HOT TOPICS IN MARINE BIOLOGY

Sea Star Catastrophe: Disease, Its Spread, and Its Diagnosis *continued* 16.1

What causes SSWD? This was initially a mystery, because no great abundance of bacteria or other organisms was visible using standard microscopy. But exposure of tissue homogenates of symptomatic sea stars homogenized and then filtered through a 0.22 μm filter resulted in the SSWD syndrome after about 10–17 days, whereas heat-treated controls resulted in no infection. These results demonstrated experimentally that nondiseased sea stars could be infected with virus-sized material. It is challenging to go to the next step. Next-generation sequencing of viral extracts of infected sea stars must be employed, along with complex metagenomic statistical techniques to assemble a viral genome. Assembly of metagenomes from the sequencing process resulted in the deduction of the sequence of a near-complete virus of the type densovirus, which was termed sea star-associated densovirus (SSaDV) (Hewson et al., 2015). This virus is in far greater concentrations in sea stars with SSWD than in normal healthy sea stars. The diagnosis is clear, but the dynamics of spread along the coast and the role of ocean warming still need to be determined. We can expect more such outbreaks in the future in many marine species and communities.

Spartina Salt Marshes

Ecosystem Engineers, Geographic Extent, and Setting

- ***Spartina*** **salt marshes are dominated by cordgrasses, which function as ecosystem engineers by binding fine sediment and causing the buildup of meadows above low water.**

Spartina salt marshes (**Figure 16.32**) develop in tidal areas of quiet water, where a variety of salt-tolerant grasses colonize the sediment and then trap fine sediment. A study of *Spartina* salt marshes on the Atlantic and Gulf coast of North America found a range of vertical sediment accretion rate of 0.09–1.78 cm per year (Turner et al., 2002). Characteristic of these grasses is an extensive **rhizome system** beneath the sediment surface, which takes up nutrients and is crucial in maintaining the structure of the marsh sediment and the entire salt marsh.

Spartina alterniflora, the dominant eastern and Gulf coast American species found lowest in the intertidal zone, must put up with long periods of immersion in saltwater, to which it is more tolerant than other grass species. The sediment pore water has little or no oxygen unless burrowing organisms aerate the sediment, and the root system of *S. alterniflora* connects to air by means of air pockets in the midcortex. Much of the leaf and stem section of the plant is highly vascularized. A cross section of the plant shows the large amount of open space near the surface, which is devoted to air and oxygen transport (**Figure 16.33**). Plants cannot use nutrients efficiently without oxygen, so this tissue allows a connection between the aerobic leaves and stems, which are surrounded usually by anoxic water.

Rhizomes extend laterally, and shoots grow above the sediment-water interface. Although these grasses develop flowers and set seed, the asexual spread of the rhizome system is usually the major form of local spread. Genetic analysis using enzymes demonstrates that marshes often

FIG. 16.32 The salt marsh at Herring Creek, near Harwich, on Cape Cod, Massachusetts. Tall form of *Spartina alterniflora* in foreground; short form behind. In the distance is the common reed *Phragmites australis* fringing the marsh. (Photograph by Jeffrey Levinton)

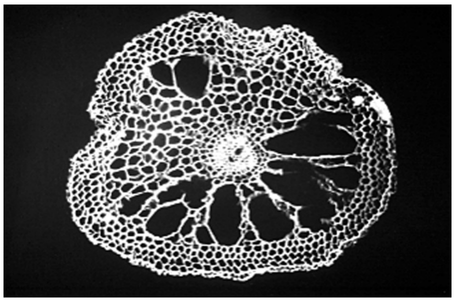

FIG. 16.33 The aerenchymal tissue allows *Spartina* to exchange gases, even when surrounded by an anoxic soil. The tissue in this photograph is visible as a series of circular passageways around the periphery. (Photograph courtesy of Mark Bertness)

consist of a few clones, or groups of genetically identical individuals, each of which has spread by asexual growth. The overall morphology of rhizome system and shoots creates a series of projections that form a baffle against water movement, which encourages sedimentation. The accumulation of sediments results in the formation of a meadow with a nearly horizontal surface. *Spartina* salt marshes are, therefore, an excellent example of the **ecosystem engineer** concept, in which one or a few species create a structural habitat on which many other species depend.

A single plant may colonize an open area of sediment (**Figure 16.34**), either by rafting or by setting of seed. After the clone has developed, the grass blades will develop a density sufficient to slow current speeds and accelerate the deposition of fine-grained sediment. This will gradually cause the development of a rising sediment surface. Thus, a salt marsh begins to spread and evolve into a meadow of sediment held together by dense grass stands. Eventually the sediment will be high in organic matter known as **peat**. Organic content varies a great deal and can range from 2 to 40 percent. Older marshes have thicker layers of peat. The meadow usually encloses a system of salt marsh **creeks**, which are often nursery grounds for juvenile crustaceans and fishes (**Figure 16.35**).

If there is no major change of local sea level, then the level of the sediment surface will rise, and the dominant plants will change gradually from low-intertidal grasses to terrestrial plants as more sediment accumulates and the surface of the sediment rises. Thus, a "mature" marsh has passed through the stages of (1) bare intertidal sediment, (2) early colonization of patches of grass, (3) extension of the grass patches and trapping of sediment, (4) gradual rise of the sediment surface and transformation into organic-rich peat, and (5) development of a higher marsh.

In North America, *Spartina* salt marshes are best developed on the east and Gulf coasts, and marshes of hundreds to thousands of acres can be found. *Spartina* marshes are also common in California, dominated by *S. foliosa*, and an American Atlantic species is an invasive element of the Pacific Northwest. Southern California salt marshes are spatially quite variable, perhaps because of the dry Mediterranean-type climate. *Spartina* marshes are also common in northern Europe. The most spectacular American marshes are found in the southeastern United States, especially in South Carolina, Georgia, and Gulf coast states. Salt marsh plants are salt tolerant, and *Spartina alterniflora* contains siliceous deposits, presumably to deter grazing by birds and mammals. The cellulose composition and the mechanically tough leaves seems to prevent much successful direct grazing. Usually much less than 10 percent of the leaf production is consumed by herbivores in the northeastern United States, but damage is greater farther south. The great majority decomposes and may support large populations of decomposing bacteria and fungi. Predation on flowers is often intense, and *Spartina* seed production is, therefore, often very limited.

FIG. 16.34 How it begins. Newly established seedlings of *Spartina alterniflora* on an open sand flat. (Photograph by Jeffrey Levinton)

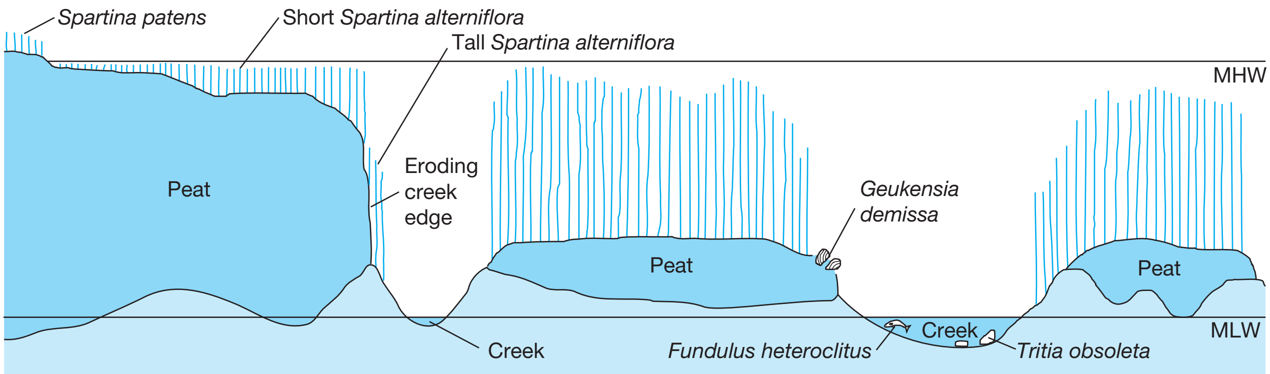

FIG. 16.35 Subhabitats of the *Spartina* salt marsh environment. A tall form of *Spartina alterniflora* is associated with the high nutrient supply of flowing creeks. (After Redfield, 1972)

Vegetational Zonation and Plant Interactions in Salt Marshes

- **Vegetational zones in salt marshes develop from the interaction of competition and physiological ability to survive salt and drowning.**

Moving from the low-water mark in a tidal creek to the terrestrial environment, one encounters a vertical zonation of vegetation, each zone dominated by a different grass species (**Figure 16.36**). In most east and Gulf coast North American marshes, zones occur in the following order, from low to high intertidal: tall form (1–1.5 m tall) of *Spartina alterniflora*, short form (< 0.5 m tall) of *S. alterniflora*, *Spartina patens*, *Juncus gerardi*, and terrestrial shrubs. The border between zones is often quite sharp and at a predictable tidal height. For example, the zone boundary between *S. alterniflora* and the higher-intertidal *S. patens*, approximately at spring high tide, is often used in legal disputes to define the marine–terrestrial border. Why are such zones present? Research by Mark Bertness (1991a) and colleagues showed that plants of the low marsh *Spartina alterniflora* grow well into the high marsh *S. patens* zone, if the latter species is absent. In other words, no physiological factor prevents *S. alterniflora* from invading upper levels. In its own zone, *Spartina patens* outcompetes *S. alterniflora*. If one transplants *S. patens* to within the typical *S. alterniflora* zone, however, the former does badly physiologically, owing to a relative intolerance to immersion in salty water and to drowning for more of the day at the lower-tide level. *Spartina patens* also lacks an efficient mechanism to survive in lower-intertidal anoxic sediments and, therefore, does badly within the lower-level *Spartina alterniflora* zone, where oxygen supply to roots is a major limiting factor. Successful dominance in a zone is

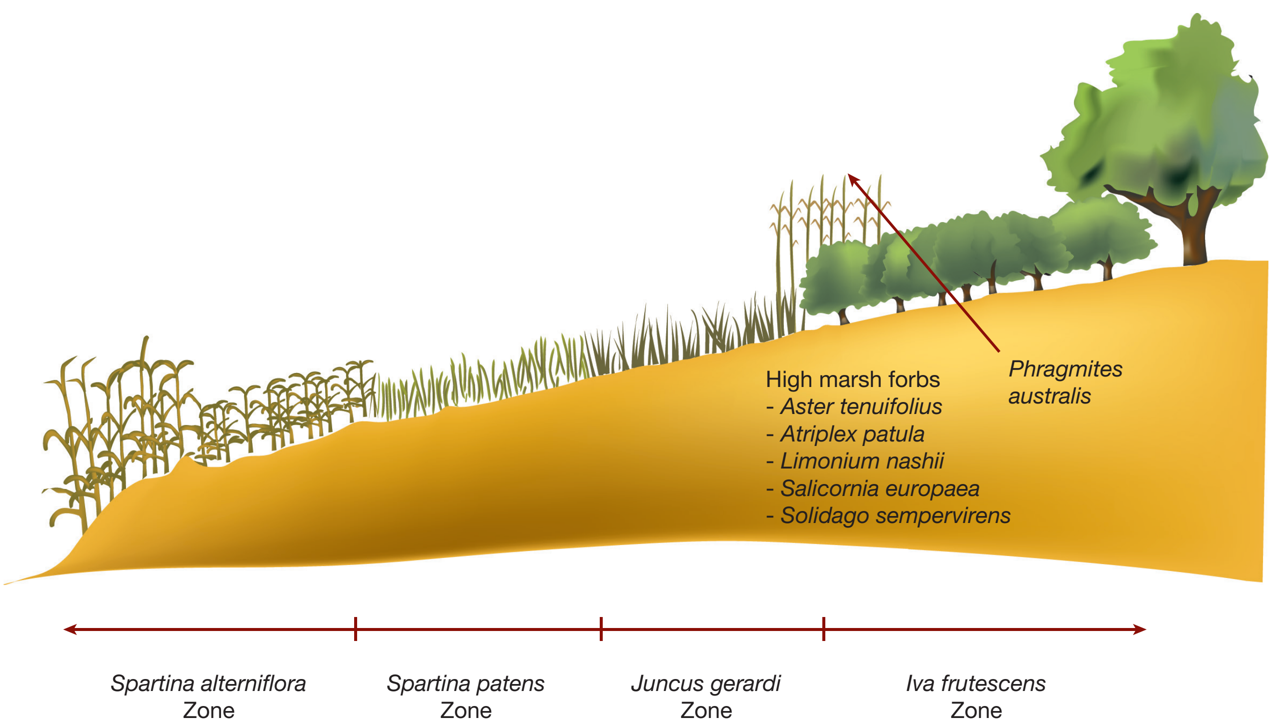

FIG. 16.36 Vegetational zonation in a southern New England salt marsh. (From Bertness et al., 2002, Copyright National Academy of Sciences, U.S.A.)

thus a combination of physiological tolerance and relative competitive ability. In the high marsh, *Juncus gerardi* outcompetes other grasses, although the grass *Distichlis spicata* is more capable of invading newly opened bare sediment patches that are often salty from evaporation. Ironically, *Distichlis* then shades the sediment, allows it to become moist and less saline, and thus facilitates the eventual invasion and predominance of *Juncus gerardi*.

Competition is therefore a major determinant of salt marsh plant dominance, but it works in reverse of dominance of invertebrate competition on rocky shores described earlier in this chapter. These are, after all, terrestrial plant species that are invading seawater. These plants tolerate salt, but the environment is more physiologically stressful as you go lower in the intertidal, because of lowered oxygen in the sediment, and high salt content of water and pore water. *Spartina alterniflora* predominates in the low zone partially because of its superior ability to survive these stresses. In higher zones, plants are good competitors because of the ability to produce a dense rhizome system, which outcompetes other species for space and nutrients.

In Florida salt marshes, *S. alterniflora* dominates the low marsh, and *S. patens* is found at higher levels that are inundated by seawater. However, large areas in this region at higher levels are often in lower-salinity water, and these areas are dominated by the black needle rush *Juncus romerianus*. Just a few centimeters of higher elevation allows the rhizome of this species to avoid exposure to salt, and this species dominates large patches. Still fresher-water expanses are dominated by the saw grass *Cladium jamaicense*, the dominant of expanses of Everglades marshes. Mangroves replace salt marsh as the dominant quiet saltwater shore habitat of southern Florida.

■ *Spartina*-dominated zones exert larger-spatial-scale impacts on adjacent ecosystems.

The presence of dense marsh growth exerts longer-distance influences on more distant ecosystems. We discuss below the potential for salt marsh systems to export nutrients, both dissolved and particulate, to nearby coastal systems, subsidizing shallow subtidal benthic systems and fueling coastal phytoplankton blooms. But the wave-buffering effect of dense *Spartina* grass growth also can influence inland, more terrestrial systems (van de Koppel and others, 2006). Without dense marsh grass, more terrestrial forbs and shrubs would be battered and drowned by salt water from wave action, and would succumb to physiological stress from salt water. But the absorption of wave shock by dense *Spartina* growth and peat development on cobble beaches of southern New England usually allows the landward development of a dense and more terrestrial plant forb community, consisting, for example, of sea lavender and glasswort.

■ Floating wrack often smothers plants and creates patches of bare sediment, which become salty and inhibit colonization for a time.

High-marsh zones often consist of acres of continuous tracts of one species of grass. Bare patches are common, however, and sometimes span several meters across. Considering the lushness of a salt marsh, the patches are surprising. Mats of cyanobacteria cover some, and others are nearly abiotic, with layers of salt on the surface. But piles of dead *Spartina* leaves, or wrack, may accumulate in marshes where there is a limited water exchange with the coastal zone. The high-marsh bare patches are often a remnant of floating rafts of decaying *Spartina* shoots, which are concentrated by currents and then float up to rest on top of grass in the high marsh. The grass is smothered, and a bare zone is created. Once the area has become bare, strong sunlight causes evaporation, which in turn greatly increases the salt content of the sediment pore waters, and sometimes a layer of salt develops on the surface. Mark Bertness (1991a, 1991b) demonstrated that the salty water prevents seed germination and the bare patch is self-sustaining. If a plant can colonize, the shading reduces evaporation immediately, and the saltiness of the water decreases. Many of the grasses can extend from the edge of the patch through vegetative growth, but a strong rain may reduce the salt content, and seeds may then be able to germinate. The patch will be eventually covered by vegetation. The rapidly colonizing grass *Distichlis spicata* is best able to colonize these patches.

■ Salt marsh assemblages may exert positive and negative effects as ecosystem engineers.

In the past few years, ecologists have come to think of **ecosystem engineers** (this term is often freely exchanged with foundation species, which is often associated with important primary producers in a community) as exerting a positive effect on the presence of a number of codependent species. *Spartina* species create a relatively quiet sedimentary environment, which may enhance the presence of species dependent on soft sediment. The tight association of grass shoots also is known to protect predators such as crabs from moving high into the marsh, which results in a refuge for a large number of salt marsh invertebrates.

Although an ecosystem engineer often creates an environment that is strongly altered, thereby favoring growth of the engineering species itself and many other associates, the local microhabitat might be no longer suitable for other groups of species. An excellent example of this is the occurrence of *Spartina* patches and patches of the lugworm *Arenicola marina* in Netherlands salt marsh habitats. The work of van Wesenbeeck and colleagues (2007) demonstrated that patches of the cordgrass *Spartina anglica* had sharp borders with patches of bare sediment, dominated by the lugworm *Arenicola marina*, an active deposit-feeding polychaete, which lives in U-shaped burrows. Modifications of the sediment by these two different dominants causes mutually negative effects, resulting in occurrence of one or the other "engineer." The lugworms burrow in the sediment, which was shown experimentally to destabilize the sediment and increase mortality of planted *Spartina* seedlings. *Arenicola* worms, on the other hand, could not burrow effectively in the sediment dominated by *Spartina*, which was dense with rhizome material.

Salt Marsh Creeks and Mudflats

- **Salt marsh systems include creeks and mudflats, which are often biologically diverse and abundant and are corridors between salt marshes and other habitats for many marine fish species.**

As mentioned earlier, salt marsh habitats are usually a series of broad *Spartina* meadows, alternating with salt marsh creeks (**Figure 16.35**). At a creek edge, a marsh may be at a standstill, eroding, or accreting in size. As the grass stands trap sediment, the marsh can grow over bare sediment and into a creek. Several species are often found in the high-intertidal zone, often at the creek edge. The marsh mussel *Geukensia demissa* lives semi-infaunally in the sediment and apparently aids marsh accretion by trapping sediment (**Figure 16.37**). It also enhances grass growth through the addition of organic-rich fecal material on the sediment surface. Fiddler crabs (genus *Uca*) burrow in the upper-intertidal zone and also are found on creek edges in marshes. The burrowing apparently enhances the growth of *Spartina*, perhaps by aerating the sediment. Normally, marsh sediment is anoxic, which inhibits the growth of fungi associated with plant roots, known as **mycorhizae**, which greatly increase the gathering of nutrients from the sediment. Crab burrowing helps aerate the sediment, which in turn increases mycorhizal growth.

The creeks themselves often have strong tidal flow, with bottoms of well-sorted sand or fine mud, depending on the degree of current strength. Marsh creeks often have dense soft-sediment faunas, including polychaete annelids and mollusks. In tidal creeks of northeastern North America, the mud snail *Tritia obsoleta* occurs in densities of hundreds per square meter. In the southeastern United States marshes, the marsh periwinkle *Littorina irrorata* feeds on the muddy surface, but climbs grass blades at high tide to avoid incoming predators. Many species of smaller crabs and shrimp are also abundant, especially the mud crab *Rhithropanopeus harrisii*. Smaller fish, such as killifish (species of *Fundulus*) and silversides (*Menidia menidia*), are also common and may attract predatory bluefish into the creeks. A variety of wading birds such as black-crowned night herons (**Figure 16.38**) and snowy egrets are also common. These birds stalk mobile forms such as crabs and shrimp. Diving birds such as terns and kingfishers also frequent the creeks, where they dive for smaller fish. Predators—including killifish, blue crabs, and other fish—are abundant in the creeks. Blue crabs move into the marsh grass to feed but cannot usually penetrate any farther than the tall form of *Spartina* adjacent to the creek.

The high density of prey invertebrates and protected waters makes tidal creeks ideal habitats for many species of fishes. Salt marsh creeks are usually regarded as nursery areas for juveniles of many fish species, but fish using marsh creeks are usually also found in associated coastal water habitats such as larger estuarine basins. The abundant predators on soft-sediment infauna create the potential for a trophic cascade. In the previous section on the soft-sediment intertidal, we discussed some of the dynamics of benthic invertebrate populations on mudflats, which are often associated with salt marshes. These include polychaetes, oligochaetes, deposit-feeding snails, and meiofauna, which are abundant in salt marsh flats of the east coast, Gulf coast, and in marsh flats in California. Many of these deposit feeders feed on microalgae, which creates a common food chain of microalgae → mudflat deposit feeders → fish–crab carnivores. Experiments on nutrient enrichment of salt marshes in New England suggest that this chain may not be tightly linked (Deegan et al., 2007). On the other hand, we mentioned earlier a very tight linkage between green seaweed input and invertebrate abundance.

Eastern American mudflats are dominated by polychaetes, oligochaetes, and bivalves and are strongly affected by inputs of particulate organic matter, especially from seaweeds. California salt marsh soft-sediment environments are less biologically diverse and dominated by oligochaetes (Levin et al., 1998; Levin and Talley, 2002). Spatial

FIG. 16.37 Population of the semi-infaunal marsh mussel *Geukensia demissa,* among *Spartina alterniflora*. (Photograph by Jeffrey Levinton)

FIG. 16.38 The black-crowned night heron *Nycticorax nycticorax*, a major predator of fish in salt marsh creeks. (Photo by Jeffrey Levinton)

variation of density and species occurrence is quite high. This difference in diversity from New England might be related to the very dry Mediterranean climate of the region. California salt marshes are highly impacted by human dredging and filling, and some active restoration projects are in process.

Spartina Marshes as Sources of Organic Matter

- ***Spartina* salt marshes produce large amounts of particulate and dissolved organic matter, which may influence the food webs of salt marsh benthos and perhaps the food webs of coastal marine systems.**

In the late fall, leaves of the dominant lower-intertidal *Spartina alterniflora* senesce, turn a lovely yellow brown, and eventually sever from the main plant. Large amounts of floating material enter the marsh system, although the material is relatively concentrated in indigestible cellulose and takes some time to be decomposed by physical fragmentation, tearing apart and ingestion by detritivores, and bacterial decomposition. This material is probably a source of nutrition for a large fraction of the deposit feeders in marsh soft sediments. Minimally, the *Spartina* fragments are substrates for bacteria and fungi, which are consumed by mussels, deposit-feeding polychaetes, and gastropods. However, these animals can also inefficiently digest particulate organic matter and probably derive some of their nutrition from the *Spartina* detritus itself. Experiments show that additions of such particulate matter can stimulate somatic and population growth of salt marsh oligochaetes.

A minority of the *Spartina* production is consumed by herbivores in New England salt marshes, and little of the high-marsh and not all of the mid-marsh grass is consumed in the southeastern United States (but see later discussion for effects of a common snail). The salt marsh ecologist John Teal showed that in Georgia salt marshes, herbivores appeared to consume a minority of the plant production, the majority of which entered into the detritus food chain (**Figure 16.39**). Many believed that the large amount of detrital material floated from salt marsh creeks into coastal continental shelf waters and was a major source of nutrition both for zooplankton and benthos of the continental shelf. This was known as the **outwelling hypothesis**. Further studies, however, showed that salt marsh plant detritus does not significantly contribute to coastal shelf secondary production but is mostly retained within marsh creeks or right near shore (see Chapter 12).

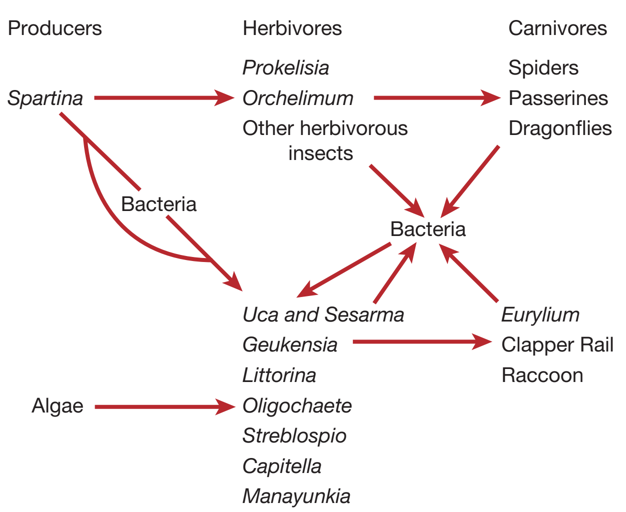

FIG. 16.39 The food web of a Georgia salt marsh. (After Teal, 1962)

Although we have few studies to bolster this idea, it appears that export of particulate organic matter may be slight but the export of dissolved nitrogen sources may be considerable in some cases. Dissolved nitrogen may be produced during decomposition, diffused from sediment pore water into the water column, and then transported away by moving waters. A study of the enclosed marsh–creek system in Sippewissett marsh on Cape Cod, Massachusetts, shows that considerable amounts of dissolved nitrogen are exported to the adjacent Buzzards Bay, which has the potential to fuel a considerable amount of the primary productivity by phytoplankton (Valiela and Teal, 1979). But large net export was not found on the north shore of Long Island, New York (Woodwell et al., 1979).

Spartina Marshes as Trophic Cascades

- ***Spartina* marshes in the southeastern United States appear to be controlled by top-down effects in a trophic cascade.**

The previous section portrays salt marshes as a source of food, which drives local and regional coastal ecosystems. But salt marshes have generally been envisioned as food-rich environments where direct grazing on *Spartina* was unimportant.

This concept of salt marsh structure has been stood on its head mainly by the creative work of Brian Silliman and colleagues. It was long known that carnivores were very important in southeastern salt marshes. Blue crabs attacked and sometimes consumed the marsh periwinkle *Littoraria irrorata*. But what ecological effect did the periwinkle have? Silliman noticed that snails appeared to be associated with wounds in *Spartina* plants, and these wounds were filled with fungi (see Figure 13.3). The scraping of the snail's radular teeth damaged the *Spartina* plants, which were attacked by fungi. Manipulative experiments (Silliman and Zieman, 2001) demonstrated that *Spartina* growth was strongly inhibited by the presence of the snails. The snails may not have been feeding directly on the plants but they were causing major damage by causing fungi to invade *Spartina* leaves, which damaged them extensively. Silliman, therefore, identified a major trophic cascade in low marshes of the Southeast: *Spartina* → snails → blue crabs (**Figure 16.40**).

The identification of this cascade has produced two very interesting interactions. First, the snails appear to have a facultative mutualism with the fungi. By damaging blades of *Spartina* grass, they facilitate fungal colonization, and the fungi is food for the snails. This is not as stable a relationship as other animal–fungi relationships, such as in leaf cutter ants, because the *Spartina* grass leaves soon die and are inhospitable for the snails. By contrast, leaf cutter ants

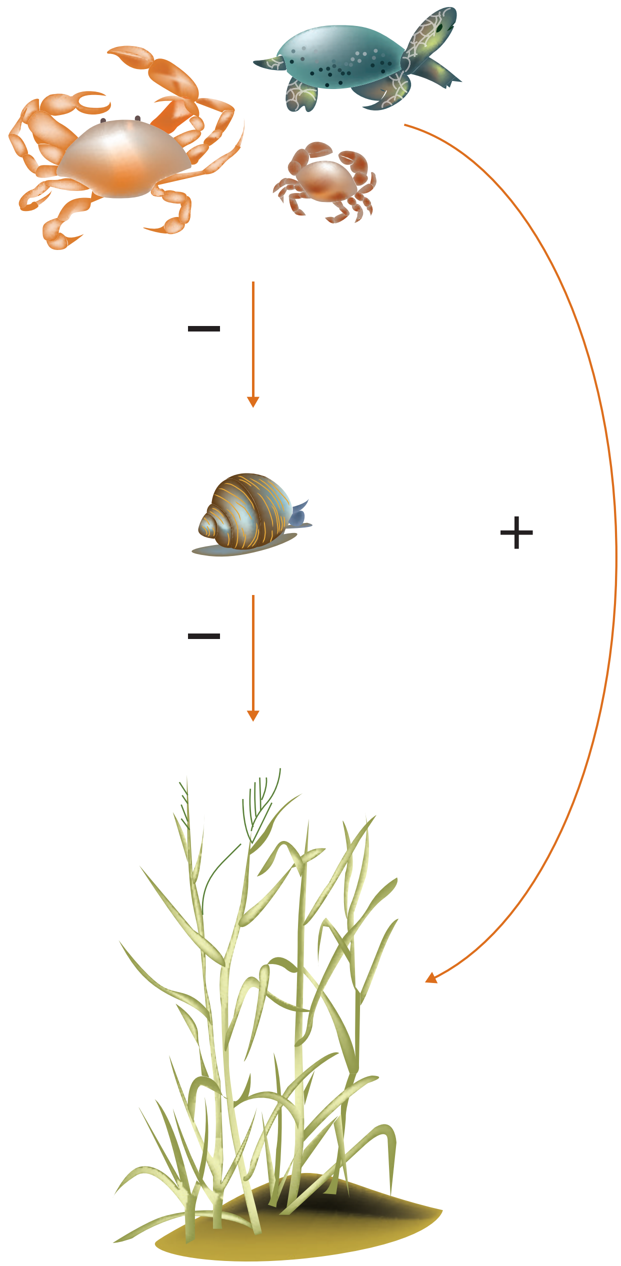

FIG. 16.40 A trophic cascade in salt marshes. Predators of the fungivorous snail *Littoraria irrorata* facilitate growth of *Spartina* because the snail strongly damages marsh plants. (From Silliman and Bertness, 2002, Copyright National Academy of Sciences, U.S.A.)

bring food (in the form of leaves) to a subterranean home for fungi.

Second, the trophic cascade has an important implication for fisheries management and conservation. Blue crabs have been exploited by commercial fishers down to very low numbers, and in the years since 2000, disease has strongly affected blue crabs in the southeastern United States. Predation on *L. irrorata* has, therefore, been depressed and may be contributing to increased mortality of low-marsh *Spartina alterniflora* populations in the Southeast in the past few years. Droughts have been very severe in the southeastern United States since about 2000 (e.g., 2006–2007, 2012), and a lack of moisture and heat stress have likely been the major contributors to this die-off. Negative effects by *L. irrorata*, however, are adding to the dieback of low-marsh plants (Silliman et al., 2005).

■ **Grazing on salt marshes of the eastern United States probably increases in intensity toward the south, as evidenced by presence of grazing species.**

Grazing by herbivores on *Spartina* plants in northern salt marshes of the northeastern United States appears to be at a low level. In contrast, grazing in the southeast is more frequent, for example, from grasshoppers. Damage from snails is absent in the Northeast but severe in the Southeast. Like many grasses, *Spartina* and other salt marsh grasses have a number of defenses against predation. *Spartina alterniflora* has phenolic acids, mainly cinammic acid esters of glucose, which are stored in cell vacuoles. Other phenolic compounds are bound to the cell walls. Lignin is also associated with the cell walls and helps to deter digestion by grazers. Silica is also used to deter grazing. Steven Pennings and Brian Silliman (2005) found that lower-latitude *Spartina* leaves are less palatable than higher-latitude leaves. This may be an evolutionary response to the increased grazing pressure in more southerly areas.

Invasion of Salt Marsh Species

■ ***Spartina* species have been introduced, accidentally and purposefully, and have greatly modified shoreline environments throughout the world.**

Spartina species have been introduced in many parts of the world and, like the brooms in the story of the sorcerer's apprentice, have spread rapidly by vegetative growth while altering greatly the nature of shoreline habitats.

The English introduction is particularly fascinating (Thompson, 1991). *Spartina alterniflora* was introduced accidentally and hybridized with the English native *S. maritima*, which produced a form known as *Spartina townsendii*, which was believed to be sterile. Somehow, a chromosome doubling in this form produced the perfectly fertile *Spartina anglica*, which spread rapidly throughout the protected coastal regions of Great Britain. This new form displaced the native marsh species in many locations. It is exceptionally efficient at spreading by rhizomes. The spread of marshes resulted in the reduction of usable habitats for some birds and spawning fishes.

The supposedly sterile *Spartina townsendii* was imported to many localities around the world for shoreline stabilization, creation of duck habitat, and so on, and somehow the reproducing *Spartina anglica* was brought along, or arose independently in many localities. Now, *Spartina anglica* and other *Spartina* species are being regarded as a scourge in the Pacific from New Zealand to Washington State, where they are spreading rapidly to protected shores along the west coast of the United States. Its major means of spread appears to be by floating seeds.

The Atlantic *Spartina alterniflora* was introduced into the state of Washington probably as packing material for oysters in the 1890s, but was not noticed growing locally until the 1940s. In Willapa Bay, Washington, *Spartina* *alterniflora* is now displacing all viable oyster grounds and intertidal mudflat spawning sites for fishes, and may be creating habitat unsuitable for the local migrating birds. The marshes, spread mainly by rhizome extension, are also displacing eelgrass beds, which are believed to be important feeding and nursery grounds for commercially important fishes. Invasive *Spartina* marshes are being controlled by herbicides.

Filling, Erosion, Nutrient Addition, and Sea-Level Rise

Dredging and filling have destroyed many salt marshes.

Salt marshes have been vulnerable to shoreline development and in many areas of the United States have been mostly filled in or dredged away. In Palm Beach County, Florida, over half of the salt marshes were removed by development. Manhattan island's coastline was largely salt marsh before 1800, and today's shoreline is less than 5 percent salt marsh. Over 75 percent of southern California marshes have been removed, and many areas have no salt marsh left. Southeastern and Gulf coast salt marshes are quite large and remain the largest areas of salt meadow coverage in North America. Salt marshes have been very important in the development of the concept of **ecosystem services**: the monetary and sociological valuing of ecosystems for human needs, both economic and recreational.

Eugene and Howard T. Odum first pointed out the possible value of salt marshes as a food source for coastal fisheries, but this has been strongly questioned. Still, the approach of placing a value on the service of salt marsh ecosystems was extremely important. Salt marshes are known to be key nursery grounds for fish and shellfish, protectors against erosion, and also of obvious aesthetic importance. Salt marshes also can absorb nutrients to a degree, and especially can process much nitrogen by denitrification. Owing to the efforts of the Odum brothers, legislation protecting salt marshes was initiated in the 1950s, and many states now have rigorous protection of salt marshes from dredging and filling. Numerous attempts have been made at restoring salt marshes, with varying success.

Nutrient addition and near-shore development has caused measurable effects on salt marshes and associated fauna.

Salt marshes are commonly in areas occupied by human populations and therefore are vulnerable to nutrient additions from sewage pipes and groundwater. To some degree, salt marshes can absorb nutrients, especially nitrogen. **Denitrifying bacteria**, common in anoxic marsh sediments, can convert a great deal of human-derived nutrients into nitrogen gas. Because of this, salt marshes have been used to some extent as sinks for sewage, as opposed to dumping sewage directly into open bays and coastal waters.

Although marshes do have the capacity to absorb nutrients, some effects have been discovered that suggest direct impacts on salt marsh communities. Bertness and colleagues (2002) found that Rhode Island salt marshes show an increase of the extent of the low-marsh species *Spartina alterniflora* in areas where shoreline development is greater. The upper limit of *S. alterniflora* increased, which may effectively squeeze out higher-marsh species and therefore decrease biodiversity. The spread of the common reed *Phragmites australis* in the high marsh is displacing other salt marsh plant species, which further threatens marsh plant biodiversity. *Phragmites* tends to occur in lower-salinity areas in New England, but in recent decades it has displaced stands of both freshwater and saltwater marsh dominant plants. This dominance is apparently the result of an invasion of a surprisingly competitive genotype (Saltonstall, 2002) that appeared in the United States in the early twentieth century. It spread from Europe or Asia and could be identified by a distinct molecular marker in herbarium specimens in U.S. museums, collected after 1910, but not before.

Coastal eutrophication may be a major cause of reduction of salt marshes throughout eastern North America. Retreat of the lower extent of the *Spartina alterniflora* zone is a major feature of salt marshes, leaving bare sediment or bare peat. Nutrient addition tends to cause *S. alterniflora* to devote more resources to shoots rather than the sediment-stabilizing rhizome system. As a result, moving water tends to rip out shoots and poorly developed root systems, resulting in the loss of *S. alterniflora* beds. The effectiveness of this hypothesized mechanism was supported by an experiment done on a Massachusetts salt marsh, involving additions of nitrogen to marshes along tidal creeks, done in comparison with control creeks that were not subjected to nutrient addition (Deegan et al., 2012). Creeks with nutrient addition showed strong retreat of *S. alterniflora* stands from the creek edges, whereas no effect was observed in the control areas. Nutrient-enriched creeks had sediment with higher-porewater content and increased slumping of sediment into the channels. After several years, more energy was devoted to shoots relative to rhizome, and more cracks in the sediment surface accumulated in the marsh creeks with experimental nutrient addition. Human nutrient additions therefore help to undermine the physical structure that stabilizes salt marsh sediments. Some *S. alterniflora* marshes have retreated because of grazing by herbivorous crabs (Schultz et al., 2016).

Salt marshes are very sensitive to sea-level fluctuations and may be affected by sea-level rise derived from anthropogenic global climate change.

Spartina salt marsh zonation is very closely tied to sea-level conditions. On the scale of thousands of years, salt marshes have had to keep pace with a rise in sea level for about 11,000 years since the end of worldwide continental glaciation. Fossilized accumulations of salt marsh peat have been used in combination with ^{14}C dating to show that the coastline of Connecticut submerged about 10 m in the past 7,000 years. Salt marshes have probably changed their areal extent substantially in response to fluctuations of sea-level rise and local basin shape. There is some concern that global warming of the past century will accelerate sea-level rise and perhaps cause damage to salt marshes by accelerating erosion or by drowning of salt-sensitive, high-marsh species. Erosion might increase because raised sea level would expose marshes to more frequent waves and current energy. Sea-level rise might also interact with the tolerance of different salt marsh species to submergence and high salinity. Initially, accelerated sea-level rise might increase the relative abundance of the salt-tolerant, low-marsh *Spartina alterniflora* and reduce biodiversity in marshes. This would combine with the effect of increased nutrient supply, which also tends to increase the dominance of *Spartina alterniflora*.

Hartig and colleagues (2002) studied the Jamaica Bay, New York, salt marshes and found a loss of about 12 percent in the period 1959–2000. Current marsh plant growth was typical of healthy marshes through the region. Nevertheless, small marsh islands were disappearing, and the fringes of marshes showed evidence of sediment slumping. Since the 1930s, sea-level rise has averaged about 0.2 cm y^{-1} in the New York region (this reflects a global rise), and projections of sea-level rise with global warming models suggest that marshes may not be able to keep pace with sea-level rise. Damage already done has included erosion, slumping, and dissection and fragmentation of marsh islands.

The growth and retreat of salt marshes may also be strongly affected by human land use patterns. After Europeans colonized the northeastern United States, much of southern New England's forests were cleared for agriculture. This resulted in erosion of agricultural lands providing sediment that could be bound up in salt marsh sediments. Forest clearing likely also increased the supply of dissolved nutrients to salt marshes from cleared fields and agricultural lands. Thus, salt marsh growth may have been stimulated by land clearing. In recent decades, however, agriculture in New England has declined and forests have returned, which may have choked off sediment supply. This may be a major factor in a widespread retreat of salt marshes that has been noticed in the Middle Atlantic states and New England (Kirwan et al., 2011). An overabundance of nutrient supply from human sources may have caused destabilization of marshes discussed above.

Mangrove Forests

- **Mangrove forests are intertidal and emergent plant communities dominated by trees, which are rooted in marine soft sediment.**

Mangrove forests (also called **mangels**) are tropical and subtropical in distribution, and over 80 mangrove species can be found in Australia, the Americas, Asia, and Africa. Dominance, however, is usually confined to fewer than five species that occur in zones. Mangrove growth in lower latitudes is continuous, and mangrove trees tend to grow taller there than mangrove trees in higher-latitude mangrove forests. Mangroves have abundant and diverse marine and terrestrial animal life. Large numbers of falling leaves provide a continual localized source of detrital material.

Mangrove forests are found along quiet-water tropical and subtropical marine coasts in water temperatures greater than 20°C, but no less than 16°C in the coldest month (**Figure 16.41**). They range in size from enormous tracts of forest, mudflats, and creeks covering an order of 10^2–10^3 km^2 to tiny cays in shallow seas such as the Caribbean. They are dominated by shrub- or treelike mangroves, which are rooted in anoxic muddy sediment that is waterlogged with seawater. Once established, they greatly decrease wave energy of the shorelines on which they live. Waterlogging is a major physiological problem for mangroves, especially because the sediment pore water is often anoxic. Mangrove belowground tissue is, therefore, subjected to long periods of exposure to anaerobic conditions, which slows nutrient uptake and allows the accumulation of toxins such as hydrogen sulfide, methane, carbon dioxide, and reducing metals.

FIG. 16.41 Mangroves along a tidal creek in Palmar, Ecuador. (Photograph by Windsor Aguirre)

Exposure to decomposing bacteria is also a problem, which may explain the high tannin concentrations in mangrove tissues that function to protect against bacterial invasion. Mangrove species have evolved independently from ancestors in a number of plant evolutionary groups, but are united in their tolerance of waterlogging and salinity stress.

Mangroves are adapted to the anoxic sediments by air-projecting and shallow roots.

Mangroves are usually broadly rooted but only to a shallow depth. This may be a response aimed at avoiding exposure to deeper-lying anoxic sediments. Above the water level, mangroves are in many ways typical terrestrial shrubs, with trunks, stems, leaves, and flowers. Their root system, however, is adapted to the anoxic sediment, and all mangrove species have root extensions that project into the air so that the underground parts of the plant root system can obtain oxygen.

The variety of root morphologies maintained by a single tree allows differentiation of function. Mangroves can have prop roots, structures that extend midway from the trunk and arch downward for support; roots that direct upward into the air (knee roots or larger pneumatophores, depending on the species); and finer roots for gathering nutrients (**Figure 16.42**). Oxygen is gathered and directed into the highly chambered upward-directing roots, which transport oxygen to belowground tissues. This assures aerobic metabolism of the plants within the anaerobic environment of the sediment. The formation of pneumatophores in the genus *Avicennia* is induced by anoxia in the sediment.

Mangroves are salt tolerant.

Mangroves live at the edge of the marine environment, and the roots penetrate into a surface sediment layer that is of high salt content, known as the **vadose layer**. The salinity of the vadose pore waters is usually less than full-strength seawater because of rainfalls. Mangroves are quite salt tolerant. They have a variety of mechanisms for excluding salt. One group of species has **salt glands** that secrete salt from the leaves (**Figure 16.43**). In the morning it is common to see small dots of moisture where the salty drops have been excreted. One often sees leaves covered with salt crystals after a few hours in the sun. In another group of mangrove species, roots are capable of reducing salt uptake to a degree by an ultrafiltration system. A membrane-bound ion channel that can exchange H^+ for Na^+ accomplishes this. Species using ultrafiltration also store Na^+ in vacuoles. Because the mangrove circulatory system fluids contain less salt than in the sediment pore waters, there is always an osmotic gradient to maintain. This is quite costly, energetically speaking.

Mangrove species show vertical zonation, which is strongly affected by seedling dispersal and invertebrate predation on seedlings.

Mangrove forests can be divided into a series of zones, with different tree species dominating with increasing distance from the shoreline. Landward of the mangrove forest one tends to find typical terrestrial trees, which differ depending on location. Although subtropical forests may have only one mangrove tree species, many tropical forests have several dominants, which are usually zoned in abundance with increasing distance from the shoreline. In southern Florida and in the Caribbean, the red mangrove *Rhizophora mangle* dominates the seaward part of mangrove forests and is the first species to colonize an unvegetated shoreline. It has prop roots, which extend into the water, and tolerates full-strength seawater and tidal inundation. The black mangrove *Avicennia mangle* lives shoreward of red mangroves and tolerates only occasional seawater inundation, usually at highest high tides. Landward may be

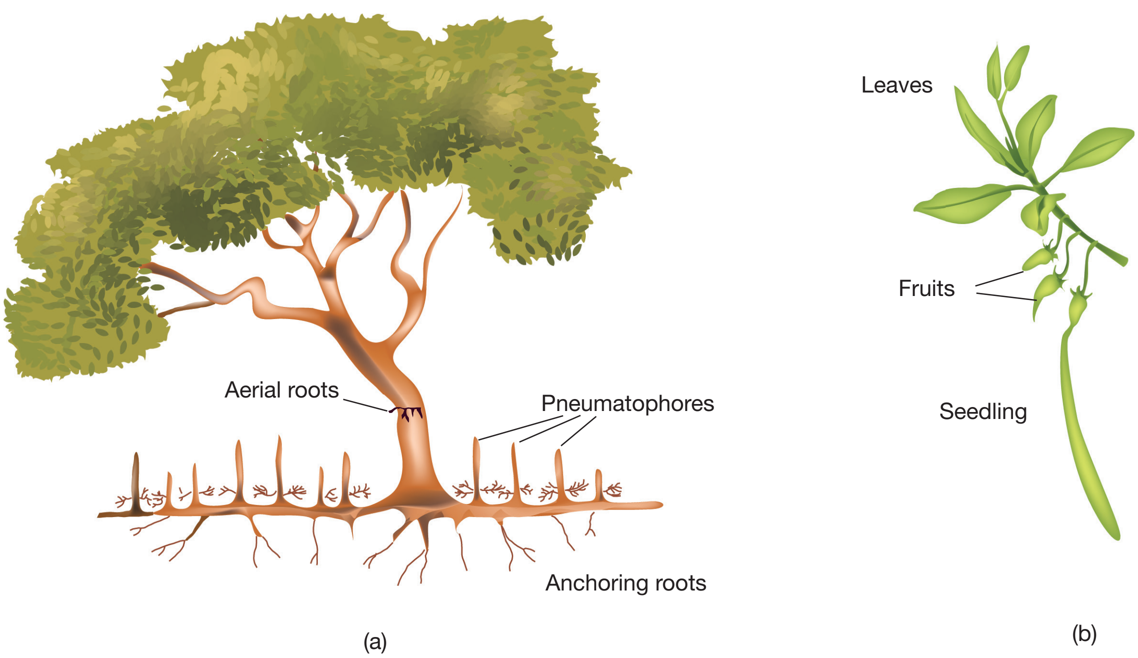

FIG. 16.42 (a) A typical mangrove tree, showing the root systems. (b) Fruits and seedling. (b after Tomlinson, 1986)

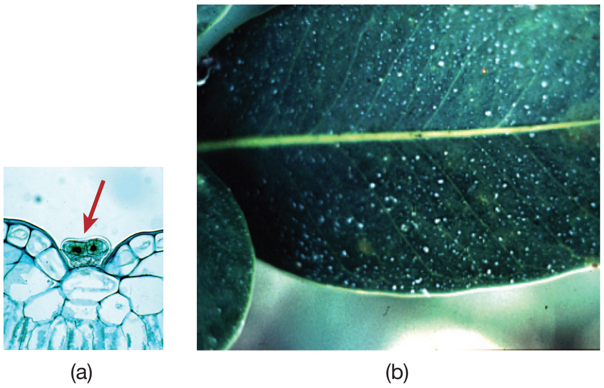

FIG. 16.43 (a) A vertical section through a mangrove leaf, showing the salt gland (arrow). (Photograph by Peter Saenger) (b) A mangrove leaf with numerous excreted salt crystals. (Photograph by Robert Twilley)

found the white mangrove, *Laguncularia racemosa*, which is rarely inundated by seawater.

Red mangrove seeds germinate while still attached to the parent plant. Seedlings develop and dangle from the parent until they either drop into the mud, like darts, or float away in the water (**Figure 16.42b**). Those that float away are finally carried by winds to another muddy shore, where they root in the sediment. A seedling coat is shed, giving the seedling negative buoyancy, which causes it to drop to the bottom. Survival of seedlings is strongly affected by predation due to grapsid crabs, which may cause total mortality of newly recruited mangrove propagules. The extent of predation may determine the species composition of individual mangrove forests. Ellison and Farnsworth (1993) found that crab predation of seedlings was especially high under existing mangrove forest canopies. Seedlings in areas where canopy was removed experimentally had faster growth rates and leaf production rates and apparently passed a threshold where crab predation did not occur. Seedlings of the red mangrove *Rhizophora mangle* tend to invest more heavily in roots and stems; this may explain its ability to rapidly colonize open, well-lit environments at the shoreline. This strategy tends to minimize crab predation and suggests that **top-down control** is important in mangrove communities in explaining species distributions. The black mangrove is far less successful in resisting predation.

Mangroves and upland vegetation compete for space, which is probably determined from differences in salt tolerance and local precipitation and evaporation in the vadose layer.

Mangroves are in competition with more terrestrial vegetation. The spatial transition between mangroves and upland coastal hardwood hammocks is often abrupt and complex. Hammocks may generally be landward of mangroves, but hardwood hammocks may also consist of a series of islands, slightly topographically higher than surrounding vegetation. Hammock species in Florida consist of species intolerant of salinity. While this would exclude them physiologically from saline soils, mangrove trees grow quite well in upland habitats with fresh water in soils. Therefore, mangroves must be excluded from these habitats by competition with upland hammock species. Sternberg and colleagues (2007) have argued that the border resulting from competition between mangroves and hammocks is unstable and based on transpiration, which is the removal of water from the soil, transport through the tree's circulatory system, and transport to the atmosphere through leaves. They argue that saline water inhibits transpiration of hardwood hammock species, which live better in fresh water. A drought or more tidal inundation tips the advantage toward mangroves, which transpire well and thus bring very saline water from deep in the soil into the vadose layer. But a modest increase in salinity within the upland hammock species tends to reduce transpiration in hardwood hammock species, which also reduces movement of saline water into the vadose layer and allows the hammock species to persist. This process maintains the two species types as separately occurring groups with a sharp boundary between them (**Figure 16.44**).

Mangrove sediments have abundant and diverse invertebrate populations, and particulate organic matter is important in the economy of mangrove communities.

The prop roots of mangroves that extend into open sea water usually support a diverse invertebrate and seaweed community. The flat tree oyster *Isognomon alatus* attaches to the roots (**Figure 16.45**), as do a variety of crabs, shrimp, and barnacles. A number of species also live on the trunks

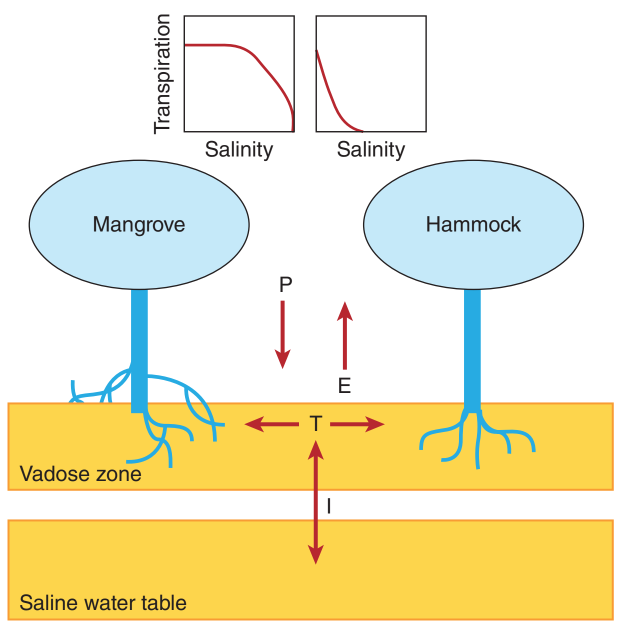

FIG. 16.44 Water uptake and transpiration in mangroves and upland hardwood hammock trees. The vadose soil layer usually has lower-salinity water and overlies a body of saline ocean water. Transpiration of mangroves is less sensitive to salinity. P = precipitation; E = evaporation; T = water uptake and transpiration; I = infiltration between the vadose layer and the layer below. (From Sternberg et al., 2007)

FIG. 16.45 Wood tree oysters attached to Caribbean mangrove roots. (Photograph by Robert Twilley)

and leaves, including barnacles and snails. A number of crab species move cyclically between the trees and mudflats, where they feed at low tide when predators are absent. The Caribbean tree crab *Aratus pisonii* is often an abundant mangrove leaf herbivore, but is only a sporadic defoliator. Unlike other marine habitats, mangrove forests are also terrestrial habitats, and southwestern Pacific mangrove forests may have large populations of herbivorous insects, monkeys, and bats.

Detritus feeders dominate the roots and sediments in the seaward part of the mangrove forest. In the inner part of the forest, mudflats are rarely inundated, and many of the dominant species live in air for extended periods of time. The mudskipper *Periophthalmus* is a small Indo-Pacific fish with excellent eyesight, capable of slithering on the surface of the intertidal mudflat and even climbing low branches. Fiddler crabs in these habitats release larvae during the rare times of tidal inundation. The soft-sediment fauna often contains crustacean species capable of deposit feeding and scavenging. This includes a number of large crabs that are exploited commercially throughout the tropics. This abundance is probably related to frequent leaf falls, which enhance the supply of particulate organic matter into the ecosystem. Stable isotopes demonstrate that a large amount of this leaf matter is consumed and used by benthic mangrove mudflat animals. Dissolved nutrients, such as N and P, appear to be retained within mangrove systems, so there is no strong export to coastal systems.

- **Mangrove shallow waters and creeks are important nursery grounds for fisheries.**

We mentioned earlier that salt marsh tidal creeks are important habitats for juvenile and adult fishes, but that most species move in and out of creeks and use other habitats as well. This is likely true for mangroves, but some species clearly spend important parts of their lifetime wholly within mangrove creek systems (**Figure 16.46**). The Goliath grouper, *Epinephelus itajara*, spends as much of its first 5 years within Florida mangrove creeks and emigrates to more open water at about 1 m body length (Koenig et al., 2007). Food of common mangrove species can be related to mangrove fishes through a tracer such as ^{13}C, a stable isotope of carbon. Abundances of this isotope can be related to a standard, and deviations from the standard can be studied in fishes and compared with potential food items. For example, a study in Tanzania by Lugendo and colleagues (2007) demonstrated that the isotopic signature of mangrove fish generally resembled that of invertebrates living in mangrove creeks. Mangroves are believed to be extremely important in sustaining coastal fisheries in the tropics.

- **Mangrove forests are very endangered throughout the tropics because of shoreline development and the dredging of mangroves for the use of shrimp farms.**

Like most coastal vegetation, mangroves have been removed to make way for human habitation. Over half of the world's mangrove habitat has been eliminated. The largest loss of mangroves, however, has been for the establishment of shrimp farms. Mangrove trees have been removed on a large scale, and have been dug out and converted into basins for shrimp farms (**Figure 16.47**). Besides the loss of mangrove habitat and loss of feeding areas for migratory birds, this activity also causes the loss of invertebrate food for fishes, subsurface salinization of otherwise fresh waters, and loading of organic matter causing anoxia. Mangrove deforestation is contributing strongly to a decline in coastal fisheries, which has been documented in Thailand, a major location of shrimp farms (Barbier and Strand, 1998). It is also a major problem in the Americas. Owing to crowded conditions, disease is a major source of shrimp mortality, and farmers respond by using high concentrations of antibiotics. These, too, are being released to freshwater canals and coastal waters.

- **Sea-level rise from global warming is a great threat to mangroves but particularly upland hammocks, which are salt intolerant.**

Global warming is a major potential source of sea-level rise, owing to thermal expansion of seawater and melting of glacial ice. As sea level rises, the frequency of incursions of seawater in coastal storms increases. This is especially a problem in the Gulf of Mexico, where hurricanes are frequent and the tidal range is very small. On the west coast of Florida, negative effects of saline water are greatest in areas with more frequent seawater flooding events. A combination of flooding, causing hypoxia, salt stress, and incursions of salt-tolerant plants has strong negative effects on salt-intolerant species such as *Sabal palmetto*, which is common throughout the Gulf of Mexico. Such plants lose their ability to regenerate and then may die several years later. This is especially worrisome because such upland hammock species are important in protecting coastlines from flood damage from hurricanes. A drought in 2000–2005 has caused major declines in cabbage palm and southern red cedar, and it is likely that sea-level rise is exacerbating the losses (Desantis et al., 2007).

Estuaries

Estuaries are environments where oceanic seawater mixes with freshwater input from a discrete source, such as a river. Because of this, estuarine biology is intimately connected

FIG. 16.46 Mangroves line the intertidal zone of tropical tidal creeks, as shown here along Estero Pargo in Terminos Lagoon, Mexico. (Photograph by Robert Twilley)

FIG. 16.47 Aerial photo showing patches of mangrove forest and excavated shrimp farms in Palmar, Ecuador. (Photograph by Windsor Aguirre)

with the **watershed**, or the surrounding land that provides water input to the estuary. Estuaries vary greatly in size, from small tidal creeks fed by rivers with watersheds that are only a few square kilometers to the relatively enormous Chesapeake Bay estuary, whose watershed is about 180,000 km^2. The interface of the watershed with the main course of the estuary provides an opportunity for the entry of nutrients, pollutants, and other substances through tributaries and general flow down slopes into the estuary.

Much of our habitat coverage above applies as coverage of subhabitats of estuaries, depending on their location. Therefore, much of our coverage here is an overview of overall estuary properties.

■ Review: Estuarine structure is controlled by seaward flow of fresh water combined with tidal mixing.

The input of fresh water through rivers causes an overall **estuarine flow**, sending lower-density water at the surface toward the ocean. There is a compensating deeper upriver flow of higher-salinity oceanic water beneath the buoyant surface flow. When the flow is strong and the tidal mixing is small (see Figure 2.27), estuaries are **highly stratified**, with a distinct low-salinity layer flowing toward the sea, and a compensating movement of higher salinity below, upriver from the ocean. From the air, one can readily see the movement of low-salinity surface water from the Mississippi

River into the Gulf of Mexico. Most estuaries are **partially mixed** from tidal action and wind. There is a stretch near the opening of the estuary where mixing occurs, but still the salinity in this zone is always lower at the surface than at depth. In very small and shallow estuaries, wind tends to fully mix the water to the bottom, creating a **vertically homogeneous** estuary.

- **Estuaries range from open marine to a range of successively decreasing salinity zones, to tidal fresh water and associated creeks and marshes, to fresh water.**

Figure 16.48 shows a series of salinity ranges and associated salinity-related habitats. The topography of the watershed, the slope and size of the river(s) feeding into the main part of the estuary, the size of the main estuary channel, and tidal flow all contribute to determining the salinity structure. The Hudson River estuary has a discrete main stem, with relatively small tributaries entering throughout its length. The slope of the main part of the Hudson River is low, and a large part of its upriver length is tidal but fresh water. By contrast, the Chesapeake Bay estuary consists of five major river systems that feed into a central estuary (see Figure 2.26). Overall, **river discharge** is also a major influence on salinity transitions, and spring increases in river flow move fresh water farther down the estuary. The main part of the estuary is strongly affected by wind and tidal action, but the rivers entering the main part of the estuary are quite variable and may not exchange as strongly with the main estuary in summer because of low river discharge, low tidal flow, and narrow openings into the main part of the estuary. In the main part of the estuary, low flow in summer combined with nutrient addition may result in sluggish circulation and low oxygen concentrations. Strong rains have very strong effects on salinity structure, and hurricanes often dump large amounts of fresh water on an estuary, causing a general decrease in salinity throughout the estuary. Storms also may cause powerful episodes of erosion and seaward sediment transport.

- **Estuaries are geologically ephemeral but abundant in nutrient supply and biological production.**

Because rather small changes of sea level can completely fill or empty out an estuarine basin, estuaries are geologically impermanent features of the coastline. As sea level rises, the sea may flood river valleys; but such basins will also empty as sea level drops, such as during a worldwide increase in glaciers, which lock up the water of the ocean as ice. It is believed that the specific form of an estuary will rarely exist for more than 10,000 years or so. On the other hand, rivers are surprisingly ancient, and therefore some type of estuary may exist for far longer periods.

Despite the ephemeral nature of estuaries, they are among the biologically richest habitats in the world. Supplies of nutrients from freshwater sources and recycling of nutrients from the seabed as in denitrification combine to

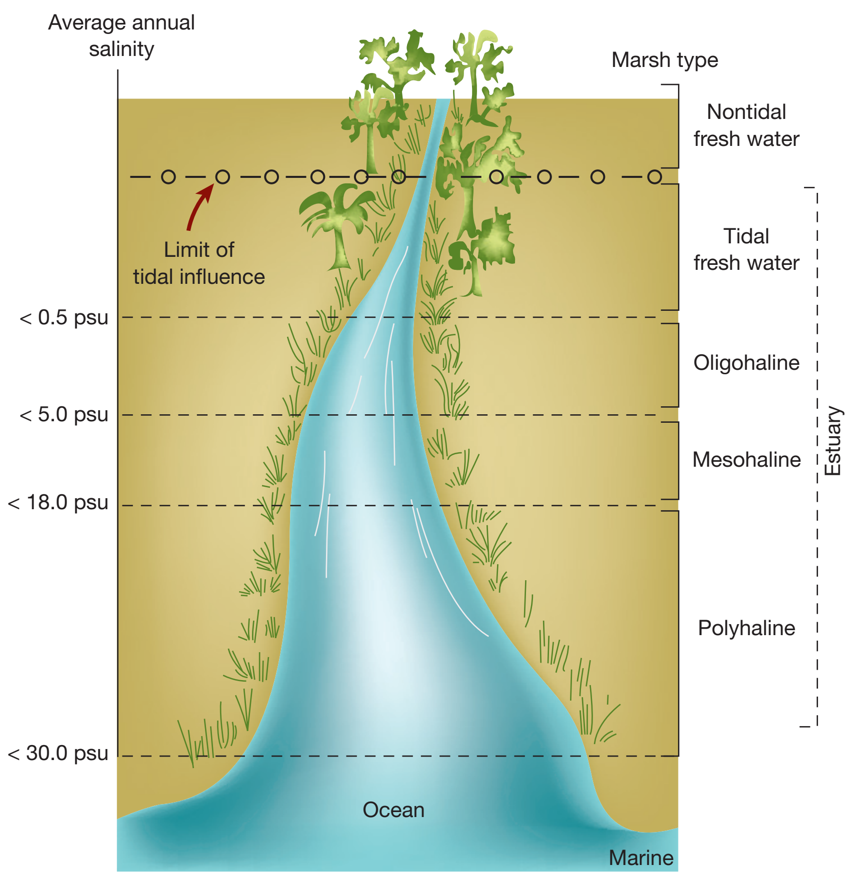

FIG. 16.48 Salinity zones in an estuary.

support high levels of primary production, which in turn supports large numbers of estuarine benthic invertebrates, fishes, plants, and birds. In eastern North America, estuaries such as the Hudson River and Chesapeake Bay support major fisheries, which have been strongly impacted by habitat destruction, overfishing, and high nutrient inputs. The Chesapeake Bay system had enormous oyster beds (they are now depleted owing to overfishing and disease) and populations of blue crabs (also overfished). The Hudson River has seasonally large populations of fishes such as shad and striped bass. The bottom is alive with annelids, mollusks, crustaceans, and insect larvae (in the freshwater parts of the estuary).

■ The decreased salinity at the headwaters of estuaries can reduce the number of marine species.

The most noticeable gradient in an estuary is that of decreasing salinity as one goes upstream. Marine species, as discussed in Chapter 5, generally can tolerate fluctuations in salinity, but their tolerance is often exceeded when salinity falls below 10–15 psu. Some major invertebrate groups, such as echinoderms (sea urchins, sea stars), tend to drop off in estuaries, due to a general incapacity to evolve resistance to lowered salinity. Others, such as crustaceans, are capable of good regulation in the face of osmotic stress and are often quite abundant in estuaries. In estuaries with some degree of vertical density stratification, the salinity is greater on the bottom than at the surface, where freshwater flow moves lower-salinity water downstream (see Chapter 2). As a result, marine bottom species can often penetrate an estuary farther upstream than surface planktonic organisms can. Infaunal species experience less salinity variation than do epifaunal species over a tidal cycle in a very-well-mixed estuary because of the buffering effect caused by sediment pore waters that exchange water slowly with the overlying water column (**Figure 16.49**).

The second major estuarine salinity transition is the critical salinity range of 3–8 psu. Many marine groups apparently find it hard to survive in this salinity range, even though many more species are capable of living either in fully fresh water or in waters of higher salinity. Along the estuarine gradient, species numbers are at a pronounced minimum in the critical salinity range (**Figure 16.50**). Mollusks may be incapable of cell volume regulation at salinities this low. Freshwater species, however, can regulate ionic concentrations and maintain a hyperosmotic state. They have lost the ability to regulate cell volume, however, and therefore cannot penetrate even the low salinities of the critical salinity range. The critical salinity is thus a no-man's land, hospitable to neither marine nor freshwater species.

Although salinity change is often a critical factor in limiting the range of marine species, many are capable of rapid regulation and adjustment to the changing osmotic stress of varying salinity. Many fish species are capable of extensive regulation of tissue fluids (see Chapter 5) and can swim across strong salinity gradients. Striped bass, salmon, and killifish are just a few examples of fishes that migrate from completely saline water to fresh water in a few weeks or even days. Some crab species are also quite adaptable to changing salinity and perform migrations over nearly the same range of salinity traveled by fishes. In the Hudson River, males of the blue crab *Callinectes sapidus* can migrate from full-strength seawater in the lower New York Bay to fresh water in the upper reaches of the estuary.

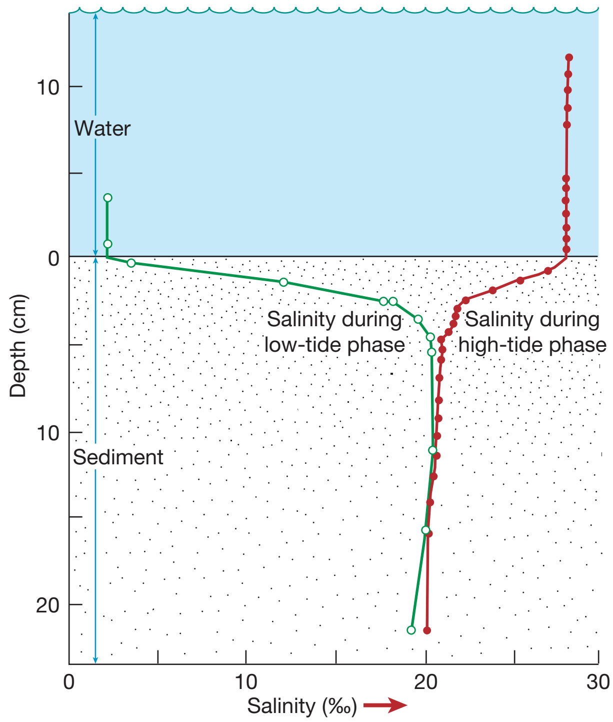

FIG. 16.49 Salinity variation in the water column and within the sediment in the small tidal Pocasset River estuary, Massachusetts. Note that the salinity varies a great deal in the water column, owing to tidal motion and freshwater flow. Within the sediment, however, the salinity is relatively constant and intermediate in value. (After Sanders et al., 1965)

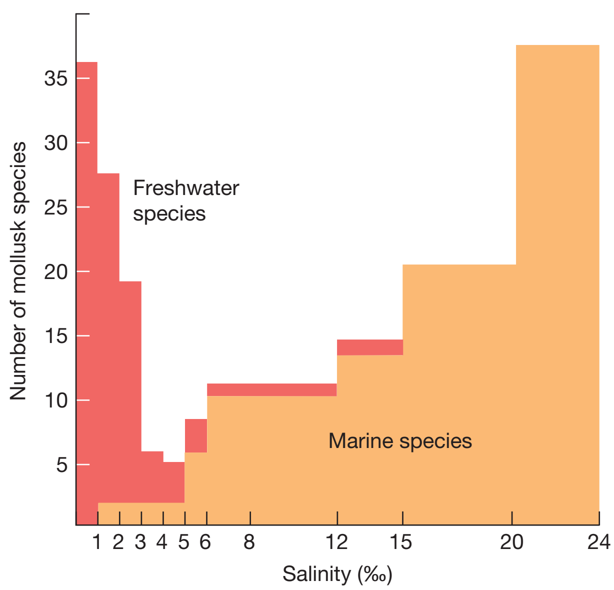

FIG. 16.50 Species richness along the estuarine gradient of the Randersfjord, Denmark. (After Remane and Schlieper, 1971)

Overall, estuaries and shelf environments comprise a two-phase system that corresponds to life-history stages of many fish and invertebrate species.

While many species, especially tidal freshwater groups, complete their entire life cycle within the estuary, a large number of species live a two-phase existence in the estuary and on the continental shelf. Clearly, differences between estuary and shelf must be driving this division, and the benefits of maintaining a two-phase life cycle must be able to counteract the cost of migrating between estuary and shelf and the likely loss of individuals, such as larvae, which fail to find their way back to the estuary. The estuary may serve as a spawning ground, nursery for juvenile fishes, or even the location of adult life, as in the case of *Anguilla* eels. The shelf may be a source of habitat and planktonic food for larvae of estuarine adults (as in blue crabs and fiddler crabs), or the location of adult feeding grounds (as in many anadromous fish species).

Changing ecological conditions within an estuary might cause strong alterations in behavior. These are most easily accomplished by nekton, which could relocate to areas with better conditions. For example, estuarine fish populations might fluctuate strongly; and there is good evidence for density-dependent effects, in which fishes grow and reproduce more poorly at high local densities (Craig et al., 2007). We would expect such species to move to more favorable habitats, reducing local densities. Changes in the structure of food webs might also stimulate such relocations. For example, invasive bivalves have reached high densities in some estuaries and have greatly reduced phytoplankton abundance (see later discussion on invasive species in estuaries). In San Francisco Bay, the invasion of the Asiatic clam *Corbula* (*Potamocorbula*) *amurensis* had such an effect, but there was a surprisingly small effect on planktivorous fishes, as might be expected from a competition-based expectation for limited food. Wim Kimmerer (2006) found that the northern anchovy *Engraulis mordax* simply moved to the higher-salinity parts of the estuary, where the Asiatic clam did not invade and had little effect on phytoplankton abundance.

Some estuarine species are adapted to counteract the estuarine flow to the sea, in order to be retained within the estuary; others are broadcasted onto the shelf and return to estuaries at the time of metamorphosis, making the estuary a two-phase system in coordination with the continental shelf.

Estuarine flow is usually seaward in the low-salinity waters at the surface. This net flow is known as **buoyant flow** and is especially strong in spring, following rains and snow melt in watersheds in higher latitudes, known as the **freshet**. Small estuaries with extensive tidal flushing cannot support large nurseries of juvenile fishes, and retention adaptations probably would be insufficient to counteract the tidal exchange with the open sea. Larger estuaries with longer flushing times and vertical density stratification can support fisheries because of the reduced loss of larvae to sea. Within large estuarine systems, such as Chesapeake Bay, tributaries like the St. Mary's River have relatively low tidal exchange rates with the rest of the estuary. The reduced exchange tends to trap larvae and may be the reason for heavy larval sets of the oyster *Crassostrea virginica*. To counteract the estuarine flow that does exist, estuarine fish and invertebrate larvae have been observed to keep to the bottom during the ebbing tide, swimming actively at the surface with the incoming tide (see Figure 7.27). Menhaden are more easily netted during flood tides, indicating their adaptations for retention within the estuarine system. The mud crab *Rhithropanopeus harrisii* is found in greater abundance upstream as the larval life period progresses. As mentioned in Chapter 7, some species export larvae to adjacent coastal waters and depend on a variety of tidal and wind sources to enable them to reinvade the estuary. Estuaries are, therefore, for many species part of an interactive two-phase system, in coordination with the continental shelf (**Table 16.2**).

A number of other species live and mate within the estuary, but larvae move in the buoyant flow toward the shelf. Good examples are the blue crab *Callinectes sapidus* (discussed in Chapter 7) and species of fiddler crabs. As mentioned, the problem for these species is to return to the estuaries, which is aided in the case of blue crabs near Delaware Bay by seasonal changes in regional wind systems. When blue crab megalopae (last larval stage, competent for settlement and metamorphosis) enter the estuary, they are adapted to swim upward on the flood and go toward the bottom on the ebb tide, in order to assure entry into the estuary. Glass eel larvae of the American eel also take advantage of flood tidal streams to enter the estuary and move upstream after they move toward the inner shelf waters.

Estuarine suspension feeders may control phytoplankton of shallow parts of large estuaries or in entire well-mixed estuaries; tidal exchange may be a driving force for suspension feeder food in smaller estuaries.

Estuaries in temperate latitudes commonly have large populations of suspension feeders, particularly bivalve mollusks such as oysters, mussels, and burrowing clams. In small estuaries with strong tidal exchange, most phytoplankton supplied to these bivalve populations come

TABLE 16.2 Examples of How Life Cycles Fit Spatially into the Two-Phase Estuary-Shelf System

BIOLOGICAL SYSTEM	ESTUARY	SHELF
Crabs type 1 (fiddler crab, blue crab)	Adults: feeding, spawning	Larvae: feeding
Invertebrates type 2 (mud crab)	Adults and larvae	None on shelf
Anadromous fish (striped bass, shad)	Larvae and early juveniles: spawning	Adults: feeding

from the adjacent ocean. The **retention time** is the average number of days that a phytoplankton cell stays in such a small estuary before it is washed out to the adjacent shelf. This value can be compared with the turnover time, which is the number of days it takes for a population of bivalves to completely filter a water column. If the turnover time is less than the retention time, then it is possible for the bivalves to completely filter the water column. For example, if the turnover time is 10 days and the retention time is 60 days, the water column will have been filtered 6 times before an average phytoplankton cell has the chance to be mixed back with the adjacent ocean.

When the estuaries are relatively well mixed by wind and tide, bivalves may have access to the entire water column, develop large populations, and greatly depress phytoplankton densities. This has been observed in two cases where invasive suspension bivalve species have appeared. The Asiatic clam *Corbula amurensis* has had a strong effect on the low-salinity phytoplankton in the very shallow San Francisco Bay. The zebra mussel *Dreissena polymorpha* invaded the tidal freshwater part of the Hudson River estuary in the late 1980s and has had a major impact on phytoplankton populations. In years of high mussel population density, well over 90 percent of the potential phytoplankton biomass is removed. If the estuary is very stratified, bivalves on the bottom may not have access to all of the phytoplankton and may not completely deplete the phytoplankton from the estuary. Also, bivalves may not be active during earlier and cooler parts of the spring when phytoplankton blooms may occur.

- **A combination of historical high nutrient inputs and removal of predators has created great ecological instability from a combination of bottom-up and top-down processes.**

Estuaries are ecologically and economically valuable and have been densely settled by human populations. Owing to human influence (see Chapter 22), estuaries have had major additions of nitrogen and phosphorus. This has greatly stimulated primary production of phytoplankton, which may greatly decrease water clarity. Much of the phytoplankton is not consumed by zooplankton or benthic suspension feeders and is broken down by bacteria, which reduces oxygen concentrations. This has had two main effects on estuarine environments. First, submerged aquatic vegetation (often called SAV), an important structural habitat in estuarine habitats, is strongly affected by low light conditions caused by the shading of concentrated phytoplankton. While eutrophication increases nutrients, which might stimulate eelgrass plant growth, the effect is more than compensated by the negative effect of strong growth of competing seaweeds, stimulation of epiphytes that grow on and intercept light from eelgrass, and the increase of phytoplankton in the water, which intercept light (Short et al., 1995). We have discussed the capacity of salt marshes to absorb nutrients and to recycle N to the atmosphere by means of denitrification. Estuaries exposed to nutrient enrichment today have a reduced means of nitrogen absorption, and **the growth of phytoplankton and epiphytes impedes eelgrass growth**. In the western part of Long Island Sound estuary, there is virtually no eelgrass left, which correlates strongly with high nutrient inputs. Eelgrass populations are still relatively abundant in the eastern third of Long Island Sound. Nutrient loading into Waquoit Bay on Cape Cod has been studied extensively, and declines of eelgrass can be related directly to increases of housing and nutrient loads (Short and Burdick, 1996). Eelgrass declines in Chesapeake Bay may be greater than the losses seen during the major eelgrass epidemic in the 1930s (Orth and Moore, 1983).

Phytoplankton in the water column that is not grazed can die and sink as **phytodetritus** to the bottom. The nature of phytodetritus can be tracked by analysis of photosynthetic pigments, which help to identify the phytoplankton types that are sinking. In the Baltic Sea, the bulk of the surface production sinks, with a successive dominance of diatoms, dinoflagellates, and cyanobacteria, from spring to late summer. Large deposits of phytodetritus results in colonization of benthic surface-feeding deposit feeders, but past a threshold, phytodetritus will overwhelm the bottom, resulting in bacterial decomposition and anoxia at the sediment surface. Such conditions can be found in late spring and summer in Chesapeake Bay, in western Long Island Sound, and in the Baltic Sea.

Along with bottom-up effects, overfishing has caused the loss of many top predators, causing trophic cascade effects from the other end of the food chain. Many top carnivores have been exterminated due to overfishing, in the same way that any possibility of top-down control by oysters and other suspension feeders has been eliminated. The oligohaline Lake Pontchartrain has lost over 96 percent of its apex predators, alligator gar and bull shark, since the early 1950s. We might not be surprised that this has initiated a trophic cascade effect through the estuarine food chain. The decline of apex predatory sharks in southeastern U.S. waters has been implicated in the increase of their prey, the rays. Cow-nosed rays have increased greatly in North Carolina estuarine waters, and these have caused large-scale mortality of their molluscan prey, especially the bay scallop *Argopecten irradians* (Myers et al., 2007). With the disappearance of scallops, the rays are digging out infaunal clams, thereby destroying more scallop sea grass habitat. In the southeastern United States, blue crabs have been severely overfished and have been recently decimated by a combination of drought and disease caused by the parasitic dinoflagellate *Hermatodinium perezi*, which proliferates in the crab's hemolymph. Drought in the Southeast since about 2000 has increased salinities in estuaries, which has in turn increased the exposure of estuarine blue crabs to the parasite. Food web effects of this decline are not well understood.

- **Large estuaries are targets for biological invasions and occasional strong ecological alteration, although the rate of invasion is quite variable.**

Large estuaries experience large environmental changes. Interannual changes in the entire watershed are likely to result in strong changes in rainfall or snowfall, and this will influence the salinity structure, temperature structure, and nutrient input of estuaries. As a result, organisms in estuaries are the targets of enormous physiological changes. A major storm may change the salinity from mesohaline to freshwater for days. Large estuaries are commonly major locations of human habitation, and therefore are strongly disturbed by pollution and shoreline habitat alteration. Of course, large estuaries are also major ports and hence targets for the introduction of alien marine species.

The combination of habitat instability, biological change, and continuous introductions of alien species makes estuaries likely hotspots for biological invasions of aquatic organisms. Human activities continuously sever the natural barriers to dispersal across large oceans. In the nineteenth century, most ballast in ships was solid material, which facilitated invasions of terrestrial plants. In the latter half of the twentieth century and beyond, the increase of ship speed combined with the use of water for ballast has exacerbated the rate of introduction of species from afar, especially because larvae and microorganisms can survive in the ballast water. Many sessile organisms arrive attached to ships' hulls. But the increased rate of introduction does not guarantee success. Introductions may fail for several reasons:

1. *No suitable habitat.* Many introduced species cannot survive the target environment because of inappropriate temperature, salinity, or substrate needs.
2. *Shipping practices.* Ships that bring species that can survive in the target region may dock in the wrong place. In Chesapeake Bay, many ships dock in salinities far too low for survival of the marine species found in ballast tanks or attached to hulls.
3. *Too small an invasive population.* The invasive population may be too small to survive random changes encountered and various challenges, such as finding appropriate larval settling sites and reproducing successfully into the next generation.
4. *Inappropriate dispersal strategy.* Invasives that survive a first generation may have a dispersal stage that precludes survival into successive generations. Planktonic larvae increase dispersal distance, but the lack of appropriate adaptations to the local hydrographic conditions might result in washout to sea or to inappropriate sites. Lack of dispersal might result in local extinction.

Despite the impediments to successful establishment, estuaries have been invaded extensively. Over 200 species have invaded San Francisco Bay, which is the most affected estuarine system in the United States (Cohen and Carlton, 1998). Its biota is completely dominated by invasive species, ranging from salt marsh domination by east coast *Spartina* cordgrass to benthic domination by the Asiatic clam *Corbula amurensis*. A 200-year record shows that San Francisco Bay invasions began to accelerate at the beginning of the twentieth century and far exceed that of other water body systems that have been studied (**Figure 16.51**).

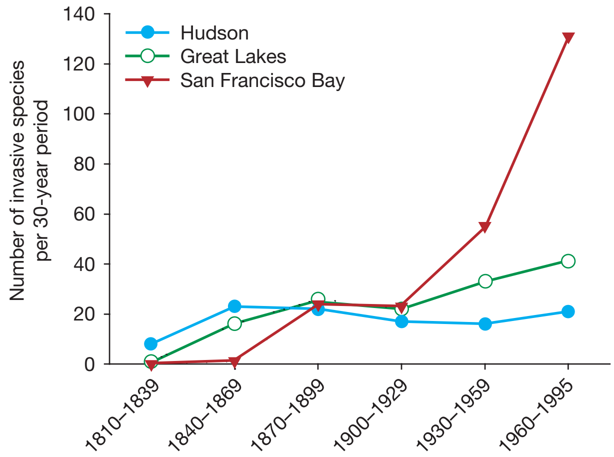

FIG. 16.51 Pattern of invasion of the Great Lakes, freshwater tidal Hudson River, and San Francisco Bay since the early nineteenth century. (From Strayer, 2006)

The ecological consequences of successful invasions are quite variable. The Hudson River tidal freshwater estuary has been invaded by over 100 species, many of which have had no strong ecological effect. The vulnerability of estuaries to ecologically significant invasions might result from three important factors:

1. *Frequent environmental overturn.* Environmental disturbances in estuaries commonly result in large-scale overturns. The timing of such overturns might increase the vulnerability of estuaries to invasion by ecologically important aliens.
2. *Ecological vacancies.* Estuaries have relatively low diversity, and some habitats may be open, remaining to be occupied. The successful invasion of the zebra mussel *Dreissena polymorpha* in the tidal freshwater Hudson might have been encouraged by the lack of common sessile suspension feeders that could attach to shallow subtidal hard bottoms.
3. *Competitive superiors.* Some invasives may simply be competitively superior to natives. The mud snail *Tritia obsoleta* successfully invaded San Francisco Bay and forced the native mud snail species into small high-intertidal refuges where the invader could not occupy.

It is likely that a number of newly appeared pathogens and toxic algae in estuaries are alien species, but we often cannot exclude the possibility that they were simply rare formerly and increased because of a recent environmental change.

Oyster Reefs

■ **Oyster reefs occur in estuarine environments throughout the world.**

Oyster reefs, especially on the east and Gulf coasts of the United States, are intimately connected with estuaries, but once were found abundantly in estuaries and along open coasts and estuaries on both coasts of North America and