CHAPTER 7

OFFSHORE PLANKTON AND BENTHOS OF THE GULF OF MEXICO

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7.1   INTRODUCTION

This chapter summarizes baseline knowledge on the benthic communities of the seafloor and the plankton of the water column on the continental shelf, continental slope, and the abyssal plain of the Gulf of Mexico up through 2009 and prior to the Deepwater Horizon oil spill. As such, this review does not consider the higher components of a typical marine food web: fishes, turtles, mammals, and birds. An overview is provided of the general characteristics of benthos and plankton in terms of community structure—abundance, biomass, and biodiversity—in each habitat within the entire Gulf of Mexico large marine ecosystem (LME) [*sensu* Ken Sherman, National Oceanic and Atmospheric Administration (NOAA)]. This is followed by discussions of what is known about each unique or different assemblage's function within its habitat. In this context, function is defined as community dynamics in terms of elemental cycling or energetics of the organisms involved to the degree that this is known. Emphasis is principally on the seafloor, with some reference to the relationships between transient phytoplankton and zooplankton assemblages and their interactions with life on the bottom. The seafloor organisms or benthos are targeted because they are geographically static in space and time and thus can serve as better indicators of each habitat's characteristics and ostensibly its health. Plankton are included because they are the base of offshore food webs; all estimations of baseline conditions up a food web will reflect the nature or health of the phytoplankton and zooplankton. Variations in community structure—abundance, biomass, productivity, and diversity—from habitat to habitat and relationships to community function will be described from the literature reviewed when appropriate. The presumption is made that offshore life is, in general, food limited, and thus, sources of energy, carbon, and nitrogen, for example, become important in ultimately determining what species survive in each habitat—that is, food supplies determine community structure. Thus, where available, the relationships between community structure and function, in terms of food supplies, will be reviewed.

Summaries of the literature will consider each major habitat separately: (1) continental shelf benthos, (2) continental slope and abyssal plain level-bottom assemblages, (3) the biota and biological processes of methane seeps, and (4) corals and live bottoms. Peculiar features in each of these habitats will be mentioned but not treated exhaustively (for example, pinnacles and banks on the shelf and canyons on the slope). The general nature of offshore life in the Gulf of Mexico will be compared to other ocean basins, marginal seas, and continental margins. In addition to the natural assemblages of organisms in different habitats (1 through 4 above), some attention will be given to those areas of the Gulf in which human activities have altered or impacted natural processes significantly. The most salient of these are eutrophication and hypoxia associated with the Mississippi River plume, enrichment that is ostensibly derived from

offshore platforms and structures, and the impact of intensive bottom trawling on resident populations. Where possible, comparisons will be made between the stocks and diversities of major continental margin habitats. For example, numerous mesoscale surveys (10–100 kilometers [km] (6.2–62 miles [mi])) have been conducted across the entire northern continental shelf, but only a few comparisons of these have been attempted (Rabalais et al. 1999b). A singular goal of this chapter will be to identify gradients in ecosystem productivity, as represented by standing stocks, along with gradients in biodiversity (the relationships between biodiversity and productivity remain obscure, at best). Likewise, while there have been numerous disparate studies that together encompass the entire continental margin and deep basin of the Gulf of Mexico (Felder and Camp 2009; Fautin et al. 2010; Ellis et al. 2011), few ecological comparisons of them all have yet been attempted because methods have varied and finding original data is not always possible.

Some important generalizations have emerged from a review of the biota of the entire offshore Gulf of Mexico. In general, the open-ocean ecosystem—from the algal phytoplankton, the vertically migrating zooplankton and mesopelagic fishes, down to the level-bottom sediment-dwelling seafloor assemblages—is dependent on the physics of the ecosystem. That is, the water mass signature characteristics, along with contributions from the continental margin, ultimately control the biota and its food webs in ecological time scales of days to months. As a marginal basin, the ratio of coastline to Gulf of Mexico basin area (or volume) is high compared to major oceans, and thus, the surrounding land masses are more important to Gulf of Mexico processes than might be expected on the Atlantic, Pacific, and even Arctic margins of the United States. On the other hand, some of the most fascinating biotic assemblages in the deep Gulf of Mexico are the fossil hydrocarbon-based communities that are linked directly to the history of the Gulf over geologic time (centuries to millennia) and not to extant physics. The hermatypic corals living on banks and domes are able to exist on the tops of salt diapirs but are thus dependent on both year-to-year climate and almost day-to-day weather. Nevertheless, the coral assemblages could not exist without the salt extrusions on which they are perched. Likewise, deep-living cold-water mesophotic corals on the upper continental slope depend on sinking detritus from the surface for food but are anchored to hard authigenic carbonate substrates that are deposited as methane seeps age. Thus, the corals are dependent on both the present and the past conditions of the Gulf of Mexico. As those corals provide a living structure to thriving fish and invertebrate assemblages, so too do thousands of offshore platforms provide a hard substrate for thriving animal–plant communities that contribute to the high biodiversity within and along the margin of the Gulf of Mexico. The obvious similarities or links between parts of the system can be linked together in mass-balance models that illustrate the interdependence of the biotas of the different habitats of the offshore Gulf. Much is still unknown about life in the deep Gulf of Mexico and thus a penultimate section is devoted to these holes in our knowledge. Finally, an analysis of ostensibly vital ecosystem services of the offshore biota will be considered.

7.2 HISTORICAL PERSPECTIVES: EXPLORING THE DEEP GULF OF MEXICO

Exploration of the fauna living in the deep Gulf of Mexico began in the late nineteenth century aboard the steamer *Blake* (Milne-Edwards 1880; Geyer 1970; Roberts 1977) under the direction of Alexander Agassiz at Harvard's Museum of Comparative Zoology [for a thorough listing of these reports, along with descriptions of the fauna by taxon, see the compendium of Felder and Camp (2009)]. In the mid-twentieth century, the U.S. National Marine Fisheries Service (NMFS), using the U.S. Bureau of Commercial Fisheries' vessel *Oregon II*, sampled the deep Gulf of Mexico using large shrimp trawls along the upper continental slope. Although no

new fisheries of economic importance were uncovered, the numerous large trawl samples continue to enhance taxonomic and zoogeographic knowledge of larger invertebrates (Wicksten and Packard 2005) and demersal fishes (McEachran and Fechhelm 1998, 2006) in the Gulf of Mexico and the Caribbean. In the early 1960s, Willis Pequegnat at Texas A&M University (TAMU) initiated studies of the deep Gulf of Mexico with support from the Office of Naval Research (ONR) using the R/V *Alaminos* and followed in the 1970s by work with the R/V *Gyre*. Pequegnat's group employed quantitative sampling for the first time in the deep Gulf of Mexico using a Campbell grab for the infauna and a skimmer to sample larger epifauna. The 2-meter (m) (6.6 feet [ft]) wide skimmer was armed with counter wheels that measured the distances over which this unique device traveled over the bottom surface. The results generated were included in numerous publications and theses by Pequegnat's associates and students, including an intricate scheme of bathymetric zonation (Roberts 1977; Pequegnat 1983; Pequegnat et al. 1990). In addition, they discovered a large area in the eastern Gulf of Mexico covered by ironstone (Pequegnat et al. 1972; Rowe and Kennicutt 2008) and deep bottom currents (Pequegnat 1972). The Woods Hole Oceanographic Institution (WHOI) also published contemporaneous quantitative data on the deep Gulf of Mexico in the 1970s. The rate of the decline in biomass with depth, they discovered, is log-normal and universal between ocean basins, but the intercept of the decline is a function of surface water primary production (PP) (Rowe and Menzel 1971; Rowe 1971; Rowe et al. 1974). The U.S. Department of Energy (DOE) supported this WHOI work, under the direction of John Ryther and David Menzel.

By the 1980s, the complexion of the investigations of the deep Gulf changed substantially. Prospects of offshore oil and gas resources led to intensified environmental studies supported by the Bureau of Land Management (BLM), which evolved, for the ocean, into the Minerals Management Service (MMS) of the U.S. Department of the Interior (DOI). This agency is now the Bureau of Ocean Energy Management (BOEM) of the DOI. All aspects of Gulf of Mexico processes have been investigated: physics, geology, chemistry, and biology. The environmental research has been conducted by competitive bidding by multi-institutional groups organized in response to requests for proposals published widely by the agency. Management of each project has been by a single academic institution or an independent consultancy. The earliest works in the 1970s dealt with the continental shelf (see separate section on Continental Shelf Studies); this was followed by several broad, rather general categories: physical oceanography; general, level-bottom seafloor ecology; methane seeps and their communities; and an experimental arena designed to determine the effects of oil and gas exploration and production in offshore waters. In addition, when special issues have been brought to the attention of the agency, such as potential response of Cetaceans or the possibility of mercury contamination, somewhat more narrow initiatives have been supported. Each of the many studies has had a distinctive name and acronym. This section of this chapter will deal only with those studies devoted to explication of deep-ocean faunal communities.

The world's view of the deep Gulf of Mexico changed abruptly again in the 1980s with the outstanding discovery of diverse communities of seafloor organisms that live apparently on oil and gas (Brooks et al. 1985; Kennicutt et al. 1985) rather than algal plankton. Alternatively, some of the foundation species of these seep communities use the sulfide produced by anaerobic bacteria as an energy source (Cordes et al. 2003). This profound discovery gave rise to almost three decades of invigorated surveys, sampling, and experimentation in the Gulf of Mexico to determine why and how organisms living on fossil hydrocarbons function and why they would appear so similar in structure to communities that survive in hydrothermal fluids rich in geothermally produced sulfide at spreading centers. These studies not only continue today in the Gulf, but also led to the realization that similar phenomena are being encountered on a yearly basis in the numerous depositional environments on continental margins (Levin and Sibuet 2012).

7.3 HABITAT DEFINITIONS

This section is a broad summary of the different physical habitats within the entire offshore ecosystem of the Gulf of Mexico. This classification is based for the most part on water depth, but also on other physical characteristics that are or can be important in determining what types of organisms live in that habitat. These categories are important because the abundance and diversity can vary widely between habitats, depending on the physical (chemical and geological) conditions. Each habitat and its biota will thus provide different ecosystem services.

7.3.1 Continental Shelf (Ken Sherman's Large Marine Ecosystem)

The most salient habitats of the northern Gulf of Mexico offshore are depicted in Figure 7.1 provided by the NOAA. This includes the northern continental shelf, which is mostly terrigenous mud west of the Mississippi Delta and carbonate material east of the delta. Note that the eastern shelf is interdigitated hard bottom and carbonate sands. The northern shelf in its entirety can be presumed to be temperate or Carolinian in composition (Engle and Summers 2000). Just west of the delta, the shelf water column becomes hypoxic due to stratification by freshwater and eutrophication from nutrient loading (Rabalais et al. 2002; Bianchi et al. 2010). The Carolinian biota transitions into tropical and semitropical species in lower Florida and about midway down the Mexican coast on the west side of the basin. The outer shelf of the northern Gulf of Mexico is characterized by banks and pinnacles whose foundations are carbonates in the eastern Gulf of Mexico or salt diapirs in the central Gulf of Mexico. The most notable is the Flower Garden Banks National Marine Sanctuary (FGBNMS), described in detail by Rezak et al. (1985). The most obvious feature of the southern Gulf of Mexico is the wide Campeche Bank and its numerous small coral islands, with some actually inhabited (West Triangles and Arrecife Alacranes).

7.3.2 Continental Slope and Abyssal Plain

It is difficult to provide a simple overview of the Gulf of Mexico continental slope because it contains so many complicated physiographic features, each being its own habitat with peculiar characteristics. Prominent among these are submarine canyons that cross isobaths. The largest—the Mississippi Trough—begins as a gouge in a narrow shelf just off the Mississippi Delta. Sediments pour out with the river plume and are deposited in the trough. Eventually the muds move offshore at unknown rates to unknown depths (Bianchi et al. 2006). This contrasts with the De Soto Canyon at the northeast corner of the Gulf; it is not off a river and thus does not actively transport material downslope that is known. Methane seeps and other fossil hydrocarbon assemblages are interspersed along the northwest slope at depths of less than 100 m (328 ft) to depths of at least 2,000 m (6,561 ft), emanating from fossil hydrocarbon deposits below kilometer-deep layers of pelagic sediments and salt. The overlying terrigenous and pelagic sediments are denser than the underlying salt. This forces the bathymetry to exhibit a varying array of diapirs (mounds) and intermediate basins between the mounds. In the north, and in similar sediments in the south, these salt and sediment deposits terminate in steep escarpments on the north (Sigsbee), south (Campeche), and east (Florida) margins of the basin. Each of these transitional physiographic features, as unique habitats, might be expected to harbor characteristic faunas. Below the steep escarpments lies the continental rise and Sigsbee Abyssal Plain (SAP). Below the Mississippi Canyon lies a thick, broad wedge of land-derived sediments—termed the Mississippi Sediment Cone—stretching down onto and bisecting the east from the west abyssal plain. The abyssal plain has been formed
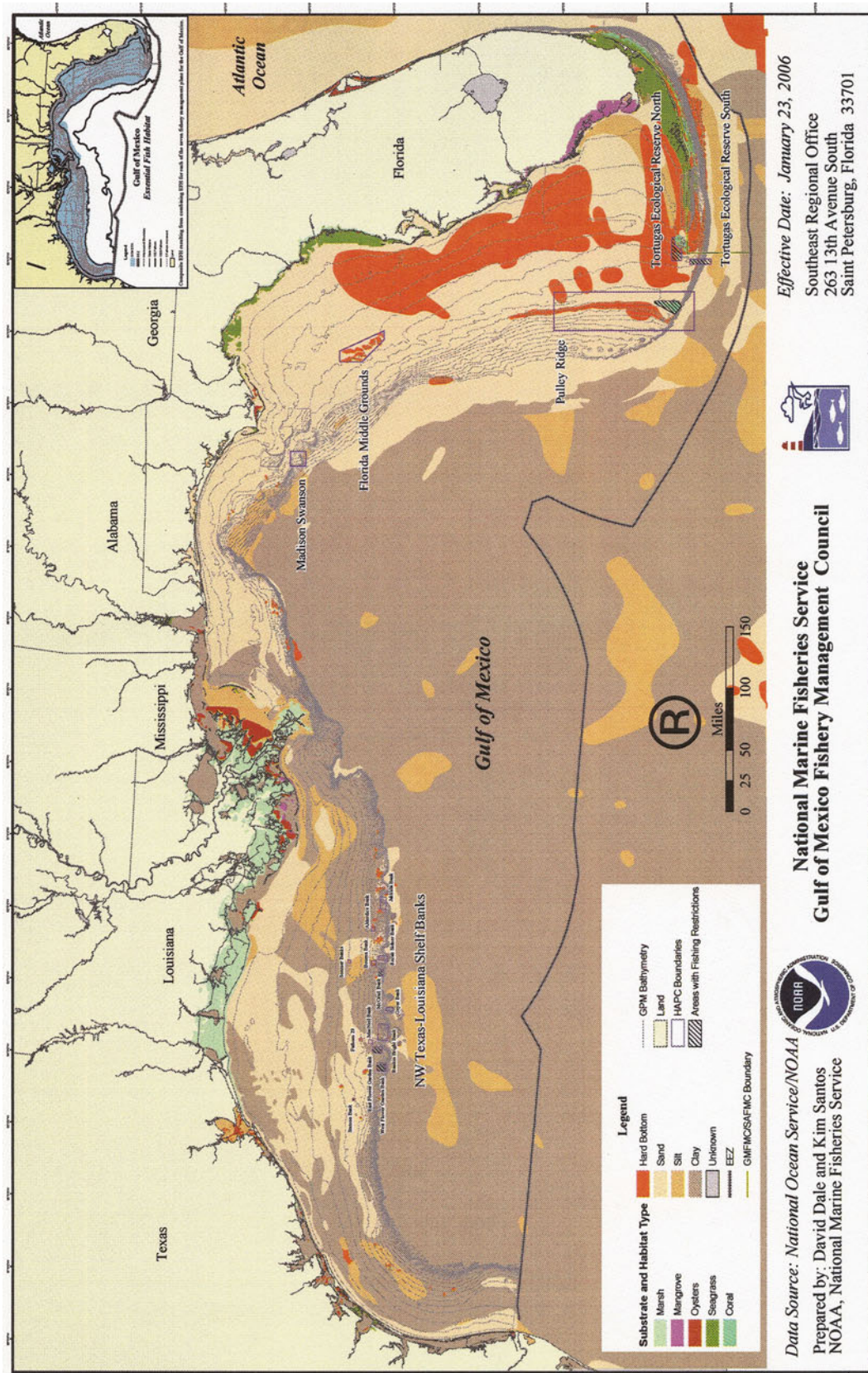
Figure 7.1. Habitats of the northern Gulf of Mexico (modified from GMFMC 2004, 2005).

by numerous intermittent turbidity flows from the margins. Its depths range from about 3.3 km (2.1 mi) down to about 3.7 km (2.3 mi) (most abyssal plains in the larger ocean basins have depths of 5–6 km [3.1–3.7 mi]). In general featureless, the SAP does contain small knolls that protrude up several hundred meters from the floor. An odd feature of the eastern boundary of the Mississippi Sediment Cone is an area of iron stone-like reddish crust that may be characterized by substantial bottom currents (Pequegnat et al. 1972).

7.4   PLANKTON

This section deals with the drifting plants and animals that occupy and drift through all habitats and depths of the open ocean. Generally small, these plants and animals together provide the food for most of the larger, often charismatic animals that make up higher levels of the food webs. The plankton are thus vital to a healthy ocean. This section treats the plankton in sections according to their function and taxonomic composition, as well as the different habitats in which they occur.

7.4.1   Functional Categories

At the base of open-ocean food webs is the plankton, defined as organisms that drift in currents. Plankton is composed of photosynthetic phytoplankton and heterotrophic zooplankton. Phytoplankton accomplishes the primary fixation of organic matter from carbon dioxide that supports the entire ecosystem biota. They are linked to higher trophic levels by the zooplankton, which is composed to a large degree of small crustaceans such as copepods. This section will describe the nature of each functional group in the Gulf of Mexico and what controls their distributions and productivity.

The plankton, or drifting organisms, is divided into two broad groups: the smaller phytoplankton, all small plant cells, and the larger zooplankton, all animals of various sizes. The phytoplankton (single-celled plants) synthesize organic matter from carbon dioxide, whereas the zooplankton (the animals) are the first step in the consumption of organic matter produced by the plants. The bulk of the biomass in all offshore ecosystems depends on this PP by the plants and the secondary (growth) production of the zooplankton, which then fall prey to larger species.

Phytoplankton is composed of single-celled organisms that are photosynthetic (use the energy of light to fix carbon dioxide into organic matter); they produce the bulk of the organic matter in aquatic ecosystems. They are divided into two general taxonomic groups: diatoms and dinoflagellates. In the open ocean, smaller nano- and pico-plankton are also important autotrophs, meaning they too are photosynthetic and produce organic matter. The growth of the phytoplankton depends on available light and inorganic nutrients such as nitrate, phosphate, and silicate to reproduce and thus produce new organic matter in the form of plant cells. The baseline characteristics of the phytoplankton outlined below are dependent on and vary directly as a function of these variables—light and inorganic nutrients.

Zooplankton is generally divided into categories based on taxonomic group and individual size of the animals. This determines the methods employed to sample them. The most frequently studied group is the *net* plankton (sometimes referred to as mesoplankton). This plankton is sampled with nets with a mesh size of about 100 micrometers (μm) up to just over 300 μm (1 μm = 3.9×10^{-5} inches [in.]). The dominant taxa are the copepod crustaceans. Nets of various sizes are held in a variety of frames, usually large rings, and these nets are hauled through the water column to filter out the drifting zooplankton. The mesh sizes are intended to be small enough to capture most zooplankton but large enough

that they do not clog up with the smaller phytoplankton. Flow meters are placed in the net opening to determine the volume of water filtered during a tow. The resultant data are then presented in terms of water volume filtered, usually cubic meters (m^3). Often the total bulk of the sampled organisms is estimated as volume displacement per m^3, meaning the amount of water displaced by the organisms is considered an estimate of their total biomass. Thus, zooplankton biomass is often expressed as milliliter(s) per cubic meter (mL/m^3). The data also can be represented as number of species or number of a particular group per m^3. These quantitative estimations allow for comparisons among Gulf of Mexico habitats, offshore regions, and even other ocean basins. The baseline characteristics in Gulf of Mexico offshore habitats will thus be presented in these general quantitative terms, as presented in the available literature.

A second category of zooplankton is the macroplankton. Because they can swim and make large diurnal vertical migrations, they are sometimes referred to as the micronekton (the nekton being large swimming species). These larger animals are measured in centimeters (cm) rather than millimeters (mm). They are sampled with large nets that can be several meters across. The nets contain wider mesh than that for net plankton and are towed at several knots because these animals can be active swimmers and thus can avoid slow-moving nets. One dominant prey is the smaller abundant copepod crustacean in the net plankton. The macroplankton is a major source of food for large predators, including billfish, marine mammals, and squid.

An additional form of plankton is the neuston. It lives at the surface interface with the atmosphere. This suite of both plants and animals that drift within the surface boundary layer are sampled with floating nets that reach just above and below the interface. A major component of the neuston in the Gulf of Mexico are large windrows of floating *Sargassum* that act as protective nursery habitats for juvenile stages of large pelagic fish.

The zooplankton also can be defined in terms of their time in the plankton. The holoplankton are always planktonic throughout their entire life cycles. The meroplankton are residents of the plankton only as larval and juvenile stages. Their adult stages are either as benthic (seafloor) invertebrates or as freely swimming nektonic predators. This resume of the plankton baselines will treat each of these categories separately. A large section is devoted to the ichthyoplankton because they grow into important pelagic and benthic fishes. This form of meroplankton is sampled in the surface 200 m (656 ft) and in the neuston.

A further distinction within the plankton is between the neritic assemblages that live nearshore and the open-water groups that live offshore. Thus, this baseline survey will include this distinction because the species composition of the two areas is different, and in the Gulf of Mexico the studies of these two habitats have been very different in nature and results.

7.4.1.1 The Phytoplankton: Physical and Chemical Controls

The base of offshore food webs is the PP by photosynthesis of diatoms, dinoflagellates, prymnesiophytes, and others, the single-celled algae that float or drift in surface currents. Phytoplankton require light and inorganic nutrients (nitrogen compounds—nitrate, nitrite, nitrous oxide, free amino acids, ammonium, primary amines and phosphate and silicon), and the rate of PP by these one-celled microorganisms is proportional to the light and nutrients available. In marine systems, including the Gulf of Mexico, nitrate is considered to be the most important limiting nutrient, although phosphate may in some cases be limiting as well when there is an overabundance of nitrate. Direct measurements of PP are accomplished on discrete water samples from standard depths taken down through the water column within the photic (lighted) zone. The general method used since the 1950s is incubation of the water with

radiolabelled bicarbonate. Carbon 14 (^{14}C) is incorporated into cells in a given volume of water over a given length of time under varying intensities of light and at varying concentrations of nutrients. At the end of the incubation, the water is filtered and the radiocarbon is then counted on a scintillation counter to determine carbon uptake rates. Alternative methods include measuring the photosynthetic pigment chlorophyll *a*, counting cell density per unit volume, or oxygen production over time. Species composition and cell densities (stock size and biomass) can be determined on the same discrete water samples. It would not be an exaggeration to say that hundreds of such measurements have been made all over the Gulf of Mexico in the last 50 years.

A less accurate but more comprehensive way to estimate PP is the use of satellite color images to estimate surface water photosynthetic pigments in cells. From this information, the total surface water phytoplankton standing stocks (biomass as mg C/m^3) can be estimated. Likewise PP can be estimated (in mg C/m^3/h [hour]) based on known relationships between photosynthetically active radiation (PAR) and pigment concentrations. The values of surface PP also can be entered into established first-order decay relationships between PP and delivery of particulate organic carbon (POC) at any depth. Surveys based on discrete samples and satellite-based maps will be used to provide an overview of present state of knowledge of the importance of phytoplankton offshore in the Gulf of Mexico.

The satellite information has been used to define ecoregions (Figures 7.2 and 7.3) that are characterized by specific levels of chlorophyll *a* concentrations based on satellite Sea-viewing Wide Field-of-view Sensor (SeaWiFS) images (Salmeron-Garcia et al. 2011). Each region also has a set of physical and chemical traits that give rise to that region's pigment concentrations. For example, the central Gulf of Mexico has very low pigments because it has no good source of nitrate. Regions 12 and 13 are bathed in Caribbean water but are characterized by upwelling
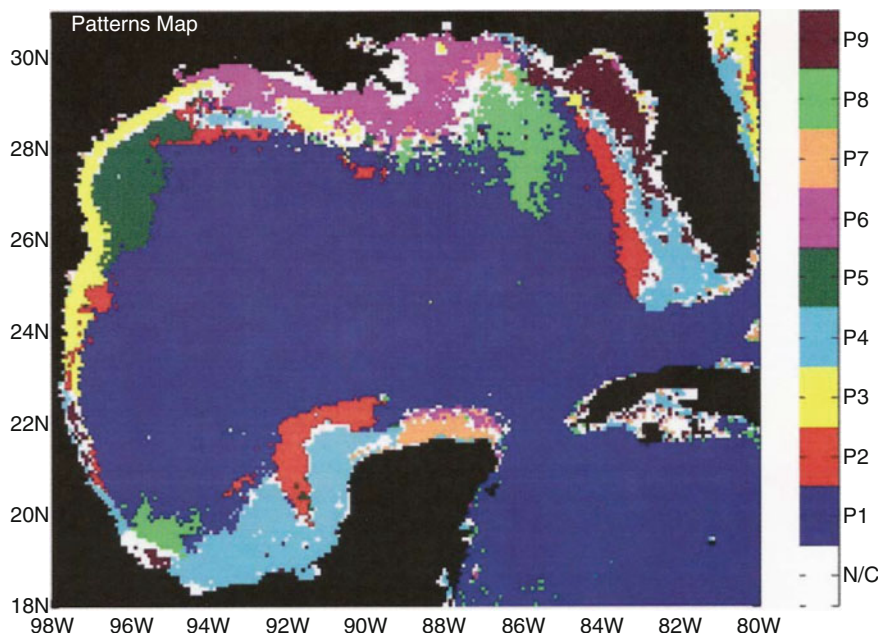

Figure 7.2. Ecoregion colors based on chlorophyll *a* concentrations assessed with SeaWiFS satellite images (from Figure 4 in Salmeron-Garcia et al. 2011; republished with kind permission from Springer Science+Business Media). The lowest levels of approximately 0.1–1 micrograms per liter (μg/L) are found in the *dark blue* (P1) area, whereas higher values are seen in the northeast (P6–P9) with values as high as 5–10 μg/L.
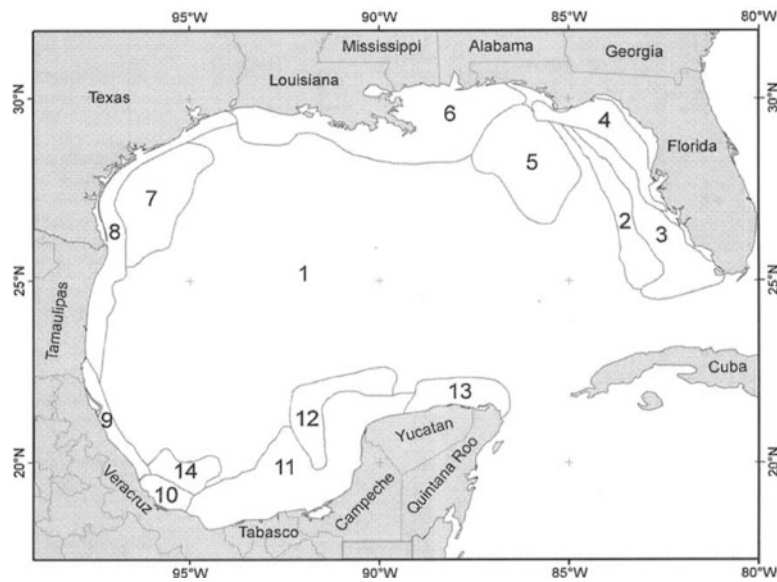
Figure 7.3. Ecoregions of surface water chlorophyll *a* pigments estimated from SeaWiFS satellite images (from Figure 5 in Salmeron-Garcia et al. 2011; republished with kind permission from Springer Science+Business Media). Each region corresponds to specific ranges of primary production (PP) and associated physical properties.

(12) and mixing (13). Mexican rivers influence regions 9, 10, 14, and 11. Region 6 is influenced by nitrate loading in the Mississippi River plume extending onto the continental shelf. Region 5 has high chlorophyll *a* concentrations because the water is pulled off of the shelf by eddies that break off from the loop current (LC). Each ecoregion, according to these authors, has its own seasonal variation patterns. The complicated set of three regions aligned with the Florida coast is a combination of upwelling and river flow.

The northeastern corner of the Gulf of Mexico is a healthy region of high PP (Figure 7.4) (Qian et al. 2003). Rate limiting nitrate is drawn offshore by warm eddies, but spatial distributions of algal biomass are controlled by riverine and estuarine input of nutrients. Both the Mississippi and the Apalachicola rivers are most important. On the other hand, the far western ecoregions of south Texas and northern Mexico are depleted of nutrients and support very low PP and algal biomass (Flint and Rabalais 1981). These two regions contrast markedly with the continental shelf just to the west of the Mississippi Delta, where hypoxia occurs during the spring, fall, and summer months when the water column is vertically stratified by freshwater (Wiseman and Sturges 1999; Rowe and Chapman 2002). The species composition of the phytoplankton in each ecoregion is also a function of the ratio of the nutrients (Dortch and Whitledge 1992). High nitrate input (greater than 100 micromoles per liter [μmol/L]) results in intense blooms that sink into and below the thermocline (Lohrenz et al. 1990). There the organic matter is respired and hypoxia ensues. As discussed in following sections, these processes have profound effects on the biota (see shelf benthos section).

To a large degree, the important role of circulation on open-ocean Gulf of Mexico productivity can be explained on the basis of sea-surface height (Figure 7.5). The best succinct description of the important processes related to the loop current system (LCS) is found in Jochens and DiMarco (2008). The water that flows into the Gulf of Mexico from the Caribbean is warm, devoid of nitrate at the surface, and has little plant biomass. It is the reddish water
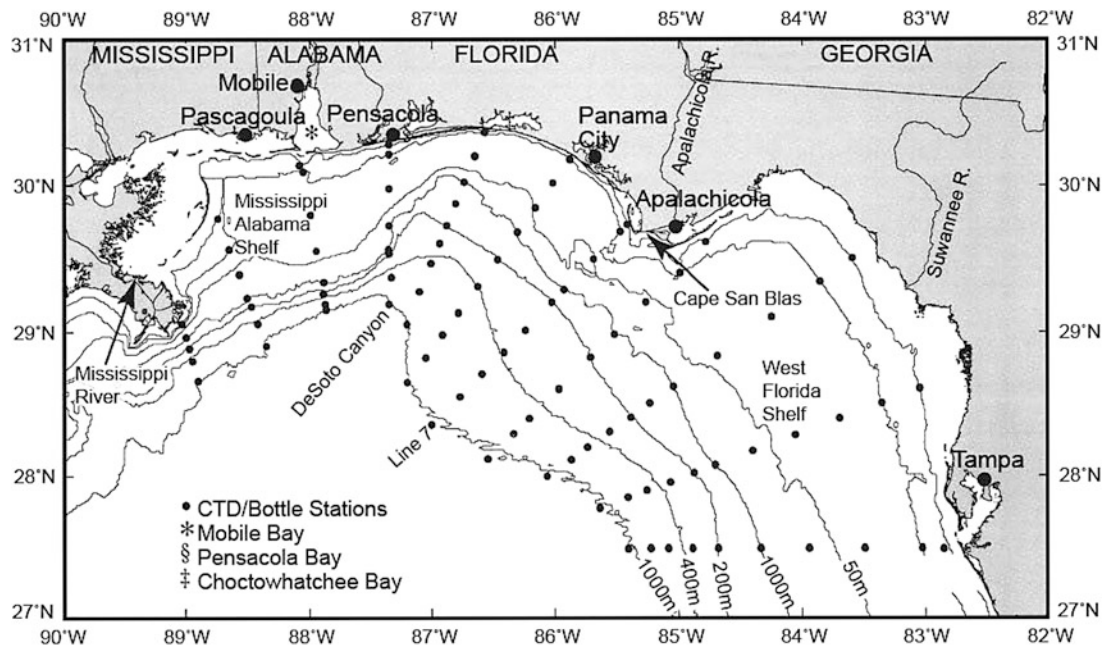
Figure 7.4. Phytoplankton study sites in the northeast Gulf of Mexico (from Figure 1 in Qian et al. 2003; reprinted with permission from Elsevier).

(Figure 7.5) flowing north between the Yucatán Peninsula and Cuba, often referred to as the loop current (LC) because it flows into the Gulf of Mexico and then abruptly curls around to the right (because it is a topographic high), returning around the Florida Keys to the Atlantic. When it penetrates deep into the north-central Gulf, it can spin off warm eddies, which are also areas of elevated sea-surface height that spin clockwise. With this flow pattern, the LC or the eddies can often pull shelf water east of the Mississippi River out into deep water, thus transferring productive water containing nitrate into deeper regions where it would normally be very oligotrophic (Maul 1974). The LC's warm eddies retain their original oligotrophic character as they move west across the entire Gulf of Mexico, degrading slowly and ending up against the continental shelf of Mexico, pictured as brown to orange blobs (Figure 7.5). The warm anticyclonic centers are topographic highs (Figure 7.5) and thus are less productive than their margins or the cool cyclonic regions adjacent to them (Biggs and Muller-Karger 1994; Biggs et al. 2008), which are topographic lows (blue in Figure 7.5). This variation all occurs in ecoregion 1 (Figures 7.2 and 7.3). The net PP in these offshore features varies between 100 and 200 mg C/m^2/day (El Sayed 1972).

An important comparison is the rate of new production between the various ecoregions of the Gulf of Mexico because this new organic matter is cycled up the food web at the surface or it is exported to the seafloor or down the water column to deep-living components. The highest PP rates on the continental shelf in the Mississippi River plume reach 3–5 g C/m^2/day (Lohrenz et al. 1990; Dagg and Breed 2003). However, narrow regions along all the coasts over much of the Gulf are substantially less—0.5 to 1.5 g C/m^2/day (Flint and Rabalais 1981; Qian et al. 2003)—and decrease offshore. The lowest rates in the central Gulf of Mexico are limited because of the depth of the nutricline at about 125 m (410 ft) (El Sayed 1972; Biggs et al. 2008); the phytoplankton in these waters produce 100–200 mg C/m^2/day at most (Bogdanov et al. 1969).
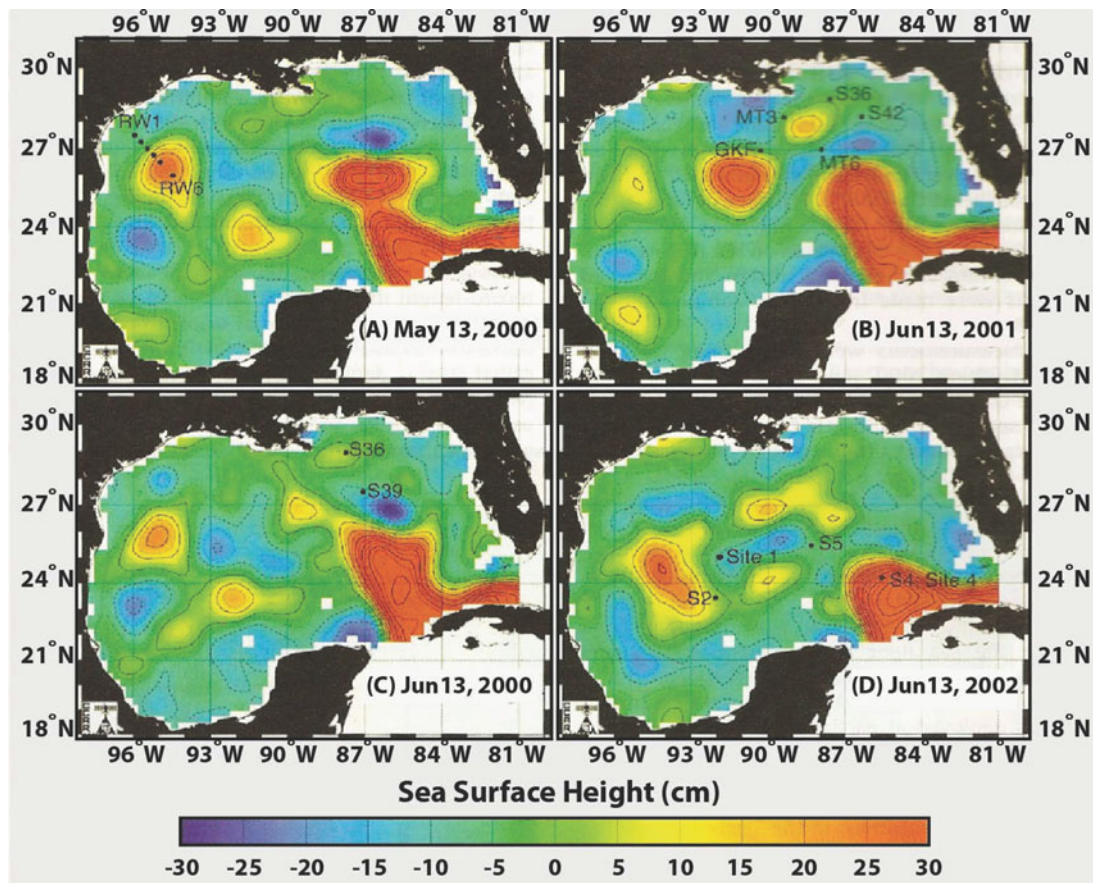
Figure 7.5. Sea-surface height showing warm eddies spun off the loop current (LC) (*reddish*) versus cold areas (*blue*) between warm eddies. Warm high areas spin clockwise; cold areas spin counterclockwise (from Plate 1 in Jochens and DiMarco 2008; reprinted with permission from Elsevier). The lowest phytoplankton production is in the *red areas*; the highest offshore is in the *blue*. However, these offshore sites are much lower than on the shelf; the highest are close to shore (see Figures 7.2 and 7.3).

The cyanobacteria, *Trichodesmium* spp., by fixing nitrogen, may play a significant role in the oligotrophic (nitrogen limited) central regions of the Gulf of Mexico (Carpenter and Roenneberg 1995; Letelier and Karl 1996). Referred to as *diazotrophs*, these organisms need energy such as light (the flat transparent surface of a calm ocean) or carbon compounds (as in the guts of termites) to transform unreactive dissolved nitrogen (N_2) into ammonium. When they are in a senescent stage, they are thought to release ammonium that could initiate a red tide bloom (see below). They could also be supplying limiting fixed nitrogen to phytoplankton in the warm oligotrophic eddies pictured in Figure 7.5. A bloom of *Trichodesmium* on the west Florida shelf may have been stimulated by iron fertilization from West African dust (Lenes et al. 2001).

Unfortunately, the phytoplankton can produce toxic blooms, often referred to as red tide. The west coast of Florida appears to be particularly susceptible to blooms of *Karenia brevis* and *Gymnodinium breve* (Chew 1956; Simon and Dauer 1972; Tester and Steidinger 1997; Gilbes et al. 1996). These can be poisonous to fish and invertebrates that consume them. The causes of such blooms remain obscure. It has been suggested that the blooms occur in the absence of adequate grazing by zooplankton to keep their densities in check.

7.4.1.2   The Zooplankton

Zooplankton are small heterotrophic organisms that also drift in currents (as opposed to swim against them). They are vital to a healthy productive ecosystem because they are the intermediary within the food web between primary producers and major consumers of economic importance—the pelagic fishes. Copepod crustaceans are the dominant taxon in both numbers and biomass in most coastal and open-ocean conditions, including the Gulf of Mexico (Bogdanov et al. 1969; Hopkins 1982; Dagg et al. 1988; Ortner et al. 1989; Elliott et al. 2012). A large fraction of the zooplankton is filter feeders that use phytoplankton cells directly, but some, such as arrow worms (chaetognaths, such as *Sagitta* spp.), are predators. The filter feeders, detritivores, and omnivores are all considered grazers of the algal standing stocks. Net zooplankton is quantified using opening and closing nets with mesh of 125–330 μm. The nets, towed at discrete depth intervals, have demonstrated that many species occupy specific depth ranges. Smaller microzooplankton are sampled with large-volume bottles and filtered. Large drifting zooplankton, such as jelly fish (Phylum Cnidaria), are important food for open-ocean turtle populations.

Most zooplankton migrate daily, swimming up to surficial waters (upper 50 m [164 ft]) at night and descending during daylight hours, and this is evident in the Gulf of Mexico (Hopkins 1982). However, as Hopkins notes, each species has its own pattern of migration, resulting in a mix of species at various depths over a 24-h cycle. Most of the migration occurs in the upper 100 m (328 ft), and it is all more or less confined to the top 1,000 m (3,281 ft) of the water column.

In continental shelf or neritic waters, the zooplankton plays a similar role—linking phytoplankton production to higher trophic levels. However, the species composition is markedly different and assemblages reach far higher biomass than offshore. In the Mississippi River plume the copepods, *Temora turbinate* and *Eucalanus pileatus*, can graze more than 50 % of the PP on a daily basis (Ortner et al. 1989; Dagg et al. 1996). The latter work documents the role of the grazers in removing lithogenic particles (suspended mud) as well as living cells. As major grazers, zooplankton can prevent toxic algal blooms before they occur.

Through frequent molting of their exoskeletons, crustacean zooplankton contribute considerable material (Dagg et al. 1988) to detrital food webs, especially offshore in deep water. Likewise zooplankton package the remains of the phytoplankton cells they graze into fecal pellets that sink far faster than the individual cells, thus adding a significant pathway for organic matter to reach great depths. Zooplankton, in sum, are a major functional group in clearing detrital organic matter out of surface layers and channeling it to food-starved deepwater biota; the slow rain of detrital particles is assumed to be a major source of food for much of the deep bottom fauna. This flux of fecal pellets, cell debris, and molts is often referred to as the *biological pump*.

The various habitats of the Gulf of Mexico neritic continental shelf contain largely the same dominant groups in the holoplankton, mostly copepod crustaceans (Ortner et al. 1989; Dagg 1995). However, the physical habitats themselves vary widely around the circumference of the Gulf of Mexico, as indicated in the above sections on phytoplankton. This variation in the physical nature of the habitats affects the species composition, diversity, productivity, and animal behavior of the assemblages. The most salient example of a modified, atypical environment is the seasonal hypoxia on the continental shelf off Louisiana. The net zooplankton between 2003 and 2008 were clustered into four assemblages dominated by calanoid copepod crustaceans (Elliott et al. 2012). Mean densities among the four groups they identified ranged from 23,000 individuals/m^3 down to 1,600/m^3. The groupings were related to temperature, salinity, and the vertical extent of hypoxic conditions, with severe restrictions (stress) in abundance below 2 mg of oxygen per liter of water (the upper limit of hypoxia) (Elliott

et al. 2012). These authors suggest that the large fecal pellets of big copepods mediate vertical flux of organic matter and thus increase the extent of bottom water hypoxia. This reinforces the suggestion of Dagg et al. (2008) that a microbial food web intensifies the Louisiana shelf's bottom water hypoxia. It is evident that hypoxia reduces habitat size for aerobic metazoans and can reduce the mean individual size within planktonic assemblages (Kimmel et al. 2009).

To the west of the Louisiana hypoxia on the south Texas shelf, the PP is drastically reduced because of minimal river runoff (see above section of continental shelf phytoplankton). This is reflected in low densities of zooplankton. However, a near-bottom layer of particulate matter is an almost universal feature of the Texas continental shelf (Flint and Rabalais 1981). Thus, the zooplankton feeds predominantly in this near-bottom, 1–2 m thick *nepheloid* layer (Bird 1983), not near the surface. The exact origin of the nepheloid layer is unclear. It may be the westward extent of mud from the Mississippi River, and/or the resuspension of mud by trawlers, tidal currents, or by resident biota. This suspended particle layer is something that differentiates the shelf habitat west of the Mississippi Delta from the relatively transparent (particle free) water east of the Mississippi Delta on the Mississippi, Alabama, and Florida coastlines (Figure 7.1).

Further to the south, the typical zooplankton assemblages reflect a gradual change in habitat types within the zoogeographic temperate regime of the northern Gulf of Mexico to habitats in the semitropical/tropical regime of the southern Gulf of Mexico. This change occurs near Tampico, Mexico, at about 24° N latitude. Below this, the seasonality is more hospitable to coral reefs and the associated biota, including the plankton (De la Cruz 1972). Densities and biomass in the southern Gulf of Mexico are low but diversity is high. Biomass is low because phytoplankton production is limited by lack of inorganic nutrients, principally nitrate. Exceptions are the areas near the mouths of the rivers at the base of the Gulf of Campeche and the narrow zones of upwelling associated with the shallow but geographically extensive Campeche Bank.

The most productive region of the Gulf of Mexico shelf is east of the Mississippi Delta over to Florida, as indicated in the section above for phytoplankton (Figures 7.1, 7.2, 7.3, and 7.4). This is due to nutrient input from rivers, the complicated physical environment, and proximity to the LC. The complicated physics includes epipelagic nutrient enhancement due to wind-driven upwelling along the shelf edge. Additionally, the Mississippi River adds nutrients. These processes were first observed in the early studies of Riley (1937) in this region. Mesoscale eddies break off of the northern extension of the LC; this can draw nutrient-rich shelf water offshore, thus enhancing PP (Hamilton 1992; Sahl et al. 1997). This PP provides food for enlarged stocks of mesozooplankton (Ressler and Jochens 2003). Upwelling enhances production all along the outer west Florida continental shelf (Weisberg et al. 2000).

The broad carbonate platform that forms the west Florida continental shelf supports abundant and diverse zooplankton populations (see area in Figure 7.1). For example, zooplankton were aligned in three separate zones along shore: one composed of a nearshore high density assemblage of larvaceans, a second inshore zone of small copepods in low densities, and a third richer zone offshore of larger species of copepods (Kleppel et al. 1996; Sutton et al. 2001). Zooplankton grazing intensity may play a role in controlling toxic blooms of the dinoflagellate phytoplankton *Karenia brevis* that plagues the west Florida shelf and coastline (Milroy et al. 2008).

The most comprehensive investigation of the offshore holoplanktonic zooplankton concentrated on the vertical distribution of all size classes of animals at an offshore location in the eastern Gulf of Mexico (27° N × 86° W) (Hopkins 1982). The sizes—larger than 1 mm (0.04 in.)—are based on opening and closing net tows with a 162-µm mesh, whereas the metazoan animals—smaller than 1 mm (0.04 in.)—are based on large-volume bottle samples. The samples were taken at 25 m (82 ft) intervals down to a depth of 150 m (492 ft), and then at
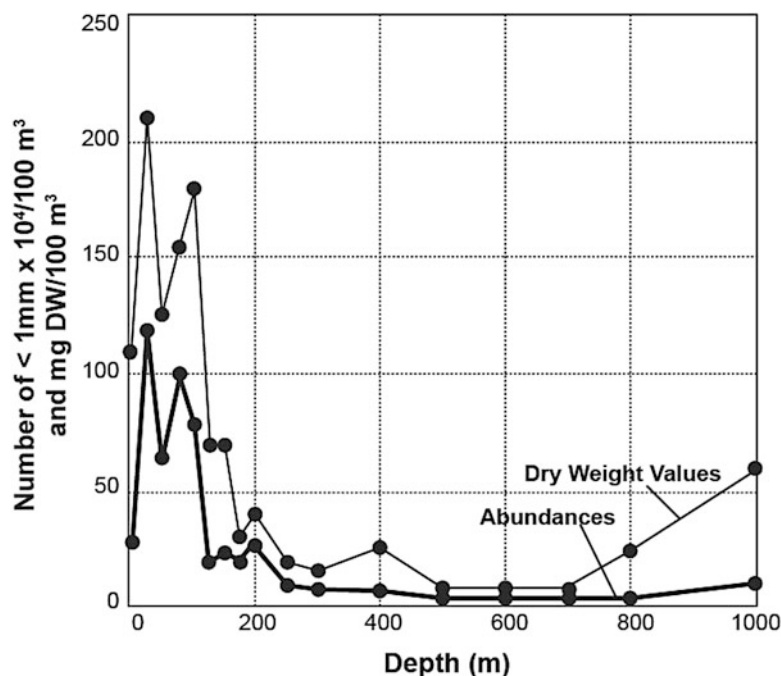
Figure 7.6. Vertical distribution of the standing stock of microzooplankton (less than 1 mm in length) at a deepwater location in the eastern Gulf of Mexico (modified from Hopkins 1982).

100 m (328 ft) intervals down to a maximum depth of 1 km (0.62 mi). The animals were sorted to species when possible and to major group, usually family or order, otherwise, for a total of 11 general categories. Of the totals, the copepod crustaceans were overwhelmingly dominant at all depths. The species composition was almost entirely different from those that dominated in the neritic habitats described above. Likewise, there was a distinct vertical partitioning of species. While much of this vertical zonation could be due to feeding habits, some of it may be related to sharp vertical gradients in temperature, according to Hopkins (1982). Hopkins' sampling was also taken during the day and at night to determine vertical migration behavior; his studies also suggested, however, that there was some net avoidance near the surface by larger motile species during daylight.

A distinct planktocline was observed in these samples at the 50–100 m (164–328 ft) depth (Figures 7.6 and 7.7). Most of the animals and the biomass were found at the surface at night and in the daytime, in spite of vertical migrations to avoid the light. The total biomass integrated over the 1 km (0.62 mi) water column that they sampled amounted to about 1.6 mg dry weight (dw)/m^2. This concentration near the surface was especially evident in the larger groups caught with the net (Figure 7.7). Of the total biomass, most was sampled in the larger size groups, amounting to about 1.2 g dw/m^2; the smaller forms amounted to 0.4 g dw/m^2. The mean size of the larger than 1 mm (0.04 in.) group was about 26 micrograms (μg) dw per individual whereas the smallest group (smaller than 1 mm [0.04 in.]) averaged about 0.25 μg dw per individual. These would be equivalent to about 10.4 μg carbon and 0.1 μg carbon per individual, respectively.

The totals observed are comparable to other oligotrophic areas such as the central Sargasso Sea, according to Hopkins (1982), in agreement with observations of phytoplankton production and biomass discussed above. The principal predators on the zooplankton appeared to be mid-water fish populations such as the myctophids, which Hopkins was also able to assess
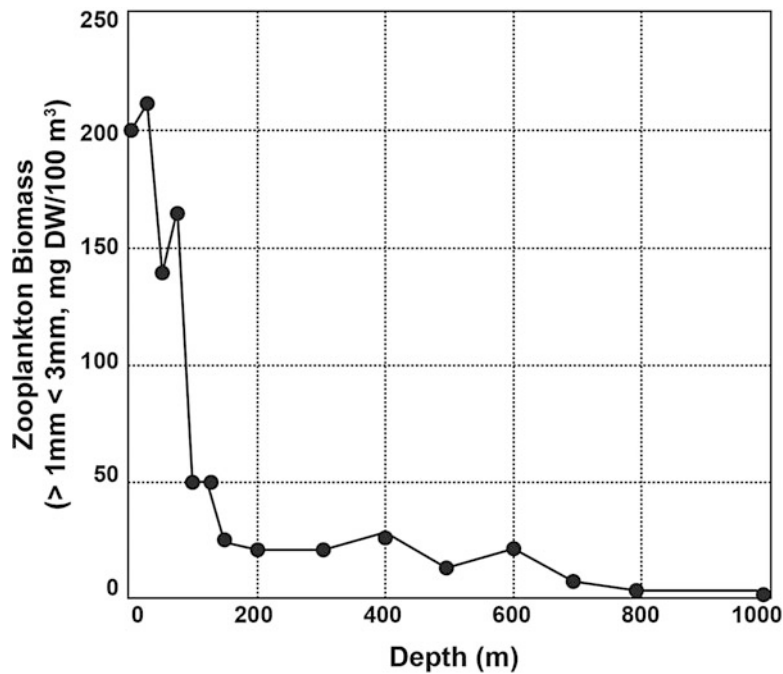
Figure 7.7. Vertical distribution of the biomass of net or mesozooplankton (larger than 1 mm, but smaller than 3 mm) sampled at night in the eastern Gulf of Mexico (modified from Hopkins 1982). Mesoplankton is traditionally sampled with a 330 μm mesh net.

with the study's opening–closing nets, but the greatest concentrations of fish were between depths of 50 and 100 m (164 and 328 ft), not near the surface.

The distribution of zooplankton is not uniform across the entire open Gulf of Mexico, as the above studies of the vertical distributions might imply. The flow from the Caribbean is the principal source of water and thus a source of plankton to the Gulf. This becomes the LC once it enters the Gulf, which pulses irregularly into the eastern gulf in an anticyclonic loop that enters through the Yucatán Channel and leaves through the Florida Straits (Hopkins 1982). On the northern boundary of the loop, warm eddies can spin off that move westward across the Gulf of Mexico (Figure 7.8), and these affect the distribution of both the phytoplankton and zooplankton. The warm anticyclonic eddies (turn clockwise and sea surface is elevated) are oligotrophic because the water comes from the Caribbean (Biggs 1992). However, small submesoscale cyclones (turn counter clockwise and are below mean sea level) can have enhanced nutrients and plankton concentrations, including mesoplankton and micronekton that can be assessed from acoustic backscatter (Ressler and Jochens 2003). Thus the open offshore Gulf of Mexico, while oligotrophic overall, is actually a patchwork of different concentrations of plankton that are controlled by physical circulation patterns on scales of tens to hundreds of kilometers (Jochens and DiMarco 2008).

The Southeast Area Monitoring and Assessment Program (SEAMAP) database contains extensive information on a wide variety of standing stocks, including zooplankton biomass distributions (Figure 7.8) in the upper 200 m (656 ft) of the water column (Rester 2011). A plot of more than 100 locations across a wide depth interval illustrates that the zooplankton baseline in general ranges from 0.025 to 0.075 mL/m^3 displacement volume over most of the Gulf of Mexico offshore (depths greater than 100 m [328 ft]), but that nearshore, the values can be much higher.
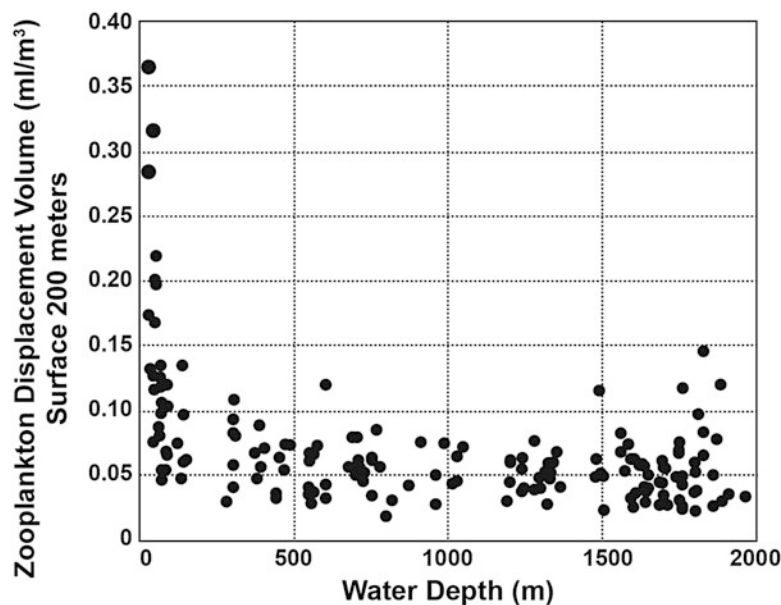
Figure 7.8. Distribution of net zooplankton (larger than 330 μm mesh net) displacement volume (a measure of biomass) in the surface 200 m (656 ft) at different water depths in the Gulf of Mexico (from SEAMAP database).

Zooplankton displacement volume (larger than 330 μm mesh net) nearshore is substantially higher than offshore (Figure 7.9). Note the parallels between the phytoplankton and zooplankton biomass levels by comparing Figure 7.9 with Figures 7.2 and 7.3: the highest are always close to shore and adjacent to river mouths.

7.4.1.3 Ichthyoplankton

A relatively small but vital component of the zooplankton in the upper 200 m (656 ft) of the water column are the ichthyoplankton, composed of fish eggs, larvae, and juveniles (SWFSC 2007). While fish eggs have their own food supply, fish larvae eat smaller plankton; both serve as an important prey base for marine invertebrates and fish. The distribution of ichthyoplankton is a function of the spawning locations of adult fish, currents, and sea-surface temperatures. Monitoring ichthyoplankton provides essential information on potential population sizes of adult fish since the survival rates of larval fish are assumed to contribute to recruitment success and year-class strength in adults (Houde 1997; Fuiman and Werner 2002; SWFSC 2007).

7.4.1.3.1 Baseline Ichthyoplankton Abundance and Distribution in the U.S. Gulf of Mexico

SEAMAP is a state/federal/university program for the collection, management, and dissemination of fishery-independent data obtained without the direct reliance on commercial or recreational fishermen (Rester 2011). A major goal of SEAMAP is to provide a large, standardized database for management agencies, industry, and scientists. The types of surveys conducted include plankton, reef fish, shrimp/groundfish, shrimp/bottomfish (trawl), and bottom longline, as well as occasional special surveys. Sampling is usually conducted at predetermined SEAMAP stations arranged in a fixed, systematic grid pattern, typically at approximately 56 km (34.8 mi) or 0.5° intervals, across the entire Gulf of Mexico (Rester 2011). All surveys are not conducted each year, and all stations and seasons are not sampled every
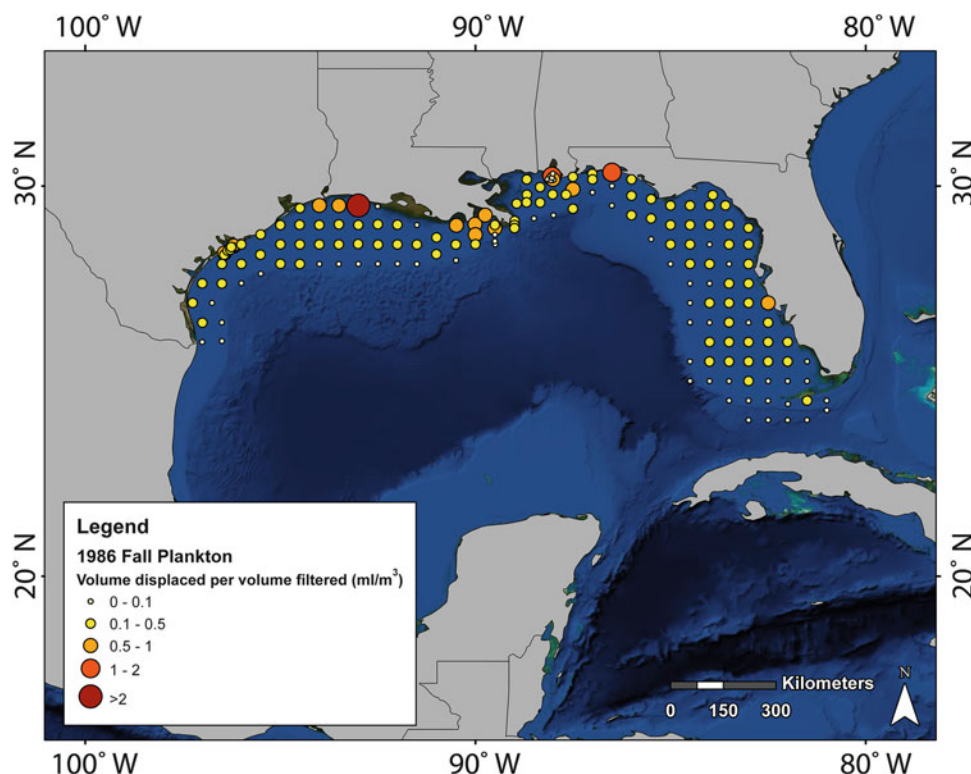
Figure 7.9. Zooplankton displacement volume in SEAMAP samples from fall sampling in the upper 200 m (656 ft) (larger than 330 μm mesh net).

year Gulf wide, with a particular deficiency in winter sampling (Lyczkowski-Shultz et al. 2004). The majority of SEAMAP plankton samples are collected using bongo nets and neuston nets. A 61 cm (24 in.) bongo net, fitted with 0.333 mm (0.013 in.) mesh netting, is fished in an oblique tow path from a maximum depth of 200 m (656 ft) or to 2–5 m (6.6–16.4 ft) off the bottom at depths less than 200 m (656 ft), and a mechanical flow meter is mounted off-center in the mouth of each bongo net to record the volume of water filtered (Rester 2011). A single or double 2 m × 1 m (6.6 ft × 3.3 ft) pipe frame neuston net, fitted with 0.937 mm (0.037 in.) mesh netting, is towed at the surface with the frame half submerged for 10 min (Rester 2011). Therefore, the two types of plankton nets used provide samples from distinct and separate segments of the water column: the neuston net samples the upper 0.5 m (1.6 ft) of the ocean surface, while the pair of bongo nets sample the entire water column from subsurface to near bottom, or to a maximum depth of 200 m (656 ft) (Lyczkowski-Shultz et al. 2004). Fish larvae are removed from the samples and identified to lowest possible taxon, typically to family.

A review of available SEAMAP data from 1982 through 2007 indicated that ichthyoplankton information collected during the spring and fall plankton surveys provided the most consistent results, both temporally and spatially; therefore, these data are summarized in the following sections.[1]

Spring plankton surveys typically cover the open Gulf of Mexico waters within the EEZ, as well as the Florida continental shelf on occasion (Figures 7.10 and 7.11), while fall plankton

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[1] ENVIRON's Baseline Information Management System (BIMS) experts provided an interpreted SEAMAP dataset that contained ichthyoplankton data from 1982 through 2007.
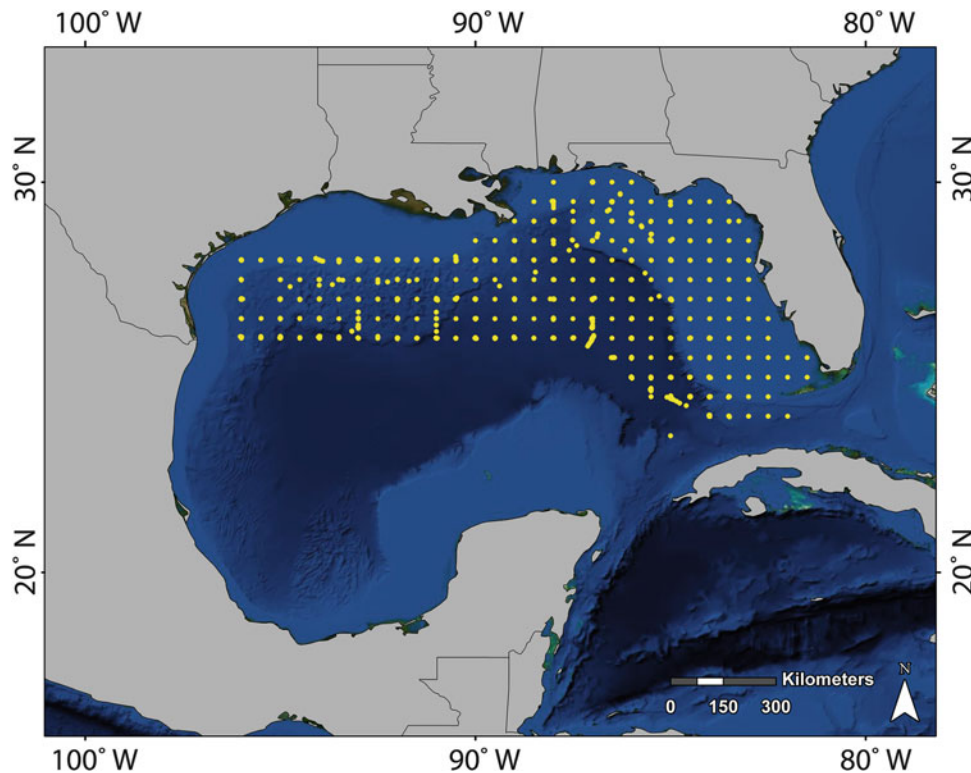
Figure 7.10. Generalized sampling locations of the SEAMAP spring plankton surveys from 1982 through 2007.

surveys typically sample the entire continental shelf of the U.S. Gulf of Mexico (Figures 7.12 and 7.13). Fish larvae in bongo net samples are expressed as number under 10 m^2 of sea surface, while larvae taken in neuston samples are expressed as number per 10-min tow. Note that the sampling sites in fall and spring were different (reason unknown).

Because of the large number of ichthyoplankton taxa collected from the U.S. Gulf of Mexico during the spring and fall from 1982 through 2007, summarizing the results for all taxa is not practical. Therefore, a small but representative number of fish taxa (11) were selected based on ecological and economic importance; baseline information for these taxa is summarized in the sections that follow. The selected taxa are listed below, and a description of the summarized SEAMAP data for each taxon is included in Tables 7.1 and 7.2.

- Family Carangidae: Jacks and pompanos
- Family Clupeidae: Herrings, shads, sardines, and menhadens
- Family Coryphaenidae: Dolphinfish
- Family Istiophoridae: Marlin and sailfish
- Family Lutjanidae: Snappers
- Family Mugilidae: Mullets
- Family Sciaenidae: Drums and croakers, includes redfish (*Sciaenops ocellatus*) and spotted seatrout (*Cynoscion nebulosus* and *Cynoscion regalis*)
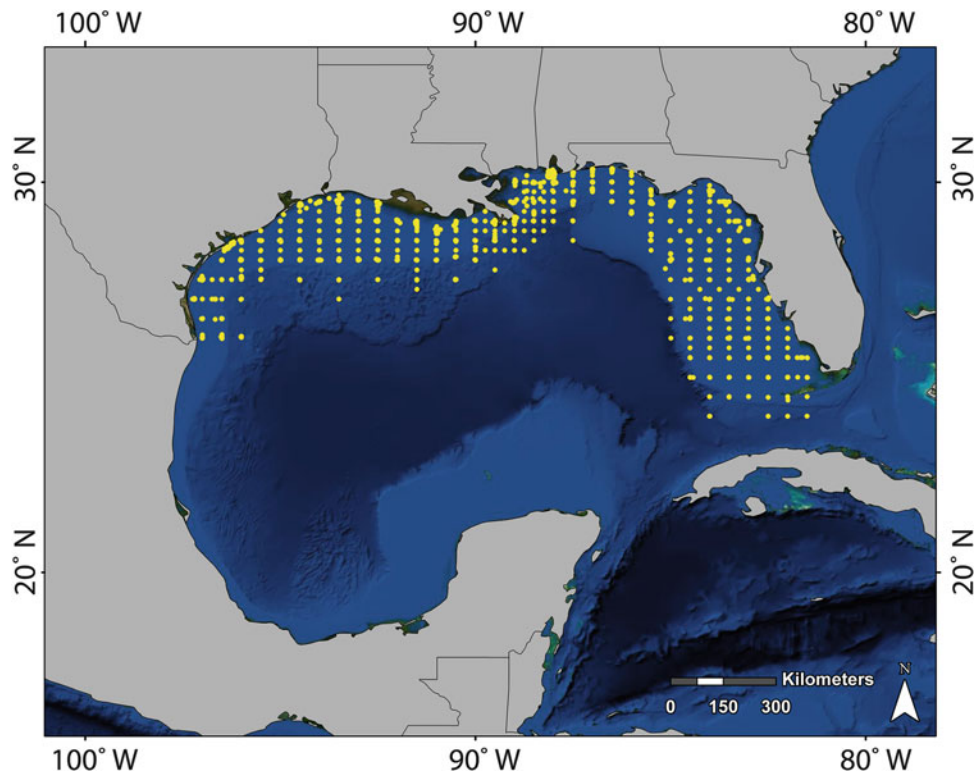- Family Scombridae: Mackerels, tunas, and bonitos (excluding *Thunnus*)

Figure 7.11. Generalized sampling locations of the SEAMAP fall plankton surveys from 1982 through 2007.
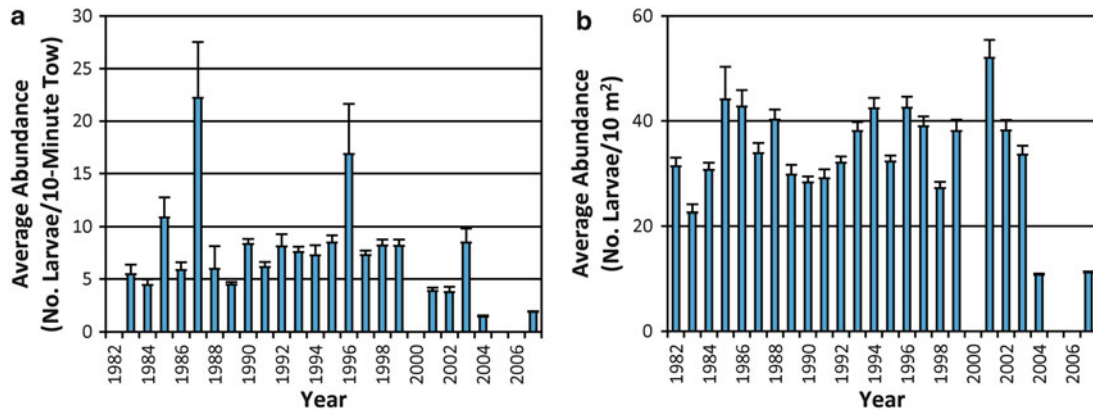

Figure 7.12. Average abundance of ichthyoplankton (all taxa combined) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.

- Genus *Thunnus*: Tuna (*Thunnus*), Atlantic bluefin tuna (*Thunnus thynnus*), blackfin tuna (*Thunnus atlanticus*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*)
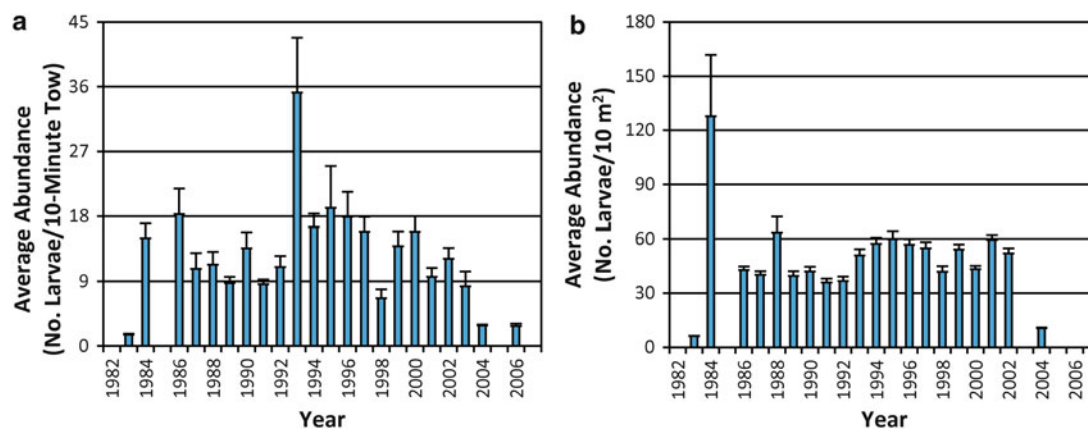- Family Serranidae: Seabasses and groupers
- Family Xiphiidae: Swordfish

Figure 7.13. Average abundance of ichthyoplankton (all taxa combined) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Table 7.1. Description of SEAMAP Data for the Spring and Fall Plankton Surveys Conducted from 1982 through 2007 for the 11 Selected Fish Taxa[a]

Family/ Genus	No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Carangidae	5,221	5.60	6,983	7.98	7,489	4,715
Clupeidae	896	0.96	3,717	4.25	2,429	2,184
Corypha enidae	1,983	2.13	436	0.50	2,072	347
Istiophoridae	456	0.49	286	0.33	644	98
Lutjanidae	577	0.62	3,608	4.12	1,320	2,865
Mugilidae	1,109	1.19	360	0.41	1,291	178
Sciaenidae	170	0.18	3,596	4.11	1,316	2,450
Scombridae (excluding *Thunnus*)	2,759	2.96	4,306	4.92	2,731	4,334
Thunnus	2,358	2.53	1,094	1.25	1,975	1,477
Serranidae	2,955	3.17	3,256	3.72	1,590	4,621
Xiphiidae	177	0.19	13	0.01	177	13

[a]Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982; fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.

Family Carangidae

Jacks and pompanos are both ecologically important as predators and prey (Lyczkowski-Shultz et al. 2004). Some species are important in the commercial and recreational fisheries in the Gulf of Mexico and are highly regarded as food (e.g., pompano), game fish (e.g.,

Table 7.2. Description of SEAMAP Data for the 11 Selected Fish Taxa for the Spring and Fall Plankton Surveys Conducted from 1982 through 2007[a]

Common Name	Scientific Name	No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Carangidae							
Amberjacks	*Seriola*	766	14.67	283	4.05	930	119
Jacks and pompanos	*Carangidae*	745	14.27	638	9.14	497	886
Round scad	*Decapterus punctatus*	672	12.87	1,556	22.28	1,166	1,062
Blue runner	*Caranx crysos*	504	9.65	557	7.98	826	235
Pompanos	*Trachinotus*	281	5.38	127	1.82	403	5
Bigeye scad	*Selar crumenoph thalmus*	271	5.19	738	10.57	483	526
Rough scad	*Trachurus lathami*	132	2.53	17	0.24	88	61
Rainbow runner	*Elagatis bipinnulata*	65	1.24	45	0.64	64	46
Lookdown	*Selene vomer*	39	0.75	365	5.23	151	253
Atlantic bumpers	*Chloroschombrus chrysurus*	31	0.59	2,051	29.37	1,074	1,008
Leatherjack	*Oligopolites saurus*	31	0.59	61	0.87	82	10
Mackerel scad	*Decapterus*	12	0.23	15	0.21	7	20
Pilot fish	*Naucrates doctor*	12	0.23	1	0.01	13	0
African pompano	*Alectis ciliaris*	9	0.17	17	0.24	24	2
Yellow jack	*Caranx bartholomai*	5	0.10	1	0.01	6	0
Crevall jack	*Caranx hippos*	4	0.08	2	0.03	1	5

(continued)

Table 7.2 (continued)

Common Name	Scientific Name	No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Palometa	*Trachinotus goodie*	3	0.06	0	0	3	0
Horse-eye jack	*Caranx latus*	2	0.04	0	0	2	0
Florida pompano	*Trachinotus carolinus*	2	0.04	1	0.01	3	0
Permit	*Trachinotus falcatus*	2	0.04	0	0	0	2
Jack mackerels	*Trachurus*	2	0.04	0	0	0	2
Threadfish	*Alectis*	1	0.02	0	0	0	1
Bumperfish	*Chloroscombrus*	1	0.02	4	0.06	2	3
Rainbow runner	*Elagatis*	1	0.02	0	0	1	0
Leatherjacks	*Oligoplites*	1	0.02	0	0	1	0
Lookdown	*Selene*	1	0.02	65	0.93	30	36
Atlantic moonfish	*Selene setapinnis*	1	0.02	10	0.14	8	3
Banded rudderfish	*Seriola zonata*	1	0.02	2	0.03	1	2
Bluntnose jack	*Hemicaranx amblyrhynchus*	0	0	1	0.01	1	0
Clupeidae							
Scaled sardine	*Harengula jaguana*	281	31.36	885	23.81	766	400
Red-eye round herring	*Etrumeus teres*	231	25.78	11	0.30	63	179
Gilt sardine	*Sardine Aurita*	198	22.10	920	24.75	568	550
Herrings, shads, and sardines	Clupeidae	105	11.72	630	16.95	438	297

Table 7.2 (continued)

Taxa		No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Common Name	Scientific Name						
Atlantic thread herring	*Opisthonema oglinum*	70	7.81	1,253	33.71	578	745
Menhaden	*Brevoortia*	6	0.67	12	0.32	10	8
Atlantic menhaden	*Brevoortia tyrannus*	2	0.22	0	0	2	0
Gulf menhaden	*Brevoortia patronus*	1	0.11	0	0	1	0
Round herrings	*Etrumeus*	1	0.11	0	0	0	1
Sardines	*Sardinella*	1	0.11	2	0.05	0	3
Finescale menhaden	*Brevoortia gunteri*	0	0	1	0.03	0	1
Herrings	*Harengula*	0	0	1	0.03	1	0
Thread herrings	*Opisthonema*	0	0	2	0.05	2	0
Coryphaenidae							
Common dolphinfish	*Coryphaenidae hippurus*	930	46.90	265	60.78	1,087	108
Dolphinfishes	*Coryphaena*	669	33.74	104	23.85	562	211
Pompano dolphinfish	*Coryphaenidae equiselis*	364	18.36	51	11.70	407	8
Dolphinfishes	*Coryphaenidae*	20	1.01	16	3.67	16	20
Istiophoridae							
Marlins	*Istiophoridae*	267	58.55	167	58.39	382	52
Indo-Pacific sailfish	*Istiophorus platypterus*	169	37.06	102	35.66	229	42
Sailfish	*Istiophorus*	10	2.19	8	2.80	16	2
Blue marlin	*Makaira nigricans*	4	0.88	0	0.00	3	1

(continued)

Table 7.2 (continued)

Taxa		No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Common Name	Scientific Name						
Spearfish	*Tetrapturus*	4	0.88	9	3.15	13	0
Atlantic white marlin	*Tetrapturus albidus*	1	0.22	0	0	1	0
Lutjanidae							
Snappers	Lutjanidae	220	38.13	1,318	36.53	312	1,226
Vermillion snapper	*Rhomboplites aurorubens*	148	25.65	856	23.73	376	628
Wenchman	*Pristipomoides aquilonaris*	95	16.46	497	13.77	218	374
Snappers	*Lutjanus*	38	6.59	372	10.31	134	276
Red snapper	*Lutjanus campechanus*	36	6.24	425	11.78	208	253
Slopefishes	*Symphysanodon*	26	4.51	8	0.22	4	30
Mangrove snapper	*Lutjanus griseus*	13	2.25	108	2.99	56	65
Jobfish	*Pristipomoide*	1	0.17	4	0.11	4	1
Snappers	Etelinae	0	0	2	0.06	0	2
Queen snapper	*Etelis oculatus*	0	0	6	0.17	1	5
Mutton snapper	*Lutjanus analis*	0	0	1	0.03	1	0
Lane snapper	*Lutjanus synagris*	0	0	11	0.30	6	5
Mugilidae							
Mullets	*Mugil*	504	45.45	167	46.39	578	93
White mullet	*Mugil curema*	327	29.49	96	26.67	401	22
Mullets	Mugilidae	274	24.71	95	26.39	307	62
Flathead mullet	*Mugil cephalus*	4	0.36	2	0.56	5	1

(continued)

Table 7.2 (continued)

Taxa		No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Common Name	Scientific Name						
Drums and croakers	Sciaenidae	57	33.53	489	13.60	102	444
Kingfish	Menticirrhus	43	25.29	677	18.83	313	407
Banded drum	Larimus fasciatus	17	10.00	225	6.26	79	163
Sciaenidae							
Sand weakfish	Cynoscion arenarius	16	9.41	496	13.79	153	359
Atlantic croaker	Micropogonias undulates	10	5.88	256	7.12	83	183
Silver seatrout	Cynoscion nothus	5	2.94	369	10.26	149	225
Spot	Leiostomus xanthu	5	2.94	94	2.61	20	79
American silver perch	Bairdiella chrysoura	4	2.35	16	0.44	7	13
Drums	Cynoscion	3	1.76	159	4.42	59	103
Star drum	Stellifer lanceolatus	2	1.18	174	4.84	68	108
Weakfish	Cynoscion regalis	1	0.59	2	0.06	1	2
Black drum	Pogonias cromis	1	0.59	1	0.03	0	2
Redfish	Sciaenops ocella	1	0.59	609	16.94	272	338
Perch	Bairdiella spp.	0	0	1	0.03	0	1
Scombridae							
Skipjack tuna	Katsuwonus pelamis	961	34.83	248	5.76	509	700
Bullet tun and frigate tuna	Auxis	940	34.07	861	20.00	846	955

(continued)

Table 7.2 (continued)

Taxa Common Name	Taxa Scientific Name	No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Mackerels, tunas, and bonitos	Scombridae	388	14.06	673	15.63	179	882
Little tunny	*Euthynnus alletteratus*	295	10.69	1,016	23.59	544	767
King mackerel	*Scomberomorus cavalla*	50	1.81	901	20.92	348	603
Spanish mackerel	*Scomberomorus macula*	46	1.67	538	12.49	269	315
Wahoo	*Acanthocybium solandri*	34	1.23	19	0.44	12	41
Mackerels	*Scomberomorus*	12	0.43	38	0.88	8	42
Tuna	*Euthynnus*	7	0.25	0	0	0	7
Kingfish	*Scomberomorus regalis*	6	0.22	11	0.26	11	6
Atlantic mackerel	*Scomber scombrus*	4	0.14	0	0	0	4
Atlantic bonito	*Sarda*	2	0.07	1	0.02	2	1
Thunnus							
Tuna	*Thunnus*	1,512	64.12	962	87.93	1,451	1,023
Northern bluefin tuna	*Thunnus thynnus*	672	28.50	50	4.57	429	293
Blackfin tuna	*Thunnus atlanticus*	163	6.91	81	7.40	89	155
Yellowfin tuna	*Thunnus albacares*	10	0.42	0	0	5	5
Bigeyed tuna	*Thunnus obesus*	1	0.04	1	0.09	1	1

(continued)

Table 7.2 (continued)

Taxa		No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Common Name	Scientific Name						
Serranidae							
Seabasses and groupers	Serranidae	1,075	36.38	1,231	37.81	446	1,860
Combers	Serranus	463	15.67	87	2.67	221	329
Sand perch	Diplectrum	254	8.60	662	20.33	285	631
Reeffish, wreckfish, and jewelfish	Anthias	203	6.87	29	0.89	51	181
Reeffish, wreckfish, and jewelfish	Hemanthias	182	6.16	27	0.83	86	123
Yellowfin bass	Anthias nicholsi	148	5.01	67	2.06	31	184
Red barbier	Hemanthias vivanus	136	4.60	11	0.34	32	115
Seabasses	Centropristis	119	4.03	325	9.98	117	327
Longtail bass	Hemanthias leptus	102	3.45	20	0.61	22	100
Pygmy seabass	Serraniculus pumilio	33	1.12	503	15.45	151	385
Streamer bass	Hemanthias aureorubens	17	0.58	3	0.09	4	16
Basslets	Liopropoma	16	0.54	7	0.21	7	16
Groupers	Epinephelus	15	0.51	0	0	1	14
Reeffish, wreckfish, and jewelfish	Anthiinae	12	0.41	1	0.03	1	12

(continued)

Table 7.2 (continued)

Taxa		No. of Occurrences in Spring Plankton Surveys	Percent Occurrence in Spring Plankton Surveys	No. of Occurrences in Fall Plankton Surveys	Percent Occurrence in Fall Plankton Surveys	No. of Occurrences in Neuston Net Samples	No. of Occurrences in Bongo Net Samples
Common Name	Scientific Name						
Roughtongue bass	*Holanthias martinicensis*	12	0.41	0	0	3	9
Streamer bass	*Pronotogrammus aureorubens*	8	0.27	0	0	1	7
Reef bass	*Pseudogramma gregoryi*	7	0.24	7	0.21	5	9
Podges	*Pseudogramma*	7	0.24	4	0.12	0	11
Groupers	*Mycteroperca*	5	0.17	0	0	0	5
Black seabass	*Centropristis striata*	4	0.14	22	0.68	2	24
Seabasses	*Pronotogrammu*	4	0.14	0	0	0	4
Reeffish, wreckfish, and jewelfish	*Plectranthias*	3	0.10	0	0	2	1
Hamlets	*Hypoplectrus*	1	0.03	0	0	0	1
Seabass	*Serraninae*	1	0.03	0	0	1	0
Yellowtail bass	*Bathyanthias mexicanus*	0	0	1	0.03	1	0
Seabasses	*Serraniculus*	0	0	1	0.03	0	1
Xiphiidae							
Swordfish	*Xiphias gladius*	176	99.44	13	100	176	13
Swordfish	*Xiphias*	1	0.56	0	0	1	0

[a]Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982; fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
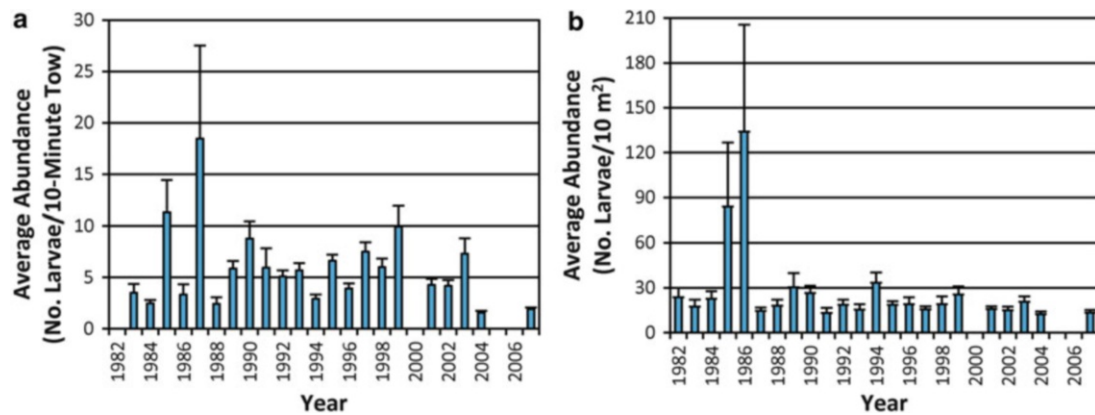
Figure 7.14. Average abundance of Carangidae for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.

amberjack), or bait (e.g., blue runner, *Caranx crysos*) (Ditty et al. 2004; Lyczkowski-Shultz et al. 2004). Larval jacks and pompanos cannot be reliably identified to species; however, they can typically be identified to genus (Lyczkowski-Shultz et al. 2004).

Jacks and pompanos made up more of the total ichthyoplankton catch than any of the other groups selected for analysis (Table 7.1). More larval jacks and pompanos were captured during the fall along the continental shelf, as compared to spring in the open Gulf of Mexico and, while larvae were captured both at the surface and in the water column, the majority of larval jacks and pompanos were captured at the water surface in neuston nets (Table 7.1).

The average abundance of Carangidae larvae collected by neuston net during the spring ranged from 1.6 (2004) to 18.5 (1987) larvae per 10-min tow, and the average abundance of carangids collected by bongo net ranged from 12.3 (2004) to 134 (1986) larvae per 10 m^2 (Figure 7.14). Carangid average abundance during the fall along the continental shelf ranged from 1.4 (1983) to 23.1 (1999) larvae per 10-min tow for neuston net samples, while bongo net samples ranged from 6.9 (1983) to 98.4 (1999) larvae per 10 m^2 (Figure 7.15). In general, the average abundance of Carangidae larvae was typically higher along the continental shelf during the fall as compared to the spring in the open Gulf for both gear types. With the exception of 1985 and 1986, the average abundance of larvae for bongo net samples was within a similar range during the spring; however, average carangid larval abundances were highly variable from year to year during the spring for neuston samples and during the fall for both gear types from 1982 through 2007 (Figures 7.14 and 7.15).

During the spring, the majority of larvae captured were jacks (*Caranx*), while most of the jack and pompano larvae that were obtained during the fall were Atlantic bumper (*Chloroscombrus chrysurus*) and round scad (*Decapterus punctatus*) (Table 7.2). Jacks were distributed throughout the open Gulf of Mexico during the spring, as well as throughout most of the continental shelf during the fall (Figure 7.16). While Atlantic bumper larvae were distributed throughout the entire continental shelf during the fall, larvae were sparsely distributed throughout the Gulf during spring plankton surveys (Figure 7.17).

Family Clupeidae

As forage fish, herrings, shads, sardines, and menhadens are abundant coastal pelagic species that constitute an important, if not primary, food source for many predatory game and commercial fishes (Shaw and Drullinger 1990a). Most of the herring, shad, sardine, and
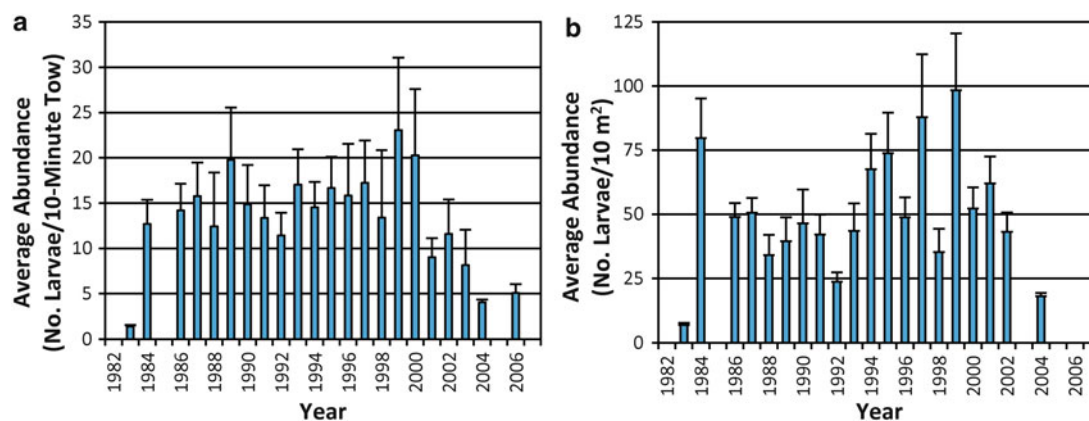
Figure 7.15. Average abundance of Carangidae for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

menhaden larvae that were captured during the plankton surveys from 1982 through 2007 were captured during the fall along the continental shelf, and similar numbers were taken in both the neuston and bongo nets (Table 7.1). Thirteen taxa are included in this group, with the most larvae being scaled sardines (*Harengula jaguana*), round herring (*Etrumeus teres*), and Spanish sardine (*Sardinella aurita*) in the spring and Atlantic thread herring (*Opisthonema oglinum*), Spanish sardine, and scaled sardines in the fall (Table 7.2). While scaled sardines and Atlantic thread herring were distributed throughout the continental shelf during the fall, they were sparsely distributed throughout the open Gulf and Florida Shelf in the spring (Figures 7.18 and 7.19).

The Gulf menhaden (*Brevoortia patronus*) is one of the most abundant pelagic fishes in the northern coastal Gulf of Mexico; it is an exploited marine resource, the principal prey for many important commercial and recreational fish species, as well as marine birds and mammals. As both a planktivore and detritivore, Gulf menhaden are an integral and key component of the Gulf of Mexico ecosystem (Vaughan et al. 2011). However, because adults spawn primarily near the mouth of the Mississippi River during the winter and the plankton surveys were conducted in the spring and fall, only one Gulf menhaden juvenile was collected in the plankton surveys (Table 7.2).

From 1982 through 2007, average clupeid larval abundances were highly variable from year to year during the spring and fall for both gear types (Figures 7.20 and 7.21). For neuston net samples, the average abundance of Clupeidae larvae ranged from 0 (2004) to 68.5 (1983) larvae per 10-min tow in the spring in the open Gulf and from 1.3 (1983) to 97.4 (1993) larvae per 10-min tow during the fall along the continental shelf (Figures 7.20 and 7.21). Average clupeid larval abundance for bongo net samples ranged from 11.7 (1982) to 247.2 (1999) larvae per 10 m^2 and from 6.7 (1983) to 225.9 (1995) larvae per 10 m^2 during spring and fall plankton surveys, respectively (Figures 7.20 and 7.21). For both gear types, the average abundance of Clupeidae larvae was typically higher along the continental shelf during the fall, compared to spring in the open Gulf of Mexico.

Family Coryphaenidae

Dolphinfishes (sometimes referred to as mahi mahi or dorado) are an important commercial and recreational species distributed throughout the tropical and subtropical seas of the world and are highly prized for food (Ditty et al. 1994). They are often associated with
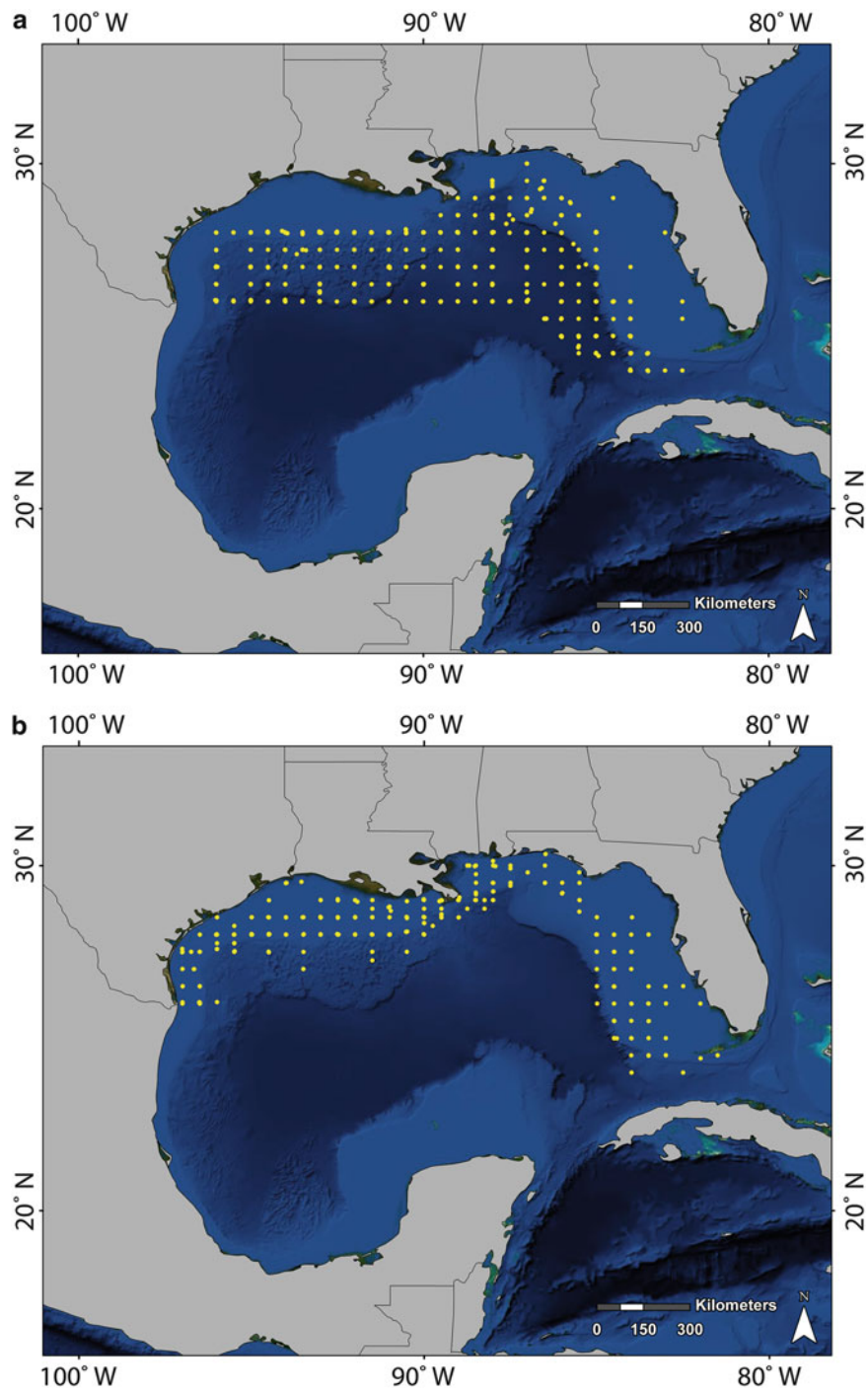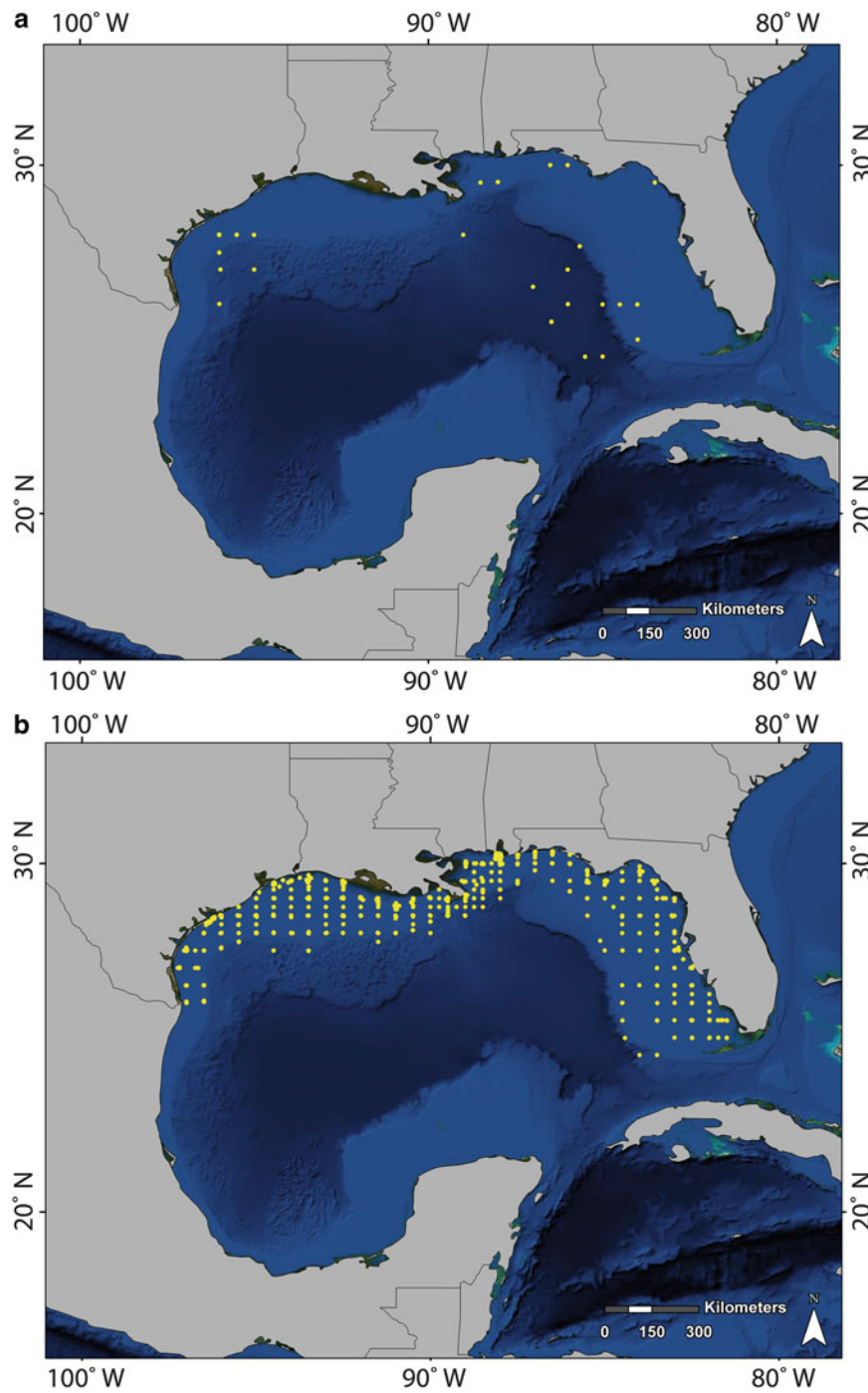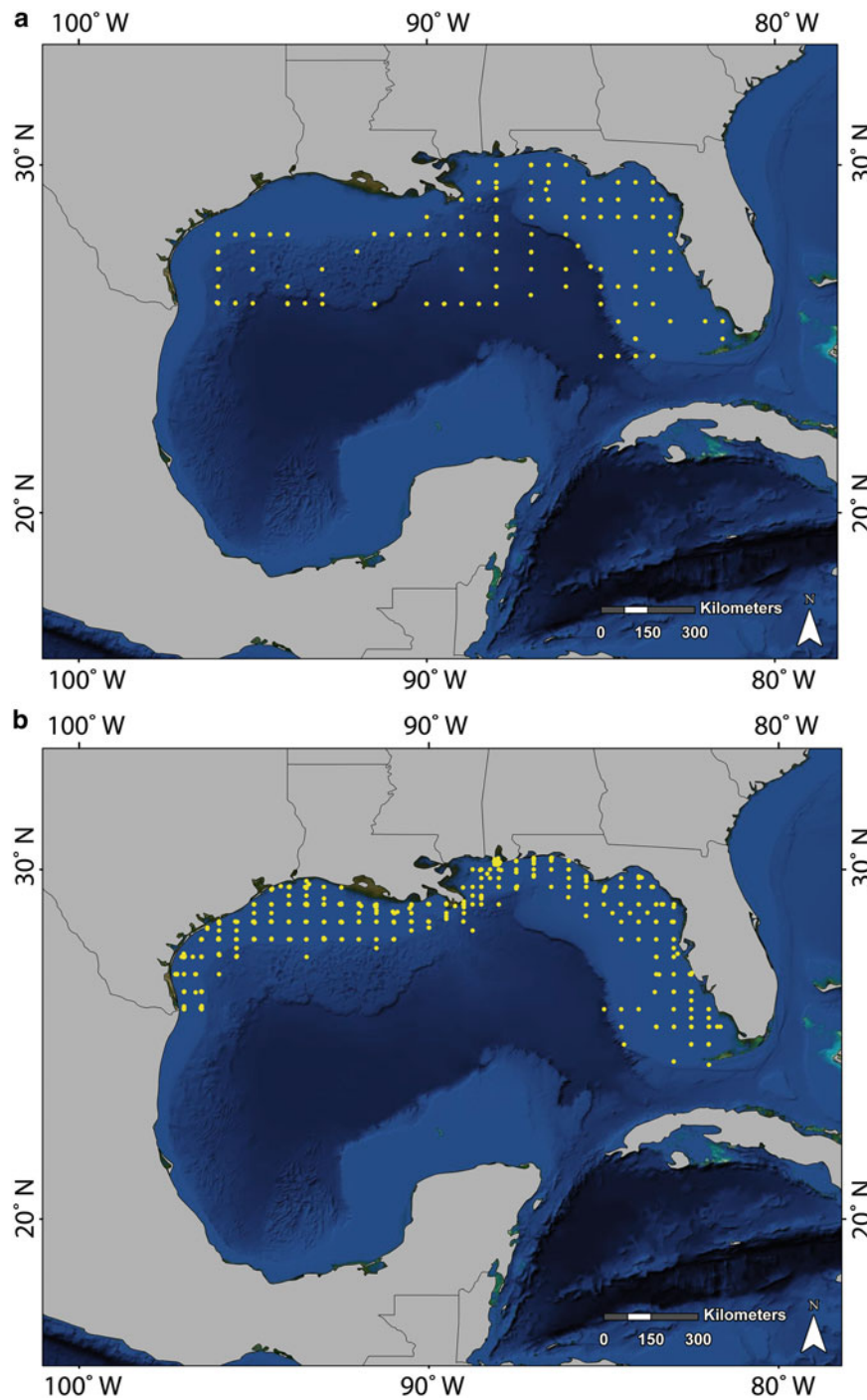
Figure 7.16. Distribution of jack (*Caranx*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
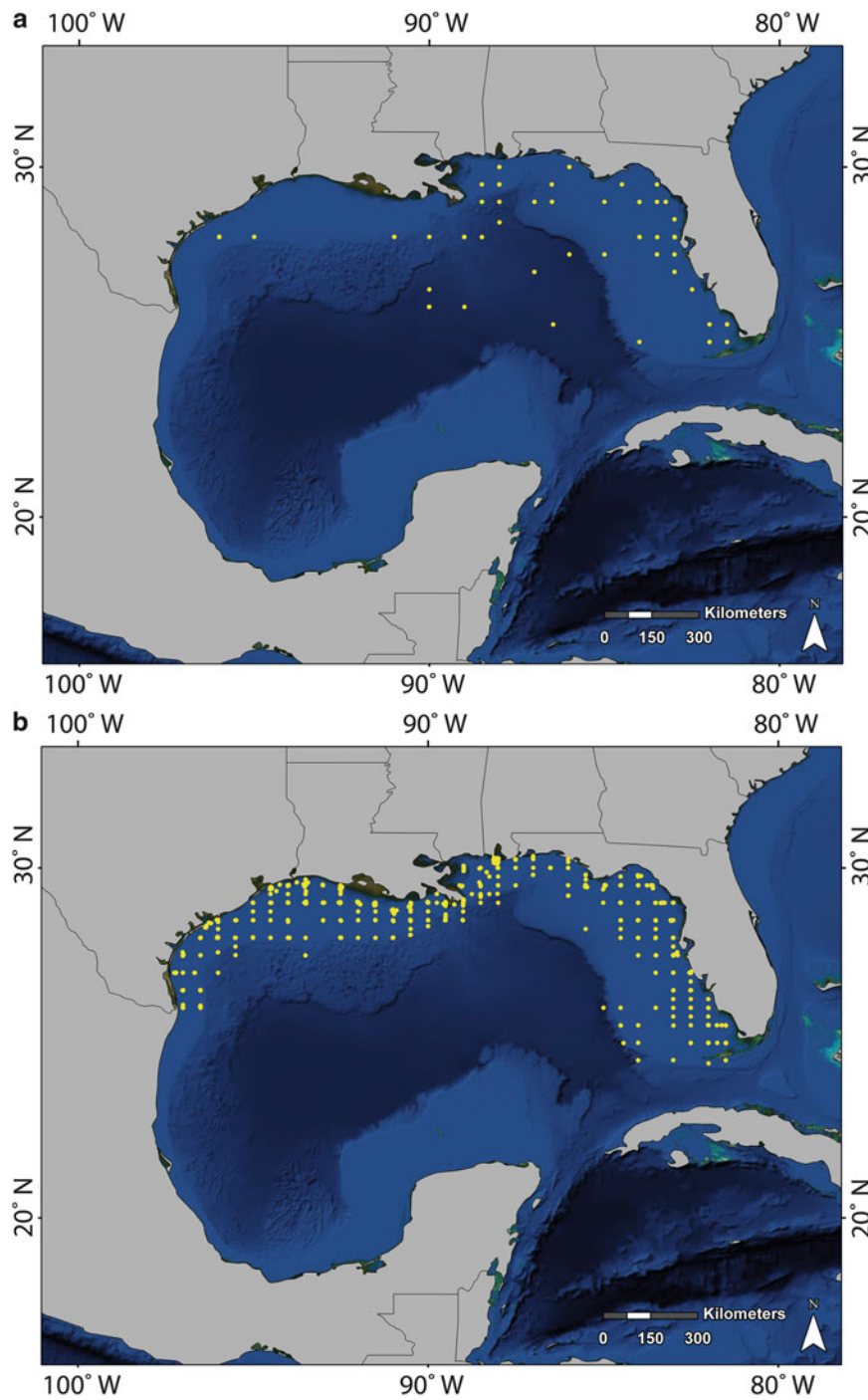
Figure 7.17. Distribution of Atlantic bumper (*Chloroscombrus chrysurus*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.

Figure 7.18. Distribution of scaled sardines (*Harengula jaguana*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.

Figure 7.19. Distribution of Atlantic thread herring (*Opisthonema oglinum*) larvae during the SEA-MAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
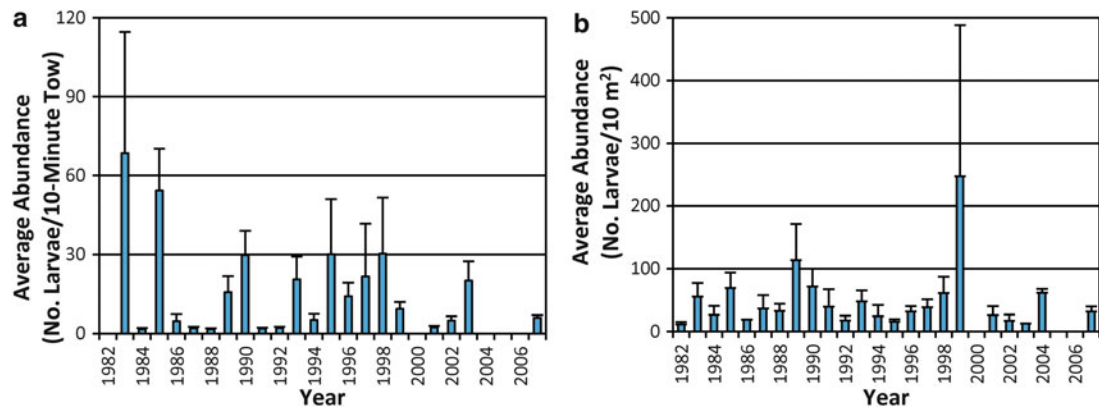
Figure 7.20. Average abundance of Clupeidae for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
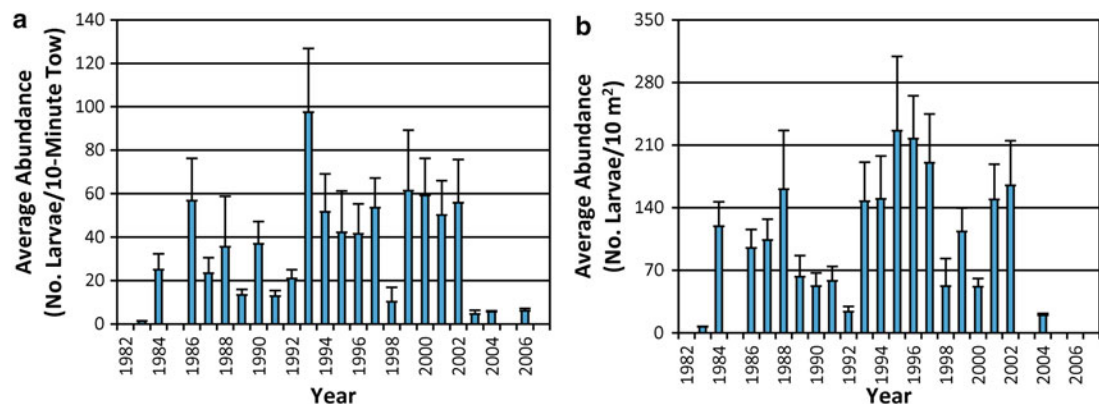
Figure 7.21. Average abundance of Clupeidae for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Sargassum spp. or other floating objects. One of the fastest growing species in the ocean, dolphinfish, serves as a primary food source for many pelagic predators (Palko et al. 1982). This group includes four taxa (Table 7.2). Most dolphinfish larvae were taken in the spring in the open Gulf of Mexico and at the water surface in neuston nets (Table 7.1). Dolphinfish were fairly well distributed throughout sampling stations during both spring and fall plankton surveys conducted from 1982 through 2007 (Figure 7.22). During the spring, as well as during the fall along the continental shelf, average abundances of dolphinfish larvae occurred at low densities and typically ranged from 1 to 3 larvae per 10-min neuston tow (Figures 7.23 and 7.24). For bongo net samples, the average abundance of coryphaenid larvae generally ranged from 5 to 9 larvae per 10 m^2 (Figures 7.23 and 7.24). In the spring in the open Gulf of Mexico, the highest average abundance of larval dolphinfish for samples collected by bongo net occurred in 2007, while the highest average abundance occurred in 1998 during the fall along the continental shelf (Figures 7.23 and 7.24).
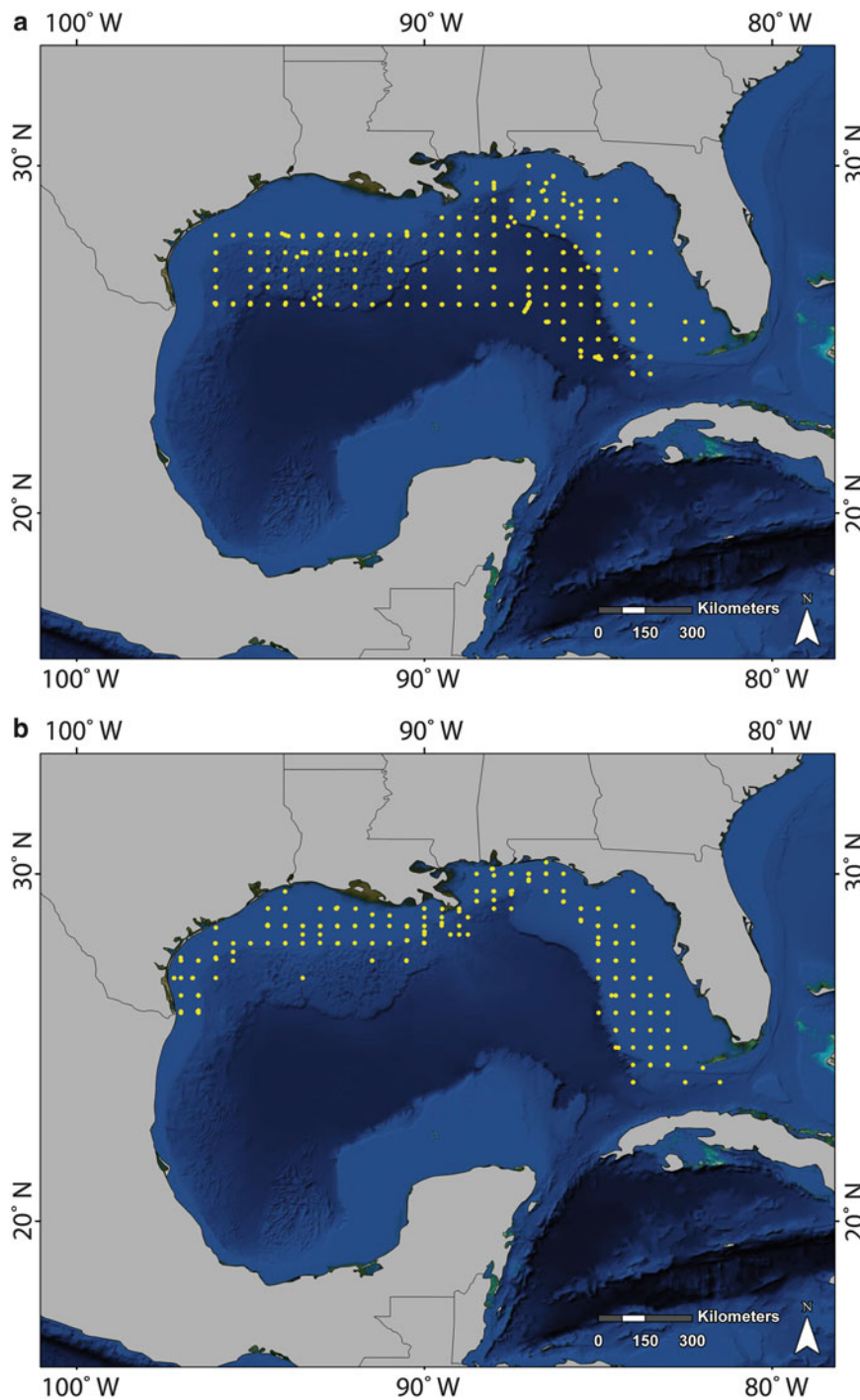
Figure 7.22. **Distribution of dolphinfish (Coryphaenidae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.**
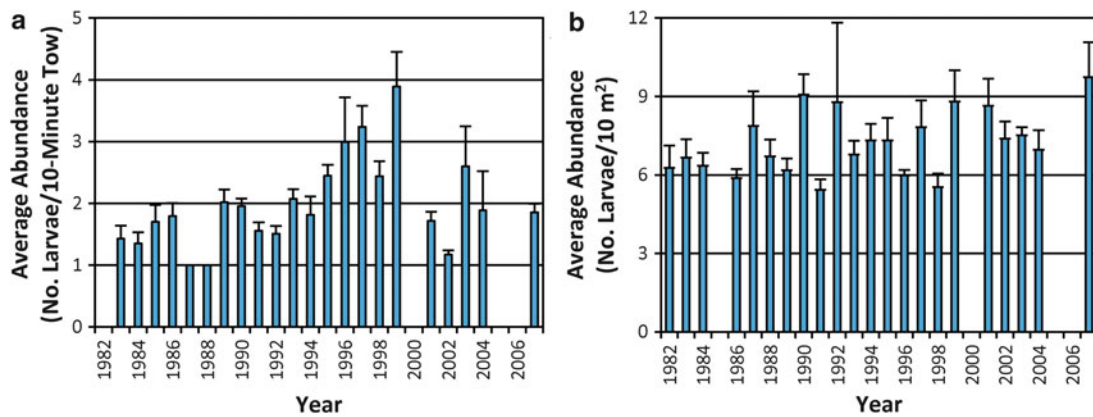
Figure 7.23. Average abundance of dolphinfish (Coryphaenidae) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
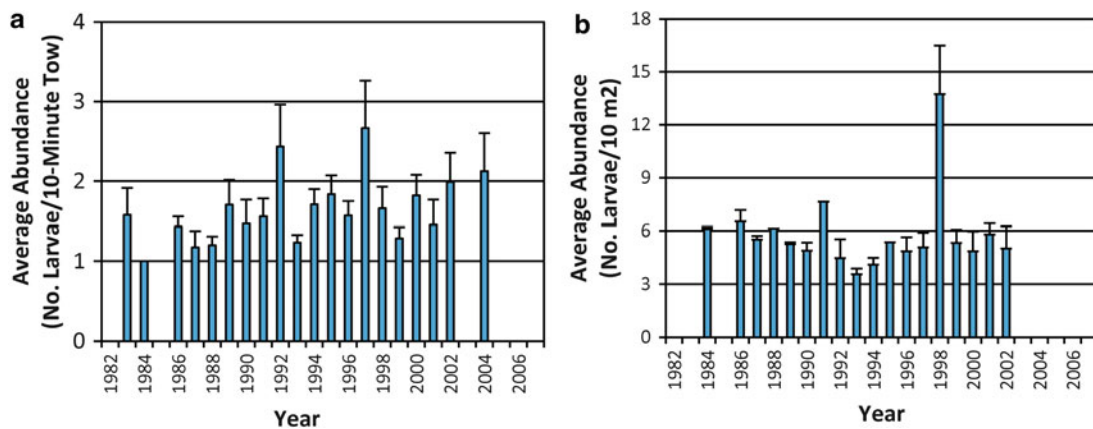
Figure 7.24. Average abundance of dolphinfish (Coryphaenidae) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Family Istiophoridae

Billfish, marlin, and sailfish are highly migratory across vast expanses of open ocean; therefore, not much is known about their life histories, especially the larval stages (Tidwell et al. 2007). Billfish support a sport fishery worth hundreds of millions of dollars each year, and as top predators play a critical role in all pelagic ecosystems (Tidwell et al. 2007; Rooker et al. 2012).

Most larval marlin and sailfish were taken in the spring in the open Gulf and at the water's surface, and seven taxa were included in this group (Tables 7.1 and 7.2). Though they did not occur at all sampling stations, billfish were fairly well represented during spring and fall plankton surveys (Figure 7.25).

Average abundances of billfish larvae for neuston net samples typically ranged from 1 to 4 larvae per 10-min tow during both the spring and fall, indicating similar surface densities in both the open Gulf and continental shelf (Figures 7.26 and 7.27). For neuston net samples from
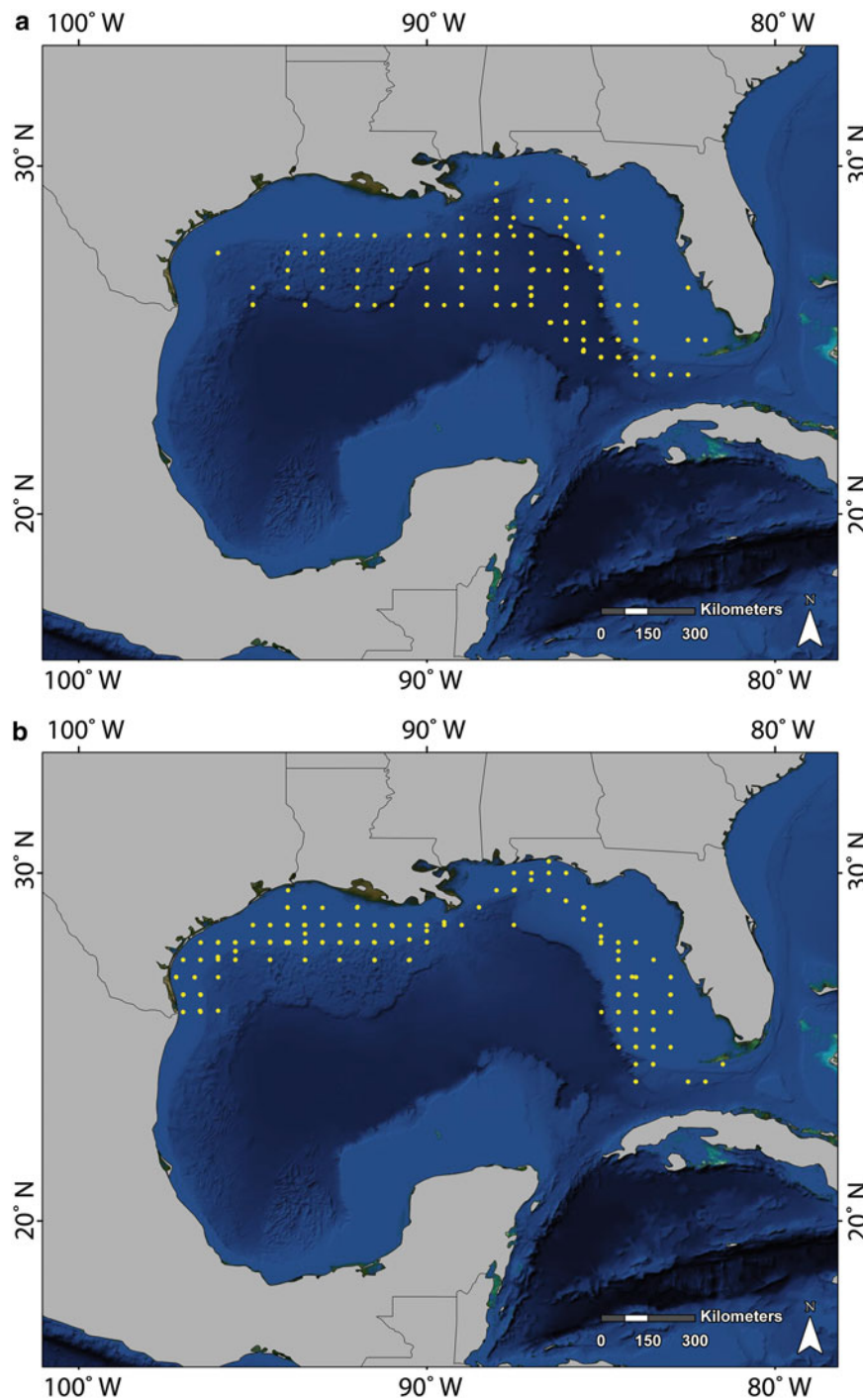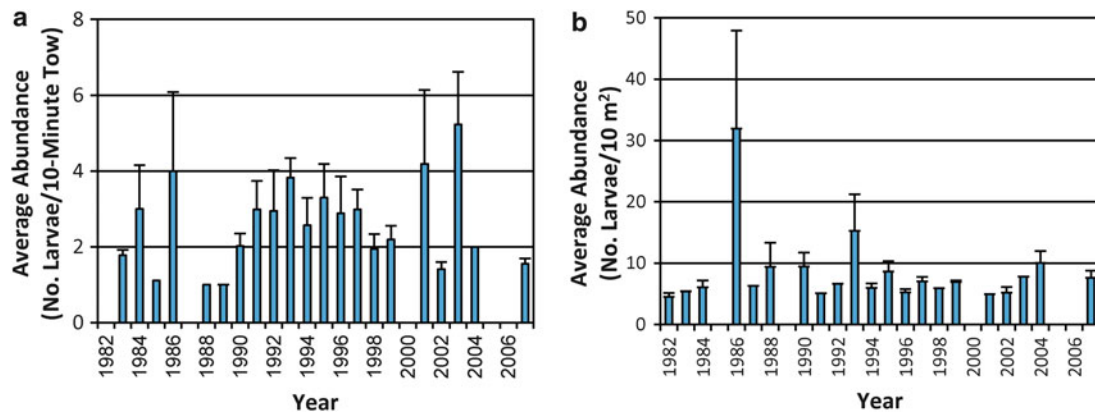
Figure 7.25. Distribution of billfish (Istiophoridae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.

Figure 7.26. Average abundance of billfish (Istiophoridae) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
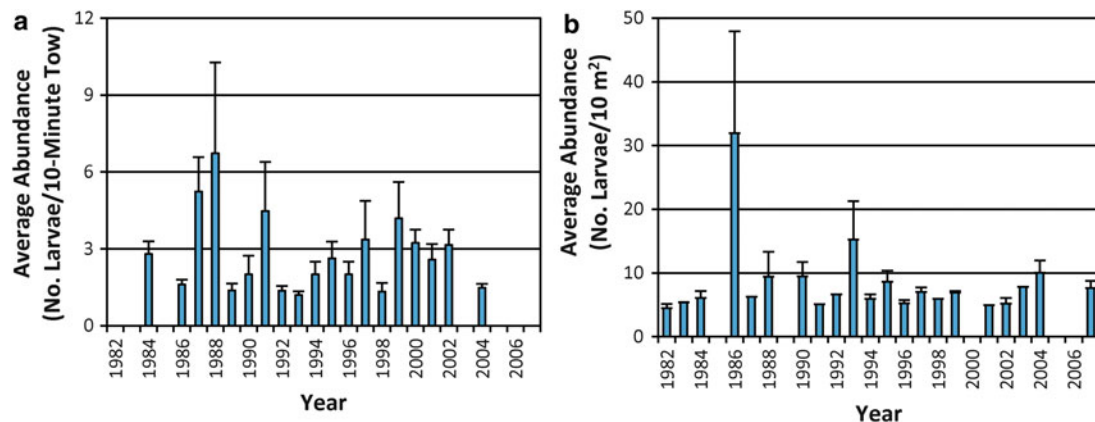
Figure 7.27. Average abundance of billfish (Istiophoridae) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

1982 through 2007, the highest average abundance of billfish larvae occurred in 2003 during spring surveys and in 1998 during fall surveys. The average abundance of billfish larvae was typically higher during the spring on the open Gulf as compared to along the continental shelf during the fall for bongo net samples (Figures 7.19 and 7.20). The highest abundance for all spring and fall bongo net samples, more than 30 larvae per 10 m^2, occurred in 1986.

Family Lutjanidae

The snapper family includes mostly reef-associated species, as well as several deepwater species; due to the excellent quality of its meat, snappers are of significant importance to the commercial and recreational fisheries in the Gulf of Mexico, and many species are overfished (Martinez-Andrade 2003). For example, red snapper (*Lutjanus campechanus*) is one of the most important food fishes in the Gulf of Mexico, and this fishery, which collapsed in the eastern Gulf of Mexico in the late 1980s, is the most controversial fishery in the U.S. Gulf of Mexico (Johnson et al. 2009; Cowan et al. 2010).

The majority of larval snapper were captured during the fall plankton surveys along the continental shelf, and most were taken in the water column in the bongo nets (Table 7.1). The snapper group includes 12 taxa, with most of the larvae captured during both the spring and fall consisting of the snapper family (Lutjanidae) and vermillion snapper (*Rhomboplites aurorubens*) (Table 7.2). Both Lutjanidae and vermillion snapper were found along the entire continental shelf during fall plankton surveys, and they were not distributed widely during spring plankton surveys (Figures 7.28 and 7.29).

From 1982 through 2007, the average abundance of lutjanid larvae collected by neuston net during the spring in the open Gulf of Mexico ranged from 0 (1983, 1988, and 2004) to 6.8 (1990) larvae per 10-min tow, while the average abundance of snapper larvae collected by bongo net ranged from 4 (1982) to 22.7 (1986) larvae per 10 m^2 (Figure 7.30). Snapper larvae average abundance during the fall along the continental shelf ranged from 0 (2006) to 12.4 (1987) larvae per 10-min tow for neuston net samples, and bongo net samples ranged from 5.6 (1983) to 24.2 (2001) larvae per 10 m^2 (Figure 7.31). For both gear types, the average abundance of snapper larvae was typically higher along the continental shelf during the fall as compared to the spring in the open Gulf (Figures 7.30 and 7.31).

Family Mugilidae

Mullet are ecologically important in the flow of energy through estuarine communities because they are primary consumers that feed on plankton and detritus. In the Gulf of Mexico, mullet typically spawn many miles offshore in deep water (Collins 1985). Mullet are important prey species for many fish and are also important to the recreational and commercial fisheries. As silvery pelagic juveniles, mullet inhabit surface waters of the open ocean for several months before migrating inshore (Lyczkowski-Shultz et al. 2004).

Four taxa are included in this group, with the majority of larvae identified to the genus *Mugil* (Table 7.2). Most mullet larvae were taken in the spring plankton surveys in the open Gulf of Mexico and were captured in the neuston nets at the surface (Table 7.1). Mullet were found in the open Gulf, as well as in the continental shelf during spring and fall plankton surveys from 1982 through 2007 (Figure 7.32).

Average abundances of larval mullet were highly variable from year to year during spring and fall for both gear types from 1982 through 2007 (Figures 7.33 and 7.34). For neuston net samples, the average abundance ranged from 0.97 (1985) to 23.8 (1999) per 10-min tow in the spring in the open Gulf and from 0 (1983, 2003, and 2006) to 15.3 (1984) larvae per 10-min tow during the fall along the continental shelf (Figures 7.33 and 7.34). Average mugilid larval abundance for bongo net samples ranged from 2.8 (1983) to 24.1 (1986) per 10 m^2 and from 0 (1983, 1986, 1998, and 2002) to 18.6 (2004) larvae per 10 m^2 during spring and fall plankton surveys, respectively (Figures 7.33 and 7.34). The average abundance of mullet larvae was typically higher during the spring in the open Gulf, compared to fall along the continental shelf for both gear types.

Family Sciaenidae

Members of the Family Sciaenidae (drums and croakers) are an important sport and commercial fishery resource along the U.S. Gulf of Mexico and are perhaps the most prominent group of northern Gulf inshore fishes (Cowan and Shaw 1988). This group includes 15 taxa, with most of the larvae consisting of the drum and croaker family (Sciaenidae), with the kingfish genus (*Menticirrhus*) in the spring and the kingfish genus and redfish in the fall (Table 7.2). The vast majority of larval drum and croaker were found during fall plankton surveys, with the
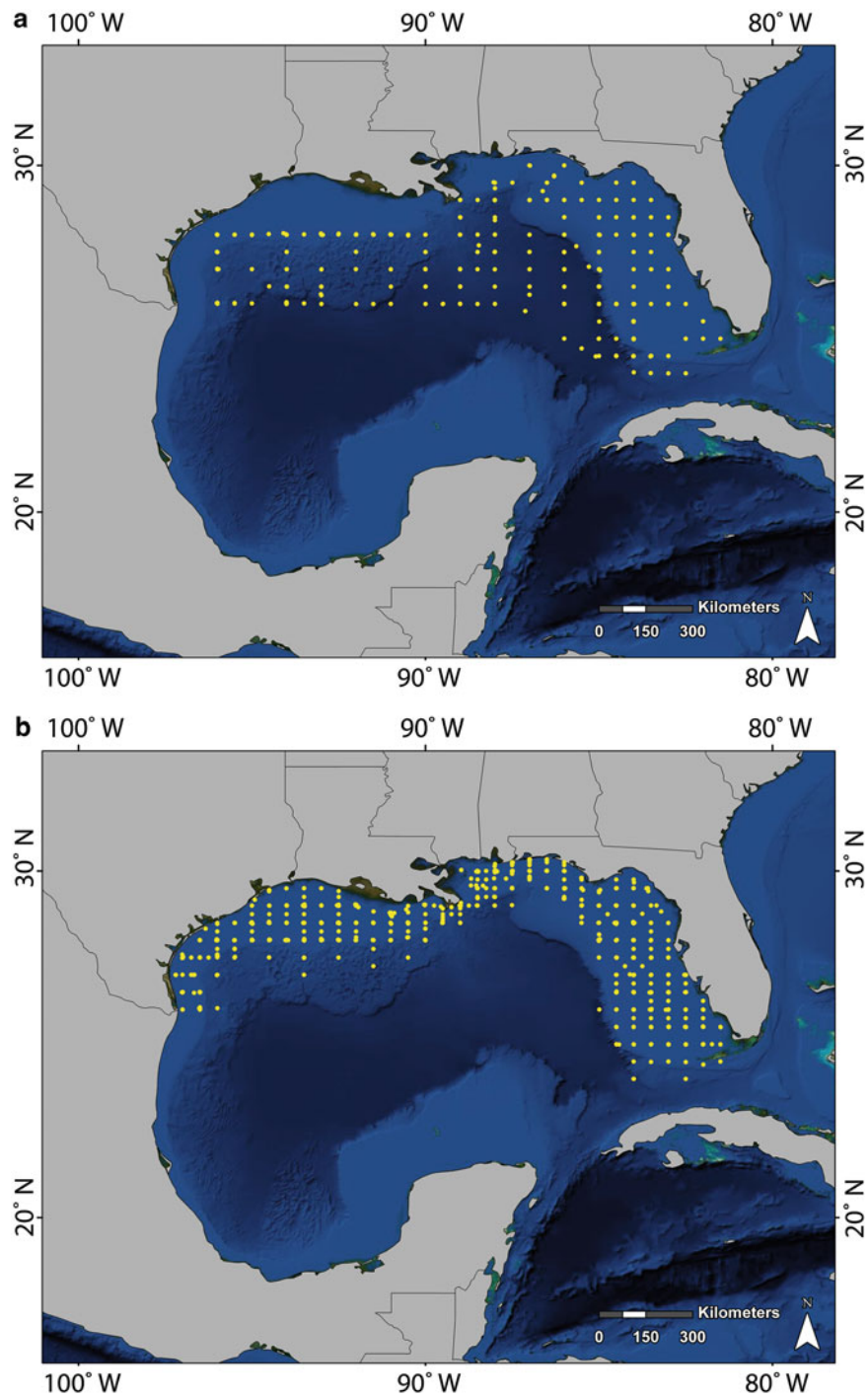
Figure 7.28. Distribution of snapper (Lutjanidae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
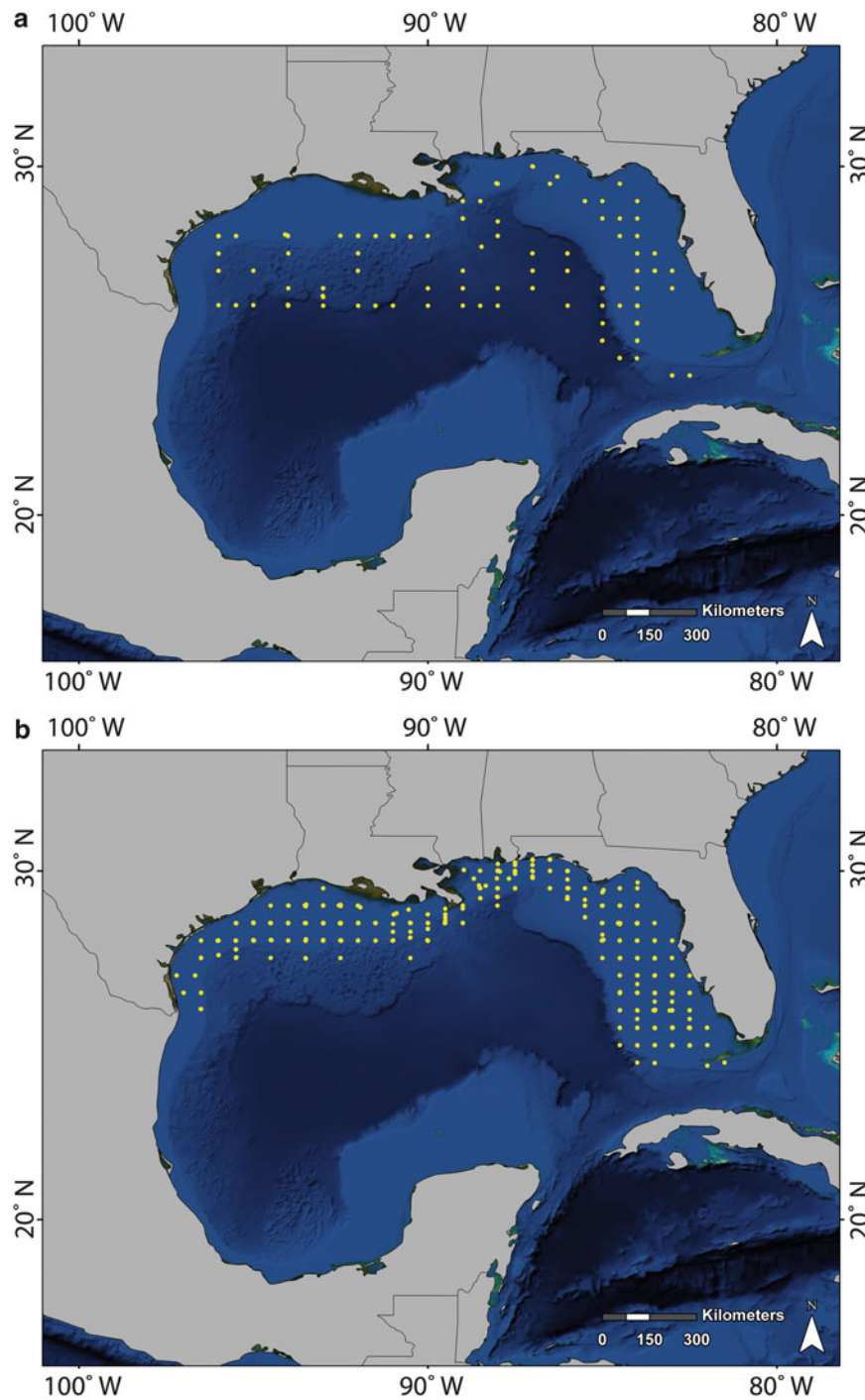
Figure 7.29. Distribution of vermilion snapper (*Rhomboplites aurorubens*) larvae during the SEA-MAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
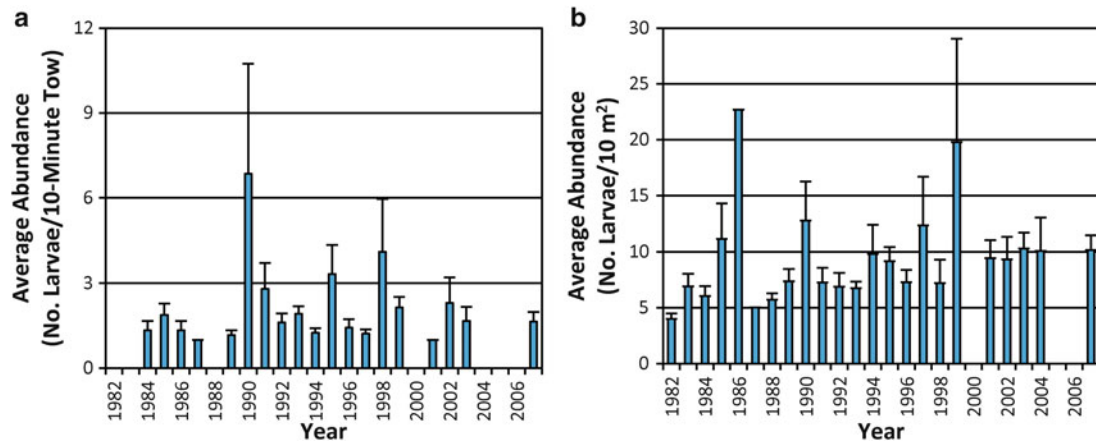
Figure 7.30. Average abundance of snapper (Lutjanidae) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
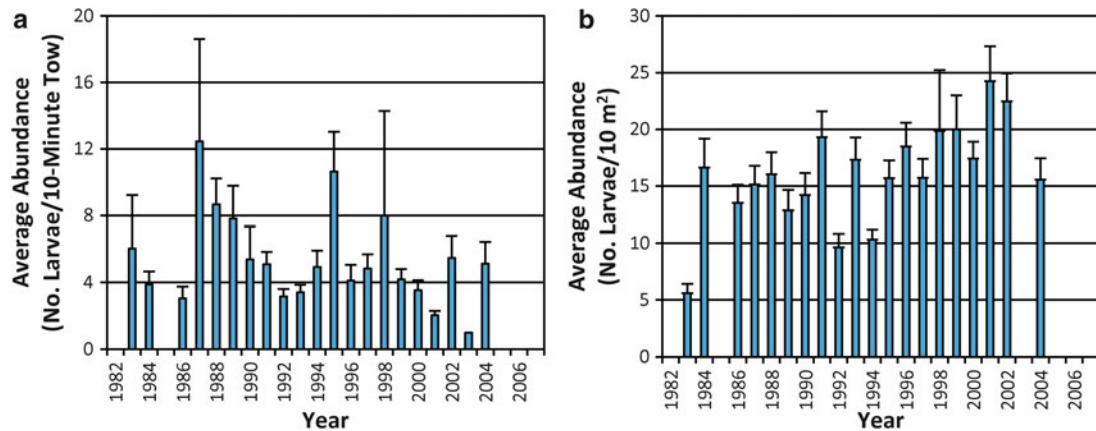

Figure 7.31. Average abundance of snapper (Lutjanidae) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

most in the water column in the bongo net samples (Table 7.1). The drum family (Sciaenidae) larvae were more extensive along the continental shelf during the fall compared to the spring (Figure 7.35); the seasonal distribution of this group was even more dramatic for the redfish (Figure 7.36).

From 1982 through 2007, with the exception of 1991 and 1995, the average abundance of sciaenid larvae collected by neuston net during the spring in the open Gulf of Mexico was fewer than 6 larvae per 10-min tow, and drum and croaker larval abundance averaged fewer than 20 larvae per 10 m^2 for bongo net samples during the spring, with the exception of 1986, when the average larval abundance was more than 120 larvae per 10 m^2 (Figure 7.36). Drum and croaker average abundance ranged from 1.3 (2006) to 32.2 (2000) larvae per 10-min tow for neuston net samples, and bongo net samples ranged from 4.8 (1983) to 208 (1988) larvae per 10 m^2 during the fall (Figure 7.38). For both gear types, the average abundance of sciaenid larvae was typically much higher along the continental shelf during the fall compared to the spring in the open Gulf (Figures 7.37 and 7.38).
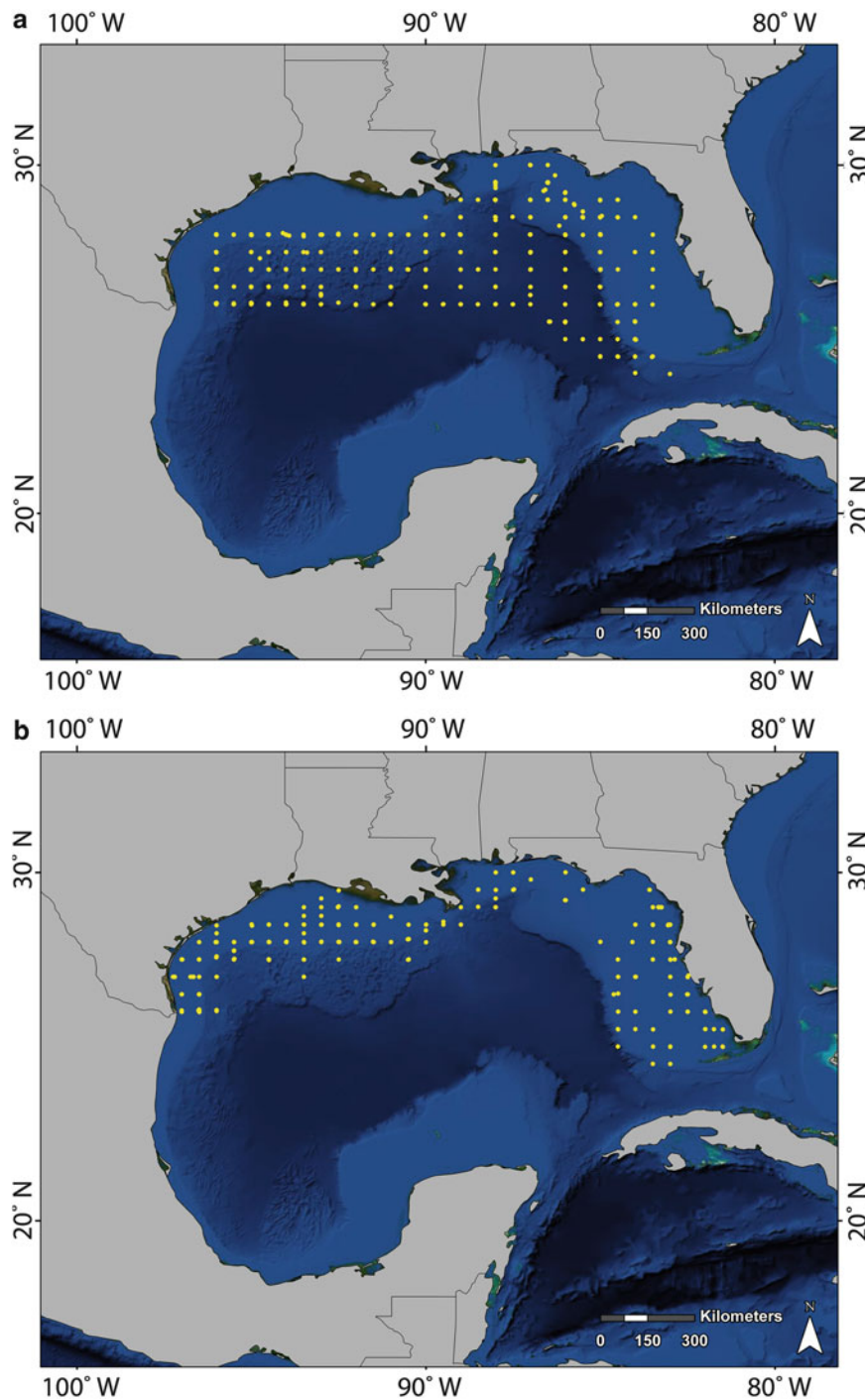
Figure 7.32. Distribution of mullet (Mugilidae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
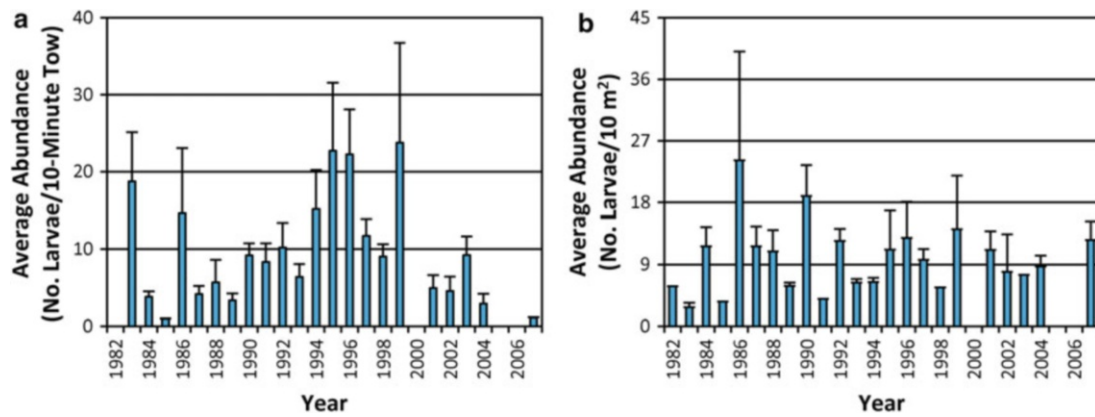
Figure 7.33. Average abundance of mullet (Mugilidae) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
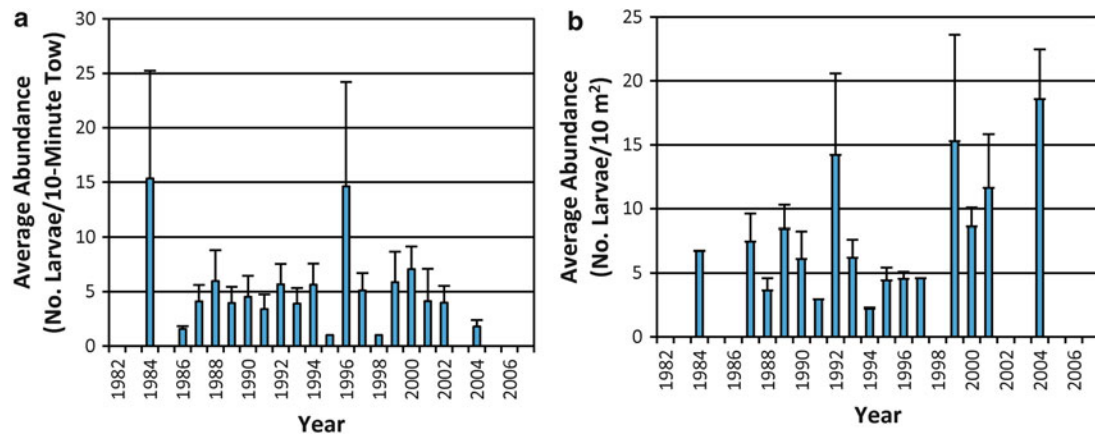

Figure 7.34. Average abundance of mullet (Mugilidae) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Redfish larvae were concentrated higher in the water column during daylight hours than at night in the general area east of the Mississippi Delta and south of the Mississippi barrier island over the East Louisiana–Mississippi–Alabama shelf in September and October 1984 and 1985 (Lyczkowski-Shultz and Steen 1991). In addition, there was no clear relationship between vertical aggregation of red drum larvae and temperature or salinity profiles or microzooplankton prey distribution. Atlantic croaker (*Micropogonias undulatus*) larvae were found to be least abundant in surface waters at night, and the highest abundances at night were observed at the deepest depths sampled during an investigation conducted in inner-shelf waters off Mississippi during September and October 1984 and 1985 (Comyns and Lyczkowski-Schultz 2004). By midmorning, Atlantic croaker larvae had moved up the water column, and highest abundances were usually found at 5 m (16.4 ft); no consistent pattern was found in the vertical stratification of Atlantic croaker larvae during the midday or afternoon.
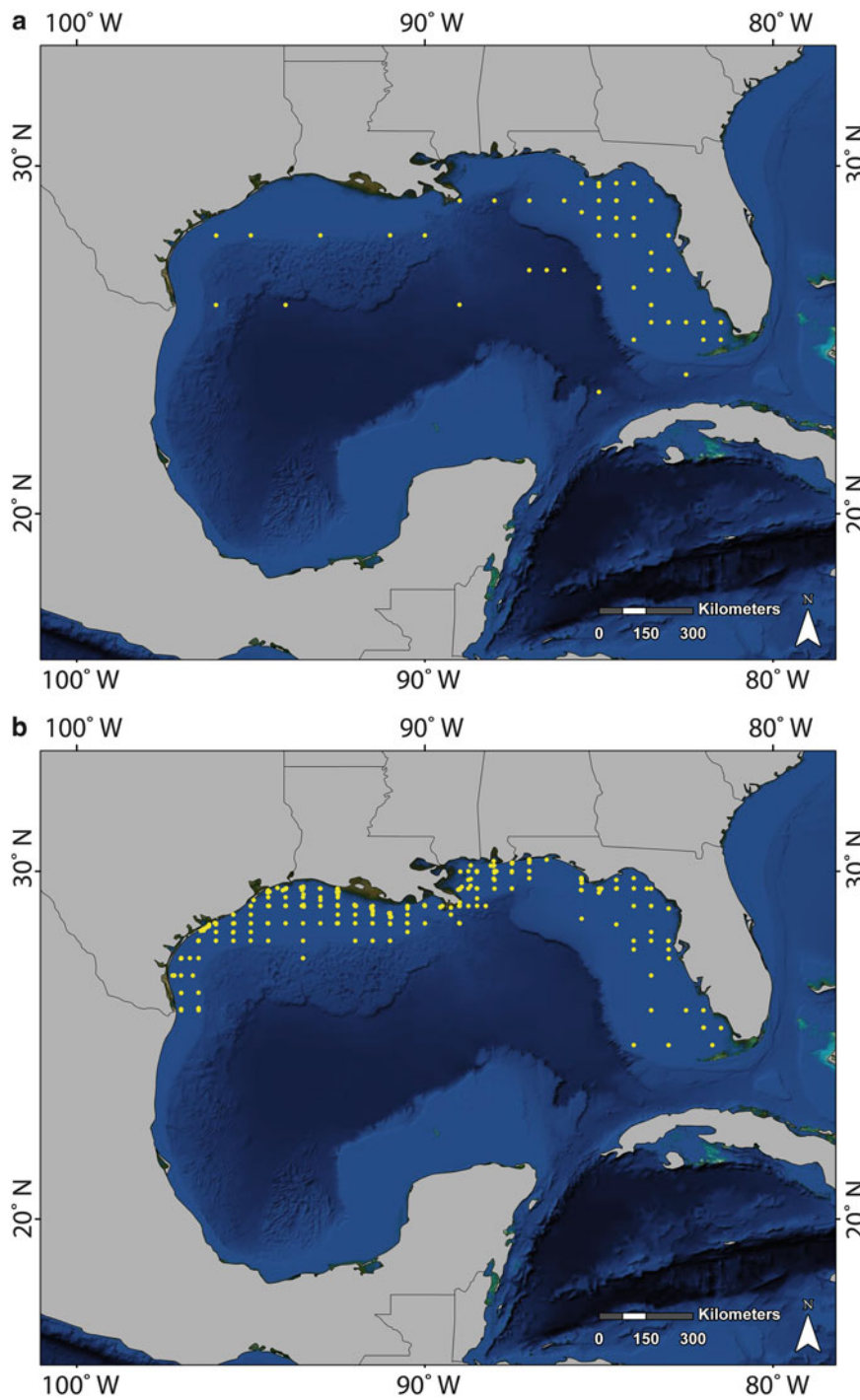
Figure 7.35. Distribution of drums and croakers (Sciaenidae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
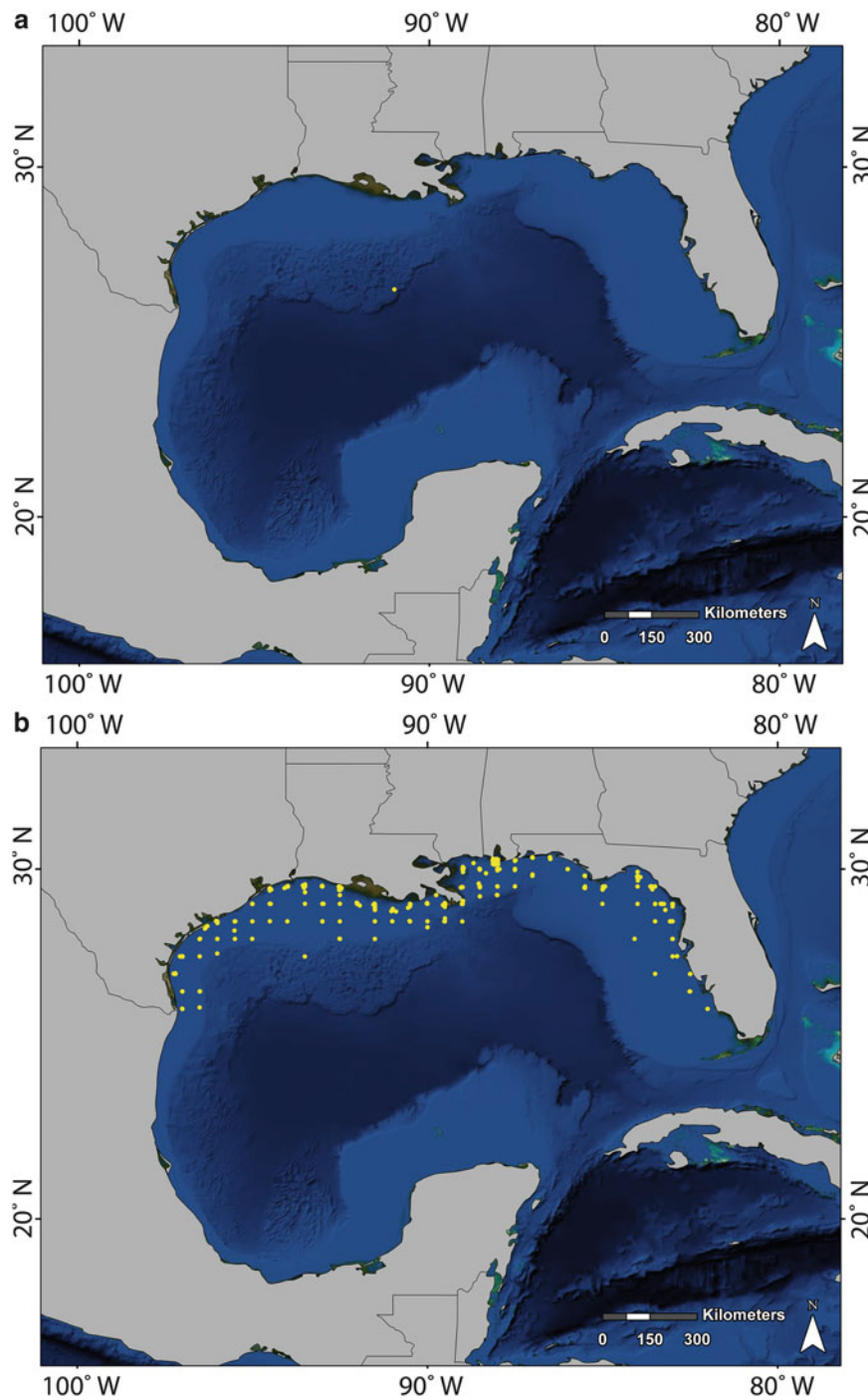
Figure 7.36. Distribution of redfish (*Sciaenops ocellatus*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
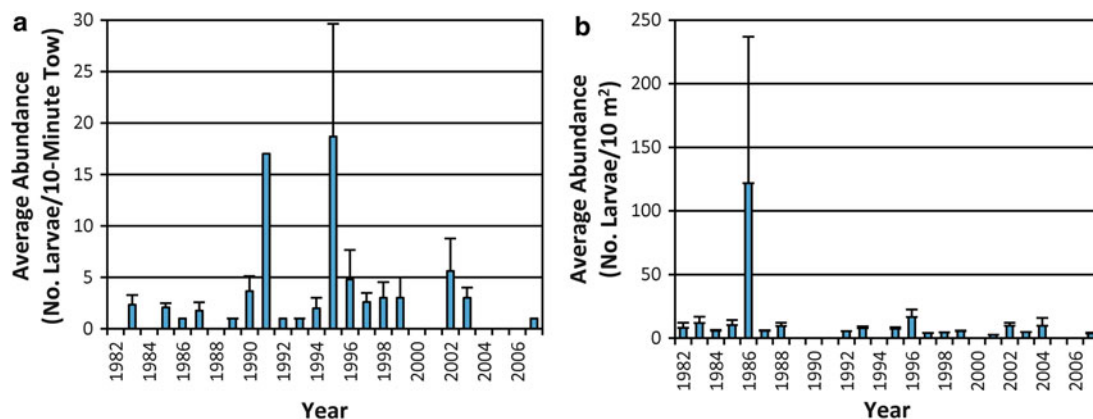
Figure 7.37. Average abundance of drums and croakers (Sciaenidae) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
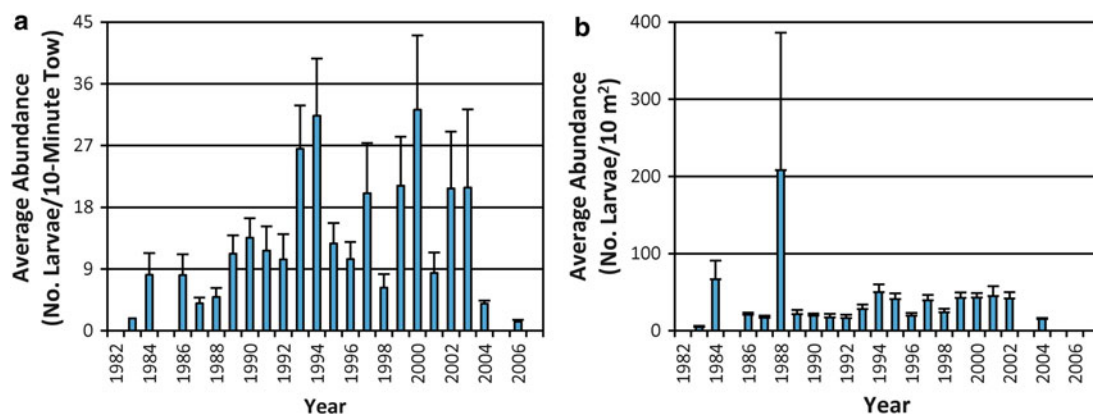

Figure 7.38. Average abundance of drums and croakers (Sciaenidae) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Family Scombridae

Mackerels, tunas (with the exception of *Thunnus*, discussed in the section below), and bonitos are important recreational and commercial fish species. For example, king mackerel (*Scomberomorus cavalla*) and Spanish mackerel (*Scomberomorus maculatus*), which are abundant and highly migratory, are coastal members of the Scombridae family and support large commercial and recreational fisheries (De Vries et al. 1990). This group includes 13 taxa; the majority of larvae for this group consisted of skipjack tuna (*Katsuwonus pelamis*) and tuna (*Auxis*) in the spring in the open Gulf of Mexico and little tunny (*Euthynnus alletteratus*) in the fall along the continental shelf (Table 7.2). Mackerel, tuna, and bonito larvae were typically taken in the fall and in bongo net samples of the water column (Table 7.1). Skipjack tuna were distributed throughout the open Gulf of Mexico during the spring. During the fall, they occurred in locations along the near edge of the continental shelf (Figure 7.39). Little tunny were found at some locations during spring plankton surveys; however, they were densely distributed throughout the entire continental shelf during the fall (Figure 7.40).
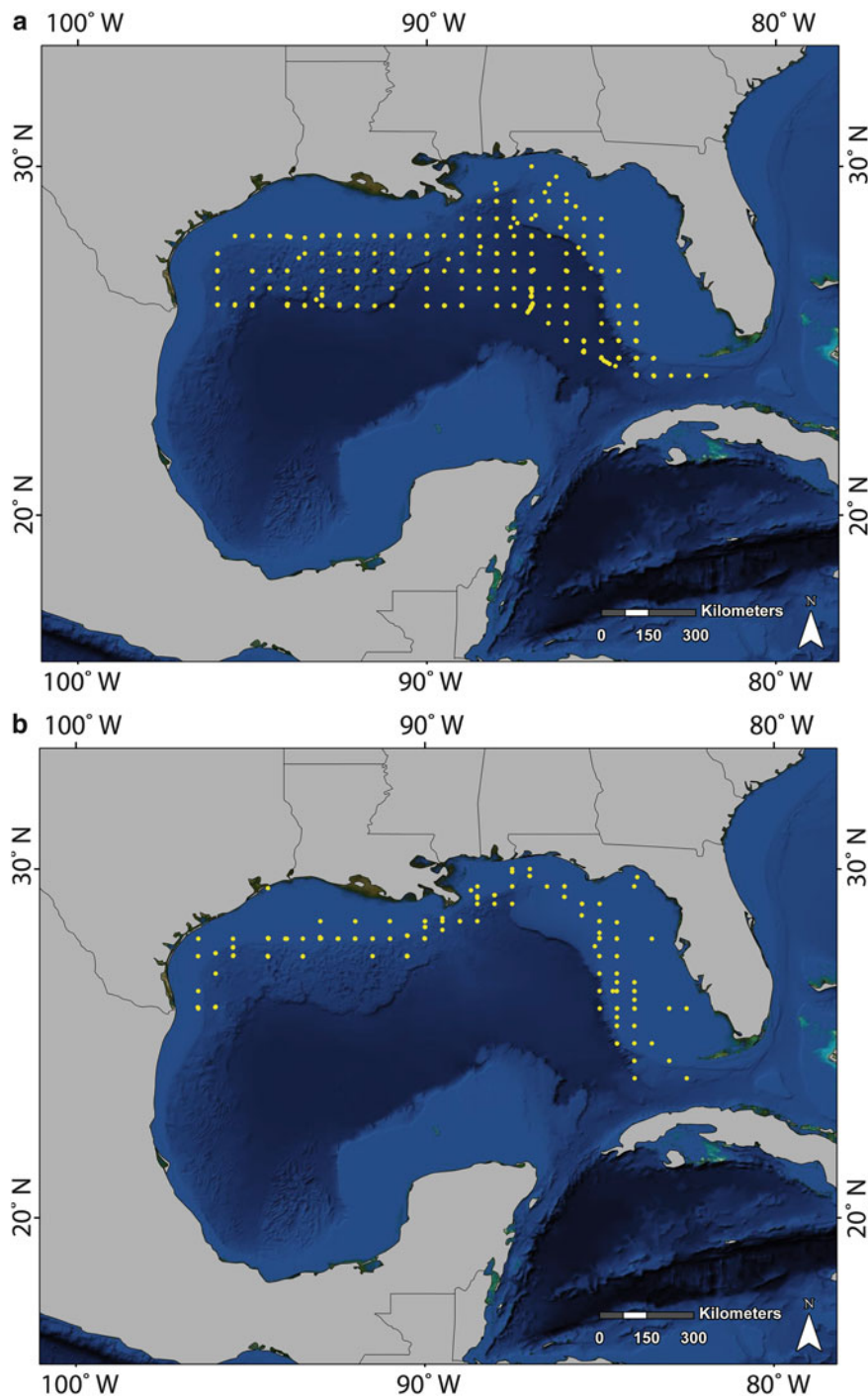
Figure 7.39. Distribution of skipjack tuna (*Katsuwonus pelamis*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
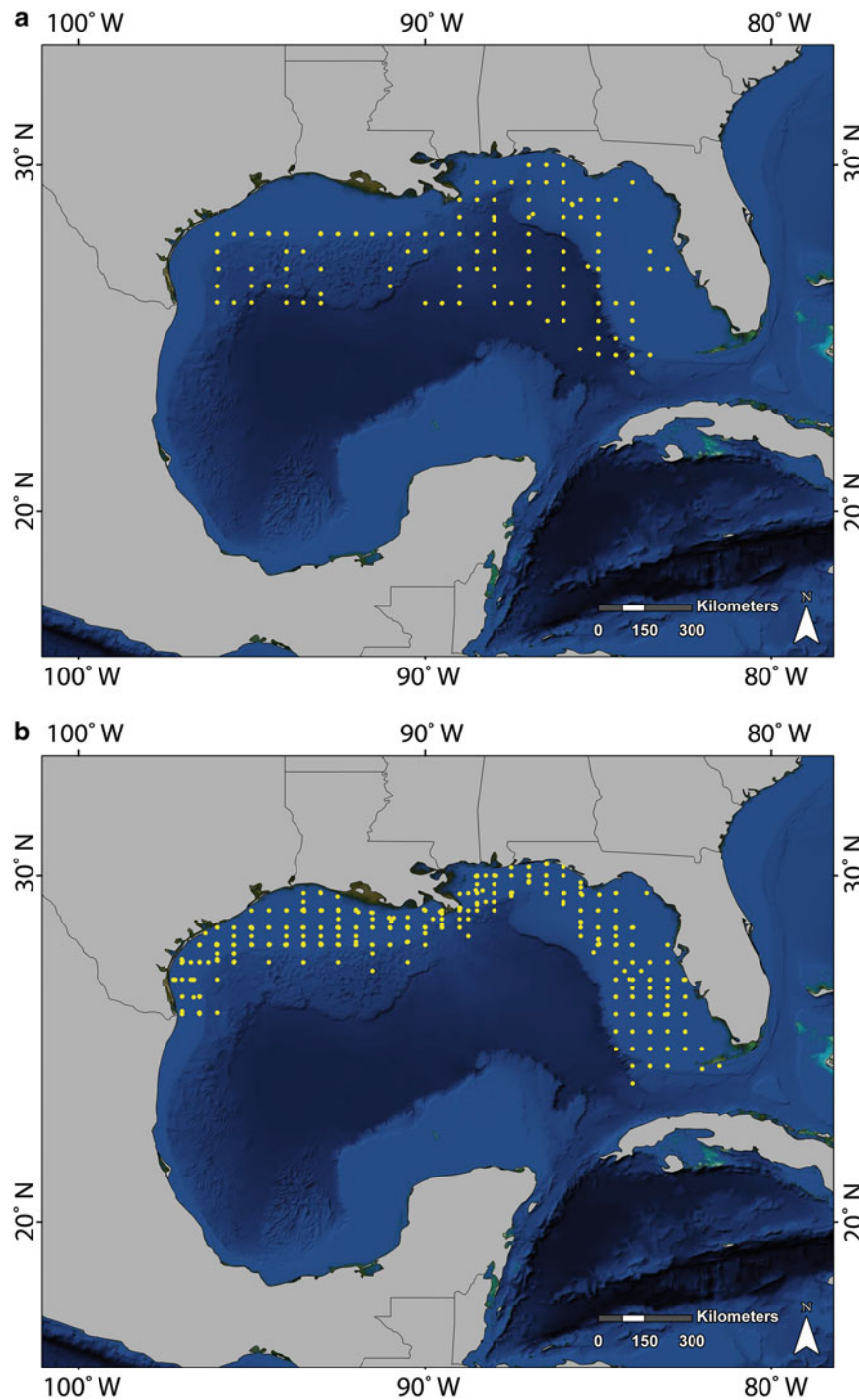
Figure 7.40. Distribution of little tunny (*Euthynnus alletteratus*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
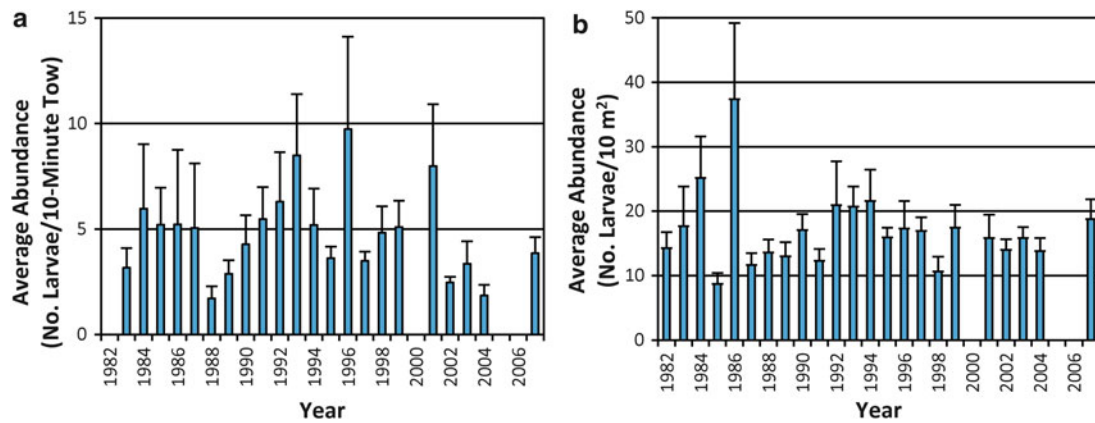
Figure 7.41. Average abundance of Scombridae for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
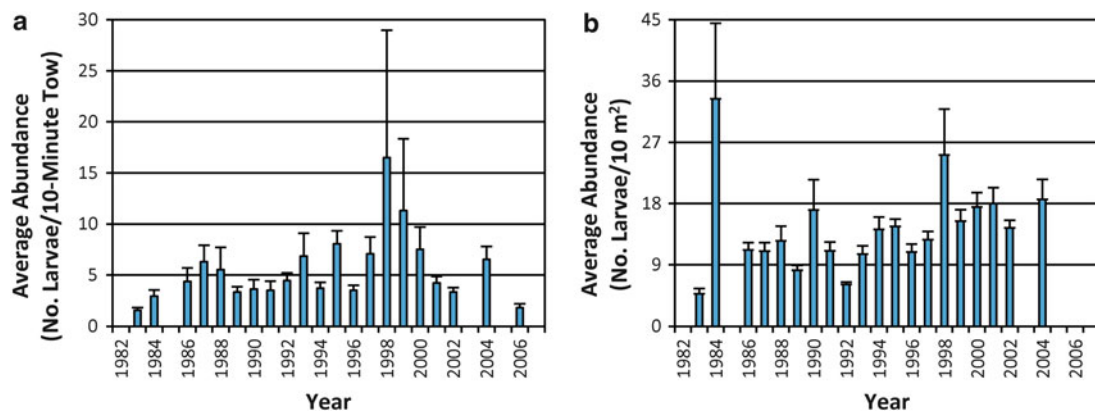

Figure 7.42. Average abundance of Scombridae for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Average scombrid larval abundances were highly variable from year to year during the spring and fall (Figures 7.41 and 7.42) for both gear types from 1982 through 2007. The average abundance of Scombridae larvae collected by neuston net during the spring ranged from 1.7 (1988) to 9.7 (1996) per 10-min tow, and the average abundance of scombrids collected by bongo net ranged from 8.7 (1985) to 37.4 (1986) larvae per 10 m^2 (Figure 7.41). During the fall, scombrid average abundance along the continental shelf ranged from 0 (2003) to 16.5 (1998) larvae per 10-min tow for neuston net samples, while bongo net samples ranged from 4.7 (1983) to 33.4 (1984) larvae per 10 m^2 (Figure 7.42). The mackerel, tuna, and bonito larvae average abundances were within a similar range during the spring in the open Gulf and during the fall along the continental shelf for both gear types (Figures 7.41 and 7.42).

Genus Thunnus

Atlantic bluefin tuna are large, highly migratory and have been heavily overfished. They spawn in the pelagic Gulf of Mexico during the spring, typically April through June (Teo et al. 2007; Muhling et al. 2010). Adult bluefin tuna have the broadest thermal niche of any of the Scombridae; they make fast, ocean basin-wide scale migrations ranging from cool subpolar foraging grounds to discrete breeding sites in subtropical waters during the spawning season (Teo et al. 2007).

Muhling et al. (2010) used a subset of SEAMAP data from 1982 through 2006 to develop a model of suitable Atlantic bluefin tuna larvae habitat in the northern Gulf of Mexico. The location and size of favorable habitat was highly variable among years. Habitats within the LC, warm-core rings, and cooler waters on the continental shelf were less favorable.

Yellowfin tuna are common in the Gulf of Mexico in pelagic waters and support one of the most valuable commercial fisheries in the Gulf of Mexico (Lang et al. 1994). Lang et al. (1994) determined that significant spawning of yellowfin tuna most likely occurred in the northern Gulf of Mexico in the vicinity of the Mississippi River discharge plume, when 801 larvae were collected during July and September 1987, and enhanced yellowfin tuna larval growth and survival occurred in the plume frontal waters.

Identification of tuna larvae of the genus *Thunnus* is very difficult (Richards et al. 1990), and because of this most of the larvae for this group were identified only to genus (Table 7.2). Tuna larvae were typically found in the spring in the open Gulf and usually at the surface in the neuston net samples (Table 7.1). They occurred throughout the open Gulf of Mexico during the spring. During the fall, they were typically found at locations near the edge of the continental shelf (Figure 7.43).

From 1982 through 2007, average abundances of tuna larvae were highly variable from year to year during spring and fall for both gear types (Figures 7.44 and 7.45). For neuston net samples, the annual abundances of larval tuna averaged fewer than 8 larvae per 10-min tow in the spring in the open Gulf, with the exception of 1985. During the fall along the continental shelf, average abundance ranged from 0 (2003 and 2006) to 16.6 (1987) larvae per 10-min tow (Figures 7.44 and 7.45). For both spring and fall plankton surveys, annual abundances of larval tuna for bongo net samples were within a similar range and typically averaged fewer than 25 larvae per 10 m^2 (Figures 7.44 and 7.45).

Family Serranidae

Twenty-eight taxa are included in this group of seabasses and groupers, with the majority of larvae identified to the seabass family (Table 7.2). Adult grouper are a commercially and recreationally important species that are highly susceptible to overfishing, largely due to their spawning behavior and slow growth (Marancik et al. 2012).

While fairly similar numbers of seabasses and groupers were captured during the spring in the open Gulf of Mexico and during the fall along the continental shelf, most larvae were collected from the water column using bongo nets (Table 7.1). In addition, seabasses and groupers were distributed throughout the open Gulf as well as the continental shelf during spring and fall plankton surveys from 1982 through 2007 (Figure 7.46).

With few exceptions (1987 and 1988 during the spring and 1986, 1990, and 1993 during the fall), annual abundances for larval serranids averaged fewer than 6 per 10-min tow for spring and fall neuston net samples from 1982 through 2007 (Figures 7.47 and 7.48). Average serranid larval abundance for bongo net samples ranged from 9.4 (2007) to 49.4 (1994) per 10 m^2 and from 7.1 (1983) to 32.4 (1984) per 10 m^2 during spring and fall plankton surveys, respectively
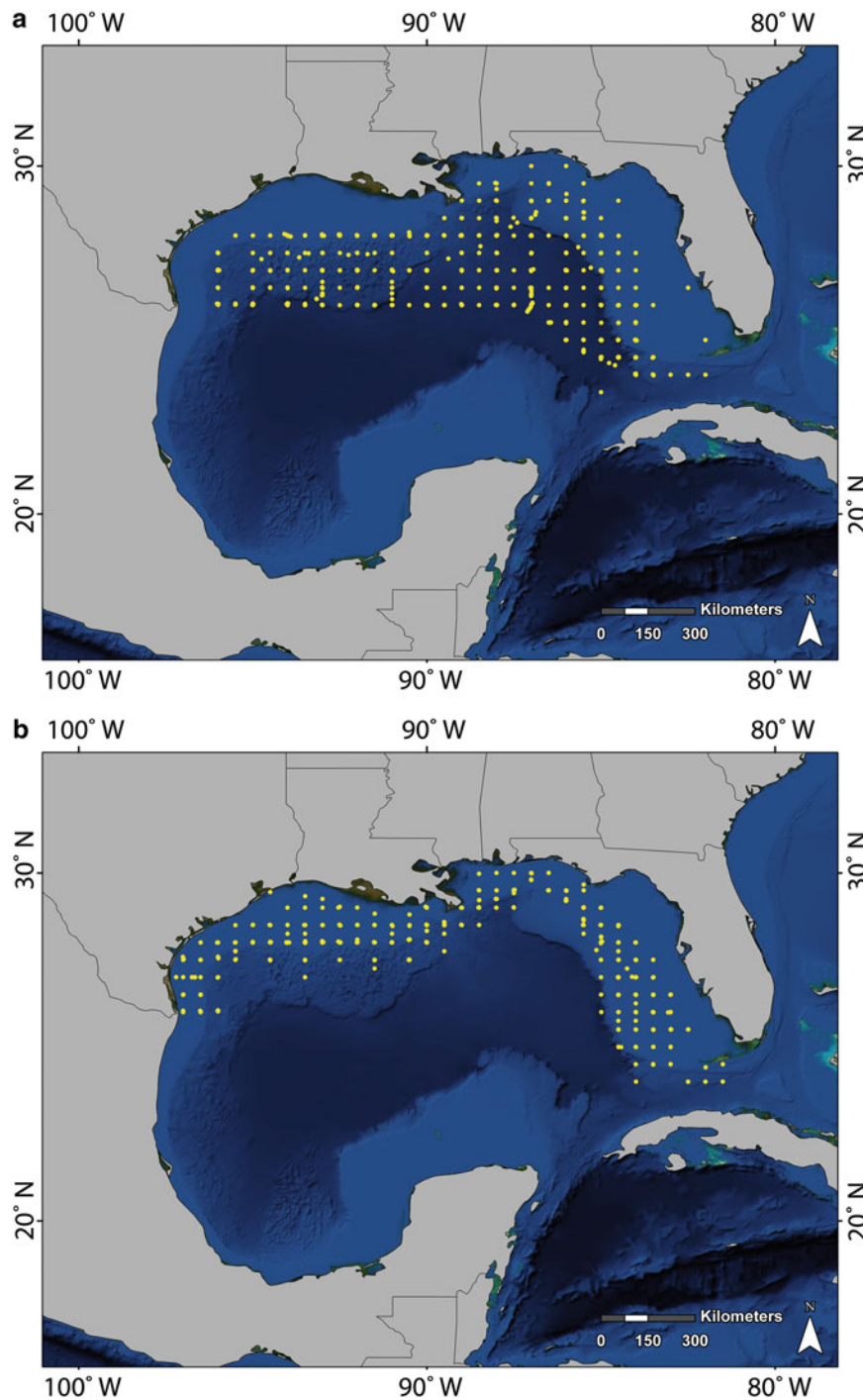
Figure 7.43. Distribution of tuna (*Thunnus*) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.
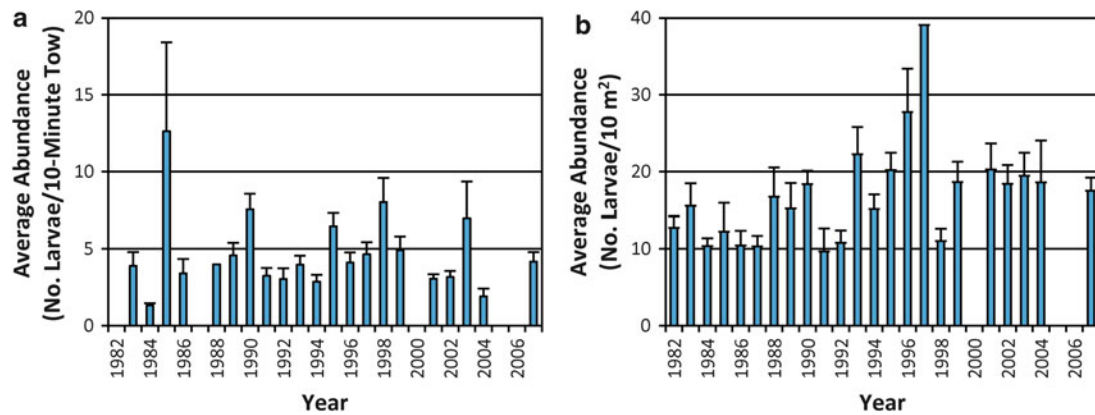
Figure 7.44. Average abundance of tuna (*Thunnus*) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
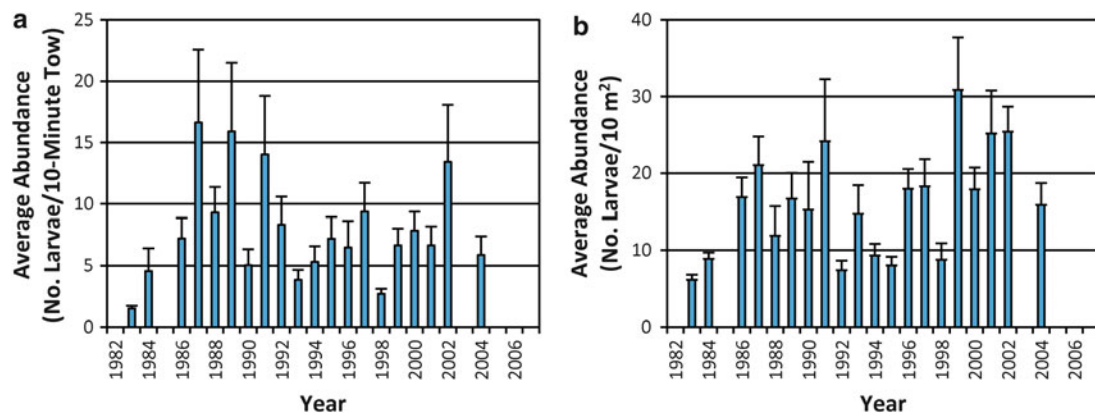
Figure 7.45. Average abundance of tuna (*Thunnus*) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

(Figures 7.47 and 7.48). For both spring and fall, the average abundance of seabasses and groupers was higher for bongo net samples than it was for neuston net samples.

Family Xiphiidae

Swordfish (*Xiphias gladius*) is the only species of the Xiphiidae family. This billfish is highly migratory and large, and while overfished, it has high value as a commercial and recreational species; as a top predator, swordfish play an important role in marine ecosystems (Rooker et al. 2012).

Swordfish larvae made up a very small percentage of the total ichthyoplankton catch; most were captured during the spring in the open Gulf at the water surface in neuston nets (Table 7.1). From 1982 through 2007, low numbers of swordfish larvae were collected by neuston net during the spring in the open Gulf, with average abundances ranging from 0 to 2.1 larvae per 10-min tow (Figure 7.49). Swordfish larvae were distributed sparsely throughout the open Gulf of
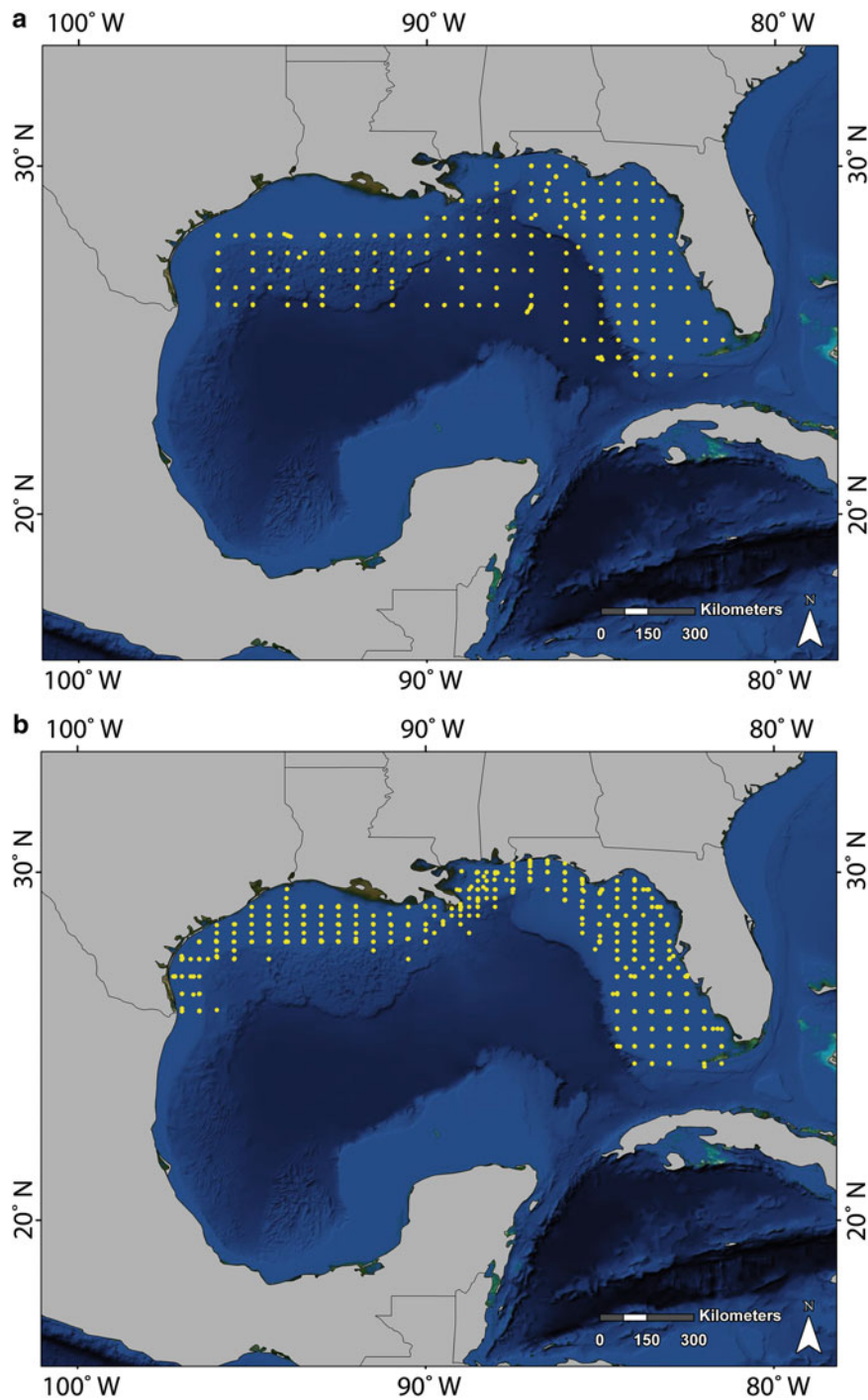
**Figure 7.46. Distribution of seabasses and groupers (Serranidae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.**
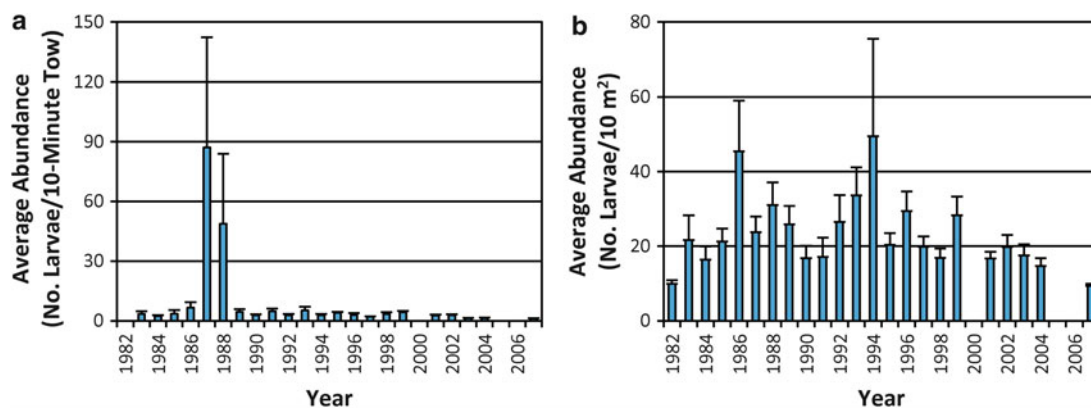
Figure 7.47. Average abundance of seabasses and groupers (Serranidae) for neuston net (a) and bongo net (b) samples for the SEAMAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
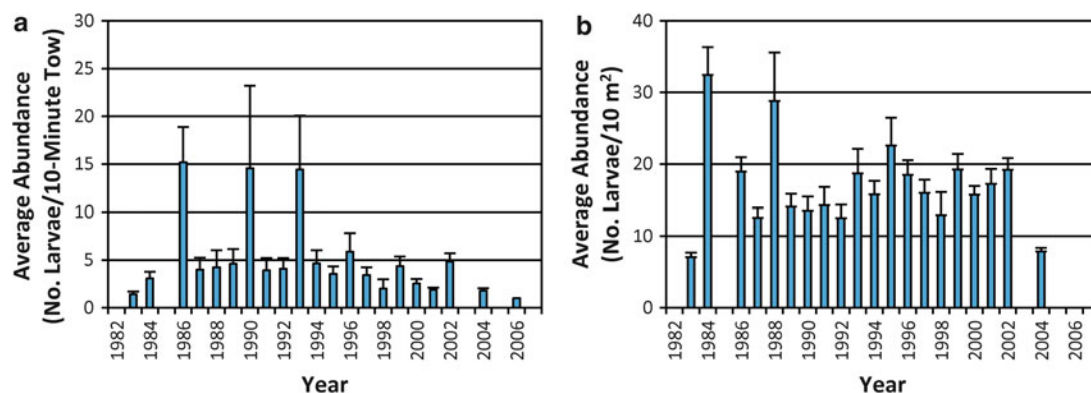
Figure 7.48. Average abundance of seabasses and groupers (Serranidae) for neuston net (a) and bongo net (b) samples for the SEAMAP fall plankton surveys from 1982 through 2007. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006. Error bars = standard error.

Mexico during the spring. In the fall, they were occasionally found near the edge of the continental shelf (Figure 7.50). Swordfish larvae were collected by bongo net during spring plankton surveys in 1982, 1983, 1989, 1991, 1992, 1995, 1996, and 2004, with average annual abundances ranging from 0 to 7.6 larvae per 10 m^2. The average abundance of swordfish larvae collected by neuston net during the fall in 1986, 1988, 1989, 1995, 1998, and 2001 was 1 larva per 10-min tow, while the average abundance in 2000 was 2.3 larvae per 10-min tow. From 1982 through 2007, swordfish larvae were collected by bongo net only in 2001, with an average abundance of 4.9 larvae per 10 m^2.

7.4.1.3.2   Summary of SEAMAP Ichthyoplankton Database Information

The large SEAMAP database is intended to be a robust resource for fisheries stock assessments that could contribute to the management of Gulf of Mexico fisheries. It allows comparison of the distribution of larval and juvenile stages of a wide range of species from different habitats as adults. Surface-living juveniles from the neuston nets can be contrasted

Figure 7.49. Average abundance of swordfish (Xiphiidae) for neuston net samples for the SEA-MAP spring plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Error bars = standard error.
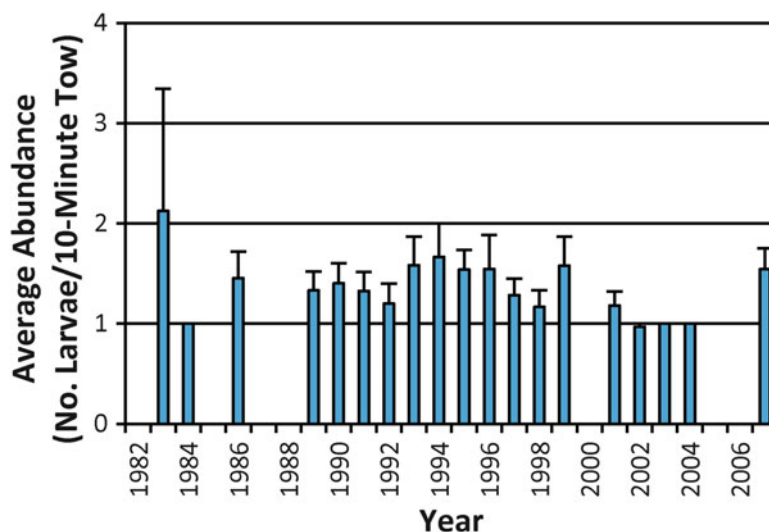
with those living throughout the water column caught with the bongo nets. Spawning season supposedly can be inferred from the season that a species appears in the ichthyoplankton. Yearly trends up or down can be inferred for each species and thus compared with variations in other species and with stock assessments of adults. However, the degree to which ichthyoplankton stock distributions are related to recruitment and adult stocks is a subject of considerable contentious debate (Haddon 2001).

The SEAMAP information does have problems. Determining trends in larval populations of the selected taxa from 1982 through 2007 is challenging because of the year-to-year variability in ichthyoplankton densities collected using both the neuston and bongo nets. In addition, comparing interannual variability is difficult because of the substantial differences in the temporal and spatial distribution of stations sampled each year under SEAMAP. The fall versus the spring sampling patterns are different for example, thus precluding seasonal comparisons. However, larval abundances appear to be stable or increasing for the majority of the selected taxa (e.g., Carangidae, Clupeidae, Coryphaenidae) that were summarized in the sections above. In addition, high densities of larvae occurred for many of the selected taxa (e.g., Carangidae, Clupeidae, Serranidae).

The SEAMAP sampling plan appears to have considered the entire EEZ as a monotypic habitat with little variation from place to place. That is, it is viewed as an LME. However, the habitats vary markedly over time and space, as reviewed in the initial section on habitat distributions. For example, what effect does the time-varying hypoxic zone off Louisiana have on ichthyoplankton distributions? How are ichthyoplankton partitioned between warm-core eddies and the cooler waters between them (Rooker et al. 2012)?

7.4.1.3.3 Baseline Ichthyoplankton Abundance and Distribution in Gulf of Mexico Regions

Various investigations have been conducted to determine the abundance and distribution of ichthyoplankton in specific regions of the Gulf of Mexico, and these are summarized below.
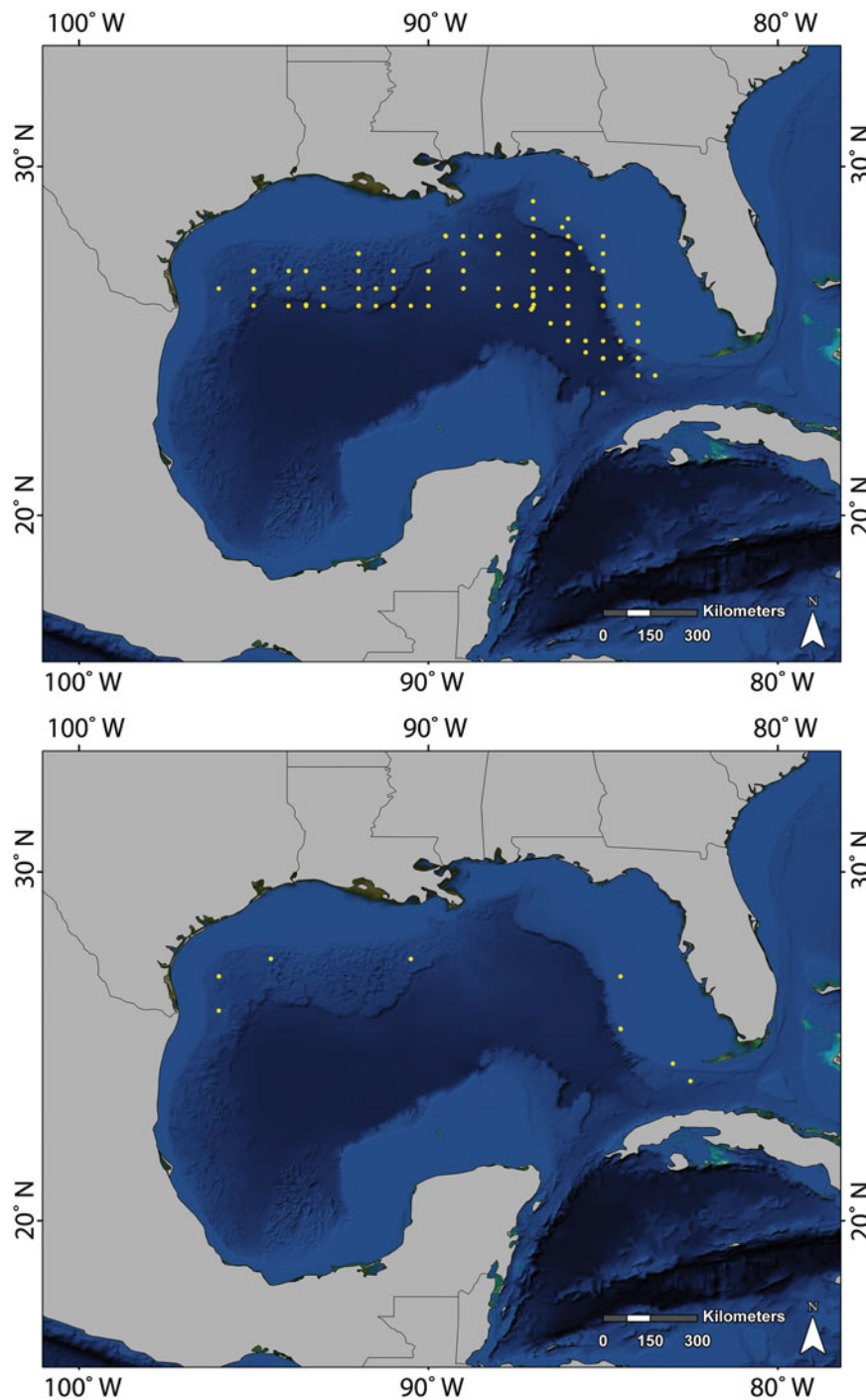
Figure 7.50. Distribution of swordfish (Xiphiidae) larvae during the SEAMAP spring (a) and fall (b) plankton surveys from 1982 through 2007. Spring plankton surveys were not conducted in 2000, 2005, or 2006, and only bongo net sampling was conducted during the spring plankton survey in 1982. Fall plankton surveys were not conducted in 1982, 1985, 2005, or 2007, and only neuston net sampling was conducted during fall plankton surveys in 2003 and 2006.

Northern Gulf of Mexico

The Gulf of Mexico continental shelf environment experiences seasonal changes in water temperature accompanied by discharges of low salinity, high nutrient water from rivers into the northern and eastern shelf areas. Using SEAMAP data, Muhling et al. (2012) characterized the spatial and temporal changes in abundances of larval fish assemblages on the northern Gulf of Mexico continental shelf from 1984 through 2008. Lanternfishes (Myctophidae) were the most common taxa collected and represented 14.65 % of the total collected ichthyoplankton, followed by codlets (Bregmacerotidae, 9.98 %) and gobies (Gobiidae, 9.29 %). Of the more than 500 taxa collected, the 20 most common fish families were evaluated. Larvae of some pelagic and mesopelagic families showed marked increases in abundance over the survey time period, while the abundances of some benthic fish families decreased (Muhling et al. 2012). Changes in fish assemblage structure were partially explained by changes in sea-surface temperature, as well as changes in the shrimp trawling effort. Interannual fish assemblage variability was also influenced by outflow from the Mississippi River. However, there was no explanation for spatial and temporal trends for many of the family groups (Muhling et al. 2012).

Carassou et al. (2012) investigated the spatial, seasonal, and depth-related structure of ichthyoplankton assemblages collected across a 77 km (47.8 mi) cross-shore gradient from March 2007 through December 2009 from highly productive estuarine waters to offshore oceanic waters on the Alabama shelf. A total of 350,766 larvae, in 17 orders and 70 families, were collected; the most common families were drums (Sciaenidae, approximately 42 % of total), followed by anchovies (Engraulidae, approximately 32 % of total). While the total density of fish larvae was significantly higher inshore, the number of families increased offshore. The total density of fish larvae also varied significantly among months, with the lowest values being observed in January and the highest in October and August. There were monthly variations in family richness, with minimum richness in December and maximum richness in May. Seven assemblages were associated with water masses characterized by distinct differences in temperature and salinity (Carassou et al. 2012). Families of larvae that were typically offshore included herrings, shads, sardines, and menhaden (Clupeidae); codlets (Bregmacerotidae); lizardfishes (Synodontidae); mackerels, tunas, and bonitos (Scombridae); and cusk-eels (Ophidiidae). Inshore families included anchovies (Engraulidae), gobies (Gobiidae), and clingfishes (Gobiesocidae). Larval fish assemblages varied seasonally and as a function of depth, but inshore and offshore assemblages remained clearly separated regardless of the season and depth considered; this strong and consistent structure was related to the combined effects of adult spawning behaviors and local oceanographic conditions, especially the influence of the Mobile River (Carassou et al. 2012).

Ichthyoplankton surveys were conducted in the northern Gulf of Mexico from 2006 through 2008 to determine the relative value of the region as early life habitat of sailfish (*Istiophorus platypterus*), blue marlin (*Makaira nigricans*), white marlin (*Kajikia albida*), and swordfish (*Xiphias gladius*) (Rooker et al. 2012). Sailfish were the dominant billfish collected in summer surveys, and larvae were present at 37.5 % of the stations sampled. Blue marlin and white marlin larvae were present at 25 % and 4.6 % of the stations sampled, respectively, and swordfish occurred at 17.2 % of the stations. Areas of peak production were detected and maximum density estimates for sailfish (22.09 larvae per 1,000 m^2) were significantly higher than the other species: blue marlin (9.62 larvae per 1,000 m^2), white marlin (5.44 larvae per 1000 m^2), and swordfish (4.67 larvae per 1,000 m^2) (Rooker et al. 2012). The distribution and abundance of billfish larvae varied spatially and temporally, and several environmental variables (sea-surface temperature, salinity, sea-surface height, distance to the LC, current velocity, water depth, and *Sargassum* biomass) were deemed to be influential variables. Densities of

billfish were typically higher in frontal zones or areas proximal to the LC. Habitat suitability was strongly linked to physicochemical attributes of the water masses they inhabited, and observed abundance was higher in slope waters with lower sea-surface temperature and higher salinity. The study suggests that the northern Gulf of Mexico is very important in the early life habitat of billfishes (Rooker et al. 2012).

Tidwell et al. (2007) confirmed that the northern Gulf of Mexico provides important nursery habitat for billfish larvae. Ichthyoplankton surveys were conducted with neuston nets in the summers of 2005 and 2006 to identify areas in the northern Gulf of Mexico with high larval billfish densities. The mean density of larvae per sample ranged from 0 to 53.8 larvae per 1,000 m^2. The highest densities of billfish larvae were located at the fronts of anticyclonic eddies. The catch of 2,589 billfish larvae from 167 stations provides powerful support that the northern Gulf of Mexico is a billfish nursery.

Monthly samples of ichthyoplankton were collected from October 2004 through October 2006 from a site off the coast of Alabama in the northern Gulf of Mexico, about 18 km (11.2 mi) south of Dauphin Island, Alabama (Hernandez et al. 2010). Mean concentrations of total fish larvae peaked in August because of very high abundances of Atlantic bumper (290.6 larvae per 100 m^3) and sand seatrout (*Cynoscion arenarius*, 301.1 larvae per 100 m^3), while taxonomic diversity was generally higher from March through October. Taxonomic richness was generally highest during the late summer and early fall. Of the 58 different families of fish collected, the dominant groups included anchovies (Engraulidae), sand seatrout, Atlantic bumper, Atlantic croaker, Gulf menhaden, tonguefishes (*Symphurus* spp.), gobies (Gobiidae), drums (Sciaenidae), and cusk-eels (Ophidiidae) (Hernandez et al. 2010). Nearly all of the Atlantic bumpers (87 %) were collected in August, while sand seatrout were present throughout the year. The Atlantic croaker was the third most abundant taxon, with an October peak in abundance of 119.5 larvae per 100 m^3 (Hernandez et al. 2010). It is important to note that the SEAMAP data are in units of number of larvae per 10 m^2 or per 10-min tow, whereas the Rooker et al. data are in numbers per 1,000 m^2 and the Hernandez et al. data are in numbers per 100 m^3.

SEAMAP spring and fall surveys from 1982 through 2005 were analyzed to provide information on location and timing of spawning, larval distribution patterns, and interannual occurrence for groupers (Marancik et al. 2012). Shelf-edge habitat was determined to be important for spawning of many species of grouper. Spawning for some species may occur year round, but two peak seasons were evident: late winter and late summer through early fall. A shift in species dominance over the last three decades from spring-spawned species (most of the commercial species) to fall-spawned species also was documented.

The more than 4,000 oil and gas platforms in the Gulf of Mexico likely affect ichthyoplankton populations (Boswell et al. 2010). Lindquist et al. (2005) collected baseline information on vertical and horizontal distribution patterns of larval and juvenile fish from five offshore platforms off the Louisiana Coast from 1995 through 2000. Light traps and passively fished plankton nets were used at night to collect fish in surface and deep waters (15–23 m [49.2–75.4 ft] in depth) within the platform structure. Light traps were also used to collect fish from surface waters directly down-current of the platforms. Compared to light traps fished in deep water, light traps fished at the surface collected higher densities and diversities of ichthyoplankton. Herrings, shads, and sardines; anchovies; lizardfishes; and presettlement blennies were the most common in surface waters within the platforms, while postflexion mackerels and tunas and settlement-size blennies, damselfishes, and clownfishes were most common in surface waters down-current of the platforms. Deep plankton nets collected higher densities of non-herring/shad/sardine ichthyoplankton, while surface plankton nets collected higher numbers of taxa. The vertical distribution patterns described for dominant larval fish collected by plankton nets were generally consistent with those from other studies: herring/

shad/sardine, jack, drum, and mackerel/tuna larvae more abundant in surface waters at platforms and lizardfish, codlet, goby, and left-eye flounder larvae more abundant in deeper waters (Lindquist et al. 2005).

Ditty et al. (2004) reviewed SEAMAP data from bongo net samples collected from 1982 through 1986 to describe the distribution of carangid larvae in the northern Gulf of Mexico relative to areas of high zooplankton. Of the 29,000 larvae from 13 species or species complexes in 11 genera, Atlantic bumper and round scad accounted for 91.7 % of all larvae, which agrees with the summaries above. Atlantic bumper densities averaged 2.9, 20.5, and 42.8 larvae per 100 m^3 for the eastern, central, and western Gulf of Mexico, respectively, while densities of round scad averaged 6.7, 0.4, and 0.1 larvae per 100 m^3, respectively, for the same regions. Carangids, including Atlantic bumper and round scad, appeared to spawn at water mass boundaries (fronts) and/or along other hydrographic features that promote higher productivity (Ditty et al. 2004).

The seasonal occurrence, distribution, and abundance of dolphinfish larvae were determined primarily from 814 neuston net collections taken during SEAMAP ichthyoplankton surveys of the Gulf of Mexico between 1982 and 1984 (Ditty et al. 2004). Larval dolphinfish were collected during all months sampled, but small larvae and pompano dolphin were found primarily during warm months. Larvae of common dolphinfish were significantly more abundant than pompano dolphin. Larval dolphinfish of both species were widely distributed in neritic and oceanic waters and most were collected near the surface. Over 90 % of common dolphinfish and about 80 % of pompano dolphin occurred over the outer continental shelf and in oceanic waters; overall densities averaged 4.8 and 0.8 larvae per 10 neuston tows, respectively.

The distribution, abundance, and seasonality of four carangids (blue runner, Atlantic bumpers, round scad, and rough scad, *Trachurus lathami*) off the Louisiana coast were evaluated using SEAMAP data from 1982 and 1983 (Shaw and Drullinger 1990b). Maximum abundances of larval blue runner, Atlantic bumper, and round scad were found in July inside the 40 m (131.2 ft) isobath. Larval Atlantic bumpers were captured in June and July only; blue runner in May, June, and July; and round scad in all seasons. Atlantic bumper larvae, concentrated mostly off western Louisiana, were by far the most abundant carangid in 1982 and 1983. Larval blue runner was the second most abundant summer-spawned carangid in 1982 and 1983; however, their abundance and depth distribution varied considerably between years (Shaw and Drullinger 1990b). The relative abundance of larval round scad off Louisiana was low, and they were captured only west of the Mississippi Delta. Rough scad were winter/spring and outer-shelf spawners; while they ranked third in overall abundance, they were the most abundant carangid on the outer shelf (Shaw and Drullinger 1990b).

Shaw and Drullinger (1990a) evaluated the distribution, abundance, and seasonality of four coastal pelagic species from the Clupeidae family—round herring, scaled sardine, Atlantic thread herring, and Spanish sardine—in the northern Gulf of Mexico using SEAMAP data from 1982 to 1983. During the summer, larval Atlantic thread herring and scaled and Spanish sardines were abundant on the inner shelf (less than 40 m or 131.2 ft) but were rare or absent in deeper waters. Scaled sardine and thread herring were found in all sampled inner-shelf water locations, but Spanish sardines were rare in the north-central Gulf (Shaw and Drullinger 1990a). During 1982, larval Atlantic thread herring were the most abundant of the four clupeids, while Spanish sardines were the most abundant during 1983. On the West Florida shelf, Spanish sardines dominated larval clupeid populations both years. Scaled sardine larvae were the least abundant of the four species both years; however, they were still captured in 20 % of the inner-shelf bongo net collections. Round herring larvae were collected from February through early June and were abundant on the outer shelf, especially off Louisiana. Over the 2-year period,

outer-shelf mean abundance for round herring was 40.2 larvae per 10 m^2, while inner-shelf mean abundance for scaled sardine, Atlantic thread herring, and Spanish sardine were 14.9, 39.2, and 41.9 larvae per 10 m^2, respectively (Shaw and Drullinger 1990a).

Ichthyoplankton cruises were conducted in continental shelf waters off west Louisiana from December 1981 through April 1982 to determine the distribution and abundance of larval drums and croakers (Cowan and Shaw 1988). The total sciaenid larval density was highest in April, and the high densities were associated with the coastal boundary layer, a horizontal density front caused by an intrusion of freshwater from the Atchafalaya River east of the study area. Sand seatrout larvae were the most abundant, followed by Atlantic croaker, spot (*Leiostomus xanthurus*), black drum (*Pogonias cromis*), southern kingfish (*Menticirrhus americanus*), and banded drum (*Larimus fasciatus*). Spawning by sand seatrout began in January. Both sand seatrout and Atlantic croaker larvae were captured at higher rates at night than during the day (Cowan and Shaw 1988). Sand seatrout larvae appeared to be somewhat surface oriented, while spot may undergo a vertical migration.

Sogard et al. (1987) collected ichthyoplankton at three inshore–offshore transects off Southwest Pass, Louisiana, Cape Sand Blas, Florida, and Galveston, Texas, from 1979 through 1981 to determine densities of larval Gulf menhaden, Atlantic croaker, and spot in the northern Gulf of Mexico. All species were more abundant at inshore than offshore stations. Gulf menhaden and Atlantic croaker were most abundant off Southwest Pass, Louisiana, a major outlet of the Mississippi River. Of the three species, only the Gulf menhaden demonstrated any consistent vertical distribution pattern. At inshore stations Gulf menhaden were concentrated near the surface at midday, while offshore and present at 70 m (229.7 ft), most were also caught near the surface (Sogard et al. 1987).

Southern Gulf of Mexico

Espinosa-Fuentes and Flores-Coto (2004) investigated the horizontal and vertical variation of ichthyoplankton assemblages in continental shelf waters of the southern Gulf of Mexico during each season in 1994 and 1995. A total of 21,814 ichthyoplankton, consisting of 25 families, 89 genera, and 92 species, was collected. Four assemblages were identified—coastal, inner neritic, outer neritic, and oceanic. Important members of the coastal assemblage in areas of the highest salinity fluctuations and in depths less than 30 m (98.4 ft) included estuarine-dependent species such as Atlantic bumper, sand weakfish, kingfishes (*Menticirrhus* spp.), croakers (*Micropogonias* spp.), and American stardrum (*Stellifer lanceolatus*). Abundant ichthyoplankton in the oceanic assemblage at depths of 50 and 100 m (164 and 328 ft) in areas with the least salinity fluctuations included pelagic species such as antenna cod (*Bregmaceros atlanticus*), lanternfishes (*Myctophum* spp.), pearly lanternfish (*Myctophum nitidulum*), large-finned lanternfish (*Hygophum macrochir*), and smallfin lanternfish (*Benthosema suborbital*) (Espinosa-Fuentes and Flores-Coto 2004). The main taxa in the inner neritic assemblage were hump-backed butterfish (*Selene setapinnis*), bigeye scad (*Selar crumenophthalmus*), shoal flounder (*Syacium gunteri*), eyed flounder (*Bothus ocellatus*), striped codlet (*Bregmaceros cantori*), and largehead hairtail (*Trichiurus lepturus*). The frequent and abundant species in the outer neritic assemblage of the outer-shelf stations and mid-depths were lanternfishes (*Diaphus* spp.), bristlemouths (*Cyclothone* spp.), fairy basslets (*Anthias* spp.), tunas (*Thunnus* spp.), bigeye scad, blue runner, rough scad (*Trachurus lathami*), bullet tuna (*Auxis rochei*), and striped codlet (Espinosa-Fuentes and Flores-Coto 2004).

Sanvicente-Añorve et al. (2000) evaluated the scales of the main physical and biological processes influencing the ichthyoplankton distribution in the southern Gulf of Mexico. These included the Bay of Campeche (spring 1983, winter 1984, and summer 1987), the littoral zone

adjacent to Terminos Lagoon (bimonthly between July 1986 and May 1987), and the Carmen Inlet between the lagoon and the sea (monthly between April 1980 through January 1981). The main circulation patterns of the southern Gulf of Mexico, continental water discharges, mixing processes, and oceanic gyres were important processes affecting ichthyoplankton distribution patterns and community structure in the Bay of Campeche, and 81 families of ichthyoplankton, which included oceanic, neritic, and estuarine-dependent species, were collected (Sanvicente-Añorve et al. 2000). The neritic zone of the Bay of Campeche contained the highest densities of ichthyoplankton; highest densities (1,000–3,000 individuals per m^3) were found near the Grijalva-Usumacinta River delta in the summer, and the lowest densities (fewer than 300 larvae per m^3) were found in the winter. Distinct ichthyoplankton assemblages were identified and included a coastal assemblage characterized by Atlantic bumper (*Chloroscombrus chrysurus*, 5.4–209 larvae per m^3), Atlantic thread herring (*Opisthonema oglinum*, 152 larvae per m^3), sand weakfish (*Cynoscion arenarius*, 10.8–24 larvae per m^3), Atlantic croaker (2.1–4.8 larvae per m^3), and hogchoker (*Trinectes maculatus*, 3.9 larvae per m^3); a neritic assemblage characterized by tonguefishes (Cynoglossidae, 2.1–6.7 larvae per m^3), codlets (Bregmacerotidae, 5.8–63.6 larvae per m^3), and left-eye flounders (Bothidae, 0.5–7.8 larvae per m^3); and an oceanic assemblage dominated by lanternfishes (Myctophidae, 0.3–3.3 larvae per m^3) and bristlemouths (Gonostomatidae, 0.1–2.3 larvae per m^3). Twenty-three families of ichthyoplankton were collected from the littoral zone adjacent to Terminos Lagoon. Littoral currents, lagoon influence, spatial salinity variability, and meteorological conditions determined the structure and function of ichthyoplankton groups (Sanvicente-Añorve et al. 2000). In the littoral zone, a high abundance of ichthyoplankton occurred from May to September, followed by a strong decrease in January and March. While they changed in size, two groups occurred throughout the year; one group, which consisted of anchovies (46–197.6 larvae per m^3) and gobies (8.5–371.5 larvae per m^3), was typically located in the area adjacent to the Carmen Inlet. The second group, located near the Puerto Real inlet, was characterized by Atlantic thread herrings (49.4–56.4 larvae per m^3), Atlantic bumpers (44 larvae per m^3), and scaled sardines, 39.9 larvae per m^3), which dominated in May, July, and September. In the Carmen Inlet between the lagoon and the sea, 38 families of ichthyoplankton were collected. Tidal- and wind-induced currents, bottom topography, and salinity gradients were the major forces controlling ichthyoplankton distribution (Sanvicente-Añorve et al. 2000). In the inlet, greatest densities of ichthyoplankton were found in the central-western section and the deepest eastern channel, and strong vertical stratification was observed; 99 % of the total catch consisted of anchovies, gobies, herrings/ shads/sardines, drums, and mojarras. Distinctive ichthyoplankton patterns were produced by the combination of the physical, biological, and oceanographic processes and the life history strategies of the fishes—the periods and spawning areas of the adults, larval stages, dispersal capabilities of larvae, and the larval stage duration (Sanvicente-Añorve et al. 2000).

7.4.1.4 Neuston and *Sargassum* spp.

The neuston are drifting organisms that inhabit the surface layer of the ocean (note above that the ichthyoplankton was sampled within this layer with a net designed to float at the surface); likewise numerous ichthyoplankton can be found in this narrow habitat. While a wide variety of organisms are encountered within this layer in general (Dooley 1972; Turner et al. 1979), the prolific assemblage is associated with the pelagic *Sargassum* algal mats (Parr 1939). These occur in the Gulf of Mexico in windrows measuring hundreds of meters long by tens of meters wide. The long, linear windrows are formed by Langmuir circulation.

In the North Atlantic and Gulf of Mexico, free-floating mats of *Sargassum*—pelagic brown algae—supplies a dynamic infrastructure for diverse assemblages of fishes, invertebrates,

sea turtles, seabirds, and marine mammals (Casazza and Ross 2008). To date, a number of studies have documented ichthyofaunal assemblages associated with *Sargassum* in these waters, most notably those of two holopelagic species: *S. fluitans* and *S. natans* (Adams 1960; Parin 1970; Zaitsev 1971; Dooley 1972; Bortone et al. 1977; Fedoryako 1980, 1989; Gorelova and Fedoryako 1986; Settle 1993; Hoffmayer et al. 2002; Wells and Rooker 2004a, b; Casazza and Ross 2008). Pelagic *Sargassum* is ubiquitous throughout the surface waters of the northern Gulf of Mexico and waters adjacent to the southeastern coastal waters of the United States. (Hoffmayer et al. 2002; Wells and Rooker 2004a, b; Casazza and Ross 2008). In general, the pelagic zone of these waters is featureless apart from free-floating *Sargassum* mats, production platforms, flotsam, buoys, and fish aggregation devices (Wells and Rooker 2004a, b). Previous studies report that *Sargassum* mats function as an essential fish habitat (EFH), affording food sources and protection from predators to juvenile and adult fishes in what is otherwise a nutrient-poor, structure-free environment (Wells and Rooker 2004a, b; Rooker et al. 2006).

Conservation interests for commercially valuable fish species have encouraged efforts to gain a better scientific understanding of nursery habitats used by these and other species at early life stages (Wells and Rooker 2004a, b). Identification and understanding of *Sargassum* community structure as an EFH is necessary in building healthy and sustainable fisheries supported by effective management strategies (Wells and Rooker 2004b). The physical nature of the various forms of *Sargassum* habitat (e.g., individual clumps, small patches, large rafts, and weed lines) makes sampling these habitats extremely difficult and potentially inconsistent (Casazza and Ross 2008). Satellite observations suggest that the Gulf of Mexico is the source of windrows of *Sargassum* in the central north Atlantic (Gower and King 2011).

Wells and Rooker (2004b) examined the spatial and temporal patterns of habitat use and evaluated the role of *Sargassum* as nursery habitat for fishes in the northwestern Gulf of Mexico. Inshore and offshore comparisons were made; inshore waters were sampled from northern (Galveston) and southern (Port Aransas) Texas from May to August 2000 and offshore waters (15–70 nautical miles) off Galveston and Port Aransas, Texas. Replicate samples (3–5) were collected monthly from May to August 2000 in each zone. *Sargassum* mats were arbitrarily chosen during a period from 08:00 to 15:00 h using a larval purse seine (20 m [65.6 ft] long, 3.3 m [10.8 ft] deep, 1,000 μm mesh). Purse seines were used as the only collection material and deployed as the boat encircled a chosen mat. Once around the mat, the net was pursed. A total of 10,518 individuals representing 36 fish species from 17 families were collected using the purse seine method only. All taxa listed in the study were included in this review since all were identified to a species level. Dominant taxa included filefishes (Monacanthidae, 4,621), jacks (Carangidae, 1,827), triggerfishes (Balistidae, 1,604), pipefishes (Syngnathidae, 1,096) and frogfishes (Antennariidae, 368), which accounted for 43.9 %, 17.4 %, 15.3 %, 10.4 % and 3.5 % of the total capture, respectively. Hoffmayer et al. (2002) on the other hand sampled a total of 18,749 fishes representing 86 species in 138 collections with combined methods of neuston nets of two sizes and paired bongo nets. However, for the purposes of this study only 10,283 were considered due to a lack of family and species identification for much of the sampling; 19 taxa identification extended only to a family level. Surface tows with a neuston net supplied the greatest abundance and diversity of species collected (9,865 fishes; 79 species identified to species level). Oblique tow with paired bongo nets yielded far less abundance and diversity (418 fishes, 36 species identified to species level). Catches were dominated by flyingfishes (Exocoetidae, 3,876) and jacks (Carangidae, 1,521) and accounted for 37.7 % and 14.8 % of the total capture, respectively.

Species and individual counts were used to determine diversity and evenness of collections for each method and study. Species richness (*S*) was highest in the Casazza and Ross (2008) (76 species) and Hoffmayer et al. (2002) (86 species) studies. Higher fish diversity (*H'*) was

observed for methods of neuston net, nightlighting, bongo nets, and purse seine. Values of evenness (J') for species collections were noticeably greater for neuston net, nightlighting, bongo nets, and purse seine methods. When studies were compared, species diversity and evenness of distribution was higher in Hoffmayer et al.'s (2002) investigation; however, the number of individuals was lower (8,968) than those of the other studies.

The mean biomass, according to Robert Webster (Texas A&M University, personal communication), is about 140 mg dw/m^2 in the Gulf of Mexico. However, this can be extremely variable. Parr (1939) estimated values of 258 g dw/m^2, standard deviation = 174, for example, in the Gulf of Mexico. The gross and net productivity are higher in neritic waters than offshore due, it is presumed, to increased levels of inorganic nutrients (Lapoint 1995). Lapoint (1995) estimated doubling time at 20 days, although Robert Webster believes it could be as short as 10 days. This would equate to about 7 mg/m^2/day or 2.5 mg dw/m^2/year. About 40 % of the dry weight is carbon, meaning the contribution of *Sargassum* to total phytoplankton PP is rather small. Although *Sargassum* windrows are considered critical habitat because they serve as a refuge for fish larvae and juveniles, as indicated abundantly in the ichthyoplankton section above (Wells and Rooker 2004a, b), when it washes ashore, it becomes a nuisance. Using satellite images of windrow movements, Webster estimates that it takes about 60 days to move across the continental shelf onto the beaches of Texas.

Data for fish assemblages associated with *Sargassum* suggest the important natural function of *Sargassum* as an EFH. Samples of fishes taken in the north-central (Hoffmayer et al. 2002) and northwestern (Wells and Rooker 2004b) Gulf of Mexico showed similarities in species diversity and abundance. A small number of taxa dominate most of the collections. These include filefishes (Monacanthidae), jacks (Carangidae), triggerfishes (Balistidae), pipefishes (Syngnathidae), and frogfishes (Antennariidae), which accounted for 52.5 % (Hoffmayer et al. 2002), 87 % (Wells and Rooker 2004b), and 94 % (Casazza and Ross 2008). Similarly, these families represent a large proportion of the total catch in studies conducted in the western Atlantic (Dooley 1972) and eastern Gulf of Mexico (Bortone et al. 1977).

Fishes at larval and juvenile stages were predominately present across all three studies and all capture methods except hook-and-line (Wells and Rooker 2004b). The relationships between the quantity of *Sargassum* and species richness and abundance and biomass of fishes can be highly variable. Dooley (1972) and Fedoryako (1980) found no correlation between numbers of fishes and quantity of *Sargassum*, but significant positive correlations between fish abundances and quantity of algae have been catalogued in other studies (Moser et al. 1998; Wells and Rooker 2004b). The sampling methods chosen by the investigator may substantially influence these results. *Sargassum* habitat is a dynamic and difficult habitat to sample, and the structural complexity of this habitat strongly affects fish assemblages (Dooley 1972).

7.5 MESOPELAGIC (MID-WATER) FISHES AND PELAGIC MEGAFAUNAL INVERTEBRATES (MICRONEKTON OR MACROPLANKTON)

Mesopelagic (mid-water) fishes are relatively small species such as the Gonostomatidae and Myctophidae (lanternfish) that vertically migrate daily from depths somewhat less than 1,000 m (3,281 ft) up to the surface waters at night. They are sampled with an Isaacs-Kidd mid-water trawl, which is difficult to quantify, or a Tucker trawl (Hopkins et al. 1973), used as sets of opening and closing nets that sample vertical stratification. Mean weight of mid-water fishes in the Gulf of Mexico is about 16 g (0.04 pounds [lb]) wet weight (ww) per individual (Bangma and Haedrich 2008). Most mid-water fishes prey on net-sized zooplankton (Hopkins and Baird 1977; Hopkins et al. 1996), but are eaten by all sizes of large pelagic species (Sutton

and Hopkins 1996). Beaked whales for example feed down to depths of 1 km (0.62 mi) preying on squid and mid-water fishes.

The Gulf of Mexico has been considered a distinct geographic region (Backus et al. 1977) on the basis of the lanternfish species distributions in the Sargasso Sea and the Caribbean. Out of about 209 species known to occur in the western Sargasso and Caribbean Sea complex (Gartner et al. 1988; Sutton and Hopkins 1996), approximately 140 have been sampled in the Gulf of Mexico. Bangma and Haedrich (2008) have suggested that the Gulf mid-water fishes be considered an *ecotone* or transition between the subtropical Atlantic and tropical faunas because the Gulf of Mexico has a mixture of species from both the north Atlantic and Caribbean. In any case, the mid-water fish play a significant role in the transfer of mass and energy up the food web to larger open-ocean pelagic species (Hopkins and Baird 1977; Hopkins et al. 1996). The deep Gulf of Mexico between about 1,500 m (4,921 ft) and 3,700 m (12,139 ft) is very poorly sampled to date. A biomass of 4.5 mg ww/m^3 (standard deviation $=$ 1.9) between the 1,500 and 3,700 m (4,921 and 12,139 ft) depth can be estimated based on the work of Sutton et al. (2008) in the central Atlantic. This would be the equivalent of about 12 g ww/m^2 between 1.4 and 3.7 km (0.87 and 2.3 mi) in depth.

Much of our knowledge of deep macroplankton or micronekton is not quantitative in terms of numbers or biomass per volume. However, extensive information is available on the number of species (Gamma diversity) of the Gulf of Mexico and adjacent Caribbean. This is due to the exploratory fishing of the NMFS (now within NOAA) (Springer and Bullis 1956; Bullis and Thompson 1965). Summaries of catches of oplophorid shrimps (Decapoda: Caridea: Oplophoridae) by Pequegnat and Wicksten (2006) illustrate the wide geographic and depth distributions of this diverse group caught in mid-water trawls and bottom-trawled nets. Of the 25 species they reviewed, 21 were sampled in the water column.

Mesopelagic micronekton standing stocks (Hopkins and Lancraft 1984; Sutton and Hopkins 1996) and composition (Hopkins et al. 1989) assessments are available for the eastern Gulf of Mexico (Figure 7.51). The latter authors have constructed an energy budget for a typical mid-water fish species that defines their importance in consuming upper water column
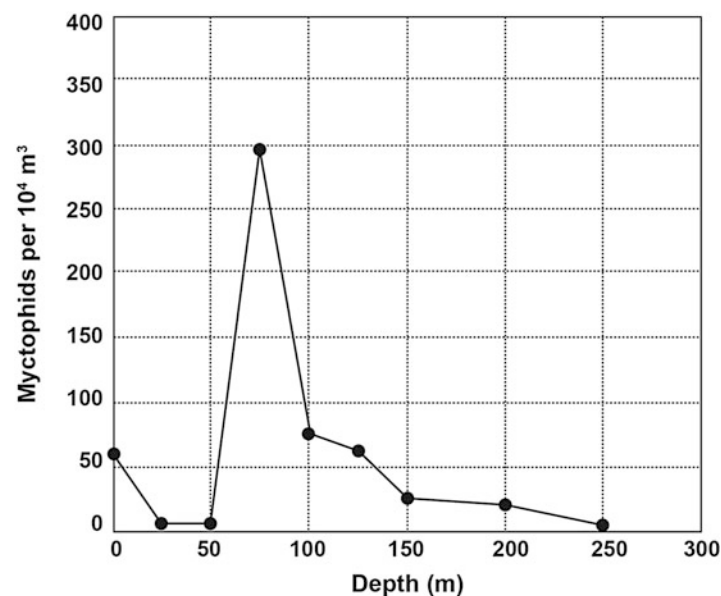

Figure 7.51. Vertical distribution of the numbers of mesopelagic myctophid fishes in the eastern Gulf of Mexico (modified from Hopkins 1982).

zooplankton, principally copepod crustaceans. They then estimate the potential production of these populations as potential prey for large terminal predators, such as billfish and beaked whales.

7.6 SEAFLOOR COMMUNITIES: THE BENTHOS

Level-bottom soft sediment (sand-, silt- and clay-sized particles) communities are composed of a wide range of size classes that are sampled by different methods. The sizes are also based on how they are sampled: the smaller the organism, the smaller the sampler (Table 7.3).

Each of these size groups will be considered separately, and a synthesis will be attempted that draws them together in a comparison and ultimately into a proposed food web. Three characteristics of biotic assemblages will be described, if adequate data are available:

1. **Densities** per unit area (or sediment volume), and associated **biomass** per unit area.
2. **Biodiversity** (a) within habitat diversity indices (Alpha diversity), (b) between habitats or species turnover or change along a gradient (Beta diversity or species turnover in space), and (c) species richness (Gamma diversity or total number of species samples).
3. **Species** composition in recurrent faunal groups or **zonation** as a function of depth (or some correlate with depth).

7.6.1 Continental Shelf Benthos

Numerous studies have been made of the biota and associated supporting habitat variables of the Gulf of Mexico. They encompass the entire Gulf periphery (Figure 7.52) (Rabalais et al. 1999b). Those studies on the northern coast (e.g., in U.S. waters) were funded by U.S. federal government agencies in anticipation of expanded offshore oil and gas exploration and production (BLM, MMS, and BOEM). Each study contains significant information that can be used to assess ecosystem processes that can be compared to each other and to other continental shelves. The databases were generated in order to establish baselines from which

Table 7.3. Level-Bottom Seafloor Assemblage Size Groupings

| Size Class	Size	Sampling Device	References
Microbiota	<1 μm (bacteria and *Archaea*), and protists up to 40 μm	1–3 cm diameter subcorer	Deming and Carpenter (2008)
Meiofauna	>40 but <500 μm	3–6 cm diameter subcorer	Baguley et al. (2008)
Macrofauna	From 250 up to 500 μm, depending on location	GOMEX corer Spade corer Ekman grab Smith-McIntyre grab	Boland and Rowe (1991), Escobar-Briones et al. (2008a, b), Harper (1977), and multiple studies (see text)
Megafauna	>1 cm	Trawls, photos Skimmer, traps	Pequegnat et al. (1970) and Pequegnat (1983)
Demersal fishes	Trawl caught, 2.5 cm stretch mesh	Trawls, photos, skimmer, longline	Pequegnat et al. (1990)

cm centimeter, *μm* micrometer
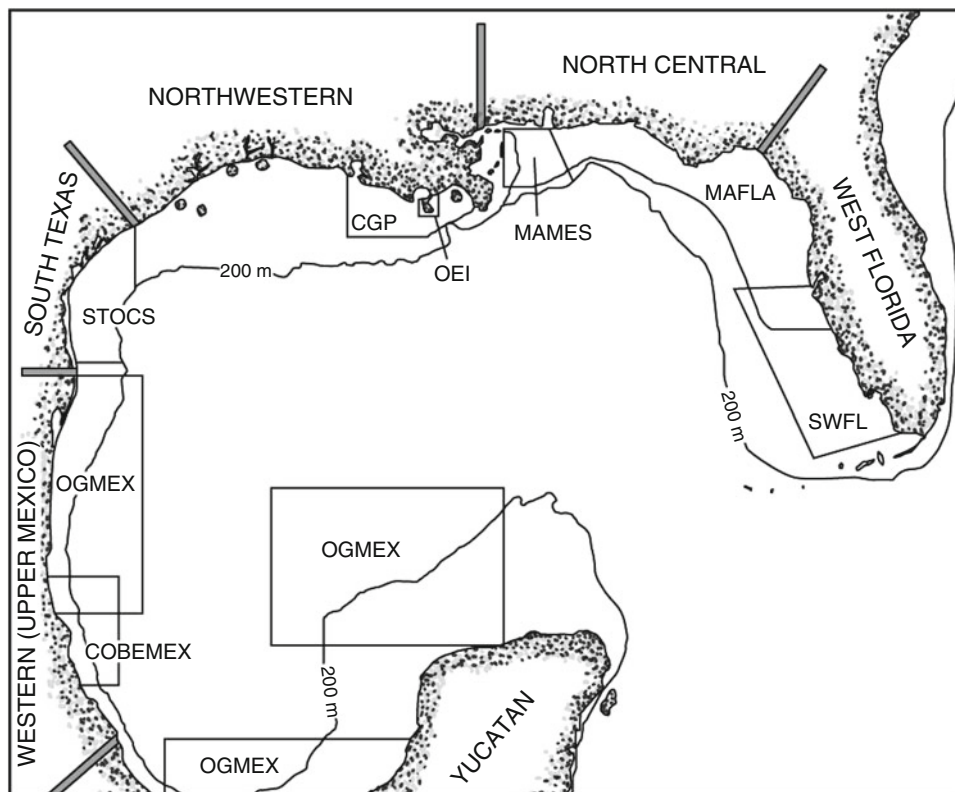
Figure 7.52. Regional studies of the continental shelf of the Gulf of Mexico (from Rabalais et al. 1999b).

damage or alterations could be assessed. In addition, extensive monitoring and associated experimental process measurements and numerical simulations have been made and are ongoing in the regional, seasonal hypoxic region that stretches west from the central Mississippi Delta to the border with Texas. NOAA (including Sea Grant), U.S. Geological Survey (USGS), U.S. Environmental Protection Agency (USEPA), and state agencies have supported the hypoxic area investigations. Studies of the biota in Mexican waters have been sponsored by the Consejo Nacional de Ciencia y Technología or National Council of Science and Technology (CNCYT) (the equivalent to the U.S. National Science Foundation). This section will attempt to summarize and compare the most salient features of the areas studied.

The faunas of the northern shelf are considered Carolinian or temperate, whereas the faunas of the southern shelf are semitropical to tropical (Engle and Summers 2000). The south Texas/northern Mexico shelf is composed of terrigenous sand, silt, and clay; the central hypoxic area of the north is mainly fluvial mud (silt and clay, with some sand), and the eastern Florida coast is hard bottom carbonate. Where the eastern Gulf of Mexico bottom off Florida is not hard carbonate (see Figure 7.1), carbonate sands replace it. The broad shelf of the Yucatán Peninsula is carbonate, but the narrow shelf at the southern end of the Bay of Campeche is terrigenous mud (silt, clay, and sand) that debouches from rivers. The biogeographic provinces and the sediment type play a big role in determining faunal composition in each area.

Quantitative seafloor samples and trawls were taken on the soft (sand, silt, and clay) substrates in each of the regions depicted in Figure 7.52 and Table 7.4 to estimate animal densities and species composition of the meiofauna, macrofauna, epibenthic megafauna, and

Table 7.4. Comparison of Macroinfaunal Assemblages, Continental Shelf (Northern Gulf of Mexico) (sample sizes varied, replication varied, all used 0.5 mm sieves) (nearshore are on the inner continental shelf at depths less than 50 m; offshore are in depths of greater than 50 m on the outer shelf)

Location/Area	Nearshore Densities	Offshore Densities	Total No. of Species
STOCS[a]	2,707 (1,561)	229 (62)	837
MAFLA	5,268 (3,533)	575 (342)	1,691
Hypoxic area[b]	3,741 (3,349)		185
Buccaneer field[c]	5,850 (2,902–10,937)		352
Bryan mound[d]	1,109 (709)		
CTGLF[e]	Range of 6–12,576		576
SWFES[f]	Range of 3,245–15,821		414

Values are arithmetic means of individuals per m^2 followed by standard deviation in parentheses; the last column is the total number of species in each study
[a]Values from Flint (1980), not Flint and Rabalais (1981)
[b]Nunnally et al. (2013)
[c]Harper (1977)
[d]September 1977 control site only—Don Harper data archived at TAMUG
[e]Bedinger (1981) (several locations subject to hypoxic conditions)
[f]Danek et al. (1985), soft-bottom locations only

demersal fishes. This information is embodied in numerous reports, government documents, and peer-refereed papers, as summarized in Table 7.4 and in the review by Rabalais et al. (1999b). Sampling locations were organized along the coast in transects that bisected the shelf, from depths as shallow as 6 m (19.7 ft) out to the edge of the shelf at depths approaching 200 m (656 ft). Recurrent groups or assemblages were determined among these sites, and maps were then used to illustrate the groupings. The entire northern Gulf of Mexico coastline exhibited some common features: (1) highest densities of macrofauna were encountered at the inshore locations, (2) lowest densities were at the outer-shelf margin, (3) macrofaunas were dominated by diverse assemblages of polychaete annelid worms followed by amphipod crustaceans and bivalve molluscs in lesser numbers, and (4) principal faunal groups were aligned parallel to the coastline within depth intervals in a predictable fashion. About 20 % of the dominant macrobenthos are shared between the three northern Gulf study areas—South Texas Outer Continental Shelf (STOCS), Mississippi Alabama Marine Ecosystem Study (MAMES), and the Mississippi, Alabama, Florida (MAFLA) ecosystem studies—and Rabalais et al. (1999b) suggest that there is regional endemism within the macrofaunal component of the benthic communities. However, that degree of overlap in similar species is substantially higher than might be expected, given the differences in the habitats (Figure 7.1).

The STOCS investigation on the south Texas shelf, summarized in Flint and Rabalais (1981), was designed to gain a quantitative understanding of how the shelf ecosystem food web functions relative to supplies of inorganic plant nutrients, phytoplankton productivity, stocks of zooplankton, and fate on the sea floor. The data clearly demonstrate that meager nutrient supply (nitrate) supports relatively low PP because chlorophyll *a* concentrations were consistently below 1 mg C/m^3 all year, with the exception of single modest spikes during brief spring and fall blooms. A carbon budget was created to illustrate how an estimated 103 g C/m^2/year of new production (a high value given the low chlorophyll *a* values) is cycled through the food web to the economically important brown shrimp (*Farfantepenaeus aztecus*) population. Modest gradients of ammonium (NH_4) at the seafloor suggested that benthic-pelagic coupling
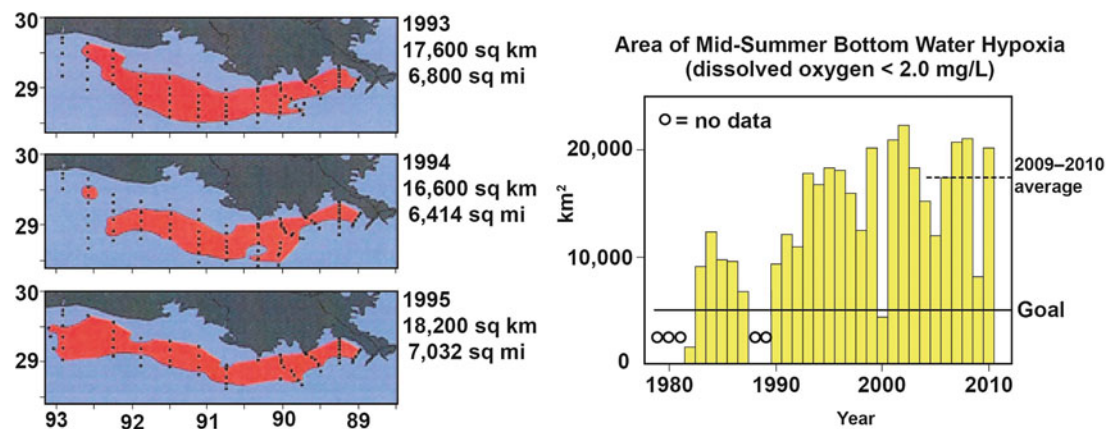
Figure 7.53. Area of continental shelf that habitually experiences seasonal hypoxia (*left*) (from Rabalais et al. 1999a); illustration of relative increase in size of hypoxic area over time (*right*) (from Rabalais and Turner (2011)); Goal refers to anticipated decrease in size if and when nitrate loading is reduced.

(regeneration by the sediment community) could be an important source of nitrogen to the water column. More recent advances in numerical modeling of food webs coupled to physical models should now be applied to this comprehensive set of shelf data.

The central and eastern Gulf of Mexico shelves are stark contrasts to the south Texas and Mexican shelves. The Louisiana shelf is bathed by freshwater from the Mississippi River and the Atchafalaya Bay diversion. This contributes high levels of inorganic nutrients (greater than 100 μmol/L nitrate concentration) that enhance PP. This is accompanied by freshwater that creates intense vertical stratification. This condition is seasonal, beginning in the late winter or early spring, and intensifying throughout the summer months of warming that contributes to the vertical stratification. The vertical stratification and surface water PP decline with water column mixing in the fall. The effect of this condition produces a large area (at times larger than approximately 20,000 km^2) of hypoxic (less than 2 mg O$_2$/L) bottom water that is stressful to most shelf biota (Figure 7.53). Motile swimmers escape; sessile organisms suffer. The region is often referred to in the public media as a *dead zone*. But this is a misnomer; it is not *dead*, although it supports a unique fauna (Gaston 1985; Rabalais et al. 2001; Baustian and Rabalais 2009; Baustian et al. 2009). The hypoxic fauna is dominated by polychaete (Rabalais et al. 2001) and nematode worms (Murrell and Fleeger 1989). A sulfur-oxidizing bacterium (*Beggiatoa* sp.) is often observed on the sediment surface under conditions approaching anoxia (Rowe et al. 2002). The diversity and abundance of the infauna is severely reduced by hypoxic conditions, and the longer hypoxic conditions persist without reoxygenation, the greater the decline in the surviving fauna (Baustian and Rabalais 2009). Recovery during the winter, when the bottom water is normoxic, is modest (Rabalais et al. 2001; Nunnally et al. 2013).

The causes, along with remedial strategies, are the subject of some debate. It has been advocated that agricultural runoff up the Mississippi River must decrease nitrogen loading from fertilizer in order to reduce the size and intensity of the hypoxia (Rabalais et al. 2002, 2007). Others question the overriding importance of fertilizer nitrogen as the cause. Dissolved organic matter (DOM) in the freshwater could contribute to the biological oxygen demand (Bianchi et al. 2010), and stratification prevents deepwater oxygenation (Rowe 2001). The plume of these discharges has been partitioned into zones in which different processes both cause and maintain hypoxia (Rowe and Chapman 2002). In the proximal zone near the river mouths (referred to as *brown*), the sediment loading prevents light penetration, and hypoxia is caused by enhanced

sedimentation. The next zone (*green*) represents the now-classic paradigm in which high levels of nitrate cause eutrophication. The final zone (*blue*) is characterized by relatively clear water with low nitrate concentrations and PP is low, but hypoxia is maintained by vertical stratification of the water column. If too much freshwater and/or DOM are primary causes of hypoxia, then reducing the nutrient load up the river will have only a minor effect on the condition.

Benthic infaunal abundance reflects the overall productivity of a coastal ecosystem. Thus, within the LME there is a substantial difference between the areas. The relatively productive northeast has twice the macrofauna as south Texas, whereas the hypoxic area lies in between. It must be noted however that the hypoxic fauna is composed of an assemblage that is adapted to low oxygen stress. It lacks the numerous species of crustaceans and mollusks common to the other two areas.

7.6.2 Corals and Live-Bottom Assemblages

Extensive areas in the Gulf of Mexico are dominated by coral growth and hard carbonate bottoms (Figure 7.1). The entire Campeche Bank off the north extension of the Yucatán Peninsula is composed of carbonate that has been formed since the Triassic–Jurassic eras. The fauna is semitropical to tropical (Tunnell et al. 2007). Hermatypic (reef-building) species are common and extensive. The most salient big reef is Alacran in the middle of the bank, more or less (Kornicker et al. 1959). Lists of species are available for many groups (Rice and Kornicker 1962; Gonzalez-Gandara and Arias-Gonzalez 2001). It is also important to artisanal fishers (Bello et al. 2005). The northern Gulf of Mexico also has patchy areas of hermatypic corals but these are encountered on the tops of salt diapirs on the outer continental shelf or upper continental slope, the most prominent being the Flower Garden Banks, which now have been designated a national marine sanctuary—FGBNMS (Figure 7.54). The many similar banks on the outer continental shelf west of the Mississippi River are plotted on the NOAA habitat map (Figure 7.1). The fauna of these banks has been studied extensively. They are important habitats for shelf fishes, and thus, recreational fishermen and amateur scuba divers frequently visit them on charter boats. Recreational hook-and-line fishing is allowed in the FGBNMS but spearfishing is not. The most extensive descriptions of the many banks on the outer shelf can be found in Rezak et al. (1985).

Rezak et al. (1985) portray many of the banks in a similar fashion. The biodiversity of the fishes, corals, and associated invertebrates in the northern Gulf of Mexico is less than the Caribbean or the southern Gulf of Mexico because these structures are at the northern boundary of the corals' ranges. All the corals release their eggs and sperm simultaneously in late summer. This synchronous spawning is observed at specific tidal and lunar conditions in many coral reefs worldwide. All coral reefs in shallow water are dependent on clear water because they contain symbiotic photosynthetic zooxanthellae. Thus, they are threatened by eutrophication that increases planktonic algal growth.

Note the layer of particle-rich water at the deep margin of the bank in Figure 7.54; this nepheloid layer is a ubiquitous feature on the shelf and upper slope of the northern Gulf of Mexico west of the central Mississippi Delta region. This is the same feature referred to above in the zooplankton section. Zooplankton grazing occurs in this near-bottom layer rather than at the surface.

Live-bottom assemblages occur on hard carbonate bottoms on the Campeche Bank, as mentioned above, but also in extensive areas of the carbonate platform off west Florida (Figure 7.1). A large fraction of the eastern continental shelf hard bottom is thus substantially different from the fauna of the northwestern Gulf of Mexico fauna living primarily on soft sediments. The boundary between the two habitat types is more or less the De Soto Canyon to the north and the Florida Keys archipelago to the south. The outer margin of the southern half
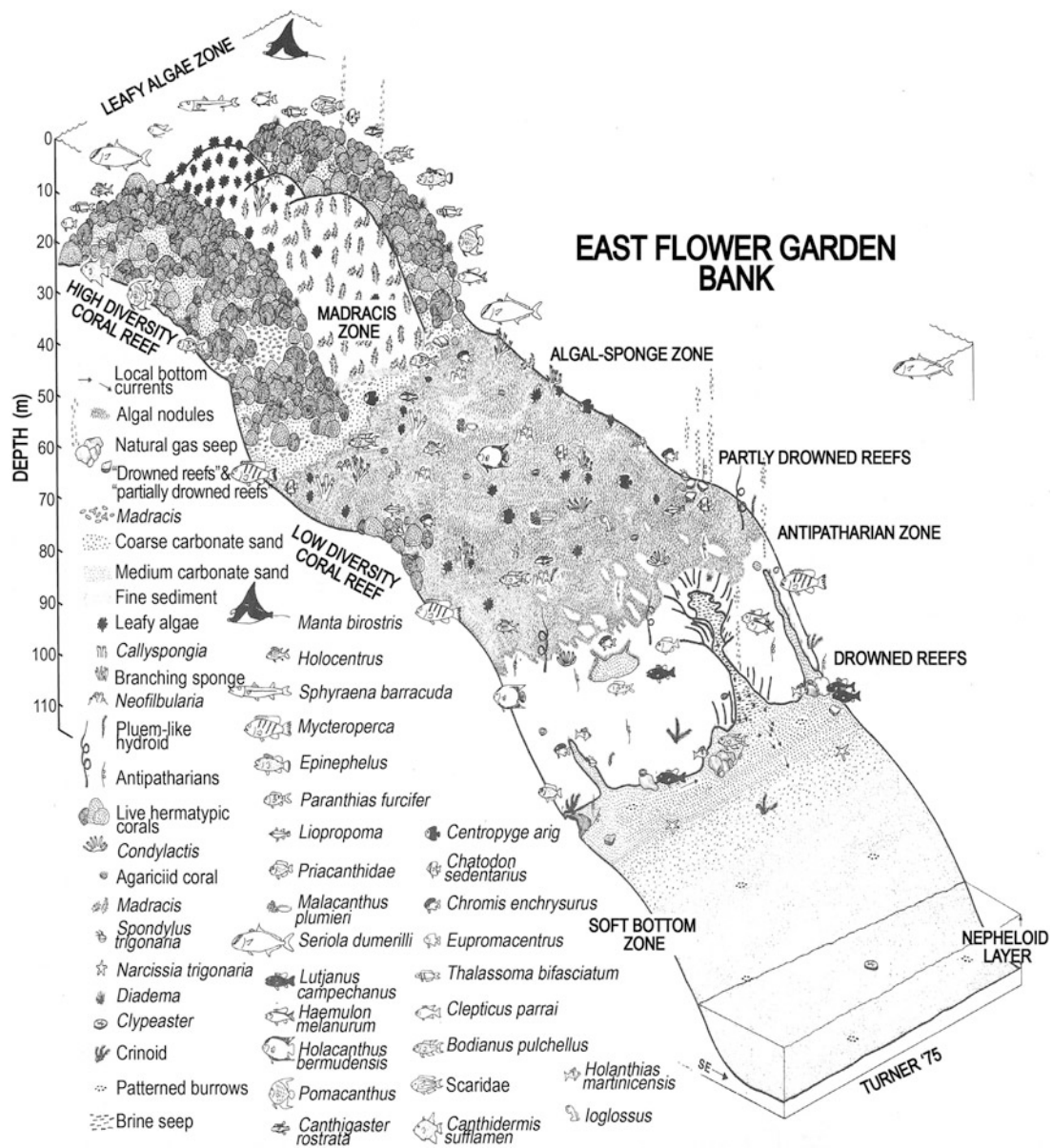
Figure 7.54. Diagram of faunal and floral zonation down the side of the East Flower Garden Bank coral reef on top of a salt diapir on the outer continental shelf off Texas. Note the salt pond and stream on the lower boundary and the bubbles appearing intermittently across the entire depth interval. Copied from Rezak et al. (1985) (republished with permission of John Wiley and Sons Inc.; permission conveyed through Copyright Clearance Center, Inc.) and based on Bright et al. (1984).

of these hard grounds is bathed by the loop current returning back south toward the Florida Straits (Figures 7.2 and 7.3). Sampling habitats sometimes referred to as *live bottoms* is far more difficult than soft bottoms of silt, clay, and sand. Scuba divers are often required to employ suction or pumping mechanisms (that sieve material through a mesh bag) or scrape off areas defined by a metal quadrat. Remotely operated vehicles (ROV) with still and video cameras have been used extensively for surveying hard bottoms. The foundation species that cover the bottom are sponges, attached algae, sea grasses such as *Zostera* and *Thalassia*,

anemones, and individual corals. Mixed among them are a diverse assemblage of polychaete worms, crustaceans, and echinoderms. The diversity of the small forms living in among the foundation species is high because of the physical variety of the available space. The principal areas on the shelf are the Alabama Pinnacles, the Florida Middle Grounds (FMG), and the smaller Madison-Swanson Banks (Figure 7.1).

The FMG evolved about 20,000 years ago when sea level was lower. The FMG is a succession of ancient coral reefs covering about 1,193 km^2 (461 square miles [mi^2]) (Figure 7.1), 128.6 km (80 mi) to the northwest off the coast of Florida. The FMG is constructed of both high and low relief limestone ledges and pinnacles that exceed 15.2 m (50 ft) in some areas. The FMG is located about 150 km (93.2 mi) south of the Florida panhandle between 28° 10′ × 28° 45′ N and 084°00′ and 084°25′ W.

Several other live bottom areas off northwest Florida are being considered as potential sanctuaries to stimulate or at least preserve some important fish species that are popular game fish (Harder and David 2009). Their depths remain just beyond the accepted maximum depth for recreational scuba (e.g., 39.6 m [130 ft]), but they are fished commercially and by recreational fishermen.

The USGS study referred to as the Northeastern Gulf of Mexico-Coastal and Marine Ecosystem Program (NEGOM-CMEP) has to date conducted the most comprehensive recent study of the Alabama Pinnacles, but earlier studies have been extensive as well (Ludwick and Walton 1957; Brooks and Giammona 1990). The USGS surveyed both the shallow reef trend (65–80 m [213–262 ft]) and deep reef trend (85–110 m [279–361 ft]). Eight main reefs (five shallow, three deep) were selected for fish community structure and trophodynamics studies, all within the region designated in Figure 7.1. The combined sampling effort by the USGS study included 326 stations, apportioned into 112 angling, 63 trap, 22 bottom trawl, 58 ROV, 15 dredge/core/grab, and 37 plankton stations. The study collected over 6,000 specimens for food habits analyses, taxonomic verification and documentation, and subsequent life history analyses, plus photographs of 113 species. The ROV observations were quantified along transects with both video and still cameras positioned 1 m (3.28 ft) above bottom to provide known areas of coverage.

The FMG ecosystem has similarities to modern patch-reefs and supports a thriving complex assemblage of species that have affinities to temperate Carolinian and tropical Caribbean origins. The fish species are tropical, with megabenthic invertebrates characterized by stony coral, gorgonians, and large basket sponges. Recent surveys have tabulated 170 species of fish, 103 species of algae, approximately 40 sponges, 75 mollusks, 56 decapod crustaceans, 41 polychaetes, 23 echinoderms, and 23 species of stony corals (NOAA CCMA 2002).

Roughtongue Reef is a roughly elliptical (400 m [1,312 ft] major base diameter), high-profile, flat-top structure with steep vertical sides. Fishermen have historically called the general area containing this and the next two target reefs the "40 Fathom Fishing Ground." Roughtongue Reef belongs to the shallow pinnacle trend, with a base depth of 80 m (262 ft). The USGS-designated name refers to the common name for the small planktivorous serranid, *Pronotogrammus martinicensis*, the roughtongue bass, which was extremely abundant on this reef. Cat's Paw Reef is a group of six small, medium-to-high profile, flat-topped mounds arranged in the pattern of a cat's paw print, with a 5–10 m (16.4–32.8 ft) relief. This cluster of mounds lies about 1,000 m (3,281 ft) west of Roughtongue Reef in the 40 Fathom Fishing Ground. Individual reef formations within the feature have flat-top communities present with limited sediment cover and highly eroded and sculpted rock surfaces with vertical faces along edges of features. Small soft corals in the USGS study were abundant on horizontal surfaces; solitary coral colonies (including *R. manuelensis*), with spiral sea whips, antipatharians, and crinoids, were also common. Yellowtail Reef is a single, elliptical (200 m [656 ft] base

diameter), high-profile, flat-top structure, that reaches the shallowest crest depth (60 m [197 ft]) of all study sites. This structure also belongs to the 40 Fathom Fishing Ground group. It forms the northwestern end of a reef arc with Cat's Paw Reef at the center and Roughtongue Reef lying at the southeastern end. Like other reef features in the group, an extensive flat-top area is present and is characterized by accumulated sediments and a dense invertebrate assemblage dominated by octocorals, antipatharians, sponges, and coralline algae. Rock outcrops characterize the northern extent of the feature, and sessile invertebrates and coralline algae are known to colonize these areas. The USGS-designated name refers to the yellowtail reef fish (*Chromis enchrysura*), which was particularly abundant on this reef.

Double Top Reef is a horseshoe shaped (100 m [328 ft] base diameter), high-profile structure that consists of multiple flat-top mounds with steep vertical sides. This area belongs to the shallow pinnacle trend in the northeastern Gulf of Mexico and also includes a similarly shaped series of mounds in the study area referred to as Triple Top Reef and an adjacent, low profile feature referred to as Pancake Reef. These features also have flat-top communities characterized by high sediment cover and dense invertebrate assemblages dominated by octocorals and antipatharians, with few solitary corals. Vertical rock walls and overhangs are dominated by *R. manuelensis* and other solitary corals. Alabama Alps is a long, narrow, north–south aligned, high-profile mound approximately 1,000 m (3,281 ft) in length. In previous studies, this same area was referred to as Lagniappe Delta Shallow and has historically been called the 36 Fathom Ridge by fishers. Alabama Alps forms the northwestern terminus of a long northwest-to-southeast-aligned ridge and pinnacle arc paralleling the shelf edge; it belongs to the shallow pinnacle trend of the northeastern Gulf. The top of this feature has sections of relatively flat terrain with scattered sections of sediment cover, particularly in the southern portion of the feature. Octocorals, antipatharians, and sponges dominate invertebrate assemblages on the flat sections. The sides of the feature range from vertical walls to large attached monoliths where the solitary coral *R. manuelensis* was the dominant sessile invertebrate with crinoids, antipatharians, coralline algae, sponges, and other solitary corals present. The USGS-designated name refers to the precipitous terrain, particularly the near-vertical west-face scarp of the structure and its position off the state of Alabama.

Ludwick and Walton Pinnacle 1 is the central member of a group of five medium- to high-profile, spire-top, shelf-edge structures with 10 m (32.8 ft) maximum relief and a base depth of 110 m (360.9 ft). This group belongs to the deep shelf-edge pinnacle trend in the northeastern Gulf. These pinnacles form a short east–west aligned arc on the shelf-slope break, bordering the northern edge of a massive shelf-edge slump of rubble. A fairly uniform coverage of debris surrounds the base with diminutive rocky reef outcrops and patch-reefs encrusted with *R. manuelensis*, octocorals, antipatharians, and crinoids. Emergent rocky features with vertical walls, rock ridges, and rock arches are distributed across the reef. Vertical rock faces had highly eroded surfaces and were densely covered with *R. manuelensis*, with low coverage of other solitary corals, octocorals, sponges, and antipatharians. Ludwick and Walton Pinnacle 2 is another of the deep shelf-edge pinnacle group. This structure, lying immediately to the east of Pinnacle 1, also was profiled and contoured by Ludwick and Walton (1957). Dense populations of *R. manuelensis*, other solitary corals, octocorals, crinoids, and basket stars colonized the elevated rocky features, while low relief hard bottom regions were characterized primarily by octocorals, antipatharians, and crinoids. Scamp Reef is a member of the Ludwick and Walton Pinnacles deep shelf-edge group with a precipitous southern reef face. This structure, lying immediately to the west of Pinnacle 1, also was profiled and contoured by Ludwick and Walton (1957). This feature has extensive vertical rock outcrops with profiles in excess of 5 m (16.4 ft). Spectacular arches, overhangs, and rugged topography occur along the southern face of the reef, with exposed rock colonized by *R. manuelensis*, antipatharians, crinoids, octocorals, and

ahermatypic coral colonies. The USGS name Scamp Reef refers to the abundance of the scamp grouper (*Mycteroperca phenax*) that reside at this site.

Qualitative observations on the physical habitat and megafaunal invertebrates associated with particular biotopes and fish assemblages were made by USGS associates from the videotapes on the ROV. Fishes on flat-topped features were assigned to six biotopes: reef top, reef face, reef crest, reef base, reef talus around a reef base, and soft bottom. Reef top biotope invertebrate assemblages had high density and species richness and were dominated by erect sponges, octocorals (particularly sea fans such as *Nicella* sp.), antipatharians, gorgono-cephalid basket stars, bryozoans, comatulid crinoids, and coralline algae. Reef crest biotopes typically were characterized by extensive rocky outcrops, with small areas of sediment cover and low invertebrate densities. The USGS report distinguished the reef crest ecotone from the adjacent flat reef top and vertical reef face biotopes to identify the possible influence of currents on the reef fish community. Reef face biotopes were rugged, vertical rocky surfaces that were characterized by lower densities of epifauna than reef tops but had an abundance of ahermatypic corals, including *R. manuelensis*, *Madrepora* sp., and *Madracis/Oculina* sp., comatulid crinoids, octocoral fans, the antipatharians spiral whip *Stichopathes lutkeni*, coral-line algae (to a depth of about 75 m [246 ft]), and sea urchins. The reef base was an ecotone between the steep reef face and the talus zone, with the rugged rocky face sometimes undercut with small cave-like overhangs. It contained vertical faces with solitary corals and the coarse sediments. Reef talus biotopes (circum-reef sediment apron) were the flat areas of reef debris and coarse carbonate sediments extending out from the base of large, high relief mounds. Coarse sediments and debris appeared to have been produced by shell and rock fragments eroded from the main reef. Small rocky outcrops in this biotope were often encrusted with solitary corals, small octocoral fans, and antipatharians. The soft-bottom/sand-plain biotopes were flat and featureless but occasionally contoured by ripples, sand waves, and excavated burrows, pits, and mounds. Sessile invertebrates in this biotope were limited to small octocorals or antipatharians attached to rock surfaces. The intermittent soft-bottom sediments should be composed of polychaete worms, crustaceans, and bivalve molluscs similar to assemblages described above for the continental shelf.

Large corals and sponges are known to occur worldwide at the outer margins of continental shelves at depths of several hundred meters (Roberts and Hirschfield 2004). These complex structures occur on hard bottoms (Brook and Schroeder 2007) and serve as habitat for a complex assemblage of invertebrates and fishes (Baker and Wilson 2001; Sulak et al. 2007, 2008). In the northern Gulf of Mexico, the corals, *Lophelia pertusa* and *Madrepora oculata,* and the black coral, *Leiopathes* sp. (Prouty et al. 2011) (Figure 7.55) are known to occur along a narrow bathymetric zone of the upper continental slope from just east of the Mississippi Delta over to the east of the De Soto Canyon (CSA 2007).

The narrow distributions (Figure 7.55) of the deep-sea coral (DSC) worldwide indicate that they all have a common set of requirements. They live in the dark. Thus, they contain no photosynthetic zooxanthellae that are vital symbionts in shallow-water hermatypic (reef-building) coral species. As they do not rely on endosymbiont photosynthesis, they are thus heterotrophic and rely on a steady rain of organic detritus that rains down from the productive surface water (Duineveld et al. 2004; Davies et al. 2010; Mienis et al. 2012) or material that is exported from the adjacent continental shelf (Walsh et al. 1981). They occupy water that is relatively cold (less than 10 degree Celsius [°C]), probably substantially colder at high latitudes), below or more or less at the permanent thermocline. At these depths (200–1,000 m [656–3,281 ft]), they would not be subject to marked seasonal temperature variations. They require a hard substrate, and in the northern Gulf of Mexico, this is provided by authigenic carbonate deposition that precipitates as fossil hydrocarbon seeps age (Roberts et al. 2010) or
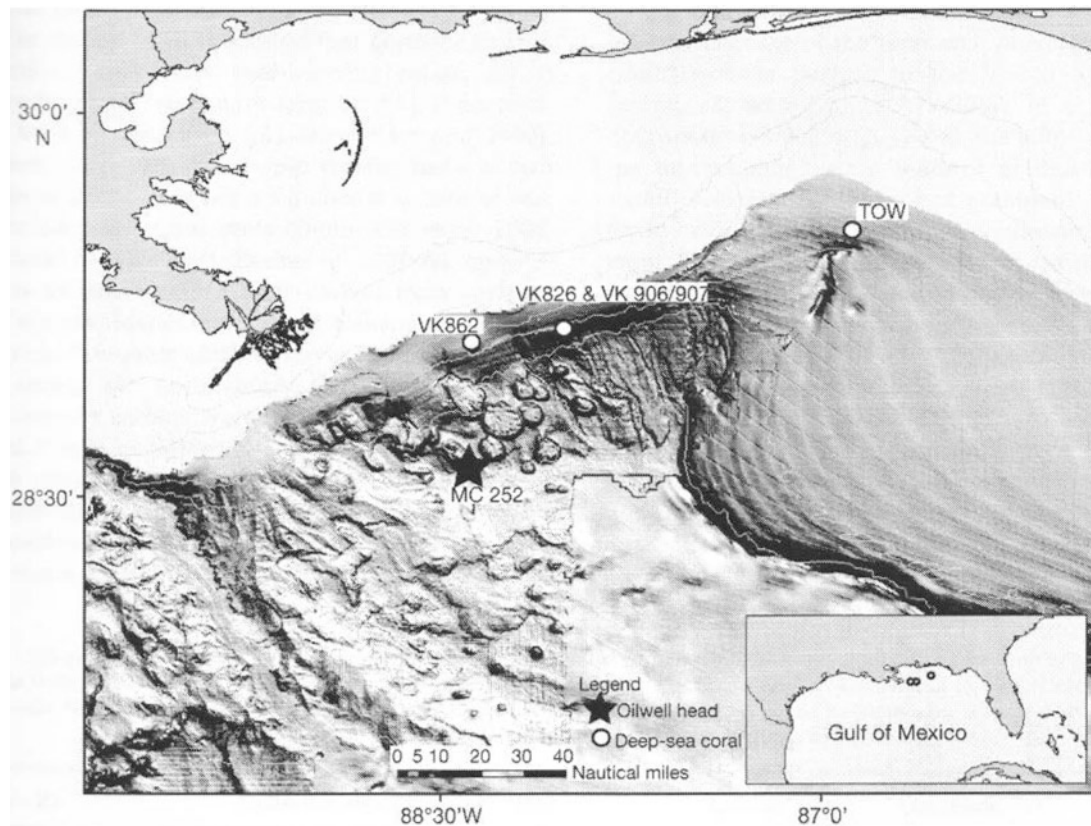
Figure 7.55. Locations of deep cold-water *Lophelia* reefs in the northeast Gulf of Mexico (from Prouty et al. 2011). The Alabama Pinnacles are located in shallower water north of the deep *Lophelia* complexes.

asphaltine solids (Williamson et al. 2008) that can support solitary sea pen and sea fan colonies. While the establishment of DSC assemblages requires these hard substrates (Hovland 1990), so far there is little evidence that the corals or sponges use the fossil organic matter as an energy or carbon source (e.g., food) (Becker et al. 2009). There is probably little to no predation on the foundation coral and sponge species themselves, but this is by inference, not actual observations. In life history models of the methane seep communities, an absence of predation is assumed because of the slow growth and long lives of the foundation species (Cordes et al. 2005a); it is thus reasonable to make this assumption—that they have no predators—with the corals as well. The DSC assemblages are considered biodiversity hot spots (Roberts et al. 2009).

West Florida *Lophelia* Lithoherms: This region consists of dozens and possibly hundreds of 5–15 m (16.4–49.2 ft) tall lithoherms (elongated carbonate mounds) off the southwest Florida shelf at depths of 500 m (1,640.4 ft), some of which are capped with thickets of live and dead *Lophelia*. The habitat extends more than 20 km (12.4 mi) along the shelf slope. In 2003, Reed et al. (2006) conducted a SEABEAM bathymetric survey over a small portion (1.85 × 1.85 km [1.15 × 1.15 mi]) of the region. They used Innovator ROV dives to ground-truth three features: a 36 m (118 ft) tall escarpment and two of the lithoherms. They examined a 36 m (118 ft) tall escarpment from 412 to 448 m (1,351.7–1,469.8 ft) at the eastern edge of the flat terrace that contained the lithoherms. The escarpment was nearly vertical and had very rugged topography with crevices, outcrops, and a series of narrow ledges. The dominant sessile fauna consisted of

Antipatharia (30 cm [11.8 in.] tall), numerous Octocorallia including Isididae (30–40 cm [11.8–15.8 in.]), and sponges, *Heterotella* spp., *Phakellia* spp., and Corallistidae. The SEA-BEAM bathymetry revealed dozens of lithoherms on a terrace west of the escarpment. Eight other lithoherms were reflected on the ROV's sonar within a 100 m (328 ft) radius. Estimated coral cover ranged from less than 5 % to greater than 50 % in some areas, with 1–20 % live. The dominant fauna was similar to the escarpment except for *Lophelia*, which was not observed on the escarpment. Common sessile benthic species included Cnidaria: Antipatharia (*Antipathes* spp. and *Cirrhipathes* spp.), *L. pertusa*, Octocorallia; and Porifera: *Heterotella* spp. and other hexactinellid vase sponges, and various plate and vase demospongiae (Pachastrellidae, Petrosiidae, Astrophorida). Common motile invertebrates included Mollusca, Holothuroidea, Crinoidea, and decapod crustaceans (*Chaceon fenneri* and Galatheidae). Nine species of fish included Anthiinae, shortnose greeneye (*Chlorophthalmus agassizi*), conger eel (*Conger oceanicus*), blackbelly rosefish (*Helicolenus dactylopterus*), codling (*Laemonema melanurum*), beardfish (*Polymixia* spp.), and hake (*Urophycis* spp.). The high number of hard bottom lithoherms revealed by the limited SEABEAM mapping effort and few ROV dives led Reed et al. (2006) to believe that there was tremendous potential for unexplored coral and fish habitat in this region.

The narrow depth distribution of the deepwater corals in the eastern Gulf of Mexico is thought to require bottom currents in addition to specific temperatures (Davies et al. 2010; Mienis et al. 2012). The corals require particulate matter from the overlying phytoplankton as a food source, but particulate matter that is not useable as nutritional food could potentially also smother the corals. The authors provide evidence that bottom currents at these depths supply adequate nutritional material but also act to sweep the areas free of suspended matter that could be detrimental. Thus, in addition to a narrow temperature range and hard substrata, these species require currents that can supply adequate nutritional POC but eliminate inorganic, terrestrial, river-derived or resuspended particulate material that can smother them. Fluxes of particulate matter into a sediment trap moored above the corals indicated that supplies of POC would be adequate to support the coral metabolism and growth (Mienis et al. 2012). The intersection of requirements of temperatures of 5–10 °C, POC nutritional levels yet to be defined, persistent bottom currents and hard substrate in this habitat may explain why these species complexes are rare: the habitat is rare. This narrow intersection of requirements could explain why similar deep corals have not been encountered on knolls west of the Mississippi River where the persistent near-bottom nepheloid layer could smother them.

Slow growth is a common biological feature of all the species involved in the DSC assemblages; they live up to several hundred years or more (Prouty et al. 2011). This remarkable phenomenon is supported by age dating with ^{210}Pb and ^{14}C concentration gradients and observations of features in the skeletal material of the black coral, *Leiopathes* sp.

Two deeper habitats that need mention are the asphaltine assemblage that was discovered in association with the very deep (about 3.6 km [2.2 mi]) Sigsbee Knolls (MacDonald et al. 2004) and the iron stone crust that covers the sediment surface on the deep (greater than 2 km [1.2 mi]) eastern margin of the Mississippi sediment fan (Pequegnat et al. 1972; Rowe and Kennicutt 2008; Rowe et al. 2008a). The asphalt-like outcroppings appear to have formed from fossil hydrocarbon deposits (Williamson et al. 2008) and harbor sessile organisms such as sea fans and sea whips. The reddish iron stone crust is thought to have been formed on the surface of slump deposits that originated in shallow water (Santschi and Rowe 2008). Both occur at depths where the vital POC input is very limited, and thus, they both support minimal benthic biomass and diversity.

7.6.3 Cold Seep Communities

The first hint of methane expulsion from the sediments was the observation that acoustic records on echo-sounder recorders (ESRs) monitoring water depth and seafloor properties were occasionally, briefly, wiped out. Such wipeouts in sound were determined to be caused by gas bubbles in the water—evidently methane and other short-chained hydrocarbons bubbling out of the sediments. The sound was not transmitted through the bubbles; that is, it was wiped out on the ESR records. This gas was assumed to be coming from the dissolution of methane clathrates or ice-like material composed of sea water, clay, and short-chained hydrocarbons that together are known to form a solid (ice) at pressures of 30 to possibly greater than 100 atmosphere (atm) and temperatures of less than 10 °C As the ice warms up or as pressure diminishes, it turns to gas, thus forming bubbles. Clathrates and associated methane releases were first discovered in the Gulf of Mexico on the upper slope (Brooks et al. 1984). The methane released was then discovered to support seafloor communities that are reminiscent of hydrothermal vent communities (Kennicutt et al. 1985; Brooks et al. 1985). The ice or gas hydrates can break off and float, giving off bubbles in the process (MacDonald et al. 2003). Most information on gas expulsion has been developed during three substantial studies supported by the MMS (now BOEM). The investigations, CHEMO I (1991) and CHEMO II (1997), concentrated on locations at depths of less than 1 km (0.62 mi), whereas, the most recent project, CHEMO III, explored the deep GoM continental slope, with support from BOEM and NOAA. CHEMO III has been summarized in the special issue *Deep-Sea Res. II*, 57 (2010), Cold seeps are distributed extensively, reaching all over the northern and southern continental slopes where they are underlain by salt deposits (Figure 7.56).
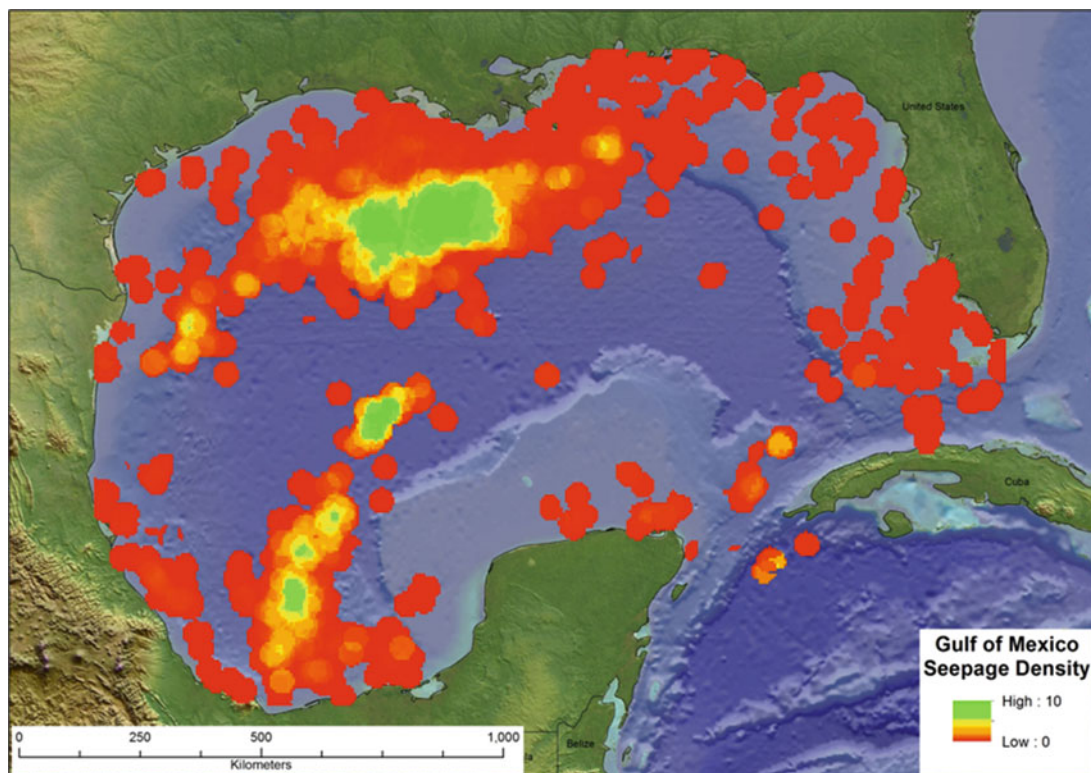

Figure 7.56. Oil and gas seepage in the Gulf of Mexico (determined from analysis of synthetic aperture radar, graphic provided by CGG's NPA Satellite Mapping, used with permission).

Finding or prospecting for seeps has taken many approaches. Sub-seafloor and seafloor surface three-dimensional seismic profiles, multibeam bathymetry, and side-scan sonar swaths are used to identify areas of potential fluid gas expulsion. Acoustic wipe out zones indicate bubbles near the seafloor. Sea surface slicks seen from satellites can be followed back to natural releases of oil and gas at the seafloor (MacDonald et al. 1993; De Beukelaer et al. 2003). With these three types of information, the next step is to confirm existence of seep communities using bottom photographic surveys, ROV observations, or deep submergence research vehicle sampling (Roberts et al. 2010). Although seafloor trawling provided some of the first clear confirmations that seep communities exist (Rosman et al. 1987), this is now frowned upon because of the damage it does to the structures. The Gulf of Mexico seeps are the most well known worldwide (Fisher et al. 2007).

The cold seep faunal assemblages occur in five categories: mussel beds, clam beds, vestimentiferan (tube worm) clumps, an epifauna of brachiopods and solitary corals, and gorgonian fields (Kennicutt et al. 1985; Rosman et al. 1987; MacDonald et al. 1989, 1990a, b, c). According to Roberts et al. (2010), of the thousands of seeps on the northern Gulf of Mexico slope, many surround the edges of the intraslope basins where shallow subsurface salt bodies give rise to bathymetry with faults that provide pathways for salt, gas, and oil to flow up to the seafloor.

Stable isotope measurements suggest that a principal energy source is hydrogen sulfide in addition to methane (Brooks et al. 1985; Demopoulos et al. 2010; Becker et al. 2010). Physiological studies have suggested that endosymbiotic relationships exist between mussels and methanotrophic bacteria, but clams and vestimentiferans contain sulfur-oxidizing bacteria (Cordes et al. 2005a). It is assumed that the seeping fossil hydrocarbons nourish sulfate-reducing bacteria that provide sulfide to the sulfide-oxidizing endosymbionts (Freytag et al. 2001). The bathymodiolids harbor at least four symbiotic functional groups: methanotrophs (consume methane as an energy and carbon source), methylotrophs (consume a methyl group at the end of a fatty acid), and two different thiotrophs (oxidize-reduced sulfur compounds for energy) (Dupperon et al. 2007). The community of organisms on the deep Florida Escarpment is not supported by fossil hydrocarbons (Paull et al. 1984).

The composition of the principal fauna associated with fluid expulsion varies over time as the seep matures. *Bathymodiolus* mussels with methanotrophic symbionts arrive first (Roberts et al. 1990; Bergquist et al. 2003). Prior to this, the sediments may need to be stabilized by carbonate precipitation that is a byproduct of the oxidation of the hydrocarbons (Aharon and Fu 2000; Joye et al. 2004; Luff et al. 2004). Vestimentiferan tubeworms follow after enough carbonate substrate is available (Cordes et al. 2003). The clumps of tubeworms and mussel beds are considered the foundation species of the seep communities (Cordes et al. 2010). The three species of mussels are *Bathymodiolus brooksi*, *B. childressi*, and *B. heckerae*. The tubeworms are known to be *Escarpia laminata* and *Lamellibrachia luymesi* (Miglietta et al. 2010) and *Seepiophila jonesi* (Gardiner et al. 2001), among others.

These foundation species serve as habitat for a speciose assemblage of smaller organisms, but the small organisms associated with the larger individual clumps are difficult to sample quantitatively (Bright et al. 2010; Cordes et al. 2010; Lessard-Pilon et al. 2010). Fauna associated with tubeworms appears to have a higher diversity than mussel beds on the upper slope (550 m [1,804 ft] depth), but at greater depths, this distinct difference is less obvious in rarefaction curves (Cordes et al. 2010). The mussel beds appear to have a mid-depth maximum (MDM) diversity but the fauna associated with the tubeworms did not. This is an interesting observation because MDMs have been observed on many continental margins, but their cause is equivocal at best. The nonseep macroinfauna of the Gulf of Mexico has a distinct MDM, but this was not apparent in the polychaete worms (Rowe and Kennicutt 2008). Many of the species associated

with the foundation fauna are obviously seep-associated organisms such as the shrimp *Alvinocaris muricola*, the polychaete worm *Methanoaricia dendrobranchiata*, and the snail *Provanna sculpta*. There seems to be minimal overlap with nonseep fauna (Wei et al. 2010a). The α or within-habitat diversity in the mussel clumps and the wormtube bushes appears to be high: of 32 samples from the middle and deep slope (about 1–2.7 km [0.62–1.7 mi] depth), the mean of the expected number of species per 50 individuals (E (50)) was 6.5, σ = 2.2 (Cordes et al. 2010). These samples of the associated animals were obtained by washing the mussel clumps and the tubeworm bush samples with filtered seawater through a 1-mm sieve in the ship's laboratory (Cordes et al. 2010). The infauna from sediment samples in studies not associated with seeps was sieved through slightly finer sieves (generally 0.3 mm) (Wei et al. 2012a), making a comparison between the seep and nonseep faunas difficult. Had the seep fauna washings been done with a finer sieve, the diversity values might have been higher. Likewise, comparisons of biomass and densities are not possible because the seep foundation species, as habitats, are three dimensional, whereas the quantitative biomass and density estimates of faunas on level silt and clay sea floor away from seeps were all estimated as individuals or biomass/m^2.

The vestimentiferans, namely *Lamellibrachia luymesi*, form aggregates or bushes of up to thousands of individuals and they are estimated to live hundreds of years (Fisher et al. 1997; Julian et al. 1999; Bergquist et al. 2000), even though the individual worms are far smaller than those encountered at hydrothermal vents (Fisher et al. 1990).

An enigma in the Gulf of Mexico is the proximity of diverse, high biomass, and productive assemblages, supported by fossil hydrocarbon, to the more general, comparatively oligotrophic (low productivity and modest biomass) level-bottom assemblages away from seeps (Wei et al. 2012a). The possibility that the sites of fossil carbon expulsion and seepage are fertilizing wide areas from nearby nonseep fauna has not been supported by stable carbon and nitrogen isotope analyses in samples of fauna near seeps (Carney 1994, 2010). That is, the many different habitats that are characterized by fossil organic matter supporting high biomass and productivity on the seafloor have had very little influence on the organisms in the habitats away from the seeps. That said, the boundaries between the two (seep versus nonseep) remain poorly defined. Demopoulos et al. (2010), for example, found stable isotope evidence that a suite of free-living invertebrates in soft sediments associated with seep sites are feeding on the free-living sulfur-oxidizing white and pink *Beggiatoa*-like bacteria species living on sulfide diffusing out of the sediment.

7.6.4 Continental Slope and Abyssal Plain Assemblages

Groups of organisms also occur along the continental slope, as well as in the abyssal plain. These assemblages are described in the following paragraphs.

7.6.4.1 Microbiota (Heterotrophic Bacteria and Archaea)

Both the density and biomass of sediment microbes have been exhaustively documented by Deming and Carpenter (2008) in conjunction with the MMS study Deep Gulf of Mexico Benthos (DGoMB) (Rowe and Kennicutt 2008). Cross-slope sampling sites were spread from the western Gulf of Mexico off south Texas across the northern Gulf of Mexico to north Florida, at depths of about 200 m (656 ft) out across the SAP to depths of 3,650 m (11,975 ft). The top 15 cm (5.9 in.) of cores were counted at four sediment intervals using a combination of DAPI and Acridine Orange stains. Values ranged from 1.0×10^8 to 1.89×10^9 cells/cm^3, while depth-integrated biomass ranged from almost Log_{10} 0.5 g C/m^2 at the shallow sites down to Log_{10} 0.05 g C/m^2, with a consistent decline from the upper slope (less than 500 m [1,640 ft])

down to the low values at 3.7 km (2.5 mi) depth. Cell numbers declined with depth in the sediments. Cell densities followed no particular pattern as a function of water depth, but biomass ranged from 2.6 down to 1.0 g C/m^2 from the upper continental slope down to the low values on the abyssal plain. The reason for this difference in counts versus biomass is related to a general decrease in measured cell size with depth. The biomass of the microbiota was positively related to POC flux (Biggs et al. 2008) and negatively related to depth. Deming and Carpenter (2008) also measured whole-core respiration and microbial production on repressurized recovered cores, and these values have been used in seafloor food web models (Rowe et al. 2008b; Rowe and Deming 2011). No more detailed information is available on the specific types of bacteria and Archaea present in these counts or incubations, just that they are presumed to be heterotrophs that consume DOM.

7.6.4.2 Meiofauna: Foraminifera and Metazoa

The meiofauna are small (>40 μm) single-celled (Foraminifera) or multicelled (metazoan) organisms that consume detritus and smaller protists and bacteria living on or within the sediments. The most prevalent of the metazoans are nematodes (round worms), harpacticoid copepods (crustaceans), and kinorhynchs. Assessing the abundance of forams is difficult because the empty (dead) shells must be differentiated from living organisms (Bernhard et al. 2008). Forams have been investigated extensively because many species have calcium carbonate shells or agglutinated tests (volcanic glass shards) that are preserved as fossils, making them important sources of information on the history of Gulf of Mexico sediments (Parker 1954; Phleger and Parker 1951; Poag 1981; Reynolds 1982). Assemblages of forams are thought to be zoned with depth and associated with specific water masses (Denne and Sen Gupta 1991, 1993; Jones and Sen Gupta 1995). Some are associated with upwelling on the Florida slope (Sen Gupta et al. 1981), while others appear to occur in association with fossil hydrocarbon seeps (Sen Gupta and Aharon 1994) and bacterial mats (Sen Gupta et al. 1997). In samples of living forams across a wide depth interval, Bernhard et al. (2008) documented a mean density of 3.9×10^4 individuals/m^2, with a mean biomass of 31.5 mg C/m^2. The highest density (8.2×10^4 individuals/m^2) and biomass (98.1 mg C/m^2) were located at a known methane seep site (Bush Hill) at a depth of 548 m (1,798 ft) on the upper continental slope. Mean densities on the upper slope (4.0×10^4 individuals/m^2, $\sigma = 2.5$) were not different from those on the abyssal plain (4.6×10^4 individuals/m^2, $\sigma = 1.9$), but the biomass was higher on the slope (52 mg C/m^2, $\sigma = 34$) than on the abyssal plain (12.9 mg C/m^2, $\sigma = 6.6$). Smaller-sized forams on the abyssal plain explain the biomass difference. The mean size among all ten locations sampled by Bernhard et al. (2008) was 0.8 μg C per individual. Fifty-nine species were encountered at the ten sites sampled, but the fauna was dominated by *Saccorhiza ramosa* (51.7 % of the total individuals).

The metazoan meiofauna abundances and biomass were determined at all the same locations as the microbiota by Deming and Carpenter (2008, see above) during DGoMB (Baguley et al. 2008), making this survey of the northern Gulf of Mexico one of the most comprehensive available anywhere. In addition, this latter study measured grazing rates and estimated respiration based on temperature and animal size. Mean biomass was 43.4 mg C/m^2, with a high of 157 on the upper slope down to a low 3.5 mg C/m^2 on the abyssal plain. Nematode worms and harpacticoid copepods dominated the biomass at all depths. Densities and biomass declined with depth, as did the estimates of total respiration of this fraction of the fauna: from about 4.5 mg C/m^2/day respiration or production of carbon dioxide on the upper slope down to almost none on the abyssal plain. Harpacticoid copepod species composition and nematode genera have been used to define recurrent groups of meiofauna over this broad area of the

slope and abyss (Baguley et al. 2006; Sharma et al. 2012). Groups of species were not aligned with depth (as is common in larger groups), but occurred in isolated patches that cross (rather than align with) depth intervals of hundreds of meters, probably due to their modes of reproduction and recruitment strategies. These estimates of respiration and biomass relative to depth are important because they are most likely controlled by food supply that is imported from the surface or exported to the seafloor from the adjacent continental shelf. Likewise, new or alien sources of organic matter, such as natural or accidentally spilled or leaked hydrocarbons, could affect them in either a positive or a negative manner.

7.6.4.3 Macrofauna

Quantitative investigations of the macrofauna were initiated in the mid-l960s (Rowe and Menzel 1971; Rowe 1971; Rowe et al. 1974; Pequegnat 1983). The published surveys used an anchor dredge or a van Veen grab to sample specific areas of the seafloor, followed by sediment sieving with a 0.42 mm mesh sieve. Since those early publications, the sieve size generally prescribed in studies supported by MMS in deep water has been reduced to 0.3 mm, meaning that total abundances of smaller organisms would have increased in the later studies (Recall that all the continental shelf studies used 0.5 mm sieves). These small changes, while affecting densities, probably have not affected biomass estimates (Rowe 1983). The most recent studies have used a GOMEX corer (Boland and Rowe 1991) or a spade corer (Escobar-Briones et al. 2008b, c), whereas some of the present ongoing sampling has gone to a multicorer (Barnett et al. 1984).

The Gulf of Mexico macrofauna biomass follows a log-normal relationship with depth, whether measured as wet weight, dry weight, or organic carbon (Rowe and Menzel 1971). The slope of the log-normal line appears to be the same regardless of which measure is used, but the slope of the densities can be less than that of the weight measures, indicating that abundances do not decline as fast as biomass; that is, animals in some ocean basins are getting smaller with depth. Recall that this was true of the microbiota and the meiofauna as well. It appears that the rate of decline of biomass with depth is a general feature on most continental margins, but the height of the line (the origin at shallow intercept on the shelf) above the x-axis is a function of the rate of PP in the surface water (Rowe 1971; Wei et al. 2010a). Thus, the biomass regression in the Gulf is steep but somewhat below most other ocean basins, a clear indication that the Gulf of Mexico is an oligotrophic ecosystem, with several exceptional habitats.

Most of the historical biomass measurements in the Gulf of Mexico (Figure 7.57) have been incorporated into a single database for the purpose of predicting macrofaunal biomass across large scales of depth and region (Wei et al. 2010b, 2012a). The densities and biomass are dominated by worms (Figure 7.58), either polychaetes or nematodes (Figure 7.59).

It is presumed that animal densities decline with depth because food becomes limiting (Rowe 1971, 1983). A log-normal relationship has been described for most of the world's oceans, including the Gulf of Mexico. The height of the line is related to the levels of PP in the surface water (Rowe 1971), as well as input from the margins (Walsh et al. 1981; Deming and Carpenter 2008; Santschi and Rowe 2008). Submarine canyons appear to concentrate organic matter, thus enhancing their biomass and animal abundances, especially in the Gulf of Mexico (Roberts 1977; Soliman and Rowe 2008; Escobar-Briones et al. 2008a; Rowe and Kennicutt 2008).

The biomass in the southern Gulf of Mexico is decidedly lower than that in the northern Gulf of Mexico, as illustrated in Figure 7.60 from Wei et al. (2012a), using data from Escobar-Briones et al. (2008a). This reflects the source of the water (the Caribbean via the Yucatán Strait) and the resulting low PP due to nitrate limitation. The high variance among the southern
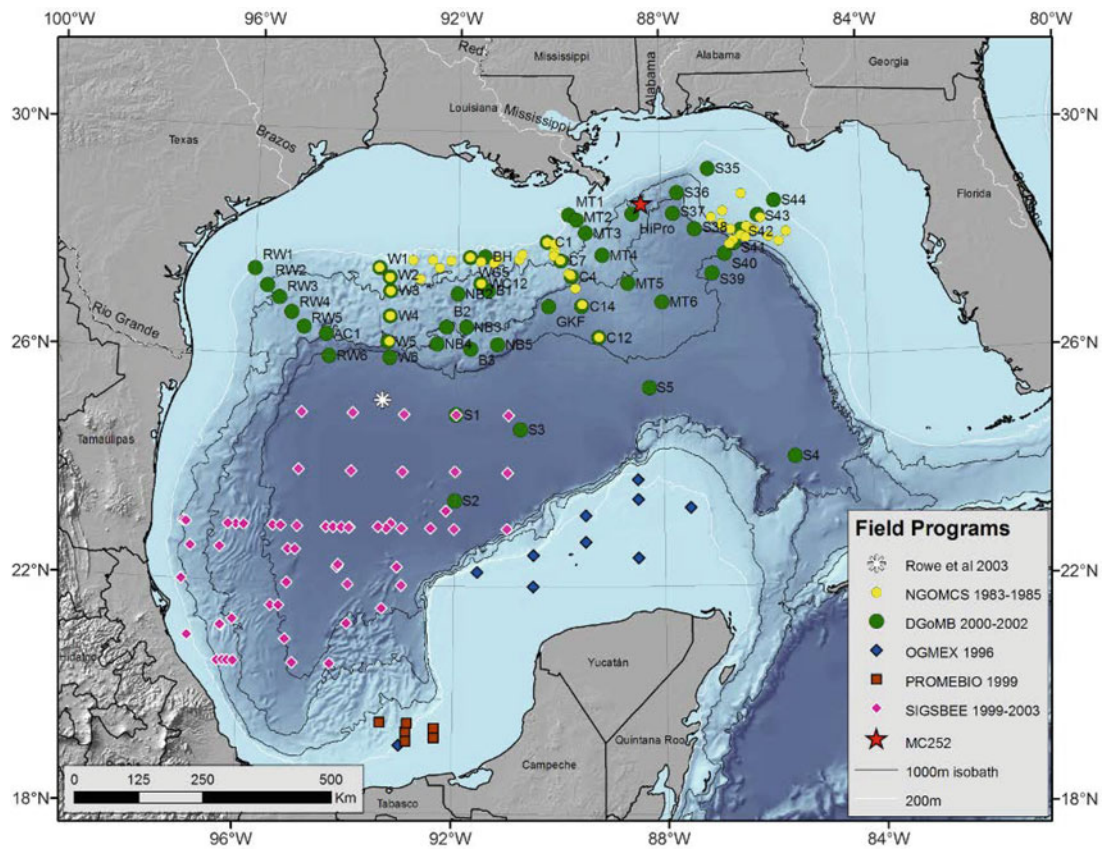
Figure 7.57. Distribution of offshore quantitative samples of macrofauna on which the biomass data are based (from Figure 1 in Wei et al. 2012a; reprinted with permission from Elsevier).
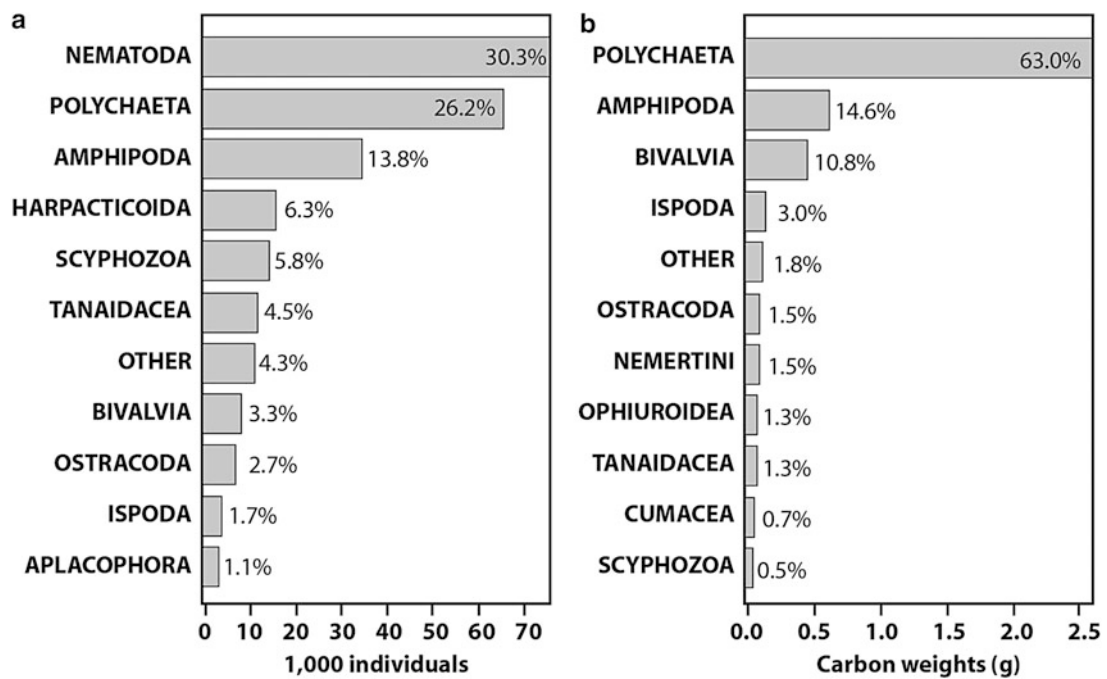

Figure 7.58. Distribution of macrofauna taxa within the samples used in the estimates of biomass (mg C per individual × total number of individuals at a location) and animal abundances (from Figure 2 in Wei et al. 2012a; reprinted with permission from Elsevier).
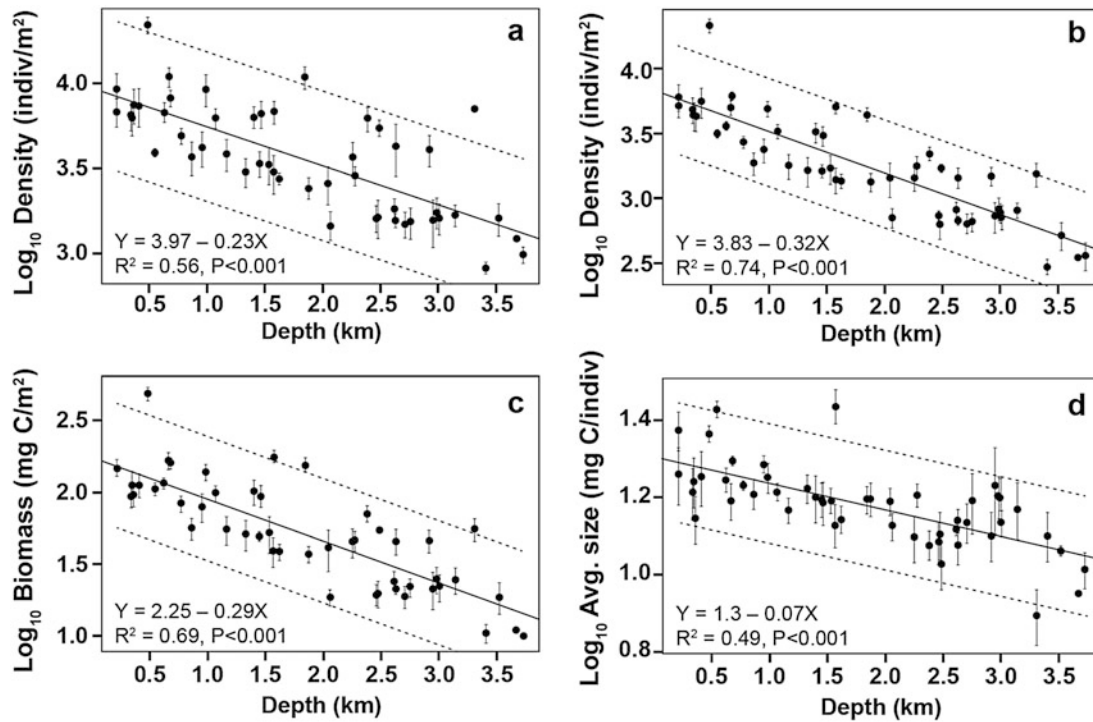
Figure 7.59. Regressions of macrofauna as a function of depth in the deep Gulf of Mexico. The *top left panel* (a) includes nematode worms and the *top right panel* (b) does not. The *bottom left panel* (c) illustrates the now classic log-normal decline in biomass as a function of depth, whereas the *bottom right panel* (d) illustrates the decline in mean size of the individuals with depth, as derived from biomass and abundance data (from Figure 3 in Wei et al. 2012a; reprinted with permission from Elsevier).
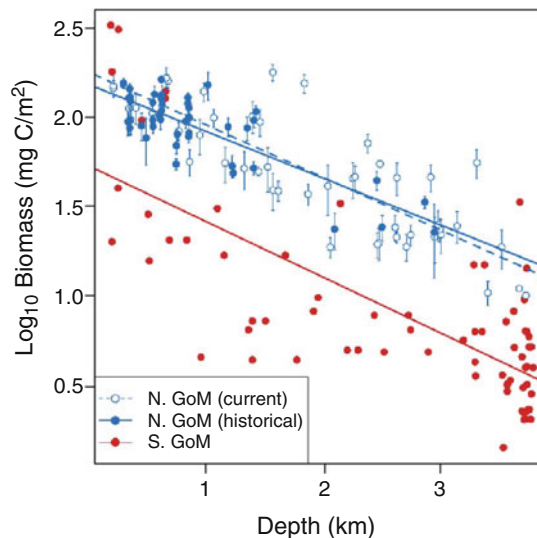
Figure 7.60. Comparison of macrofaunal biomass in the northern and southern Gulf of Mexico (from Figure 6 in Wei et al. 2012a; reprinted with permission from Elsevier). Current refers to the Deep Gulf of Mexico Benthos (DGoMB) sampling (2000–2003) versus the historical, which is the Northern Gulf of Mexico Continental Slope (NGoMCS) samples (1983–1985).
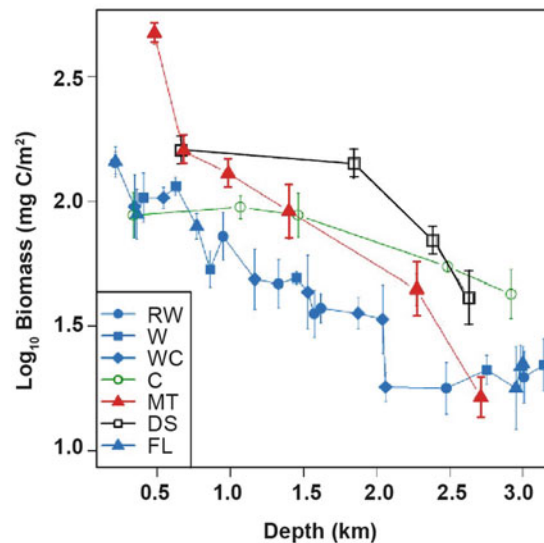
Figure 7.61. Comparison of biomass of macrofauna on transects in the MMS-sponsored DGoMB study across the northern Gulf of Mexico. The lines went from west (RW) to east (FL). While there is no apparent difference in these longitudinal extremes as illustrated, the highest values were in two large canyons (*DS* De Soto Canyon, *MT* Mississippi Trough) and the central transect, which was just west of the MT line (from Figure 5 in Wei et al. 2012a; reprinted with permission from Elsevier). Original data in or derived from Rowe and Kennicutt (2008).

Gulf of Mexico samples reflects their use of small subcores from a spade corer or a multicorer, which takes small samples (about 125 cm^2 versus 2,000 cm^2 in the GOMEX corer).

The transects across the northern margin of the Gulf of Mexico (Figure 7.61) illustrate that the highest macrofauna abundances and biomasses are found in the central locations of the Gulf, at all depths. All transects merge to very low values on the SAP. The highest numbers were encountered at a depth of 500 m (1,640 ft) in the head of the Mississippi Trough (Soliman and Rowe 2008). Much of this high density can at times be attributed to a single species of a small tube-dwelling amphipod crustacean (*Ampelisca mississippiana*) (Soliman and Rowe 2008). At mid-slope depths, however, the highest abundances and biomass were encountered in the De Soto Canyon.

Comparisons of biomass values between the Northern Gulf of Mexico Continental Slope (NGoMCS) (1983–1985) and DGoMB studies (2000–2003), about 20 years apart, revealed no significant differences (Wei et al. 2012a) (Figure 7.61). There was no indication that mid-slope basins, proximity to methane seeps or the base of steep escarpments affected the biomass or animal densities (Figure 7.62) in any of the previous studies (Wei et al. 2012a). Variations that could be attributed to season have not been tested adequately as yet, although Wei et al. (2012a) did try to estimate possible effects of what they termed *arrival time lag* of POC input to the seafloor. This is almost impossible because the settling rate of the surface-derived POC is unknown, and the rate at which newly arrived POM is incorporated into the biota is unknown and probably is a function of the different size or functional groups. Additionally, the horizontal contribution of material from the margins is thought to be important but is impossible to quantify (Bianchi et al. 2006; Rowe et al. 2008b; Santschi and Rowe 2008). Thus, the organic detritus has two sources—lateral transport from the margins and vertical transport from the surface—neither of which is well constrained or understood.

It is presumed that the severe decline in biomass and abundance of the fauna (all sizes) as a function of depth reflects the decline in POC input with depth (Figures 7.62 and 7.63). Thus, it
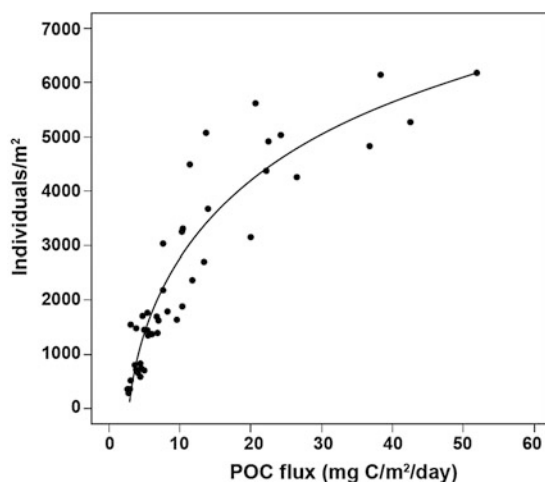
Figure 7.62. Density of macrofauna individuals in the Gulf of Mexico as a function of delivery of POC as estimated from sea surface—satellite estimated chlorophyll *a* concentration (modified from the data in Biggs et al. 2008 and Wei et al. 2012a).
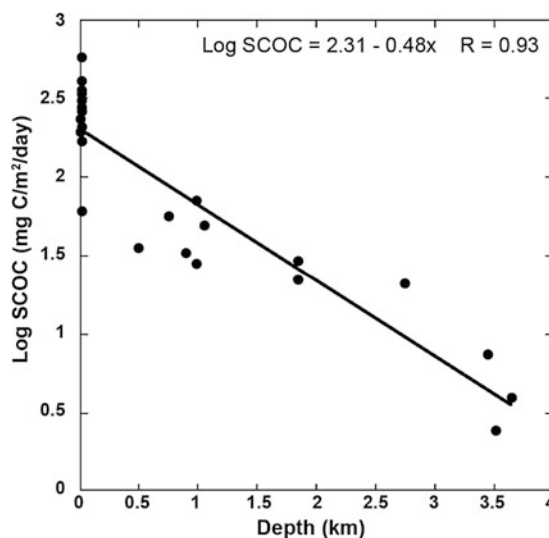

Figure 7.63. Sediment community oxygen consumption (SCOC) in the northern Gulf of Mexico (Rowe et al. 2008a). The deep samples on the slope and abyssal plain are from Rowe et al. (2003, 2008a), whereas the shallow (less than 100 m) data are from studies of the continental shelf, many of which were measured on sediments in the hypoxic area off Louisiana (Rowe et al. 2002).

would stand to reason that any additional input of labile (easily biodegradable) organic matter would enhance biomass locally. This is true for food falls or carcasses of fishes and marine mammals. That no effects could be discerned in the continental slope mesoscale basins (which could trap particulates), near methane seeps or at the base of escarpments indicates that the methods used cannot extract the effects from the highly variable database, or in fact these features do not enhance food resources.

Sediment community oxygen consumption (SCOC) (Figure 7.63) illustrates that the model-estimated POC flux and carbon turnover by the seafloor organisms are in good agreement. Both decline in significant log-normal fashion as a function of depth. However, the rate of

decline in the SCOC is almost two times that of the biomass. This suggests that total community heterotrophic metabolic rates decline faster than biomass. It also demonstrates that the metabolic rate of the community as a function of biomass declines as a function of depth.

In the DGoMB samples (2000–2003), a total of about 957 different species were enumerated at the 43 designated locations. Taxonomic specialists at many different institutions generated the lists of these species. Type material is now archived in the benthic invertebrate collections at Texas A&M University—Galveston (TAMUG), whereas material collected in the earlier offshore MMS programs is housed at the Texas Cooperative Wildlife Collections Marine Invertebrate Collections at TAMU—College Station or has been deposited in the U.S. National Museum of Natural History (the Smithsonian). A large fraction of the macrofauna-sized material remains undescribed, although putative species designations have been given to each different species based on the judgment of the taxonomist in charge of a group.

A list of all the described species and the putative species with separate designations has been assembled into a single database. This database has been used to identify recurrent groups of organisms using measures of similarity (shared species) between each pair of samples across the entire northern Gulf of Mexico, excluding the continental shelf. Four major depth-related zones were apparent (Figure 7.64) (Wei et al. 2010a). The middle two were separated longitudinally as well. Each location in each demarcated group shared at least 20 % of its species with all the other locations in the zone. Wei et al. (2010a) concluded that the most important factor
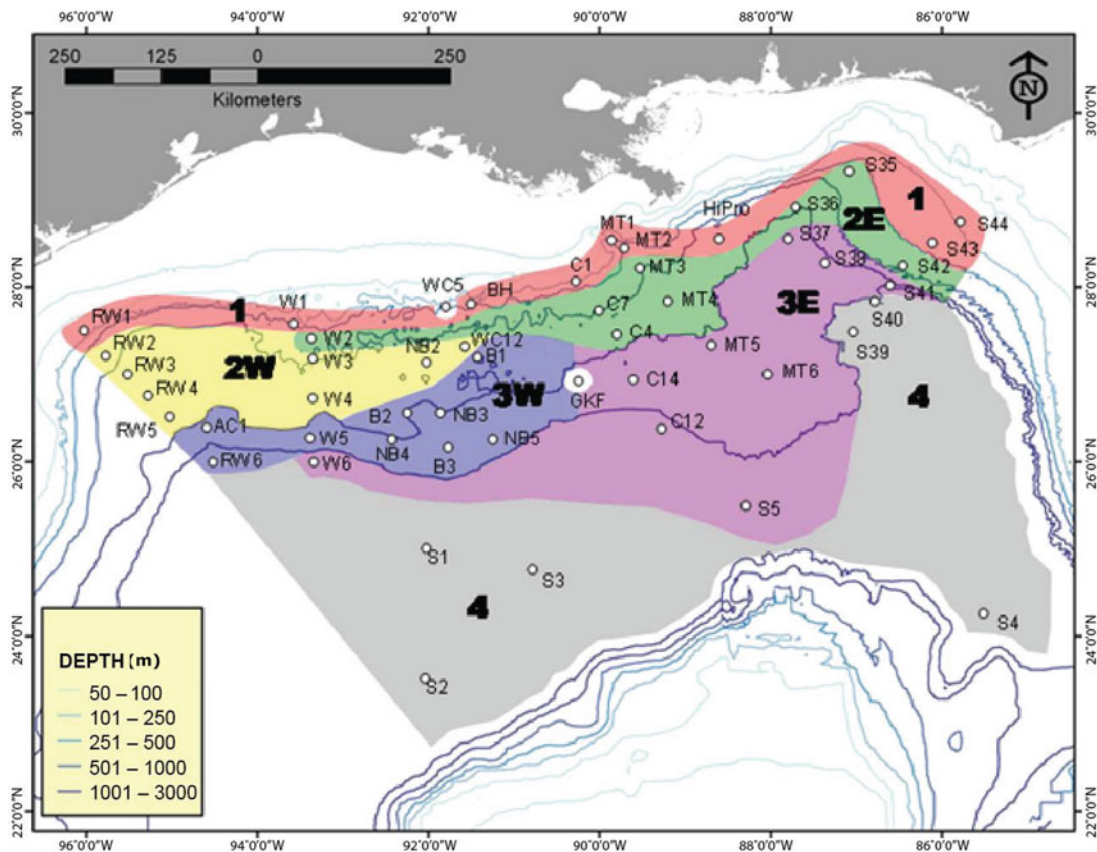

Figure 7.64. Zonation of macrofaunal species into four major depth-related zones based on percent species shared between locations, with the two intermediate zones divided between east versus west subzones (from Wei and Rowe 2006; Wei et al. 2010a).

giving rise to this pattern is the decline in POC input. That is, the variable that controls the sharp fall in biomass has also given rise to this alignment of groups of species along isobaths. The intermediate east versus west separations appeared to be a function of a difference in sediment grain sizes: a coarse sand fraction (composed of $CaCO_3$ pelagic foram tests) with a mean of 25 % in the east versus a coarse fraction of less than 5 % among the western locations. The western locations were dominated by terrigenous clays that were thought to dilute the pelagic carbonate fraction. It is not clear whether it was the sediment grain size or the mode of the pelagic input that was important. Roberts (1977) also describes four zones in the area of the De Soto Canyon based mostly on megafauna from skimmer samples (Pequegnat et al. 1970); likewise Powell et al. (2003) describes four zones of demersal fishes from the upper slope down to the shallow margin of the abyssal plain.

Biodiversity is often used as a measure of community, ecological, or environmental health. However, the causes of variations in diversity are numerous and inconclusive. The zonation referred to in Figure 7.64 is beta diversity, or the turnover or replacement of species along a physical gradient. Wilson (2008) described the *within-habitat* (alpha) diversity of isopod crustaceans in the macrofauna along the transects occupied by both NGoMCS (1983–1985) and DGoMB (2000–2002). This group, based on *expected species*, $E(s)$, displayed an MDM that occurred at the 1–1.5 km (0.62–0.75 mi) depth. To Wilson (2008), the distribution appeared to suggest that the deep Gulf of Mexico might have suffered some extinction events, and thus, the present-day deep fauna reflects invasions of shallow species from the margins. Haedrich et al. (2008) used species richness (total numbers of species or gamma diversity) to demonstrate that the MDM is not an artifact of the overlapping bathymetric ranges of multiple species with little ecological significance, but rather a significant nonrandom response to variations in the ecosystem. However, the species richness of different large taxonomic groups appeared to respond to different sets of environmental variables. Wei and Rowe (unpublished manuscript) use the macrofauna species list database to illustrate the response of within-habitat diversity [as E (100 individuals)] to POC flux estimates among all the DGoMB locations (Figure 7.65). This odd parabolic pattern could illustrate a relaxation in competitive exclusion that follows the sharp decline in POC input as depth increases (right side of the parabola); diversity in that data
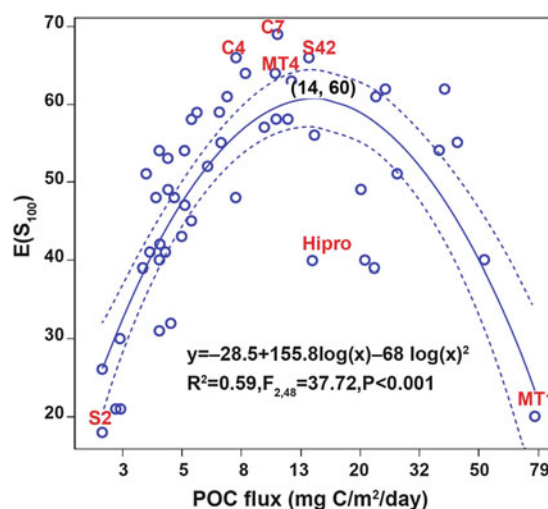

Figure 7.65. Macrofauna diversity (alpha or within-habitat diversity index Expected Number of Species per number of individuals), or rarefaction, (E (100) = number of species per 100 individuals) plotted as a function of estimated POC flux onto the seafloor (from Wei and Rowe, unpublished data, manuscript in preparation).

set attained a maximum at POC input values that are encountered on the mid- to upper slope at a depth of approximately 1.2–1.5 km (0.75–0.93 mi); then the E (100) declined again on the left arm of the parabola as POC input becomes more and more severely limiting on the abyssal plain. The "relaxation of competitive exclusion" hypothesis is just one of several possible explanations for the MDM and the increase as POC input declines offshore. An alternative is the MDM occurs in a region of intermediate levels of disturbance by physical and biological processes.

7.6.4.4   Megafaunal Invertebrates

Megafauna is defined in size as being identifiable in seafloor photographs, larger than 1 cm (0.4 in.) in diameter and caught in trawls with stretch mesh of about 2.5 cm (1 in.) (Table 7.4). It includes large sessile and motile invertebrates and in some instances authors have included bottom-living or demersal fishes as well. Here the demersal fishes have been treated separately (see below). Most of the invertebrate species encountered are documented in the monograph of Gulf of Mexico biota edited by Felder and Camp (2009); only a small fraction of this size group remains undescribed, compared to the macrofauna above, in which approximately 50 % remain undescribed.

An early goal of megafauna studies in the deep Gulf of Mexico was to document and describe patterns of bathymetric (depth) zonation (Roberts 1977; Pequegnat 1983; Pequegnat et al. 1990). The simplest approach has been to tabulate the depths with the most rapid change in species composition. This is done by observing the depth range of each species or the depths at which each species starts and then stops along the entire bathymetric gradient. Pequegnat (1983) and Pequegnat et al. (1990) used this approach and followed the overly intricate zonation nomenclature of Menzies et al. (1973) to describe Gulf of Mexico zonation patterns. Rather than looking at bathymetric starts and stops, Roberts (1977) and Pequegnat (1983) calculate percent similarities between individual skimmer samples. Roberts (1977) described four depth-related zones in the De Soto Canyon. As noted above, Wei et al. (2010a) used percent similarities to describe four zones that conformed to broad depths in the macrofauna across the entire northern Gulf of Mexico.

The compendium by Pequegnat (1983) is the most comprehensive account of Gulf of Mexico megafauna (Figure 7.64). It is a product of the environmental consultancy TerEco Corporation as a report of contract work for the MMS, but unfortunately, it was never published in the open literature either as a stand-alone book or as an individual or set of peer-refereed papers.[2] The groupings of species were determined using percent similarities, and then illustrated with a cluster diagram and a site-by-site foldout matrix illustration that is rarely used. An atlas-like section gives bathymetric distributions and quantitative abundances relative to depth of numerous species. These species distributions are presented as modified whisker plots. Each species has a dedicated page that includes the depth/abundance data, an illustration of the organism and a map of the sites where it was encountered in the Gulf of Mexico. Both fishes and large invertebrates captured with the skimmer are included. A peculiar feature of this survey was the lack of sampling in the prominent Mississippi Trough, which later studies found to be very important to deep Gulf processes and faunal groupings (see Rowe and Kennicutt 2008). It may be that Pequegnat was trying to describe the natural six zone zonation pattern with depth that Menzies et al. (1973) suggested was a worldwide feature, and Pequegnat suspected that a canyon fauna would be an exception to the rule. Or it may be

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[2] It is however available online at http://www.data.boem.gov/PI/PDFImages/ESPIS/3/3898.pdf, thanks to the DOI's BOEM.
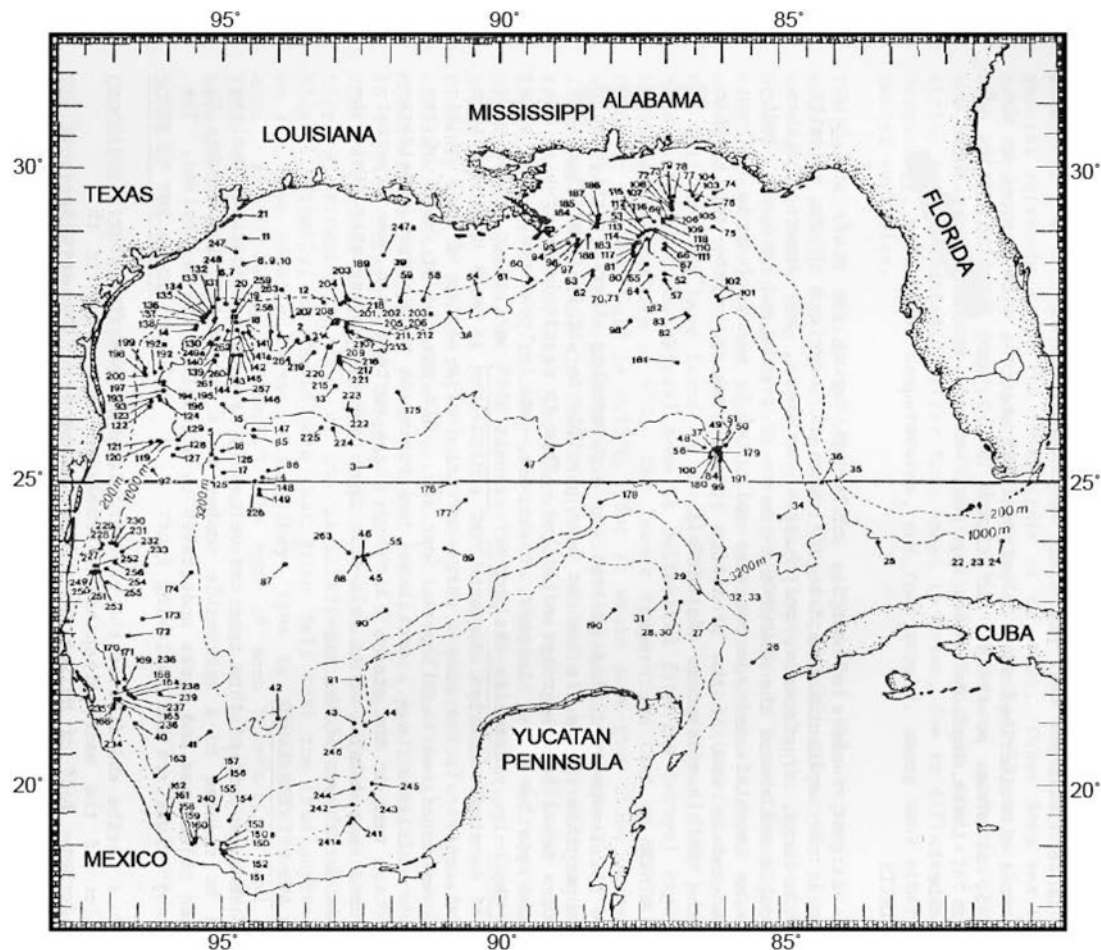
Figure 7.66. Distribution of sites sampled in the Gulf of Mexico for deepwater benthos by the R/V *Alaminos*, Office of Naval Research vessel operated by Texas A&M University (from Pequegnat 1983).

that the contractors (MMS) had advised Pequegnat against sampling there. It is interesting to note that the R/V *Alaminos* sampling (Figure 7.66) was not excluded from the Mexican EEZ as would be the case today without special permissions or participation with a Mexican institution on a Mexican research vessel.

An example of the illustrations in Pequegnat (1983) is the sea star, *Dytaster insignis*, with its broad depth distribution (Figure 7.67). The sea star is also common on the northwest Atlantic coast. The skimmer was particularly good at sampling the Echinodermata. Note that each major group within the echini has an MDM, as was observed in the macrofauna discussed above (Figure 7.68). However, note too that each major group's depth of maximum number of species is somewhat different. It is presumed that the megafauna prey on the macrofauna (Rowe et al. 2008b), but how this predation shapes or alters the variations in macrofauna diversity, as a function of depth is not known.

The megafauna are assumed to decline in numbers and biomass as a function of depth. They conform to the following equation:
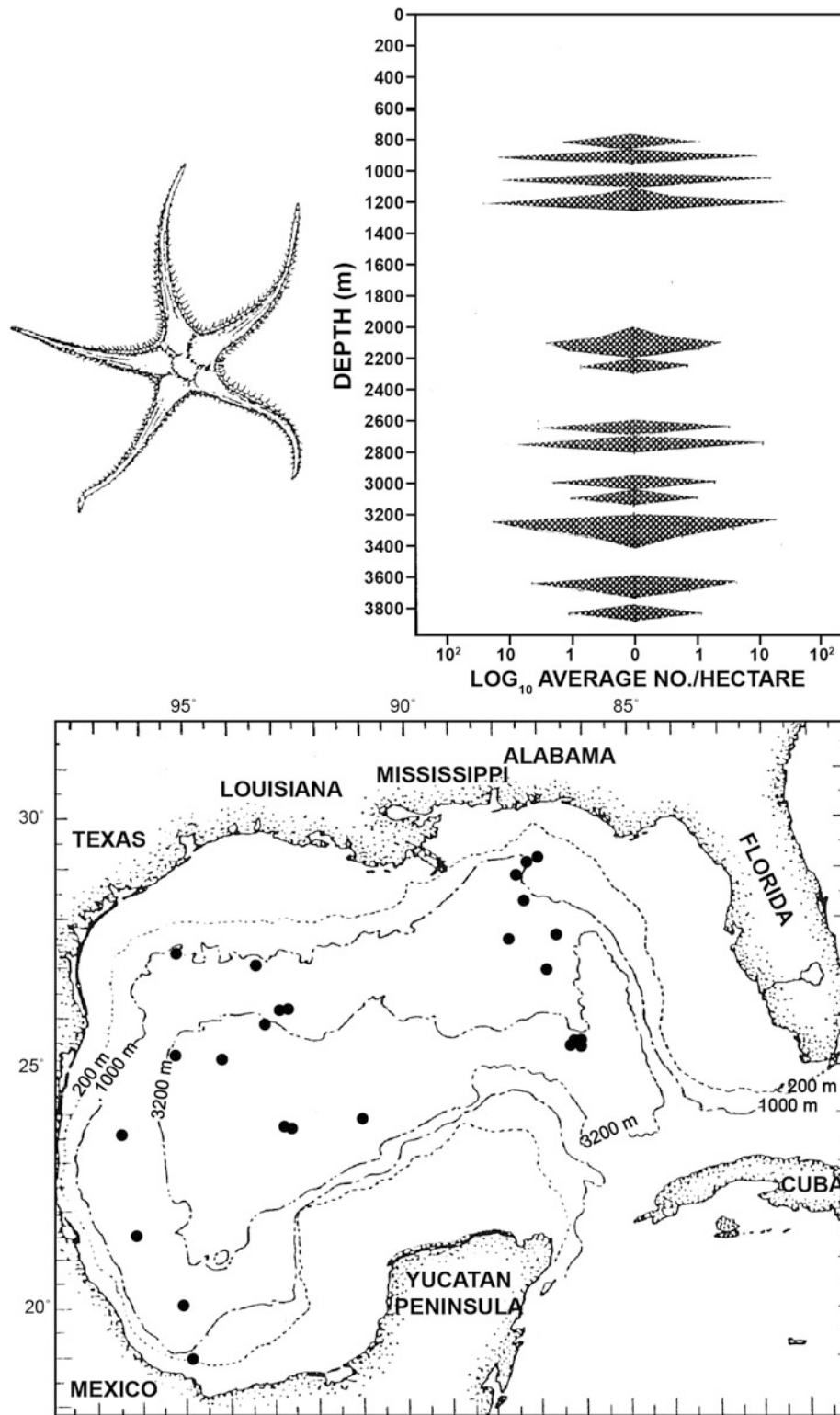
Figure 7.67. *Dytaster insignis*, a sea star, as an example of numerous illustrations of megafauna and fish distributions (from Pequegnat 1983).
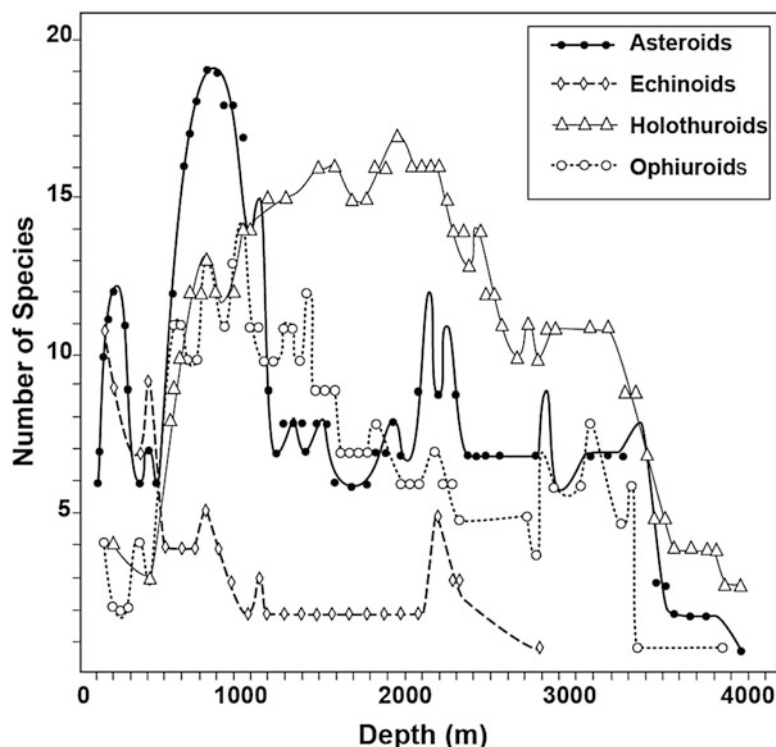
Figure 7.68. Bathymetric distribution of numbers of echinoderm species sampled by the R/V Alaminos using a skimmer (from Pequegnat 1983).

$$\text{Megafauna biomass } \left(\text{mg C/m}^2\right) = 12.1 - 2.36(\text{depth in km}), \quad r^2 = 0.02$$

But the relationship presented in Rowe et al. (2008b) was not statistically significant at the $P = 0.05$ level. Mean values ranged from about 12 mg up to a maximum of 55 mg C/m^2 on the upper slope down to less than 0.5 mg C/m^2 on the SAP.

Among the most fascinating megafauna of the Gulf is the giant isopod, *Bathynomus giganteus*, the largest isopod known (Briones-Fourzan and Lozano-Alvarez 1991). Individuals can be more than 35 cm (13.8 in.) in length. The largest weigh up to 1.4 kilograms (kg) (3.1 lb) wet weight. An exponential length–weight relationship was developed from collected specimens, and a linear relationship was found between body length (BL, cm) and body width (BW, cm), as demonstrated by the two equations below (Briones-Fourzan and Lozano-Alvarez 1991):

$$\text{Log Weight(kg)} = (-1.428 \log \text{BL}) + 2.957, \quad r^2 = 0.996$$

$$\text{BW} = 0.4338 \text{BL} - 0.092, \quad r^2 = 0.982$$

These peculiar organisms occupy the upper slope at depths from about 200 to 1,000 m (656–3,281 ft). Although often taken in deep trawls, the most successful sampling has used large, steel wire baited traps. The animals are assumed to be general scavengers of small macrobenthos but also feed on slow-moving megafauna such as echinoderms. They appear to exhibit seasonal reproduction, although evidence for this is equivocal. Their age, respiration, and growth rates remain unknown, but it is reasonable to suggest that they play a role in cropping seafloor macrofauna. They can be kept alive in the laboratory for months and thus

could be valid subjects of experimentation in the future (Mary Wicksten, 2012, Texas A&M University, personnel communication).

Solitary Cnidaria (sea fans, sea pens, anemones) are salient sessile members of the megafauna. Sea fans occur on small tar pillows on the Shenzi (oil and gas) field but not on soft mud nearby (Williamson et al. 2008). MacDonald et al. (2004) observed them associated with asphalt volcanism in the Campeche Knolls in the southern Gulf of Mexico. Trawl surveys in the northern margin of the deep Gulf of Mexico have noted that large anemones occur most frequently associated with submarine canyons and are especially common in the De Soto Canyon (Ammons and Daly 2008). It should be noted that these sessile organisms are all filter feeders that depend on a rain of detritus for nutrition, thus limiting their distributions to locations where a nutritional POC source is available. For food, they may also depend on horizontal or depth-contour controlled bottom currents to supply them with organic particulate material.

As illustrated in Figure 7.68, the echinoderms are an important component of the deep megafauna. Within this diverse phylum, the holothuroids (sea cucumbers) appear to be the most widely distributed in the deep Gulf of Mexico, with a prominent MDM. However, they are difficult to sample. This is suspected because of trawling and multishot seafloor photography in the same locations of the seafloor. For example, photographs of a species of *Peniagone* sp. illustrated that it maintained a density of about 160,000 individuals per hectare (10,000 m^2 or 107,640 ft^2). The mean length of this species in these photographs was about 2.75 cm, or just over an inch. But individuals of this species were never captured in the trawls at the same location and time. Many holothuroids are more or less neutrally buoyant and thus it was thought that these individuals were not captured because they were pushed or swept away by the trawl's bow wave. Many species of holothuroid are known to be able to swim or drift slowly over the deep seafloor. This information is contained in the *Northern Gulf of Mexico Continental Slope Study Annual Report, Year 3, Vol II, Technical Report* (Gallaway et al. 1988). This preliminary report is a font of knowledge that is not found in the final report (Pequegnat 1983) or a lone published summary of the work (Pequegnat et al. 1990).

According to Ziegler (2002), the invertebrate megafauna densities of the continental slope and abyssal plain of the Gulf of Mexico are one to two orders of magnitude less than equivalent depths in other studies at higher latitudes (Rowe and Menzies 1969; Ohta 1983; Lampitt et al. 1986; Mayer and Piepenburg 1996). This supports the suggestion that in general the Gulf of Mexico is oligotrophic (Smith and Hinga 1983), based on low densities and biomass of macrobenthos (see above section on macrofauna), but this generalization ignores the numerous slope assemblages supported by fossil hydrocarbons or the fauna in the Mississippi and De Soto canyons. While this generalization may apply to the open continental slope and the abyssal plain, it may not apply to exceptional habitats such as seeps and canyons where food supplies are enhanced.

7.6.4.5 Deepwater Demersal Fishes

The deep bottom-dwelling or demersal fish assemblages of the Gulf of Mexico are fairly well known (McEachran and Fechhelm 1998, 2006). Most species can be found in FishBase, where their worldwide distributions, age, maximum size, growth rates, and reproduction are documented. In the northern Gulf of Mexico, the species appear to occur in at least four somewhat overlapping depth-related assemblages (Roberts 1977; Pequegnat 1983; Pequegnat et al. 1990; Powell et al. 2003). Sampling deep-living species began in the 1950s by NMFS conducting exploratory fishing in the Gulf of Mexico and Caribbean aboard the *Oregon* II. Beginning in the 1960s, deep sampling on the R/V *Alaminos* by Pequegnat (1983) using a
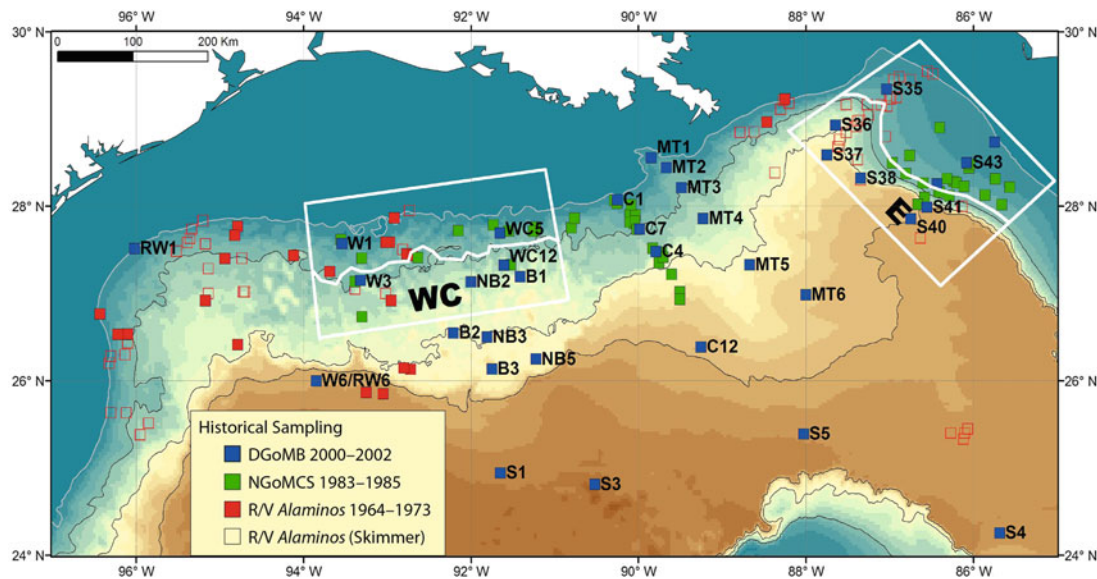
Figure 7.69. Epibenthic fish sampling in the deep northern Gulf of Mexico. The *solid symbols* are otter trawls versus *open symbols* for benthic skimmer. *Gray line* = 200 m isobath. The *black line* = 1,000 m isobath. The station names are used in the 2000–2002 sites (from Wei et al. 2012b).

skimmer resulted in a large dataset that sampled fish and invertebrates across a large spectrum of sizes. A creditable contribution of the latter was the semiquantitative estimates of fishes and megafauna that were based on the skimmer's bottom distance measuring odometer. Two other large surveys in 1983–1985 to 2000–2002 both used 40 ft semi-balloon or otter trawls (shrimp trawls) on a single warp to sample both megafauna and fishes.

Wei et al. (2012b) assembled all the demersal fish data from the above three *Alaminos* and *Gyre* surveys to determine if the fish faunal composition taken by the skimmer and the shrimp trawl were the same and also if there was any evidence that the fauna has changed during the 40 years over which the surveys were conducted (Figure 7.69). As indicated by the map, not all of the sampling was done at the same sites.

A cluster diagram of all the historical *Alaminos* samples (Figure 7.70, top) illustrates that there were four zones, according to all the data reviewed by Wei et al. (2012b). These are mapped across the area (Figure 7.70, bottom) and can be compared with the zones documented for smaller organisms above. They found no evidence that the skimmer data or time had affected the composition or the abundance of the fishes.

A cluster diagram of all the pooled data from 1964 through 2002 (Figure 7.70, top) was used to illustrate that the four zones were evident in both the old and the more recent data, according to Wei et al. (2012b). These are mapped across the area (Figure 7.71, bottom) and can be compared with the zones documented for smaller organisms above in the section on the megafauna and macrofauna. Wei et al. (2012b) found no evidence that the skimmer data or time had affected the composition or the abundance of the fishes with a 10 % similarity in species (the solid line); however, the cluster diagram does suggest that further structure exists within these large groups. This can be related to depth, but is likely a function of subtle differences in the habitats (Levin and Sibuet 2012).

Wei et al. (2012b) used violin diagrams to represent the depth and abundances of occurrences of the groups across the depth intervals using lumped data (Figure 7.72) and they separated the data as well into the most abundant species (Figure 7.73). These represent the range of the groups and the depths at which they are most abundant.
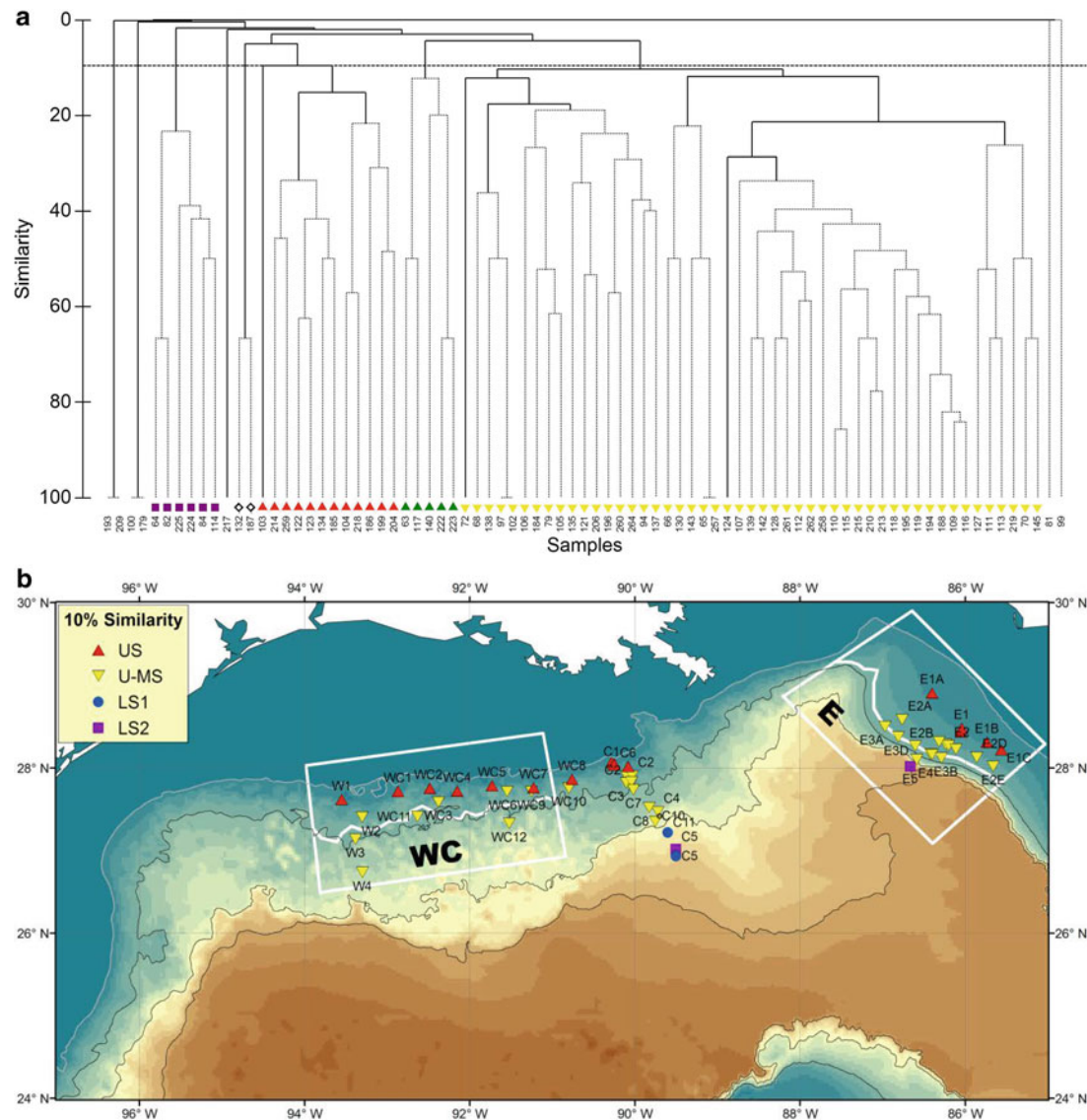
Figure 7.70. Epibenthic fish species composition and faunal zonation during the R/V *Alaminos* cruises from 1964 to 1973. (a) Group-average cluster analysis on intersample Sørensen's similarities. The *solid lines* indicate significant structure (SIMPROF test, *P* < 0.05). The *horizontal dashed line* shows 10 % similarity. (b) Distribution of the fish faunal zones with at least 10 % faunal similarity. *US* Upper-Slope Group, *U-MS* Upper-to-Mid-Slope Group, *LS1* Lower-Slope Group, *LS2* Lower-Slope-to-Abyssal Group. The *colors* on the cluster analysis dendrogram correspond to the locations of the *colors* on the map (from Wei et al. 2012b).

Multidimensional scaling (MDS) was used by Wei et al. (2012b) to view how environmental factors (as MDS1 and MDS2) affected the groups as a function of depth and as a function of the different cruises (Figure 7.74). The distances over the space in the figure are proportional to the similarity in species of the samples. That is, the shallow sites on the right were far different from the deep locations on the left. However, the red, yellow, green, and blue sites in the middle were different, but not by much (they hover close together in the center of space) in the top panel. On the other hand, the bottom panel illustrates that the colors representing cruises overlap a lot, indicating that the fauna was the same between them.
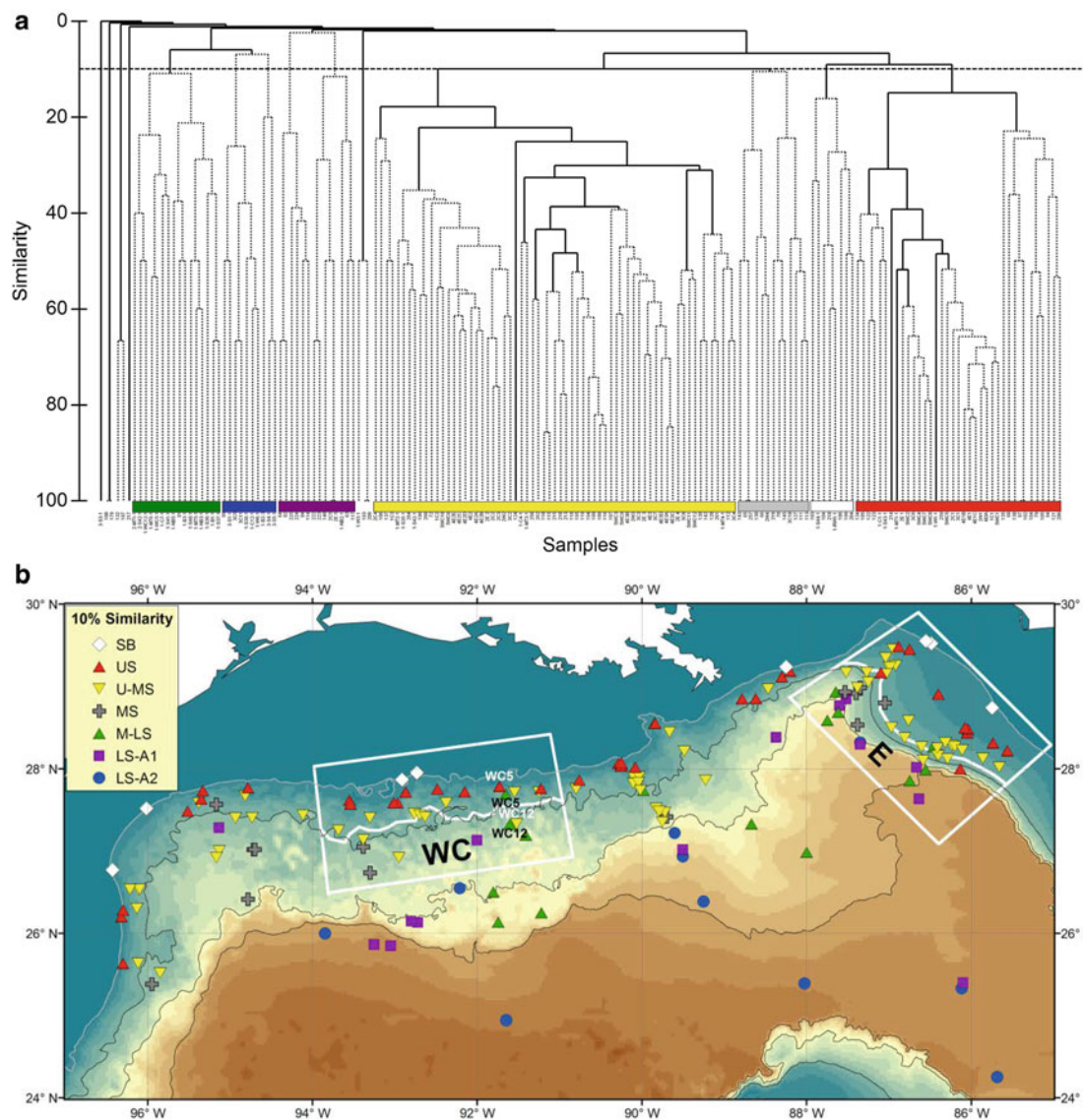
Figure 7.71. Epibenthic fish species composition and faunal zonation for the pooled data from 1964 to 2002. (a) Group-average cluster analysis on intersample Sørensen's similarities. The *solid lines* indicate significant structure (SIMPROF test, *P* < 0.05). The *horizontal dashed line* shows 10 % similarity. (b) Distribution of the fish faunal zones with at least 10 % of faunal similarity. *SB* Shelf-Break Group, *US* Upper-Slope Group, *U-MS* Upper-Slope-to-Mid-Slope Group, *MS* Mid-Slope Group, *M-LS* Mid-to-Lower-Slope Group, *LS-A1* Lower-Slope-to-Abyssal Group 1, *LS-A2* Lower-Slope-to-Abyssal Group 2. The *colors* on the cluster analysis dendrogram correspond to those on the map (from Wei et al. 2012b).

Wei et al. (2012b) plotted the fish similarities of MDS1 as a function of both depth and macrofauna biomass (Figure 7.75). The coherence of the dots indicates that depth is very important in determining where fish species live, and the right panel implies that this pattern exhibited by the fishes agrees with that of the biomass of the macrofauna. This could mean that they either depend on the macrofauna for food or that the same set of conditions that control the macrofauna also has a substantial influence on the distribution of the fishes, both of which seem logical.
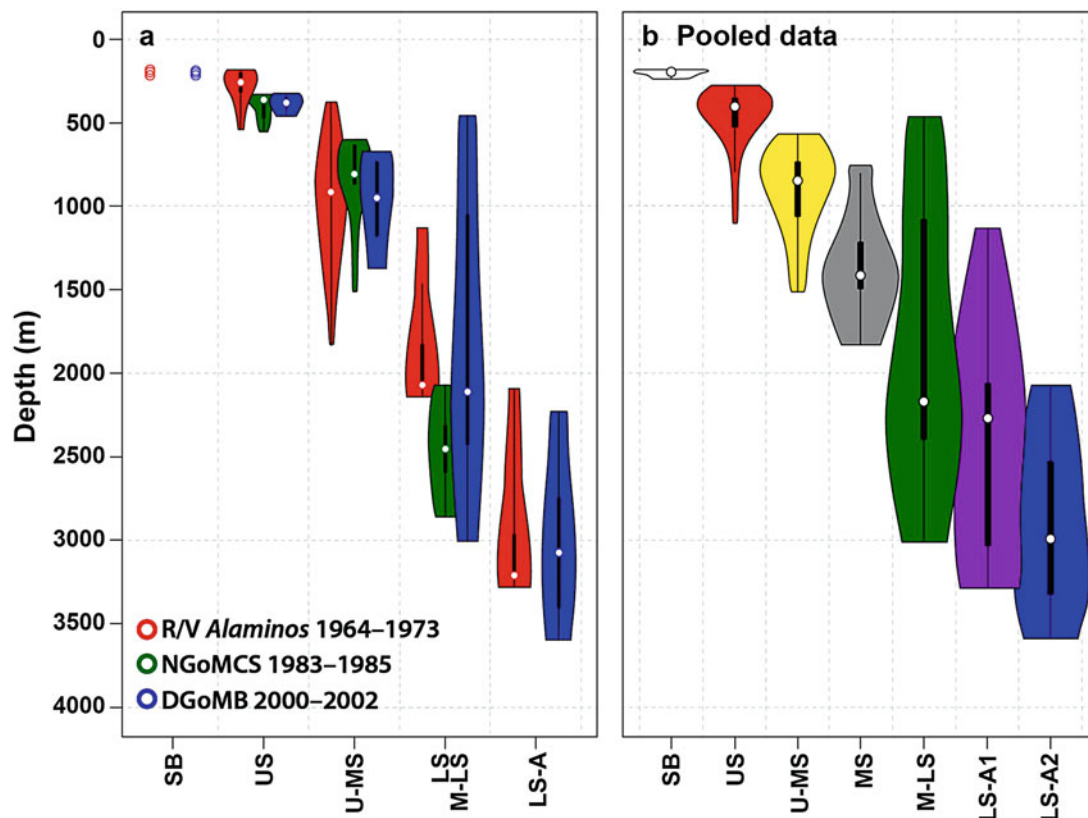
Figure 7.72. *Violin plots* of sampling depths for homogenous faunal groups in (a) R/V *Alaminos*, NGoMCS, and DGoMB studies, and (b) pooled data of all three surveys. A *violin plot* is a combination of *box plot* and kernel density plot (Wei et al. 2012b) that shows the probability of data at different values, the median and kernel density estimation. *SB* Shelf-Break Group, *US* Upper-Slope Group, *U-MS* Upper-Slope-to-Mid-Slope Group, *LS* Lower-Slope Group, *M-LS* Mid-to-Lower-Slope Group, *LS* Lower-Slope-to-Abyssal Group, *LS-A1* Lower-Slope-to-Abyssal Group 1, *LS-A2* Lower-Slope-to-Abyssal Group 2.

Biomass of the demersal fish assemblages declined with depth, according to Rowe et al. (2008b), in the following manner:

$$\text{Fish}\left(\text{mg C/m}^2\right) = 10.20\, e^{-0.93(\text{depth in km})}, \quad r^2 = 0.21$$

That is, demersal fish biomass declined exponentially down the continental margin to the abyssal plain. It can be surmised, therefore, that food supplies are increasingly limiting, and this lack of food supply is exacerbated as depth and distance from shore increase. However, it should be noted that while the above equation would predict about 10 mg C/m^2 at the shallow margin of the sampling, the shallow water data ranged from more than 40 mg down to about 2 mg C/m^2, suggesting that the upper margin is extremely variable. Also, there were hot spots of high biomass observed along the boundary between the shelf and the slope. Two of these were the De Soto Canyon and the Mississippi Trough in particular, according to Rowe et al. (2008b).

Commercial fisheries are extending down the continental slope in some regions of the world. However, this is unlikely in the Gulf of Mexico because the surface productivity is inadequate to support such a fishery, based on the data gathered to date.
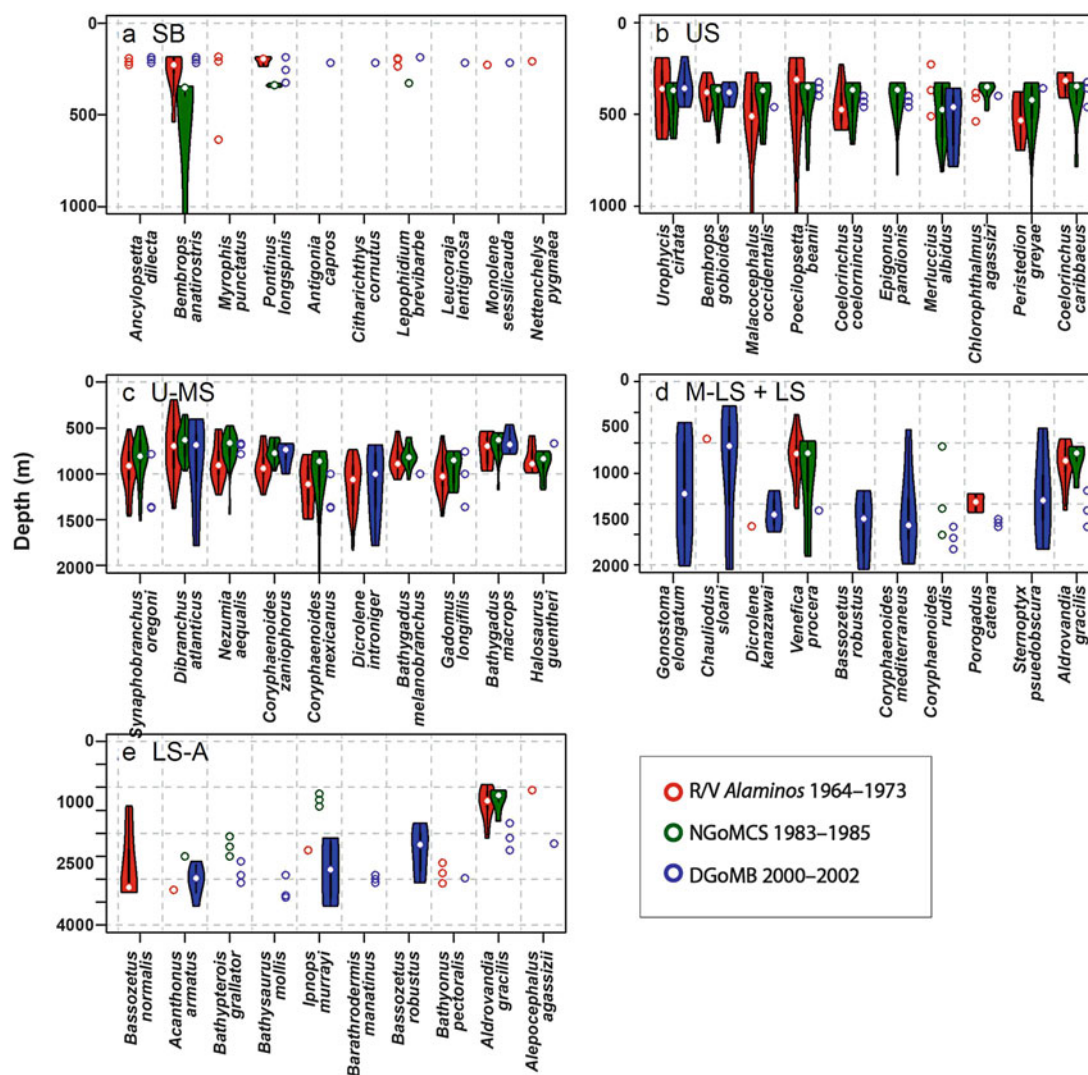
Figure 7.73. *Violin plots* of sampling depths for the top ten most common species (with highest occurrence) from (a) Shelf Break, (b) Upper Slope, (c) Upper-to-Mid-Slope, (d) Mid-to-Lower and Lower Slope, and (e) Lower-Slope-to-Abyssal Groups. *Colors* indicate different sampling times. The *violin plot* is a combination of *box plot* and kernel density plot (See Fig. 7.72). When the sampling depths were equal or fewer than three observations, the raw depth values are shown (from Wei et al. 2012b).

7.7 OFFSHORE COMMUNITY DYNAMICS, CARBON CYCLING, AND ECOSYSTEM SERVICES

Community function refers to the dynamics of the living components of assemblages of organisms. In the context of deep-ocean habitats this is considered to include such variables as growth, feeding, reproduction, recruitment, predation, mortality, respiration, and excretion (Figure 7.76). It can also include responses of the latter list to variables such as pollution, organic matter input, temperature, oxygen, and currents. In the deep ocean, these features of a
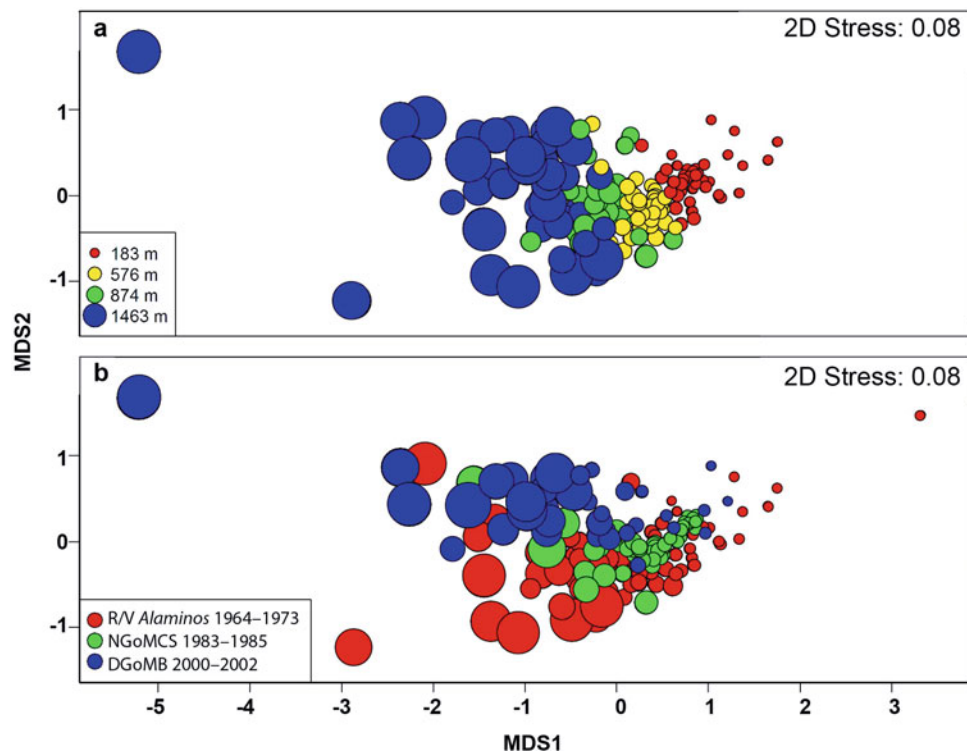
Figure 7.74. Nonmetric multidimensional scaling (MDS) on intersample Sørensen's similarities of pooled demersal fish data (from Wei et al. 2012b). The distances between samples represent dissimilarities in species composition. (a) Symbol sizes are relative water depth, with *small circles* being very shallow on the right and very deep on the left; *colors* indicate four depth intervals with equivalent numbers of samples. (b) Symbol sizes show relative depth, and *colors* indicate three studies of different sampling times.

community are substantially more difficult to assess than in shallow environments or compared to community structure characteristics (e.g., biomass, species composition, and diversity).

Methods for measuring community function include sediment traps to assess input of POC to the seafloor; use of natural and introduced radionuclides to define rates of change in time (Yeager et al. 2004; Santschi and Rowe 2008; Prouty et al. 2011); stable isotopes to infer food web structure; incubations in the laboratory or in situ to determine uptake rates of biologically active compounds such as oxygen, nitrate, and sulfide (Rowe et al. 2002, 2008a); and numerical simulations that solve for rates that are impossible to measure (Cordes et al. 2005b; Rowe et al. 2008b; Rowe and Deming 2011).

In the deep Gulf a number of studies have been undertaken to determine aspects of total level-bottom sediment community processes on the seafloor. Baguley et al. (2008) labeled sediment bacteria with ^{14}C and made them available to free-living nematode populations in small, repressurized incubation chambers. The results were inconclusive. There was little evidence that nematodes rely to any degree on bacterial cells as a food source. However, total microbial heterotrophic uptake of a ^{14}C labeled mixture of dissolved free amino acids was used to determine microbial uptake rates in combination with production of ^{14}C carbon dioxide and utilization of 3-H thymidine to determine respiration and growth rates simultaneously (Deming and Carpenter 2008). A free-falling benthic lander was used to implant incubation chambers on the seafloor to measure total SCOC (Figure 7.63). The secondary production of the
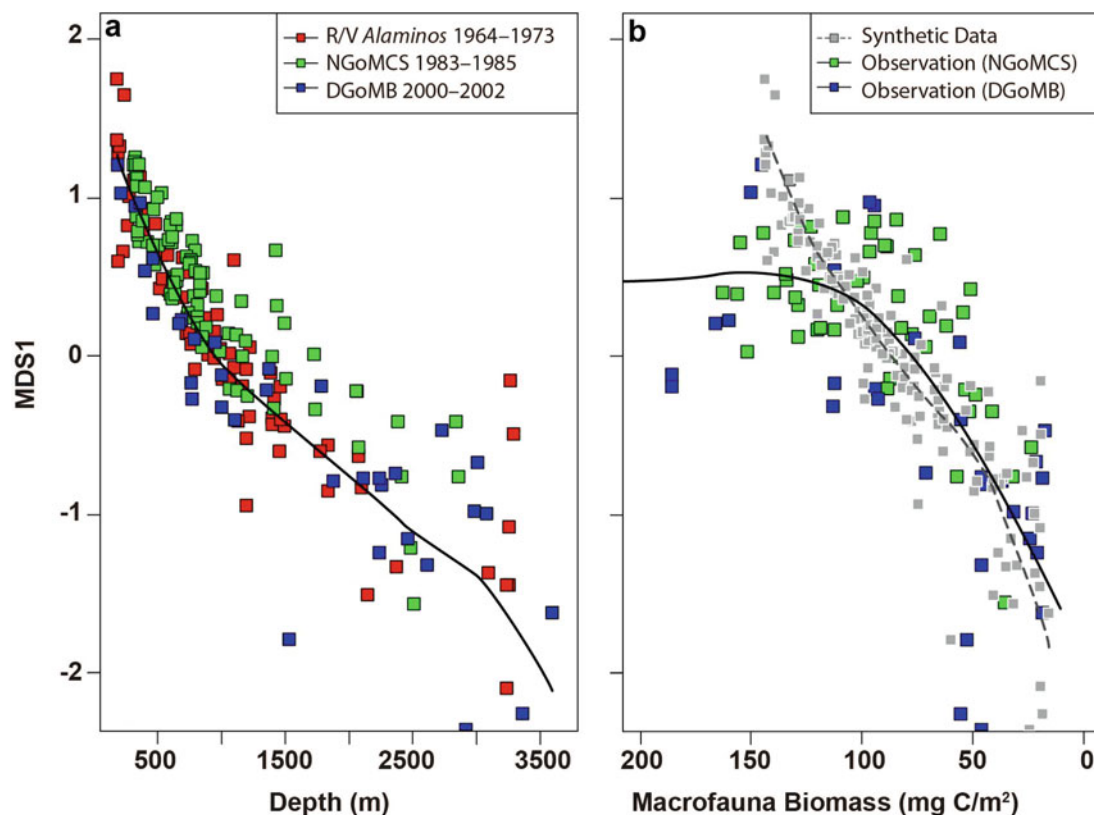
Figure 7.75. The *x*-axis of the nonmetric multidimensional scaling (MDS1) plotted against (a) depth and (b) total macrofaunal biomass, where MDS1 represents species composition of demersal fishes in multivariate space. The trend lines show the MDS1 as smooth spline functions of depth or macrofaunal biomass (from Wei et al. 2012b).

Rain of POC = Predation and Export + Community
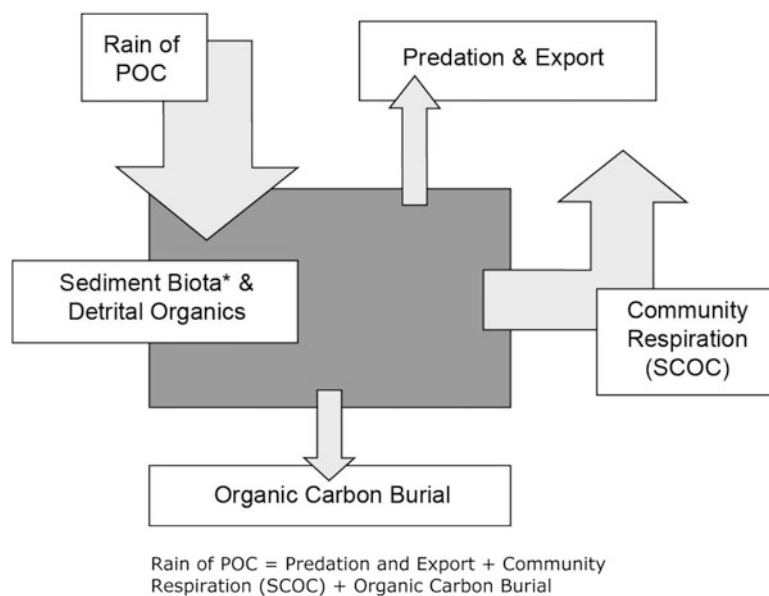Respiration (SCOC) + Organic Carbon Burial

Figure 7.76. Organic carbon budget for deep-sea bottom biota; * refers to "total living biomass" on and in the sea floor (microbes, meiofauna, macrofauna, and megafauna (from Rowe et al. 2008b; republished with permission of Elsevier Science and Technology Journals, permission conveyed through Copyright Clearance Center, Inc.).

Figure 7.77. Four food web carbon budgets at depths 0.4 km (*upper left*), 1.5 km (*upper right*), 2.6 km (*lower left*), and 3.6 km (*lower right*) (from Rowe et al. 2008b; republished with permission of Elsevier Science and Technology Journals, p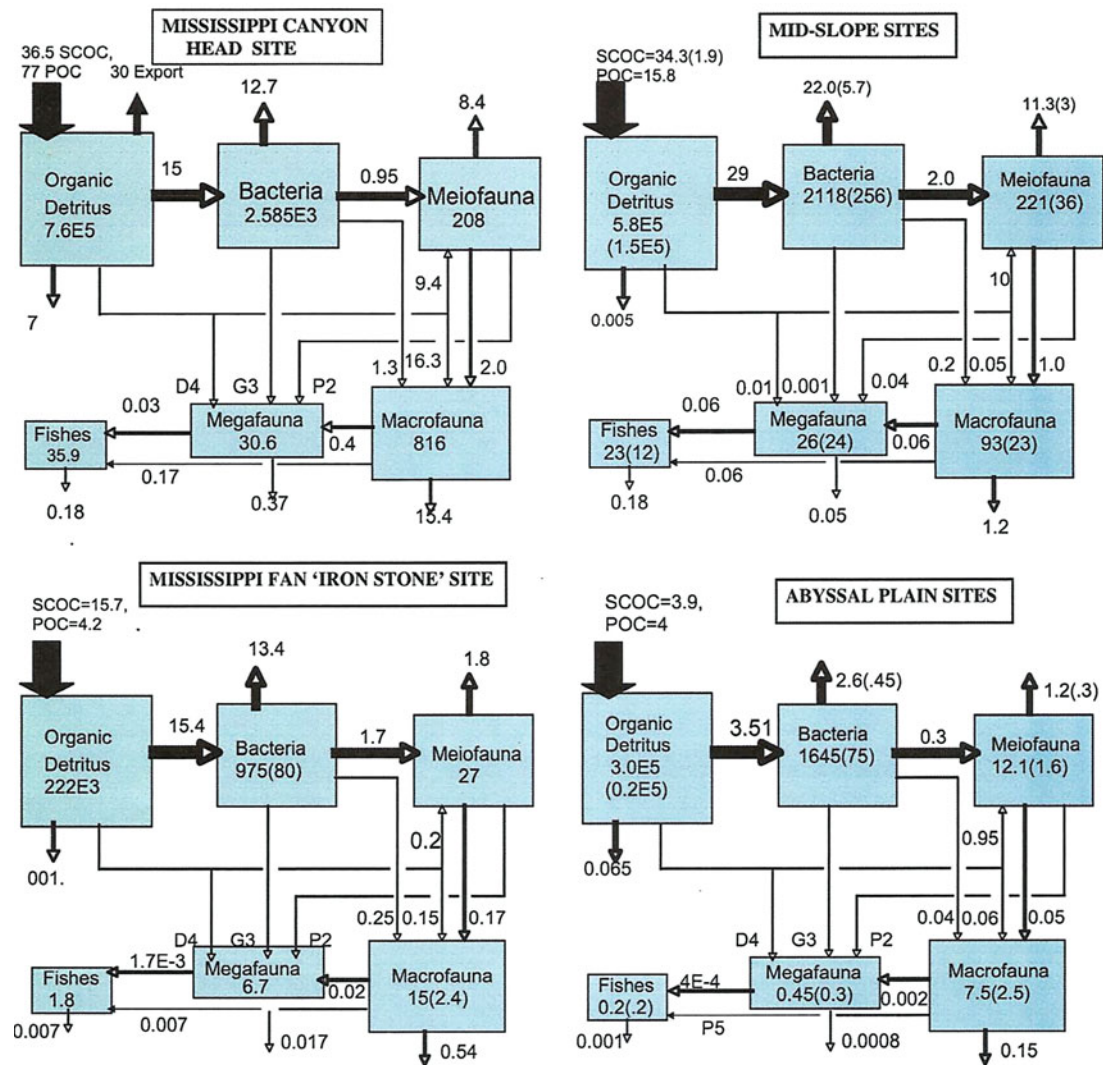ermission conveyed through Copyright Clearance Center, Inc.), in mg C m⁻² for the *boxes* and mg C m⁻² day⁻¹ for the *arrows*.

dominant amphipod *Ampelisca mississippiana* was estimated in the head of the Mississippi Trough using size frequencies in the population (Soliman and Rowe 2008), but it is rare that such rates can be measured in deep water because growth is slow, organisms are small, and numerous samples are required over time.

All of the stock and process data collected above during the DGoMB 2000–2002 survey have been incorporated into a model of presumed food webs at four deep locations: the Mississippi Trough head, at mid-slope depths, in the lower slope/abyssal iron stone region and on the abyssal plain (Rowe et al. 2008b) (Figure 7.77). Processes are driven by the input of POC as estimated from the SCOC regression equation (Figure 7.63) and model-estimated input inferred from satellite-determined surface chlorophyll *a* estimates (Biggs et al. 2008). This POC input to the organic carbon pool (Morse and Beazley 2008) is then divided up into five biological size categories (bacteria, meiofauna, macrofauna, megafauna, and fishes) using
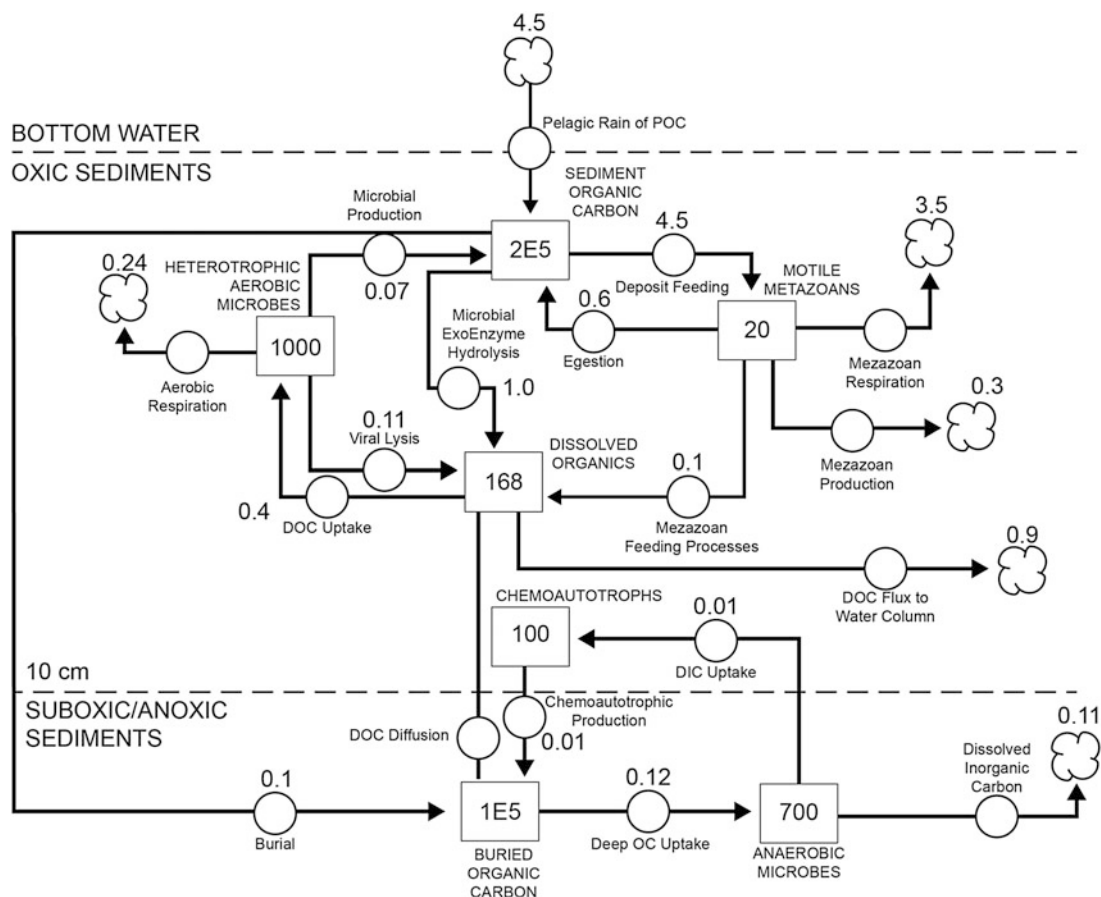
Figure 7.78. Model of carbon cycling by seafloor bacteria in relation to transformations from POC, by invertebrates, into DOC, thus reducing the role of bacteria in the processes (redrawn from Rowe and Deming 2011; reprinted by permission of Taylor & Francis Ltd.). The units are mg organic C/m^2 for the stocks (*boxes*) and mg organic C/m^2/day for the fluxes (*arrows*).

carbon as the basic model currency. The habitats at four depths are pictured: Mississippi Trough, mid-slope, iron stone area on the Mississippi Fan, and the abyssal plain, with standing stocks and total carbon flow decreasing exponentially as depth increases.

In the original rendition, most of the organic carbon was recycled by the bacteria, but a more recent assessment of the original rates in Deming and Carpenter (2008) led to a considerable downward revision of the microbial component (Rowe and Deming 2011) (Figure 7.78) because the microbes consume dissolved organic carbon (DOC) and not POC. The POC must be released into a dissolved form (DOC) before it is accessible to the bacteria. The authors suggest that this remobilization is done through "messy feeding" by motile invertebrates, viruses, or exoenzymes produced by the bacteria. How the bacterial assemblage as a whole would respond to an oil spill or free methane remains to be seen.

Table 7.5, accompanied by Figure 7.79, is a simplified summary of quantitative information on the major stocks and the fluxes or transfers between those stocks in the deep Gulf of Mexico as gleaned from the reviews in the above sections. This carbon cycle would require about 33 mg new N/m^2/day for the organic matter production by photosynthesis. The sources of this could be rain, dust, mixing up through the nutricline by storms, recycling from the zooplankton and

Table 7.5. Relationships in Carbon Biomass and Food Web Exchanges between Living Components of the Deep Offshore Water Column and Seafloor Generated from the Reviews in the Above Sections Taken from the Literature

Category	Biomass (mg C/m^2)	Gains (mg C/m^2/day)	Transfers (mg C/m^2/day)
Phytoplankton[a]	1,000 (euphotic zone, 0–100 m)	100–200 (net primary production)	50–150 (grazing zooplankton, loss to DOC, or sinks)
Zooplankton and mid-water fishes[b]	500 (0–1,500 m)	50–100 (by grazing on phytoplankton)	15–30 (eaten by predators, wastes sink to deeper layers)
Pelagic predators	5–50	10–20 (predation on zooplankton and mid-water fishes)	1–3 (sinks as dead carcasses or feces)
Deepwater scavengers[c]	1,200 (poorly known, low concentrations but integrated over 2.7 km of water column)	12[d] (consumed over the deep water column, most lost to respiration)	3–5 (transferred as particulate matter or aggregates sinking to the bottom)
Seafloor communities[e]	1,660 (mostly inactive microbes), 3–3.7 km depth	3–5 (rain of particles from above)	0.2 (long-term burial)

The five listed stocks are represented in Fig. 7.79. Respiration is not explicit
[a]El Sayed (1972) and Biggs et al. (2008)
[b]Hopkins (1982) and Hopkins and Baird (1977)
[c]Estimated from Sutton et al. (2008) from the Atlantic Ridge
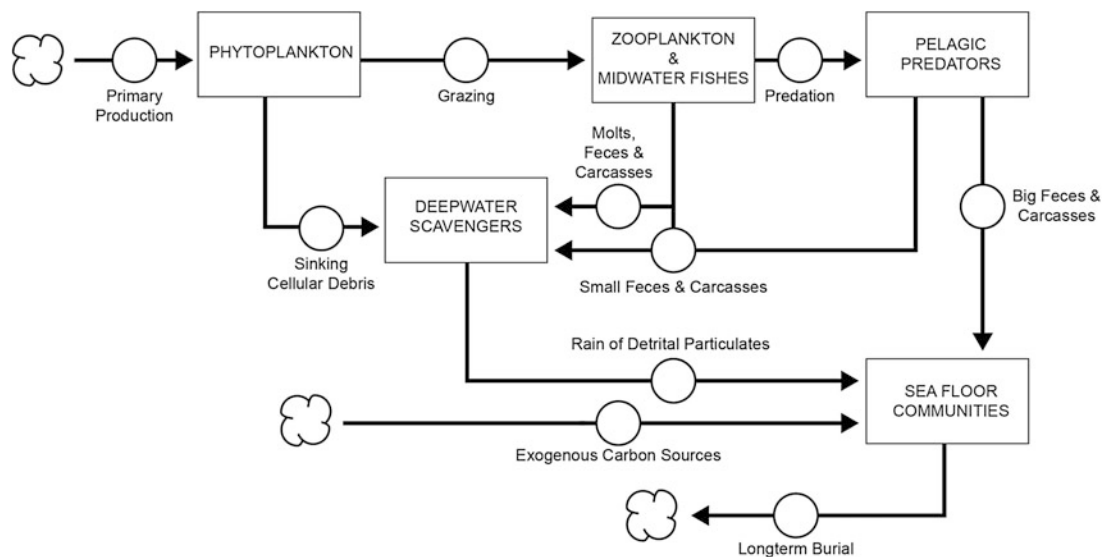[d]Modified from Del Giorgio and Williams (2005)
[e]Rowe et al. (2008b)

Figure 7.79. Simplified relationship between surface-produced organic matter and its routes to the deep ocean floor biota (modified from Rowe 2013).

microbiota, and nitrogen fixation by the species complex *Trichodesmium*. The major loss of organic matter from each heterotrophic stock is respiration, but that is not explicit in the budget. Even so, considerable carbon dioxide is produced over the deepwater column as the organic material that sinks into it is metabolized. The deep consumers in the water column are obscure deepwater scavengers. Although present in very low concentrations, this stock is integrated over a water column of about 2.5 km (1.6 mi). While this rendition represents the extreme deep abyssal plain of the Gulf of Mexico at a 3.2–3.7 km (2–2.3 mi) depth, at lesser depths up the continental slope, more particulate matter would reach the seafloor resulting in higher biomass, as is the case.

The effects of new or alien organic matter are not immediately apparent. Large plant detritus such as *Thalassia, Zostera* or *Sargassum* is probably of some importance. Carcasses may be as well. How fossil organics such as oil or gas would be incorporated into such a carbon budget is not as yet known.

7.8   STRESSORS AND ALTERED HABITATS

The Gulf of Mexico overall is an oligotrophic basin, in spite of its high margin-to-basin ratio and the input of nutrient-rich water from rivers, principally the Mississippi. The reason is that the largest source of water is the warm, nutrient-poor Caribbean. The nutricline is deep below the mixed layer and the euphotic zone. The result is that standing stocks of all levels of the complex, offshore food web are below comparable levels along the margins of other much larger ocean basins.

On the other hand, the Gulf suffers from a large region of hypoxia (less than 2 mg O_2/L) along the continental shelf of Louisiana. This is caused by nutrient loading and stratification resulting from the freshwater plume of the Mississippi River. The freshwater creates a vertical stratification that prevents mixing of oxygen-rich eutrophic surface water through the pycnocline into the bottom salty water. It is presumed that recreational and commercial fisheries are hampered by the condition, but the evidence for this is mixed. The fauna on the seafloor is composed of an assemblage of invertebrates that are adapted to low oxygen and organic enrichment. The area affected is directly proportional to spring flooding. The water depths of the hypoxia are 10–50 m (32.8–164 ft) and thus deepwater populations offshore are not affected by it.

The oil and gas industry at present has over 6,000 platforms in the Gulf of Mexico (Figure 7.80). This does not include PEMEX in the southern Gulf. These platforms serve as habitat unlike any other, for better or worse. It is well documented that the platforms support large populations of sessile plants and animals within the surface euphotic zone and sessile attached animals at depths below the euphotic zone (Boswell et al. 2010). The effects on the seafloor appear to be mixed. Right below a platform, the bottom fauna can be diminished, whereas a halo several kilometers away can be enriched with greater numbers and biomass than would be encountered without the platform. Detailed surveys in deep water indicate that drilling mud disposed of adjacent to a well can result in anoxic or reducing sediments for a restricted area (several kilometers at most) where the fauna is low in diversity and numbers.

A risk that is sometimes acknowledged is that the seep communities rely on fossil hydrocarbons for carbon and energy. If the supplies are diminished by withdrawal by the oil and gas industry, what is left to support these peculiar communities?

Platforms increase the primary and secondary productivity within an ecosystem by increasing the surface area on which plants can grow. This new PP is supplied with adequate nutrients by recycling of plant organic matter by the attached invertebrates and browsers within the complex of producers and consumers within the restricted habitat. Excess detritus that sinks
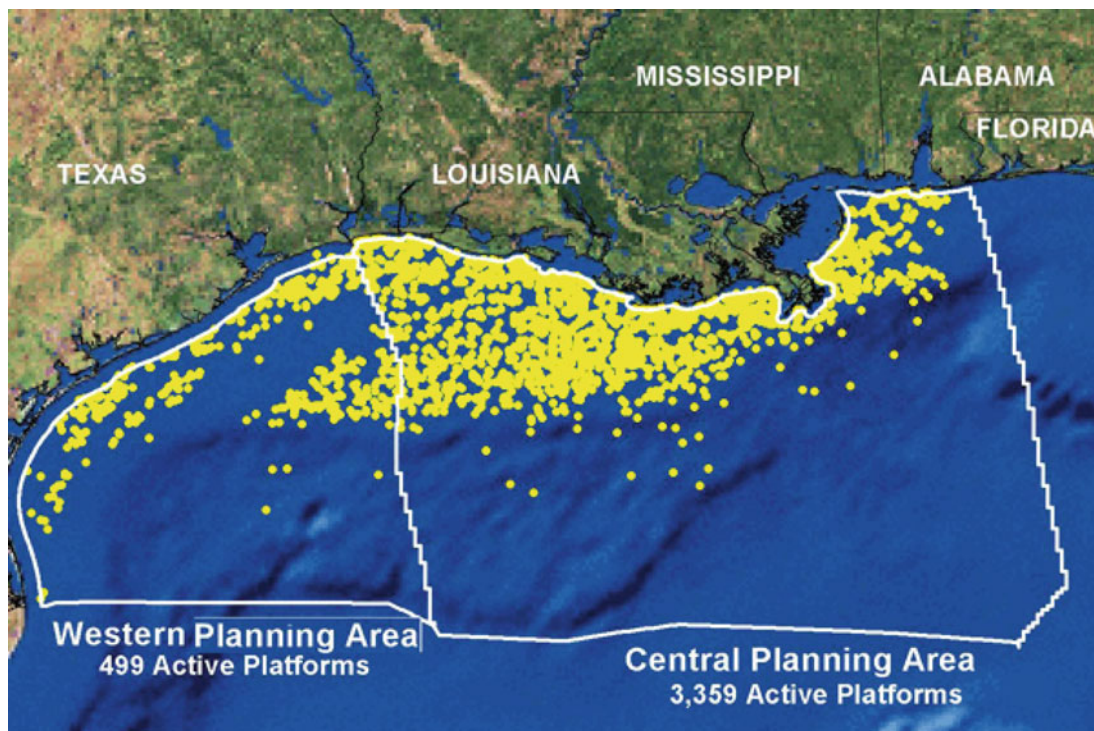
Figure 7.80. Offshore platforms in the Gulf of Mexico that serve as substrate for epibenthic organisms and habitat for numerous species of fishes popular in recreational fisheries and to commercial party boat patrons: map of the 3858 oil and gas platforms in the Gulf of Mexico in 2006. The size of the *dots* used to note platform locations is highly exaggerated and the density of platforms is low (http://oceanexplorer.noaa.gov/explorations/06mexico/background/oil/media/ platform_600.html).

below the platform nourishes a deeper fauna. These processes can theoretically lead to low oxygen below a platform, but the rates of this input have not been established. The productivity of the continental shelf ecosystem would be substantially less without the platforms, but it is presently impossible to calculate this difference.

The numerous platforms are popular sites for recreational fishers and charter boat captains. Many fear that the removal of platforms after wells are no longer producing will remove and eliminate these important habitats. Some believe the removal of this widespread spatial rugosity will have severe effects on recreational fishing in the northern Gulf of Mexico (Joe Surovik, Coastal Safari Charters, personal communication).

The continental shelf of the Gulf has been subjected to shrimp trawling for almost a century (Watling and Norse 1998; Wells et al. 2008). Practically every square kilometer of surface is dragged over on a yearly basis. The exceptions are the sanctuaries such as the FGBNMS and where corals or platforms physically prevent bottom trawling. The effects of the trawling are not immediately apparent because the baseline prior to trawling is not known (Peterson et al. 2011).

It is widely believed that fishing pressure in general, worldwide, has led to an overall decrease in the mean size of the largest predatory species of finfish (Pauly et al. 1998). This is probably true for the Gulf of Mexico, but there is no historical baseline on which to verify this.

There is widespread support for regulating human activities in the upper continental slope zone because of the sensitive nature of the vulnerable DSC biotope (Rogers 1999). This

assemblage is restricted to a limited set of environmental variables (rain of organic particulate matter, low and invariable temperatures, solid substrate, lack of predation), foundation species appear to be slow growing and old (decades to centuries), and the foundation species provide habitat structure to a wide variety of organisms, even though they are structurally delicate. These areas are termed vulnerable marine ecosystems (VMEs) by the International Council for the Exploration of the Sea (ICES). In addition to the corals, VMEs can contain large sponge aggregates (*Geodia* spp., *Pheronemia* spp.). Organizations supporting efforts to protect the upper continental slope VMEs are the Alaska Conservation Foundation, Earth Friends, The Rockefeller Brothers Fund, the Surdna Foundation, and the Pew Charitable Trusts, among others (Roberts and Hirschfield 2004), in addition to ICES. International agreements and national legislation to protect VMEs would be similar to marine protected areas (MPAs) and critical fisheries habitats (CFHs) in terms of regulating activities deemed harmful. According to Roberts (2002) the biggest threat to upper continental slope VMEs from human activity is bottom trawling, although oil and gas industry prospecting and production, anchoring, and some other forms of fishing might also pose some potential threats.

Overburdened sediments on the outer margin of the shelf and the upper continental slope can collapse, moving large masses of sediments downslope. These cataclysmic movements leave scars in the margin they left and hillocks where they come to rest. This process erodes away the shallower seafloor communities and then buries others, both potentially wiping out the biota of areas that are tens of kilometers in cross section. Altered or unexpected patterns in natural and bomb-produced radionuclides in the sediments are good after-the-fact evidence of where mass sediment slumping has occurred (Santschi and Rowe 2008). Such mass movements can also threaten oil and gas activities on the seafloor.

While the effects of actions near well heads on the biota on the shelf and offshore are fairly well documented (CSA 2006), the effects of massive blowouts and excessive oil, gas, and dispersant contamination remain unknown as yet. Human-derived trash is frequently encountered (Wei et al. 2012c), but deleterious effects of these alien materials have not been documented.

While hurricanes are known to have profound effects on coastlines, it should be recognized that they can resuspend sediments down to tens of centimeters out on the continental shelf to water depths of at least 50 m (164 ft). The wave action on the bottom is known to completely reorganize seafloor assemblages of organisms. For example, the well-adapted polychaete worm fauna that survives hypoxia off Louisiana was replaced by a more typical invertebrate assemblage after hurricane Katrina. Ironically, that new fauna turned out to be more susceptible to the stress of the following summer's hypoxia (Nunnally et al. 2013).

The effects of climate change on the offshore biota of the Gulf of Mexico are open to conjecture. More drought conditions will increase salinities nearshore and in isolated or closed embayments. Wet conditions will have the opposite effect: flooding will intensify or enlarge the hypoxic region off Louisiana. Increased water temperatures may be deleterious to organisms during the summer that are already near their upper limit of temperature tolerance. Lowered pH may make calcium carbonate deposition by organisms more difficult. A slight rise in seafloor temperatures in the areas of methane clathrate deposits may cause them to de-gas more intensively or even to break loose from the bottom.

7.9 REMAINING UNKNOWNS

Although the data to date suggest that seeps do not influence the nonseep fauna, it is difficult to accept that multiple seeps occurring in close proximity over an extended area of the bottom do not harbor their own associated sediment fauna. The hydrocarbon sources could

fertilize adjacent fauna that is characteristic of a depth range or they could be supporting their own unique assemblage of species adapted for gassy or oily sediments. The continental shelf and slope are composed of layers of pelagic and terrigenous mixtures of sediment that overlay thick salt deposits. It is reasonable to assume that the salt is squeezed out horizontally when it reaches the steep escarpments that line much of the basin. If salt does squeeze out from the escarpments horizontally, it could be forming slow-moving rivers of dense salt that would have unknown effects on the biota (William Bryant, TAMU, personal communication). The deep basin of the central Gulf of Mexico is bordered on three sides by extremely steep escarpments. The fauna that lives on these unique formations is virtually unknown, except for small targeted areas (Paull et al. 1984; Reed et al. 2006). No consistent investigations to date have documented how the fauna might be changing offshore as a function of time. Such changes could be seasonal and a function of PP that responds to sunlight, nutrients, or mixing. The continental shelf hypoxia associated with the Mississippi River plume is an example of recurrent seasonality nearshore, but offshore the deepwater effects of the spring bloom have not been demonstrated in the Gulf of Mexico, although seasonality is widely recognized on other continental margins.

In the *Year 3* report on the NGoMCS investigation in 1982, a section prepared by Greg Boland illustrated that the small (2–5 cm [0.80–2 in.]) sea cucumber, *Peniagone* sp., was observed in great abundances (hundreds per mi^2), but they were not sampled by a trawl. It is not known if this was a function of gear or timing of the sampling. We can thus ask what other organisms have not been sampled because we have not had the means to capture them? At great depths (between about 2–3.7 km [1.2–2.3 mi]) in the water column, the resident fauna is relatively unknown; presumably the sparse fauna subsists on a meager rain of detrital particles from the surface, but that is just a presumption: no data is available on what lives in this large volume of water and what supplies this fauna with nutrition. While some information is available on this layer in some ocean basins (Sutton et al. 2008), we know almost nothing of this layer in the deep Gulf of Mexico. This is a huge volume of water, and its biota will undoubtedly prove to be sparse; quantifying it needs to be accomplished nonetheless.

7.10 SUMMARY

The purpose of establishing a baseline for the status of the plankton and benthos of the open Gulf of Mexico is because these broad categories of organisms support, as food sources, all the major groups of larger organisms of economic importance or charismatic megafauna (mammals, birds, turtles). The health of the benthos and plankton groups—defined by their abundance, biomass, diversity, and productivity—determines or controls the larger organisms in the food web. The terminal elements of a food web are not sustainable if their food supplies fail or if their food sources are altered significantly. This summary does not include finfish, commercially important invertebrates, mammals, turtles, or birds.

This summary addresses communities or assemblages of organisms, sometimes referred to as biotopes, in a variety of habitats. These assemblages of organisms can each be defined by their quantitative abundances and biomasses and their biodiversities within volumes of water or sea surface areas, usually per m^2. In addition, where useful and available, the several dominant organisms are listed by their common and scientific names. Species lists are not provided, although references in the literature that contain such lists are given. The Gulf of Mexico offshore ecosystem is divided up into salient habitats, and each contains its own suites of organisms (e.g., assemblages or biotopes). These include (1) continental shelves, (2) deep continental margins and adjacent abyssal plain, (3) methane seeps, and (4) live (hard) bottoms, partitioned according to water depths [hermatypic coral reefs in the Mexican EEZ, coral banks

on diapirs (e.g., the FGBNMS, Alabama Pinnacles, FMG, Viosca Knolls, and Florida Litho-herms)]. In addition, some important exceptional habitats within those habitats are highlighted (shelf hypoxia off Louisiana, large submarine canyons [Mississippi, De Soto, Campeche], deep iron stone sediments, and asphaltine outcroppings).

The functional groups of organisms reviewed are (1) phytoplankton, separated into near-shore (neritic) and open-ocean assemblages, (2) zooplankton, again separated into neritic and offshore populations, with somewhat more extensive coverage of the ichthyoplankton because of its potential importance to fisheries, and (3) benthos, divided by habitat into level-bottom soft sediments, hard bottom coral-supporting sea floor and fossil hydrocarbon-supporting communities. In each case, some explanations are given about what biological processes or environmental characteristics of a particular habitat control the distributions of the organisms in question.

Several significant generalizations can be made based on the baseline information referred to above. In general, the low productivity and biomass of many of the larger habitats indicate that the Gulf of Mexico is oligotrophic compared to similar habitats at higher latitudes or continental margins characterized by tropical or equatorial upwelling. This generalization is based on geographically widespread assessments of phytoplankton, zooplankton, and benthic biomass. Deep benthos, regardless of size category, declines exponentially as a function of depth and delivery of detrital organic matter to the seafloor; the well-established statistical regressions of these declines tend to be below similar biomass estimates on other continental margins where such studies have been conducted. Likewise, the benthic biomass down across the continental margin of the northern Gulf of Mexico appears to be higher than that across the continental margin of the southern Gulf of Mexico. The deep zooplankton and the benthos species composition fall into depth-related zones along the continental margin of the northern Gulf of Mexico. That is, all groups of organisms appear to be zoned into discrete depth intervals, but with substantial overlap in species composition between zones.

Several important exceptions to oligotrophy are evident. The Louisiana continental shelf west of the Mississippi Delta is subjected to seasonal hypoxia because of excessive nitrate delivery in the river water and stratification caused by the freshwater. Ameliorating this harmful recurring condition is problematic; improving farming practices to reduce the nitrate loading and diverting the freshwater before it reaches the Gulf are possible helpful alternatives (Peterson et al. 2011). Much of the continental slope is characterized by patches of larger benthic organisms that are sustained by fossil hydrocarbons that seep up to the seafloor from deposits within the sediments. While many similar cold seep communities have now been discovered on continental margins worldwide, the Gulf of Mexico appears to support some of the most prolific that have been described to date. Clearly, what is known now about the species composition and the chemistry and physiological modes of existence of such communities is based on studies conducted in the Gulf of Mexico.

Another exceptional habitat type with high diversity and biomass are several large subma-rine canyons. It is presumed that they support high regional biomass by accumulating or focusing organic detritus. Likewise such habitats provide physical complexity that enhances species richness. Hard bottoms, sometimes referred to as live bottoms, are intermittently scattered across the entire Gulf of Mexico continental margin. They are inherently more difficult to evaluate because quantitative evaluations have to consider three dimensions in many cases. The hard bottom makes sampling difficult. Numerous sessile large benthic organisms, both animals and plants, attached to the seafloor in such habitats provide a diverse physical environment that provides niches for a long list of inhabitants, from small cryptic invertebrates to large finfishes. While diversity and species lists in such habitats have been evaluated with cameras and direct observations, quantifying biomass and rates of processes

remains extremely difficult if not impossible; comparisons are relative between such habitats. The shallow banks on the continental shelf contain hermatypic corals that depend on light because the corals contain photosynthetic zooxanthellae. Many such banks are important to recreational fisheries, as are the many habitats formed by offshore platforms. Such complex structures are also fascinating destinations for scuba divers. An important example is the FGBNMS. At greater depths, such as the Alabama Pinnacles, hard bottoms on seafloor prominences have long provided popular fishing spots, although they are too deep for recreational scuba. We know little about what lives on the unexplored escarpments surrounding the deep Gulf of Mexico central basin.

A major shortcoming of a summary of the diversity, abundance, biomass, and productivity of the lower-level components of the various habitats of the Gulf is a general lack of valid long-term (centuries-long) baseline information. This is especially true for the continental shelves; they have been fished extensively for decades or more and what is now observed may not resemble the biota that existed prior to extensive exploitation. The continental slope of the northwest Gulf of Mexico is composed of alternating mesoscale basins and diapirs. Each basin might present a different habitat, depending on its underlying fossil hydrocarbon deposits and its relation to settling particulate matter. Virtually nothing is known about the fauna of the many individual basins and how they compare with each other or with the biota outside of a basin. In terms of food webs, the case has been made in the appropriate sections that the major supplies of energy and carbon that support the food webs of most habitats are either (1) PP in surface water that creates the slow rain of POC through the water column, and (2) seeps of naturally occurring fossil hydrocarbons that support extensive but patchy seep communities. However we know little of the relative importance of alternative sources such as carcasses or *Sargassum* and shallow water-attached plants. While it is widely acknowledged that the continental slopes of the Gulf are subject to slumps of sediments and that turbidity flows have formed the Mississippi Fan and adjacent abyssal plain, we know little of how such dynamic physical processes might affect the fauna.

This review of the plankton and benthos of the Gulf of Mexico demonstrates that the principal ecosystem components, at the lower end of the food web (phytoplankton, zooplankton, mid-water fishes, and seafloor organisms) in most habitats are characteristic of an oligotrophic ecosystem; that is, the biota is relatively low in numbers and biomass compared to other continental margins (e.g., upwelling regions, temperate and polar latitudes). The principal cause of this oligotrophy is the source water from the Caribbean depleted of nitrate in about the surface 125 m (410 ft). The penetration of the LC coming up through the Yucatán channel spins off warm anticyclonic (clockwise) eddies that travel west across the Gulf of Mexico. These features induce a counter flow in the opposite direction. Depending on location, this combination of complicated surface currents can draw nutrient-rich water off the continental shelf into deep water, and phytoplankton production can thus be marginally enhanced offshore. Upwelling zones along the west coast of the Yucatán Peninsula and Florida are also characterized by some intensification of PP. Most of the offshore regions of modestly enhanced productivity can be observed remotely by satellites.

Populations of plankton offshore represent a near-surface fauna that declines with depth in a biocline: the further from the surface, the more depauperate the biomass. This biocline occurs in the top 100–200 m (328–656 ft), and by a depth of 1 km (0.62 mi) the standing stocks are extremely limited. All size groups of multicellular organisms decline exponentially as a function of depth and distance from land, so that the abyssal plain supports only a few mg C/m^2 of total seafloor biota (fishes, zooplankton, mega-, macro-, and meiobenthos). Biodiversity of the macrobenthos, measured as alpha or within-habitat diversity, follows a different pattern as a function of depth, depending on the taxon studied. In general there is a

mid-depth maximum (MDM) of the macrofauna alpha diversity at a depth of about 1.2 km (0.75 mi). Beta diversity (zonation or recurrent groups across a physical gradient) is clearly apparent in the macrofauna, megafauna, and fishes (Pequegnat 1983; Pequegnat et al. 1990; Powell et al. 2004; Wei et al. 2010a), and the steep decline of POC flux with depth has been suggested as a cause (Wei et al. 2010a). The oligotrophic (depauperate in biomass) conditions are reflected in low sediment mixing and biodegradation (Yeager et al. 2004; Santschi and Rowe 2008) and sediment community biomass and respiration (Rowe et al. 2008a, b).

The deep continental margin of the Gulf of Mexico has exceptionally complex layers of pelagic and terrigenous sediments overlying thick salt that is associated with fossil organic deposits (oil and gas). This oil and gas seeps up to the seafloor where it supports a peculiar fauna. The seep-supported assemblages are believed to live upwards of centuries, based on in situ growth rate experiments. Authigenic carbonate deposited at old seeps provides substrate for deep-living cold-water corals such as *Lophelia pertusa* that provide habitat for deep-living demersal fish, crustaceans, and echinoderms in a narrow depth band at the upper margin of the continental slope in the northeastern Gulf of Mexico (Sulak et al. 2008). Given that the open Gulf is relatively oligotrophic, these corals would not be expected to be as abundant in the Gulf of Mexico as they are in other more productive basins or at high latitudes.

Potential problems in sustaining the biota offshore include the possible effects of climate change, turbidity currents and slumps, eutrophication, oil and gas industry accidents, hypoxia, overfishing, trawling the bottom, and hurricanes. The luxuriant growths associated with pinnacles and salt diapirs are threatened by all the above, one way or the other. The establishment of areas such as the FGBNMS offers some protection from directly intrusive activities, but not from climate-induced changes that are more global. The thousands of oil and gas industry platforms in the Gulf seem to have had a positive effect on biodiversity and fishing, but there is no uniform acceptance of these relationships. Removal of platforms on the other hand is thought to be a threat to thriving recreational fishers and charter boat operators.

ACKNOWLEDGMENTS

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APPENDIX A: WEBSITES SUPPORTED BY BOEM, NOAA, AND USGS WITH COMPREHENSIVE INFORMATION ON THE BIOTA OF THE DEEP GOM

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www.gomr.mms.gov/PI/PDFImages/ESPIS/4/4320.pdf and 4/4877.pdf

NGOMCSS Study from l988:
www.gomr.mms.gov/PI/PDFImages/ESPIS/3/3773.pdf
www.gomr.mms.gov/PI/PDFImages/ESPIS/3/3774.pdf
www.gomr.mms.gov/PI/PDFImages/ESPIS/3/3695.pdf
www.gomr.mms.gov/PI/PDFImages/ESPIS/3/3696.pdf

Previous *Lophelia* studies:

www.tdi-bi.com/Lophelia/Data/Loph_Cru1_Rpt-Final.pdf
Also Cru2_Rpt-Final.pdf

Ongoing *Lophelia* studies by BOEM and NOAA:
http://fl.biology.usgs.gov/coastaleco/OFR_2008-1148_MMS_2008-015/index.html.