CHAPTER 6

COASTAL HABITATS OF THE GULF OF MEXICO

Irving A. Mendelssohn,¹ Mark R. Byrnes,² Ronald T. Kneib³ and Barry A. Vittor⁴

¹Louisiana State University, Baton Rouge, LA 70808, USA; ²Applied Coastal Research and Engineering, Mashpee, MA 02649, USA; ³RTK Consulting Services, Hillsboro NM 88042, USA; ⁴Barry A. Vittor & Associates, Mobile, AL 36695, USA imendel@lsu.edu

6.1 INTRODUCTION

The Gulf of Mexico (GoM) is the ninth largest body of water in the world (including ocean basins) with an outer shoreline extending approximately 6,077 kilometers (km) (3,776 miles [mi]) from the Florida Keys to the northwest coast of Cuba (Moretzsohn et al. 2012). The Gulf encompasses an area of approximately 1.5 million km² (0.58 million mi²), and with an average depth of about 1,615 meters [m] (5,300 feet [ft]), it provides habitat for a myriad of marine, shoreline, and estuarine flora and fauna that occupy a diverse suite of coastal ecosystems (NOAA 2011). The Gulf is among the most biologically productive marine environments in the world, producing 78, 62, and 16 % of U.S. shrimp, oyster, and fishery landings, respectively (NOAA 2011). The productive value (market value) of the Gulf has been estimated at 124 billion U.S. dollars annually for Mexico and the United States from oil and gas, fisheries, ports and shipping, and tourism (Yoskowitz 2009). The Gulf provides a variety of important ecosystem services from regulating greenhouse gases to providing food to supporting recreational activities, all of which enhance the diverse social cultures within the GoM region (see Section 6.4.4).

The GoM shoreline includes a variety of coastal habitats, ranging from submerged seagrass beds to intertidal wetlands to supratidal sand dunes and maritime forests. Included in this habitat diversity are barrier islands, hypersaline lagoons, herbaceous marshes, forested wetlands of mangroves and cypress swamps, beaches, intertidal flats, oyster and coral reefs, subaquatic vegetation, and sponge beds (NOAA 2011). The following review emphasizes vegetated habitats of coastal strand beaches, as well as adjacent saline wetlands and subaqueous environments.

Coastal strand beaches, and adjacent marsh and subaqueous habitats of the GoM, extend as far north as approximately 30.5°N near the Florida Panhandle shoreline to as far south as 18°N along the Veracruz-Tabascan shoreline of Mexico. The westernmost extent is approximately 98°W along the Tamaulipas shoreline of Mexico, and the far eastern extent is along the Matanzas shoreline in Cuba at about 80.6°W (Figure 6.1). This geographic range spans geophysical boundaries and climatic zones (temperate, subtropical, and tropical), giving rise to physiographic and ecological classifications of shoreline habitats.

The primary goal of this paper is to provide a conceptual framework from which to understand the ecology of coastal habitats in the GoM including the physical and geological processes that control their formation. Given the importance of vegetated habitats along coastal beaches and marshes of the GoM, their documented societal value, and the present pressures for development, emphasis will be placed on vegetated shoreline habitats. These include intertidal wetlands, such as salt marshes and mangroves, intertidal to subtidal seagrasses and



Figure 6.1. Geographic extent of the Gulf of Mexico (basemap from CEC, 2007; French and Schenk, 2005).

flats, and supratidal barrier strand habitats, including beaches, sand dunes, and maritime forests on barrier islands. The landward limit of this review is the boundary between salt and brackish marshes, although when relevant, processes, biota, and/or habitats farther landward will be discussed. The seaward limit to which physical and biotic processes are addressed is the extent of active littoral transport (approximate location of the 10-m [33-ft] depth contour). From a geological standpoint, Holocene processes and sedimentary deposits are emphasized.

Although much is known about vegetated marine habitats of the GoM, no single document has attempted to review the diverse geology and ecology of coastal shoreline habitats in this vast geographic region. This review provides a summary of the geological and ecological status of shoreline habitats in the GoM, emphasizing vegetated ecosystems. It provides a baseline and general understanding of the operative physical and geological processes influencing coastal habitat formation and evolution, as well as the ecological structure and function of habitats.

6.2 PHYSIOGRAPHIC FRAMEWORK

Gulf Coast margins are characterized by persistent geochemical and biological interactions where continental and marine waters mix, and there is a continual exchange of large amounts of sediment, organic matter, and energy with the open Gulf. Topographic features, coastal and nearshore circulation, tidal mixing, and freshwater inflow from rivers and groundwater all contribute to small-scale interactions that control coastal habitat distribution and response (see Section 6.4). Along the north and south margins of the Gulf, river systems deliver large quantities of organic matter, sediments, and nutrients, resulting in high rates of sediment deposition and primary productivity, along with episodic sediment resuspension and redistribution (Robbins et al. 2009). On the eastern and western Gulf margins, river input is relatively small, and Loop Current and upwelling processes predominate (Schmitz 2003; Hine and Locker 2011).

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Various classification systems have been used to describe marine and terrestrial ecosystems within and adjacent to the GoM relative to watershed characteristics and oceanographic processes. Because the primary focus of this review is to describe the evolution of vegetated marine habitats of coastal strand beaches and adjacent wetlands (coastal habitat at the land–water interface), the marine ecoregion classification of Wilkinson et al. (2009) was used to illustrate natural environmental variability and the potential impact of human activities along the margins of the GoM. However, terrestrial ecoregions describe the inland character of subaerial coastal habitats at the marine boundary. As such, both systems are described below and referred to throughout the text when discussing shoreline change and coastal habitat distribution.

6.2.1 Marine Ecoregions

The GoM provinces of Robbins et al. (2009) largely overlap marine ecoregions established by Wilkinson et al. (2009), including (1) the South Florida/Bahamian Atlantic Marine Ecoregion, (2) the Northern GoM Marine Ecoregion, (3) the Southern GoM Marine Ecoregion, and (4) the Caribbean Sea Marine Ecoregion (Figure 6.2). Furthermore, Spalding et al. (2007) classified waters surrounding Cuba and a larger portion of the central Caribbean as the Greater Antilles Marine Ecoregion. The marine ecoregion classification was established to address ecosystembased conservation and sustainable development strategies. Three levels were identified for each ecoregion, except for the Greater Antilles. Level I captures largest-scale ecosystem differences, such as large water masses and currents and regions of consistent sea surface



Figure 6.2. Level I marine ecoregions of the GoM (data from Spalding et al. 2007; Wilkinson et al. 2009; and basemap from CEC 2007; French and Schenk 2005).



Figure 6.3. Level III marine ecoregions for the GoM (data from Wilkinson et al. 2009 and basemap from CEC 2007; French and Schenk 2005).

temperature (Figure 6.2). Level II reflects the break between neritic and oceanic areas and is delineated based on physiographic features (e.g., continental shelf and slope). This sub-level indicates the importance of depth for determining the location of benthic marine communities and primary physiographic features for controlling current flows and upwelling. Level III is limited to the continental shelf and based on differences within the neritic zone as determined by local water mass characteristics, regional landforms, and biological community type (Figure 6.3). Spalding et al. (2007), Wilkinson et al. (2009), Yáñez-Arancibia and Day (2004), and Yáñez-Arancibia et al. (2009) summarized these ecological regions and related environmental characteristics.

Although marine province and ecoregion characterizations for the GoM basin are generally consistent, marine ecoregion classification provides details more closely related to coastal habitat identification. The South Florida/Bahamian Atlantic region includes the southern tip of the Florida Peninsula, where groundwater discharge is important and sandy beaches, mangroves, seagrasses, and coral reefs dominate. This marine ecoregion extends from the Florida Keys north to southern Keewaydin Island (just south of Naples, Florida) and comprises four subregions that reflect physiographic and hydrologic complexities associated with this biologically unique area. Level III subregions include the Dry Tortugas Reef Tract, Florida Keys, Florida Bay, Shark River Estuarine, and Southwest Florida Neritic (Figure 6.3). Habitats of this region are often underlain by a calcium carbonate substrate, a driver of vegetation structure and function. Sea surface temperatures vary from 22.5 °C (72.5 °F) in the winter to 28 °C (82 °F) in the summer (Figure 6.4). Although the Cuban shoreline of the GoM is not included in this classification level, it is part of the Greater Antilles Marine Ecoregion (Level I)

and is dominated by limestone substrate similar to that of southern Florida. Furthermore, physical processes and ecological characteristics along the northwestern Cuban shoreline are similar to those of the Florida Keys.

The Caribbean coast of Mexico is the northern portion of the Caribbean Sea Ecoregion, named the Contoyan Neritic sub-region (Wilkinson et al. 2009). The sub-region name reflects proximity to Isla Contoy, located just east of the Campeche/Yucatán Inner Neritic zone (Figure 6.3). The area generally has lower average sea surface temperatures (28 °C [82 °F] in summer and 22.5 °C [72.5 °F] in winter; Figure 6.4) and lower nutrient loading than the Southern GoM Marine Ecoregion. Coral reefs, carbonate beaches, mangrove forests, and seagrass meadows are common coastal habitats, and water flow through the Yucatán Channel has a primary influence on coastal and shelf ecosystems. Beaches are primary tourist attractions of economic importance to the region.

The Northern GoM Ecoregion is a warm-temperate area in the GoM basin that contains approximately 60 % of tidal marshes in the United States, freshwater inputs from 37 major rivers, and numerous nursery habitats for fish (Figure 6.2) (Wilkinson et al. 2009). Average sea-surface summer temperatures in this region range from 28 to 30 °C (82 to 86 °F), while winter temperatures range from 14 to 24 °C (57 to 75 °F) (Figure 6.4). This is generally a region of high nutrient loading and includes biotic communities such as mangroves, salt marshes, and seagrasses, coastal lagoons and estuaries, and low river basins. This ecoregion extends from southern Keewaydin Island on the west coast of Florida to just south of Barra del Tordo in the State of Tamaulipas, Mexico and comprises six subregions that reflect the influence of tropical currents from the Caribbean Sea through the Yucatán Channel, the Loop Current and associated warm-water eddies, freshwater contributions from major river systems and groundwater, and outflows through the Straits of Florida. Level III subregions include the Western Florida Estuarine, Eastern Gulf Neritic, Mississippi Estuarine, Texas Estuarine, Laguna Madre Estuarine, and the Western Gulf Neritic (Figure 6.3).

The Southern GoM Ecoregion encompasses tropical waters of Mexico that support a variety of coastal habitats, including coastal lagoons, estuaries, beaches and dunes, mangroves, seagrass beds, and coral reefs. Air temperatures vary little between winter and summer, averaging about 26 °C (79 °F), although sea surface temperatures vary between 24 and 28.5 °C (75 and 83 °F), respectively (Figure 6.4). This is also a region of generally high nutrient loading and some local upwelling. The continental margin in this region is very topographically diverse, including a relatively narrow continental shelf (6 to 16 km [3.8 to 10 mi] wide) in the southwestern portion of the ecoregion with beaches and estuaries composed primarily of reworked fluvial sediment, interspersed with coastal rocky outcrops (Moreno-Casasola 2007; Contreras-Espinosa and Castañeda-Lopez 2007). In contrast, the southeastern coast of Campeche and Yucatán is fronted by a wide and shallow carbonate continental shelf and carbonate sand beaches. Many of the same biotic communities present in the northern GoM are common in this ecoregion, although coastal salt marshes are almost completely replaced by mangroves, and coral reefs and seagrasses become important. The Southern Gulf ecoregion extends from Barra del Tordo, along all six Gulf-facing States in Mexico, to the northeastern end of the Yucatán Peninsula. Subregions include Veracruz Neritic, Tabasco Neritic, Campeche/Yucatán Inner Neritic, and Campeche/Yucatán Outer Neritic (Figure 6.3).

Marine ecoregions for Cuba were not classified beyond Level I (Greater Antilles; Spalding et al. 2007); however, coastal systems within the Central Caribbean Ecoregion described by Sullivan-Sealey and Bustamante (1999) (equivalent to the Greater Antilles Ecoregion of Spalding et al. 2007) were classified based on dominant community type. Coral reefs, seagrass beds, and mangrove-dominated habitat are common along the northwestern Cuba coast. Further discussion of this classification is presented below in Section 6.4.2.



Figure 6.4. Average sea surface temperatures for winter and summer seasons for the GoM (data from Casey et al. 2010; basemap from French and Schenk 2005).

6.2.2 Terrestrial Ecoregions

Although oceanographic processes associated with specific marine ecoregions influence habitat development at the land-sea interface, geology, soils, and watershed characteristics associated with terrestrial ecoregions exert primary control on physiography of coastal habitats and nearshore water bottoms (Griffith et al. 2007). As such, coastal habitat descriptions within the context of GoM marine ecoregions may refer to terrestrial ecoregions when examining habitat distribution and change. Like marine ecoregions, their terrestrial counterparts portray areas within which relative homogeneity exists among physical and biological components of an ecosystem. Thirteen terrestrial ecoregions border the GoM from Florida to Cuba; four in the United States and ten in Mexico and Cuba (Figure 6.5).

The Southern Coast and Islands portion of the Southern Florida Coastal Plain Ecoregion extends from Keewaydin Island south to Key West and the Dry Tortugas (Griffith et al. 1997). The region includes the Ten Thousand Islands and Cape Sable, the islands of Florida Bay, and the Florida Keys (Figure 6.6). It is an area of mangrove swamps and coastal marshes, coral reefs, coastal strand vegetation on beach ridges, and limestone rock islands. The area has a nearly frost-free climate with mean annual temperature of 22 to 25 °C (72 to 77 °F) and mean annual precipitation of 1.34 m (4.4 ft) (Figure 6.7; Wiken et al. 2011). It is characterized by low-relief topography with wet soils. Relatively minor differences in elevation have significant impact on vegetation and diversity of habitat. Limestone underlies surficial sand and gravel and areas of peat and clay.

North of this area lies the Southwestern Florida Flatwoods portion of the Southern Coastal Plain Ecoregion (Level III), which includes barrier islands and Gulf coastal flatlands between



Figure 6.5. Level III terrestrial ecoregions surrounding the GoM (data from Wiken et al. 2011 and basemap from CEC 2007; French and Schenk 2005). Cuban ecoregions were developed by Olson et al. (2001).



Figure 6.6. Level IV terrestrial ecoregions for the U.S. GoM coast (data from USEPA 2011 and basemap from Amante and Eakins 2009).

Anclote Key and Keewaydin Island (Figure 6.6) (Griffith et al. 1997). The terrain consists mostly of flat plains, and also includes sandy beaches, coastal lagoons, marshes, and swampy lowlands. The Pinellas Peninsula portion of the Southern Coastal Plain Ecoregion is underlain by deeply weathered sand hills of Miocene age in the north and Pleistocene-age sand, shell, and clay deposits in the south. Besides the coastal strand, natural vegetation consists of longleaf pine and pine flatwoods. The dominant characteristic of the region is the Clearwater/St. Petersburg urban area. North of Anclote Key is the Big Bend Coastal Marsh segment of the Southern Coastal Plain Ecoregion, where Miocene to Eocene-age limestone resides at or near the surface to the mouth of the Ochlockonee River near the western margin of Apalachee Bay (Figure 6.6). Coastal salt marshes and mangroves characterize most of the coast.

The Gulf Barrier Islands and Coastal Marshes Ecoregion (Level IV) represents the westernmost extent of the Southern Coastal Plain Ecoregion (Figure 6.6). This area contains salt and brackish marshes, dunes, beaches, and barrier islands that extend from Saint George Sound near Apalachicola Bay to western Mississippi Sound at the Pearl River. Quaternary quartz sand, shell fragments, silt, clay, muck, and peat are primary physical components of coastal deposits. Cordgrass and saltgrass are common in the intertidal zone, while coastal strand grasses and pine scrub vegetation occur on parts of the dunes, spits, and barrier islands (Griffith et al. 2001). Average annual precipitation is approximately 1.5 m (4.9 ft), and average annual temperature is about 20 °C (68 °F) (Figure 6.7).

The Deltaic Coastal Marshes and Barrier Islands component (Level IV) of the Mississippi Alluvial Plain Ecoregion (Level III) encompasses brackish and saline marshes of the south Louisiana deltaic plain between the Pearl River and Vermilion Bay (Daigle et al. 2006). The region supports vegetation tolerant of brackish or saline water including salt marsh cordgrass, marshhay cordgrass, black needlerush, and coastal saltgrass. Black mangrove occurs in a few areas, and some live oak is found along old natural levees. Barrier islands in this region are low relief, medium to fine sand deposits with beach grasses in elevated dune and backshore environments. Extensive organic deposits lie mainly at or below sea level in periodically flooded settings, and inorganic silts and clays are soft and generally have high water content. Wetlands and marshes act as a buffer to help moderate flooding and tidal inundation during storm events. Flood control levees and channelization of the Mississippi River have led to a reduction



Figure 6.7. Average annual temperature (data from CEC 2011a) and precipitation (data from CEC 2011b) for terrestrial areas adjacent to the GoM. Basemap credits: © 2014 ESRI, DeLorme, HERE.

in sediment input to marshes and bays, resulting in delta erosion and accelerated relative sea-level rise (due primarily to subsidence) that threaten the environmental and economic stability of the region. This ecoregion has a humid subtropical climate with an average annual temperature of about 21 °C (70 °F) and mean annual rainfall of about 1.7 m (5.6 ft) (Figure 6.7).

In southwestern Louisiana and southeastern Texas, marginal deltaic deposits of the Mississippi-Atchafalaya River system form the Texas-Louisiana Coastal Marshes section (Level IV) of the Western Gulf Coastal Plain Ecoregion (Level III). The region is characterized by extensive brackish and saline marshes, few bays, and thin, perched barrier beaches at the GoM marsh-water edge that extend from western Vermilion Bay (LA) to High Island, Texas (Figure 6.6). Streams and rivers north of this region supply nutrients and sediments to coastal marshes from poorly consolidated Tertiary coastal plain deposits and Quaternary alluvium, terrace deposits, or loess. Soils are very poorly drained with muck or clay surface textures. Narrow, low relief ridges paralleling the modern shoreline are called *cheniers*, for the live oak trees that grow on these relic sand and shell shoreline deposits (McBride et al. 2007). Extensive cordgrass marshes occur in more saline areas. Estuaries and marshes support abundant marine life, supply wintering grounds for ducks and geese, and provide habitat for small mammals and alligators (Daigle et al. 2006). This coastal marsh ecoregion has a humid subtropical climate and average temperature and precipitation similar to the Deltaic Coastal Marshes ecoregion to the east.

The Mid-Coast Barrier Islands and Coastal Marshes portion of the Western Gulf Coastal Plain Ecoregion extends approximately 350 km (217 mi) from the Bolivar Peninsula on the southeast margin of Galveston Bay to Mustang Island, just south of Port Aransas, TX (Figure 6.6). The climate is sub-humid and average annual precipitation ranges from 0.9 to 1.2 m (3.0 to 3.9 ft) (Figure 6.7). The region includes primarily Holocene sediments with saline, brackish, and freshwater marshes, barrier islands with minor washover fans, and tidal flat sands and clays. In estuarine areas between Matagorda Bay and Corpus Christi Bay, some older Pleistocene barrier island deposits occur. Smooth cordgrass, marshhay cordgrass, and coastal saltgrass vegetation dominate in more saline zones. Barrier islands support extensive foredunes and back-island dune fields (Griffith et al. 2007). Salt marsh and wind-tidal flats are mostly confined to the backside of the barrier islands with fresh or brackish marshes associated with river-mouth delta areas. Black mangroves become common from San Antonio Bay south.

The Laguna Madre Barrier Islands and Coastal Marshes section of the Western Gulf Coastal Plain Ecoregion extends approximately 200 km (124 mi) from Corpus Christi Bay to the Rio Grande River; however, the Western Gulf Coastal Plain Ecoregion encompasses an extra 250 km (155 mi) of coastal habitat in the State of Tamaulipas, Mexico from the Rio Grande south to La Pesca (Figure 6.5). The Laguna Madre sections in Texas and Mexico are distinguished by their hypersaline lagoon systems, vast seagrass meadows, wide tidal mud flats, and long, narrow barrier islands with numerous washover fans. Surficial geology is primarily Holocene alluvium, beach ridges, and barrier island-tidal flat sands. The coastal zone of south Texas and northeastern Mexico has a semi-arid climate and average annual precipitation of 0.7 to 0.8 m (2.3 to 2.6 ft); average annual temperatures range from 22 to 25 $^{\circ}$ C (72 to 77 $^{\circ}$ F) (Figure 6.7). There is extreme variability in annual rainfall, and evapotranspiration is generally two to three times greater than precipitation. Tropical storms and hurricanes can bring large changes to this ecoregion. Grass vegetation of barrier island systems consists mostly of bitter panicum, sea oats, and gulf dune paspalum. Marshes generally are less extensive on the southern Texas and northern Mexico coast. A few stands of black mangrove occur along the south Texas coast; however, mangrove and herbaceous marsh habitat are more common in the Mexican part of this ecoregion along the fringes of backbarrier lagoons. Along the Tamaulipas coast, beaches are low profile and sand rich with narrow or no lagoons.

As no major rivers flow into the Texas Laguna Madre, the lagoon water can be hypersaline. Combined with the Laguna Madre of Tamaulipas, Mexico, it is the largest hypersaline system in the world (Tunnell 2002a). The shallow depth, clear water, and warm climate of this lagoon are conducive to seagrass production. Nearly 80 % of all seagrass beds in Texas are now found in the Laguna Madre (Tunnell 2002a).

The Veracruz Moist Forests Ecoregion along the eastern coast of Mexico extends from La Pesca to the Farallón Lagoon in Veracruz (Figure 6.5). This ecoregion encompasses lowlands of the eastern slopes of the Sierra Madre Oriental. It is composed of sedimentary rocks from the Cretaceous period, and the soils are shallow but rich in organic matter. The climate is tropical humid, with rain during 7 months of the year. Mean annual temperatures fluctuate between 20 and 24 °C (68 and 75 °F), and average annual precipitation ranges between 1.1 and 1.6 m (3.6 and 5.2 ft) (Figure 6.7) (WWF 2014a). Numerous fluvial systems drain geologic deposits that provide sediment and water to coastal saltwater lagoons and Gulf beaches (Contreras-Espinosa and Castañeda-Lopez 2007; Moreno-Casasola 2007). The ecoregion encompasses a variety of coastal physiography from sandy beaches and lagoons to rocky cliffs composed primarily of Mesozoic and Cenozoic sedimentary rocks. Between Laguna de Tamiahua to the rocky headland at Playa Munéco, clastic sediment beaches are supplied by upland sedimentary sandstone, shale, and limestone (Wiken et al. 2011). Extensive coastal sand dunes are common and sandy/cobble pocket beaches exist between rocky headlands. Mangroves are common in coastal lagoons and estuaries.

The Veracruz Dry Forests Ecoregion is located in central Veracruz, surrounded by tropical forest ecoregions (Figure 6.5). The region is located in the coastal plain of central Veracruz, north of the Santa Martha and San Andrés volcanoes. The climate is tropical dry due to the influence of the Chiconquiaco Sierra Mountains. The soils are calcareous and derived from sedimentary rocks, and the area is relatively humid (<1 m/year [3.3 ft/year] rainfall). These characteristics allow the development of a dry forest along the coast, near Veracruz City. The forests constitute the preferred habitat for many birds, including migratory species that use coastal environments of the region as a stopover during their migratory route (WWF 2014b).

Adjacent and south of the Veracruz dry forests is the Petén-Veracruz Moist Forests Ecoregion. This moist forest ecoregion consists of a mixture of wetlands, riparian habitats, and moist forests that extend from southern Veracruz and into the State of Tabasco (Figure 6.5). Soils of this ecoregion are some of the most productive in the country, resulting in high species richness and high desirability for local agriculture. As such, much of the natural habitat has been cultivated for agriculture, and it is estimated that only a small percentage of the original habitat remains (Hogan 2013a). Beach and estuarine deposits in the Petén-Veracruz Moist Forests Ecoregion are influenced by fluvial systems that primarily drain Cenozoic sedimentary sandstones. Quaternary alluvial, marsh, and lacustrine deposits are common near the coast. The Papaloapan watershed is a dominant physiographic feature in this ecoregion (Wiken et al. 2011).

The Sierra de los Tuxtlas small coastal ecoregion is bounded on landward sides by the Petén-Veracruz Moist Forests Ecoregion. Formed from volcanic activity, coastal deposits are primarily rocky cliffs and sandy pocket beaches between rocky headlands. Upland environments are thickly forested and the area is recognized as an important zone for migratory birds (Valero et al. 2014).

The Pantanos de Centla Ecoregion is located in the eastern part of Tabasco and the western portion of Campeche south and west of Laguna de Términos (Figure 6.5). The ecoregion is biologically rich and contains almost 12 % of aquatic and sub-aquatic vegetation in Mexico. Soils of this ecoregion are quite productive and species richness is high. Deltaic deposits and extensive marsh habitat are primary components of the Centla region of Tabasco from the

Grijalva-Usumacinta watershed. Lowlands fringing Laguna de Términos (Campeche) contain large expanses of mangroves (ParksWatch-Mexico 2003).

The Mesoamerican Gulf-Caribbean Mangroves Ecoregion resides at various locations along the Mexican GoM coast, primarily associated with saltwater lagoons and estuaries (Figure 6.5). Mangroves north and west of the Alvarado Lagoon (Veracruz) thrive in coastal areas exposed to riverine water and sediment input throughout the states of Tamaulipas and Veracruz. Mangroves grow on flat terrain and are influenced by the Tonala River near the border between Tabasco and Veracruz, the Papaloapan in northern Veracruz, and the Pánuco River near the border between Tamaulipas and Veracruz. Mangroves grow on clay soils that are deep and rich in organic matter. The climate is tropical sub-humid with summer rains; temperature oscillations are very slight, and the levels of humidity are relatively high with between 1.2 and 2.5 m (3.9 and 8.2 ft) of annual rainfall. Red, black, and white mangroves are the dominant species, and as with most mangrove areas, local herbaceous flora is not abundant because they are generally intolerant to frequent flooding (Hogan 2013b; WWF 2014c).

Mangrove habitat flourishes surrounding Laguna de Términos in the State of Tabasco, Mexico. The delta of the Usumacinta and Grijalva Rivers supports mangrove habitat in this region as well. Soils are deep and rich in organic matter, which make them among the most productive soils in Mexico. The climate is warm and humid with abundant rain in summer, and this mangrove ecoregion is one of the wettest, with about 1.6 m (5.2 ft) of rain annually. Usumacinta mangroves and the nearby floodlands are considered the most important wetlands of the country, referred to as the Pantanos de Centla (Figure 6.5). The Grijalva-Usumacinta fluvial system and deltaic plain supply the largest discharge of fresh water to the southern GoM. Intrusions of salt water during the dry season allow mangroves to form up to 30 km (18.6 mi) inland. Vegetation is established in soils with very high organic matter content. Red, white, and black mangroves are key species in the community (WWF 2014d).

Homogenous limestone layers from Tertiary and Quaternary periods characterize the western portion of the Yucatán Peninsula, where the Yucatán Dry Forest Ecoregion abuts the coast near the city of Campeche (Figure 6.5) (WWF and Hogan 2013). The area is relatively dry, with average annual rainfall of about 0.5 m (1.6 ft) and average annual temperatures between 24 and 26 °C (75 and 79 °F) (Figure 6.7) (Wiken et al. 2011). Mangroves dominate coastal vegetation and very little surface water drains to the coast; drainage is primarily subterranean. Beach sand is primarily limestone particles (Moreno-Casasola 2007). Petenes mangroves characterize the northwestern edge of the Yucatán Peninsula (WWF and Hogan 2014a). The area is continuously flooded, though rivers are absent from this portion of the Mesoamerican Gulf-Caribbean Mangroves Ecoregion. Instead, springs form in the bottom of the mangroves, providing fresh water to help regulate salinity and raise nutrient concentrations. The Celestún Lagoon is the most important hydrologic feature within Petenes mangroves portion of the ecoregion. Soils form on a karstic limestone platform and are shallow in some areas and deep in others. Different types of mangroves grow in this area depending on the levels of salinity and the amount of nutrients present. Coastal fringe mangrove habitat contains greater nutrients and is composed of taller trees (15 to 20 m [49 to 66 ft]) as compared with pygmy mangrove habitat inland of the fringe where shorter trees (less than 5 m) dominate. Both types of mangrove habitat contain primarily red and white tree species; black mangroves are scarce because they are relatively intolerant of persistent floods.

The eastern Yucatán Peninsula has similar physiographic and ecologic characteristics. It has a mean annual temperature of 26 °C (79 °F), and there are warm, sub-humid climates with intermediate rains (Wiken et al. 2011). Mangroves dominate coastal vegetation, and white limestone sand beaches are present. Drainage is completely subterranean, and carbonate rocks are of Upper Tertiary origin.

Two terrestrial ecoregions dominate coastal habitats in western Cuba adjacent to the GoM. The Cuban Cactus Scrub Ecoregion is always associated with dry coastal climates and is located in patches along west coast shorelines (Figure 6.5) (WWF 2014e). The ecoregion has a desert-like appearance with average annual precipitation of 0.8 m (2.6 ft) or less and average temperatures of 26 °C (79 °F) (Figure 6.7). The principal soil type is derived from coralline limestone rock and has a karstic structure. Beaches are generally narrow and are composed of coralline sand and pebble fragments. Although the Bahamian-Antillean Mangroves Ecoregion is primarily associated with the Bahamas islands, coastal habitat on the submerged limestone bank along the northwestern Cuban shoreline is included in this ecoregion (Figure 6.5) (WWF and Hogan 2014b). Porous limestone substrate and relatively low precipitation means no major rivers supply nutrients and sediment to the coast. Coral reefs and carbonate islands are common seaward of the mainland coast, and mangroves thrive in these environments. Mainland beaches are composed of coralline sand and carbonate shell deposits, and seagrass beds in association with mangroves are common.

6.3 PHYSICAL SETTING

River-dominated shelves and energetic tropical cyclonic events that control the development of coastal habitats characterize the GoM ocean basin. Gulf waters are bordered by the United States to the north (Florida, Alabama, Mississippi, Louisiana, Texas), six Mexican states to the south and west (Tamaulipas, Veracruz, Tabasco, Campeche, Yucatán, Quintana Roo), and the island of Cuba to the southeast (Figure 6.1). The Gulf basin extends approximately 1,600 km (994 mi) from east to west and about 900 km (560 mi) from north to south. The Gulffacing shoreline from Cape Sable, Florida to the tip of the Yucatán peninsula extends approximately 5,700 km (3,542 mi), with another 380 km (236 mi) of shore on the northwest margin of Cuba. When bays and other inland waters are included, total shoreline length increases to at least 27,000 km (16,777 mi) in the United States alone (Moretzsohn et al. 2012). Based on bathymetric contours for the Gulf basin, shallow and intertidal regions (<20 m [66 ft] deep) represent about 11 % of the Gulf basin, whereas shelf, slope, and abyssal regions comprise approximately 25, 38, and 26 %, respectively (Figure 6.8). Average water depth for the basin is on the order of 1,615 m (5,300 ft), and maximum depth is about 4,400 m (14,435 ft) (Sigsbee Deep).

Water and sediment presently are supplied to the Gulf by more than 150 rivers, including 20 major river systems (Robbins et al. 2009). Freshwater inflow to the Gulf is approximately 10^{12} cubic meters per year (m³/year) (35 × 10^{12} ft³/year), with about 63 % of the total arriving via the Mississippi-Atchafalaya watershed (Moretzsohn et al. 2012). Other U.S. rivers contribute another 14 %, and the remaining 23 % is supplied from Mexico and Cuba. South Texas receives the least rainfall among Gulf coastal areas. Groundwater contributions are significant in many areas, especially the eastern and southern margins of the Gulf.

Thirty-nine major estuarine systems exist along the Gulf coastline, of which 82 % are located within the Northern Gulf Marine Ecoregion and 18 % along the Southern Gulf coast (Wilkinson et al. 2009; Moretzsohn et al. 2012). Marine-dominated bays occur in the eastern Gulf, whereas river-dominated estuaries characterize the northern Gulf and coastal lagoons are common in the Southern Gulf (Moretzsohn et al. 2012). More than 14,500 km² (5,600 mi²) of estuarine wetlands reside along Gulf coastlines. Approximately one-third consist of forested mangrove wetlands, with the remainder being herbaceous marsh (Wilkinson et al. 2009). Tidal influence on estuaries is relatively uniform (in contrast to freshwater influence), with tide ranges generally less than 1 m (3.3 ft) (Stumpf and Haines 1998).



Figure 6.8. Map illustrating primary depth contours defining the GoM basin (contour data from Becker et al. 2009; basemap from Amante and Eakins 2009).

The following sub-sections provide a summary of geologic controls regarding formation of the GoM Basin, terrestrial and watershed controls on coastal habitat formation, primary oceanographic processes influencing basin-wide circulation patterns and coastal habitat evolution, and historical shoreline change patterns relative to longshore sediment transport magnitude and direction. These geological and physical processes are the primary factors influencing the spatial distribution of coastal habitats and their ecology (Sections 6.4.3 and 6.5) within an ecoregion context (Section 6.2).

6.3.1 Formation of the Gulf of Mexico Basin

The GoM has been described as a relatively small oceanic basin that evolved in response to separation of the North and South American plates by crustal extension and seafloor spreading during the Mesozoic breakup of Pangea (Galloway 2011). As such, topographic relief and bathymetry reflect the overall geologic structure of the basin. Furthermore, physiography of the Gulf basin has been influenced by sea-level changes in response to alternating glacial and interglacial periods on the North American continent. Sea-level changes driven by episodic influxes of meltwater generally controlled drainage systems of the region, the morphology of coastal plain alluvial systems, and sediment volumes supplied to the basin (Bryant et al. 1991).

The general geographic limits of the GoM basin correspond with structural features (Figure 6.9). The Florida and Yucatán carbonate platforms mark the eastern and southern flanks of the basin. The western flank of the basin corresponds to the location of the Chiapas massif and the Sierra Madre Oriental of Mexico, whereas the northern border flanks the

Ouachita orogenic belt, the Ouachita Mountains, the central Mississippi deformed belt, and the southern reaches of the Appalachian Mountains (Salvador 1991a). Along the north and north-west margins of the basin, the coastal plain and continental shelf of the GoM are widest and have a relatively gentle slope toward the center of the Gulf, similar to the slope of the basement in the region. In eastern Mexico, the coastal plain and shelf are quite narrow and steep, just like the basement surface (Bryant et al. 1991). Adjacent to the east and southeast margins of the basin, some of the deepest parts of the GoM rise rapidly at the submarine escarpments fronting the Florida and Yucatán platforms, under which basement rocks are flat and featureless.



Figure 6.9. General outline of the GoM basin. Second-order structural features include: (1) Macuspana basin; (2) Villahermosa uplift; (3) Comalcalco basin; (4) Isthmus Saline basin; (5) Veracruz basin; (6) Cordoba platform; (7) Santa Ana massif; (8) Tuxpan platform; (9) Tampico-Misantla basin; (10) Valles-San Luis Potosi platform; (11) Magiscatzin basin; (12) Tamaulipas arch; (13) Burgos basin; (14) Sabinas basin; (15) Coahuila platform; (16) El Burro uplift; (17) Peyotes-Picachos arches; (18) Rio Grande embayment; (19) San Marcos arch; (20) East Texas basin; (21) Sabine uplift; (22) North Louisiana salt basin; (23) Monroe uplift; (24) Desha basin; (25) La Salle arch; (26) Mississippi salt basin; (27) Jackson dome; (28) Central Mississippi deformed belt; (29) Black Warrior basin; (30) Wiggins uplift; (31) Apalachicola embayment; (32) Ocala uplift; (33) Southeast Georgia embayment; (34) Middle Ground arch; (35) Southern platform; (36) Tampa embayment; (37) Sarasota arch; (38) South Florida basin (republished with permission of the Geological Society of America from Salvador 1991a; permission conveyed through Copyright Clearance Center, Inc.).

The Late Triassic breakup of Pangea preceded the formation of the GoM Basin, which began about 230 million years ago with the collapse of the Appalachian Mountains (Bird et al. 2011). As a result of rifting within the North American Plate during the Middle to Late Jurassic, it began to crack and drift away from the African and South American plates (Salvador 1991b). Although differing evolutionary models for the basin exist, most researchers believe that counterclockwise rotation of the Yucatán Peninsula block away from the North American Plate, involving a single ocean-continent transform boundary, led to the formation of the basin (Bird et al. 2011). Opening of the Gulf required approximately 500 km (310 mi) of extension accompanied by southward migration and counterclockwise rotation of the Yucatán block (Galloway 2011). Most of the structural basin is underlain by transitional crust that consists of continental crust that was stretched and attenuated primarily by Middle to Late Jurassic rifting (Galloway 2011).

The separation of what became North and South America produced a narrow belt of ocean about 170 million years ago. Initial conditions in what is now the GoM basin consisted of shallow, hypersaline seas in which extensive salt deposition took place. Deposition of Louann salt and associated evaporites spread across the hypersaline basin formed by stretching of continental crust (Figure 6.10) (Galloway 2011). Salt deposition during the Jurassic eventually resulted in the formation of numerous salt domes that are scattered throughout the GoM.

Since the Late Jurassic, the basin has been a stable geologic province characterized by the persistent subsidence of its central part, likely due at first to thermal cooling and later to sediment loading as the basin filled with prograding sediment wedges along its northwestern and northern margins, particularly during the Cenozoic (Salvador 1991b). Approximately 155 million years ago, the Yucatán Peninsula and the Florida Peninsula were connected land-masses and the ancestral GoM was a shallow marine sea (Figure 6.11). The coast in Mexico and Texas was inland of the present coast and was dominated by reefs with shallow basins that precipitated evaporite minerals on their landward side. These conditions required sea level to be about 100 m (328 ft) above its present position. Persistent subsidence of the basin eventually opened the Gulf between the Yucatán and Florida peninsulas.

Carbonate deposition in the Middle Cretaceous (about 100 million years ago) included large reef complexes throughout the basin. Landward of these deposits in the northeastern GoM, terrigenous sediment from the southern Appalachians provided clastics for the initial phase of coastal plain development and fluvial delta formation (Figure 6.12). Near the end of the Cretaceous, tectonic activity caused ocean basins to experience a significant increase in volume that produced falling sea level in the Gulf. Lowered sea level resulted in significant erosion of adjacent landmasses, causing substantial sediment transport to the northern GoM coast. By the end of the Early Cretaceous, deposition and subsidence created the modern morphology of the Gulf Basin.

The sedimentary section of the GoM was deposited under stable tectonic conditions. Subsidence of the basin was modified only by local deformation of Jurassic salt and growth faulting adjacent to primary depocenters (Galloway 2011). As a consequence, environments of deposition and lithologic composition of the sedimentary sequence persisted from Late Jurassic to present. Overall, three distinct provinces were formed in the sedimentary sequence of the GoM basin: (1) carbonate and evaporite deposits associated with Florida and Yucatán platforms; (2) carbonates and fine-grained terrigenous sediment along the Tamaulipas, Veracruz, Tabasco, and Campeche coasts of Mexico; and (3) coarse-grained terrigenous sediment in the northern GoM, indicating the importance of fluvial input from the continental interior to the area between eastern Mexico and northern Florida (Salvador 1991b; Galloway 2011).

Although the basin was stable, uplift of the Appalachians during the Miocene produced extensive fluvial sediment that was transported to the northern Gulf coast. Large deltaic



Figure 6.10. Crustal types, depth to basement, and original distribution of Jurassic Louann salt beneath the GoM basin. Principal basement structures include: *SrA* Sarasota Arch, *TE* Tampa Embayment, *MGA* Middle Ground Arch, *AE* Apalachicola Embayment, *WA* Wiggins Arch, *MSB* Mississippi Salt Basin, *MU* Monroe Uplift, *NLSB* North Louisiana Salt Basin, *SA* Sabine Arch, *ETB* East Texas Basin, *SMA* San Marcos Arch, *RGE* Rio Grande Embayment, *TA* Tamaulipas Arch (from Galloway 2011; republished with permission of the Texas A&M University Press).

systems were developed along the northern coast of the basin. Sea level was tens of meters above the present position. During the Pliocene, terrigenous sediments from the mainland dominated the northern Gulf. The Yucatán platform remained controlled by carbonate sedimentation because of a lack of siliclastic sediment (Figure 6.13). The shoreline had a configuration similar to present time but at a more landward position (Salvador 1991b).

6.3.2 Terrestrial Controls on Coastal Evolution

Two primary factors control the development of terrestrial habitat at the interface between marine and freshwater environments: geology of coastal deposits and watershed contributions. Coastal geology refers to existing deposits that are subject to erosion and transport by modern marine processes and watershed input refers to terrestrial supply of sediment, nutrients, and fresh water to estuarine and fluvial deltaic deposits, and neritic carbonate environments, at the marine land–water interface. Coastal habitats of the GoM reflect the variety of geologic controls and watershed processes operating along the modern Gulf shoreline. Figure 6.14



Figure 6.11. Paleogeography of the GoM basin around 155 million years ago (republished with permission of the Geological Society of America from Salvador 1991b; permission conveyed through Copyright Clearance Center, Inc.).

depicts the age and type of geologic deposits coincident with the land-water interface around the GoM. Most low-lying shorelines are composed of Quaternary sedimentary deposits of carbonate and terrigenous origin. However, Eocene, Oligocene, and Miocene deposits are common along the Big Bend coastline of northwestern Florida and along the Tamaulipas and Veracruz coast of Mexico. Furthermore, Quaternary volcanic rocks intersect the land-water interface in two locations along the Veracruz coast (Palma Sola and Tuxtla). Finally, Cretaceous carbonate deposits are encountered along the northwest margin of Cuba (Figure 6.14). Most prominent Quaternary deposits are those associated with riverine deltas in the northern GoM marine ecoregion (e.g., Rio Grande, Mississippi, and Apalachicola) and carbonate deposits along the southwest Florida coast, the Yucatán Peninsula, and the northwest coast of Cuba.

Coastal Habitats of the Gulf of Mexico



Figure 6.12. Paleogeography of the GoM basin around 100 million years ago (republished with permission of the Geological Society of America from Salvador 1991b; permission conveyed through Copyright Clearance Center, Inc.) For explanation of patterns, see Figure 6.11.

Although geologic deposits with direct exposure at the marine land–water interface have significant impact on coastal habitat formation, freshwater input from riverine watersheds and coastal groundwater sources provide vital nutrients and sediment to estuaries and outer coast shoreline habitat. Riverine contributions to coastal habitat in Mexico are important in the States of Tamaulipas, Veracruz, and Tabasco, but annual freshwater and sediment input to the Gulf from the United States vastly exceeds input from Mexico. Figure 6.15 illustrates primary watersheds adjacent to the GoM, showing the spatial extent of each watershed. The Mississippi-Atchafalaya watershed drains nearly two times as much area as all other watersheds combined. Furthermore, average discharge from this watershed contributes about 63 % of freshwater input to the Gulf annually. Table 6.1 provides a summary of freshwater discharge to the Gulf by watershed. Groundwater contributions to coastal habitat evolution are relatively minor but important for carbonate environments of the Yucatán Peninsula and the southwest Florida coast. In both areas, precipitation associated with tropical cyclones and other rain events provides the primary source of fresh water to recharge carbonate aquifers (Beddows et al. 2007).

The interaction among fluvial water/sediment supply, coastal geology, and marine physical processes produces the variety of coastal depositional environments bordering the GoM. Although marine ecoregions provide a reasonable framework for describing primary coastal habitats at the land–water interface, terrestrial ecoregions emphasize land-based characteristics above sea level (see Section 6.2.2). Section 6.4.2 presents depositional characteristics of



Figure 6.13. Paleogeography of the GoM basin around 5 million years ago (republished with permission of the Geological Society of America from Salvador 1991b; permission conveyed through Copyright Clearance Center, Inc.). For explanation of patterns, see Figure 6.11.

vegetated marine habitats and adjacent subaqueous environments along the Gulf shoreline that provide more detail regarding habitat type and distribution than discussed previously under terrestrial ecoregions. First, the distribution of dominant coastal depositional systems will be presented within the context of coastal processes controlling sediment transport and deposition.

6.3.3 Oceanographic Processes

The formation and evolution of coastal habitats within the Gulf are a direct response to water, sediment, and nutrient input to the basin relative to physical oceanographic processes that control erosion and deposition at the land–water interface in response to long- and short-term fluctuations in water level. Far-field forces such as basin-scale circulation, tide dynamics, and eustatic sea-level rise exert significant control on long-term habitat evolution, whereas intense periodic events such as storms and floods present short-term perturbations to the coast that can create habitat in a given locale as fast as it is destroyed in another. As such, coastal habitats are always changing in response to physical disturbances. The following section summarizes dominant physical processes in the GoM.



Figure 6.14. Terrestrial geologic deposits bordering the GoM (geology data from Garrity and Soller 2009). Basemap credits: ESRI, GEBCO, NOAA, CHS, CSUMB, National Geographic, DeLorme, and NAVTEQ.

6.3.3.1 Meteorological Conditions

The GoM is influenced by a maritime subtropical climate controlled primarily by clockwise circulation around a high barometric pressure area known as the Bermuda High. This pressure system dominates circulation throughout the year, weakening in the winter and strengthening in the summer. The Gulf is located southwest of this center of circulation, resulting in a predominantly southeasterly flow throughout the GoM. Two types of cyclonic storms may be superimposed on this circulation pattern depending on time of year. During winter months (December through March) when strong north winds bring drier air into the region, cold fronts associated with cold continental air masses primarily influence northern Gulf coastal areas, but also reach the southern GoM. Tropical cyclones develop and/or migrate into the Gulf and substantially alter local wind circulation. Severe weather events such as thunderstorms, lightning, floods, and tornadoes are common in the Gulf as well. While tornadoes and floods are primarily inland weather hazards, the coastal zone is most vulnerable to hurricanes and their accompanying impacts such as storm surge.

For coastal areas along the GoM, prevailing wind directions are generally from the southeast and south, except for the coastal areas in the northeastern Gulf, where the prevailing winds are from the north (BOEM 2011). Average wind speeds from shoreline and buoy stations



Figure 6.15. Primary watersheds supplying freshwater, nutrients, and sediment to the GoM (watershed data from CEC 2010; basemap from Amante and Eakins 2009).

are relatively uniform, ranging from 5.2 to 6.4 m/s (17.1 to 21.0 ft/s). In general, wind speeds are highest in winter months and lowest in summer months. In coastal areas, sea breezes may become the primary circulation feature during summer months. The humid subtropical climate of the GoM exhibits abundant and fairly well distributed precipitation throughout the year. Precipitation in coastal cities along the Gulf tends to peak in summer months. As such, relative humidity in coastal areas is high. Lower humidity occurs during late fall and winter when cold, continental air masses regularly bring dry air into the northern Gulf. Maximum humidity occurs during spring and summer when prevailing southerly winds introduce warm, moist air. Typically, highest relative humidity occurs during the warmest part of the day (around sunrise), while lowest relative humidity occurs during the subtropical maritime climate in the southwestern GoM is relatively dry. Overall, the subtropical maritime climate is a dominant feature driving weather patterns in this region. As such, the GoM climate shows very little diurnal or seasonal variation.

6.3.3.2 Tides

Astronomical tide range throughout the GoM is relatively small (generally less than 1 m [3.3 ft]), but what it lacks in magnitude is compensated for by variety of tide types. While semidiurnal tides (two highs and two lows per day) are dominant along most coasts, GoM water levels are controlled by diurnal tides (one high and one low per day) due to the near resonance of Gulf water with diurnal tidal forcing (Kantha 2005). Diurnal tide in the GoM is driven by

Watershed	Drainage Area (km²)	Average Daily Discharge (m ³ /s)	% Total Discharge	Primary River(s) (water years)	Source
South Florida Gulf	30,960	46	0.1	Caloosahatchee (1966–2011)	USGS (2012a)
West Florida Gulf	67,370	401	1.2	Ochlockonee (1926–2011), Peace (1932–2011), Suwanee (1931–2011), & Withlacoochee (1928–2011)	USGS (2012b, c, d, e)
Apalachicola	52,200	683	2.0	Apalachicola (1978–2011)	USGS (2012f)
Choctawhatchee- Escambia	37,230	389	1.1	Choctawhatchee (1931–2011) & Escambia (1988–2011)	USGS (2012g, h)
Mobile	114,450	1,709	4.9	Tombigbee (1961–2011) & Alabama (1976–2011)	USGS (2012i, j)
Pascagoula-Pearl	51,520	518	1.5	Pascagoula (1994–2011) & Pearl (1939–2011)	USGS (2012k, I)
Mississippi- Atchafalaya	3,282,169	21,940	63.3	Mississippi & Atchafalaya (1980–1996)	Battaglin et al. (2010)
Texas Gulf Coast	484,678	1,081	3.1	Calcasieu (1923–2011), Sabine (1961–2011), Neches (1951–2011), Trinity (1924–2011), Brazos (1967–2011), Colorado (1948–2011), Guadalupe (1935–2011), San Antonio (1924–2011), & Nueces (2000–2011)	USGS (2012m, n, o, p, q, r, s, t, u)
Rio Grande/Bravo- Conchos ^{ab}	558,360	177	0.5	Rio Grande	NWCM (2010)
San Fernando-Soto La Marina ^a	54,720	115	0.3	San Fernando & Soto La Marina	NWCM (2010)
Pànuco ^a	97,820	645	1.9	Pànuco	NWCM (2010)
Tuxpan-Nautla ^a	26,190	384	1.1	Tuxpan, Cazones, Tecolutla, & Nautla	NWCM (2010)
Papaloapan ^a	57,480	1,565	4.5	La Antigua, Jamapa, & Papaloapan	NWCM (2010)
Coatzacoalos ^a	29,770	1,252	3.6	Coatzacoalcos & Tonala	NWCM (2010)
Grijalva- Usumacinta ^{abc}	103,300	3,727	10.8	Grijalva-Usumacinta & Candelaria	NWCM (2010)
Yucatán West (Campeche)	21,620	N/A	0	Groundwater only	NWCM (2010)
Yucatán North	56,270	N/A	0	Groundwater only	NWCM (2010)

(continued)

Table 6.1. (continued)

Watershed	Drainage Area (km²)	Average Daily Discharge (m ³ /s)	% Total Discharge	Primary River(s) (water years)	Source
Total	5,126,107	34,633	100.0		
United States	4,120,577	26,768	77.3		
Mexico	1,005,530	7,865	22.7		

^aThe data on average daily discharge represent the mean value of their historical registry

^bThe mean daily discharge includes imports from other countries

^cThe watershed area refers only to the Mexican portion



Figure 6.16. Spatial distribution of tide type based on water level form number for the GoM (modified from Kjerfve and Sneed 1984; basemap from French and Schenk 2005). Tide stations from which harmonic constituents were used to create the map are illustrated as *green dots*.

in-phase co-oscillations of the Atlantic Ocean and the Caribbean Sea through the Straits of Florida and the Yucatán Channel and exhibits a natural period of oscillation from 21 to 28.5 h (Reid and Whitaker 1981; Seim et al. 1987). Whereas direct tidal forcing explains about 13 % of the diurnal water level variance, more than half of the semidiurnal water level variance is in

response to direct tidal forcing (Kjerfve and Sneed 1984). Because the semidiurnal (M_2) tide is dominant in the North Atlantic, it influences tides in the Gulf via flows through the Straits of Florida and indirectly through the Yucatán Channel. Even though semidiurnal tides tend to get amplified across wide continental shelves, only tides in the eastern Gulf from Apalachicola Bay south along the West Florida Shelf are measurably influenced by the semidiurnal signal (Kantha 2005).

Although astronomical tides often are considered unimportant for the GoM, many studies have measured and analyzed tide and current data for the Gulf (e.g., Marmer 1954; Seim et al. 1987; DiMarco and Reid 1998; He and Weisberg 2002). Dominant constituents were found to be the luni-solar diurnal (K_1), principal lunar diurnal (O_1), and the principal lunar semidiurnal (M_2). Along with the principal solar semidiurnal (S_2) tidal component, He and Weisberg (2002) found these tidal constituents accounted for 90 % of the tidal variance along the West Florida Shelf. The distribution of tide type within the Gulf was determined by Kjerfve and Sneed (1984) and Seim et al. (1987) using the water level form number (F) of Defant (1960). A common way of defining form number or amplitude ratio is

$$F = (K_1 + O_1)/(M_2 + S_2)$$

when F < 0.25, tide is classified as semidiurnal. Within the range 0.25 < F < 1.5, tide is mixed but primarily semidiurnal. For the range 1.5 < F < 3.0, tide is mixed but primarily diurnal, and when F exceeds 3.0, tide is classified as diurnal. Figure 6.16 illustrates the distribution of tide type within the GoM, indicating a dominant diurnal signal.

6.3.3.3 Circulation

The GoM has been characterized as a two-layered circulation system with a surface layer up to 1,000 m (3,300 ft) deep and a bottom layer reaching the ocean floor at depths of approximately 4,000 m (13,120 ft) (Lugo-Fernandez and Green 2011). Circulation patterns in the Gulf are the result of complex interactions among bathymetry and forcing mechanisms such as wind, atmospheric conditions, water density (variations in temperature and salinity), and the Loop Current (e.g., Oey et al. 2005; Sturges and Kenyos 2008). Even though the Loop Current and associated eddies are dominant circulation features in the GoM, Cochrane and Kelly (1986) identified a cyclonic (rotating counter-clockwise) gyre present over the Texas-Louisiana continental shelf in response to prevailing wind stress. On the inner shelf, currents flow west-southwest, and a corresponding countercurrent along the shelf break completes the gyre system (Figure 6.17) (Nowlin et al. 1998; Zavala-Hidalgo et al. 2003).

Although circulation on the Mississippi-Alabama-Florida (MAFLA) shelf is variable due to interactions among the Loop Current and associated intrusions, tides, winds, and freshwater inflow, Kelly (1991) documented a dominant westward wind-driven flow on the inner shelf and an eastward return flow over the middle and outer shelf, creating a pattern of complex cyclonic and anticyclonic eddy pairs with strong inter-annual variability (Brooks and Giammona 1991; Jochens et al. 2002). Flow structure on the west Florida continental shelf consists of outer shelf, middle shelf, and coastal boundary layer regimes. The Loop Current and associated eddies more directly affect circulation on the outer shelf, whereas in water depths less than 30 m (98 ft), wind-driven flow is predominantly alongshore with a weak, southward-directed mean surface flow. In the coastal boundary layer, longshore currents driven primarily by winds and tides dominate cross-shelf flows.

The Loop Current is a horseshoe-shaped circulation pattern that enters the Gulf through the Yucatán Channel and exits through the Florida Straits (Figure 6.17) (BOEM 2011). The extent of intrusions of the Loop Current into the Gulf varies and may be related to current location on the



Figure 6.17. Generalized circulation patterns for the GoM (modified from BOEM 2011 and MMS 2007; contour data from Becker et al. 2009; basemap from French and Schenk 2005).

Campeche Bank at the time it separates from the bank. The Loop Current encompasses approximately 10 % of the GoM (Lugo-Fernandez and Green 2011), has surface current speeds up to 1.8 m/s (5.9 ft/s) (Oey et al. 2005), and exists to depths of 800 m (2,625 ft) (Nowlin et al. 2000; Lugo-Fernandez 2007). Water entering the Gulf through the Yucatán Channel typically is warmer and saltier than GoM waters, which generates energetic conditions that drive circulation patterns in the Gulf (Lugo-Fernandez 2007; Jochens and DiMarco 2008; Lugo-Fernandez and Green 2011). Location of the Loop Current varies, as it periodically extends to the northwest and onto the continental slope near the Mississippi River Delta (Oey et al. 2005). As the Loop Current spreads north to approximately 27°N, instability causes formation of anticyclonic warm-core eddies (closed, clockwise-rotating rings of water) shed from the Loop Current (Vukovich 2007). Even though the physical mechanisms that trigger eddy formation are not fully understood (Chang and Oev 2010; Sturges et al. 2010), the period between eddy separations ranges from 0.5 to 18.5 months (e.g., Vukovich 2007). Loop Current eddies typically have a diameter of 300 to 400 km (186 to 249 mi), surface current speeds between 1.5 and 2 m/s (4.9 and 6.6 ft/s), and west-southwest migration speeds ranging from 2 to 5 km/day (1.2 to 3.1 mi/day) (Brooks 1984; Oey et al. 2005).

Cold-core cyclonic (counter-clockwise rotating) eddies have been observed in the Gulf as well. These cyclones surround a central core of seawater that is cooler and fresher than adjacent waters. Cyclonic circulation is associated with upwelling, which brings cooler, deeper water toward the surface. A cyclone can form north of a Loop Current eddy encountering northern

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GoM bathymetry due to off-shelf advection (Frolov et al. 2004). Schmitz (2005) has also associated cyclones with the Loop Current. Small cyclonic eddies around 50 to 100 km (31 to 62 mi) wide have been observed over the continental slope off Louisiana (Hamilton 1992). These eddies can persist for 6 months or longer and are relatively stationary.

In addition to currents associated with the Loop Current and meso-scale eddies, two other significant circulation features have been reported in the GoM (MMS 2007). The first is a permanent anticyclonic feature oriented approximately east-northeast and aligned with 24°N in the western half of the Gulf (Monreal-Gomez et al. 2004). The generating mechanism for this anticyclonic circulation and associated western boundary current along the coast of Mexico is a point of debate (Sturges and Blaha 1975; Elliott 1979, 1982; Blaha and Sturges 1981; Sturges 1993); however, the feature is suspected of being wind driven (Oey 1995). The second circulation feature is a cyclonic gyre centered in the Bay of Campeche, also thought to be wind driven (Figure 6.17) (Vazquez de la Cerda 1993; Nowlin et al. 2000; Monreal-Gomez et al. 2004).

6.3.3.4 Wind Waves

Wave climate is one of the primary factors controlling sediment transport, deposition, and erosion in coastal habitats, and is defined as the average wave condition over a period of years based on wave height, period, direction, and energy. In coastal and nearshore environments, wind speed and direction, and nearshore bathymetry, are the primary forcing mechanisms of wave climate. Changing geomorphic characteristics of coastal habitats are dependent upon short-term fluctuations in wave climate, long-term cycles of wind and wave activity (including the effects of frontal passages and hurricanes), and the availability of sediment and fresh water to deltaic, estuarine, and marine coastal settings. Wind directions and intensities vary seasonally with southerly winds prevailing most of the year. During winter months, wind-circulation patterns and low barometric pressures preceding the passage of cold fronts can cause strong onshore winds and increased wave heights that typically erode beaches. After frontal system passage, wind direction shifts and northerly winds can generate waves that erode north-facing shorelines at many locations.

Various moored buoys and coastal wave gauges are situated throughout the GoM (Figure 6.18). Average deep-water wave heights range from 0.5 m (1.6 ft) in summer months to 1.5 m (4.9 ft) in winter months (NDBC 2012). However, most fair-weather average significant wave heights in Gulf coastal environments are less than 0.6 m (2.0 ft) high (Li 2012; BOEM 2011). Average fair-weather wave periods are on the order of 3.5 to 4 s. Although fair-weather waves contribute to coastal habitat evolution throughout the Gulf, greatest sediment redistribution along the coast occurs during tropical cyclones and winter cold fronts for this storm-dominated region.

6.3.3.5 Tropical Cyclones

A tropical cyclone is a warm-core, low-pressure system (organized system of clouds and thunderstorms) without an associated frontal weather zone. These systems develop over tropical and subtropical waters and have a closed low-level circulation (includes tropical depressions, tropical storms, and hurricanes) (NHC 2012). Tropical cyclones affecting the Gulf originate over portions of the Atlantic basin, including the Atlantic Ocean, the Caribbean Sea, and the GoM. They occur as early as May and as late as December, but most frequently from mid-August to late October (Figure 6.19) (NHC 2012). On average, about 11 tropical cyclones occur in the Atlantic Basin annually, many of which remain over the ocean and never impact U.S. coastlines. Approximately six of these storms become hurricanes each year (Blake



Figure 6.18. Location of National Data Buoy Center (NDBC) wave buoys and WAVCIS coastal wave gauges in the GoM (data from NDBC 2012 and WAVCIS 2012; basemap from French and Schenk 2005).

et al. 2007). Historical data indicate that hurricane tracks are relatively predictable based on a storm point of origin. Figure 6.20 illustrates the likelihood of hurricane occurrence for August, September, and October of any given year relative to storm origin and tracking. Data illustrate that hurricanes formed in the southern Caribbean in September have the greatest chance of impacting coastal habitat within the GoM, followed by August storms formed in the eastern Atlantic (Figure 6.20).

Gulf coastal areas generally experience hurricane return periods ranging from 7 to 20 years for hurricanes passing within 100 km (62 mi) of a given location (Keim et al. 2007; NHC 2012). Hurricanes and tropical storms can increase surface current speeds to between 1 and 2 m/s (3.3 and 6.6 ft/s) in nearshore and continental shelf regions (Nowlin et al. 1998; Teague et al. 2007). Recorded offshore wave heights during major hurricanes have exceeded 30 m (98 ft) (MMS 2005), attesting to the impact these storms can impose on coastal habitat. Furthermore, hurricane storm surges have been reported to range between 2 and 8 m (6.6 and 26.2 ft) for hurricanes throughout the Gulf, inundating large expanses of coastal marine and freshwater habitat (Fritz et al. 2007; Sullivan 2009).

Numerous studies have documented the destructive nature of hurricanes on coastal and nearshore habitat (e.g., Meyer-Arendt 1993; Cahoon 2006; Morton and Barras 2011). However, storm events may rejuvenate coastal marshes by delivering sediment that raises soil elevations and stimulates organic matter production (e.g., Turner et al. 2006; McKee and Cherry 2009).



Figure 6.19. Historical distribution of tropical cyclones in the Atlantic Basin, with peak occurrence between 20 August and 1 October (from NHC 2012).

Barrier strand deposits generally absorb the brunt of destructive storm forces as these sand deposits provide the first line of defense to storm energy. Consequently, beach erosion and overtopping during storm surge may result in significant geomorphic change in barrier strand environments and adjacent salt marshes, but erosion and resuspension of coastal and estuarine sediment during storms often leads to nourishment of interior marshes via fine-grained sediment deposition.

6.3.3.6 Relative Sea-Level Rise

Long-term changes in coastal habitat type and extent are controlled by rate at which sediment is supplied to the coastal zone relative to sea level. When sea-level rise exceeds sediment deposition and organic matter accumulation required to maintain wetlands at or above water level, land loss predominates. As sea level has risen throughout the Gulf over the past 15,000 years, previously exposed upland environments on the modern continental shelf surface were inundated and reworked by waves and currents, not unlike the slow but steady submergence of coastal uplands that continues today (Balsillie and Donoghue 2011; Davis 2011a). Rates of coastal inundation and subaerial deposition fluctuate in space and time, but the fate of coastal habitats is dependent on long-term sea-level trends. Douglas (2005), Balsillie and Donoghue (2011), and Davis (2011a), as well as many others, provide detailed discussions on geologic and historical variations in sea-level change throughout the Gulf relative to coastal habitat evolution. For the following discussion, 21 tide gauge time series are used to document variations in relative sea-level rise around the GoM as a function of geographic setting (Figure 6.21).



Figure 6.20. Climatological areas of origin and typical hurricane tracks for August through October (from NHC 2012).



Figure 6.21. Distribution of tide gauge stations around the GoM illustrating sea-level rise trends (data from the Permanent Service for Mean Sea Level [PSMSL] database (see Woodworth and Player 2003) and U.S. Army Corps of Engineers, New Orleans District (USACE 2014); basemap from French and Schenk 2005).

Due to a variety of geologic controls in Gulf coastal environments, sea-level changes vary significantly. Carbonate geology of the Florida Gulf Peninsula provides a stable platform upon which sea level rises at a rate similar to eustatic (global) change due to a lack of sediment runoff from the continent and distance from areas of tectonic activity in the Earth's crust (Davis 2011a). Recent sea-level changes recorded in tide gauge time series data are relatively small but sea level is rising at a rate of about 1.6 to 2.5 mm/year (0.06 to 0.1 in/year) (Figure 6.22), very similar to the present rate of global sea-level rise (about 2 mm/year [0.08 in/year]) (Douglas 2005). As such, the Florida Gulf Peninsula provides baseline conditions upon which sea-level changes can be compared with other coastal locations in the Gulf.

Although coastal habitats along the Florida Panhandle, Alabama, and Mississippi are primarily wave-dominated barrier beaches and backbarrier estuarine marshes that are supplied by significant riverflows into estuaries and the Gulf (Isphording et al. 1989; Isphording 1994), tide gauge data for the northeast Gulf coast illustrate sea-level change trends consistent with eustatic sea-level rise (Figure 6.23). In fact, tide gauge data for Apalachicola illustrate a lower rise rate (1.5 mm/year [0.06 in/year]) than any recorded changes along the west coast of Florida, even though the gauge is located in close proximity to the Apalachicola River Delta. One might expect sediment compaction in this area to contribute significantly to the present rate of sea-level rise; however, deltaic sediment deposits are relatively thin (Twichell et al. 2007) and



Figure 6.22. Sea-level change rates for tide gauges located along the Florida Gulf Peninsula using time series of monthly water levels from the PSMSL database.

the tide gauge is situated near a stable Pleistocene interfluve adjacent to the Apalachicola River. As one moves west toward Pensacola Bay and the entrance to Mobile Bay (Dauphin Island), relative sea-level rise increases to about 2.9 mm/year (0.11 in/year), reflecting gauge proximity to thicker sequences of Holocene sediment infilling drowned river valleys (Hummell and Parker 1995).

Relative sea-level rise on the Mississippi River Deltaic Plain is the highest of any location in the GoM primarily due to compactional subsidence of thick Holocene sediment and peat deposits that filled the Mississippi River valley during the most recent rise in sea level (Törnqvist et al. 2008). Subsidence, in addition to eustatic sea-level rise and reduced sediment supply associated with levee fortification of the river since the 1920s, has resulted in dramatic land loss in coastal Louisiana since the 1930s (Blum and Roberts 2009). Although only two NOAA tide gauge records have been used to characterize relative sea-level rise on the delta plain since the 1940s (Figure 6.24), various U.S. Army Corps of Engineers water-level gauges on the delta plain support the trend documented at these sites (e.g., Penland and Ramsey 1990). Relative sea-level rise at the Grand Isle gauge is approximately 9 mm/year (0.35 in/year), about 4.5 times greater than eustatic sea-level rise. The Eugene Island gauge recorded an even higher



Figure 6.23. Sea-level change rates for tide gauges located along the northeastern GoM coast using time series of monthly water levels from the PSMSL database.



Figure 6.24. Sea-level change rates for tide gauges located along the Louisiana Deltaic Plain coast using time series of monthly water levels from the PSMSL database.

rate of relative sea-level rise (9.6 mm/year [0.38 in/year]), but record length is about half that of Grand Isle. Even though subsidence has been active since sedimentation at the river mouth was initiated, prior to dam construction within the watershed and levee construction for flood control, sediment loads were sufficient to create thousands of square kilometers of vegetated wetlands and barrier beaches. As such, a prograding delta complex and marginal deltaic wetlands flourished. Although Holocene deltas experienced landloss due to river abandonment in the past, only after civil works projects constricted sediment yield to within the confines of the dam/levee systems did delta-scale wetland losses become a chronic problem.



Figure 6.25. Sea-level change rate for the Calcasieu Pass tide gauge located on the Louisiana Chenier Plain using time series of annual mean sea level obtained from the U.S. Army Corps of Engineers, New Orleans District.



Figure 6.26. Sea-level change rates for tide gauges located along the Texas coast using time series of monthly water levels from the PSMSL database.

As recorded at the Calcasieu tide gauge, relative sea-level rise remains high along the LA/TX Chenier Plain (Figure 6.25), but less than half that recorded along the delta plain and about 2 mm/year (0.08 in/year) less than the rate recorded for Galveston. Although relative sea-level rise is high at Galveston, due in part to groundwater withdrawal in the Houston area (Gabrysch 1984), as one proceeds southwest along the Texas coast toward Rockport and Port Isabel, a reduction in relative sea-level rise is documented (Figure 6.26). Between Galveston Island and Port Isabel, relative sea-level rise decreased from 6.3 to 3.9 mm/year (0.25 to 0.15 in/year), both greater than eustatic sea-level rise and change trends in the eastern GoM. The Texas coastal plain includes a number of river systems that have contributed sediment to the coast. As such, compaction of fluvial sediment deposits may be contributing to higher relative sea-level rise in coastal Texas.



Figure 6.27. Sea-level change rate for the tide gauge located along the Veracruz coast at Tuxpan using time series of monthly water levels from the PSMSL database.



Figure 6.28. Aerial view of Tuxpan Beach with elevated upland areas producing a more stable and forested coastal setting. Image credit: ArcGIS World Imagery.

Approximately 580 km (360 mi) south of the Rio Grande in Tuxpan, Veracruz (Mexico), short-term tide gauge records indicate a sea-level rise rate of about 2.9 mm/year (0.11 in/year) (Figure 6.27), similar to that recorded at Dauphin Island, AL. The rise rate is about 1 mm/year (0.04 in/year) less than that recorded in south Texas on the northern margin of the Rio Grande delta where upland runoff had a significant impact on coastal sedimentation. Even though coastal deposits north of Tuxpan to the Rio Grande primarily are composed of terrigenous clastic sediments from upland sources that commonly form barrier islands and lagoons, beaches narrow with distance south of the Rio Grande resulting in mainland beach morphology and a more stable coast toward Tuxpan (Figure 6.28) (Carranza-Edwards et al. 2007). Sea-level



Figure 6.29. Sea-level change rates for tide gauges located along the Veracruz coast near Tuxtlas using time series of monthly water levels from the PSMSL database.

rise may reflect this southward change in coastal geomorphology adjacent to the east Mexico shelf.

South of Tuxpan for about 480 km (298 mi) to Coatzacoalcos is the most geologically diverse coastal region of the southern GoM. The area includes low-lying sandy beaches backed by lagoons and wetlands, bluffed mainland beaches, and rocky volcanic coasts with sandy pocket beaches between rock headlands. Relative sea-level rise for this coastal segment (Veracruz, Alvarado, and Coatzacoalcos) is between 1.8 and 3.2 mm/year (0.07 and 0.13 in/year) (Figure 6.29). The rocky coasts of Veracruz and Alvarado provide a stable platform upon which to record eustatic sea-level changes (1.8 and 2.2 mm/year [0.07 and 0.09 in/year]), but the coast south of the volcanic Los Tuxtlas area is more influenced by fluvial sedimentation from the Coatzacoalcos River and tributaries. Fluvial deposition and Holocene sediment compaction may have contributed to increased relative sea-level rise rates at the Coatzacoalcos gauge.

The southern Gulf coast between Coatzacoalcos and Ciudad del Carmen encompasses the entire Tabascan coast, as well as the eastern section of Veracruz and western Campeche. Coastal geomorphology is controlled by fluvial sedimentation from the Coatzacoalcos and Grijalva-Usumacinta River systems. Deltaic environments associated with the Grijalva-Usumacinta and San Pedros Rivers contain some of the most extensive marshes in Gulf coastal Mexico known as the Centla Marshes (Moreno-Casasola 2007). Deltaic settings provide for greatest magnitudes of relative sea-level rise due to compactional subsidence. However, the closest tide gauge to these active deltaic environments is at Ciudad del Carmen (Campeche), just east of the Grijalva-Usumacinta delta and marginal deltaic beach ridge plain adjacent to Isla del Carmen. Relative sea-level rise at this location (Figure 6.30) is slightly greater than that recorded at Coatzacoalcos (Figure 6.29), and both rates exceed present eustatic sea-level rise by at least 1.2 mm/year (0.05 in/year).

Farther east along the Yucatán Peninsula, one tide gauge is available to describe the relative sea-level history of this predominantly carbonate environment. River runoff from this area


Figure 6.30. Sea-level change rates for tide gauges located along the Campeche and Yucatán coast using time series of monthly water levels from the PSMSL database.



Figure 6.31. Sea-level change rate for the tide gauge located along the northwestern coast of Cuba using time series of monthly water levels from the PSMSL database.

does not exist; instead, all exchange of fresh water between upland and the Gulf is accomplished via groundwater (Isphording 1975). As such, one might expect this area to be a relatively stable platform upon which to monitor sea-level rise. However, a 38-year record of water level changes at Progreso along the northern Yucatán coast indicated a 5 mm/year (0.20 in/year) rise in sea level (Figure 6.30), the highest rate of sea-level rise along the Gulf coast of Mexico.

The final gauge used to document variations in relative sea-level rise within the Gulf is located at Cabo San Antonio, along the northwestern coast of Cuba (Figure 6.31). Similar to the Yucatán Peninsula and southwestern Florida coast, the geologic setting is primarily carbonate, and clastic sediment is composed of shell, coral, and other limestone fragments. A 38-year time series of water level measurements indicates a relative sea-level rise rate of about 2.2 mm/year (0.09 in/year), very similar to that recorded for eustatic sea-level rise. This rate is almost equivalent to that recorded at Key West (2.3 mm/year), about 400 km (250 mi) northeast across the Florida Straits. The consistency in sea-level rise trends between these sites leads to questions regarding measurements at Progreso, an area of similar geologic setting.

6.3.4 Shoreline Change and Longshore Sediment Transport

Although three distinct sedimentary provinces characterize the modern GoM basin (Section 6.3.1), a variety of coastal depositional systems have evolved along the 6,077 km (3,776 mi)

land–water interface in response to upland drainage; groundwater supply; sediment availability; wind, wave, and current processes; relative sea-level rise; and physiographic characteristics of margin deposits. Carbonate deposits dominate the Mexican States of Campeche (east of Laguna de Términos), Yucatán, and Quintana Roo, as well as the northwestern coast of Cuba and the southwestern coast of Florida. Terrigenous sediment is dominant in the northern GoM where 77 % of all fluvial flow entering the basin originates. Smaller fluvial watersheds along the Tamaulipas, Veracruz, and Tabascan coasts of Mexico contribute the remaining 23 % of fluvial input to the Gulf, resulting in a mixture of fine-grained terrigenous clastics and carbonate sediment.

Shorelines fronting coastal habitats in the GoM evolve as a function of geologic setting and climatological factors affecting the balance between sediment erosion and deposition. Previous sub-sections under Physical Setting (Section 6.3) describe the dominant processes that control land changes along the margins of the Gulf, resulting in sediment erosion, transport, and deposition. On a geologic scale, coastal habitats evolve in response to long-term sea-level changes relative to sediment supply and land movements. Although historical changes in coastal habitats (century time scale) are influenced by these same processes, storm and wave energy controls sediment transport magnitude and direction, resulting in shoreline and habitat change. This section documents historical shoreline changes and associated net sediment transport pathways and magnitudes throughout the GoM over the past century or so. When available, a qualitative description of interior habitat changes is provided in Section 6.4.2.

6.3.4.1 South Florida Marine Ecoregion

One of the most diverse areas of the GoM coast is associated with habitats along the southwestern Florida peninsula where groundwater discharge has significant influence on habitat distribution and sandy beaches, mangroves, seagrasses, and coral reefs dominate. Specific shorelines of interest encompass the Florida Keys and Ten Thousand Islands areas of southwest Florida (Figure 6.32). The Florida Keys is an arcuate complex of Pleistocene coral reef islands and ooid shoals that accumulated approximately 120,000 years ago when sea level was 2 to 3 m above its present position (Hine and Locker 2011). These islands are bedrock based and are separated by tidal passes. Individual keys (islands) are stable but very low in elevation, making them vulnerable to storm surge during tropical storms and hurricanes. Landward of the keys is Florida Bay, a very shallow bay with a soft, carbonate mud bottom (Davis 2011b). The mud is quite thin (<1 m [3.3 ft] thick) and is deposited on Pleistocene limestone of the Key Largo Limestone and the Miami Oolite formations (Hine and Locker 2011). Mud deposits generally are quite cohesive, resulting in only minor sediment resuspension due to tidal currents; however, resuspension does occur during non-tidal wind events (Enos and Perkins 1979).

There are approximately 58 km (36 mi) of beaches in the Florida Keys, extending from the head of Florida Bay southwest to the Dry Tortugas (Clark 1990). Florida Keys beach sand is derived from erosion of limestone, precipitation of aragonite particles from seawater, and fragments of corals, shells, and calcareous algae (Clark 1990). Although shoreline change estimates are not well documented, historical analyses of beach erosion have been completed at a few locations along the Florida Keys (Clark 1990; FDEP 2012a). In addition, aerial photography documents numerous erosion control structures that were constructed to protect against beach erosion in this area. Beach erosion along the Keys primarily is associated with tropical cyclones and geomorphic changes associated with natural variations in littoral sediment transport. However, most of the 16.4 km (10.2 mi) of critically eroding beaches (Figure 6.33) can be associated with coastal protection structures (e.g., seawalls, revetments, groins) located at



Figure 6.32. Image illustrating the Florida Keys and Ten Thousand Islands within southwestern Florida. Net longshore sediment transport direction is indicated with *arrows* (data from Clark 1990; Dean and O'Brien 1987). Image credit: Microsoft Bing Maps Aerial.



Figure 6.33. Critically eroding beaches along the Florida Keys (from FDEP 2012a).

the ends of many small pocket beaches (FDEP 2012a). The Florida Department of Environmental Protection (FDEP), Bureau of Beaches and Coastal Systems, defined a critically eroding beach as a segment of shoreline where natural processes or human activity have caused or contributed to erosion and recession of beach or dune systems to such a degree that upland development, recreational interests, wildlife habitat, or important cultural resources are threatened or lost. For beaches fronting the Straits of Florida, net littoral sand transport is to the southwest.

North of Florida Bay to Marco Island are the predominantly vegetated shorelines of Cape Sable and the Ten Thousand Islands, an area containing numerous mangrove-covered islands and marsh habitat (Figure 6.32). Tidal channels separate the series of small islands, and oyster reefs are common in brackish waters that result from freshwater runoff from Big Cypress swamp and the Florida Everglades (Davis 2011b). Marsh habitats are the result of gradual deposition of sediment over the inner shelf during the late Holocene following early Holocene transgression (Parkinson 1989). South of Marco Island and Cape Romano, there is a noticeable transition from dominantly terrigenous sand to biogenic sediment. Beaches generally are absent with only a few local accumulations of shell and skeletal debris (Davis 2011b). The coast is quite stable due to an abundance of mangrove vegetation. Although hurricanes are common in this area, their impact has had little influence on coastal geomorphology (Davis 1995). Furthermore, because of its remote location, there is relatively little human impact on the coastal system.

According to Clark (1990), GoM beaches in southwestern Florida (north of Florida Bay) include about 42 km (26 mi) of sandy shoreline. Average beach width is on the order of 8 to 15 m (26 to 49 ft) and sediment composition is predominantly carbonate. Figure 6.34illustrates historical shoreline changes south of Gordon Pass (north end of Keewaydin Island) to the Marco Island area between the 1970s and 2000s. Although critically eroding beaches have been identified along both islands, beach nourishment in historically eroding areas has been an effective management technique for mitigating chronic erosion, resulting in a net sand surplus along much of Marco Island (Figure 6.34). Shoreline change since the 1970s for Keewaydin Island was about -0.4 m/year (-1.3 ft/year), and Marco Island illustrated net shoreline advance of approximately 5.7 m/year (18.7 ft/year). The Cape Romano shoreline is not managed for erosion, resulting in net shoreline recession of approximately 5 m/year (16 ft/year) between 1978 and 2010. This segment of coast is classified by the Bureau of Beaches and Coastal Systems as critically eroding. Net littoral sand transport along the southwestern Florida coast is to the south-southeast. Longshore transport rates at the north end of Keewaydin Island (Gordon Pass) were estimated at about 54,000 m³/year (71,000 cubic yards per year [cy/year]), decreasing to about 42,000 m³/year (55,000 cy/year) south of Marco Island at Caxambas Pass (Dean and O'Brien 1987).

Although limited studies document historical shoreline/wetland changes for the coast south of Cape Romano, Wanless and Vlaswinkel (2005) illustrated the impact of human activities and hurricane processes on the Cape Sable area. Significant changes in shoreline position were recorded by comparing historical aerial photography. Figure 6.35 documents net shoreline position change for the Cape Sable area since 1928 illustrating natural variations in shoreline response primarily due to tropical cyclone impacts. Although shoreline recession ranges from 1 to 4 m/year (3.3 to 13.1 ft/year) near the entrances to Lake Ingraham and in the Northwest Cape area, other portions of the coast exhibit net stability in this relatively sheltered coastal area. The presence of truncated ridge deposits along the shoreline suggests geologic variations in sediment supply and possibly transport direction; however, net transport direction during historical times is to the south-southeast toward Florida Bay.



Figure 6.34. Shoreline change from Keewaydin Island to Cape Romano. Most critically eroding shorelines occur in the Cape Romano area at rates of about 5 m/year. *Sources*: Shoreline change data, Absalonsen and Dean (2010); Cape Romano shoreline position (1978), NOAA (2013a); beach nourishment locations, Miller et al. (2004), FDEP (2008); critical erosion areas, FDEP (2012a). Image credit: Microsoft Bing Maps Aerial.

6.3.4.2 Northern Gulf of Mexico Marine Ecoregion

The Northern GoM Marine Ecoregion extends from Keewaydin Island on the west coast of Florida to just south of Barra del Tordo in the State of Tamaulipas, Mexico, and includes barrier beaches and coastal marshes of Florida, Alabama, Mississippi, Louisiana, and Texas (Figure 6.2). This area encompasses a variety of coastal geological deposits formed by the interaction between fluvial drainage systems and coastal processes in the GoM. Most coastal depositional systems are composed of terrigenous clastic sediment; however, karstic shoreline deposits are dominant in the Big Bend area of Florida (Hine 2009). Shoreline changes throughout this region are a function of sediment supply, changes in relative sea level, and the level of energy associated with dynamic coastal processes (winds, waves, and currents under normal and storm conditions). Eight geographic areas are used to illustrate patterns of shoreline change within the Northern Gulf Ecoregion: (1) Central West Florida Barrier Islands, (2) Big Bend Coast, (3) Northeastern Gulf Barrier Islands, (4) Mississippi River Delta Plain Coast, (5) Chenier Plain Coast, (6) Texas Mid-Coast Barrier Islands, (7) Laguna Madre Barrier Islands, and (8) Laguna Morales Barrier Beaches.

6.3.4.2.1 Central West Florida Barrier Islands

The barrier-inlet system along the central west Florida coast consists of approximately 27 barrier islands and inlets extending from Gordon Pass (just north of Keewaydin Island) to Anclote Key, northwest of Tampa. The islands range from a few kilometers to tens of kilometers long and all were formed in the past 3,000 years. According to Davis (2011b), no



Figure 6.35. Shoreline change for the Northwest, Middle, and East Cape portions of Cape Sable. Most eroding shorelines occur adjacent to the entrances to Lake Ingraham and along the southernmost portion of the Northwest Cape (shoreline position data from NOAA 2013b). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS World Imagery (inset); John Strohsahl (2008) (photo inset), used with permission.

significant terrigenous sediment is transported to the coast in this area; barrier island formation results from reworking of pre-Holocene deposits over the past 3,000 years. Large quantities of sediment from reworking of inner shoreface deposits have been transported landward during historical time (Hine et al. 1987; Hine and Locker 2011). The prism of sediment that includes the barrier island system begins at a water depth of about 6 m (20 ft) and extends landward with maximum thickness at the dunes where it reaches an elevation of only 4 to 5 m (13 to 16.4 ft) in most places (Davis et al. 2003). According to data in Table 6.1, discharge from watersheds in this area is relatively minor, indicating that modern drainage systems do not deliver significant amounts of sediment to the coast.

The balance between tide and wave energy controls morphodynamics of the central West Florida barrier islands (Davis 2011b). The net direction of littoral sand transport along the coast is to the south; however, transport reversals do exist in several locations due to changes in shoreline orientation (Davis 1999). Additionally, bedrock outcrops on the inner shoreface cause wave refraction that contributes to reversals in transport. According to Dean and O'Brien (1987), longshore transport rates vary between 35,000 and 85,000 m³/year (46,000 and 111,000 cy/year).

Most of the central West Florida barrier islands have been developed for residential and commercial activities. Coastal protection structures are prevalent on the islands, often resulting in buildings being situated too closely to the shoreline (Davis 2011b). As such, beach erosion



Figure 6.36. Shoreline change for the central West Florida barrier island coast. Long-term and recent shoreline changes illustrate the impact of beach nourishment throughout this coastal region. Shoreline change data from Absalonsen and Dean (2010); beach nourishment data from Miller et al. (2004) and FDEP (2008). Image credit: Microsoft Bing Maps Aerial.

near these structures has been alleviated by beach nourishment, which has been an integral part of beach management activities since the 1970s (Figure 6.36). The highest rates of erosion in this area typically are located near tidal inlets. Overall, average rates of shoreline change were approximately zero between the mid-1800s and the 1970s, even though net change along the islands ranged from 9 m (30 ft) of erosion to 9 m (30 ft) of deposition. Between the 1970s and 2000s, beach nourishment was an integral component of beach management along the islands, and net deposition prevailed at an average rate of about 0.9 m/year (3.0 ft/year) (Figure 6.36) (data from Absalonsen and Dean 2011). Although beach erosion hot spots are common along the islands and beach nourishment has been successful at mitigating erosion, Davis (2011b) indicates that natural accretion has occurred in several places along the islands. Furthermore, tropical cyclone impacts along the central West Florida barrier beaches have been reduced by the presence of a shallow and gently sloping shoreface which limits large waves from reaching subaerial beaches (Davis 2011b). Land loss in the bays and lagoons is minor because these water bodies generally are small or are already protected by erosion control structures such as bulkheads (Doyle et al. 1984).

6.3.4.2.2 Big Bend Coastal Marshes

The Big Bend region of Florida is typified by a shallow sloping submarine surface, general lack of wave activity, and lack of sediment supply. These three characteristics have created an



Figure 6.37. Big Bend coastal marshes along the northwestern Florida peninsula illustrating few critical erosion areas in a low energy marsh environment. *Inset* areas illustrate regions for coastal change assessment in Figures 6.39 through 6.41. Critical erosion areas defined by FDEP (2012a). Image credit: Microsoft Bing Maps Aerial.

extensive salt marsh system that rims the Big Bend coast north of Anclote Key to Ochlockonee Bay (Figure 6.37). This swath of coastal wetlands is a mixture of marsh, mangrove, and hammock vegetation, influenced by porous limestone bedrock (FDEP 2012b).

The geology of the Big Bend region is characterized by karstified Eocene and Oligocene limestone deposits over which thin muddy marsh dominated by *Juncus* sp. flourishes (Figure 6.38). According to FDEP (2012b), fluctuations in sea level during glaciation caused infilling of karstic features with Holocene and Pleistocene quartz sands and sandy clays. Holocene intertidal calcitic mud commonly overlies Pleistocene sand, and organic material derived from decaying marsh grasses intermixed with sand form the surface layer in coastal marshes. Although the Big Bend coastal area is considered sediment starved, Holocene sediment deposition continues along rivers such as the Aucilla, Suwannee, and Withlacoochee (FDEP 2012b). Big Bend karstic features generate a tight connection between the Floridian aquifer system and surface waters of the region. Because of the low topographic gradient on the limestone surface, the Big Bend area has low wave energy at the coast, similar to that of an incipient epicontinental sea (Hine 2009).

Earlier observations of coastal change in the Big Bend area by Tanner (1975a) indicated that marshes in the vicinity of Ochlockonee Bay have been stable or receding at slow rates since 1950 (on the order of 0.2 m/year [0.7 ft/year]). Tanner (1975a) also noted that average wave breaker heights in the "zero energy" coast (St. Marks to Anclote Key) were less than about 4 cm (1.6 in), that there were no integrated littoral drift cells, and that marshes along the GoM shoreline were



Figure 6.38. Distribution of Eocene-age and Oligocene-age limestone in the Big Bend area (*left*; geologic data from Scott et al. 2001). Image credit: Microsoft Bing Maps Aerial. Photograph of exposed karst surface near Rock Island (*right*; photo by Doug Alderson, used with permission).

well developed, suggesting that wave attenuation over a wide nearshore shelf decreases sediment transport energy to near zero. This implies that shoreline recession in coastal marshes is driven by submergence associated with relative rising sea level rather than erosion due to variations in wave energy.

In a more recent analysis, Raabe et al. (2004) documented coastal change in the Big Bend area using historical maps and aerial imagery. Inset locations shown in Figure 6.37 are used to illustrate changes in Big Bend historical record. Figure 6.39 documents shoreline and habitat change for a portion of the southern Big Bend for the period 1896 to 1995. Although conversion from marsh to water (blue) is present throughout the area, greatest loss of tidal marsh is present north of the Weeki Wachee River. Raabe et al. (2004) conducted field surveys of this area and found large mudflat areas with salt marsh rhizome remnants on the surface. Hernando Beach provides an example of coastal wetland loss due to development, and coastal forest retreat and oyster bar submergence illustrates the influence of slowly rising sea level during the period of record.

Figure 6.40 illustrates a comparison of 1858 and 1995 shorelines for the marshes between Withlacoochee Bay and Waccasassa Bay. Rapid expansion of tidal marsh inland 1 km (0.6 mi) or more over a gently sloping exposed limestone platform replaced coastal forest habitat as slowly rising marine waters submerged inland habitat (Raabe et al. 2004). Minor amounts of shoreline erosion were documented along outer margins of the marine marsh; however, marine submergence under rising sea level appears to be the dominant factor influencing coastal change in this area. According to Raabe et al. (2004), a number of natural and anthropogenic factors may have contributed to the inland expansion of coastal marsh, including soil damage during tree harvest, dissolution of limestone, change in freshwater flow from the Waccasassa River, and concentrated storm surge in the Waccasassa embayment that would focus marine

Intertidal Zone Changes from 1886 to 1995 for Topographic Survey T-1700 From Bayport, Hernando County to Aripeka, Pasco County, Florida



Figure 6.39. Coastal change for T-sheet 1700 (see Figure 6.37) between Horse Island and the Pine Island area documenting submergence of the intertidal zone between 1896 and 1995 (from Raabe et al. 2004).

Coastal Habitats of the Gulf of Mexico



Scale 1:143000

25

20

A

3150

et al. 2004).

Figure 6.40. Coastal change for T-sheet 699 (see Figure 6.38), Withlacoochee Bay to Waccasassa Bay, documenting inland expansion of marsh from marine submergence, 1858 to 1995 (from Raabe

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energy and flooding inland. All of these factors may exacerbate the impact of rising sea level in the area.

Along the northwest portion of the Big Bend coast, between the Fenholloway River and the Aucilla River, is an area illustrating changes most common to the Big Bend marshes and coastal forests. Figure 6.41 shows relatively small losses along the marine marsh boundaries but rather significant inland recession of the coastal forest boundary as tidal marshes expand inland. According to Raabe et al. (2004), increased tidal flooding has resulted in loss of hammocks in tidal marsh and widespread inland recession of the upland forest boundary. Although marsh shoreline recession is most common along the coast, small areas of shoreline advance are present, primarily the result of high marsh bank slumping and recolonization by low marsh species (Raabe et al. 2004).

Overall, Big Bend shoreline change documents relatively minor movement in both directions with significant growth of intertidal marsh over adjacent uplands in response to sea-level rise over an approximate 100-year period. As documented by Raabe et al. (2004), dieback of coastal forests is common in the low-gradient Big Bend area as marine water submerges the limestone surface under rising seas.

Northeastern Gulf Barrier Islands and Beaches 6.3.4.2.3

The barrier island-inlet system of the northeastern GoM extends from the western margin of Ochlockonee Bay, FL (eastern margin of the Apalachicola River Delta) west to Cat Island,

1995 Upland Vegetation



Figure 6.41. Coastal change for T-sheet 1424a (see Figure 6.38), Fenholloway River to Aucilla River, documenting small to moderate changes along the marine and coastal forest boundaries, 1875 to 1995 (from Raabe et al. 2004).

MS (Figure 6.42). Geomorphic features include barrier islands, sand spits, mainland beaches, and inlet systems of various sizes. Shorelines of the Apalachicola River Delta vary in orientation, resulting in an array of sand transport directions and magnitudes relative to dominant wave approach. Broad and gently sloping inner continental shelf deposits seaward of the delta result in relatively low littoral transport rates versus those present along the east-west barrier strandplain west of the delta (Davis 2011b). Overall, the dominant direction of longshore sand transport is from east to west, and transport magnitudes vary based on shoreline orientation.

Historical shoreline change along most of the northeastern GoM beaches has been net erosional since the mid-1800s, primarily the result of tropical cyclone impacts. Storm-driven wave and current processes are the primary erosional forces responsible for instantaneous geomorphic changes, whereas more frequent climatological occurrences that produce normal wave and current processes rework storm-induced beach changes, resulting in long-term coastal evolution. Overall, shoreline recession is dominant throughout this portion of the GoM; however, beach nourishment since the 1970s has mitigated erosion hot spots, augmenting the littoral transport system and reducing erosion. Although sea-level rise for this section of coast is slightly greater than the eustatic rate (see Section 6.3.3.6), it has not caused significant shoreline recession during the period of record (Davis 2011a; Byrnes et al. 2012).



Figure 6.42. Location of shoreline reaches for the Northeastern Gulf Barrier Islands and Beaches region extending from Ochlockonee Bay, FL to Cat Island, MS. Image credit: Microsoft Bing Maps Aerial.

Based on geomorphic characteristics, shoreline change and longshore transport are summarized for three distinct areas of the northeastern GoM (Figure 6.42). The coast between Ochlockonee Bay and St. Joseph Peninsula is characteristic of deltaic and marginal deltaic environments of the Apalachicola River delta (Figure 6.43). Shoreline orientation varies significantly, and patterns of sand transport and beach change reflect shoreline orientation relative to incident waves. Although reversals in net littoral sand transport are common for this section of the coast, net longshore sand transport is from east to west.

According to Dean and O'Brien (1987), net longshore transport along Dog Island and St. George Island (south of Apalachicola) is to the west at a rate of about 130,000 m³/year (170,000 cy/year), even though transport at the eastern end of Dog Island is to the east. As shoreline orientation shifts to more southerly in the St. Vincent Island area (east of St. Joseph Peninsula), west-directed transport decreases to about 90,000 m³/year (118,000 cy/year). North of Cape San Blas (southern point of St. Joseph Peninsula), the shoreline faces a more westerly direction and net longshore transport is to the north-northwest at approximately 130,000 m³/ year (170,000 cy/year) (Dean and O'Brien 1987). Historical shoreline change rates for the Apalachicola delta coast vary from 8.2 to -8.2 m/year (26.9 to -26.9 ft/year) between the mid-1800s and 1970s/1980s (Figure 6.43). However, net shoreline recession was dominant at a rate of about 0.2 m/year (0.7 ft/year). Although beach nourishment was completed along the southern extent of St. Joseph Peninsula in 2009, net shoreline recession rates for the period 1970s/1980s to 2009 increased to an average of 0.6 m/year (2.0 ft/year), perhaps due to increased storm impacts since the 1970s.

The next segment of coast is concave and extends from Port St. Joe (near the northern end of St. Joseph Peninsula) to Mobile Point on the eastern side of Mobile Pass (Figure 6.42). Although net longshore sand transport is to the east at about 100,000 m³/year (131,000 cy/year) along a short length of beach at the eastern end of this 300-km (186-mi) segment of coast (near Mexico Beach Inlet), net transport for the western 270 km (168 mi) of beach is to the west at rates between 115,000 and 400,000 m³/year (150,000 and 523,000 cy/year) (Dean and O'Brien 1987; Byrnes et al. 2010). Seven inlets interrupt sand transport between Port St. Joe and Mobile Pass, and all but three are maintained by the U.S. Army Corps of Engineers, Mobile District. Mexico Beach Inlet in Florida, a natural entrance that exchanges water and sediment between the GoM and Saint Andrew Sound, is maintained by the City of Mexico Beach, and Little Lagoon Pass is maintained by the State of Alabama. Historical shoreline change rates for the 1800s to 1970s/1980s illustrate hot spots of erosion and accretion east of St. Andrew Bay Entrance that range from -8.4 to 7.2 m/year (-27.6 to 23.6 ft/year) (Figure 6.44); however, most beaches document shoreline changes between -1 and 1 m/year (-3.3 and 3.3 ft/year).



Figure 6.43. Historical shoreline change for sandy beaches for the Apalachicola River delta region. Variations in net shoreline change between the mid-1800s and 1970s/1980s are illustrated in the *top panel*, whereas net shoreline changes between the 1970s/1980s and 2000s are shown in the *bottom panel* relative to beach nourishment (*black line* segments) and the direction of net littoral sand transport (*white arrows*). Shoreline change data from Absalonsen and Dean (2010) and Miller et al. (2004). Beach nourishment data from Miller et al. (2004) and FDEP (2008). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS National Geographic World Map (overview).

Overall, net shoreline recession of -0.1 m/year (-0.3 ft/year) was recorded for this 300-km (186-mi) coastal segment. Between the 1970s/1980s and 2000s, sand nourishment was imposed along a number of beaches (FDEP 2008), contributing to a shift in net shoreline change to 0.1 m/year (0.3 ft/year) (Absalonsen and Dean 2011) (Figure 6.44).

The westernmost 100 km (62 mi) of the northeastern Gulf barrier islands and beaches encompasses the barrier islands fronting Mississippi Sound (Figure 6.42). The barrier islands extend from Dauphin Island (AL) to Cat Island (MS) and provide the first line of protection to mainland Mississippi and Alabama from storm waves and surge. The islands are composed of beach sand derived from updrift beaches east of Mobile Pass and from ebb-tidal shoals at the entrance. Four tidal passes between the islands promote exchange of sediment and water between marine waters of the GoM and brackish waters of Mississippi Sound (Figure 6.45). Tidal passes also interrupt the flow of littoral sand to the west from Mobile Pass ebb-tidal shoals are federally maintained navigation channels since the early 1900s (Byrnes et al. 2010, 2012).

Byrnes et al. (2010) and Byrnes et al. (2013) document long-term beach changes for the Mississippi Sound barrier islands, emphasizing the dominance of east-to-west longshore transport processes on erosion and deposition along the coast. Net shoreline recession of about



Figure 6.44. Historical shoreline change for sandy beaches from Port St. Joe to Mobile Pass. Variations in net shoreline change between the mid-1800s and 1970s/1980 are illustrated in the *top panel*, whereas net shoreline changes between the 1970s/1980s and 2000s are shown in the *bottom panel* relative to beach nourishment (*black line* segments) and the direction of net littoral sand transport (*white arrows*). Shoreline change data from Absalonsen and Dean (2010) and Byrnes et al. (2010). Beach nourishment data from Miller et al. (2004) and FDEP (2008). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS National Geographic World Map (overview).

1.5 m/year (4.9 ft/year) was documented for Gulf facing beaches for the period 1847 to 1981/1986 (Figure 6.45); storm processes and inlet dynamics in the dominant east-west littoral transport environment control shoreline position change. Shoreline recession since 1981 increased to 2.4 m/year (7.9 ft/year), perhaps due to an increase in tropical cyclone impacts during this 30-year period. Cross-shore island changes are particularly important along central Dauphin Island and along East Ship Island where long-term rates of change have been documented at up to -3 m/year (-10 ft/year) and -6 m/year (-20 ft/year), respectively (Byrnes et al. 2012). However, lateral island migration (from east to west) controls long-term island morphologic changes at rates between 10 and 50 m/year (33 and 164 ft/year), emphasizing the dominance of net longshore transport processes (Figure 6.46) (Byrnes et al. 2013). The systematic pattern of updrift erosion and downdrift deposition illustrates sand movement from east to west and promotes westward migration, and has reduced island areas by about one-third since the 1850s (Byrnes et al. 2012).

As illustrated in Figure 6.46, littoral sand transport along the Mississippi Sound barrier islands is predominantly from east to west in response to prevailing winds and waves under normal and storm conditions from the southeast. Reversals in longshore transport occur at the eastern ends of the islands, but their impact on net sediment transport is localized and minor



Figure 6.45. Historical shoreline change for sandy beaches from Mobile Pass to Cat Island. Variations in net shoreline change between the mid-1800s and 1970s/1980 are illustrated in the *top panel*, whereas net shoreline changes between the 1970s/1980s and 2000s are shown in the *bottom panel* relative to beach nourishment (*black line* segments) and the direction of net littoral sand transport (*white arrows*). Shoreline change data from Byrnes et al. (2010) and Byrnes et al. (2013). Beach nourishment data from Miller et al. (2004). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS National Geographic World Map (overview).

relative to dominant transport processes from the southeast. Net longshore transport magnitude was estimated using historical survey datasets encompassing an approximate 90-year period to quantify sand flux along the barrier-inlet system (littoral sediment budget). According to Byrnes et al. (2013), longshore sand transport magnitudes range from about 230,000 m³/year (300,000 cy/year) along the western end of Dauphin Island to approximately 320,000 m³/year (420,000 cy/year) along Horn Island to 110,000 m³/year (145,000 cy/year) near Ship Island (Figure 6.47).

6.3.4.2.4 Mississippi River Deltaic Plain

The Mississippi River deltaic plain extends from the Chandeleur Islands to Southwest Pass (west margin of Marsh Island) (Figure 6.48). Mississippi River delta growth over the past 7,000 years has produced millions of acres of wetlands that form and degrade as the river switches course every 1,000 to 2,000 years. Channel gradients become so low that hydraulic flow inefficiencies result in river channel realignment to a more efficient route to the Gulf (Roberts 1997). As delta lobes are abandoned (that is, fluvial processes no longer contribute significantly to sedimentation and land building), erosive wave and current forces begin to rework the outer margins of the delta. Erosion and sediment reworking are exacerbated by







Figure 6.47. Macro-scale sediment budget for the Mississippi Sound barrier island chain, 1917–1918 to 2005–2010. *Arrows* illustrate the direction of sediment movement throughout the system and *black numbers* reflect the magnitude of net sediment transport (from Byrnes et al. 2013; used with permission of the Journal of Coastal Research).



Figure 6.48. Location diagram for the Mississippi River deltaic plain extending from the Chandeleur Islands west to Southwest Pass. Image credit: Microsoft Bing Maps Aerial.

compactional subsidence, as the primarily depositional system evolves (Williams et al. 2011). Eventually, headland beaches and barrier islands are formed as transgression proceeds on the sediment-starved abandoned delta lobe (Kulp et al. 2005). Headland beaches and barrier islands formed along the outer margin of the Mississippi River delta plain reflect various stages of delta lobe evolution, and because the natural source of river sediment has been reduced from interior watersheds via dams and isolated from the modern deltaic plain via levees, deltaic habitats are rapidly deteriorating. Coastal habitats are particularly vulnerable to change where direct exposure to storm waves and currents results in rapid shoreline changes and significant sediment transport rates.







Figure 6.49. (continued)



Figure 6.50. Deterioration and rapid shoreline recession along the Chandeleur barrier island system, mid-1800s to 2005 (data from Martinez et al. 2009). *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.

In response to high subsidence rates, diminished sediment supply to coast habitats, and continued exposure to storm waves and currents, the Mississippi-Atchafalaya River deltaic plain experiences the highest rates of laterally continuous shoreline retreat and land loss in the GoM (Penland et al. 1990; Miner et al. 2009). While land loss associated with shoreline change along the Gulf shore and around the margins of large coastal bays is extreme, loss of the interior wetlands is even more extensive due to submergence and deterioration of the Mississippi River delta plain. Wetland erosion along the Louisiana deltaic shoreline (excluding accretion along the modern delta fringe) averaged about 4.8 m/year (15.7 ft/year) between 1855 and 2005; however, the rate of erosion increased to approximately 14.1 m/year (46.3 ft/year) between 1996 and 2005 (Martinez et al. 2009). Highest rates of Gulf shoreline recession along the Mississippi River deltaic plain coincide with subsiding marshes and migrating barrier islands such as the Chandeleur Islands, Caminada-Moreau headland, and the Isles Dernieres (Figure 6.49).

The Chandeleur Islands barrier system represents the final stage of delta lobe deterioration where transgressive sand deposits reside along the outer margin of a submerged delta lobe under rapid shoreline recession and frequent overwash (Figure 6.50). Historical shoreline recession (1855 to 2005) for this segment of coast was 6.4 m/year (21.0 ft/year) (Figure 6.49a); between the 1930s and 2005, the rate increased to -8.6 m/year (-28.2 ft/year) (Reaches 57 to 59 on Figure 6.49b). Most sand transport within this low-profile barrier island system is directed

landward during storm events (washover); however, longshore transport is characterized as bi-directional (north and south of the central portion of the island chain), and net rates estimated using wave modeling varied between 60,000 and 130,000 m³/year (78,000 and 170,000 cy/year) (Ellis and Stone 2006; Georgiou and Schindler 2009).

The Plaquemines barrier system protects Barataria Bay from Gulf waves and currents and extends from Sandy Point (east) to West Grand Terre Island at Barataria Pass (Figure 6.51). Longshore transport is eastward from Barataria Pass and westward from Sandy Point, converging near the eastern end of East Grand Terre Island (Figure 6.51; USACE 2012). Annualized maintenance dredging from the bar channel at Barataria Pass (1996 to 2007) was approximately 140,000 m³/year (183,000 cy/year) (USACE 2010). Of this quantity, about 90,000 m³/year (118,000 cy/year) was sand; however, this quantity is an estimate of gross transport to the pass from east and west. Georgiou et al. (2005) estimated that approximately 10,000 m³/year (13,000 cy/year) of sand was transported westward along the Plaquemines shoreline based on survey data, and USACE (2012) estimated sand transport along Shell Island at approximately 33,000 m³/year (-23.0 ft/year) (1884 to 2005); however, shoreline change rates average about -7.0 m/year (26.6 ft/year) between the 1930s and 2005 (Reaches 44 to 48, Figure 6.49b; Martinez et al. 2009).

The Bayou Lafourche barrier system extends approximately 60 km (37 mi) from Barataria Pass (eastern end of Grand Isle) to Cat Island Pass at the western end of Timbalier Island (Figure 6.51). The Caminada-Moreau Headland is included in this coastal segment and contains some of the highest rates of shoreline recession in south Louisiana (11.2 m/year [36.7 ft/year]; Reach 42, Figure 6.49a). Timbalier Island has experienced rapid lateral migration to the west, reflecting the dominant direction of longshore transport west of the Caminada-Moreau Headland (McBride et al. 1992). Based on shoreline change analyses and nearshore sedimentation trends, Georgiou et al. (2005) estimated net longshore transport for this area to be approximately 146,000 m³/year (191,000 cy/year) eastward. According to Rosati and Lawton (2011), net westward transport of maintenance dredging material from Cat Island Pass (Houma Navigation Canal) was about 100,000 m³/year (130,000 cy/year) toward the Isles Dernieres. However, Georgiou et al. (2005) estimates that a maximum of 50,000 m³/year (65,000 cy/year) of sand moves westward along the Timbalier Islands. Based on data from Martinez et al. (2007), historical shoreline change for the Bayou Lafourche barrier shoreline was about -8.8 m/year (-28.9 ft/year) (1884–2005). Shoreline recession rates decreased to about 5.8 m/year (19.0 ft/ year) between the 1930s and 2005 (Figure 6.49b).

The westernmost barrier island system along the south Louisiana coast is the Isles Dernieres. In the mid-1800s, the Isles Dernieres (then known as Last Island) was home to the first coastal resort in Louisiana (Davis 2010). At that time, the island was continuous, about 50-km (31-mi) long, and approximately 1 km (0.6 mi) wide. The hurricane of 1856 destroyed the resort community and the island has continued to deteriorate since that time. Although the east-to-west longshore sediment transport pathway is well defined for the Isles Dernieres (Figure 6.51), littoral transport rates estimated using wave modeling routines vary from about 33,000 m³/year (43,000 cy/year) (Georgiou et al. 2005) to 60,000 m³/year (78,000 cy/year) (Stone and Zhang 2001). Based on the sediment budget for Cat Island Pass (Rosati and Lawton 2011) developed using survey data, net transport quantities of Stone and Zhang (2001) and Georgiou et al. (2005) likely underestimate annualized transport rates. Historical shoreline change rates (–11.3 m/year [–37.1 ft/year]; 1887–2005) are of similar order to those recorded for the Caminada-Moreau headland. For the 1930s to 2005 period, recession rates increased slightly to 12.0 m/year (39.4 ft/ year) (Reaches 33 to 36; Figure 6.49b).



Figure 6.51. Net longshore sediment transport pathways for the barrier island shoreline between Sandy Point and Raccoon Point fronting the Mississippi River deltaic plain. Image credit: Microsoft Bing Maps Aerial.

6.3.4.2.5 Mississippi River Chenier Plain

The Chenier Plain coast of southwestern Louisiana and southeastern Texas is a unique marginal-deltaic depositional environment indirectly influenced by high levels of riverine input from the Mississippi-Atchafalaya River system. The area extends from Southwest Pass (LA) to Rollover Pass (TX) (Figure 6.52). The Chenier Plain coast is approximately 200 km (124 mi) long and extends up to 30 km (19 mi) inland from the GoM. Chenier Plain deposits are composed primarily of mud, interspersed with thin sand- and shell-rich ridges. Coastal deposits were formed from sediments supplied by longshore transport of primarily fine-grained Mississippi-Atchafalaya River sediment (Hoyt 1969) when the river mouth was oriented to the west. When the river mouth was located eastward and sediment supply to the Chenier Plain was limited relative to erosive wave energy, previously deposited mud-rich sediment was reworked by coastal processes, concentrating coarse-grained sediments and forming shore-parallel ridges (Penland and Suter 1989). Subsequent shifts in sediment supply created the alternating ridge and swale topography so common to the Chenier Plain (McBride et al. 2007).

Although no direct measurements of littoral sediment transport have been made along mixed sediment coastal and nearshore deposits of the Chenier Plain, Holocene geomorphic records illustrate an east to west longshore transport direction (McBride et al. 2007). Only three primary waterways interrupt longshore transport along the Chenier Plain coast, two of which have significant inland bays (Calcasieu and Sabine). All three waterways are structured with jetties that illustrate net longshore sediment transport direction (sand accumulation at the eastern jetties). Sediment transport magnitude is more difficult to estimate; however, net transport quantities estimated by Georgiou et al. (2008) between Calcasieu Pass and Sabine Pass using numerical modeling were reported as a maximum of about 40,000 m³/year (52,000 cy/year). Shepsis et al. (2010) used survey data and numerical modeling to estimate a net west-directed longshore transport rate of approximately 70,000 m³/year (92,000 cy/year) for the same coastal segment. Furthermore, Taylor Engineering (2010) documented a series of longshore sand transport rates for the Rollover Pass area that ranged between 44,000 and 73,000 m³/year (96,000 cy/year) to the southwest.

Shoreline change along the Louisiana Chenier Plain coast is dominated by erosion between Southwest Pass and the Mermentau River Outlet at a rate of about 5.3 m/year (17.4 ft/year)



Figure 6.52. Historical shoreline change trends for the Mississippi-Atchafalaya River Chenier Plain coast. Shoreline change data from Martinez et al. (2009) and Paine et al. (2011). *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.

(Figure 6.52) (Byrnes et al. 1995; Martinez et al. 2009). However, a 23-km (14-mi) segment of coast east and west of Freshwater Bayou illustrates net shoreline advance between 1884 and 2005 (2.9 m/year [9.5 ft/year]; Figure 6.52), perhaps reflecting sediment supplied to this area by the Atchafalaya River (Huh et al. 1991). West of this deposition zone to a position 7.5 km (4.7 mi) west of the Mermentau River Outlet is a 68-km (42 mi) shoreline segment that illustrates greatest historical recession rates along the Chenier Plain (8.7 m/year [28.5 ft/ year]). Further west of this point to Sabine Pass, net deposition and shoreline advance (1.6 m/ year [5.2 ft/year]) becomes dominant (Byrnes et al. 1995). This alternating trend of shoreline recession and advance shifts to net recession west of Sabine Pass to Rollover Pass, where beach erosion dominates shoreline dynamics (Figure 6.52), particularly when tropical cyclones impact the area (Byrnes and McBride 2009). Thin sand and shell beaches, perched on inland herbaceous marsh deposits, exist along the entire coast, and net shoreline recession rates average about 2.6 m/year (8.5 ft/year). Overall, temporal and spatial trends in shoreline response illustrate increasing shoreline recession with time (Byrnes et al. 1995). Besides being a function of incident wave energy, shoreline change data indicate that factors such as shoreline orientation to dominant wave processes, sediment supply, and engineering structures have a profound influence on coastal response.

6.3.4.2.6 Texas Mid-Coast Barrier Islands

Barrier beaches along the central Texas coast extend approximately 300 km (186 mi) southwest between Rollover Pass and Packery Channel (North Padre Island) (Figure 6.53). The area between Rollover Pass and San Luis Pass encompasses Bolivar Peninsula and Galveston Island, a zone of sandy beaches and dune systems with ridge and swale topography (Bernard et al. 1970). In historical times, navigation structures at Bolivar Roads (Houston Ship Channel Entrance) have influenced sediment transport pathways along the southeast Texas coast. In addition, the Galveston seawall and groin system on the eastern part of Galveston Island, while protecting the island, has limited sediment to downdrift beaches, resulting in a net



Figure 6.53. Long-term shoreline change trends for the Texas Mid-Coast Barrier Islands (mid 1800s to 2007 for the area between Rollover Pass and San Luis Pass; 1930s to 2007 for the area southwest of San Luis Pass to Packery Channel). Shoreline change data from Paine et al. (2011). *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.

deficit to the sediment budget along south Galveston Island. These structures serve to compartmentalize the coast by blocking southwest-directed longshore sand transport to downdrift beaches. As a result of these structures and natural processes, approximately 88 % of the coast in this area illustrates long-term shoreline recession (Figure 6.53) (Paine et al. 2011). Net shoreline recession for the period 1882 to 2007 was about 0.2 m/year (0.7 ft/year). Although shoreline recession is dominant, small areas of net deposition occur at shoreline segments adjacent to the north and south jetties at Bolivar Roads, and the southwestern end of Galveston Island (Paine et al. 2011). Longshore sand transport measurements obtained by Rogers and Ravens (2008) for the surf zone on Galveston Island ranged from 86,000 m³/year (112,000 cy/ year) to 231,000 m³/year (302,000 cy/year).

The coast southwest of San Luis Pass to Pass Cavallo encompasses the headland of the Brazos and Colorado River deltas and associated barrier peninsulas called Follets Island and Matagorda Peninsula. Sediments eroded by waves reworking muddy and sandy deltaic headland deposits supplied sandy sediment to beaches adjacent to the headland deltas. Three navigation channels have been controlled with jetties along this section of coast, resulting in disruption of natural littoral transport to downdrift beaches. These include the Freeport Ship Channel jetties just north of the Brazos River entrance, the relatively short jetties that extend seaward from the Colorado River Navigation Channel entrance, and the Matagorda Ship Channel jetties. These structures and channels have effectively compartmentalized sediment transport patterns along this section of coast (Paine et al. 2011). According to Paine et al. (2011), approximately 85 % of this coastal segment recorded shoreline recession. South of the San Bernard River to Pass Cavallo, average long-term recession rates averaged about 1.2 m/year (3.9 ft/year), whereas north of this point to San Luis Pass, shoreline recession averaged about 0.2 m/year (0.7 ft/year) (Figure 6.53). Areas of significant long-term shoreline recession include Follets Island, the Brazos headland, and a segment of Matagorda Peninsula southwest of the Matagorda Ship Channel. Beaches illustrating net shoreline advance are focused along short segments of the Matagorda Peninsula, including 3 km (1.9 mi) of beach northeast of the Colorado River mouth, a 5.5 km (3.4 mi) segment adjacent to the north jetty at the Matagorda Ship Channel, and a 2 km (1.2 mi) long segment at the southwestern tip of Matagorda Peninsula (Figure 6.53) (Paine et al. 2011). Net longshore sand transport between San Luis Pass and the Brazos River is consistent with transport direction and rates for Galveston Island. South of the Brazos headland along the Matagorda Peninsula, Heilman and Edge (1996) and Thomas and Dunkin (2012) estimated net longshore transport at between 38,000 and 250,000 m³/year (50,000 and 327,000 cy/year) to the southwest.

Southwest of Pass Cavallo to Packery Channel, long-term shoreline recession is prevalent along most beaches (0.8 m/year [2.6 ft/year]; Figure 6.53). Coastal engineering structures that impact sand transport for this shoreline segment include jetties at the Matagorda Ship Channel entrance that restrict sand transport to Matagorda Island, jetties at Aransas Pass that interrupt sand transport between San Jose and Mustang Islands, and the small Packery Channel jetties (Paine et al. 2011). Paine et al. (2011) documented net shoreline recession along about 80 % of this shoreline segment. However, approximately half the Gulf shoreline of Matagorda Island has advanced at relatively low rates since 1937. Highest rates of net shoreline recession (averaging 9.7 m/year [31.8 ft/year]) were recorded along a 6 km (3.7 mi) segment of Matagorda Island southwest of Pass Cavallo (Figure 6.53) (Paine et al. 2011). Net recession rates greater than 1 m/year (3.3 ft/year) were measured along most of San Jose Island, the central portion of Mustang Island, and the southern end of Mustang Island. Net shoreline recession rates elsewhere were less than 1 m/year (3.3 ft/year).

Although limited information is available regarding longshore sand transport rates, the predominant transport direction appears southwestward north of Packery Channel and variable south of this point. As such, net transport rates decrease to the southwest as the difference between northeast- and southwest-directed transport becomes minimized. Based on wave simulations, Kraus and Heilman (1997) determined the net longshore sand transport rate for Mustang and north Padre Islands to be about 34,000 to 53,000 m³/year (39,000 to 69,000 cy/ year) to the southwest. However, deposition at the Aransas Pass jetties between 1866 and 1937 suggests net northward transport (Figure 6.54). Conversely, Morton and Pieper (1977) document deposition at the southern end of San Jose Island, southward channel migration at Aransas Pass, and shoreline recession along the north end of Mustang Island prior to jetty construction as evidence of net southwest longshore transport. Williams et al. (2007) documented deposition south of the jetty (Figure 6.54). Based on these and other observations, the coast southwest of Aransas Pass to Padre Island National Seashore appears to be a nodal area for changes in the dominant direction of littoral sand transport (McGowen et al. 1977).

6.3.4.2.7 Laguna Madre Barrier Islands

The Laguna Madre of Texas and Tamaulipas is separated by the Rio Grande Delta at the United States–Mexico border and bounded by barrier islands and peninsulas along the GoM coast and mainland deposits along its western margin. The Laguna Madre extends



Figure 6.54. Patterns of deposition adjacent to the jetties at Aransas Pass and Packery Channel documenting variable transport directions. Shorelines from Miller et al. (2004). Image credit: ArcGIS World Imagery.

approximately 445 km (277 mi) from Corpus Christi Bay to La Pesca at the mouth of the Rio Soto la Marina (Figure 6.55). The Texas and Tamaulipas lagunas each encompass approximately 185 km (115 mi) of coast, and the Rio Grande Delta occupies about 75 km (47 mi) between the lagunas (Tunnell 2002b). The delta lobe protrudes about 35 km (22 mi) into the Gulf relative to shoreline orientation adjacent to the delta. Padre Island extends the entire length of the Texas Laguna Madre, except for an inlet cut through southern Padre Island in 1962 called Mansfield Channel (Figure 6.55). The southern terminus of the Texas Laguna Madre is marked by Brazos-Santiago Pass, which connects Port Isabel to the GoM. Brazos Island State Park (Boca Chica beach) is located along the southern 12 km (7.5 mi) of Texas coast that terminates at the Rio Grande River mouth.

Along the Tamaulipas coast, a deltaic headland/peninsular beach called Barra el Conchillal protects the northern portion of the Mexican Laguna Madre from Gulf waves and currents. This relatively low-profile beach averages approximately 2 km (1.2 mi) wide where it fronts northern Laguna Madre and extends approximately 115 km (71 mi) from the Rio Grande to Boca de Sandoval. Three washover barrier islands, with widths of 500 m (1,640 ft) or less, protect Laguna Madre south of Boca de Sandoval to the mouth of Rio Soto la Marina at La Pesca. Between Boca de Sandoval and Boca de Catán, Barra los Americanos and Barra Jesus Maria encompass about 56 km (35 mi) of coast marked by ephemeral inlets and washover features formed during storm events (Figure 6.55; Tunnell 2002b). The southernmost 78 km (48 mi) of barrier shoreline fronting Laguna Madre (Barra Soto la Marina) extends to the jetties



Figure 6.55. Long-term shoreline change trends for the Laguna Madre Barrier Islands (1930s to 2007). Shoreline change data from Paine et al. (2011). *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.

at the mouth of Rio Soto la Marina. Although all beaches along the Tamaulipas coast are prone to washover during storms, beach widths tend to decrease from the Rio Grande south and beach face slopes increase (Carranza-Edwards et al. 2007). Fine-grained terrigenous sands are dominant, with grain size increasing as beach slopes become steeper.

Longshore sand transport for Padre Island beaches varies depending on shoreline orientation. Although literature indicates that net littoral transport along northern Padre Island is to the south, sedimentation at the Packery Channel jetties indicates a nearly symmetrical deposition pattern, suggesting variable transport direction (Figure 6.54). Because transport direction varies depending on season and year along this section of coast, net transport rates are relatively low (Williams et al. 2007). Based on 8 years of wave data, Kraus and Heilman (1997) calculated net southward transport near Packery Channel at an average rate of 34,000 m³/year (44,500 cy/

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Figure 6.56. Shoreline offset at Mansfield Channel jetties illustrating net longshore transport to the north along South Padre Island, Texas. Image credit: ArcGIS World Imagery.

year). When shoreline orientation shifts from southwest to southeast along central Padre Island, net northward transport is well illustrated at jettied entrances (Figure 6.56). Heilman and Kraus (1996) calculated average net longshore transport rates along South Padre Island to be about 115,000 m^3 /year (150,000 cy/year) to the north. South of the Rio Grande, along the deltaic headland beach of Barra El Conchillal, net transport direction shifts southward based on shoreline orientation and dominant wave climate. This pattern of transport continues south to La Pesca. Although no information is available on net transport rates for beaches fronting the Tamaulipas Laguna Madre, deposition patterns at jettied entrances document the net direction of longshore transport (Figure 6.57).

Between Packery Channel and Mansfield Channel, a longshore sand transport convergence zone shifts north and south depending on annual variation in wave energy relative to shoreline orientation. As such, a 38-km (24-mi) section of beach along north central Padre Island illustrates net accretion (~0.1 m/year [0.3 ft/year]) since 1937 (Figure 6.55). Conversely, the 20-km (12-mi) shoreline segment to the north toward Packery Channel and the 53-km (33-mi) segment south toward Mansfield Channel recorded net shoreline recession of about 1.0 m/year (3.3 ft/year) and 0.9 m/year (3.0 ft/year), respectively. The shoreline recession rate increased substantially for the 7-km (4.3-mi) segment north of Mansfield channel to about 4.1 m/year (13.5 ft/year), perhaps due to interruption of north-directed longshore sediment transport by the jetties at Mansfield Channel entrance. South of the channel, sand deposition within 1.5 km (0.9 mi) of the south jetty resulted in beach accretion and shoreline advance of about 1.9 m/year (6.2 ft/year). However, south of this deposition zone for approximately 50 km (31 mi), shoreline recession was prevalent at an average rate of about 3.1 m/year (10.2 ft/year). Only the southern 5 km (3.1 mi) of beach fronting South Padre Island was net depositional (1.6 m/year [5.2 ft/ year]), likely the result of beach nourishment. South of Brazos Santiago Pass, the coast was net depositional during the Holocene as fluvial sediment from the Rio Grande supplied sand to form barrier islands (Paine et al. 2011). Since 1937, the northern 4.5 km (2.8 mi) of beach recorded net deposition from north-directed longshore sand transport, resulting in average shoreline advance of 0.8 m/year (2.6 ft/year). Conversely, the southern 7.5 km (4.8 mi) of beach to the Rio Grande documented shoreline recession of about 2.9 m/year (9.5 ft/year).

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Figure 6.57. Shoreline offset at the El Mezquital and Boca de Soto la Marina entrances along the Tamaulipas Laguna Madre coast illustrating net longshore transport to the south. Image credit: Microsoft Bing Maps Aerial.

Quantitative shoreline change data are not available for the Tamaulipas Laguna Madre beaches, however, Moreno-Casasola (2007) stated that the barrier island coast south of the Rio Grande is presently eroding or migrating landward due to storm impacts, rising sea level, and limited new sand supply to the coast. Beaches along this coastal segment are low profile and highly susceptible to storm overwash. Relatively low net recession rates have been observed along most of this coastal segment (Carranza-Edwards 2011).

6.3.4.2.8 Laguna Morales Barrier Beaches to Barra del Tordo

This 85-km (53-mi) segment of coast extends from Boca de Soto la Marina at La Pesca to Barra del Tordo near the mouth of the Rio Carrizales (Figure 6.58). Narrow lagoons and waterways back beaches along this section of coast from Laguna Morales in the north to the estuary at Barra del Tordo. Beaches are relatively narrow and similar to those in the southern portion of the Laguna Madre region (Carranza-Edwards et al. 2007). Net longshore sand transport is to the south and onshore; however, deposition patterns at the mouth of Rio Carrizales, where a single jetty currently exists along the south side of the entrance, indicates that north and south transport is fairly balanced. Figure 6.58 illustrates sand spit development at the mouth of Rio Carrizales prior to jetty placement along the southern shoreline.



Figure 6.58. North-south shoreline between Boca de Soto la Marina and Barra del Tordo illustrating bi-directional transport at Rio Carrizales in an overall net south-directed longshore transport system. *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.

6.3.4.3 Southern Gulf of Mexico Marine Ecoregion

The Southern GoM Marine Ecoregion extends from Barra del Tordo at the mouth of Rio Carrizales along the southern GoM shoreline through Veracruz, Tabasco, and Campeche to the northeastern tip of the Yucatán Peninsula (Figure 6.2), a shoreline distance of about 1,700 km (1,056 mi). These shorelines encompass a variety of coastal geological deposits primarily formed by the interaction between fluvial drainage systems and coastal processes in the GoM. Most coastal depositional systems are composed of terrigenous clastic sediment; however, limestone shoreline deposits are dominant east of Isla del Carmen along the Yucatán Peninsula. Furthermore, volcanic headlands exist along the Veracruz coast adjacent to barrier beaches and deltaic deposits. Three geographic areas are used to illustrate patterns of shoreline change within the Southern Gulf Ecoregion: (1) Veracruz Neritic Barrier Shoreline, (2) Tabascan Neritic Rocky and Deltaic Shoreline, and (3) Campeche/Yucatán Carbonate Beach.

6.3.4.3.1 Veracruz Neritic Barrier Shoreline

Between Barra del Tordo and Tuxpan, the coast is composed of terrigenous clastic beaches, primarily sourced by Rio Panuco, that commonly form as barrier islands. The largest barrier island along this section of coast is Cabo Rojo, an island with extensive ridges and active dune fields (Figure 6.59). According to Stapor (1971), Rio Panuco is the primary source of sediment via southerly longshore transport leading to the development of Cabo Rojo. Sand beaches are generally wide and accretionary, and dune elevations are several meters high along most of the island. Between Barra del Tordo and Tampico, barrier islands are low profile, and beach widths are relatively narrow (<40 m [131 ft]) (Carranza-Edwards et al. 2007). Beaches are composed of terrigenous sand but shell fragments are frequently present. Three structured entrances that indicate net transport to the south are present along this section of coast. Croonen et al. (2006) analyzed the rate at which sand accumulated along the north jetty at the Port of Altamira and estimated south-directed transport at $300,000 \text{ m}^3/$ year (392,000 cy/year). The jetty is a significant littoral barrier for sand transport to downdrift beaches, thereby creating a narrow, erosive barrier island protecting the lagoon south of the Port. Shoreline recession rates in this area were reported at 5 to 10 m/year (16.4 to 32.8 ft/ year) (Croonen et al. 2006).

Between the Tampico Harbor jetties and Tuxpan, the most prominent coastal feature is Cabo Rojo, an extensive late-Quaternary barrier island extending approximately 100 km (62 mi) along the Gulf margin of Laguna Tamiahua (Figure 6.59) (Stapor 1971). Beaches are low profile and wide between Cabo Rojo and Tuxpan with extensive dune ridges behind the beaches. Net sand transport along the coast is to the south, as indicated by excess deposition along the north jetties at the Laguna Tamiahua and Tuxpan (Rio Pantepec) entrances and the prograding beach ridge plain along the southern leg of the cape. Although a net depositional feature, Cabo Rojo has experienced net erosion over the past few decades at rates of approximately 1 m/year (3.3 ft/ year) (Peresbarbosa-Rojas 2005). Although net longshore transport quantities have not been estimated for this coastal segment, deposition patterns at jettied entrances suggest that transport rates are less than that identified for the beaches north of Tampico.

Except for a 7 km (4.3 mi) section of coast north of the mouth of Rio Cazones (Veracruz), where volcanic outcrops intersect the coast, beaches extending from Tuxpan to Playa Punta Delgada (50 km [31 mi] south of Nautla) are characterized as low, sandy mainland deposits that are relatively narrow. Rio Tecolutla and Rio Nautla supply relatively large volcanoclastic sediment loads directly to beaches along this section of coast (Figure 6.59) (Okazaki et al. 2001). However, dunes are absent in this area and beaches appear primarily erosional. Shorelines between Playa Punta Delgada and Playa Salinas are composed of bluffs and rocky points of volcanic origin (referred to as the Trans-Mexican Volcanic Belt), interspersed with small lagoons and narrow flood plains (Moreno-Casasola 2007). Sandy beaches are observed throughout this section of coast, and active dune fields are prominent north of Veracruz to Laguna de Farallón (Carranza-Edwards 2011). Although less common, rocky headlands persist as far north as Playa Punta Delgada, interrupting littoral sand transport along beaches. Most beaches within this ecoregion are undergoing erosion, as illustrated by active erosion or scarping of the primary dune ridge along the coast (Tanner 1975b). Sediment transport is primarily to the south but is variable in response to localized fluvial inputs, lithologic boundaries, and sedimentation accumulation landforms (Psuty et al. 2008, 2009).

6.3.4.3.2 Tabascan Neritic Rocky and Deltaic Shoreline

This 570-km (354-mi) shoreline segment has the greatest variety of shoreline types and extends from southeastern Veracruz through Tabasco to southwestern Campeche (Figure 6.60). Coastal areas in Veracruz, particularly the barrier beaches in the Alvarado region, are low lying

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Figure 6.59. Veracruz Neritic shoreline between Barra del Tordo and Playa Salinas illustrating a net south-directed longshore transport system. *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.



Figure 6.60. Tabascan Neritic shoreline between Playa Salinas and Isla Aguada illustrating variability in the net longshore transport system. *White arrows* show the direction of net littoral sand transport. Image credit: Microsoft Bing Maps Aerial.

and vulnerable to storm surge and rising sea level (Moreno-Casasola 2007). Southeast of this area, between Punta Puntilla and Laguna Ostión, the coast is a mixture of low-lying sandy beaches and rocky headlands within Los Tuxtlas Biosphere Reserve (associated with the San Andres Tuxtla volcanic massif). East of Laguna Ostión to Coatzacoalcos, beaches are low profile and extensive dune fields are present. Between Rio Coatzacoalcos and Rio Tonalá, numerous small rivers supply clastic sediment to the coast; however, most beaches are erosional (Carranza-Edwards 2011). Sediment within the Tabascan coastal zone is terrigenous, primarily sourced from the Tonalá, Grijalva, Usumacinta, and San Pedro y San Pablo Rivers (Thom 1967). Sand grain size varies from fine to very fine, and heavy mineral concentrations are common (Carranza-Edwards et al. 2007). Beach ridges are associated with deltaic deposition during an accretionary phase of development when sediment loads were high. However, historical changes in coastal evolution have been dominated by beach erosion (Tanner and Stapor 1971). Deltaic shorelines extend east into Campeche, terminating at the channel between Zacatal and Isla del Carmen at Laguna de Términos (Figure 6.60). Isla del Carmen, a barrier island fronting Laguna de Términos, is located in the transition area between limestone of the Yucatán Peninsula and alluvial terrain of deltaic deposits to the west (Contreras-Espinosa and Castañeda-Lopez 2007).

Based on aerial imagery and Stapor (1971), net longshore sediment transport rates vary in this east-west oriented coastal segment depending on local shoreline orientation and sediment supply from the river systems. Near Alvarado and the Papaloapan River system, net transport is to the east. This trend continues along the Tuxtlas shoreline, only to be interrupted by rapid changes in shoreline orientation at headland outcrops. Pocket beaches often are shielded from wave approach depending on headland size and orientation, meaning longshore transport may vary significantly relative to open-coast sandy beaches. South of Laguna Ostión, net transport is from west to east until the jetties at Coatzacoalcos. East of the jetties, transport appears balanced with slightly greater transport from east to west. However, at the entrance to Laguna del Carmen at Sánchez Magallanes (~60 km [37 mi] east of Coatzacoalcos), the offset in sand deposition at the east and west jetties illustrates dominant littoral transport from east to west (Figure 6.61). This pattern of transport continues to the mouth of Laguna de Términos. Net transport rate estimates do not exist for this area.



Figure 6.61. Shoreline offset at the Laguna del Carmen jetties at Sánchez Magallanes illustrating net west-directed longshore sand transport (A; Image credit: Microsoft Bing Maps Aerial). Downdrift beach erosion west of the jetties has resulted in significant property damage (B; photo from Hernández-Santana et al. 2008, used with permission).

Although quantitative shoreline change information is not available for the coast between Plava Salinas and Rio Tonalá, Carranza-Edwards et al. (2007) indicated that coastal processes for most sandy beaches in this area are net erosional. East of Rio Tonalá, Tanner and Stapor (1971) recorded erosion along the seaward edge of the beach-ridge plain where younger beach ridges are truncated or scarped rather than tapered. Furthermore, trunks of dead trees were found in the surf zone as a result of beach erosion and shoreline recession. Ortiz-Pérez (1992) and Ortiz-Pérez and Benítez (1996) used historical maps to compare shoreline positions for the periods 1943 to 1958 and 1972 to 1984 to illustrate that shoreline recession is widespread for the deltaic shorelines of Tabasco and Campeche. At the mouth of Rio San Pedro y San Pablo, they found net shoreline recession was dominant at about 8 m/year. Hernández-Santana et al. (2008) supplemented these data with a 1995 shoreline and documented change between Rio Tonala and the Rio San Pedro y San Pablo entrance from 1943 to 1995. Estimates of shoreline change between 1984 and 1995 for the mouth of the Rio San Pedro v San Pablo were consistent at about -8 to -9 m/year (-26 to -30 ft/year) (Figure 6.62). Comparison of shoreline position for 1972, 1984, and 1995 at other coastal locations illustrated shoreline recession for most of the Tabascan/Campeche deltaic coast.

Ortiz-Pérez et al. (2010) updated previous shoreline change studies to include a 2008 aerial imagery shoreline. Figure 6.63 documents net changes quantified for nine segments of coast east of Rio Tonalá for the period 1995 to 2008. The western portion of segment 1 shows shoreline advance (0.97 m/year [3.2 ft/year]) near Rio Tonalá and the eastern side indicates net erosion (0.5 m/year [1.6 ft/year]). Sánchez Magallanes is located on the western margin of the jettied entrance to Laguna del Carmen (Figure 6.64), where west-directed longshore sand transport is blocked by the east jetty (Figure 6.61). This interruption in littoral transport produces significant net erosion immediately downdrift of the entrance (3 to 5 m/year



Figure 6.62. Shoreline position change adjacent to Rio San Pedro y San Pablo for the periods 1943–1972, 1972–1984, and 1984–1995 (from Hernández-Santana et al. 2008), used with permission.



Figure 6.63. Net annual rates of shoreline advance (avance) and recession (retroceso) from Rio Tonalá to the Rio San Pedro y San Pablo delta plain, 1995 to 2008 (from Ortiz-Pérez et al. 2010, used with permission). *Arrows* pointing to the Gulf indicate shoreline advance; *arrows* pointing toward land imply recession.


Figure 6.64. Shoreline change locations for the Tabasco/Campeche coast. Image credit: Microsoft Bing Maps Aerial.

[9.8 to 16.4 ft/year] from 1972 to 2005) (Hernández-Santana et al. 2008), resulting in net erosion (0.5 m/year [1.6 ft/year]) for about 19 km (11.8 mi) west of the jetties. Although net deposition does occur adjacent to the east jetty, the next 28.5 km (17.7 mi) of coast (segment 2) east of the entrance is net erosional at approximately 1.05 m/year (3.4 ft/year) (Figure 6.63). From Boca Panteones east to Barra Tupilco (~17 km [10.5 mi]; segment 3) (Figure 6.64), shoreline recession is dominant at about 1.07 m/year (3.5 ft/year). The magnitude of erosion increases slightly along the 24.8 km (15.4 mi) shoreline east of Barra Tupilco (segment 4) to approximately 1.35 m/year (4.4 ft/year) but increases to 4.34 m/year (14.2 ft/year) over the next 5 km (3.1 mi) near Puerto Dos Bocas (Ortiz-Pérez et al. 2010). Between Rio Gonzaléz and the eastern flank of the Rio Grijalva delta (~73 km [45 mi]; segments 7 and 8), the shoreline experiences net advance of between 0.16 and 1.04 m/year [0.5 and 3.4 ft/year]. However, the coast adjacent to Rio San Pedro y San Pablo and east about 20 km (12.4 mi) eroded at about 3.05 m/year (10.0 ft/year) (segment 9) between 1995 and 2008 (Ortiz-Pérez et al. 2010) and has been consistently eroding since at least 1943 (Figure 6.62) (Hernández-Santana et al. 2008).

Torres-Rodríguez et al. (2010) and Bolongaro Crevenna Recaséns (2012) evaluated erosion trends along the Campeche coast at selected locations east of the Rio San Pedro y San Pablo between 1974 and 2002/2008. Seven locations were used to document erosion trends, including shorelines adjacent to the Rio San Pedro y San Pablo mouth that overlap with shoreline change information compiled by Ortiz-Pérez et al. (2010) (Figure 6.64). Bolongaro Crevenna Recaséns (2012) documents a change rate of -4.8 m/year (-15.7 ft/year) between 1974 and 2006 and Ortiz-Pérez et al. (2010) calculated a rate of about -3.1 m/year (-10.2 ft/year) for the period 1995 to 2008. Although rates differ, variations in time interval and/or beach extent perhaps had the greatest influence on change rates. East of Rio San Pedro y San Pablo, the Nitrogenoducto area illustrated shoreline recession of about 0.7 m/year (2.3 ft/year) (1974 to 2004) whereas the Atasta shoreline area recorded -14.3 m/year (-46.9 ft/year) (1974 to 2008) (Bolongaro Crevenna Recaséns 2012). The very eastern portion of the delta plain near Playa la Disciplina and the channel to Laguna de Términos recorded a change rate of -17.1 m/year (-56.1 ft/year) between 1974 and 2008 (Torres-Rodríguez et al. 2010). The large change rates at Atasta and Playa la Disciplina reflect the influence of hurricanes impacting this area in 2005 and 2007. Additionally, three shoreline areas were evaluated for Isla del Carmen at Playa Norte, Club de



Figure 6.65. Index map illustrating net longshore sediment transport pathway for the Campeche-Yucatán coast (Image credit: Microsoft Bing Maps Aerial). Two *inset* images indicate the net direction of transport via sand spit growth and differential shoreline change at structured entrances. (Image credit: ArcGIS World Imagery).

Playa, and Cases (Figure 6.64). Large change variations existed but the Gulf facing shoreline was net erosional at all locations and the eastern two locations illustrated greatest change (-5.2 m/year [-17.0 ft/year] at Club de Playa; -3.6 m/year [-11.8 ft/year] at Cases). Playa Norte is at the eastern end of Isla del Carmen, the downdrift end of the longshore transport system, and had the smallest net erosion rate (0.3 m/year [1.0 ft/year]) (Bolongaro Crevenna Recaséns 2012).

6.3.4.3.3 Campeche/Yucatán Carbonate Beach

The Campeche-Yucatán carbonate beaches extend approximately 700 km (435 mi) from Isla Aguada at the eastern margin of Laguna de Términos to the northeastern end of Yucatán Peninsula near Cabo Catoche (Figure 6.65). The coast in this area is primarily a low-relief limestone platform through which rainfall filters and supplies coastal habitats with fresh water. Between Isla Aguada and Champotón, calcareous sand beaches are narrow and low relief. North of Champotón to Campeche, the coast is primarily limestone rock. Concrete bulkheads and other coastal structures protect the city of Campeche from flooding and erosion, and narrow calcareous sand and rock beaches are common south of the city. North of Campeche to Celestún, the shoreline is protected from energetic Gulf waves and the dominant shoreline type is mangrove. The northern Yucatán coast includes a beach-ridge plain overlying the limestone platform of the Yucatán Peninsula. Calcareous sand beaches along the Yucatán coast protect

shallow and narrow lagoons from GoM waves and currents (Meyer-Arendt 1993). In many locations along northern Yucatán, beaches are quite narrow and low-relief dunes are common. River runoff is not present in this area, so beach sand is composed of carbonate particles derived from limestone deposits, coral reefs, and shells. As such, organic content in coastal waters is low and water clarity is excellent.

Carbonate sand beach ridges along the northern Yucatán coast reflect a period of sand abundance and accretion during the Holocene, but the present lack of sand in the littoral transport system has resulted in net erosion in recent years (Meyer-Arendt 1993). The dominant east-to-west longshore sediment transport system has produced several westward-curving sand spits (e.g., Celestún) and shoreline offsets at shore-perpendicular structures (e.g., jetties, groins) (Figure 6.65). Along the north-south shoreline between Celestún and Isla Aguada, net sand transport direction is to the south-southwest. The only section of coast where longshore transport is not a significant coastal process is along the low-energy coast between Celestún and Campeche where mangroves are dominant. Estimates of longshore transport magnitude are not available for the area between Isla Aguada and Celestún; however, shoreline change rates for the sandy beaches between Isla Aguada and Champotón are consistent with change rates along the northwestern Yucatán coast where transport rates vary from approximately 48,000 to 60,000 m³/year (63,000 to 78,000 cy/year) (Appendini et al. 2012).

Between Celestún and Cabo Catoche, numerous coastal communities and industrial ports are present among the carbonate beaches and shallow coastal lagoons. Navigation structures associated with port development have resulted in large differences in shoreline position on either side of entrances (e.g., Puerto de Sisal, Puerto de Chuburná, Puerto de Telchac) indicating the dominant direction of littoral transport. The net direction of longshore sand transport in this area is illustrated well based on sand accumulation at shore-perpendicular structures and the natural growth of sand spits; however, the magnitude of net longshore transport requires knowledge of wave and current processes or a time series of shoreline and hydrographic surveys for documenting long-term sediment erosion and accretion patterns. Long-term regional survey datasets are not available for the northern Yucatán coast, so Appendini et al. (2012) used 12 years of wave hindcast data to estimate potential longshore sediment transport rates. The reliability of transport estimates was verified by comparing calculated rates with infilling rates at a shore-perpendicular structure that acts as a total littoral barrier to longshore transport. Based on transport simulations, Appendini et al. (2012) determined a range in transport from approximately 20,000 to 80,000 m³/year (26,000 to 105,000 cy/year). Figure 6.66 illustrates variability in potential longshore sand transport rates for the northern coast of the Yucatán Peninsula, suggesting that approximately 60,000 m³/year (78,000 cy/year) is being transported from the northwestern coast toward Celestún, creating an extensive sand spit deposit (Figure 6.65).

Torres-Rodríguez et al. (2010) document shoreline changes along the Campeche coast between Isla Aguada and Champotón for the period 1974 to 2002/2008. Greatest rates of change were recorded for a 10 km (6.2 mi) beach segment at Sabancuy (-6.8 m/year [-22.3 ft/ year]) where jetties protecting navigation between Estero Sabancuy and the Gulf caused significant erosion downdrift of the entrance (Torres-Rodríguez et al., 2010). About 35 km (21.7 mi) north of this area, Torres-Rodríguez et al. (2010) document shoreline recession of about 4.4 m/year (14.4 ft/year) near Punta de Xen. Near Champotón, shoreline recession decreased to about 2.4 m/year (7.9 ft/year); however, much of the coast is rocky, implying a more stable shoreline type. The most stable carbonate beaches along the Campeche coast were identified near Isla Aguada where net shoreline recession rates of 0.2 m/year (0.7 ft/year) were calculated near the southwestern end of the littoral drift zone (Torres-Rodríguez et al. 2010). Sand accumulation from longshore transport perhaps resulted in lower net shoreline recession relative to updrift beaches.



Figure 6.66. Potential longshore sediment transport estimates (m^3 /year \times 1,000) for the northern coast of the Yucatán Peninsula (modified from Appendini et al. 2012). Areas of erosion and deposition are identified based on gradients in longshore transport rates. Negative and positive values represent westward and eastward transport, respectively.

Along the northern Yucatán coast, long-term accretion has been the primary process associated with barrier beach formation during Holocene time. However, during historical times, beach erosion has been the principal geomorphic response to coastal processes shaping the coast. Despite past accretion trends, dune scarping is common at several locations along the northern Yucatán coast, especially east of Progreso near Puerto de Chuburná (Meyer-Arendt 1993). Although shoreline recession rates of about 1.8 m/year (5.9 ft/year) have been documented by Gutierrez-Espadas (1983) for a 110-year period for this area, short-term rates averaged about 0.3 to 0.6 m/year (1.0 to 2.0 ft/year) for the period 1948 to 1978 (Meyer-Arendt 1993). Greatest shoreline changes along the northern Yucatán coast occur in response to jetty construction at harbor entrances and in association with sand spit growth (e.g., near Celestún). Natural coastal erosion generally is attributed to the passage of nortes (winter cold fronts) and hurricanes; normal waves and currents contain relatively low energy not capable of producing significant sand transport or shoreline changes.

6.3.4.4 Caribbean Sea Marine Ecoregion: Cabo Catoche to Cancún

The northeast outer coast of Quintana Roo, from Cabo Catoche to Punta Cancún, is composed of Holocene carbonate sediment derived from marine and coral reef limestone of Upper Pleistocene and Holocene age (Ward 2003). Coastal ecosystems include coral reefs, beaches and dunes, and coastal lagoons (Figure 6.67). Beaches are composed of fine, well-sorted sand, primarily derived from ooliths with skeletal mollusk detritus and coral fragments, and sand sources are from reef degradation and onshore sand transport (Morán et al. 2007; González-Leija et al. 2013). Prominent features along the coast include barrier islands and sand spits connected to the mainland that create coastal lagoons (e.g., Isla Blanca), and offshore islands (Isla Contoy and Isla Mujeres) that formed partly as remnants of Upper Pleistocene dune ridges (Ward 2003). This part of the Quintana Roo coast is particularly vulnerable to tropical cyclones and nortes. As such, the coast is typically erosional (Molina et al. 2001). When storms impact the area, limestone rock ledges are often exposed until coastal sand transport processes cover the rock ledges during post-storm depositional periods. Most beaches in this region are narrow (40 to 400 m [130 to 1,300 ft] wide) and have low elevations (Molina et al. 2001).

According to Carrillo et al. (2015), the general pattern of surface water currents along the Quintana Roo coast is from south to north, as is the Yucatán Current (Figure 6.68). Although reversals in longshore transport south of Cancún occur in the nearshore reef between rock



Figure 6.67. Index map illustrating net longshore sediment transport pathways for the northeast Quintana Roo coast. Image credit: Microsoft Bing Maps Aerial.

headlands, the Yucatán Current, coupled with wave refraction, produces a net northward current for all littoral areas along the northeast coast of Quintana Roo (Krutak and Gío-Argáez 1994). Longshore sand deposition resulted in the formation of numerous Holocene beach ridges along the northern coast of Isla Blanca, illustrating the dominant direction of littoral transport. Overall, this information is consistent with the potential longshore sediment transport modeling estimates of Appendini et al. (2012); however, predicted transport for approximately 15 km (9.3 mi) east of Cabo Catoche is to the southeast, not to the north (see Figure 6.66). Review of aerial imagery for this section of coast indicates that a reversal in longshore transport is evident based on sand deposition patterns at entrances between the islands. This localized departure from overall transport trends does not diminish the fact that both studies recognize a dominant south to north, then east to west, longshore transport pathway for coastal flows around Cabo Catoche. Although transport direction in this area is well documented, the magnitude of longshore sand transport is lacking.

The beach south of Punta Cancún was evaluated for shoreline change by Dibajnia et al. (2004) to document erosion trends relative to proposed beach replenishment in the area. They identified variations in shoreline response, illustrating net shoreline recession of about 1.5 m/year (4.9 ft/year) for beach extending approximately 3 km (1.9 mi) south of Punta Cancun, 0.5 m/year (1.6 ft/year) for the 6-km (3.7-mi) long central beach segment, and about 2.6 m/year (8.5 ft/year) for the 2 km (1.2 mi) segment south to Punta Nizuc for the period 1989 to 2000.



Figure 6.68. Pattern of surface water currents along the Quintana Roo coast (reprinted from Carrillo et al., 2015, with permission from Elsevier).

Based on change measurements, Dibajnia et al. (2004) estimated beach losses at approximately 33,000 to 76,000 m³/year (43,000 to 99,000 cy/year). If one assumes beach changes primarily are associated with longshore transport processes, estimated quantities can be used to approximate littoral transport rates. Because equivalent shoreline studies are not available north of this area, and exposure to waves and currents is similar for both regions, the estimates of Dibajnia et al. (2004) may provide a proxy for beaches along the northeastern Quintana Roo coast.

6.3.4.5 Greater Antilles Marine Ecoregion: Northwestern Cuba

The northwestern coast of Cuba, between Cabo San Antonio and Havana, has a coastline length of approximately 350 km (217 mi) and is highly diverse in terms of geology, soils, and plant communities (González-Sansón and Aguilar-Betancourt 2007). West of Havana to Bahía Honda, the coast is characterized by low cliffs and sandy beaches with inlets and bays (Figure 6.69) (Rodríguez 2010). Moving west of Bahía Honda, a chain of coral reefs and cays becomes the Archipelago de los Colorados, sheltering the inland coast and fringing mangrove habitat (González-Sansón and Aguilar-Betancourt 2007). Mangrove habitat flourishes when protected by sandy barrier beaches and spits or fringing coral reefs. Although narrow, fringing beaches are present between Havana and Mariel, sandy carbonate beach



Figure 6.69. Index map illustrating the location of sand beaches and net longshore sediment transport pathway for northwest Cuba. Image credit: Microsoft Bing Maps Aerial.

environments become more common west of Mariel where source material for carbonate sands (degrading reefs) becomes more abundant. Along the southwestern end of Golfo de Guanahacabibes is a limestone peninsula with rocky beaches with narrow carbonate sand deposits.

The longshore sand transport system in this area is very complicated by the presence of coral reefs and limestone rock shores that dissipate and reflect wave energy depending on distance from shore and orientation relative to dominant wave approach. However, where sand beaches are present, the dominant direction of transport is from east to west due to predominant winds and waves from the east-northeast (Figure 6.69) (UNEP/GPA 2003; González-Sansón and Aguilar-Betancourt 2007). Sand spits at inlets and along the western ends of cays support this direction of net transport. Although longshore sand transport magnitudes are not available for the northwest coast of Cuba, predicted annualized sand transport rates for beaches at Varadero (east of Havana) are estimated at 89,000 to 134,000 m³/year (116,000 to 175,000 cy/year) (Kaput et al. 2007). Beaches along the northwest coast are more protected from predominant waves than those at Varadero, so net littoral transport rates are perhaps lower than those simulated by Kaput et al. (2007).

Shoreline change rates for northwestern Cuba beaches are lacking as well. Again, if measurements made for Varadero beaches over the past 30 years are indicative, the net rate of shoreline recession would be approximately 1.2 m/year (3.9 ft/year) (Kaput et al. 2007). Dead trees and stumps exposed on the beaches along the northwestern coast indicate chronic beach erosion (Figure 6.70); however, change rates are difficult to estimate. Using similar logic as stated for estimating net littoral transport rates, long-term shoreline recession rates would perhaps be on the order of 1 m/year (3.3 ft/year).

6.4 **BIOGEOGRAPHIC SETTING**

The coastal strand and its associated vegetated marine habitats consist of several characteristic habitats that are qualitatively similar throughout the world. These habitats include supratidal barrier islands and beaches; intertidal saline wetlands, including salt marshes and mangroves; subtidal seagrasses; and intertidal flats and subtidal soft bottoms (Christensen 2000; Mendelssohn and McKee 2000; Hester et al. 2005; and references therein). These habitats provide a suite of societal benefits as described in Section 6.4.4 of this chapter.



Figure 6.70. Erosion along the northwest coast of Cuba; (a) Playa Las Canas (UNEP/GPA 2003) and (b) Cayo Levisa (photo credit: van Lieshout (2007), used with permission).

6.4.1 Introduction to Vegetated Marine Habitats

6.4.1.1 The Barrier Strand

The barrier strand, composed of shore-parallel accumulations of sand and shell in the form of barrier islands, beaches, and related shoreline types, is best considered a habitat-complex. Several unique habitats, such as beach, dune, swale, maritime shrub and forest, salt pan, back barrier marsh, and submerged seagrass occur as part of the barrier strand complex



Figure 6.71. (a) Barrier strand habitats in the northern GoM (from Mendelssohn et al. 1983; used with permission from ASCE). (b) Oblique aerial photo of a segment of the Chandeleur Islands (photo credit: I. A. Mendelssohn).

(Figure 6.71a, b). Although the physiography of the barrier strand may differ in specific geographical locations in the GoM, the habitats therein and the primary factors controlling their biotic communities are quite similar. This introduction draws examples from the Deltaic Coastal Marshes and Barrier Islands Terrestrial Ecoregion (Figure 6.6).

The beach habitat is a strip of generally sandy substrate that extends from the low tide line to the top of the foredune, or in the absence of a foredune, to the farthest inland reach of storm waves (Barbour 1992) (Figure 6.72). This habitat is characterized by shifting sands, intense salt-spray, periodic saltwater inundation, and sand-washover. Only those plant species highly adapted to these stressors (e.g., *Cakile edentula* (sea rocket)) can survive on the beach.



Figure 6.72. Beach habitat includes the foreshore and backshore of the barrier strand and is subject to periodic wave runup, shifting sands, and saltwater from salt spray and surf (photo credit: I. A. Mendelssohn).

Landward of the beach, sand dunes, which can vary greatly in height, form as accumulations of aeolian transported sand and fine shell (Figure 6.73). Some dunes remain unvegetated and mobile, while those that are more stable become vegetated, which further promotes stability. Dune vegetation is usually distinct from beach vegetation. Because sand dune habitat seldom experiences saltwater inundation, the substrate, although infertile, has little salt accumulation, and thus, plant salt tolerance is not necessary. However, salt spray, the salt-laden aerosol generated from onshore winds blowing across breaking waves, is a common environmental stressor on primary dunes, and vegetation, like *Uniola paniculata* (sea oats), must be adapted to this stressor to survive in the sand dune habitat.

Landward of the primary dune, and between secondary and tertiary dunes, are low elevation depressions called swales or dune slacks (Figure 6.74). Swales have greater soil moisture than beach or dune habitats, and the types of vegetation occurring in swales are more flood-tolerant than beach and dune vegetation. Because of generally greater plant growth in the swale habitat and the lesser probability of plant-derived litter being removed by tides, soils in the swale are relatively high in organic matter (compared to the dune and beach), and therefore, have a greater water holding capacity and are more fertile for plant growth (Dougherty et al. 1990). Many of the mostly herbaceous plants that dominate the swale occur only, or primarily, in this habitat. On wider and more stable barrier islands, protected portions of the swale are usually dominated by shrubs and trees, e.g., *Myrica cerifera* (wax myrtle) and *Quercus virginiana* (live oak), respectively, and have been termed maritime forests (Christensen 2000).

On larger, more stable barrier islands, dune and swale topography often repeats multiple times, but when moving landward, elevation decreases and seawater inundation from back-barrier lagoons and bays occurs. This portion of a barrier island system is dominated by backbarrier salt marshes and in the more tropical climates, mangroves (Figure 6.75a, b). Salt



Figure 6.73. Dune habitat is characterized by accumulations of sand, either mobile or stabilized, depending on the extent of vegetation cover. As such, vegetation must be adapted to sand burial and salt spray, as well as moisture deficiency, to survive (photo credit: I. A. Mendelssohn).



Figure 6.74. Swale habitat is an interdunal topographical depression that occurs landward of the primary dune. Because the environment is more benign here, species diversity is generally high (photo credit: I. A. Mendelssohn).



Figure 6.75. Backbarrier marsh (a) occurs on the landward side of a barrier island/beach and is composed of both regularly flooded low marsh, dominated by *Spartina alterniflora* or *Avicennia germinans*, and (b) infrequently flooded high marsh, dominated by *S. patens* and *Distichlis spicata*, among other species (photo credit: I. A. Mendelssohn).

pan habitat (Figure 6.76) generally occurs between the swale and the backbarrier wetlands. This is an area where infrequent tidal incursions result in salt accumulation in the soil and thus high soil salinities. Where salinities are exceptionally high (more than twice sea-strength), salt pans can be devoid of vegetation. However, more often than not, sparse populations of the most salt-tolerant halophytes dominate salt pans. At somewhat lower elevations, tidal incursions occur more frequently, but still not on a daily basis. This is the high marsh, which consists of



Figure 6.76. Salt pan habitat has hypersaline soils in which few plant species can survive, and those that do are stunted and of low productivity (photo credit: I. A. Mendelssohn).

salt-tolerant plants that can only withstand intermittent flooding, usually only on spring or wind tides. Further bayward is the low marsh, where tidal inundation occurs daily. Salt marshes and mangroves that occur in regularly flooded portions of backbarrier environments reach their greatest development here. Intertidal flats are only exposed at very low water, and therefore are generally unvegetated by macrophytes.

Within shallow waters landward of the barrier strand, seagrass beds may occur where turbidity conditions permit. Their presence is determined primarily by water clarity and low-nutrient conditions. Also associated with the barrier strand are intertidal flats (Figure 6.77), which occur throughout the GoM, and are herein considered an independent coastal habitat (see Section 6.5.6). Often they are associated with barrier islands, but they also occur along shorelines in bays and lagoons.

6.4.1.2 Marine Intertidal Wetlands

Salt marshes, mangroves, and reed beds generally are low-energy coastal shoreline intertidal wetlands. Salt marshes are dominated by halophytic forbs, graminoids, and shrubs that periodically flood with seawater as a result of lunar (tidal) and meteorological (primarily wind) water level changes. Like other wetlands, salt marshes are characterized by a pronounced hydrology, soil development under flooded conditions (hydric soils), and the dominance of vegetation (hydrophytes) adapted to saturated soil conditions (Lyon 1993). Salt marshes (Figure 6.78a) usually dominate in temperate climates, but to a lesser degree are also found in subtropical and tropical environments (Costa and Davy 1992). Mangrove habitats (Figure 6.78b), which primarily occur in tropical and subtropical climates, share many of the same characteristics, but are dominated by woody plant species. The word, mangrove, is an ecological term used to describe salt- and flood-tolerant trees and shrubs that inhabit the intertidal zone (Mendelssohn and McKee 2000). In addition to the typical saline wetlands that occur along



Figure 6.77. Unvegetated tidal flats, adjacent to vegetated salt marshes, are exposed at low tides and provide habitat for wading birds and benthic fauna (photo credit: I. A. Mendelssohn).

the GoM coastline, reed beds, dominated by *Phragmites australis*, are a unique habitat of the northern GoM. The largest expanse of coastal reed beds in North America occurs along the coastal shorelines of the Mississippi River Birdfoot Delta (Figure 6.78c). Because it is a shoreline coastal habitat and occupies the position of saline wetlands elsewhere in the Gulf, it is included in this review of coastal habitats. The *Phragmites* reed habitat at the terminus of the Mississippi River is structured by the Mississippi River and the high subsidence rates that occur there. Salinities are fresh to intermediate and both native and European strains of *Phragmites australis* occur (Lambertini et al. 2012).

6.4.1.3 Seagrass Beds

Seagrass beds or meadows are primarily composed of clonal marine flowering plants that occur in shallow, generally soft-sediment habitats along the shores of bays and estuaries in temperate and tropical environments (Williams and Heck 2001) (Figure 6.79). Seagrasses comprise a very important vegetative habitat in the GoM. These flowering angiosperms are entirely restricted to underwater habitats where water clarity, salinity, and substrate are suitable. They often are referred to as "submerged aquatic vegetation" or SAV. Five genera occur in the Gulf, including *Thalassia*, *Halodule*, *Syringodium*, *Halophila*, and *Ruppia*. *Ruppia maritima* is generally associated with low-salinity brackish waters in bays and estuaries and is not addressed in this chapter. Estimates of the areal extent of seagrass beds in the GoM range from approximately 17,000 km² (4,250,000 acres) to 19,000 km² (4,695,000 acres) (Table 6.2) (Onuf et al. 2003; Handley et al. 2007). They are unevenly distributed with sizable areas occurring along Cuba's northwestern coast, the southern tip and Big Bend areas of Florida, the southern Texas coast, and Mexico's Yucatán Peninsula. Lesser amounts of seagrasses are found along the northern GoM from the Florida Panhandle to north Texas. Areas of seagrass also occur in the Mexican states of Tamaulipas, Tabasco, and Veracruz.



Figure 6.78. Oblique aerial photographs of (a) salt marsh dominated by *Spartina alterniflora*, (b) mangrove islands dominated by *Avicennia germinans*, and (c) *Phragmites australis*-dominated reed beds, all located in coastal Louisiana (photo credit: I. A. Mendelssohn).



Figure 6.79. Mixed meadow of seagrasses from the Big Bend area of Florida (photo credit: Barry A. Vittor & Associates).

Location	Area, Ha (Acres)	Source(s)
NW Cuba	205,500 (507,790)	а
Tamaulipas, MX	35,700 (88,215)	а
Tabasco, MX	810 (2002)	а
Yucatán Peninsula, MX	591,100 (1,460,640)	а
Texas, excl. Laguna Madre	16,763 (41,422)	b, c
Texas, Laguna Madre	70,817 (174,987)	d
Louisiana	12,525 (30,949)	е
Mississippi	1,280 (3,164)	f
Alabama	682 (1,685)	g
Florida, Panhandle	15,864 (39,200)	h
Florida, Springs Coast	250,100 (618,000)	h
Florida, South	526,100 (1,299,993)	h
Totals	1,727,241 (4,268,048)	

Table 6.2. Areal Estimates of Seagrass Extent for the GoM

(a) Onuf et al. (2003); (b) Pulich (2001); (c) Pulich et al. (1997); (d) Handley et al. (2007); (e) NOAA (2004); (f) Barry A. Vittor and Associates, Inc. (2009); (h) Yarbro and Carlson (2011)

6.4.1.4 Intertidal Flats and Subtidal Soft Bottoms

Although GoM intertidal flats and subtidal soft-bottom habitats lack rooted vascular vegetation, they represent a significant interface between vegetated coastal habitats and nearshore waters. These sedimentary habitats adjoin or surround seagrass meadows, salt

marshes, and mangroves, and many of their motile fauna move freely between vegetated and non-vegetated habitats. Non-vascular plants (marine macroalgae or "seaweeds") do occur in intertidal and subtidal areas, but are a minor component of those habitats. Epibenthic and benthic fauna obtain some nutrients from seaweeds but primarily convert organic production by vegetated habitats to forms available to epifauna and nekton. This trophic linkage is critical to fishery resources in the GoM.

Intertidal flats are less prominent in the GoM than along the Atlantic and Pacific coasts because amplitudes of lunar tides are much lower in the Gulf, and exposure of these habitats results mainly from wind-driven tidal action, especially during winter months. Subtidal soft-bottom habitats encompass those substrates that are deeper than the beach swash zone, and for this chapter, extend seaward to a depth of less than 10 m.

Gulf seaweeds are associated primarily with hard substrates, but genera such as *Avrain-villea*, *Caulerpa*, *Halimeda*, *Penicillus*, and *Udotea* include species that are found mainly on sand or mud surfaces. *Ceramium* may occur in seagrass beds as well as on hard bottom. Other taxa, including *Ulva*, can occur on intertidal flats and subtidal soft-bottoms where there are hard surfaces on which to attach. Fredericq et al. (2009) listed 673 seaweed species in the GoM; however, only 50 of these species occur predominantly on sand or mud bottoms. Only three of these soft-bottom species have been reported from the Mississippi Estuarine or Texas Estuarine Ecoregions; most are found in the Eastern Gulf Neritic Ecoregion. Because seaweeds generally exhibit patchy distributions, no estimates of surface area coverage are available for the GoM.

6.4.2 Depositional Characteristics of Vegetated Marine Habitats

The ecological structure and function of coastal flora and fauna in the GoM varies in response to spatial changes in depositional environments and climatic regime (temperate to subtropical to tropical). As a result, the distribution of vegetated marine habitats and their depositional environments within the GoM can best be summarized from an ecoregion perspective, given that marine and terrestrial ecoregions are in large part climatically driven (Wilkinson et al. 2009; Yáñez-Arancibia and Day 2004). At the broadest geographical scale, coastal habitats of the GoM occur in five primary marine ecoregions: (1) South Florida/Bahamian Atlantic, (2) Northern GoM, (3) Southern GoM, (4) Caribbean Sea, and (5) Greater Antilles (Figure 6.2). Because coastal habitats represent transitional environments between marine and terrestrial ecosystems (see Section 6.2), ecoregions based on terrestrial characteristics will be used as necessary when describing coastal habitats and their distribution.

6.4.2.1 South Florida/Bahamian Atlantic Marine Ecoregion

The most diverse area of the GoM coast is that of the southwestern Florida peninsula, where coastal habitats of the South Florida/Bahamian Atlantic Marine Ecoregion occur. The variety of habitats in this area is immense, where groundwater discharge is important and sandy beaches, mangroves, seagrasses, and coral reefs dominate. This marine ecoregion extends from the Florida Keys north to southern Keewaydin Island (just south of Naples, Florida) and comprises the Southern Coast and Islands Terrestrial Ecoregion. This part of the southwest Florida coast has many physiographic and hydrologic complexities associated with this biologically unique area. The entire Mesozoic and most of the Cenozoic geological sequence associated with the Florida peninsula is composed of carbonate rock (Hine and Locker 2011). As such, habitats of this region are often underlain by a calcium carbonate substrate, a driver of vegetation structure and function. As a consequence of this carbonate underpinning, the southwest Florida area is quite stable with little sediment compaction or subsidence.



Figure 6.80. Coastal habitats for and adjacent to the Southern Coast and Islands Terrestrial Ecoregion (data from Beck et al. 2000; FFWCC-FWRI 2003; Giri et al. 2011a; IMaRS/USF et al. 2010). Image credit: Microsoft Bing Maps Aerial. Inset photo: Chauta 2012, used with permission.

The Southern Coast and Islands Terrestrial Ecosystem portion of the South Florida/ Bahamian Atlantic Marine Ecoregion encompasses the Florida Keys and Ten Thousand Islands areas of southwest Florida (Figure 6.6). This highly diverse marine vegetated ecosystem consists of mangroves, seagrass beds, coral reefs, and marshes (Griffith et al. 2002) (Figure 6.80). Seagrass habitat has been cited as the largest in the northern hemisphere and is dominated by species such as *Thalassia testudinum* (turtlegrass), *Halodule wrightii* (shoalweed), and *Syringodium filiforme* (manatee grass) (Yarbro and Carlson 2011). Mangroves that dominate intertidal wetlands in the region consist of four primary tree species: *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), and *Conocarpus erectus* (buttonwood). The southwestern Florida coast is characterized by a subtropical climate, modulated by the Gulf Stream, cold fronts, and hurricanes.

The Ten Thousand Islands area north of Florida Bay to Marco Island is characterized by numerous mangrove-covered islands (Figures 6.80 and 6.81). Beaches generally are absent along the southwestern coast with only a few local accumulations of shell and skeletal debris (Davis 2011b). The coast is quite stable due to an abundance of mangrove vegetation. Although hurricanes are common in this area, their impact has had little influence on coastal geomorphology (Davis 1995).

Ecosystem changes for the Southern Coast and Islands ecoregion have been documented using core data and information on historical hydrologic changes in the Everglades. Willard et al. (2001) and Wingard et al. (2007) documented long-term increases in salinity in Florida Bay and the Ten Thousand Islands area due to a combination of sea-level rise and hydrologic changes in the Everglades. These hydrologic changes produced a shift in wetland habitat from brackish/fresh-water marshes to dwarf mangrove stands. Although historical shoreline/wetland changes are primarily related to storm events and human activities (Section 6.3.4.1), Davis (2011a) suggests minimal long-term changes may be expected due to the stability of carbonate substrate in this relatively low-energy coastal region.



Figure 6.81. Image from Google Earth illustrating the Ten Thousand Islands area of southwest Florida. Map data: Google, U.S. Geological Survey.

6.4.2.2 Northern Gulf of Mexico Marine Ecoregion

The Northern GoM Marine Ecoregion is the most geographically expansive of the GoM ecoregions and extends from southern Keewaydin Island on the west coast of Florida to just south of Barra del Tordo in the State of Tamaulipas, Mexico, and includes coastal areas of Alabama, Mississippi, Louisiana, and Texas (Figure 6.2). Climate within this region is temperate to subtropical, with relatively distinct seasonal patterns in temperature resulting from temperate cold fronts during the winter and warm tropical currents in the summer. The region generally has high nutrient loading and includes biotic communities such as mangroves, salt marshes, and seagrasses; coastal lagoons and estuaries; and low river basins. It contains approximately 60 % of tidal marshes in the United States, freshwater inputs from 37 major rivers, and numerous nursery habitats for fish (Wilkinson et al. 2009).

6.4.2.2.1 Southwestern Florida Flatwoods Terrestrial Ecoregion

The barrier-inlet system along the central west Florida coast consists of approximately 27 barrier islands and inlets extending from Keewaydin Island (just south of Naples) to Anclote Key, just northwest of Tampa (Figure 6.82). Coastal habitats in this subtropical area include seagrasses, mangroves, and barrier islands and beaches. This ecoregion is underlain by a carbonate limestone on which sand and silts support large seagrass beds, dominated by *Thalassia*, that are key nursery, spawning, and feeding habitats for a variety of fish species (Zieman and Zieman 1989). Groundwater discharge is a notable source of freshwater and nutrients in the area. Mangroves are important intertidal wetland plants, but lose dominance at higher latitudes because of their relatively low cold tolerance (Mendelssohn and McKee 2000).



Figure 6.82. Coastal habitats for and adjacent to the Southwestern Florida Flatwoods Terrestrial Ecoregion (data from Beck et al. 2000; FFWCC-FWRI 2003; Giri et al. 2011a). Image credit: Microsoft Bing Maps Aerial.

Extensive barrier islands and the replacement of mangroves with herbaceous salt marshes characterize the northern reaches of this ecoregion.

Davis (2011b) refers to this area as the most morphologically complex barrier system in the world. The barrier islands range from 1 kilometer to tens of kilometers long, and inlets include a wide variety of sizes and morphologies under natural and engineered conditions. This coastal segment is classified as microtidal (range <2 m [6.6 ft]) with a mean annual wave height of less than 0.5 m (1.6 ft). Furthermore, this part of the central West Florida coast generally has avoided significant hurricane landfall compared with the northern Gulf.

Tidal inlets associated with the central West Florida barrier island system show a wide variety of scales and morphologies. Tide-dominated inlets tend to be stable and have existed throughout the historical record. Mixed-energy inlets respond to a general balance in tide and



Figure 6.83. Coastal habitats for and adjacent to the Big Bend Coastal Marsh Terrestrial Ecoregion (data from Beck et al. 2000; FFWCC-FWRI 2003; Giri et al. 2011a). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS World Imagery (inset); FL Department of Environmental Protection, http://www.dep.state.fl.us/coastal/images2/spartina_marsh.jpg (inset photo).

wave energy, whereas wave-dominated inlets typically are unstable and tend to close due to the dominance of wave transport energy relative to the flushing capabilities of tidal flow. Overall, tidal prism and the volume of water that flows into and out of backbarrier estuaries/bays during each tidal cycle control the scale and stability of inlets. Flood tidal shoals are the largest sand bodies extending into estuaries in this region, often formed during hurricanes through breaching of barrier islands (Davis 2011b).

6.4.2.2.2 Big Bend Coastal Marsh Terrestrial Ecoregion

North of Anclote Key, barrier islands cease to exist as sediment supply to the coast is negligible and coastal habitats are characterized by open-water marsh (primarily *Juncus*) in a tide-dominated environment (Figure 6.6). Coastal marshes experience spring tides up to 1.3 m (4.3 ft) and average wave heights of <0.3 m (1 ft). Because the coast is sediment starved, extensive limestone outcrops exist in subtidal and supratidal environments. As such, the Big Bend region of Florida has extensive seagrass beds, some extending into relatively deep water >12 m (39 ft) (Figure 6.83). Open-coast marshes that characterize the area can extend several kilometers inland, covering a karstic limestone surface along the coast (Hine et al. 1988). According to Davis (2011a), the Big Bend coastal area is similar to an open-water estuary with large freshwater discharge from springs that form the headwaters of rivers that empty into the Gulf. Linear oyster reefs that are fixed on the Tertiary limestone that crops out at the surface dominate the shallow inner shelf in this region. The presence of open-coast marshes indicates the degree to which wave and current processes rework coastal deposits. The broad,

shallow shelf provides significant protection to coastal environments, and storms have had only minor impacts on the area, primarily by adding sediment to the marsh surface (Goodbred et al. 1998; Davis 2011a).

6.4.2.2.3 Gulf Barrier Islands and Coastal Marshes Terrestrial Ecoregion

Barrier islands and marshes of the northeastern GoM extend from the Apalachicola River Delta west to the Pearl River (Mississippi) (Figure 6.6). Coastal depositional systems include barrier islands, sand spits, mainland beaches, and backbarrier marshes. Inlets of various sizes separate coastal strand environments along this 550 km (342 mi) stretch of coast (Figure 6.84). A variety of shoreline orientations and ranges in shoreface slopes produce a complex pattern of longshore sediment transport associated with wave refraction patterns. However, a general east-west net transport direction is dominant along the coast (Section 6.3.4.2.3; Byrnes et al. 2010; Byrnes et al. 2012; Morang et al. 2012). Coastal sediments are terrigenous and derived from mainland and shoreface erosion under rising sea level.

Coastal habitats of this ecoregion are characterized by a series of barrier islands and beaches that are separated from narrow mainland salt marshes by elongate sounds (Figure 6.84). Barrier islands and beaches are well developed with relatively large dune fields on which *Uniola paniculata* (sea oats) often dominates. Mainland salt marshes are generally infrequently flooded and *Juncus roemerianus* (black needlerush) is the primary salt marsh plant species, as is the case for the salt marshes of the Florida panhandle. Only one species of mangrove is



Figure 6.84. Coastal habitats for and adjacent to Gulf Barrier Islands and Coastal Marshes Terrestrial Ecoregion (data from Beck et al. 2000; FFWCC-FWRI 2003; Giri et al. 2011a; NOAA et al. 2004; NOAA et al. 2007; NOAA and DHS 2009). Image credits: Microsoft Bing Maps Aerial (main, inset); ArcGIS World Imagery (overview).

present, *Avicennia germinans*, which is the most cold tolerant of the four new world mangrove species commonly found in south Florida (Sherrod and McMillan 1985). The northern limit of the black mangrove in the GoM occurs on Horn Island, Mississippi. Seagrass beds are also limited in this ecoregion because of a lack of clarity in coastal waters.

Along the eastern boundary of this region, barrier islands fringe the Apalachicola Delta, a large promontory that abruptly changes shoreline orientation west of the Big Bend. As such, the delta marks the western limit of the low wave-energy coast of the Florida Gulf Peninsula. Between Alligator Point, just west of Ochlockonee Bay on the eastern margin of the Apalachicola Delta, and Pensacola Pass (about 330 km [205 mi]), white sandy barrier island and mainland beaches characterize what is known as the Florida Panhandle coast (Davis 2011b). Inland bays and lagoons provide estuarine habitat for herbaceous marshes and seagrass meadows. The inner shelf adjacent to the Apalachicola Delta coast is broad and gently sloping; however, the shoreface west of this area is steeper and wider. Consequently, wave energy at this coast generally is higher. Beach erosion along southeast facing shorelines often is coupled with deposition along the southwest margin of barrier beaches (Donoghue et al. 1990). Littoral sediment transport along the coast and deposition and erosion patterns in bays are controlled by storm processes associated with tropical cyclone and winter cold front passage (Stone et al. 2004).

The western extension of the Florida Panhandle coast encompasses the Morgan Peninsula coast between Pensacola Pass and Mobile Bay entrance. Morgan Peninsula, the most prominent geologic feature along this 75 km (47 mi) coastal segment, forms the southeastern terminus of Mobile Bay and consists of an extensive beach backed by parallel dunes and numerous sub-parallel beach ridges, formed as a result of west-directed net longshore sediment transport processes (Bearden and Hummell 1990; Stone et al. 1992). The eastern Alabama coast is similar to Florida Panhandle coast where sandy barrier beaches are close to but separated from the mainland by lagoons.

Seafloor topography and Holocene sediment distribution on the Alabama shelf reflect a combination of processes, including regression during the late-Pleistocene and reworking of the exposed shelf surface by ancient fluvial systems, and reworking of the exposed shelf surface by coastal processes during the subsequent Holocene rise in sea level (Parker et al. 1997). Redistribution of sediment by waves and currents during transgression partially or totally destroyed geomorphic features associated with Pleistocene fluvial environments. Concurrently, these same processes formed modern shelf deposits as subaerial coastal features became submerged and reworked during relative rising sea level. As such, much of the shelf offshore Alabama and the Florida Panhandle is sand (Byrnes et al. 2010).

Along the western quarter of the Gulf Barrier Islands and Coastal Marshes Terrestrial Ecoregion (Figure 6.84), adjacent to the eastern margin of the Mississippi River delta (i.e., the St. Bernard delta complex), resides Mississippi Sound and barrier island coastal habitat. The barrier islands extend approximately 100 km (62 mi) from Dauphin Island (AL) to Cat Island (MS) and provide the first line of protection to mainland Mississippi and Alabama from storm waves and surge. The islands are composed of beach sand that is derived from updrift beaches east of Mobile Pass and from ebb-tidal shoals at the entrance. Four tidal passes between the islands promote exchange of sediment and water between marine waters of the GoM and brackish waters of Mississippi Sound. Tidal passes also interrupt the flow of littoral sand to the west from Mobile Pass ebb-tidal shoals and Dauphin Island.

According to Otvos and Carter (2008) and Otvos and Giardino (2004), the Mississippi Sound barrier islands formed during a deceleration in sea-level rise approximately 5,700 to 5,000 years ago. At that time, the core of Dauphin Island at its eastern end was the only subaerial feature in the location of the modern barrier island system through which predominant west-directed littoral sand transport from the Florida panhandle via Mobile Pass ebb-tidal



Figure 6.85. Barrier Island and St. Bernard delta lobe development as envisioned by Otvos and Giardino (2004) (reprinted with permission from Elsevier).

shoals could transit and deposit as elongate sand spits and barrier islands. The laterally prograding barrier island system originally extended west to the Mississippi mainland shoreline near the Pearl River, marking the seaward limit of subaerial deposition and the formation of Mississippi Sound.

Beginning approximately 3,500 years ago, the Mississippi River flowed east of New Orleans toward Mississippi Sound, creating the St. Bernard delta complex (Figure 6.85) (Otvos and Giardino 2004). Delta deposition extended over the western end of the Mississippi barrier island system, west of Cat Island. By about 2,400 years ago, fluvial sediment from the expanding St. Bernard delta created shoals as far west as Ship Island (Otvos 1979), changing

wave propagation patterns and diminishing the supply of west-directed littoral sand to Cat Island. With changing wave patterns and reduced sand supply from the east, the eastern end of Cat Island began to erode, resulting in beach sand transport perpendicular to original island orientation (Rucker and Snowden 1989; Otvos and Giardino 2004). Persistent sand transport from the east has been successful at maintaining island configuration relative to rising sea level for much of the barrier system; however, reduced sand transport toward Ship Island has resulted in increased island erosion and segmentation from tropical cyclones (Rucker and Snowden 1989).

Mississippi Sound is considered a microtidal estuary because its diurnal tide range is only about 0.5 m (1.6 ft). The Sound is relatively shallow and elongate (east-west) with an approximate surface area of 2,000 km² (772 mi²) (Kjerfve 1986) and a tidal prism of about 1.1×10^9 m³ (1.4×10^9 cy). Although tidal currents account for at least 50 % of flow variance, the Sound responds rapidly to meteorological forcing, as evidenced by subtidal sea-level variations of up to 1 m (3.3 ft) and persistent net currents in the tidal passes (Kjerfve 1986). The relatively shallow and large area of the Sound creates strong currents in tidal passes between the barrier islands, ranging from 0.5 to 1.0 m/s (1.6 to 3.3 ft/s) and 1.8 to 3.5 m/s (5.9 to 11.5 ft/s) on flood and ebb tides, respectively. Overall, circulation within Mississippi Sound is weak and variable, and the estuary is vertically well mixed.

Barrier islands protecting Mississippi Sound experience a low-energy wave climate. Littoral sand transport along the islands is predominantly from east to west in response to prevailing winds and waves from the southeast. Reversals in longshore transport occur at the eastern ends of the islands but their impact on net sediment transport is localized (Byrnes et al. 2012). Although beach erosion and washover deposition are processes that have influenced island changes, the dominant mechanism by which sand is redistributed along the barrier islands and in the passes is by longshore currents generated by wave approach from the southeast (primarily storms).

6.4.2.2.4 Deltaic Coastal Marshes and Barrier Islands Terrestrial Ecoregion

The Mississippi River Delta Plain consists of large expanses of coastal wetlands within a geomorphologic framework of lakes, estuaries, and natural levee systems associated with active and abandoned distributaries (Figure 6.86). Locally, barrier island systems form the seaward edge of the delta plain, constituting an important component of the delta-plain ecosystem due to the habitat they provide, their storm-surge buffering capabilities, and their role in regulating marine to estuarine gradients (Kulp et al. 2005). Modern depositional models describe the Holocene history of the Mississippi River Delta Plain as a dynamic, multistage process that reflects the collective influence of changes in patterns of local relative sea-level rise and fluvial-sediment dispersal (Penland et al. 1988; Boyd et al. 1989). Sedimentary deposits of the Holocene delta plain consist of fine-grained sediment deposited within a variety of fluvial, deltaic, and coastal depositional environments. These sedimentary deposits formed in response to deltaic progradation and abandonment, resulting in an assemblage of overlapping regressive and transgressive units that consist of unconsolidated fluvial sediment (Kulp et al. 2005).

The present Mississippi River delta consists of two active delta complexes (Balize and Atchafalaya) and several inactive delta complexes (Figure 6.87). A delta complex encompasses the sedimentary deposits from a sequence of smaller delta lobes that are linked to a common distributary (Kulp et al. 2005). According to Roberts (1997), deposition within a delta complex generally occurs for approximately 1,000 to 2,000 years. During delta expansion, wetlands fringing the delta front and distributary network grow laterally, creating wetland habitat dominated by fluvial distributaries and bays adjacent to active distributary networks. Aerial



Figure 6.86. Coastal habitats for the Deltaic Coastal Marshes and Barrier Islands Terrestrial Ecoregion (data from Beck et al. 2000; Giri et al. 2011a; NOAA et al. 2004; NOAA and DHS 2009). Image credit: Microsoft Bing Maps Aerial.



Figure 6.87. Distribution and chronology of Holocene Mississippi River delta complexes (from Kulp et al. 2005; used with permission of the Journal of Coastal Research).

expansion of a delta complex produces elongated distributary networks, which lead to a reduction in hydraulic gradient and eventual abandonment of the delta for a shorter, more hydraulically efficient route. Distributary switching and delta abandonment are natural processes by which marine inundation and delta erosion commence as a result of decreased



Figure 6.88. Conceptual model of delta lobe evolution. Distributary abandonment results in erosion and reworking of the delta lobe, ultimately forming an inner-shelf, sand-rich shoal (from Penland et al. 1992).

sediment supply and substrate compaction (Figure 6.88) (Roberts 1997; Williams et al. 2011). At abandoned deltaic headlands, relative sea-level rise results in erosional headland retreat as marine processes rework the shoreline. Sediment is dispersed laterally by waves and contributes to construction and nourishment of flanking beaches, beach ridges, and marginal deltaic deposits.

As a result of high subsidence rates and diminished sediment supply to the coast from a controlled river system, the Mississippi-Atchafalaya River Deltaic and Chenier Plains experience the highest rates of laterally continuous shoreline retreat and land loss in the GoM. While land loss associated with shoreline change along the Gulf shore and around the margins of large coastal bays is extreme, loss of the interior wetlands is even more extensive due to submergence and destruction of the Mississippi River Delta Plain (Penland et al. 1990). The result has been substantial land loss on the delta plain since the 1930s (Figure 6.89).

6.4.2.2.5 Texas-Louisiana Coastal Marshes Terrestrial Ecoregion

The Texas-Louisiana Coastal Marshes Terrestrial Ecoregion encompasses marginal deltaic depositional environments indirectly influenced by high levels of riverine input from the Mississippi-Atchafalaya River system. The region includes coastal habitats of southeastern Texas and southwestern Louisiana, an area known as the Chenier Plain (Figure 6.6). Coastal waters in this ecoregion generally are variable in salinity, and water clarity is low because of sediment load. Bottom sediments tend to be fine clays and muds, and conditions are ideal for growth of marshes and oyster reefs (Beck et al. 2000) (Figure 6.90).

The Chenier Plain extends approximately 200 km (124 mi) from Southwest Pass at Vermilion Bay to eastern Texas (Figure 6.91). This Late-Holocene, marginal-deltaic environment is up to 30 km (19 mi) wide and is composed primarily of mud deposits that are capped by marsh and interspersed with thin sand- and shell-rich ridges known as cheniers. In the Chenier Plain, oak trees line these ridges, which are better drained and topographically higher than the surrounding marsh.



Figure 6.89. Wetland change on the Louisiana deltaic plain, 1932 to 2010 (data from Couvillion et al. 2011). Image credit: ArcGIS World Imagery.



Figure 6.90. Coastal habitats for the Texas-Louisiana Coastal Marshes Terrestrial Ecoregion (data from Beck et al. 2000; BEG 1995; Giri et al. 2011a; NOAA et al. 2004). Image credit: Microsoft Bing Maps Aerial. Inset photo: White 2011, used with permission.

The Chenier Plain evolved during the Holocene as a series of progradational mudflats that were intermittently reworked into sandy or shelly ridges to form the modern Chenier Plain physiography (Gould and McFarlan 1959; Byrne et al. 1959; McBride et al. 2007). Numerous cycles of deposition and erosion created alternating ridges separated by marshlands. Sediment of the Chenier Plain has been primarily supplied by longshore transport of fine-grained



Figure 6.91. General geomorphic characteristics of the Mississippi River Chenier Plain (modified from McBride et al. 2007).

Mississippi River sediments (Hovt 1969). These sediments, transported by westward-flowing nearshore currents, were eventually deposited along the Chenier shoreline as mudflats that built seaward. When deposition ceased or declined because of a shift in Mississippi River delta depocenters in the east, the previously deposited mud-rich sediment was reworked by coastal processes, concentrating coarse-grained sediments and forming shore-parallel ridges (Penland and Suter 1989). Renewed mudflat progradation, stemming from the introduction of new sediment by Mississippi River distributaries, resulted in isolation of these ridges by accretion of new material on the existing shoreline. Thus, repeated seaward growth and retreat along the Chenier Plain is a consequence of deltaic deposition farther east and the periodic cessation of sediment supply to the Chenier Plain as deltaic depocenters become abandoned and Chenier coast marine processes dominate. Currently, the Atchafalaya River is supplying the Chenier Plain with fine sediments by westward-directed longshore transport (Kineke et al. 2006). Distinct ridges, most of which represent relict shoreline positions, are interspersed in the mud-dominated coastal depositional system. Ridges typically are oriented shore-parallel to sub-parallel, are approximately 10 to 90 km (6.2 to 56.0 mi) long, 1 to 5 m (3.3 to 16.4 ft) thick, and 1 km (0.6 mi) wide (McBride et al. 2007).

Marginal deltaic coastal habitats evolved in a low-energy, microtidal, storm-dominated environment that experiences episodic sediment supply. Mean spring tide is mainly diurnal, ranging from 0.6 to 0.8 m (2.0 to 2.6 ft). Dominant nearshore currents are to the west and are controlled by winds and waves that are predominantly from the southeast (McBride et al. 2007). According to tide gauge data, the average rate of relative sea level rise for the Chenier Plain is 4.15 mm/year (0.16 in/year) (Figure 6.25), most of which can be attributed to compactional subsidence of Holocene sediment.

The upper Texas coast extends about 141 km (88 mi) from Sabine Pass to San Luis Pass. From a geologic perspective, Galveston Island is included with barrier island deposits south of Galveston Bay. Beach and marsh deposits east of Galveston Bay are more closely aligned with Chenier Plain deposits of southwestern Louisiana. Like southwestern Louisiana, the eastern portion of the upper Texas coast is characterized by a modern strandplain-chenier system with well-preserved chenier ridges with marsh-filled swales adjacent to Sabine Pass. These deposits reflect late-Holocene sedimentation associated with marginal deltaic environments of the Mississippi/Atchafalaya River system (McBride et al. 2007). Swales between relic chenier ridges are the sites of extensive brackish marshes. The strandplain-chenier system has gradually evolved through cycles of deposition, erosion, and compaction. The strandplain extends southeast along the Gulf shore toward High Island as thin sandy beach deposits perched on marsh. High Island is a salt dome near the Gulf shoreline with elevations exceeding 7.5 m (24.6 ft).

6.4.2.2.6 Mid-Coast Barrier Islands and Coastal Marshes Terrestrial Ecoregion

This central east Texas terrestrial ecoregion extends approximately 300 km (186 mi) southwest from the Bolivar Peninsula to north Padre Island (Figures 6.6 and 6.92). Bolivar Peninsula, to the northeast of Bolivar Roads (Houston Ship Channel Entrance), is a sandy beach and dune system that has accretionary topography and is characterized by two large relict flood-tidal shoal/washover fan deposits extending into East Bay. These fans are the sites of extensive salt and brackish marshes. Adjacent to Bolivar Roads, Galveston Island is a modern progradational barrier island with well-preserved ridge-and-swale topography (Bernard et al. 1970). Relict beach ridges and intervening swales have an orientation roughly parallel to the present island shoreline marked by the Gulf beach. Bayward of the ridge and swale features on Galveston Island are numerous truncated channels, the remnants of past tidal inlets and



Figure 6.92. Coastal habitats for the Mid-Coast Barrier Islands and Coastal Marshes Terrestrial Ecoregion (data from Beck et al. 2000; BEG 1995; Giri et al. 2011a). Image credit: Microsoft Bing Maps Aerial.

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storm washover channels along with extensive marshes. Galveston Island is relatively wide along its northeastern half and tapers and narrows toward San Luis Pass to the southwest (White et al. 2004b). Landward of Galveston Island is Galveston Bay. Although impacted by human activities including the Houston Ship Channel and extensive industrial and petrochemical activities, Galveston Bay has extensive intertidal wetlands dominated by *Spartina alterniflora*. Seagrasses are of lesser importance in this bay. South of Galveston Bay, the barrier strand continues with a series of backbarrier lagoons and, in some cases, adjacent bays. Coastal habitats including salt marshes, mangroves, seagrasses, tidal flats, and barrier beaches and associated dunes and swales are present (Figure 6.92). Although riverine freshwater input has been altered in many of these areas, hypersaline conditions do not normally occur because of sufficient rainfall. However, this situation progressively changes approaching Laguna Madre.

The segment of coast between San Luis Pass and Pass Cavallo encompasses the headland of the Brazos and Colorado River deltas with flanking barrier peninsulas called Follets Island and Matagorda Peninsula (about 143 km [89 mi] long). Primary natural geomorphic features along the shoreline include the Brazos and Colorado deltaic headlands, consisting of muddy and sandy sediments deposited by the Brazos and Colorado Rivers and overlain by a discontinuous, thin veneer of sandy beach deposits; a narrow, sandy peninsula extending northeastward from the Brazos headland toward San Luis Pass; and a narrow, sandy peninsula extending southwestward from the Colorado headland toward Pass Cavallo (Paine et al. 2011).

Sediments eroded by waves reworking deltaic headland deposits supplied sandy sediment to the flanking barrier peninsulas. Furthermore, the Brazos and Colorado Rivers supply sediment to the coast from their drainage basins. The drainage basin of the Brazos River encompasses approximately 116,000 km² (44,800 mi²) of Cretaceous, Miocene, and Pleistocene sedimentary deposits, but the river capacity for carrying sediment to the coast during major floods has been reduced by completion of several dams and reservoirs between 1941 and 1969 (Paine et al. 2011). The drainage basin of the Colorado River is slightly smaller (103,000 km² [40,000 mi²]), and nine dams completed in the upper and central basin between 1937 and 1990 have reduced its sediment-carrying capacity.

Further south, between Pass Cavallo and Packery Channel, much of the coast illustrates net shoreline recession. This section of shore includes Matagorda Island, San Jose Island, and Mustang Island. These sand-rich islands are characterized by broad sandy beaches and dune systems that reflect the position of the islands within a longshore current convergence zone between the Brazos/Colorado and Rio Grande deltaic headlands (White et al. 2002). Although tidal inlets separate these islands, no rivers supply water/sediment directly to the Gulf. Instead, rivers provide freshwater and sediment to the headwaters of Corpus Christi Bay, Copano Bay, and San Antonio Bay.

6.4.2.2.7 Laguna Madre Barrier Islands and Coastal Marshes Terrestrial Ecoregion

This ecoregion encompasses parts of Texas and Mexico included in the Western Gulf Coastal Plain Terrestrial Ecoregion and the Texas Estuarine, Laguna Madre Estuarine, and Western Gulf Neritic Marine Ecoregions (see Figures 6.6 and 6.3, respectively). The southern Texas coast comprises about 183 km (114 mi) of beach where the principal natural geomorphic feature is Padre Island, a long Holocene barrier island system with a well-developed dune system (Figure 6.93) that extends from Packery Channel near Corpus Christi Bay south to a narrow peninsula at Brazos Santiago Pass (White et al. 2007) (Figure 6.94). Padre Island developed initially as a spit extending from the relict Rio Grande Holocene deltaic system that has been eroding for hundreds of years. The Rio Grande enters the GoM along the border with Mexico and has created a large fluvial-deltaic headland that forms the southern boundary of a regional longshore current cell bound on the north by the Brazos-Colorado headland.



Figure 6.93. Generalized barrier island profile for Padre Island illustrating prominent features (modified after Paine et al. 2011).

The Rio Grande has a large drainage basin (558,400 km² [215,600 mi²]) that extends into Mexico, New Mexico, and Colorado, but dams constructed in the middle and lower parts of the basin, combined with extensive irrigation use of Rio Grande water on the coastal plain, have reduced sediment delivered to the coast (Paine et al. 2011). Most of Padre Island is undeveloped, except for the town of South Padre Island. Engineering structures for this stretch of coast include the jetties and channels at Brazos Santiago Pass and the shallower Mansfield Channel.

The Laguna Madre of Texas and Tamaulipas (Mexico) is the only set of coastal, hypersaline lagoons on the North American continent. Extending along approximately 485 km (301 mi) of shoreline in south Texas and northeastern Mexico, the lagoons are separated by 85 km (53 mi) of Rio Grande Delta. The Laguna Madre system lacks significant precipitation, riverine input, and tidal flux, and in combination with high evapotranspiration rates and shallow depths, results in a classic hypersaline lagoon. The Texas lagoon is about 190 km (118 mi) long and the Mexico lagoon is about 210 km (130 mi) long, and each contains extensive tidal flats (Figure 6.94). Adjacent coastal habitats reflect this arid and hypersaline environment. Because the climate is harsh north and south of the Rio Grande, many bayshores are fringed by sparse vegetation and open sand flats, and barrier islands are characterized by sparsely vegetated dune fields. Extreme salinities have been moderated in recent decades due to channel dredging and the cutting of passes in the Texas Laguna Madre (Beck et al. 2000). The lagoons are protected on the east by barrier islands and peninsulas, and on the mainland side by large cattle ranches, farmlands, and the brush country. Laguna Madre also has the most extensive wind-tidal flats and clay dunes in North America (Beck et al. 2000).

The coast from Brazos Island State Park in Texas to Barra del Ostión in Mexico is dominated by deltaic sediment from the Rio Grande. This area also is referred to as the Mexican Laguna Madre region, where riverine sediment is dominant along the mainland coast of the lagoon and reworking of deltaic deposits by coastal waves and currents along the GoM provides vast quantities of sand to barrier beaches along the Tamaulipas coast (Moreno-Casasola 2007). Furthermore, the Mexican Laguna Madre in Tamaulipas consists of extensive barren tidal flats from which salt is commercially collected (Tunnell 2002a). Moving south from the Rio Grande, beach widths generally decrease and beach slopes increase. Terrigenous particle size is smaller on gentle slopes and larger on steep slopes. The predominant sediment size along Tamaulipas beaches is fine-grained sand, and sand distribution tends to be well sorted (Carranza-Edwards et al. 2007). Beaches in this region tend to be erosional (Figure 6.95).

The Laguna Madre is a region of high humidity but low precipitation, and consequently, emergent salt marshes fringing the Laguna Madre are dominated by succulent halophytes (salt loving plants) that have very high salt tolerances. Taxa such as *Salicornia* (glasswort), *Batis* (saltwort), *Distichlis* (saltgrass), *Borrichia* (sea oxe-eye), and *Limonium* (sea lavender), all common salt pan inhabitants, dominate the hypersaline wetlands of the Laguna Madre. Black

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Figure 6.94. Coastal habitats for the Laguna Madre Barrier Islands and Coastal Marshes Terrestrial Ecoregion (data from Beck et al. 2000; BEG 2000; Giri et al. 2011a; Green and Short 2003). Image credit: Microsoft Bing Maps Aerial.

mangroves dwarfed by the hypersaline conditions also occur. In addition to hypersaline marshes, extensive fringing tidal flats, which are virtually unvegetated except for cyanobacteria algal mats, are common in the Laguna Madre. Interestingly, seagrass beds are much more abundant in the Laguna Madre than in other Texas bays due to clear and shallow waters of the former, resulting from the absence of riverine sediment input and the presence of a sandy lagoonal substrate. Barrier islands in this region are relatively simple compared to those on the Atlantic Coast (Judd 2002) and lack the multi-layer shrub-tree canopy structure of barrier islands in much of northern and eastern GoM. For example, virtually all plant species on southern Padre Island are herbaceous, although woody black mangroves occur sporadically. *Opuntia* spp. (prickly pear cactus) and *Prosopis glandulosa* (mesquite) also occur as individuals



Figure 6.95. Distribution of coastal types and geological sediment trends for the southern GoM coast of Mexico (modified from Moreno-Casasola 2007; basemap from French and Schenk, 2005).

on these barrier strands. The live oak, *Quercus virginiana*, which is considered the climax habitat of barrier islands in the rest of the GoM, is absent except for a small stand on the Laguna Madre side of northern Padre Island (Judd 2002).

6.4.2.3 Southern Gulf of Mexico Marine Ecoregion

The Southern GoM Marine Ecoregion extends from approximately Barra del Tordo (about 40 km [25 mi] south of the terminus of the Laguna Madre Ecoregion) south and then east along the southern GoM shoreline to the northeastern tip of the Yucatán Peninsula (Figure 6.2), a shoreline distance of approximately 1,700 km (1,056 mi). This ecoregion includes the shorelines of Veracruz, Tabasco, Campeche, and Yucatán. Shorelines encompass a diverse suite of coastal habitats that include barrier beaches and islands, deltaic systems, coastal lagoons, estuaries, mangroves, seagrass beds, and coral reefs. Although climate in this area is primarily tropical, low-pressure cold fronts (locally called nortes) episodically traverse the region during autumn, winter, and spring, producing cooler conditions. High aquatic productivity in this region is thought due to wind-driven nutrient upwelling and freshwater input to the Gulf from the Usumacinta-Grijalva River, the second largest river system in the GoM (Table 6.1).



Figure 6.96. Coastal habitats for the Veracruz Neritic Marine Ecoregion (data from Giri et al. 2011a; Green and Short 2003). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS World Imagery (inset).

6.4.2.3.1 Veracruz Neritic Marine Ecoregion

The northern boundary of the Veracruz Neritic Marine Ecoregion begins just south of Barra del Tordo, where the arid environment of Laguna Madre and the Rio Grande basin gives way to higher precipitation coastlines of the Veracruz barrier beaches (Britton and Morton 1989). Summer rainfall increases greatly, allowing a moderately diverse tropical flora to occur. Coastal topography of central Veracruz consists of fluvial and marine sediment draped around volcanic promontories (Psuty et al. 2008). Between Barra del Tordo and Tuxpan, the coast is composed of terrigenous clastic beaches that commonly form as barrier islands. The most extensive barrier island along this section of coast is Cabo Rojo, an island with extensive ridges and active dune fields, the highest of the western GoM (Figure 6.96). Rio Panuco is the primary source of sediment via southerly longshore transport leading to the development of Cabo Rojo

(Stapor 1971). The island protects Laguna de Tamaihua, where mangroves are common along the shoreline, and extends from Tampico to Tamaihua (about 120 km [75 mi]). Seagrass is present along the Gulf shoreline of Cabo Rojo and seaward of the beaches fronting Veracruz and Playa Salinas. Sand beaches are generally wide and accretionary, and dune elevations are several meters high along most of the island. North of Tampico to Barra del Tordo, low-profile barrier islands with relatively narrow beach widths protect shallow, narrow lagoons (Carranza-Edwards et al. 2007). Beaches are composed of terrigenous sand, and shell fragments are frequently present.

Beaches extending from Tuxpan to Playa Punta Delgada (50 km [31 mi] south of Nautla) are characterized as low, sandy mainland deposits that are relatively narrow, except for a 7-km (4.3-mi) section of coast north of the mouth of Rio Cazones (Veracruz), where volcanic outcrops intersect the coast. Dunes are absent in this area and beaches appear primarily erosional. Coastal habitat between Playa Punta Delgada and Playa Salinas is composed of bluffs and rocky points of volcanic origin, interspersed with small lagoons and narrow flood plains (Moreno-Casasola 2007). Sandy beaches are observed throughout this section of coast, and active dune fields are prominent north of Veracruz to Laguna de Farallón. Although less common, rocky headlands persist as far north as Playa Punta Delgada, interrupting littoral sand transport along beaches. The port of Veracruz occurs along this shoreline, but in a relatively low relief section. Most beaches within this ecoregion are undergoing erosion, as illustrated by active erosion or scarping of the primary dune ridge along the coast (Tanner 1975b).

6.4.2.3.2 Tabascan Neritic Marine Ecoregion

Tuxtlas Volcanic Coast. A prominent volcanic feature along the coastal portion of the Tabascan Neritic Marine Ecoregion in the State of Veracruz is an area known as Sierra de los Tuxtlas (Figure 6.97). The coastal area west of Tuxtlas is known as the Papaloapan region where an extensive sand barrier protects the Alvarado estuarine system (Figure 6.97) (Moreno-Casasola 2007). The 70 km (43 mi) stretch of coast between Playa Salinas and Punta Puntilla contains relatively wide sandy beaches with elevated dune fields that extend up to several kilometers inland. It is classified as a stable to accreting coast (Figure 6.95); however, Tanner (1975b) documented dune scarping by waves 2 to 3 km (1.2 to 1.9 mi) south of Alvarado Lagoon. The area between Punta Puntilla and Playa Linda (Los Tuxtlas region) is characterized by mixed abrasive-accumulative coastlines, alternating between projections of volcanic rocks and sandy beaches. Within this matrix of coastal geologic deposits are Laguna de Sontecomapan and a prominent sandy beach fronting the lagoon. Moving east along the coast from Laguna del Ostión, an abrupt change in shoreline orientation is encountered at the lagoon entrance to the Gulf, just west of Coatzacoalcos.

Tabascan Barrier Beaches and Marshes. The area east of Laguna del Ostión to Isla Aguada (Campeche) is within the Tabascan Neritic Marine Ecoregion where riverine input to the coast influences the sedimentological character of beaches. The non-calcareous deltaic shoreline extends along the southernmost arc of the GoM to a point just north of Laguna de Términos, where bedrock gradually changes to limestone of the Yucatán (Britton and Morton 1989). West of Laguna de Términos, coastal deposits are dominated by deltaic sedimentation from the Grijalva, Usumacinta, and San Pedro Rivers (Figure 6.95) (Thom 1967). As fluvial sediment accumulated at the Gulf shoreline, waves and currents redistributed sediment as ridges along the eastern Campeche and Tabascan coast. Modern sedimentation processes in the eastern portion of this area are dominated by fluvial input from the Grijalva and Usumacinta Rivers, the two longest rivers in Mexico, as they meander through mountainous uplands and lowlands of the Centla Marsh Biosphere Reserve. Beaches along the Tabascan lowlands are composed of light brown to gray, fine-grained clastic sediment of riverine origin, in contrast to


Figure 6.97. Coastal habitats for the Tabascan Neritic Marine Ecoregion (data from Giri et al., 2011a; Green and Short, 2003). Image credits: Microsoft Bing Maps Aerial (main); Ela 2016, distributed under a CC-BY 2.0 license (left inset); ArcGIS World Imagery (right inset).

the bright white calcareous sand of the Yucatán/Campeche area. Isla del Carmen, a barrier island fronting Laguna de Términos, is located in the transition area between limestone of the Yucatán Peninsula and alluvial terrain of deltaic deposits to the west (Figure 6.98) (Contreras-Espinosa and Castañeda-Lopez 2007). Beaches are wider and more elevated in the Isla Aguada transition area than beaches to the east, but carbonate sediment composition is very similar for both areas. Moreno-Casasola (2007) indicates that deposition in coastal beach and marsh habitat dominates Holocene sedimentation patterns along the coast (Figure 6.95).

Large wetland and barrier beach systems are associated with Tamiahua Lagoon, Alvarado Lagoon, Términos Lagoon, and lagoons adjacent to the west and north coasts of the Yucatán (Herrera-Silveira and Morales-Ojeda 2010). The most extensive mangrove stands in the GoM occur along the southern GoM shorelines (Dugan 1993; Thom 1967). Of all the coastal systems in the Southern GoM Ecoregion, Términos Lagoon (Laguna de Términos) has probably received the most scientific attention. Barrier islands and beaches, seagrass beds, mangroves, and even freshwater marshes are found in the Términos ecosystem (Figure 6.98), which occupies approximately 1,500 km² (580 mi²). These are some of the most productive natural habitats in the southern GoM.

Coastal processes along the Tabascan shore and beach-ridge plain are presently causing beach erosion along most of the coast. Tanner and Stapor (1971) recorded erosion along the seaward edge of the beach-ridge plain where younger beach ridges are truncated or scarped rather than tapered. Furthermore, trunks of dead trees were found awash in the surf zone as a



Figure 6.98. Habitats associated with Laguna de Términos in the Southern GoM Marine Ecoregion (data from Giri et al. 2011a; Rojas-Galaviz et al. 1992). Black arrows indicate water circulation pattern. Image credit: ArcGIS World Imagery.

result of beach erosion and shoreline recession. Finally, Tanner and Stapor (1971) found no evidence of beach ridges presently forming, implying that coastal erosion is a dominant process along the Tabascan shore. Although erosion along the beach-ridge plain does not appear extensive, beach ridges are eroding rather than growing.

6.4.2.3.3 Campeche/Yucatán Inner Neritic Marine Ecoregion

The Campeche-Yucatán carbonate beaches and mangroves are located adjacent to the Campeche-Yucatán Inner Neritic and Contoyan Neritic Marine Ecoregions (Figure 6.3). The coast extends approximately 700 km (435 mi) from Sabancuy, just north of Términos Lagoon, to the northeastern end of the Yucatán Peninsula near Holbox Lagoon (Figure 6.99). The Yucatán Peninsula is mainly a low-relief karst limestone platform. Few streams and no rivers drain the flat land or reach the sea, but rainfall filters through porous limestone and is stored underground (Britton and Morton 1989). Along the northern Yucatán coast, calcareous sand beach deposits provide low-relief coastal strands often fronting shallow and narrow lagoons (Meyer-Arendt 1993). Seagrass fronting Gulf beaches is dominant along the entire coast. Beaches can be quite narrow, and low-relief dunes are common. This area has limited mangrove habitat due to low precipitation and little terrestrial freshwater runoff. However, mangrove habitat can occur locally where lagoons persist, such as Rio Lagartos and Holbox Lagoons along the northeastern tip of the Yucatán peninsula and the coast between Campeche and Celestún (Britton and Morton 1989; Herrera-Silveira and Morales-Ojeda 2010).



Figure 6.99. Coastal habitats for the Campeche/Yucatán Inner Neritic Marine Ecoregion (data from Giri et al., 2011a; Green and Short, 2003). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS World Imagery (inset).

North of Sabancuy to Champotón, seagrass beds are common in nearshore areas and mangroves populate lagoonal areas landward of the beach. Calcareous sand beaches become wider in this area but relief remains low (Figure 6.99) (Moreno-Casasola 2007). A few limestone cliffs are present along the coast between Champotón and Campeche, but most limestone shores in this ecoregion are low, narrow platforms that have elevations approximately 2 m (6.6 ft) above the surrounding sand veneer (Britton and Morton 1989). Concrete bulkheads and other coastal structures protect the city of Campeche from flooding and erosion, and narrow calcareous sand and rock beaches are common south of the city. North of the city of Campeche to Celestún, the inner coast is dominated by mangroves and low-relief calcareous lagoonal deposits landward of the shoreline, and the nearshore area has extensive seagrass beds.

As orientation of the coast shifts from north-south to east-west, a large calcareous sand peninsula at Celestún marks the terminal location to dominant westward longshore sand transport adjacent to the primarily low-energy mangrove coast to the south (Figure 6.99). This location is nearly coincident with the boundary between the Mexican States of Yucatán and Campeche, and is characterized by low precipitation (less than 50 cm/year [1.6 ft/year]) and shallow lagoons, which during drought, evaporate and form salt pans. The lagoons become hypersaline when precipitation allows. In spite of these conditions, much of the region north of Celestún to Progreso consists of relatively extensive, low stature mangroves (Britton and Morton 1989; Herrera-Silveira and Morales-Ojeda 2010).



Figure 6.100. Coastal habitats for the Contoyan Neritic Marine Ecoregion (data from Giri et al., 2011a; IMaRS/USF et al., 2010; Green and Short, 2003). Image credits: Microsoft Bing Maps Aerial (main); Maas 2006, distributed under a CC-BY 2.0 license (inset).

6.4.2.4 Caribbean Sea Marine Ecoregion

6.4.2.4.1 Contoyan Neritic Marine Ecoregion

The Contoyan Neritic region (extends from the northern part of the Yucatán Peninsula adjacent to Holbox Lagoon to Cancun; named after Isla Contoy) along the northeastern margin of the Yucatán Peninsula is characterized by coral reefs, seagrass meadows, and mangrove forests (Figure 6.100). Coralline beaches are narrow and dunes are low and not very extensive due to the presence of thick mangrove wetlands (Moreno-Casasola 2007). Lagoons in the region are shallow and often contain extensive seagrass beds and mangrove habitat. Low annual rainfall combined with severe dryness has eliminated rivers from the landscape. As such, freshwater necessary for productive mangrove ecosystems comes from springs (groundwater). Figure 6.95 illustrates that the barrier beach shoreline along the northern Yucatán Peninsula is net erosional, but beaches along the northeast margin of the Yucatán are net depositional, primarily due to longshore sedimentation processes (Moreno-Casasola 2007).

6.4.2.5 Greater Antilles Marine Ecoregion

Although Cuba was not specifically classified by Wilkinson et al. (2009), a quite comprehensive classification of marine ecoregions by Spalding et al. (2007) placed Cuba in their Greater Antilles Marine Ecoregion. The Cuban archipelago is typically Caribbean with regard to its marine ecosystems (González-Sansón and Aguilar-Betancourt 2007), composed primarily of small islands, mangroves, coral reefs, and seagrasses (Figure 6.101). Much of the underlying substrate for coastal habitats in this ecoregion is mixed calcium carbonate sands over which organic plant materials create mangrove swamps. The nearshore subtidal seafloor generally



Figure 6.101. Coastal habitats for northwestern Cuba (data from Giri et al., 2011a; IMaRS/USF et al., 2010; Green and Short, 2003; Sullivan-Sealey and Bustamante, 1999). Image credits: Microsoft Bing Maps Aerial (main); ArcGIS World Imagery (bottom and upper right insets); Ji-Elle 2015, distributed under a CC-BY 2.0 license (left inset).

consists of unconsolidated sediment, either devoid of vegetation or forming large seagrass meadows dominated by *Thalassia testudinum* (turtle grass) or rocky bottom with extensive corals. Mangroves (*Rhizophora mangle, Avicennia germinans, Laguncularia racemosa*, and *Conocarpus erectus*) also are prevalent in protected, intertidal habitats along the northwestern Cuban shoreline (Figure 6.101) (Green and Short 2003; Sullivan-Sealey and Bustamante 1999). The Greater Antilles Marine Ecoregion has a wet-tropical climate characterized by a rainy season (May to October) and a dry season (January to March), interrupted by random, large-scale disturbances, primarily hurricanes and tropical storms. Similar to the Southern GoM Ecoregion, the northwestern Cuban coast is subject to nortes that punctuate the dry season. Predominant winds blow from the east and northeast.

Sullivan-Sealey and Bustamante (1999) describe four depositional systems encompassing the northwestern and southwestern Cuban coast. The Western High Energy Rocky Shore/ Fringing Reef Coastal System faces Yucatán Channel, where water flowing from the Caribbean Basin funnels to the eastern GoM and the Florida Straits, forming the Loop Current in the GoM (Figure 6.101). The coastline to the south is mostly rocky with long sandy beaches facing a narrow shelf that drops steeply to the southern entrance of the Yucatán Channel (Sullivan-Sealey and Bustamante 1999). Reefs fringe the entire edge of the shelf (Figure 6.101). Beaches along most of the western coast of Cuba are relatively stable due to the presence of offshore reefs to dissipate wave energy. The Northwestern Mixed Mangrove-Reef-Seagrass Coastal System has a coastline length of about 375 km (233 mi), a mangrove-coastline length of about 355 km (221 mi), and is highly diverse in terms of geology, soils, and plant communities. Mountains of moderate height, sandy plains, lagoons, marshes, and flat and conical karst outcrops characterize the landscape (Borhidi 1996). This region includes an offshore barrier reef and an extensive shelf that is particularly wide in the Gulf of Guanahacabibes (Figure 6.101) (Sullivan-Sealey and Bustamante 1999). The shallow water Gulf contains numerous mangrove cays, seagrass beds, and patch reefs that extend to westernmost Cuba near Cabo San Antonio. Barrier reefs run along the outer border of the shelf, parallel to the Archipelago las Coloradas, which is composed of hundreds of mangrove cays.

The Havana-Matanzas Mixed Shore/Fringing Reef coastline is a coral reef dominated system that has a coastline length of 280 km (174 mi), of which about 30 km (19 mi) is populated with mangroves (Figure 6.101). This mixed-shore fringing reef system has an extensive rocky shore with terraces and cliffs with extended beaches (Sullivan-Sealey and Bustamante 1999). The coastal system is relatively narrow, and the continental shelf seaward of the coast is 1 to 3 km (0.6 to 1.9 mi) wide. The largest Cuban coastal population centers (Havana and Matanzas) are located within this coastal system.

6.4.3 Introduction to Aquatic Fauna of Vegetated Marine Habitats

Faunal components of vegetated marine habitats considered in this section, as well as adjacent intertidal flats and subtidal soft bottoms, are primarily macrobenthic epifauna (living on the sediment surface), infauna (living within the sediments), and nekton (natant or swimming organisms). The habits and distributions of these faunal components often overlap in coastal habitats. Some nekton are associated with the surface and mid-level depths of the water column, but many others have a distinct orientation toward the bottom, placing them in close proximity to the macrobenthic invertebrate assemblages. These demersal forms (e.g., flatfishes, gobies, natant decapod crustaceans) may also be categorized among epifaunal assemblages that dwell largely on the surfaces of sediments, submerged vegetation, or other structural elements in wetlands. This section does not include benthic meiofauna (organisms that pass through a 0.5 mm (0.02 in) mesh sieve usually used to collect macrofauna) nor does it include nektonic taxa (e.g., sea turtles, dolphins) that are the focus of other contributions to this collection of white papers.

Invertebrate assemblages of the GoM have been described in numerous reports and publications. Large-scale ecosystem surveys, such as the Bureau of Land Management (now Bureau of Ocean Energy Management [BOEM]) benchmark programs in the South Texas Outer Continental Shelf (STOCS) (Flint and Rabalais 1980), Mississippi-Alabama-Florida (MAFLA) (Dames and Moore 1979), and Southwest Florida Shelf (SOFLA) (Woodward-Clyde Consultants 1983), included some inshore sampling and characterized assemblages comprising a large array of decapod and stomatopod crustaceans, relatively small crustaceans such as cumaceans and amphipods, mollusks (especially gastropods), echinoderms, cnidarians, and some polychaetous annelids.

Defenbaugh (1976) grouped the epifauna of the northern Gulf into 12 assemblages. In zones immediately seaward of the coastal strand, decapods such as the portunid *Callinectes similis*, spider crab (*Libinia*), shame-faced crab (*Calappa*), purse crab (*Persephone*), and hermit crab (*Pagurus*) are common scavengers. Mud shrimp (e.g., *Callianassa*) form burrows in silty sand substrates while the stomatopod *Squilla* is more motile and carnivorous. Sea pansies (*Renilla*) are less common but noteworthy indicators of higher salinity waters. The gastropods *Nassarius*, *Littoridina*, and *Cantharus* and the bivalves *Mulinia* and *Nuculana* are

common inhabitants of muddy sand and sand substrates throughout the GoM. Mollusks are generally most diverse in the southern Gulf, where sediments contain more carbonate and fewer large rivers discharge into the coastal area, but most dominant taxa in the southern Gulf also are found in other Gulf coastal habitats (Solis-Marin et al. 1993). Echinoderms such as the ophiuroid *Hemipholis* and the asteroids *Astropecten* and *Luidia* are associated with muddy sand and sand sediments throughout the Gulf. The echinoids *Diadema* and *Encope* are typical of subtidal waters in the Southern GoM Ecoregion (Solis-Marin et al. 1993). Figure 6.102 illustrates the distributions of three echinoid species in the GoM. The habitats of these species range into greater water depths than coastal wetlands but echinoids are found in littoral mud habitats, although some ophiuroids are detritivores and burrow in soft sediment.

Some epifaunal invertebrates, such as the penaeids *Farfantepenaeus aztecus*, *Farfantepenaeus duorarum*, and *Litopenaeus setiferus* also are nektonic and occur throughout the GoM, migrating offshore to spawn. Prevailing currents and behavioral adaptations allow their larvae to return to the estuaries that serve as primary nursery grounds. Blue crab (*Callinectes sapidus*), another key commercial epifaunal nektonic invertebrate species, exhibits similar migratory behavior. Coastal wetlands serve as the principal nursery areas for many commercially harvested decapod crustaceans, including penaeid shrimp (Figure 6.103).

Distributions of the juveniles of these species are closely linked with coastal wetlands. While some species, such as *F. aztecus* (Figure 6.103a) and *L. setiferus* (Figure 6.103c) are common in most coastal wetlands throughout the GoM, others such as *F. duorarum* (Figure 6.103b) seem dependent on specific wetland types (e.g., seagrass beds). Epifaunal invertebrate assemblages in vegetated habitats such as seagrass meadows generally exhibit higher densities and diversity than those on adjacent unvegetated soft bottoms; those metrics are often significantly correlated with aboveground plant biomass (Heck and Wetstone 1977).

Coastal benthic macroinfauna are among the best-known groups of marine invertebrates because they feed on detrital material produced in coastal wetlands and convert it to biomass production usable by secondary consumers of commercial value such as penaeid shrimp (e.g., Zimmerman et al. 2000). Infauna also are important indicators of habitat quality and the effects of environmental perturbation because they represent an integration of chronic and persistent natural and anthropogenic conditions (Rakocinski et al. 1998). Benthic surveys often are conducted to address specific potential or actual environmental impacts in the GoM, including effects of navigation dredging, oil spills (especially IXTOC in 1979) (Boehm and Fiest 1982), petroleum exploration and production, brine discharges from salt caverns, and effluent outfalls. Shallow-water benthic assemblages are sometimes categorized by substratum type (i.e., mud, sandy mud, muddy sand, or sand assemblages), but there are many species that occupy a wide range of sediment types. Mud habitats are depositional areas that support an infaunal assemblage adapted to elevated organics and periodic dissolved oxygen (DO) depletion; at the other extreme, sand habitats are characterized by species that require higher DO concentrations and greater flushing, with fewer burrowing taxa such as depositfeeding polychaetes. The amphipods Ampelisca abdita and A. cristata occur mainly on siltysand bottoms, but differences in the species' distributions within the GoM (Figure 6.104) suggest that habitat factors other than sediment type are also important. Uebelacker and Johnson (1984) described 593 polychaete species alone on the continental shelf of the United States regions of the Gulf; most of these were reported from coastal waters. They noted that some common polychaete species exhibited a faunal break east of Mobile Bay; some syllids were only found east of this area while some magelonids and ampharetids were only found west of the break. Other polychaetes exhibited disjunct distributions and were present in both the Eastern Gulf Neritic and Texas Estuarine subregions but not in the Mississippi Estuarine



Basin

léxico Cit

[A] Lytechinus variegatus.

Photo credit: Hillewaert 2011; © Hans Hillewaert/CC BY-SA 4.0



[B] Diadema antillarum.

Photo credit: Smith 2003; © Daniel P.B. Smith/GNU Free Documentation License.







Figure 6.102. Distributions in the GoM of three echinoids found in seagrass, reefs [A, B] or sandy unvegetated sediments including beaches [C]. The GoM base map and species distributions were modified after data downloaded from http://www.eol.org on 21 March 2014.

Cuba



[A] Farfantepenaeus aztecus.

Photo credit: downloaded from http://txmarspecies.tamug.edu/inv ertdetails.cfm?scinameID=Farfant epenaeus aztecus in March 2014.



[B] Farfantepenaeus duorarum.

Photo credit: downloaded from http://txmarspecies.tamug.edu/in vertdetails.cfm?scinameID=Farf antepenaeus duorarum in March 2014.





[C] Litopenaeus setiferus.

Photo credit: downloaded from http://txmarspecies.tamug.edu/in vertdetails.cfm?scinameID=Litop enaeus setiferus in March 2014.



Figure 6.103. Distributions of important nursery areas for juveniles of three species of penaeid shrimp in the GoM. The GoM base map was modified from http://www.eol.org on March 21, 2014 and species distributions were modified from maps of penaeid nursery areas downloaded from http://www.ncddc.noaa.gov/website/DataAtlas_1985/atlas.html in March 2014. Photo images from the Identification Guide to Marine Organisms of Texas web site, http://txmarspecies.tamug.edu/ index.cfm, used with permission.



Figure 6.104. Distributions of two benthic amphipods associated with intralittoral bay, estuarine and beach island habitats in the GoM. The GoM base map and distributions were modified after data downloaded from http://www.eol.org on 22 March 2014.

subregion. Tubicolous filter feeders and surface-dwelling carnivores are more abundant in sand habitats, and diversity overall is higher in the Southern GoM Ecoregion and in the South Florida/ Bahamian Atlantic Ecoregion.

Seagrasses, salt marshes, and mangroves provide habitat for diverse assemblages of infaunal organisms, especially crustaceans, mollusks, and polychaetes. Diversity and abundance of infauna in seagrass meadows are greater than in surrounding non-vegetated areas (Lewis 1984), while salt marsh and mangrove infaunal assemblages generally exhibit lower diversity and abundance than adjacent mudflats, possibly due to the presence of thick roots, dense rhizome mats, and dense organic sediments (Sheridan 1997). However, lower levels of diversity and abundance in marsh and mangrove habitats also may be attributed to lesser degrees of inundation and oxygenation. Dominant species of infauna in these habitats are generally ubiquitous in the GoM, with very little difference among assemblages in the Southern GoM Ecoregion, Northern GoM Ecoregion, and South Florida/Bahamian Atlantic Ecoregion. Fiddler crabs (*Uca* spp.) can be found within any saline or brackish marsh as well as mangrove-dominated areas, but within such common genera, there can be distinctly different distributions among species (Figure 6.105).



[A] Uca rapax. Photo credit: Richard Heard. Distribution modified from:

www.usm.edu/gcrl/public/gulf.creature s/fiddler.crabs.php_in March 2014.



[B] Uca longisignalis. Photo credit: Richard Heard. Distribution modified from: www.usm.edu/gcrl/public/gulf.creature s/fiddler.crabs.php in March 2014.



[C] *Uca speciosa.* Photo credit: Richard Heard. Distribution modified from:

www.usm.edu/gcrl/public/gulf.creature s/fiddler.crabs.php in March 2014.



Figure 6.105. Distributions of three species of fiddler crabs (*Uca* spp.) commonly found in salt marsh and/or mangrove habitats of the GoM. The GoM base map and distributions were modified after data downloaded from http://www.eol.org on 22 March 2014. Photographs by Richard W. Heard, University of Southern Mississippi Gulf Coast Research Laboratory Campus, used with permission (Heard, 1982).

The term *nekton* describes an animal type that resides in water all or most of the time and is capable of self-directed propulsion through that medium even against currents. The ability to achieve deliberate and sustained horizontal movements in a dynamic fluid environment separates this group of aquatic organisms from plankton and places a lower limit on the size of nekton at about 2 cm in most estuarine/marine circumstances (Aleyev 1977). Although fishes usually comprise the highest species diversity among nekton, coastal habitats of the GoM are used by a variety of other groups classified as nekton, including some natant decapod crustaceans (penaeid and caridean shrimps, portunid crabs and lobsters), molluscs (squid, octopus, scallops), reptiles (turtles, alligators and crocodiles) and mammals (dolphins, whales and manatees). No nekton studies have targeted the full suite of nekton species (invertebrates, fishes, reptiles and mammals) that occur in coastal wetlands of the GoM. This discussion focuses primarily on the fishes and decapod crustaceans of vegetated marine habitats because these nekton groups are the most abundant and species-rich, but information on other groups is provided where appropriate.

There are more than 1,500 fish species, 150 natant decapod crustacean species, and less than 100 cephalopods represented among the GoM nekton, but as with the macrobenthos, relatively few species are endemic or even characteristic of the GoM (McEachran 2009; Felder et al. 2009; Judkins et al. 2009). The GoM nekton communities are derivatives of assemblages found in the Carolinian Atlantic and the Caribbean Sea. Fishes of the GoM include fewer than 5 % endemics, and many of these have sibling species in adjacent waters (McEachran 2009). However, a substantially higher proportion of such endemic species among fish families are typically associated with the shallow, intertidal vegetated coastal habitats of the GoM, particularly within the Eastern Gulf Neritic, Mississippi Estuarine and Texas Estuarine regions. For example, among the 28 species within the fish families Poeciliidae (live-bearers), Fundulidae (fundulids), and Cyprinodontidae (killifishes), which are commonly found in coastal wetland habitats of the GoM, 20, 46, and 60 %, respectively, are endemic. This is approximately an order of magnitude more than the average proportion of endemics among GoM fishes. One likely reason for the higher rate of endemism among these families is that species tend to be small, lack a planktonic life stage, and are not strong swimmers, so they do not travel extensively over their usually brief lifespans (1 to 3 years). All of these species are closely associated with coastal wetland habitats and never venture far from shore. Some are tolerant of a wide range of environmental conditions and are broadly distributed throughout the coastal wetlands of the GoM, while others may be so closely tied to specific habitats that their ranges are very limited (Figure 6.106). There is no single principal reason for constrained GoM distributions of small nekton species with relatively weak swimming abilities.

For example, the goldspotted killifish, *Floridichthys carpio*, is a very hardy species that inhabits only the quiet, shallow waters of mangroves, marshes, and coastal impoundments along the western coast of Florida and the Yucatán (Figure 6.107a) while the dwarf seahorse, *Hippocampus zosterae*, tolerates a narrow range of environmental conditions and is restricted largely to seagrass habitats (Figure 6.107b). This dependence on a single habitat type exposes seahorse populations to increased risk associated with habitat degradation (Musick et al. 2000; Hughes et al. 2009), in addition to negative pressures connected to their commercial exploitation in the GoM to meet demand in the aquarium trade and overseas medicinal markets (Baum and Vincent 2005).

Greater mobility of most other nekton, coupled with the location of coastal wetlands near the boundary of freshwater and marine environments, results in spatially and temporally dynamic nekton assemblages that may draw representatives from a range of marine, brackish, and freshwater groups within each ecoregion of the GoM. Consequently, most nekton assemblages found in these transitional habitats comprise a limited number of small, stress-tolerant

Coastal Habitats of the Gulf of Mexico





[A] Fundulus grandis.

Photo credit: W.M. Howell/ R. L. Jenkins (http://www.fishbase.org/summary/F undulus-grandis.html); Downloaded

March 12, 2013. Used with permission.



[B] Fundulus jenkinsi.

Photo credit: G.L. Grammer (http://www.fishbase.org/summary/F undulus-jenkinsi.html). Downloaded March 12, 2013. Used with permission.





[C] Fundulus grandissimus.

Photo credit: T. Aarud (http://www.fishbase.org/summary/F undulus-grandissimus.html). Downloaded March 12, 2013. Used with permission.



Figure 6.106. Distributions of three fundulids (killifishes) found in vegetated coastal wetlands (marshes, mangroves, and seagrass beds) of the GoM. *F. grandis* [A] also occurs along the Atlantic coast of Florida, but *F. jenkinsi* [B] and *F. grandissimus* [C] are GoM endemics. The GoM base maps and distributions were modified after data and references downloaded from http://www.eol.org on 10 March 2014.



Figure 6.107. Examples of two habitat-restricted nekton species in the GoM. The GoM base map and species distributions were modified after data downloaded from http://www.eol.org on 21 March 2014.

species of year-round estuarine residents (Figure 6.106), as well as a complement of transient species (Figures 6.104 and 6.108) composed of seasonally abundant juvenile fishes and decapod crustaceans whose entire habitat within the GoM is more extensive, but encompasses coastal wetlands (Kneib 1997, 2000; Minello 1999; Heck et al. 2003).

Short-term (e.g., diel or tidal) and long-term (e.g., seasonal or ontogenetic) migrations also commonly occur between adjacent coastal wetlands (e.g., mangroves and coral reefs), with nekton providing a source of connectivity and the transfer of production among otherwise isolated environments comprising more sessile species (e.g., Kneib 1997, 2000; Deegan et al. 2000; Ellis and Bell 2008; Hammerschlag and Serafy 2009; Jones et al. 2010).

Major transfers of production from coastal wetlands occur when large numbers of species that use these habitats as nurseries (e.g., Figures 6.103 and 6.108) undertake offshore or coastal migrations as schooling species mature from juveniles to adults, or when coastal predators (e.g., Figure 6.109) forage on small resident nekton and benthic/epibenthic invertebrates in shallow coastal wetlands. Common predatory nekton associated with coastal wetlands in the GoM also exhibit a range of tolerances and preferences for certain environmental conditions.



[A] Anchoa mitchilli.

Photo credit: W.M. Howell/ R.L. Jenkins: downloaded from http://www.fishbase.org/summary/5 45 in March 2014. Used with permission.



[B] Mugil cephalus.

Photo credit: J.E. Randall; downloaded from http://www.fishbase.org/summary/ Mugil-cephalus.html in March 2014. Used with permission.





[C] Brevoortia patronus.

Photo credit: Joel Boumje, free and unrestricted use of image provided by author through Wikimedia Commons.



Figure 6.108. Distributions of three species of abundant schooling nekton in the GoM. The GoM map and distribution shown in [A] were modified after data and references downloaded from http:// www.eol.org on 10 March 2014. Distributions for [B, C] were modified after distribution maps downloaded from http://www.ncddc.noaa.gov/website/DataAtlas1985/atlas.html in March 2014 and show only principal spawning/nursery areas for these species, which otherwise range throughout the GoM.





[A] Cynoscion nebulosus.

Photo credit: Donald Flescher, NOAA Fisheries; http://www.nefsc.noaa.gov/rcb/ photogallery/flescher.html, accessed February 20, 2017.



[B] Sciaenops ocellatus.

Photo credit: Texas Parks & Wildlife; downloaded from http://www.tpwd.state.tx.us/huntwild/ wild/images/fish/reddrum2.jpg downloaded March 2014.



[C] Centropomus undecimalis.

Photo credit: Matthew Hoelscher; downloaded from <u>http://commons.wikimedia.org/wiki</u> /File:Centropomus.jpg in March 2014. Distributed under a CC BY-SA 2.0 license.



Figure 6.109. Three common predatory nekton species in coastal wetland habitats of the GoM. The GoM base map was modified after data downloaded from http://www.eol.org on 10 March 2014. Distributions were modified after maps downloaded from http://www.ncddc.noaa.gov/website/DataAtlas1985/atlas.html in March 2014.

For example, spotted seatrout (*Cynoscion nebulosus*) and red drum (*Sciaenops ocellatus*) may be widely distributed throughout the Gulf (Figure 6.109a, b) and elsewhere, while snook (*Centropomus undecimalis*) prefer clear waters associated with seagrass and mangrove habitats mostly in the southern GoM (Figure 6.109c).

In general, species richness of plants and animals in the GoM tends to be inversely related to water depth and is greatest along the south Florida coast, north through the Eastern Gulf Neritic (NOAA 2011). Approximately 40 % of fishes, 60 % of natant decapod crustaceans, and 12 % of cephalopods known from the GoM are from bay, nearshore, beach, coral reef, or estuarine habitats (McEachran 2009; Felder et al. 2009; Judkins et al. 2009) where they could be considered a source assemblage of nekton species for coastal wetland habitats. As with macrobenthos, most nekton families, and many species, are ubiquitous within the GoM. Fishes in the families Sciaenidae (drums), Ariidae (sea catfish), Gobiidae (gobies), Engraulidae (sardines), Clupidae (herrings), Mugilidae (mullets), and Sparidae (porgies) are among the most widely distributed according to trawl samples within Gulf estuaries (see McEachran 2009), but these groups are not always abundant in coastal wetland habitats, which are not usually sampled by trawling. Among the natant decapod crustaceans, species representing the families Penaeidae (penaeid shrimps), Palaemonidae (grass shrimps), and Portunidae (swimming crabs) are among the most widespread and abundant but there are major gaps in knowledge concerning these and other crustacean groups, particularly in the southern GoM (Felder et al. 2009). Only a few species of cephalopods, mostly within the family Loliginidae (inshore squids), are widespread in shallow estuarine waters associated with coastal wetlands (Judkins et al. 2009).

Table 6.3 is a summary of nekton families comprising the most abundant species closely associated with shallow coastal wetland habitats within most of the major nearshore ecoregions of the GoM. It suggests that fishes dominate coastal wetland assemblages in most ecoregions except in the Mississippi and Texas Estuarine regions, where natant decapod crustaceans may be far more abundant. Sedimentary environment characteristics and influence of freshwater riverine input and nutrients from extensive watersheds supplying these regions (Figure 6.15, Table 6.1) may favor the production of crustaceans, or the observation could be related to differences in the emphasis of research efforts within each region. For example, the 22 studies summarized in Minello (1999), which represent nekton samples primarily in the Mississippi and Texas Estuarine regions (Table 6.3) were all collected with small enclosure samplers usually deployed from the bow of small boats primarily sampling the edges of tidal marshes (e.g., Baltz et al. 1993; Minello et al. 1994). This presents a perspective on the nekton assemblages that may differ from that obtained using other methods applied in flooded intertidal habitats and smaller channels/ponds within interior marshes (e.g., Weaver and Holloway 1974; Herke and Rogers 1984; Felley 1987; Peterson and Turner 1994; Rozas and Minello 2010). Samples collected from the flooded interior portions of tidal marshes in the northern GoM are dominated by few very abundant species in the families Cyprinodontidae, Fundulidae, and Palaemonidae (Rozas 1993).

Nekton sample collection in the Campeche/Yucatán Inner Neritic Ecoregion used beach seines and trawls with a focus on fishes, and as such, did not report the abundance of any decapod crustaceans occurring within samples. However, penaeid shrimps (*Litopenaeus* spp., *Farfantepenaeus* spp.) and Mayan octopus (*Octopus maya*) support valued fisheries harvests presumably associated with the nursery function of lagoonal estuaries along the Mexican coast (Yáñez-Arancibia and Day 2004; Yáñez-Arancibia et al. 2009). Consequently, it seems reasonable to infer that natant decapod crustaceans are an important component of nekton in coastal wetlands of these regions as well. Shrimps in the family Hippolytidae are commonly associated with seagrass beds and while they appear to be abundant among the nekton of southern Florida, one might also expect this group to be well represented in the seagrass-dominated lagoonal

	Ecoregion – Level III					
Nekton Family	Florida Bay	Western Florida Neritic	Eastern Gulf Neritic	Mississippi/ Texas Estuarine	Campeche/ Yucatán Inner Neritic	
Fishes						
Ariidae (sea catfishes)						
Atherinidae (silversides)						
Belonidae (needlefishes)						
Carangidae (jacks)						
Cichlidae (cichlids)						
Clupeidae (herrings)						
Cyprinodontidae (killifishes)						
Engraulidae (anchovies)						
Fundulidae (funduluids)						
Gerridae (mojarras)						
Gobiidae (gobies)						
Mugilidae (mullets)						
Poeciliidae (livebearers)						
Polynemidae (threadfins)						
Sciaenidae (drums)						
Sparidae (porgies)						
Syngnathidae (pipefishes)						
Tetradontidae (puffers)						
Natant Decapod Crustaceans						
Hippolytidae						
Palaemonidae						
Penaeidae (penaeid shrimps)						
Portunidae (swimming crabs)						
# of species required to achieve > 85% of total nekton abundance	41	28	26	29	33	
References	2, 7, 11	5, 9	3, 8, 10	4	1, 6, 12	

Table 6.3. Dominant Nekton Families in or Adjacent to Vegetated Marine Habitats (mangroves, marshes, seagrass) Within GoM Ecoregions

Only studies reporting numerical abundance were included. Dominant families were those that together accounted for >85% of the nekton abundance within a study. Total number of species within families accounting for >85% of individuals is documented in the table.

(1) Arceo-Carranza and Vega-Cendejas (2009); (2) Ley et al., (1999); (3) Livingston et al., (1976); (4) Minello (1999) (summary of 22 studies); (5) Mullin (1995); (6) Peralta-Meixueiro and Vega-Cendejas (2010); (7) Sheridan et al. (1997); (8) Stevenson (2007); (9) Krebs et al. (2007); (10) Subrahmanyam and Coultas (1980); (11) Thayer et al. (1987); (12) Vega-Cendejas and Hernández de Santillana (2004).

systems of the southern GoM ecoregion (e.g., Barba et al. 2005). The presence of schooling species in the fish families Atherinidae (silversides), Clupeidae (herrings), and Engraulidae (anchovies) listed among the dominants suggests that samples were collected in, or very near, open water and not within structurally complex habitats (e.g., mangrove prop roots or among the stiff, dense stems of emergent marsh vegetation) where fishes would be unable to maintain the group integrity of a school.

Relatively few species (averaging 26 to 41 per study) seem to compose the bulk of nekton assemblages from coastal wetland habitats in the GoM (Table 6.3). Most individuals are the juveniles of estuarine transient species (e.g., mullets, menhaden, drums, penaeid shrimps,

portunid crabs), and all life stages of small estuarine resident species (e.g., gobies, killifishes, livebearers, grass shrimp) (Rozas 1993; Rozas and Reed 1993). At least one of these (i.e., *Fundulus jenkinsi*) is considered a species of special concern (Lopez et al. 2011) due to its apparent limited distribution (Figure 6.106b).

Although more species are associated with the southern neotropical portions of the GoM (Florida Bay and Campeche/Yucatán Inner Neritic) than the temperate northern regions, it should be noted that no attempt was made to standardize the collecting methods or focus of studies across regions (Table 6.4). Still, such a pattern would be expected and corresponds with the general spatial pattern of species richness around the GoM (NOAA 2011).

Many species of nekton are widespread within the GoM but only a few are both ubiquitous and abundant. Anchoa mitchilli (Figure 6,108a) is a clear standout among the fishes and is a dominant nekton component in all regions. Others (e.g., Brevoortia patronus) are distributed throughout the GoM (Figure 6.108c), but are among the most abundant nekton only within the Mississippi/Texas Estuarine Ecoregion (Table 6.4), suggesting a connection between riverine discharges and production of certain groups. The Mississippi/Texas Estuarine also includes a relatively high species richness of demersal gobiids (e.g., Gobiosoma spp., Gobionellus spp.) among the dominant nekton. Although gobies are common in estuarine habitats almost everywhere, their abundance in the Mississippi/Texas Estuarine region is noteworthy. A similarly high species richness of engraulids (Anchoa spp.) occurs in the Campeche/Yucatán Inner Neritic. Tropical waters of southern Florida and Yucatán include the greatest number of fish species that are not dominant elsewhere (Table 6.4). Greater species richness and lower abundance of fishes in these tropical regions may explain this observation (i.e., more species are required to account for at least 85 % of the individuals). However, these areas also contain extensive seagrass beds and/or coral reefs, which contribute substantially to diversity of fishes found in adjacent coastal wetlands, such as mangrove forests. Snappers (e.g., Lutjanus spp.) and mojarras (e.g., *Eucinostomus* spp.) tend to be among the dominants in mangroves. Pipefishes (e.g., Syngnathus spp.), sea horses (e.g., Hippocampus spp.) and porgies (e.g., Lagodon *rhomboides*) are dominant in areas where extensive seagrass habitats exist, such as in the Florida Bay (Table 6.4). The Mississippi/Texas Estuarine appears to include more dominant natant decapod crustaceans than are counted among the dominants in other regions. The lack of dominance among the fundulids (Fundulus spp.) collected from the Mississippi/Texas Estuarine is surprising, given that this region of the northern GoM contains most of the tidal marsh, which is usually the principal habitat of fundulids (Table 6.4, Figure 6.106). One possible explanation is that a majority of nekton samples from this region have been collected at the interface between vegetated tidal marshes and adjacent open waters (i.e., marsh edge), and fundulids may be more closely associated with the interior portions of shallow vegetated coastal habitats (e.g., Peterson and Turner 1994).

A pairwise comparison of the percentage of abundant fish species shared in common between ecoregions (Table 6.5) shows that the most abundant fishes of the neotropical southern GoM (Campeche/Yucatán Inner Neritic) are relatively distinct from those in all other regions, including southern Florida. The neotropical environment of Florida Bay and the Florida Keys share a substantial number (about 25 %) of abundant species with temperate wetlands of the Western Florida Estuarine and Eastern Gulf Neritic, but less similarity in the most abundant fishes is found on the coast of the Mississippi/Texas Estuarine compared with other regions. This is likely due to the higher diversity of habitat types and species found in the eastern GoM compared with more productive regions of the northern GoM, which tend to be dominated by tidal marshes and fewer nekton species at higher densities. Coastal currents (Figure 6.17) may contribute to the similarity in nekton assemblages along the west coast of the Florida peninsula,

Table 6.4. Species Comprising the Dominant Nekton Families Accounting for >85 % of Individuals in Field Studies Within or Immediately Adjacent to Vegetated Marine Habitats (e.g., marshes, mangroves, seagrass beds) in Each of the Listed Ecoregions.

		Ecoregion			
	Florida Bay	Western Florida Estuarine	Eastern Gulf Neritic	Mississippi/ Texas Estuarine	Campeche/ Yucatán Inner Neritic
Fishes]				
Adinia xenica					
Anchoa cayorum					
Anchoa cubana					
Anchoa hepsetus					
Anchoa lamprotaenia					
Anchoa lyolepis					
Anchoa mitchilli					
Archosargus probatocephalus					
Archosargus rhomboidalis					
Atherinomorus stipes					
Bairdiella chrysoura					
Bathygobius soporator					
Belonesox belizanus					
Brevoortia patronus					
Calamus arctifrons					
Chilomycterus schoepfi					
Ctenogobius smaragdus					
Cynoscion arenarius					
Cynoscion nebulosus					
Cyprinodon artifrons					
Cyprinodon variegatus					
Diapterus auratus					
Diapterus rhomboides					
Dorosoma cepedianum					
Eucinostomus argenteus					
Eucinostomus gula					
Eucinostomus harengulus					
Eucinostomus melanopterus					
Eugerres plumieri					
Evorthodus lyricus					
Floridichthys carpio					
Floridichthys polyommus					
Fundulus confluentus					

(continued)

Table 6.4. (continued)

	Ecoregion				
Nekton Family	Florida Bay	Western Florida Neritic	Eastern Gulf Neritic	Mississippi/ Texas Estuarine	Campeche/ Yucatán Inner Neritic
Fundulus grandis					
Fundulus grandissimus					
Fundulus jenkinsi					
Fundulus majalis					
Fundulus persimilis					
Fundulus seminolis					
Fundulus similis					
Gambusia spp.					
Gambusia affinis					
Gambusia holbrooki		-			
Garmanella pulchra					
Gerres cinereus					
Gobioides broussoneti					
Gobionellus boleosoma					
Gobionellus oceanicus					
Gobionellus shufeldti					
Gobiosoma bosc					
Gobiosoma robustum					
Harengula jaguana					
Hippocampus erectus					
Hippocampus zosterae					
Heterandria formosa					
Hypoatherina herringtonensis					
Lagodon rhomboides					
Leiostomus xanthurus					
Lucania parva					
Lophogobius cyprinoides					
Lutjanus apodus					
Lutjanus griseus					
Lutjanus jocu					
Menidia martinica					
Menidia peninsulae					
Menidia spp.					
Menticirrhus americanus					
Microgobius gulosus					
Microgobius thalassinus					
Micropogonias undulatus					
Mugil cephalus					
Mugil curema					
Opisthonema oglinum					
Poecilia latipinna					
Pogonias cromis					
Saratherodon melanotheron					
Sciaenops ocellatus					
Strongvlura marina					
Strongvlura timucu					
Strongvlura notata					
	1	1		1	

(continued)

Table 6.4. (continued)

	Ecoregion				
	Florida Bay	Western Florida Estuarine	Eastern Gulf Neritic	Mississippi/ Texas Estuarine	Campeche/ Yucatán Inner Neritic
Sphoeroides nephalus					
Sphoeroides spengleri					
Sphoeroides testudineus					
Syngnathus dunkeri					
Syngnathus floridae					
Syngnathus louisianae					
Syngnathus scovelli					
Species abundant only in this Ecoregion	19	8	4	8	22
Natant Decapod Crustaceans					
Callinectes ornatus					
Callinectes sapidus					
Callinectes similis					
Hippolyte zosericola					
Hippolyte curacaoensis					
Farfantepenaeus aztecus					
Farfantepenaeus duoarum					
Leander tenuicornis					
Litopenaeus setiferus					
Macrobrachium ohione					
Palaemonetes intermedius					
Palaemonetes paludosus					
Palaemonetes pugio					
Palaemonetes transverus					
Palaemonetes vulgaris					
Tachypenaeus constrictus					
Thor floridanus					
Tozeuma carolinense					
Species abundant only in this Ecoregion	4	0	0	7	0

Referenced studies are the same as in Table 6.3. Aqua shading indicates the species was among those in a family considered abundant (not necessarily that the species itself was abundant) and *blue* shading indicates a species that was the most abundant in a given family in at least one study within the indicated ecoregion.

while the Mississippi River may function as a physical barrier to east-west movement of certain nekton species associated with shallow coastal waters.

Quantitative information on nekton from vegetated marine habitats in the extreme southeastern portion of the GoM along the northwestern coast of Cuba is scarce, so data were not included in Tables 6.3 through 6.5. However, Ortiz and Lalana (2005) provide some useful qualitative insights from their general description of the marine biodiversity of the Cuban Archipelago. The families and species reported as noteworthy in seagrass beds, mangroves, and coastal lagoons include fishes in the families Lutjanidae (snappers), Serranidae (sea basses), Atennariidae (frogfishes), Ogocephalidae (batfishes), Synodontiae (lizardfishes), Pomadacidae (damselfishes), Gerridae (mojarras), Mugilidae (mullets), and Centropomidae (snooks). Other Table 6.5. Matrix of Pairwise Comparisons Between Indicated Ecoregions Showing the Percentage of Species from Abundant Fish Families That are Shared in Common. Referenced studies are the same as in Table 6.3.

	Ecoregion				
Ecoregion	Florida Bay	Western Florida Estuarine	Eastern Gulf Neritic	Mississippi/ Texas Estuarine	Campeche/ Yucatán Inner Neritic
Florida Bay		25.5%	25.0%	13.0%	12.9%
Western Florida Estuarine			35.3%	7.7%	9.3%
Eastern Gulf Neritic				9.6%	8.3%
Mississippi/Texas Estuarine					6.7%

fishes associated with shallow subtidal flats included Scaridae (parrotfishes)—especially adjacent to coral reefs—and Dasyatidae, specifically the bluntnose stingray (*Dasyatis say*). Except for frogfishes and batfishes, which are rarely reported as abundant or important in other regions of the GoM, the nekton of the Cuban coast, at least at the family level, is similar to that of the southern Florida and Yucatán assemblages, with substantial contributions from coral reef and mangrove nekton assemblages (e.g., snappers, mojarras, damselfishes). Likewise, nektonic decapod crustaceans associated with shallow macroalgal beds, mangroves, and coastal lagoons included Portunidae (crabs in the genera *Portunus* and *Callinectes*) and shrimps in the family Penaeidae, with specific mention of *Farfantepenaeus notialis* and *Litopenaeus schmitti* (Ortiz and Lalana 2005). Most of these are either the same or sibling species that occur throughout the GoM (e.g., the northern white shrimp, *Litopenaeus setiferus* and the southern white shrimp, *L. schmitti* are sibling species as are the northern pink shrimp *Farfantepenaeus duorarum* and the southern pink shrimp *F. notialis*).

Some nekton species are restricted to narrow regional coastal reaches by their habitat requirements or physiological tolerances to variable environmental factors. For example, the American crocodile (*Crocodylus acutus*) occurs in the neotropical regions of the southern GoM, primarily from the Florida Keys, Florida Bay, Shark River Estuarine, and southwest through the Veracruzan Neritic, including a large population in Cuba. Crocodiles are limited to the southern GoM largely because of a low tolerance for cold even for short periods (Kushlan and Mazotti 1989). The related American alligator (*Alligator mississippiensis*), which can tolerate water temperatures below 8 °C (46 °F) for extended periods (Lance 2003) is distributed in the GoM throughout inshore coastal wetlands from south Florida north and west through the Texas Estuarine Ecoregion. Although alligators are more widely distributed within the GoM, crocodiles have a higher salinity tolerance and are more likely to be abundant in saline wetlands within their range, including mangrove habitats throughout the southern Gulf. Both species of crocodilians are top predators within the region, feeding on a diverse diet that includes other nekton (especially fishes) as well as terrestrial mammals, reptiles, and insects.

The diamondback terrapin (*Malaclemys terrapin*) is another nektonic reptile that is even more characteristic of tidal marshes and mangroves of the GoM than crocodilians, and is considered by some to be among the imperiled species of special regional interest (Beck et al. 2000). The distribution of terrapin subspecies within the GoM is particularly interesting because the subspecies appear to follow the distribution of Level III Ecoregions shown in Figure 6.3. Although there are seven recognized subspecies of diamondback terrapin, only four of these occur within the GoM (Ernst and Lovich 2009). *M. terrapin rhizophorarum* (mangrove diamondback terrapin) is restricted to mangrove habitats of the Florida Keys, Florida Bay,

and the Shark River Estuarine Ecoregions (Ernst and Lovich 2009; Hart and McIvor 2008). *M. t. macrospilota* (ornate diamondback terrapin) occurs primarily within the marshes of the Western Florida Estuarine and Eastern Gulf Neritic. *M. t. pileata* (Mississippi diamondback terrapin) ranges within the tidal marshes of the Mississippi Estuarine. The fourth subspecies, *M. t. littoralis* (Texas diamondback terrapin) occupies the Texas Estuarine from western Louisiana to Corpus Christi, Texas. The conformity between the distributions of the subspecies of diamondback terrapins and Level III Ecoregions within the GoM is matched by few other nekton. Diamondback terrapins consume a variety of estuarine invertebrates including snails, crustaceans, and bivalves. Although strong swimmers, they tend to have limited home ranges, which may help to explain how the distinct subspecies persist.

Water depth, salinity, seasonal temperatures, dissolved oxygen, freshwater inputs, sediment type, availability of physical or biogenic structure (Day et al. 1989), as well as the size and spatial configuration of aquatic habitats within the coastal landscape (Boström et al. 2011), are among the multiple interacting factors controlling the composition and structure of nekton assemblages within coastal wetlands. Environmental variability on multiple spatial and temporal scales is a hallmark of estuarine systems, but the high mobility of nekton allows assemblages to persist by emigrating in response to unfavorable environmental conditions that might develop over the short-term or on limited spatial scales, and quickly immigrating to repopulate the same areas when conditions improve (Hackney et al. 1976; Day et al. 1989; Tyler et al. 2009).

Water depth usually affects the size of the species or life stages of nekton found in coastal wetlands. Shallow waters associated with most coastal wetlands generally are dominated by smaller (mostly <15 cm) individuals. Mean size and species richness of nekton assemblages tends to decrease from deeper to shallower waters, as does swimming ability, but densities often increase along the same depth gradient, with greater nekton densities occurring in shallow water (e.g., Peterson and Turner 1994; Eggleston et al. 2004; Ellis and Bell 2004). Within shallow vegetated habitats of the coast, the fish families Fundulidae (fundulids), Cyprinodontidae (killifishes), and Poecilidae (live-bearers) are abundantly represented (e.g., Rozas 1993; Peterson and Turner 1994). Water depth and physical structure (emergent and submergent plants and reefs) attract a subset of the Penaeidae (white, brown, and pink shrimp), Palaemonidae (grass shrimp), and Portunidae (swimming crabs such as the blue crab), at least near the edges of intertidal wetland habitats (e.g., Minello et al. 2008).

Aquatic accessibility to coastal wetlands is a key factor controlling the composition and abundance of nekton assemblages, particularly in intertidal habitats (Rozas 1995; Kneib 1997; Minello et al. 2012). Several factors may affect the accessibility of coastal wetlands to nekton including the frequency and duration of tidal or storm-driven inundation of intertidal habitats (e.g., marshes, mangroves, tidal flats) and the presence of structural landscape features (e.g., passes, creek channels, and ditches) that facilitate nekton movements (Saucier and Baltz 1993; Raynie and Shaw 1994) among otherwise isolated aquatic elements (e.g., lagoons, ponds, and impoundments) embedded within coastal landscapes (Knudsen et al. 1989; Herke 1995). Unlike most coasts, which experience semidiurnal tides (i.e., two high and two low tides daily), much of the GoM experiences diurnal tides (i.e., 1 high and 1 low tide daily) as illustrated in Figure 6.16. Mixed tides have the characteristic of exhibiting appreciably different amplitudes in successive high and low water events and may be either diurnal or semidiurnal. All tides within the GoM are considered microtidal in that tidal amplitude is considerably <2 m. Note that tides along the west coast of Florida, as well as most of the Cuban coast, are semidiurnal while all other portions of the GoM experience diurnal tides. Increased accessibility to intertidal habitats associated with twice daily high tides (semidiurnal) in the eastern GoM may explain at least some of the greater similarities in dominant nekton species shared by these regions (Table 6.5).

The dominance of small amplitude diurnal tides within the GoM may restrict the extent to which nekton have access to coastal wetlands and sometimes limit the effective use of these habitats to edges adjacent to open water (Baltz et al. 1993; Minello et al. 1994) or to habitats that remain submerged, such as subtidal seagrass beds and permanent or ephemeral ponds and impoundments. Even in the latter case, physical access routes in the form of passes between barrier islands into lagoons or embayments, or channels connecting natural ponds or artificial impoundments to open estuarine waters, are essential for immigration and emigration of most transient species of nekton that use these habitats as juvenile nurseries but spawn elsewhere (Day et al. 1989; Raynie and Shaw 1994; Herke 1995).

The association between productivity of inshore waters and nutrient dynamics of vegetated marine habitats has long been recognized (Odum 2000; Chesnev et al. 2000; Beck et al. 2001), as have relationships between the area of vegetated coastal wetlands and fisheries production (e.g., Turner 1977, 1992), particularly in the northern GoM. However, in the neotropical southern GoM, the area of emergent vegetated wetlands appears to be less important in controlling fishery production than river discharge and freshwater inputs (Deegan et al. 1986; Yáñez-Arancibia and Day 2004), which are delivered to the coastal wetlands via relatively small watersheds compared to those in the northern GoM (Figure 6.15, Table 6.1). Secondary productivity in the GoM, as elsewhere, is driven by primary productivity and water quality, which control habitat quality and the production of higher trophic levels such as nekton (Yáñez-Arancibia and Day 2004). Although some coastal wetland nekton species have digestive tracts capable of assimilating energy from diets of algae and detritus (e.g., Cyprinodon variegatus, Poecilia latipinna, Mugil cephalus, Brevoortia patronus) (Odum and Heald 1972; Deegan et al. 1990), many supplement their diet by feeding on small invertebrates (Harrington and Harrington 1961, 1982). For the most part, nekton found in coastal wetlands are omnivorous and opportunistic, relying primarily on small surface-dwelling or epibenthic invertebrates as their primary food source (Stoner and Zimmerman 1988; Kneib 1997; Llansó et al. 1998). These benthic invertebrate food resources are capable of using algal and microbial assemblages associated with detritus as their primary energy source (see Figure 1 in Kneib 2003), and thus are likely to provide the most important links between coastal wetland primary production and nekton populations.

The role of different coastal wetland habitat types (e.g., seagrass, salt marsh, mangrove) in support of nekton secondary production remains a topic of some debate, but it does not appear that all types of wetland habitats contribute equally to estuarine nekton production. Beck et al. (2001) hypothesized that seagrass, marsh, and oyster reef habitats serve a nursery role in contributing to the production of nekton, but mangroves, tidal flats, and intertidal beaches do not provide a significant source of nekton production, though may serve a role as predator refugia for some species.

6.4.4 Ecosystem Services and Societal Benefits of Vegetated Marine Habitats

Natural ecosystems provide a suite of goods and services that have societal benefits (Costanza et al. 1997). These benefits are especially important relative to coastal ecosystems given that 41 % of the world population lives within 100 km (62 mi) of the coast (Martínez et al. 2007). Ecosystems of the GoM are no exception in providing goods and services that support human populations.

Ecosystem Services of the GoM by Service Level				
Level 1	Level 2	Level 3		
Ecosystem Foundation or Support Services	Provisioning Services—Goods and Services Produced by, and Dependent on, Support Services	Outcomes and Benefits to Society		
Nutrient Balance Hydrological Balance Biological Interactions Soil and Sediment Balance	Pollution Attenuation Air Supply Water Quantity Water Quality Food Raw Materials Medicinal Resources Gas Regulation Ornamental Resources Climate Regulation	Hazard Moderation Aesthetics and Existence Spiritual and Historic Science and Education Recreational Opportunities		

Table 6.6.	Ecosystem Services o	of the GoM (from	Yoskowitz et al.	2010; republished	with permis-
sion of th	e Texas A&M University	y Press)			

Although there are many definitions for ecosystem services, the Gulf of Mexico Ecosystem Services Workshop (Yoskowitz et al. 2010) specifically defined GoM ecosystem services as "...the contributions from Gulf of Mexico marine and coastal ecosystems that support, sustain, and enrich human life." The central concept of this definition, and most others commonly used, is the emphasis on services that support human well-being and the identification of different classes of ecosystem services such as: (1) Ecosystem Foundation or Support Services, which are regulatory in nature and consist of processes that maintain the structure and function of ecosystems, (2) Provisioning Services, which are goods and services produced by or dependent on the support services, and (3) Outcomes and Benefits to Society, which include a suite of direct societal benefits (Table 6.6).

This organization has the advantage of being hierarchical in nature. Level I (Support Services) provides the foundation upon which all other ecosystem services depend. The higher the level, the more closely linked things are to direct human benefits. The Millennium Ecosystem Assessment (WHO 2005) uses a similar classification that groups ecosystem services into Supporting, Regulating, Provisioning, and Social and Cultural Services.

Nineteen ecosystem services provided by the GoM can be segregated by coastal habitat and prioritized as illustrated in Table 6.7. Specific ecosystem services provided by any particular coastal habitat vary with habitat. For example, ecosystem services performed by salt marshes are qualitatively and quantitatively different from those provided by barrier strand dunes or maritime forests. The importance of each service for a particular habitat is indicated. Although it can be argued whether or not the list is complete and/or the priorities correct, the table provides a summary from 30 coastal scientists and resource managers relative to their perceptions of ecosystem services provided by a suite of coastal habitats of which those presented in Table 6.6 are just a subset.

The goods and services provided to society by one particular coastal habitat, mangrove forests, have been studied and reviewed (Ewel et al. 1998). Although their relative importance varies among forest types and geographic locations, the primary goods and services include shoreline stabilization, buffering storms and hurricanes, sediment trapping, sinks for nutrients and carbon, nursery grounds for commercially important fisheries, wildlife habitat, and recreation opportunities. All mangrove forests contribute to soil formation and help stabilize

	Ecosystem Services	Dune/Beach	Salt Marsh	Mangrove	Seagrasses	Intertidal Flat	Subtidal Flat
1.	Nutrient balance		6		6	5	2
2.	Hydrological balance						
3.	Biological interactions	6	1	1	2	2	1
4.	Soil & sediment balance	3	11	3	4	1	3
5.	Pollution attenuation			7			
6.	Air supply					6	
7.	Water quantity		10				
8.	Water quality	7	9	6	3		
9.	Food		4	8	1	4	5
10.	Raw materials					8	4
11.	Medicinal resources						
12.	Gas regulation		8				
13.	Ornamental resources						
14.	Climate regulation		7				
15.	Hazard moderation	1	2	2	8	9	
16.	Aesthetics & existence	2	5	4	7	7	6
17.	Spiritual & historic						
18.	Science & education	5					
19.	Recreational opportunities	4	3	5	5	3	7

Table 6.7. Coastal Habitats and Their Ecosystem Services (modified from Yoskowitz et al. 2010)

coastlines; however, fringe forests dominated by *Rhizophora mangle* (e.g., in Florida) may be especially important in this regard. Sediment trapping is a related function most often attributed to riverine forests (e.g., the Shark River in the Everglades, Florida) (Ewel et al. 1998), but the scrub mangrove habitats found in the Mississippi River Delta along secondary waterways may also capture sediment (Perry and Mendelssohn 2009). Depending on geomorphology and hydrodynamics, mangroves may act as sinks or sources for nutrients and carbon. Basin forests

are thought to be sinks for organic matter and nutrients (Twilley 1985; Twilley et al. 1986). Scrub or dwarf forests may also be sinks due to their restricted hydrology. Forest types with more open exchange (fringe, overwash island) may be sources of nutrients and carbon to adjacent estuaries. Mangrove forests are also thought to protect human communities against storm surge, with the trees contributing to wave attenuation (Bao 2011). Additionally, mangrove forests serve as nurseries and refuge for a variety of marine organisms of commercial or sport value, such as snapper (*Lutjanus* spp.), tarpon (*Megalops atlanticus*), barracuda (*Sphyraena barracuda*), jack (*Caranx* spp.), sheepshead (*Archosargus probatocephalus*), and red drum (*Sciaenops ocellatus*). In addition to serving as habitat for a variety of wildlife such as birds, reptiles, and mammals, mangrove forests also provide habitat for threatened or endangered species such as the West Indian manatee and American crocodile. Mangrove forests are important in terms of aesthetics and tourism; many people visit these areas to engage in fishing, boating, bird watching, and snorkeling.

Various scientists have identified the ecosystem services ascribed to coastal habitats differently. For example, Peterson et al. (2008) listed the following ecosystem services for tidal marshes, which include salt marshes: habitat and food web support, buffer against storm wave damage, shoreline stabilization, hydrological processing (flood water storage), water quality, biodiversity preservation, carbon storage, and socioeconomic services for humans. Many of these services are similar to those listed for salt marshes in the Yoskowitz et al. (2010) classification (Table 6.6). Costanza et al. (1997) estimated the economic value of tidal marshes and mangroves at \$9,990/ha/year. Seagrass habitats were valued even higher at \$22,832/ha/year. The coastal barrier strand, although not given a monetary evaluation, per se, provides a number of ecosystem services including protection of the mainland from storms and waves; buffering of wave energy to allow for formation of marshes and estuaries; creation of habitat for a variety of fish, shellfish, waterfowl and shorebirds, furbearing mammals, and endangered species such as sea turtles; recreation; vacation and retirement living; and economic benefits for tourism for coastal communities (Wells and Peterson 1982). In total, the ecosystem services provided by coastal habitats, including tidal marshes, mangroves, and the offshore coastal zone, were estimated at \$63,563/ha/year (Costanza et al. 1997).

6.5 COASTAL HABITAT ECOLOGY

Coastal habitats that occur in the GoM represent a relatively finite list and are similar to those occurring worldwide. Factors such as climate, wave energy, water clarity, salinity, submergence, propagule availability, among others, determine the specific coastal habitat present in any particular geographic location and the flora and fauna comprising these habitats. In addition, factors such as disturbance type and frequency, biotic interactions such as herbivory, soil chemical condition, and others modulate many of the large-scale controls.

Coastal habitats are generally characterized by their dominant vegetation type. For example, mangrove trees define mangrove habitat, while seagrasses identify the seagrass habitat; halophytic graminoids and forbs distinguish a salt marsh. Barrier islands, in contrast, are primarily identified by their geomorphological characteristics (e.g., beach, dune, swale, etc.). Regardless, coastal habitats are important and conspicuous biogeomorphic features in the GoM. Intertidal wetlands are found throughout the GoM, but as mentioned briefly before, salt marshes dominate in the more temperate environments of the GoM, and mangroves dominate in more tropical settings. Mangroves, which are intertidal tropical and subtropical trees, are restricted to certain parts of the GoM by temperature. They dominate in the Southern GoM and Greater Antilles (Cuba) Marine Ecoregions, and become less prevalent and of lower stature in the more temperate regions of the Gulf (Mendelssohn and McKee 2000). The geographic limit of mature mangrove stands in the GoM is approximately 29.2°N latitude in

coastal Louisiana in the Northern GoM region. Here, both plant communities co-occur (Patterson and Mendelssohn 1991); this ecotone also exists along the Florida and Texas shorelines. Mangrove plants also occur on the Chandeleur Islands (~29.8°N latitude) in Louisiana, and recent observations¹ have identified black mangroves on Horn Island, Mississippi (~30.2°N latitude), which, if persistent, is the farthest northern population in the GoM. Seagrass habitats in the GoM also have a somewhat restricted distribution due to low water clarity and/or low temperatures in much of the northern GoM. Seagrasses reach their dominance in clear waters of the subtropical and tropical southern Gulf, and their distribution is further limited in the Northern GoM Ecoregion by high turbidity associated with Mississippi River-influenced coastal waters (Hale et al. 2004). Barrier islands and beaches, as well as tidal flats, occur throughout the GoM wherever physical conditions allow. The following is a description of the major coastal strand habitats and their associated wetlands.

6.5.1 Barrier Strand Habitats

6.5.1.1 Dominant Forcing Functions

The barrier strand is a stressful environment where factors such as salt spray from saline waters of the GoM, soil moisture deficiencies, limited nutrient supply, and soil instability may negatively affect biota, especially barrier strand vegetation (Barbour et al. 1985; Packham and Willis 1997). Salt spray occurs when effervescence in the surf propels droplets into the air where they are concentrated and transported inland by the wind. The active agent in salt spray is the chloride ion, which enters the windward portions of plant parts through cracks and lesions in the epidermis. The degree of injury is related to the wind speed above the critical value of 7 m/s, where an abrupt increase in salt spray intensity occurs as turbulent air flow increases. In addition to affecting growth, salt spray is the primary environmental factor determining the distribution, architecture, and zonation of maritime plant species (Christensen 2000). Many plants that grow on foredunes (e.g., *Uniola paniculata* [sea oats]) are resistant to salt entry and can survive the intense salt-spray zones of the barrier strand. Plants that are less well adapted (e.g., *Andropogon* (*=Schizachyrium*) spp. [broomsedge]) are found in the lee of dunes or other vegetation. Salt spray is an important factor, along with sand burial, in preventing the establishment of some annual species (Van der Valk 1974; Miller et al. 2008).

Although dune species may be stressed by water deficits, especially on tall sand dunes, freshwater availability is greater than one might expect. Sand below the top few centimeters of a dune is often moist, even though the soil surface is dry. In fact, it has been suggested that the dry surface acts as a vapor trap, which impedes drying of deeper substrate. The water table, which may be several meters from the active root zone depending on the size of the dune, acts as an indirect source of water via vapor phase diffusion upward to the rooting zone. Because the capillary rise of water from a free water surface in very fine sand is not more than 40 cm, the water table in a dune of only a few meters can make no direct contribution to the moisture requirements of most dune plants. Rainfall and condensation provide important sources of water to dune vegetation. Regardless of the source of water. Many beach and dune species control water loss via a number of mechanisms including sunken stomates, strong stomatal control, and waxy leaf surfaces. Also, numerous beach and dune species are succulent and accumulate water in their leaf tissue. Still other plant species, especially dune grasses, have

¹ http://blog.al.com/live/2012/07/mangrove_trees_show_up_on_horn.html

a high capacity for the acquisition of water via deep roots that penetrate into moist soil. Because of these multiple adaptations to conserve and acquire water, water deficiency stress is not generally a major constraint to barrier strand species (Barbour et al. 1985).

A primary limitation to plant growth and expansion is the relatively nutrient-deficient sandy soils that compose the barrier strand. Major nutrient inputs to the dune system are salt spray, precipitation, and nitrogen fixation by both symbiotic and free-living bacteria. The mineralization of organic matter in the dunes is of limited importance because aeolian processes remove most lightweight organic matter; however, in protected swales and back-barrier marshes, soil organic matter may accumulate. Nitrogen is generally the primary plant-limiting nutrient, although phosphorus can be of secondary importance (Dahl et al. 1974; Dougherty et al. 1990; Laliberté et al. 2012). In fact, research on nutrient limitations of European dunes and swales indicates that phosphorus often co-limits primary productivity, especially in early stages of dune development (Lammerts et al. 1999).

Soil instability, and resulting sand burial, is another problem that dune vegetation encounters (Maun and Perumal 1999). Plants have a more difficult time becoming established in shifting windblown sand than in a stable substrate and can easily be buried with sand in large mobile dune fields. Dune plants, in particular, have adapted to this environment by developing the capacity to grow upward through considerable accumulations of sand. In fact, moderate sand burial has a stimulatory effect on the growth of dune grasses, but too much sand burial can cause plant mortality. In general, however, perennial grasses are more resistant to sand burial than annual forbs (20 cm limit for annuals and more than a meter for grasses) (Van der Valk 1974).

Although less investigated, herbivory is another factor that can limit the growth and expansion of dune vegetation (Hester et al. 1994). Grazing by rabbits, deer, nutria, and other mammals can dramatically reduce the structure of vegetation. However, this disturbance is often missed in the absence of adjacent areas where herbivores are excluded.

6.5.1.2 Plant Communities and Associated Vegetation

Because barrier strand vegetation throughout the GoM is subject to similar environmental stressors, as described above, plant form and habitat structure vary little. Even species composition can be quite similar, especially within the same latitudinal bands. Beach species are often prostrate herbaceous perennials capable of vegetative reproduction by stolons or rhizomes. Leaves are frequently small and lobed, with waxy surfaces and exhibiting succulence to various degrees. These are adaptations to plant water loss and/or low water availability, whether the cause is high transpiration, low water availability, soil salinity, or a combination (Barbour et al. 1985). Dune species are often grasses, like Uniola paniculata (sea oats) or Panicum amarum (bitter panicum), whose long roots can tap moisture deep in the soil, and whose rapid growth rates allow for tolerance to sand burial. Non-grass herbs, like *Hydocotyle* spp. (pennywort), found in the dune environment often have shallow roots to readily absorb frequent but short episodes of precipitation and strong stomatal control to reduce water loss. A mixture of graminoids and herbaceous dicots usually dominates swales. Because swales are generally protected from many of the stressors influencing beach and dune species, they do not show these same adaptations. However, swales often have higher water tables, and species such as Spartina patens, Schoenoplectus olneyi, and Andropogon (=Schizachyrium) scoparius (shore little bluestem) tolerate high soil moisture and even flooding. The swale habitat is the location where maritime forests and shrub thickets occur. Trees such as pines (Pinus spp.) and live oak (*Quercus virginiana*), and shrubs like Myrica cerifera (wax myrtle) and Baccharis halimifolia (groundsel bush), dominate swales located on more stable barrier islands and beaches. Backbarrier salt marshes, dominated by Spartina alterniflora (smooth cordgrass)

Texas	Louisiana	Mississippi, Alabama, and Florida Panhandle	South Florida
Croton punctatus Ipomoea stolonifera Panicum amarum	Spartina patens Cenchrus incertus Sporobolus virginicus	Uniola paniculata Schizachyrium maritimum Chrysoma pauciflosculosa Paronvchia erecta	Iva imbricata Opuntia spp. Paspalum distichum Scaevola plumieri

Table 6.8. Characteristic and Distinguishing Beach Flora in Each of the Four Regions of the Northern GoM as Identified by Barbour et al. (1987)

and S. patens (wiregrass), and where climate allows, Avicennia germinans, are frequent occurrences, as are seagrass beds.

The beach and foredune vegetation on the backshores of barrier strands in the GoM can be divided into four geographic clusters: (1) a western region consisting of shorelines south of Galveston, Texas, (2) a northwest region of Louisiana beaches, (3) a northeast region consisting of Mississippi, Alabama, and the Florida panhandle, and (4) the south Florida beaches (Barbour et al. 1987). These groupings are separated by geographical and environmental discontinuities, such as differences in parent material of the sand and geological stability, as well as the influence of the Mississippi River. The beach survey of Barbour et al. (1987), which covered a shoreline distance of 2,500 km (1,550 mi), found that the northern GoM from the Texas-Mexico border to south Florida was dominated by a changing mixture of approximately a dozen plant species in nine genera. Only five of these dominants, and nine species overall, occurred in all four regions. Uniola paniculata was the dominant, except along the Louisiana coastline, where Spartina patens (wiregrass) replaced it. Other widespread beach species throughout the GoM were Ipomoea stolonifera (fiddle leaf morning glory), Croton punctatus (beach tea), Sporobolus virginicus (seashore dropseed), and Heterotheca subaxillaris (camphorweed), with the dune grass Panicum amarum (bitter panicum) prevalent, but decreasing in an eastward direction. Table 6.8 presents the distinguishing beach species for each region.

Considerable local variation occurs depending on the age and successional stage of the barrier strand. Figure 6.110 presents an elevation-vegetation transect across a young (12 years from formation) segment of Crooked Island West in northwest Florida (Johnson 1997). The embryo dunes along this profile are dominated by grasses, such as *Panicum amarum* var. *amarulum* (=*P. amarulum*, coastal panicgrass). More mature and stable shorelines formed as long as 53 years before the study on Crooked Island West show a transition from grasses to shrubs as dominants. The oldest and most stable dune ridges (some older than 100 years) are dominated by shrub species (Johnson 1997). One or two species dominate each community across the island: Foredunes—*Panicum amarum* var. *amarulum* and *Uniola paniculata* (with *Iva imbricata* (seacoast marsh elder) and *Schizachyrium maritimum* (gulf bluestem) as frequent associates); Swales—although diverse, species such as *Fimbristylis castanea* (marsh fimbry) and *Paspalum distichum* (knotgrass) are prevalent, as well as *Andropogon virginicus* (broomsedge) and *Dichanthelium aciculare* (needleleaf rosette grass); Maritime Forests—*Pinus clausa* (sand pine) and *P. elliottii* (slash pine) communities with *Ilex glabra* (inkberry) and *I. vomitoria* (yaupon), and many other small trees and shrubs in the understory.

Barrier strand communities associated with barrier islands and beaches of the Mississippi River Deltaic Complex in Louisiana are distinctly different from those to the east. Because of a limited sand supply, frequent winter cold fronts and episodic hurricanes, and rapid subsidence



Figure 6.110. Vegetation—elevation profile along a dune-swale transect (A-A') (from Johnson 1997; used with permission of the Journal of Coastal Research) on Crooked Island, located east of Panama City in northwest Florida. Letters indicate dominant plant species on each numbered ridge and swale (*Pa* = *Panicum amarum* var. *amarulum*, *Sm* = *Schizachyrium maritimum*, *Pd* = *Paspalum distichum*, *Ee* = *Eragrostis elliotii*, Av = Andropogon virginicus).

of the coastal deltaic landscape, barrier strand development is quite limited. Sand dunes are generally small in stature (Figure 6.111) and subject to frequent overwash. Consequently, beaches are predominantly erosional and relatively narrow. Some of these environmental and geologic features are, in part, responsible for the almost complete absence of *Uniola paniculata* (sea oats) along the Louisiana barriers, west of the Mississippi River (Hester and Mendelssohn 1991). Figures 6.111 and 6.112 present many of the common coastal strand species found in Louisiana.

Shorelines of southeastern Texas are very similar to those in southwestern Louisiana, but progressing southward, differences develop. Sand dunes and beaches become larger and more expansive and *Uniola paniculata* (sea oats) again gains dominance. Common plant species on Padre Island are provided in Table 6.9 (Smith 2002).

Beaches and barrier islands occur throughout the southern GoM (Figure 6.95). Coastal strand vegetation of this region has been described in a series of papers (Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988, 1993, 2007; Silvia et al. 1991). As expected, the barrier strand flora of northern Tamaulipas is similar to that of southern Texas. Just south of the United States-Mexico border at Playa Washington, Uniola paniculata (sea oats) and Ipomoea *pes-caprae* (goat foot morning glory or bayhops) frequently occur along exposed parts of the dune and are sometimes replaced by Croton punctatus (beach tea) and Scaevola plumieri (gullfeed). Landward of this zone, Croton mixes with other species like Clappia suaedifolia (fleshy claydaisy), *Phyla cuneifolia* (wedgeleaf), *Sabatia arenicola* (sand rose gentian), and others. In southern Tamaulipas and northern Veracruz, dunes generally reach a height of 3-5 m (10 to 16 ft), with the exception of 30 m (98 ft) dunes in Cabo Rojo, and include the same species as previously mentioned, plus others like *Sesuvium portulacastrum* (shoreline sea purslane), Coccoloba uvifera, and Canavalia maritima. In general, tropical species like those present in south Florida are more prevalent. Figure 6.113 presents a vegetation profile at Bocatoma, Tamaulipas (Moreno-Casasola 1993). Uniola does not occur here, but rather Sporobolus *virginicus* (seashore dropseed) becomes the primary beach and dune grass. *Lippia* (=*Phyla*) nodiflora (frog fruit or fogfruit) is a typical swale species, and the mangrove associate, Conocarpus erecta (=C. erectus), (buttonwood or button mangrove), dominates the lagoonal shoreline.

One of the most interesting features of the Tamaulipas shoreline is Cabo Rojo, which has been described as a tombolo extending into the sea (Britton and Morton 1989). Because of the difference in shoreline orientation between the northern and southern sections of Cabo Rojo, the northern section of the barrier strand receives the full force of frequent winter nortes, while



Figure 6.111. Vegetation—elevation profile across one section of the Caminada-Moreau Beach, west of Grand Isle, LA (modified from Mendelssohn et al. 1983). (*Andropogon scoparius = Schizachyrium scoparium; Scirpus americanus = Schoenoplectus olneyi; Lippia = Phyla*).

the southern section is somewhat protected. This difference both affects topography and species composition. Because of the extensive presence of aeolian sands on the northern leg, the dunes here can reach more than 30 m (98 ft). Strong winter winds and wave energy create a steep beach backed by sand dunes. Stable vegetated dunes occur behind the primary dune line, forming shrub thicket and forest habitats. *Coccoloba uvifera* (seagrape) is the most common leading species in the northern section. The southern section is composed of a series of old beach ridges that shield the strand from winds and accumulating sand. As a result, dunes are virtually absent, and *Ipomoea pes-caprae* (goatfoot morning glory) and *Croton punctatus*



Figure 6.112. Vegetation—elevation profile across the northern segment of the Chandeleur Islands, Louisiana (modified after Mendelssohn et al. 1983) (*Andropogon scoparius = Schizachyrium scoparium*).

Table 6.9. Comm	ion Plant Species on the Ba	rrier Strand of Padre Island	(data from Smith 2002)

Backshore	Primary Dunes	Low Coastal Sand and Swales
Uniola paniculata Sesuvium portulacastrum Sporobolus virginicus	Uniola paniculata Paspalum monostachyum Paspalum setaceum Oenothera drummondii Ipomoea pes-capre Ipomoea imperati Chamaecrista fasciculata	Paspalum monostachyum Eragrostis secundiflora Fimbristylis castanea Heliotropium curassavicum Hydrocotyle bonariensis Erigeron procumbens Phyla nodiflora Stemodia tomentosa

(beach tea) dominate the leading vegetation on the beach. Plant diversity of strand vegetation in the northern section (25 species) is much greater than in the southern section (12 species) probably because the frequent washovers and disturbances in the northern leg create greater habitat heterogeneity and more microenvironments suited for more species (Poggie 1962).

The Veracruz shoreline is complex and gives rise to a variety of barrier strand physiognomies from narrow beaches in some areas in the northern part to the enormous dune systems along the central Veracruz shoreline (Britton and Morton 1989). Sands can vary from primarily light-colored quartz to dark, heavy mineral sand, derived from volcanic rocks. *Uniola paniculata* (sea oats), a dominant dune grass in the northern GoM, basically disappears south of the state of Tamaulipas. Plant zonation is generally distinct with definable plant communities extending from the beach landward to the large fixed dunes and semi-deciduous tropical forests (Figure 6.114a). Numerous microenvironments occur within such large coastal strands,



including wet swales and inter-dunal lagoons. Common species and their zonation are depicted in Figure 6.114b (Moreno-Casasola 1993, 2007).

Further to the east is the state of Tabasco, which has a relatively small coastline. Here, a complex of active and abandoned river channels and their associated deltas characterize the coastal plain. Quartz-sand beaches occur along the shoreline between the river mouths. Although dunes occur in scattered places, the area is characterized by a low-elevation beachridge system (Figure 6.115) (Moreno-Casasola 1993). In some areas (e.g., San Pablo), sand dune-ridges are backed by mangroves, which are further fringed by marsh shrubs, e.g., *Borrichia frutescens* (marsh elder) and *Hibiscus tiliaceus* (sea hibiscus). In the wet swales between beach ridges, a distinct community of low palms such as *Bactris* (bactris palm) and *Paurotis* (Everglades palm) alternate with solid stands of *Xylosma* sp. (logwood).

The State of Campeche, on the Yucatán peninsula, is characterized by its karst basement material and its almost continuous low-elevation barrier beach composed of shell and other calcareous materials (Moreno-Casasola 1993). The beach is often separated from the mainland by shallow, but wide lagoons and salt flats. The sand flats flood during the winter when nortes push seawater through the inlets. Where calcareous sands dominate, the coastal vegetation becomes more Caribbean-like with inclusions of *Coccoloba uvifera* (seagrape), *Scaevola plumieri* (gullfeed), *Suriana maritima* (bay cedar), and others (Figure 6.116).

Along the northern Yucatán shorelines, beach sand is primarily calcareous, and the beach is narrow with a parallel ridge (1 to 2 m [3.3 to 6.6 ft]). As described by Moreno-Casasola (1993), a vegetation gradient exists from beach to mainland. Pioneer vegetation consists of species such as *Chamaesyce buxifolia* (coastal beach sandmat), *Croton punctatus* (beach tea), *Scaevola plumieri* (gullfeed), *Sesuvium portulacastrum* (shoreline seapurslane), *Suaeda linear*is (annual seepweed), and *Tournefortia gnaphaloides* (sea rosemary). The pioneer zone ends at a shore-parallel thicket dominated by *Suriana maritima*. The landward swale consists of species such as



Figure 6.114. (a) Idealized vegetation profile of a mature dune system from beach to maritime forest (from Moreno-Casasola 2007). (b) Plant species composition and distribution of a dune system in the central part of Veracruz, Mexico (from Moreno-Casasola 1993; used with permission).



Figure 6.115. Vegetation profile from Las Flores, Tabasco, Mexico (modified after Moreno-Casasola 1993).

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Figure 6.116. Vegetation profile from Champotón, Campeche, Mexico (modified after Moreno-Casasola 1993).

Hymenocallis littoralis (beach spiderlily), *Agave silvestris* (agave), *Scaevola plumieri*, and others. Along other parts of the northern Yucatán, *Coccoloba uvifera* (seagrape) is the dominant species, gradually increasing in height landward from the beach. Species of wild cotton (*Gossypium hirsutum* and *G. punctatum*) are interesting inclusions in this flora. *Gossypium punctatum*, closely related to commercial cotton, grows on the outer beach ridges and overlaps with the distribution of *Coccoloba uvifera* (seagrape) (Sauer 1967). Figure 6.117 presents a generalized vegetation profile for the northern Yucatán coastline.

Along the northwestern coast of Cuba, beach and dune habitats are especially well developed in the Guanahacabibes Peninsula and the shoreline between Havana and Varadero (Borhidi 1996) (Figures 6.101 and 6.118). This coast consists mainly of Pliocene limestone, which is seldom interrupted by muddy or sandy beaches. Flat karsts and cliffs are most common, with some rocky hills. The vegetation in this region consists of coastal thickets, dry evergreen forests and shrubwoods, fragments of semi-deciduous forests on the slopes, and small stands of mangroves. The dominant pioneer species of the strand line are *Ipomoea pes-capre* (goat foot morning glory) and *Canavalia maritima* (baybean). Landward of the pioneer species, but still on the beach, are combinations of species such as *Sporobolus virginicus* and *Baccharis halimifolia* (groundsel bush), *Borrichia arborescens* (tree seaside tansy), *Tournefortia gnaphaloides* (sea rosemary), *Spartina juncea* (=*S. patens*), and others. Many of these species also occur on the northern shoreline of the Yucatán. The primary dunes are often covered by the shrub seagrape, *Coccoloba uvifera*. Further landward the coastal gradient terminates with dry coastal evergreen shrubs (Figure 6.118) (Borhidi 1996).

A somewhat unique coastal habitat present along the shoreline is the coastal rock pavement community. Although widespread along the southern coast of eastern and central Cuba, it also occurs at Havana and Matanzas. The more open pioneer community is composed of succulent



Figure 6.117. Vegetation profile for beach and wide ridge system in Yucatán, Mexico (from Moreno-Casasola 1993; used with permission). 1=beach; 2=embryo dune and foredune; 5=sheltered zone; 6=fixed dunes; 4=humid and wet slacks.



Figure 6.118. Vegetation of beach and dune habitats in the Casilda Peninsula, near Trinidad, Cuba (from Borhidi 1996, used with permission).

creepers such as *Lithophila muscoides* (talustuft), *Trianthema portulacastrum* (desert horse purslane), and *Sesuvium* spp. Landward is the coastal rocky shrub zone composed of *Rachicallis americana* (seaside rocket shrub), *Borrichia arborescens* (tree seaside tansy), *Conocarpus erecta* (mangrove button), *Opuntia dillenii* (erect pricklypear), and others. On cliffs exposed to salt spray and winds, *Rachicallis* sp. (seaside rocket shrub) and *Conocarpus* form a community. Sometimes *Coccoloba uvifera* (sea grape) will occur further landward on shallow sands, or thorn shrubs, dominated by species of *Mimosa* (mimosa), may dominate (Figure 6.119) (Borhidi 1996).



Figure 6.119. Vegetation of coastal rock pavement communities. (a) Aroya Blanco near Jibacoa, Cuba and (b) Punta Guanal near Matanzas, Cuba. *Em Eugenia maleolens, Tm Tabebuia myrtifolia, Ph Piscidia havanensis* (from Borhidi 1996, used with permission).

6.5.1.3 Fauna: Swash Zone and Shallow Tidal Pass Habitats

Relatively few studies in the past 20 to 30 years have focused on faunal assemblages associated with shallow (3 to 15 m [10 to 50 ft]) water swash zone habitats in the GoM. These sandy habitats are pervasive on mainland beaches from Texas to Florida and beaches found on the Louisiana, Mississippi, Alabama, and Florida barrier islands. Sandy beach and beach flat habitats in the Northern GoM are under continual pressure due to population growth along coastal areas, coastal resource utilization, recreational development, shoreline manipulation, tropical storms, and sea-level rise. Sandy sediments define coastal beaches; their geomorphology can be either narrow and steep (reflective) or wide and flat (dissipative) (Aagaard et al. 2013; Schlacher et al. 2008). Erosional beaches are typical in the Northern GoM (Buster and Holmes 2011). Their geological origin and the sorting effects of waves and currents influence the particle size of beach sand. Short-term geomorphic dynamics of sand beaches are typically linked to a source of sand and the energy to move it (Aagaard et al. 2013). Sand transport is greatest in the exposed surf zone and sand storage greatest in coastal dunes and nearshore sandbars. The intertidal and subtidal beach habitats and the shallow tidal pass habitats represent harsh habitats for organisms and often are characterized by steep gradients of environmental factors including wave action, currents, water depth, sediment composition, temperature, food availability, and regional/seasonal climatic factors (e.g., hurricanes) (Rakocinski et al. 1993; Schlacher et al. 2008).

6.5.1.3.1 Biotic Community Structure

A number of large-scale surveys and summaries have listed marine invertebrate species that occur in habitats throughout the GoM, including shallow, swash zone habitats (e.g., Rakocinski et al. 1991, 1993, 1998; Felder and Camp 2009). Barry A. Vittor and Associates, Inc. (2011) studied beach zone macroinfauna for the U.S. Army Corps of Engineers (USACE) Mississippi Coastal Improvements Program (MsCIP). The USACE Mississippi Sound and Adjacent Areas study (Shaw et al. 1982) broadly characterized benthic habitats based on sediment texture and macroinvertebrate assemblages, and feeding guilds present. Considerable variability in faunal assemblages occurred in similar sediment types. For example, sandy sediments of shallow sound habitats were characterized as having a macroinvertebrate assemblage dominated by the small bivalve, Gemma gemma, the polychaete, Paraonis fulgens, and the amphipod, Lepidactylus triarticulatus. This habitat had the lowest average taxa richness. the highest station mean density, and the lowest taxa diversity. The large variability in taxa richness and abundance seen between stations was due to the clumped distribution of G. gemma and L. triarticulatus. In contrast, a shallow tidal pass habitat with >95 % sand was characterized as having a macroinvertebrate assemblage dominated by surface and subsurface deposit feeders. including the polychaetes *Polygordius* spp., *Mediomastus* spp., and *Spiophanes bombyx*; the chordate Branchiostoma spp.; the crustacean Acanthohaustorius spp.; and suspension/filter feeders such as the bivalve Crassinella lunulata.

Rakocinski et al. (1991) studied the macroinvertebrate assemblages associated with barrier islands bordering the mainland of Mississippi, Alabama, and Florida. The Mississippi and Alabama barrier islands provide a wide range of environmental conditions for macroinvertebrate assemblages, the most influential being protected beaches on the north or "sound" sides of the islands versus exposed beaches located on the south or GoM sides of the islands. Early studies have also shown that macroinvertebrate assemblages on barrier island beaches have lower taxa richness and abundance than mainland beach habitats. A variety of environmental variables play a role in determining the macroinvertebrate assemblage in a given barrier island habitat, including wave action, sediment properties (primarily the percentage of sand), turbulence, salinity, dissolved oxygen (the occurrence of hypoxia), water depth, the frequency of tropical storms//hurricanes, and seasonal variability in these factors. Rakocinski et al. (1993) also studied benthic habitats seaward from the swash zone at Perdido Key (Florida) in an attempt to determine zonation patterns in macroinvertebrate assemblages. The authors sampled at 0, 25, 50, 75, 100, 150, 300, 500, and 800 m along a transect perpendicular to the beach. Crustaceans and polychaetes made up 75 % of the total number of individuals and species, with taxa richness and abundance increasing with depth (seaward). Total densities increased an order of magnitude from the shore to the deeper seaward stations and ranged from 2,000 individuals/m² to 20,000 individuals/m². The authors identified four unique zones along the depth gradient and land/sea interface: (1) the swash zone had a macroinvertebrate assemblage composed of motile. burrowing and/or tube-dwelling suspension feeders of medium body size; the dominant taxa were the polychaete, *Scolelepis squamata*, the decapod crustacean, *Emerita*, and the bivalve, Donax; (2) an inner subtidal zone which ranged from the shoreline to 100 m (330 ft) with depths <2 m (6.6 ft) and including nearshore troughs and sand bars; this habitat was dominated by small to large deposit and suspension feeding crustaceans and polychaetes; (3) a subtidal transition zone which ranged from 10 to 300 m (33 to 984 ft) offshore with depths of 2 to 4 m (6.6 to 13.1 ft); the macroinvertebrate assemblage was dominated by small and large bodied polychaetes; and (4) an outer subtidal zone which ranged from 300 to 800 m (984 to 2,625 ft) offshore, with depths between 4 and 6 m (13.1 and 19.7 ft); and a macroinvertebrate assemblage dominated by polychaetes, gammarid amphipods, gastropods, and the chordate *Branchiostoma*.

The macroinvertebrate assemblages at the shallow sand pass stations associated with the Mississippi barrier islands (Barry A. Vittor and Associates, Inc. 2011) were similar to the Shallow Sound Sand and Tidal Pass habitats characterized in the MSAW study (Shaw et al. 1982), and the Shallow Subtidal and Inner Subtidal (shoreline to 100 m [328 ft], depths <2 m [6.6 ft]) habitats recognized by Rakocinski et al. (1991, 1993). The macroinvertebrate assemblages characteristic of the Inner Subtidal habitat recognized by Rakocinski et al. (1993) were also similar to assemblages associated with the barrier islands in the MsCIP study with a dominance of polychaetes, haustorid amphipods, and bivalves; in addition, macroinvertebrate assemblages in the Shallow Subtidal habitats recognized by Rakocinski et al. (1991) were similarly dominated by polychaetes and amphipods.

Taxa richness and density data collected from sandy beach stations at distances of 3, 6, and 16 m (9.8, 19.7, and 52.5 ft) from shore in the MsCIP study had low taxa richness, extremely variable densities based on the patchy distribution of several habitat-specific macroinvertebrate taxa, and no discernible seasonal patterns. One factor that consistently separated macroinvertebrate assemblages on Petit Bois, Horn, and Ship Islands was whether or not the stations were located on the Mississippi Sound side of the islands or on the Gulf side. Stations located on the Mississippi Sound side of the islands had two to four times as many taxa and an order of magnitude higher densities than stations located on the GoM side of the islands. These data were similar to those found by Rakocinski et al. (1991) for Alabama, Mississippi, and Florida barrier islands with exposed GoM beaches and protected Sound beaches.

Epifaunal organisms associated with swash zone and shallow tidal pass habitats are typically opportunistic, large, active predatory and grazing organisms. The swash zone habitats in the GoM are dominated by various highly mobile decapod taxa (hermit crabs, *Pagurus*; blue crabs, *Callinectes*; ghost crabs, *Ocypode*; pinnixid crabs; portunid crabs, *Arenaeus*), shallow burrowing decapods (mole crabs, *Emerita*), echinoderms (sand dollars, *Mellita*), bivalves (*Donax*), and various gastropods (naticid moon snails; olives, *Olivella*).

Nekton assemblages associated with the waters surrounding the beaches along the barrier strand habitat are generally dominated by very few species, most of which are larval and juvenile life stages (Ruple 1984; Ross et al. 1987). Samples collected over several years along Horn Island, part of a barrier chain along the Mississippi-Alabama coast, included >75 species of fishes and natant decapod crustaceans, but >95 % of the individuals were represented by only four fish families (Clupeidae—herrings, Engrualidae—anchovies, Sciaenidae—drums, Carangidae—jacks) and one family (Portunidae) of natant decapod crustacean (Modde and Ross 1980; Ross et al. 1987). Only a few species within each family were abundant. Harengula *jaguana* (scaled sardine) dominated the clupeids. Anchoa lvolepis (dusky anchovy), A. hepsetus (striped anchovy), and A. mitchilli (bay anchovy) comprised almost all of the engraulids. The most abundant carangids were Trachinotus carolinus (Florida pompano) and Caranx hippos (crevalle jack), and the sciaenids were mostly Menticirrhus littoralis (gulf kingfish) and Leiostomus xanturus (spot). Callinectes sapidus (blue crab) was the most abundant portunid. A similar assemblage of surf zone fishes occurred along the beaches of Padre Island, Texas in the northwest GoM (Smith and Smith 2007), where in addition to the species listed above, mullet (Mugil cephalus and M. curema) were among seasonal dominants (M. cephalus in winter and *M. curema* in spring).

Although surf zone nekton have not been a focus of many studies throughout the GoM, samples collected from barrier strands along the Atlantic coasts of the United States (e.g., Layman 2000; Wilbur et al. 2003) and South America (e.g., Monteiro-Neto et al. 2003) are remarkably similar, even with respect to the dominant species. For example, *Trachinotus carolinus* is a prominent carangid and *Menticirrhus* spp. represent most of the sciaenids

along barrier strand beaches at all of these locations. In some areas, mullet (Mugilidae) and silversides (Atherinidae) are also abundant (Layman 2000; Monteiro-Neto et al. 2003).

Shallow waters have been recognized as potentially important predator refugia for coastal marine and estuarine species, particularly in areas where SAV has been reduced or is absent (Ruiz et al. 1993). The shallow waters along barrier strand beaches of the GoM may serve a similar function, but a number of factors affect the occurrence and abundance of nekton along beach habitats, including seasonal reproductive patterns (Modde and Ross 1980; Gibson et al. 1993; Monteiro-Neto et al. 2003), diurnal or tidal foraging activity (Robertson and Lenanton 1984; Ross et al. 1987; Gibson et al. 1996), wind direction and intensity (Ruple 1984), and changes in beach configuration or composition of sediments resulting from storms or anthropogenic activities such as beach nourishment (Wilbur et al. 2003). Short-term episodic changes in physical attributes of nearshore waters, such as the onshore movement of hypoxic bottom waters, may drive onshore migrations of nekton populations as occurs at infrequent intervals in Mobile Bay, where the well-known summer phenomenon has been termed "Jubilee" (Loesch 1960; May 1973).

The physically dynamic nature of the barrier strand often results in the creation and extirpation of ponded aquatic habitats at different distances inland from the surf zone. These semi-permanent pools serve as habitat for a sometimes-ephemeral assemblage of nekton (Ross and Doherty 1994). Depending on distance from the shore, frequency of aquatic connections with the surf zone, and colonization dynamics, these assemblages are either dominated by nekton commonly found in back-barrier marsh habitats (e.g., Cyprinodontidae, Fundulidae, Poeciliidae), which exhibit a moderate level of stability, or a much less persistent assemblage of accidental colonists (Engraulidae, Sciaenidae, Carangidae, Clupeidae, Mugilidae) from the surf zone. Pools containing marsh colonists include reproductively active adults, thereby maintaining a persistent assemblage over time. However, surf zone colonists are represented only by juveniles that are unlikely to survive, and hence, form only ephemeral nekton assemblages.

6.5.2 Salt Marshes

6.5.2.1 Dominant Forcing Functions

Salt marshes generally occur along shorelines with sufficient protection from wave action, e.g., in protected shallow bays and estuaries, lagoons, and on the landward sides of barrier islands. Excessive wave action prevents establishment of seedlings, exposes the shallow root systems, and limits deposition of fine sediments that promote plant growth. Salt marshes are more extensive along low-relief coastlines where tidal intrusion reaches far inland and where there is abundant availability and accumulation of silts and clays, such as found in the north central GoM.

The hydrologic regime exerts a tremendous influence on the structure and function of wetlands, including salt marshes. Hydrology affects abiotic factors such as salinity, soil moisture, soil oxygen, and nutrient availability, as well as biotic factors such as dispersal of seeds. These factors, in turn, influence the distribution and relative abundance of plant species and ecosystem productivity. The tides constitute both a stress and a subsidy (Odum and Fanning 1973) for salt marsh development (Mendelssohn and Morris 2000). Tidal inundation leads to soil anaerobiosis and, depending on the flood tolerance of species, may inhibit survival, growth, and expansion. For salt marsh species, effects of low oxygen may limit vegetative spread via rhizomes (underground stems) and/or seed germination. Tides also import high concentrations of potentially toxic ions such as Na⁺ and Cl⁻. Tidal fluctuation, however, acts as a subsidy to

salt marsh systems by importing nutrients, aerating the soil porewater, flushing accumulated salts and reduced compounds (e.g., hydrogen sulfide) that are phytotoxic, and enhancing the dispersion of seeds and/or vegetative fragments. The tidal subsidy effect is readily apparent along hydrodynamically active creekbanks, where marsh grasses, like *Spartina alterniflora*, are taller and more productive than in the interior of the marsh, where belowground tidal water movement is minimal (Mendelssohn and Seneca 1980; Howes et al. 1986).

Although salt marshes achieve best development on fine-grained sediments, they occur on a variety of substrates, including sands and volcanic lava. Terrigenous sediments are carried by rivers from inland areas to be deposited along the GoM or may originate from adjacent eroding shorelines. Fine silts and clays contain abundant exchangeable ions that fertilize and enhance productivity of the plants. Marshes may also develop on sandy substrata, particularly in stable, sheltered areas where the sand mixes with silt or organic matter (Chapman 1976). In the case of autochthonous deposits, the marsh vegetation itself contributes to sedimentation and soil development through production of organic matter, primarily below ground (Nyman et al. 1993; Turner et al. 2000). The organic matter content of soils may vary from <10 to >90 %, depending on the relative contribution of organic versus mineral deposits. High rates of root production combined with slow decomposition rates in the anaerobic soil environment may promote large accumulations of organic matter. Other biogenic deposits include carbonate skeletons of calcareous algae (e.g., *Halimeda* spp.), which are the major source of sand in the Caribbean, and shells of oysters and other invertebrates, which can be important constituents of salt marsh sediments.

Salt marsh soils are typically saline, but salinity varies depending on freshwater input, the ratio of rainfall to evapotranspiration, and hydrology (Thibodeau et al. 1998). In the low marsh, regular tidal inundation maintains salinities near that of seawater. At higher elevations, the interaction between frequency and duration of tidal flooding, on one hand, and evapotranspiration and freshwater runoff, on the other, results in substantial variability in soil salinity. During periods of high rainfall or in regions receiving freshwater runoff, salinities may be low between tidal flooding events. Salt marshes immediately adjacent to the Mississippi River, for example, may experience wide fluctuations in porewater salinity with average salinities less than 15 ‰ (ppt) (Mendelssohn and Kuhn 2003). Areas with high evapotranspiration rates and irregular tidal flushing develop hypersaline conditions with porewater salinities sometimes exceeding 70 ‰. Salt marsh plants are able to survive and grow at elevated salinities due to a number of unique adaptations. Localized freshwater discharges in seasonally dry regions may also prevent hypersaline conditions and promote vegetative development. However, along some arid tropical and subtropical coasts, for example the Laguna Madre of southern Texas and northern Mexico, extended periods of hypersaline conditions may stunt or even prevent the survival of perennial vegetation.

Inundation of salt marsh soils with water leads to anaerobic conditions due to a 10,000times slower diffusion rate of oxygen in aqueous solution compared to air (Gambrell and Patrick 1978). Once oxygen is depleted by soil and plant root respiration, it is not quickly replaced and anaerobic conditions prevail. In the absence of oxygen, soil microorganisms utilize alternate oxidants (NO³⁻, Mn⁺⁴, Fe⁺³, SO₄²⁻) as electron acceptors. This process results in an increased soil oxygen demand, variation in availability and form of plant nutrients, and a build-up of toxic, reduced compounds in the soil. Soil Eh is a measure of the intensity of soil reduction, and low (\leq -100 millivolts [mV]) values are characteristic of strongly reducing conditions. Values ranging from +300 to -250 mV are typical of flooded soils and vary depending on soil texture, concentrations of redox elements, and flooding regime. The oxidation-reduction status of marsh soils is influenced by the presence of plant roots (Mendelssohn and Postek 1982; McKee et al. 1988). Leakage of oxygen from the plant roots into the surrounding soil creates an oxidized rhizosphere in which redox potentials can be higher than in the bulk soil. Thus, the growth of salt marsh vegetation is influenced by the anoxic condition of the soil substrate, but the plants themselves also modify the oxidation–reduction status.

The nutritional status of salt marshes is greatly influenced by tidal and riverine processes. Tides distribute mineral sediment and affect the redox status of the substrate, which in turn controls nutrient transformations, form, and/or availability. Rivers deliver nutrient-rich sediments to coastal salt marshes, resulting in some of the highest productivities (Sasser et al. 1995). The primary productivity of the vast majority of salt marshes is nitrogen limited (Mendelssohn and Morris 2000). Availability of phosphorus in anaerobic sediments typically exceeds that of ammonium, the dominant nitrogen form (Mendelssohn 1979), and is therefore of lesser importance. Numerous fertilization experiments in salt marshes have consistently demonstrated that nitrogen is the primary growth-limiting nutrient (see Mendelssohn et al. 1982 and references therein), although phosphorus can limit plant growth in sandy environments where phosphorus availability is low (Broome et al. 1975).

Another important controller of plant production, in addition to nutrients, is phytotoxin accumulation, which can occur in anaerobic sediments. In the marine environment a major phytotoxin produced under anaerobic conditions is hydrogen sulfide, which results from the bacterial reduction of sulfate to sulfide. Sulfate is the second most abundant anion in seawater and begins to be reduced under anaerobic conditions after NO^{3-} , Mn^{+4} , and Fe⁺³ have been reduced. The reduction of sulfate is carried out by true anaerobes, e.g., *Desulfovibrio*, and is thus dependent on anoxic conditions. Considerable research has demonstrated that sulfide is a primary driver of salt marsh primary productivity by impairing nitrogen uptake and assimilation (Mendelssohn and Morris 2000 and references therein).

On the broadest scale, climate, in particular temperature and rainfall, are primary controllers of species distribution and productivity. In the GoM, salt marshes are restricted in both growth and distribution in arid regions that generate high soil salinities. High temperature, per se, is not a direct constraint on the distribution of salt marsh vegetation but, as discussed previously, allows for development of mangroves, which outcompete salt marsh plants and thereby prevent salt marsh dominance (Mendelssohn and McKee 2000).

6.5.2.2 Vegetation

6.5.2.2.1 Structure and Zonation

Salt marsh communities are relatively species-poor and, in fact, along some shorelines of the northern GoM consist of monospecific stands of *Spartina alterniflora* (smooth cordgrass). Species richness generally decreases with increasing salinity (Mendelssohn and McKee 2000). For example, while as many as 93 species have been documented in Louisiana's coastal freshwater marshes, species richness in nearby salt marshes does not exceed 17 and, as previously mentioned, most individual salt marshes contain far fewer species (Chabreck 1972).

Most salt marshes are composed of plant communities dominated by graminoids such as grasses, sedges, and rushes; non-graminoid herbaceous communities dominated by forbs and succulents; and dwarf-shrub communities, especially common along arid and semi-arid coasts (Adam 1990). Unlike forests, which contain a number of strata, the vertical structure of salt marshes is relatively simple. Minor strata development is generated by different plant growth forms and the presence of benthic and epiphytic algae, where light penetration through the canopy allows.

Two physiographic zones, differing in hydrology and resulting soil and vegetation, occur in salt marshes. The low marsh, or regularly flooded marsh, is inundated by each tidal event, once or twice a day depending on whether the tides are diurnal or semidiurnal, respectively. The high

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marsh, sometimes referred to as the irregularly flooded marsh, is higher in elevation than the low marsh and thus is flooded less frequently, sometimes only during spring tides or extreme wind tides. Species richness tends to increase along an elevation gradient from the sea to the marsh/terrestrial ecotone. The low marsh has very low species richness, sometimes with only one species present, whereas the high marsh often exhibits a much greater number of species, especially where freshwater runoff from adjacent uplands occurs. The highest elevations of the salt marsh can develop into hypersaline areas called salt pans. The salt pan is inundated only by the highest spring tides, and then may not be inundated again until the next spring tide. As a result, salt often accumulates to lethal or near-lethal levels due to evapotranspiration in the absence of tidal dilution and leaching. Consequently, salt pans are often devoid of vegetation or are characterized by stunted halophytes and low species richness (Hoffman and Dawes 1997).

Zonation of species is a frequently observed characteristic of plant communities in habitats with strong physical and/or chemical gradients. In wetlands, spatial segregation of species often occurs in conjunction with elevation gradients that determine depth and duration of flooding and edaphic conditions influencing plant growth (Pielou and Routledge 1976; Vince and Snow 1984). Much work has centered on the role of abiotic factors as determinants of plant growth and distribution. However, the capacities of species to tolerate environmental conditions along elevation gradients greatly overlap, suggesting that factors other than environmental must play a role in generating zonation. In fact, biotic factors such as dispersal, competition, and herbivory may play a major role, along with abiotic constraints, in determining actual zonation (Pennings et al. 2005; Keddy 2010).

In salt marshes, species zonation is generally a ubiquitous feature, although species within a zone may vary from one geographical location in the GoM to another. However, where elevation gradients are shallow and/or occur over large distances, such as in the Mississippi River delta, zonation is visually less apparent, although quantifiable at larger spatial scales. Plant salt marsh zonation occurs along the elevation gradient from the seaward limit of the wetland to the terrestrial border. This elevation gradient is a complex gradient composed of multiple environmental factors that vary in time and space. The two most important abiotic factors controlling zonation along this gradient are inundation and salinity. Salt marsh species exhibit differential tolerances to these stressors. For example, *Spartina alterniflora*, a low marsh dominant, is more flood-tolerant than *S. patens*, a high marsh dominant, as documented in a Virginia salt marsh (Gleason and Zieman 1981). However, the species' tolerance limits to both inundation and salinity overlap considerably so that, for example, where inundation and salinity stresses are minimal many of these species could theoretically coexist. Thus, as briefly mentioned previously, abiotic factors alone cannot completely explain the observed zonation in salt marshes.

Competition also influences species zonation. Bertness and Ellison (1987) demonstrated in a New England salt marsh that zonation of *Spartina alterniflora* and *S. patens* is controlled by both environmental tolerances and competition. Competition between the species plays a more important role at the less stressful landward boundary of the marsh while abiotic factors control species pattern along the more stressful seaward end of the elevation gradient. For example, *Spartina patens* (wiregrass or saltmeadow cordgrass) does not occur at the most seaward limit of salt marshes because it cannot tolerate the inundation conditions. In contrast, *S. alterniflora* cannot exist at higher elevations because it is outcompeted by *S. patens*. As a result, competitive subordinates, in this example, *S. alterniflora*, are displaced to the more stressful zones of the gradient, while competitive dominants, in this case, *S. patens*, occupy the more benign areas. Similar conclusions were drawn from a number of studies throughout North America and elsewhere (Snow and Vince 1984; Bertness and Ellison 1987; Pennings et al. 2005). Disturbance in the form of wrack deposition or herbivory can also influence zonation patterns in salt marshes. Bertness and Ellison (1987), for example, found that the pattern of species occurrence in a New England high marsh was generated by tidal deposition of large mats of dead plant material (wrack), causing differential plant mortality. *Spartina alterniflora* and *Distichlis spicata* (saltgrass) are more tolerant of wrack burial than other marsh plants and their relative abundance increases in disturbed areas. When the disturbance is more severe and of longer duration, all the underlying vegetation can be killed by the wrack and bare patches are generated. *Distichlis spicata, Salicornia europaea* (glasswort), and *Spartina alterniflora* rapidly colonize these patches and dominate compared to adjacent non-disturbed areas. However, over time, these disturbance communities are outcompeted and replaced by the surrounding communities of *Spartina patens* and *Juncus gerardii* (saltmeadow rush). This pattern mosaic can reoccur or even persist if wrack disturbance is frequent. Disturbances, such as wrack deposition, also promote greater plant species richness by opening gaps in the canopy and thereby facilitating species recruitment and establishment (Ellison 1987; Bertness 1992).

6.5.2.2.2 Salt Marsh Zonation and Distribution in the Gulf of Mexico

The GoM contains the largest area of salt marshes in North America, 55 % of the United States total (Mendelssohn and McKee 2000). Although the majority of these salt marshes occur in the northern GoM, salt marshes occur sporadically in the more southerly locations of the Gulf. The plant species composition and salt marsh area vary greatly due to a combination of factors including differential climate, tidal range, local relief, and wave energy.

Although salt marshes are limited within the South Florida Ecoregion, they do occur, often in association with mangroves, in areas of disturbance, or associated with salt pans (Figure 6.120). Where mangroves dominate the shoreline, salt marsh vegetation generally occurs along the seaward and landward intertidal fringes (Montague and Wiegert 1990). At the landward edge, where seawater inundation is infrequent, narrow bands or larger of *Juncus roemerianus* (black needlerush) and high marsh plant communities often occur. Farther landward, high marshes can become salt pans with little vegetation or dominated by *Cladium jamaicense* (sawgrass) in the presence of freshwater. In contrast, at the seaward edge of *Rhizophora mangle* (red mangrove) forests, a narrow fringe of *Spartina alterniflora* (smooth cordgrass) can occur (Figure 6.121) (Montague and Wiegert 1990). In the Ten Thousand Islands region of southwestern Florida (Figures 6.80 and 6.81), mangrove coverage has increased by approximately 35 % over 78 years, probably due to sea-level rise and possibly altered freshwater input (Krauss et al. 2011). Hence, the prevalence of coastal herbaceous marsh in the South Florida Ecoregion may be at risk.

Salt marshes of the eastern GoM (western Florida, Alabama, and Mississippi) are primarily irregularly flooded marshes dominated by *Juncus roemerianus*. Twenty-eight percent of U.S. *J. roemerianus* marshes occur in the eastern region of the GoM, an area containing only 8 % of U.S. marshland (Stout 1984). Other common salt marsh species in this region include *Spartina alterniflora*, *S. patens*, *S. cynosuroides* (big cordgrass), *Distichlis spicata*, *Salicornia* spp., *Schoenoplectus americanus* (=*Scirpus olneyi*) (chairmaker's bulrush or three-square), and *Schoenoplectus robustus* (=*Scirpus robustus*) (sturdy bulrush or leafy three-square) (Figure 6.122). *Spartina alterniflora* frequently occurs as a narrow fringe seaward of the *Juncus* (Figure 6.122). About half of all salt marshes in Florida occur between Tampa Bay and the Alabama border (Montague and Odum 1997). This region, called the Big Bend area, where wave energy is low, shoreline relief is shallow, and tide range relatively high, has the greatest development of salt marshes in Florida. Similar to Alabama and Mississippi, the salt marshes here are irregularly flooded and dominated by *J. roemerianus*. In fact, about 60 % of northwest



Figure 6.120. Salt marsh distribution in Florida and physical features of the coast; tidal range in cm (*small numbers*), relative wave energy (*block letters*), and relative sea-level rise in cm per century (numbers in *parentheses*) (from Montague and Wiegert 1990; Figure 14.2. Occurrence of salt marshes in Florida and physical features of the coast, from "Salt Marshes" by Clay L. Montague and Richard G. Wiegert in Ecosystems of Florida, Edited by Ronald L. Myers and John J. Ewel. Gainesville: University Press of Florida, 1990, pp. 483. Reprinted with permission of the University Press of Florida.).



Figure 6.121. Typical south Florida mangrove-associated salt marsh. Notice *Spartina alterniflora* on the seaward fringe and *Juncus roemerianus* on the landward fringe (modified from Montague and Wiegert 1990).



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Figure 6.122. Generalized profiles of irregularly flooded gulf coast salt marshes as found in the northeastern GoM for (a) protected low energy shorelines and (b) open moderate energy shorelines (modified from Stout 1984).

Florida salt marshes are covered with monospecific stands of *J. roemerianus* (Montague and Wiegert 1990). *Juncus* throughout the northeast GoM often occurs as two growth forms: tall *Juncus* near shorelines and open water and short *Juncus* more inland. Further landward of the short *Juncus* is a suite of common high marsh species (Figures 6.122a, b). At the southern extent of the Florida Big Bend area at Cedar Key, *J. roemerianus* co-dominates with the black mangrove, *Avicennia germinans*.

Physiognomy of coastal marshes changes greatly west of the Pearl River at the Mississippi-Louisiana border. This is the Mississippi Estuarine Ecoregion, where *J. roemerianus* loses its dominance in the low-lying deltaic marshes of Louisiana (Figure 6.123). Here, regularly flooded salt marshes, the largest areal extent in the continental United States, are dominated by *S. alterniflora, Avicennia germinans*, and *Juncus roemerianus. Spartina patens* and *Distichlis spicata* are often subdominant species, depending on local topography and salinity (Visser et al. 1998). In the higher elevation Chenier Plain of southwestern Louisiana and southeastern Texas, the high marsh species, *Spartina patens* and *Distichlis spicata*, dominate brackish coastline marshes (Visser et al. 2000). Salt marsh vegetation dominates the shorelines of the eastern section (Delta Plain) of the Louisiana coast while both brackish and saline marshes occur along the western Louisiana coastline (Chenier Plain) (Figure 6.123). Westward flow of



Figure 6.123. (a) Vegetation types of Louisiana coastal wetlands (red = saline marsh, blue = brackish marsh, pink = intermediate marsh, green = fresh marsh, and yellow = other) (modified from Sasser et al. 2008). (b) Idealized vegetation profile across the diverse marsh types of coastal Louisiana (modified from Mendelssohn and McKee 2000).

freshwater from the Atchafalaya River is a primary controlling factor, as is freshwater from the Mississippi River, in reducing coastal salinity enough to allow the occurrence of intermediate salinity marshes along the shorelines of the Birdfoot Delta.

Visser et al. (1998) classified saline coastal marshes of the Delta Plain into two primary types: polyhaline mangrove and polyhaline oystergrass (also commonly known as smooth cordgrass). Polyhaline mangrove is characterized by the presence of *Avicennia germinans*, but is equally dominated by *Spartina alterniflora* and *Batis maritima* (turtleweed), a common associate of the black mangrove. Polyhaline oystergrass is always dominated by *Spartina alterniflora*, and sometimes co-dominates with *J. roemerianus*. In contrast, the coastal marshes of the Chenier Plain are divided into two primary types: mesohaline wiregrass and mesohaline mixture, both of which have brackish salinities (Visser et al. 2000). The mesohaline wiregrass type is co-dominated by *Spartina patens* and *Schoenoplectus americanus* (=*Scirpus olneyi*). This marsh type is mostly found along the fringing marshes of Vermillion Bay, but is also present along the eastern shore of Calcasieu Lake and south of Sabine Lake (Visser et al. 2000). The mesohaline mixture type is co-dominated by *Spartina alterniflora* and *Distichlis spicata*, but *S. patens* also frequently occurs. Visser et al. (2000) found this vegetation type in the marshes fringing the GoM and the western shoreline of Calcasieu Lake.

Salt marshes along the central Texas shoreline, for example in Galveston and adjacent East and West Bays, are once again dominated by *S. alterniflora*. Galveston Bay is unique in Texas in having relatively extensive emergent marshes instead of submerged seagrass beds as the



Figure 6.124. Salt marsh profile at Smith Point, East Bay, Texas showing relative elevations of plant communities (from White and Paine 1992; note, *Scirpus maritimus* is synonymous with *Schoenoplectus maritimus*).

major estuarine vegetation type. Salt marsh coverage is estimated at 120 km² (29,700 ac) (U.S. Department of Commerce 1989), although total wetland area is 1,594 km² (394,000 ac) (Moretzsohn et al. 2012). Of these, brackish marshes compose the greatest proportion at 65 to 70 %, with salt marshes composing approximately 25 to 30 % and fresh marshes 5 to 10 % (White and Paine 1992). For salt marshes, plant species such as *S. alterniflora*, *Batis maritima*, *Salicornia* spp., and *Juncus roemerianus* are most common in the lower elevation, more frequently flooded areas (Figure 6.124). In the high marsh, where flooding frequency is sporadic, species such as *Distichlis spicata*, *Salicornia bigelovii* (dwarf saltwort), *S. perennis* (=*Sarcocornia perennis*) (chickenclaws), *Monanthochloe littoralis* (shoregrass), and *Batis maritima* tend to dominate (Shew et al. 1981; U.S. Department of Commerce 1989; White and Paine 1992). *Spartina patens* and *S. spartinae* (gulf cordgrass) also occur in Galveston Bay salt marshes, but are more prevalent in brackish marshes (U.S. Department of Commerce 1989) (Figure 6.124).

The intertidal Spartina alterniflora-dominated marshes of central Texas are replaced in southern Texas and northern Mexico by succulent-dominated, hypersaline marshes. Succulent species such as *Batis maritima*, *Borrichia frutescens* (bushy seaside tansy), *Suaeda maritima* (herbaceous seepweed), *Sesuvium portulacastrum* (shoreline seapurslane), and others are dominant (Mendelssohn and McKee 2000). In the Texas Laguna Madre (Laguna Atascosa National Wildlife Refuge), salt marsh species are clearly zoned along elevation gradients with *Batis maritima* at lower elevations and *Spartina spartinae* at higher elevations (Judd and Lonard 2002). *Monanthochloe littoralis*, found farthest from the shoreline, occurs at intermediate elevations (Judd and Lonard 2002). Based on importance values, four species dominate the salt marsh shoreline of the Laguna Atascosa National Wildlife Refuge in southernmost Texas, *Spartina spartinae*, *Borrichia frutescens*, *Monanthochloe littoralis*, and *Sporobolus virginicus* (seashore dropseed), although as many as 32 species can be found in these salt marshes (Judd and Lonard 2002). Associations consisting of *Suaeda nigra* (=*Suaeda moquinii*) (Mojave seablite) and *Salicornia ambigua* (=*Salicornia perennis*) occur in some of the highest

salinity regions of the Laguna Madre in Mexico (Contreras-Espinosa and Castañeda-Lopez 2007). This association can be replaced by *Batis maritima*, and sometimes, by *Distichlis spicata* and *Monanthochloe littoralis*. In somewhat better-drained areas, *Spartina spartinae* and *Spartina densiflora* (denseflower cordgrass) are more frequent (Contreras-Espinosa and Castañeda-Lopez 2007). Costa and Davy (1992) also listed many of the same species as prevalent in salt marshes near Veracruz. Salt marsh area decreases greatly in the southern GoM, but salt marshes still occur in pockets adjacent to mangroves—especially at higher elevations (Olmsted 1993).

Olmsted (1993) estimated the extent of major wetlands of Mexico, including coastal lagoons; fresh, brackish, and salt marshes; mangrove swamps; freshwater lakes; and riverine forests, at 3,318,500 ha. At this time, an accurate estimate of salt marsh area for Mexico is not available, but salt marshes, per se, likely comprise only a small percentage of the total, which includes both freshwater and saline wetland types, like mangroves. The largest continuous wetland in the southern GoM is located in Tabasco and Campeche and is approximately 1,400,000 ha. Other large wetlands are located in Quintana Roo and the Yucatán (335,000 and 184,000 ha, respectively). These wetlands, together with those in Tabasco, Veracruz, Campeche, and Chiapas, make southeastern Mexico the most significant wetland region of Mexico (Olmsted 1993). Although salt marshes in tropical latitudes are often outcompeted and replaced by mangroves, West (1977) has cited three environmental situations where salt marsh species may exist, usually on the margins or within mangrove woodlands: (1) colonizing recently formed mudflats that fringe mangrove woodlands, (2) occupying saline soils on the inner edge or within the mangrove woodland, and (3) colonizing disturbed areas within a mangrove woodland.

In more tropical Mexico, brackish and saline marshes are commonly found in association with mangroves along the Gulf and Caribbean coasts, especially near coastal lagoons or near river deltas with low sediment load. Figure 6.125 presents vegetation zonation along a shoreline northwest of Laguna de Mecoacán in Tabasco, Mexico. Here, mangrove and herbaceous habitats occur adjacent to each other.

Infrequently inundated hypersaline salt flats, although small in areal extent, also occur along the coastlines of Mexico. Salt flats on the northern Gulf coast of Mexico contain three associations: (1) *Suaeda nigra* and *Salicornia ambigua*; (2) *Batis maritima, Borrichia frutescens, Clappia suaedifolia* (fleshy clapdaisy), and *Maytenus phyllanthoides* (Florida mayten); and (3) *D. spicata* and *Monanthochloe littoralis* (Olmsted 1993). On the Yucatán Peninsula, dominant plant species on salt flats include *Salicornia* spp., *B. maritima, Suaeda linearis* (annual seepweed), and *Sesuvium portulacastrum* (Johnston 1924).



Figure 6.125. Cover of plant species along a mangrove-marsh transect near Laguna de Mecoacán, Tabasco, Mexico. (*Rhizophora mangle = fine broken line, Avicennia germinans = fine line, Batis maritima = dotted line, Spartina spartinae = bold line, Pithecellobium lanceolatum = bold broken line* (modified from Lopez-Portillo and Ezcurra 1989)).

6.5.2.2.3 Salt Marsh Primary Productivity

One of the most important and best-quantified functions of salt marshes is primary productivity, the rate of organic matter production per unit surface area per unit time. Factors controlling the primary productivity of coastal salt marshes dominated by Spartina alterniflora, the primary intertidal herbaceous salt marsh plant in the northern GoM, have been extensively reviewed (Mendelssohn et al. 1982; Smart 1982; Howes et al. 1986; Mendelssohn and Morris 2000). In general, the primary factors determining the growth of this species are salinity and soil waterlogging, both of which affect plant nitrogen utilization and allocation. Prolonged flooding results in soil anoxia, biochemically reduced soil conditions, and the accumulation of hydrogen sulfide in coastal salt marshes (DeLaune et al. 1983; Mendelssohn and McKee 1988). Soil anaerobiosis and phytotoxin accumulation inhibit the uptake of ammonium-nitrogen, the primary nutrient limiting plant growth in these systems (Morris 1984; DeLaune et al. 1984; Koch et al. 1990). Additionally, the roots may become deficient in oxygen and exhibit limited aerobic respiration and reduced energy for nutrient uptake (Mendelssohn et al. 1981; Koch et al. 1990). Hydrogen sulfide accumulation further inhibits root energy production and, hence, exacerbates plant nitrogen deficiencies (Koch et al. 1990). Elevated salinities can also negatively affect the growth of S. alterniflora by competitively inhibiting ammonium uptake (Morris 1984). In addition, nitrogen-containing cellular organic compounds (osmotica) that aid in maintaining plant water status are synthesized at elevated salinities; the allocation of nitrogen to osmotica production decreases the amount of nitrogen available for growth (Cavalieri and Huang 1979). Considerably less is known about the factors controlling the production of other salt marsh plant species. However, since hydrology and salinity are recognized as primary forcing functions in coastal salt marsh systems (Mitsch and Gosselink 1993), the primary productivity of other marsh species are likely controlled, at least qualitatively, by similar factors.

In addition to environmental controls, biotic factors may also influence salt marsh productivity. Bertness (1984, 1985) has shown that both fiddler crabs and mussels can enhance the production of *Spartina alterniflora*, the former by aerating the soil and the latter by increasing soil fertility through the production of feces and pseudofeces. Moderate grazing by snow geese in Canadian salt marshes also stimulates vascular plant primary production via the input of nitrogen from feces (Hik and Jefferies 1990); however, intense grazing can result in the denuding of the marsh (Abraham et al. 2005). There is also evidence for autogenic control of plant productivity. The accumulation of peat by the vegetation over time can inhibit plant growth possibly due to the increased hardness of the substrate and/or to the lower fertility of a peaty soil (Bertness 1988). These biotic controls on salt marsh plant production have generally been overlooked and require corroboration in other marsh types.

Coastal salt marshes are one of the most productive ecosystems in the world (Dring 1982). Although primary producers include the emergent vascular plants and benthic and epiphytic algae, most research has concentrated on quantifying the productivity of the emergent vascular vegetation. Rates of primary production can vary greatly depending on the methodology, plant species, environmental condition, latitude, grazing pressure, and temporal variability. For example, mean regional aboveground productivities of salt marshes in North America range from 76 g dry matter/m²/year (30 g C/m²/year) in Alaska to 1,976 g dry matter/m²/year (812 g C/m²/year) in the north central GoM (Mendelssohn and McKee 2000; Mendelssohn and Morris 2000). Although considerable overlap in primary productivity occurs for various geographic regions, productivities generally increase in a southward direction in North America. In the GoM, per se, salt marsh primary productivity varies longitudinally, with generally lower productivities in the western GoM (673 to 1,283 g dry matter/m²/year) than in the central GoM (1,578 to 2,374 g dry matter/m²/year) (95 % confidence intervals as modified from

Table 6.10. Range of Aboveground Primary Productivity Values for Salt Marshes Dominated by *Spartina alterniflora* and *Juncus roemericanus* in the Northern GoM (data from Eleuterius 1972; Kirby and Gosselink 1976; Turner and Gosselink 1975; Turner 1976; Kruczynski et al. 1978; de la Cruz 1974; Hackney and Hackney 1978; Hackney et al. 1978; Hopkinson et al. 1978; Stout 1984; Webb 1983)

	Aboveground Net Primary Productivity (g/m ² /year)			
Location	Spartina alterniflora	Juncus roemerianus		
Florida	130–1,281	245–949		
Alabama	175–2,029	580–3,078		
Mississippi	1,084–1,964	372–2,000		
Louisiana	754–2,658	991–3,416		
Texas	438–1,846	_		

Mendelssohn and McKee 2000). Belowground rates of production are highly variable, possibly due to smaller sample sizes than for aboveground estimates as well as greater inherent variation in the data (Mendelssohn and McKee 2000). Regardless, belowground productivities are as high or even higher than aboveground (Mendelssohn and McKee 2000) (Table 6.10). For example, in one Louisiana salt marsh, belowground production was 11,676 g dry matter/m²/ year compared to 1,821 g dry matter/m²/year for aboveground production (Darby and Turner 2008), although this belowground estimate was exceptionally high.

6.5.2.3 Fauna

Salt marshes may exhibit high infaunal and epifaunal invertebrate species diversity, compared to other habitats such as freshwater marshes (Odum 1988), but faunal species diversity in salt marsh systems varies across multiple temporal and spatial scales. For example, infaunal and epifaunal forms may show strong patterns of intertidal zonation, and epifaunal species richness may increase during warmer months due to seasonal abundance peaks of nektonic epifauna such as penaeid shrimps and blue crabs.

The effects of ecological stressors vary across the salt marsh landscape (Fleeger et al. 2008). Duration of tidal inundation (i.e., relative intertidal elevation) is a key factor determining infaunal and epifaunal community changes across the marsh landscape, and also controls intertidal access for nekton. Consequently, distributions of many salt marsh infauna and epifauna vary along an elevation continuum of habitat change on which are superimposed effects of cyclic patterns of environmental change, reproductive events, and predator–prey interactions at multiple temporal scales (e.g., diel, tidal, seasonal).

Most salt marshes in the GoM are located within the northern region and so, not surprisingly, much of the research on the fauna in this habitat has been conducted between Florida's Big Bend area of the Eastern Gulf Neritic Ecoregion to Corpus Christi in the Texas Estuarine Ecoregion. Across all GoM ecoregions, diversity tends to be greater in lower salt marsh elevations compared to the less frequently flooded areas of the high marsh. Subrahmanyam et al. (1976) found that low marsh zones had significantly more invertebrate species than did the upper marsh in *Juncus*-dominated marshes of the Eastern Gulf Neritic Ecoregion. Similarly, Humphrey (1979) found that the low *Juncus* marsh of the Mississippi Estuarine Ecoregion contained the greatest diversity and densities. Comparison of the two studies, however, reveals that low marsh diversity (H') was higher in the Subrahmanyam et al. (1976) study (H' = 2.49) compared to that found in Mississippi (0.77) (Humphrey 1979). Stout (1984) suggested that the Mississippi marsh may represent the lower end of salinity tolerances for many estuarine and marsh organisms, but is still too salty for most freshwater or terrestrial species. Macroinvertebrate Shannon-Wiener H' diversity in an Alabama study (Ivester 1978) found that diversity in *Juncus* (0.69) and *Distichlis* (0.66) marshes was similar to Humphrey's (1979) findings in Mississippi. Alabama *Spartina* marshes had low macroinvertebrate diversity (0.37), with a decline in diversity in both late winter-early spring and in early fall (Ivester 1978). These diversity values for Alabama likely are underestimated because oligochaetes and insect larvae were not identified to species.

Subrahmanyam et al. (1976) reported a low marsh/upper marsh community dominated by the marsh periwinkle *Littoraria irrorata*, the isopod *Cyathura polita*, and tanaid crustaceans, with several abundant polychaetes (*Scoloplos fragilis*, *Nereis succinea*, and *Laeonereis culveri*). Mollusk populations increased toward a landward salt flat. The high marsh community had abundant fiddler crabs (*Uca* spp.) and the gastropods *Melampus bidentatus* and *Cerithis-dea scalariformis*. At Bay St. Louis, Mississippi, dominant species by both density and biomass in the low needlerush marsh were the bivalves, *Polymesoda caroliniana* and *Geukensia demissa*, and the snail, *Neritina reclivata* (Humphrey 1979). The high marsh zone was dominated by the snail, *M. bidentatus*, fiddler crabs, and *P. caroliniana*.

Whaley and Minello (2002) examined the fine-scale (1 to 10 m) distributions of infauna in relation to the edge of a salt marsh in the Texas Estuarine Ecoregion. Surface-dwelling annelid worms and peracarid crustaceans were most abundant in low elevation sediments near the marsh edge for most sampling periods. Distributions of common surface-dwelling species were often unrelated to elevation but almost always negatively related to distance from the marsh edge. Abundances of near-surface direct deposit feeders and omnivores were related to both distance from the edge and elevation. In contrast to surface dwellers, densities of abundant subsurface deposit feeders (mainly oligochaetes) were frequently greatest in sediments located away from the marsh edge (Whaley and Minello 2002).

The relative value of salt marsh habitats for juvenile fishery species appears to be related to two environmental characteristics: the amount of marsh/water interface and the elevation of the marsh surface (Minello et al. 1994; Whaley and Minello 2002). Thus, there is decreasing use of the vegetated marsh by nekton with increasing distance from the marsh edge. Partyka and Peterson (2008) suggested that the faunal response to the presence of salt marsh habitat is more dependent on characteristics of the broader landscape that provide access to the shallow intertidal marsh surface and intertidal and subtidal creeks than on characteristics of the vegetated marsh.

Heard (1979) compiled a guide to 88 species of marine and estuarine invertebrates reported in marshes of the northeastern GoM, specifically along the Mississippi-Alabama coast and immediately adjacent areas of Florida and Louisiana. He identified three major groups of salt marsh infauna and benthic epifauna: polychaete worms, bivalve and gastropod mollusks, and crustaceans. Stout (1984) noted that the Heard (1979) listing would be greatly expanded with the addition of oligochaetes and insects, which are abundant in GoM salt marshes. The insect fauna of northeastern GoM marshes comprise aquatic species that also occur in freshwater systems, and include fly (dipteran) larvae (especially those of the Culicidae, Chironomidae, and Ceratopogonidae), heteropterans, coleopterans, and certain trichopteran larvae (Stout 1984).

Many salt marsh invertebrates occur across all ecoregions of the GoM coast, including taxa such as fiddler crabs (*Uca* spp.) (Figure 6.105) and nektonic taxa such as penaeid shrimps (Figure 6.103), and blue crabs (*Callinectes* spp.). In addition to widely occurring taxa, studies of salt marsh invertebrates from different regions of the northern GoM have found differences in community composition for some of the most abundant species.

Region	Florida	Alabama	Mississippi	Texas
Common infauna <i>Littoraria irrorata</i> and epifauna (G)		Littoraria irrorata (G)	Polymesoda caroliniana (B)	Streblospio benedicti (P)
	Scoloplos fragilis (P)	Guekensia demissa (G)	Guekensia demissa (B)	Capitella capitata (P)
	Nereis succinea (P)	Polymesoda caroliniana (B)	Neritina reclivata (G)	Hargeria rapax (T)
	Cyathura polita (I)	Neritina reclivata (G)	Melampus bidentatus (G)	Corophium spp. (A)
Data source	Subrahmanyam et al. (1976)	lvester (1978)	Humphrey (1979)	Whaley and Minello (2002)

Table 6.11. Abundant Invertebrates in Marsh Systems of the Northern GoM.

Key: A amphipod, B bivalve, G gastropod, I isopod, P polychaete, T tanaid

Table 6.11 lists abundant invertebrates in marsh systems of the northern GoM. Subrahmanyam et al. (1976) sampled infauna and epifauna in two Florida black needlerush (*Juncus roemerianus*) marshes, at Wakulla and St. Marks. Four major groups comprised the invertebrate community, including crustaceans (44 %), mollusks (31 %), annelids (24 %), and insect larvae (1 %). Numerically dominant taxa included the marsh periwinkle (*Littoraria irrorata*), the isopod *Cyathura polita*, and the polychaete *Scoloplos fragilis*.

Pure stands of black needlerush, intertidal smooth cordgrass (*Spartina alterniflora*), and salt grass (*Distichlis spicata*) were sampled by Ivester (1978) for invertebrate community comparisons along a salt flat in Alabama. A total of 19 taxa were identified, along with unidentified oligochaetes and insects. Six species represented over 90 % of total numbers of the community in each zone. Marsh periwinkle (*L. irrorata*) and the mussel, *Guekensia demissa*, were important only in smooth cordgrass. Marsh periwinkle was replaced by the gastropod *Melampus bidentatus* and increased numbers of the gastropod *Neritina reclivata* in black needlerush and salt grass stands. The bivalve *Polymesoda caroliniana* was prevalent in needlerush, as seen in both north Florida (Subrahmanyam et al. 1976) and Mississippi (Humphrey 1979). Oligochaetes dominated each of the three plant community types, ranging in relative abundance from 80 % in smooth cordgrass to 53 % in salt grass.

Epifauna utilize salt marsh tidal creeks in addition to the vegetated marsh surface, often entering vegetated areas after inundation by tides. Nektonic epifauna typically include grass shrimp (*Palaemontes* spp.), white shrimp (*Litopenaeus setiferus*), brown shrimp (*Farfantepenaeus aztecus*), and blue crab (*Callinectes sapidus*). These important decapod fishery species are seasonally abundant in salt marshes of the northern GoM coast (Zimmerman and Minello 1984; Thomas et al. 1990; Peterson and Turner 1994). Remarkably similar nekton assemblages occur in the tidal channels and ponds of *Spartina*-dominated marshes of Louisiana and Texas and the *Juncus*-dominated marshes in the northeastern GoM (Subrahmanyam and Drake 1975; Subrahmanyam and Coultas 1980).

Most nekton studies conducted in marshes of the GoM have emphasized samples collected from the interface (edge, with 5 to 10 m) between vegetated marsh and adjacent open water habitats and usually used drop samplers deployed from the bow of a boat (Baltz et al. 1993; Minello et al. 1994; Minello 1999; Minello and Rozas 2002; Zeug et al. 2007). Nekton samples collected at or near the marsh edge included species that use the flooded interior marsh surface as well as those that tend to be associated with nearshore shallow water. Thus, samples collected only from the marsh edge may not distinguish among assemblages of nekton that actually make

extensive use of the majority of the interior marsh (e.g., resident species) and those visiting the periphery of that habitat (e.g., transients or schooling species).

The perception and emphasis on the dependence of nekton on marsh edge in the GoM has been incorporated into models of penaeid shrimp production that have linked changes in edge and wetland loss with growth rates (Haas et al. 2004), habitat fragmentation (Roth et al. 2008), and future shrimp harvests (Browder et al. 1989). Other research has recognized that the extent to which the marsh surface is used by nekton in the GoM also depends on the frequency and duration of tidal inundation (Rozas 1995), and that even deteriorating tidal marshes undergoing submergence in both Louisiana and Texas continue to be used extensively by nekton during the process by which the vegetated wetland is replaced by open water (Rozas and Reed 1993).

A few studies in the GoM have attempted to address edge-bias in marsh nekton collections by using different sampling methods. For example, bottomless lift nets were designed to provide quantitative samples of nekton from any location on the flooded marsh surface (Rozas 1992) and when used to sample nekton from intertidal marsh habitats at different relative tidal elevations (high, medium, and low) result in a very different view of nekton assemblages (Rozas and Reed 1993) than collections from the marsh edge (Minello 1999). Samples collected at the marsh edge often are dominated by decapod crustaceans and include relatively low densities of many fish species, but sometimes include high densities of schooling fishes such as clupeids (Table 6.12, Figure 6.108). Samples collected on the marsh surface contained approximately equal densities of natant decapod crustaceans and fishes, but with the fishes being dominated by only a few species of resident fundulids and cyprinodontids (Figures 6.106 and 6.107a), particularly in the high marsh habitats that may be infrequently flooded. Low marsh collections with lift nets comprised nekton assemblages that were most similar to the edge marsh samples collected by drop traps (Table 6.12), suggesting that the differences represented real patterns of zonation and not simply differences in the effectiveness of the sampling gear types.

Peterson and Turner (1994) used flume nets of different lengths and seine samples collected at high and low tide to address this issue as well. Their findings suggested a zonation pattern consisting of four groups (Figure 6.126). Group A consisted of resident species that quickly use the interior marsh whenever it is inundated, gaining access and moving through the habitat by way of small channels and low-lying microtopographic characteristics of the marsh surface. Fishes dominate this group and comprise representatives of the Fundulidae, Cyprinodontidae, and Poeciliidae. Group B had interior marsh users, which may require slightly deeper inundation of the marsh surface and tend to return to more permanent water at the creek edge at low tide. This group included the larger fundulid, Fundulus grandis, caridean shrimp in the genus Palaemonetes, and smaller individuals of the portunid crab, Callinectes sapidus. Some of the species in this group, particularly the fundulids, exhibited foraging habits (Rozas and LaSalle 1990; Lopez et al. 2010a, b) and life history characteristics such as reproductive activity synchronized with tidal cycles (Greeley and MacGregor 1983) and delayed hatching of eggs (Harrington 1959) that suggest specific adaptations to the intertidal marsh environment. Group C contained species that are commonly associated with the flooded edges of tidal marshes but rarely venture more than a few meters into the vegetation. These could include some of the Gobiidae (e.g., Gobiosoma bosc and Gobionellus boleosoma) as well as schooling species of Atherinidae (e.g., Menidia bervllina) or Mugilidae (e.g., Mugil cephalus), and the penaeid shrimps (e.g., Farfantepenaeus aztecus and Litopenaeus setiferus). Piscivorous predators such as spotted seatrout (Cynoscion nebulosus) would likely also find marsh edge habitats to be advantageous in ambushing prey. Group D comprised a group of shallow subtidal estuarine species that rarely made direct use of the vegetated tidal marsh, but instead were commonly found in the open water adjacent to vegetated wetlands and beaches, including a group of Table 6.12. Densities (per m²) of the Most Abundant Nekton in Collections from Drop Traps at Marsh Edges (*Spartina* and mixed vegetation) Reported by Minello (1999) and From Lift Nets in Marsh Vegetation at Different Relative Tidal Elevations (high, medium, low) Reported in Rozas and Reed (1993)

	Edge Marsh		Marsh Elevations		
	Spartina	Mixed	High	Medium	Low
Fishes					
Adinia xenica	0.1	0.1	4.2	2.2	0.8
Brevoortia patronus	0.8	5.0	0.0	0.0	0.0
Cynoscion nebulosus	0.2	< 0.1	< 0.1	< 0.1	< 0.1
Cyprinodon variegatus	0.2	1.1	6.0	2.8	0.9
Evorthodus lyricus	0.0	0.0	0.2	< 0.1	0.2
Fundulus grandis	0.4	1.0	10.7	2.3	1.3
Gobionellus boleosoma	0.9	0.1	< 0.1	0.0	0.0
Gobiosoma bosc	2.7	4.0	< 0.1	0.1	0.2
Lagodon rhomboides	1.3	0.1	< 0.1	0.0	0.0
Lucania parva	0.5	1.0	0	0	< 0.1
Menidia beryllina	0.6	0.8	0.3	1.2	0.4
Mugil cephalus	0.2	0.2	1.1	2.4	2.5
Natant Decapod Crustaceans					
Callinectes sapidus	6.2	2.7	2.0	1.0	1.7
Hippolyte zostericola	0.7	0.0	0.0	0.0	0.0
Farfantepenaeus aztecus	7.5	2.6	0.3	0.5	1.4
Farfantepenaeus duorarum	1.0	0.5	0.0	0.0	0.0
Litopenaeus setiferus	5.5	1.5	0.1	0.4	1.7
Palaemonetes pugio	58.8	25.7	10.5	5.4	14.6

Red shaded cells show the top six species in each marsh type

flatfishes (e.g., *Symphurus plagiusa* and *Achirus lineatus*) and common schooling species found in GoM estuaries such as the ubiquitous engraulid, *Anchoa mitchilli*, and the clupeid, *Brevoortia patronus*.

Natural (e.g., ponds and tidal channels) and anthropogenic (e.g., impoundments and oil/gas pipeline canals) aquatic features embedded within the matrix of the intertidal vegetated marsh landscape function as important habitat for marsh nekton (Peterson and Turner 1994; Rozas and Reed 1994; Akin et al. 2003; Rozas and Minello 2010). Nekton assemblages found in these tidal marsh sub-habitats are affected by size and depth of the habitat (Akin et al. 2003; Rozas and Minello 2010), temperature and salinity (Herke et al. 1987; Akin et al. 2003), and perhaps most importantly, accessibility to open water (McIvor and Rozas 1996). Blocked or restricted channels that impair movement of nekton among adjacent habitats (e.g., bays, lagoons, and the coastal neritic zone) can be expected to have a more limited nekton assemblage than those with open and free connections to other aquatic habitats (Neill and Turner 1987; Herke 1995). There



Figure 6.126. Zonation patterns of different nekton groups in tidal marshes of Louisiana (after Peterson and Turner 1994; republished with permission of Springer Science and Bus Media BV, provided by Copyright Clearance Center, Inc.). Species that use the interior marsh extensively tend to be "true residents" that are primarily fishes in the families Fundulidae, Cyprinodontidae, and Poeciliidae, while the marsh edge is visited by a diverse group of fishes and abundant natant decapod crustaceans, many of which commonly occur in other estuarine habitats within the GoM.

appear to be no substantial differences between nekton assemblages using anthropogenic aquatic habitats such as open pipeline canals and natural marsh channels (Rozas 1992; Granados-Dieseldorff and Baltz 2008). The species composition and spatial distribution of nekton using pipeline canals and marsh creek channels is similar to that shown in Figure 6.126, with the same suite of fish and natant decapod crustacean taxa dominating on the adjacent interior and edge marsh habitats and a similar subtidal group found in the deeper portions of the channels. Marsh ponds also show a similar nekton assemblage structure, with small resident fish species and natant decapod crustaceans associated with pond vegetation and schooling species such as *Anchoa mitchilli* and *Brevoortia patronus* (Figure 6.108) sometimes abundant in the adjacent unvegetated open waters of larger ponds (Rozas and Minello 2010), lagoons (Rozas et al. 2012), or embayments (Akin et al. 2003).

The presence of SAV, such as *Ruppia maritima* (Akin et al. 2003; Rozas and Minello 2010) in brackish canals and ponds, or *Thalassia testudinum* and *Halodule wrightii* in more saline bays and lagoons (Rozas et al. 2012), creates a hybrid emergent/SAV habitat that can affect the species composition of the nekton assemblage even in an adjacent tidal marsh. For example, pink shrimp (*Farfantepenaeus duorarum*) and hippolytid shrimp (e.g., *Hippolyte zostericola, Tozeuma* spp.), pinfish (*Lagodon rhomboides*), pipefish (*Syngnathus* spp.), and gobiid species tend to be more abundant in habitats associated with seagrasses (Rozas et al. 2012), and so could occur in samples from the adjacent marsh.

Salt marsh is one of the most biologically productive ecosystems in the world (Teal 1962). The high primary productivity that occurs in the marsh provides the base of the food chain supporting invertebrate detritivores or omnivores that provide an important link to higher-level consumers in the food web (Stout 1984). Infauna densities and biomass are positively associated with percent organic matter in salt marshes (Minello and Zimmerman 1992; Levin et al. 1996, 1998). Many small crustaceans and annelids consume organic detritus, and these fauna represent a trophic pathway to higher predators, most of which do not have the ability to derive much nutrition directly from detritus (Kneib 2003). Nekton associated with salt marshes can have a prominent role in the export of energy and materials from these productive coastal



Figure 6.127. Transferring coastal wetland production from shallow to deeper waters via the trophic relay as depicted for salt marshes in the southeastern United States (from Kneib 2000; reprinted with permission of Springer). Key resident species include palaemonid shrimps as well as fundulid, cyprinodontid and poecilid fishes. Gauntlet species tend to be subject to predation both when immigrating to estuaries as early life stages from coastal spawning grounds and when emigrating as juveniles and adults. Typical gauntlet species for the region would be penaeid shrimps and gulf menhaden as depicted in the figure. Important transient predators include fishes in the families Sciaenidae, Ariidae, and Pleuronectiform flatfishes.

wetlands to open estuaries and the coastal ocean through multiple mechanisms. Some species, such as Gulf menhaden (Deegan 1993; Deegan et al. 2000) or natant decapod crustaceans (Zimmerman et al. 2000), which use coastal estuaries and wetlands as nurseries during their juvenile life stages, often show ontogenetic patterns of emigration to nearshore or offshore coastal water effectively transferring substantial biomass and energy between habitats. Permanent estuarine resident species (e.g., fundulid fishes and palaemonid shrimps) also contribute to these production transfers through spatially overlapping distributions along a stream-order gradient (Granados-Dieseldorff and Baltz 2008) that involve size-specific predator–prey interactions in which smaller nekton from shallow water are consumed by larger nekton (Figure 6.109) that move with the tide or seasons into adjacent deeper habitats (Figure 6.127) in a process often referred to as the trophic relay (Deegan et al. 2000; Kneib 1997, 2000).

Predator-prey interactions driving production transfers in salt-marsh ecosystems are mediated primarily by tidal dynamics, local physiography (i.e., landscape structure), and vegetation density (Moody 2009). Many salt marshes are drained by a network of tidal creeks, and the transfer of marsh production to aquatic estuarine predators appears to be facilitated by tidal flushing that provides nekton access to small detritivores, herbivores, and omnivores residing in the marsh (Zimmerman and Minello 1984; Kneib 1987; Rozas 1995; Zimmerman

et al. 2000). Collectively, tidal creeks and the adjacent intertidal marsh function as tightlyconnected nursery areas providing both high density food resources and structural refugia for the juvenile life stages of many commercially harvested fishes, decapod crustaceans, as well as a larger subset of other GoM taxa.

Various aspects of the predator-prev interactions controlling production transfers from tidal marshes have been studied for decades in the GoM and elsewhere (Kneib 1997). For example, Rozas and LaSalle (1990) examined the foraging habits of the abundant marsh resident fundulid, Fundulus grandis, and found that the guts of specimens leaving a Mississippi intertidal marsh on the ebbing tide were substantially fuller than when they entered the habitat on flooding tides. In addition to short-term tidal patterns in predator-prev dynamics, strong seasonal patterns of foraging activity thought to be driven by the seasonal abundance of juvenile transient nekton species have been evidenced by intra-annual variability in the densities of infaunal and small epifaunal marsh invertebrates (Zimmerman et al. 2000). For example, Subrahmanyam et al. (1976) measured a maximum late winter invertebrate density of 578 individuals/m² in tidal marshes of northwestern Florida corresponding with peak recruitment for certain species, and minimal densities in summer (375 individuals/m²) when potential predators tend to be most abundant (Akin et al. 2003). Whaley and Minello (2002) also found that populations of infaunal prey fluctuated seasonally in a Texas salt marsh, with the greatest densities occurring during winter and early spring when epibenthic predator densities were generally low.

Predatory decapods likely play an important role in these energy transformations from tidal marshes. For example, Kneib (1986) found that the blue crab, *Callinectes sapidus*, was probably a major predator of adult mummichogs (*Fundulus heteroclitus*) in North Carolina salt marshes. Given the higher densities of blue crab in marshes of the GoM (Zimmerman et al. 2000) when compared to the U.S. Atlantic coast, one can reasonably infer a similar predator–prey relationship exists between blue crabs and small resident nekton in the GoM. The inference is supported by the findings of West and Williams (1986) who observed that blue crabs preferentially selected marsh periwinkles (*Littoraria irrorata*) and gulf killifish (*Fundulus similis*) over infaunal prey (the ribbed mussel *Geukensia demissa*) in an Alabama salt marsh. In a study of habitat use by decapod crustaceans among transplanted and natural smooth cordgrass marshes in Galveston Bay, Minello and Zimmerman (1992) found that grass shrimp (*Palaemonetes pugio*) and juvenile brown shrimp (*Farfantepenaeus aztecus*) were positively correlated with densities of macroinvertebrate prey in sediment cores. Whaley and Minello (2002) suggested that there was a strong trophic link between infauna and nekton near the marsh edge, and that this relationship contributed to the high fishery productivity derived from GoM marshes.

6.5.3 Mangroves

Mangroves generally displace intertidal coastal salt marshes in the Southern GoM Ecoregion, with exceptions noted above. With a longer growing season and warmer conditions, the tree stature of mangroves allows them to outcompete shorter salt marsh vegetation for light. In the absence of frost, mangroves eventually become dominant.

The term *mangrove* refers to an ecological group of salt- and flood-tolerant trees and shrubs that inhabit the intertidal zone (Tomlinson 1994). Synonymous terms that refer to the entire assemblage include mangrove community, mangrove ecosystem, mangrove swamp, mangrove forest, and mangal. Mangrove species may not be closely related taxonomically, with members of a community often from different plant families. Mangroves, however, have various morphological and physiological adaptations in common, which allow avoidance or tolerance of the anoxic and saline soils typical of the mangrove habitat. According to

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Tomlinson (1994), true mangrove species are further distinguished by their complete fidelity to the intertidal habitat and by their taxonomic isolation (at least at the generic level but often at the subfamily or family level). Mangrove "associates," which may be herbaceous, epiphytic, or arboreal species, are found within the mangrove habitat but may also occur in more upland habitats and play a minor role in mangrove forest structure.

There are 65 species of mangroves worldwide (excluding hybrids), but only five species occur in North America (excluding Central America) (Spalding et al. 2010). Of these five species, only four occur in the GoM: *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), and *Conocarpus erectus* (buttonwood). These species have a wide distribution, occurring in Florida, the Caribbean, and Mexico. Other plant species found in association with mangroves in the GoM include *Batis maritima*, *Sesuvium portulacastrum* (shoreline seapurslane), *Salicornia* spp. (glasswort), *Sporobolus virginicus* (seashore dropseed), *Monanthochloe littoralis* (shore grass), *Paspalum vaginatum* (seashore paspalum), *Distichlis spicata* (saltgrass), *Spartina alterniflora* (smooth cordgrass), and *S. patens* (wiregrass or saltmeadow cordgrass).

6.5.3.1 Dominant Forcing Functions

Similar to salt marshes, the hydrologic regime exerts a tremendous influence on the structure and function of mangroves. Hydrology affects abiotic factors such as porewater salinity, pH, oxygen, and phytotoxin accumulation, and soil factors, such as organic matter, texture, and nutrient availability, as well as biotic factors such as dispersal of seeds (Marchand et al. 2008). Disturbances from insect herbivores and woodborers are additional disturbances seen by mangroves (Feller and McKee 1999; Feller et al. 2007). Climate-related factors such as hurricanes, drought, and sea-level rise as well as human-pressures associated with the expanding human footprint also are important forcing functions. Given that the majority of mangrove-associated forcing functions are identical to those occurring in salt marshes and described in detail in Section 6.5.2.1, we herein only provide a brief summary. However, see Krauss et al. (2008) for specific examples of dominant forcing functions in mangroves.

6.5.3.2 Vegetation

6.5.3.2.1 Structure and Zonation

Mangrove forests are often classified into six basic types: overwash island, fringe, basin, riverine, dwarf, and hammock (Lugo and Snedaker 1974) (Figure 6.128). All of these types can be found in Florida, and each is characterized by certain tidal characteristics, hydroperiod, and forest structure. Riverine forests, which occur along tidal rivers and creeks with high input of freshwater, sediment, and nutrients, exhibit the highest productivity of all six types (see below). The high productivity and dynamic hydrology lead to high rates of organic matter export. Forest stands found along portions of the Shark River in Florida fall into the riverine category. The fringe forest type develops along the seaward edge of protected shorelines, has an open exchange with the sea and is well flushed by the tides. Fringe forests experience sea-strength salinity and receive fewer nutrients than riverine forests. Consequently, their productivity is somewhat lower. Overwash islands, which are sometimes considered to be a special case of fringe forest, experience higher tidal velocities that "overwash" the island and flush out accumulated litter. The overwash island type is found throughout the Ten Thousand Island region of Florida. Basin mangrove forests develop in topographic depressions, typically inland of fringing or riverine forests. Water movement is less, with tidal inundation occurring seasonally or with spring or storm tides. Once inundated by tides or freshwater, basin forests

			RIVERINE	FRINGE	BASIN	SCRUB/DWARF
PHYSIOGNOMY &	Prof	ile				Alt and
REST	Canopy He	eight (m)	12.64 ± 1.43	7.65 ± 0.94	12.14 ± 1.29	0.83 ± 0.09
<u>6</u>	Litter Pro (MT/h	duction a/yr)	12 ± 10	9 ± 0.7	6.6 ± 0.7	1.9 ± 0.6
βGY	Water S	ource	Ocean Tides & Stream Flow	Ocean Tides	Ocean Tides & Saline Groundwater	Ocean Tides & Saline Groundwater
GL0		Duration	Hours-Days	Hours	Days-Months	Perennial
YDR	Hydroperiod	Frequency	Daily Or Seasonal	Daily	Seasonal	Continuous
т		Depth	Shallow-Deep	Shallow	Shallow	Shallow
RY	Salinity	(psu)	0/26	33/38	25/60	33/46
SOIL MIST	Redox Pote	ntial (mV)	-48/+116	-96/+103	+87/+279	-244/-105
CHE	Sulfide	(mM)	0.0/0.2	0.1/0.3	0.1/0.2	0.9/2.2

Figure 6.128. A summary of four primary mangrove forest types originally described by Lugo and Snedaker (1974) (modified after Mendelssohn and McKee 2000).

may remain flooded for extended periods and leaf litter often accumulates on the forest floor. Basin mangroves may exhibit high productivity but low export of organic matter. The basin mangrove forest, often dominated by *A. germinans*, can be found along the southwest coast of Florida and wherever mangrove development is expansive, such as much of the southern GoM shoreline. Small trees characterize dwarf or scrub mangrove forests, often less than 1.5 m (4.9 ft) tall, with low density and extended hydroperiod. Hydrologic energy is low, and the near-continuous flooding leads to slow growth and low productivity. Extensive stands of scrub mangroves occur throughout the GoM. At higher latitudes in the northern GoM, forest stands are often scrub-like, with trees never exceeding heights of 3 to 4 m (9.8 to 13.1 ft). These stands, however, often predominate along tidal creeks and shorelines where they function more like fringe forests with a more open exchange of water and nutrients. Their short stature is caused by cold temperatures and periodic freezes, which limit plant growth and cause pruning of distal branches.

Mangrove zonation occurs where more than one species inhabit a shoreline and where a strong environmental gradient exists. In the northern Gulf, mangrove stands display typical zonation patterns found throughout the Neotropics (McKee 2012). Along shorelines and creekbanks *R. mangle* often predominates, but landward zones may contain monospecific stands of *A. germinans* or mixed stands of *R. mangle*, *A. germinans*, and/or *L. racemosa*. However, specific zonation patterns vary with local conditions and species composition. Spatial patterns of species dominance vary depending on propagule dispersal and seedling survival (Rabinowitz 1978; McKee 1995a, b; Sousa et al. 2007), physiochemical conditions (flooding, salinity, nutrients) (Krauss et al. 2008), competition, and disturbance history (Lopez-Portillo and Ezcurra 1989). During dispersal or stranding stages, mangrove propagule viability may be compromised by damage inflicted by herbivorous crabs or snails, and survival rates may influence species dominance patterns (Smith et al. 1989; Patterson et al. 1997; Cannicci et al. 2008).

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Within the Deltaic Marshes of the Mississippi Estuarine Ecoregion, at the northern limits of mangrove distribution and where Spartina alterniflora salt marshes dominate, zonation of mangrove stands is simple, but striking. The pattern most frequently encountered is created by monospecific bands (10 to 20 m [33 to 66 ft] wide) of A. germinans along creekbanks, abutting large expanses of salt marsh dominated by S. alterniflora in the marsh interior. There also may be occasional patches of A. germinans occurring in the marsh interior and, if not killed by freezes, these may ultimately coalesce to form a larger, monospecific stand. Some research has examined factors influencing this spatial pattern in salt marsh-mangrove zonation (Patterson et al. 1993, 1997). In coastal Louisiana, snails attack the propagules of A. germinans, and the damage contributes to lower survival and establishment in the marsh interior (Patterson et al. 1997). Propagules also tend to strand at higher elevations on creekbanks in Louisiana marshes and sustain less damage by predators compared to those stranding at lower elevations. Those seedlings that do become established in salt marshes may be suppressed by competition from grasses such as S. alterniflora (McKee and Rooth 2008). Only when S. alterniflora is disturbed, reducing competition or creating bare patches of ground, can A. germinans recruit to the sapling stage (McKee et al. 2004). However, herbaceous vegetation may act as nursery species, promoting mangrove establishment and survival in highly stressful environments (McKee et al. 2007b).

6.5.3.2.2 Distribution

Total mangrove area in the United States is estimated to be $3,030 \text{ km}^2$ (749,000 ac) (Spalding et al. 2010). The largest expanse occurs along the southwestern coast of Florida around Florida Bay and Ten Thousand Islands where mangrove extent reaches 10 to 20 km (6.2 to 12.4 mi) inland in the Shark River Estuary region of the Everglades (Figure 6.129). Extensive stands also occur farther north in the Rookery Bay Estuary near Naples and around Tampa Bay and Charlotte Harbor. Above Tampa Bay, mangrove stands in Florida diminish and are gradually replaced



Figure 6.129. Distribution of mangrove species in the northern GoM (from Sherrod and McMillan 1985; used with permission).

with salt marsh vegetation. With increasing frequency of winter frosts, mangroves cannot persist, especially those species such as *R. mangle*, which are sensitive to colder temperatures. The only mangrove species found along the northernmost region of the GoM is *A. germinans*, which is the most cold tolerant of these four species (Markley et al. 1982). Scattered individuals of *R. mangle* and *L. racemosa* are periodically observed at mid-latitudes in the northern GoM, e.g., Cedar Keys (Markley et al. 1982; McMillan and Sherrod 1986; Stevens et al. 2006), but they often never exceed the juvenile stage of development (Zomlefer et al. 2006). No substantial mangrove stands have been reported between the Cedar Keys and the Mississippi River Delta. Mangrove populations do, however, exist along the Louisiana coast (Patterson et al. 1993; McKee et al. 2004; Perry and Mendelssohn 2009; Giri et al. 2011b). Mangrove area in Louisiana has varied from 2,180 ha (5,400 ac) in 1983 to 57 ha (141 ac) in 1986 with current stands (2010) estimated at 434 ha (1,072 ac) (Giri et al. 2011b). Scattered populations of *A. germinans* occur in Texas, e.g., around South Padre Island, but current estimates of area are not available (Sherrod and McMillan 1981; McMillan and Sherrod 1986; Everitt et al. 1996).

Mangroves are generally limited to tropical and subtropical climates between 32°N and 28°S latitudes (Lugo and Patterson-Zucca 1977; Tomlinson 1994; Duke et al. 1998). Their distributional limits usually correlate with the 20 °C (68 °F) winter isotherm of seawater (Duke et al. 1998). Sensitivity to freezing temperatures is widely regarded as the primary constraint on distributional limits (Sherrod and McMillan 1985; McMillan and Sherrod 1986; Sherrod et al. 1986; Kao et al. 2004; Stevens et al. 2006; Stuart et al. 2007). Latitudinal limits in the Northern Hemisphere vary spatially and temporally because of local variation in air and water temperatures (Stevens et al. 2006). Historically, the northernmost limit of mangroves along the Florida Gulf coast has been the Cedar Keys in the Big Bend region (29°08'N). Closedcanopy, monospecific stands of A. germinans occur at Cedar Keys, presumably because freeze intensity is not as great due to the insulating effect of surrounding water (Lugo and Patterson-Zucca 1977; Stevens et al. 2006). Stands of A. germinans have been reported as far north as 28°18'N on the northern GoM coast in Louisiana (Sherrod and McMillan 1985). However, a recent observation of A. germinans on Horn Island, Mississippi (~30.2°N latitude) may document the northernmost mangroves in the GoM.² In Texas, A. germinans has occurred as far north as Galveston Island, but may not persist due to winter freezes (McMillan 1971). This species is more abundant at Laguna Madre and south to the Rio Grande (Sherrod and McMillan 1981). Populations of L. racemosa and R. mangle have been reported as far north as $29^{\circ}10'N$ latitude at Cedar Key on the west coast of Florida (Rehm 1976). A fourth species, C. erectus, is found as far north as 28°50'N in Florida. The persistence of A. germinans at subtropical latitudes is attributed in part to its coppicing (stump sprouting) ability (Tomlinson 1994). Although periodic freezes kill portions of the shoot, the trees are able to recover by producing new shoots from reserve meristems located near the base of the trunk. More recent work comparing temperature tolerance of A. germinans found that the dispersal stage had the highest survivorship compared to stranded or seedling stages (Pickens and Hester 2011). Consequently, cold tolerance of dispersing propagules, in combination with the ability to coppice following freeze damage, both contribute to persistence of A. germinans along the northern GoM.

Mangrove communities in the northern GoM are characterized by few species (Figure 6.129) and relatively simple stand structure. In southwest Florida, mangrove forests are typically composed of two or three species with few, if any, mangrove associates in the understory. Depending on stand age, disturbance history, and other factors, mixed stands composed of

² http://blog.al.com/live/2012/07/mangrove_trees_show_up_on_horn.html

R. mangle, A. germinans, and *L. racemosa* may be found in the Everglades and Ten Thousand Islands. In some areas, there may be stands of tall *R. mangle* along tidal creeks or on small islands. In interior areas, dwarf stands of red mangrove may be extensive. At higher latitudes, monospecific stands of *A. germinans* occur (e.g., Louisiana), but pale in aerial extent compared to co-occurring salt marshes.

Extensive stands of mangrove forests occur on both coasts of Mexico and together total more than 488,000 ha. South of the Rio Grande, in the southernmost part of Laguna Madre de Tamaulipas near La Pesca, the climate is mostly tropical and winter freezes are rare. Here, all three mangrove species occur. *Rhizophora*, as is typical for new world mangroves, lines the seaward shoreface. The *Rhizophora* zone here is not well developed, but it is characteristic (Britton and Morton 1989). Because of the steep sloping foreshore in this area, both *Avicennia* and *Laguncularia* mix in a narrow band landward of *Rhizophora*. Hence, at this location the typical zonation of *Rhizophora*, *Avicennia*, and *Laguncularia* is not generally present. Seaward of the *Rhizophora* fringe, extensive beds of the seagrass, *Syringodium filiforme* (manatee grass), dominate the subtidal (Britton and Morton 1989).

The five Mexican states along the southern GoM have a total of 194,043 ha of mangroves (Loza 1994). This is 40 % of the total mangrove area in Mexico. The most well-developed mangrove forests occur in Campeche (80,369 ha), much of which occur in the Laguna de Términos, which has a total area of 130,000 ha (Flores-Verdugo et al. 1992). This area is subject to a dry season from February to May, a tropical rainy season from June to October, and a season of frequent cold front passages (nortes) from October to February. Freshwater input into the lagoon is from four rivers and annual precipitation ranges from 110 to 200 cm (Rojas-Galaviz et al. 1992). The lagoon is an area of high habitat diversity as a result of a relatively heterogeneous environment underpinned by patterns in wind, freshwater input, and water circulation (Figure 6.98).

The mangrove habitat of the northern Yucatán, which in many ways is similar to hypersaline lagoons of Texas and northern Mexico, is, in contrast, quite different from mangrove habitat in the Laguna de Términos, where freshwater input is plentiful. The lagoon system of the northern Yucatán has been described as one of the most biologically depauperate tropical marine environments on Gulf shorelines (Britton and Morton 1989). The combination of an arid environment (low precipitation and high evapotranspiration) and infrequent tidal inundation, due to dune ridges and sills that retard water exchange, results in what amounts to evaporation ponds that concentrate salt far above sea strength. It is within this lagoonal system that small circular mangrove stands are scattered across lagoonal bottoms. These are topographical highs that are apparent even when the lagoons are dry, but in the presence of water, resemble small islands. Two variations on this theme occur. Along the margins of the lagoon, Avicennia dominates the centers of the hummocks where elevation is highest due to accumulated sand and organic matter. Fringing the Avicennia, but at somewhat lower elevations, are tufts of Monanthochloe littoralis (shoregrass), Sesuvium portulacastrum (shoreline seapurslane), Salicornia virginica (Virginia glasswort), and Batis maritima (turtleweed)—common hypersaline salt marsh herbs that often occur in salt pans. Avicennia's high salt tolerance allows it to survive under these conditions. On hummocks located closer to the center of lagoons, large masses of sand and organic matter have accumulated. Here Avicennia fringes the outer periphery of the hummocks, but *Rhizophora* dominates the center. The higher elevations in the center of these hummocks may allow *Rhizophora* to avoid the highest soil salinities, thus being able to survive; Rhizophora has a lower salt tolerance than Avicennia (Tomlinson 1994). Herbaceous plant species similar to those found around the Avicennia hummocks occur here as well. A unique faunal feature of the hypersaline lagoons in the Yucatán is the greater flamingo. These beautiful birds feed upon small brine shrimp and other invertebrates adapted to hypersaline conditions.



Figure 6.130. Terrestrial ecoregions of Cuba (data from Olson et al. 2001).

In the Greater Antilles Ecoregion, the largest tracts of mangroves occur in Cuba (532,400 ha) (Carrera and Santander 1994), although the northwestern portion of Cuba that borders the GoM includes only a small fraction of the total (Figure 6.130). Many of the mangroves inhabit the numerous small islands or cays in the Golfo de Guanahacabibes eastward through the Archipelago de los Colorados. The Guanahacabibes Peninsula at the far western extent of Cuba is characterized by flat karsts composed of Quaternary coral limestone. Broad mangrove habitat occurs on the peaty silt deposits on the northern shore, although the largest mangrove area in western Cuba occurs along the southern shoreline of Cuba on the Zapata Peninsula. Further to the east along Golfo de Guanahacabibes is the seashore area between Bahia Honda and Varadero, the latter being the approximate eastern boundary of the operationally defined Cuban GoM shoreline. Northwestern Cuba has a seasonal tropical climate characterized by a rainy season (May to October) and a dry season (November to April). Between January and March, frequent cold fronts (nortes) occur, similar to the Yucatán climate. The four primary mangrove trees are the same as along the Mexican GoM shoreline: Rhizophora mangle, Avicennia germinans, Lagucularia racemosa, and Conocarpus erectus. Herbaceous species are also similar, such as *Batis maritima*. However, in Cuba mangrove associates such as Dalbergia ecastaphyllum (coinvine), Acrostichum aureum (golden leatherfern) and others (Carrera and Santander 1994) are also found. Mangroves occur along shallow muddy beaches protected by coral reefs or in embayments. As in the rest of the Caribbean, *Rhizophora mangle* is the most seaward species, forming a zone between low tide and mean tide. In contrast, Avicennia germinans is found between mean tide and high tide. Laguncularia racemos is often intermingled with Avicennia. The Rhizophora community is usually free of other plant species, while the Avicennia community often includes species such as Agrostichum spp., Batis maritima, Lycium carolinianum (Carolina desert-thorn), Cynanchum salinarum

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Figure 6.131. Zonation along a mangrove shoreline at La Isabela, Las Villas province, Cuba. 1 = Rhizophora mangle, 2 = Avicennia germinans (Ag), 3 = Laguncularia recemosa (Lr), 4 = Conocarpus erectus (Ce), 5 = Batis maritima (Bm), 6 = Notoc commune (Nc), 7 = Chloris sagraeana(Cs) sand dune vegetation; Od = Opuntia dillenii (from Borhidi 1996; used with permission).

(swallow-wort), and others. Finally, at the highest intertidal elevation is *Conocarpus erectus*, which is the most salt tolerant of the species, and can be found in monoculture or mixed with *Avicennia* and *Conocarpus* (Borhidi 1996). This shoreline zonation is presented in Figure 6.131. Landward of the *Conocarpus* zone are often expansive salt pans, only reached by the highest tides. The mangrove associates, *Batis maritima*, *Suaeda linearis* (annual seepweed), and *Salicornia* (=*Sarcocornia*) perennis (chickenclaws) are found here (Borhidi 1996).

6.5.3.2.3 Primary Productivity

Mangrove forests are highly productive ecosystems with net primary production rates reaching 13 metric tons/ha/year in some neotropical forests (McKee 2012). Productivity of mangroves is highest in lower latitudes (0 to 20°N), however, and decreases toward the subtropics. Most of the data on mangrove biomass production is based on annual litterfall rates, determined by monthly collections of leaf, wood, and reproductive materials that have fallen into litter traps. This approach does not include wood produced in tree trunks, above- and below-ground root production, or net production by other autotrophs (e.g., epiphytic and benthic algae). Thus, although litterfall rates provide a relative indication of primary production, they are underestimates of the net primary production by the ecosystem. However, most estimates of mangrove productivity are based on this method and will be emphasized here.

In general, litterfall rates vary among forest types: Dwarf (120 g/m²/year), basin (730 g/m²/ year), fringe (906 g/m²/year), and riverine (1,170 g/m²/year) (Twilley and Day 1999). In the northern GoM, values for annual litterfall ranged from 50 to 1,724 g/m²/year with an overall mean of 736 g/m²/year (Table 6.13). Highest values are reported for overwash islands (1,132 g/ m²/year) and a restored forest (1,099 g/m²/year), intermediate values for basin and fringe forests (295 to 906 g/m²/year), and lowest values for scrub and tidally restricted forests (101 to 250 g/m²/year). These values fall within the range reported for mangrove forests at more tropical latitudes and for the same forest types. Mangrove productivity along the Mexican GoM has best been documented in the Laguna de Términos. Species of mangrove here include *R. mangle, A. germinans, L. racemosa, and C. erectus*. The structure and function of the mangrove habitat have been described in a suite of publications (e.g., Rojas-Galaviz et al. 1992). Net primary productivity was much higher at a riverine site (2,458 g/m²/year) compared to a fringing mangrove location (1,606 g/m²/year) (Table 6.14), apparently due to greater nutrient and freshwater input at the riverine location. Also, higher seasonal productivity values occur during the rainy season and lowest during the period of frequent nortes.

Biomass Dominant Production (g/m²/year) Location Latitude Longitude Source **Species** Forest Type Litterfall Rookery Bay 26°02'N 81°45′W A. germinans Basin mixed 810 Twilley & Estero Bay, R. mangle et al. (1986) FL L. racemosa 25°02'N 81°34′W A. germinans Basin 444 Twillev monosp. et al. (1986) Cockroach 27°41′N 82°31′W R. mangle Overwash 1,132 Dawes island Bay Tampa et al. (1999) Bay, FL Rookery Bay, 26°3'N 81°42′W A. germinans Basin mixed 1,724 McKee and FL R. mangle Faulkner (2000)L. racemosa Restored 1,108 McKee and Faulkner (2000)81°47′W McKee and Windstar, FL 26°7'N A. germinans Basin mixed 1,065 R. mangle Faulkner (2000) McKee and R. mangle Restored 1,170 L. racemosa Faulkner A. germinans (2000)Rookery Bay, 26°3'N 81°42′W 1,278 A. germinans Basin mixed Raulerson FL R. mangle (2004)L. racemosa 1,241 Raulerson R. mangle Fringe (2004)L. racemosa Restored 1,205 Raulerson (2004)Windstar, FL 26°7'N 81°47′W A. germinans Basin mixed 986 Raulerson R. mangle (2004)L. racemosa R. mangle Fringe 1,132 Raulerson (2004) R. mangle Restored 913 Raulerson (2004) L. racemosa A. germinans Rookery Bay, 26°3′N 81°42′W 264 A. germinans Basin mixed Giraldo FL R. mangle (2005) L. racemosa A. germinans Basin 145 Giraldo (2005)monosp. R. mangle Fringe 247 Giraldo (2005) 101 Giraldo R. mangle Scrub (2005)

Table 6.13. Biomass Production of Mangrove Forests in the Northern GoM (maximum reported value for each location)

(continued)

Table 6.13. (continued)

Location	Latitude	Longitude	Dominant Species	Forest Type	Biomass Production (g/m²/year)	Source
Windstar, FL	26°7′N	81°47′W	A. germinans R. mangle L. racemosa	Basin mixed	220	Giraldo (2005)
			R. mangle	Fringe	192	Giraldo (2005)
Captiva Island, FL	26°42′N	82°14′W	A. germinans R. mangle L. racemosa	Unrestricted tide	151	Harris et al. (2010)
				Restricted tide	50	Harris et al. (2010)
Sanibel Island, FL	26°34′N	82°12′W	A. germinans R. mangle L. racemosa	Unrestricted tide	900	Harris et al. (2010)
Sanibel Island, FL	26°34′N	82°12′W	A. germinans R. mangle L. racemosa	Restricted tide	450	Harris et al. (2010)
Root production	on		I	r	r	ſ
Rookery Bay, FL	26°3′N	81°42′W	A. germinans R. mangle	Basin mixed	610	McKee and Faulkner (2000)
			L. racemosa	Restored	797	McKee and Faulkner (2000)
Windstar, FL	26°7′N	81°47′W	A. germinans R. mangle	Basin mixed	453	McKee and Faulkner (2000)
			R. mangle L. racemosa A. germinans	Restored	412	McKee and Faulkner (2000)
Rookery Bay, FL	26°3′N	81°42′W	A. germinans R. mangle	Basin mixed	182	Giraldo (2005)
			A. germinans	Basin monosp.	198	Giraldo (2005)
			R. mangle	Fringe	200	Giraldo (2005)
			R. mangle	Scrub	211	Giraldo (2005)
Windstar, FL	26°7′N	81°47′W	A. germinans R. mangle L. racemosa	Basin mixed	144	Giraldo (2005)
			R. mangle	Fringe	144	Giraldo (2005)

(continued)

Table 6.13. (continued)

Location	Latitude	Longitude	Dominant Species	Forest Type	Biomass Production (g/m ² /year)	Source
Bayou Lafourche, LA	29°10′N	90°14′W	A. germinans	Scrub	346	Perry and Mendelssohn (2009)
Shark River, Everglades, FL	25°22′N	81°01′W	R. mangle L. racemosa A. germinans	Riverine	643	Castaneda- Moya et al. (2011)
Taylor Slough, Everglades, FL	25°44′N	80°51′W	R. mangle	Scrub	407	Castaneda- Moya et al. (2011)

Table 6.14. Structure and Productivity of Mangrove Stands at a Fringing Mangrove Site (Estero Pargo) and a Riverine Mangrove Site (Boca Chica) in Términos Lagoon (from Rojas-Galaviz et al. 1992)

	Estero Pargo	Boca Chica				
Structural characteristics						
Mean canopy height (m)	6	20				
Stem density	7,510	3,360				
Basal area (m²/ha)	23	34				
Complexity index	69	32				
Net primary productivity (g/m²/year)						
Woody growth	772	1,206				
Leaves	594	881				
Fruits	192	253				
Branches	48	118				
Total	834	1,252				
Net annual primary productivity	1,606	2,458				

Very few estimates of belowground production have been reported due to the difficulties involved in measuring root production and turnover. A few estimates of root accumulation rates have been made through the use of ingrowth bags. The bags, constructed of flexible mesh material, are filled with root-free sediment or another standardized substrate, and inserted vertically into the ground. After a time interval, the bags are retrieved and the ingrown root mass is measured. This approach reflects the net effect of root production, turnover, and decay during the time interval. Thus, the values are an underestimate of root production, but allow a relative comparison of root matter accumulation in the soil. Values reported for Florida mangroves are slightly less than rates of litterfall, ranging from 144 to 797 g/m²/year with an overall mean of 365 g/m²/year (Table 6.15). Highest values were reported for a riverine soil (643 g/m²/year) and a restored forest (605 g/m²/year), with intermediate values for basin mixed

able 6.16. Abundant macro-invertebrate Groups Associated with mangrove bystems in the Go						
Infauna	Encrusting Epifauna	Motile Epifauna				
Oligochaeta	Oysters (M)	Gastropods (M)				
Capitellidae (P)	Barnacles (C)	Hermit crabs (C)				
Nereididae (P)	Sponges	Brachyuran crabs (C)				
Spionidae (P)	Tunicates (Ch)	Penaeid shrimps (C)				
Amphipoda (C)						
Tanaidacea (C)						
Alongi and Christoferssen (1992), Sheridan (1997), Dittmann (2001), Ellison and Farnsworth (2001), Lee (2008), Metcalfe and Glasby (2008)	Nagelkerken et al. (2008)	Henriques (1980), Alongi and Christoferssen (1992), Caudill (2005), Nagelkerken et al. (2008)				

Table 6.15. Abundant Macro-Invertebrate Groups Associated with Mangrove Systems in the GoM

Key: C =crustacean, Ch =chordate, M =mollusk, P =polychaete

forests (347 g/m²/year), and lowest values for fringe, basin monospecific, and scrub/dwarf forests (172 to 321 g/m²/year).

6.5.3.3 Fauna

Information on the infauna and epifauna of GoM mangrove systems is relatively sparse compared with mangal systems in the tropical Indo-Pacific (see mangrove reviews by Nagelkerken et al. 2000; Faunce and Serafy 2006). This is due, in part, to the restricted regional distribution of this wetland type in the GoM and the fact that mangroves are almost always contiguous to other vegetated wetlands (e.g., seagrasses and tidal marshes) where benthic assemblages are somewhat less complicated to sample (i.e., woody structures such as prop roots and pneumatophores associated with mangroves make sampling the benthos more difficult: see Lee 2008). The numerically dominant benthic invertebrates in mangrove systems of the GoM are small crustaceans (e.g., amphipods and tanaidaceans) and polychaetes, which may occur at high densities (e.g., >52,000 individuals/m²) but low biomass (e.g., ≤ 8.2 g wet/m²) and diversity when compared to seagrass (e.g., $\leq 24,000$ individuals/m² and ≤ 87.4 g wet/m²) or even shallow unvegetated habitats (Sheridan 1997; Escobar-Briones and Winfield 2003). Most studies of mangrove invertebrate assemblages in the GoM have been conducted in southern Florida (e.g., Sheridan 1992, 1997; Vose and Bell 1994) and Mexico (e.g., Vega-Cendejas and Arreguín-Sánchez 2001; Lango-Reynoso et al. 2013). Much of this work has focused on the value of mangrove habitat as foraging areas and nurseries for marine and estuarine nekton (Faunce and Serafy 2006). Unlike other coastal wetland habitats in the GoM, the role of mangroves as important nurseries for nektonic fishes and decapod crustaceans appears to be equivocal (Barbier and Strand 1998; Sheridan and Hays 2003).

Detritus has long been considered the base of mangrove food webs (Odum and Heald 1972) and that notion has persisted in more recent studies of trophic structure and dynamics in GoM mangrove systems, especially in Mexico (Rosado-Solórzano and Guzmán del Próo 1998; Vega-Cendejas and Arreguín-Sánchez 2001; Rivera-Arriaga et al. 2003). Mangrove leaf detritus is more refractory than seagrass or marsh plant detritus and alternative perspectives on the base of GoM mangrove food webs have also emerged, placing emphasis on the importance of benthic algae and phytoplankton (Dittel et al. 1997) or detritus from other sources of riparian vegetation (Mendoza-Carranza et al. 2010). Regardless of the source of detritus or primary

production, there appears to be general agreement that most energy transformations to higher trophic levels such as fishes and nektonic decapods in mangrove systems occur through small benthic and epibenthic invertebrate prey resources (mostly micro- and macro-crustaceans, polychaetes, and gastropods) that can use detritus as a source of nutrition (Vose and Bell 1994; Sheridan 1997; Llansó et al. 1998; Vega-Cendejas and Arreguín-Sánchez 2001; Sheridan and Hays 2003). The feeding activities of intertidal and semiterrestrial sesarmid crabs (e.g., *Aratus pisonii*) and gastropods (e.g., *Melampus coffeus*) found in GoM mangroves often function to process larger fractions of living and dead mangrove leaves into smaller particles that can be consumed by microcrustaceans and annelids (Beever et al. 1979; Erickson et al. 2003; Proffitt and Devlin 2005). Mangroves, like tidal marshes, also provide habitat for a guild of omnivorous xanthid crabs (e.g., *Eurytium limosum*) that can be involved in complex trophic interactions, which may ultimately terminate in the transfer of mangrove production to foraging nekton (Sheridan 1992; Vose and Bell 1994; Llansó et al. 1998).

In many areas of the world where mangroves are a dominant wetland type, macroinvertebrate community structure is influenced by the degree of tidal inundation, availability of organic matter, and sediment characteristics (Lee 2008). There is at least some evidence that the same factors affect assemblages in the GoM (e.g., Sheridan 1997; Vose and Bell 1994). Infaunal and epifaunal assemblages in high and low intertidal mangroves are often distinctly different, due in part to horizontal variation (landward–seaward) in environmental conditions (Nagelkerken et al. 2008). Metcalfe and Glasby (2008) found the highest diversity and abundance of polychaetes in the soft, unconsolidated substrates of seaward assemblages, with these measures decreasing progressively in the landward assemblages. Ellison and Farnsworth (1992) documented epifaunal assemblages on mangrove prop roots at six sites in Belize that ranged from nearshore to offshore sites. Species richness of all encrusting epifauna increased with distance offshore and duration of tidal inundation, with only two sponge species present in the most nearshore site, while there were nine at the most offshore site.

Structurally complex wetland habitats are usually associated with an enriched local faunal diversity (Heck and Wetstone 1977; Summerson and Peterson 1984; Thompson et al. 1996; Cocito 2006; Eriksson et al. 2006; Van Hoey et al. 2008). Biodiversity of some groups of molluscs and crabs may be enhanced by the presence of mangrove (Henriques 1980; Ellison and Farnsworth 2001) but, in general, infaunal diversity is relatively low in mangrove systems. There have been numerous studies of infaunal diversity in mangroves compared to adjacent vegetated and unvegetated habitats in Australia and New Zealand, and these have confirmed the relatively low diversity of infauna assemblages in mangroves (Dittmann 2001; Ellis et al. 2004; Alfaro 2006). Mangrove infaunal assemblages of the GoM show similar low diversity (Sheridan 1997). Lower diversity in some mangrove sediments may have resulted in part from organically enriched silt, which was unsuitable for certain taxa, such as many larger suspension feeders (Ellis et al. 2004).

Table 6.15 lists the most abundant invertebrate groups found in mangrove systems. Mangrove infauna and epifauna are relatively poorly known compared to other components of the mangrove ecosystem, such as floristics and trophic ecology (Lee 2008). Some of the abundant groups of mangrove infauna, such as polychaetes, have been much less frequently studied than other groups, such as brachyuran crabs. For the poorly studied groups, little is known of their overall diversity, abundance, and functional role in mangroves (Nagelkerken et al. 2008).

Microhabitats occupied by mangrove invertebrates include the hard substrata offered by the trunk, aerial roots, and foliage of mangrove trees, and the surrounding soft, unconsolidated sediments (Ellison and Farnsworth 1992). In addition, motile epifauna are attracted to inundated areas of mangroves for foraging and refuge from predators. The peaty mucks in which
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mangroves grow have a high silt content and are inhospitable to most larger suspension-feeding invertebrates (Ellison and Farnsworth 2001). Consequently, mangrove infauna tends to be small, surface-dwelling annelids (polychaetes and oligochaetes) and crustaceans (Lee 2008). Alongi and Christoferssen (1992) found that small, surface-dwelling polychaetes and amphipods were dominant mangrove taxa, followed by tanaid crustaceans. Similarly, annelids, and tanaids were the dominant infaunal taxa in mangroves of Rookery Bay, Florida (Sheridan 1997).

A variety of encrusting and sessile benthic invertebrates, including oysters, barnacles, sponges, and tunicates, occupy mangrove prop root and pneumatophore surfaces in intertidal and subtidal areas. Invertebrates such as the isopod *Sphaeroma terebrans* burrow into the roots of mangroves in south Florida (Brooks and Bell 2002). Of the motile epifauna, gastropods and semiterrestrial crabs (e.g., ocypodids, grapsids, and some xanthids) tend to be most abundant in mangrove ecosystems (Nagelkerken et al. 2008; Beever et al. 1979; Erickson et al. 2003; Proffitt and Devlin 2005). Gastropods occupy a wide range of ecological niches in mangroves and include herbivorous grazers, deposit feeders, and predators (Nagelkerken et al. 2008). Various crabs, including hermit crabs and the tree crab, *Aratus pisonii*, are also conspicuous community constituents. Erickson et al. (2003) reported that *A. pisonii* feeds on the leaves of mangroves in Florida Bay, while Alongi and Christoferssen (1992) found that juvenile crabs and penaeid shrimps were common epifauna occupying mangrove sediments.

Mangroves in most areas, including the GoM, rarely occur in the absence of other adjacent and structurally complex shallow estuarine (e.g., seagrass and marsh) or marine (e.g., coral reef) habitats with which the mangrove habitat shares elements of common highly mobile nekton assemblages (Sheaves 2005). Consequently, mangroves do not appear to be associated with a "characteristic" faunal assemblage. Where present along Gulf shorelines, mangroves attract populations of locally occurring epifauna. In a Louisiana black mangrove stand, Caudill (2005) found that the most abundant epifaunal species in lift nets were grass shrimp (Palaemonetes spp.), which contributed 53.5 % of all collected individuals, followed by white shrimp (Litopenaeus setiferus) and blue crabs (Callinectes sapidus). These species are consistently among the numerically dominant nekton occurring in Gulf coast marine wetlands. Structural complexity may increase apparent biomass production in mangroves by attracting motile fauna (Tolley and Volety 2005; Eriksson et al. 2006). Spatially complex habitats such as submerged mangrove trunks and roots mitigate predator-prey interactions by providing places for prey to hide or escape from predators (Figure 6.132). Juvenile brown shrimp and blue crabs, for example, primarily seek and occupy vegetated habitats (Zimmerman and Minello 1984; Peterson and Turner 1994; Howe et al. 1999; Rakocinski and Drury 2005; Moksnes and Heck 2006).

The composition of nekton assemblages found in mangroves appears to be strongly influenced by species that occur in adjacent habitats. In upstream mangrove forests adjacent to uplands, the nekton assemblages tend to be dominated by small estuarine resident species similar to those commonly found in interior tidal marsh and marsh edge habitats, but in downstream fringing mangrove habitats adjacent to seagrasses or coral reefs, juveniles of species in the families Lutjanidae (snappers) and Haemulidae (grunts), which occur as adults on reefs or in seagrass habitats, are added to the nekton assemblage (Ley et al. 1999; Serafy et al. 2003). Such observations have led to a considerable focus on habitat matrix upon which some species are dependent at different stages in their life histories (Nagelkerken et al. 2001, 2002; Mumby 2006; Jones et al. 2010).

The basic nekton assemblage structure of mangroves in much of the GoM appears to be very similar to that of tidal marshes, with the shallow waters inundating the structurally complex elements of prop roots and pneumatophores offering attractive habitat (Figure 6.132),



Figure 6.132. Illustration of nekton attraction to submerged structural features of mangrove habitat. (http://www.naturefoundationsxm.org/education/mangroves/red_mangrove_illustration. gif; used with permission). Mangrove aerial roots may provide food, in the form of epiphytes and epifauna, habitat, and protection from predation for many nektonic species.

mostly for small estuarine resident species (Table 6.16). Although many of the dominant species may vary across regions, the most abundant fish families in mangroves are Cyprinodontidae (killifishes), Fundulidae (fundulids), Poeciliidae (live-bearers), and Gobiidae (gobies), as well as the juveniles of a number of transient species, often representing the fish families Gerridae (mojarras), Mugilidae (mullets), Sciaenidae (drums), and Sparidae (porgies). At the edges of the embayments and channels immediately adjacent to the mangrove vegetation, schooling species in the fish families Engraulidae (anchovies), Atherinidae (silversides), and Clupeidae (herrings) are often common (Figure 6.108), as are the much less abundant larger predatory species they attract, such as Sphyraenidae (barracudas), Eleopidae (tarpons), and Centropomidae (snooks) (Figure 6.109c).

The absence of natant decapod crustaceans from some studies is noteworthy (Table 6.16) and has two likely explanations. First, the methods used to collect nekton from among the sturdy prop roots and pneumatophores of mangroves often rely on the application of rotenone which, especially in its most commonly used formulation, is much more effective on fishes than crustaceans (Robertson and Smith-Vaniz 2008), so it is not surprising that fishes predominate in the collections. Second, natant decapod crustaceans may not be as abundant in mangroves as in other coastal wetland habitats. Some researchers have noted that penaeid shrimp were rarely collected or observed in mangroves, but were more commonly associated with adjacent seagrass beds (Thayer et al. 1987), even though there is some evidence that juvenile penaeid shrimp appear to satisfy at least a portion of their nutritional requirements from mangrove-associated bacteria and benthic macrofauna (Nagelkerken et al. 2008).

A variety of unconventional methods for sampling nekton have been applied in highly structured wetlands such as mangroves, and sometimes the findings provide complementary representations of the fauna because no two methods are equally effective in capturing nekton Table 6.16. Nekton Species Comprising at Least 90 % of the Total Individuals in Mangrove Samples Collected with Block Nets or Enclosure Nets from Prop Roots in Florida (FL Bay 1: Thayer et al. 1987; FL Bay 2: Ley et al. 1999; Placido Bayou, FL: Mullin 1995; Tampa Bay, FL: Krebs et al. 2007) or Lift Nets Among the Pneumatophores of Black Mangroves in Louisiana (Caudill 2005)

		Lift Nets			
	FL Bay 1	FL Bay 2	Placido Bayou, FL	Tampa Bay, FL	Caminada Bay, LA
Fishes					
Atherinidae					
Atherinomorus stipes	Х	Х			
Membras martinica	Х				
Menidia penninsulae	Х				
Menidia beryllina					Х
<i>Menidia</i> spp.		Х	Х	Х	
Cichlidae					
Sarotherodon melanotheron		Х	Х		
Unidentified cichlid				Х	
Clupeidae					
Brevoortia gunteri			Х		
Brevoortia patronus				Х	
Harengula humeralis	Х				
Harengula jaguana	Х	Х			
Jenkensia lamprotaenia	Х				
Opisthonema oglinum		Х			
Cyprinodontidae					
Floridichthys carpio	Х	Х	Х	Х	
Cyprinodon variegatus	Х	Х	Х	Х	Х
Engraulidae					
Anchoa mitchilli	Х	Х	Х	Х	
Anchoa hepsetus	Х				
Anchoa cayorum		Х			
Fundulidae					
Lucania parva	Х	Х	Х		
Fundulus grandis	Х	Х	Х	Х	Х
Fundulus similis	Х	Х		Х	
Fundulus confluentus	Х	Х		Х	
Fundulus jenkinsi			Х		
Adinia xenica		Х		Х	
Gerridae					
Diapterus plumeri		Х	Х	Х	
Eucinostomus gula	Х	Х			
Eucinostomus argentus	Х	Х	Х		
Eucinostomus harengulus		Х		Х	

(continued)

Table 6.16. (continued)

		Lift Nets			
	FL Bay 1	FL Bay 2	Placido Bayou, FL	Tampa Bay, FL	Caminada Bay, LA
Eucinostomus spp.				Х	
Gerres cinereus		Х			
Gobiidae					
Bathygobius soporator	Х				
Ctenogobius smaragdus	Х			Х	
Evorthodus lyricus					Х
Gobiosoma bosc	Х	Х			
Gobiosoma robustum	Х	Х	Х		
Gobiosoma spp.				Х	
Gobionellus boleosoma					Х
Lophogobius cyprinoides	Х	Х			
Microgobius gulosus	Х	Х	Х	Х	
Mugilidae					
Mugil cephalus	Х	Х		Х	Х
Mugil curema	Х	Х			
Mugil gyrans				Х	
Mugil liza		Х			
Poeciliidae					
Belonesox belizanus		Х			
Gambusia holbrooki				Х	
Gambusia sp.	Х	Х			
Poecilia latipinna	Х	Х	Х	Х	
Sciaenidae					
Cynoscion nebulosus	Х			Х	
Leiostomus xanthurus			Х	Х	
Pogonias cromis	Х			Х	
Sciaenops ocellatus	Х			Х	
Sparidae					
Archosargus probatocephalus	Х			х	
Lagodon rhomboides	Х		Х	Х	Х
Natant Decapod Crustacean	s				
Portunidae					
Callinectes sapidus				Х	Х
Penaeidae					
Farfantepenaeus aztecus					Х
Farfantepenaeus duorarum				Х	
Litopenaeus setiferus					Х
Palaemonidae					
Palaemonetes spp.					Х

Red shaded cells indicate the presence of dominant families at each location

of all species, sizes, or at all locations (Loftus and Rehage 2005). For example, rotenone in aqueous solution, as it is commonly used in marine sampling programs in coral reef and mangrove habitats, is strongly selective in affecting fishes, but has little or no effect on most natant decapod crustaceans or other types of nekton (Robertson and Smith-Vaniz 2008). Consequently, nekton-sampling programs relying on rotenone are biased toward fishes, even if they may not be the most abundant nektonic organisms in the assemblage.

Table 6.17 compares the nekton assemblage from a mangrove habitat in Florida Bay using a combination of nets and rotenone poisoning with results from visual censusing and video recording. Only half of the top ten most abundant fish families appear in all three lists, and these were represented by species considered as resident nekton (families Gerridae, Cyprinodontidae, Fundulidae, Poecilidae, and Gobidae). However, there are also some striking differences in the importance of dominant groups. Engraulids (anchovies) were the top-ranked family captured in nets but accounted for only 1.4 % of fishes in the video recording and do not even rank in the top ten families in the visual census. Also, in the visual census, the atherinids (silversides) comprised nearly 84 % of the fishes, but were not detected in the video recording data. Species diversity and evenness were greater in the net sample than in either the visual census or the video recording collections. For example, only two families represented by six species accounted for nearly 88 % of all nekton in the visual census, but five families and 15 species were required to account for a similar percentage of nekton in the net samples. The video recording samples were intermediate in this regard, requiring seven families and >11 species to account for 88 % of the individuals. The video data also included a high percentage (9.6%) of juvenile individuals that could not be identified to either species or family. The three methods clearly paint a very different picture of the nekton assemblage in this single mangrove system. The enclosure nets with rotenone likely represented the species found among the mangrove prop roots while the visual census may have better represented the nekton assemblage immediately adjacent to the mangrove forest per se.

There is considerable debate over the relative contribution of mangrove habitat in supporting estuarine nekton assemblages. While some studies have suggested a positive relationship between the areal extent of fringing mangrove forests and regional fisheries production (Aburto-Oropeza et al. 2008), others have questioned the importance of mangroves as nursery habitat for nekton (Sheridan and Hays 2003; Faunce and Serafy 2006). Unlike other coastal wetland habitats in which production by the dominant plant species tends to support a trophic structure on which nekton assemblages derive considerable nutrition, mangroves generally do not directly contribute much trophic support for nekton (Stoner and Zimmerman 1988; Sheridan and Hays 2003). Alternative sources of trophic support from nearby habitats such as seagrasses may contribute more to the diets of nekton found in mangroves (Nagelkerken and van der Velde 2004). Nonetheless, mangrove habitats seem to provide at least some nursery functions for both recreationally and commercially important fishery organisms and their food resources (Odum et al. 1982).

6.5.4 *Phragmites* Reed Beds

Phragmites australis (common reed) is a warm-season, rhizomatous, stoloniferous perennial grass that grows in tidal and non-tidal habitats throughout the world (Chambers et al. 1999; USDA 2002). In the northern GoM, *Phragmites australis* (hereafter *Phragmites*) inhabits stream banks and interior marsh locations from Texas to Florida, but occurs in greatest abundance along the Balize, or Birdfoot, Delta and Chenier Plain regions of Louisiana (Tiner 2003; Rosso et al. 2008; Stanton 2005). *Phragmites* has been part of the marsh communities of North America (including the Gulf Coast) for millennia (Lamotte 1952), but has drastically Table 6.17. Top Ten Fish Families in Mangrove Prop Roots in Florida Bay Based on Sampling With: (1) Enclosure Nets + Rotenone, (2) Visual Censusing (Ley et al. 1999), and (3) Video Recording (Ellis and Bell 2008)

Rank Order	Fish Family	Abundance	Cumulative %	Number of Species
Enclosur	e nets + rotenone			
1	Engraulidae – anchovies	18,598	21.3	2
2	Atherinidae – silversides	17,683	41.6	3
3	Cyprinodontidae – killifishes	15,277	59.1	2
4	Poeciliidae – livebearers	13,410	74.4	3
5	Fundulidae – fundulids	11,753	87.9	5
6	Gobiidae – gobies	3,915	92.4	4
7	Gerridae – mojarras	3,321	96.2	4
8	Cichlidae – cichlids	1,066	97.4	2
9	Belonidae – needlefishes	1,040	98.6	2
10	Batrachoididae – toadfishes	572	99.3	2
	TOTAL above and others	87,257	100.0	48
Visual Ce	nsus			
1	Atherinidae – silversides	407,772	83.9	3
2	Lutjanidae – snappers	19,186	87.8	3
3	Peociliidae – livebearers	15,377	91.0	3
4	Fundulidae – fundulids	12,149	93.5	3
5	Gerridae – mojarras	11,122	95.9	4
6	Cyprinodontidae – killifishes	9,004	97.7	2
7	Haemulidae – grunts	2,901	98.3	2
8	Belonidae – needlefishes	1,974	98.7	1
9	Gobiidae – gobies	1,743	99.9	3
10	Muglidae – mullets	1,377	99.3	2
	TOTAL above and others	485,846	100.0	42
Video Re	cord			
1	Gerridae – mojarras	4,121	46.2	1?
2	Sparidae - porgies	1,715	65.4	2
3	Haemulidae – grunts	1,354	80.6	2?
4	Lutjanidae – snappers	294	83.9	2
5	Peociliidae – livebearers	198	86.1	2
6	Gobiidae – gobies	151	87.8	1?
7	Engraulidae – anchovies	122	89.2	1?
8	Fundulidae – fundulids	61	89.9	1
9	Cyprinodontidae – killifishes	39	90.3	1
10	Ephippidae - spadefishes	4	90.3	1
	TOTAL above and others	8,919	100.0	16

increased its distribution over the past century (Chambers et al. 1999). This range expansion has occurred at the expense of other species, as *Phragmites* often forms large, dense, near-monotypic stands that outcompete other species for resources (Phillips 1987; Minchinton and Bertness 2003). Increased *Phragmites* density also alters ecosystem services and reduces available habitat for many species of wading birds, fish, and mammals that utilize wetlands (Hauber et al. 1991; Chambers et al. 1999). However, *Phragmites* marshes do provide habitat for a variety of species, and may play an important role in stabilizing some of the most erodible wetland habitats in the northern GoM (Rooth and Stevenson 2000).

6.5.4.1 Dominant Forcing Functions

The primary drivers that control the ecological structure and function of *Phragmites* beds in the central GoM (i.e., Mississippi River Delta) are similar to those discussed for salt marshes and mangroves, with a few notable exceptions. Salinity in *Phragmites* marshes at the mouth of the Mississippi River is low to absent due to freshwater input from the river. Marshes here are classified as the intermediate type, between fresh and brackish, or fresh. However, salinity is an important environmental factor outside of the Birdfoot Delta, such as in the Chenier Plain region, where *Phragmites* stands are normally exposed to brackish water conditions (Stanton 2005). Also, reed beds at the mouth of the Mississippi River are continuously flooded with a few meters of water during the spring flood period. Water may not drain from the beds during this period. However, *Phragmites* has an efficient internal aeration system that provides oxygen to underground plant organs (Brix et al. 1996), allowing this species to not only tolerate these conditions, but also thrive. The input of nutrient-rich sediments from the Mississippi River may assist in this regard. The high land subsidence rate is another driver impacting the attached reed beds in the region. In the Birdfoot Delta, relative sea-level rise (the combination of subsidence and global sea-level change) is more than a centimeter a year (Penland and Ramsey 1990). This process has been a primary driver of wetland loss in the region, as has the natural abandonment of the sub-deltas comprising the Birdfoot Delta and the infilling of their distributary channels (Wells and Coleman 1987), and is an added force for ecological change.

6.5.4.2 Vegetation

6.5.4.2.1 Origin and Structure

Phragmites australis occupies a range of habitats in the northern GoM and can proliferate in a wide variety of water depths (Hauber et al. 1991; White et al. 2004a). Historically, *Phragmites* was only a minor component of tidal marsh vegetation assemblages and was confined to higher elevations at the upland boarders of marshes and areas along creek banks (Niering et al. 1977; Warren et al. 2001). However, recent expansion of *Phragmites* into more diverse habitats has been occurring along the U.S. Atlantic and Gulf coasts (Chambers et al. 1999; Peterson and Partyka 2006; Hauber et al. 2011). Reasons for the *Phragmites* expansion vary by location but can include tidal restrictions, habitat modification, disturbance, and invasion by a more competitive European population (Chambers et al. 1999; Burdick et al. 2001; Howard et al. 2008; Hauber et al. 2011). For example, in coastal Mississippi Peterson and Partyka (2006) found that *Phragmites* was widespread along creek banks in up-estuary/low salinity environments where there was little anthropogenic disturbance, but *Phragmites* also occurred in high elevation/high salinity areas that were heavily modified by man.

The situation in Louisiana is somewhat unique, particularly in the Mississippi River's Birdfoot Delta, where distinct genotypes of *Phragmites* can occupy different areas within the same marsh (White et al. 2004a; Hauber et al. 2011; Lambertini et al. 2012) (Figure 6.133).



Figure 6.133. *Phragmites australis* forms circular patches in the Mississippi River Birdfoot Delta. Molecular genetic analyses have demonstrated that these patches, which have identifiable aerial signatures (color and height), are genetically distinct populations (Lambertini et al. 2012) (photo credit: I. A. Mendelssohn).

Phragmites is the dominant vegetation type in the outer two-thirds of the Birdfoot Delta, yet within these *Phragmites* areas are patches of the reed that are both phenotypically and genetically distinct (Hauber et al. 1991, 2011; White et al. 2004a) (Figure 6.133). However, the occurrence of *Phragmites* on the outer portions of the delta is a mixed blessing. On one hand, *Phragmites* populations stabilize an easily erodible landscape (Rooth and Stevenson 2000) and protect the more diverse and fragile interior marshes of the delta (Hauber et al. 2011). On the other hand, *Phragmites* populations provide little in the way of habitat and food for migrating waterfowl that overwinter in the Mississippi River delta (Hauber et al. 1991).

The *Phragmites* marshes of the Mississippi River's Birdfoot Delta are unique in that they contain the most phenotypically and genetically diverse *Phragmites* populations in the world (Hauber et al. 2011). The most common phenotype, known as the Delta phenotype, tends to occur in the outer portions of the delta and is considered the oldest *Phragmites* lineage in the Birdfoot Delta (Hauber et al. 1991; Fournier et al. 1995; White et al. 2004a). More recently the interior marshes of the delta have been colonized by at least two other lineages, the Gulf Coast subspecies and the introduced haplotype M, which has Eurasian origins (Hauber et al. 2011). Another *Phragmites* haplotype, AD, was also recently discovered by Hauber et al. (2011), but its distribution is presently unknown.

6.5.4.2.2 Ecosystem Function

The processes responsible for controlling ecosystem function in *Phragmites* marshes along the Gulf Coast have gone largely unstudied. In fact, much of the data regarding primary production, decomposition, nutrient cycling, and elevation change comes from a single source—Stanton (2005). *Phragmites* is a tenacious ecosystem engineer that can colonize a wide range of water depths (White et al. 2004a), and build soil upwards through the accumulation of organic and inorganic materials to increase soil elevation and potentially reduce flooding stress (Rooth and Stevenson 2000; Stanton 2005). For example, Stanton (2005) found that elevation in the center of a 40-year-old *Phragmites* colony in Louisiana was 10 cm higher than the surrounding marsh. Interestingly, the elevation increase did not lead to a change in the interstitial water chemistry of the *Phragmites* colony, although this was likely due to the hydrology of the marsh being manipulated by control structures (Stanton 2005).

Organic matter decomposition in wetlands depends on flooding frequency, flooding duration, soil temperature, soil redox potential, and organic matter quality (Brinson 1977; Neckles and Neil 1994; Windham 2001). *Phragmites* litter is of particularly poor quality (high carbon to nitrogen ratio) making decomposition rates in *Phragmites* marshes slow (Windham 2001) and the accumulation of organic matter rapid (Stanton 2005).

Above- and below-ground biomass production rates in *Phragmites* marshes can be very high due to the large stature of the plant and its ability to outcompete other species for resources (Burdick and Konisky 2003; Stanton 2005; Howard and Rafferty 2006). Above-ground biomass production in *Phragmites* marshes varies depending on stem densities and heights, but is proportional to stem diameter (Stanton 2005), and stem heights can increase in response to flooding (Howard and Rafferty 2006). As *Phragmites* colonies age, stem densities tend to increase, but stem height and diameters tend to decrease (Stanton 2005). Aboveground productivity determined in Louisiana ranged from 990 to 2,318 g dry mass/m²/year (Hopkinson et al. 1978). Belowground, *Phragmites* produces roots and rhizomes that often extend greater than 50 cm below the soil surface (Windham 2001). This allows *Phragmites* to utilize resources unavailable to many other common marsh species, put more energy toward aboveground growth, capture more light for photosynthesis, and ultimately outcompete and displace other marsh species (Stanton 2005).

6.5.4.3 Fauna

The fauna of *Phragmites* marshes has been the focus of few studies, particularly in the GoM. Much of the available data on benthic, epibenthic and nektonic fauna associated with *Phragmites* has been collected in the northeastern United States, but it is not clear how widely the results of these studies may apply to *Phragmites* environments in other geographic regions (Meyerson et al. 2000). Nevertheless, there are likely to be similarities in faunal assemblage structure in GoM *Phragmites* marshes when compared with GoM smooth cordgrass and needlerush marshes.

Phragmites australis occurs as various haplotypes with different growth forms and habits (Howard et al. 2008) that vary with respect to potential effects on faunal assemblages. Generally, the most important impacts of *Phragmites* in coastal wetlands occur in association with a very robust Eurasian haplotype that has an aggressive growth habit (Burdick and Konisky 2003; Philipp and Field 2005; Howard et al. 2008). The invasive Eurasian variety of the common reed is very productive in terms of both above and below ground biomass generated annually (Windham 2001), which alters soil properties, increases elevation, and reduces microtopographic relief of intertidal wetlands (Windham and Lathrop 1999).

Posey et al. (2003) found that while vegetation type (i.e., smooth cordgrass or *Phragmites*) had a detectable effect on benthic invertebrate assemblage structure, microhabitat characteristics, such as local topography, had a stronger relation to faunal abundance patterns. Infaunal and epifaunal assemblages in high and low intertidal salt marsh (Stout 1984) and mangroves (Nagelkerken et al. 2008) are often distinctly different depending on the degree and duration of tidal flooding. Angradi et al. (2001) found that invertebrate abundance and assemblage composition did vary with distance from the marsh edge of *Phragmites* marsh in southern New Jersey. It is assumed that benthic community structure in Gulf *Phragmites* marshes is influenced to some degree by tidal inundation.

Angradi et al. (2001) found that invertebrate taxon richness was significantly higher in *Spartina alterniflora* marsh compared with *Phragmites* marsh. Moreover, dominance by the most abundant taxa was greater in *Phragmites* marsh (>85 %) at most sampling locations, also indicating lower benthic diversity in *Phragmites* (Angradi et al. 2001). Yuhas et al. (2005), however, found no clear pattern of difference in taxa abundance and richness comparing *Phragmites* and *S. alterniflora* marshes in New Jersey, though they only sampled creek bank and the marsh edge and not the interior vegetated marsh. Taxonomic diversity of invertebrate assemblages in GoM *Phragmites* marshes is likely to vary by location and time of year.

Table 6.18 lists the most abundant invertebrates found in *Phragmites* systems. Infaunal assemblages in *Phragmites* marsh are broadly similar to those of salt marsh. For example, Angradi et al. (2001) found that the most abundant infauna in *Phragmites* included oligo-chaetes and the polychaete *Manayunkia aestuarina*. Fell et al. (1998) sampled sites along the Connecticut River and found that certain high-marsh invertebrates (snails, amphipods and isopods) were common to abundant in salt marshes with and without *Phragmites*. Posey et al. (2003) found that *Phragmites* marshes in the Chesapeake Bay were numerically dominated by the polychaetes *Capitella capitata*, *Hobsonia florida* and *Laeonereis culveri*, oligo-chaetes, and chironomid fly larvae. They found that a typical mesohaline assemblage numerically dominated the infaunal community. Yuhas et al. (2005) collected benthic samples in *Phragmites* marshes in New Jersey, and found that oligochaetes were the most abundant infauna, comprising 24.4 % of all collected individuals.

Where present, intertidal *Phragmites* habitats along GoM shorelines can be expected to provide habitat for populations of locally occurring epifauna and nekton as is the case in the northeastern United States, but there is considerable debate over the relative habitat value of *Phragmites* compared to other marsh types. Able and Hagan (2000) examined decapod

Infauna	Epifauna		
Oligochaeta	Blue crab (C)		
Capitella capitata (P)	Fiddler crab (C)		
Hobsonia florida (P)	Mud crab (C)		
Laeonereis culveri (P)			
Amphipoda (C)			
Isopoda (C)			
Chironomidae (Di)			
Fell et al. (1998), Angradi et al. (2001), Posey et al. (2003), Yuhas et al. (2005)	Able and Hagan (2000)		

Table 6.18. Abundant Invertebrates in *Phragmites* Systems

Key: C crustacean, Di dipteran, P polychaete

crustacean use of *Phragmites* and *S. alterniflora* marsh in the brackish water reaches of the Mullica River (NJ). Fiddler crabs (*Uca* spp.) and mud crabs (*Rhithropanopeus harrisii*) were more abundant in *Phragmites* (Able and Hagan 2000). Angradi et al. (2001) found that a *Spartina* marsh had greater production of benthic infauna than a *Phragmites* marsh, with higher overall abundance of benthic invertebrates. Posey et al. (2003) found only a small effect on faunal abundance patterns, with most species exhibiting slightly higher mean density in smooth cordgrass compared to adjacent *Phragmites* marshes. It has been suggested that fewer refugia from predators during high tide in *Phragmites* marsh may explain some of the differences in faunal abundance and community structure in comparison to *Spartina* habitat (Angradi et al. 2001).

The relative value to nekton of intertidal areas dominated by *Phragmites* compared to other marsh plant species remains unclear. Samples collected by trawling adjacent to subtidal creeks (Grothues and Able 2003) or using block net-type gear in intertidal creeks (Kimball et al. 2010) or on intertidal vegetated edges (Meyer et al. 2001) have not detected substantial differences in nekton assemblages in *Phragmites*-dominated sites compared to marsh habitats dominated by other plant species (e.g., *Spartina*). Also, the gut contents of at least one resident fundulid fish species collected from the inundated surface of *Phragmites* marshes contained similar invertebrate prey items as those foraging in marshes dominated by other vegetation types (Fell et al. 1998) and stable isotope analyses of several transient species of estuarine fishes have shown that *Phragmites* contributes to trophic support (Wainright et al. 2000; Litvin and Weinstein 2003; Weis and Weis 2003; Mendoza-Carranza et al. 2010; Weinstein et al. 2010).

Other studies have revealed a somewhat different picture. For example, Raichel et al. (2003) found that adults of the fundulid fish, *Fundulus heteroclitus*, were equally abundant in marshes dominated by *Phragmites* compared to those dominated by *Spartina*, but larvae and early juveniles of the fish were significantly less abundant in *Phragmites*. Furthermore, they also found that abundance of potential prey resources (e.g., copepods and other small crustaceans) for these early stages of resident nekton was significantly lower in *Phragmites* relative to *Spartina* marsh.

A key element that seems to drive the observed differences between *Phragmites* reed beds and other marsh types with respect to effects on benthic and nektonic fauna is that the robust rhizome and root growth of *Phragmites* affects elevation, microtopographic features and hydrologic characteristics of the intertidal marsh (Weinstein and Balletto 1999; Osgood et al. 2003; Buchsbaum et al. 2006). Many fundulid fishes spawn in intertidal marshes and often rear their young in shallow intertidal pools and puddles on the marsh surface. The robust growth of rhizomes and roots in *Phragmites* beds raises and flattens the marsh surface (Figure 6.134), reducing the availability of intertidal spawning and rearing sites for resident fishes (Able et al. 2003; Hunter et al. 2006) as well as the production of early life stages (Hagan et al. 2007).

Jivoff and Able (2003) used an otter trawl to sample tidal creeks adjacent to *Phragmites*and *Spartina*-dominated marshes near high tide and found a tendency toward greater abundance of adult and fewer small recruit blue crabs (*Callinectes sapidus*) associated with *Phragmites* beds. They suggested that the observed differences in size-specific abundance were due to the effect of marsh surface vegetation type on high tide use of the marshes. Specifically, they proposed that smaller blue crabs made greater use of the less densely vegetated and more tidally inundated *Spartina* marsh surfaces compared to *Phragmites* sites. Of course, this assumes that greater abundance of blue crab life stages in tidal creeks at high tide occurs as a result of the inaccessibility of the marsh surface.



Figure 6.134. Changes in the micro-topographic features of the vegetated marsh surface with the growth and expansion of *Phragmites australis* as it replaces *Spartina alterniflora*, filling in small intertidal creeks and aquatic microhabitats and flattening the marsh surface (from Able et al. 2003; republished with permission of Springer Science and Bus Media BV, permission conveyed through Copyright Clearance Center, Inc.).

Questions regarding the quality of potential food resources derived from *Phragmites* production also have been raised. Stable isotope studies conducted primarily in New Jersey have indicated that an abundant resident fundulid fish (*Fundulus heteroclitus*) derives most of its nutrition for growth, reproduction and survival from a combination of primary producers including benthic microalgae and extant marsh grasses such as *Spartina* and *Phragmites*. However, in *Phragmites* reed beds there is reduced production of benthic microalgae due to shading effects of the robust aboveground growth of the reed relative to other marsh grasses (Currin et al. 2003). Consequently, the food webs associated with *Phragmites* are more dependent on detrital pathways based on reed decomposition.

Recent stable isotope studies have shown that there are potentially important differences in the allocation of lipids and free fatty acids when fish depend on food webs based on *Phragmites* production rather than benthic microalgae or other marsh plants. In particular, triacylglycerols which are essential for reproduction and survival during times when food resources may be limited (e.g., winter) are substantially lower in tissue samples of not only resident fundulids (Weinstein et al. 2009), but also certain marsh transient species such as *Morone americana* (white perch) (Weinstein et al. 2010). These findings have led some to the conclusion that *Phragmites* reed beds provide an inferior source of trophic support for nekton compared to food webs based on noninvasive primary producers.

Although the studies described in this section were conducted in marshes along the Atlantic coast, very similar species of benthic invertebrates and nekton, including a sibling suite of fundulid (*Fundulus grandis*, *F. pulvereus*, *F. jenkinsi*) species in the northern GoM (Figure 6.106) could reasonably be expected to respond to *Phragmites* reed beds in ways that are similar to responses observed in the common fauna along the U.S. Atlantic coast. *Fundulus jenkinsi* (salt marsh topminnow) may be of particular interest in this regard because it is a federally listed species of concern in the GoM and is sensitive to the types of physical marsh surface features (e.g., stem density, bank slope, and marsh elevation) (Lopez et al. 2010a, b, 2011) that are most affected by the common reed *Phragmites australis*. At a broader spatial scale, faunal assemblages of *Phragmites* marshes within the GoM are likely sensitive to their location within the coastal landscape, so that the composition and functioning of the faunal components are likely influenced by connectivity to adjacent habitats (Partyka and Peterson 2008). However, the overall contribution of *Phragmites* to secondary production in coastal areas has not been adequately investigated.

6.5.5 Seagrass Meadows

Seagrasses are unusual among the vascular flowering plants (i.e., angiosperms) in being entirely restricted to underwater marine habitats (den Hartog 1970). The more general term *submerged aquatic vegetation* or SAV is occasionally used interchangeably, although with the understanding that it can refer to freshwater species as well. Species occurring primarily in brackish or fresh water are not considered in this discussion.

Evolutionarily, the seagrasses are not true grasses (i.e., family *Poaceae*), but instead represent a diverse taxonomic group of four phylogenetically related plant families all belonging to the order Alismatales (Green and Short 2003; APG III 2009; Stevens 2001). There are approximately 60 known species of seagrasses worldwide with the majority of species being placed in three primary families: Hydrocharitaceae (3 genera with 17 species), Cymodoceaceae (5 genera and 16 species), and Zosteraceae (2 genera with 14 species). The small family Posidoniaceae is represented by a single genus (Posidonia) with only 2 species (Green and Short 2003). Some species of *Ruppia* (family Ruppiaceae) are treated as seagrasses by various authors, although they do not typically occur in the higher salinity waters considered in this summary.

6.5.5.1 Dominant Forcing Functions

Yáñez-Arancibia and Day (2004) divide the GoM into several different ecological regions and subregions based on the interactions of various physiographic, oceanographic, and biogeographic features including climate, geomorphology, freshwater input, and coastal drainage patterns (i.e., hydrologic units), physical chemistry, wildlife, estuarine vegetation, and human influences (Yáñez-Arancibia and Day 2004; Wilkinson et al. 2009). A description of seagrass communities of the South Florida/Bahamian Atlantic Marine Ecoregion, Northern GoM Marine Ecoregion (Eastern Gulf Neritic, Mississippi Estuarine, Texas Estuarine), and Southern GoM Marine Ecoregion, as well as their distribution, are provided below.

Broad patterns in species composition and the spatial positioning of seagrass beds are apparent across the ecoregions of the GoM. These patterns generally correlate with latitude, although many other complex factors likely contribute, including both large-scale and local differences in geomorphology, salinity, and hydrology.

6.5.5.2 Vegetation

6.5.5.2.1 Structure and Zonation

Seagrass species exhibit autecological (relationship of an individual species to its environment) differences in their natural history that affect their spatial distribution within beds. Where multiple seagrass species co-occur, a general pattern of zonation can be observed. For example, a survey of SAV distribution in East Bay (Bay County, Florida) conducted during 2011 documented three seagrass species. *Halodule wrightii* (shoalweed) dominates the SAV community closest to shoreline, and is most frequently found at depths of 1 to 3 ft. Thalassia becomes prevalent at depths of 3 to 6 ft. Syringodium filiforme (=Cymodocea filiformis) (manatee grass) is often interspersed with *Thalassia* at shallower depths, but becomes the dominant species at depths greater than 5 ft. No SAV was observed at depths greater than 8 ft. Halophila engelmanni (Engelmann's seagrass) is often found at great depths. In the Big Bend area of Florida, it can be found in monotypic stands away from the primary grass beds down to a depth of 20 m (66 ft) (Continental Shelf Associates, and Martel Laboratories 1985, cited in Zieman and Zieman 1989). Halophila decipiens, another species adapted to low-light conditions, covers approximately 20,000 km² (4,900,000 ac) of seagrass habitat off the west coast of Florida (Hammerstrom et al. 2006). Seagrass meadows typically contain a variety of rhizophytic and drift algae. Mattson (2000) summarized macroalgae associated with the Big Bend area of Florida, including *Caulerpa* spp. (rhizophytic forms) and *Hypnea* spp. (drift algae).

The landscape position of seagrass beds differs among the ecoregions. On the west coast of Florida in the South Florida/Bahamian Atlantic and Eastern Gulf Neritic ecoregions (Yáñez-Arancibia and Day 2004; Wilkinson et al. 2009) seagrasses are frequently found fronting the GoM, especially around the Florida Bay, Springs Coast, and Big Bend areas and also the eastern Florida Panhandle including Apalachee Bay (Yarbro and Carlson 2011; Onuf et al. 2003; Zieman and Zieman 1989; Iverson and Bittaker 1986). Moving westward along the coastline of the Panhandle, seagrasses gradually become more associated with sheltered embayments and areas behind protective barrier islands (e.g., Apalachicola Bay, St. Joseph Bay, St. Andrews Bay, Choctawhatchee Bay, and Santa Rosa Sound) (Yarbro and Carlson 2011). In the Mississippi Estuarine Ecoregion (Yáñez-Arancibia and Day 2004), which includes all of Alabama, Mississippi, and Louisiana, seagrasses are restricted to areas behind barrier islands (Onuf et al. 2003). Similarly, seagrasses are also found in the protective bays and coastal lagoons in the Texas Estuarine Ecoregion and along the northwestern coast of Cuba, seagrasses occur in several embayments as well as in the Gulf itself (Onuf et al. 2003).

There also are differences in species composition of seagrass beds among the subregions. *Thalassia, Halophila*, and *Syringodium* tend to be much more common at lower latitudes in Florida and Texas, and these species gradually become less prevalent as one moves northward into Alabama, Mississippi, Louisiana, and north Texas (i.e., the Mississippi Estuarine Ecoregion and portions of the Texas Estuarine Ecoregion). In this broad central GoM area, *Halodule wrightii* predominates and the three other species are largely absent. When present, they generally represent a minor component of the seagrass community, unlike the southern areas of Florida and Texas, and Mexico and Cuba, where they occur abundantly. This distributional pattern based on latitude probably reflects a number of various physiographic processes. Examples include regional differences in climate, salinity, and hydrology (e.g., variations in freshwater input especially from the Mississippi River), turbidity (which relates to hydrology),

the geochemistry and texture of bottom sediments (muddy silts in the upper Gulf near the Mississippi River versus gravel, shell, and sands in the Eastern Gulf Neritic), shelf geomorphology, nutrient loads, and geologic histories (Wilkinson et al. 2009; Onuf et al. 2003). Zieman and Zieman (1989) and references therein report on species-specific differences in seagrasses that are related to species substrate preferences, depth and light regimes, and salinity tolerance; all of these factors are likely responsible for current day distributional patterns in the GoM.

6.5.5.2.2 Distribution

Seagrass beds in the South Florida/Bahamian Atlantic Ecoregion are characterized by *Thalassia testudinum, Syringodium filiforme*, and *Halodule wrightii*; *Halophila* species (e.g., *H. engelmanni and H. decipiens*) are abundant primarily in deeper or more turbid waters (Yarbro and Carlson 2011). This ecoregion includes Florida Bay and Florida Keys, and covers nearly 6,000 km² (1,480,000 ac) or over 55 % of the seagrasses in Florida's GoM coastal waters (Onuf et al. 2003). Distributions and abundances of seagrasses in Florida Bay and the Florida Keys have been studied extensively; Fourqurean et al. (2002) described the results of three monitoring programs focused on changing habitat conditions and die-off of some seagrasses in that area. Seagrass communities are similar in northwestern Cuba, and are dominated by *Thalassia, Syringodium, Halophila engelmanni*, and *Halophila decipiens*; perhaps 2,000 km² (494,000 ac) of grassbeds occur in this area (Onuf et al. 2003).

In the Eastern Gulf Neritic Ecoregion of the GoM, *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* are the most frequently encountered species of seagrass (Zieman and Zieman 1989; FNAI 2010; Yarbro and Carlson 2011). *Halophila engelmanni* is generally considered an uncommon and minor component of marine SAV beds in the northern reaches of the Florida Gulf Coast, where it is often found intermixed with other species (Zieman and Zieman 1989; FNAI 2010; Yarbro and Carlson 2011). Approximately 15,864 ha (39,200 acres) of SAV have been mapped in Florida waters, north of Crystal River to Escambia Bay (Yarbro and Carlson 2011). SAV is most abundant in the Big Bend area and in the St. Andrew Bay system.

Along the northern Gulf in the centrally located Mississippi Estuarine Ecoregion (Yáñez-Arancibia and Day 2004), *Halodule wrightii* predominates as the major species of seagrass (Barry A. Vittor and Associates, Inc. 2004, 2009; Onuf et al. 2003). The other species (e.g., *Thalassia, Syringodium*, and *Halophila*) reach the northern extent of their distribution and are generally rare in occurrence (Onuf et al. 2003). Minor areas of *Thalassia testudinum* are documented in Louisiana, Mississippi, and Alabama. In Alabama only one small extant population (0.02 ha) is currently known to exist (Barry A. Vittor and Associates, Inc. 2004, 2010; Heck and Bryon 2005). *Syringodium filiforme* and *Halophila engelmanni* have been recorded from Mississippi and Louisiana waters (Onuf et al. 2003); these two species have not been documented in Alabama and likely do not occur in the state (Kral et al. 2011). Approximately 14,487 ha (35,747 acres) of SAV occur in this subregion: the greatest coverage is found in the area of the Chandeleur Islands, along the eastern coast of Louisiana (NOAA 2004). Seagrass abundance in this ecoregion is highly variable, but all areas have experienced significant declines in SAV during the past 50 years, with only occasional periods of re-growth or expansion.

Within the Texas Estuarine Ecoregion, there is a gradual shift in species composition of seagrass beds moving southward down the GoM coastline. In the upper reaches of the ecoregion, *Halodule* is practically the only species present, continuing the pattern seen in the adjacent Mississippi Estuarine Ecoregion. Along the upper Texas coast *Thalassia testudinum* is found at only a single location near the west end of Galveston Bay. Moving southward, there is a transition of *Halodule*-dominated beds to *Thalassia*, which becomes increasingly prevalent in

the central and southern Texas coast. At Aransas Pass, for example, *Thalassia* is the dominant species and comprises nearly 25 % of the bay bottom. *Thalassia* is even more dominant along the lower Texas coast. At the southern end of Laguna Madre, it comprises over 90 % of the seagrass beds near the Gulf outlet there (Onuf et al. 2003). *Halophila engelmanni*, along with *Ruppia maritima*, is found sporadically across the entire Texas coast. Seagrasses in Texas are spatially confined to protected areas located behind the state's coastal barrier islands and are not found seaward along its frontage with the GoM. While roughly 87,580 ha (216,410 acres) of SAV occur in Texas coastal waters, most (over 95 %) are found south of Matagorda and Galveston Bays (Handley et al. 2007); approximately 1,310 ha (3,237 acres) of SAV occur in those embayments. Estimates of seagrasses have varied widely: NOAA (2004) estimated that there are nearly 123,834 ha (306,000 acres) of seagrasses in Texas, or approximately 30 % more than described by Onuf et al. (2003) and 40 % more than reported by Handley et al. (2007).

According to Onuf et al. (2003), seagrass distributions within the Southern GoM Ecoregion were described mainly by studies that date to the 1950s. The same five genera reported in the rest of the GoM (*Thalassia, Syringodium, Halodule, Halophila, Ruppia*) also occur along the coast of Mexico. In the State of Tamaulipas, *Halodule wrightii* is the dominant species in the hypersaline Laguna Madre, and comprises approximately 18 % (35,700 ha) of the Lagoon's extent. Tabasco and Veracruz contain fewer seagrasses: Onuf et al. (2003) reported that only *H. wrightii* and *Ruppia maritima* occur in the coastal estuaries of Tabasco, probably due to heavy sediment loads and elevated turbidities caused by discharges from the Grijaval-Usumacinta River system. *Thalassia testudinum, Syringodium filiforme, Halodule wrightii*, *Halophila decipiens* has been found to a depth of over 10 m. The Yucatán Peninsula contains extensive seagrass beds populated by *Thalassia testudinum, Syringodium filiforme, and Halophila* is least abundant. *Thalassia testudinum, Syringodium filiforme, and Halophila* is least abundant. *Thalassia* is especially dominant in areas around coral reef lagoons.

6.5.5.3 Fauna

Seagrasses are important as both habitat for adult animals, as well as a nursery habitat for post-larval and juvenile individuals. The faunal assemblages found in these seagrass beds consist of groups of animals with many different life forms and ecological characteristics. The assemblages have been subdivided into several categories based on where the animal spends most of its time (Kikuchi and Peres 1977). Epifaunal species live on leaves, and include microfauna and meiofauna, sessile fauna, mobile creeping and walking epifauna (e.g., gastropods), and swimming epifauna (e.g., caridean shrimp), which may also be considered as nekton. Infaunal species include burrowers and tube–dwellers as well as those animals creeping or crawling at the sediment water interface (Orth et al. 1984). The seagrass epifauna and infauna are primarily composed of crustaceans, mollusks, and polychaetes. The final category of seagrass fauna is made up of mobile nektonic species living freely under and over the leaf canopy (e.g., fishes, marine mammals, and marine reptiles).

Seagrasses and macroalgae commonly form an extensive bottom cover in the brackish and saline shallow coastal lagoon bay systems that are prominent features throughout much of the GoM (Sheridan and Minello 2003; Contreras-Espinosa and Warner 2004; Rozas et al. 2012). Seagrass meadows rarely occur in physical isolation from other coastal wetland habitats so it is not surprising that their faunal assemblages include many species in common with other adjacent coastal wetlands such as mangroves, tidal marshes, intertidal and subtidal flats, or



Figure 6.135. Generalized illustration of the variety of nekton species and size classes associated with seagrass meadows. The depiction is from an Australian seagrass habitat but can be generalized to the GoM (McKenzie et al. 2006–2012; www.seagrasswatch.org/seagrass.html, reprinted with permission).

with coral reefs, particularly in the southern GoM (e.g., Yáñez-Arancibia et al. 1993; Ortiz and Lalana 2005).

Most seagrass habitat is largely subtidal and, unlike intertidal mangrove and marsh habitats, is always accessible to aquatic fauna. Consequently, seagrass assemblages include a diverse group of benthic, epibenthic, and nektonic species and size classes of organisms (Figure 6.135). Primary production in seagrass ecosystems can be quite high reaching up to $8 \text{ g C/m}^2/\text{day}$ for seagrasses alone (Zieman and Wetzel 1980). Studies of seagrass systems have also indicated the important role that epibenthic algae play in the total primary productivity of seagrass systems. These epiphytes have been found to be very productive and important sources of high-quality food for benthic marine consumers (Fry 1984; Kitting et al. 1984; Moncreiff et al. 1992; Williams and Heck 2001). The primary production of epiphytic algae can represent a substantial percentage of the total primary production of a seagrass meadow, sometimes matching or exceeding that of the seagrasses (Morgan and Kitting 1984; Mazella and Alberte 1986; Thom 1990; Williams and Heck 2001). Epiphytic algae have been found to be important determinants of epifaunal abundance (Hall and Bell 1988, 1993; Edgar 1990; Williams and Heck 2001). The high primary productivity of seagrasses and their associated epiphytic algae form the basis of complex food webs involving mammals, reptiles, fishes, crustaceans, mollusks, polychaetes, echinoderms, sponges, bryozoans, cephalochordates, and phytoplankton, as well as the algae and seagrasses themselves (Figure 6.136). Among the invertebrates, crustaceans and mollusks are very important groups in seagrass food webs, with taxa that play key roles in several trophic levels. Polychaetes also make up a high percentage of most seagrass faunal assemblages. The dominant fishes and natant decapod crustacean components of seagrass systems are strongly affected by seasonal recruitment patterns (Livingston et al. 1976), salinity (Arceo-Carranza and Vega-Cendejas 2009), proximity to inlets and passes (Reese et al. 2008), diel and tidal activity patterns of individual species (Sogard et al. 1989;



Figure 6.136. Generalized seagrass meadow food web (modified from Greenway 1995).

Hammerschlag and Serafy 2009) as well as a suite of short-term (Renaud 1986; Roth and Baltz 2009) and chronic water quality variables (Livingston 1984; O'Connor and Whitall 2007).

There is a paucity of available research related to the infaunal assemblages inhabiting the relatively isolated seagrass beds of Alabama, Louisiana, and northern Texas, which accounts for a lack of species-specific distributional information for the Mississippi and Texas Estuarine subregions. However, most seagrass research on benthic invertebrates in the northern Gulf is derived from areas of extensive seagrass meadows in Florida. In the northern GoM, these areas are represented by Gulf-fronting seagrass beds within the Eastern Gulf Neritic subregion (Figure 6.3), which includes a large portion of the Florida Gulf coast from its Springs Coast area northward through the Big Bend and westward along the northern panhandle to the vicinity of Escambia Bay near the Alabama–Florida stateline. This subregion is characterized by an extensive shelf system with nearshore substrates consisting primarily of sand, gravel, and shell with areas of limestone (Wilkinson et al. 2009). *Thalassia testudinum, Syringodium filiforme*, and *Halodule wrightii* are frequently encountered species in this subregion (Zieman and Zieman 1989; FNAI 2010; Yarbro and Carlson 2011).

Expansive seagrass beds that exist in the Eastern Gulf Neritic provide habitat for some organisms that are common to this subregion, but that may be rare in other areas of the northern Gulf. Examples are the bay scallop (*Argopecten irradians*), the green sea urchin (*Lytechinus variegatus*) (Figure 6.102a), and the sea star (*Echinaster serpentarius*) (Zieman and Zieman 1989). The limited distributions of these and other organisms in the northern Gulf is likely influenced by salinity, and the fact that a large portion of the northern Gulf is heavily

impacted by freshwater input from the Mississippi River. Bay scallops for example, are usually associated with seagrass beds in salinities greater than 25 ppt (Nelson 1992).

A variety of crustacean taxa representing both infaunal and epifaunal groups are prevalent within seagrass meadows (Table 6.19). Copepods, ostracods, and amphipods comprise the majority of the infaunal crustacean taxa. Epifaunal crustaceans include several taxa of isopods,

	Marine ecoregion						
-		Eastern Gulf	Mississippi	Texas	Southern		
Taxon	South Florida	Neritic	Estuarine	Estuarine	GOM		
	× ×	× ×	X	X	× ×		
Arabella iricolor	X	X	X	X	X		
Armandia agilis	X	X	X	X	X		
Bhawania goodei	X	X	X	X	X		
Capitella capitata	Х	Х	Х	Х	Х		
Cossura candida					Х		
Glycinde solitaria		Х	Х	Х	Х		
Laeonereis culveri	Х	Х	Х	Х	Х		
Malacoceros vanderhorsti	X	х	х	х	х		
Parandalia vivanneae					Х		
Pista cristata	Х	Х	Х	Х	Х		
Spio pettibonae	Х	Х	Х	Х	Х		
Streblospio benedcti	Х	Х	Х	Х	Х		
Mollusca-Bivalvia							
Americardia guppyi	Х	Х	Х	Х	Х		
Argopecten gibbus	Х	Х	Х	Х	Х		
Argopecten irrdians		Х	Х	Х			
Macoma constricta	Х	Х	Х	Х	Х		
Pitar simpsoni	Х	Х			Х		
Semele bellastriata	Х	Х	Х	Х	Х		
Tagelus divisus	Х	Х	Х	Х	Х		
Tellina tampaensis					Х		
Mollusca-Gastropoda							
Bulla striata	Х	Х	Х	Х	Х		
Caecum plicatum	X	Х	Х	Х	Х		
Calliostoma pulchrum	X	Х	Х	Х	Х		
Crepidula planum	Х				Х		
Haminoea glabra					Х		

Table 6.19. Common Invertebrates in GoM Seagrass Systems

(continued)

Table 6.19. (continued)

	Marine ecoregion					
		Eastern Gulf	Mississippi	Texas	Southern	
Taxon	South Florida	Neritic	Estuarine	Estuarine	GoM	
Neritina virginea	Х	Х	Х	Х	Х	
Nitidella nitida	Х				Х	
Petalifera ramose	Х				Х	
Tectura antillarum	Х				Х	
Mollusca-Cephalopoda						
Octopus maya					Х	
Pickfordiateuthis pulchella	х				Х	
Crustacea-Decapoda						
Alpheus heterochaelis	х	х	х	х	Х	
Armases cinereum	Х			Х	Х	
Callinectes sapidus	х	х	х	х	Х	
Cardiosoma guanhumi	Х	Х		Х	Х	
Clibanarius vittatus	Х	х	х	Х	Х	
Dyspanopeus texana	Х	Х		Х	Х	
Macrobrachium acanthurus	Х	Х	х	Х	Х	
Tozeuma carolinense	Х	Х	х	Х	Х	
Crustacea-Others						
Americamysis almyra	х	х	х	х	Х	
Ampelisca holmesi	Х					
Apocorophium Iouisianum	Х	х	х	Х	Х	
Batea catharinensis	Х	Х	Х	Х	Х	
Cyathura polita		Х	Х	Х		
Erichthonius brasiliensis	Х	Х	Х	Х	Х	
Leucothoe spinicarpa	Х	Х	Х	Х	Х	
Paracereis caudata	Х					
Photis macromanus		х	х	Х		
Echinodermata						
Echinaster serpentarius	Х	Х	Х	X	Х	
Lytechinus variegatus	Х	Х	Х	Х	Х	

References: Hall and Bell (1993), Heck and Valentine (1995), Leber (1985), Lewis (1984), Livingston (1984), Mendoza-Carranza et al. (2010), Sheridan (1997), Stoner (1980a), Virnstein et al. (1983), Zieman and Zieman (1989)

copepods, ostracods, and amphipods (Hemminga and Duarte 2000). Hall and Bell (1993) found that harpacticoid copepods and nauplii were the most abundant meiofaunal taxa on seagrass blades at Egmont Key, FL. Based on the apparent ubiquitous nature of this taxonomic group, it is likely that harpacticoid copepods play an important role in seagrass ecosystems in the GoM. As previously noted, crustaceans play key roles in multiple trophic levels within seagrass systems, and in addition to the important epiphytic taxa, larger mobile crustaceans (particularly decapods such as shrimp and crabs) are also common within seagrass meadows. Crustaceans derive their nutrition from a wide range of food sources available in the seagrass beds. Some taxa (such as brachyuran crabs) are at least partially herbivorous, consuming live seagrass tissue (including both leaves as well as root and rhizome material) and epiphytic algae (Leber 1985; Livingston 1984; Woods and Shiel 1997), while others are largely predatory. The carnivorous pink shrimp (Farfantepenaeus duorarum), for example, is a dominant decapod predator in seagrass meadows (Figure 6.103b), preying on caridean shrimp, amphipods, bivalve mollusks, polychaetes, gastropods, crabs, and detritus (Livingston 1984). The majority of smaller crustaceans inhabiting seagrass beds rely on algae or detrital particles as a food source (Klumpp et al. 1989).

Crustaceans are an important food source for fishes foraging in seagrass beds, and may play a prominent role in the energy transfer from primary producers to higher trophic levels, via the food web that links microalgae and detritus through epifaunal crustaceans to smaller fish, and ultimately to larger fish predators (Edgar and Shaw 1995). Crustaceans are very important in another aspect as well; several decapod species that spend at least part of their life cycle in seagrass beds are highly valued as food sources for humans. These species are the basis for extensive fisheries in warm-temperate and tropical areas throughout the world. In the GoM, important commercial fisheries are in place for penaeid shrimp and blue crabs (*Callinectes sapidus*). Among the crustaceans associated with seagrasses, decapods have received the most scientific attention, due to their ecological significance and commercial value (Perry 1984; NMFS 1988; Orth and van Montfrans 1984; Olmi and Orth 1995; Heck et al. 2001). Seagrass beds have long been recognized as an important nursery habitat, providing structure where settlement and growth of decapod post-larvae and juveniles may occur (Lewis and Stoner 1981; Lewis 1984; Zieman and Zieman 1989; Fonseca et al. 1996; Orth et al. 1996; Bell et al. 2001; Heck et al. 2003; Dawes et al. 2004).

Mollusks (gastropods and bivalves) also make a significant contribution to the fauna of seagrass beds in the GoM (Table 6.19). Gastropod species employ a variety of feeding strategies. While most feed on microalgae and detritus particles present on the sediment and leaf surfaces (Hemminga and Duarte 2000), others are carnivorous, feeding on other members of the faunal community. Bologna and Heck (1999), for example, observed large predatory gastropods (e.g., whelks [*Busycon* spp.]), horse conchs (*Pleuroploca gigantea*), and tulip snails (*Fasciolaria* spp.) preying on bay scallops in seagrass beds in the northern GoM. Bivalves can be suspension feeders, deposit feeders, or both. True suspension feeders collect food by filtering particles from the water column. The availability of this food depends on waterflow and water-column mixing. Research suggests that suspension-feeding bivalves grow faster when near-bottom water velocities are higher (Hemminga and Duarte 2000). This waterflow is reduced inside seagrass canopies. Therefore, bivalves inhabiting the interior portions of seagrass beds might experience a reduced food supply. The reduction of food supply, and subsequent lower growth rate of suspension feeders, is potentially balanced by positive aspects of living in the seagrasses. Possible positive aspects include decreased chance of dislodgement

of the animals during storms (Reusch and Chapman 1995), a reduction of predation intensity within the seagrass canopy (Irlandi and Peterson 1991), and larger degree of sediment stability within the seagrass beds (Irlandi 1994, 1996).

While many studies have illustrated the importance of seagrass beds to the survival rates of infaunal bivalves (Blundon and Kennedy 1982; Peterson 1982, 1986; Coen and Heck 1991), less is known about the effects that the presence of these bivalves have on the seagrasses themselves. Some more recent studies have suggested a mutualistic relationship between suspension feeding bivalves and seagrasses. Peterson and Heck (2001) tested two possible beneficial effects of the presence of tulip mussel aggregates (*Modiolus americanus*) in *Thalassia testudinum* beds. First, the suspension-feeding bivalves filter particulates from the overlying water column, and excrete nutrients in the form of ammonium and phosphorus, enriching the sediments in the seagrass bed. Additionally, mussel aggregates provide increased structural complexity that may provide a refuge from predation for epiphytic grazer species (e.g., small gastropods and amphipods). Higher densities of grazer species may lead to increased grazing activity on seagrass leaves. These two possible mechanisms (nutrient enrichment and increased light absorption), both due to the presence of suspension-feeding bivalves, can positively affect seagrass productivity.

As with commercially important crustaceans, which spend at least a portion of their life cycle associated with seagrass beds, some mollusk species are prized for their value as a source of seafood. An example is the bay scallop, *Argopecten irradians*. An important commercial and recreational fishery is established for bay scallops in the GoM (primarily in the Big Bend area of Florida). Scallops are intimately tied to seagrass systems, which they utilize as a primary settlement site as well as a refuge from predation (Gutsell 1930; Eckman 1987; Bologna and Heck 1999).

Polychaetes are an important part of the faunal community within all soft bottom habitats, including seagrass meadows (Table 6.19). Although there are no commercially important polychaete species and the majority of seagrass research focuses on decapods and mollusks, polychaetes represent a key part of seagrass food webs, and make up a relatively high percentage of total seagrass faunal abundance (Stoner 1980a; Lewis and Stoner 1983). Due to their generally high fecundity, polychaetes can exhibit seasonal pulses of abundance in temperate habitats (Orth and van Montfrans 1984). Dominant polychaete families in GoM seagrass beds include Nereidae, Capitellidae, Syllidae, Spionidae, Cirratulidae, Terebellidae, Sabellidae, and Maldanidae (Gloeckner and Luczkovich 2008). Although the majority of polychaetes are burrowing infaunal species, some are epiphytic, building tubes on seagrass leaves. Polychaetes represent a variety of feeding guilds, including predators, but most are suspension or deposit feeders.

Seagrass meadows differ from emergent vegetated wetlands in a number of important features that may be reflected in their nekton assemblages. For example, certain groups of natant decapod crustaceans (e.g., Hippolytidae) and fishes (e.g., Syngnathidae) are more common and abundant in this habitat than in other coastal wetlands (Minello 1999). Seagrasses lack the rigid physical structure of emergent intertidal vegetation, so the habitat does not constitute a substantial physical barrier to either the movement of nekton or collecting gear (trawls or seines) normally used to sample nekton in estuaries. As observed in other coastal wetland habitats, differences in the sampling methodology of seagrass-dominated systems (Pérez-Hernández and Torres-Orozco 2000) and differences in targeted groups (e.g., fishes, decapod crustaceans, or species of commercial or recreational importance) (Gilmore 1987) can have a strong influence on the results and conclusions of individual nekton studies. The numerically abundant resident species of nekton (e.g., Gobiidae, Syng-nathidae, and Hippolytidae) are small and often cryptic in habit and so may be underrepresented in seagrass nekton samples that use conventional gears (Gilmore 1987; Zieman and Zieman 1989).

The widespread use of small quantitative sampling devices such as throw traps and drop samplers has been popular largely in the northern and eastern GoM, while most nekton samples from seagrass-dominated habitats in the southern GoM are collected by trawling or seining. Also, there are regional differences in the types of species included among nekton samples from seagrass meadows in the United States, where natant decapod crustaceans are included, compared to collections in the southern GoM, which have focused on fishes or species of commercial importance. Effects of this regional difference in sampling approach and emphasis may explain some principal differences in the dominant nekton families and species reported from marine ecoregions around the GoM (Table 6.20).

The most obvious feature of these data is the apparent lack of natant decapod crustaceans and greater number of abundant fish families in seagrass-dominated lagoonal systems along the Mexican coast. Even though it has been suggested that fishes comprise most of the nekton assemblages of lagoon-estuarine habitats in the southern GoM (Yáñez-Arancibia et al. 1994), natant crustaceans are generally not reported in many studies within this region. The use of smaller quantitative sampling gear types in the northern GoM results in the capture of smaller resident nekton that numerically dominate these systems, particularly natant crustaceans representing the families Hippolytidae and Palaemonidae. It appears that palaemonids tend to dominate the natant decapod crustacean assemblage in temperate seagrass meadows near tidal marshes (Minello 1999; Rozas et al. 2012), but hippolytid shrimps are the numerical dominants in tropical and subtropical portions of the GoM where marshes are not as extensive (Sheridan et al. 1997; Sheridan and Minello 2003).

In contrast, trawls and seines are the gears of choice for sampling nekton in the southern GoM, where fishes and natant decapod crustaceans tend to be reported in separate studies rather than as elements of a nekton assemblage. Natant decapod crustaceans are important and abundant components of seagrass nekton assemblages in the southern GoM, but their importance must be inferred from separate studies that have targeted decapod crustaceans or considered the diets of predatory fishes. For example, penaeid shrimps are the most valuable artisanal fisheries in the coastal lagoons of the southern GoM but focused studies on this group are relatively rare (Pérez-Castañeda and Defeo 2001; May-Kú and Ordóñez-López 2006). In the seagrass- and macroalgal-dominated lagoons of the southern GoM, the predominant penaeids are the spotted pink shrimp (Farfantepenaeus brasiliensis), the southern pink shrimp (Farfantepenaeus notialis) and the northern pink shrimp (Farfantepenaeus duorarum) (Pérez-Castañeda and Defeo 2001; May-Kú and Ordóñez-López 2006). In contrast, the northern brown shrimp (Farfantepenaeus aztecus) and northern white shrimp (Litopenaeus setiferus) tend to be the most abundant penaeid species in areas of extensive salt marsh habitat (e.g., Louisiana and Texas) (Minello 1999), and the northern pink shrimp (Farfantepenaeus duorarum) is most often associated with seagrass meadows wherever they occur (Figure 6.103b), from the Florida Keys through the northern GoM (Bielsa et al. 1983; Rozas et al. 2012).

The sparse information available on the nekton of the northwestern Cuban coast does not mention many natant decapod crustaceans as being abundant in seagrass meadows, but

	Marine Ecoregion					
	Florida Bay	Eastern Gulf Neritic	Mississippi Estuarine	Texas Estuarine	Campeche/ Yucatán Inner Neritic	
Fishes						
Achiridae						
Achirus lineatus					Х	
Ariidae						
Ariopsis felis	Х					
Atherinidae						
Menidia colei					Х	
Menidia penninsulae	Х					
Menidia beryllina			Х			
Belonidae						
Strongylura notata					Х	
Clupeidae						
Harengula jaguana					Х	
Cyprinodontidae						
Floridichthys carpio	Х					
Floridichthys polyommus					Х	
Cyrprinodon antifrons					Х	
Cyprinodon variegatus			Х			
Engraulidae						
Anchoa mitchilli	Х				Х	
Fundulidae						
Lucania parva	Х	Х	Х		Х	
Fundulus perisimilis					Х	
Gerridae						
Eucinostomus gula	Х				Х	
Eucinostomus argenteus		Х			Х	
Gobiidae						
Gobiosoma bosc			Х			
Gobiosoma robustum	Х			Х		
Ctenogobius boleosoma		Х		Х		
Microgobius gulosus	Х					
Haemulidae						
Haemulon bonariense					Х	
Mugilidae						
Mugil trichodon					Х	
Poeciliidae						
Heterandria formosa			Х			
Poecilia latipinna			Х			
Poecilia velifera					Х	
Sciaenidae						
Bairdiella chrysoura	Х					

Table 6.20. Nekton Species Comprising at Least 90 % of the Total Individuals in Seagrass Samples from the Indicated Marine Ecoregions of the GoM

(continued)

Table 6.20. (continued)

	Marine Ecoregion						
	Florida Bay	Eastern Gulf Neritic	Mississippi Estuarine	Texas Estuarine	Campeche/ Yucatán Inner Neritic		
Sparidae							
Lagodon rhomboides	Х	Х		Х	Х		
Syngnathidae							
Syngnathus scovelli	Х		Х				
Tetradontidae							
Sphoeroides testudineus					Х		
Natant Decapod Crustaceans	_		_				
Portunidae							
Callinectes sapidus		Х	Х	Х			
Callinectes similis				Х			
Penaeidae							
Penaeidae - Unidentified				Х			
Farfantepenaeus aztecus			Х				
Farfantepenaeus duorarum	Х	Х		Х			
Litopenaeus setiferus			Х	Х			
Palaemonidae							
Palaemonetes spp.			Х	Х			
Palaemonetes pugio		Х	Х	Х			
Palaemonetes intermedius		Х		Х			
Palemon floridanus		Х					
Periclimenes americanus	Х						
Periclimenes longicaudatus		Х					
Hippolytidae							
Hippolyte zostericola		Х		Х			
Thor floridanus	Х						
Tozeuma carolinense		Х		Х			
References Cited:	8,13,14	6,11	3,5,7	2,4,10,12	1,9,15		

Red shaded cells indicate the presence of dominant families at each location. The most abundant species reported in each family are indicated by an "X". Studies in southern GoM ecoregions reported only fishes but natant decapod crustaceans are important fisheries species in the region.

References: (1) Arceo-Carranza and Vega-Cendejas (2009), (2) Burfeind and Stunz (2006), (3) Kanouse et al. (2006), (4) King and Sheridan (2006), (5) La Peyre and Gordon (2012), (6) Livingston (1984), (7) Mairaro (2007), (8) Matheson et al. (1999), (9) Peralta-Meixueiro and Vega-Cendejas (2011); (10) Reese et al. (2008); (11) Rozas et al. (2012), (12) Sheridan and Minello (2003), (13) Sheridan et al. (1997), (14) Thayer et al. (1987), (15) Vega-Cendejas and Hernández de Santillana (2004)

identifies areas of macroalgal beds and coastal lagoons surrounded by mangroves as a principal habitat for portunid crabs, including *Callinectes sapidus* and *C. ornatus*. The same coastal lagoons are identified as important habitat for penaeid shrimps *Farfantepenaeus notialis* and *Litopenaeus schmitti* (Ortiz and Lalana 2005).

The smaller and most abundant natant decapod crustaceans reported from seagrass systems in the United States are rarely reported in nekton studies from the Mexican and Cuban coasts of the GoM. However, caridean shrimps, particularly the Hippolytidae, are reported to be among the most abundant crustaceans within SAV in the major lagoonal systems of the southwestern GoM (Negreiros-Fransozo et al. 1996). Also, the diets of common fishes, such as the sparid *Lagodon rhomboides* and the batrachoidid *Opsanus phobetron*, from GoM lagoons along the Yucatán Peninsula include caridean shrimps, presumably Hippolytidae or Palaemonidae (Canto-Maza and Vega-Cendejas 2007, 2008). Consequently, it is reasonable to infer that natant decapod crustaceans may be of greater importance among the nekton assemblages of seagrass meadows in the southern GoM than suggested by the literature on fish assemblages from these systems.

Seagrass meadows have different trophic dynamics than other coastal wetland habitats in that seagrass primary production is consumed by some nekton as both live and dead (detritus) material (Heck and Valentine 2006), whereas the trophic role of emergent marsh plant production in the support of nekton populations is largely through a detrital pathway in marshes and the role of mangrove primary production may not contribute significantly to trophic support of nekton (Beck et al. 2001). Some nekton, such as the pinfish (*Lagodon rhomboides*) (Livingston 1982; Montgomery and Targett 1992) and a few larger nektonic herbivores, such as green sea turtles (*Chelonia mydas*) and manatees (*Trichechus manatus*) consume live seagrass and contribute to recycling of nutrients and maintenance of seagrass productivity (Thayer et al. 1984; Heck and Valentine 2006).

Seagrass meadows have long been recognized as important foraging sites for the juveniles of predatory fishes, especially members of the Sciaenidae (drums) and Lutjanidae (snappers) (Gilmore 1987; McMichael and Peters 1989; Rutherford et al. 1989; Rooker et al. 1999), but these species are commonly found in other coastal wetlands as well, and so are not characteristic of seagrass meadows *per se*. The smaller species of fishes, such as members of the Gobiidae and Fundulidae (especially *Lucania parva*) and natant decapods such as shrimps in the family Hippolytidae, are widely distributed and abundant in seagrass habitats within all regions of the GoM (Table 6.20). Many members of the Syngnathidae (pipefishes), such as the dwarf seahorse (*Hippocampus zosterae*) (Figure 6.107b) and fringed pipefish (*Anarchopterus criniger*) are even more dependent upon seagrass habitats within the GoM and have been identified by some as species of special concern (Beck et al. 2000). It has been suggested that the refuge value of seagrass structure is a key feature in maintaining these assemblages of smaller nekton (Heck et al. 2003).

6.5.5.4 Ecosystem Services and Function

Seagrasses represent a valuable natural resource to human culture and society. The benefits provided by their ecological services are innumerable. Some studies have estimated the economic contribution of seagrasses to be worth 20 billion dollars annually (Orth et al. 2006; Costanza et al. 1997; Yarbro and Carlson 2011). Seagrasses also constitute a significant ecological and functional guild, one that serves many diverse roles in marine environments. Seagrasses act as essential nursery habitats for many economically important fish and shellfish species and thus are vital to recreational and commercial fisheries (Hemminga and Duarte 2000; Beck et al. 2001; Heck et al. 2003; Yarbro and Carlson 2011). They provide crucial food resources for waterfowl, sea turtles, fishes, and other wildlife (Hemminga and Duarte 2000). Seagrasses offer habitat for endangered marine species (Orth et al. 2006). Structurally, the rhizomes and roots of seagrasses can stabilize sediments (Orth et al. 2006; Hemminga and Duarte 2000) and seagrass beds provide shoreline protection *via* wave attenuation

(Koch et al. 2009). Seagrasses also play a crucial role in natural biogeochemical processes, receiving, transforming, and exporting various compounds trophically through marine ecosystems (Orth et al. 2006). Their presence contributes significant amounts of organic carbon to marine food webs in the form of detrital material (Orth et al. 2006), and as such, are an important component of nutrient cycling in the environment. A large portion of this carbon may be transported to the food-limited deep sea where it becomes a vital contributor of organic material to these systems (Suchanek et al. 1985).

Seagrass meadows are productive ecosystems. Estimates of primary production in seagrass meadows have indicated an average net production of approximately 1,012 g dry weight/m²/year, when production of both above-ground and below-ground components are considered (Duarte and Chiscano 1999; Hemminga and Duarte 2000). This estimate of primary productivity places seagrass meadows among the most productive ecosystems in the biosphere (Hemminga and Duarte 2000). When these estimates are scaled to the estimated global cover of seagrasses, the result is a contribution of about 1.13 % of the total marine primary production (Duarte and Cebrian 1996; Hemminga and Duarte 2000). Unlike phytoplankton, where most of the primary production is used up in the marine system, much of the seagrass production is either stored in the sediments or exported to neighboring ecosystems (Duarte and Cebrián 1996; Duarte and Agusti 1998; Hemminga and Duarte 2000). It is currently believed that approximately 16 % of seagrass production is stored in the sediments, representing a net sink of carbon in the ecosystem. The carbon stored in the sediments annually by seagrasses is estimated to be in the order of 0.08×10^{15} g C/year (about 12 % of the total carbon storage in marine ecosystems) (Duarte and Cebrián 1996; Duarte and Chiscano 1999; Hemminga and Duarte 2000). Therefore, seagrass meadows represent important parts of the marine carbon cycle and are responsible for a significant portion of the net CO₂ uptake by marine biota.

The high primary productivity of seagrass systems provides an abundant supply of organic matter that can be used as the basic energy source for food webs (Zieman and Wetzel 1980; Williams and Heck 2001). When considering the secondary production provided by these seagrass systems, it is important to understand the important contribution that epiphytic and benthic algae make to the seagrass system in terms of their production. Stable isotope studies conducted over the past 10 to 20 years have led to a paradigm shift in our view of seagrass trophic dynamics. At one time, seagrasses were thought to be the most important material for secondary production. It is now believed that benthic microalgae are the primary source of organic matter to higher trophic levels in seagrass food webs (Fry 1984; Kitting et al. 1984; Morgan and Kitting 1984; Mazella and Alberte 1986; Kenworthy et al. 1987; Dauby 1989, 1995; Thom 1990; Moncreiff et al. 1992; Loneragan et al. 1997; Yamamuro 1999; Lepoint et al. 2000; Williams and Heck 2001; Mateo et al. 2006). Valentine and Duffy (2006) suggested that seagrass food webs contain two key conduits for the transfer of primary production to higher order consumers. Seagrass grazing ecosystems are characterized by moderate to intense grazing on living seagrass tissue (leaves and rhizomes) by abundant large vertebrate, and some invertebrate, herbivores. This grazing results in low seagrass biomass and a direct conversion of seagrass production into vertebrate biomass. Seagrass detrital ecosystems are primarily devoid of large vertebrates, and herbivory is dominated by small invertebrate grazers that feed preferentially on epiphytic algae. This strategy indirectly enhances seagrasses, resulting in high seagrass biomass, much of which enters the detrital food chain (Valentine and Duffy 2006).

Historically, most seagrass ecosystems, especially in the tropics, were believed to be seagrass grazing ecosystems. More recently, due in large part to human impacts, reductions in abundances of large vertebrate herbivores such as green sea turtles, sirenians (manatees and dugongs), and waterfowl, have decreased the importance of these large herbivores as primary consumers in seagrass systems (Jackson et al. 2001; Valentine and Duffy 2006). Consequently, many present-day seagrass systems are of the detritus-based type, with little seagrass production being grazed directly (Robertson et al. 1982; Chin-Leo and Benner 1991; Ziegler and Benner 1999; Cebrián 1999, 2002; Mateo et al. 2006; Valentine and Duffy 2006).

Decomposition in situ appears to be the most probable fate for both seagrass leaf detritus and below-ground (rhizomes and roots) production (Mateo et al. 2006). The total amount of seagrass production (both above- and below-ground) that is decomposed is generally large. Research suggests that the amount of seagrass detritus that is transferred to decomposers and detritivores tends to be larger than for many other aquatic and terrestrial producers (Cebrián 1999, 2002; Mateo et al. 2006). It appears that most seagrass production is supported through internal nutrient recycling, and also that seagrass meadows maintain high levels of secondary production by microbial decomposers and invertebrate detritivores. Therefore, research suggests that the abundant faunal communities that are normally associated with seagrass beds are supported primarily through the detritus-based food chain (Mateo et al. 2006). Estimates of seagrass decomposition (and rates of decomposition) can be highly variable and are affected by several factors, including environmental physical conditions (water temperature, sediment oxygen content, water nutrient content, desiccation), the nutrient content of the detritus, and methodological approach used (Harrison 1989; Mateo et al. 2006).

Seagrasses play an important role in global carbon and nutrient cycling. Seagrass biomass, along with that of macroalgae within seagrass beds, has been identified as a substantial sink for carbon in the ocean (Smith 1981; Mateo et al. 2006). The majority of seagrass biomass ends up as detritus (Cebrián 1999, 2002; Mateo et al. 2006; Valentine and Duffy 2006). As a result, the amount of seagrass carbon available to be stored in the sediments can be large. In fact, research suggests that the carbon resulting from seagrasses represents approximately 12 % of the total carbon storage in the ocean, despite the fact that seagrass production represents only a small percentage (1 %) of the total oceanic production (Duarte and Cebrián 1996). In addition to burial of nutrients, seagrass beds require high nitrogen incorporation and likely play an important role in the cycling of nitrogen in shallow estuarine systems (Kenworthy et al. 1982; Bethoux and Copin-Montégut 1986; Hemminga et al. 1991; Lee and Dunton 1999).

Seagrass beds have been found to support higher faunal density and species diversity than unvegetated areas in the same environment (Orth 1977; Heck and Orth 1980; Stoner 1980a, b; Virnstein et al. 1983; Lewis 1984; Orth et al. 1984; Heck and Crowder 1991; Heck et al. 1997; Williams and Heck 2001). Furthermore, an increase in seagrass biomass results in an increase in habitat complexity or heterogeneity, which provides microhabitat space in the grass bed that is not found in the surrounding bare substratum (Stoner 1980a, b; Coen et al. 1981; Lewis and Stoner 1983; Lewis 1984). Consequently, aboveground plant biomass often is significantly correlated with invertebrate species number and abundance (Heck and Wetstone 1977; Stoner 1980a; Lewis 1984). This is especially true of epiphytic species. The high abundance of epiphytes present in seagrass meadows provides the primary pathway to higher trophic levels (Virnstein et al. 1983) via decapod crustaceans and other predators. Some infaunal species may exhibit an inverse relationship between abundance and macrophyte biomass. Thick roots and/or heavy rhizome mats may prevent certain types of infauna from inhabiting dense seagrass beds, which leads to the observed decrease in some infaunal species with increased seagrass biomass (Stoner 1980a; Brenchley 1982; Orth et al. 2006).

6.5.6 Intertidal Flats and Subtidal Soft Bottoms

6.5.6.1 Dominant Forcing Functions

The dominant forcing functions affecting faunal assemblages in unconsolidated soft sediments are components of the physical environment, including the prevailing hydrodynamic and sedimentary regimes. Biological interactions, such as competition and predation, occur to varying degrees within the constraints of the physical environment. Intertidal and subtidal flats occur along a gradient of inundation and physical exposure to wind and wave energy.

Unlike the exposed beaches of barrier islands, flats tend to have little or no slope and experience considerably less wave action, especially when facing a bay. As a shore becomes more protected from wave action, sediment particle size becomes finer and there is an accumulation of organic materials. Consequently, the sediments of flats grade from sandy to muddy along a decreasing gradient of wave and wind exposure. Water movement is minimal across mud flats, which can be a more stable substratum for benthic faunal assemblages. This stability is a favorable environment for organisms that construct permanent burrows. However, the presence of fine sediments combined with little or no slope means that pore water is retained, resulting in poor exchange between pore water and overlying water. These conditions favor the growth of dense microbial assemblages and often result in depletion of oxygen and even anaerobic conditions in the sediment below the first several centimeters. Low oxygen content in pore water may limit chemical and biological degradation processes, affecting the development and the productivity of the mud flat benthic community.

All marine and estuarine sediments are anoxic at some depth below the sediment-water interface. The boundary zone separating upper sediments dominated by aerobic processes from subsurface anaerobic sediments is defined as the redox potential discontinuity (RPD) (Fenchel 1969). Coarse sediments such as sand, gravel, or shell fragments allow more current flow into and through the substratum allowing for the RPD layer to penetrate deeper into these types of sediments. In muddy and silty habitats, subsurface hydrology is further limited due to occlusion of interstitial spaces, which allows oxygen to diffuse only a few millimeters into the sediment (Revsbech et al. 1980). Environments with more shallow RPDs tend to support deposit-feeding taxa that are able to maintain some form of hydrologic contact with the sediment-water interface by the manufacture of tubes or construction of burrows for irrigation. Burrowing and irrigation activity of infauna can distribute oxygen much deeper into the sediment (Rhoads et al. 1977). Other factors that affect the position and thickness of the RPD are the oxygen content of bottom water, sedimentation of organic matter, sediment grain size, and temperature (Vismann 1991; Diaz and Rosenberg 1995). Controlling for differences in sediment type, habitats with thinner RPDs tend to be associated with some type of environmental instability or stress, while habitats with deeper RPDs usually have flourishing epifaunal and infaunal assemblages.

Infauna that inhabit soft sediments in the GoM comprise assemblages that exhibit spatial and seasonal variability in their distributions (Boesch 1972; Dames and Moore 1979; Tenore 1985; Weston 1988; Byrnes et al. 1999). Shallow coastal waters are characterized by a variety of environments having great diurnal, seasonal, and annual fluctuations in their chemical, hydrographic, and physical properties. These factors contribute to the temporal variability of population occurrence and individual abundance of marine invertebrates (Flint and Holland 1980; Byrnes et al. 1999). Patterns of reproductive periodicity in marine systems apparently are related to ambient climatic conditions, primarily temperature, for most marine invertebrates (Sastry 1978). In tropical zones, seasonality is less pronounced.

Within seasons, benthic community structure in subtidal sediments is determined largely by disturbances and physical stresses, including riverine inputs, sedimentation, and currents (Oliver et al. 1980; Probert 1984; Hall 1994; Thrush et al. 1996). Changes in infaunal assemblage composition along broad depth gradients have been noted in numerous studies of shelf ecosystems, including in the GoM. Relatively shallow areas of the coastal strand and inner shelf comprise a turbulent zone (Day et al. 1971), where benthic fauna are adapted to unstable sediments.

Benthic boundary layer hydrodynamic flow is a significant factor regulating the composition of soft sediment invertebrate assemblages (Nowell and Jumars 1984; Hall 1994; Snelgrove and Butman 1994; Newell et al. 1998; Crimaldi et al. 2002; Hentschel and Herrick 2005). Hydrodynamic forcing has important effects on sediment regime (particle size, degree of sorting, organic content), sediment stability, and pore water oxygenation (Hall 1994), all of which affect habitat suitability for members of the various invertebrate guilds. Contrasting different sedimentary habitats in terms of how they determine infaunal community patterns can be complex because, in addition to sediment regime, other important parameters vary with hydrodynamic condition (Snelgrove and Butman 1994).

The influence of sedimentary regime on benthic community composition has been recognized since the pioneer studies of Peterson (1913), Thorson (1957), and Sanders (1958). Benthic faunal assemblages comprise taxa that are adapted to particular sedimentary habitats through behavioral, morphological, physiological, and reproductive adaptations. Fine-textured sediments are generally characteristic of depositional environments, where occluded interstitial space and accumulated organic material support surface and subsurface deposit feeders. Coarse sediments in high water current habitats, where finer particles are maintained in suspension in the water column, favor the occurrence of suspension-feeding taxa and facilitate feeding by carnivorous fauna that consume organisms occupying interstitial spaces (Fauchald and Jumars 1979).

6.5.6.2 Vegetation

Although intertidal flats and subtidal soft bottoms are generally characterized by the absence of rooted vegetation and might not be normally considered in an overview of vegetated coastal habitats, their close spatial association with vegetated coastal habitats and their inherent ecological importance make them worthy of discussion in the context of coastal habitats. Of course, these habitats are not completely devoid of photosynthesizing organisms. Primary producers, in the form of benthic microalgae (diatoms), cyanobacteria (blue-green algae) and macrophytic algal species (e.g., the green alga *Ulva* and *Enteromorpha*) are integral components of most coastal marine flats along the shorelines and within the many protected tidal lagoons of the GoM. The only primary producers on exposed beaches are benthic diatoms and swash-zone phytoplankton, which are often patchy in distribution and can exhibit vertical migration within sediments. Coastal sandflats generally have low productivity (McLachlan 1996). Allochthonous sources (originating from outside sources) of organic material, such as macroalgae (e.g., *Sargassum*) and estuarine plant detritus, provide episodic, localized enrichment when transported to intertidal and subtidal flats by currents and tides.

6.5.6.3 Fauna

The fauna of mud and sand flats are either opportunistic generalists that occupy a variety of habitats or specialists found only within a particular habitat type (Shaw et al. 1982). Infauna of the GoM occurs in distinct assemblages that are associated with certain sedimentary regimes

and water depths (Dames and Moore 1979; Flint and Holland 1980; Baker et al. 1981; Shaw et al. 1982; Harper 1991). Although some invertebrate taxa occur across a range of sedimentary habitats, most species predominate in areas with particular sediment characteristics. The spatial distribution and size of habitats in a subtidal landscape play an important role in the functioning and structure of benthic communities (Thorson 1957; Andrew and Mapstone 1987; Morrisey et al. 1992; Rakocinski et al. 1998; Zajac et al. 1998, 2003; Pineda 2000; Thrush et al. 2000, 2005; Levinton and Kelaher 2004). Subtidal benthic assemblages on the shallow shelf also may be influenced by proximity to estuarine outflow. Generally, in coastal areas, inshore estuarine endemics and euryhaline opportunists grade into fully marine assemblages of the shelf (Boesch 1977). The nature of cross-shelf faunal change depends on local hydrographic and hydrologic environment, including the rate and volume of riverine input (e.g., silts and organic fines) to adjacent shelf areas.

Species diversity in tidal flat systems is generally lower than occurs in the subtidal environment, due in part to continually changing physical parameters, such as tidal fluctuation. Although diversity may be relatively low on tidal flats, these systems are highly productive in terms of invertebrate biomass.

The dominant groups of infauna found on mud flats (polychaetes, bivalves, and crustaceans) are similar to those on sand beaches, but the specific taxa are different in response to adaptations necessary for life in a habitat with fine sediments and anaerobic pore water conditions. Most organisms inhabiting the mud flat are either adapted to burrowing into and through the soft substrate or build and live in tubes in or on the substrate. Deposit-feeding organisms, such as the polychaete *Capitella*, burrow through the substrate, ingest sediment, and digest the organic matter with the help of bacteria; the polychaete, *Arenicola*, builds a u-shaped burrow with one arm of the burrow open to the surface and one filled with sediment to feed upon. Deposit-feeding bivalves are also common on mud flats (e.g., tellinid clams). Clams on mud flats are typically buried in the sediment, but have long siphons that extend to the surface for deposit feeding. Common polychaetes include bloodworms (*Glycera*) and clam worms (*Nereis*).

Dittmann (2000) found that benthic fauna in a tropical tidal flat showed a zoned distribution between the high and low tide marks. Defined groups were found, corresponding to a zonation of distinct assemblages at the high intertidal mudflat, the mid-intertidal *Callianassa* and sandflat sites, and the lower intertidal sandflat (Dittmann 2000). Bourget and Messier (1983) found that intertidal biomass was highest in the lower half of the intertidal zone compared to the upper half. Alternatively, Brown (1982) found that mean body size of the polychaete *Scoloplos fragilis* varied spatially across a tidal flat system, with body sizes significantly larger in the high-tide zone compared to the low-tide zone. The relative importance of physical versus biological controls on faunal distributions across tidal flat systems remains poorly understood.

Generally, shallow subtidal and inner shelf infaunal assemblages are dominated by polychaetes in terms of overall abundance (Day et al. 1971; Tenore 1985; Weston 1988; Barry A. Vittor and Associates, Inc. 1991). Other important groups of coastal infauna include amphipods and bivalves. Notable studies of benthic infauna in the Gulf include baseline investigations such as STOCS (Flint and Rabalais 1980), MAFLA (Dames and Moore 1979), Mississippi Sound and adjacent area study (Shaw et al. 1982), SOFLA (Woodward-Clyde Consultants 1983), and NOAA investigations of Florida Bay and Florida Keys (Barry A. Vittor and Associates, Inc. 1999). These studies showed that polychaetes typically account for half of all infaunal taxa, while mollusks and crustaceans each account for less than 25 % of the taxa. Uebelacker and Johnson (1984) noted that some common polychaete species exhibited a faunal break east of Mobile Bay: some syllids only were found east of this area while some magelonids and ampharetids only were found west of the break. Other polychaetes exhibited disjunct distributions and were present in both the Eastern Gulf Neritic and Texas Estuarine Area subregions but not in the Mississippi Estuarine subregion.

Shaw et al. (1982) performed a large baseline survey of infauna that included the barrier strand areas of Alabama and Mississippi out to Gulf depths of 30 m (98 ft). Infauna of the clean sand habitat in tidal passes included the archiannelid *Polygordius*, cephalochordate *Branchiostoma caribaeum*, polychaetes *Mediomastus* spp. and *Spiophanes bombyx*, and the burrowing amphipod *Acanthohaustorius*. Offshore (shallow Gulf) assemblages varied with sedimentary habitat type. Mud habitats supported polychaetes such as *Magelona* cf. *phyllisae*, *Mediomastus* spp., *Diopatra cuprea*, and *Myriochele oculata*, and the cumacean *Oxyurostyllis smithi*. Offshore sand had assemblages dominated by *Polygordius*, *B. caribaeum*, and the polychaetes *Lumbrineris* spp., *Mediomastus* spp., and *Paraprionospio pinnata*.

Coastal Louisiana invertebrate assemblages include widespread taxa such as the polychaetes *Paraprionospio pinnata*, *Magelona* cf. *phyllisae*, and *Sigambra tentaculata* (Baker et al. 1981; Gaston and Edds 1994), that commonly occur inshore to mesohaline (18 to 5 ppt) environments (Shaw et al. 1982; Gaston et al. 1995). The Southwest Research Study (Baker et al. 1981) collected infauna from the central Louisiana shelf (inshore to 90 m [295 ft] depths) and found that sand habitats supported amphipods *Ampelisca verrilli* and *Photis macromanus*, and the polychaetes *Ceratonereis irritabilis*, *Prionospio cristata*, and *Glycera americana*.

Benthic community analysis of the Laguna Madre (Texas) conducted for the U.S. Army Corps of Engineers showed that Upper Laguna Madre assemblages were dominated mainly by polychaetes, while the Laguna Madre south of Baffin Bay was characterized primarily by several mollusk species (Barry A. Vittor and Associates, Inc. 1996). However, nearly all numerically important species in the Laguna Madre were typical of marine waters throughout the Gulf, including *Capitella capitata*, *Streblospio benedicti*, *Prionospio heterobranchia*, *Grandidierella bonnieroides*, and *Mulinia lateralis*. Similar infaunal assemblages were described in Laguna de Términos, which is located in a sedimentary transition zone on the Campeche coast: 173 species of mollusks and over 120 species of polychaetes have been identified, including *M. lateralis*, *Abra aequalis*, *Macoma constricta*, *C. capitata*, *S. benedicti*, and *Mediomastus californiensis* (Contreras-Espinosa and Castañeda-Lopez 2007).

Epifaunal benthic species assemblages in the coastal waters of the northern Gulf are fairly uniform across the region and are distinguished mainly by large differences in sediment texture/type and salinity (Defenbaugh 1976). Carbonate-dominated sand sediments, such as those found along the Florida Panhandle and the Eastern Gulf Neritic subregion, are populated by many species also found farther to the west, including the sand dollar (*Mellita quinquie-sperforata*), the starfish (*Luidia clathrata*), rock shrimp (*Sicyonia brevirostris*), and the spider crab (*Libinia dubia*). However, a change in epifaunal assemblages occurs between shallow sand habitats of the Florida Panhandle and muddy sand sediments west of Mobile Bay. Species not commonly found west of the Bay include *Encope michellini* (sand dollar) (Figure 6.102c), *Arbacia punculata* (sea urchin), the decapod crabs *Podachela riisei*, *Ovalipes guadalupensis*, *Iliacantha intermedia*, *Calappa flamea*, *Stenorhychus seticornis*, and *Parthenope serrata*, the cnidarian *Calliactis tricolor*, and the poriferan *Cliona celata* (Barry A. Vittor and Associates, Inc. 1986).

Brittle stars (*Hemipholis elongatus* and *Ophiolepis elegans*) are very abundant in subtidal flats near tidal inlets, where they feed on detritus borne by tidal currents. Penaeid shrimps are also present on these sand sediments, but at far lower densities than found on muddy sediments (Swingle 1971). In addition to echinoderms, dominant epifaunal species include the cnidarian

Renilla mulleri (sea pansy), the gastropods *Sinum perspectivum* and *Cantharus cancellarius*, the bivalve *Chione clenchi*, the stomatopod *Squilla empusa*, and the decapods *Persephone crinata*, *Hepatus epheliticus*, *Callinectes similis*, and *Pagurus pollicaris*.

The nekton assemblages of sandy and muddy tidal flat habitats in the GoM often have been sampled to make comparisons with the nekton assemblages of adjacent vegetated (marsh, mangrove, seagrass) habitats. Consequently, the same sampling gear has been used in both vegetated and shallow unvegetated estuarine bottom habitats. If it can be assumed that effectiveness of the collecting methods are similar, unvegetated flats almost invariably yield lower densities of nekton, particularly small natant decapod crustaceans, than occur in more structurally complex coastal wetlands (Orth et al. 1984; Minello 1999; Beck et al. 2001; Heck et al. 2003). As in all of the other coastal wetlands discussed here, proximity to adjacent wetland types (e.g., seagrass, tidal marsh, mangrove) influences the species composition of the nekton assemblage in intertidal flats and on subtidal soft bottoms within the GoM. This can be illustrated by a comparison of dominant nekton families and species in quantitative collections from the U.S. coasts of the GoM (Table 6.21).

Decapod crustaceans dominate numerically the collections represented in the table in all northern and southeastern GoM regions represented, and fishes appear to be better represented on intertidal and subtidal flats in areas with adjacent marsh habitat. Where seagrasses are a dominant habitat adjacent to the flats, the hyppolytid shrimps are a major component of the natant decapods, but where marshes are adjacent to the flats, palaemonid and penaeid shrimps are more abundant. Except for the gobiid and engraulid fishes, which are common components of the nekton in most regions of the GoM, there is little commonality in the dominant fish families or species reported among individual studies. One possible reason for this is that most nekton using intertidal or shallow subtidal flats to forage or escape predators are constantly moving, so the assemblage at a particular location may change quickly.

The data summarized in Table 6.21 represents only a small portion of the nekton assemblage that occurs on the intertidal and subtidal flats because most of the quantitative samples represented in the table used collecting gear of relatively small sample unit size (e.g., 1 m^2), which is less effective in capturing larger nekton, highly mobile schooling species, or species that may be common and even abundant at the broader spatial scales sampled by trawls within the estuaries. Many of these species forage in shallow flats, where benthic invertebrate prey can be abundant, or are in the process of moving among more structurally complex coastal wetland habitats.

Among the nekton that are widely distributed on intertidal and subtidal flats are several common species in the families Sciaenidae (drums) and Ariidae (sea catfishes), which occur in most estuaries throughout the GoM (Nelson 1992; Gilmore 1987; Yáñez-Arancibia and Lara-Dominguez 1988). Because of their economic importance in commercial and recreational fisheries, the Sciaenidae, Penaeidae, and Portunidae are among the best studied of the nekton commonly found on estuarine flats (e.g., Gilmore 1987; McMichael and Peters 1989; Grammer et al. 2009; Rooker et al. 1999; Pérez-Castañeda and Defeo 2001; Luna et al. 2009). Other epibenthic species of nekton that are particularly well adapted to intertidal and subtidal flat habitats in GoM estuaries are the stingrays (e.g., *Dasyatis sabina*, *D. say*) and several species within the flatfish families Achiridae (e.g., *Citharichthys spilopterus*), which are widely distributed in both the northern and southern GoM (Contreras-Espinosa and Castañeda-Lopez 2007). These species are not considered of much economic importance, so their requirements and functional roles within this system have not been as clearly defined.

Table 6.21. Nekton Species Comprising at least 90 % of the Total Individuals in Samples From Unvegetated Shallow Subtidal and Intertidal Flats in the GoM (most prominent adjacent wetland type is shown in parentheses)

			Marine Ecoregion	I	
	Florida Bay (seagrass)	Eastern Gulf Neritic (marsh/ seagrass)	Mississippi Estuarine (marsh)	Texas Estuarine (marsh/ seagrass)	Texas Estuarine (seagrass)
Fishes					
Batrachoididae					
Opsanus beta			Х		
Clupeidae					
Brevoortia patronus			Х		
Cynoglossidae					
Symphurus plagiusa		Х			
Engraulidae					
Anchoa mitchilli			Х	Х	Х
Fundulidae					
Lucania parva	Х				
Gerridae					
Eucinostomus argenteus		Х			
Gobiidae					
Gobiosoma bosc			Х	Х	
Gobiosoma robustum	Х				
Ctenogobius boleosoma		Х	Х		
Gobiesocidae					
Gobiesox strumosus			Х		
Mugilidae					
Mugil curema		Х			
Sciaenidae					
Bairdiella chrysoura		Х			
Leiostomus xanthurus				Х	
Ophichthidae					
Myrophis punctatus			Х		
Natant Decapod Crustacea	ns				
Hippolytidae					
Thor floridanus	Х				
Tozeuma carolinense					Х
Palaemonidae					
Palaemonetes intermedius		Х			
Palaemonetes pugio				Х	
Palaemonetes spp.			Х		
Penaeidae					
Farfantepenaeus aztecus			Х	Х	Х
Farfantepenaeus duorarum	Х	Х			
Portunidae					
Callinectes sapidus		Х	Х	Х	
Callinectes similis					Х
Data References:	Sheridan et al., 1997	Rozas et al., 2012	Mairaro, 2007; Plunket, 2003	Minello, 1999	Sheridan and Minello, 2003

Red shaded cells indicate the presence of dominant families at each location. The most abundant species reported in each family are indicated by an "X"

Most marine food webs share fundamental structural and ordering characteristics with those of estuarine, fresh water, and terrestrial systems (Dunne et al. 2004). Benthic invertebrates have an important role in transferring energy from detrital production to higher trophic levels (Newell et al. 1998). Decapods are among the chief consumers of the benthos, and in general are opportunistic predators. Many decapods feed on the predominant invertebrates of coastal sediments, including polychaetes, bivalves, echinoderms, and smaller crustaceans (Stehlik 1993). Blue crabs (*Callinectes sapidus*) consume locally abundant infauna, epifauna, and fish (Tagatz 1968). Where abundant, blue crabs play a major role in energy transfer within estuaries (Baird and Ulanowicz 1989). Blue crabs and other decapods provide an important link between benthic secondary production and higher trophic levels.

The diet of many of the most common demersal fishes consists of benthic invertebrates (Grosslein 1976). Fishes such as flounders, skates (*Raja* spp.), and spot (*Leiostomus xanthurus*) are predominantly bottom feeders that consume infaunal and epibenthic crustaceans and polychaetes. Amphipods are known to be important in the diets of some demersal fishes, including Atlantic croaker (*Micropogonias undulatus*). The affinity of certain demersal fishes for particular sediment types often is related to the types of prey items supported by those sediments (Rogers 1977). Decapods are a primary component of the diets of demersal fishes (Bowman et al. 2000).

Epifauna associated with intertidal flats are predominantly mobile predatory species such as portunid crabs (e.g., *Callinectes sapidus*) that consume small bivalves, polychaetes, and crustaceans. Other mud and sandy-mud associated epifauna include brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), swimming crabs such as *Portunus gibbesii* and *Portunus spinimanus*, the mantis shrimp (*Squilla empusa*), the gastropods *Pollinices lunulata* and *Nassarius acutus*, and the bivalves *Nuculana concentrica* and *Macoma tageliformis*. Intertidal flats also provide migratory corridors for taxa such as penaeid shrimps and blue crab, which feed on polychaete worms and other tubicolous infauna as they move from estuarine nurseries into nearshore spawning grounds (Franks et al. 1972).

6.6 DISTURBANCES AND ECOLOGICAL IMPACTS

The ecological structure and function of coastal habitats discussed previously are the result of the interaction among environmental characteristics of habitats, the biology of the species occurring within habitats, and the numerous disturbances that periodically impact and often reset ecosystem processes. Coastal habitat disturbances vary widely, being both natural and anthropogenic, and acute and chronic. Here, we provide a brief overview of many primary disturbances structuring coastal habitats mentioned within this chapter. Our discussion is not meant to be exhaustive, but rather serves as a summary of diverse disturbances and their ecological impacts.

6.6.1 Natural Disturbances

Disturbance is a physical event that disrupts at least some aspects of the physical or biological structure of an ecosystem, and consequently, plays an important role in restructuring the ecosystem and altering its ecological functions. Disturbance can be natural, as in the case of tropical storms that cause coastal marsh and beach erosion, or human-induced, such as introduction of excessive nutrients to coastal waters and resulting depletion of dissolved oxygen. The relative influence of different types of natural disturbance varies with geographic location; northern populations of mangroves, for example, are subject to freeze damage while southern populations, especially outside of the United States, experience human impacts, such as harvesting, as well as the natural impacts from frequent tropical storms and hurricanes. This section will address small- and large-scale natural disturbances in coastal habitats.

6.6.1.1 Tropical Cyclones

Coastal habitats, such as beaches, salt marshes, and mangroves, can experience severe alteration from hurricanes and other tropical storms. Hurricane Andrew, which made landfall in Florida and Louisiana in late August 1992, removed sections of salt marsh and deposited them in shallow ponds and bays (Cahoon 2006). Hurricane Katrina similarly impacted brackish marshes east of the Mississippi River resulting in more than 80 ha (200 acres) of land loss (Morton and Barras 2011). Sediment and wrack deposition during hurricanes can bury marsh vegetation and result in plant mortality (Guntenspergen et al. 1995; Valiela and Rietsma 1995). Also, saltwater intrusion in lower salinity coastal marshes disrupts system ecology, resulting in short-term vegetation dieback (Cahoon 2006). In contrast to the negative effects of hurricanes and storms, hurricane-generated sediment input can counterbalance relative sea-level rise and promote wetland sustainability (McKee and Cherry 2009). In addition, bare patches resulting from wrack deposition allow for the recruitment of other plant species, generating habitat heterogeneity and increasing plant diversity (Guntenspergen et al. 1995).

Mangrove forests in Florida have been periodically disturbed by hurricanes, such as Hurricane Donna in 1960 (Craighead and Gilbert 1962), Hurricane Andrew in 1992 (Smith et al. 1994; Baldwin et al. 1995), and Hurricane Wilma in 2006 (Whelan et al. 2009). These and other studies have documented the impacts of such storms on subsequent structure and function of mangrove forests, including defoliation and losses of branches or entire trees (Davis 1995; Baldwin et al. 2001; Davis et al. 2004; Milbrandt et al. 2006; Profitt et al. 2006; Ward et al. 2006; Smith et al. 2009; Whelan et al. 2009; Castaneda-Moya et al. 2010; Harris et al. 2010). Recovery of mangroves after hurricane disturbance is a function of a complex interaction of factors, including seedling recruitment and survival, resprouting capability, and colonization by herbaceous vegetation (Baldwin et al. 2001). Post-disturbance site productivity (Ross et al. 2006) and spatial variation in hurricane impact (Thaxton et al. 2007) further influence regeneration success. Recovery of ecological structure generally occurs, but it is a relatively slow process compared to herbaceous systems.

Hurricane damage to seagrass beds can be highly variable and depends on location as well as hurricane characteristics (Smith et al. 1994; Courtemanche et al. 1999; Paerl et al. 2001; Coles and Brown 2007; Cebrián et al. 2008; Anton et al. 2009). Hurricanes have been observed to cause widespread damage to seagrasses, but also to pass with little or no damage (Poiner et al. 1989; Hemminga and Duarte 2000). For example, a cyclone and its associated rainfall caused a loss of approximately 1,000 km² (247,000 ac) of seagrass in Hervey Bay, Australia (Preen et al. 1995). Other reports have shown hurricanes having only small impacts on seagrass beds and associated macrophytes (Fourqurean and Rutten 2004; Tilmant et al. 1994).

Hurricane Katrina was one of the most destructive storms in U.S. history, with winds over 264 km/h (164 mi/h) and a storm surge of 7.8 to 8.5 m (25.6 to 27.9 ft) in the western coast of Mississippi (Hsu et al. 2005). Anton et al. (2009) showed that this powerful hurricane had no major impact on seagrass density, biomass, or community structure (abundance of producers and consumers) in a seagrass bed located approximately 100 km (62 mi) to the east of the hurricane's landfall. Overall, this research showed that natural temporal changes in seagrass metabolism, recorded before the hurricane, were larger than any post-storm changes. Conversely, a combination of tropical storm activity and higher-than-average watershed discharge in the Big Bend area of Florida is believed to have caused severe reductions in seagrass distribution and abundance up to 2005; absence of storm activity and relatively low river
discharges have resulted in significant expansion of seagrass cover, including into areas where seagrass species had not been observed for many years³ (FDEP 2012b) Even when there are significant changes in the coastal wetland vegetation after hurricanes, faunal assemblages, especially mobile nekton, are resilient, and any immediate effects tend to be quickly reversed (Piazza and La Peyre 2009).

6.6.1.2 Floods and Drought

Flooding may elicit major changes in morphology and sediments of barrier beaches, salt marshes, seagrasses, and subtidal substrates, and result in significant (albeit temporary) losses of fauna associated with those habitats. Nearly freshwater conditions (freshets) may occur in areas normally classified as marine waters during extreme flooding events. Although best known for their damaging effects on oysters, freshets also can be responsible for mass mortalities among sessile epifauna (cnidarians such as *Renilla*) and many infaunal species. Motile epifauna (portunid crabs and penaeid shrimps) may move out of areas exposed to extreme reductions in salinity.

Adequate light levels have been identified as one of the most important factors influencing the presence of seagrasses (Hemminga and Duarte 2000). Water column turbidity can be influenced by a number of factors, both natural and anthropogenic. Regardless of source, the primary detrimental effect of turbidity is increased attenuation of light. Reduced light over a prolonged period can deplete seagrass carbon reserves, resulting in increased shoot mortality and ultimately the decline of whole meadows. In extreme cases, the lack of photosynthetically produced oxygen can lead to sediment anoxia and a more rapid rate of seagrass mortality (Ralph et al. 2006). Additionally, it has been suggested that elevations in turbidity may reduce irradiance to a point that stresses seagrasses, reducing their vitality and making them more vulnerable to disease (Giesen et al. 1990; Hemminga and Duarte 2000).

Drought conditions may favor expansion of drought-resistant vegetative community types. For example, mangrove populations survived while competing species, such as *Spartina alter-niflora*, had high mortality caused by a regional drought in 2000 in coastal Louisiana (McKee et al. 2004). Hypersaline zones created in salt marshes during droughts may exhibit changes in vegetation composition, from species such as *Juncus roemerianus and Spartina patens* to salt-tolerant species such as *Sarcocornia pacifica* and *Distichlis spicata*. Bertness (1992) observed in a New England salt marsh that these salt-tolerant species shade the soil, reduce evaporation, and ameliorate salinity; as salinity decreases, other species (for example, *Juncus* and *Spartina*) can re-populate the area and outcompete earlier colonizers until they dominate the patches after 2 to 4 years. However, since 2000, numerous examples of drought-induced plant mortality have been documented along the Atlantic seaboard of the United States (Alber et al. 2008). These events have resulted in salt marsh dieback, often in the absence of significant recovery.

6.6.1.3 Subsidence and Sea-Level Rise

Natural subsidence in the northern GoM has resulted in loss of salt marsh habitat and its associated fauna, but expands habitats for other species. Subsidence in coastal Louisiana has converted large areas of marsh in Barataria Bay, Timbalier Bay, and other embayments to open-water habitat (Britsch and Dunbar 1993; Couvillion et al. 2011), resulting in reductions in primary productivity but increases in subtidal habitats and populations of infauna and epifauna. Work in Florida found that mangrove areas in the Ten Thousand Islands National

³ Carl M. Way, Barry A. Vittor and Associates, Inc.

Wildlife Refuge had increased 35 % from 1927 to 2005; this increase was attributed to sea-level rise as well as factors such as subsidence, enhanced propagule dispersal via new waterways, and reduced freshwater delivery from overland flow (Krauss et al. 2011). Mangroves are also predicted to replace freshwater forests in the eastern Gulf (Doyle et al. 2010). Although some workers have examined rates of sediment accretion in expanding mangrove stands at their northern limits (Perry and Mendelssohn 2009), no information exists on the relative capacity of mangroves to keep up with sea-level rise compared to salt marsh habitat. Relative sea-level rise throughout the GoM is discussed in detail in Section 6.3.

6.6.1.4 Herbivory

Disturbances caused by herbivores may have important consequences for vegetated marine habitats. Grazers in wetlands include insects, crustaceans, snails, fish, waterfowl, and mammals (McKee and Baldwin 1999 and references therein). Arguably, two of the most damaging grazers in salt marshes of the GoM are mammals: nutria (*Myocaster coypus*) and muskrat (*Ondatra zibethicus*), nutria being introduced. Geese also are damaging grazers, but their impacts in the GoM are more localized. These animals can cause "eatouts" that result in denuded marsh surfaces that often recover slowly or not at all (Kerbes et al. 1990; Linscombe and Kinler 1997; Gough and Grace 1998; Randall and Foote 2005). Herbivore impacts from invertebrates (for example, snails in Louisiana and Georgia (Silliman et al. 2005) and crabs in New England (Holdredge et al. 2008)), causing denuding of marshes, also have been reported.

Mangrove forests can be damaged by wood-boring beetles (xylovores), which may cause death of individual trees or small groups of trees (Lugo and Patterson-Zucca 1977; Feller 1995; Smith et al. 1994). Such biotic agents of disturbance were unrecognized until Feller (1995) reported that up to 30 % of the canopy in a red mangrove forest in Belize was removed by the activities of wood-boring beetles. The larvae of the beetles are active in the phloem and outer xylem where they create extensive feeding galleries that are still evident in the standing dead wood and fallen litter for many years. Feller (1995) found that the activity of a single larva can ultimately girdle a branch or bole, resulting in a thinning of the canopy, and terminating in the creation of a light gap and standing dead wood that is secondarily invaded by other xylovores. Only a few estimates of herbivory rates have been made in mangrove forests in the northern GoM, mainly in Florida (Onuf et al. 1977; Erickson et al. 2004; Feller et al. 2007).

Herbivorous animals consume live seagrass blades, epiphytes, and macroalgae. Animals from several different taxonomic groups, such as gastropods, fish, sea urchins, waterfowl, sea turtles, and manatees can all be significant consumers of seagrasses. Sea urchins are primary invertebrate grazers in seagrass beds. In some instances, sea urchin grazing can be so intense that much of the seagrass primary production is consumed, occasionally resulting in the elimination of extensive seagrass patches (Larkum and West 1990; Hemminga and Duarte 2000). Such overgrazing is correlated with sea urchin population density, and can be common in some areas. As a result of these overgrazing events (and subsequent bare patches), young sea urchins are exposed to higher predation rates. This increase in predation results in a decline in the urchin population, which in turn results in a recovery of the seagrass vegetation. In this way, the grazing pressure exerted by sea urchins on seagrass systems may show an oscillating pattern over time, due to consecutive cycles of growth and decline of the sea urchin population (Heck and Valentine 1995; Hemminga and Duarte 2000). Herbivory by certain fish species can be intense under specific conditions; however, the proportion of seagrass production consumed by fish is generally low when compared to the intense grazing observed by sea urchins (Klumpp et al. 1993; Greenway 1995; Cebrián et al. 1996; Hemminga and Duarte 2000).

6.6.1.5 Other Natural Disturbances

Naturally occurring hypoxia has been reported in coastal waters for many years; as summer water temperatures and salinities rise and winds decrease, the potential for mass mortalities among motile fauna as well as benthic and sedentary fauna increases. While this phenomenon (known locally as a "jubilee") occurs mainly in estuarine waters, hypoxic events also occur in nearshore marine waters. In areas of the GoM that are frequently or chronically impacted by hypoxia, benthos tends to be dominated by short-lived, small deposit-feeding polychaetes, and long-lived infauna and epifauna are rare (Rabalais et al. 2002). Some common nekton species in the GoM, including penaeid shrimps, have a degree of tolerance for low oxygen conditions (Rosas et al. 1999), but most actively avoid hypoxic conditions (Renaud 1986). Localized and short-term cyclic hypoxic episodes may be common in tidal creeks of estuaries (Tyler et al. 2009), but nekton are capable of quickly emigrating from areas affected by localized hypoxia and repopulating the area when conditions improve (Hackney et al. 1976).

Mangroves are susceptible to damage by prolonged freeze conditions. Stevens et al. (2006) reported on the role of freezing on mangrove density and seedling establishment, and fluctuations in comparison to salt marsh species. Others have examined the effects of freezing on the structure of dwarf mangrove forests in Florida and how this may change mangrove diversity in the future with a warmer climate (Ross et al. 2009).

6.6.2 Human-Induced Disturbances

Human-induced stressors in coastal habitats are associated primarily with waste discharges, nutrient enrichment, navigation improvements, flood control measures, coastal development, and petro-chemical-related development. Unlike most natural stressors, humaninduced disturbances are typically chronic and persistent. This section describes the major anthropogenic factors that affect coastal habitats in the GoM.

6.6.2.1 Nutrient Enrichment and Pollution

Worldwide population growth has led to an exponential increase in nutrient inputs into the coastal zone, primarily though massive use of fertilizers for agriculture (Nixon and Buckley 2002). Introduction of excess nutrients via the Mississippi River has caused a large area of GoM bottom waters (over 20,000 km² [7,722 mi²] in 2000) to become hypoxic on an annual basis, resulting in die-offs of many epifauna and infauna (Rabalais et al. 2002). At the Louisiana Offshore Oil Port, densities of infauna decreased by over 80 % during persistent hypoxic conditions in the spring-summer seasons of 1990 to 1993; however, taxa richness only decreased by about 50 %, suggesting that some infauna are adapted to nearly anaerobic conditions (Barry A. Vittor and Associates, Inc. 1995). Chronic hypoxia also has been observed in Chandeleur Sound and western Mississippi Sound (Lopez et al. 2010a, b). Waste discharges into coastal waters also include municipal storm water, treated effluents from wastewater treatment plants, and industrial effluents. In general, ecological impacts are relatively minor due to the dilution effects of relatively large receiving waters, and due to improved levels of treatment for such discharges.

Although wetland primary productivity is nutrient limited, recent research has indicated that the input of nutrients, especially nitrogen, can accelerate the expansion of invasive genotypes of *Phragmites australis* into brackish marshes in New England (Bertness et al. 2002) and alter biomass allocation, possibly impacting the capacity of coastal wetlands to keep pace with rising sea levels, as reported for coastal Louisiana (Darby and Turner 2008). Increased inputs of nutrients to mangrove forests as a consequence of agriculture, urban

sewage, and industrial effluents may have significant effects on forest structure and function by modifying net photosynthesis and other physiological processes (Lovelock et al. 2004), rates of herbivory (Feller and Chamberlain 2007), production-decomposition rates (Feller et al. 2007), organic matter accumulation and contribution to soil elevation maintenance (McKee et al. 2007a), or nutrient recycling (Feller et al. 1999; McKee et al. 2002; Whigham et al. 2009). Much of the foregoing work has been conducted outside the northern GoM but the findings are relevant to understanding the general responses of mangroves to nutrient enrichment.

Nutrient excess can also affect the competitive interactions between coastal wetland vegetation types. For example, McKee and Rooth (2008) examined effects of nitrogen addition on the competition between the mangrove, *Avicennia germinans*, and the salt marsh dominant, *Spartina alterniflora*, in coastal Louisiana. When grown in mixture in greenhouse mesocosms, nitrogen addition greatly favored *S. alterniflora*, which is a stronger competitor for nitrogen. Also, seedlings established in nitrogen-fertilized field plots in coastal Louisiana were more susceptible to crab herbivory than unfertilized seedlings (McKee and Rooth 2008). Consequently, nutrient enrichment in this plant community would be expected to modify the outcome of species interactions. Another study, conducted in the Florida Everglades (Castaneda-Moya et al. 2011), found that variation in the availability of phosphorus to below-ground roots could influence future response of mangroves in that system to sea-level rise through modifications of root production and organic contributions to soil volume.

Although eutrophication does not directly cause declines in seagrass because seagrasses generally benefit from higher nutrient levels, eutrophication results in a bottom-up effect in which other marine primary producers, such as phytoplankton and macroalgae, are allowed to proliferate (Hemminga and Duarte 2000). Nutrient requirements for seagrasses tend to be lower than those for phytoplankton and macroalgae (Duarte 1995). Therefore, at similar nutrient inputs, seagrasses are able to maintain primary production well above that of phytoplankton and macroalgae. Seagrasses also experience lower grazing than the other marine primary producers (Cebrián and Duarte 1994; Duarte 1995). For these reasons, seagrasses are able to maintain higher biomasses and outcompete other primary producers under nutrient-limited conditions (Hemminga and Duarte 2000).

As nutrient inputs increase, light becomes the limiting factor and the balance between primary producers is altered. Phytoplankton biomass in the water column increases and microand macroalgae proliferate, sometimes overgrowing the seagrasses. Carpets of epiphytes may cover seagrass leaves, further reducing light available for seagrass photosynthesis. This reduction of light is ultimately the most important factor responsible for the decline of seagrasses in eutrophied waters (Hemminga and Duarte 2000). Along with a reduction in light availability, eutrophication can also lead to decreased sediment oxidation status, anoxia of bottom waters, and, in some cases, concentrations of nutrients that reach toxic levels (Hemminga and Duarte 2000).

6.6.2.2 Fishery Activities

Coastal marine faunal communities are heavily exploited for commercial and recreational uses, especially as key components of fisheries. Penaeid shrimps, blue crab, stone crab, and bay scallop comprise vital fisheries in the GoM. Although infauna are not harvested for commercial use, they provide a major source of food for many fishery species, and environmental disturbances that decrease the abundance of infauna can also reduce populations of important epifauna. Fishing practices, such as trawling and dredging, can disturb bottom sediments, damage shoots and rhizomes, or completely remove seagrasses from the substratum, possibly resulting in severe local reductions of seagrass cover (Hemminga and Duarte 2000). In areas where small boats are numerous, the cumulative effect of boat moorings and propeller scars can result in considerable loss of vegetation (Walker et al. 1989; Creed and Amado Filho; 1999; Hemminga and Duarte 2000), although losses due to these mechanical disturbances are likely small relative to damage caused by elevated water turbidity (Onuf 1994).

Rapid degradation and loss of coastal wetland habitats may be considered the greatest threat to many nekton species of special interest in the GoM (Thomas 1999; Contreras-Espinosa and Warner 2004). However, nekton assemblages in both the northern (Gravitz 2008) and southern (Contreras-Espinosa and Warner 2004; Contreras-Espinosa and Castañeda-Lopez 2007; Ortiz and Lalana 2005) GoM are affected directly and indirectly by activities associated with commercial and recreational fisheries exploitation. The status of many managed fisheries in the GoM is poorly understood with respect to overharvest, but there are some well-known examples of depressed populations of formerly abundant inshore fish families such as the Sciaenidae, especially red drum (Tilmant et al. 1989) and reef fishes, whose juveniles commonly use coastal wetland habitats (Contreras-Espinosa and Warner 2004; Ortiz and Lalana 2005; Gravitz 2008). Removal of larger predatory fishes targeted in many recreational and commercial fisheries can have important implications for trophic dynamics within estuaries that result in shifts in associated nekton assemblages (Pauly et al. 1998; Hall et al. 2000).

Although it has been suggested that heavy fishing pressure following periods of high weather-related natural mortality events has hampered the recovery of some penaeid stocks within the GoM (Kutkuhn 1962), the penaeid shrimp fisheries of the GoM were long considered virtually impervious to overharvesting (Lindner and Anderson 1956). Unlike many larger, long-lived fish species targeted in recreational and commercial fisheries, penaeids are annual species that are reproductively prolific and population variation is largely controlled by environmental conditions, especially in estuarine wetland nursery habitats. In fact, because the fishery is considered fully exploited but not overharvested, it was proposed that trends in shrimp landings could be used as indicators of regional estuarine habitat quality (O'Connor and Matlock 2005). However, recent concerns have arisen about growth overfishing (i.e., decreases in the size of shrimp harvested) of some penaeid stocks in the GoM (Caillouet et al. 2008).

The unintended effects of fishing gear on nekton populations may have an even greater effect on nekton that are not specifically targeted by the principal fisheries in the GoM. Most mobile fishing gear disturbs habitats and potential prey resources for nekton populations (Watling and Norse 1998). Incidental taking of non-targeted species in by-catch is considered by many to be the most significant problem in fisheries management, with shrimp trawling producing the highest discard/catch ratio (Hall et al. 2000). The blue crab fishery, which uses largely stationary gear (i.e., crab traps), also has important indirect effects on many other nekton in the GoM. At least 23 species of fishes, including important recreational fisheries species among the Sciaenidae (drums), have been incidentally killed or injured in crab traps (Guillory et al. 2001). Diamondback terrapins (*Malaclemys terrapin*) are also among the coastal wetland nekton negatively impacted as by-catch of the crab fishery in the GoM (Butler and Heinrich 2007; Hart and Crowder 2011). Like many other long-lived species that are subjected to overharvesting, even unintentionally, it is the juvenile terrapins that are most susceptible to mortality in crab traps (Dorcas et al. 2007).

6.6.2.3 Invasive Species

Introduction of non-native plant species can alter diversity, productivity, and resilience of natural habitats, including mangrove forests. In south Florida, non-native mangrove species (from the Indo-Pacific) have become established in botanical gardens and these populations are reportedly expanding on the Atlantic coast (Fourqurean et al. 2010). However, the mangrove habitat is considered to be difficult to invade by non-mangrove species due to the fact that flooding and high salinity exclude most other plant species unadapted to these conditions (Lugo 1998). Nevertheless, some studies show negative effects of invasives, such as Brazilian pepper, through allelopathic effects of leached chemicals from the fruits on growth and leaf production of mangrove species (Donnelly et al. 2008). In salt marshes, invasive species are relatively few in number in the GoM, perhaps because few plant species have been able to evolutionarily adapt to salinity and flooding, and the niche space for invasion is limited. The European genotype of Phragmites australis, however, has become problematic along the mid-Atlantic and New England coasts of the United States, where it has replaced the native form of this species in many locations while expanding into brackish and saline marshes (Chambers et al. 1999). In the GoM, it also appears to have expanded its dominance, especially within the Birdfoot Delta of the Mississippi River (White et al. 2004a; Hauber et al. 2011) and coastal Mississippi (Peterson and Partyka 2006).

Invasions of seagrass systems by non-native producer species have not been reported to cause large-scale declines in seagrasses, although such a situation is not unlikely (Hemminga and Duarte 2000). Proliferation of *Caulerpa taxifolia* (a tropical green alga) was first noted in the Mediterranean in 1984 (Meinesz and Hesse 1991), and is considered potentially dangerous to that region's native seagrass meadows. These fears have been somewhat reduced by observations that algae appear to be successful colonizers only in polluted environments where seagrass vitality is poor, or in sparse meadows (DeVillèle and Verlaque 1995; Chisholm et al. 1997; Hemminga and Duarte 2000).

Unlike with non-native producer species, there are examples of unanticipated, indirect effects arising from the introduction into coastal marine systems of invasive consumer species. Arguably the most damaging invasive animal affecting coastal marshes in the northern GoM is the nutria, or marsh rat, Myocaster coypus. This rodent was introduced into the United States in the 1930s and 1940s, when it was brought to Louisiana to farm its fur (Wilsey et al. 1991). After escaping captivity, it spread throughout the northern GoM and elsewhere in the United States, with an estimated population size of 20 to 30 million (Byers 2009). Nutria not only consume marsh vegetation, they are also a cause of marsh loss due to their consumption of belowground plant parts and the resulting disturbance of the soil (McFalls et al. 2010). Invasive invertebrates in the GoM have also taken their toll. For example, the boring isopod, Sphaeroma terebrans, can cause substantial damage to red mangrove roots (Brooks and Bell 2002). The Asiatic green mussel, Perna viridis, has been found in estuaries of the eastern GoM, where it can occur in numbers that outcompete native species of mollusks, such as Crassostrea virginica (Baker et al. 2011). Other non-native introductions have led to some well-known examples of marine trophic cascades. The introduction of non-native green crabs (Carcinus maenas) from Europe to the Gulf of Maine reduced periwinkle (Littorina littorea) feeding and allowed ephemeral green algae (the periwinkle's preferred food) to dominate the substrate rather than less palatable brown and red algae (Lubchenko 1978; Vadas and Elner 1992). Other examples include the effects of the Asian clam (Potamocorbula amurensis) in San Francisco Bay (Carlton 1999), the non-native ctenophore (*Mnemiopsis leidyi*) in the Black Sea (Malyshev and Arkhipov 1992), and the invasive seastar (Asterias amurensis) in Australia (Buttermore et al. 1994). While such examples do not specifically refer to any situations occurring in the northern GoM, they serve

to illustrate the ability of invasive predatory species to dramatically change food web structure of benthic ecosystems (Heck and Valentine 2007). The impacts of invasive species observed elsewhere also justify concerns about the potential effects in the GoM of recent exotic introductions of species such as lionfish (*Pterois* spp.) (Schofield 2010; Fogg et al. 2013) and penaeid shrimp species (e.g., Wakida-Kusunoki et al. 2011).

6.6.2.4 Navigation Improvements and Flood Control

Navigation improvements (channel dredging and dredged material disposal) can have localized impacts on coastal habitats, including marshes, seagrass beds, and subtidal soft bottoms. Construction of channels and basins involves deepening of existing open-water habitats, or converting vegetated areas to open-water. For example, dredging may have a direct mechanical impact on seagrass beds (Onuf 1994). Biota in such areas are destroyed or displaced by these activities. Excavated channels tend to accumulate fine-grained sediments which can become anaerobic; these areas support very few infaunal organisms and are generally avoided by motile epifauna and demersal fauna especially during warm months. Maintenance of navigation channels requires that re-dredging be performed periodically. Generally, sediments removed during maintenance dredging are placed in upland-confined disposal facilities or in open-water dredged material disposal sites. Biota in the latter sites are subject to periodic smothering or displacement, but recolonization is relatively rapid due to the presence of abundant fauna outside the affected areas, the ability of many burrowing infauna to survive smothering by reestablishing themselves in the new sediment layer, and the generally small spatial scale of disposal impacts.

Canal dredging to support oil and gas development has had a more significant impact on coastal habitats, especially salt marshes along the coasts of Louisiana and Texas. In Louisiana, which has approximately 40 % of the coastal wetlands in the conterminous United States, canal dredging for oil and gas well access has modified the coastal landscape and resulted in direct conversion of wetland to open water (Turner 1990). The resulting fragmentation of coastal marshes has been blamed in part for the rapid rate of marsh loss in Louisiana (estimated at 6,400 ha/year [Britsch and Dunbar 1993]), but the primary causes of marsh loss include regional subsidence and faulting and restriction of natural freshwater and sediment input to marshes due to construction of flood control levees along the Mississippi River. Furthermore, levees disrupt the natural delta cycle process that allows the Mississippi River to change course every 1,000–1,500 years, enabling new deltas to become established over time. The Mississippi River levee system, as well as construction of dams within the watershed, has reduced the amount of river-borne sediment that enters coastal marshes, resulting in an imbalance between subsidence and sedimentation. The resulting decrease in salt-marsh habitat has resulted in a decrease in primary productivity and detrital production that are key factors in fisheries production in the Gulf, and in the infaunal and epifaunal communities that inhabit marshes. Assemblages of organisms associated with open-water habitat, including species that have value to commercial and recreational fisheries, replace these communities.

6.6.2.5 Petroleum-Related Development

Oil and gas development in the GoM began in the 1920s and continues today. Aside from disturbances associated with canals and other access channels, petroleum-related activities have created ecosystem disturbances through installation of pipelines, discharges of drilling muds and fluids, discharges of produced water at well sites, installation of hard structures such as production platforms and wellheads, and incidental releases of oil. Oil pollution, *per se*,

appears to have had little long-term impact on coastal vegetation, even though acute effects often occur during spill events (Pezeshki et al. 2000). Vegetation responses to petroleum hydrocarbons and vegetation capacity to recover are dependent on the toxicity of the oil, the volume of oil and extent of plant coverage, whether oil penetrates the soil, plant species impacted, oiling frequency, season during which the spill occurred, and cleanup methodologies employed (Lin and Mendelssohn 1996; Hester and Mendelssohn 2000; Pezeshki et al. 2000).

The literature describing the effects of petroleum hydrocarbons on coastal wetlands and their flora and fauna is vast and beyond the scope of this chapter. For published reviews on this topic, see, for example, Fang (1990), Baker et al. (1993), Catallo (1993), Proffitt (1998), Pezeshki et al. (2000), Ko and Day (2004), Michel and Rutherford (2013).

6.6.2.6 Marsh Burns

Besides natural lightning strikes, fire associated with managed burns is a relatively frequent disturbance in herbaceous wetlands such as salt marshes, although small burns do occur in mangroves, killing trees, but usually not initiating a large fire (McKee and Baldwin 1999). Fire creates disturbance patches that allow for subdominant species to gain dominance, often increasing diversity, until finally outcompeted by the surrounding climax vegetation (Nyman and Chabreck 1995). Fire in wetlands becomes particularly problematic when peat burns occur, reducing marsh elevation, increasing inundation, and stressing marsh vegetation.

6.7 SUMMARY

Vegetated marine habitats of the GoM provide a wealth of ecosystem services including food, employment, recreation, and natural system maintenance and regulation to the countries bordering the GoM: the United States, Mexico, and Cuba. The economic, ecological, and aesthetic values of these habitats benefit human well being as illustrated by the desire of humans to live on or near the coast. Ironically, the attraction of coastal shorelines and their habitats to people, along with associated demands for exploitation of natural resources, have led to environmental pressures that have taken their toll on many marine habitats. Nonetheless, coastal habitats of the GoM continue to represent vital components of the GoM ecosystem.

This chapter has reviewed the physical and biological processes that control habitat formation, change, and ecological structure and function. The goal has been to provide baseline information by which resource managers and decision makers can better manage these important natural resources. Those marine habitats that occur immediately adjacent to the GoM, including barrier islands and beaches, salt marshes and mangroves, seagrasses, intertidal and subtidal flats, and reed marshes at the mouth of the Mississippi River have been emphasized.

Although three distinct sedimentary provinces characterize the modern GoM basin, a wide variety of coastal depositional systems have evolved along the 6,077 km (3,776 mi) land–water interface in response to upland drainage; groundwater supply; sediment availability; wind, wave, and current processes; relative sea-level rise; and physiographic characteristics of margin deposits. Carbonate deposits dominate the Mexican States of Campeche (east of Laguna de Términos), Yucatán, and Quintana Roo, as well as the northwestern coast of Cuba and the southwestern coast of Florida. Terrigenous sediment is dominant in the northern GoM where 77 % of all fluvial flow entering the basin originates. Smaller fluvial watersheds along the Tamaulipas, Veracruz, and Tabasco coasts of Mexico contribute the remaining 23 % of flow to the Gulf, resulting in a mixture of fine-grained terrigenous clastics and carbonate sediment.



Figure 6.137. Summary distribution of coastal habitat type throughout the GoM (for data sources see Figures 6.80, 6.82–6.84, 6.86, 6.90, 6.92, 6.94, 6.96–6.101; basemap from French and Schenk, 2005).

Vegetated marine habitats are qualitatively similar throughout the GoM, though they vary in relative importance depending upon their location (Figure 6.137). Regional climate, geology, and riverine influence are key drivers of geographical habitat differences. For example, tropical and subtropical mangroves are more prevalent in the Southern GoM Ecoregion, as well as the South Florida/Bahamian Atlantic and Greater Antilles Ecoregions, compared with the Northern GoM Ecoregion, where temperate salt marshes dominate. Seagrasses occur throughout much of the GoM, but areal extent is less abundant in the northern GoM due to reduced water clarity and salinity associated with major riverine discharges of the Mississippi/Atchafalaya drainage basins. Also, arid environments resulting from low precipitation and high evapotranspiration in southern Texas-northwestern Mexico and the northern Yucatán generate hypersaline conditions and sedimentary habitats where rooted vegetation is stunted, absent, or replaced by algal assemblages. Such conditions stand in contrast to much of the remainder of the GoM, where high precipitation and lush vegetated marine habitats occur.

Mangroves in the GoM are dominated by four species: red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and button mangrove (*Conocarpus erectus*). The cold-tolerant black mangrove dominates in the northern extremes of the GoM, while all four species are important along the more southern shorelines

of the GoM. Salt marshes also show distinct differences in species composition with smooth cordgrass (*Spartina alterniflora*) dominating many of the frequently flooded marshes of the northern GoM and black needle-rush (*Juncus roemerianus*) more prevalent in higher elevation, infrequently flooded salt marshes of the northeastern GoM (Mississippi, Alabama and the Florida panhandle). Salt marshes do occur in the more southern GoM, but generally where mangroves cannot dominate due to various stressors and disturbances (e.g., hypersaline and infrequently flooded areas, where herbaceous halophytes may co-occur with stunted mangroves).

Seagrasses consist of five major species in the GoM: turtlegrass (Thalassia testudinum), shoalgrass (Halodule wrightii), manatee grass (Svringodium filiforme), Engelman's seagrass (Halophila engelmanni), and widgeon grass (Ruppia maritima). Seagrass species composition varies regionally in the GoM. Across the northern Gulf, Thalassia, Halophila, and Syringodium tend to be much more common at lower latitudes in Florida and Texas, and these species gradually become less prevalent northward into Alabama, Mississippi, Louisiana, and north Texas. In this broad central GoM area, Halodule wrightii predominates and the three other species are largely absent. When present, they generally represent a minor component of the seagrass community unlike the southern areas of Florida and Texas where they occur abundantly. Seagrass beds are regionally extensive in the southern GoM, where many of the same species occur. Intertidal flats and subtidal soft bottoms lack rooted vascular vegetation but may contain marine macroalgae (seaweeds) such as Avrainvillea, Caulerpa, Halimeda, and Udotea. Although barrier islands and beaches are ubiquitous and many plant species are common throughout the GoM, unique species distributions do occur. For example, sea oats (Uniola paniculata) dominates much of the northern GoM, but is virtually absent along shorelines from the Mississippi River to northeastern Texas. In the tropical areas of the southern GoM, sea oats again disappears and species such as seagrape (Coccoloba uvifera), gullfeed (Scaevola plumieri), bay cedar (Suriana maritima), baybean (Canavalia maritima), sea rosemary (Tournefortia gnaphaloides), and others with more tropical affinities dominate.

GoM macroinvertebrates that live at or above the seafloor (epifauna) and on or within the substrate (infauna) are distributed primarily on the basis of sediment texture and quality, and vegetative cover type. Fewer species are adapted to the rigorous habitats provided by salt marshes and *Phragmites* marshes, despite the presence of abundant organic matter: epifauna such as the bivalves Guekensia demissa and Polymesoda caroliniana occur at the base of marsh plants, while fiddler crabs (Uca spp.) and mud crabs (Rhithropanopeus harrisii) forage across marsh mud flats. Marsh infauna have low diversity but the species that are present (e.g., the polychaetes Capitella capitata, Neanthes succinea, and Laeonereis culveri) can be relatively abundant. Diversity generally increases as the frequency and duration of inundation increases. Mangroves contain many more species than marshes, but include many of the same taxa, in addition to species such as penaeid shrimps (e.g., Litopenaeus setiferus and Farfantepenaeus aztecus), portunid crabs (especially blue crab, Callinectes sapidus), various sponges and tunicates, and spionid polychaetes. Beach habitats support higher numbers of epifaunal and infaunal taxa, including a wide variety of burrowing forms such as capitellid and nereid polychaetes, bivalves such as Donax variabilis, and crustaceans such as Emerita talpoida, Lepidactylus triarticulatus, and Acanthohaustorius spp. Intertidal flats and subtidal soft bottoms contain diverse and abundant faunal communities. These include many burrowing deposit feeders (especially polychaetes), as well as various bivalves, gastropods, echinoderms, and crustaceans. Epifauna and infauna are most diverse in seagrass meadows, which provide relatively stable habitat conditions, high productivity, and structure. Bay scallop (Argopecten *irradians*), green sea urchin (Lytechinus variegates), and sea star (Echinaster serpentarius) are associated primarily with seagrass beds, but may also occur on other soft bottoms.

Most of the numerically dominant epifaunal and infaunal taxa are found throughout the GoM, while others exhibit more limited geographic distributions. Species that are adapted to finer and organic-rich sediments characterize the Mississippi Estuarine and Texas Estuarine Ecoregions, while some species in the Eastern Gulf Neritic Ecoregion and South Florida/Bahamian Atlantic Ecoregion are associated primarily with biogenic sediments on the West Florida Shelf and Campeche Banks in the Southern GoM Ecoregion. A faunal break has been described between the Eastern Gulf Neritic and Mississippi Estuarine Ecoregions (as defined by the DeSoto Canyon), but changes in species distributions are less abrupt in most other areas of the Gulf. Coastal habitat epifauna and infauna play an important role in the trophic dynamics of GoM ecosystems. They exhibit a wide range of feeding strategies and are critical to the conversion of vegetative detritus available to higher trophic levels. Few of these taxa are migratory; rather they are typically sedentary or have limited ranges of movement. As a result, their abundance and diversity serve as ideal indicators of habitat quality and perturbation.

Nekton are characterized by their mobility, and their assemblages in the region's vegetated marine habitats are a subset of the fishes, natant crustaceans, molluscs, marine reptiles, and marine mammals found along the beaches, bays, lagoons, and tidal channels of the GoM. It is difficult to describe a characteristic nekton assemblage for individual marine habitats because the habitat of many nekton species includes multiple types of coastal wetlands; species richness and abundance are often greatest at the boundaries (i.e., edges) between subtidal (e.g., embayments) and intertidal (e.g., salt marshes) wetland habitats. A few species like bay anchovy, Anchoa mitchilli, are ubiquitous in almost every coastal marine habitat within the GoM (Figure 6.108), while others like zostera shrimp, Hippolyte zostericola, and dwarf seahorse, *Hippocampus zostericola*, are closely associated with specific habitats such as subtidal seagrass beds (Figure 6.107). The relatively few species (e.g., fishes in the families Fundulidae and Cyprinodontidae and shrimps in genus Palaemonetes) that are abundant year-round residents of intertidal vegetated marine habitats in the northern GoM (Figure 6.106) are adapted to the wide range of environmental conditions typical of temperate intertidal estuaries. Many other species (e.g., penaeid shrimps, Gulf menhaden) are seasonally abundant as a result of life histories that involve the use of shallow coastal wetlands as nurseries by juvenile life stages (Figures 6.103 and 6.108) during seasons when environmental conditions are favorable for their survival and growth. Overall, nekton assemblages connect vegetated marine habitats across the coastal landscape of the GoM by facilitating significant energy transformations and production transfers among coastal wetland habitats and from estuaries to nearshore coastal marine environments via either diel, tidal, and ontogenetic migrations (e.g., penaeid shrimps, Gulf menhaden) or size-structured predator-prev interactions.

Greatest changes in coastal marine habitats occur in areas most susceptible to relative sea-level rise, tropical cyclones, and human disturbances. As such, the deltaic coast of Louisiana has experienced the greatest land and habitat changes in the GoM. Conversely, the more stable coasts of the Yucatán Peninsula, Cuba, and southwestern Florida have illustrated the least amount of change. Although vegetated marine habitats of the GoM are quite productive, human disturbances are recognized in areas of significant industrial activity and tourism. Human impacts are in large part tied to periodic and chronic stressors and disturbances associated with urban, agricultural, and industrial activities. The draining and filling of wetlands for human habitation, agricultural development, and industrial expansion have dramatically impacted coastal habitats throughout the GoM. Also, over-fishing and related activities have threatened important commercial fisheries in some areas of the Gulf. Other stressors such as nutrient enrichment, and resulting eutrophication and hypoxia, altered hydrology from multiple causes, invasive species, and chemical pollutants from agriculture and industry have challenged the health and sustainability of vegetated marine habitats. In addition, natural phenomena such as hurricanes, the underlying geology, and floods and drought exacerbate the human impacts. Information provided in this review is intended to help natural resource managers and policy makers better understand, manage, and restore these important natural ecosystems.

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A manuscript of this breadth required multiple authors to adequately address the physical and biological aspects of marine vegetated habitats. To that end, Irving A. Mendelssohn was responsible for documenting the vegetative characteristics of coastal habitats, Mark R. Byrnes was responsible for describing geological controls and physical processes affecting sedimentation and hydrodynamics in coastal habitats, Ronald T. Kneib summarized nekton population dynamics in and adjacent to coastal habitats, and Barry A. Vittor discussed benthic fauna and the distribution and ecology of seagrass habitat in the coastal GoM.

Maps throughout this chapter were created from World Imagery (credits: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, and the GIS User Community) and Bing Maps Aerial (credits: © 2010 Microsoft Corporation and its data suppliers) aerial imagery web mapping services using ArcGIS® software by Esri. ArcGIS® and ArcMap[™] are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com. All original figures used in this document were reproduced with permission from copyright holders.

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