Introduction to Ocean Sciences

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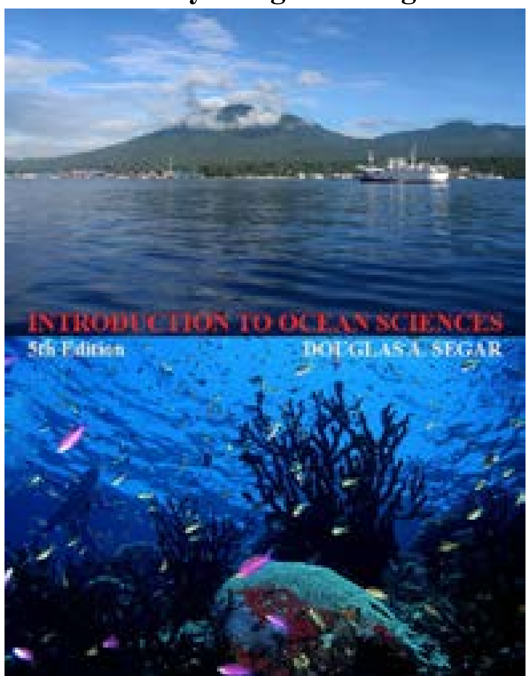

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CHAPTER 13

Coastal Oceans and Estuaries

CRITICAL CONCEPTS USED IN THIS CHAPTER
CC5 Transfer and Storage of Heat by Water
CC8 Residence Time
CC11 Chaos
CC12 The Coriolis Effect
CC15 Food Chain Efficiency
CC16 Maximum Sustainable Yield

The oceans and the land are intimately related where they meet. The vegetation, rocks, beach, waves, clouds, kelp seen floating on the water surface, and all the unseen plants and animals living within the coastal waters in this California bay are the result of processes that take place in the coastal oceans and estuaries.

In the coastal oceans, **salinity,** temperature, water **density, turbidity,** chemical composition, and water movements are affected by freshwater discharges from rivers, and by the physical presence of land and shallow seafloor. These influences vary in **spatial** extent as seasonal changes in rainfall affect **runoff** and river input of freshwater and as **weather** and seasonal changes in winds affect wind-driven **currents**. Hence, the boundaries of the **coastal zone** are not defined precisely. On **passive margins** where the **continental shelf** is wide, the coastal zone is generally the area between the **coastline** and the continental **shelf break.** Where large river discharges occur on tectonically active margins with narrow continental shelves, the coastal zone may extend beyond the continental shelf.

The continental shelf comprises approximately 8% of the total area of the oceans. The coastal zone, which includes only limited areas beyond the shelf, comprises less than 10%. Nevertheless, the coastal ocean is disproportionately important because more than 99% of the total world fishery catch is taken from coastal waters. The coastal ocean is also important for ports and shipping; recreational activities; mining of sand, gravel, and other minerals; oil exploration and extraction; energy production or potential production from winds, tides and currents, thermal differences between surface water and deep water, and waste disposal. This chapter examines the factors that make the coastal zone and its **ecosystem** different from the open ocean. It also describes the characteristics of **estuaries** and **lagoons** and their relationships to ocean ecosystems.

SPECIAL CHARACTERISTICS OF THE COASTAL OCEANS

Because the coastal oceans are shallow, water movements are affected by the seafloor and the coastline. In addition, rivers discharge freshwater into coastal waters. As a result,

The salinity and temperature of coastal waters are more variable than those of open-ocean waters.

- Coastal currents are generally independent of the open-ocean gyre currents.
- The mixed layer has more sources of nutrients in coastal waters than in the open ocean.
- Benthos of the coastal oceans are more diverse, abundant, and commercially valuable than open- ocean benthos.

These factors make the coastal oceans different and generally more variable than the open oceans. Some of the ways in which these factors affect the coastal oceans are discussed in this section. However, you should remember that each coastal area has its own unique characteristics and this chapter provides only a general overview and some examples of coastal and estuarine processes in some specific locations.

Salinity

Freshwater from rivers reduces the salinity of coastal waters. Where river discharges are large, low-salinity water spreads as a surface layer over higher-salinity ocean water unless vertical mixing is intense. Consequently, near mouths of major rivers, a **halocline** often is present a few meters below the surface. The area affected by the halocline and the halocline's strength depend on the rate of discharge of low-salinity water from the river and on the extent of wind-, wave-, and **tide**-induced vertical mixing of the water column (Fig. 13-1). Haloclines inhibit **upwelling** and vertical mixing.

Low-salinity water discharged by rivers is mixed with ocean water primarily by winds and is transported away from the river mouth by coastal currents. Chapter 8 explained that coastal currents generally flow parallel to the coastline and are often separated from the open-ocean gyre currents by sharply defined **fronts**. Thus, mixing of coastal water with water from the open oceans is slow, and **residence times** of water in the coastal ocean can be long.

The residence time of freshwater in the coastal **water mass** can be calculated if the volume input of freshwater from rivers, the average salinity in the coastal waters, and the volume of the coastal water mass are known (CC8). For example, the residence time of freshwater in the coastal oceans of the northeastern United States from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina, is about 2½ years. The long residence time has implications for the use of this area for ocean waste disposal. Although the volume of coastal water is large, the quantities of potential **contaminants** released into the northeastern United States coastal ocean in discharges from cities (primarily treated sewage wastewater and storm water runoff) and industries are also large. For potential contaminants not removed by **sedimentation** or decomposition (Chap. 16), an amount equivalent to 2½ years of discharges is retained within this region.

Salinity varies seasonally with river flow in many coastal areas. In mid and low **latitudes,** salinity is usually lowest in the local rainy season. At high latitudes, salinity is always lowest in late spring or summer when snowmelt swells rivers and seasonal sea ice melts.

Salinity extremes occur in **marginal seas,** lagoons, or other bays with restricted connections to the oceans. In locations such as the eastern Mediterranean and the Red Sea, evaporation is

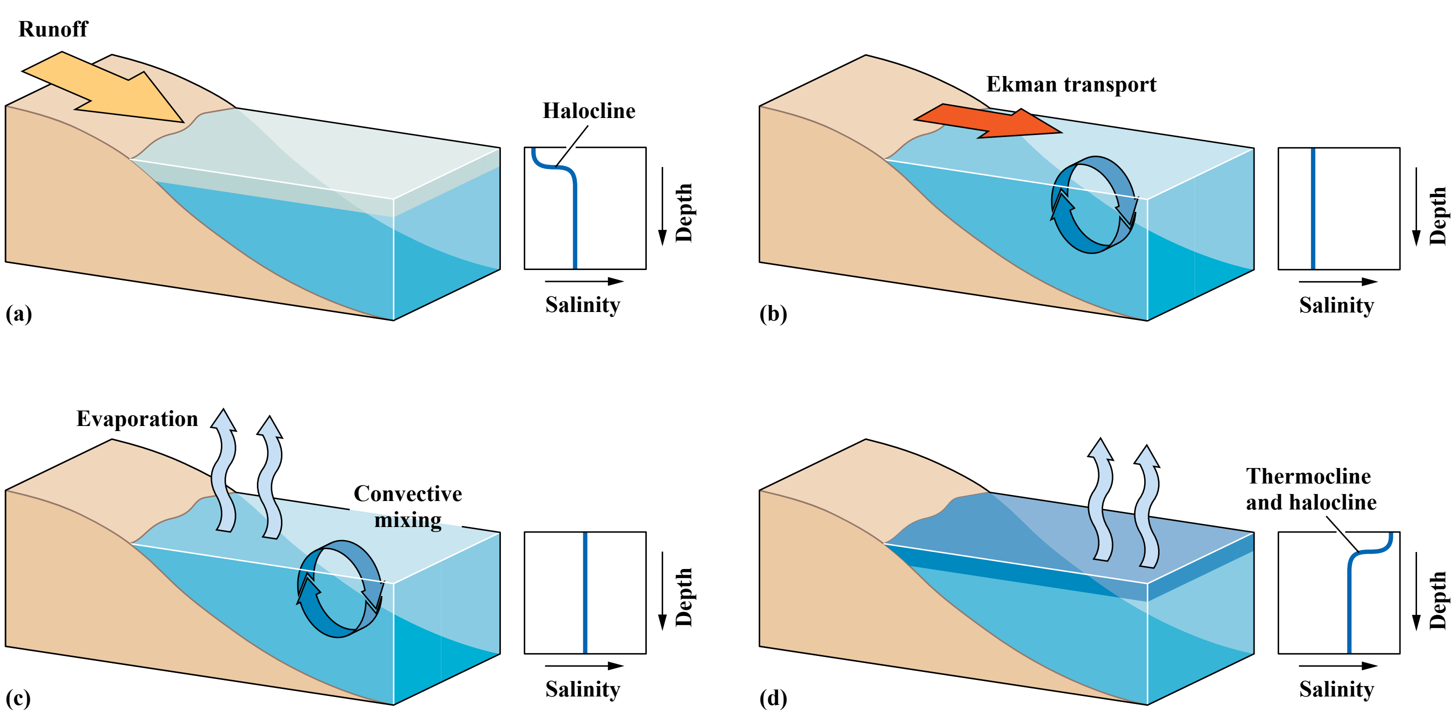


FIGURE 13-1 Salinity distributions in the coastal-ocean water column. (a) Near major rivers, discharges of low-salinity river water over higher-salinity ocean water create a halocline. Where winds transport surface waters offshore, the layer of low-salinity water may spread farther and be thinner. Lower-volume river discharges produce thinner, low-salinity layers that do not extend far from the river mouth. (b) Where winds are strong and river discharge is relatively small, the low-salinity river water may be completely mixed with ocean water, and as a result, there is no halocline. (c) In areas of strong evaporation and low rainfall, warm, high-salinity surface water is produced that may be dense enough to sink all the way to the seafloor. (d) Conversely, this warm, high-salinity water may be warm enough that its density is lower than the lower-salinity but cooler offshore water. In this case, the warm, high-salinity water forms a higher-salinity surface layer overlying a halocline in which salinity decreases with depth.

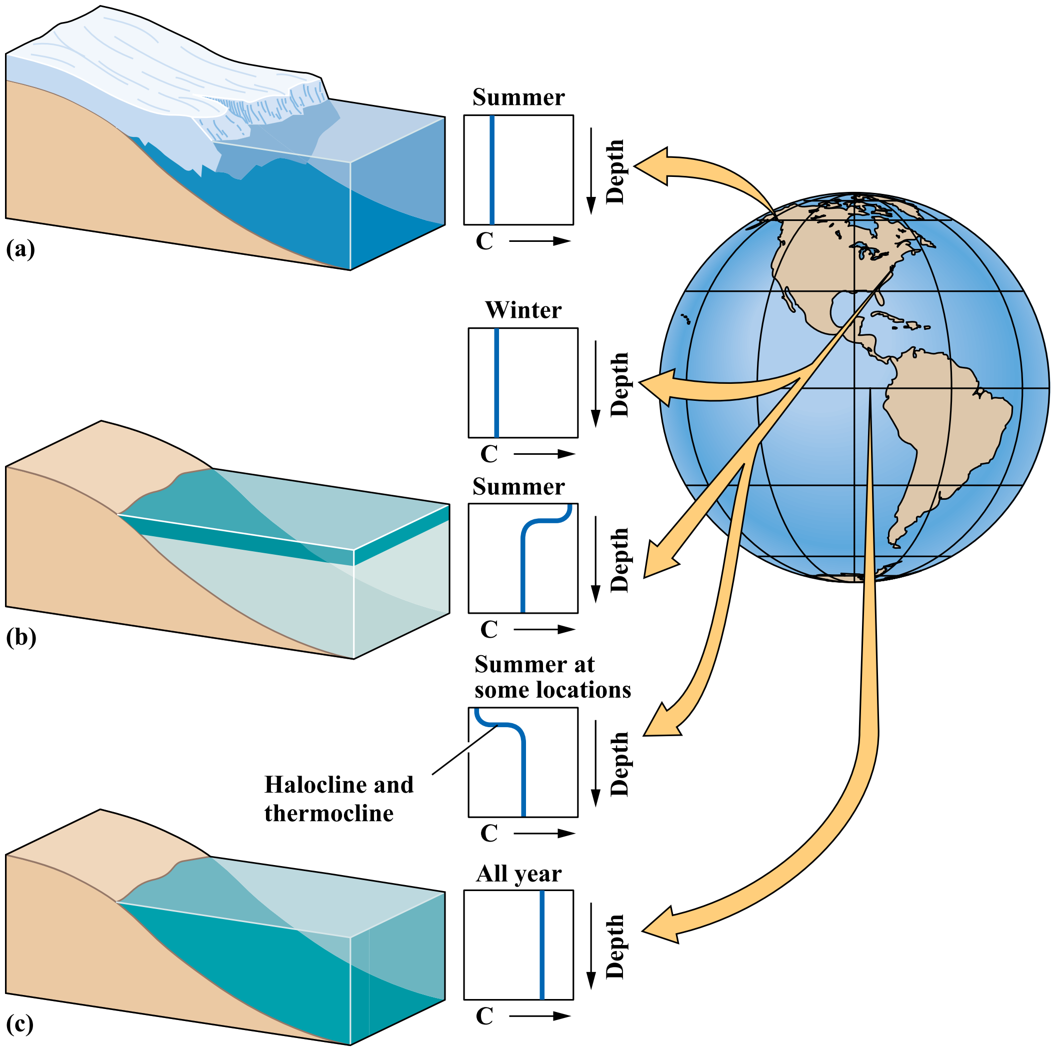


FIGURE 13-2 Temperature distributions in the coastal-ocean water column. (a) In high-latitude regions where ice is forming or melting throughout the year, the water column is uniformly at or near the freezing point. (b) In mid latitudes, surface waters are warmed in summer, producing a shallow seasonal thermocline. In winter the surface water is cooled and sinks, and the water column is generally well mixed by this convection and by winds. In some areas, low-salinity runoff may produce cool but low-salinity surface water and a shallow pycnocline that is both a halocline and a thermocline in which temperature increases with depth. (c) In low-latitude regions where freshwater inputs are limited, the temperature of the water column above the permanent ocean thermocline depth is usually uniform and high.

high and rainfall low, so surface salinity is high—in some areas exceeding 40. In these regions, the mixed layer is usually deep because vertical circulation is enhanced by the formation of surface waters with relatively high density due to high salinity. The mixed layer often extends to the seafloor and consists of warm, high-salinity water. The vertical circulation helps to recycle nutrients from relatively deep waters into the **photic zone.** Consequently, many of these regions have moderately high productivity, despite their limited inputs of nutrients in runoff from land. However, in some parts of such regions, lower-salinity surface water from the open ocean may flow as a surface layer over the high-salinity water created by evaporation in another part of the basin (**Fig. 13-1c**). In some basins with high evaporation and low rainfall, higher-salinity but warmer surface water has lower density than the lower-salinity but colder open-ocean water. Thus, a warm, high-salinity surface layer is formed (**Fig. 13-1d**).

Salinity is lowest where river outflow is large and evaporation is low. Such conditions generally occur in mid- and high-latitude locations, including many **fjords** and the Baltic Sea. The huge **monsoon** flows of the Ganges and Brahmaputra rivers lower the surface salinity of the entire Bay of Bengal (**Fig. 7-14**).

Temperature

Seasonal changes in solar intensity and air temperature cause larger temperature changes in shallow coastal waters than in the open ocean. Temperature variations are particularly large in enclosed marginal seas, fjords, and other embayments that have restricted exchange with the open ocean. In tropical regions, coastal water temperature is uniformly high year-round, and the water column is often **isothermal** to the seafloor, particularly in shallow lagoons (**Fig. 13-2c**). In deeper coastal waters, the depth of the mixed (or isothermal) layer is determined by physical processes, including wind-, tide-, and wave-induced mixing.

In high latitudes, coastal water temperatures vary little between seasons (**Fig. 13-2a**). Sea ice in these regions melts during summer and re-forms during winter. This process maintains the water temperature at the freezing point of seawater, usually above –2°C (**Chap. 5**, **CC5**).

Seasonal temperature changes in coastal waters are most evident in mid latitudes (**Fig. 13-2b**). In these regions, the surface water layer becomes warmer and less dense as solar heating increases in spring, reaching a temperature maximum in summer. In addition, in many locations, mixing by wind and waves decreases during summer. As a result, a shallow **thermocline** is formed and the mixed-layer depth is reduced to about 15 m (**Fig. 13-2b**). This seasonal thermocline breaks down in winter when surface water is cooled and **convection** and wind mixing increase. A uniformly cold mixed layer is produced that extends to the top of the permanent thermocline (about 100 m) or to the seafloor, if it is shallower. Because most coastal waters are less than 100 m deep, the mixed layer extends to the seafloor in most of the temperate coastal region during winter.

Coastal-ocean water temperature in mid latitudes is usually lower in summer and higher in winter than air temperatures over the adjacent coastal land. This difference affects the **climate** of coastal regions (**Chap. 7**) by moderating temperature variations.

Waves and Tides

Tidal-current speed increases as the tide wave enters shallow coastal waters and its energy is compressed into a shallower depth (**Chap. 10**). Consequently, tides are an important contributor to vertical and horizontal mixing in the coastal zone.

As tides **ebb** and **flood,** they cause **turbulence** that enhances vertical mixing. Tides also mix water across the shelf. Near-bottom tidal currents are slowed by **friction** with the seafloor. In addition, tidal currents may be different above and below a **pycnocline** when one is present. Thus, water in different layers moves different distances across the shelf during a tidal cycle. Turbulent mixing between layers transfers water from one layer to another.

Wind-driven waves create turbulence and vertical mixing. In the coastal zone, vertical mixing is enhanced where waves move into shallow waters and break. **Langmuir circulation** and **internal waves** (**Chap. 8**) also contribute to vertical mixing.

Turbidity and the Photic Zone

The photic zone extends to the seafloor in many areas of the coastal oceans. In these areas, **kelp** and other **macroalgae** (**Fig. 13-3**) can live and **photosynthesize** on the seafloor. However, the photosynthetic **community** of the shallow seafloor is often dominated by **species** of single-celled **algae** similar to **phytoplankton**. These algae **encrust** rocks, dead **coral**, and other organisms that live on the seafloor. A number of such species live inside the tissues of corals, clams, and other **benthic** animals in a **symbiotic** relationship (**Chap. 14**).

The photic zone is generally shallower and more variable in depth in the coastal oceans than in open-ocean waters because the concentration of suspended particles, and hence turbidity, is higher. Turbidity is higher primarily because of the proximity of river discharges that can carry large quantities of **suspended sediment**. The finest particles are continuously **resuspended** and transported in the coastal zone by waves and currents, so their concentration remains high. Once they have been transported to the lower-energy deep oceans, these particles sink below the photic zone.

The concentration of suspended sediment in coastal waters is variable because it depends on such factors as location in relation to river discharges, river discharge rates, intensity of wave resuspension activity, and the speed of coastal currents. Each of these factors varies spatially and temporally. Similarly, phytoplankton concentrations are highly variable in the coastal zone. As a result, the photic-zone depth can vary substantially over short distances and time periods. Populations of benthic algae, particularly in the relatively deep waters of the mid-shelf region, vary accordingly. High turbidity also affects the health and distribution of **coral reefs** by reducing the light available for photosynthesis by their symbiotic algae, the **zooxanthellae**.

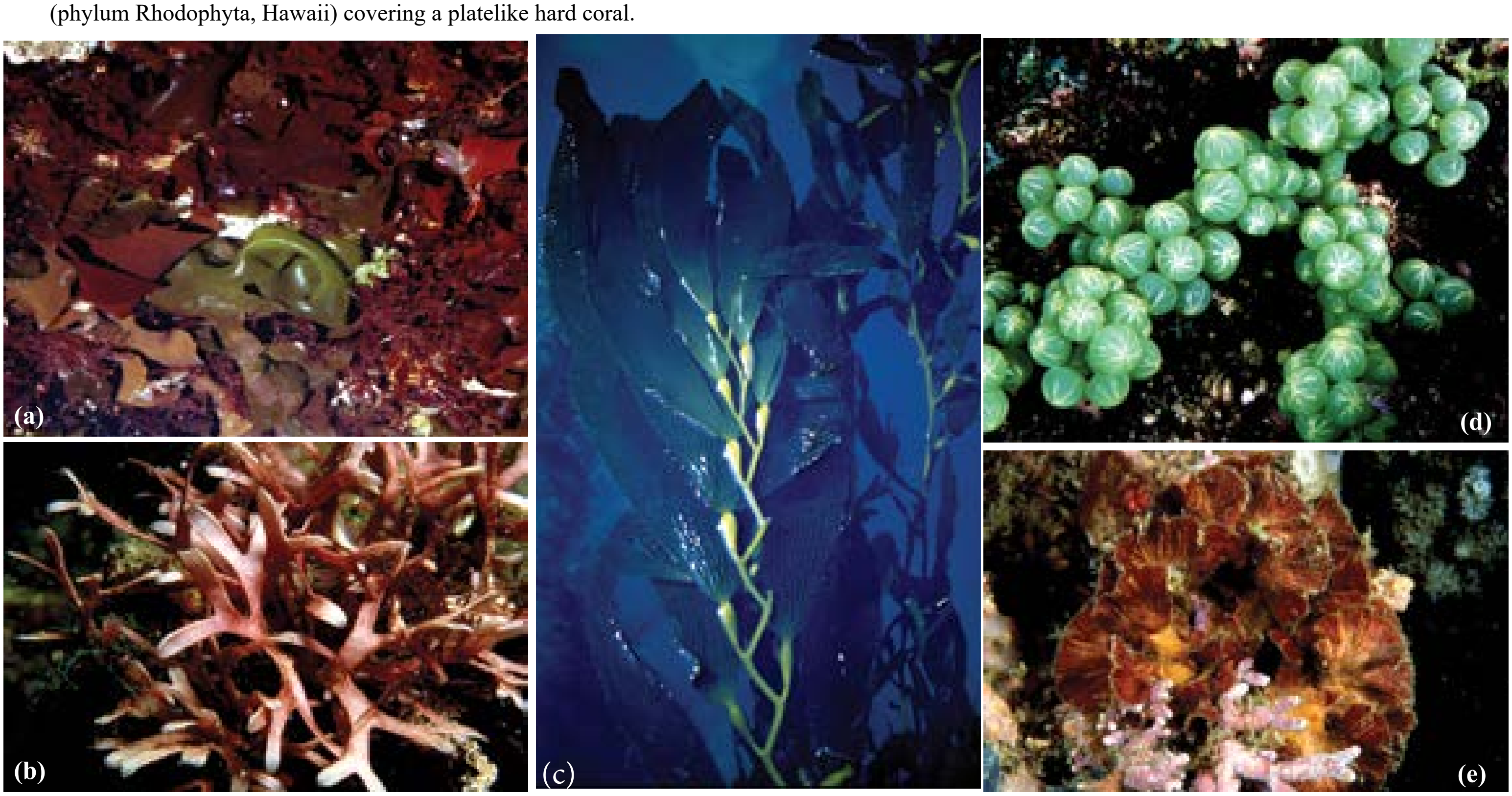
Currents

Because coastal currents (**Chap. 8**) are dominated by local winds, they vary seasonally and on shorter timescales in response to weather systems. Coastal currents are generally steered by their interaction with the seafloor, so they flow parallel to the coastline. However, interactions between currents and the seafloor or **shoreline** can also cause permanent or semipermanent **eddies** to form.

Nutrients

The supply of nutrients to the coastal photic zone is generally

FIGURE 13-3 Benthic algae. (a) Various species of green, brown, and red macroalgae in a tide pool on the California coast near San Francisco. (b) A red calcareous macroalga (phylum Rhodophyta, Philippines). (c) The upper fronds of kelp (*Macrocystis sp.*) floating on the water surface in Monterey Bay, California. (d) A coral reef green macroalga called “grapeweed” (*Caulerpa racemosa*, Papua New Guinea). (e) An encrusting red alga (phylum Rhodophyta, Hawaii) covering a platelike hard coral.



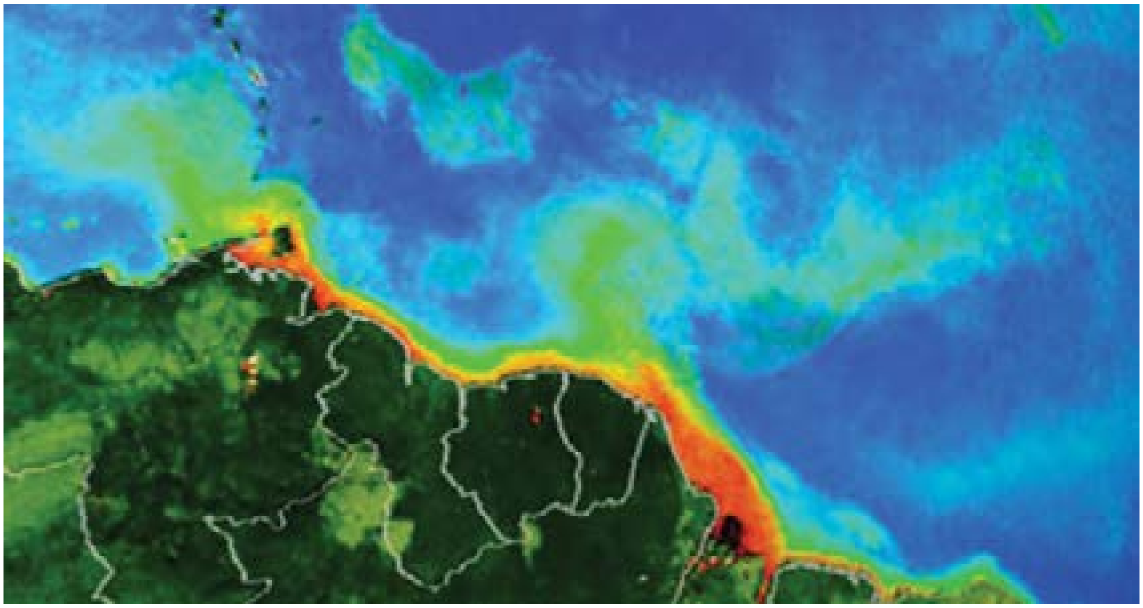


FIGURE 13-4 This false color–enhanced satellite image of the Atlantic coast of South America depicts the elevated (red colors) chlorophyll concentrations associated with the nutrient inputs in the outflow of the Amazon and Orinoco Rivers. The river outflow is transported north along the coast by the coastal currents

greater and more variable than the supply to open-ocean photic zones. The sources of, and variations in, nutrient supply are important to the biological characteristics of coastal waters and are discussed in detail in the next section.

NUTRIENT SUPPLY TO THE COASTAL PHOTIC ZONE

The most productive areas of the oceans are in coastal regions (**Fig. 14.12**). With only a few exceptions, coastal waters have higher **primary productivity** than the adjacent open-ocean waters because a variety of mechanisms supply or resupply nutrients to the photic zone in coastal regions. The most important mechanisms are river inputs and coastal upwelling.

Some rivers discharge large quantities of nutrients into coastal waters, where currents carry water parallel to the coastline so that it mixes only slowly with offshore waters. Consequently, nutrients discharged by rivers tend to be distributed along the **coast** in the direction of the prevailing coastal current. The influence of river-borne nutrients and coastal-current transport can be seen in the high primary productivity near the Amazon River mouth in Brazil (**Fig. 13-4**).

River-borne nutrients are important in many areas, but in other areas, much larger quantities of nutrients are supplied to the coastal photic zone by wind-driven coastal upwelling (**Chap. 8**). In addition, various other physical mechanisms mix nutrients into photic-zone waters of the continental shelf.

Wind-Driven Coastal Upwelling

Coastal upwelling occurs when wind-driven **Ekman transport** (**Figs. 8-3, 8-5**) moves the surface water layer offshore. Coastal upwelling brings offshore water from depths of 100 m or more to the surface to replace the mixed-layer water that is transported offshore. If the water raised to the surface has high nutrient concentrations and replaces nutrient-depleted surface water, and if the upwelling occurs where photosynthesis is not **light-limited,** the nutrients enhance primary productivity. In coastal-ocean regions where these conditions are met and where winds that cause the upwelling are persistent, primary productivity is high and remains high while upwelling persists (**Fig 13-5**). The term "**coastal upwelling** region" is usually applied to such areas. Ekman transport also causes upwelling in other areas where the upwelled water originates from above the permanent thermocline. This water typically is poor in nutrients, and the upwelling has little effect on productivity.

Nutrient-rich water from below the permanent thermocline generally does not penetrate far onto the continental shelf off mid-latitude east coasts because of the swiftly flowing, deep **western boundary currents** of the ocean gyres (**Fig. 8-10**). In contrast, nutrient-rich water does penetrate onto the continental shelf off the west coasts of the continents. Hence, high-productivity coastal upwelling regions are concentrated off the west coasts of the continents, notably off California, Peru, and the western

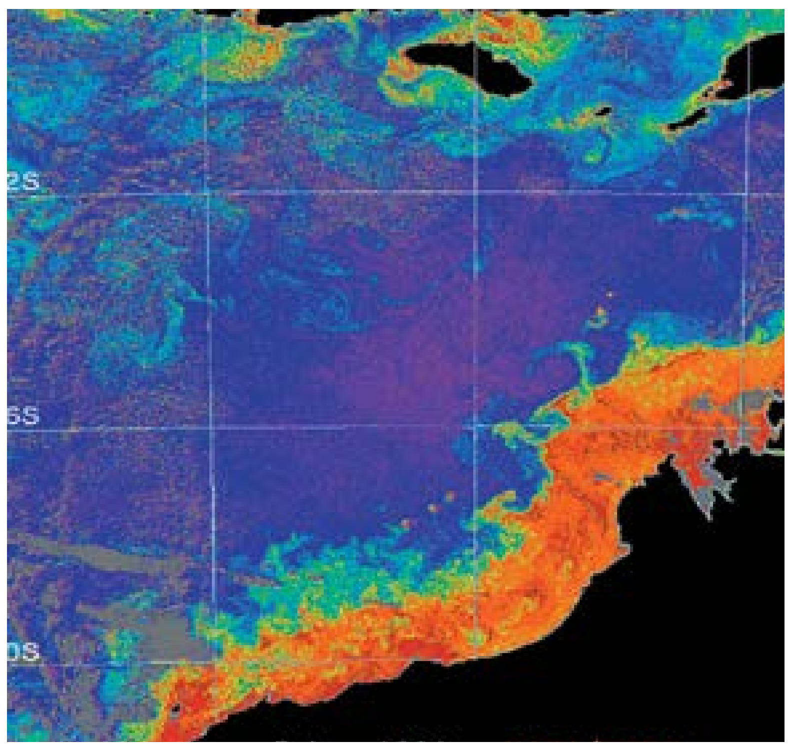
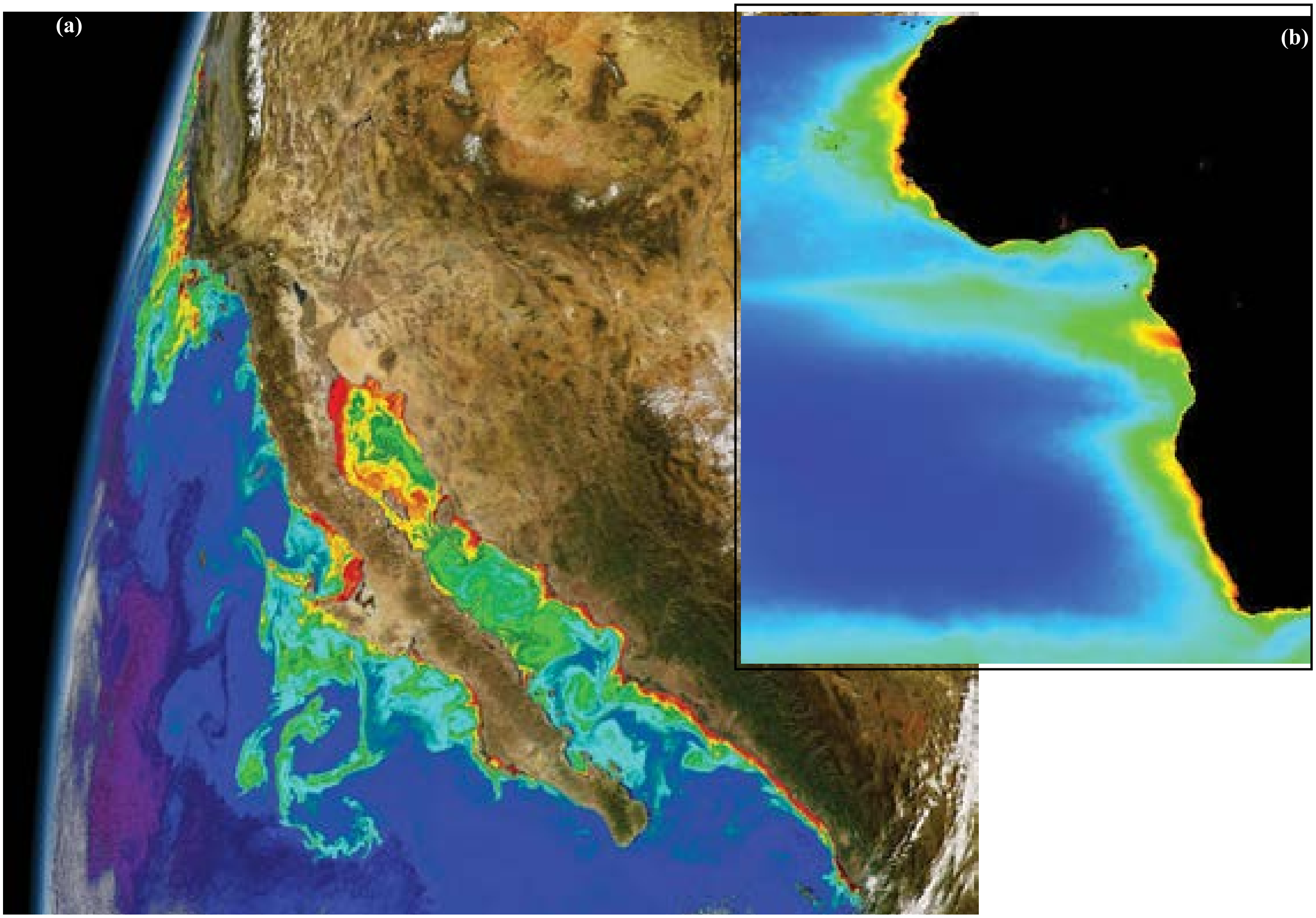


FIGURE 13-5 Surface water chlorophyll concentrations in the Indian Ocean region between Indonesia and northwestern Australia (June 1981). High concentrations are shown in red and are associated with high rates of primary production. The high productivity off northwestern Australia occurs because winds cause offshore Ekman transport and coastal upwelling. Note the complex local variations along the coast. The productivity is much lower near Indonesia, where there is no major coastal upwelling.



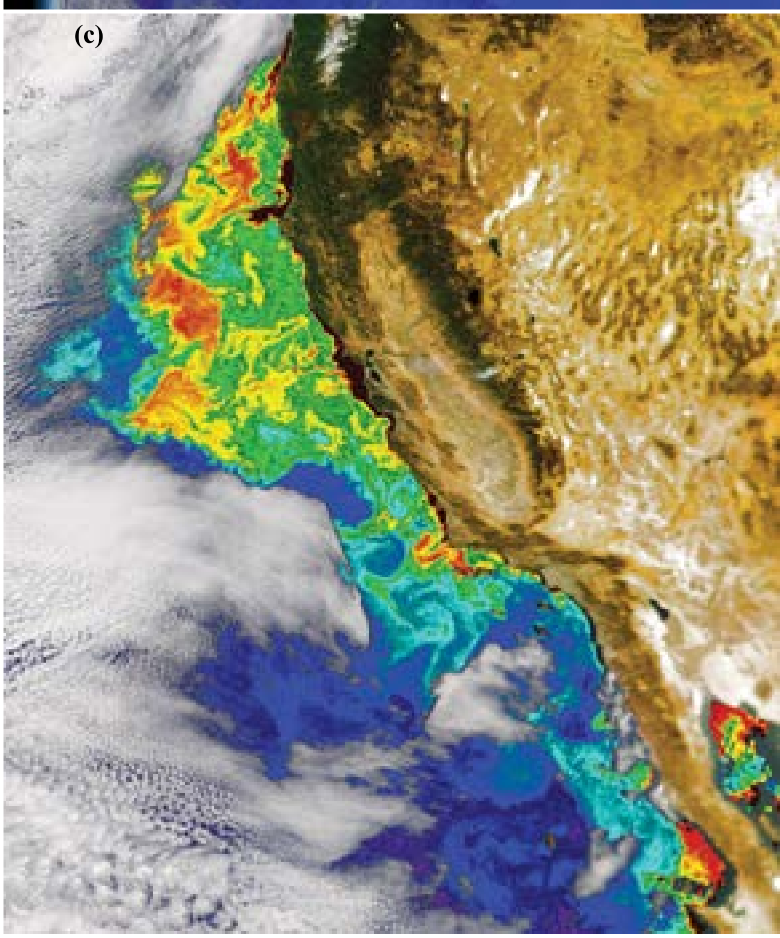


FIGURE 13-6 These false color–enhanced satellite images show the elevated (red colors) chlorophyll concentrations associated with the interaction of coastal currents and capes. . (a) The complex gyres that form at capes and that support enhanced primary productivity are clearly seen in this image of the coastal region off Baja California. (b) Upwelling is especially strong and extends farther offshore at each of the several capes on the western Africa coast. (c) This image shows the intense upwelling that sustains the abundant marine species populations of the California coastal zone. This, and other eastern boundary current coastal upwelling zones, are difficult to capture from satellites since they are often obscured by the marine layer clouds and fog that you can see offshore in the image and that characterize these zones

Africa coast both north and south of the equator (**Fig. 12-12**).

The intensity of upwelling varies locally in coastal upwelling regions (**Fig. 13-5**). It is especially strong and persistent off coasts where prevailing winds produce offshore Ekman transport in regions with dry or desert climates, such as California and Peru. In some other coastal regions, winds cause offshore Ekman transport, but river inputs of freshwater are substantial. In these areas, the low-salinity water discharged by the rivers spreads to form a low-density, relatively shallow surface layer. Because this layer "slides" relatively easily over the higher-density water below it, offshore Ekman transport tends to spread it farther offshore to be replaced by additional low-salinity water from the river. The low-salinity, low-density surface layer inhibits upwelling. If Ekman transport is strong and river flow rate relatively low, upwelling does occur, but the upwelled water may be low-nutrient shelf water from below the shallow halocline rather than high-nutrient water from below the deeper permanent thermocline. Upwelling of nutrient- rich water from below the permanent thermocline can occur only if the winds and offshore Ekman transport are persistent and strong, and if river input remains relatively low.

For coastal upwelling to occur, winds must blow in the appropriate direction long enough to initiate Ekman transport, which then must move sufficient surface water offshore to bring nutrient-rich waters to the surface. This process may take many hours or several days, depending on the wind strength and direction and the depth of the thermocline. In locations where winds are variable in strength and direction, upwelling may be sporadic and highly variable from day to day and from year to year. Coastal upwelling is generally most consistent in the **trade wind** region because trade winds are less variable than winds at other latitudes (**Chap. 7**).

In many regions, such as off the California coast, climatic winds and coastal currents change direction seasonally (**Fig. 8-14**) and upwelling is also seasonal. For example, upwelling occurs during summer and fall off the California coast, when winds blow from the north. Seasonal upwelling may occur each year, but the timing, intensity, and persistence of upwelling vary from year to year. These variations are important to major fisheries that depend on the upwelling.

Coastal upwelling often extends farther offshore and is stronger and more persistent near capes (**Fig. 13-6**). Fishers have long known about this phenomenon because capes have especially abundant fish, seabird, and often **marine mammal** populations. The reason is still not totally understood, but the phenomenon appears to be the result of an interaction of coastal currents with the undersea **topographic** ridge that usually extends onto the continental shelf as an extension of the cape. The coastal current flows parallel to the coastline, and as it meets the ridge, it is deflected first offshore and then back toward the **shore** as it passes up and over the ridge. This deflection sets up a complex eddy circulation similar to the mesoscale eddies discussed in **Chapter 8**. Upwelling is especially intense immediately downstream of the ridge, but upwelled water is also entrained in the eddy circulation and carried farther offshore.

Biology of Coastal Upwelling Zones

In most highly productive coastal upwelling regions, upwelling persists for several months or more each year. During this period, continuous, although variable, onshore–offshore transport processes are established (**Fig. 13-7**). Surface layer water flows offshore and is replaced by cold, nutrient-rich water that flows inshore near the seafloor. As the upwelled cold water is transported offshore, it is progressively warmed by solar heating and mixed

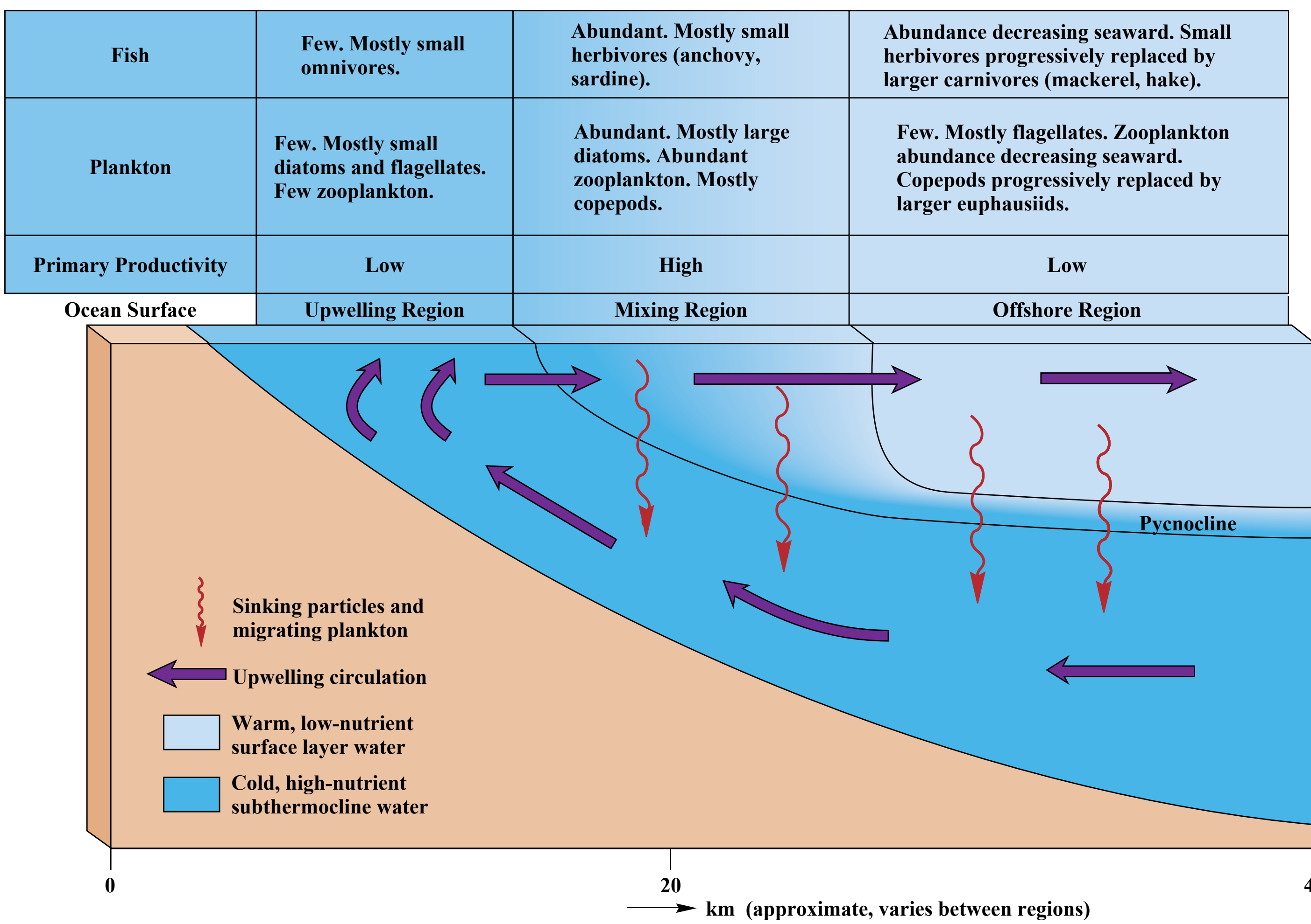


FIGURE 13-7 In coastal upwelling regions, the distribution of water properties and biota is related to the upwelling circulation. Upwelled water, high in nutrients, supports only low levels of primary production at first, but as it moves offshore as the surface layer, it supports a diatom bloom that depletes the nutrients, after which flagellates become dominant. Zooplankton and fish species are distributed to take advantage of this distribution of food. Many species of plankton use the upwelling circulation by changing their depth to be transported either onshore or offshore. Many fish and invertebrate species also use the circulation by placing their eggs and larvae at the right place and depth so that they are transported to a location where the appropriate food source is available at the different stages of their life cycle.

with warmer offshore surface water.

Although the newly upwelled water near the coast has high nutrient concentrations and adequate light, phytoplankton growth does not begin immediately. There may be several reasons for the time lag, including the following:

- Newly upwelled water contains few viable phytoplankton or other primary producer cells.
- Dissolved **micronutrient** organic compounds may be lacking in newly upwelled water.
- Dissolved trace metals in the newly upwelled water may be in a more toxic ionic form because the concentration of dissolved organic compounds is low.
- Dissolved nutrient trace metals, such as iron, may be in an ionic form unavailable to some species of primary producers, again because the concentration of dissolved organic compounds is low.

The toxicity and biological availability of metals in solution are known to be changed by chelation, a process in which the metal atom or **ion** is surrounded by an organic molecule or molecules and stable bonds are formed with part of the organic molecule structure. Generally, toxicity is decreased by chelation, and the metal may become more readily available for uptake by living organisms. In laboratory experiments, the addition of a simple organic compound known to be a chelating agent to newly upwelled water reduces the lag time. Therefore, either toxicity or unavailability of metals must account for at least some of the lag time. In newly upwelled water, a variety of small **flagellate** phytoplankton species are apparently less affected by the factors that create the lag time. These species are the first to grow and reproduce actively in the newly upwelled water. In doing so, they are thought to synthesize a variety of organic compounds that they then, at least in part, release to solution. These compounds must include chelating agents and/or the micronutrients needed by other phytoplankton species, which then allows those species to grow.

As upwelled water moves offshore, larger phytoplankton, including chain-forming **diatoms**, reproduce rapidly. In the mid-shelf region, these **blooms** peak, and phytoplankton **biomass** reaches more than 100 times that present in nutrient-poor surface waters farther offshore. The blooms consume and thus deplete nutrients (nitrogen, phosphorus, and silica) in the previously upwelled water. As the nutrient-depleted water is transported farther offshore and mixed with offshore surface waters, the phytoplankton, which are now **nutrient-limited** and no longer actively growing, are reduced by **grazers**. Consequently, the larger phytoplankton are replaced by smaller numbers of flagellate species that are able to grow at low nutrient concentrations.

Zooplankton and **nekton** populations within the coastal upwelling ecosystem are distributed to take advantage of the local food supply. Few zooplankton or nekton are present in newly upwelled water, where primary productivity is still low. The mid-shelf area where concentrations of diatoms are highest has large populations of **herbivorous** fishes and zooplankton. Farther offshore, larger **carnivorous** zooplankton and carnivorous fishes feed on the herbivores brought to them by the offshore flow. These **food webs** are short in comparison with open-ocean food webs (**CC15**). Hence, coastal upwelling fisheries use photosynthetically produced organic matter more efficiently than open-ocean fisheries do (**CC16**).

Fecal pellets and **detritus** produced by organisms in the

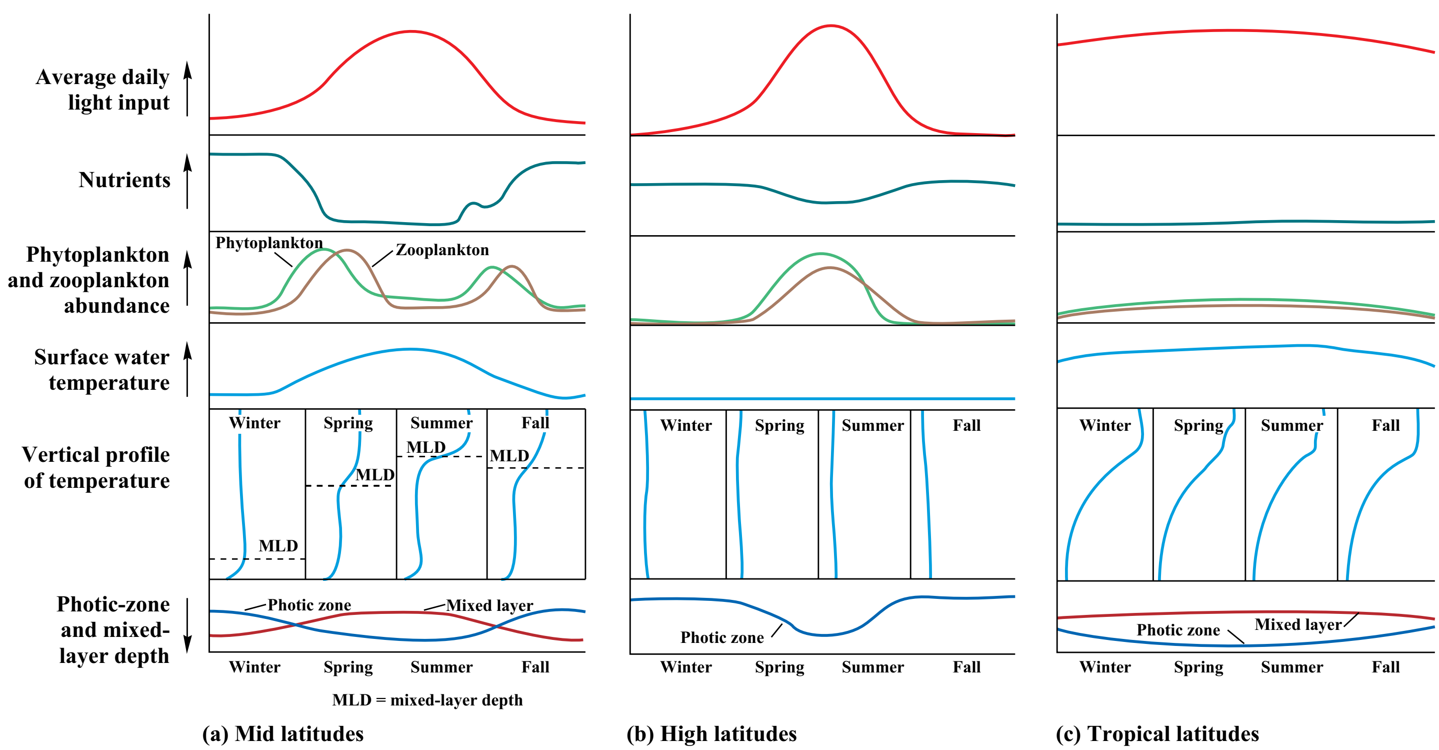


FIGURE 13-8 Seasonal variations in solar intensity, nutrient concentrations, phytoplankton and zooplankton biomass, and surface water temperature are different in mid (temperate), high, and tropical latitudes. (a) In mid latitudes, there is a distinct seasonal cycle in which a shallow thermocline forms in summer, a spring bloom of plankton depletes the nutrients, and a smaller fall bloom sometimes occurs as nutrients are recycled. (b) In high latitudes, there is an intense plankton bloom in the short summer when light intensity is sufficient for growth. Nutrients are not depleted, because strong vertical mixing occurs and this mixing prevents the formation of a thermocline. (c) In tropical latitudes, a strong permanent thermocline exists. This thermocline inhibits vertical mixing, and nutrients in the surface layer are permanently depleted. As a result, primary production is limited to uniformly low levels throughout the year.

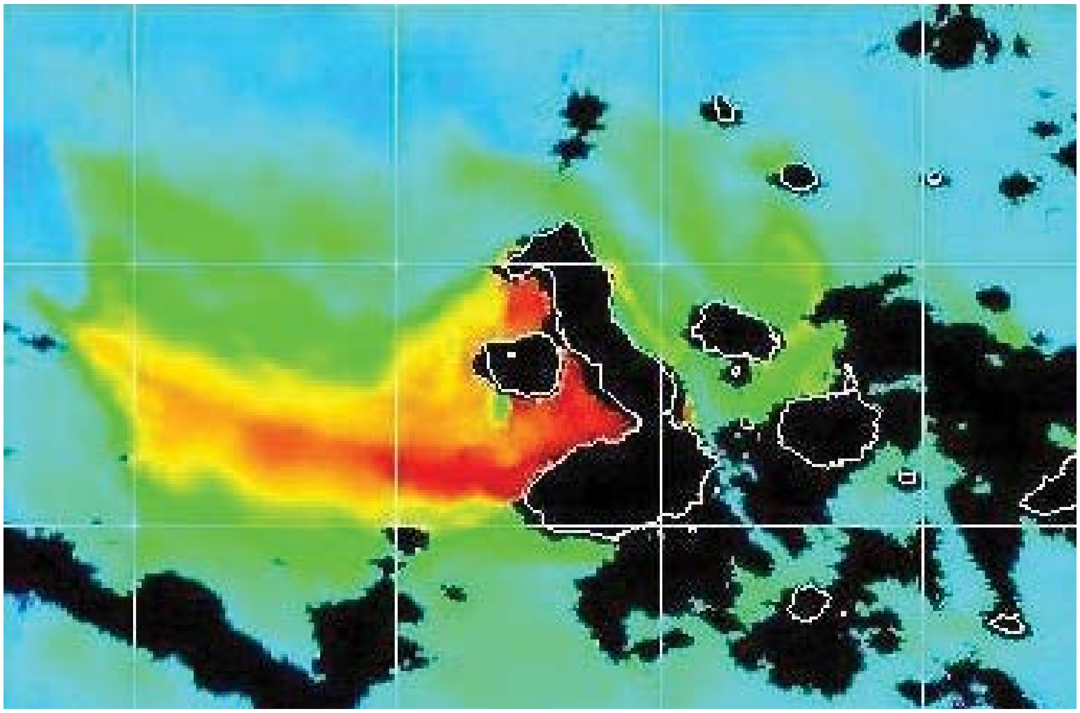


FIGURE 13-9 Elevated chlorophyll concentrations are found around islands, including the Galapagos Islands, which are depicted in this false color–enhanced satellite image. Primary productivity is enhanced by the vertical mixing that is caused by the interaction of ocean currents with the island topography, which brings nutrients to the surface layer, and by nutrients in freshwater runoff from the islands

surface water layer of the upwelling zone fall below the surface layer into the near-bottom water or to the seafloor, where they are decomposed. Nutrients released by this decomposition are added to the water that moves inshore to be upwelled. Thus, upwelling-zone circulation ensures that nutrients are rapidly recycled.

Coastal upwelling circulation is also important to the life cycles of species in the upwelling-zone ecosystem, particularly **plankton,** because they are continuously transported offshore in the mixed layer. If they are carried offshore beyond their optimal location, members of these species can return by sinking through the water column so that they are carried onshore by the upwelling circulation. Many phytoplankton species form resting phases called **spores** or **cysts,** and zooplankton species lay eggs in offshore waters, where they sink into cold subthermocline water that moves onshore. Once upwelled into an area where nutrients or food is available, the phytoplankton revive and zooplankton eggs hatch.

Nekton use a similar strategy to distribute their eggs and **larvae** to favorable locations. Many nekton species migrate inshore or to estuaries to **spawn,** but others may spawn offshore. Their eggs are carried in the near-bottom waters toward shore, where they are upwelled and then hatch. The larvae may change their physical form and feeding strategy several times to exploit different food sources as they are transported offshore as plankton. A final change to the adult nektonic form occurs when an appropriate location in the upwelling circulation is reached.

Many upwelling-zone species rely on the upwelling circulation to deliver their eggs and larvae to locations where appropriate food is available at specific times during their life cycles. Consequently, in years when upwelling occurs at a different time or differs in intensity and duration, some species may be advantaged or disadvantaged in relation to others. The result is considerable year-to-year variation in the breeding success of many species. The cause of the collapse of fisheries for many species has likely been that they were **overfished** during one or more years when environmental factors substantially reduced reproduction.

Other Mechanisms of Nutrient Supply

Coastal upwelling and runoff from the land are the two most important mechanisms of nutrient supply to the coastal photic zone. However, there are other mechanisms of nutrient supply that depend on waves and tides, the interaction of ocean currents with the seafloor, and thermal convection.

The mixed-layer depth is partially determined by the intensity and duration of winds. Winds cause vertical mixing due to Langmuir circulation (**Chap. 8**) and wave action. In regions where a seasonal thermocline is formed, intense storms in summer or fall generate waves with long **wave periods** that disrupt the thermocline. This disruption mixes water from above and below the thermocline, weakens the thermocline, and transports some nutrient-rich waters upward into the mixed layer. Nutrients are also returned to the mixed layer by convection that occurs when the surface layer water cools in fall–winter and the seasonal thermocline disappears (**Fig. 13-8a**). Where the seafloor is shallower than the permanent thermocline depth, detritus falls through the photic zone and accumulates on the shallow seafloor. As this detritus is decomposed, nutrients are released into near-bottom waters, from where they can be returned to the photic zone by vertical mixing.

Long-**wavelength** internal waves that form on the thermocline are slowed as they reach shallow water, and they eventually break on the outer portion of the continental shelf (**Chap. 9**). In some areas, such as the outer continental shelf next to Long Island and New Jersey, these waves may transport nutrient-rich subthermocline water into the mixed layer.

Tides in certain regions generate swift currents, particularly in bays, estuaries, and gulfs. Turbulence created by these currents can prevent a seasonal thermocline from forming. Thus, nutrients are recycled more effectively in such locations.

Where currents encounter seafloor topographic features, such as ridges, plateaus, **seamounts,** banks, or islands, water must flow over or around the feature, and nutrient-rich deep water can be mixed into the photic zone by complex eddies and turbulence. The increase in productivity caused by the interaction of ocean currents with islands can be seen in the increased **chlorophyll** concentrations around some such islands (**Fig. 13-9**).

When surface mixed-layer water is cooled, it becomes dense and sinks while convective motions replace it with nutrient-rich water from below. Convective mixing is extremely important in the high-latitude oceans (**Fig. 13-8b**). In these regions, surface waters are cooled continuously except in midsummer, so there

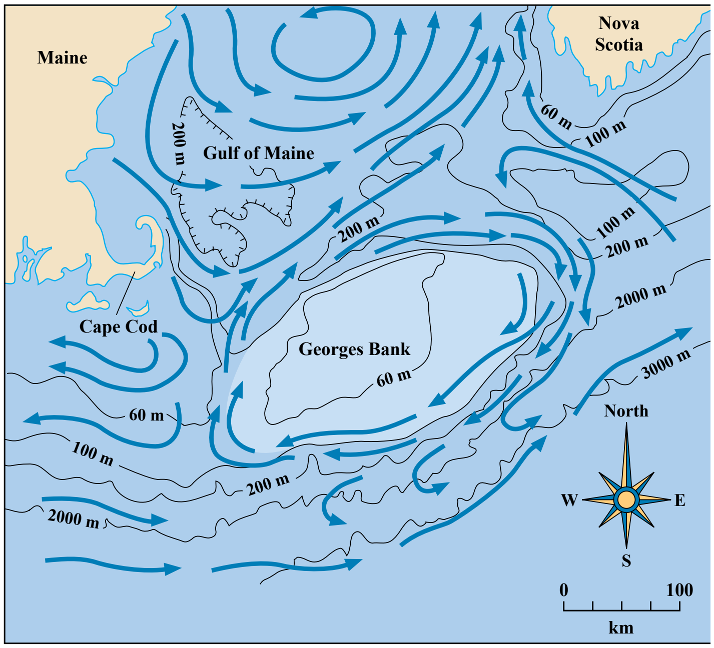


FIGURE 13-10 The water circulation around Georges Bank, New England, is characterized by two permanent gyres. One is a clockwise-rotating gyre that runs around the edge of Georges Bank. The other is a counterclockwise gyre in the Gulf of Maine. The circulation around the bank causes upwelling of nutrients and retains plankton in the water over the bank so that they are able to reproduce to high population densities. These plankton provide food for large fish populations.

is no thermocline, and convective mixing is nearly continuous. When light intensity is sufficient, these regions sustain intense phytoplankton blooms that are rarely slowed by nutrient depletion.

Georges Bank off the New England coast is an extremely productive fishery, primarily because of a plentiful supply of nutrients. The bank is a huge shallow **shoal** in the mouth of the Gulf of Maine (Fig. 13-10). Cold, nutrient-rich water flows out of the Gulf of Maine and intersects the north side of the bank, where it is deflected. Some water flows over the bank, but most forms a huge eddy, and a large fraction (approximately 10% to 30%) flows all the way around the bank. Wind waves, tidal currents, and turbulence and upwelling caused by deflection of the water mass into and around the bank continuously inject nutrients into the eddy and the water on the bank.

Productivity is especially high because the eddy that circulates around the bank enables phytoplankton to remain in the water on the bank, where nutrient supplies are high. The residence time of water and plankton on the bank is about 2 to 3 months, so phytoplankton may go through many cell divisions before being swept off the bank. The phytoplankton provide abundant food for zooplankton, which also remain on the bank long enough to feed and reproduce, ensuring that their young have ample food. Fishes, in turn, exploit the abundant phytoplankton and zooplankton. Unfortunately, Georges Bank fisheries declined substantially because of overfishing especially prior to 1994 when some fishing restrictions were put in place. The populations of commercially valuable species of fishes have recovered very slowly but not yet to their previous abundance.

SEASONAL CYCLES

Substantial seasonal variations in primary productivity occur in mid and high latitudes, but not in the tropics and subtropics (Figs. 14.12, 13-8). Seasonal variations are complex and controlled by the availability of light and nutrients and the depth of the mixed layer, each of which varies with latitude, location, and year-to-year climatic variations. As a result, seasonal cycles in high latitudes, mid latitudes, and tropical latitudes have different general characteristics that are representative of each of these broad regions, but there are no sharply defined latitudinal boundaries between areas with these characteristics, and characteristics are substantially modified by local conditions. Seasonal cycles are generally similar in coastal and open-ocean waters within each latitudinal region. However, seasonal cycles are especially important in coastal and estuarine ecosystems.

Polar and Subpolar Regions

Figure 13-8b is a simplified representation of the annual cycles of light intensity, nutrient concentrations, phytoplankton biomass, zooplankton biomass, and water temperature in subpolar seas remote from major freshwater inputs. In these regions, the water column remains well mixed year-round. Frequent storms and low light intensity (limited solar heating) prevent the formation of a seasonal thermocline, and surface cooling produces year-round convective circulation, so there is no permanent thermocline. Nutrients are plentiful because they are supplied continuously by this convective mechanism, but light intensity is sufficient to sustain phytoplankton growth only during a short period in summer, when an explosive bloom of mostly diatoms occurs. Because nutrients are continuously resupplied and do not become **limiting**, the bloom continues unchecked, except by predation, until light intensity declines at the end of summer.

In polar regions, subpolar regions near land, and areas of seasonal sea ice, this seasonal cycle is modified by freshwater inputs. During spring and summer, substantial quantities of freshwater mix with surface waters. The freshwater comes from river runoff fed by snowmelt and from the melting of seasonal sea ice or **glacial** ice. It is mixed with surface ocean water to form a cold but low-salinity surface layer separated from the water below by a halocline. In many areas, the surface layer has high turbidity due to suspended particles from river or glacial ice inputs. High turbidity and low sun angle restrict the photic zone to a very shallow depth. Because the halocline restricts the vertical movement of nutrients and the photic zone does not extend below this layer, **primary production** quickly becomes nutrient-limited after an initial bloom that occurs in early summer when light intensity first increases. Frequent and intense storms in many subpolar regions vigorously mix subpolar seas, break down the halocline, and resupply nutrients to the surface layer. Hence, primary production is nutrient-limited primarily in protected inshore regions such as fjords.

Productivity is also nutrient-limited throughout most of the Arctic Ocean that is ice-free in summer (Fig. 8-26). With the exception of a few areas of upwelling, these ice-free waters have a steep, almost permanent halocline a few meters below the surface for several reasons. First, freshwater input from rivers and from the melting of the permanent ice pack is large in volume and continuous during the short summer. In addition, salt is removed from the surface layer by **ice exclusion** (Chap 8), which creates high salinity brines that sink below the surface layer. Water exchange between the Arctic Ocean and the Pacific and Atlantic Oceans is limited, so the low salinity Arctic Ocean surface water is transported to lower latitudes very slowly. Furthermore, because the Arctic coast is close to the polar atmospheric downwelling area (Chap. 9), there are relatively few storms in summer. Storms that do occur have only a limited fetch in which to build wind waves because the ice-free Arctic Ocean is restricted to the zone between the polar ice and the coast. The continuing loss of permanent sea ice in the Arctic Ocean is modifying these factors such that the nutrient limited area in the Arctic Ocean is declining producing significant shifts in the distribution and composition of Arctic species.

In the Southern Hemisphere, the oceans around Antarctica do not have a halocline like the Arctic Ocean halocline, because Antarctica is a desert and the continental ice sheet melts very little during summer. The very limited freshwater input from the melting of sea ice and from runoff is readily and rapidly mixed and transported into the much larger volume of the Southern Ocean. Because persistent haloclines do not form in the oceans around Antarctica, the area has higher annual productivity than the Arctic Ocean ice-free regions have.

Tropical Regions

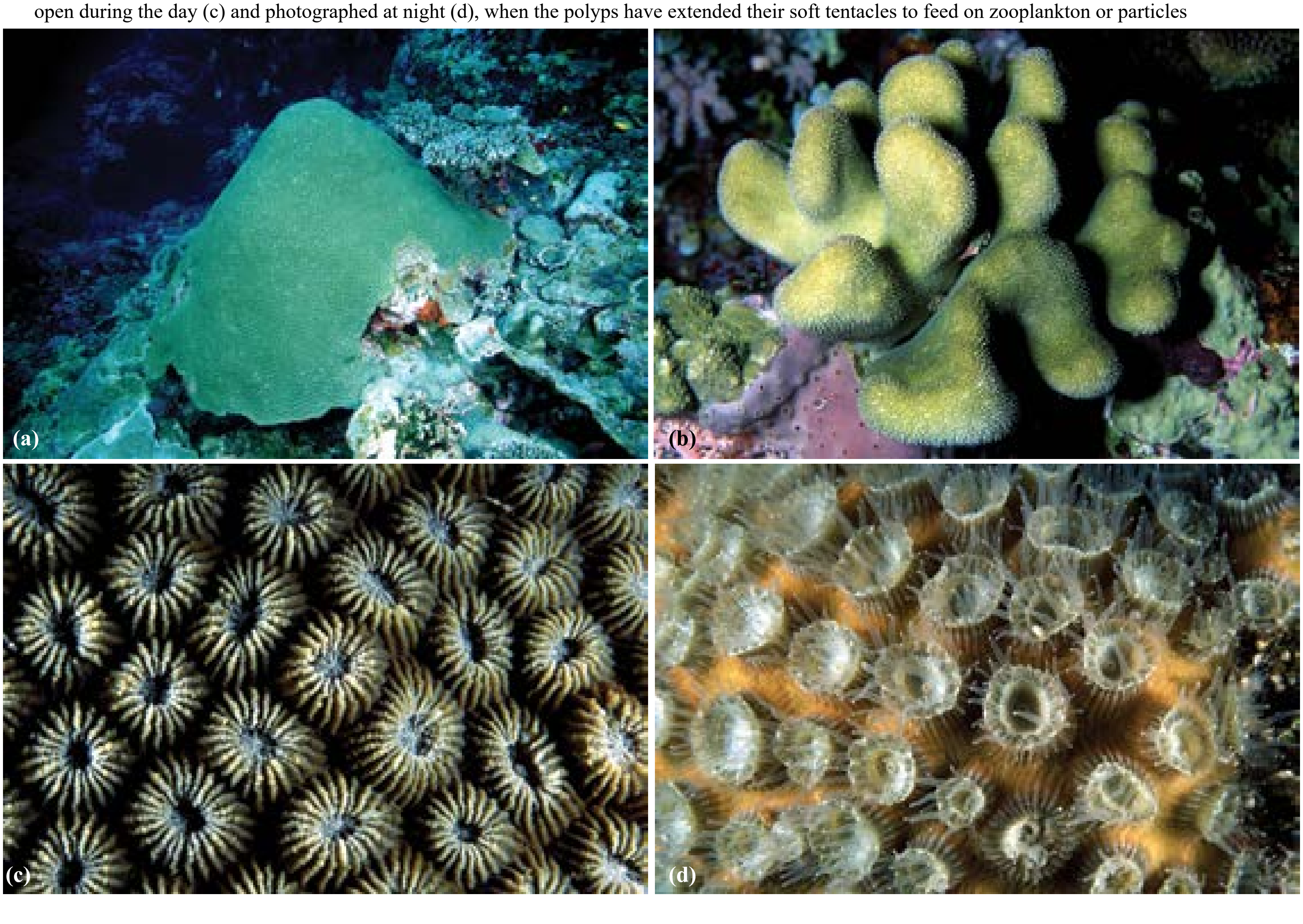
In the tropical and subtropical oceans, there is generally little seasonality of plankton growth because of the general uniformity of light intensity year-round and a very steep permanent thermocline that begins below a relatively shallow mixed layer (**Fig. 13-8c**). Hence, light intensity is always high and the photic zone is deep. However, nutrients transported below the relatively shallow mixed layer are removed from the photic zone. Consequently, everywhere in tropical regions other than in upwelling regions, primary productivity is low because of nutrient limitation.

Although productivity is nutrient-limited throughout the tropical oceans, most coastal areas are characterized by extremely rich and abundant coral reef communities, except where turbidity is high or salinity is variable because of runoff. Despite the extremely low nutrient concentrations in the water column above, the coral communities thrive as a result of a unique symbiotic relationship between algae and **reef**-building corals.

Reef-building corals consist of millions of individual tiny animals whose **hard parts** are cemented together to form the coral mass (**Fig. 13-11**). Each coral animal, or **polyp**, contains within its tissues a large number of dinoflagellate algae known as zooxanthellae. The relationship between coral and zooxanthellae is complex and not fully understood, but one of the principal effects of, or reasons for, this partnership is thought to be more efficient utilization of the small amounts of nutrients available in tropical waters. The zooxanthellae and coral polyps continuously and rapidly recycle nutrients between themselves, thus retaining these nutrients in the photic zone.

Reef-building corals can grow only in the photic zone, where their zooxanthellae can photosynthesize. Hence, these corals are present only in relatively shallow water. In high-turbidity regions, the depth of the photic zone is reduced and coral reef communities do not develop. Coral polyps are adversely affected by high concentrations of suspended particulates, as they have

FIGURE 13-11 Reef-building corals. (a) A typical reef-building hard coral colony (probably *Diploastrea heliopora,* Papua New Guinea). (b) Another typical hard coral (possibly *Pocillopora sp*., Papua New Guinea). (c, d) Individual polyps of *Diploastrea heliopora* (Papua New Guinea) when not open during the day (c) and photographed at night (d), when the polyps have extended their soft tentacles to feed on zooplankton or particles



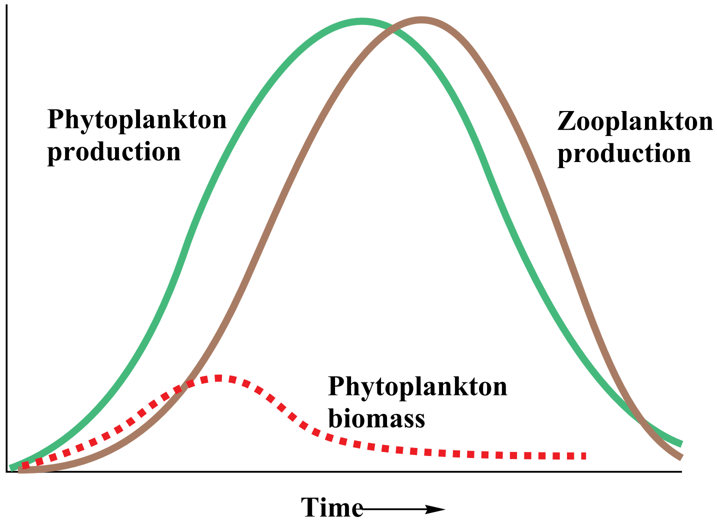


FIGURE 13-12 During a phytoplankton bloom, such as the spring bloom in mid latitudes, the production rate of new biomass by phytoplankton rises rapidly and is followed, with a time lag of a few days, by a similar increase in zooplankton production. The phytoplankton biomass (standing stock) increases somewhat during the early part of the bloom, but it is rapidly reduced by zooplankton feeding, even though the phytoplankton production rate continues to increase.

limited ability to remove that are deposited on them to avoid being smothered and high turbidity reduces the amount of light available for their zooxanthellae to photosynthesize. Thus, reef building corals die if high concentrations of suspended sediment are sustained. Increased turbidity due to human activities has destroyed or damaged many such coral reef communities (**Chap. 16**).

Mid Latitudes

During winter in mid latitudes, cooling of surface waters and mixing by wind waves eliminate the seasonal thermocline and mix water that has high nutrient concentrations from below the thermocline into the mixed layer (**Fig. 13-8a**). Phytoplankton are distributed almost randomly throughout the mixed layer because of their limited swimming capabilities. Because the mixed layer is much deeper than the photic zone, phytoplankton are within the photic zone during only a small percentage of the time. Therefore, during winter, phytoplankton are light-limited, populations are low, and many species are in a hibernation-like resting phase.

In spring, light intensity increases and the photic zone becomes deeper. At the same time, storms are reduced, surface waters begin to warm, the mixed-layer depth is reduced, and a seasonal thermocline begins to form. Phytoplankton are now in the photic zone for an increased percentage of their time, and nutrients remain plentiful. The phytoplankton begin to photosynthesize, grow, and reproduce rapidly.

The **standing stock** (biomass) of phytoplankton increases rapidly at the beginning of the spring bloom period, but the zooplankton population, which now has an increasing food supply, also begins to feed, grow, and reproduce rapidly. Consequently, the majority of new phytoplankton cells are eaten by zooplankton, and the rapid reproduction of phytoplankton does not lead to sustained high phytoplankton concentrations (**Fig. 13-12**). The standing stock of phytoplankton represents only a small percentage of the total production. The remaining fraction is lost to consumption by herbivores or to sinking.

As spring continues, phytoplankton rapidly deplete nutrients in the mixed layer. In addition, the mixed layer becomes shallower (about 10 to 15 m) as the seasonal thermocline forms. At this time, the phytoplankton have adequate light but are nutrient-limited. Consequently, their growth slows and the spring bloom collapses as zooplankton continue to feed on them. Soon the zooplankton population also declines as its food supply decreases, but the zooplankton continue to be eaten by their predators.

During summer, primary productivity continues at a low level, supported by nutrients recycled by the consumers and **decomposers** in the mixed layer. However, most of these nutrients are recycled below the seasonal thermocline, where light levels are too low to support significant phytoplankton growth.

In fall, cooling and winter storms again weaken the seasonal thermocline, and nutrients are mixed into the photic zone from waters below. The addition of nutrients often supports a fall bloom of phytoplankton. However, the photic zone is now shallower because of the declining light intensity. Variations in timing, location, and year-to-year climate are particularly important in determining the magnitude of the fall bloom. If nutrients are mixed into the surface layer before the light intensity declines too much and before the mixed layer becomes too deep, a fall bloom occurs. Fall blooms are generally smaller and of shorter duration than spring blooms. If the nutrients are not mixed into the surface layer until late fall, when light intensity is already very low, no fall bloom occurs. In addition, no fall bloom occurs if intense cooling or strong storms eliminate the seasonal thermocline early and create a continuously mixed, very deep mixed layer.

In early winter, the enhanced mixing by storm winds, surface water cooling, and declining light levels combine to return the system to its winter state, in which the phytoplankton are light-limited.

Each year, at each location, the seasonal phytoplankton cycle is different from that of the previous years because of variations in weather. In addition, the details of the cycle vary in response to other influences, such as the composition of planktonic species and the concentrations of nutrients other than nitrogen and phosphorus (particularly the concentration of silicate). The subtle and complex interactions between ocean physics, chemistry, and biology that control the seasonal plankton cycle are further complicated in some coastal regions by other processes, such as the introduction of suspended sediment and nutrients by rivers and coastal upwelling.

Phytoplankton Species Succession

Many herbivores are selective feeders that require or prefer certain characteristics in the phytoplankton they eat. Most commonly, the requirement or preference is that the food species be within a range of sizes suited to the animals' feeding methods. Larger zooplankton and juvenile fishes generally require large phytoplankton cells that are easy to capture and provide large amounts of food. Smaller zooplankton specialize in eating smaller phytoplankton. Most coastal **food chains** that lead to commercially valuable fish and **shellfish** species are short and based primarily on zooplankton and juvenile fishes that eat larger phytoplankton species. Food chains based on the smaller phytoplankton species are generally longer and less efficient (**CC15**), and support fish and shellfish species of generally lesser commercial value. Microbial food chains may be short, but they are thought to be partially self-contained, with much of the organic matter produced being recycled by microbial species rather than consumed in food chains leading to commercially valuable species.

Many factors influence phytoplankton species composition, including temperature, salinity, light intensity, and nutrient concentrations. Because these factors vary seasonally, phytoplankton species composition also varies during the year in most locations. Many different species of phytoplankton are always present at any location, but one or, at most, a few species generally dominate and constitute the majority of phytoplankton. As environmental factors change, one dominant species is replaced by another in a progression called **species succession**.

Phytoplankton species succession can be highly complex and can vary, often greatly, from year to year. One species may become dominant at approximately the same time of year for many years, but may not become dominant at all in other years.

In high latitudes and in regions of persistent upwelling, nutrients are present in relatively high concentrations throughout the phytoplankton growth period. High nutrient concentrations favor larger phytoplankton species, which are predominantly diatoms. Diatoms dominate the phytoplankton community throughout the active growth period in these regions, which consequently support short, efficient food webs (**CC15**).

In mid latitudes, nutrient concentrations vary during the summer growing period. In spring, nutrient concentrations are high, and, consequently, diatoms dominate. The spring bloom of diatoms removes most nutrients from the water column, causing the bloom to collapse and to be replaced by flagellates (**Fig. 13-13**). During summer, after the spring diatom bloom, flagellates (sometimes a succession of different species) dominate the phytoplankton community. The flagellates can obtain their nutrients from the very low concentrations that are sustained by nutrient recycling in the photic zone. In fall, storms return enough nutrients to the photic zone to support fall diatom blooms in some years and areas.

As a result of the seasonal availability of diatoms, many species of zooplankton and juvenile fishes that prefer or require diatoms as food have life cycles that are attuned to the seasons. For example, some fish and **invertebrate** species spawn in spring, and their eggs hatch into larvae that feed voraciously on diatoms. The juvenile fishes reach a sufficient size by late spring, when the diatom bloom collapses, to be able to feed on zooplankton. Some species spawn twice during the year to take advantage of both spring and fall blooms.

Many mid-latitude fish and invertebrate species have life cycles that depend on the availability of abundant diatoms as food for their juveniles during only a few days or weeks at a specific time of year. However, the timing, intensity, and dominant species of seasonal diatom blooms vary from year to year. As a result, the survival rate of the larval stages of many fish and invertebrate species also varies from year to year. The number of juveniles that survive their first critical year of life is called the "year class strength." Year class strength may be high if the species spawns at the optimal time and locations in relation to the seasonal phytoplankton cycle. If year-to-year variability causes spawning and the phytoplankton seasonal succession to be misaligned in time or location in any specific year, sufficient food is not available when needed and year class strength is low.

Phytoplankton species succession is further complicated by variations in the availability of specific nutrients, particularly silicate and nitrogen compounds. During the spring diatom bloom in mid latitudes, silicate may be depleted before other nutrients (**Fig. 13-13**), causing diatoms to be replaced by flagellates that do not require silica. Silica is recycled extremely slowly into solution once it has been incorporated in diatom **frustules**. As a result, silica is not returned to the photic zone until the fall, when nutrient-rich waters from below the seasonal thermocline are mixed back into the mixed layer. These deeper waters have relatively high concentrations of silica dissolved from diatom

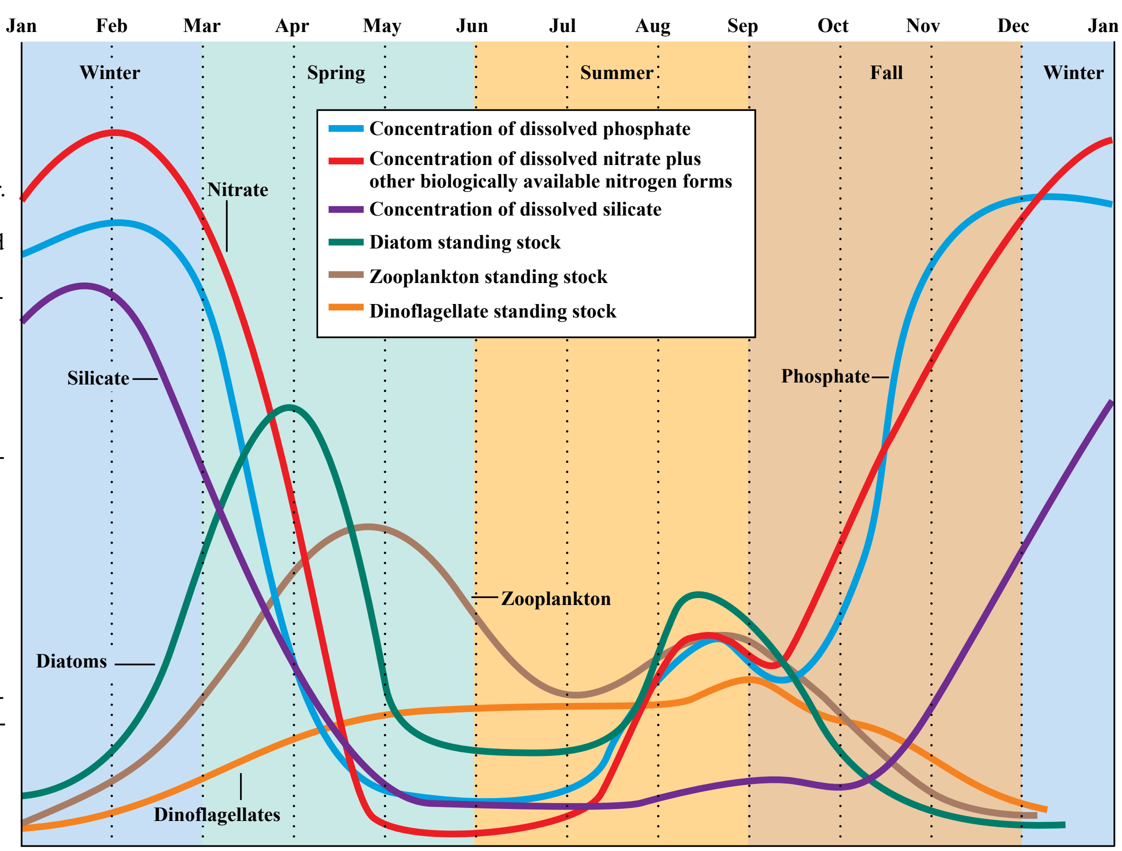


FIGURE 13-13 The seasonal variations of nitrogen, phosphorus, silicon, diatoms, flagellates, and zooplankton in the mid-latitude coastal oceans usually follow a similar pattern each year. The spring bloom of diatoms rapidly depletes the nutrients, and the diatoms are superseded by dinoflagellates. Because the dinoflagellates are not suitable food for many zooplankton species, the zooplankton population also declines. By utilizing nutrients recycled within the photic zone, flagellates and some diatoms continue primary production at relatively low levels throughout the summer. A fall bloom of diatoms often occurs when storms and cooling weaken the thermocline and return some nutrients to the surface layer by mixing. In late fall, the light intensity becomes too low to support substantial primary production. Thus, decomposition, cooling, and wind mixing enable the return of nutrients to the surface layer before the following spring.

frustules and **terrigenous** particles.

All phytoplankton cells require and take up phosphorus and nitrogen in approximately the same ratio as these elements occur in seawater. Similarly, diatoms require and take up silica in a reasonably constant ratio to other nutrients. The proportions of silicate, phosphate, and nitrogen compounds in water below the permanent thermocline are remarkably constant throughout the oceans. In coastal regions, terrestrial runoff normally contains high concentrations of dissolved silicate.

Consider what might happen if there were an excess of nitrogen compounds and phosphate in relation to silicate at the onset of the spring diatom bloom. The diatom bloom would deplete silicate sooner than nitrogen and phosphorus. Flagellates would replace diatoms and could bloom explosively because nitrogen and phosphorus would still be ample. This bloom might produce very large standing stocks of flagellates if, as is often true, herbivores that are able to graze the tiny flagellate cells efficiently were not abundant and could not reproduce quickly. Flagellate blooms do occur periodically, although infrequently, in limited regions where runoff has high nitrogen and phosphorus concentrations but low silicate concentrations. Blooms are becoming more frequent and widespread in regions near centers of human population, particularly where coastal waters have long residence times. Some of these blooms are caused by or substantially strengthened by the huge volumes of treated or untreated human sewage wastes and agricultural fertilizer discharged to the oceans (**Chap. 16**). Untreated sewage has high concentrations of nitrogen compounds and phosphate but relatively low silicate concentrations and sewage treatment employed in most locations in the US and worldwide does not remove nitrogen or phosphorus.

ALGAL BLOOMS

Intense **dinoflagellate** blooms occur naturally, but infrequently, in many parts of the coastal oceans, particularly in subtropical to temperate climates. The frequency of such blooms has been observed to be increasing, and they are occurring in areas where they have not been seen before.

Dinoflagellate blooms can be caused by a variety of mechanisms. For example, a large increase in freshwater runoff can form a shallow surface layer of low-salinity water in a previously well-mixed water column. Phytoplankton that were previously light-limited because they were frequently mixed below the photic zone may be restricted to this shallow surface layer where they are always in the photic zone. This situation may trigger a bloom. In some instances, it is thought that runoff containing dissolved inorganic or organic compounds may trigger blooms because these substances react with toxic substances, such as copper or mercury, and reduce their toxicity to the phytoplankton. Many blooms are caused by such natural events, but increasing nutrient fertilization due to human activity (**Chap. 16**) is generally believed to be a significant causative factor in the increasing frequency and severity of blooms.

Because the nitrogen compound concentration in discharges of treated sewage wastewater and of agricultural runoff and industrial waste are high in relation to the silicate concentration, such discharges are generally believed to be responsible for the higher frequency of dinoflagellate, as compared to diatom, blooms. However, several **cyanobacteria** (also called "blue-green algae") convert dissolved molecular nitrogen, a nitrogen form that most phytoplankton cannot use, to usable nitrate. In some areas, these cyanobacteria may provide the nitrogen needed to initiate or sustain dinoflagellate blooms.

Dinoflagellate blooms can appear quickly but often disappear within a few days as nutrients become limiting. However, under appropriate conditions, blooms can last for many weeks if the source of nutrients is sustained. Dinoflagellates reproduce very rapidly. In optimal conditions, dinoflagellate populations can double in as little as a few hours. Accordingly, blooms can grow within a few days to concentrations of dinoflagellate cells a million or more times greater than normal. Dinoflagellates can also concentrate themselves into blooms by using their weak swimming ability to congregate at depths where light levels are optimal.

The dense concentration of phytoplankton in blooms colors the surface water yellow, green, brown, or reddish, depending on the species. Many dinoflagellates are reddish in color, so their blooms are often called "red tides."

Dinoflagellate blooms often have adverse effects on other marine organisms and, occasionally, on human health. These effects are caused by toxic substances synthesized by certain phytoplankton species, particularly when they are stressed in bloom situations, or by the depletion of oxygen caused by the decaying organic matter that remains when the bloom collapses.

Dinoflagellate and Other Plankton Toxins

Like many terrestrial plants, certain phytoplankton species produce toxic substances as a defense against herbivores. Some, but not all, species of dinoflagellates produce particularly virulent toxins, including saxitoxin, brevetoxin, okadaic acid, and domoic acid. These substances are complex organic compounds and often mixtures of several compounds, some of which are many times more toxic than, for example, strychnine. The toxins are selective: some are toxic to **vertebrates** only, whereas others also affect some invertebrates, particularly **crustaceans** such as shrimp and crabs. Toxins produced by dinoflagellate blooms often kill large numbers of fish.

In addition to fish kills, dinoflagellate toxins can cause serious human health problems because the toxicity is selective for vertebrates. Most **filter-feeding** organisms (organisms that strain or sift food particles from the water), including clams, mussels, and oysters, are unaffected by dinoflagellate toxins but concentrate the toxins in their body tissues. Other invertebrates such as crabs that feed on filter feeding invertebrates can also become contaminated with these toxins from their food. If any of these contaminated invertebrates shellfish are then eaten by vertebrates, the toxins can still produce their deadly effects in the vertebrates. Unfortunately, humans are one of the vertebrate species that feed on shellfish and other invertebrates.

Human poisoning by dinoflagellate toxins concentrated in shellfish is well known. At least four major pathologies are caused by shellfish-borne toxins. The most widespread is paralytic shellfish poisoning (PSP). The toxins that cause PSP are strong nerve poisons that can cause permanent nerve injuries or, if the concentrations are high enough, paralysis and death. There are an estimated 1600 annual cases of PSP worldwide, and an estimated 300 fatalities among these cases. Neurotoxic shellfish poisoning (NSP) is less common and less serious than PSP, but it produces symptoms that are often mistaken for the more common types of **bacterial** food poisoning. Diarrhetic shellfish poisoning (DSP) is also less serious but probably more widespread than NSP, and it causes severe diarrhea. Amnesic shellfish poisoning (ASP) is much rarer pathology in which short-term memory is destroyed, perhaps permanently.

Winds can blow ashore sea spray containing dinoflagellate cells or their detritus from nearshore blooms. When this happens, the toxins cause the local human population to suffer from allergylike reactions, such as irritated eyes, running noses, coughs, and sneezes.

Most dinoflagellate toxins are stable compounds that remain toxic even after prolonged cooking of contaminated shellfish. Once the bloom has disappeared, some shellfish lose their toxicity within days, but other species may remain toxic for months. The only certain way to avoid human poisoning by these toxins is to identify affected shellfish and prevent them from reaching the marketplace. Many countries, including the United States, have extensive seafood monitoring programs to ensure toxin-free shellfish. Unfortunately, these monitoring programs are extremely expensive and difficult to implement. As an alternative, in areas where dinoflagellate blooms occur with reasonable frequency, shellfish areas are closed to harvesting during the summer and fall, when blooms are most likely. Such closures lead to substantial loss of income to fishers. Areas closed to shellfishing because of dinoflagellate blooms are expanding each year, perhaps indicating an increase in the frequency and geographic extent of such blooms.

At one time, only dinoflagellates were thought to produce the powerful toxins that affect people and other vertebrates. However, blooms of at least two different diatom species have now been observed to produce domoic acid. An event that occurred in 1987 in Prince Edward Island, Canada, left several victims afflicted with ASP. The victims suffered short-term memory loss that lasted at least 5 years. A second event, in 1991 off the west coast of California, Oregon, and Washington, did not affect people. In this case, pelicans were poisoned by domoic acid produced by a diatom species that had been consumed by anchovies, on which the pelicans were feeding. Shellfisheries throughout this huge area were closed to harvesting for many weeks.

Other groups of planktonic organisms also produce toxins. For example, cyanobacteria produce toxins that have caused numerous fish kills in freshwater. In 2010, a toxin from cyanobacteria was found to be responsible for the deaths of marine mammals, specifically sea otters. This event was the first know occurrence of hepatotoxic shellfish poisoning (HSP) in the marine environment. The cyanotoxins apparently originated in freshwater rivers but were consumed by coastal shellfish which were, in turn consumed by the sea otters. It has been hypothesized that the toxins may be produced by bacteria or **viruses** living in the phytoplankton cells, rather than by the phytoplankton themselves.

Humans and pelicans are not the only vertebrates poisoned by phytoplankton toxins. For example, in 1986, hundreds of bottlenose dolphins died off the coasts of New Jersey and Maryland after consuming menhaden contaminated with a dinoflagellate toxin, and more died in the same way off the Carolina coast in 1987. In these cases, the menhaden were either less susceptible to the toxin than the dolphins, or the dolphins accumulated more of the toxin as they fed on large quantities of menhaden and were unable to destroy or **excrete** the toxin.

Harmful algal blooms are now known to occur in the waters of almost every coastal state of the United States and are estimated to be responsible for direct economic losses in the United States of between $10 million and $100 million annually. Costs are incurred in public health, closure of commercial fisheries, management, and monitoring. The most frequent toxic algal blooms occur off the coast of Florida every year. It has been estimated that impacts of these blooms alone cost tens of millions of dollars annually, and a 2018 red tide event in Florida is estimated to have a $184 million loss in tourism dollars alone. Algal bloom in other areas have caused deaths of many species, including pelicans, sea otters, and bottlenose dolphin and tainted commercially valuable species, causing closures of recreational and commercial fisheries and major economic losses. In 2015, one of the largest and most severe HABs occurred along the entire West Coast of North America from southern California to the Aleutian Islands. The principal organism in the bloom was a diatom that produced domoic acid, but, in some parts of the affected area, dinoflagellates that produced toxins that cause PSP and DSP were also found. The bloom lasted from May until October and resulted in the closure of several important fisheries. Closures imposed an estimated $48 million in economic losses for the Dungeness crab fisheries, which remained closed until March 2016, $22 million in Pacific razor clam harvest, and major losses in other closed shellfisheries. The bloom toxins were also implicated in the deaths of many top predators, especially sea lions, and several sea bird species.

Oxygen Depletion and Dead Zones

Below the permanent thermocline, oxygen concentrations are reduced by oxygen consumption during **respiration** and decomposition of detritus that has been transported through the thermocline from the photic zone (**Chap. 12**). The same processes consume oxygen below seasonal thermoclines, but the reduction in oxygen concentration is usually small for two reasons. First, the residence time of water in the layer below a seasonal thermocline (but above any permanent thermocline) is at most a few months. When the seasonal thermocline breaks down in the fall, oxygen is returned to this water when it becomes part of the mixed layer in contact with the atmosphere. In addition, in locations where a seasonal thermocline forms, the total production of phytoplankton during the summer is limited by nutrient availability in the shallow mixed layer above the seasonal thermocline. Hence, only a limited quantity of organic matter is transported through the thermocline to be decomposed. Areas with high productivity are generally areas of upwelling or other physical processes that prevent the formation of a steep thermocline. Vertical mixing in these areas continuously transports oxygen-deficient water to the surface, where it regains oxygen from the atmosphere.

Severe oxygen depletion does not generally occur below seasonal thermoclines, but it may occur in specific circumstances when the cumulative **oxygen demand** in the subthermocline layer is very large. The cumulative oxygen demand is the total amount of oxygen consumed before the water mass recontacts the atmosphere or before additional oxygen is supplied by mixing with water that has a higher oxygen concentration. Two circumstances tend to produce high cumulative oxygen demand: high productivity in the overlying water, and long residence time of water below the thermocline. If oxygen concentrations become too low, many animal species cannot survive for more than a short period of time. This low oxygen condition is called **hypoxia**. If the oxygen concentration drops to zero—a condition called **anoxia**—animals cannot survive at all.

Residence times of water below seasonal thermoclines on the continental shelf are generally short, but residence times of water

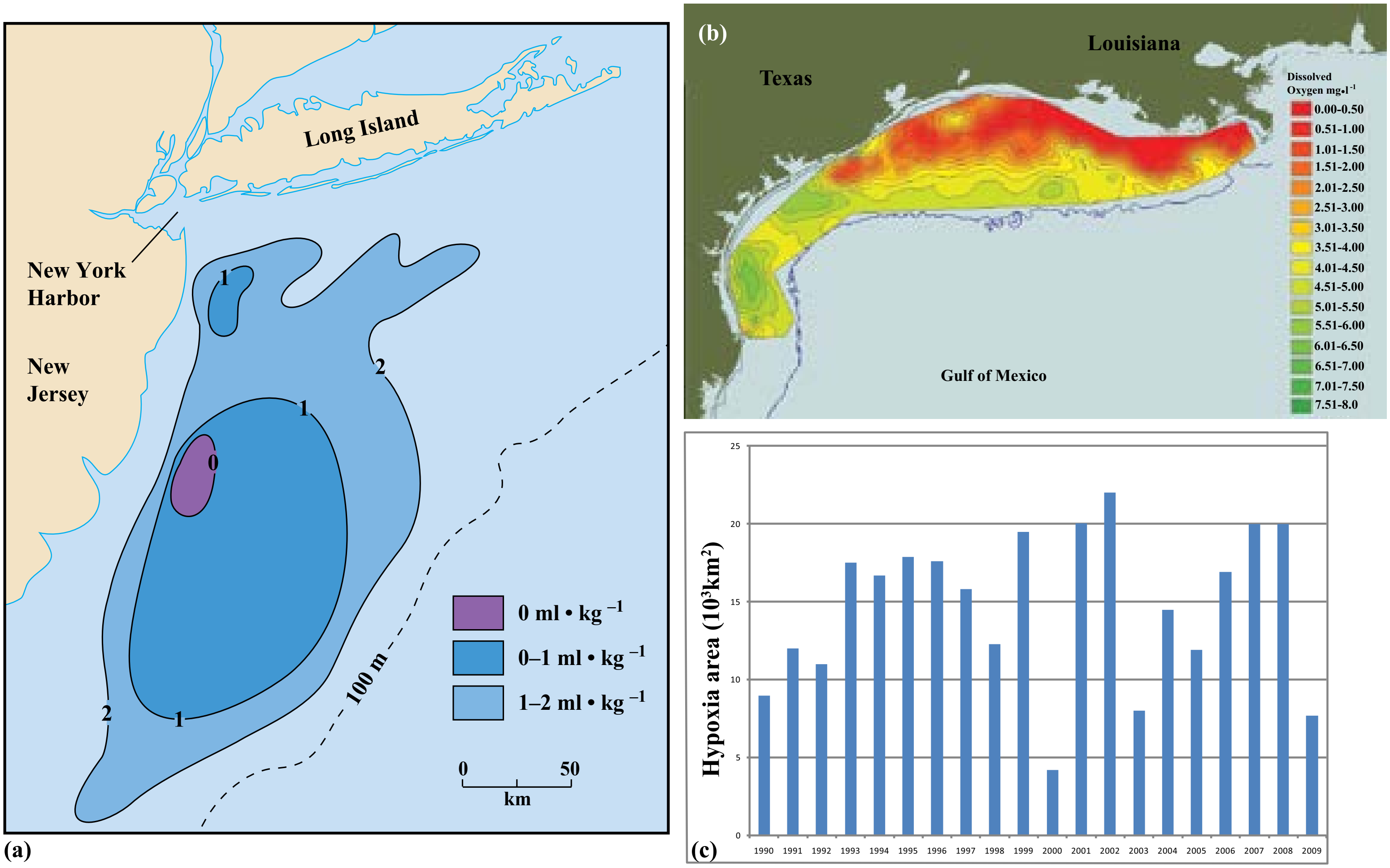


FIGURE 13-14 Anoxia (a) During the summer of 1976, eutrophication and unusual climate conditions combined to produce anoxia or conditions in which oxygen concentrations were too low to support animal life (values of less than 2 in this figure) throughout a large area of the New Jersey continental shelf. This event caused the deaths of massive numbers of clams and other benthic fauna. (b) Hypoxia and anoxia now occur annually each summer in a large area of the Gulf of Mexico continental shelf. This map shows the extent of the hypoxia in summer of 2008. Levels of oxygen above 2.0 are considered essential for marine animals to survive. (c) The Gulf of Mexico “dead zone” affects an area of the Gulf that varies in extent each year. However, the area is now comparable to or greater than the maximum area of fisheries closures during the Deepwater Horizon oil spill of 2010.

below permanent thermoclines in marginal seas or ocean inlets and bays may be very long (often many decades). Consequently, despite the relatively low productivity of marginal seas that have steep thermoclines, the cumulative oxygen demand is sufficient in certain locations to deplete oxygen. The result can be anoxia and the formation and accumulation of toxic sulfide in bottom waters. Examples of such locations are many Norwegian and other fjords and in the Baltic Sea, where anoxic conditions have been present continuously in the deep waters of the central region for at least 100 years. The geographic area of anoxic bottom waters in the Baltic has grown during that time in response to increasing inputs of nutrients and oxygen-demanding organic matter by humans (**Chap. 16**).

In some marginal seas or other coastal areas, normal conditions result in periodic (often seasonal) or permanent hypoxia. In some of these regions, increased phytoplankton growth and blooms can occur as a result of nutrient inputs from sewage, agriculture, and other human sources. Blooms produce large amounts of detritus, and as a result, the naturally low oxygen concentrations below the thermocline are reduced further. This may lead to occurrences of anoxia, causing most benthic **biota** and some deep-water nekton to be either killed or deprived of these areas as **habitat.**

Anoxia may occur in any particular year in a coastal region if primary productivity is high and/or residence time is long. For example, on the continental shelf of New York and New Jersey in 1976, wind mixing was limited, and an intense bloom of phytoplankton developed. The combination of long residence time and high productivity caused a widespread anoxia that extended for hundreds of miles along the coast in a band tens of miles wide across the shelf (**Fig. 13-14a**). The anoxia killed enormous numbers of many marine species, including clams and other shellfish valued at more than $500 million.

The 1976 anoxia was not caused directly by excess nutrients discharged to the oceans from New York and New Jersey, because natural conditions were responsible for the unusually long residence time of that year. However, nutrient inputs to this region in sewage increase productivity and, thus, the probability of blooms. If nutrient inputs are allowed to increase, hypoxia and anoxia would occur at shorter residence times and, hence, probably more frequently.

Overfertilization of natural waters with nutrients that cause blooms and sometimes hypoxia or anoxia is called **eutrophication**. It has been well known in lakes for decades, but has only more recently become the subject of intense study in the coastal oceans.

Temporary or permanent hypoxia or anoxia has been found in a growing number of areas of the coastal zone, increasing from just a handful of locations in the mid-20th century to hundreds today and still increasing. This problem is now so widespread that a new term "dead zone" has become a common way to describe such occurrences. For example, in the Adriatic Sea, the Saronikos Gulf in Greece, the Sea of Japan, and many bays and harbors, periodic massive algal blooms exceed the consumption capacity of the zooplankton population and cause anoxia in the bottom waters. The blooms have been so bad in some years in the Adriatic Sea that the rotting algae have fouled **beaches** and the air, severely affecting tourism in Italy and Croatia. In the United States, hypoxia or anoxia has occurred in the North Atlantic coastal zone, the Gulf of Mexico, Chesapeake Bay, the Oregon coastal region and a number of other bays and estuaries. Extensive efforts have been made to reduce nutrient inputs to Chesapeake Bay to lessen the severity of anoxia but progress has been disappointing so far. In the Gulf of Mexico, there is a seasonal dead zone that now develops annually and often extends from near the mouth of the Mississippi River to the Mexican border of Texas (**Fig. 13-14b**).

The anoxia that now occurs most years on the Oregon continental shelf is apparently caused by a new mechanism not previously seen. The mid depth water mass in the Pacific Ocean has an oxygen minimum zone due to the prolonged time this water mass has been below the thermocline. This oxygen minimum zone appears to be expanding and becoming thicker since it is now shallow enough to extend onto the Oregon continental shelf when winds create seasonal upwelling in summer. The cold high-nutrient water that is upwelled normally supports abundant marine life in this region. However, the upwelled water now often contains insufficient oxygen for respiration and causes a dead zone with massive kills of marine animals. The apparent expansion and deepening of the oxygen minimum layer at mid depths in the North Pacific may be a reflection of either a slowing of the MOC circulation (**Chap. 8**) or an increase in ocean primary production due to increased temperatures and nutrient availability in ocean surface waters, or perhaps both. If the expansion continues, more coastal upwelling regions will likely experience periodic hypoxia and the area of the oceans that has a mid-depth water mass that has too little oxygen to support animal life will expand.

FISHERIES

Because they ultimately depend on primary production for their food, fishes are most abundant in areas where primary productivity is high (**Fig. 12-12, Fig 13-15a**). Hence, fish population density and productivity are higher in the coastal oceans, espe-

FIGURE 13-15 (a) Primary productivity, measured as the total amount of organic carbon produced annually in each square meter of water column, is much higher in upwelling areas than in coastal (nonupwelling) or oceanic areas. (b) The average trophic efficiency is high in upwelling regions, intermediate in coastal regions, and lowest in oceanic regions. (c) Most of the ocean is oceanic in character, whereas upwelling areas constitute only a very small percentage of the total area. (d) Because the area occupied by oceanic regions is so large, the oceanic regions are responsible for most of the worldwide primary production. (e) The total production of fish biomass in oceanic areas is small, despite the high primary production, because this primary production is performed mostly by dinoflagellates and because the average trophic efficiency is low. Dinoflagellates must pass through more trophic levels than the diatoms that dominate in coastal and upwelling regions before they are used to build fish tissue. Thus, more dinoflagellate biomass than diatom biomass is needed to sustain the same fish biomass. Fish production is high in coastal regions because of the relatively high primary productivity and trophic efficiency. Despite their very small area, upwelling regions are responsible for a large proportion of the world's fish production because of their very high primary productivity and high trophic efficiency.

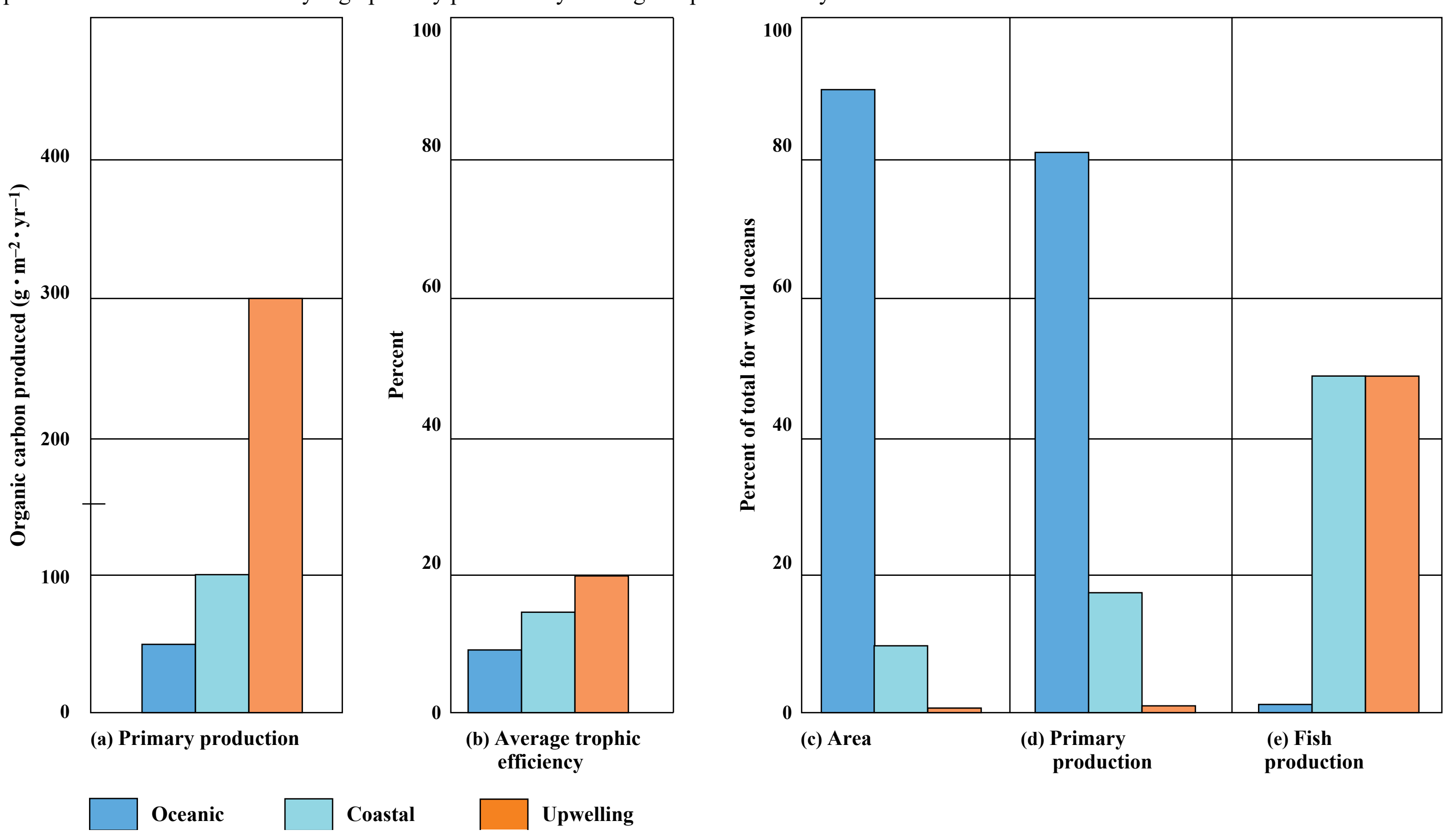


FIGURE 13-16 The ancient Greek city of Ephesus, now in Turkey. In ancient Greek times, Ephesus was a port city. The waterfront was just at the foot of the hill behind the temple in the center of this photograph. The ruins of the port are now several kilometers inland. In the background, you can see the wide flat coastal plain. This was once a large bay, but since ancient times it has filled with sediments

cially in upwelling regions, than in open-ocean areas where there is no upwelling.

The average **trophic efficiency** (**CC15**) is higher in coastal food webs than in open-ocean food webs and is highest in food webs of upwelling areas (**Fig. 13-15b**). As a result, the total fish production of upwelling areas is about half of the world's total (**Fig. 13-15e**), despite the very small area (0.1% of the total area of the oceans) in which upwelling occurs (**Fig. 13-15c**). Coastal regions constitute about 10% of the ocean area and account for about 50% of the world's fish production. Open-ocean regions constitute 90% of the oceans but sustain less than 1% of the world's fish production (**Fig. 13-15e**).

The most successful fisheries are **herring,** anchovy, and sardine fisheries in upwelling regions. These species constitute about 25% by weight of the global catch. Because they feed primarily on zooplankton at the second **trophic level,** they are extremely abundant, and their harvest represents an efficient use of ocean resources. Much of the catch of these species is used to feed animals and not directly to feed people, so we are using these resources at only about 10% of their potential efficiency. About 40% of the global fishery catch of all species is used as animal food.

Because of the distribution of fish biomass production, the world's major fisheries are almost all located in the coastal zone, especially in upwelling areas. Most of these major fisheries are being exploited at or near their **maximum sustainable yield** (**CC16**), and many are overfished. It is believed that the total world fishery catch cannot be increased substantially from its present level without causing detrimental effects on the entire ocean ecosystem, and particularly on higher carnivores (including the largest fishes, marine mammals, and seabirds) that rely on fish stocks for their food. Further, various anthropogenic influences including overfishing, increasing ocean water temperatures and acidity are projected to cause a decline in future fisheries food production potential. Global fishery catch data is hard to estimate due to poor accuracy in data reporting from many fishers and their nations. However, it is believed that the world fishery catch peaked somewhere during the late 1990s and is now declining steadily. Fortunately, the total worldwide production of seafood has remained reasonably stable due to a rapid expansion in aquaculture but it is not know whether aquaculture can continue to make up for declining wild fisheries into the future. Also, aquaculture can not yet, and perhaps will never be able to, economically produce the high trophic level species such a tuna that are of the highest value so some shift in species used for human consumption is inevitable if aquaculture is to replace declining wild fisheries resources

Natural variations in fish stocks are caused by complex interactions of ocean physics, chemistry, and biology. For example, many fish species release their eggs into the plankton community that drifts with the ocean currents. The eggs hatch into larvae that must have the right type of food. For example, anchovy larvae, which eat only phytoplankton that are at least 40 mm in diameter throughout the first few days after hatching. Larval survival of anchovies varies from year to year because the availability of such phytoplankton varies, as do many other factors, including the concentrations of species that compete for food with or prey on the larvae. Survival and success are no less complicated for the larval fish of other species or of the larvae when they become a juveniles, because juveniles also have to find food and are subject to predation, disease, **parasitism**, and the direct and indirect effects of **pollution.** Each of these factors, in turn, can be variable from year to year, at least in part because of year-to-year climatic variations.

Life cycles and their interactions with physical, chemical, and biological variables are so complex that studies must be conducted over many years to obtain even a limited understanding of the population variations in a single fish species. Even after such extensive studies, it is impossible to predict the future of the fish stock with any certainty. Many of the influences on fish stock size and age composition are nonlinear. Consequently, fish stocks of many species are inherently **chaotic** (**CC11**) and appear to fluctuate in a random or unpredictable way. It may be impossible to predict future fish stocks accurately, just as it is impossible to forecast the weather accurately more than a day or so in advance.

ESTUARIES

As freshwater flows into the oceans, it mixes with seawater. Regions where this mixing occurs are called "estuaries." The seaward limit of an estuary is where the dilution of ocean water by freshwater is insignificantly small. The landward boundary, or "head," of the estuary is the maximum landward limit of saltwater movement. Estuaries are present at mouths of major rivers and in many other semi-enclosed inlets or arms of the ocean into which streams and rivers flow. If freshwater discharge is very large, the seaward boundary of the estuary can be many kilometers offshore. The inland boundary can be tens or even hundreds of kilometers inland. The boundaries are not fixed. They can move seaward if freshwater flow rate increases and farther inland if it decreases.

The fact that most major cities are located on estuaries reflects the historical importance of estuaries as harbors and ports. Estuaries are also important to marine ecosystems because many species of fishes and invertebrates spend part of their life cycle in the oceans and part in an estuary or river, and many major fisheries and shellfisheries are in estuaries.

Estuaries differ in characteristics that include their length, width, depth, **tidal range,** freshwater flow rate, shape, and coastal character. These factors affect ocean and river water movements and mixing processes in the estuary. Consequently, there is no simple description of a typical estuary, and no single classification system can capture the many variations. Every estuary is different from all others and has its own unique behavior. However, estuaries are classified into general groups according to the geological processes that formed their embayment or, alternatively, according to their water circulation and mixing characteristics.

Geological Origin of Estuaries

Almost all present-day estuaries were formed as sea level rose in the past 19,000 years from a low point approximately 130 m below current sea level (**Fig. 8.17e**). As the most recent ice age ended and glacial ice melted, sea level rose. River and glacial valleys were flooded and coasts were modified by erosion, forming barrier islands in some locations (**Fig 13-17**, **Chap. 11**).

Estuaries are filled progressively with **sediment** supplied by the river. If sea level were to remain stable long enough, most estuaries would eventually become filled with sediment and **deltas** would form (**Chap. 11**). The inexorable process of sediment filling can be seen at locations such as the former Greek port of Ephesus, now in Turkey. This city, a bustling seaport less than 3000 years ago, is today many kilometers inland, behind a low **coastal plain** formed by the accumulation of sediment eroded from surrounding mountains (**Fig. 13-16**).

In the past, during periods when sea level was falling, there were few estuaries. As sea level falls, the coastal landform con-

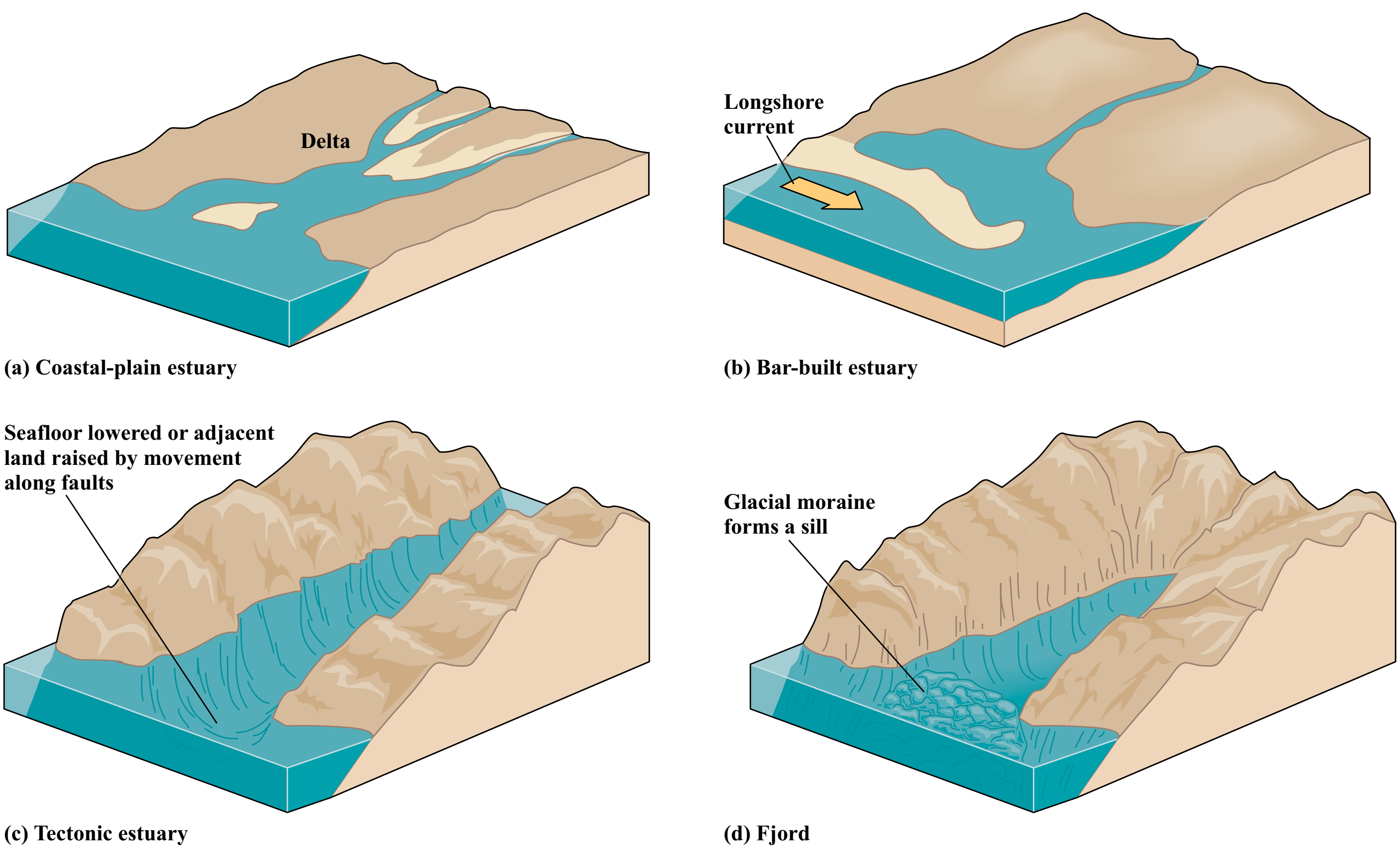
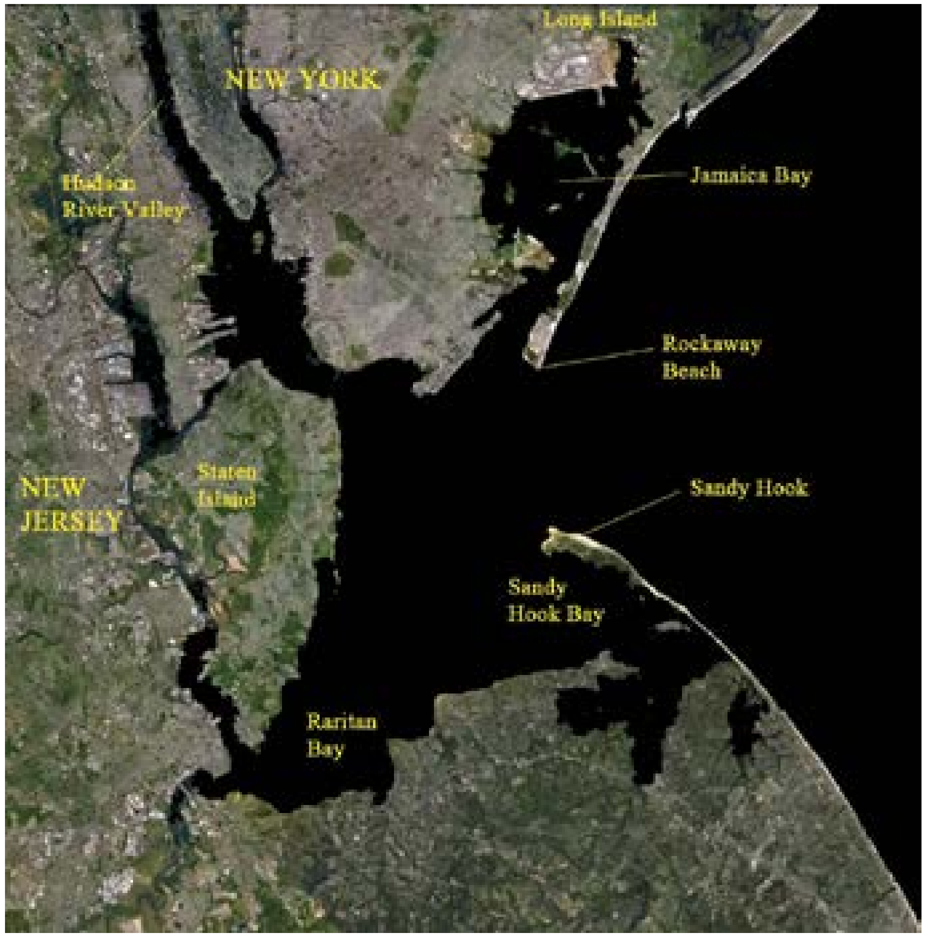


FIGURE 13-17 (Above) The rise of sea level during the past 19,000 years has been a major factor in the creation of all present-day estuaries. Estuaries have a variety of geological settings and origins. (a) The most common estuary is a coastal-plain estuary (also sometimes called a "drowned river valley") that forms as rising sea level floods the mouth of a river. (b) Some estuaries form where longshore drift builds a bar, spit, or barrier island that isolates a bay from free exchange with the ocean. (c) Tectonic estuaries are formed where a block of the Earth's crust is lowered by tectonic processes at earthquake faults. (d) Fjords are created when rising sea level floods the steep-sided valleys that are cut by glaciers and exposed after the glaciers retreat.

FIGURE 13-18 (Right) This satellite image of the Hudson River basin–New York Harbor–Raritan Bay estuary shows the complex character of this estuary. The Hudson River valley is a drowned river and glacier-cut valley and so can be considered a coastal-plain estuary. Parts of the river are steep-sided and deep enough that they may even be considered a fjord. Sandy Hook Bay and Jamaica Bay are bar-built. Raritan Bay and New York Harbor could be considered either coastal-plain estuary segments or bar-built, or both.



sists of newly exposed continental shelf. This new coastal plain is relatively featureless because the topographic lows in the shelf floor are filled with sediment transported by tides, waves, and currents. Estuaries will virtually disappear again when sea level falls in the future.

Rising sea level has created estuaries that differ according to the character of land that has been inundated. Four types are recognized: **coastal-plain estuaries, bar-built estuaries, tectonic estuaries,** and fjords. Coastal-plain estuaries were formed as sea level rose to flood river valleys (**Fig. 13-17a**). These estuaries, often called "drowned river valleys," are especially abundant on passive margins, such as the east coast of the United States. Chesapeake Bay, Delaware Bay, and the New York Harbor are examples of coastal-plain estuaries. The Mississippi River delta is an example of a former coastal-plain estuary that has been filled with river-borne sediment.

Bar-built estuaries are formed when a sandbar is constructed parallel to the coastline by wave action and **longshore drift** (**Chap. 11**), and the bar separates the ocean from a shallow lagoon (**Fig. 13-17b**). Lagoons behind barrier islands are bar-built estuaries. Examples include Albemarle Sound and Pamlico Sound in North Carolina. Some estuaries have mixed characteristics. For example, the Hudson River estuary that passes through the New York Harbor and Raritan Bay is primarily a drowned river valley, but the Sandy Hook **spit** gives Raritan Bay certain bar-built estuary characteristics (**Fig. 13-18**

Tectonic estuaries are formed when a section of land drops or tilts below sea level as a result of vertical movement along a **fault** (**Fig. 13-17c**). Such estuaries are most often present on coasts along **subduction zone** or **transform fault** plate boundaries. The best-known tectonic estuary in North America is San Francisco Bay (**Fig. 13-22**), which is on a **transform plate boundary.**

Fjords are estuaries in drowned valleys that were cut by glaciers when sea level was lower (**Fig. 13-17d**). These estuaries are generally steep-sided, both above and below sea level, and are often deep. Many fjords have a shallow **sill** near the mouth that was formed by sediment deposited at the lower end of the glacier when it flowed through the valley. Fjords are common on the Norwegian coast, the southwest coast of New Zealand, and the Pacific coast of Canada and southern Alaska. Puget Sound in Washington State is also a fjord.

Estuarine Circulation

In estuaries, less dense river water flows over seawater, causing vertical mixing between the two layers. The movements and mixing of freshwater and seawater are affected by many factors, including tidal currents and mixing, wind-driven wave mixing, shape and depth of the estuary, rate of freshwater discharge, friction between the moving freshwater and seawater layers and between the water and seafloor, and the **Coriolis effect** (**CC12**). Because some or all of these factors vary among estuaries between seasons within individual estuaries, and from one part of an estuary to another, estuaries have a wide variety of circulation patterns.

Estuarine circulation is extremely important because many major cities are located on estuaries. These cities discharge large quantities of wastes, particularly sewage treatment plant **effluents** and storm water runoff, into the estuaries (**Chap. 16**). Estuarine circulation patterns determine the fate of these contaminants.

In many estuaries, circulation is altered by piers and other port structures, dredging of navigation channels, filling of **wetlands**, and construction of **levees** and other coastal structures. These alterations can affect life cycles of marine species that

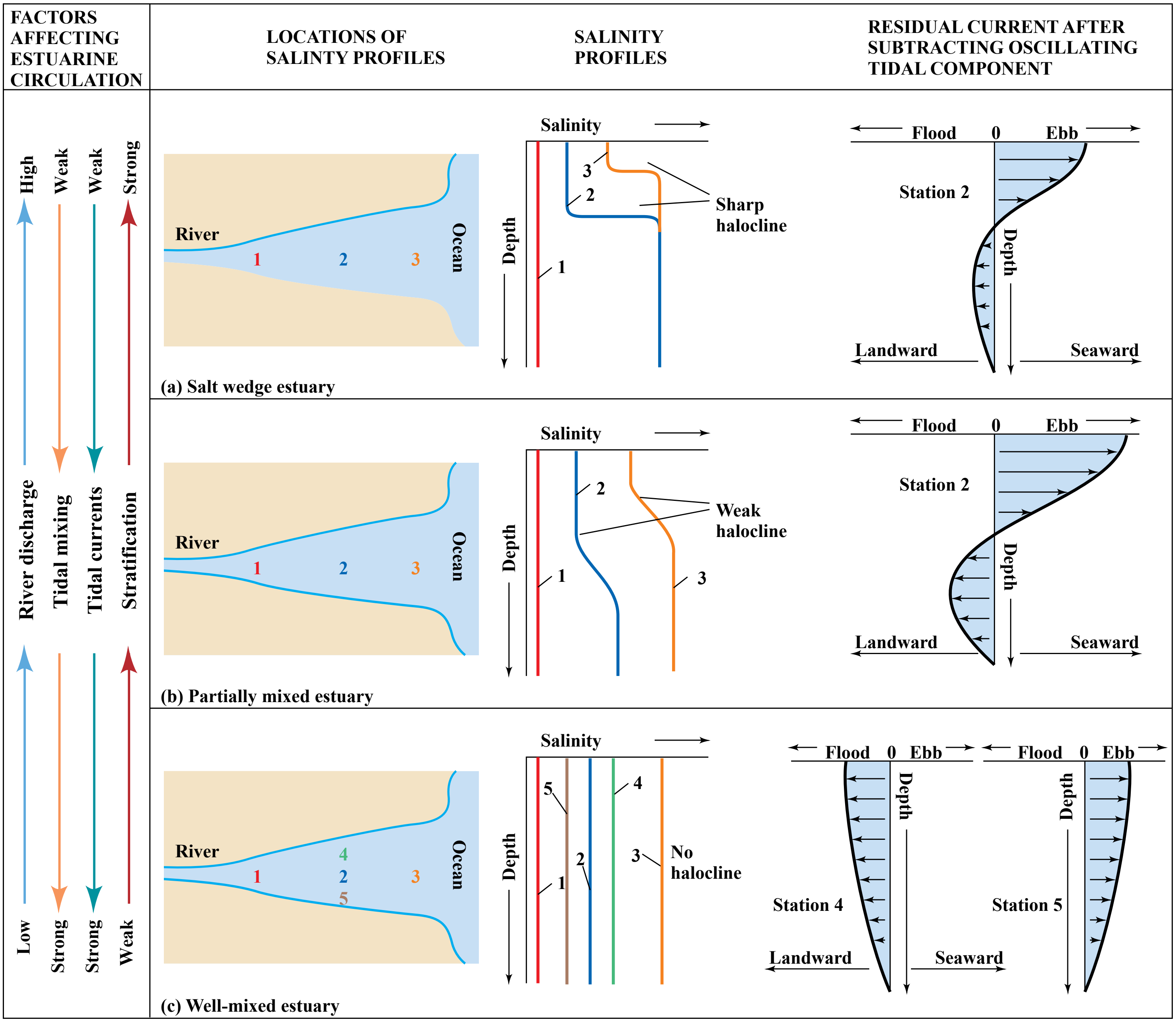


FIGURE 13-19 One way to classify estuaries is on the basis of their circulation characteristics and the factors that influence their circulation. (a) Salt wedge estuaries are river-dominated and are strongly stratified with a sharp halocline. (b) Partially mixed estuaries have a weak halocline because the surface and bottom layers are partially mixed by turbulence induced by tidal currents. (c) In well-mixed estuaries, the water column is thoroughly mixed from surface to seafloor, and there is no halocline. However, salinity does increase progressively with distance from the head of the estuary to the sea and across the estuary as a result of the Coriolis effect.

inhabit or transit the estuary (Chap. 16).

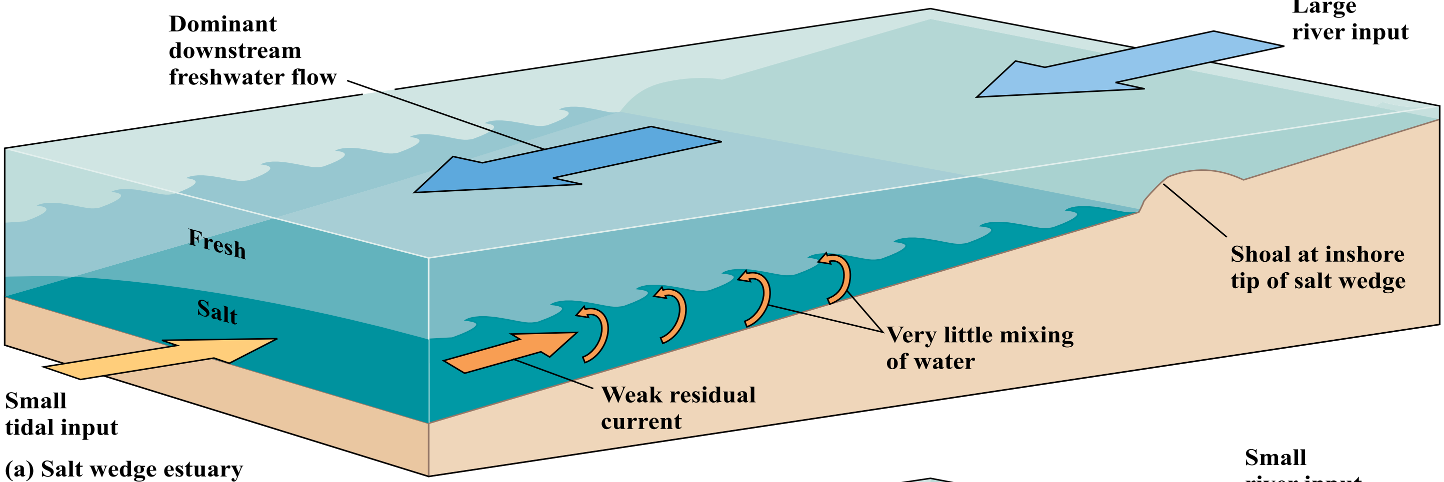
Because circulation within each estuary is complex, varies temporally, and is unique to that estuary, detailed, multiyear physical oceanography studies of each estuary are necessary to understand its circulation. Such studies are difficult and expensive, particularly in large, complex estuaries such as Chesapeake Bay or San Francisco Bay.

Types of Estuarine Circulation

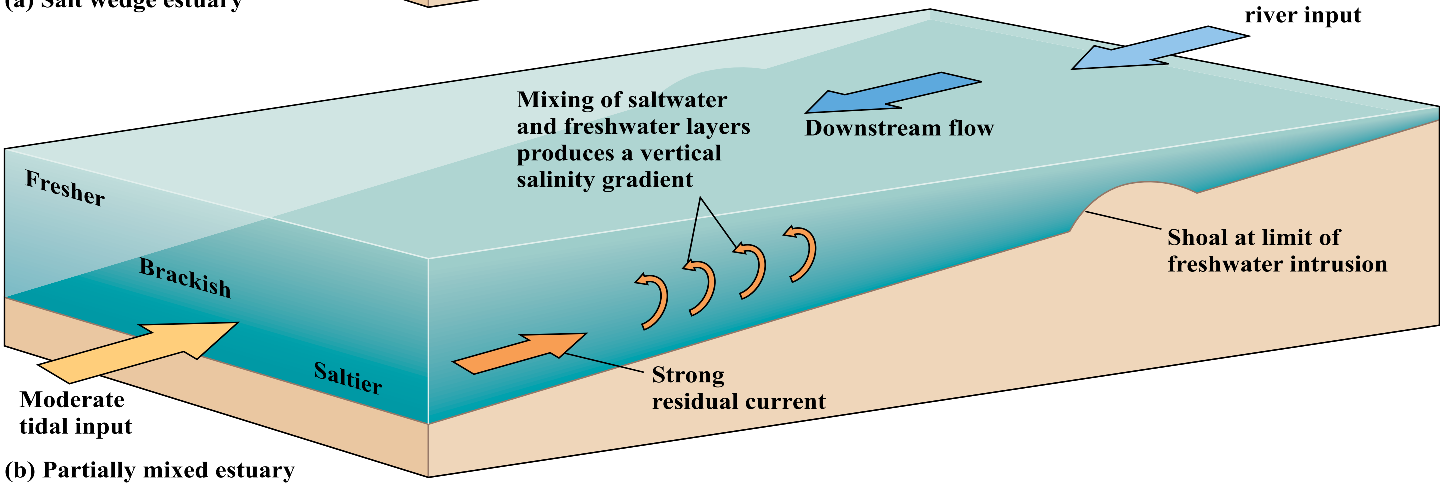
Estuaries can be classified according to the major characteristics of their circulation. The major types are **salt wedge estuaries, partially mixed estuaries, well-mixed estuaries,** fjord estuaries, and inverse estuaries

Salt Wedge Estuaries.

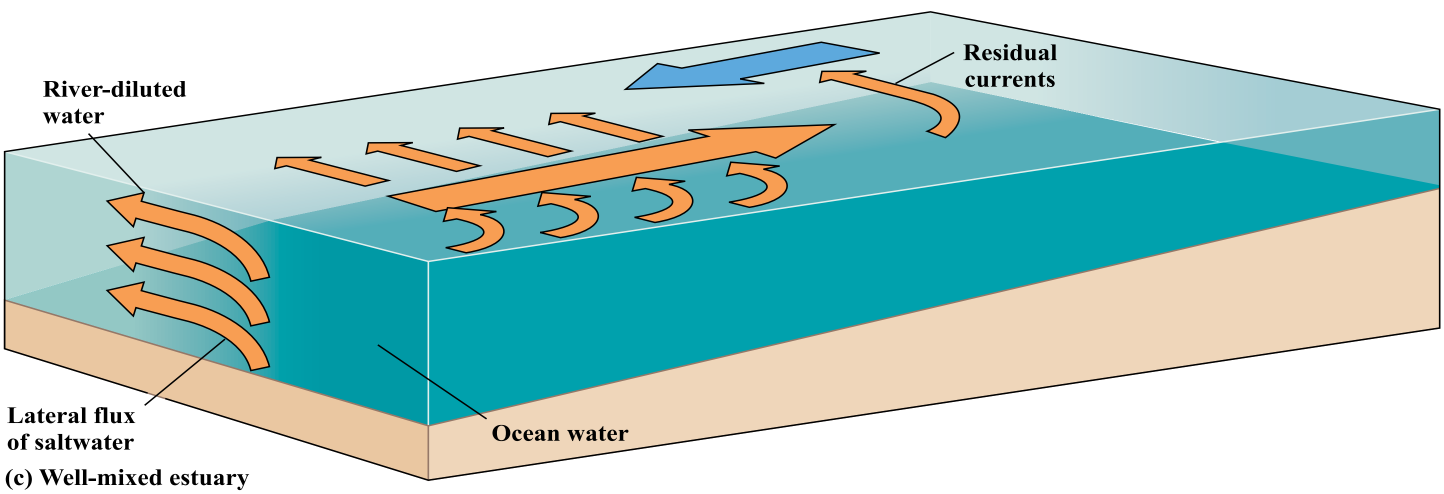
In a salt wedge estuary, freshwater flows down the estuary as a surface layer separated by a steep density interface (halocline) from seawater flowing up the estuary as a lower layer that forms a wedge-shaped intrusion (Figs. 13-19a, 13-20a). Vertical mixing across the steep density gradient is slow in salt wedge estuaries, but the velocity difference between seaward-flowing river water and the underlying seawater creates friction between these layers. The friction causes turbulence and internal waves at the interface. The internal waves grow, and when they break, small quantities of high-salinity water are injected and mixed into the upper layer, which progressively increases in salinity toward the estuary



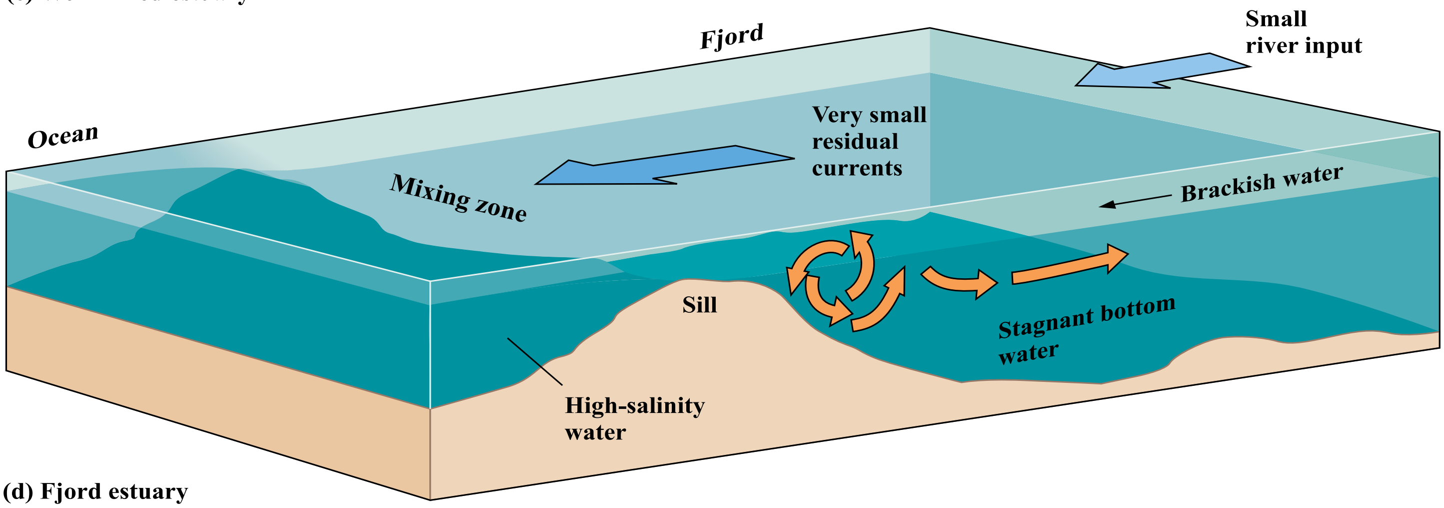
(a) Salt wedge estuary



(b) Partially mixed estuary



(c) Well-mixed estuary



(d) Fjord estuary

FIGURE 13-20 (Opposite page) Types of estuaries. (a) Salt wedge estuaries are characterized by a net (after tidal motions are averaged out) landward current in the lower layer and a net seaward current in the upper layer. There is little vertical mixing, but breaking internal waves on the halocline mix some seawater up into the surface layer. (b) Partially mixed estuaries are characterized by relatively strong net landward currents near the seafloor and relatively strong net seaward currents in the surface layer. (c) Well-mixed estuaries have no vertical salinity variations, but they do have variations in salinity both across and down the length of the estuary. The net estuarine currents are landward at all depths on the right side of the estuary in the Northern Hemisphere (viewed from the ocean), and seaward at all depths on the left side. These currents are on the reverse sides in the Southern Hemisphere. (d) Estuaries in fjords have little current in the deep water below the depth of any sill. In the upper layers above the sill depth, there is generally a salt wedge or sometimes a partially mixed estuary circulation pattern.

mouth (**Figs. 13-19a, 13-20a**). Almost no freshwater is transferred into the lower seawater layer.

Salt wedge estuaries are most likely to be present where freshwater input is relatively large and allows a thick, freshwater surface layer to develop. Estuaries that are narrow in relation to their depth also favor the development of a thick freshwater layer. Other conditions that favor salt wedge estuaries are small tidal range, and hence limited tidal currents and tidal mixing, and limited vertical mixing due to wind-induced motions (e.g., waves, Langmuir circulation, and Ekman transport). To understand how these factors favor the two-layer salt wedge configuration, compare the estuary with a blender filled with water and cooking oil. If the blender runs at high speed, the cooking oil is quickly mixed with and dispersed in the higher-density water. If the blender runs more slowly, the oil will tend to remain in a distinct upper layer, particularly if there is enough oil to create a thick oil layer. A thin oil layer will mix and disperse at a lower blender speed than a thick oil layer.

Partially Mixed Estuaries.

Vertical mixing between freshwater and seawater is greater in partially mixed estuaries than in salt wedge estuaries, and therefore the density gradient between the two layers is much less pronounced (**Fig. 13-19b**). The most important process that causes vertical mixing across an estuarine halocline is the friction and resulting turbulence created by reversing tidal currents. Hence, partially mixed estuaries are most common where tidal currents are relatively fast, river flow rate is moderate, and river current speed does not greatly exceed tidal current speed. As in a blender running at moderate speed with roughly equal volumes of water and oil, some mixing occurs at the interface, but two distinct layers persist.

In partially mixed estuaries, freshwater and seawater layers are separated by a relatively weak halocline. Seawater moves landward up the estuary as a bottom layer and is diluted progressively with freshwater from above (**Figs. 13-19b, 13-20b**). Both layers move up and down the estuary with each tidal cycle. The distance that water moves in the estuary with each ebb and flood is the tidal excursion. The tidal excursion is usually much greater than the landward or seaward net movement that occurs as a result of the **residual currents** of the estuarine circulation (currents caused by the river flow and landward flow of seawater). **Figure 13-19** shows only these residual currents. Residual currents are often difficult to measure because they are masked by the faster reversing tidal currents that must be averaged out to reveal the residual current.

As seawater moves landward and freshwater moves seaward in an estuary, the moving water is deflected by the Coriolis effect. Consequently, if we look at an estuary from the sea in the Northern Hemisphere, seawater moving up the estuary tends to be deflected to our right, and freshwater moving down the estuary tends to be deflected to our left. In salt wedge estuaries, this deflection causes the halocline to be tilted slightly upward toward the right bank (**Fig. 13-20a**). In partially mixed estuaries, the Coriolis deflection affects not only the mean flow, but also tidal currents. As tidal currents flow into the estuary, they are deflected to the right side (as viewed from the sea); as they ebb, they are deflected to the left side. Consequently, in a partially mixed estuary, movement of seawater landward in the lower layer is concentrated on the right side, and the lower-salinity estuarine outflow is concentrated on the left side. The halocline is strongly inclined upward to the right (as viewed from the sea) in many partially mixed estuaries. The incline is in the opposite direction in the Southern Hemisphere.

Well-Mixed Estuaries.

In estuaries with swift tidal currents, mixing is very strong (like the blender at high speed), the water column is completely mixed, and no halocline is present (**Fig. 13-19c**). In these well-mixed estuaries, seawater moving landward is continuously mixed with freshwater moving seaward. Salinity decreases progressively from the ocean toward the head of the estuary. Although the salinity is uniform from surface to bottom, it varies during the tidal cycle, increasing as the tide floods and decreasing as it ebbs.

In large well-mixed estuaries, the Coriolis effect tends to separate the landward and seaward estuarine flows, so they are concentrated on opposite sides of the estuary. This separation is especially important in wide and shallow estuaries. Many such estuaries have a small residual landward movement of water along the right side (as viewed from the sea in the Northern Hemisphere), and a small residual seaward current on the left side. This is made possible by a residual current that flows from one side of the estuary to the other (**Fig. 13-20c**). This circulation causes salinity to be higher on the right side of the estuary and to gradually decrease across the estuary to the left side (**Fig. 13-19c**).

Well-mixed estuaries tend to be wide and relatively shallow. They usually have limited freshwater inputs and strong tidal currents. These factors and others that determine the circulation characteristics change with location in the estuary and sometimes with time. Consequently, an estuary's circulation can vary from well mixed, to partially mixed, and to salt wedge at different times and at different locations within the estuary. San Francisco Bay is a good example (**Fig. 13-22**). The central portion of the bay (closest to the ocean) has relatively strong tidal currents, is wide, and is generally partially mixed. The upper part of the estuary, which is closer to the Sacramento and San Joaquin rivers, is narrower and generally has salt wedge characteristics because tidal currents are somewhat reduced and freshwater inputs are large enough to form a thick, low-salinity surface layer. The southern part of San Francisco Bay is shallow, has very little freshwater input, and is generally well mixed. When river flow rates are low, seasonally or in drought years, the northern part of the estuary becomes partially mixed. During high spring river runoff, the southern and central parts of the bay can become partially mixed

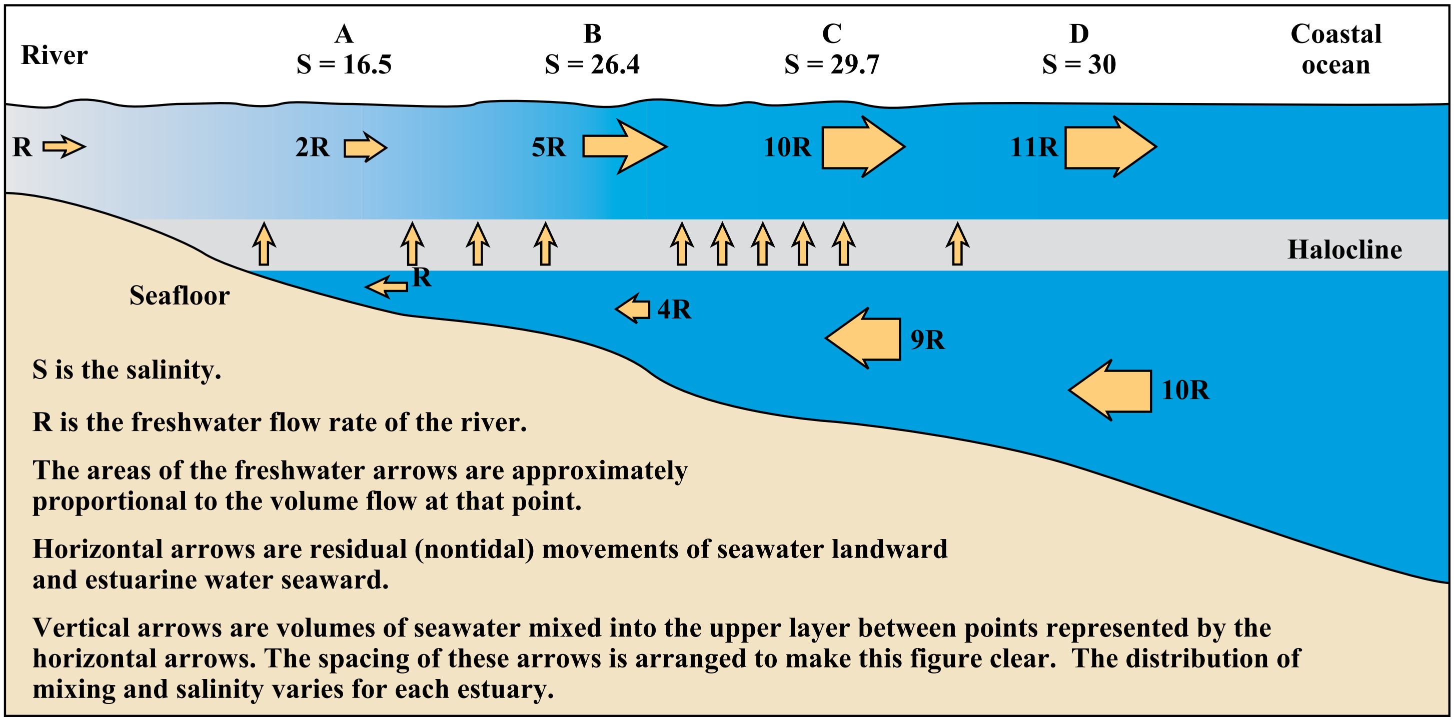


FIGURE 13-21 Seaward-moving surface water increases in salinity from nearly zero at the head of the estuary to 30 where it enters the ocean. Ocean water entering the estuary has a salinity of 33. Where seaward-flowing water reaches a salinity of 16.5 (half that of ocean water), it must consist of one-half river water and one-half ocean water. Seawater must flow landward to point A at a rate (volume per unit time) equal to the river flow rate, and seaward transport of low-salinity estuarine water must equal twice the river flow rate. Similarly, the landward flow rate of seawater at point B must equal 4 times the river flow rate, and the seaward flow rate of low salinity estuarine water must be 5 times the river flow rate

or even salt wedge estuaries.

Fjord Estuaries.

Fjords are generally narrow and usually much deeper than most other estuaries. Most fjords are deep enough that vertical mixing does not reach the bottom waters, even if tidal currents are strong. Consequently, almost all fjords have a halocline separating high-salinity bottom water from lower-salinity surface water, and fjords are almost never well-mixed.

Circulation in many fjords is complicated by the presence of a shallow sill at the seaward end of the estuary that prevents the free exchange of deep water between ocean and fjord (**Fig. 13-20d**). Therefore, estuarine circulation is established only above the level of the sill. The fjord's interior above the sill depth behaves as a salt wedge or partially mixed estuary. At the sill, vertical mixing is enhanced by turbulence caused by the flow of water over the sill (**Fig. 13-20d**). The deep water below the sill depth within the fjord is stagnant and is not involved in the estuarine circulation. In many fjords, the deep water becomes anoxic because of the decomposition of organic particles that have settled from above. Periodically this deep water may be displaced by high-salinity ocean water that floods over the sill in response to some unusual set of water movements. In such circumstances, hydrogen sulfide in the fjord bottom water is displaced into surface waters of the fjord and ocean, where it may cause extensive fish mortality.

Inverse Estuaries.

Shallow estuaries in arid regions can sustain sufficiently high rates of evaporation that salinity is higher than that of ocean water outside the estuary. In this situation, estuarine circulation is inverted. High-salinity estuarine water flows seaward in a bottom layer, and ocean water flows landward as a relatively lower-salinity (and less dense) surface layer. Inverse estuaries generally occur at about 30°N or 30°S, in the region of atmospheric subtropical highs, where evaporation is strong and rainfall typically is low. Some well-known examples of inverse estuaries are the Red Sea, San Diego Bay in California, and Laguna Madre in Texas. In addition, the Mediterranean Sea behaves as though it were an exceptionally large inverse estuary.

Particle and Contaminant Transport in Estuaries

Most major cities have developed next to rivers and estuaries, partly because of their convenience for the disposal of sewage and other wastes. The common belief is that wastes discharged to a river or estuary are simply swept out to the ocean, where they are diluted in the vast volume of ocean water. However, a simple explanation of water movements and suspended-particle transport within estuaries reveals that this is not what happens.

Freshwater input at the head of the estuary creates the estuarine circulation. To sustain this circulation, the amount of seawater that flows through the estuary must greatly exceed the volume of freshwater discharged during the same period of time. To understand this process, we must first observe that freshwater entering the head of most estuaries has a salinity close to zero, whereas water discharged from the estuary mouth into the ocean has a salinity almost equal to that of the seawater. Freshwater mixes with seawater, so the salinity of the seaward-moving water progressively increases along the length of the estuary (**Figs. 13-19, 13-21**).

Figure 13-21 depicts the relative residual flow rate (the volume of water that passes a particular point in the estuary per day) in various parts of an estuary. From the figure, we can see that the

FIGURE 13-22 This image of San Francisco Bay, taken by the Landsat satellite, shows the high turbidity in the upper estuary, where there is a salt wedge circulation, and the location of the Alcatraz dredged-material dump site near the estuary mouth, where the circulation is partially mixed

residual flow rate of seawater moving landward and the residual flow rate of estuarine water flowing seaward at the mouth of an estuary are both many times greater than the river flow rate. In addition, the seaward and landward flow rates are highest near the mouth of the estuary and decrease toward the head of the estuary. The residual flow rate is equal to the residual current speed multiplied by the cross-sectional areas of the estuary. Consequently, flow rate does not always translate directly into current speed, because the cross-sectional area of an estuary changes, sometimes in complex ways, along its length. However, the large differences in flow rate along an estuary generally cause both landward and seaward residual currents to be higher near the mouth of the estuary than near the head.

Rivers carry large quantities of suspended sediment particles, the largest of which are quickly deposited when the river reaches the flat coastal plain or, if there is no coastal plain, when the river enters the head of an estuary. The finest particles could remain in suspension as they are transported to the oceans, but the increased salinity in the estuary causes most of them to clump. Because the clumps are larger, they are then deposited.

Particles of intermediate size, which fall slowly through the water column, are usually deposited within the estuary. In well-mixed estuaries, these particles are deposited primarily on the left side (as viewed from the sea in the Northern Hemisphere). In other estuaries, seaward-moving particles fall through the water column into the landward-moving bottom layer, where they are transported back toward the head of the estuary. These particles often are deposited near the estuary's head where tidal and residual currents are low, often accumulating as a shoal (**Fig. 13-20a,b**). However, when elevated river flows extend the head of the estuary seaward, the particles may be resuspended by the swifter river currents. In many estuaries, these recycled particles

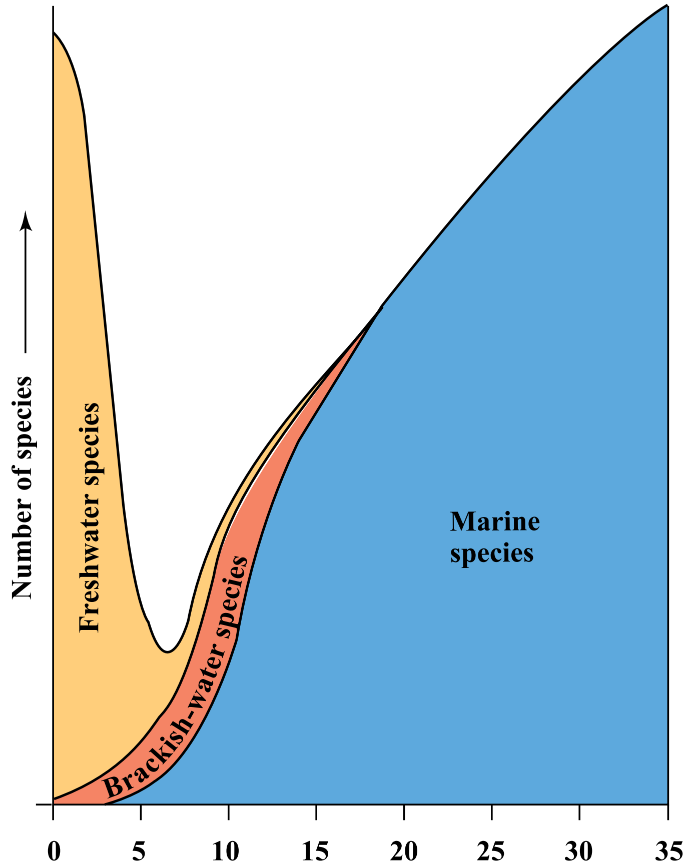


FIGURE 13-23 The number of species of marine, estuarine, and freshwater origin varies within the salinity gradient of a typical estuary. The fact that the total number of species is much lower in the brackish-water zone than in the freshwater or the marine zones reflects the stressful environmental conditions, particularly variable salinity, in the brackish-water region.

are eventually deposited in wetlands (Chap. 11).

Sediments also can be transported from the ocean into estuaries, particularly in estuaries where tidal currents are strong enough to resuspend sediments that accumulate on the nearshore continental shelf.

Substantial quantities of suspended sediment can be transported from the ocean into well-mixed estuaries, where they accumulate along the right side (as viewed from the sea in the Northern Hemisphere). Smaller quantities of suspended sediment are carried from the ocean into partially mixed and salt wedge estuaries. Even particles carried into the ocean by the seaward-moving surface layer may return to the estuary if they sink and are transported landward in the seawater layer.

The fate of particles in an estuary depends on the particle size and where the particles are introduced to the estuary. Floating and extremely small particles introduced to the surface layer (or to the left side of a well-mixed estuary) are transported to the oceans, although many will clump at higher salinities. Small or low-density particles in bottom waters are transported landward until the current slows and they are deposited. Such particles may accumulate in the estuarine sediments or in the sediments of adjacent wetlands, and they may be resuspended and carried seaward when river flow rates are high. Particles of intermediate size in the surface layers of salt wedge or partially **stratified** estuaries are carried seaward until they sink below the halocline, then are transported landward until they settle out in the upper parts of the estuary where current speeds are lower. Large particles tend to accumulate near the point of introduction.

The important point of the preceding discussion is that suspended particles tend to be retained within the estuary by the estuarine circulation and are not simply flushed into the open ocean. Because most toxic metals and organic compound attach

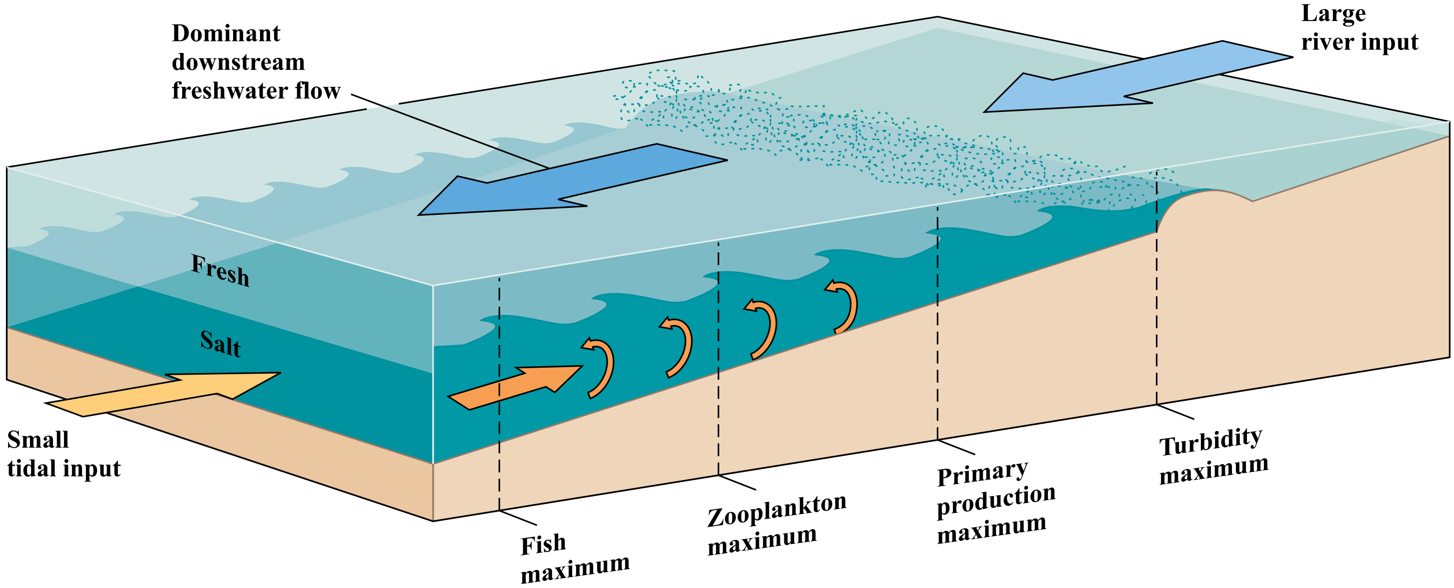


FIGURE 13-24 In many estuaries, an accumulation of particulate matter creates high turbidity near the landward extent of seawater intrusion. Particles transported seaward in the upper layer may sink to the lower layer before leaving the estuary and then return to the high-turbidity area in the landward-flowing lower layer. Many planktonic estuarine organisms use this pathway to stay within the estuary or to reach an appropriate point in the estuary at the right time in their life cycle. The maximum primary productivity in an estuary is usually just seaward of the high-turbidity zone. In this region, more light can penetrate. In addition, nutrients are available because they are regenerated by the decomposition of suspended detritus particles transported up the estuary in the lower layer and are then mixed into the surface water at the turbidity maximum. Maximum zooplankton populations and growth occur downstream of this area to take advantage of the phytoplankton drifting seaward in the upper layer.

to particles, particularly the organic particles in treated sewage effluents, they tend to accumulate in the estuary and are not flushed out to the ocean.

A lack of understanding of estuarine circulation and its effect on particles and the fates toxic metals and organic compounds is one reason that many estuarine ecosystems have been and continue to be severely impacted by human activities. One of many examples of the misuse of estuaries for waste disposal is in San Francisco Bay, where navigation channels, marinas, and ports must be dredged to maintain desired depths. Most of the dredged sediments were, for decades, and some still are, dumped near the bay's mouth at a site between Alcatraz Island and San Francisco (**Fig. 13-22**). The swift tidal currents were expected to flush the material out to the ocean, where it would be dispersed. However, the dump site is near the right bank (viewed from the sea) of a partially mixed estuary, and the dumped dredged sediments instead fall to the floor of the bay and disperse in the lower part of the water column.

With an understanding of estuarine circulation, we realize that much of the dredged material dumped at the Alcatraz dump site, with its toxics load, is not transported to the ocean. It is instead transported back within San Francisco Bay by estuarine circulation and eventually is deposited in low-energy areas, including the same channels and harbors from which it was originally dredged. Perhaps more importantly, continual dredging and disposal disturbs the particle-associated toxic metals and organic compounds, which were relatively safe when buried in sediments, and resuspends them in the estuarine circulation, where they are more directly in contact with the biota (**Chap. 16**). Fortunately, the most contaminated dredged material is no longer dumped at this dump site.

Estuarine Biology

Estuaries are difficult places for organisms to inhabit because they are subject to rapid and irregular changes in environmental factors such as salinity, temperature, and current speed. The stress induced by salinity changes is particularly challenging because organisms must be able to cope with widely varying **osmotic pressures** (**Chap. 14**).

Because estuaries are high-stress **environments**, they support fewer species than the adjacent ocean or freshwater environments support (**Fig. 13-23**). However, there is an abundant supply of nutrients and sunlight in most estuaries. As a result, estuarine biomass is typically much greater than biomass in freshwater and ocean environments, with the exception of the most productive coastal upwelling areas.

Although estuaries typically have relatively high turbidity, they are also generally shallow, and in many, light penetrates to the bottom. In such estuaries, primary production is dominated by benthic **microalgae**, particularly diatoms, that form mats that carpet the sediments. Macroalgae can grow on the estuary floor in areas where current speeds are low. In addition, rooted aquatic plants are abundant in the tidal **salt marshes** and **mangrove** forests along the edges of many estuaries. In contrast, because phytoplankton are continually being swept seaward with the estuarine surface layer flow, their populations are relatively limited in estuaries that have short residence times.

Nutrients are generally abundant in estuaries because they are supplied in substantial quantities in river water that has **leached** them from soils and rocks of the drainage basin. In addition, once in the estuary, nutrients tend to be retained and recycled within the estuarine circulation. Nutrient-containing detritus, which flows seaward in the surface layer, sinks below the halocline and then returns with the landward-flowing ocean water. This circulation tends to concentrate detritus in the region near the landward limit of seawater intrusion (**Fig. 13-24**), which has low residual currents. This region has high turbidity as a result of the accumulated detritus and other particles. The nutrient-rich detritus supports a varied community of fish and invertebrate larvae and juveniles.

In many estuaries, much of the detritus that accumulates in the upper part is derived from algal mats from the adjacent wetlands (**Chap. 11**). Where residual currents are slow, or the estuary is long, a food chain from phytoplankton to zooplankton to estuarine fishes is established that is analogous to the food chain in the coastal upwelling ecosystem described previously in this chapter. Zones of high phytoplankton abundance, high zooplankton abundance, and high fish abundance form a seaward progression from the head of the estuary (**Fig. 13-24**). Some planktonic organisms and larval fishes that are being transported seaward in the estuary's upper layer and away from the region of abundant food supply sink into the seawater layer. They are then transported back into the food-rich region.

Because they provide abundant food and substantial protection, estuaries are ideal habitats for the larvae and juvenile stages of marine animals. Particularly in wetlands, there are many shallow-water hiding places that are accessible to small swimming organisms but not to their larger predators. In addition, predators are less common in estuaries than in less stressful freshwater or ocean environments. Many marine fishes and invertebrates use estuaries as nursery grounds. Some species briefly visit the estuary to spawn, and others release vast numbers of eggs in the adjacent ocean so that they are transported into the estuaries by the estuarine circulation. Along the southeast coast of the United States, more than half of the commercially important marine fish species are known to use estuarine wetlands as nursery areas or for breeding. Because of the abundant supply of detritus, estuaries also support huge populations of commercially important shellfish, including clams, oysters, mussels, and crabs.

Anadromous and Catadromous Species

Estuaries are important to two categories of migratory fishes that live most of their lives either in the oceans or in freshwater. **Anadromous** fishes, such as salmon and striped bass, live most of their lives in the ocean but return to freshwater to spawn. The stress involved in the return to freshwater and the energy lost in spawning are such that the adults die soon after they spawn and do not return to the ocean. Their offspring develop in freshwater and migrate to the estuary, which provides abundant food and relative safety from predators. Eventually, they migrate out to sea, where they live several years before returning to the rivers to spawn.

Catadromous fishes use a strategy opposite that of anadromous fishes. Catadromous species live most of their lives in freshwater and then journey to the oceans to spawn and die. Freshwater eels are the best-known and most abundant catadromous species. Sexually mature eels in rivers on both sides of the North Atlantic Ocean make a one-way journey to spawn in the southwest part of the Sargasso Sea. Their offspring return to the rivers, riding part of the way on the Gulf Stream. North Pacific eels make a similar journey to the equivalent southwest area of the North Pacific Gyre, and their offspring use the Kuroshio

(Japan) Current for the ride home.

Anadromous and catadromous species do not generally spend much time in the estuary during their reproductive migration, but being there is especially stressful because they must make the osmotic-pressure adjustment from seawater to freshwater, or vice versa, very quickly. Striped bass, for example, rest in the outer part of the estuary to adjust to lower salinity before moving farther upstream. Many estuaries also have relatively high concentrations of toxic metals and organic compounds that are likely to cause additional stress on anadromous and catadromous species as they transit the estuary. Such contamination by toxics may account, in part, for the decline of these species in some areas.

CHAPTER SUMMARY

Special Characteristics of the Coastal Oceans.

Salinity and temperature are more variable, and turbidity is generally higher in coastal waters than in the open ocean. River discharges often lower salinity and increase turbidity near river mouths, and a shallow halocline is often present in this region. Coastal currents are driven by local winds and are generally independent of ocean gyre currents, often flowing in the opposite direction. Benthos of the coastal oceans are more diverse and abundant than open-ocean benthos.

Nutrient Supply to the Coastal Photic Zone.

The mixed layer in many coastal regions receives nutrients from river runoff, coastal upwelling, decomposition of organic matter on the shallow seafloor, eddies formed around shallow seafloor topographic features, and breaking internal waves. Nutrients tend to be retained in coastal waters because residence times of coastal water masses are often long. Coastal upwelling is most prevalent off the west coasts of continents where Ekman transport moves the surface layer offshore. Newly upwelled water may support only limited primary productivity until needed organic compounds are synthesized by flagellates. As upwelled water moves offshore, diatoms bloom and are consumed by zooplankton, and eventually nutrients are depleted and primary productivity declines.

Nutrients may be recycled as they are transported into subthermocline waters in fecal pellets, released there by decomposers, and transported back inshore and upwelled. The eggs or spores of many species are carried inshore in subthermocline water, are then upwelled, **metamorphose** or hatch, and move back offshore where phytoplankton food supply increases. There they mature and produce eggs or spores that sink and reenter the circulation.

Seasonal Cycles.

In subpolar regions, primary productivity is very low, except during a short summer when light intensity is sufficient for photosynthesis. Nutrients are plentiful in areas where strong vertical mixing prevents a pycnocline from forming. In polar and some subpolar regions, vertical mixing is restricted by a halocline formed by freshwater runoff and sea-ice melt; hence, nutrients are limited, and productivity is low.

In tropical regions, there is little seasonality, and nutrients are always limiting, except in upwelling areas. However, coral reef ecosystems are highly productive because of nutrient recycling, primarily between corals and their symbiotic zooxanthellae.

In mid latitudes, the winter water column is well mixed, and primary production is light-limited. In spring, as light intensity increases, a plankton bloom occurs and continues until nutrients are depleted. Nutrient depletion is often accelerated by the formation of a shallow seasonal thermocline. Productivity remains low until fall, when storms provide additional nutrients by vertical mixing and a limited fall phytoplankton bloom may occur. Nutrients are returned to the photic zone by winter mixing.

There is a succession of dominant phytoplankton species during seasonal cycles of mid and high latitudes. Generally, diatoms dominate when nutrients are abundant and are replaced by flagellates as nutrients decline or as silica is depleted. Species succession is similar each year, but it varies in timing and dominant species because of differences in climate and the physical and chemical characteristics of the ocean water. Juveniles of many animal species rely on particular phytoplankton species or types at particular times and locations. When the species succession is altered, and this food is unavailable, these species' larval survival can be drastically reduced.

Algal Blooms and Dead Zones.

Intense blooms of dinoflagellates occur infrequently in coastal water, primarily at subtropical and temperate latitudes. These episodic blooms can be natural. However, their frequency appears to be increasing off many coasts, and evidence suggests that sewage-derived nutrients may favor the dominance of dinoflagellates over diatoms and contribute to some blooms. Certain dinoflagellates and diatoms produce substances toxic to vertebrates. Hence, blooms can kill fishes. They can also adversely affect human health, because the toxins do not harm shellfish but are toxic to people who eat the shellfish. The most prevalent dinoflagellate toxin causes paralytic shellfish poisoning in humans. Many valuable shellfishing areas are closed to harvesting during months when dinoflagellate blooms may occur.

When phytoplankton blooms collapse as a result of nutrient depletion, their decomposing remains can deplete oxygen in bottom waters, particularly where residence times are long and bottom waters are separated from surface waters by a seasonal thermocline. Anoxia can decimate benthic communities. The number of coastal areas experiencing periodic or permanent anoxia has grown for just a handful in the mid 20th century to many hundreds and the number continues to grow. There is strong evidence that nutrients, especially nitrogen, in sewage is responsible for much of the increase in the frequency and geographic extent of hypoxia and anoxia in coastal waters adjacent to major cities.

Fisheries.

Fishes are most abundant in areas of high primary productivity, especially in coastal waters, where trophic efficiency is higher because food webs are shorter. Coastal upwelling regions account for about half of the world's fishery production. Natural variations in fish stocks and reproductive success are so great that maximum sustainable yield cannot be established accurately. Many fisheries are currently exploited at or above their maximum sustainable yield, and a number have collapsed. Global fisheries production appears to have peaked and is now declining.

Estuaries.

Estuaries are regions where seawater mixes with freshwater from rivers. Most present-day estuaries were formed as sea level rose during the past 19,000 years. Coastal-plain estuaries are drowned river valleys, and are abundant on passive margins. Bar-built estuaries are located landward of sandbars or barrier islands. Tectonic estuaries are formed by uplift or subsidence of the coast at a fault. Fjords are drowned valleys previously cut by glaciers.

In salt wedge estuaries, seawater forms a lower layer separated by a sharp halocline from a low-salinity surface layer. Seawater progressively mixes into the surface layer as this layer moves seaward, raising its salinity. In partially mixed estuaries, the halocline is much broader, usually because of greater vertical mixing by tidal currents. In well-mixed estuaries, the water column has vertically uniform salinity, but salinity progressively increases seaward. In all but inverse estuaries, residual (nontidal) currents due to the estuarine circulation flow landward in the bottom part of the water column and seaward in the surface layers. The flow rates of seawater into the estuary and of lower-salinity water into the ocean are many times greater than the flow rate of freshwater into the estuary. In the Northern Hemisphere, the Coriolis effect deflects flow into the estuary toward the right side as viewed from the ocean and deflects the outflow to the left side. Fjords have estuarine circulation only at depths above the top of their sill. Water below the sill depth is stagnant and often anoxic. Occasional flushing of anoxic bottom water enriched in hydrogen sulfide can cause fish kills.

Particles and associated toxic metals and organics tend to be trapped in estuaries. They can move seaward in the upper layer, but they sink to the lower layer that moves landward in estuarine circulation.

Estuaries are stressful environments for organisms because of variable temperature, salinity, turbidity, currents, and other environmental factors. However, they provide food and shelter from ocean predators, particularly in bordering wetlands. The estuarine circulation enables weakly swimming or planktonic species or their eggs and larvae to remain within the estuary. Anadromous fishes live in the ocean and transit estuaries to spawn in rivers. Catadromous fishes live in rivers and transit estuaries to spawn in the oceans.

KEY TERMS

You should be able to recognize and understand the meaning of all terms that are in boldface type in the text. All of those terms are defined in the Glossary. The following are some less familiar key scientific terms that are used in this chapter and that are essential to know and be able to use in classroom discussions or on exams.

algae
anadromous
anoxia
bar-built estuary
barrier island
benthic
benthos
biomass
bloom
carnivorous
catadromous
chlorophyll
coast
coastal plain
coastal-plain estuary
coastal upwelling
coastal zone
coastline
community
mangrove
marginal sea
maximum sustainable yield
microalgae
micronutrient
mixed layer
nekton
nutrients
nutrient-limited
osmotic pressure
overfished
oxygen demand
partially mixed estuary
photic zone
photosynthesis
phytoplankton
plankton
polyp
contaminant
continental shelf
coral
coral reef
cyanobacteria
delta
detritus
diatoms
dinoflagellates
ebb
ecosystem
eddy
effluent
Ekman transport
estuary
eutrophication
fjord
flagellate
flood
food chain (web)
habitat
halocline
hard parts
herbivorous
hypoxia
internal wave
invertebrates
isothermal
kelp
lagoon
larva
longshore drift
macroalgae
primary production
primary productivity
pycnocline
residence time
residual current
respiration
resuspended
runoff
salt marsh
salt wedge estuary
shelf break
shellfish
shoal
shore (shoreline)
sill
spawn
species succession
spit
standing stock
stratified
suspended sediment
symbiotic
tectonic estuary
thermocline
trophic level
turbidity
turbulence
upwelling
vertebrates
water mass
well-mixed estuary
wetland
zooplankton

STUDY QUESTIONS

1. What characteristics of the coastal oceans make them different from the deep oceans?
2. How does coastal upwelling occur? How could you tell whether upwelling is likely in waters off a particular coast without making any direct observations of the oceans?
3. Describe the circulation in coastal upwelling zones. How do organisms take advantage of this circulation?
4. What are the sources of nutrients to the coastal photic zone? Discuss their distribution in the oceans.
5. Why are there seasonal cycles in populations of marine organisms in mid latitudes and polar regions? Why is there little or no seasonality in tropical regions?
6. Why does primary production slow during midsummer in mid latitudes, and why is there sometimes a fall bloom?
7. Why is there a succession of dominant phytoplankton species during a typical seasonal cycle? Why are diatoms usually replaced by flagellates during this succession?
8. What are the relative magnitudes of fish biomass and production in the deep oceans and coastal regions? Why are these not proportional to the relative areas of these regions?
9. What are the major types of estuarine circulation? Why do they occur in different estuaries?
10. If you were in Australia and operating a boat that had only a weak engine, on which side of an estuary would you choose to travel out to the ocean, and on which side would you

choose to return? Why?

11. Why are estuaries stressful environments for marine organisms?

CRITICAL THINKING QUESTIONS

1. Some areas of the coastal oceans have lower oxygen concentrations and a greater probability of developing periodic anoxia in the lower part of the water column than other areas. List and explain the factors that make some coastal areas more susceptible to anoxia than others.
2. Describe what would happen to the low-density organic particles in sewage if they were discharged to the surface layer at the center of a partially mixed estuary. Would the fate of these particles be different if they were discharged to the lower layer? If so, how?
3. It has been suggested that, if the Earth's climate does warm by several degrees, the seasonal cycle of primary production may be disrupted more in polar coastal regions than anywhere else on the Earth. Do you agree or disagree with this prediction? Explain the reasons for your answer.
4. Is it likely that a global climate change in which the Earth's atmosphere warms by several degrees will alter the frequency or intensity of dinoflagellate blooms? Why? Is it likely that the frequency and geographic extent of periodic anoxia in coastal waters will change? If so, how and why?
5. Many marine species are overfished. The current method of managing fisheries is to restrict the total catch of individual species to below the maximum sustainable yield of that species. However, this approach does not prevent adverse effects on other species that may depend on the targeted species for food. For example, it is hypothesized that Pribilof seal populations in the Bering Sea are declining because the fish species that they consume are being heavily fished, reducing the seals' food supply. A new approach to fishery management is developing in which ocean ecosystems are managed as a whole. For example, the growing fishery for krill in the Southern Ocean is managed by an ecosystem-based international treaty. Krill are the food supply on which a number of whale and seal species are dependent. Populations of these whale and seal species were drastically reduced by hunting in the first half of the twentieth century and have not yet recovered. Populations of penguin species that also rely on krill have increased to take advantage of the food previously eaten by whales and seals. If the krill fishery is to produce close to its maximum sustainable yield and contribute significantly to the solution of world hunger and protein deficiency, the whale and seal populations will never recover to their previous population levels, and it may be necessary to reduce penguin populations to protect whales and seals from renewed decline.
   (a) Do you think that marine ecosystems and fishing should be managed in this way? Explain your reasons.
   (b) What alternatives would you propose to solve the world hunger problem?
6. A swarm of locusts threatens the crops of a large area of North Africa. Should the locusts be eradicated to protect the food? A growing population of fur seals threatens to consume a growing percentage of fish from a regional fishery where the human population depends heavily on seafood. If the fish populations are not to crash from overfishing, the catch must be reduced, creating high prices and market shortages, or the fur seal population must be controlled. Would you kill seals to keep the population from growing so large as to damage the fishery? Did you have different reactions to these two scenarios? If so, why?

CRITICAL CONCEPTS REMINDERS

CC5 Transfer and Storage of Heat by Water: Water's high heat capacity allows large amounts of heat to be stored in the oceans and released to the atmosphere without much change in the ocean water temperature. Water's high latent heat of fusion allows ice to act as a heat buffer, which keeps the ocean surface water layer temperatures in high latitudes relatively uniform and near the freezing point.

CC8 **Residence Time**: The residence time of seawater in a given segment of the oceans is the average length of time the water spends in that segment. The residence times of some coastal water masses are long and therefore some contaminants discharged to the coastal ocean can accumulate to higher levels in these regions than in areas with shorter residence times.

CC11 **Chaos**: The nonlinear nature of many environmental interactions, including some of those that control annual fluctuations in fish stocks, mean that fish stocks change in sometimes unpredictable ways. .

CC12 **The Coriolis Effect:** Water masses move freely over the Earth and ocean surface, while objects on the Earth's surface, including the solid Earth itself, are constrained to move with the Earth in its rotation. This causes moving water masses to be deflected as they flow. The apparent deflection is at its maximum at the poles, is reduced at lower latitudes, and becomes zero at the equator. In Northern Hemisphere estuaries, the Coriolis effect tends to concentrate the lower salinity water that flows down the estuary toward the left side of the estuary as viewed from the ocean, while the high salinity water flowing up the estuary tends to be concentrated toward the right side (In the Southern Hemisphere these directions of concentration are reversed). .

CC15 **Food Chain Efficiency:** All organisms use some of their food as an energy source in respiration and for reproduction. They also lose some of their food in excretions (including wastes). On average, at each level in a food chain, only about 10% of food consumed is converted to growth and biomass of the consumer species. .

CC16 **Maximum Sustainable Yield:** The maximum sustainable yield is the maximum biomass of a fish species that can be depleted annually by fishing but that can still be replaced by reproduction. This yield changes unpredictably from year to year in response to the climate and other factors. The populations of many fish species worldwide have declined drastically when they have been overfished (beyond their maximum sustainable yield) in one or more years when that yield was lower than the average annual yield on which most fisheries management is based.

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