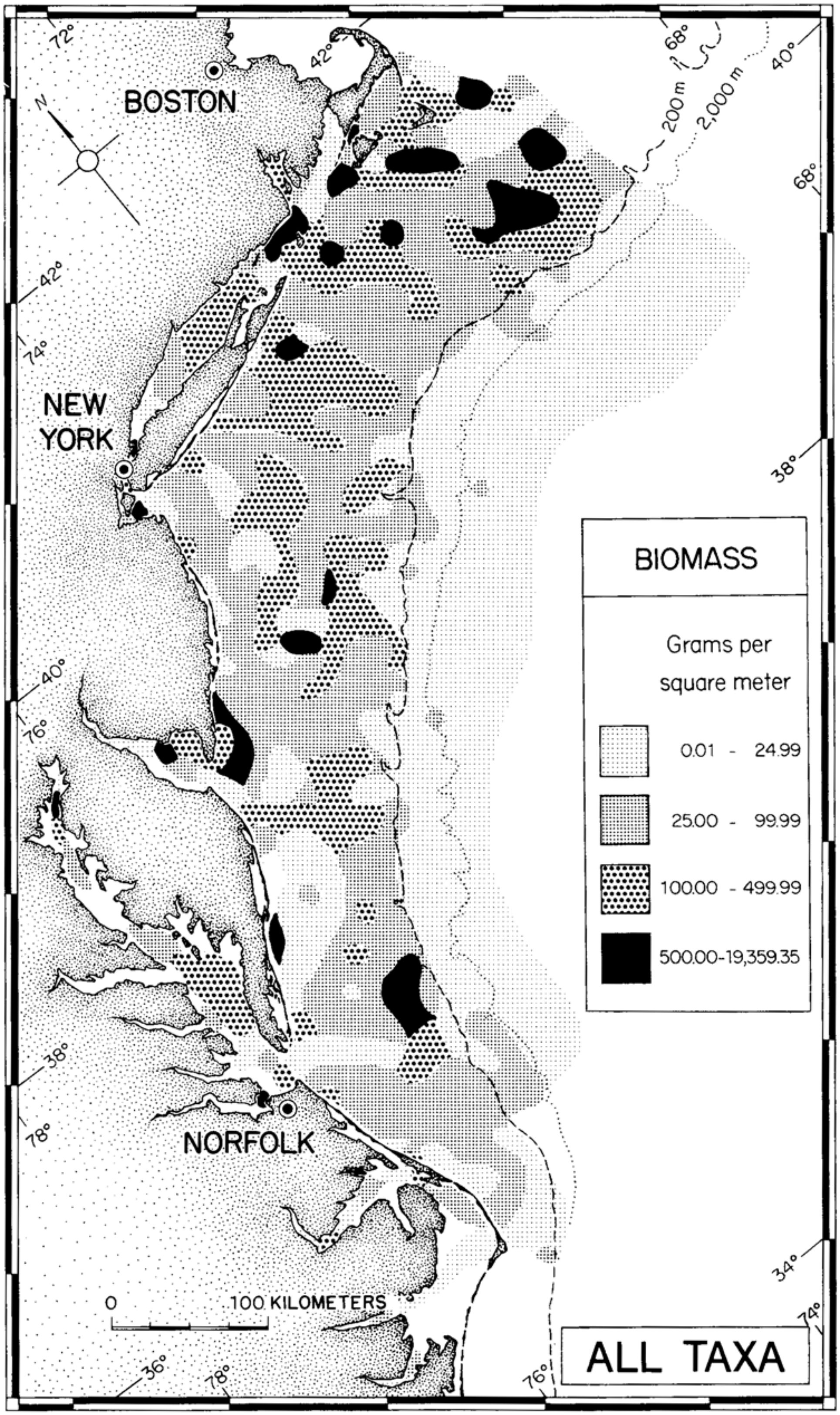


Figure 2.17. Geographic distribution of the biomass (as mean wet weight in grams per square meter) of all taxonomic groups of benthic invertebrates in the Mid-Atlantic region, 1956-1965. (Source: Wigley and Theroux (1981).)

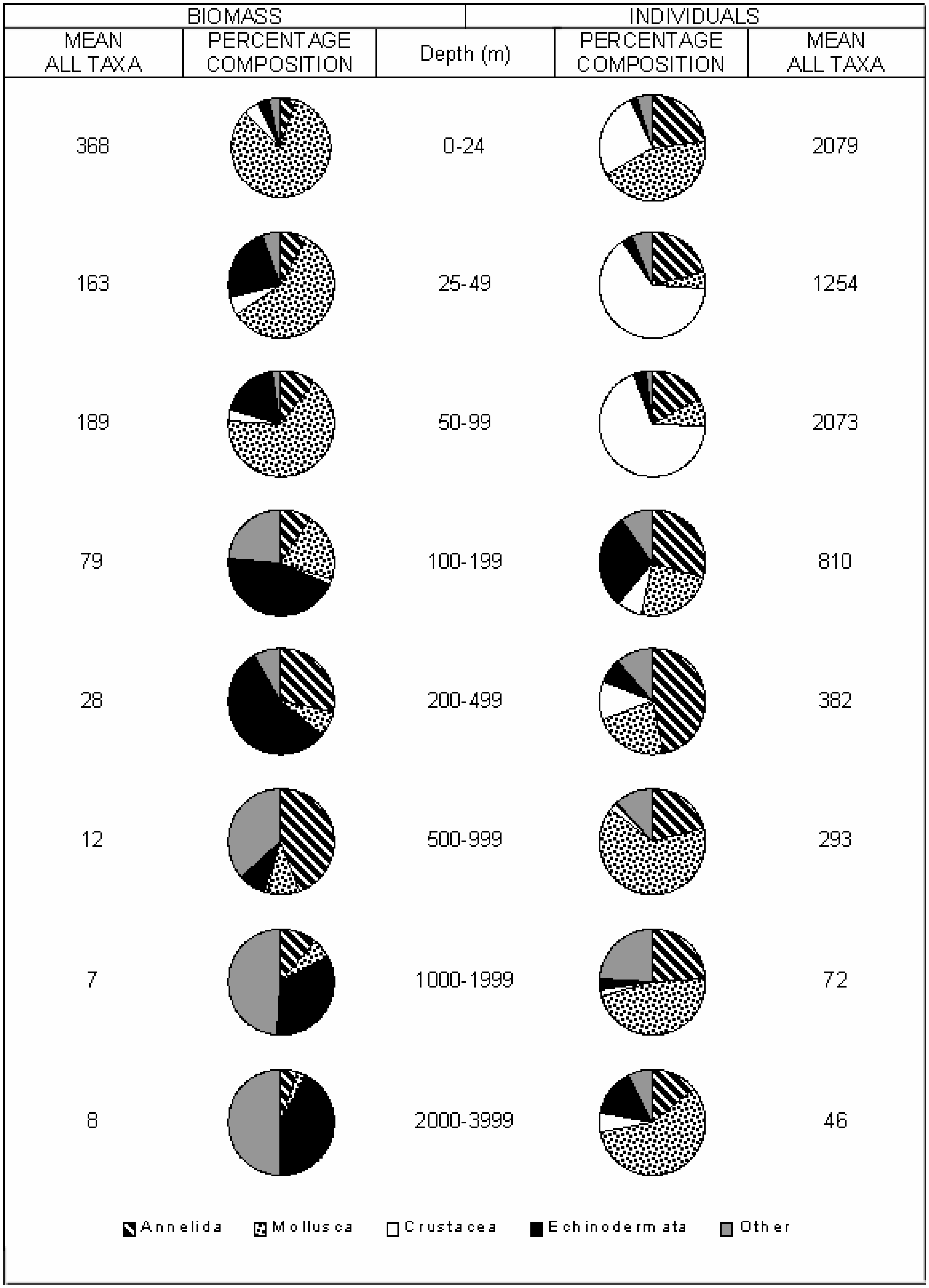


Figure 2.18. Percentage composition (by number of individuals and by wet weight) and density and biomass (as mean number and wet weight (in grams), respectively, of individuals per square meter of bottom area) of the major taxonomic groups of Mid-Atlantic benthic invertebrate fauna in relation to water depth. (Source: Wigley and Theroux (1981).)

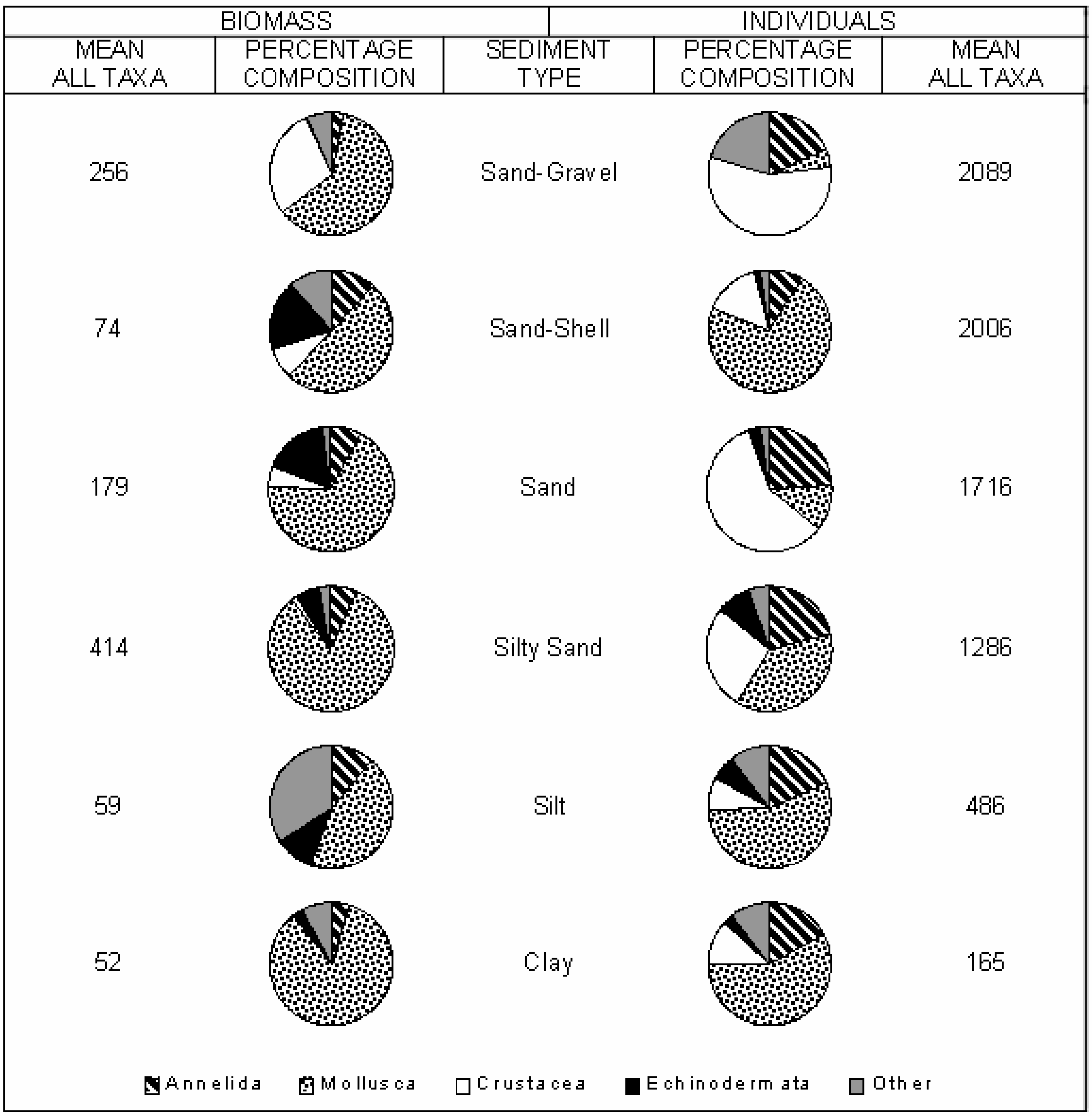


Figure 2.19. Percentage composition (by number of individuals and by wet weight) and density and biomass (as mean number and wet weight (in grams), respectively, of individuals per square meter of bottom area) of the major taxonomic groups of Mid-Atlantic benthic invertebrate fauna in relation to bottom type. (Source: Wigley and Theroux (1981).)