Chapter 14

Estuaries: Where Rivers Meet the Sea

THEME Patterns

By studying the structure of estuaries, scientists have classified four main types of estuaries, as well as four main estuarine communities.

BIG IDEA

Estuaries have unique physical and chemical properties and are of great importance to both the ecology of oceans and to human society.

About the photo The red mangrove (*Rhizophora mangle*) is common in estuaries in tropical and subtropical regions. Their prop roots provide habitats for fishes and invertebrates.

Vilainecrevette/Alamy

14.1 Origins and Types of Estuaries

Main Idea

The four main types of estuaries are categorized by how they formed.

Key Questions

1. What are estuaries?
2. How do estuaries differ between the Atlantic and Pacific coasts of North America?

VOCABULARY

- estuaries
- drowned river valleys
- coastal plain estuaries
- bayous
- bar-built estuary
- tectonic estuaries
- fjords

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, and are therefore lower in biodiversity, than rocky shores. Nevertheless, they are among the most productive environments on Earth and are the breeding ground of many food species.

Estuaries also rank among the environments most affected by humans. Most natural harbors are estuaries, and many of the world's great cities—New York, London, and Tokyo, among others—developed along them.

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, like the Baltic and Black seas, as estuaries.

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.

DIVE IN!

Where are the world's largest estuaries? Many scientists consider the St. Lawrence River, a 1,200 km waterway that connects the Great Lakes to the Atlantic Ocean, to be the world's largest estuary. The largest estuary in the United States is Chesapeake Bay, which covers over 165,000 km^2. The Rió de la Plata is the world's widest estuary. The mouth of the estuary is about 200 km wide, and the length of the estuary forms the border between Uruguay and Argentina.

Drowned River Valley and Coastal Plain Estuaries

Many estuaries were formed when sea level rose because of the melting of ice at the end of the last ice age during the Pleistocene, 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. 14.1, p. 420), the mouth of the St. Lawrence River in eastern Canada, and the mouth of the River Thames in England. Also considered estuaries are the extensive **bayous** that are affected by tides along the low-lying mouth of the Mississippi River and adjacent coastal areas on the northern Gulf of Mexico.

IN CONTEXT

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

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

- 2.3, Modern Ocean Basins

IN CONTEXT

Pleistocene Geological period that began around 2.5 million years ago and during which sea levels fluctuated during several ice ages.

Bar-Built and Tectonic Estuaries

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 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. 14.1), and along the North Sea coast of the Netherlands and Germany.

Other estuaries, like 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**.

Fjords

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, Greenland, southern Chile, and the South Island of New Zealand (Fig. 14.2). Large glaciers, currently melting faster as a result of global climate change are still found in many fjords, particularly in Alaska, Greenland, and southern Chile.

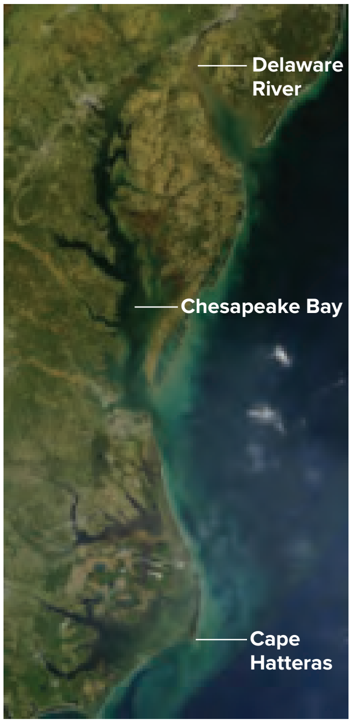


Figure 14.1 Two types of estuaries are found along the eastern coast of the United States. Chesapeake Bay and the mouth of the Delaware River are drowned river valley estuaries; the Cape Hatteras islands form a bar-built estuary.

Figure 14.2 Milford Sound, on the southwestern coast of New Zealand's South Island, is a fjord. 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.

Section Review

1. **Classify** Make a table to classify the different types of estuaries.
2. **Contrast** What are the differences in estuaries on passive margins versus those on active margins?

14.2 Physical Characteristics of Estuaries

Main Idea

Estuaries have wide fluctuations in salinity and dissolved oxygen, and contain various types of sediments.

Key Questions

1. How does salinity change with depth and distance from the ocean in an estuary?
2. What is a salt wedge?
3. How do suspended sediments in estuaries affect water quality and the type of organisms living there?

VOCABULARY

salt wedge

tidal currents

negative 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‰) from rivers or melting glaciers, 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. 14.3).

Salinity also varies with depth in the estuary. The salty seawater is more dense and stays on the bottom. 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. 14.4, p. 422). 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

DIVE IN!

Can seagrasses survive in hypersaline water? Seagrasses are commonly found in subtidal marine habitats, where salinities average 35‰. In Laguna Madre, along Texas's Gulf of Mexico coast, however, salinities routinely reach over 80‰! It is one of only about six coastal hypersaline lagoons in the world. Despite this seemingly inhospitable salinity, Laguna Madre is home to 80% of Texas's seagrass habitat. The shallow lagoon receives ample sunlight year round. The limited connection to the ocean and low fresh water inflow result in low turbidity, a major benefit for seagrasses. The seagrass beds are vital nursery grounds for many fishes, crabs, and shrimps.

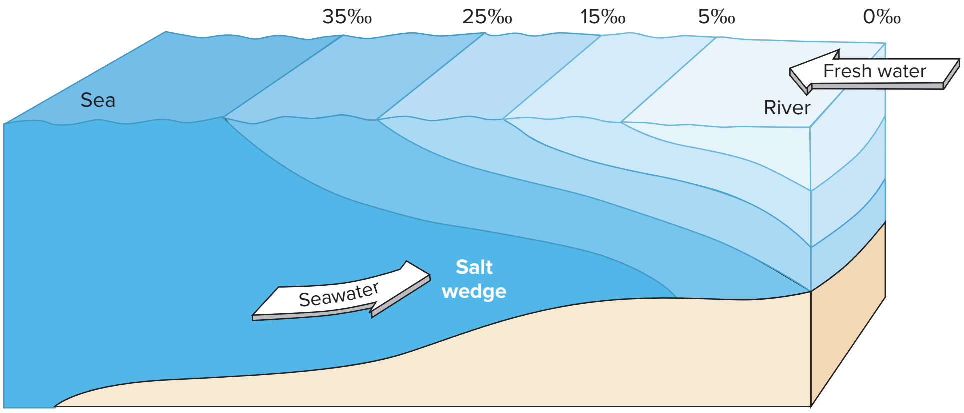


Figure 14.3 Profile of an idealized estuary. The lines across the estuary connect points of similar salinity and are known as *isohalines*.

IN CONTEXT

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.

• 4.3, The Tides

Coriolis Effect Because of Earth's rotation, anything that moves large distances on Earth's surface tends to deflect to the right in the northern hemisphere and to the left in the southern hemisphere.

• 5.1, Atmospheric Circulation

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.

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, including fjords, 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! 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 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 an estuary can be higher than in the surrounding ocean. An example is Laguna Madre, a shallow bar-built estuary with limited access to the open ocean that

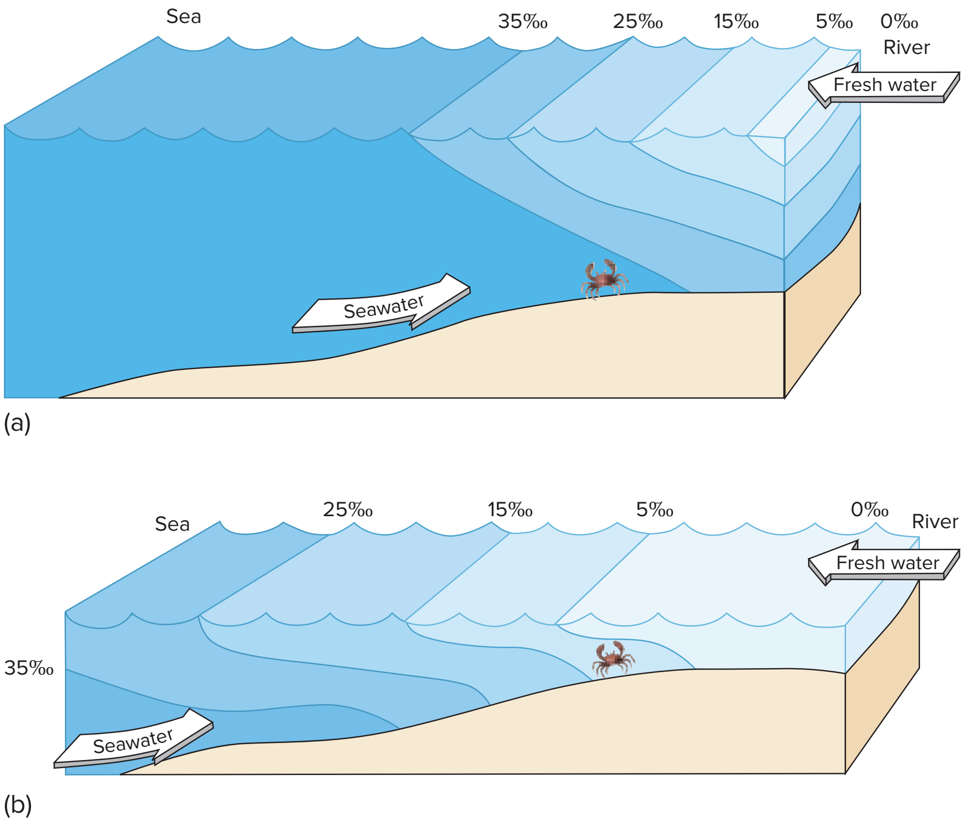


Figure 14.4 The salt wedge in a typical estuary moves in and out with the tide. (a) At high tide the crab is covered by water with a salinity of 35‰. (b) At low tide it is covered by water with a low salinity, between 5‰ and 15‰.

parallels the Texas coast for 185 km. The average salinity is over 50‰ in some areas, and it can 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 can 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, 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. 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.

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 like fjords (see Fig. 14.2, p. 420), 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 can 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 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, like some sponges, that are sensitive to sediment.

Section Review

1. **Relate** How are salt wedges and tidal rhythms related to fluctuations in salinity in estuaries?
2. **Describe** the substrate in estuaries and the organisms found there.

14.3 Estuaries as Ecosystems

VOCABULARY

euryhaline
stenohaline
brackish
succulents
mudflats
salt marshes
wetlands
rhizomes
mangals
pneumatophores
outwelling

Main Idea

There are four main types of estuarine communities, each with organisms specially adapted to live there.

Key Questions

1. What challenges do organisms living in estuaries face?
2. What are pneumatophores?
3. Within estuaries, what is the main form of organic material that is available to consumers?

An estuary may at first look bare, but this 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 animals. Estuarine ecosystems consist of several distinct communities, each with a characteristic assemblage of organisms.

DIVE IN!

Can invasive cordgrass be biologically controlled? Smooth cordgrass (*Spartina alterniflora*) is an invasive species on the Pacific coast of North America, where it outcompetes native salt marsh plants. In an attempt to combat the spread of smooth cordgrass, scientists released a leaf-hopping insect (*Prokelisia*) that feeds on the sap of Spartina. Some studies have shown that *Prokelisia* is effective in reducing smooth cordgrass populations, but worryingly, other studies have found that certain genetic strains are quite tolerant of *Prokelisia*. Biologists and coastal managers must combine biological control with other measures (chemical or manual removal) to reduce smooth cordgrass populations.

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 can be more extreme—they can be colder or more saline, for instance—none changes so rapidly or in so many ways as an estuary. Accumulation of sediment or the opening up of barrier islands as a result of storms can bring even faster changes. 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 as a consequence of fresh water from rivers or melting glaciers (Fig. 14.5). How far they can move up the estuary depends on just how tolerant they are. Most estuarine 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.

Salinity adaptations in animals 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. Some animals

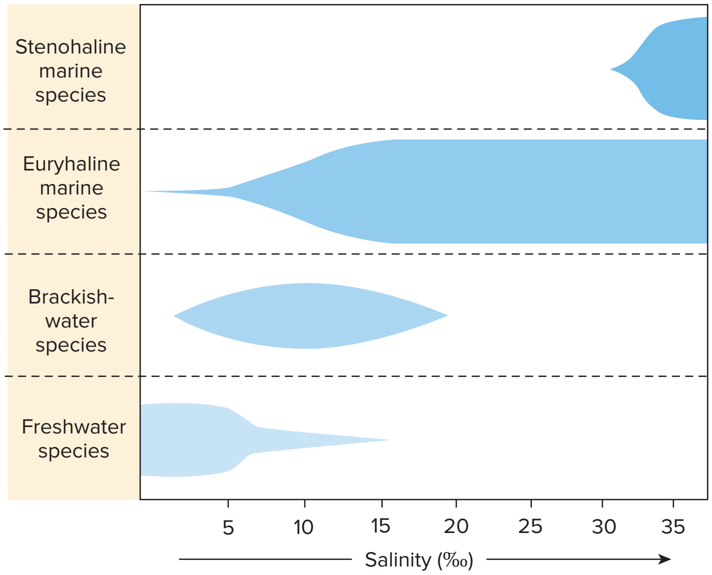


Figure 14.5 Types of species living in an idealized estuary in relation to salinity. The width of the bars represents the relative number of species, or biodiversity.

adapt by simple changes in behavior. They 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.

Soft-bodied estuarine animals, like 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. 14.6, p. 426). 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. They adapt to different salinities by regulating the concentration of their body fluids. For example, when the salinity of the water is lower than that of the blood, osmoregulators 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. 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.

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 like salmon and freshwater eels do not keep *exactly* the same concentration of salts and other solutes in their blood as salinity changes.

Salinity adaptations in plants 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.

IN CONTEXT

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.

- 6.5, Challenges of Life in the Sea

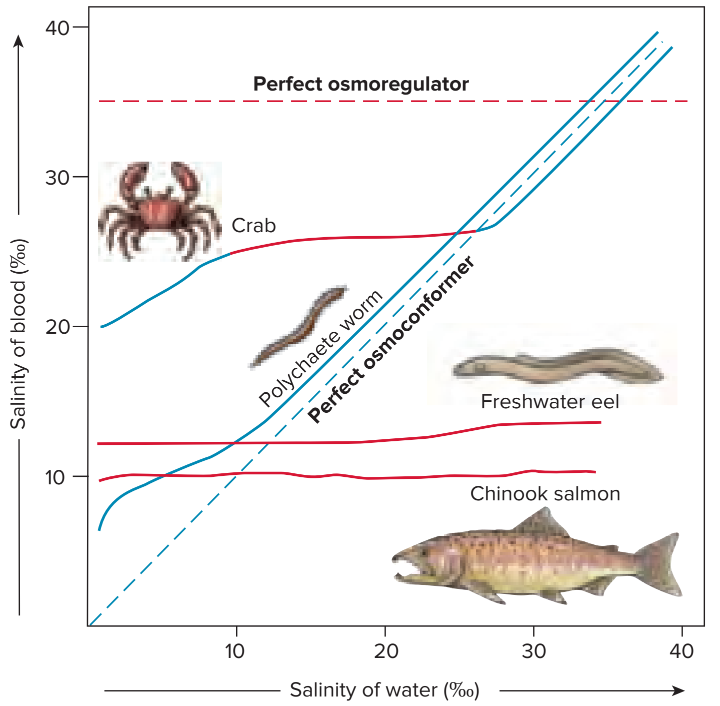


Figure 14.6 The salinity of the body fluids of estuarine animals responds in various ways to the salinity of the surrounding water. In a perfect osmoconformer, the salinity of the blood exactly matches that of the water. In a perfect osmoregulator, blood salinity stays the same no matter what the water salinity is. 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.

Several types of adaptations have evolved in some estuarine plants. Cordgrasses (*Spartina*; Fig. 14.7), other salt-marsh plants, and some mangroves actually excrete excess salts by way of salt glands in their leaves. Some estuarine plants, like pickleweed (*Salicornia*), accumulate large amounts of water to dilute the salts they take up (Fig. 14.8). Such fleshy plants are known as **succulents**.

Adapting to the Mud As discussed in Chapter 13, 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.

Figure 14.7 Cordgrass (*Spartina*) is an important component of salt marshes on both the Atlantic and Pacific coasts of North America and other temperate shores worldwide.

Figure 14.8 Pickleweed (*Salicornia*) is a common succulent plant in salt marshes around the world.

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 estuarine ecosystem.

Estuarine communities show low biodiversity. The relatively low number of estuarine species, however, are typically represented by many individuals. The low biodiversity is therefore compensated by a high biomass, the amount of living material measured as weight. A surprising number of estuarine species, particularly those inhabiting temperate estuaries, are widely distributed around the world. Humans have introduced many of this species, 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 can limit primary production by phyto-plankton, even when the density of plankton is typically very high. Most of the phytoplankton and zooplankton in small estuaries are marine species flushed in and out by the tides. Larger estuaries can 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 commer-cially 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.

IN CONTEXT

Plankton Primary producers (phytoplankton) and consumers (zooplankton) that drift with the currents.

- 12.2, Major Marine Lifestyles and Environments

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

- 6.1, The Ingredients of Life

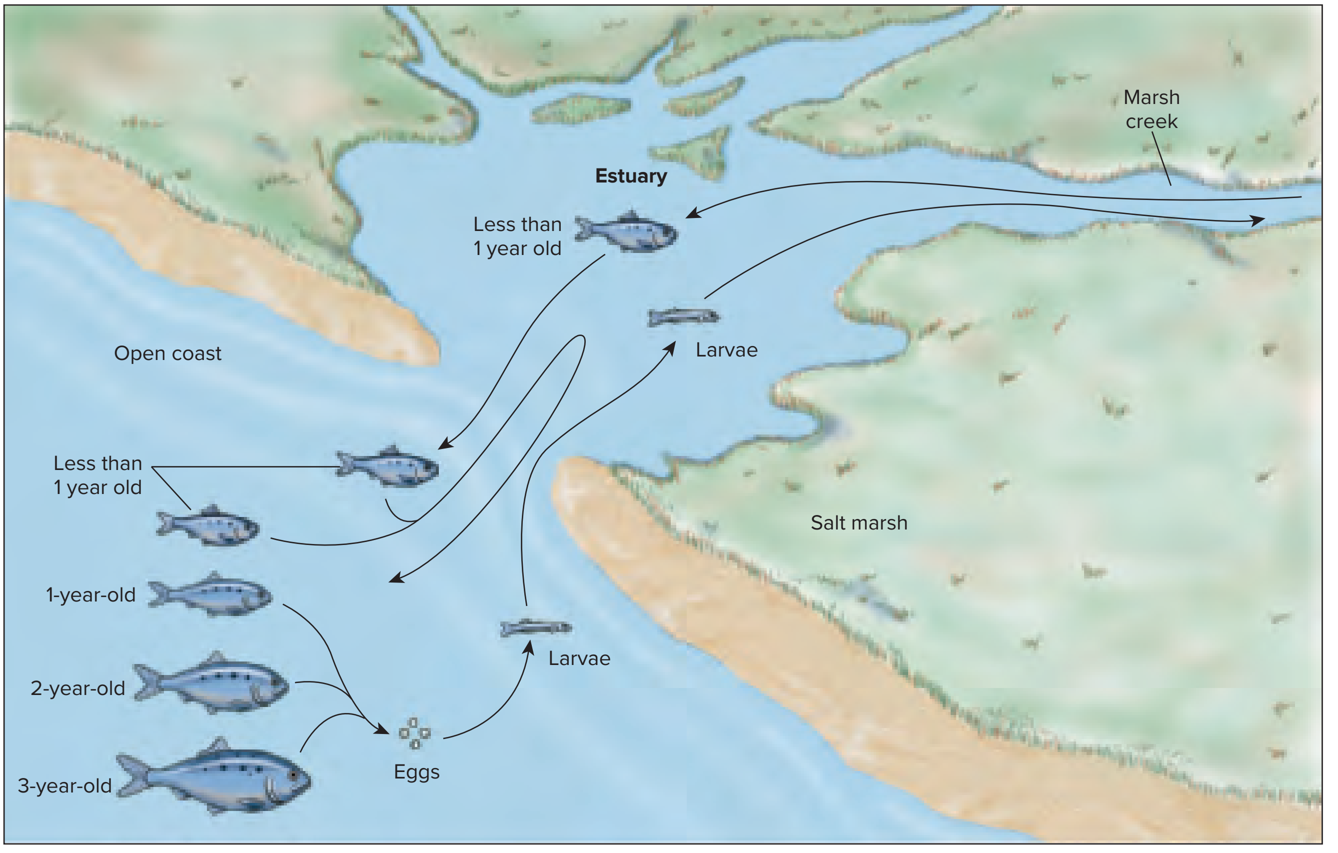


Figure 14.9 The Atlantic menhaden (*Brevoortia tyrannus*) is one of the most important commercial fishes in the United States. Adult fish (one to three years old) spawn offshore and the larvae drift with the tides and currents into estuaries, moving into shallow areas in the salt marshes to grow.

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. 14.9), 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 are one example.

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

Mudflats The bottoms of estuaries that become exposed at low tide often form **mudflats** (see Fig. 14.14, p. 433). 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 can accumulate to create sand flats near river mouths and in the tidal creeks that form as the tide changes. The calmer central part the mudflat contains more fine, silty material. Mudflats can also be found in fjords (see Fig. 14.2), where they occur mostly on the inner margin because the sides of fjords are steep and the bottom rapidly slopes to deep water.

Mudflat communities in estuaries are similar to those on muddy shores. Low tides expose organisms to desiccation, wide variations in temperature, and predation, just as in any other intertidal community. For these reasons mudflat communities could be classified as intertidal communities. In estuaries,

IN CONTEXT

Anadromous Fishes Those that migrate from the sea to spawn in fresh water.

Catadromous Fishes Those that migrate from fresh water to spawn at sea.

- 10.3, Fish Adaptations

however, mudflat organisms must also withstand regular, often drastic, variations in salinity that define estuaries.

Primary producers Although not always evident, primary producers do flourish on mudflats. A few seaweeds—like the green algae *Enteromorpha* (Fig. 14.10) sea lettuce, and some red algae—grow on bits of shell. These and other primary producers can be particularly common during the warmer months. Large numbers of benthic diatoms grow on the mud and 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 and archaea 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 sulfur bacteria, chemosynthetic bacteria that derive energy by breaking down sulfur compounds like hydrogen sulfide (see Table 5.1). Diatoms and bacteria, including photosynthetic bacteria, actually account for most of the primary production on mudflats.

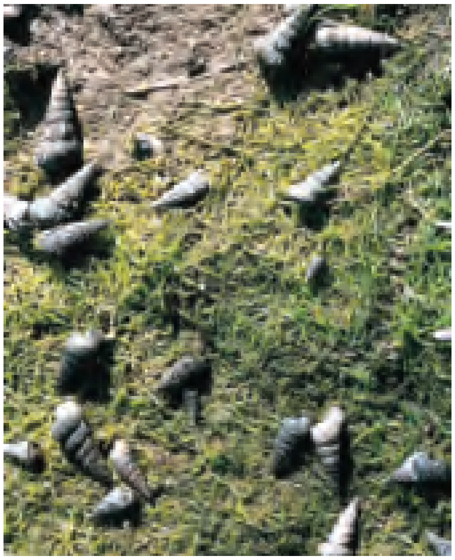


Figure 14.10 The California horn snail (*Cerithidea californica*), a deposit feeder, is abundant on mudflats. The green alga is *Enteromorpha*, which tolerates wide fluctuations in salinity and temperature as well as pollution.

Infauna The dominant animals on mudflats burrow in the sediment and are known as infauna (Fig. 14.11, p. 430). Burrowers, like the fat innkeeper (*Urechis caupo;* Fig. 14.11), actively excavate burrows in the sediment. 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. Though there are not many species of these burrowing animals, they often occur in immense numbers. At low tide their presence is often 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.

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. On the Pacific coast of North America the fat innkeeper secretes a funnel-shaped net of mucus. It pumps water through this net to filter out food. 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.

Many deposit feeders and some other members of the infauna are known as bioturbators because they move and mix sediment when burying or digging.

IN CONTEXT

Chemosynthetic Bacteria Autotrophic bacteria that use energy contained in inorganic compounds rather than sunlight to make organic matter.
- 7.2, Prokaryotes

Detritus Particles of dead organic matter.
- 12.3, The Flow of Energy and Materials

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.
- 9.1, Sponges, Cnidarians, and Comb Jellies

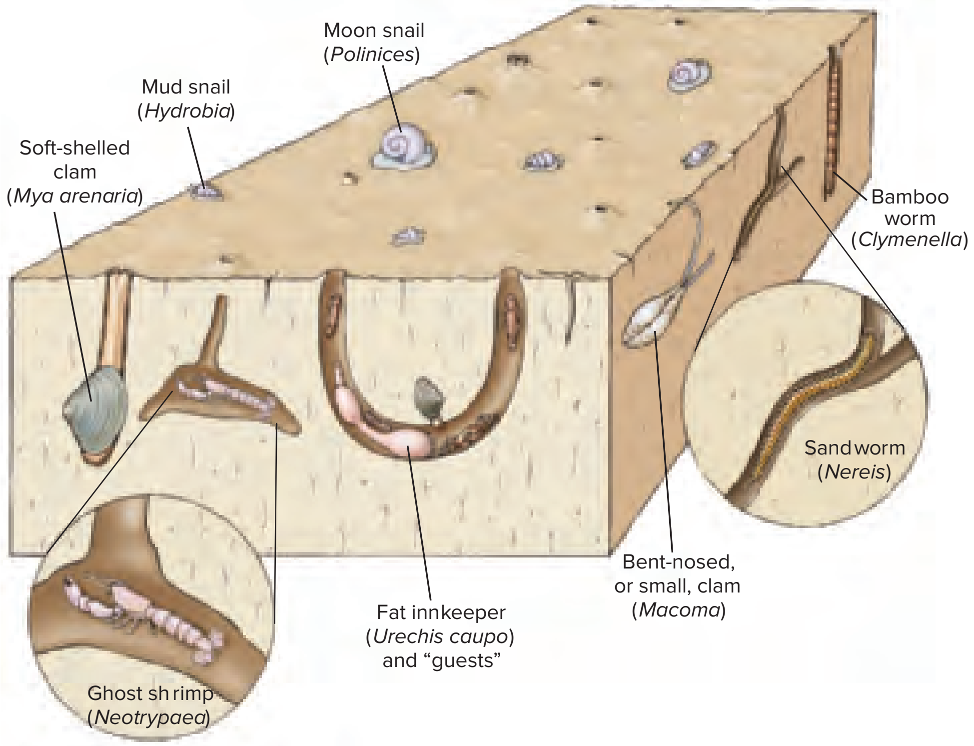


Figure 14.11 Some representative inhabitants of mudflats in temperate estuaries. Many mudflat organisms also can be found on muddy bottoms outside estuaries.

Bioturbation helps in the oxygenation of sediment, a most important role in the case of the typically anoxic sediments of estuaries.

Meiofauna Protozoans, nematodes, and many other minute animals that compose the meiofauna also thrive on detritus. The meiofauna are also known as interstitial animals. The larger burrowing animals, or infauna, include many polychaetes. 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.

Epifauna 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. Crabs and some other animals can temporarily bury by covering themselves with sediment. Bivalves often abound on mudflats. Many are filter feeders that are also found on muddy and sandy shores outside estuaries. Examples from temperate waters are the quahog, or hard clam (*Mercenaria mercenaria*), the soft-shelled clam (*Mya arenaria;* Fig. 14.11), and razor clams. Some of these are of considerable commercial importance. Bent-nosed, or small, clams (*Macoma;* Fig. 14.11) are deposit feeders that use their long incurrent siphons to vacuum the surface.

The ghost and mud (*Upogebia*) shrimps make elaborate burrows that, as bioturbators, 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. They process the mud and extract the detritus, which they eat.

Fiddler on the Mud

What lives in mud, feeds on mud, and finds mates by calling and waving across the mud? Of course—fiddler crabs!— best known as the ultimate mud aficionados.

The many species of fiddler crabs (*Uca*) are inhabitants of mud and sand flats in estuaries and other sheltered coasts. They are found mostly in the tropics and subtropics, but can be found as far north from the equator as Massachusetts and as far south as Argentina. Fiddlers are deposit feeders, which consume detrital food sources that have been passively deposited in the mud. Fiddler crabs feed at low tide when tidal flats are exposed to air. The detritus in the mud is extracted with the help of brush-like mouthparts. Water is pumped from the gill chambers into the mouth to make the lighter detritus float and thus help separate it from the mud. The detritus is swallowed, and the 'clean' mud is spat out on the substrate in neat little balls.

The importance of tides Fiddlers are active at low tide and retreat into their burrows at high tide. Each burrow has an entrance (revealed by the neat little balls of mud around it) that the occupant can plug when the tide comes in. At the next low tide, crabs emerge from home to feed and do whatever healthy, active fiddlers like to do. The tidal cycle is so ingrained in the crabs that if crabs are taken away and isolated in an environment of constant light and temperature, they will continue to be active at the times that correspond to low tide and sit quietly when they were expected to be in their burrows at high tide! Not only activity patterns but color changes that normally take place in their natural environment (darker color during the day, lighter at night) continue to be observed in isolation. These patterns are examples of biological clocks, repeated rhythms that are synchronized with time. In the case of fiddlers, activity patterns and color changes are synchronized with tides and with day-night changes.

The claw Fiddlers have an exciting sex life. Males feature one tremendously enlarged claw. It is brightly colored or highlighted with markings in many species. Males use their big claw to advertise their availability to females. They also use the claw to threaten away any other males that may be around. They wave the claw at low tide on territories established around their burrows. Claw-waving gets so heated sometimes that a whole mudflat seems to move up and down with hundreds of displaying males. Males entice females into their burrows, and a female may visit a few pads before deciding on a particular one. Males often fight for prospective mates but are also known to establish partnerships with neighbor males to defend their territories against intruders. Fighting with a stronger neighbor may cause a fiddler to end up with a lost claw, a more costly alternative than peaceful cooperation. A lost claw means disaster – the male can neither attract a mate nor defend himself. It takes many molts to regenerate one. A fiddler with a lost claw is also not as cool as his neighbor- literally. The enlarged claw is also used in temperature regulation, and crabs with an enlarged claw cool faster than those without it. On the other hand, while a large claw does have its advantages for attracting potential mates, it can also attract potential predators. A large claw would be easier for a bird to grab than a small one.

In those areas co-inhabited by several species of fiddlers, waving is used to prevent a male from attracting females of the wrong species. Some species wave up and down, others sideways. The angle and frequency of waving also vary, and bowing, fancy steps, and other body movements may form part of the ritual. Some beat the claw on the ground, and males of many species even produce sound by vibrating a joint of the large claw. It pays to advertise!

Signaling in a male fiddler crab (*Uca*)

Figure 14.12 Differences in the bill length of wading shorebirds from the west coast of North America allow them to feed on particular mudflat animals.

Some animals live on the surface of the mud or move in and out with the tide. These include deposit feeders like mud snails (*Cerithidea, Hydrobia;* Figs. 14.10 and 14.11 pp. 429-430), amphipods, and shrimps. Carnivores include polychaete worms (*Nereis;* Fig. 14.11), moon snails (*Polinices;* Fig. 14.11) and other predatory snails and swimming crabs.

Predators 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. 14.12 and 14.13). These include the willet, godwits, dowitchers, and many species of plovers and sandpipers such a curlews and phalaropes. They feed on polychaetes, ghost shrimps and other small crustaceans, clams, and mud snails. Oystercatchers specialize on clams and other bivalves.

Figure 14.13 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.

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 (see Fig. 14.12). In addition, shorebirds use different strategies to locate their food. Birds like sandpipers rely mostly on their bills, probing in the mud as they walk around (Fig. 14.13a). Others, like plovers, use their eyesight to detect slight movements on the surface of the mud (Fig. 14.13b). 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 swimming prey. Birds that feed by swimming or diving in the estuary, like ducks, terns, and gulls, are often seen resting on mudflats.

Salt Marshes Estuaries in temperate and subarctic regions worldwide are usually bordered by extensive grassy areas that extend inland from the mudflats. These intertidal areas are partially flooded at high tide and are known as **salt marshes**, or sometimes tidal marshes (Fig. 14.14). Sometimes they are

IN CONTEXT

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

- 12.1, The Organization of Communities

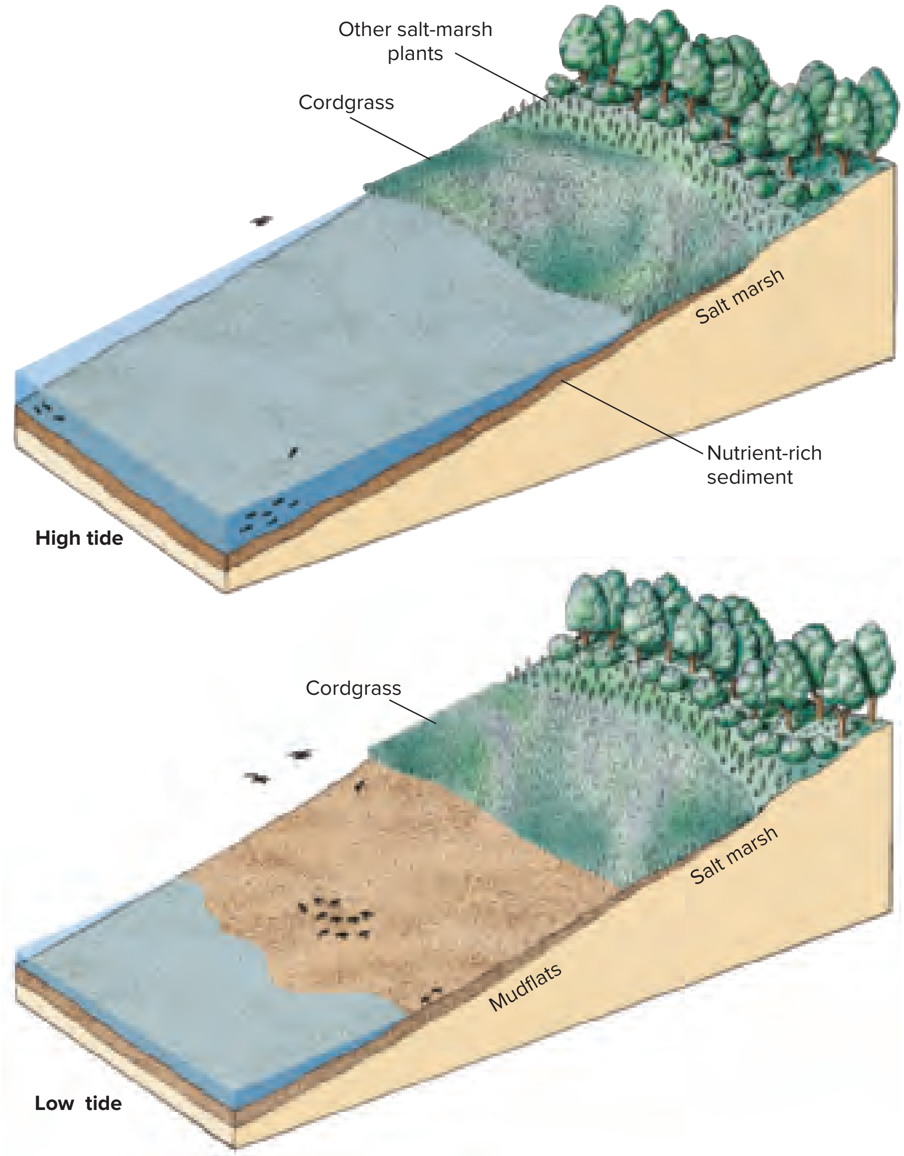


Figure 14.14 The daily tides play a crucial role in salt marshes. They help circulate detritus and nutrients and expose mudflat organisms to predation by shorebirds and other animals.

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. Salt marshes may also develop along the inner margins of fjords as long as there is an accumulation of muddy sediments free from the ice of glaciers. Tidal creeks, freshwater streams, and shallow pools frequently cut through the marsh. Salt marshes are typically replaced by mangrove forests along sheltered coasts in the tropics.

In North America, salt marshes are particularly extensive along the Atlantic and Gulf of Mexico coasts (see foldout map of North America at the end of the book). The broad estuaries and shallow, protected 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, exposed to wave action, so that 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 live on a muddy bottom, but the mud 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

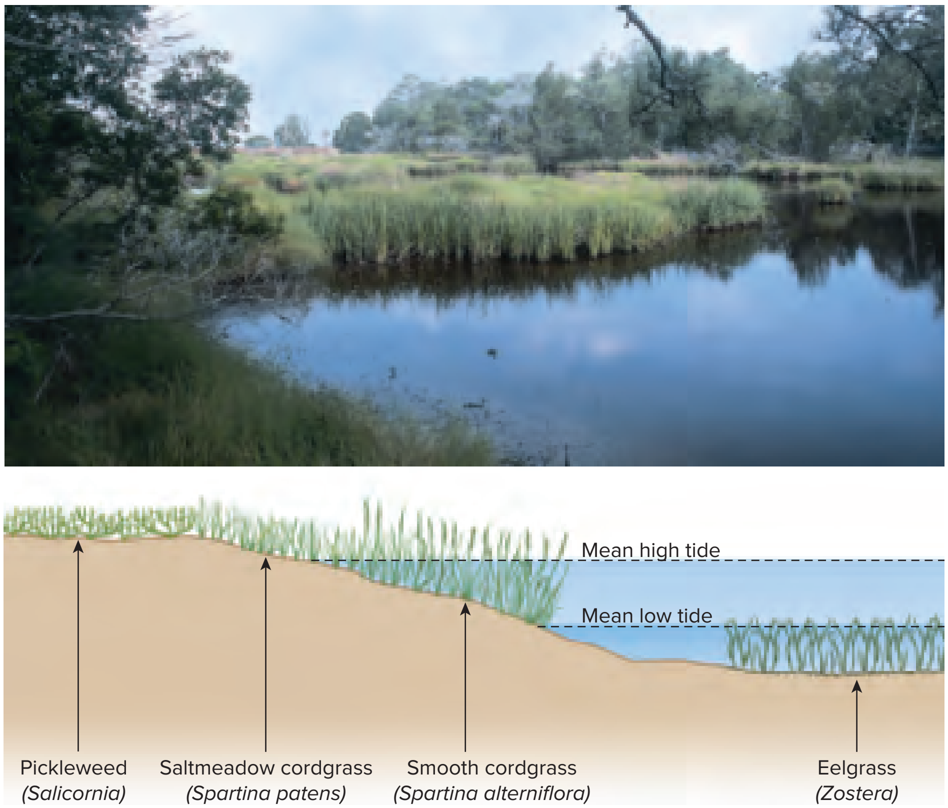


Figure 14.15 A salt marsh near Atlantic Beach, North Carolina. As in other Atlantic marshes, the smooth cordgrass (*Spartina alterniflora*) occupies the edge of the marsh that is flooded the most by seawater. It is replaced higher up in the marsh by saltmeadow grass, or salt-marsh hay (*Spartina patens*), a shorter and finer grass that is less salt tolerant and can form extensive meadows. It grows where the marsh is flooded only at high tide.

plants in salt marshes (Fig. 14.15). 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 can become particularly high at intermediate heights as a result of higher evaporation in marshes closer to hot, dry regions. This can result in areas bare of vegetation.

Salt marsh plants Cordgrasses (smooth cordgrass, *Spartina alterniflora*, on the Atlantic coast; California cordgrass, *Spartina foliosa,* on the Pacific coast; see Fig. 14.7) are typically the most common plants along the seaward limit of the salt marsh, where it meets the mudflats (Figs. 14.14 and 14.15). 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, or **rhizomes**, that stretch out underground. The leaves and roots develop from the stems. Rhizomes spread horizontally, farming extensive growths of genetically identical plants, or clones. Roots just below the soil also take in oxygen from the air, a crucial adaptation for living anoxic sediments.

Cordgrass can 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 because such a high density of plant biomass, 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.

Cordgrass gives way to other plants in the higher parts of the marsh. On the Atlantic coast, a second species of cordgrass (the salt-meadow, or salt-marsh hay, *Spartina patens*) dominates (Fig. 14.15), but rushes, 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. 14.8, p. 427). 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, like salt grasses 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.

Bacteria 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 marsh animals Some burrowing animals of mudflats also inhabit salt marshes. In addition, nematodes, small crustaceans, larvae of land insects, and

IN CONTEXT

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

• 7.2, Prokaryotes

Figure 14.16 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.

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 sediments, another example of bioturbation. Other marsh crabs 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 and marsh periwinkles 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. 14.16). Killifishes and juvenile silversides 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 like 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. Mangroves are flowering land plants adapted to live in the intertidal. These trees and shrubs often form dense forests called **mangals** to distinguish them from, the actual plants themselves, or mangroves. Mangroves are typical of tropical and subtropical regions, where they replace the temperate salt marshes. The two communities nevertheless coexist in some areas, as on the northern coast of the Gulf of Mexico, southeastern Australia, and northern New Zealand.

Global distribution 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. Mangroves are killed by frost so their worldwide northern and southern limits are determined by low temperatures. A change in the distribution of mangroves as a result of global climate change has already been noted. Florida mangroves have been growing father north along the Atlantic coast, those in southern Australia have been expanding into salt marshes. Similar extensions of the geographical range of mangroves have also been recorded in Perú and on the Pacific coast of Mexico. Mangrove forests are been directly affected by humans in other ways.

Mangroves grow on protected coasts where muddy sediments accumulate. Though mangroves usually grow in tropical and subtropical estuaries, they are not restricted to them. Nevertheless, all mangroves require fresh water. 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.

The Indo-West Pacific region has the world's most extensive mangrove forests with by far the largest number of mangrove species, which include species of *Aegiceras, Avicennia, Ceriops, Rhizophora,* and *Sonneratia*. Mangrove forests extend as far as 320 km 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.

IN CONTEXT

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

Diversity 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. 14.17) and is easily identified by its peculiar prop roots, which support the trees very much like stilts. Flexible aerial roots drop down from the higher branches, helping extend the tree laterally. The trees can be as tall as 9 m. Under optimal conditions they form dense forests noted for their high primary production as a result of such high plant biomass. Other species of *Rhizophora* are found on tropical coasts around the world.

Along the Atlantic and Pacific coasts of the western hemisphere and the Atlantic coast of Africa, the black mangrove (*Avicennia germinans*) and the white mangrove (*Laguncularia racemosa*) live inland from the red mangrove (Fig. 14.17). 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. 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.

As land plants living at the sea edge, mangroves live under very stressful conditions. They are nevertheless adapted to the marine environment in several ways. Mangroves must get rid of salts from the water that is taken in by the roots.

Figure 14.17 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*).

Most salts are actually not taken in by the roots of the red mangrove, a process that requires energy. Salt glands on the leaves of the black and white mangroves and several other mangrove species excrete salts, with salt crystals usually visible on the leaves as the drops containing the salts dry up (Fig. 14.18). The salt glands of the white mangrove are clearly visible as two bumps at the base of each leaf. Living in anoxic mud is also stressful, and the roots of all mangrove species have different types of root extensions, like the prop-roots of the red mangrove, for obtaining oxygen from the atmosphere. Several species of mangroves, like the black mangrove of the tropical western hemisphere and the Atlantic coast of Africa and the Indo-West Pacific species of *Sonneratia,* develop **pneumatophores**, conspicuous, unbranched extensions of the roots that grow upward from the anoxic mud to help aerate the plant tissues (Fig. 14.19).

Mangrove forest communities Many marine and land animals live in mangrove forests. Crabs are particularly common. Many feed on the abundant leaf litter that accumulates below the mangrove trees. Some species of crabs also feed on leaves, flowers, and seedlings still attached to mangrove trees. Mangrove crabs spend most of their lives on land, but when eggs are ready to hatch, females must release the larvae at sea.

Many types of organisms attach to, or take shelter among, the submerged mangrove roots (Fig. 14.20). These include cyanobacteria, seaweeds, sponges, polychaetes, gastropods, oysters, barnacles, and tunicates. Particularly rich in attached organisms are mangrove roots subject to a wide tidal range. Large sponges living on the roots have been found to provide significant amounts of

Figure 14.18 Leaves of the Indo-West Pacific black mangrove (*Aegiceras corniculatum*) from Australia, showing the salt crystals that form as the salty secretions of the salt glands dry up under the sun.

Figure 14.19 Pneumatophores, the vertical extensions of shallow roots, obtain additional oxygen in mangroves like *Sonneratia alba* in Palau.

(l)James Harrop/E+/Getty Images, (r)©Peter Castro nitrogen compounds to mangrove plants. They also help protect the roots from burrowing isopods, which otherwise can cause considerable damage.

Figure 14.20 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*).

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. Several species of fiddler crabs excavate burrows in the mud. As in temperate mudflats and salt marshes, burrowing crabs help oxygenate the sediment. Mudskippers (*Periophthalmus;* Fig. 14.21) 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.

The channels that cross mangrove forests are rich nurseries for many species of commercially important shrimps, spiny lobsters, crabs, and fishes (Fig. 14.22, p. 440). They are also nurseries for coral reef fishes. Several species of oysters and other bivalve molluscs that live on or even within the roots of mangroves are used as food in some places around the world.

Many species of land animals use mangrove forests for shelter and food. Insects feed on leaves, flowers, and the attached seedlings, while bees and bats feed on the pollen and nectar of some mangrove flowers. Birds make their homes in the branches and feed on fishes, crabs, and other prey. Snakes, frogs, lizards, bats, and other land animals also live in the mangrove trees.

Figure 14.21 A mudskipper (*Periophthalmus*) from the mudflats of a mangrove forest in Singapore. Its protruding eyes are adapted to see in air. Each eye can be retracted into a moist pocket to keep it from drying out.

Figure 14.22 Small fishes, many of which are juveniles of commercially important species, seek shelter from predators and find food among the roots of mangrove. Shown here is the red mangrove (*Rhizophora mangle*) in a Florida mangrove forest.

Bianca Lavies/National Geographic/Getty Images

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 and fungi. 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.

Besides its ecological importance, mangrove forests have an incalculable value to humans. They contribute significant portions of the economy of many developing nations, not only in terms of fishery resources but as a source of timber, charcoal, and revenue from the tourist industry. Mangrove forests improve water quality by removing pollutants and particulate matter and help protect coasts from wave action and increasing sea levels. There is evidence that damage by the 2004 Indian Ocean tsunami would have not been as severe if mangrove forests had not been cleared in some of these areas.

Other Estuarine Communities The bottom of estuaries beyond the intertidal mudflats and salt marshes is typically muddy and inhabited by organisms similar to those characteristic of muddy subtidal communities. Brackish-water species are gradually replaced by euryhaline marine species and ultimately by stenohaline marine species (see Fig. 14.5). Fjord bottoms are typically anoxic and support communities there are characterized by low biodiversity but high biomass. The abrasive effect of drift ice from glaciers is also an important factor in some fjords. Deep-water coral "reefs" high in biodiversity have nevertheless been discovered in some fjords.

Seagrasses 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, which is restricted to temperate waters, and turtle grass, 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 meadows are not restricted to estuaries and are discussed in more detail in Chapter 15.

Oyster reefs Oysters can form extensive beds on the muddy bottoms of estuaries in temperate waters in North America, Europe, and Australia. These oyster reefs, sometimes known by the more general name of shellfish reefs, gradually develop as successive generations of oysters grow on the shells of their predecessors (Fig. 14.23). 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 beds, though the mussels require a hard substrate for attachment.

Oyster reefs, once an important feature of many estuaries along the Atlantic coast of North America, have sharply declined as a result of pollution, overharvesting, disease, and disturbance by boats. This decline has had a major impact on the biodiversity in these estuarine communities. In addition to providing a habitat to many species, oysters increase the clarity and light transmission of water for seagrasses and other plants by filtering the water; an adult oyster filters as much as 270 liters of water daily. Oyster reefs also help protect shores from erosion by waves.

Figure 14.23 An oyster reef formed by the eastern oyster (*Crassostrea virginica*) on the Atlantic coast of the United States, exposed at low tide.

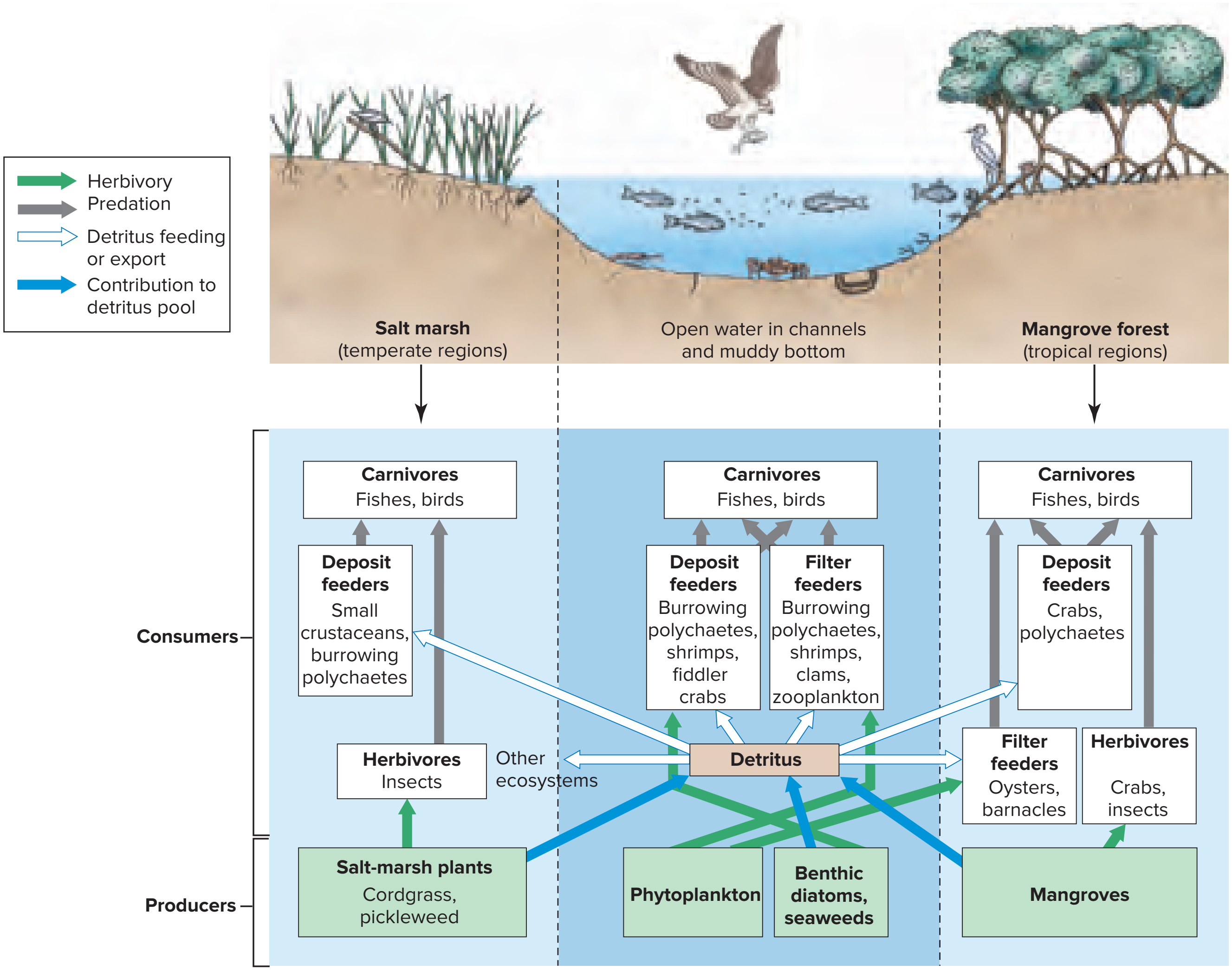


Figure 14.24 Generalized food webs in estuarine ecosystems. Salt marshes (left) occur in temperate regions, mangroves (right) in the tropics.

Feeding Interactions Among Estuarine Organisms

Though estuaries are low in biodiversity when compared to rocky shores, they reap the benefits of living in a very productive ecosystem. The generalized food webs shown in Figure 14.24 summarize the feeding relationships among different organisms in estuarine ecosystems.

Productivity 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 high biomass 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.

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 weight/m^2/year for cordgrasses in salt marshes on the Atlantic coast of the United States. See Table 12.1 for a summary of the typical rates of primary production for salt marshes, mangroves, and seagrass meadows.

Detritus-based Food Web 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.

Section Review

1. **Identify** What are some of the adaptations estuarine plants and animals have to manage the fluctuations in salinity?
2. **Summarize** What are the four main types of estuarine communities and the dominant organisms in each?

Estuary	Substrate	Producers	Consumers
Open water			
Mudflats			
Salt marshes			
Mangroves			

3. **Explain** Why do estuaries have such high primary productivity?

14.4 Human Impact on Estuarine Communities

VOCABULARY

invasive species

eutrophication

Main Idea

Estuaries provide many important functions, both to the marine environment and to humans, which are lost and when humans impact estuaries by dredging or filling them.

Key Questions

1. What are the ecosystems services of estuaries?
2. How much of estuaries have been lost worldwide due to human activities?

DIVE IN!

How might rising sea level affect estuaries? The current average rate of sea level rise is about 3.2 mm per year. Scientists are concerned about the potential impacts of rising sea level on estuaries. As the sea level rises, ocean water will reach further upstream, increasing salinity in the upper reaches of estuaries. This could change the composition of estuarine communities, resulting in the local extiction or migration of species that cannot withstand higher salinities. The types of habitats within an estuary could also shift. With rising sea levels, mudflats, salt marshes, and mangrove forests that are regularly exposed at low tide would be covered and destroyed by exposure to wave action.

The worldwide economic value of marine wetlands as sources of food and as nurseries of many food species, in recreation and tourism, as sources of wood and other materials, in protection against storms and erosion, as well as in the maintenance of biodiversity and water quality, is enormous. Estuaries also serve as critical stopovers for migratory seabirds around the world. Furthermore, mangrove forests and seagrass meadows that often develop in tropical estuaries help reduce terrestrial runoff that protects coral reefs from sedimentation. Yet, the environmental consequences of human intrusion in marine wetlands, particularly in highly productive salt marshes and mangrove forests, have been disastrous. Countless have been obliterated, and many surviving ones are in danger of disappearing. What's more, oyster reefs are now considered by many as the world's most imperiled marine habitat.

Threats to Estuaries

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 in some estuaries is the reduction or elimination of normal freshwater input when rivers are dammed or diverted. Sediment input from rivers is decreased so that erosion of sediments by tides is not replenished. The opposite can also be a problem. Deforestation and agriculture brings about an increase in sediment, which in estuaries like Chesapeake Bay, decreases water quality and increases pollution.

Threats to Salt Marshes Oil spills can be particularly harmful to salt marshes, as evidenced by the 2010 *Deepwater Horizon* spill in the Gulf of Mexico. Wetlands along the Louisiana coast of the Gulf of Mexico have also

Restoration of Salt Marshes

The destruction of salt marshes by human activities is a major worldwide problem. The restoration of disturbed salt marshes to their natural condition is being carried out as part of efforts to protect and preserve coastal wetlands. Some biologists encourage the natural regeneration of disturbed salt marshes, but others prefer to accelerate recovery by replanting dominant species, particularly cordgrass (*Spartina*). For example, the University of Southern Mississippi operates a nursery that grows salt marsh plants that are transplanted in damaged marshes.

Does restoration work? The success of replanting depends on factors such as wave action and tides, water chemistry (salinity, dissolved nutrients), and the substrate (slope, sediment size, oxygen content). Recovery can take many years, and the length of the recovery period depends on the degree of disturbance, environmental factors, and the relative maturity of marshes. The more mature marshes take the longest to recover. Restoration does not always lead to a community where species diversity matches that of a targeted natural state. Invasive plants, feral animals, unusual weather, and other unpredictable disruptions often disrupt restoration. Systematic monitoring is vital to restoration efforts.

Why restore marshes? The technology behind salt-marsh restoration is also being applied other habitats. Flooded areas previously cut off from the ocean, construction mitigation projects, and salt marshes affected by oil spills are habitats that can benefit from restoration. Restoring salt marshes can defend against erosion, provide flood management, and create habitats for seabirds and other wildlife.

Restoration is also undertaken in salt marshes impacted by invasive species of cordgrass, as in the case of smooth cordgrass (*Spartina alterniflora*). *S. alterniflora* is native to the Atlantic coast of North America and has become a pest on the Pacific coast. Seeds were probably accidentally introduced when oysters were transplanted to the Pacific, but some may have come in ships' ballast water. In some areas of the Pacific coast the plant was intentionally introduced for erosion control. Smooth cordgrass has spread over mudflats, tidal creeks, oyster grounds, and eelgrass beds. Its roots accumulate additional sediment, which turns natural habitats into swampy land within a decade or so. Smooth cordgrass can hybridize with the native Pacific cordgrass (*Spartina foliosa*), and the hybrids are taller, spread into deeper water, and release more pollen and seeds than the native cordgrass. Spreading is accelerated because smooth cordgrass, unlike the native species, can self-pollinate. These hybrids are by now the dominant cordgrass in many Pacific salt marshes. Efforts to control invasive cordgrass are being undertaken in places such as San Francisco Bay and Willapa Bay on the west coast of the United States.

been gradually eroded away as the result of the cutting of canals to install pipelines and haul oil drilling equipment. Another threat, particularly along the Pacific coast of North America, is the effect of cordgrass **invasive species**.

About one-third of all salt marshes in the United States have disappeared altogether; close to 70% of those in California have been lost. Similar or even higher losses have been documented in many countries. Erosion and flooding as a result of sea level rise brought about by global climate change is another threat to salt marshes.

Threats to Mangrove Forests The same factors that threaten salt marshes are menacing mangrove forests in the tropics. Mangrove forests once fringed around 75% of all sheltered tropical coastlines, but 35 to 50% of these forests have been destroyed. The figure is higher for the very diverse mangrove forests of Southeast Asia. It has been estimated that mangrove forests are disappearing at an annual rate of at least 1 to 2% worldwide, possibly higher than coral reefs and tropical rain forests. The United Nations' Environment Program estimated in 2014 that about 20% of mangrove forests had been lost worldwide between 1980 and 2005.

Mangrove forests have been cleared at this alarming rate to provide space for agriculture, urban and industrial development, roads, and garbage dumps. Shrimp aquaculture, a booming operation and an important source of revenue and employment in the developing nations of Southeast Asia, South America, and other tropical and subtropical regions, has nevertheless been particularly destructive. Forests have been destroyed to build the ponds to raise the shrimp; many others have been built to raise fish (Fig. 14.25). Water from the ponds, which contains large amounts of waste, excess nutrients, and uneaten food, is often flushed out to sea, causing serious pollution. Excess nutrients are responsible for **eutrophication**, the increased growth of algae as a consequence of excess nutrients.

The growing use of mangrove wood as fuel and timber in some areas is another cause for concern. Mangrove forests have also been impacted by increased boat traffic, oil spills, and pollution by plastics and solid waste

Figure 14.25 Shrimp and fish aquaculture has been responsible for the destruction of many mangrove forests, particularly in Southeast Asia and South America. Waste that is released into coastal waters from ponds like this, where fish are farmed, is an important source of pollution.

Figure 14.26 Solid waste, especially plastics and other durable materials, often accumulate in mangrove forests. Some of the waste is brought in by high tide, but forests are sometimes used as convenient garbage dumps.

(Fig. 14.26). Together with salt marshes, it has been predicted that mangrove forests will be among the first marine communities to be adversely affected by sea level rise due to global climate change. Increased temperatures, however, are promoting the extension of mangroves further north or south from the Equator.

Mangrove forests remove carbon dioxide (CO_2) from the atmosphere and trap an unusually high proportion of their primary production as organic carbon in the leaves and detritus that are deposited in the sediments. When the mangroves are destroyed, much of this trapped CO_2 is released back to the atmosphere when the organic matter decays. Mangrove deforestation accounts for an estimated 10% of all CO_2 emissions caused by deforestation, even though mangrove forests occupy only 0.7% of the area of tropical forests.

Conservation Efforts

Conservation efforts through protective legislation, restoration projects involving the mass replanting of mangrove seedlings, proper management, and the creation of marine protected areas and reserves have nevertheless resulted in a reduction in the rate of loss of mangrove forests in some areas. Of particular importance is the development of sustainable exploitations of fishery resources in developing countries, where economic development is often in conflict with the conservation of natural resources. Many conservation programs thus emphasize the education of local communities on the economic and ecological values of mangrove forests, and on providing economic alternatives to practices that lead to mangrove destruction.

Section Review

1. **Describe** How have human activities led to the reduction of estuaries worldwide?
2. **Relate** How might the reduction of mangrove forests affect global climate change?

Chapter 14 Review

REVIEW QUESTIONS

Multiple Choice

1. Estuarine organisms that are euryhaline
   - a. tolerate only a narrow range of salinities.
   - b. tolerate a wide range of salinities.
   - c. are limited to the upper end of an estuary.
   - d. are limited to the lower end of an estuary.

2. Some estuarine plants accumulate large amounts of water to dilute the salts they take up. Fleshy plants such as these are known as
   - a. anadromous.
   - b. catadromous.
   - c. osmoregualtors.
   - d. succulents.

3. Which type of estuarine community consists of extensive beds of filter feeders on the muddy bottom?
   - a. mangrove forests
   - b. mudflats
   - c. oyster reefs
   - d. seagrass beds

Short Answer

4. What factors affect the behavior of water masses and circulation in estuaries?

5. What are the ecosystem services of mangroves? What conservation efforts help protect mangroves?

Critical Thinking

6. A proposal is made to deepen the entrance and main channel of an estuary. What do you think will happen to the salt marshes that surround the channel? What do you predict will happen to the primary production of the estuary as a whole?

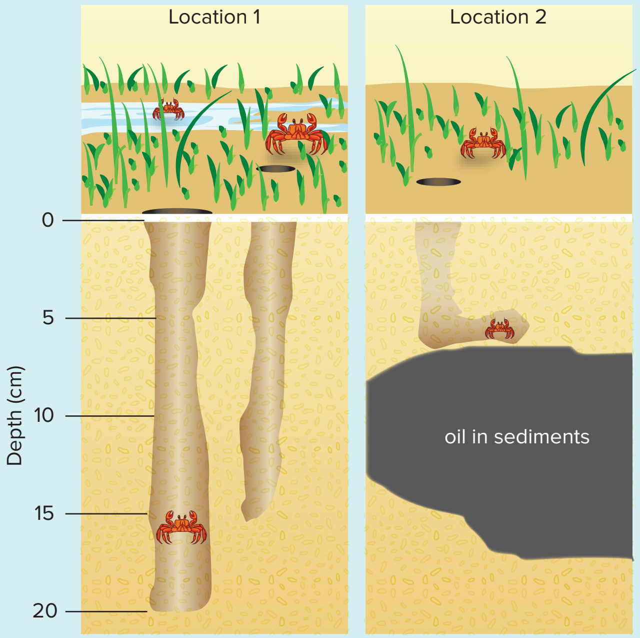
7. Some of the organic material manufactured in estuarine communities is exported to other ecosystems. What type of ecosystems receive this material? How is this material transported?

DATA ANALYSIS LAB

Can an oil spill affect salt marshes decades later? In 1969, 189,000 gallons of oil was spilled onto the coast of Massachusetts. In 2000, scientists found around 100 kg of oil remaining in salt marsh sediments. Biologists collected data on the depth and shape of fiddler crab burrows in two salt marsh locations—one where oil from the spill was still present and one which had never been affected by the spill.

Data and Observations

The illustration shows the depth and shape of the burrows at Location 1 (never affected by the oil spill) and Location 2 (oil from spill still present in sediment).



Think Critically

1. What are some differences in the fiddler crab burrows between the two locations?

2. What effect do you think a shallower burrow would have on predation on fiddler crabs?

3. Fiddler crabs are bioturbators who move sediments around as they dig their burrows. Why would any affects on this process be important to salt marsh communities?

**Data obtained from: Reddy, C., 2007. Still toxic after all these years. Oceanus, vol. 45, no. 3, July, pp. 26–29.*