This chapter reviews tidal wetlands that occur along the Atlantic coast of the United States from the northern border of North Carolina to the northern distribution limit of mangroves in central Florida. The South Atlantic coast has a warm climate, a wide tidal range, and fewer anthropogenic impacts than the North and Central Atlantic coasts. It is a gently sloping coast that supports extensive tidal salt marshes. Tidal brackish marshes are common where rivers provide a source of freshwater. Rivers upstream of estuaries are bordered by tidal freshwater marshes and swamps. Below, we discuss the historical human use of the area. Then, building on Pomeroy and Wiegert (1981), Wiegert and Freeman (1990), and Dame, Alber, et al. (2000), we review the ecology of South Atlantic tidal wetlands and discuss regional conservation concerns.

Historic Human Use of the Landscape

Around 2200 b.c., coastal populations of Native Americans in the South Atlantic began intensively harvesting oysters, *Crassostrea virginica*, and other shellfish (DePratter 1979; Thomas 2008), leaving thick shell deposits, including shell rings up to 150 m across, on barrier and back-barrier islands (Crusoe and DePratter 1976; Thompson 2007). When Europeans arrived, Native American populations were at their peak (DePratter 1978; Thomas 2008; Thompson and Turck 2009). By the late 1600s, however, Native American populations were severely reduced by Old World diseases and forced relocation by Europeans (Worth 1995). By the late 1600s, however, Native American populations were severely reduced by Old World diseases and forced relocation by Europeans (Worth 1995). The shell deposits that they left behind, however, were so extensive that European inhabitants mined them for road fill and construction material (Sullivan 2001).

After 1600, human use of coastal wetlands shifted in focus. Rice was farmed in diked tidal marshes in Georgia and South Carolina from the mid-1700s to circa 1900 (Coclanis 1989, 1993). Some former rice fields are currently maintained as habitat for waterfowl. Cypress and other wetland trees were harvested in coastal wetlands, and pine and hardwoods on coastal highlands, and they were floated downstream to coastal docks during the late 19th and early 20th centuries (Sullivan 2001). Ballast stone offloaded into coastal wetlands by ships receiving timber formed novel back-barrier islands. Dredging of channels began in the late 1800s to accommodate shipping and continues today. Dredge spoil was deposited onto adjacent marshes, forming another type of novel island (Sullivan 2001). Finally, commercial and recreational harvesting of oyster, crab, shrimp, and fish expanded in the 20th century. How these various impacts affect the current functioning of tidal wetlands in the South Atlantic is largely unknown.

The Physical Setting

Geology

The South Atlantic coastline receives sediment from erosion of the Appalachian Mountains, the deeply weathered soils and bedrock hills of the Piedmont, and the thick, sandy soils of the Coastal Plain (Fig. 4.1) (Kennedy 1964). Rivers draining the Piedmont typically transport more water and an order of magnitude more sediment than those draining the Coastal Plain (Meade 1982). Early farming practices increased sediment loads, but this effect has decreased since the 1940s (Trimble 1974). Most transported sediment is trapped behind dams or in estuarine wetlands, and little reaches the continental shelf (Milliman, Pilkey, et al. 1972; Meade 1982).

Coastal marshes (Fig. 4.2) formed several thousand years ago behind developing barrier islands that moderated wave action (Alexander and Henry 2007; Mallinson, Burdette, et al. 2008). Barrier islands in North Carolina, northern South Carolina, and Florida are composed of unconsolidated sands (Hayes 1994). In contrast, barrier islands in southern South Carolina and Georgia are compound, with younger, sandy components on their eastern sides and older, stratigraphically variable deposits on their western sides. Back-barrier islands (= hams) occur between barrier islands and the mainland, and were created either by erosion of uplands, progradation of the shoreline, or anthropogenic deposition of dredge-spoil, ballast stone, or oyster shell.
Climate and Oceanographic Context

The southeastern United States has a generally warm and wet climate, driven by the interaction between marine tropical and continental polar air masses. Tropical air is unstable and driven into the region by clockwise circulation around the subtropical Atlantic high-pressure cell (the Bermuda High), giving rise to thunderstorm activity during the summer. The continental polar air mass interacts with the marine tropical air mass during winter, forming baroclinic instabilities that promote cyclogenesis, leading to the bulk of the winter precipitation. South Florida, however, has drier winters than the rest of the region because the Atlantic high-pressure cell tends to move toward the equator during winter, leading to sinking air and inhibiting convective storm activity (Soulé 1998). The strength and location of the Bermuda High are major factors determining the supply of freshwater to Georgia coastal systems (Sheldon and Burd unpublished) and historic patterns of rainfall in the Southeast (Stahle and Cleaveland 1992).

Tidal patterns in the South Atlantic are primarily driven by the semidiurnal lunar tide (M2) and the solar tide (S2). The tidal range varies from 1 to 3 m depending on location and M2–S2 interactions. When the dominant M2 tidal wave enters bays and estuaries, nonlinear interactions with irregular creek geometries and bottom topography produce overtides (harmonics) and more complicated tidal cycles (Huang, Chen, et al. 2008). These overtides generally produce asymmetric tidal currents, with the ebb current stronger and shorter than the flood current. Water stored in intertidal marshes also contributes to ebb dominance in the channel.

River flow, precipitation, and groundwater discharge create an along-channel salinity gradient as high as 1 PSU km⁻¹ (Blanton, Alber, et al. 2001). Because the estuaries are shallow, vertical stratification is easily destroyed by tidal stirring (vertical mixing) (McKay and Di Iorio 2010). Ocean inputs are mediated by seasonal wind patterns that cause sea level to fall or rise by up to 0.4 m in the summer versus fall and winter, respectively (Di Iorio unpublished).

Land Use and Freshwater Inputs

Rivers are a major source of nutrients and freshwater to coastal wetlands, and estuarine salinity is well predicted by river discharge (Sheldon and Alber 2002; Di Iorio unpublished). Nutrient delivery varies with flow within a river: nitrate+nitrite dominates dissolved nitrogen (N) loading of the Altamaha River during periods of low flow, whereas dissolved organic nitrogen increases in importance during high flow (Weston, Hollibaugh, et al. 2003). The 12 largest watersheds are dominated by forest (33 to 70%) and agriculture (18 to 43.5%). The most important watershed N inputs are fertilizer (33%), net import of food and livestock feed (31%), and agricultural N fixation (26%) (Schaefer and Alber 2007a). Riverine N export is correlated with watershed N input (Schaefer and Alber 2007a), but the proportion of N exported to the estuary is only 9% (Table 4.1), less than half of global estimates of ~25% (Boyer, Goodale, et al. 2002; Galloway, Dentener, et al. 2004), possibly due to temperature-driven differences in denitrification (Schaefer and Alber 2007a).

Another source of freshwater and nutrients to coastal wetlands is submarine groundwater discharge (Moore 1999). Groundwater fluxes of nutrients, metals, and dissolved inorganic and organic carbon (C) can rival or exceed riverine fluxes (Krest, Moore, et al. 2000; Moore, Krest, et al. 2002; Crotwell and Moore 2003). The nature of groundwater discharge has been altered by dredging, which can breach underlying confining layers (Duncan 1972), and by groundwater use, which can lower potentiometric surfaces in aquifers, causing seawater infiltration (Landmeyer and Stone 1995).

Soils and Biogeochemistry

Tidal salt and brackish marshes of the Southeast generally have sandy, mineral soils, with higher bulk density and less organic C and N than marshes of the North Atlantic and Gulf coasts (Coultais and Calhoun 1976; Daniels, Kleiss, et al. 1984; Gardner, Smith, et al. 1992; Craft 2007). Soils are typically high in sulfides and have poorly developed horizons or layers. Porosity is high, ranging from >50% in mineral soils to 90% in organic soils (Craft, Seneca, et al. 1991). The pH of moist salt and brackish marsh soils is neutral to slightly basic, but some soils become acidic upon drying as sulfide is oxidized to sulfate (Daniels, Kleiss, et al. 1984). Cation exchange capacity varies depending on clay and organic content, but exchange sites are dominated by base cations, Na, K, Ca, and Mg. Brackish and fresh marshes and swamps tend to have organic or organic-rich mineral soils (Daniels, Kleiss, et al. 1984; Loomis and Craft 2010). Tidal freshwater marshes and swamps contain little sulfide and are slightly more acidic than brackish and salt marshes (Loomis and Craft 2010).

Within the Southeast, tidal-marsh soil properties vary depending on salinity, geomorphic position, tide range, vegetation type, and other factors (Table 4.2). Barrier-island salt marshes have very sandy soils, with high bulk density and low nitrogen compared with lagoonal salt marshes (Table 4.2).
FIG. 4.2. A. Aerial view of creek network permeating *Spartina alterniflora* salt marsh, Georgia. B. Aerial view of part of the Georgia coast, with light-green barrier islands to right, mainland to left, and dark green tidal wetlands between. C. Creekbank of *S. alterniflora* salt marsh at high tide. D. Wrack disturbance in upper levels of salt marsh, with *S. alterniflora* in foreground and *Juncus roemerianus* behind. E. Creekbank of *S. alterniflora* salt marsh at low tide, with oyster reef at water’s edge. (Photo credits: A: Clark Alexander; B: 2000 Landsat ETM+ produced by the U.S. Geological Survey; C: K. Więski; D: C. Hladik; E: S. Pennings. Used by permission.)
<table>
<thead>
<tr>
<th>Watershed</th>
<th>Watershed Area (km²)</th>
<th>Forest (%)</th>
<th>Agriculture (%)</th>
<th>Urban (%)</th>
<th>Wetlands (%)</th>
<th>Water (%)</th>
<th>Other (%)</th>
<th>Watershed N input (kg N km⁻² yr⁻¹)</th>
<th>Specific runoff (mm yr⁻¹)</th>
<th>Riverine N export (kg N km⁻² yr⁻¹)</th>
<th>Percent N export (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roanoke (NC)</td>
<td>21,984</td>
<td>69.6</td>
<td>22.2</td>
<td>2.8</td>
<td>1.7</td>
<td>2.5</td>
<td>1.4</td>
<td>2,889</td>
<td>352</td>
<td>197</td>
<td>7</td>
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<tr>
<td>Pamlico (NC)</td>
<td>5,748</td>
<td>58.8</td>
<td>26.5</td>
<td>2.7</td>
<td>10.3</td>
<td>0.6</td>
<td>1.0</td>
<td>4,118</td>
<td>334</td>
<td>446</td>
<td>11</td>
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<tr>
<td>Neuse (NC)</td>
<td>7,033</td>
<td>51.0</td>
<td>29.3</td>
<td>7.6</td>
<td>9.8</td>
<td>1.5</td>
<td>0.7</td>
<td>4,884</td>
<td>341</td>
<td>446</td>
<td>9</td>
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<tr>
<td>Cape Fear (NC)</td>
<td>13,599</td>
<td>62.8</td>
<td>20.8</td>
<td>7.0</td>
<td>6.0</td>
<td>1.5</td>
<td>1.8</td>
<td>3,604</td>
<td>355</td>
<td>248</td>
<td>7</td>
</tr>
<tr>
<td>Pee Dee (NC)</td>
<td>21,448</td>
<td>61.2</td>
<td>27.0</td>
<td>5.5</td>
<td>3.8</td>
<td>1.1</td>
<td>1.4</td>
<td>4,039</td>
<td>467</td>
<td>390</td>
<td>10</td>
</tr>
<tr>
<td>Santee (SC)</td>
<td>32,017</td>
<td>69.7</td>
<td>18.1</td>
<td>7.0</td>
<td>0.8</td>
<td>2.2</td>
<td>2.1</td>
<td>2,676</td>
<td>433</td>
<td>312</td>
<td>12</td>
</tr>
<tr>
<td>Black (SC)</td>
<td>3,274</td>
<td>33.3</td>
<td>43.5</td>
<td>3.0</td>
<td>18.1</td>
<td>0.2</td>
<td>1.9</td>
<td>3,282</td>
<td>286</td>
<td>158</td>
<td>5</td>
</tr>
<tr>
<td>Edisto (SC)</td>
<td>6,944</td>
<td>45.0</td>
<td>32.3</td>
<td>1.6</td>
<td>15.2</td>
<td>0.7</td>
<td>5.3</td>
<td>2,913</td>
<td>337</td>
<td>228</td>
<td>8</td>
</tr>
<tr>
<td>Savannah (GA)</td>
<td>25,488</td>
<td>65.9</td>
<td>18.0</td>
<td>2.8</td>
<td>4.7</td>
<td>3.6</td>
<td>4.9</td>
<td>2,762</td>
<td>418</td>
<td>272</td>
<td>10</td>
</tr>
<tr>
<td>Ogeechee (GA)</td>
<td>8,415</td>
<td>44.9</td>
<td>33.6</td>
<td>0.7</td>
<td>14.2</td>
<td>0.6</td>
<td>5.9</td>
<td>3,098</td>
<td>330</td>
<td>283</td>
<td>9</td>
</tr>
<tr>
<td>Altamaha (GA)</td>
<td>35,112</td>
<td>57.9</td>
<td>24.5</td>
<td>3.5</td>
<td>7.3</td>
<td>1.2</td>
<td>5.7</td>
<td>3,099</td>
<td>339</td>
<td>273</td>
<td>9</td>
</tr>
<tr>
<td>Satilla (GA)</td>
<td>7,348</td>
<td>45.9</td>
<td>30.4</td>
<td>1.0</td>
<td>14.4</td>
<td>0.6</td>
<td>7.7</td>
<td>3,203</td>
<td>275</td>
<td>365</td>
<td>11</td>
</tr>
<tr>
<td>Area-weighted average</td>
<td>59.7</td>
<td>24.5</td>
<td>3.9</td>
<td>6.6</td>
<td>1.7</td>
<td>3.5</td>
<td></td>
<td>3,199</td>
<td>379</td>
<td>294</td>
<td>9</td>
</tr>
</tbody>
</table>

**Note:** Watershed N input was obtained by summing all inputs (net atmospheric deposition, fertilizer, N fixation, and net food and feed import) and subtracting non-food crop export. Adapted from Schaefer and Alber (2007a). Specific runoff is calculated as annual river flow divided by watershed area, thus allowing comparisons among watersheds of different sizes.
Some tidal freshwater and brackish marshes (i.e., those in the Albemarle-Pamlico estuaries) are underlain by several meters of peat, due to the microtidal tide regime, low sediment inputs, and low salinity relative to marshes elsewhere (Craft, Seneca, et al. 1993). Phosphorus content does not vary strongly among barrier-island, riverine, and lagoonal marshes (Table 4.2).

As in all wetlands, biogeochemical conditions in sediments vary as a function of plant production, microbial processes, macrofauna, and hydrology. The relative importance of these factors varies spatially, driving variation in biogeochemical zonation in both horizontal (across the marsh) and vertical (over depth) directions. Bioturbation and plant roots affect vertical structure, creating fine-scale spatial variation in redox conditions (Bull and Taillefert 2001; Kostka, Gribsholt, et al. 2002; Gribsholt, Kostka, et al. 2003). Large-scale horizontal zonation occurs along the salinity gradient in estuaries. In salt marshes, inundation with seawater rich in sulfate favors organic matter decomposition and mineralization via microbially mediated sulfate reduction, whereas in tidal fresh marshes, decomposition of organic matter is limited by the availability of terminal electron acceptors, and methanogenesis is of more pronounced importance (Weston and Joye 2005; Weston, Dixon, et al. 2006). Soil biogeochemical conditions vary seasonally (Bull and Taillefert 2001), driven by variation in availability of labile dissolved organic carbon more than by variation in temperature (Weston and Joye 2005; Weston, Porubsky, et al. 2006).

### Microbial, Plant, and Animal Communities

#### Microbial Communities

Microbes drive the detritus-based food webs of South Atlantic wetlands and surrounding waters through their activities in mineralizing plant biomass and processing carbon. Four or five species of ascomycetous fungi are the primary decomposers of *Spartina alterniflora* along the entire U.S. Atlantic coast, complemented by seven major bacterial taxa (Newell, Blum, et al. 2000; Newell 2001; Buchan, Newell, et al. 2003). *Spartina patens* hosts a higher diversity of ascomycete species than *S. alterniflora* (Lyons, Alber, et al. 2009). A different suite of ascomycetous fungi are the major decomposers of black needlerush, *Juncus roemerianus* (Newell 2003). Less work has been done on the microbial decomposers of tidal brackish and fresh marshes. Recent studies using molecular techniques have shown that the sediment bacterial communities of *Spartina*-dominated salt marshes in the South Atlantic Bight are quite diverse, with estimates of “species” richness comparable to those in terres-

#### Table 4.2

Selected properties of tidal marsh soils (0–30 cm) of the southeast Atlantic coast (North Carolina, South Carolina, Georgia, and Florida) as a function of geomorphic position and location on the salinity gradient

<table>
<thead>
<tr>
<th></th>
<th>Sand (%)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
<th>Bulk density (g cm⁻³)</th>
<th>Organic matter (%)</th>
<th>Total N (%)</th>
<th>Total P (μg g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>BARRIER/SEA ISLAND</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salt marsh b,c,d</td>
<td>65 ± 8</td>
<td>16 ± 2</td>
<td>13 ± 2</td>
<td>0.94 ± 0.14</td>
<td>4 ± 1</td>
<td>0.19 ± 0.04</td>
<td>690 ± 240</td>
</tr>
<tr>
<td><strong>RIVERINE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salt marsh b,c,d</td>
<td>57 ± 10</td>
<td>20 ± 7</td>
<td>11 ± 4</td>
<td>0.56 ± 0.09</td>
<td>12 ± 2</td>
<td>0.36 ± 0.05</td>
<td>530 ± 100</td>
</tr>
<tr>
<td>Brackish marsh c,g,k</td>
<td>16 ± 16</td>
<td>29 ± 16</td>
<td>27 ± 27</td>
<td>0.33 ± 0.07</td>
<td>28 ± 7</td>
<td>0.81 ± 0.26</td>
<td>620 ± 10</td>
</tr>
<tr>
<td>Tidal freshwater marsh c,k</td>
<td>32</td>
<td>41</td>
<td>2</td>
<td>0.23 ± 0.02</td>
<td>25 ± 4</td>
<td>0.73 ± 0.05</td>
<td>740 ± 190</td>
</tr>
<tr>
<td>Tidal forest n</td>
<td>66</td>
<td>7</td>
<td>1</td>
<td>0.45</td>
<td>26</td>
<td>0.64</td>
<td>490</td>
</tr>
<tr>
<td><strong>LAGOONAL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brackish marsh h,o,p</td>
<td>13</td>
<td>30</td>
<td>6</td>
<td>0.17 ± 0.02</td>
<td>51 ± 3</td>
<td>1.58 ± 0.12</td>
<td>860 ± 60</td>
</tr>
</tbody>
</table>

* Craft, Seneca, and Broome 1993.
* Four barrier-island salt marshes and one riverine salt marsh (Craft unpublished data).
* Two salt marshes (Sapelo River estuary) (Craft 2007). Sand, silt, and clay content (Craft unpublished data).
* Two salt marshes, one brackish marsh, and one tidal freshwater marsh (Paludan and Morris 1999).
* Three salt marshes and one brackish marsh (Bradley and Morris 1990).
* One salt marsh (Goni and Thomas 2000).
* Two salt marshes. Silt content is silt plus clay (Gardner, Smith, Michener 1992).
* Two salt marshes (Sharma, Gardner, et al. 1987).
* One salt marsh (Vogel, Kjerfve, and Gardner 1996).
* Three rivers (Ogeechee, Altamaha, Satilla) (Loomis and Craft 2010). Sand, silt, and clay content (Craft unpublished data).
* Coulas and Calhoun 1976.
* Craft unpublished data.
* Craft, Broome, and Seneca 1986.
* Craft, Seneca, and Broome 1991.
trial soil (Caffrey, Bano, et al. 2007; Lasher, Dydzszyński, et al. 2009). A variety of protist species consume bacteria but may not control their densities (First and Hollibaugh 2008).

**Benthic Algae**

Benthic microalgae (diatoms and cyanobacteria) are abundant in South Atlantic salt marshes compared with Central and North Atlantic sites, but are less abundant than in some Gulf coast marshes (Joye unpublished data). Macroalgae are rare in South Atlantic marshes due to the combination of turbid water, which limits photosynthesis when algae are submerged, and hot temperatures, which cause desiccation when algae are exposed. Microalgal biomass is often greatest on mudflats, because these areas are fully exposed to sunlight and constantly moist. Water stress at higher elevations favors cyanobacteria at the expense of diatoms. Macroalgae are also common in lower-salinity marshes, though data are limited (Neubauer, Miller, et al. 2000; Neubauer, Givler, et al. 2005).

Macroalgal production can rival that of angiosperms in coastal marshes (Tyler, Mastronica, et al. 2003; Porubsksy, Velasquez, et al. 2008), and enters the food web more directly (Currin, Newell, et al. 1995). Benthic microalgal account for 10 to 60% of gross primary production (Pinckney and Zingmark 1993a,b; Sullivan and Currin 2000) and 20 to 25% of net vascular plant production (Tobias and Neubauer 2009). Cyanobacteria are an important source of fixed nitrogen during periods of nitrogen limitation (Tyler, McGlathery, et al. 2003), whereas benthic microalgae can release copious dissolved organic carbon to the water under nutrient-replete conditions (Porubsksy, Velasquez, et al. 2008).

**Angiosperms**

The dominant salt-marsh plant in the South Atlantic is the grass *Spartina alterniflora* (Fig. 4.2a–e), which occurs in mono-specific stands at low to intermediate elevations, sometimes mixed with *Salicornia virginica* or other species at intermediate elevations (Wieghert and Freeman 1990). High marsh elevations are dominated by *Juncus roemerianus* (Pennings, Grant, et al. 2005) and *Borreria frutescens* (Pennings and Moore 2001). This zonation pattern is driven by competition and varying sensitivities of the different plants to flooding and salinity stress. In some marshes, the border between *S. alterniflora* and high-marsh vegetation is interrupted by an unvegetated salt pan with porewater salinities several times those of seawater (Pennings and Bertness 1999) that is surrounded by a group of highly salt-tolerant plant species (Wieghert and Freeman 1990).

Latitude variation in climate drives variation in plant ecology. North of Virginia, aboveground parts of grasses and rushes senesce in the fall, but plants south of Virginia grow year-round (Gallagher, Reimold, et al. 1980). Due to this difference in phenology and warmer temperatures, primary production is greater at low than at high latitudes (Turner 1976). A number of low-latitude plants, such as *J. roemerianus* and *B. frutescens*, do not occur north of Virginia (Pennings and Bertness 1999), likely because they cannot tolerate harsh winters. Because salt-marsh plants can benefit each other by shading the soil and ameliorating high soil salinities, and because low-latitude marshes are hotter than high-latitude marshes, it is reasonable to hypothesize that low-latitude plant communities would be strongly structured by positive interactions (Pennings and Bertness 1999). This hypothesis, however, is false. Instead, competitive interactions predominate among salt-marsh plants in the South Atlantic, in part because the more salt-sensitive plant species are rare at low latitudes and in part because low-latitude species are stronger competitors due to their larger size (Pennings, Selig, et al. 2003).

Brackish marshes are dominated by *Spartina cynosuroides* and *Juncus roemerianus* (Higinbotham, Alber, et al. 2004). The distribution of *S. cynosuroides* and *S. alterniflora* on creek-banks shifts depending on river discharge and estuarine salinity (White and Alber 2009). The dominant plant in tidal fresh marshes is the grass *Zizania palustris* (Higinbotham, Alber, et al. 2004), and tidal swamps are dominated by the trees *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (tupelo gum) (Conner, Doyle, et al. 2007). Several aspects of the marsh-plant community vary systematically along the estuarine salinity gradient. Species richness increases fivefold from saline to fresh sites (Więski, Guo, et al. 2010). Plants are tallest, and nitrogen stocks in plants greatest, at fresh sites, but standing biomass and carbon stocks in vegetation are greatest at brackish sites.

**Marine and Terrestrial Invertebrates**

Southeastern salt marshes support dense populations of mollusks and crustaceans (Fig. 4.3a–g). The mud snail *Ilyanassa obsoleta* occurs in the low marsh and feeds on carrion and algae (Currin, Newell, et al. 1995). The periwinkle *Littoraria irrorata* occurs in the mid-marsh and feeds on fungal decomposers of *Spartina alterniflora* (Silliman and Newell 2003). The pulmonate *Melampus bidentatus* occurs at high elevations, especially in areas not frequented by *Littoraria* (Lee and Silliman 2006), and feeds on biofilms and fungi. The oyster *Crassostrea virginica* is the dominant bivalve, forming low-lying reefs. The ribbed mussel, *Geukensia demissa*, forms mounds in the mid-marsh (Smith and Frey 1985; Stiven and Gardner 1992). The Carolina marsh clam *Polymesoda caroliniana* occurs at low densities in the high marsh.

Eight crab and several shrimp species are common. Predatory mud crabs, *Panopeus herbstii* and *Euritium limosum*, occur throughout all *Spartina* zones (Silliman, Layman, et al. 2004). Predatory blue crabs, *Callinectes sapidus*, enter and leave marshes with the tides. The deposit-feeding sand fiddler, *Uca pugilator*, and mud fiddler, *U. pugnax*, occur in sandy and muddy salt habitats, respectively, while the larger *U. minax* occurs in brackish habitats. Finally, the omnivorous wharf crab, *Armases cinereum*, and the herbivorous purple marsh crab, *Sesarma reticulatum*, occur, respectively, at the terrestrial border and lower edge of the marsh. The commercial brown, white, and pink shrimp and the smaller grass shrimp use salt marshes for feeding and nursery habitats. Finally, a variety of meso- and microinvertebrates occupy marshes, living in association with plants or in marsh soils. These taxa represent an important trophic link between detritus or macroalgae and larger consumers, but only a few have been well studied (Haines and Montague 1979; Kneib 1986; Kneib, Newell, et al. 1997; Graça, Newell, et al. 2000; Griffin and Silliman 2011).

The marshes are also populated by “terrestrial” invertebrates (Fig. 4.4a–e), most notably insects and spiders (Davis and Gray 1966; Pfeiffer and Wieghert 1981). More is known about arthropod food webs in salt marshes than about those in low-salinity marshes. *Spartina alterniflora* supports several herbivores including the planthoppers *Prokelisia marginata* and *P. dolus*, the bug *Trigonotylus uhleri*, several stem borers, and the tettigonid Orche-
Orchelimum fidicinium (Smalley 1960; Stiling and Strong 1984). These are fed on by a variety of parasitoids and predatory insects and spiders (Pfeiffer and Wiegert 1981; Stiling and Bowdish 2000).

The shrub Borrichia frutescens supports several herbivores, including the planthopper Pissonotus quadripustulatus, the gall fly Asphondylia borrichiae, and the lepidopteran Argyresthia sp. (Moon and Stiling 2004), all of which are attacked by hymenopteran parasitoids (Moon, Rossi, et al. 2000). The shrub Iva frutescens supports several herbivores, including leaf-galling mites, the aphid Uroleucon ambrosiae, the beetles Ophraella notulata and Paria aterrima, and the grasshoppers Paroxya clavuliger and Hesperotettix floridensis (Ho and Pennings 2008; Pennings, Ho, et al. 2009). Predators include ladybugs, spiders, and the crab Armases cinereum.

Vertebrates

Vertebrate utilization of marsh habitat for feeding, foraging, and reproduction is one of the most understudied aspects of...
Biogeography of Wetland Communities

The biogeographic paradigm for Atlantic coast marine communities involves transitions at Cape Cod, Cape Hatteras, and Cape Canaveral (Fig. 4.5). These boundaries, however, may not apply to wetland communities. For example, the strong transition zone at Cape Hatteras, where the Gulf Stream diverges from the coastal shelf (Briggs 1974), primarily affects species with low dispersal ability and those distributed far out on the continental shelf (Fischer 1960; Briggs 1974; Schwartz 1989; Roy, Jablonski et al. 1998). In contrast, estuarine invertebrates show other biogeographic transitions associated with temperature gradients (Engle and Summers 1999) (Fig. 4.5). Similarly, phylogeographic surveys along the Florida coast indicate that the canonical transition zone at Cape Canaveral is strongest for species with restricted dispersal (Pelc, Warner, et al. 2009), although the Florida peninsula does act as a barrier for many species (Avise 1992).

Phylogeographic studies of *Spartina alterniflora* show genetic transitions across Chesapeake Bay (Blum, Bando, et al. 2007), reflecting the transition between the Upper and Lower Virginian provinces documented by Engle and Summers (1999). Similarly, the planthopper *Prokelisia marginata* is divided into a mid-Atlantic and a South Atlantic–Gulf coast clade, with a boundary in Virginia (Denno, Peterson, et al. 2008). A number of other wetland animals, including fiddler crabs, bivalves, and sheepshead minnow, also display a transition between the Upper and Lower Virginian provinces (Diaz-Ferguson, Robinson, et al. 2009). The transition from high to low latitudes across the mid-Atlantic region is associated with changes in climate that affect the life history and productivity of *Spartina* (Turner 1976; Kirwan, Guntenspergen, et al. 2009), a large increase in wetland habitat (Bertness 1999), a transition from dominance by *S. patens* to *ficus romerianus* in the middle elevations of salt marshes, an increased abundance of salt-tolerant plant species such as *Salicornia* spp. (Pennings and Bertness 1999), and turnover in dominant insect herbivore species (Wason and Pennings 2008). These transitions lead to variation in ecological interactions at different latitudes (Pennings and Silliman 2005; Pennings, Selig, et al. 2003; Pennings, Ho, et al. 2009).

Key Ecological Processes

Disturbance

The primary disturbance in South Atlantic tidal marshes is the deposition of floating mats of dead vegetation (wrack) onto the marsh by high tides (Fig. 4.2d). Wrack disturbance is more common in North Atlantic than South Atlantic tidal marshes because the aboveground biomass of plants at high latitudes completely dies back in the winter (Turner 1976) and is vulnerable to erosion by ice. In contrast, plants at low latitudes grow year-round, and tend to decompose in place (Newell 1993). Wrack tends to be moved by wind and currents into
predictable locations that are regularly disturbed (Fischer, Klug, et al. 2000). Although heavy mats of wrack harm vegetation, thin layers may benefit it by shading the soil and ameliorating salinities or by leaching nutrients (Pennings and Richards 1998). In addition, wrack creates habitat for spiders and is a major food source for detritivores (Zimmer, Pennings, et al. 2004). Wrack exported from estuaries can trap sand and nucleate the formation of dunes on beaches. Little is known about wrack in tidal brackish or fresh marshes, but the tall vegetation in these marshes probably limits effects to the marsh edge.

**Microbial Decomposition**

Angiosperm production of South Atlantic wetlands enters the food web primarily through decomposition rather than herbivory. In salt marshes, the dominant grasses decay in a standing position, and initial decomposition of dead stalks and leaves occurs in the air, with periodic wetting by rain and tides. Ascomycete fungi are the predominant mediators of this phase of decomposition, and production of fungal organic mass is on the order of 535 g m⁻² y⁻¹ (Newell 2003). Fungi-laden decaying leaves are attractive foods for a variety of consumers, including snails and amphipods (Graça 2000; Kneib, Newell, et al. 1997; Silliman and Newell 2003). These detritivores fragment leaves, which fall into sediments alongside collapsing stalks. Bacteria replace fungi as the dominant decomposers in salt-marsh sediments, but fungal activity remains high in low-salinity sediments (Newell 2003). Fungal biomass is low, but fungal activity per unit of biomass is high, in low-salinity systems (Newell 2003), and detritivorous periwinkles, amphipods, and crabs are less abundant in fresh than in salty marshes (Graça, Newell, et al. 2000; Newell and Porter 2000). The bulk of angiosperm biomass enters the sediments and water column as detritus composed primarily of lignocellulose (Benner, Newell, et al. 1984), which is highly recalcitrant to decomposition. Microbial decomposition of lignocellulose in the sediments is highest during the summer, and is primarily mediated by bacteria (Benner, Maccubbin, et al. 1986).

**Ecosystem Engineering**

Several species in South Atlantic salt marshes are ecosystem engineers, changing the physical environment through nontrophic mechanisms. *Spartina alterniflora* creates the marsh platform by trapping sediment and producing peat (Grosholz, Levin, et al. 2009). Emergent plants also ameliorate desiccation at low tide and hinder access by predators, benefitting small animals that live in the marsh. Burrowing by fiddler crabs, *Uca* spp., oxygenates salt-marsh soils, and crabs excrete wastes in burrows, transporting nutrients from the marsh surface to plant root zones; consequently, crabs stimulate plant growth (Montague 1982). Patches of mussels, *Geukensia demissa*, on the marsh platform engineer mounds capped with vigorous plant growth (Kuenzler 1961; Smith and Frey 1985). Mussels bind sediments and deposit nutrient-rich feces and pseudofeces onto the marsh surface (Kraeuter 1976; Newell and Krambeck 1995). Because mussels are largely absent from marsh edges in the South Atlantic due to predation (see below), they are less important engineers than in New England (Bertness 1984), but oyster reefs at the lower edge of South Atlantic salt marshes (Fig. 4.2e) may play a similar role. Ecosystem engineers are likely also important in tidal brackish and fresh marshes, but this has not been studied.

**Herbivory and Predation**

Early studies in the South Atlantic found that most of the carbon flow from *Spartina alterniflora* to the ecosystem was through detrital processing rather than herbivory (Teal 1962). From this arose the conclusion that herbivory was unimportant in marsh processes. In fact, herbivory rates in salt marshes are similar to those in most terrestrial ecosystems (Cebrian 1999). As described above, herbivores in salt marshes include insects, crabs, and snails. Most of these can suppress plants when common (Denno, Peterson, et al. 2000; Silliman and Ziemann 2001; Stiling and Moon 2005; Ho and Pennings 2008), and two, the snail *Littoraria irrorata* and the crab *Sesarma reticulatum*, have been implicated in contributing to localized dieback of vegetation (Silliman et al. 2005; Hughes, Fitzgerald, et al. 2009). Herbivory in salt marshes is affected by the abiotic gradients across which the plants grow (Denno, Lewis, et al. 2005). For example, *Littoraria* caged at 600 m⁻² reduced *S. alterniflora* biomass by 90% in creekbank plots, versus 65% in mid-marsh plots (Silliman and Bertness 2002). How stress affects herbivory differs as a function of plant and herbivore species (Moon and Stiling 2002a,b; Goranson, Ho, et al. 2004; Stiling and Moon 2005). Little is known about herbivore communities and impacts in tidal brackish and fresh marshes.

Herbivores are more abundant and do more damage to salt-marsh plants in the South than in the North Atlantic (Pennings, Ho, et al. 2009). This pattern, which is probably driven by cold climates limiting herbivore growth rates and densities at high latitudes, may be an important selective factor on plant traits. Salt-marsh plants are tougher, less nutritious, and more chemically defended at low versus high latitudes (Siska, Pennings, et al. 2002). As a result, high-latitude plants support better herbivore growth (Ho, Pennings, et al. 2010).

Predation rates vary with elevation, and are usually highest at the creekbank (Lin 1989; Silliman and Bertness 2002). Predation rates are probably higher in South than in North Atlantic salt marshes, but the evidence is largely anecdotal. For example, the ribbed mussel occurs along creekbanks in the North Atlantic but is relegated to higher elevations in the South Atlantic. Mussels transplanted to lower elevations were quickly eaten (Stiven and Gardner 1992), suggesting that southern marshes experience higher predation rates than northern ones; however, this hypothesis has not been tested with rigorous comparative studies. Similarly, predation rates in arthropod food webs are probably higher in South than in North Atlantic salt marshes (Pennings pers. observation), but again rigorous comparisons are lacking. Herbivorous arthropod food webs are strongly structured by top-down control from parasites and predators (Ho and Pennings 2008; Marczak, Ho, et al. 2010).

**Ecosystem Metabolism**

The metabolism of South Atlantic estuaries has long been of interest due to their high productivity and potential role in subsidizing marine food webs (Oдум 1961, 1968; Schelske and Odim 1962). The simplest depiction of the C cycle of an estuary includes production, respiration, organic C storage, and burial, and exchanges with the atmosphere, uplands,
and ocean (Fig. 4.6a). Few of these processes are easily measured. Consequently, most attempts to quantify C fluxes have employed indirect measures, such as mass balance of offshore C budgets (Hopkinson 1985) or mass balance of all the producer and consumer communities (Wiegert, Christian, et al. 1981; Hopkinson and Hoffman 1984; Hopkinson 1988). Organic C fluxes associated with rivers are well documented (Mulholland and Kuenzler 1979; Hopkinson and Hoffman 1984; Hopkinson 1988). Estimates of production and respiration are similar throughout the South Atlantic and Gulf coasts, but are considerably reduced in the North Atlantic (Hopkinson 1988). Estimates of export to the ocean are considerably higher on the South Atlantic (up to 59%) than on the Gulf and Northeast coasts (1 to 38%), probably reflecting both high primary production and the high tidal range in the South Atlantic.

Salt-marsh estuaries are often conceptualized as separate marsh and aquatic systems with linked C budgets (Fig. 4.6b). This approach indicates that the salt marsh is autotrophic (P/R = 4,500/3,213 = 1.4:1) while the aquatic system is heterotrophic (P/R = 326/574 = 0.56:1), and that each square meter of marsh exports 1,500 gC yr⁻¹ to estuarine creeks and bays. This is equivalent to an input of almost 10,000 gC to each square meter of water. Mass balance for the aquatic portion (tidal creeks and bays) suggests a flux in excess of 5,000 gC m⁻² of water surface yr⁻¹ to the ocean. In addition, rivers contribute 1,852 kgC m⁻² shoreline yr⁻¹ to the coastal zone, much of which passes to the ocean with little alteration or loss during estuarine transit.
Cai and coworkers (Cai, Pomeroy, et al. 1999; Cai, Wang, et al. 2003; Wang, Cai, et al. 2005; Cai 2011) conceptualized southeastern estuaries as a benthic subsystem and an aquatic subsystem (Fig. 4.6c). They used free water measurements of dissolved O₂ and CO₂ to document metabolism of both aquatic components and those portions of the benthic subsystem flooded at any time. This was a significant advance, as it did not rely solely on transport of organic C to tidal creeks to satisfy heterotrophic demands; instead, the water subsystem moves onto the marsh and there integrates some aspects of respiration occurring on the marsh. This approach indicated that the estuarine, bay, and inner-shelf waters of the Georgia Bight are heterotrophic and respire large quantities of organic C exported from intertidal marshes.

Conservation Concerns

Between 1980 and 2003, coastal counties of the Southeast Atlantic had the largest rate of population increase (58%) of any coastal region in the coterminous United States. Most of this growth occurred in Florida (EPA 2008), but tourists and retirees are also placing pressure on the Carolinas and Georgia, which are projected to gain 11 million residents by 2025 (U.S. Census Bureau 2000). These human population changes will drive changes in land use and increase demand for water supply, wastewater disposal, and coastal resources. Conservation concerns for the region include freshwater delivery, eutrophication, management of top consumers, climate change, and marsh die-back.

Freshwater Delivery to the Coast

Changes in industrial and human demand for water are likely to affect freshwater delivery to the coast. Because nutrients, pollutants, sediment, and organic material are all carried along with freshwater, changes in freshwater delivery will affect the delivery of these materials as well (Alber 2002). Similarly, changes in land cover, such as clearing and draining land for agriculture, will also affect the delivery of freshwater and associated materials to the coast. Anthropogenic impacts on freshwater delivery will be layered on top of natural variability in freshwater discharge to estuaries. All five Georgia riverine estuaries exhibit at least a 29-fold interannual difference between minimum and maximum discharge (GCRC 2002). For example, the onset of drought led to increasing salinities in the Satilla River as freshwater discharge declined from almost 150 m³ s⁻¹ in February 1999 to below 10 m³ s⁻¹ in May and June 1999 (Blanton, Alber, et al. 2001). Freshwater inflow also undergoes a regular annual cycle, with seasonal maxima in discharge during the spring and minima in the fall.

Potential changes in freshwater inflow are of concern because they will affect estuarine resources (Alber 2002). For example, a tide gate and diversion canal near the Savannah River National Wildlife Refuge displaced the salt wedge 6 to 8 miles upstream, causing a shift toward salt-tolerant marsh vegetation and changes in fauna (Pearlstine, Kitchens, et al. 1993). When the tide gate and canal were later removed, there was a shift back toward a tidal freshwater community. Similarly, natural variation in freshwater inflow in the Altamaha River estuary between drought and wet years altered the distribution of Spartina cynosuroides (White and Alber 2009) and affected sediment deposition on the marsh surface (Craft unpublished) and productivity of Spartina alterniflora (Pennings unpublished). Finally, drought promotes marsh die-back (below).

Eutrophication

Eutrophication is increasing on the South Atlantic coast. Nitrogen and phosphorus inputs to watersheds have increased over the last 50 years, reflecting fertilizer input and an increase in the human population (Schaefer and Alber 2007b). Dissolved oxygen levels at the Skidaway Institute of Oceanography in Georgia show a steady drop over 19 years (Verity, Alber, et al. 2006). Symptoms of eutrophication (nourishment and toxic algal blooms, hypoxia/anoxia, fish and shellfish mortality) exist in nearly half of the major southeastern estuaries, with future deterioration predicted (Bricker, Longstaff, et al. 2007). In the recent National Coastal Condition Report (EPA 2008), 54% of the water-quality index ratings in the South Atlantic were fair or poor, and 59% of chlorophyll a concentrations were fair. Eutrophication would be expected to stimulate microbial activity (Sundareshwar, Morris, et al. 2003), increase plant productivity (Gallagher 1975), and favor some plant species, especially Spartina alterniflora, over others (Pennings, Stanton, et al. 2002). Moreover, because plants commonly respond to eutrophication by investing more biomass aboveground and less below, eutrophication may reduce belowground production and thereby reduce the ability of marshes to keep pace with rising sea levels (Darby and Turner 2008). In addition, fertilization may increase the palatability of plants to herbivores by increasing plant nitrogen content (Silliman and Ziemann 2001; Moon, Rossi, et al. 2000; Moon and Stiling 2002a,b).

Management of Top Consumers

Humans have markedly affected the densities of many top consumers in southeastern estuarine systems. Alligator densities are rebounding from historic hunting, but landings of commercially important fish and shellfish are declining (EPA 2008). Impacts of recreational anglers are difficult to assess but will likely increase as population densities rise. We lack good data on anthropogenic impacts on most top consumers in southeastern wetlands; however, humans typically reduce the populations of large marine predators to a fraction of their natural densities (Jackson, Kirby, et al. 2001; Myers, Baum, et al. 2007), and so it is likely that populations of many predators in southeastern coastal wetlands have been similarly depressed. The consequences of depressed predator densities for southeastern marsh food webs remain largely unexplored.

Climate Change

Changing climate probably will lead to accelerated sea-level rise and increased storm activity in the South Atlantic. The contemporary rate of relative sea-level rise (RSLR) along the South Atlantic is 2–3 mm yr⁻¹ (Craft, Clough, et al. 2009), and vertical accretion rates in the region range from 2 mm yr⁻¹ for salt marshes to 4–6 mm yr⁻¹ for brackish and tidal freshwater marshes (Craft 2007), indicating that they are able to keep pace with RSLR by trapping sediment and accumulating soil organic matter. Climate projections suggest that SLR will accelerate in the coming century. Although marsh accretion
rates increase with greater sea level (Morris, Sundareshwar, et al. 2002), accelerated RSLR is likely to lead to some losses of tidal marshes, with losses unequal among tidal fresh, brackish, and salt marshes (Craft, Clough, et al. 2009). Rising sea levels will also move saltwater farther into estuaries, which will likely accelerate decomposition of soil organic matter (Weston, Dixon, et al. 2006; Craft 2007), further limiting the ability of low-salinity marshes to keep pace with RSLR.

Hurricanes and storms can drive saltwater upstream, uproot vegetation, and either deposit or erode sediments (Nyman, Crozier, et al. 1995; Cahoon 2006). Hurricane effects on Gulf coast wetlands have been severe (Chabreck and Palmisano 1973). In North Carolina, heavy rainfall from hurricanes lowered salinity and increased N and organic C loadings to estuaries, with cascading effects on estuarine food webs (Paerl, Bales, et al. 2001). Georgia and South Carolina receive relatively few hurricanes (Hopkinson, Lugo, et al. 2008); however, the frequency of storms in the South Atlantic is projected to increase in the future (Hayden and Hayden 2003).

Marsh Die-Back
In 2001–02, salt marshes in Georgia and South Carolina experienced a sudden die-back event that left bare patches in multiple parts of marshes and affected both Spartina alterniflora and Juncus roemerianus (Ogburn and Alber 2006). Many areas were naturally revegetating by 2009. Sudden die-back has also been observed in other years in the Southeast and in other areas of the country (Alber, Swenson, et al. 2008; Osgood and Silliman 2009). In the South Atlantic, die-back was associated with low rainfall and low river inflow. In 2001–02, the Palmer Drought Severity Index for Georgia and South Carolina was characterized as “extreme drought,” and soils at several sites were cracked and desiccated. Die-back was also associated with drought in Louisiana but not in other areas of the country (Alber, Swenson, et al. 2008).

The variety of die-back patterns makes it difficult to come up with a single explanation for these events. When present at high densities, the snail Littoraria irrorata can strongly suppress Spartina alterniflora, and drought may increase plant vulnerability to grazing (Silliman and Bertness 2002; Silliman, van de Koppel, et al. 2005). An interaction between snail grazing and drought may explain die-back events on barrier islands, where snail densities are often high, but is less likely to explain die-back at inland locations, where snail densities are generally low. Other possibilities include drought-induced changes in soil chemistry or the presence of fungal pathogens (McKee, Mendelsohn, et al. 2004; Osgood and Silliman 2009). Rigorous evaluation of the various hypotheses is difficult because transient die-back events are often not noticed until they are well developed, at which point the factor causing die-back may no longer be present.

Conclusions
The warm climate, high sediment supply, and high tidal range of the South Atlantic have combined to produce geologically resilient, biogeochemically dynamic, and biologically productive wetlands. Gaps in our scientific understanding include a paucity of research on lower-salinity tidal marshes and swamps (but see Conner, Doyle, et al. 2007), a weak but rapidly emerging understanding of microbial diversity, and a poor understanding of the ecology of top consumers. South Atlantic coastal wetlands are not pristine, but have been less affected by anthropogenic impacts and climate change than coastal marshes elsewhere in the U.S.; however, they are likely to deteriorate in coming decades as sea levels and human populations rise unless they are protected by proactive and strong management policies that regulate land use, freshwater delivery to the coast, eutrophication, and harvesting of top consumers.

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