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An Overview of the Northern Gulf of Mexico Ecosystem

ROBERT B. SPIES, STANLEY SENNER, AND CHRISTOPHER S. ROBBINS

The Gulf of Mexico is a large marine ecosystem (LME) bordered by the southern United States, Mexico, and Cuba. This general overview of its northern portion covers physiography, significant oceanographic features, the influence of major rivers and freshwater, biological productivity, and food web characteristics. It then describes the pelagic and benthic components of the major habitats: oceanic (continental slope and abyssal plain), continental shelf and bays, estuaries, and marshes, with descriptions of prominent processes and some dominant organisms. For each habitat several species from a variety of trophic levels are introduced and their general role in the ecosystem discussed. In 2010 the northern portion of the Gulf was the site of the largest U.S. marine oil spill in history and is now the focus of an unprecedented restoration effort. Successful restoration of the northern Gulf will depend on an integrated view of this LME and the forces that maintain and change it. This introduction to the northern Gulf marine ecosystem should be useful for policy makers, informing decisions on proposed restoration actions.

INTRODUCTION

The Gulf of Mexico (Gulf), a productive, warm-water, large marine ecosystem (Heileman and Rabalais, 2005), accounts for about 20% of the commercial fisheries landings in the United States (NOAA, 2010), supports a very large recreational fishery, and produces 23% of the U.S. domestic oil supply and 7% of the domestic dry natural gas supply (USEIA, 2014). It is the ninth largest body of water in the world and supports a great variety of warm temperate and tropical marine species (Felder and Camp, 2009). The northern Gulf ecosystem has been greatly altered by human activities, including nutrient and pesticide loading, altered patterns of sediment transport and deposition from the Mississippi and Atchafalaya Rivers, rapid destruction of coastal wetlands, introduction of invasive species, heavy fishing pressure, and development associated with intense oil and gas activities, including spills (Odum, 1970; Turner and Rabalais, 1991; Boesch et al., 1994; Turner, 1997; Chambers et al., 1999; Clark et al., 1999; Rabalais et al., 2002; Nilsson et al., 2005; Priest, 2005, 2007; NRC, 2006; Howarth, 2008; Hupp et al., 2009; NOAA, 2014). Global climate change, ocean acidification, and sea level rise will likely cause further widespread changes in this ecosystem (e.g., Justic et al., 1996; Foodrie et al., 2009; Biasutti et al., 2012; Lowe et al., 2012).

This condensed overview of the northern Gulf ecosystem updates earlier, longer reviews (USFWS, 1954; Darnell and Defenbach, 1990; Gore, 1992) and describes the main features, processes, and structure of this ecosystem,

emphasizing the northern Gulf, the site of the April 2010 Deepwater Horizon MC 252 oil spill [hereafter referred to as the Deepwater Horizon oil spill (see papers in *Proceedings of the National Academy of Sciences* 90(8), 2012)]. The review begins with the physiography, climate, and oceanography, productivity and biodiversity, and climatic forces and oceanography. Then the main habitats of the Gulf are described: the pelagic and benthic habitats of the oceanic, continental shelf (near and offshore), and bays, estuaries, and marshes. For each habitat, the general biological features, processes, and a few of the prominent organisms and their roles are described.

There was—and still is—an enormous amount of attention directed at the northern Gulf following the Deepwater Horizon oil spill, and subsequent restoration programs are liable to be substantial, given the expected billions of dollars in restoration expenditures. Those restoration programs and any associated monitoring efforts will be most effective if they are grounded in an understanding of how the ecosystem is structured and functions and how ocean conditions affect the abundance, distribution, and resilience of species and habitats. Hence, an underlying purpose of this article is to provide an introduction to the northern Gulf of Mexico ecosystem, particularly for the benefit of decision makers and resource managers. We do not discuss the impacts of the Deepwater Horizon spill or other man-made or natural disasters, as they are beyond the scope of this brief overview, and the available information in spill effects is still very incomplete. Likewise, we do not discuss the fisheries of the Gulf, which would be a subject unto itself.

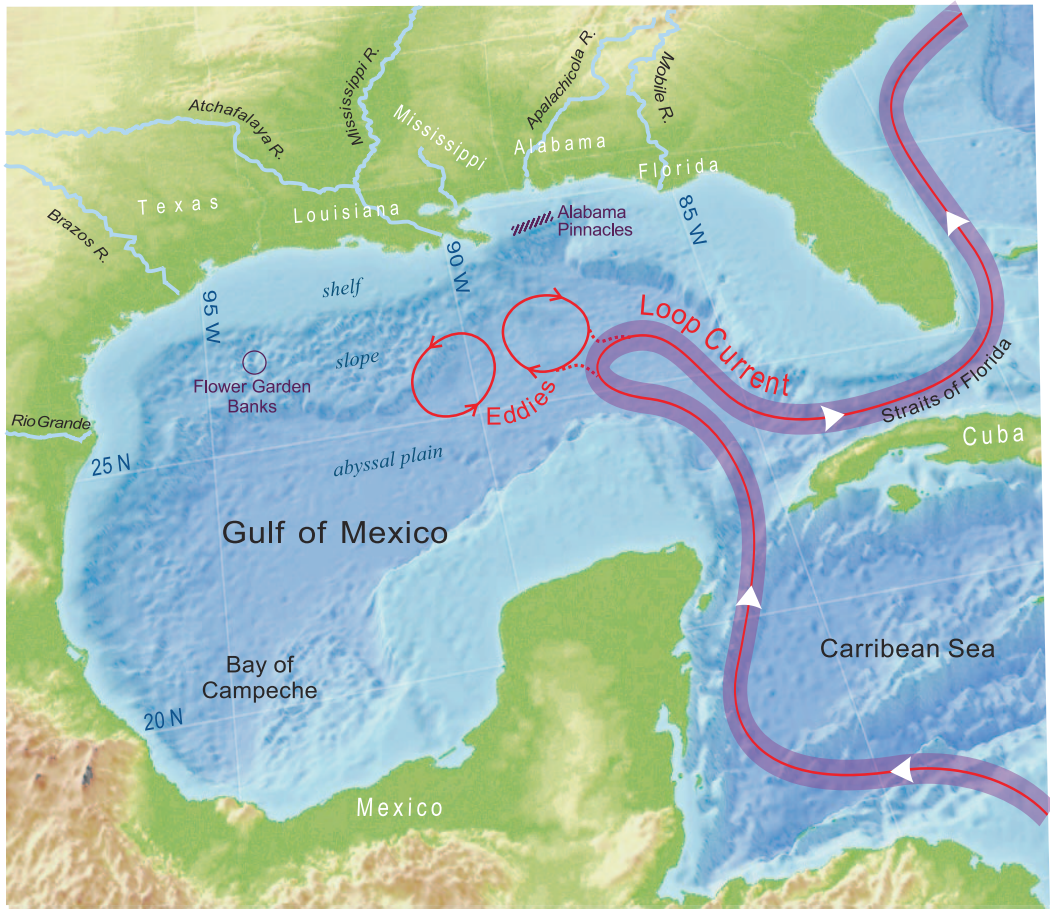


Fig. 1. Gulf of Mexico bottom topography, major rivers, and currents.

OVERVIEW OF THE NORTHERN GULF OF MEXICO ECOSYSTEM

Physiography.—The Gulf of Mexico is a semi-enclosed, warm temperate to tropical sea that is approximately 1.5 million km² in area, communicating with the Caribbean Sea north and south of the Island of Cuba and bounded by the United States to the north and by Mexico to the west and south (Fig. 1). The continental shelf off the west coast of Florida, most of Texas and Louisiana, and the Yucatan Peninsula is broad, but the shelf narrows near the outlet of the Mississippi River. The northern Gulf shelf is incised by river-derived canyons, notably the Mississippi and DeSoto Canyons.

The most extensive slope environments are located off northeastern Mexico, Bay of Campeche, Texas, and Louisiana and consist mainly of muddy sediments derived from continental erosion (Uchupi, 1968). Underlying salt diapirs provide some topographic complexity, the Flower

Garden Banks off Texas and Louisiana and the pinnacles off Mississippi and Alabama being prime examples. They affect local to meso-scale oceanography, as deep-water currents tend to be guided by bottom topography. Much of the sediment outflow of the Mississippi River continues downslope through the Mississippi Trough and Canyon, which bisects the continental slope close to its narrowest point.

The Gulf's abyssal plain (below 3,000 m), the long axis of which has a southwest to northeast orientation, has a maximum depth of approximately 4,000 m within the Sigsbee Deep in the central western sector and accounts for about 20% of the area of the Gulf [Harte Research Institute, 2014 (and references therein)]. The most biologically productive habitats occur in water depths of less than 20 m and account for 38% of the Gulf area. The seafloor is predominately muds in the north central Gulf (Balsam and Beeson, 2003), with some terrigenous sands along barrier islands. Continental

erosion is the main sediment source in the northern and western and southwestern Gulf of Mexico; biogenic carbonate sands derived from corals, mollusks, and algae dominate the seafloor off western Florida and the Yucatan Peninsula (Ewing et al., 1958; USGS, 2006a). Fringing barrier islands front much of the U.S. Gulf Coast, and warm-water coral reefs occur in southern Florida and off Texas and the Yucatan Peninsula (Aronson et al., 2005; Tunnell et al., 2007; Cancelmo, 2008). The varying climate, geology, and freshwater inputs interact to create habitats for sea life that range from beaches, marshes, shallow estuaries and lagoons, oyster reefs, bays, and continental shelf to rocky reefs, coral reefs, banks, deep-water cold seeps, extensive deep-water soft bottoms, and oceanic pelagic areas. The northern outer continental shelf has numerous drowned reefs and banks, including the salt diapirs, with hard substrate and epibiota that may help maintain reef fish populations (NOAA, 2014a).

Climate and oceanography.—The northern Gulf of Mexico is greatly influenced by semipermanent weather patterns in the western Atlantic Ocean, namely the Bermuda High for much of the year, but also by the dry, cooler, continental air flow in winter from the north (Wang et al., 1998). Summer winds are generally from a southerly direction. The Bermuda High results in a predominant southeasterly flow of air into the Gulf of Mexico. These winds and the annual insolation cycle produce marked seasonality in the northern Gulf: rapid warming with heavy runoff from land in the spring; quiescent hot summers with occasional wind events; rapid cooling in the fall, with the potential for major tropical storms; and moderate winters, with occasional cold-air outbreaks from the north. Water temperatures are about 13–15°C in the coldest months and about 29–31°C in the warmest months, varying with year and location. Annual mean sea surface temperature fluctuates between 26°C and 27°C (Heileman and Rabalais, 2005). As is the case elsewhere, long-term climate change is affecting the Gulf. For example, in Mobile Bay, the onset of the spring phytoplankton bloom is now about 2 wk earlier than it was in 1947 (M. Graham, Southern Mississippi University, pers. comm.), consistent with a warming climate.

The main water circulation features in the Gulf of Mexico are (1) a large, elongated clockwise circulation, the Loop Current, the dominant feature of the eastern Gulf, that enters through the Yucatan Straits and extends north before exiting between the southern tip of Florida and Cuba; (2) large-scale eddies that

dominate the central and western Gulf of Mexico (Sturges and Lugo-Fernandez, 2005); and (3) wind-driven coastal currents. The eddies are shed from the Loop Current in the eastern Gulf and move to the west along the continental shelf edge, eventually shoaling and degrading in the northwest Gulf (Sturges and Leben, 2000). Eddies are shed from the Loop Current as clockwise-circulating (anticyclonic) warm-core eddies. Eddies tend to be found in cyclonic (cold-core) and anticyclonic pairs. The prevailing southeasterly winds also contribute to eddy formation in the northern Gulf. Interactions of eddies with each other and with the shelf edge as they move westward have important consequences for local biological production due to associated upwelling (in cold-core eddies) and downwelling (in warm-core eddies) and their role in onshore and offshore transport of nutrients and organisms. It seems likely that global warming will weaken the Loop Current and associated eddies during this century (Liu et al., 2012), which could substantially alter pelagic ecology. There appears to be a slow anticlockwise circulation in the Gulf below 2,000 m (DeHaan and Sturges, 2005).

Surface water circulation on the continental shelf is quite variable and is controlled mainly by local wind fields, but also by the outflow of major rivers, influences from deep-water circulation, and, to a small extent, tides. The average surface water current speeds range up to 0.7 m/sec (Johnson, 2008). Currents on the northern Gulf of Mexico continental shelf can be divided between summer and the rest of the year. Average summer surface currents are generally weak and variable over most of the Gulf, but there are strong easterly flowing offshore currents on the outer shelf from the Mississippi River Delta through central Florida. This pattern reverses in late summer, and the strongest currents are to the west on the inner shelf of western Louisiana and Texas until the following summer (Johnson, 2008).

Shelf fronts, where water masses with differential temperature, salinity, or suspended solid properties meet, occur along the northern Gulf, from northern Mexico through Florida as well as along the northern portions of the Yucatan Peninsula. Shelf fronts can be important aggregation areas for plankton, nekton, and marine pelagic predators (from Cowan et al., 2008).

More than 150 rivers supply fresh water to the Gulf. The Mississippi River is the largest source and supplies well over half of the annual total volume of more than $10 \times 10^{11} \text{ m}^3$ of the fresh water entering the Gulf. The Mississippi, the fifth largest river in the world, carries large quantities



Fig. 2. Satellite photo of Louisiana's Mississippi River birdfoot delta and surrounding area, spring 2007, with plankton bloom evident (Photo by NASA).

of nutrient, sediments, and pollutants garnered from draining about 40% of the area of the continental United States, including the farm belt (Turner and Rabalais, 1991; Goolsby et al., 2000). The plume of the Mississippi River, entering either from the Atchafalaya River or from the so-called bird-foot delta of the Mississippi River, is a major influence on the oceanography of the central Gulf and the productivity of its shelf (Wawrik and Paul, 2004). Its freshwater plume flows westerly as less dense water overriding saltier, deeper offshore water.

Freshwater runoff from the combined rivers of the northern Gulf contributes to a low-salinity, highly turbid, nearshore water mass or plume within a westward-flowing coastal current, which is constrained within a steep, horizontal salinity front on the midshelf about 20–50 km offshore (Crout, 1983; Cochran and Kelly, 1986).

Productivity.—The Gulf is a moderately high-primary-productivity basin (250–300 gC/m²/yr) in comparison to other portions of the world's oceans, although within-region annual rates vary from 100 to 500 gC/m²/yr (Biggs and Sanchez, 1997; Chen et al., 2000), and daily rates can be highly variable (e.g., Quigg et al., 2011). There are two major gradients of biological mass and activity in the Gulf: (1) productivity is highest on the continental shelf, decreasing generally offshore; and (2) productivity and biomass decrease with depth. These gradients reflect the supporting primary productivity from photosynthesis

that is highest in shallow water close to land, where nutrients and light are plentiful, and offshore in well-lit surface waters above the compensation depth, where photosynthesis is greater than respiration. As might be expected from this pattern of productivity, abundance and biomass of living organisms decreases rapidly with depth (Pequegnat et al., 1990; Rabalais, 1990; Powell et al., 2003).

In the northern Gulf of Mexico primary productivity occurs year round, but it is generally higher in the spring and early summer (Fig. 2), coinciding with peak river flows into coastal waters (Lehrter et al., 2009). The spring phytoplankton bloom is followed by a peak in zooplankton abundance.

Primary and secondary production of the northern continental shelf is greatly influenced by the Mississippi River because of the nutrients in the river discharge (Darnell, 1990; Lohrenz et al., 1997), but perhaps also because of the plume buoyancy that keeps phytoplankton near the surface. The nearshore marshes, estuaries, and the areas influenced by the Mississippi River and other rivers have greater-than-average productivity compared to other areas of the Gulf (Lehrter et al., 2009). In addition, the riverine organic matter that enters the Gulf is a very important source of nutrition for marine life throughout the shelf and down the continental slope (Murrell et al., 2013) and accounts for a major part of total respiration. Outflow of nutrients and carbon from local bays comprises apparently only a fraction of that delivered by the Mississippi River (Gordon and Goni, 2003; Das et al., 2011). Unfortunately, increased inputs of anthropogenic nutrients, mainly from the Mississippi River, have resulted in very large phytoplankton blooms and more labile organic matter sinking toward the bottom, followed by seasonal hypoxia over a broad area of the northern Gulf shelf west of the Mississippi River (e.g., see review of Rabalais et al., 2002; Dagg and Breed, 2003). The nutrient contributions from deepwater upwelling in cold-core eddies appear to not yet have been quantitatively compared to those from river inputs as catalysts for shelf and slope production.

Gulf fisheries are supported by the high shelf productivity and large inputs of terrestrial nutrients. Major fisheries include three species of shrimp (brown, *Farfantepenaeus aztecus*; white, *Litopenaeus setiferus*; and pink, *Farfantepenaeus duorarum*), oysters (*Crassostrea virginica*), blue crab (*Callinectes sapidus*), menhaden (*Brevoortia patronus*), red snapper (*Lutjanus campechanus*), swordfish (*Xiphias gladius*), tuna (*Thunnus* spp.), amberjack (*Seriola* spp.), and tilefish (*Lopholatilus*

Gulf of Mexico Food Web

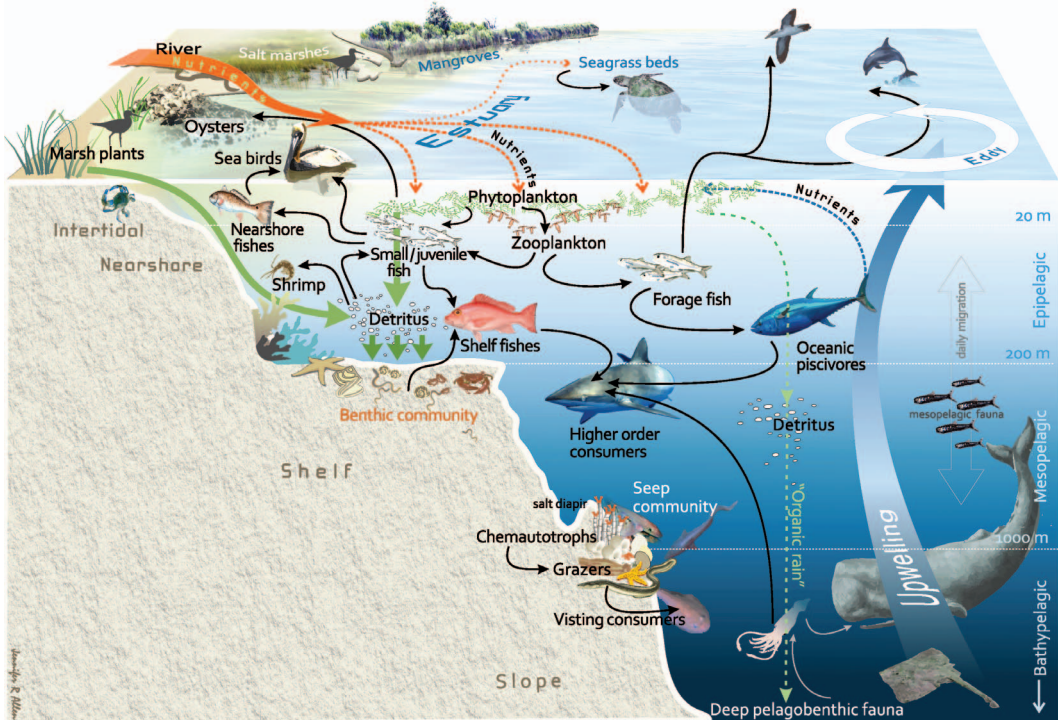


Fig. 3. Diagrammatic representation of a cross section of the northern Gulf of Mexico, showing some major habitats and the geological and biological features involved in primary and secondary production and some representative species in the food web (diagram by J. R. Allen).

chamaelonticeps). The top five fisheries in terms of economic value are shellfish (brown shrimp, white shrimp, eastern oyster, and blue crab). The menhaden fishery is the fifth most economically valuable in the Gulf but the second largest commercial fishery in the United States by landings (weight).

Biodiversity.—Biodiversity, or the variety of life, is another important ecosystem attribute. It is often defined as the variety of genuses, species, and ecosystems in a region (e.g., Larsson, 2001). Biodiversity includes the different things that organisms do in the ecosystem and how many different species there are to do them. Ecosystems are optimized through natural selection on the species level to use energy wherever and whenever it is available. Different organisms fill different roles in ecosystem dynamics through production, consumption, and recycling of materials, as well as through habitat modification, under a host of different circumstances. The warm, temperate, and subtropical waters of the northern Gulf harbor a larger diversity of organisms than are found in colder, temperate

waters to the north, but the Gulf's diversity is not as great as that associated with the tropics. Recently, the Harte Research Institute for Gulf of Mexico Studies in Corpus Christi, TX, undertook a survey of marine biodiversity in the Gulf (Felder and Camp, 2009). It was estimated that out of a total of 224,787 described marine species in the world, 15,419 of those species are found in the Gulf. This compares to the 26,927 found in Europe, 6,150 found in Hawaii, and 10,836 found in South Africa. The variety of habitats in the northern Gulf of Mexico contributes greatly to its biodiversity, and with potentially more exploration of the deep Gulf and the application of molecular techniques we can expect significant increases in the numbers of described species.

HABITATS

In this section the main habitats of the northern Gulf are described based on their physical characteristics and biological activity, and representative species from various trophic levels are highlighted (Fig. 3). The main habitat

definitions used here follow closely the guidance from the Federal Geographic Data Committee (2012). The species discussed under each habitat comprise a fraction of the thousands that live in the Gulf; they were chosen because of their importance ecologically or to humans. In this section the main habitats are discussed, starting offshore and moving shoreward and from the deepest to the shallowest. The pelagic or neritic habitats are discussed first, and then the benthic habitats within each major province (i.e., oceanic; continental shelf; bays, estuaries, and beaches) are discussed.

Oceanic.—The deep-water habitats in the central Gulf of Mexico are not well studied, and ecological data are sparse. There are some notable exceptions, including the extensive geological and geochemical data gathered for petroleum exploration and the unique chemosynthetic communities of deep-water petroleum seeps, methane hydrates, and brine seeps. Most of these data are for the continental slope rather than the abyssal plain.

The deep ocean basin accounts for about 20% of the area of the Gulf (Harte Research Institute, 2014). The oceanic area (seaward of the shelf break) is treated here in two habitat categories: pelagic and benthic.

Pelagic: The narrow continental shelf off the Mississippi River brings oceanic epipelagic (0–200 m deep) habitats relatively close to land. Eddies migrating along the shelf break entrain the plume of the Mississippi River and transport it offshore, producing a nutrient-rich, oceanic pelagic habitat, supporting nektonic fishes and squids as well as top-level predators, such as sperm whales (*Physeter macrocephalus*), relatively close to shore (Davis, 2000). Cyclonic, cold-core eddies, producing slight elevations of the sea surface, generally have higher concentrations of nutrients and chlorophyll associated with them and a shallower deep chlorophyll maximum. Cyclonic eddies also have a higher biomass of zooplankton (Davis, 2002) than do anticyclonic eddies (Biggs, 1992).

Like other oceans and seas, the oceanic habitat in the northern Gulf of Mexico has progressively deeper zones: the epipelagic (0–200 m); mesopelagic (200–1,000 m); bathypelagic (1,000–4,000 m), where no sunlight penetrates; and abyssal pelagic (>4,000 m). Ecosystem biomass decreases rapidly below 200 m, the lower boundary of the mixed layer. In the Gulf, the mesopelagic animals comprising the deep-scattering layer (named for its acoustic reflectivity) are located between 450 and 550 m during the day, avoiding day-time

surface predators, and rise close to the surface at night to feed on the more abundant plankton (Hopkins et al., 1994; Kaltenberg et al., 2007). Prominent organisms in the deep-scattering layers include copepods, decapods, mysids, ctenophores, salps, tunicates, polychaete worms, shrimp, squid, and myctophid (lantern fishes). These vertically migrating layers support a variety of predatory fish, squids, night-foraging seabirds, and marine mammals (Fig. 4).

The bathypelagic fauna is not well characterized. Large bathypelagic organisms collected in trawls and seen from submersibles include bristlemouth fish, decapod shrimps, squid, dragonfish, and gulpers (e.g., Burghart et al., 2010). The bathypelagic micronekton include a high proportion of species that brood their eggs, while the shallower mesopelagic zone has many fewer brooders (Burghart et al., 2007). Apparently brooding and direct development are adaptations to an environment in which pelagic larvae are less likely to survive.

The very deep sea (meso- and bathypelagic zones) contains a rich variety of single-celled organisms (Protista) that are even less well known than the multicellular fauna. The bacteria and archaea are single-celled prokaryotes that along with the eukaryotes comprise the two great divisions of cellular organisms. Some prokaryotes fix dissolved inorganic carbon and others metabolize it. Dissolved organic matter is a huge reservoir of carbon, as much as 200 times greater than living biomass in the ocean. The dissolved organic matter exists in a reversible equilibrium with microscopic gels that provide habitat for bathypelagic protists (Verdugo and Santschi, 2010). In addition, dissolved inorganic carbon fixation rates (supported by chemoautotrophy) that rival those of heterotrophic microbes have recently been shown in the bathypelagic zone of the deep Atlantic (Reinthaller et al., 2010) and are also likely to play the same role in the deep Gulf. Among the archaea the methane-oxidizing species are abundant near sources of this gas, such as natural petroleum seeps. This genetically diverse community of prokaryotes is a food source for heterotrophic nanoflagellates and ciliates, forming complex interactions at the base of the meso- and bathypelagic food webs, comprising the well-known microbial loop (Nagata et al., 2010).

On the surface of the Gulf, two species of the brown macroalgae *Sargassum* form large floating rafts in the late spring and summer and constitute an important surface habitat for a variety of creatures (Rooper et al., 2006), some of which are found only in these rafts (Fig. 5). Common fishes found here include sargassumfish (*Histrio*

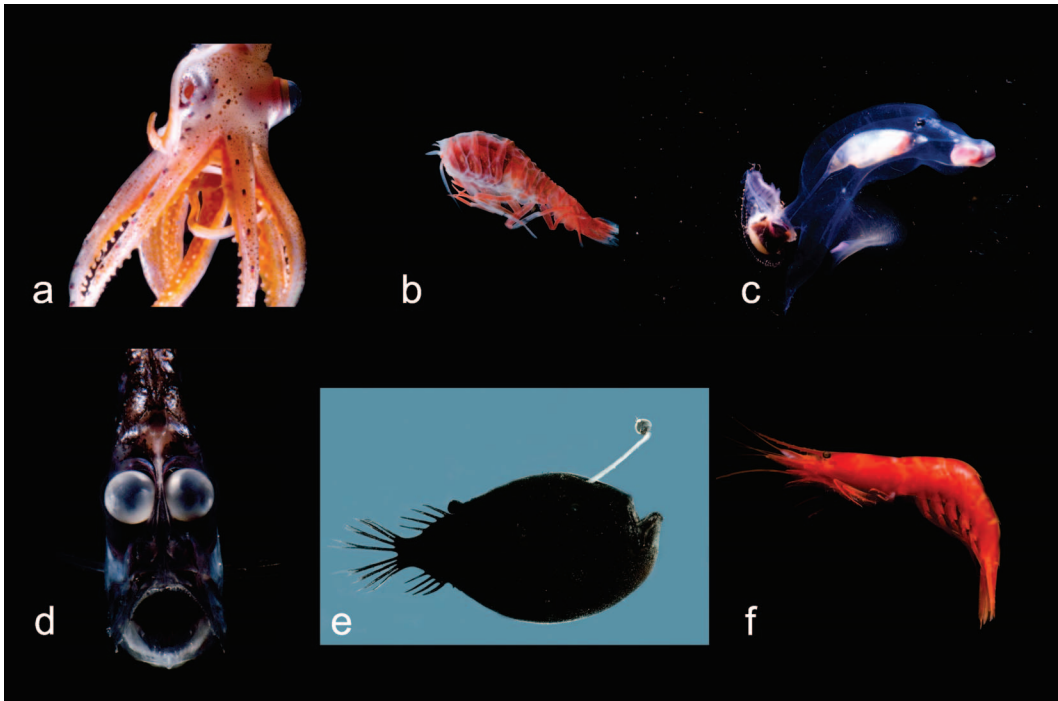


Fig. 4. Bathypelagic and mesopelagic species in the Northern Gulf of Mexico. (a) The squid *Stigmatoteuthis arcturi*. (b) Mesopelagic amphipod. (c) The heteropod mollusk *Caranaria lamarki*. (d) The globe-eye hatchetfish *Argyropelecus aculeatus*. (e) The anglerfish *Cryptosaurus* cf. *couelsii*. (f) The prawn *AcanthePHYra purpea* (all photos, copyright Dante Fenolio, used by permission).

histrio), sargassum pipefish (*Syngnathus pelagicus*), planehead filefish (*Stephanolepis hispidus*), and sargassum triggerfish (*Xanthichthys ringens*). Common invertebrates include crustaceans, nudibranchs, hydrozoans, and bryozoans. *Sargassum* is also a good habitat for juvenile fishes,

including mahi mahi (*Coryphaena hippurus*), cobia (*Rachycentron canadum*), and wahoo (*Acanthocybium solandri*), as well as for sea turtles (Wells and Rooker, 2009; Witherington et al., 2012), providing food and protection from pelagic predators.

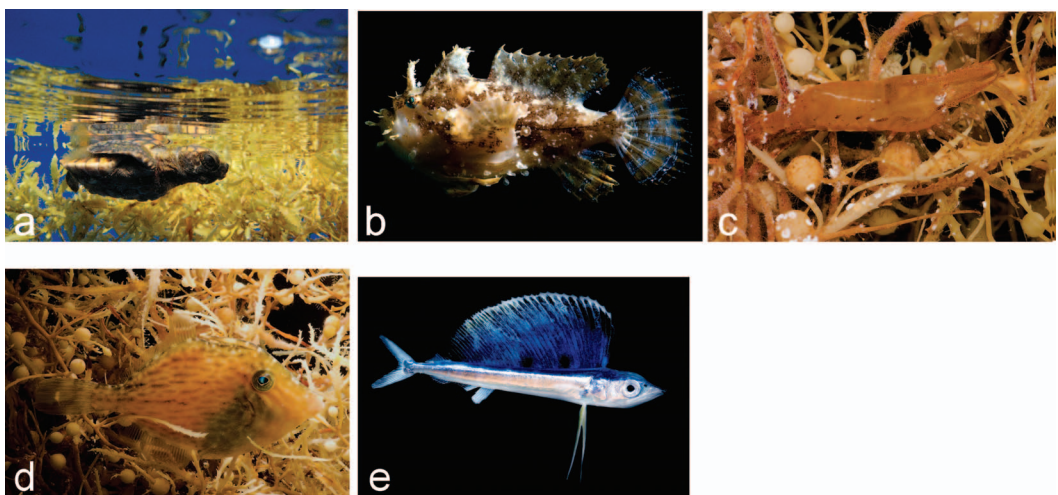


Fig. 5. The Sargassum community. (a) A bed of floating Sargassum with a juvenile loggerhead turtle, *Caretta caretta*. (b) The sargassum angler fish *Histrio histrio*. (c) The sargassum shrimp *Latreutes fucorum*. (d) The sargassum filefish *Stenolepis hispidus*. (e) juvenile sailfish (all photos, copyright Dante Fenolio, used by permission).

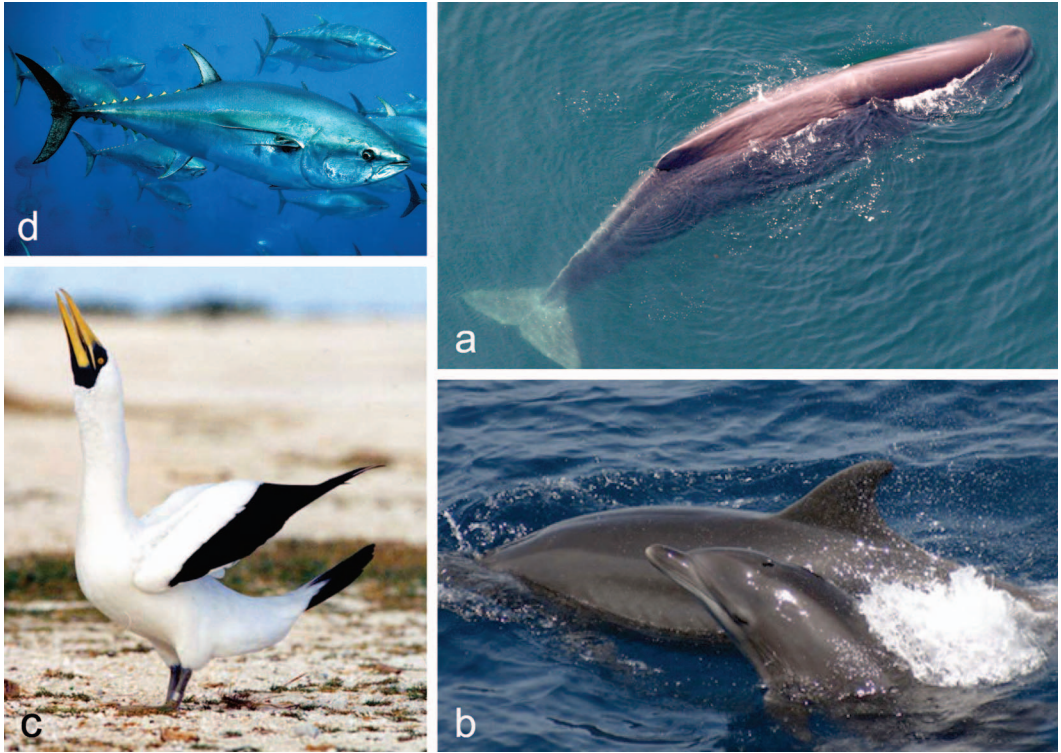


Fig. 6. Some pelagic marine vertebrates of the Gulf of Mexico. (a) Sperm whale, *Physeter macrocephalus* (photo by Tim Cole, NMFS). (b) Bottlenose dolphin and calf, *Tursiops truncatus* (photo by NMFS). (c) Masked booby, *Sula dactylatra* (photo by W. Montevicchi). (d) Atlantic bluefin tuna (*Thunnus thynnus*) (photo by Richard Hermann).

Floating rafts of *Sargassum* are particularly common in the northwest Gulf in spring and then move eastward and are injected into the Atlantic Ocean starting in July, and the Gulf may be the main source of Atlantic Ocean *Sargassum* (Gower and King, 2008). Total *Sargassum* biomass may reach 6 million tons in the Gulf in some years. In the open waters of the Gulf *Sargassum* may contribute as much as 60% of the primary production in the upper meter of water (Carpenter and Cox, 1974; Pères, 1982). *Sargassum* is also often washed ashore in the Gulf, adding nutrients to coastal habitats and providing feeding opportunities for shorebirds and other wildlife as it decays and is consumed by invertebrates.

Prominent megafauna of the oceanic epipelagic zone include swordfish (*Xiphias gladius*), white (*Tetrapturus albidus*) and blue (*Makaira nigricans*) marlin, blue runners (*Caranx crysos*), yellowfin (*Thunnus albacorus*) and bluefin tuna (*Thunnus thynnus*), and whale sharks (*Rhincodon typus*) (Fig. 6). There are also many species of seabirds, dolphins, and whales. Some of the prominent species of this habitat are seen in Figure 6.

Atlantic Bluefin tuna, an iconic top predator, is one of the largest and fastest fishes in the

world; it once supported an extremely lucrative fishery but is now greatly depleted by overfishing (Safina, 1997). Bluefin tuna have adaptations to an energetically demanding, highly mobile life in the open ocean. A high rate of metabolism, endothermy, and unique molecular adaptations underlie a remarkable physiology for sustained high-speed swimming (Block and Stevens, 2001). Satellite tagging data indicate mixing of the eastern and western stocks on either side of the central North Atlantic Ocean (Block et al., 2001).

The oceanic pelagic portion of the Gulf contains one of the two known spawning grounds for this species (Rooker et al., 2007). Based on tagging and genetic data it has been suggested that the spawning stocks in the Gulf and the Mediterranean Sea are different, but there is no consensus on this view. Based on larval distribution, the greatest spawning activities of bluefin tuna occur in association with the shelf break in the northern Gulf. Spawning is thought to be associated with cyclonic eddies (TAG, 2012). The frontal systems on the shelf have the greatest concentrations of larvae. Bluefin tuna in the Gulf mature at 8 yr, and the average age of females in the spawning grounds

is 11 yr. Peak spawning occurs from mid- to late May (Brothers et al., 1983). Tuna are batch spawners, each female spawning more than once per season. Large tunas can spawn 30–60 million eggs annually (Baglin, 1982). The eggs hatch in just a few days in the warm water of the Gulf, and peak egg and larval abundances are found in April, May, and June.

Bluefin tuna in the western Atlantic forage mainly in the upper mixed layer of the ocean, feeding on forage fishes, such as sand lance (*Ammodytes* spp.) and Atlantic herring (*Clupea harengus*), and cephalopods. While mainly pelagic foragers, a significant portion of their diet in shallow areas comprises benthic organisms (Chase, 2002). Nevertheless, bluefin tuna prey are primarily from trophic levels higher than that fed upon by other tunas.

Prominent oceanic seabirds of the Gulf include parasitic jaegers (*Stercorarius parasiticus*), Audubon's shearwaters (*Puffinus lherminieri*), band-rump storm petrels (*Oceanodroma castro*), sooty terns (*Onychoprion fuscatus*), and black terns (*Clidonia niger*) (Davis et al., 2000). There is much seasonal variability in many Gulf seabird populations due to the migration patterns of these species. Many seabirds are associated with areas of higher phytoplankton and zooplankton biomass within cyclonic eddies and in sheer zones between eddies (Ribic et al., 1997; Hess, 1999).

The masked booby (*Sula dactylatra*) is an oceanic seabird in the gannet family. It is the largest of the boobies, with a wingspan up to 150 cm and weighing up to 1.5 kg. It breeds on tropical islands in the southern Gulf of Mexico and Caribbean (Tunnell and Chapman, 2000); otherwise it spends its entire life at sea. Masked boobies feed on pelagic fish and squid, particularly on flying fish. They plunge dive, from as high as 30 m, to catch their prey. Aggregations of masked boobies are often found near schools of dolphin or tuna, both top-level predators also attracted to schools of pelagic fish. In the western North Atlantic Ocean these boobies forage over *Sargassum* (Moser and Lee, 2012), so this behavior may also occur in the Gulf.

There are 28 species of cetaceans (whales and dolphins) reported in the Gulf (Davis et al., 2002). Several species of dolphins are commonly sighted during shipboard and aerial surveys, including bottlenose (*Tursiops truncatus*), spinner (*Stenella longirostris*), Atlantic spotted (*Stenella frontalis*), pantropical spotted (*Stenella attenuata*), risso (*Grampus griseus*), striped (*Stenella coeruleoalba*), and clymene (*Stenella clymene*) dolphins, as well as melon-headed (*Peponocephala electra*) and short-finned pilot (*Globicephala macrorhynchus*) whales. Many whales and dolphins concentrate

over the continental slope, where convergences occur between eddies and, presumably, where their food (small fishes, plankton, and micro-nekton) is concentrated (Baumgartner et al., 2001). The offshore transport of nutrient-rich water by shelf-edge eddies is a key process in supplying a productive trophic base and in determining high-quality cetacean habitat. Other dolphins and whales tend to be found all along the shelf break, not preferentially associated with cyclonic eddies and confluences.

A resident population of Gulf sperm whales congregates within 100 km of the mouth of the Mississippi River (Davis et al., 2002), mainly because of the elevated chlorophyll concentrations in the surface waters (O'Hern and Biggs, 2009). Sperm whales feed mainly on mesopelagic and bathypelagic squids, which may by inference be linked to higher production areas of the epipelagic zone. The average diving depth of sperm whales in the Gulf is 644 m. Acoustic recordings made during the dives had signals consistent with the use of long-range biosonar to locate patches of prey (Watwood et al., 2006). Recent genetic evidence suggests that females in the Gulf population breed exclusively there and that males move among Gulf populations and those in the Mediterranean Sea, western North Atlantic, and North Sea (Englehaup et al., 2009).

Continental slope and bathyl benthos: Salt domes, or salt diapirs, are common features on the outer continental shelf and slope (and some coastal areas) of the northwestern (Murray, 1961; Halbouty, 1967) and southwestern (Worzel et al., 1968) Gulf, including the Flower Gardens and many of the other offshore banks. Salt domes are the result of hypersaline deposits from late Mesozoic seas that formed buoyant pillars after burial that then penetrated overlying sediments and are important areas for oil and gas production (Halbouty, 1979; Henderson and Varner, 2011). Drowned ancient coral reefs are also important features in some areas.

As much as 140,000 tons of oil seep naturally into the Gulf of Mexico every year (NRC, 2002), and much of this seepage occurs on the continental slope. Areas of oil and gas seepage and brine seepage have unusual biological activity on the otherwise mostly homogeneous deep-sea muddy bottoms of the continental slope, occurring between depths of 250 and 2,200 m (MacDonald et al., 1990a). Brine seeps occur over salt-core diapirs and are scattered over the shelf break and continental slope of the northern Gulf. They support cold-seep chemosynthetic communities that are mainly decoupled in their

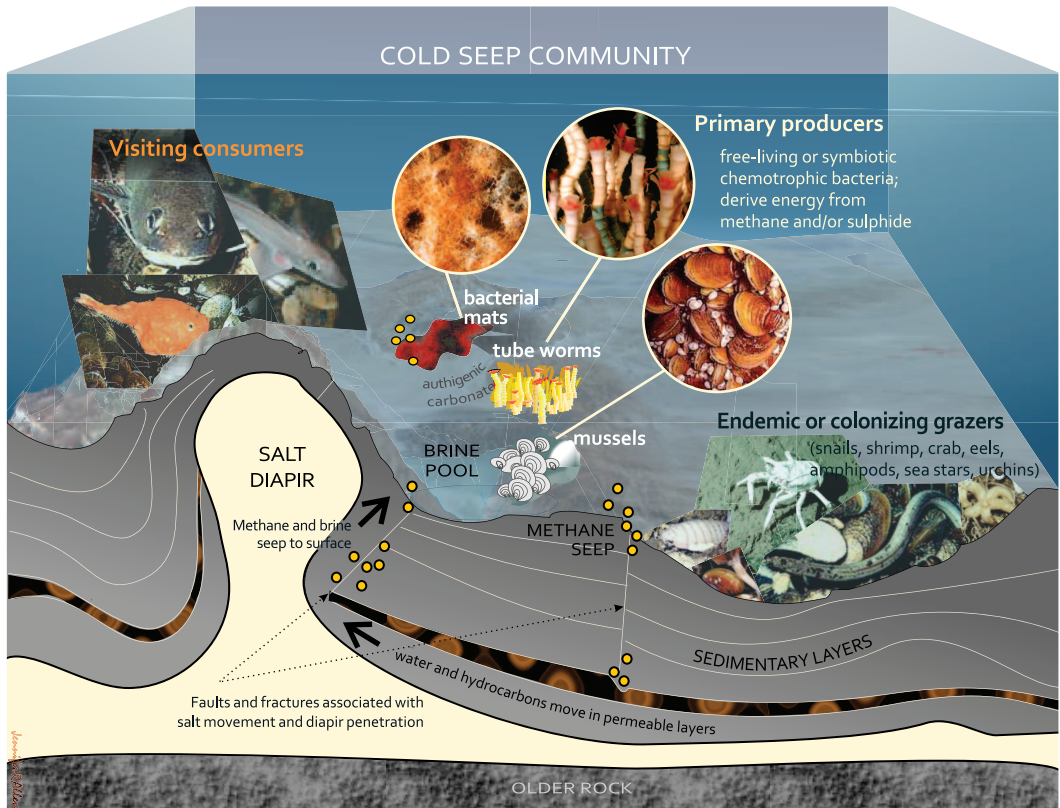


Fig. 7. Diagram of geological and biological features and dominant species of a cold seep community on the continental slope (diagram by J. R. Allen).

energy supply from overlying photosynthetic communities near the ocean surface and that depend on high-energy chemically reduced compounds in the seepage (H_2S and methane) for their metabolic energy and carbon (Childress et al., 1986; Fisher et al., 1987) (Fig. 7).

The dominant organisms in these slope seep communities are either mussels or vestimentiferan worms, although epibenthic and infaunal bivalves can also be prominent. In one case, chemosynthetic-dependent mussels live at the edge of hypersaline methane-rich pools at a depth of 650 m on the continental slope (MacDonald et al., 1990b). Cold seeps and brine seeps support a diverse epibenthic fauna dependent on mussels and vestimentiferan worms for structure and habitat in an environment otherwise lacking much habitat diversity (Berquist et al., 2003). Similar biocenoses involving chemosynthetic bacterial mats in petroleum seeps are apparently common on the upper continental shelf of the Gulf (Sassen et al., 1993) as well as elsewhere, such as in the Santa Barbara Channel in California (Spies et al., 1980).

Hard-bottom habitat consisting of authigenic carbonate deposits is also scattered along the continental slope. These deposits form from the combined activity of sulfate-reducing and methane-oxidizing bacteria, their metabolism resulting in the deposition of carbonates in areas of natural gas seepage (Boetius et al., 2000; Birgel et al., 2011; Chevalier et al., 2011). These elevated carbonate-based substrates allow large fixed animals to settle and grow, including ahermatypic (cold-water) corals, gorgonians, sponges, hydroids, and anemones. These hard-bottom communities developing on petroleum seepages appear to be the endpoint of a succession of colonizing animals, such as corals, gorgonians, and anemones, that, unlike the original colonizers (tube worms and mussels, etc.), are not dependent on the chemosynthetic processes in the seeps for nutrition (CSA, 2007).

The patterns of occurrence of benthic species biomass on the continental slope correlate negatively with depth and positively with export rate of particulate organic carbon from overlying waters (Baguley et al., 2008; Wei et al., 2010).

Away from areas of seepage, the majority of the continental slope consists of soft sediments and has a diverse benthic and benthopelagic fauna. Animals living here rely mainly on the rain of organic matter from the waters above or on the organic material coming downslope from the continental shelf, in particular from the Mississippi River. At depths greater than 700 m sedimentation rates are apparently <0.44 cm/yr (Yaeger et al., 2004). The numbers and biomass of bacteria, meiofauna, and the infauna sampled by grabs and cores, as well as the macrofauna sampled by dredge, all decrease with depth as material from the photic zone sinks and is metabolized. For example, the density of macrofauna is correlated with the amount of particulate organic matter in sediments below 700 m (Yaeger et al., 2004); benthic bacterial biomass decreases with depth and with the amount of particulate organic carbon from the overlying water (Deming and Carpenter, 2008). Benthic community oxygen consumption decreases from values of 30 mM $O_2/m^2/d$ at the top of the slope near the shelf break to 1 mM $O_2/m^2/d$ at 3,000 m depth (Rowe and Kennicut, 2002; Rowe et al., 2008). The biomass and abundance of benthic macrofauna and meiofauna also decrease with depth on the continental slope in the northern Gulf (Pequegnat et al., 1990). An unusual feature of the northern Gulf continental slope communities is that the meiofauna (0.063–0.5 mm) have a higher biomass than do the macrofauna (>0.5 mm). An extensive trawl survey of the macrofauna on the continental slope east and west of the Mississippi Canyon found 126 species of deepwater fish and 432 species of invertebrates in 46 bottom trawls conducted between depths of 200 and 3,000 m. Shrimps, crabs, sea pens, and sea cucumbers were some of the prominent invertebrates comprising the trawl catches and appearing in deep-sea photographs. Skates, rays, batfish, rattail fish, hakes, cod-like fish, and gapers were some of the more common fish encountered (Galloway et al., 2001).

In the abyssal plain there is a low density of organisms, as is seen elsewhere in the world's oceans. In the Sigsbee Deep the size of organisms was inversely related to the biomass of the populations, with meiofauna and bacteria populations constituting the greatest share of biomass (Rowe et al., 2003).

Large predators are apparently quite abundant on at least the continental slopes and perhaps throughout the bathyl region (Pequegnat et al., 1990; Carney, 1994; P. Montagna, pers. comm.). Benthic feeding fishes appear to be very active in the Gulf, and some highly mobile

species, such as rattails and eels, derive most of their nutrition from chemosynthetic communities, while others use production from such brine and methane seeps as well as from surface water photosynthesis (McAvoy et al., 2002).

The continental slope environment of the northern Gulf is perhaps more heavily polluted than are comparable areas in other parts of the United States, likely as a result of the disposal of wastes from the thousands of wells drilled in the northern Gulf, including leaking and uncapped boreholes, and the deposition of contaminated sediments from the Mississippi River. A wide-ranging survey was recently conducted in the northern Gulf from west Florida to mid-Texas. Enrichment of polynuclear aromatic hydrocarbons in concentrations up to ~ 1 ppm was found at several sites. The elements Ba, Ni, Pb, Cd, As, Cu, and Mn were variously enriched from two-fold to 10-fold measures over background (Wade et al., 2008).

Continental shelf.—The broad shelf extending through most of the northern Gulf is rich in marine life, supported by plentiful nutrients, warm temperatures, and high primary productivity from plankton and submerged aquatic vegetation. In addition, imported terrestrially produced plant material supplements the diets of the large number of detrital feeders.

Neretic: Most of the biological production in the central northern Gulf pelagic zone occurs over the shelf, with higher rates on the inner shelf (Chen et al., 2000; Murrell et al., 2013). The peak spring flows of the Mississippi River carrying an influx of nutrients and organic matter are followed by water stratification and the annual phytoplankton bloom as the days lengthen in April and May (Dagg and Breed, 2003). The spring phytoplankton bloom is followed by a zooplankton bloom, mainly in June; copepods are a particularly important component of the zooplankton for passing energy and biomass to higher trophic levels (Dagg et al., 1991; Dagg, 1995). Other common zooplankters include protozoans, chaetognaths, polychaete worms, decapods, and euphausiid crustaceans (Ortner et al., 1989). Most of these species spend their whole lives as plankton, but there are also the temporary zooplankters, mostly larval forms of larger animals, such as fish, corals, gastropods, bivalves, polychaetes, echinoderms, and crabs.

Fish communities associated with parts of the shelf dominated by muddy bottoms have relatively low diversities, and seasonal migrations are common. In the eastern Gulf, however, rock- and

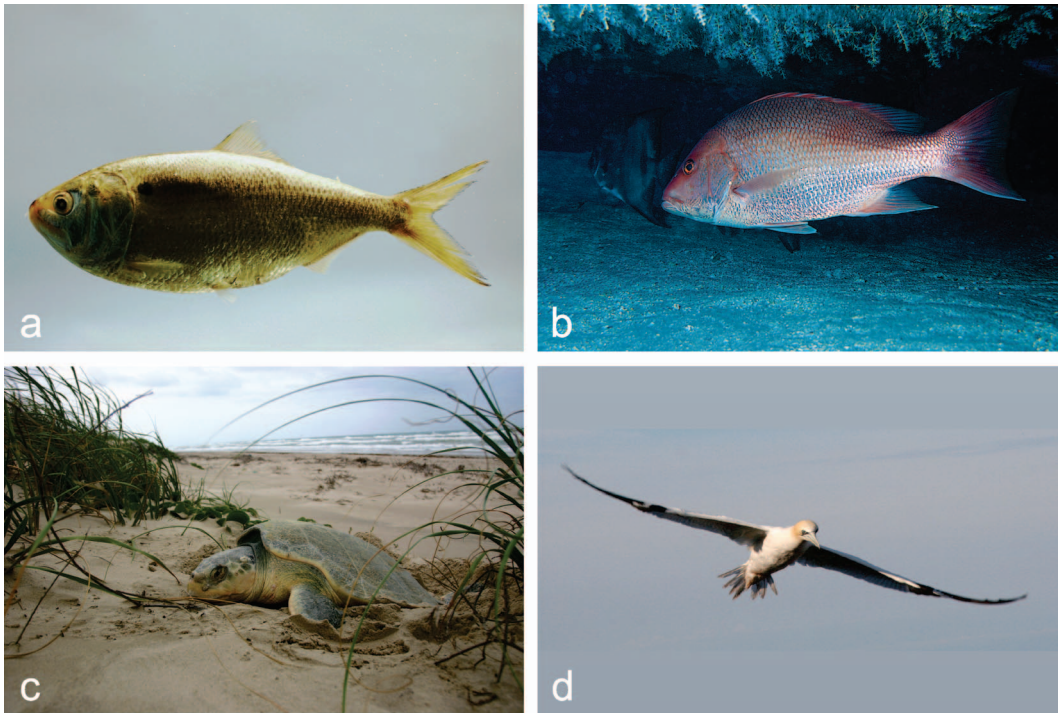


Fig. 8. Some species on the continental shelf of the northern Gulf of Mexico. (a) Gulf menhaden, *Brevoortia patronus* (photo by NMFS). (b) Red snapper *Lutjanus campechanus* (photo by Ned DeLoach). (c) Kemp's ridley sea turtle, *Lepidochelys kempii* (photo by National Park Service). (d) Northern gannett, *Morus bassanus* (photo by W. Montevicchi).

reef-related species are more important, diversity is greater, and there are more species endemic to this portion of the Gulf (Darnell, 1990) (Fig. 8).

Many species on the shelf are estuarine for at least part of their life cycle. As in other temperate and subtropical marine environments, the sexually mature adults of many commercially important marine species move out of estuaries and spawn on the shelf. The life cycle of brown shrimp (*Farfantepenaeus aztecus*) illustrates the linkage between offshore spawning areas and inshore estuarine rearing habitat (Fig. 9). After spawning has occurred, the newly hatched postlarval brown shrimp descend and ride the northward-flowing bottom currents, generated from the passage of cold fronts in the spring, into the mouths of the estuaries (Rogers et al., 1993).

Similar processes bring postlarval blue crabs from the shelf environment to the mouths of estuaries, depending on favorable winds, but sometimes tidal regimes, particularly nocturnal, summertime flood tides with minimal amplitude, play a larger part (Morgan et al., 1996). Pink shrimp (*Farfantepenaeus duorarum*) that spawn in the Dry Tortugas also have larvae with behavioral adaptations that place them in cross-shelf tidal currents and apparently transport them 100 km

into the mouths of Florida estuaries (Crales et al., 2007). Blue crabs spend much of their life cycle in bays and estuaries, with males often going extensively into freshwater areas for overwintering and then moving seaward in late winter and spring to encounter females and mate.

Common shelf forage fish include Gulf menhaden, sardines, and anchovies (Gelwick et al., 1996; Lewis et al., 2007). Gulf menhaden are the most abundant forage fish in the Gulf of Mexico and support the second largest fishery by weight in the United States—mainly a reduction fishery for fish oil and animal feed (Vaughan et al., 2007)—of about 480,000 metric tons per year. Fluctuations in the Gulf menhaden population appear to be inversely related to Mississippi River discharge volume (Vaughan et al., 2011). Adults spawn offshore and in bays in winter, and the young menhaden are transported shoreward, arriving later in the year in coastal estuaries, where they mature (Vaughan et al., 2011). Adult Gulf menhaden are filter-feeding planktivores and detritivores and live up to 6 yr (Ahrenholz, 1991). Juveniles appear to sight-select microzooplankton and dinoflagellates as prey and also consume macrodetritus (Gavoni et al., 1983;

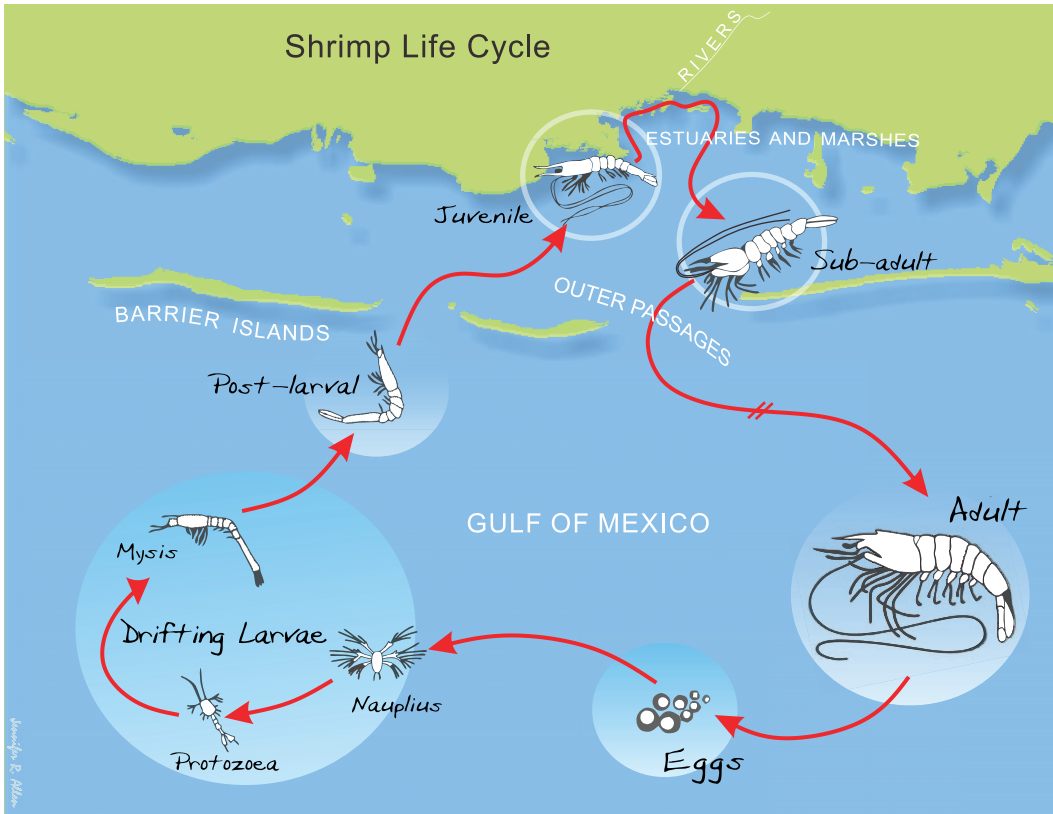


Fig. 9. Life cycle of shrimp (brown and white) in the Gulf of Mexico (diagram by J. R. Allen).

Stoeker and Gavoni, 1984). In addition to supporting a large commercial fishery, menhaden form an important trophic step from plankton to higher-level predators: large fish, seabirds, and marine mammals (Scharf and Schlicht, 2000; Withers and Brooks, 2004; Vaughan et al., 2011).

Red snapper occupy a trophic level above the forage fishes, with adults feeding on small fishes, crustaceans, and other benthic invertebrates. The species is a prominent but depleted sport fish and supports active recreational and commercial fisheries throughout the northern Gulf shelf (Wells et al., 2008). Red snapper is found in greatest abundance at depths of 15 to 90 m; adults are often associated with hard-bottom or artificial platforms, but they also occur in shallower inshore waters, especially in cooler months. They become sexually mature before they reach 30 cm in length and have lifespans of up to 50 yr (Gallaway et al., 2009). Adult females are batch spawners, spawning frequently between late May and early Oct. (Collins et al., 2001).

Sea turtles are prominent members of the Gulf shelf vertebrate fauna. There are five species in the Gulf of Mexico: green (*Chelonia mydas*),

leatherback (*Dermochelys coriacea*) Kemp's ridley (*Lepidochelys kempi*), loggerhead (*Caretta caretta*), and hawksbill (*Eretmochelys imbricata*) sea turtles. All five species are endangered or threatened under Federal law. The most commonly encountered species are greens, followed by loggerheads, leatherbacks, and Kemp's ridley. Kemp's ridley, an endangered species, is the smallest of these five species of sea turtle, with adults weighing an average of 45 kg; there are about 7,000 individuals in the Gulf. This species feeds mainly on the continental shelf across the northern Gulf; it is omnivorous, feeding mostly on crabs, but also on jellyfish, other crustaceans, and mollusks (NOAA, 2014). Juvenile Kemp's ridleys spend most of their time near the sea surface and in association with the *Sargassum* community (Witherington et al., 2012). They mature in 11–13 yr (Zug et al., 1997). Adults mate offshore, and females come ashore during daylight three times in spring and summer to lay eggs. The only known spawning beaches for the Kemp's ridley turtle are in the Gulf of Mexico, mainly Playa de Rancho Nuevo, Tamaulipas, Mexico. They are occasionally caught at public fishing piers by recreational fisherman and are

also caught in the commercial trawl fisheries for shrimp and in gill nets (Rudloe and Rudloe, 2005). As with other Gulf sea turtles, this species is cold sensitive and can be stunned by unusually cold winter temperatures and killed during prolonged cold spells in shallow waters (Foley et al., 2007). With the implementation of turtle exclusion devices in shrimp trawls and increased enforcement, the population in the Gulf appears to be starting to recover, although direct or subtle impacts on the species resulting from the BP oil spill could be influencing the species' recovery (Antonio et al., 2012; Barron, 2012).

The Gulf of Mexico shelf seabird fauna comprises a mixture of temperate and tropical species, with many more northerly forms wintering in the Gulf. Most of the seabirds in the Gulf feed on forage fish, but some have other prey; black skimmers (*Rynchops niger*), for example, feed on zooplankton as well as fish (Gochfeld and Burger, 1994). The northern gannett (*Morus bassanus*) is a large prominent fish-eating seabird in the Gulf of Mexico shelf environment. Gannets, like the closely related pelicans, are plunge-diving seabirds (Birdlife International, 2012). This species nests on rocky headlands on the North Atlantic coast, and the young birds migrate south, swimming at first and then later flying during their first winter migration. Young birds spend their first few years in the Gulf foraging on small shoaling fish. Adults are very efficient flyers, often cruising up to 30 m above the ocean while searching for fish, or at other times just above the wave tops, taking advantage of the updrafts from the ocean (USFWS, 2010).

Benthos: The continental shelf benthic habitat of the northwestern Gulf is characterized by gradually accelerating depths in the offshore direction, with a variable depth gradient dependent usually on the shelf width. The area offshore of Louisiana from about Terrabonne Bay west to about Corpus Christi, TX, is wide, with the steepest depth gradients beyond 80 m, while the narrower shelf off the Mississippi River has a steep depth gradient seaward from about 40 m (Rezak et al., 1990). East of the Mississippi River and its associated canyons, the shelf again widens and grades into the very broad, gently sloping Florida Platform that drops off steeply on its outer edge as the Florida Escarpment. The nearshore benthos in Texas, Louisiana, Mississippi, and western Alabama less than 10 m deep experiences lower salinity, turbid water subject to rapid winter cooling to below 10°C (Rezak et al., 1985). A near-bottom nepheloid layer extends farther into the Gulf than the 10-m isobath.

The continental shelf benthic communities reflect the substrates, depths, turbidity of overlying waters, minimum temperatures, and available dissolved oxygen. Much of the shelf west of the Mississippi River is under the influence of seasonal hypoxia from organic enrichment (Rabalais et al., 2002). However, sandy shoals elevated off the otherwise-muddy bottoms in this region and above the deep-water hypoxic zone in the summer have a diverse array of infauna. The predominant infaunal groups of the continental shelves are polychaete worms and amphipod crustaceans (Brooks et al., 2008; Dubois et al., 2009). Some of the most notable features of the continental shelf are the more than 30 reefs and banks below the 50-m isobath on the outer continental shelf west of the Mississippi River Delta (Rezak et al., 1990) and about 30 more to the east of the Delta, notably the Pinnacles and the Florida Middle Grounds (T. Shirley, unpubl.). The banks in east Texas and Louisiana are salt diapirs, while those in south Texas, the Pinnacles, and the Florida Middle Grounds are relict coral-algal carbonate reefs and shorelines. Biological and geological information on the south Texas outer continental shelf banks is summarized by Nash et al. (2013), who showed that some 943 species have been identified from these outer shelf banks.

The Flower Garden Banks are a unique habitat on the shelf directly south of the Texas-Louisiana border (Fig. 10). These banks have been well studied, as they occur in an area of active oil and gas production and are protected because of their diverse fauna. The banks consist of coral reef structures that have grown up on salt diapirs. Coral reefs are found in other parts of the Gulf, but nowhere else are they as diverse and as close to natural as in the Flower Gardens (Rezak et al., 1985, 1990). The banks have living corals from about 20 to 45 m in depth, comprising mainly the genera *Monastrea*, *Diploria*, and *Porites*. Two species of Gulf coral (the staghorn, *Acropora cervicornis*, and the elkhorn, *A. palmata*) are federally listed endangered species. The carbonate sediments of the banks are derived from corals and numerous calcareous algae that thrive in the warm, clear water. There is greater than 50% cover of corals here (Aronson et al., 2005), which is the highest in the Western Hemisphere. The coral provide a habitat for 175 species of tropical reef fishes and numerous species of invertebrates, including seafans and whips, sponges, anemones, and crinoids. Like other banks and reefs in the Gulf of Mexico, biological zonation occurs with depth (Dennis and Bright, 1988; Rezak, 1990). Hermatypic corals at the Flower Garden Banks appear



Fig. 10. Underwater photo of coral and associated fish fauna on Flower Garden Banks (NMFS).

to be the source for coral populations located at the many oil and gas platforms in the northern Gulf (Sammarco et al., 2012). At the base of the diaper-supported structures comprising the Flower Garden Banks are high-density, gas-saturated brine seeps that discharge into brine pools in the seafloor.

The Florida Platform and southwest Florida continental shelf, dominated by carbonate sands with some rock outcrops, extend a great distance from shore. Although rock outcrops are rare here, sessile epifauna such as corals, coralline algae, and sponges occupy more than 30% of the benthos (Phillips et al., 1990). The sandy substrates on this platform are often a thin veneer over limestone rock and have a macroinfauna dominated by crustaceans, polychaetes, and mollusks. Epibenthic life is dominated by crustaceans, mollusks, fishes, algae, and coelenterates.

Bays, estuaries, and beaches.—Numerous bays, lagoons, and estuaries line the Gulf coast; 40 are listed in the Gulfbase Web site for Texas,

Louisiana, Mississippi, Alabama, and Florida coasts (Harte Research Institute, 2014). The particular habitats within these areas are defined by salinity, tide, geomorphology, sediments, and especially by the predominant vegetation types. There are bays, barrier islands, sand beaches, estuaries, marshlands, and mangroves. A good general account of the broad Louisiana coastal area, including the landscape, vegetation, wildlife, human activities, wetland loss, and attempts at restoration, is provided by Gomez (2008). Britton and Morton (1989) provide another good general account of shoreline ecology, including terrestrial, estuarine, and marine waters from the Mississippi Delta west to Brownsville, TX, and then along the Gulf coast of Mexico to the Yucatan Peninsula. There are extensive lagoons in the western Gulf. Tunnell and Judd (2002) offer an excellent treatment of the ecology of the Laguna Madre system, which stretches from Corpus Christi, TX, to La Pesca, Mexico.

Many of the bays and lagoons in Florida and south Texas have relatively clear water and seagrass beds (Fig. 11), whereas bays and estuaries of Louisiana, Mississippi, and Alabama have more extensive marshes, but also have some seagrass habitats (GMP, 2004). The Big Bend area of Florida and Florida Bay have very extensive seagrass beds (Iverson and Bittaker, 1986), covering many square kilometers of coastal waters. Seagrass beds (also called submerged aquatic vegetation, SAV, which includes other types of plants as well) can include seven species of vascular plants rooted in the sediments.

Three of the more common varieties of seagrasses are turtle grass (*Thalassia testudum*), shoal grass (*Halodule wrightii*), and manatee grass (*Syringodium filiforme*). Seagrass beds are important as habitat for a variety of invertebrates and fishes (including many commercially important species), sea turtles, and marine mammals.

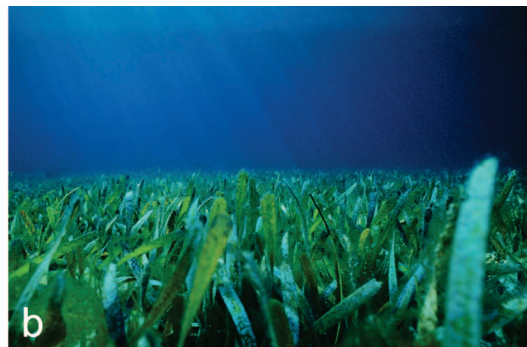
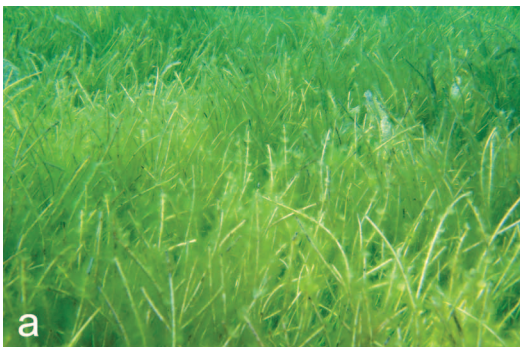


Fig. 11. Some Gulf of Mexico seagrasses. (a) Manatee grass, *Syringodium filiforme* (photo by Nancy Diersing, NOAA, NMS). (b) Turtle grass, *Thalassia testudum* (photo by Heather Dinn, NOAA, NMS).

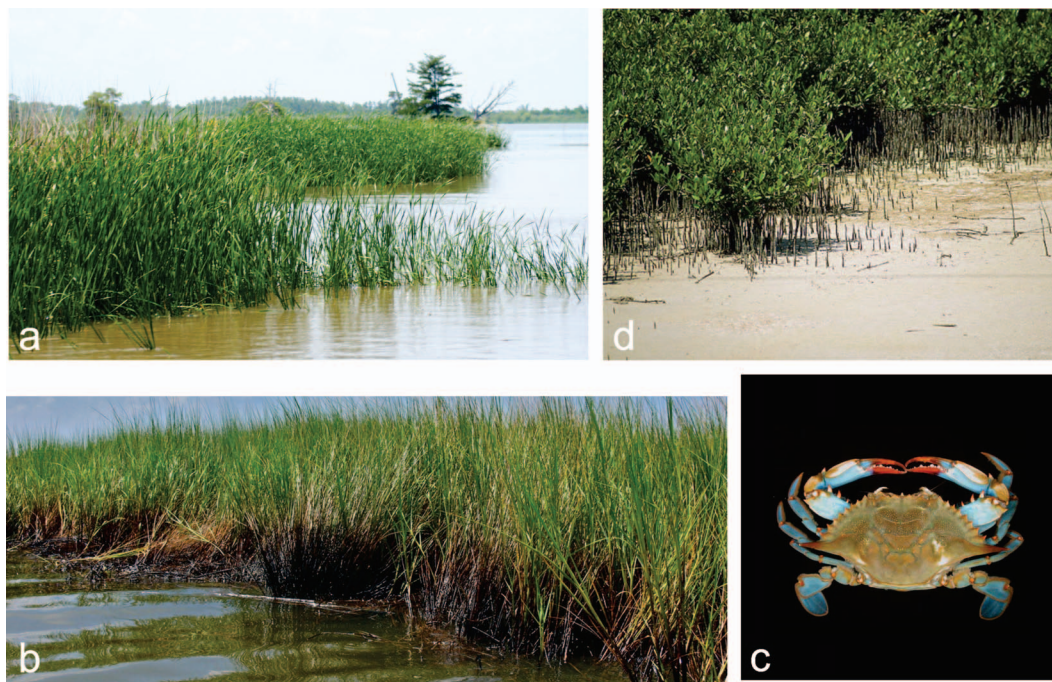


Fig. 12. Coastal marsh habitat and some of its inhabitants. (a) Marsh edge reeds, (b) cordgrass, *Spartina alterniflora*, at marsh edge with oil (photo by Mark Schrope), (c) blue crab, *Callinectes sapidus* (photo by University of South Carolina DNR), (d) black mangroves, *Avicennia germinans* (photo by J. Rayney, University of Texas).

Seagrass meadows are also valuable winter feeding habitat for ducks. For example, 75% of the world population of redhead ducks (*Aythya americana*) overwinters in the vast meadows of seagrasses in the Laguna Madre of Texas and Tamaulipas (Weller, 1964). Seagrasses dampen the effects of wave action and storm surge and thereby stabilize sediments. Blades shed from seagrasses break down into detritus, an important source of organic matter in shallow-water ecosystems. The macrobiota of seagrass beds include algae, polychaetes, crustaceans, mollusks, other invertebrates, and fishes (Britton and Morton, 1989). The fish fauna of the northern Gulf seagrass beds has apparently been affected by rising seawater temperatures in the last 40 yr, given the northern range extensions of many new tropical fishes (Fodrie et al., 2009). The seagrass beds of the northern Gulf of Mexico have been in decline for the last 60 yr (USGS, 2006).

The Gulf of Mexico has a very small tidal range, about half a meter at the maximum. This small range combined with the often very gradual increase in landward elevations exposes large areas of some habitats (e.g., marsh) during low tide. Salt marshes are very extensive in the north central Gulf, defining much of the

shoreline features and habitat (Fig. 12). At the water's edge the predominant emergent aquatic vegetation is smooth cordgrass (*Spartina alterniflora*), which thrives in salinities of about 16 ppt (Shiftlet, 1963). As cordgrass and other vegetation dies back or sheds its aboveground leaves, the leaves break down into detritus, an important potential source of food for invertebrates and some small fishes (Marinucci, 1982).

Algae also appear to be major sources of primary production for macrofauna living in marshes (Winemiller et al., 2007). Shrimp and blue crab are associated with marsh and wetland vegetation and are found in highest abundances close to the edge of marsh vegetation. Juvenile brown shrimp, white shrimp (*Litopenaeus setiferus*), and blue crab are most abundant within 1 m of the vegetative edge of marshes in the northwest Gulf (Minello and Rozas, 2002), showing the importance of marsh vegetation not only for sediment stabilization but also as structured habitat for commercially important estuarine invertebrates and small fishes, which are prey for sea trout (*Cynoscion nebulosus*) and red drum (*Sciaenops ocellatus*). Minello and Rozas (2002) estimated that degradation of marshes resulting in greater than 70% open water is likely to lead to decreases in these crustaceans.



Fig. 13. Artificial oyster reef before deployment (photo by author).

The northern Gulf is the northerly limit of black mangroves (*Avecinnia* spp.), which form another vegetative shoreline type. Climate warming may well result in the expansion of their populations into areas where *Spartina* spp. are currently dominant, with accompanying changes in marsh geophysical and geochemical properties (Comeaux et al., 2012). Biological uses of mangroves and marshes are unlikely to be identical, so changes in shrimp, crabs, and marsh-dependent finfishes may be expected.

In slightly less saline and inland areas of estuaries are brackish marshes—the habitat for marsh hay cordgrass (*Spartina patens*) in higher elevations and widgeon grass (*Ruppia maritima*) in the lower elevations and partly submerged areas. Approximately 20 species of SAV were identified in a survey of the northern Gulf; widgeon grass was the most commonly encountered species (Merino et al., 2009). Here open water is less extensive, with ponds and channels being predominant. Brackish marsh is a very important habitat for young stages of crabs, shrimps, and various fishes. Farther inland, brackish marshes grade into intermediate marsh areas, which have even more restricted open water and a lower salinity, in the range of 3 ppt. Reeds and rushes are important components of the vegetation, and these areas also serve as important habitat for young stages of estuarine and marine organisms.

In apparent contrast to the trophic structure of estuaries elsewhere in the United States (e.g., San Francisco Bay and Chesapeake Bay), the benthic communities of northern Gulf of Mexico estuaries and bays are dominated by detritivores, which may account for as much as 90% of the biomass of these communities (Gaston et al., 1997). Suspension feeders appear to be a relatively minor component of the benthic fauna, in contrast to other estuaries. There are biogeographical differences in benthic invertebrate communities of estuaries around the Gulf of Mexico with two provinces: Rio Grande, TX to northern Florida and south Florida (Engle

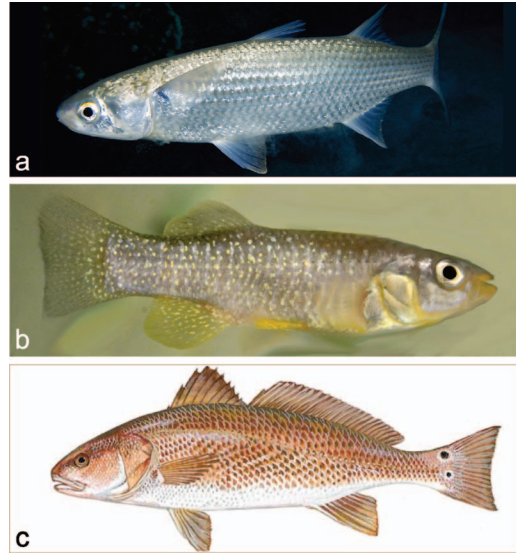


Fig. 14. Some bay and estuarine fish, Gulf of Mexico. (a) Stripped mullet, *Mugil cephalus* (photo by Keoki Stender), (b) gulf killifish, *Fundulus grandis* (photo by B. Dubjanski, LSU), (c) red drum, *Sciaenops ocellatus* (drawing courtesy of State of Louisiana).

and Summers, 2000). Crustaceans, bivalves, polychaetes, other invertebrates, and benthic fish are dominant faunal groups of these communities throughout the intertidal and subtidal areas of the Gulf.

Another major biogenic habitat is oyster reefs, which harbor a variety of estuarine species and help protect estuaries from storm-caused erosion. Oysters are sensitive to changes in salinity, and long-term changes in freshwater supply and saltwater incursion have had marked effects on the location of oyster reefs in estuaries (Berquist et al., 2006). Given the decline in oyster reefs, increases in the appreciation of their ecosystem services provided by oysters and advances in oyster hatchery technology have increased emphasis on oyster restoration throughout the northern Gulf (Fig. 13).

In the bays of Texas alone there are 550 species of fish (Murdy, 1983). We include here just a few comments on bay and estuarine fishes that are commonly prey for higher trophic level species, including some of the larger sport and commercial fish species (Fig. 14). As with invertebrates, there is a great deal of overlap in the schooling forage fishes found in bays and estuaries and those found on the shelf. Gulf menhaden (discussed in the section on the shelf), striped mullet (*Mugil cephalus*), and bay anchovy (*Anchoa mitchelli*) are abundant in bays. The three species of Gulf mullets are schooling, bottom-feeding detritivores, and their feeding

activity suspends large amounts of sediments (Britton and Morton, 1989). Among the many smaller species of fish that live in bays and marshes, the Gulf killifish (*Fundulus grandis*) are prominent permanent inhabitants.

Red drum is in the next trophic level higher than forage fishes and is a prominent sport fish across the northern Gulf, feeding on small fishes, crustaceans, and molluscs. They are a long-lived species, living up to 37 yr, and can weigh up to 27 kg in the Gulf (Texas Parks and Wildlife, 2014). They spawn inshore in the fall and winter. At first, young fish live in very shallow water, but they can spend more time offshore as they mature. Adult red drum, however, are often found in very shallow water and even in freshwater many miles from the ocean.

The brown pelican (*Pelicanus occidentalis*) is ubiquitous in the shallow bays and estuaries of the northern Gulf of Mexico. It is one of the largest birds on the Gulf coast: it weighs up to 5 kg and has a wingspan of up to 2.5 m. Brown pelicans are plunge divers, feeding almost exclusively on fish in the marine environment. They nest in colonies on coastal islands and raise their young in clutches of about three chicks, which they tend for up to 9 mo.

The West Indian manatee (*Trichechus manatus*) is a seasonal inhabitant of shallow coastal environments of the northern Gulf of Mexico (Pabody et al., 2009) and is frequently also seen in freshwater rivers. It is most commonly found in Florida, being limited to warm water habitats because of the manatee's lack of body insulation. Manatees can succumb to long cold spells in winter. They are herbivores, feeding on a variety of aquatic vegetation, such as seagrass, in large quantities. Manatees may live as long as 60 yr and may be up to 4 m in length. They mature sexually at approximately 4 yr and generally have one calf at a time. An adult female manatee can expect to have a calf approximately every 2 to 5 yr.

In contrast to the muddy sediments that predominate in coastal Louisiana, Mississippi, and to some extent in Alabama, the shorelines of Texas and Florida have mainly sandy beaches. These sandy beaches, many of them on barrier islands facing the open Gulf, have distinct groups of animals including bean clams (*Donax variabilis*), amphipods, mole crabs (*Emerita benedicti*), polychaetes, and small fishes (Kindinger, 1981; Britton and Morton, 1989; Rocha, 1995). The sandy beach invertebrates are fed upon by surf fishes, such as pompano (*Trachinotus carolinus*) and Gulf kingfish (*Menticirrhus littoralis*). The diversity of fauna in these sediments seems to increase with decreasing grain size.

CONCLUSION

The northern Gulf is a dynamic, large marine ecosystem supporting a high diversity of species and is influenced by terrestrial and oceanographic features that define its unique ecology. The estuarine, nearshore, pelagic, and deep-sea environments are interconnected, necessitating an integrated, ecosystem-wide approach to restoration planning and natural resource management. There are at least three major ecosystem features or processes that demonstrate the scale and importance of connectivity in the Gulf that should be considered in restoration: (1) the Loop Current and its associated eddies are mechanisms for chemical and biological dispersal within and beyond the Gulf and contribute nutrients through upwelling; (2) the Mississippi River is a significant source of freshwater, sediments, food and nutrients driving marine productivity and conditions in the northern Gulf; and (3) many Gulf species use both estuarine and offshore habitats during their life cycle. Long-term, Gulf-wide monitoring can improve our understanding of how these factors interact with one another and affect Gulf function and condition within the context of an ever-changing ocean.

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