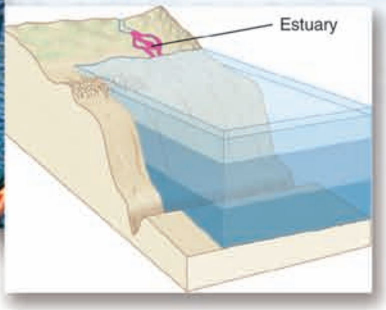
Salt marsh and mudflat.

CHAPTER 12

Estuaries: Where Rivers Meet the Sea



A unique environment develops where fresh water from rivers enters the sea. **Estuaries** are semi-enclosed areas where fresh water and seawater meet and mix. They therefore represent a close interaction between land and sea. Estuaries are typically inhabited by fewer species than rocky shores. Nevertheless, they are among the most productive environments on earth.

Estuaries also rank among the environments most affected by humans (see "Human Impact on Estuarine Communities," p. 281). Most natural harbors are estuaries, and many of the world's great cities—New York, London, and Tokyo among others—developed along them. And this was just the beginning.

ORIGINS AND TYPES OF ESTUARIES

Estuaries are scattered along the shores of all the oceans and vary widely in origin, type, and size. They may be called lagoons, sloughs, or even bays, but all share the mixing of fresh water with the sea in a partially enclosed section of the coast. Some oceanographers go as far as classifying enclosed seas with restricted circulation, such as the Baltic and Black seas, as estuaries.

Estuaries are partially enclosed coastal regions where fresh water from rivers meets and mixes with seawater.

Many estuaries were formed when sea level rose because of the melting of ice at the end of the last ice age, about 18,000 years ago. The sea invaded lowlands and river mouths in the process. These estuaries are called **drowned river valleys** or **coastal plain estuaries.** They are the most common type of estuary. Examples are Chesapeake Bay and the mouth of the Delaware River on the east coast of the United States (Fig. 12.1). Other examples are the mouth of the St. Lawrence River in eastern Canada and the mouth of the River Thames in England.

A second type of estuary is the **bar-built estuary.** Here the accumulation of sediments along the coast builds up **sand bars** and **barrier islands** (see "Sand on the Run, or What to Do with Our Shrinking Beaches," p. 418) that act as a wall between the ocean and fresh water from rivers. Bar-built estuaries are found, for instance, along the Texas coast of the Gulf of Mexico, the section of the North Carolina coast protected by the Outer Banks and Hatteras barrier islands (Fig. 12.1), and along the North Sea coast of the Netherlands and Germany.

FIGURE 12.1 Two types of estuaries are found along the eastern coast of the United States. Chesapeake Bay and the mouth of the Delaware River are drowned river valley estuaries; the Cape Hatteras islands form a bar-built estuary.

Other estuaries, such as San Francisco Bay in California, were created not because sea level rose but because the land sank, or **subsided,** as the result of movements of the crust. These are known as **tectonic estuaries.**

Another type of estuary was created when retreating glaciers cut deep, often spectacular, valleys along the coast. The valleys were partially submerged when sea level rose, and rivers now flow into them. These estuaries, or **fjords,** are common in southeastern Alaska, British Columbia, Norway, southwestern Chile, and the South Island of New Zealand (Fig. 12.2).

Estuaries can be classified into four basic groups based on their origins: drowned river valleys, bar-built, tectonic, and glacier-carved estuaries, or fjords.

Broad, well-developed estuaries are particularly common in regions with flat coastal plains and wide continental shelves, a feature typical of **passive margins.** This is the case along the Atlantic coast of North America. The opposite is true for the steep coasts and narrow continental shelves of the Pacific coast of North America and other **active margins.** Here narrow river mouths carved along the steep coast have restricted the formation of estuaries.

FIGURE 12.2 Milford Sound, on the southwestern coast of New Zealand's South Island, is a fjord. It is a finger-like inlet surrounded by sheer walls that rise 1,200 m (3,900 ft) above sea level and plunge to depths of 500 m (1,640 ft). Its entrance is only 55 m (180 ft) deep. As in other fjords, the shallow entrance restricts the exchange of water between the fjord and the open sea, resulting in stagnant, oxygen-depleted, deep water.

PHYSICAL CHARACTERISTICS OF ESTUARIES

Influenced by the tides and the mixing of fresh and salt water, estuaries have a unique combination of physical and chemical characteristics. These factors govern the lives of the organisms that live there.

Salinity

The salinity of estuaries fluctuates dramatically both from place to place and from time to time. When seawater, averaging about 35‰ salinity, mixes with fresh water (nearly 0‰) the mixture has a salinity somewhere in between. The more fresh water that is mixed in, the lower the salinity. Salinity therefore decreases as one moves upstream (Fig. 12.3).

Salinity also varies with depth in the estuary. The salty seawater is more dense and stays on the bottom (see "Salinity, Temperature, and Density," p. 45). It flows in along the bottom in what is frequently known as a **salt wedge.** Meanwhile, the fresher, less dense water from the river flows out on the surface.

The salt wedge moves back and forth with the daily rhythm of the tides (Fig. 12.4). It moves up the estuary on the rising tide, then recedes as the tide falls. This means that organisms that stay in one place are faced with dramatic fluctuations in salinity. They are submerged under the salt wedge at high tide and under low-salinity water at low tide. If the area has a **diurnal tide,** the organisms are subjected to two shifts in salinity every day: one as the tide moves upstream and a second as it retreats. In an estuary with **semidiurnal tides,** salinity changes four times a day.

Estuaries are subject to wide fluctuations in salinity.

The behavior of water masses in estuaries is not always this simple. The shape of the estuary and its bottom, the wind, evaporation of water from the surface, and changes in the tide all influence the distribution of salinity. Also of importance are seasonal variations in freshwater runoff from rivers as a result of rainfall patterns or snowmelt. Currents are especially important. Because most estuaries are long and narrow, the tide doesn't just rise; it rushes in, often creating strong **tidal currents.** In a few places the tide actually comes in as a nearly vertical wall of water known as a **tidal bore.** Tidal bores in the Qiantang River, China, can generate waves as high as 6 m (20 ft)! Such strong water movements greatly affect the pattern of salinity in an estuary.

Another factor that affects circulation in estuaries is the **Coriolis effect.** North of the Equator, the fresh water that flows from rivers toward the sea is deflected toward the right. South of the Equator, the flow is to the left. This means that in estuaries located

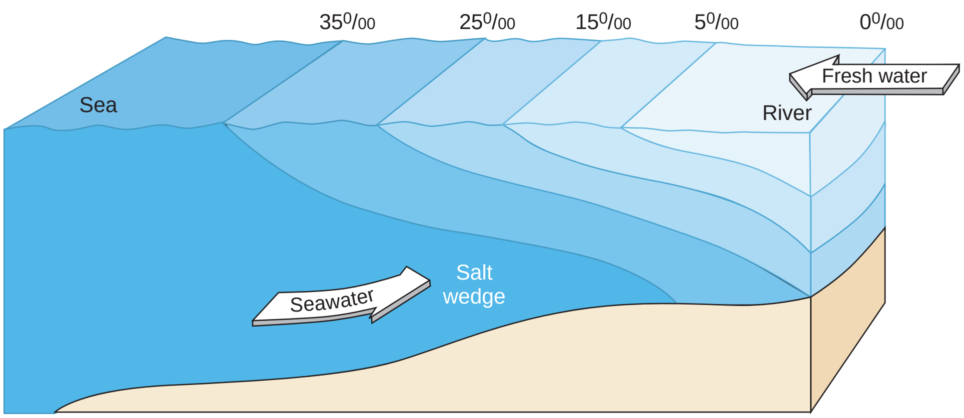


FIGURE 12.3 Profile of an idealized estuary. The lines across the estuary connect points of similar salinity and are known as *isohalines.*

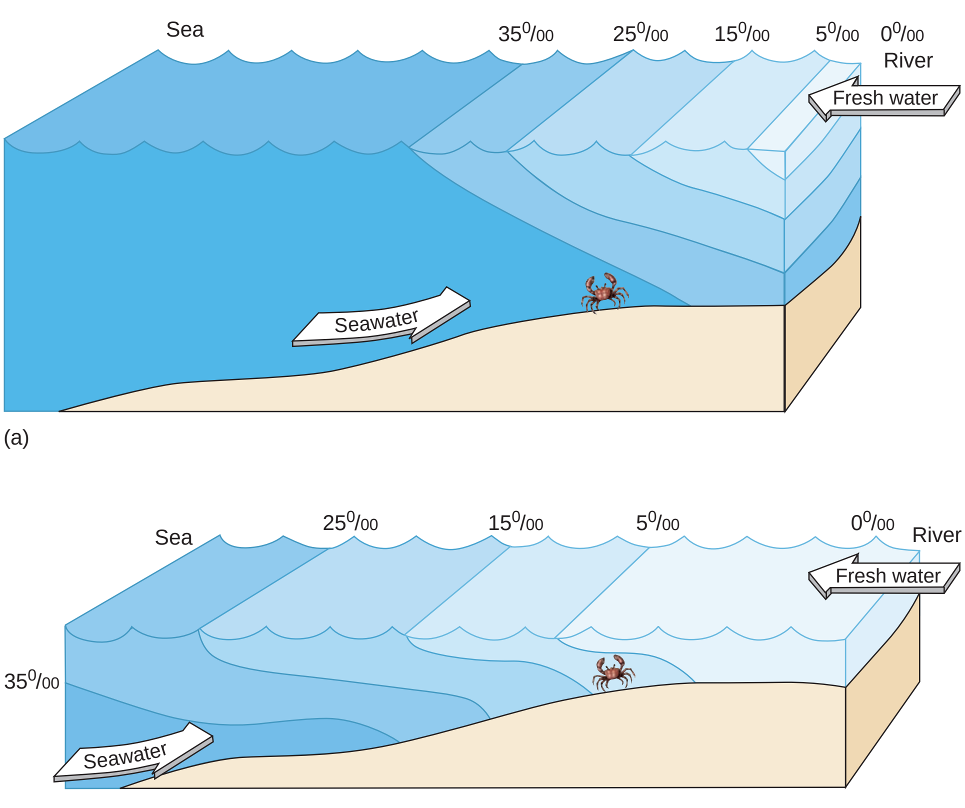


FIGURE 12.4 The salt wedge in a typical estuary moves in and out with the tide. (*a*) At high tide the crab is covered by water with a salinity of 35‰. (*b*) At low tide it is covered by water with a low salinity, between 5‰ and 15‰.

Plate Tectonics The process in which large sections of the earth's crust move about.

• Chapter 2, p. 23

Passive Continental Margin One that is on the "trailing edge" of a continent and therefore has little geological activity.

• Chapter 2, p. 35; Figure 2.22

Active Continental Margin One that is colliding with another plate and therefore has a lot of geological activity.

• Chapter 2, p. 34; Figure 2.22

Semidiurnal Tide A tidal pattern with two high and two low tides each day.
Diurnal Tide A tidal pattern with one high and one low tide each day.
Mixed Semidiurnal Tide A tidal pattern in which two successive high tides are of different heights.

• Chapter 3, p. 61; Figure 3.34

Coriolis Effect As a result of the earth's rotation, anything that moves large distances on the earth's surface tends to bend to the right in the Northern Hemisphere and to the left in the Southern Hemisphere.

• Chapter 3, p. 49

in the Northern Hemisphere marine organisms can penetrate farther upstream on the left side when one faces seaward. In the Southern Hemisphere they extend up the right side.

In regions of little freshwater runoff and high evaporation, the salinity of the water increases. An example is Laguna Madre, a shallow bar-built estuary with limited access to the open ocean that parallels the Texas coast for 185 km (115 mi). The average salinity is over 50‰ in some areas, and it may reach 100‰ or more during dry spells. These high-salinity estuaries are called **negative estuaries**.

Substrate

Rivers carry large amounts of sediment and other materials, including pollutants, into most estuaries. Sand and other coarse material settle out in the upper reaches of the estuary when the river current slows. The fine, muddy particles, however, are carried further down the estuary. There, many of them settle out when the current slows even more, though the finest particles may be carried far out to sea. The **substrate,** or type of bottom, of most estuaries is therefore sand or soft mud.

Mud, which is actually a combination of silt and clay (see Fig. 11.27), is rich in organic material. As in other organic-rich sediments, respiration by decay bacteria uses up oxygen in the **interstitial water,** the water between sediment particles. Water cannot easily flow through the fine sediments to replenish the oxygen supply. As a result, the sediments in estuaries are often devoid of oxygen, or are **anoxic,** below the first few centimeters (see Fig. 11.29). They have the black color and rotten-egg smell typical of anoxic sediments, in which **hydrogen sulfide (H_2S),** which is toxic to most organisms, accumulates. Anoxic sediments are not completely devoid of life. **Anaerobic bacteria,** which do not need oxygen to carry out respiration, thrive under these conditions.

Fine, muddy sediments brought into estuaries by rivers settle out in the relatively quiet waters. Bacterial respiration in these organic-rich sediments depletes the oxygen in them.

In estuaries that have unimpeded tidal flow, which includes most shallow ones, there is plenty of oxygen dissolved in the water. Some deep-water estuaries such as fjords (see Fig. 12.2), however, have a shallow "sill" at the entrance that restricts water circulation. Low-salinity water flows out unimpeded on the surface. The sill, however, prevents seawater from flowing in along the bottom. The stagnant deep water may become depleted in oxygen because of bacterial respiration associated with the decomposition of organic matter that sinks and accumulates on the bottom.

Other Physical Factors

Water temperature in estuaries, except fjords, varies markedly because of their shallow depths and large surface area. Organisms that are exposed at low tide may have to face even more drastic daily and seasonal temperature fluctuations.

Large amounts of suspended sediments are typical of estuaries, greatly reducing the water clarity. Very little light thus penetrates through the water column. The particulate material in the water can also clog the feeding surfaces of some filter feeders and even kill organisms, such as some sponges, that are sensitive to sediment.

ESTUARIES AS ECOSYSTEMS

To the uninitiated, an estuary may at first look like a wasteland. This impression is far from the truth. Estuaries are tremendously productive and are home to large numbers of organisms, many of which are of commercial importance. Estuaries also provide vital breeding and feeding grounds for many birds, fishes, shrimps, and other animals. Estuarine ecosystems consist of several distinct communities, each with its own characteristic assemblage of organisms.

Living in an Estuary

Life in an estuary revolves largely around the need to adapt to extremes in salinity, temperature, and other physical factors. Though other marine environments may be more extreme—they may be colder or more saline, for instance—none changes so rapidly or in so many ways as an estuary. Living in an estuary is not easy, so relatively few species have successfully adapted to estuarine conditions.

Coping with Salinity Fluctuations Maintaining the proper salt and water balance of cells and body fluids is one of the greatest challenges facing estuarine organisms. Most estuarine organisms are marine species that have developed the ability to tolerate low salinities (Fig. 12.5). How far they can move up the estuary depends on just how tolerant they are. Most estuarine

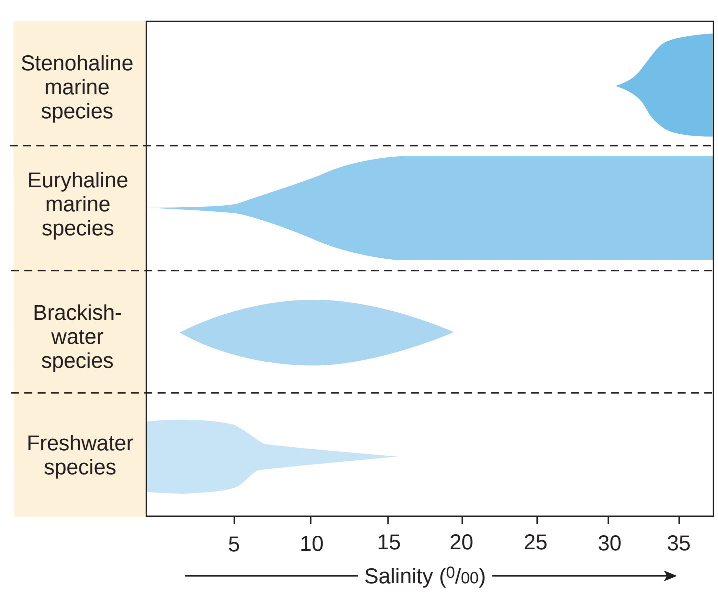


FIGURE 12.5 Types of species living in an idealized estuary in relation to salinity. The width of the bars represents the relative number of species.

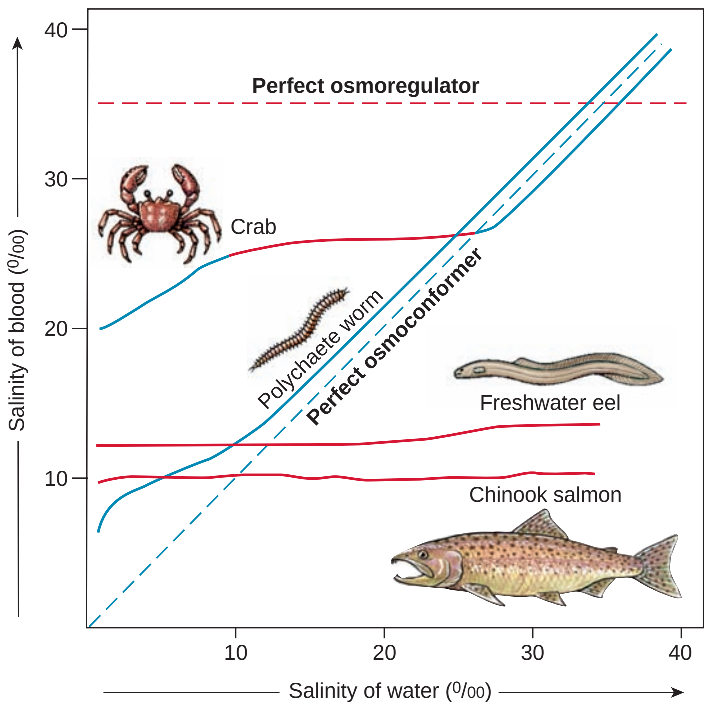


FIGURE 12.6 The salinity of the body fluids of estuarine animals responds in various ways to the salinity of the surrounding water. In a perfect osmoconformer, the salinity of the blood exactly matches that of the water. In a perfect osmoregulator, blood salinity stays the same no matter what the water salinity is. We have drawn the line for an imaginary perfect osmoregulator at 35‰. The salmon and freshwater eel are nearly perfect osmoregulators even though their bloods are more dilute. The important point is not the actual salinity of the blood but the fact that it remains relatively constant. Notice that some organisms, like the crab in the diagram, can only osmoregulate within a certain range of salinity; they are osmoconformers outside this range.

organisms are **euryhaline** species, that is, they tolerate a wide range of salinities. The relatively few **stenohaline** species, those that tolerate only a narrow range of salinities, are limited to the upper or lower ends of the estuary and rarely penetrate into the estuary proper. Stenohaline species can be either marine or freshwater in origin. Some species are adapted to live in **brackish water,** or water of intermediate salinity. Some of these species are stenohaline; others are euryhaline.

Because of their marine background, most estuarine organisms face the problem of the water in estuaries being diluted with fresh water. Those having an internal salt concentration higher than that of the surrounding water tend to take on water through **osmosis** (see Fig. 4.13*a*). Some animals adapt by simple changes in behavior. They may hide in their mud burrows, close their shells, or swim away if the salinity drops. These strategies are not widespread in estuaries, however, and most organisms rely on other mechanisms.

FIGURE 12.7 Cordgrass (*Spartina*) is an important component of salt marshes on both the Atlantic and Pacific coasts of North America and other temperate shores worldwide.

Soft-bodied estuarine animals, such as many molluscs and polychaete worms, often maintain osmotic balance simply by allowing their body fluids to change with the salinity of the water. They are called **osmoconformers** (Fig. 12.6). Many fishes, crabs, molluscs, and polychaetes are instead **osmoregulators.** They keep the salt concentration of their body fluids more or less constant regardless of the water salinity. When the salinity of the water is lower than that of the blood, they get rid of excess water and, via **active transport,** absorb some solutes from the surrounding water to compensate for those lost in the elimination of water. The gills, kidneys, and other structures accomplish this.

Bony fishes that inhabit estuaries also need to osmoregulate, since their blood is less salty than seawater (see Fig. 4.14 and "Regulation of the Internal Environment," p. 164). Salmon and freshwater eels migrate back and forth between rivers and the sea and still maintain a stable internal environment, thanks to the active transport of solutes by their kidneys and gills.

Organisms in estuaries have adapted to salinity fluctuations in various ways. Osmoconformers let the salinity of their body fluids vary with that of the water. Osmoregulators keep the salt concentration of their body fluids constant.

Few animals can be neatly classified as perfect osmoconformers or perfect osmoregulators. Many invertebrates, for instance, osmoregulate at low salinities and osmoconform at higher salinities. Even efficient osmoregulators such as salmon and freshwater eels do not keep *exactly* the same concentration of salts and other solutes in their blood as salinity changes.

Estuarine plants must also handle salinity variations. Grasses and other salt-marsh plants are land plants that have developed high salt tolerance. Some of these plants actively absorb salts and concentrate harmless solutes like sugars to match the outside concentrations and prevent water from leaving their tissues. Notice that this is opposite to the situation in marine organisms that live in estuaries, which have to adapt to reduced, not increased, salinities.

Different adaptations have evolved in some estuarine plants. Cordgrasses (*Spartina;* Fig. 12.7), other salt-marsh plants, and some mangroves actually excrete excess salts by way of salt glands in their leaves. Some estuarine plants, such as pickleweed

Osmosis The movement of water from high to low concentrations across a membrane.

Active Transport The transfer of substances across membranes by a cell against a *concentration gradient.*

• Chapter 4, p. 72

FIGURE 12.8 Pickleweed (*Salicornia* is) a common succulent plant in salt marshes around the world.

(*Salicornia*), accumulate large amounts of water to dilute the salts they take up (Fig. 12.8). Fleshy plants such as these are known as **succulents.**

Adapting to the Mud As discussed in Chapter 11 (see "Living in the Sediment," p. 260), living in mud has its problems. There is nothing to hold on to, so most animals either burrow or live in permanent tubes beneath the sediment surface. Clams do well because they can extend their siphons through the mud to get water for food and oxygen. Because it is difficult to move through mud, the inhabitants tend to be stationary or slow-moving. Living in mud, however, has a benefit: Salinity fluctuations are less drastic than in the water column.

The depletion of oxygen caused by the decay of organic matter in the mud presents another challenge. This is no problem to burrowers that pump oxygen-rich water into their burrows. Burrowers without this luxury have special adaptations to low-oxygen environments. Some have blood that contains **hemoglobin,** which has a particularly high affinity for oxygen. It can hold and carry oxygen even when only minute quantities are available. Some clams and a few other mud-dwellers can even survive for days without oxygen.

Types of Estuarine Communities

Several distinct communities are associated with estuaries. One consists of the **plankton,** fishes, and other open-water organisms that come in and leave with the tide. Several other communities are permanent parts of the ecosystem.

Estuarine communities consist of relatively few species. These species, however, are typically represented by many individuals. A surprising number of estuarine species, particularly those inhabiting temperate estuaries, are widely distributed around the world. Many have been distributed by humans, often with undesirable consequences.

Open Water The type and abundance of plankton inhabiting estuaries vary tremendously with the currents, salinity, and temperature. The murky water restricts the penetration of light and may limit **primary production** by phytoplankton. Most of the phytoplankton and zooplankton in small estuaries are marine species flushed in and out by the tides. Larger estuaries may also have their own, strictly estuarine, species.

One reason many of the world's great cities developed around estuaries is the rich supply of fish and shellfish in or near estuaries. Many species of commercially important fishes and shrimps use estuaries as nurseries for their young, taking advantage of the abundant food and relative safety from predators. About 90% of the marine commercial catch in the northern Gulf of Mexico, for example, is of species that depend on estuaries at some point in their lives.

A relatively rich variety of fishes live in most estuaries. Many are the juveniles of marine species that breed at sea but use estuaries as nurseries. Examples are the menhaden (Fig. 12.9), anchovies, mullets, croakers, and many species of flatfishes. Some fishes move through estuaries during their migrations. Such fishes are either **anadromous**—like salmon, smelts, and shad—or **catadromous**—like freshwater eels. Relatively few fishes spend their entire lives in estuaries. Killifishes (*Fundulus*) are one example.

Shrimps and crabs are often common in estuaries, and many commercially valuable species use estuaries as nurseries.

Mudflats The bottoms of estuaries that become exposed at low tide often form **mudflats** (see Fig. 12.14 and photo on p. 265). Mudflats are especially extensive in estuaries where there is a large **tidal range** and a gently sloping bottom. It all looks pretty much the same, but the mudflat can vary widely in particle size. Sand may accumulate to create sand flats near river mouths and in the tidal creeks that form as the tide changes. In the calmer central part the mudflat contains more fine, silty material.

Mudflat communities in estuaries are similar to those on muddy shores (see "Soft-Bottom Intertidal Communities," p. 259). Low tides expose organisms to desiccation, wide variations in temperature, and predation, just as in any other intertidal community. In estuaries, however, mudflat organisms must also withstand regular variations in salinity.

Primary producers are not usually evident on mudflats. A few hardy seaweeds—such as the green algae *Enteromorpha* (Fig. 12.10) and *Ulva,* the sea lettuce, and the red alga *Gracilaria*—manage to grow on bits of shell. These and other primary producers may be particularly common during the warmer months. Large numbers of benthic diatoms grow on the mud and

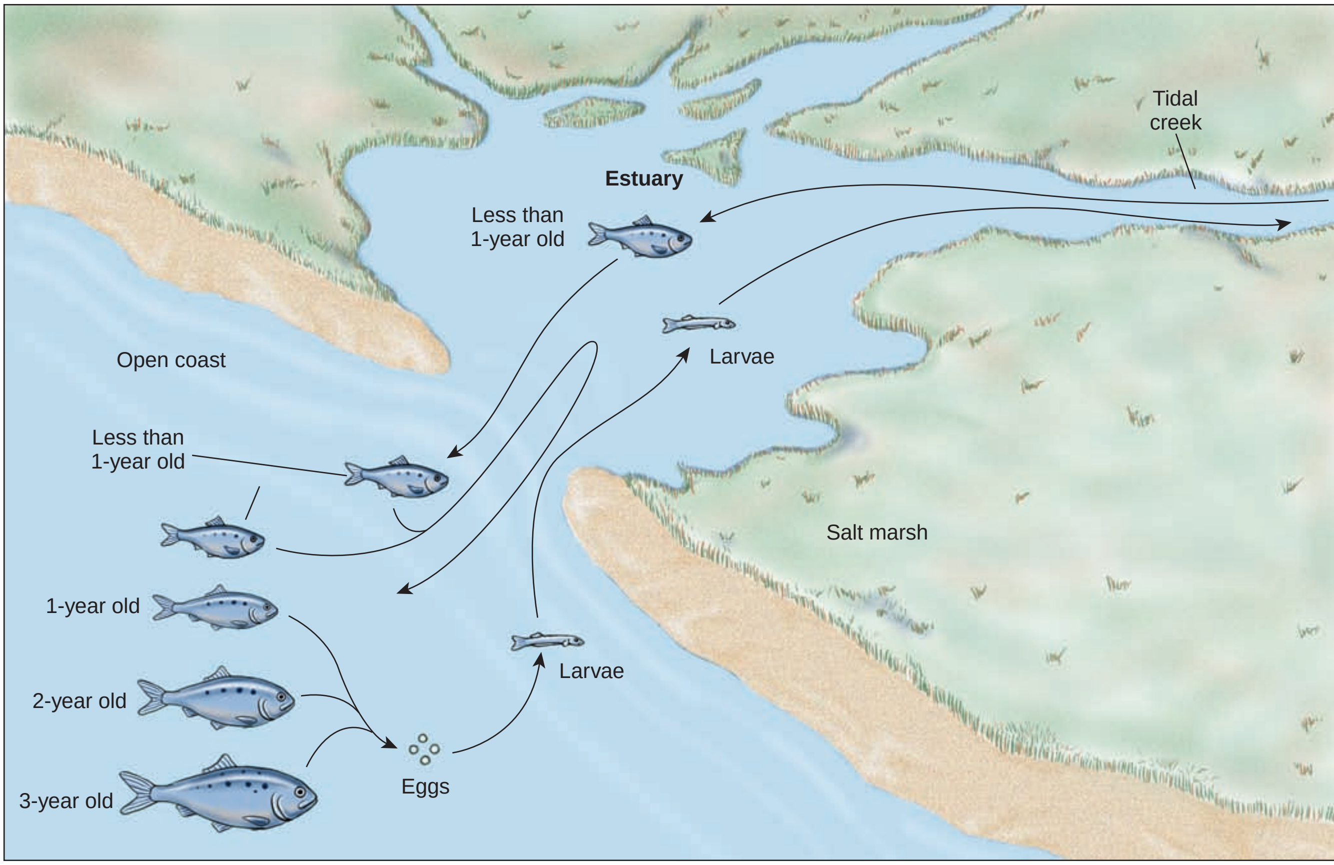


FIGURE 12.9 The Atlantic menhaden (*Brevoortia tyrannus*) is one of the most important commercial fishes in the United States. Adult fish (one to three years old) spawn offshore and the larvae drift with the tides and currents into estuaries, moving into shallow areas in the salt marshes to grow.

often undergo extensive blooms, forming golden-brown patches. In tide pools left by the receding tides these patches become coated with oxygen bubbles as intense photosynthesis takes place in the sunlight.

Bacteria are extremely abundant on mudflats. They decompose the huge amounts of organic matter brought in by rivers and tides. When the oxygen is used up by decay, some bacteria produce hydrogen sulfide. This in turn is used by

FIGURE 12.10 The California horn snail (*Cerithidea californica*), a deposit feeder, is abundant on mudflats. The green alga is *Enteromorpha,* which tolerates wide fluctuations in salinity and temperature as well as pollution. It can be found on rocky shores as well as along the shores of estuaries. It thrives during the long, sunny days of summer, when it can turn mudflats into bright-green "meadows."

Hemoglobin A blood protein that transports oxygen in many animals; in vertebrates it is contained in *erythrocytes,* or red blood cells.
- Chapter 8, p. 164

Plankton Primary producers (*phytoplankton*) and consumers (*zooplankton*) that drift with the currents.
- Chapter 10, p. 220; Figure 10.11

Primary Production The conversion of carbon from an inorganic form, carbon dioxide, into organic matter by autotrophs—that is, the production of food.
- Chapter 4, p. 68

Anadromous Fishes Those that migrate from the sea to spawn in fresh water.
- Chapter 8, p. 168

Catadromous Fishes Those that migrate from fresh water to spawn at sea.
- Chapter 8, p. 169

Tidal Range Difference in water level between successive high and low tides.
- Chapter 3, p. 60

sulfur bacteria, chemosynthetic bacteria that derive energy by breaking down sulfur compounds such as hydrogen sulfide (see Table 5.1, p. 88). Diatoms and bacteria, including photosynthetic bacteria, actually account for most of the primary production on mudflats.

The dominant animals on mudflats burrow in the sediment and are known as **infauna** (Fig. 12.11). Though there are not many species of these burrowing animals, they often occur in immense numbers. At low tide their presence may be revealed only by small sediment mounds topped by a hole or piles of feces and other refuse. They feed on the abundant **detritus** in the sediment and water. Most of the food for these animals is brought in by the rivers and tides and is not actually produced on the mudflat. Very few mudflat animals can be classified as **epifauna,** those that either live *on* the sediment surface or are attached to a surface as **sessile** forms.

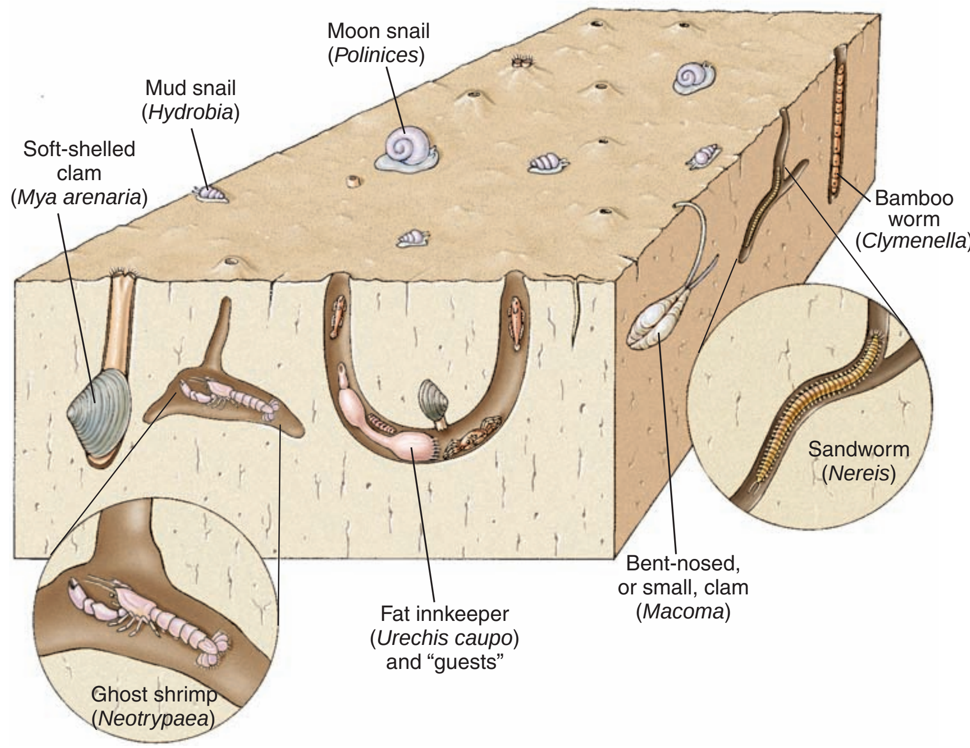


FIGURE 12.11 Some representative inhabitants of mudflats in temperate estuaries. Many mudflat organisms also can be found on muddy bottoms outside estuaries (also see Fig. 13.6).

Mudflat inhabitants that feed on detritus are **deposit** and **suspension feeders,** including **filter feeders.** Deposit feeders are more common than suspension feeders on mudflats and other muddy bottoms (see Fig. 13.12). Suspension feeders are at a disadvantage because their filtering mechanisms tend to get clogged by the high amounts of sediment that rains on soft bottoms. Furthermore, deposit feeders actually exclude many suspension feeders by disturbing the sediments, which clogs the suspension feeders' feeding structures and buries their newly settled larvae.

Suspension feeders, on the other hand, dominate where the sediment is more sandy. The wider interstitial spaces between the larger sand particles hold less detritus for deposit feeders to eat, and the abrasive sand is hard on their digestive systems.

The dominant primary producers on mudflats are diatoms and bacteria. Most of the animals are burrowing deposit and suspension feeders that feed on detritus.

Protozoans, nematodes, and many other minute animals that compose the **meiofauna** (see "Life in Mud and Sand," p. 291) also thrive on detritus. The meiofauna are also known as **interstitial** animals. The larger burrowing animals, or infauna, include many polychaetes (see Figs. 11.31 and 12.11). Most are deposit feeders. Other polychaetes are suspension feeders that filter water or extrude tentacles to collect the detritus that falls from the water column. Yet another detritus-feeding strategy among some polychaetes is to switch back and forth between suspension and deposit feeding, depending on the amount of suspended material in the water.

Bivalves often abound on mudflats. Many are filter feeders that are also found on muddy and sandy shores outside estuaries (see Fig. 11.30). Examples from temperate waters are the quahog, or hard clam (*Mercenaria mercenaria*), the soft-shelled clam (*Mya arenaria;* Fig. 12.11), and razor clams (*Ensis*). Some of these are of considerable commercial importance. Bent-nosed, or small, clams (*Macoma;* Fig. 12.11) are deposit feeders that use their long incurrent siphons to vacuum the surface.

The ghost (*Neotrypaea,* Fig. 12.11) and mud (*Upogebia*) shrimps make elaborate burrows that, as a side effect, help oxygenate the sediment. These shrimps feed on detritus that they filter from the water and sift from the mud. Fiddler crabs (*Uca*) also live in burrows but are active on the mudflats at low tide (see "Fiddler on the Mud," p. 273). They process the mud and extract the detritus, which they eat.

On the Pacific coast of North America the fat innkeeper (*Urechis caupo;* Fig. 12.11), an echiuran worm, secretes a funnel-shaped net of mucus. It pumps water through this net to filter out food. It gets its common name because it shares its U-shaped burrow with a polychaete (*Hesperonoe adventor*), a crab (*Scleroplax granulata*), one or more fish (*Clevelandia ios*), and other guests.

Some animals live on the surface of the mud or move in and out with the tide. These include deposit feeders such as mud snails (*Cerithidea, Hydrobia;* Figs. 12.10 and 12.11), amphipods, and shrimps. Carnivores include polychaete worms (*Nereis;* Fig. 12.11), moon snails (*Polinices;* Fig. 12.11) and other predatory snails (*Busycon*), and swimming crabs (*Callinectes*).

By far the most important predators in the mudflat community are fishes and birds. Fishes invade mudflats at high tide, whereas birds congregate at low tide to feed. Estuaries are important stopover and wintering areas for many species of migratory birds. The open spaces offer them safety from natural enemies, and food is plentiful. The most significant predators on mudflats are wading shorebirds (Figs. 12.12 and 12.13). These include the willet, godwits, dowitchers, and many species of plovers and sandpipers. They feed on polychaetes, ghost shrimps and other small crustaceans, clams, and mud snails. Oystercatchers specialize on clams and other bivalves.

These birds do not all exploit the same type of prey. The varying lengths of their bills represent a specialization in prey because different types of prey live at different depths in the mud (Fig. 12.12). In addition, shorebirds use different strategies to locate their food. Birds such as sandpipers rely mostly on their bills, probing in the mud as they walk around (Fig. 12.13*a*). Others, like plovers, use their eyesight to detect slight movements on the surface of the mud (Fig. 12.13*b*). Some biologists think that these differences in feeding habits are an example of **resource partitioning.**

Herons and egrets compose yet another group of wading birds. They specialize in catching fishes, shrimps, and other small

Chemosynthetic Bacteria *Autotrophic bacteria* that use energy contained in inorganic compounds rather than sunlight to make organic matter.

• Chapter 5, p. 92; Table 5.1

Detritus Particles of dead organic matter.

• Chapter 10, p. 223

Deposit Feeders Animals that feed on organic matter that settles in the sediment.

Suspension Feeders Animals, including *filter feeders,* that feed on particles suspended in the water column.

• Chapter 7, p. 116; Figure 7.3

Resource Partitioning The sharing of a resource by two or more species to avoid competition.

• Chapter 10, p. 214

swimming prey. Birds that feed by swimming or diving in the estuary, such as ducks, terns, and gulls, are often seen resting on mudflats.

Salt Marshes Estuaries in temperate and subarctic regions are usually bordered by extensive grassy areas that extend inland from the mudflats. These areas are partially flooded at high tide and are known as **salt,** or **tidal, marshes** (Fig. 12.14). Sometimes they are grouped with coastal environments flooded at high tide and with freshwater marshes and collectively called **wetlands.** Though mostly associated with estuaries, salt marshes can also develop along sheltered open coasts. They develop as long as disturbance from wave action is minimal to allow the accumulation of muddy sediments. Tidal creeks, freshwater streams, and shallow pools frequently cut through the marsh.

In North America, salt marshes are particularly extensive along the Atlantic and Gulf coasts (see Fig. 2.22). The broad estuaries and shallow bays of these gently sloping coastlines provide optimal conditions for the development of salt marshes. The Pacific coast of North America, on the other hand, is generally steeper, and most of the estuaries have formed along narrow river valleys. This has resulted in less extensive development of salt marshes. In the Northern Hemisphere salt marshes tend to be more extensive on the left side than on the right side of estuaries, since the turbulence caused by the flow of freshwater from rivers is stronger on the right side as a result of the Coriolis effect.

Salt marshes are subject to the same extremes in salinity, temperature, and tides that affect mudflats. They also have a muddy bottom, but it is held together by the roots of marsh plants and thus is more stable.

Salt-marsh communities are dominated by a few hardy grasses and other salt-tolerant land plants. These plants thrive in the marsh, though the environment is too harsh for most other land plants. There is a pronounced zonation of plants in salt marshes (Fig. 12.15). The location of a given zone is related to the height relative to the tide, but it varies according to geographical location, type of substrate, and other factors. For instance, soil salinity may become particularly high

FIGURE 12.12 Differences in the bill length of wading shorebirds from the west coast of North America allow them to feed on particular mudflat animals.

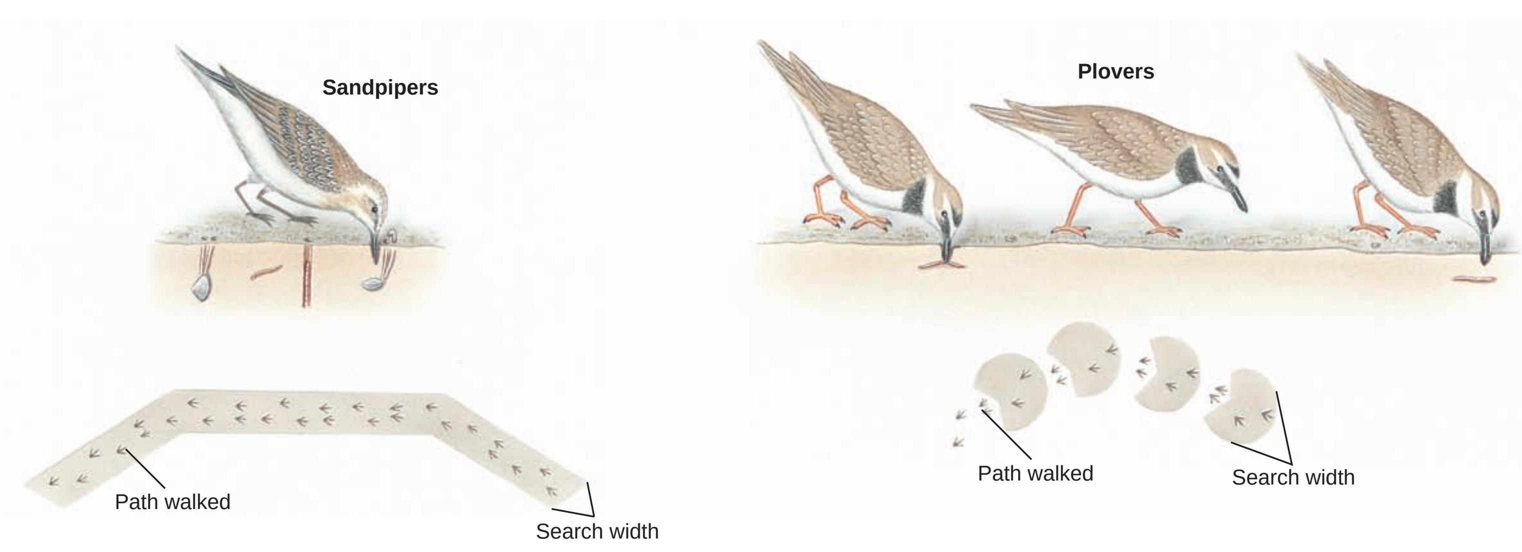


FIGURE 12.13 Feeding behavior also varies among shorebirds. (*a*) Sandpipers use their bills to search for food and follow a roughly straight path. (*b*) Plovers rely mostly on their vision, turning their heads sideways as they move.

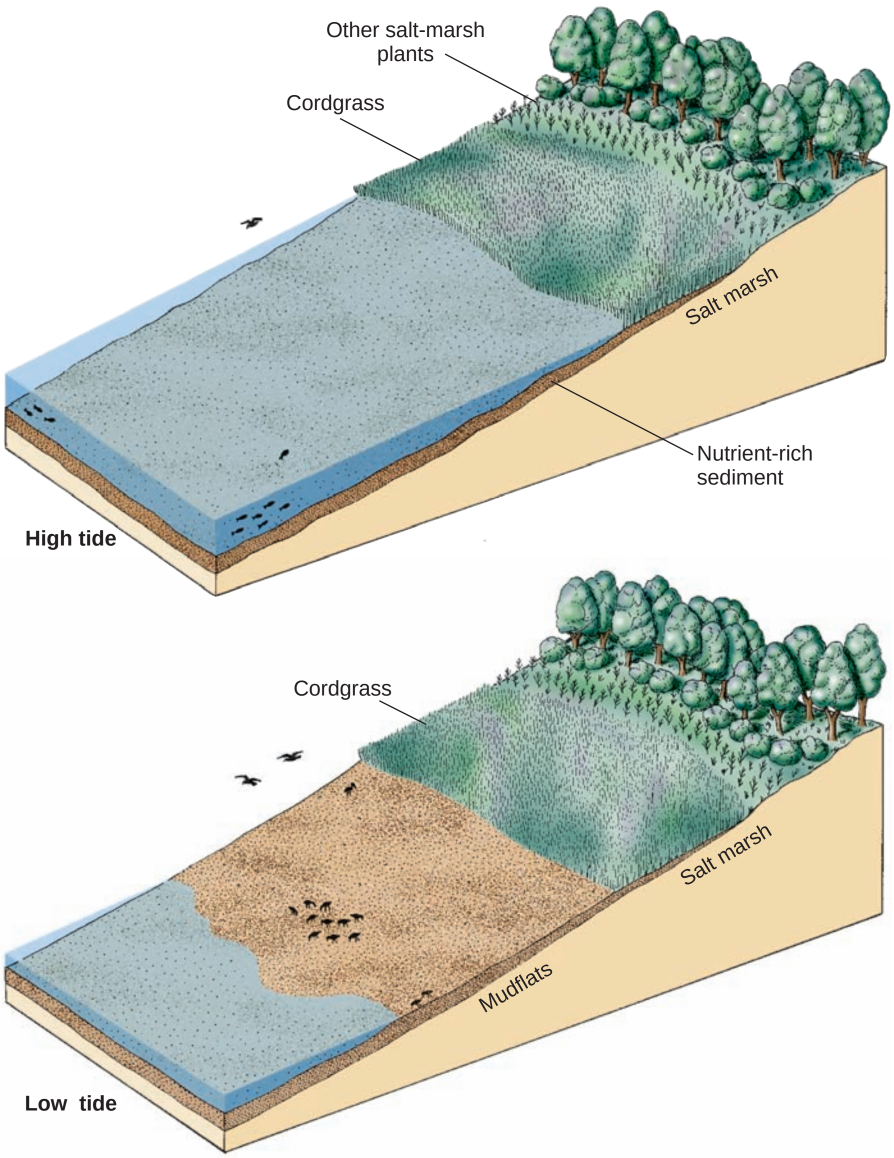


FIGURE 12.14 The daily tides play a crucial role in salt marshes. They help circulate detritus and nutrients and expose mudflat organisms to predation by shorebirds and other animals.

at intermediate heights as a result of higher evaporation in marshes closer to hot, dry regions. This may result in areas bare of vegetation.

Cordgrasses (the smooth cordgrass, *Spartina alterniflora*, on the Atlantic coast; the California cordgrass, *S. foliosa,* on the Pacific coast; see Fig. 12.7) are typically the most common plants along the seaward limit of the salt marsh, where it meets the mudflats (Figs. 12.14 and 12.15). These grasses invariably occupy the fringe above the mean low tide level. Plants do better here because the soil is well drained and therefore richer in oxygen and less salty. The tops of their tall leaves remain exposed to the air even when the bottom is covered at high tide. The plants have extensive horizontal stems that stretch out underground. The leaves and roots develop from the stems. Roots just below the soil may take in oxygen from the air.

Cordgrass may gradually invade mudflats because the plants slow down the tidal flow and thus increase the amount of sediment trapped among the roots. The landward extension of the salt marsh is eventually limited by the height of the highest tide. In addition to providing a significant portion of the high primary production of estuarine communities (see "Feeding Interactions among Estuarine Organisms," p. 279), salt-marsh plants like cordgrass help stabilize soils by decreasing the effects of wave action. Smooth cordgrass from the Atlantic has been introduced in other parts of the world for the protection of shorelines, sometimes with negative effects (see "Biological Control of Invasive Cordgrass," p. 276).

Cordgrass gives way to other plants in the higher parts of the marsh. On the Atlantic coast, a second species of cordgrass (the saltmeadow, or salt-marsh hay, *Spartina patens*) dominates (Fig. 12.15), but rushes (*Juncus*), pickleweed, and several other plants often form distinct zones. The higher levels of salt marshes on the Pacific coast are usually dominated by pickleweed (see Fig. 12.8). The landward limit of salt marshes is a transition zone with adjacent terrestrial, or land, communities. It is characterized by a large variety of plants resistant to salt spray, such as salt grasses (*Distichlis*) and several species of pickleweed. It appears that in most salt marshes zonation is determined not only by the effects of flooding by tides but also by the combined effect of other factors. They include competition for space among salt-marsh plants, increased soil salinity in warm areas due to evaporation, and even the effect of burrowing animals.

The muddy salt-marsh substrate is home to decay bacteria, diatoms, and thick mats of filamentous green algae and cyanobacteria. Bacteria play a crucial role by decomposing the large amounts of dead plant material produced in the salt marsh. These bacteria and the partially broken-down organic matter are a major source of the detritus that feeds many of the inhabitants of the estuary. Some bacteria are **nitrogen fixers** that enrich the sediment.

Salt marshes are dominated by grasses and other marsh plants. Bacteria in the mud decompose dead plant material and contribute a large portion of the detritus in the estuary.

Some burrowing animals of mudflats also inhabit salt marshes. In addition, nematodes, small crustaceans, larvae of land insects, and other small invertebrates live among the algal mats and decaying marsh plants. Crabs are conspicuous inhabitants of salt marshes. Fiddler crabs build burrows along the mudflat edges, where they increase the oxygenation of soils. Other marsh crabs (*Sesarma,*

Nitrogen Fixation Conversion of nitrogen gas (N_2) into nitrogen compounds that can be used by primary producers as nutrients.

• Chapter 5, p. 93; Table 5.1

Hemigrapsus) are scavengers that eat dead organic matter. Some of these species live in burrows.

Marsh plants provide shelter and food to many marine and land animals. Coffee bean snails (*Melampus*) and marsh periwinkles (*Littorina, Littoraria*) are air-breathing snails that feed on detritus, minute algae, and fungi that grow on marsh plants. They move up the plants as the high tide moves in. Though they are air-breathers, they lay their eggs in the water and the larvae that hatch develop in the plankton. The ribbed, or horse, mussel (*Geukensia demissa*) is a suspension feeder that lives half buried in the mud among the cordgrass (Fig. 12.16). Killifishes and juvenile silversides (*Menidia*) are examples of fishes that inhabit tidal creeks and pools in the marsh at low tide. They move into the salt-marsh grass at high tide to escape predators such as crabs and larger fishes, which enter the creeks with the rising tide. Crustaceans and small fishes retreat to pools or tidal creeks at low tide. Rails and American coots are among the birds that feed and nest here. Many other land birds and mammals, from ospreys to raccoons, are common visitors.

Mangrove Forests Mangrove forests are not limited to estuaries, but in some ways they are the tropical equivalents of salt marshes, though the two coexist in many places. **Mangroves** are flowering land plants adapted to live in the intertidal (see "Flowering Plants," p. 110). These trees and shrubs often form dense forests called **mangals** to distinguish them from mangroves, the actual plants themselves (see Figs. 6.14 and 6.15). Mangroves are typical of tropical and subtropical regions, where they replace the temperate salt marshes (Fig. 12.17 and foldout map). It has been estimated that around 75% of all sheltered tropical shores were at one time fringed with mangroves, a figure that suggests their tremendous importance. Mangrove forests, however, are being rapidly destroyed by humans (see "Human Impact on Estuarine Communities," p. 281).

Mangrove forests, or mangals, are formed by mangroves, tropical and subtropical trees and shrubs adapted to the intertidal environment.

Mangroves grow on protected coasts where muddy sediments accumulate. Though mangroves grow in estuaries, they are not restricted to them. As in salt-marsh plants, the various species of mangroves have different tolerances to immersion by high tide. Partly as a result of these differences in tolerance, they show a distinctive zonation in the intertidal, from a marine to a progressively terrestrial environment.

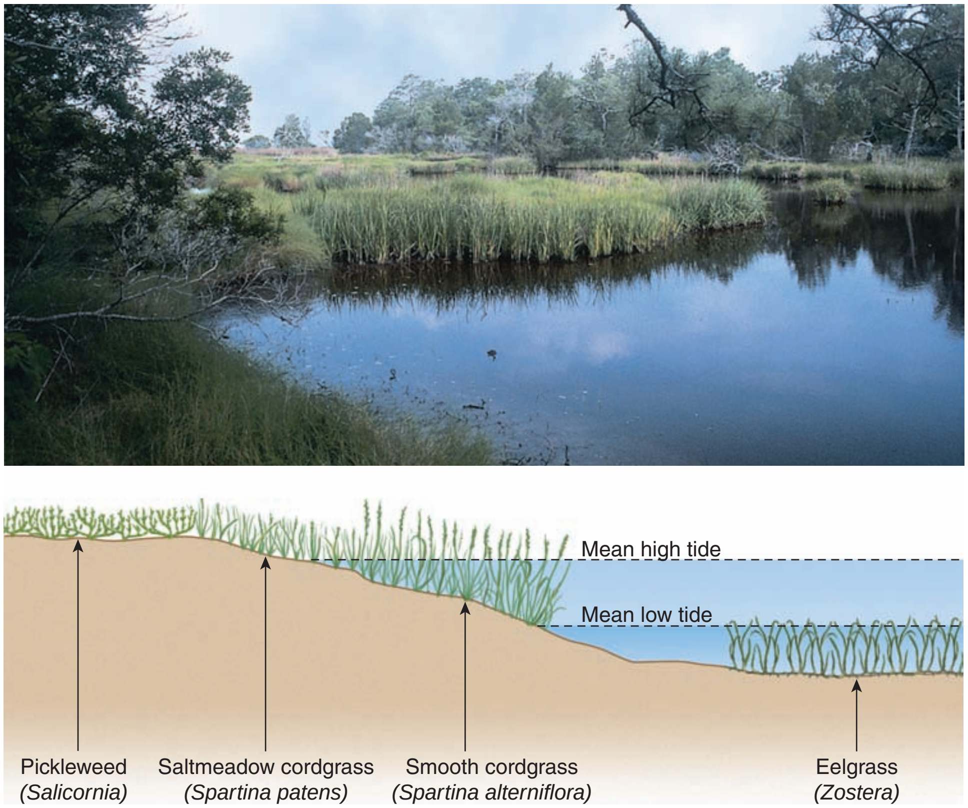


FIGURE 12.15 A salt marsh near Atlantic Beach, North Carolina. As in other Atlantic marshes, the smooth cordgrass (*Spartina alterniflora*) occupies the edge of the marsh that is flooded the most by seawater. It is replaced higher up in the marsh by saltmeadow grass, or salt-marsh hay (*Spartina patens*), a shorter and finer grass that is less salt tolerant and may form extensive meadows. It grows where the marsh is flooded only at high tide. Many of these marshes have been filled in and destroyed.

FIGURE 12.16 The Atlantic ribbed, or horse, mussel (*Geukensia demissa*) lives half buried in the mud. It has the unusual ability to slightly open its valves, or gape, at low tide and take in oxygen from the air.

Some mangroves need fresh water for growth. Since they live at the sea edge, mangroves must get rid of salts from the water that is taken in by the roots. Most salts are actually not taken in by the roots, and salt glands on the leaves of some species excrete salts.

The **Indo-West Pacific region** has the world's most extensive mangrove forests

Indo-West Pacific Region The tropical Indian and western and central Pacific oceans.

• Chapter 14, p. 315

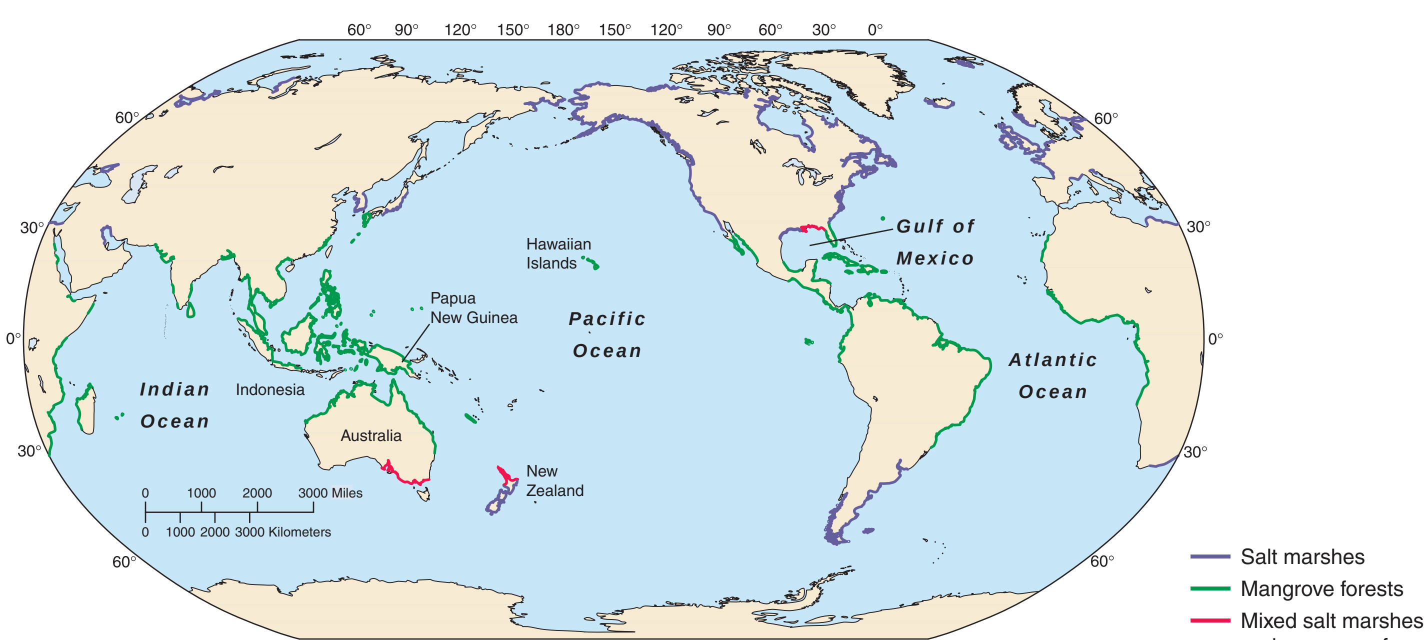


FIGURE 12.17 The world distribution of salt marshes and mangrove forests. Mangroves tend to replace salt marshes in tropical regions. The two overlap in such areas as the Gulf of Mexico, southern Australia, and New Zealand. Mangroves were introduced by humans to the Hawaiian Islands.

FIGURE 12.18 Aerial view of a mangrove forest on the southern coast of Puerto Rico. The outer seaward edge of the forest is dominated by the red mangrove (*Rhizophora mangle*). As in Florida and most of the Western Hemisphere, the inner margin of the red mangrove is bordered by a broad belt of black mangrove (*Avicennia germinans*). Farther away from the black mangrove is the white mangrove (*Laguncularia racemosa*).

FIGURE 12.19 Pneumatophores, the vertical extensions of shallow roots, obtain additional oxygen in mangroves such as *Sonneratia alba.* Here in Palau, western Pacific, this species is found along the seaward fringe of mangrove forests.

with by far the largest number of mangrove species. Mangrove forests extend as far as 320 km (200 mi) inland in southern New Guinea and some islands in Indonesia, where the influence of the tides extend far up estuaries.

Atlantic and eastern Pacific mangrove forests, though not as extensive and diverse as those in the Indo-West Pacific region, are nevertheless of great ecological significance. The most common species of mangrove along the shores of southern Florida, the Caribbean, and the gulfs of California and Mexico is the red mangrove (*Rhizophora mangle*). It lives right on the shore (Fig. 12.18) and is easily identified by its peculiar prop roots, which branch downward and support the tree-like stilts (see Fig. 6.14). Flexible aerial roots drop down from the higher branches, helping extend the tree laterally. The trees can be as high as 9 m (30 ft). Under optimal conditions they form dense forests noted for their high primary production. Other species of *Rhizophora* are found on tropical coasts around the world.

Along the Caribbean and Atlantic coasts of the Western Hemisphere, the black mangrove (*Avicennia germinans*) and the white mangrove (*Laguncularia racemosa*) live inland from the red mangrove (Fig. 12.18). Black mangrove seedlings can survive the high salinity of the water that remains standing after high tide flooding. As a result, the black mangrove grows higher in the intertidal than the red mangrove. The black mangrove, like several Indo-West Pacific mangroves, develops **pneumatophores,** conspicuous, unbranched extensions of the shallow roots that grow upward from the oxygen-poor mud to help aerate the plant tissues (Fig. 12.19). White mangrove seedlings do not easily tolerate flooding by seawater, and as a consequence, the white mangrove is found only along the landward edge of the mangrove forest. Its leaves have two clearly visible salt glands at the base for the excretion of salts. Salts are also excreted by the leaves of the black mangrove.

Many marine and land animals live in mangrove forests. Crabs are particularly common. Many, such as species of *Sesarma* and *Cardisoma,* feed on the abundant leaf litter that accumulates below the mangrove trees. These crabs spend most of their lives on land, but when eggs are ready to hatch, females must release the larvae at sea. Several species of fiddler crabs (see "Fiddler on the Mud," p. 273) excavate burrows in the mud. As in temperate mudflats and salt marshes, burrowing crabs help oxygenate the sediment.

Mudskippers (*Periophthalmus;* Fig. 12.20) are unique fishes found in Indo-West Pacific mangrove forests and mudflats. They have burrows in the mud but spend most of their time out of the water, skipping over the mud and crawling up mangrove roots to catch insects and crabs. When out of the water, mudskippers can take oxygen from the air through blood-rich surfaces in the mouth and on the skin as long as the surfaces remain moist.

FIGURE 12.20 A mudskipper (*Periophthalmus*) from the mudflats of a mangrove forest in Papua New Guinea. Its protruding eyes are adapted to see in air. Each eye can be retracted into a moist pocket to keep it from drying out.

Many organisms attach to, or take shelter among, the submerged mangrove roots (Fig. 12.21). Large sponges living on the roots have been found to provide significant amounts of nitrogen compounds to mangrove plants. They also help protect the roots from burrowing isopods, which otherwise can cause considerable damage.

The muddy bottom around mangroves is inhabited by a variety of deposit and suspension feeders, as on mudflats. These include polychaetes, mud shrimps, and clams. The channels that cross mangrove forests are rich nurseries for many species of commercially important shrimps, spiny lobsters, and fishes. They are also nurseries for coral reef fishes. In Thailand alone, mangrove forests annually contribute an estimated \$3.5 million per km^2 (\$1.4 million per mi^2) to the economy.

Birds make their homes in the mangrove branches and feed on fishes, crabs, and other prey. Snakes, frogs, lizards, bats, and other land animals also live in the mangrove trees.

FIGURE 12.21 Seaweeds, sponges, oysters, sea anemones, barnacles, sea squirts, and many other types of organisms live attached to the roots of the red mangrove (*Rhizophora mangle*).

Large amounts of leaves and other dead plant material accumulate in the mangrove forest. Considerable amounts are eaten by crabs, and some is exported to other ecosystems. Much of the detritus, however, is broken down by bacteria. This makes the mud among the mangrove roots black and oxygen-deficient, much like that in salt marshes. Because of the oxygen-poor sediments, and toxic substances released by the leaves, life on muddy bottoms in mangrove forests is less abundant than on similar bottoms elsewhere.

Other Estuarine Communities The muddy bottoms below low tide levels are sometimes covered by beds, or meadows, of grass-like flowering plants known as **seagrasses.** They include eel grass (*Zostera;* see Fig. 6.13*b*), which is restricted to temperate waters, and turtle grass (*Thalassia;* see Fig. 6.13*d*), a warm-water species often found around mangrove forests. The roots of seagrasses help stabilize the sediment, and their leaves provide shelter to many organisms as well as being an additional source of detritus. Seagrass beds are not restricted to estuaries and are discussed in more detail in Chapter 13 (see "Seagrass Beds," p. 290).

Oysters (*Ostrea, Crassostrea*) may form extensive beds on the muddy bottoms of estuaries in temperate waters. These **oyster reefs** gradually develop as successive generations of oysters grow on the shells of their predecessors (Fig. 12.22). They provide a complex, three-dimensional surface for many organisms. The oyster-reef community includes seaweeds, sponges, tubeworms, barnacles, and other organisms that attach to the hard shells. Other animals take shelter among or even inside the shells. A similar estuarine community develops in association with mussel (*Mytilus*) beds, though the mussels require a hard substrate for attachment.

FIGURE 12.22 An oyster reef formed by the eastern oyster (*Crassostrea virginica*) on the Atlantic coast of the United States, exposed at low tide.

Feeding Interactions among Estuarine Organisms

Though relatively few species live in estuaries when compared to rocky shores, they reap the benefits of living in a very productive ecosystem. The generalized food webs shown in Figure 12.23 summarize the feeding relationships among different organisms in estuarine ecosystems.

Why do estuaries have a high primary production? There are several reasons. Nutrients brought in by the tide and rivers, together with those generated by nitrogen-fixing organisms and the decomposition of detritus, are used by plants, algae, and bacteria, the primary producers. Primary production is especially high in the communities that surround estuaries. The dense stands of cordgrass and other salt-marsh plants (or mangroves in the tropics) are particularly adapted to live on the mud and thus take advantage of the high concentration of nutrients in the sediments. The diatoms and bacteria in the mud and the phytoplankton in the water also contribute significantly to primary production.

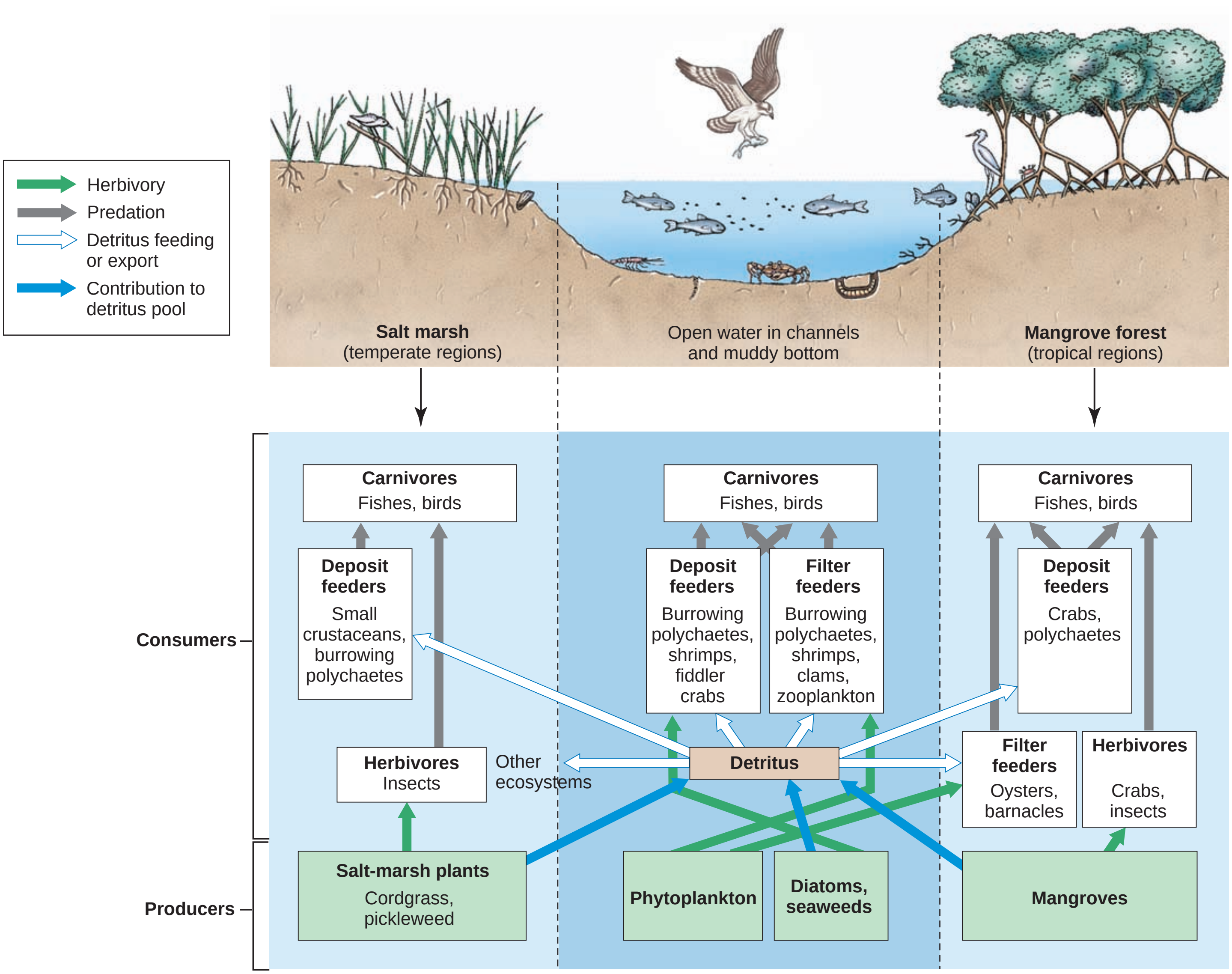


FIGURE 12.23 Generalized food webs in estuarine ecosystems. Salt marshes (left) occur in temperate regions, mangroves (right) in the tropics.

Detritus also tends to sink to the bottom. Bottom water, which has a higher salinity and density than shallower water, thus acts as a nutrient trap in deep estuaries. Some phytoplankton are known to migrate to deep water at night to take in nutrients and move up to shallow, sunlit water the next day to carry out photosynthesis.

Primary production by estuary plants and other organisms varies geographically and seasonally, as does their relative contribution to the ecosystem as a whole. Estimates of primary production range from 130 to nearly 6,000 grams dry wt/m^2/year for cordgrasses in salt marshes on the Atlantic coast of the United States. See Table 10.1 (p. 225) for a summary of the typical rates of primary production for salt marshes, mangroves, and seagrass beds.

The organic material manufactured by primary producers is made available to consumers mainly in the form of detritus. A distinctive feature of estuarine ecosystems is that most of the animals feed on dead organic matter. Except for insects, geese, and some land animals on the fringes, relatively few herbivores actually graze on salt-marsh plants. Many detritus feeders obtain more energy from the bacteria and other decomposers in the detritus than from the dead organic matter itself. They excrete any detritus that remains undigested, however, returning it to the detritus pool. The surplus detritus is exported to the open ocean and neighboring ecosystems in a process known as **outwelling.** The exported detritus serves as a valuable source of food and nutrients to other ecosystems. The amount of exported detritus varies among estuaries, and some are actually net importers. Nonetheless, outwelling is an important role of estuaries, an additional reason that they should be preserved and protected.

Estuaries include plant-dominated communities with very high primary production. Much of the food manufactured by these plants is made available to consumers by way of detritus.

HUMAN IMPACT ON ESTUARINE COMMUNITIES

The environmental consequences of human intrusion in estuarine communities, particularly in highly productive salt marshes and mangrove forests, have been disastrous. Countless have been obliterated (see Fig. 18.1), and many surviving ones are endangered.

All around the globe estuaries are being dredged to make marinas, artificial harbors, and seaports. Others are filled to create everything from industrial parks and urban development to garbage dumps. The dredging of navigation channels increases the exposure of estuaries to wave action, which often results in the destruction of salt marshes. Another problem is the reduction or elimination of normal freshwater input when rivers are dammed or diverted. About one-third of all estuaries in the United States have disappeared altogether; close to 70% of those in California have been lost.

The same factors that threaten salt marshes are menacing mangrove forests in the tropics. Shrimp mariculture, a booming operation in Southeast Asia, South America, and other tropical and subtropical shores (see "Mariculture," p. 392), has been particularly destructive to mangrove forests. Forests have been destroyed to build the ponds to raise the shrimp. Water from the ponds, which contains large amounts of waste, excess nutrients, and uneaten food, is sometimes flushed out to sea, causing serious pollution.

Mangrove forests have also been cleared at an alarming rate to provide space for crops, urban development, roads, and garbage dumps. The growing use of mangrove wood as fuel and timber in some areas is another cause for concern. Mangrove forests once fringed around 75% of all sheltered tropical coastlines, but 35 to 50% of these mangrove forests have been destroyed. The figure is higher for the highly diverse mangrove forests of Southeast Asia. There is evidence that damage by the 2004 Indian Ocean tsunami (see "Waves That Kill," p. 58) would have not been as severe if mangrove forests had not been cleared in some of these areas.