

CHAPTER 4



CHAPTER OUTLINE

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new caption to come

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Marine Plants

Benthic marine plants are probably more familiar to even casual seashore observers than are phytoplankton because they are conspicuous, coastal, macroscopic, multicellular organisms typically large enough to pick up and examine. They all belong to a single kingdom, the Plantae (Fig. 4.1). Like phytoplankton, these plants need sunlight for photosynthesis and are confined to the photic zone, but the additional need for a hard substrate on which to attach limits the distribution of benthic plants to that narrow fringe around the periphery of the oceans where the sea bottom is within the photic zone (the inner shelf of Fig. 1.45). Some benthic plants inhabit intertidal areas and must confront the many tide-induced stresses that affect their animal neighbors (discussed in Chapter 9). Their restricted near-shore distribution limits the global importance of benthic plants as primary producers in the marine environment. Yet within the near-shore communities in which they live, they play major roles as first-trophic-level organisms.

The abundant plant groups so familiar on land—ferns, mosses, and seed plants—are poorly represented or totally absent from the sea. Instead, most marine plants belong to two divisions, Phaeophyta and Rhodophyta, that are almost completely limited to the sea. Two other divisions, Chlorophyta and Anthophyta, are found most commonly in fresh water and on land, yet they are important members of some shallow coastal marine communities. The characteristics of these divisions are summarized in Table 4.1. We begin our examination of marine plants with a familiar group, the Anthrophyta or flowering plants, and then proceed to the seaweeds.

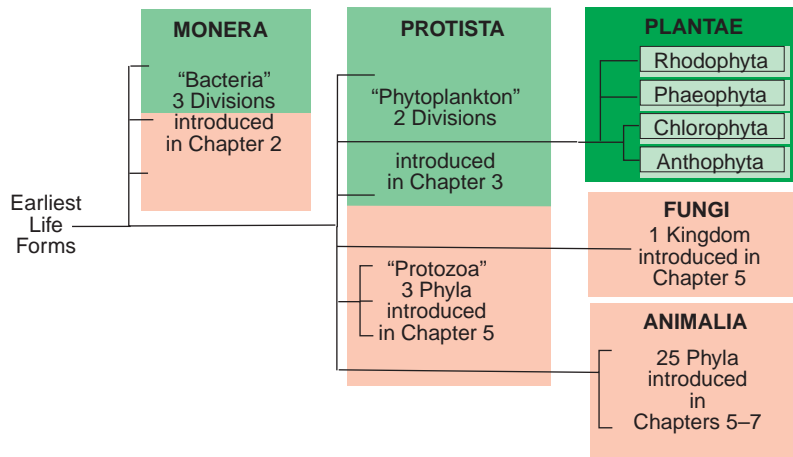


Figure 4.1

The phylogenetic tree introduced in Figure 2.7, emphasizing the four divisions of kingdom Plantae described in this chapter.

Major Divisions of Marine Plants and Their General Characteristics

Table 4.1

Division (common name)	Approximate number of living species	Percentage of species marine	General size and structure	Photosynthetic pigments	Storage products	Habitat
Phaeophyta (brown algae)	1500	99.7	Multicellular, macroscopic	Chlorophyll <i>a, c</i> Xanthophylls Carotenes	Laminarin and others	Mostly benthic
Rhodophyta (red algae)	4000	98	Unicellular and multicellular, mostly macroscopic	Chlorophyll <i>a</i> Carotenes Phycobilins	Starch and others	Benthic
Chlorophyta (green algae)	7000	13	Unicellular and multicellular, microscopic to macroscopic	Chlorophyll <i>a, b</i> Carotenes	Starch	Mostly benthic
Anthophyta (flowering plants)	250,000	0.018	Multicellular, macroscopic	Chlorophyll <i>a, b</i> Carotenes	Starch	Benthic

Adapted from Segal et al., 1980; Dawson, 1981; and Kaufman et al., 1989.

4.1 Division Anthophyta

Marine flowering plants are abundant in localized areas along some seashores and in backwater bays and sloughs. Seagrasses are exposed to air only during very low tides, whereas salt marsh plants and mangroves are emergent and are seldom completely inundated by seawater. These plants represent a secondary adaptation to the marine environment by a few species of a predominantly terrestrial plant group, the flowering plants (division Anthophyta). Flowering plants are characterized by leaves, stems, and roots, with water- and nutrient-conducting structures running through all three of these basic structures.

Submerged Seagrasses

Twelve genera of seagrasses (classified in four families), including about 60 species, are dispersed around coastal waters of the world. Half of these species are restricted to the tropics and subtropics and are seldom found deeper than 10 m. The four common genera found in the United States are *Thalassia*, *Zostera*, *Phyllospadix*, and *Halodule*. *Thalassia*, or turtle grass (Fig. 4.2a), is common in quiet waters along most of the Gulf Coast from Florida to Texas. *Zostera*, or eelgrass (Fig. 4.2b), is widely distributed along both the Atlantic and Pacific coasts of North America. *Zostera* normally inhabits relatively quiet shallow waters but occasionally is found as deep as 50 m in clear water. Surf grass, *Phyllospadix* (Fig. 4.2c), is found on both sides of the North

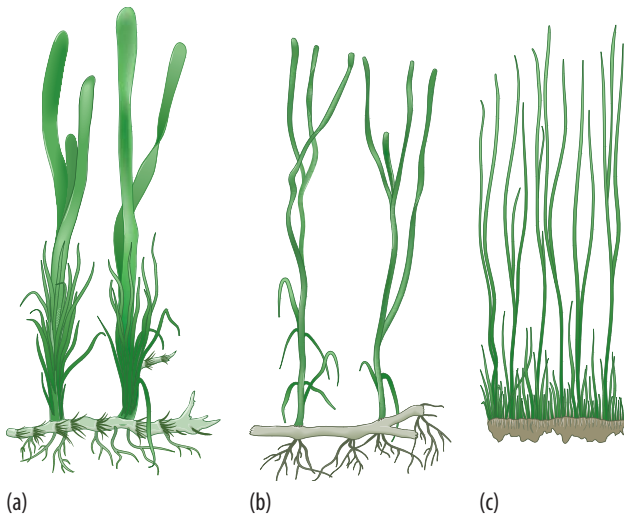


Figure 4.2

Three common seagrasses from different marine climatic regions: (a) turtle grass, *Thalassia*; (b) eelgrass, *Zostera*; and (c) surf grass, *Phyllospadix*.

Pacific and inhabits lower intertidal and shallow subtidal rocks that are subjected to considerable wave and surge action. *Halodule* prefers sandy areas with lower salinity.

Most seagrasses produce horizontal stems, or **rhizomes**, that anchor the plants in soft sediments or attach them to rocks (Fig. 4.2). From the buried rhizomes, many erect leaves develop to form thick green lawns of vegetation. These plants are a staple food for near-shore marine animals and migratory birds. Densely matted rhizomes and roots also accumulate sediments and organic debris to alter further the living conditions of the area.

Seagrasses reproduce either vegetatively by sprouting additional vertical leaves from the lengthening horizontal rhizomes or from seeds produced in simple flowers. The purpose of most showy flowers on land plants is to attract insects or birds so that **pollen** grains are transferred from one flower to another and cross-fertilization occurs. Pollen grains contain the plant's sperm cells, but submerged seagrasses use water currents for pollen transport. In all seagrasses, pollination occurs underwater.

Some seagrasses, including *Zostera*, produce threadlike pollen grains about 3 mm long (about 500 times longer than their cargo, the microscopic chromosome-carrying sperm cells). After release, the pollen grains of *Zostera* become ensnared on the **stigma**, the pollen-receptive structure of the female flower, and fertilization occurs. *Thalassia* produces small round pollen grains released in a thread of sticky slime. When the slime thread lands on the appropriate stigma of

another plant (also covered with a surface film of slime), the two slime layers combine to produce a firm bond between the pollen grain and the stigma, and fertilization follows. This two-component adhesive acts like epoxy glue to produce a strong bond after the separate components are mixed. It also provides a mechanism for selecting between compatible and foreign types of pollen grains. Only on contact with pollen of the same species will the stigma–pollen bond be formed. Foreign pollen grains do not adhere and are washed away, possibly to try again on another plant.

Mature seeds of each type of seagrass are adapted to their preferred habitat. Eelgrass seeds drop into the mud and take root near the parent plant, whereas the fruits of *Thalassia* may float for long distances before releasing their seeds in the surf. The fruits surrounding individual seeds of *Phyllospadix* are equipped with bristly projections. When shed into the surf, these bristles snag branches of small seaweeds, and the seeds germinate in place.

Like reef-forming corals and tropical mangroves, countless seagrass blades growing in all tropical lagoons provide a prodigious surface area on which other organisms (**epibionts**) can attach and grow. In St. Ann's Bay, Jamaica, Silvia Maciá determined that, on each square meter of seafloor, seagrass blades provide an average of nearly 300 m² of surface on which epibionts can attach. This vast expanse of surface area does not go unnoticed by local organisms. About 175 species of plants and animals have been observed living attached to blades of turtle grass in the Caribbean region, including various algae, sponges, hydroids, sea anemones, amphipods, ectoprocts, tunicates, annelids, and snails. These same seagrass beds support the foraging activities of a few species of unusual marine tetrapods that are unusual simply because they are herbivores (see later here).

If you were to visit a tropical seagrass meadow with a mask and snorkel, your first impression would likely be that there is very little life in seagrass beds (Fig. 4.3). This is because, other than the epibionts, which simply appear as a whitish fuzz on older blades, you would encounter very few animals. The primary reason for the paucity of animals among seagrass is that this habitat experiences a great deal of sedimentation. Waves arrive from the open sea and break on the reef flat, creating sediment-laden currents that stream into the lagoon. In the lagoon, the currents slow as they are forced to meander through millions of seagrass blades. This decreased current velocity is insufficient to transport larger sediment particles, and they begin to settle onto the sea floor among the

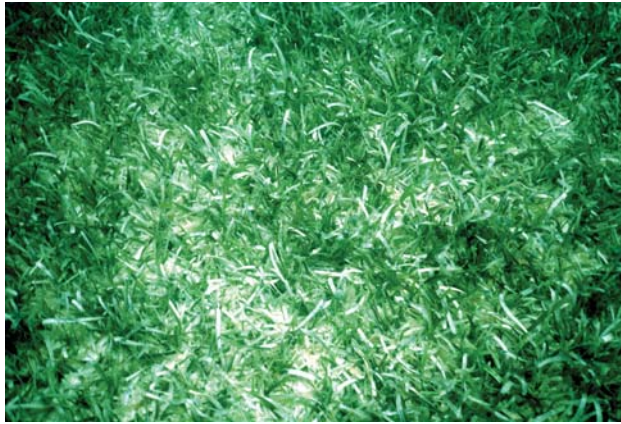


Figure 4.3

A typical view of a seagrass-covered lagoon floor.

seagrass. Many organisms cannot endure this high rate of sedimentation because it interferes with feeding, it hinders respiration by clogging gills, it easily abrades soft tissues, and it buries smaller organisms in an avalanche of particles; however, the high sedimentation rates that repel many potential seagrass residents is actually attractive to deposit-feeding sea cucumbers and mojarras, silvery fishes that make a living by straining mouthfuls of sediment through their gill rakers in search of organic morsels.

Macroalgae such as *Halimeda*, *Penicillus*, *Acetabularia*, and *Caulerpa* are often very common in tropical lagoons, and because some of these also precipitate CaCO_3 that they have extracted from seawater (like corals), they contribute additional carbonate sediment to the sea floor after they die. About 85% of the biomass of the Caribbean's *Halimeda* is CaCO_3 , and this genus alone can contribute three kilograms of carbonate sand per square meter in just 1 year.

The expansive meadow of seagrass and macroalgae that grows in most tropical lagoons is an irresistible source of food to several common herbivores. In addition to high concentrations of herbivorous parrotfishes and surgeonfishes that leave the safety of the adjacent reef at night to forage in seagrass, green sea turtles and a few species of large marine mammals rely extensively on tropical seagrass beds and are important components of seagrass communities.

Mammalian Grazers of Seagrasses

Manatees and dugongs (order Sirenia) are the only marine mammals that are herbivores (see Chapter 7). Manatees and dugongs consume a wide variety of tropical and subtropical seagrasses, including *Enhalus*, *Halophila*, *Halodule*, *Cymodocea*, *Thalassia*, *Thalasso-*

dendron, *Syringodium*, and *Zostera*. Algae also are eaten but only in limited amounts if seagrasses are abundant. At the very southern extent of their range, dugongs in subtropical Moreton Bay, Australia also consume sessile benthic invertebrates including sea squirts and polychaete worms, presumably to augment the protein content of their otherwise low-protein diet of seagrasses.

The strongly down-turned snout of the dugong causes its mouth to open almost straight downward, and it is virtually an obligate bottom feeder subsisting on seagrasses less than 20 cm high. Manatees, in contrast, have only a relatively slight deflection and are generalists, feeding at any level in the water column from bottom to surface, and are able to take floating vegetation easily. Manatees graze on a large variety of coastal and freshwater vegetation, including several species of submerged seagrasses, floating freshwater plants (*Hydrilla* and water hyacinths), and even the leaves and shoots of emergent mangroves.

Sirenians are the only marine mammals that have a prehensile snout. The short muscular snout of manatees is covered with modified vibrissae that have a prehensile function to bring vegetation to the mouth (Fig. 4.4). During feeding, dugongs gouge visible tracks into seagrass stands and bottom sediments while grubbing seagrasses from the bottom. Each track follows a serpentine course and appears to represent the continuous feeding effort of a single dive. Like terrestrial mammalian herbivores, the cheek teeth of both manatees and dugongs are adapted for grinding cellulose-rich vegetation.

Even though seagrass meadows are very productive, green sea turtles, manatees, and dugongs are the only large herbivores to graze on them commonly. The



Figure 4.4

A Caribbean manatee manipulating plant food with its vibrissae snout and flippers.

low energy value and protein content of a seagrass diet for manatees and dugongs has been suggested as contributing factors to their slow and sluggish behavior, low metabolic rates relative to other marine mammals, and the consequent need for these endotherms to remain in tropical and warm subtropical waters. Several other species of marine mammals (described in Chapter 7) also occupy tropical waters, but none is as completely restricted to warm and shallow waters as these large, slow, herbivorous sirenians.

Emergent Flowering Plants

Several other species of flowering plants often exist partially submerged on bottom muds of coastal salt marshes protected from strong ocean wave action. These plants are usually situated so that their roots are periodically, but not constantly, exposed to tidal flooding. They are terrestrial plants that have evolved various degrees of tolerance to excess salts from sea spray and seawater. Some even have special structural adaptations for their semi-marine existence. The cordgrass, *Spartina* (see Fig. 8.9a), for example, actively excretes excess salt through special two-celled salt glands on its leaves. Even so, several species of *Spartina* have higher experimental growth and survival rates in freshwater than in seawater. This difference strongly suggests that the salt marsh does

not provide optimal growth conditions for *Spartina*, even though the salt marsh is its natural habitat. Competition with other land and freshwater plants may have forced *Spartina* and other salt-tolerant species into the more restricted areas of the salt marshes.

Salt marsh plants contribute heavily to detritus production in their protected environments as well as in nearby bays and estuaries. Some feature extensive stands containing several species of emergent grasses, especially various species of *Spartina*. At slightly higher elevations, these grasses give way to succulents (*Salicornia* and *Suaeda*), a variety of reeds and rushes, and the brush and smaller trees of the local woodland. These lush pastures are extremely productive and harbor a unique assemblage of organisms, including commercially important shellfish and finfishes. Yet as large urban centers develop near them, they have become popular sites for waste dumping, recreation, dredging and filling, and other detrimental uses. The degradation of salt marshes is a serious and worldwide problem that becomes more severe as human populations expand and place more pressure on these fragile habitats. The issues surrounding modification and degradation of salt marshes are discussed further in Chapter 8.

Several species of shrubby to treelike plants, the mangroves, create dense thickets of tidal woodlands known as **mangals** (Fig. 4.5). Mangals dominate large



Figure 4.5

Dense mangal thicket lining a tidal channel.

RESEARCH

in progress

Can an Army of Snails Destroy a Salt Marsh?

Shoreline communities are the most popular communities in America. The U.S. Census Bureau estimates that 53% of Americans reside within our 673 coastal counties, even though they constitute just 17% of the total land area in America (excluding Alaska). This high density of shoreline-dwelling humans (300 people per square mile in U.S. coastal counties vs. a national average of less than 100 persons per square mile) has transformed coastal areas into extremely valuable real estate, with \$150 billion per year being generated by near-shore communities via tourism, aquaculture, and fisheries.

Such fondness for the coast is not unique to Americans, and coastal population explosions worldwide are often blamed for global degradation of seagrass beds, mangrove swamps, coral reefs, salt marshes, oyster reefs, and kelp forests via anthropogenic habitat destruction, eutrophication, or alteration of food webs. One such die-off has occurred in recent years along the southeastern and gulf coasts of America, where greater than 100,000 hectares (250,000 acres) of salt marsh have been lost along more than 1500 km of coastline. These salt

marshes are the most important communities, economically and ecologically, along the eastern seaboard and Gulf of Mexico because they serve as shoreline buffers, sediment stabilizers, nutrient and sediment filters, and essential habitat for juvenile and adult fishes and seabirds; thus, determining the cause of this cordgrass die-off is crucial.

Much like subtidal eel grass in New England, red mangroves along the world's tropical coasts, and giant kelp off America's west coast, cordgrass (*Spartina alterniflora*) is the dominant, habitat-forming, soft-shoreline plant from Newfoundland to Florida and throughout the Gulf of Mexico. For more than half a century, salt marsh ecologists have been dogmatically constrained by the paradigm that cordgrass health was primarily under the control of soil-related stresses (such as salinity or pH) or nutrient availability, so-called bottom-up factors. Thus, much of the investigation into the recent cordgrass die-off in the southeastern United States has centered around edaphic, or soil-related, stressors, especially because a severe drought in the southern United States from 1999 to 2001 resulted in increases in salinity and decreased moisture and pH of marsh soils.



Figure B4.1 Marsh periwinkles in unusually high densities on cordgrass in Louisiana.

Enter Dr. Brian Silliman, an ecologist in the Department of Zoology at the University of Florida in Gainesville. Dr. Silliman knew that the most abundant herbivore in coastal communities of the eastern United States was the marsh periwinkle, *Littoraria irrorata*, a gastropod grazer (Fig. B4.1) that damaged healthy cordgrass while grazing on their fungal food (pathogenic fungi exhibit enhanced growth when growing in periwinkle-created grazer wounds on cordgrass). Thus, these snails kill cordgrass not through direct consumption of the plant, but indirectly via facilitating the growth of pathogenic fungi during their fungal-farming activities. He also knew that southeastern populations of blue crabs, *Callinectes sapidus*, a major predator of periwinkles, had declined 40% to 85% in recent years because of overfishing. Moreover, he had observed that snail densities in die-off sites reached 2000 individuals per m², that snails were essentially absent on

exposed mudflats, that snail density peaked in “snail fronts” along the die-off/healthy border, and that snail density decreased markedly within stands of healthy cordgrass. Thus, he hypothesized that fungal-farming snails at high density could destroy the marsh canopy in a “top-down” manner and wondered whether drought-related stress could act synergistically with the periwinkles to worsen the die-off. In short, he sought to determine whether drought-induced elevations in soil salinity, recent increases in snail abundance because of crab decreases, or a synergistic interaction between both factors was responsible for the loss of cordgrass.

To test his hypothesis, Dr. Silliman conducted two experiments, and his results were quite unexpected. First, to determine whether snail fronts alone contribute to marsh die back, he excluded snails from the marsh borders and watched the cordgrass grow (Fig. B4.2). This experiment showed that marsh periwinkles leave exposed mudflats in their wakes as they pass in

fronts and that the presence of snail fronts results in an increase in the die-off area of 15% to 185%. Second, to test whether the drought and the snails could have interacted together to cause the initial marsh die-off and localized disturbances, he manipulated snail densities and soil salinities at 12 field sites in Georgia and Louisiana. When grazing snails were removed, cordgrass biomass increased by more than three orders of magnitude, a strong indication that top-down control of growth by snails is significant. When Dr. Silliman increased soil salinity to 56‰ (to simulate drought conditions), *Spartina* growth was reduced by 45%, demonstrating that bottom-up factors also could contribute to a cordgrass die-off. Finally, when *Spartina* was exposed to both increased soil salinity and dense populations of grazing periwinkles, the biomass of cordgrass decreased by 84%. Hence, Dr. Silliman was able to conclude that environmental stress (a drought) had a significantly greater negative effect on cordgrass growth and survival when coupled with

unusually high densities of grazing snails. A likely scenario that Dr. Silliman has proposed to explain this extreme die-off includes several stages. First, an intense multiyear drought initiated the *Spartina* die-off while a concomitant reduction in blue crab predators en-

Can an Army of Snails Destroy a Salt Marsh?

abled snail populations to increase dramatically. Next, snail density was further increased by the loss of cordgrass because the snails were forced to clump on whatever vegetation remained. Finally, runaway grazing by snails in density-dependent, marching fronts persisted for more than 1 year after the drought ended, resulting in even greater loss of wetland vegetation.

These exciting results challenge traditional views of salt marsh ecology and the relative importance of top-down versus bottom-up causal factors. When coupled with similar observations of grazing fronts mowing their way through other marine habitats (e.g., sea urchins in kelp forests, crown-of-thorns sea stars on coral reefs, and snow geese in arctic salt marshes), Dr. Silliman was led to the sobering conclusion that rapid and extensive marine habitat loss is usually coupled with anthropogenic alterations of food webs or nutrient cycling. Could such large-scale die-offs of marine communities become more common if global warming continues at predicted rates?



Figure B4.2 Snail-exclusion cages permit exuberant cordgrass growth in the center of a snail-ravaged mudflat.

expanses of muddy shores in warmer climates and are excellent examples of emergent plant-based communities. Mangroves range in size from small shrubs to 10-m-tall trees whose roots are tolerant to seawater submergence and are capable of anchoring in soft muds. Collectively, mangrove plants, the major component of mangal communities, line about two thirds of the tropical coastlines of the world (Fig. 4.6).

Members of these mangal communities are supported on their muddy substrate by numerous prop roots that grow down from branches above the water. The pattern of mangrove development illustrates well a series of adaptations needed to exist on muddy tropical shores (Fig. 4.7). Red mangroves (*Rhizophora*) produce seeds that germinate while still hanging from the branches of the parent tree. As the seedlings

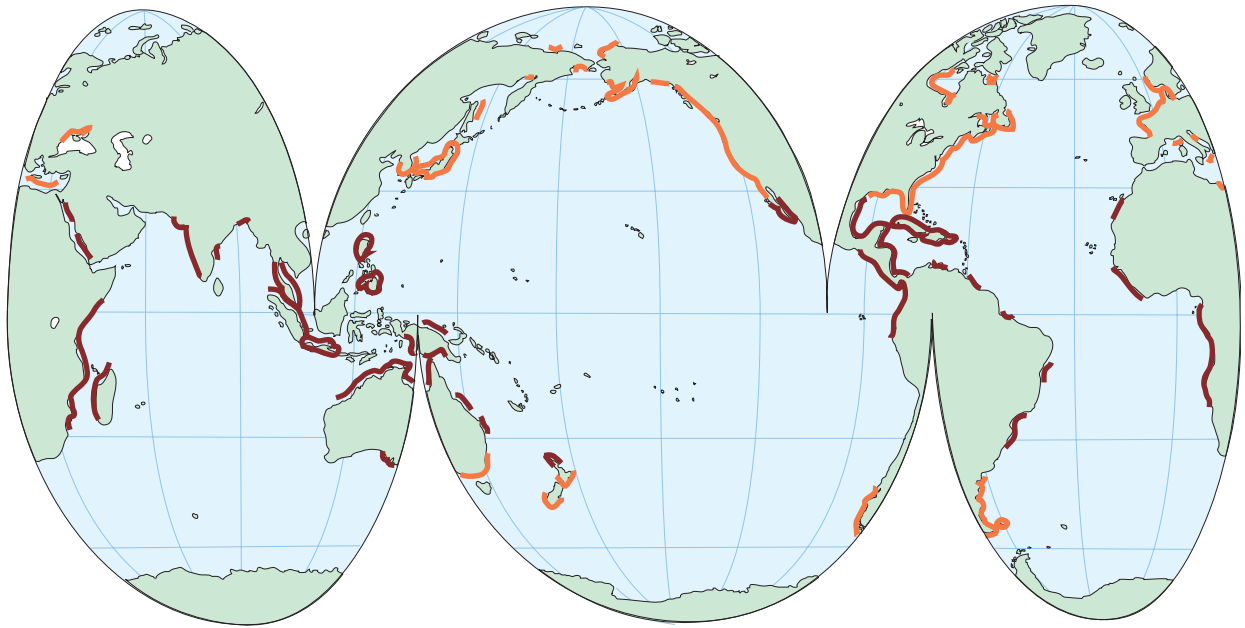


Figure 4.6

Distribution of salt marshes (orange) and mangals (maroon).

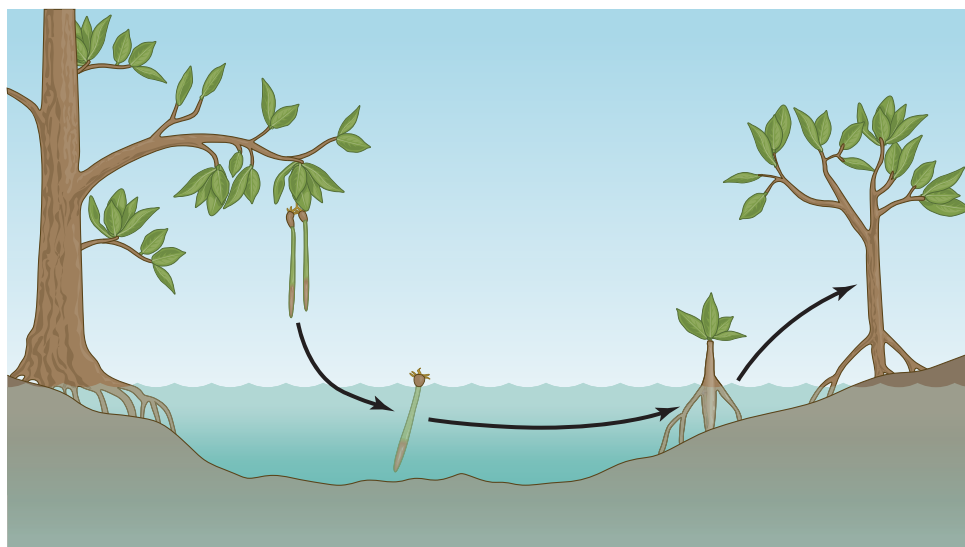


Figure 4.7

Germination cycle of a mangrove seedling.

develop and grow longer, their bottom ends become heavier. When the seedlings eventually drop from the parent plant into the surrounding water, they float upright, bobbing at the water's surface, are dispersed by winds or tides, and finally implant in muddy sediments along shallow shorelines. There, the seedlings promptly develop small roots to anchor themselves and continue to mature. The resulting tangle of growing roots traps additional sediments and increases the structural complexity of mangal communities. Birds, insects, snails, and other terrestrial animals occupy the upper leafy canopy of the mangroves, and a variety of fishes, crustaceans, and mollusks live on or among the root complex growing down into the mud. Because the leafy portions of these plants are above the water level, few marine animals graze directly on mangrove plants. Instead, leaves falling from these plants into the quiet waters surrounding their roots provide an important energy source for the detritus-based food webs of these communities.

In the United States, the distribution of mangals reflects their need for warm waters protected from wave action; they are found only along portions of the Gulf of Mexico and the Atlantic coast of Florida. The south coast of Florida is dominated by extensive interconnected shallow bays, waterways, and mangals. These mangals form a nearly continuous narrow band along the coast, with smaller fingers extending inland along creeks. Inland, toward the freshwater Everglades, the mangroves are not high, but tree height of red, black, and white mangroves (the three most common species in the southeast United States) increases to as much as 10 m at the coast. It is these taller coastal members of mangal communities that are especially prone to hurricane damage. In 1992, Hurricane Andrew cut a swath of destruction across south Florida with sustained winds up to 242 km/hr. The accompanying storm surge lifted the sea surface more than 5 m above normal levels. Some of the more exposed coastal mangal communities experienced greater than 80% mortality, due mostly to wind effects and lingering problems of coastal erosion.

On August 29, 2005, Hurricane Katrina struck the coasts of Louisiana, Mississippi, and Alabama. This important coastline houses 15 major fishing ports, nearly 200 seafood processing plants, and nearly 15,000 state- and federally permitted fishing vessels, which together produce 10% of the shrimp and 40% of the oysters consumed in the United States. Two months after Katrina made landfall, her effects on seafood production, and coastal fauna and habitats were assessed. It is estimated that Katrina caused \$1.1 billion in

losses to seafood production for Louisiana and about \$200 million in losses to Alabama and Mississippi, respectively. Moreover, these initial losses to seafood production may persist because benthic communities along this coastline experienced significant reductions in biodiversity as well as shifts in the composition and ranking of dominant taxa.

SUMMARY POINTS

Division Anthophyta

- Multicellular plants in the sea are dominated by brown and red algae, with green algae and some flowering plants also playing important roles.
- About 60 species of seagrasses thrive throughout the world along subtidal soft-bottom shorelines. Most seagrasses reproduce vegetatively via horizontal rhizomes or sexually via underwater pollination of tiny flowers followed by fruit production.
- Additional flowering plants, such as marsh grasses and mangals, grow on soft bottoms in the intertidal zone. All types of marine flowering plants host a unique community of organisms within the habitat that they create.
- Manatees and dugongs are the only herbivorous marine mammals. They use their prehensile snouts to graze on a variety of sea grasses and the occasional macroalga.

4.2 The Seaweeds

By far, most large conspicuous forms of attached marine plants are seaweeds. The term *seaweed* is used here in a restricted sense, referring only to macroscopic members of the plant divisions Chlorophyta (green algae), Phaeophyta (brown algae), and Rhodophyta (red algae) (Table 4.1). These are multicellular plants that do not produce seeds or flowers, yet meet all the criteria for kingdom Plantae as summarized in section 2.2.

Seaweeds are abundant on hard substrates in intertidal zones and commonly extend to depths of 30 to 40 m. In clear tropical seas, some species of red algae thrive at depths as great as 200 m, and one species has been reported as deep as 268 m in the Bahamas. Many seaweeds tolerate or even require extreme surf action on exposed rocky intertidal outcrops, where they are securely fixed to the solid

substrate. Where they are abundant, seaweeds can greatly influence local environmental conditions for other types of shallow-water marine life by protecting them from waves and providing food, shade, and sometimes a substrate on which to attach and grow.

Structural Features of Seaweeds

Seaweeds are not as complex as the flowering plants. Seaweeds lack roots, flowers, seeds, and true leaves. Nevertheless, within these structural limitations, seaweeds exhibit an unbridled diversity of shapes, sizes, and structural complexity. Microscopic filaments of green and brown algae can be found growing side by side with encrusting forms of red algae and flat sheet-like members of all three divisions. The more obvious members of all three seaweed divisions typically develop into similar general forms, consisting of a **blade**, a **stipe**, and a **holdfast** composed of many small fingerlike **haptera** (Fig. 4.8).

The Blade

The flattened, usually broad, leaflike structures of seaweeds are known as blades. Seaweed blades often exhibit a complex level of branching and cellular

arrangement. Several larger species of brown algae produce distinctive blade shapes and blade arrangements (Fig. 4.9), yet each begins as a young plant with a single, unbranched, flat blade nearly identical to other young kelp plants.

The blades house photosynthetically active cells, but photosynthesis typically occurs in the stipes and holdfasts as well. In cross-section, seaweed blades (Fig. 4.10a) are structurally unlike the leaves of terrestrial plants (Fig. 4.10b). The cells nearer the surface of the blade are capable of absorbing more light and are photosynthetically more active than those cells near the center of the blade. “Veins” of conductive tissue and distinctions between the upper and lower surfaces are lacking in the blades of seaweeds. Because the flexible blades either droop in the water, float erect, or are continuously tossed by turbulence, there is no defined upper or lower surface. The two surfaces of the seaweed blade are usually exposed equally to sunlight, nutrients, and water and are therefore equally capable of carrying out photosynthesis. Unlike seaweeds, flowering plants (including seagrasses) exhibit an obvious asymmetry of leaf structure, with a dense concentration of photosynthetically active cells crowded near the upper surface (Fig. 4.10b). Below the upper epidermis and palisade mesophyll is a spongy layer of cells separated by large spaces to enhance the exchange of carbon dioxide, which is often 100 times less concentrated in air than in seawater.

Pneumatocysts

Several large kelp species have gas-filled floats, or **pneumatocysts**, to buoy the blades toward the sunlight at the surface. Pneumatocysts are filled with the gases most abundant in air, N_2 , O_2 , and CO_2 , although some kelp pneumatocysts also contain a few percent of carbon monoxide, CO . Again, there is a large diversity in size and structure. The largest pneumatocysts belong to *Pelagophycus*, the elkhorn kelp (Fig. 4.9). Each *Pelagophycus* plant is equipped with a single pneumatocyst, sometimes as large as a basketball, to support six to eight immense drooping blades, each of which may be 1 to 2 m wide and 7 to 10 m long.

In strong contrast to *Pelagophycus*, *Sargassum* has numerous small pneumatocysts (Fig. 4.11). A few species of *Sargassum* lead a pelagic life afloat in the middle of the North Atlantic Ocean (the “Sargasso Sea”). In the Sargasso Sea, *Sargassum* creates large patches of floating plants that are the basis of a complex floating community of crabs, fishes, shrimp, and other animals uniquely adapted to living among the *Sargassum*. Large

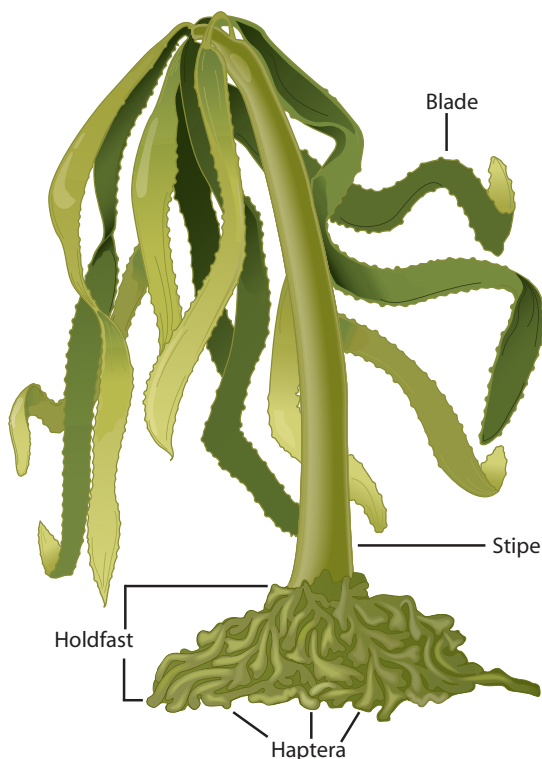


Figure 4.8

The northern sea palm *Postelsia* (Phaeophyta) is equipped with a relatively large stipe and a massive holdfast.

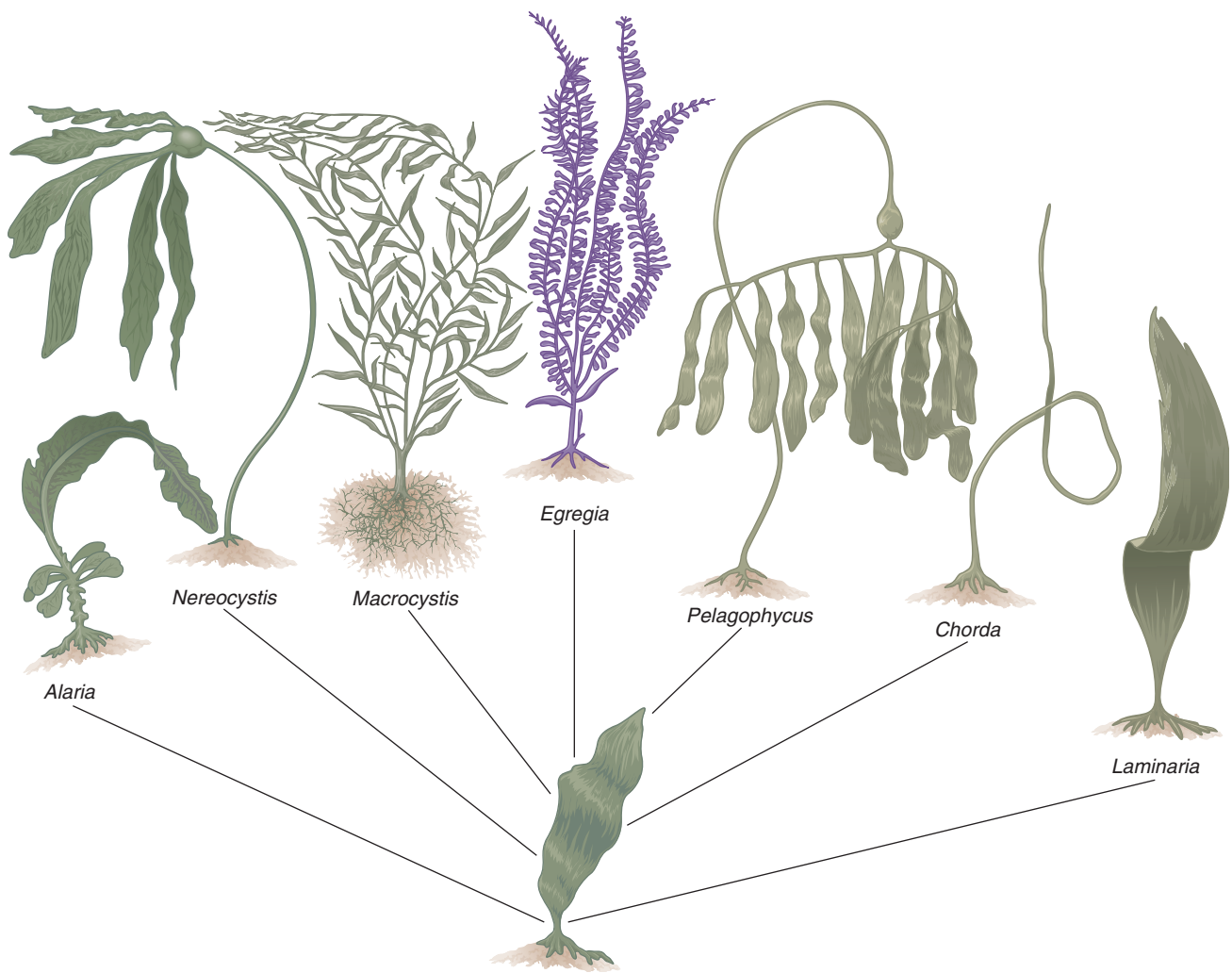
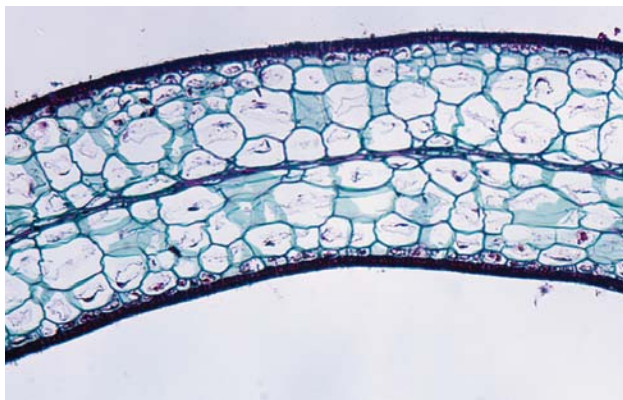
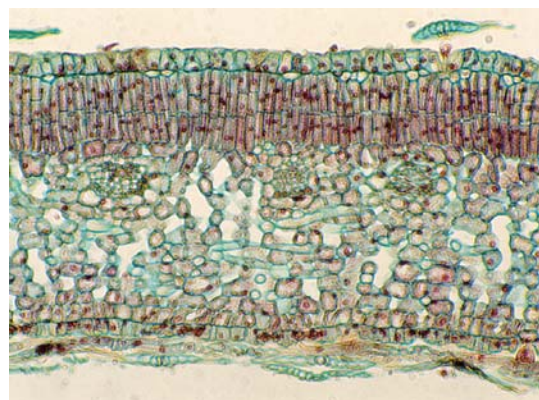


Figure 4.9

Some large kelp plants of temperate coasts. Each mature plant develops from a young plant with a single flat blade.



(a)



(b)

Figure 4.10

Cross-sections of a blade of a typical marine alga, *Nereocystis* (a), and a typical flowering plant leaf (b). Note the contrasting symmetry patterns.



Figure 4.11

A portion of the floating brown alga, *Sargassum*, containing numerous small pneumatocysts, becomes a temporary home for a baby sea turtle.

masses of this plant community sometimes float ashore on the U.S. East and Gulf Coasts, creating odor problems for beachgoers as the dying plants decompose. In the Sea of Japan, other species of attached intertidal *Sargassum* break off and also become free-floating for extended periods of time.

The Stipe

A flexible stemlike stipe connects the wave-tossed blades of seaweeds to their securely anchored holdfasts at the bottom. An excellent example is *Postelsia*, the sea palm (Fig. 4.8), which grows attached to rocks only in the most exposed surf-swept portions of the intertidal zone. Its hollow resilient stipe is remarkably well suited for yielding to the waves without breaking.

The blades of some seaweeds blend into the holdfast without forming a distinct stipe. In others, the stipe is very conspicuous and occasionally extremely long. The single long stipes of *Nereocystis*, *Chorda*, and *Pelagophycus* (Fig. 4.9) provide a kind of slack-line anchoring system and commonly exceed 30 m in length. The complex multiple stipes of *Macrocystis* are often even longer.

Special cells within the stipes of *Macrocystis* and a limited number of other brown and red algal species form conductive tissues strikingly similar in form to those present in stems of terrestrial plants. Radioactive tracer studies have shown that these cells transport the products of photosynthesis from the blades to other parts of the plant. In smaller seaweeds, the necessity for rapid efficient transport through the stipe is minimal, and such internal transport is lacking.

The Holdfast

Holdfasts of the larger seaweeds often superficially resemble root systems of terrestrial plants; however, the basic function of the holdfast is to attach the plant to the substrate. The holdfast seldom absorbs nutrients for the plant as do true roots. Holdfasts are adapted for getting a grip on the substrate and resisting violent wave shock and the steady tug of tidal currents and wave surges. The holdfast of *Postelsia* (Fig. 4.8), composed of many short, sturdy, rootlike haptera, illustrates one of several types found on solid rock.

Other holdfasts are better suited for loose substrates. The holdfast of *Macrocystis* has a large diffuse mass of haptera to penetrate muddy or sandy bottoms and stabilize a mass of sediment for anchorage (Fig. 4.12). Holdfasts of many smaller species do the same thing on a much smaller scale, with many fine filaments embedded in sand or mud on the sea bottom.

A variety of small red algae are epiphytes and demonstrate special adaptations for attaching themselves to other marine plants. Figure 4.13 illustrates two common red algal epiphytes attached to a strand of surf grass. Using other marine plants as substrates for attachment is a common habit of many smaller forms of red algae.

Photosynthetic Pigments

Each seaweed division is characterized by specific combinations of photosynthetic pigments that are reflected in their color and in the common name of each division (Table 4.1). The bright grass-green color of



Figure 4.12

Complex interlocking mass of haptera that make up the holdfast of *Macrocystis*.

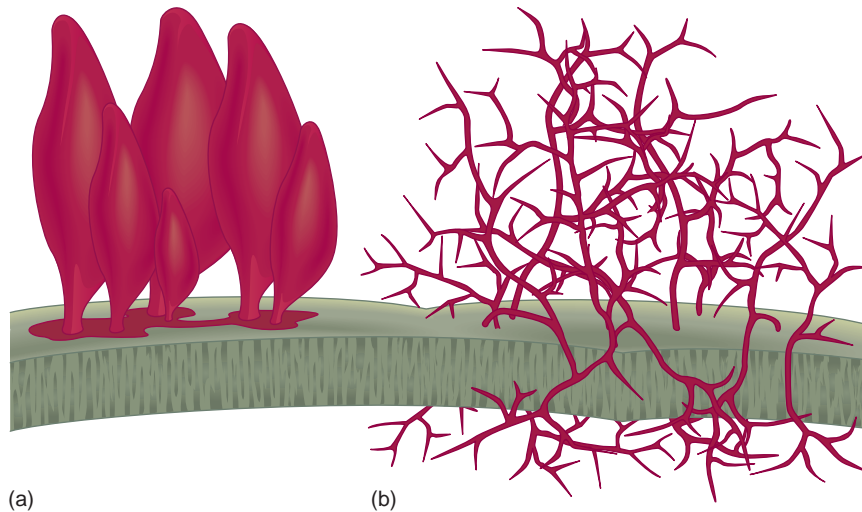


Figure 4.13

Two red algal epiphytes: (a) *Smithora* and (b) *Chondria* attached to a leaf of *Phyllospadix*.

green algae is due to the predominance of chlorophylls over accessory pigments. Green algae vary in structure from simple filaments to flat sheets (Fig. 4.14) and diverse complex branching forms. They are usually less than half a meter long, but one species of *Codium*



Figure 4.14

A healthy growth of the green alga *Ulva* lies on the sand during low tide.

from the Gulf of California occasionally grows to 8 m in length. When compared with brown and red algae, the Chlorophyta have fewer marine species, yet in some locations their limited diversity is compensated with dense populations of individuals from one or two species.

The photosynthetic pigments of the Phaeophyta sometimes appear as a greenish hue, but more often, the green of the chlorophyll is partially masked by the golden xanthophyll pigments, especially fucoxanthin, characteristic of this division. This blend of green and brown pigments usually results in a drab olive-green color (Fig. 4.15). Many of the larger and more familiar algae of temperate seas belong to this division. A number of species are quite large and are sometimes



Figure 4.15

The brown alga *Fucus* growing on a rocky intertidal shoreline.

collectively referred to as **kelp** (Fig. 4.9). In temperate and high latitudes, these species usually dominate the marine benthic vegetation. Numerous smaller, less obvious brown algae are also common in temperate and cold waters, as well as in tropical areas.

Red algae, with red and blue phycobilin pigments, as well as chlorophyll, exhibit a wide range of colors. Some are bright green, such as *Porphyra*, the popular seaweed known as nori that is used in sushi rolls, and others are sometimes confused with brown algae; however, most red algae living below low tide range in color from soft pinks to various shades of purple or red (Fig. 4.16). Red algae are as diverse in structure and habitat as they are in coloration, and they seldom exceed a meter in length.

The adaptive significance of accessory photosynthetic pigments for phytoplankton was described in Chapter 3. At first glance, it might appear that the green algae and seagrasses, with their preponderance of chlorophyll pigments, do not fare well at moderate depths because of their limited ability to absorb the deeper-penetrating green wavelengths of sunlight, but plants can adapt to low- or limited-wavelength light conditions in other ways; for example, because some green algae have dense concentrations of chlorophyll that appear almost black, they are able to absorb light at essentially all visi-

ble wavelengths. In addition, most green plants have chlorophyll *b* as well as chlorophyll *a*. Chlorophyll *b* has a strong light-absorbing peak in the blue region of the visible spectrum and can collect a good fraction of the deep-penetrating blue light available in tropical waters. Still, red and brown algae, with their abundant xanthophyll and phycobilin pigments working in concert with chlorophyll, generally have a slight competitive advantage in occupying the deeper portions of the photic zone in turbid coastal waters and function at no disadvantage in shallow waters or intertidal zones.

Reproduction and Growth

Reproduction in seaweeds, as well as in most other plants, can be either sexual, involving the fusion of sperm and eggs, or asexual, relying on vegetative growth of new individuals. Some seaweeds reproduce both ways, but a few are limited to vegetative reproduction only. The pelagic species of *Sargassum*, for instance, maintain their populations by an irregular vegetative growth followed by fragmentation into smaller clumps. The dispersed fragments of *Sargassum* are capable of continued growth and regeneration for decades. Sexual reproduction is lacking in the pelagic species of *Sargassum* but not in the attached benthic forms of the same genus.

Much of the structural variety observed in seaweeds is derived from complex patterns of sexual reproduction, patterns that define the life cycles of seaweeds. For our purposes, these complex life cycles can be simplified to three fundamental patterns. The sexual reproduction examples of the first two types described here are not meant to cover the entire spectrum of seaweed life cycles but are used to illustrate the basic patterns that underlie the complexity and variation involved in sexual reproduction of seaweeds.

In the life cycle of most of the larger seaweeds, an alternation of **sporophyte** and **gametophyte** generations occurs. The green alga *Ulva* represents one of the simplest patterns of alternating generations (Fig. 4.17). This basic life cycle is a hallmark of the kingdom Plantae. The cells of the macroscopic *Ulva* sporophyte are diploid; that is, each cell contains two of each type of chromosome characteristic of that species. Some cells of the *Ulva* sporophyte undergo meiosis to produce single-celled flagellated **spores**. As a result of meiosis, these spores contain only one chromosome of each pair present in the diploid sporophyte and are said to be haploid.



Figure 4.16

Calcareous red alga, *Jania*, in a small tide pool.

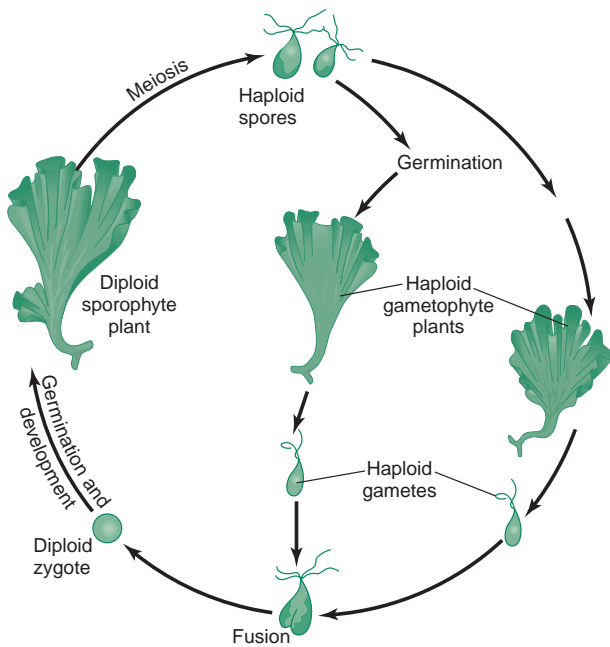


Figure 4.17

The life cycle of the green alga, *Ulva*, alternating between diploid sporophyte and haploid gametophyte generations. (Adapted from E.Y. Dawson. *Marine Botany of Marine Plants*. Holt, Rinehart and Winston, 1966.)

The spores of *Ulva* and other green algae each have four flagella, whereas each gamete has two flagella that are equal in length and project from one end of the cell. Spores produced by *Ulva* are capable of limited swimming and then settle to the bottom.

There they immediately germinate by a series of mitotic cell divisions to produce a large, multicellular, gametophyte generation that still is haploid. Cells of the gametophyte in turn produce haploid gametes, each with two flagella, that are released into the water. When two gametes from different gametophyte individuals meet, they fuse to produce a diploid single-celled zygote. By repeated mitotic divisions, the zygote germinates and completes the cycle by producing a large, multicellular, diploid sporophyte once again. In *Ulva*, the sporophyte and gametophyte generations are identical in appearance. The only structural difference between the two forms is the number of chromosomes in each cell; diploid sporophyte cells have double the chromosome number of haploid gametophyte cells.

The life cycles of numerous other seaweeds are characterized by a suppression of either the gametophyte or the sporophyte generation. In the green alga *Codium* and the brown alga *Fucus*, the multicellular haploid generation is completely absent. The only haploid stages are the gametes. In other large brown algae, the gametophyte stage is reduced. The life cycle of *Laminaria* is similar to that of most other large kelp plants and serves as an excellent generalized example of seaweeds with a massive sporophyte that alternates with a diminutive gametophyte (Fig. 4.18). Special cells (called **sporangia**) on the blades of the diploid sporophyte undergo meiosis to produce several flagellated microscopic spores. These haploid spores swim to the

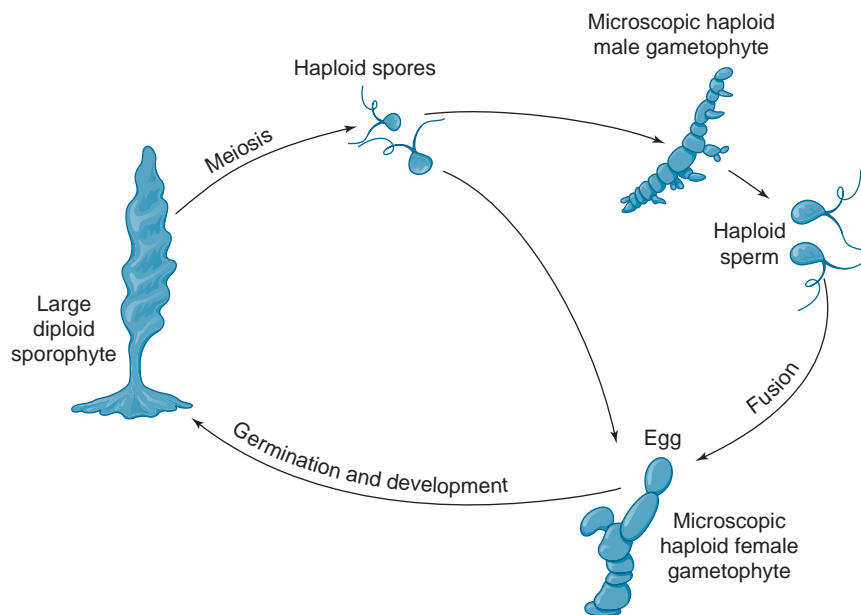


Figure 4.18

The life cycle of *Laminaria* (similar to the cycles of other large kelps) alternates between large diploid sporophyte and microscopic haploid gametophyte generations.

bottom and quickly attach themselves. They soon germinate into very small, yet multicellular, gametophytes. The female gametophyte produces large, nonflagellated eggs. The egg cells are fertilized in place on the female gametophyte by flagellated male gametes, the sperm cells produced by the male gametophyte. After fusion of the gametes, the resulting zygote germinates to form another large sporophyte. The flagellated reproductive cells of brown algae always have two flagella of unequal lengths, and they insert on the sides of the cells rather than at the ends.

Red algae lack flagellated reproductive cells and are dependent on water currents to transport the male gametes to the female reproductive cells. The most common life cycle of red algae has three distinct generations, somewhat reminiscent of the reproductive cycle outlined for *Ulva* (Fig. 4.17). A diploid sporophyte produces haploid spores that germinate into haploid gametophytes. Instead of producing a new sporophyte, however, the gametes from the gametophytes fuse and develop into a third phase unique to red algae, the **carposporophyte**. The carposporophyte then produces **carpospores** that develop into sporophytes, and the cycle is completed.

The development of a large, multicellular seaweed from a single microscopic cell (either a haploid spore or a diploid zygote) is essentially a process of repeated mitotic cell divisions. Subsequent growth and differentiation of these cells produce a complex plant with many types of cells, each specialized for particular functions. After the plant is developed, additional cell division and growth occur to replace tissue lost to animal grazing or wave erosion; however, such cell

division is commonly restricted to a few specific sites within the plant that contain **meristematic tissue** capable of further cell division. These meristems frequently occur at the upper growing tip of the plant. In kelp plants and some other seaweeds, additional meristems situated in the upper and lower portions of the stipe provide additional cells to elongate the stipe and blades. The meristematic activity of a cell layer near the outer stipe surface of some kelp species provides lateral growth to increase the thickness of the stipe. The stipes of a few perennial species of kelp, including *Pterygophora* and *Laminaria*, retain evidence of this secondary lateral growth as concentric rings that resemble the annual growth rings of trees.

In the spring, during periods of rapid growth, the rate of stipe elongation in large *Nereocystis*, *Pelagophycus*, and *Macrocystis* plants often exceeds 30 cm/day. Many kelp species produce kelp blades resembling moving belts of plant tissue (Fig. 4.19), growing at the base and eroding or being eaten away at the tips. At any one time, the visible plant itself (the standing crop) may represent as little as 10% of the total material it produced during a year.

Kelp Forests

Most kelp plants are perennial. Although they may be battered down to their holdfasts by winter waves, their stipes will regrow from the holdfast for several successive seasons. Thus, the extent of the kelp canopy and the overall three-dimensional structure of the kelp forest are quite variable over annual cycles. Occasionally, herbivore grazing or the pull of strong waves frees the

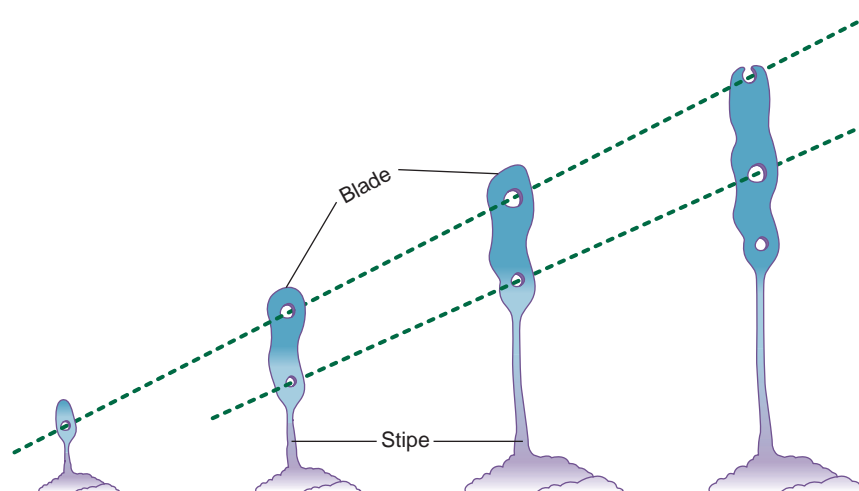


Figure 4.19

Generalized growth pattern of a kelp. Punched holes and dashed lines indicate the pattern of blade elongation. (Adapted from K. H. Mann, *Marine Biology* 14(1973):199–209.)

holdfast and causes the plant to wash ashore. More commonly, small fragments of blades and stipes are continually eroded away to decompose into food for detritus feeders.

Along most of the North American west coast, subtidal rocky outcrops are cloaked with massive growths of several species of brown algae, dominated by either *Macrocystis* or *Nereocystis* (Fig. 4.20). West coast kelp forests occur as an offshore band paralleling the coastline because wave action tears these plants out nearer to shore and light does not penetrate to the sea floor farther offshore. In the dimmer light below the canopy of these large kelps exists a shorter understory of mixed brown and red algae. Together, these large and small kelp plants accomplish very high rates of primary production and support a complex community of grazers, suspension feeders, scavengers, and predators (Fig. 4.21). From Central California northward, kelp abundance varies seasonally, and the fishes are dominated by several species of rockfishes in the genus *Sebastes*. In contrast, southern California kelp forest abundance varies irregularly and is especially vulnerable to the influences of El Niño–Southern Oscillation events. Here, the dominant fishes are not rockfishes; instead, perches, damselfishes, and wrasses abound, reflecting the more tropical affinities of these fishes.

Compared with the richness of species observed in western North American kelp forests, the kelp beds of the northwestern Atlantic Coast exhibit low diversity in most taxonomic groups. Unlike the U.S. west coast, the rocky intertidal and subtidal shores

of New England states and neighboring Canadian Maritime Provinces were scoured to bare rock (in places to several hundred meters below sea level) by several episodes of continental glaciation. Only since the retreat of the most recent glacial episode 8000 to 10,000 years ago have these shores been recolonized, and that recolonization is not yet complete.

The lower species diversity of northwestern Atlantic kelp beds leads to somewhat simpler trophic interactions than those occurring in U.S. west coast kelp forests; still, similar species occupy the same major trophic roles (Fig. 4.22). The macroscopic primary producers are dominated by the kelp, *Laminaria*, with an understory of mixed red and brown foliose algae. In clear patches below about 10 m, encrusting coralline red algae cover rock surfaces with a bright pink pavement of CaCO_3 . These coralline crusts are maintained indirectly by the constant grazing actions of sea urchins on the larger kelp plants. On this coast, the lower limit of growth for *Laminaria* and other large kelps is controlled not by low light intensity as it is on the west coast but by the presence of grazing urchins.

On the U.S. West coast, too, kelp beds exist in a delicate balance with their major grazers, sea urchins. Since World War II, kelp beds on both coasts have been devastated by dense aggregations of sea urchins grazing on the holdfasts, causing the remainder of the plant to break free and wash onto the shore. These large urchin populations, capable of completely eliminating local kelp beds, seem free of the usual population regulatory mechanisms—predation and starvation.

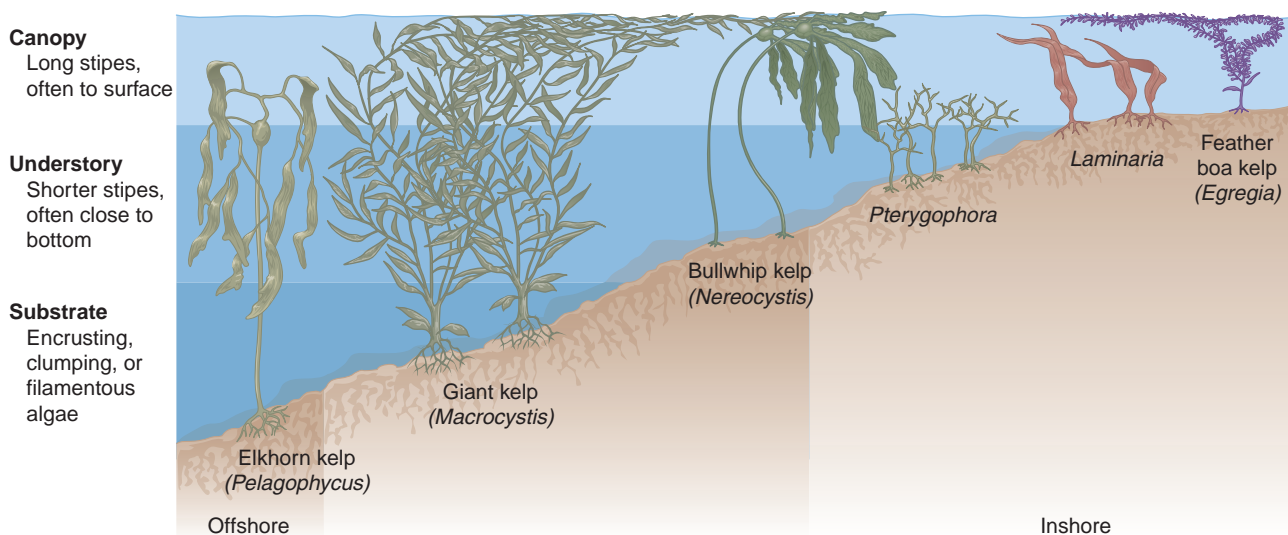


Figure 4.20

General structure of a U.S. west coast kelp forest, with a complex understory of plants beneath the dominant *Macrocystis* or *Nereocystis*.

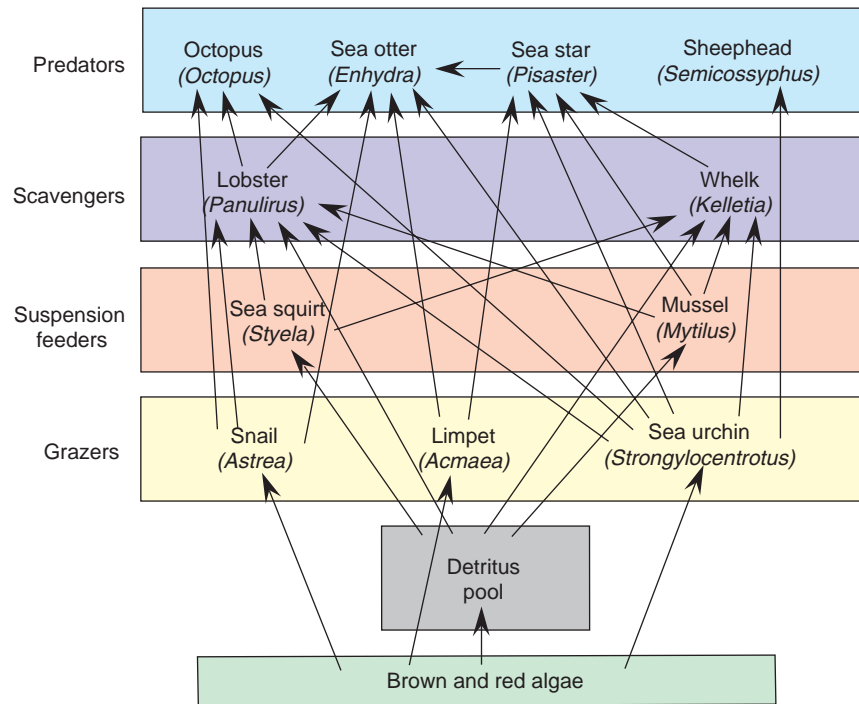


Figure 4.21

Trophic relationships of some dominant members of a southern California kelp community.

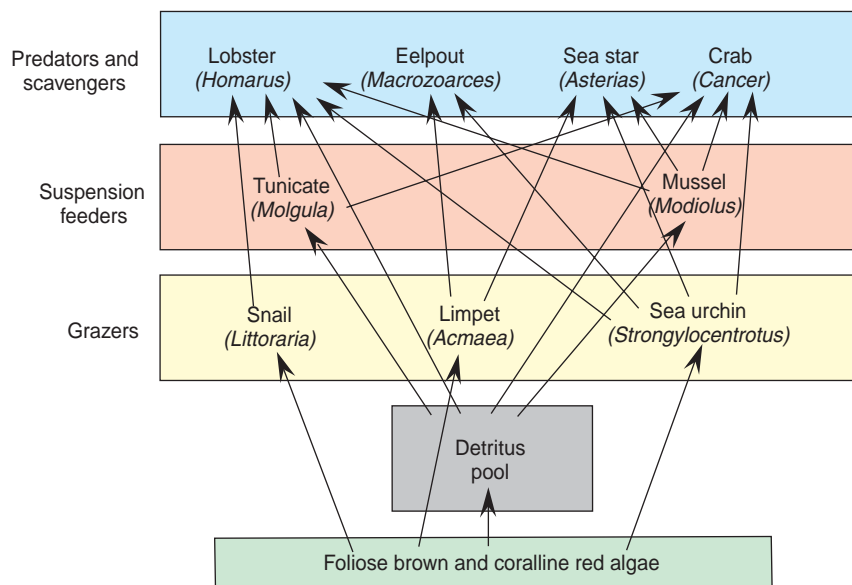


Figure 4.22

Trophic relationships of the common members of a New England kelp community.

A major predator of West Coast kelp bed urchins is the sea otter (*Enhydra*, see Fig. 7.13). East Coast sea urchins are similarly preyed on by the lobster (*Homarus*); however, both of these predators have been subjected to intensive commercial harvesting and have ex-

perienced major population reductions in the past 2 centuries.

Available evidence indicates that the effects of this reduced predation have been magnified by increased concentrations of dissolved and suspended

organic materials in coastal waters (mostly from urban sewage outfalls). The U.S. Office of Technology Assessment has identified over 1300 major industries and 600 municipal wastewater treatment plants that discharge into the coastal waters of the United

States. Standard secondary treatment of sewage is intended to separate solids and to reduce the amount of organic matter (which contributes to biochemical oxygen demand), nutrients, pathogenic bacteria, toxic pollutants, detergents, oils, and grease in wastewater.

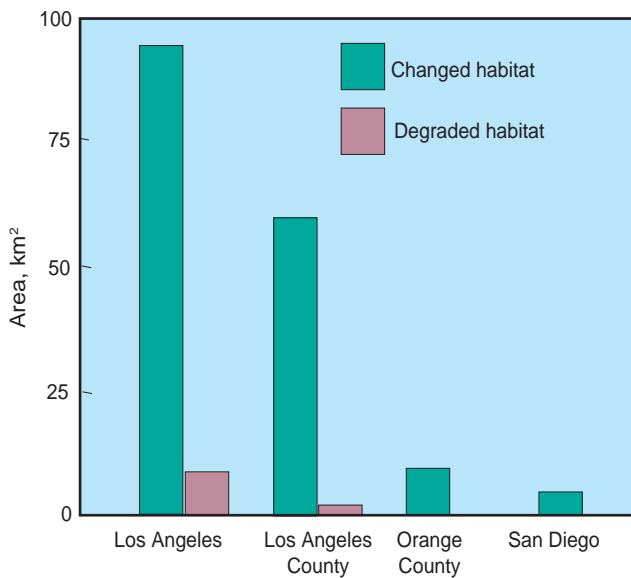


Figure 4.23

Extent of areas changed or degraded by four major sewage outfalls in the California Bight, 1978–1979. (Data from A. J. Mearns. *Marine Environmental Pollution*, Elsevier, 1981.)

In the United States, most ocean discharges of wastewater are supposed to meet those secondary treatment standards, but many still do not, including some that discharge into southern California coastal waters. Until the mid 1980s, treated sewage containing about a quarter of a million tons of suspended solids was discharged from 4 large and 15 small publicly owned sewage treatment plants each day. These solids are similar to detritus from natural marine sources in its general composition and nutritional value for zooplankton and benthic detritus feeders. Measurable changes in species diversity and biomass of benthic infauna and kelp beds can be found, but these changes depend on the rate of discharge and the degree of treatment before release. Increased abundance of fishes and benthic invertebrates have been noted in the vicinity of some outfalls; at others, benthic communities have been noticeably degraded. Of the four major sewer outfalls emptying into the Southern California Bight, two had caused obvious degradation in several square kilometers around the outfall site (Fig. 4.23). Collectively, the four outfalls significantly changed or degraded nearly 200 km² of seafloor during the 1970s and 1980s.

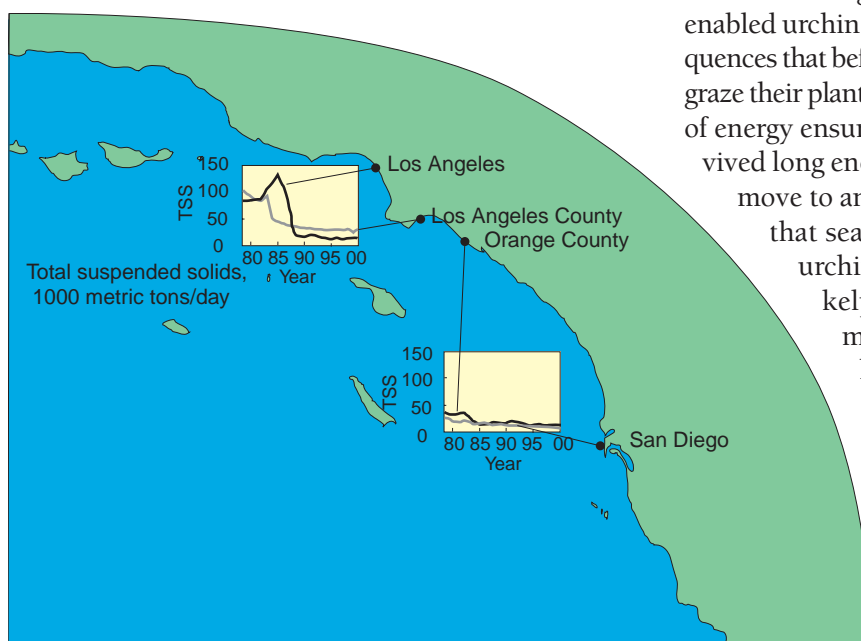


Figure 4.24

Graphs showing the reduction in discharged total suspended solids (TSS) for the past two decades at the four major sewage outfalls in the California Bight. (Data from Steinberger and Schiff, 2002.)

These energy-rich substances from treated sewage enabled urchin populations to evade the usual consequences that befall animal populations when they overgraze their plant food sources. These alternative sources of energy ensured that large numbers of urchins survived long enough after decimating one kelp bed to move to another. In central California kelp beds that sea otters have recolonized since 1950, urchin populations are now kept low, and kelp forests have recovered throughout most of the otters' geographic range. The kelp beds just off San Diego, however, have made a dramatic recovery since 1960 without sea otters. The recovery there was more likely due to improved urban sewage treatment, especially reducing the amounts of discharged solids (Fig. 4.24). The activities of other predators, particularly sea stars and the California sheephead, also played important roles. In an unusual turnabout, these recovered urchin populations,

so recently considered pests in need of eradication, are now themselves targets of a rapidly expanding commercial fishery to supply urchin roe to local and international sushi markets.

SUMMARY POINTS

The Seaweeds

- Most large conspicuous plants in the sea are macroalgae (seaweeds and kelps), growing from rocky or sandy substrates with their characteristic blades, stipes, holdfasts, and pneumatocysts (in some species).
- The common names of seaweeds often are motivated by their colors, which in turn reflect the various photosynthetic pigments that they contain. Just as in phytoplankton, there is adaptive significance for all accessory photopigments possessed by seaweeds.
- Reproduction in seaweeds can be either vegetative and asexual or complex and sexual. Sexual reproduction tends to follow three fundamental patterns, all variations of alternating sporophyte, gametophyte, and/or carposporophyte generations.
- Luxurious kelp communities dominate in temperate areas, with North America's west coast hosting a more complex and extensive kelp community than New England.

4.3 Geographic Distribution

The interplay of a multitude of physical, chemical, and biological variables influences and controls the distribution of marine plants on a local scale. For instance, on an exposed rock in the lower intertidal zone on the Oregon coast, *Postelsia* may thrive, but 10 m away, the conditions of light, temperature, nutrients, tides, surf action, and substrate may be such that *Postelsia* cannot survive. Nevertheless, on an ocean-wide scale, only a few factors seem to control the presence or absence of major groups of seaweeds. Significant among these are water and air temperature, tidal amplitude, and the quality and quantity of light. With these factors in mind, we can make a few generalizations concerning the geographic distribution of benthic plants.

In marked contrast to the impoverished seaweed flora of the Red Sea, the tropical western coast of

Africa, and the western side of Central America, seaweeds thrive in profusion along the coasts of southern Australia and South Africa, on both sides of the North Pacific, and in the Mediterranean Sea. The U.S. West Coast is somewhat richer in seaweed diversity than is the East Coast. From Cape Cod northward, the East Coast is populated with subarctic seaweeds. South of Cape Cod, the effects of the warm Gulf Stream become more evident, until a completely tropical flora is encountered in southern Florida.

Red algae are not rare in cold-water regions but are more abundant and conspicuous in the tropics and subtropics. Calcareous forms of red algae (and some browns and greens as well) are characterized by extensive deposits of calcium carbonate (CaCO_3) within their cell walls. The use of calcium carbonate as a skeletal component by warm-water marine algae is apparently related to the decreased solubility of CaCO_3 in water at higher temperatures. In the tropics, plants expend less energy to extract CaCO_3 from the water, and here, coralline red algae contribute to the formation and maintenance of coral reefs. Encrusting coralline algae grow over coral rubble, cementing and binding it into larger masses that better resist the pounding of heavy surf. Some Indian Ocean "coral" reefs completely lack coral animals and are constructed and maintained entirely by coralline algae. The few calcareous forms of green algae that exist are also limited to tropical latitudes and play a large role in the production of CaCO_3 sediments.

The small green alga *Halimeda* is one of the few green algae to also secrete a CaCO_3 skeleton, giving it a stony feel. *Halimeda* is a member of a remarkable group of Chlorophytes known as siphonous green algae. Although some siphonous green algae reach several meters in size, each plant consists of an enormously long, tubular, single cell containing millions of nuclei by uncoupling the process of nuclear division from that of cell division. Two other members of this group, *Caulerpa taxifolia* and *Codium fragile*, recently have become notorious for their explosively rapid invasions as introduced exotics, *Caulerpa* in the Mediterranean Sea (Fig. 4.25) and *Codium* in shallow coastal waters of New Zealand and the U.S. Northeast. These invasions have been enhanced by the ability of these plants to fragment in storms and quickly regrow from the wave-scattered pieces.

A few of the larger species of benthic marine plants flourish in such profusion that they dominate the general biological character of their communities. Such community domination by plants is common on land but is exceptional in the sea. Away from the near-shore



Figure 4.25

A dense growth of *Caulerpa* has invaded the Mediterranean Sea.

habitats occupied by benthic plants, the microscopic phytoplankton prevail as the major primary producers of the sea, and it is their larger animal consumers that define the visual character of their pelagic communities. In the near-shore fringe, however, mangals, salt marshes, seagrasses, and kelp beds thrive where the appropriate bottom conditions, light, and nutrients exist.

Kelp are temperate to cold-water species, with few tropical representatives. Large kelps are especially abundant in the North Pacific. Kelp beds abound with herbivores that graze directly on these plants and in turn become prey for higher trophic levels. The cool-water kelp plants form extensive layered forests of mixed species in both the Atlantic and Pacific Oceans. The blades of the larger *Macrocystis*, *Laminaria*, or *Nereocystis* form the upper canopy and the basic structure of these plant communities. Shorter members of other brown algal and red algal species provide secondary understory layers and create a complex three-dimensional habitat with a large variety of available niches (Fig. 4.26). The maximum depth of these kelp beds, usually 20 to 30 m, is limited by the light available for the young growing sporophyte. The larger kelp plants, with their broad blades streaming at the

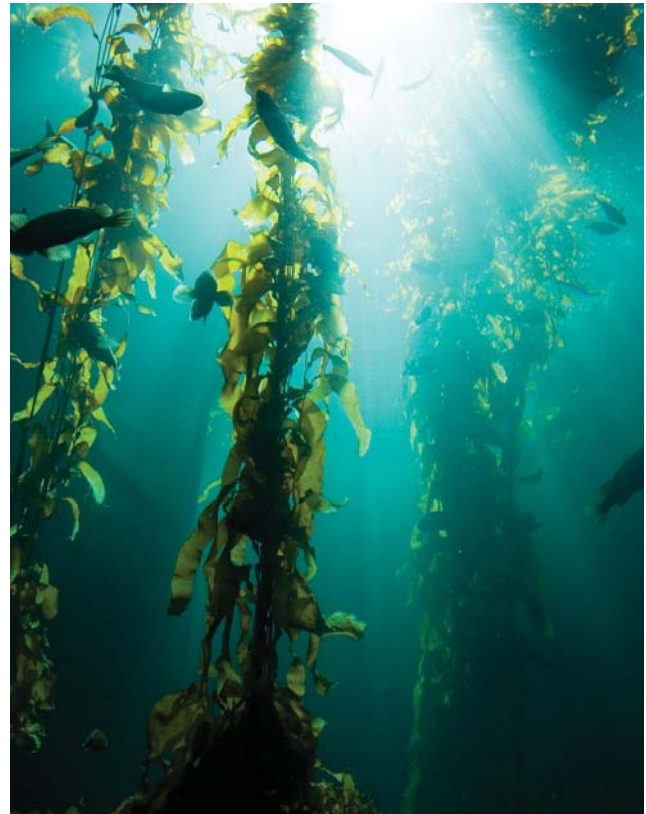


Figure 4.26

A kelp forest off the California coast, dominated by *Macrocystis*, a brown alga.

sea surface, create substantial drag against currents and swells and are susceptible to storm damage by waves and surge. Cast on the shore, these decaying plants are a major food source for beach scavengers.

SUMMARY POINTS

Geographic Distribution

- A complex interplay of a multitude of physical, chemical, geological, and biological factors determines the distribution of marine plants on both small and large scales.
- A knowledge of these variables helps one understand why opposite sides of an intertidal rock or an entire continent may host different species of plants.

4.4 Seasonal Patterns of Marine Primary Production

In Chapter 3, the influence of sunlight, nutrients, and grazers on marine primary productivity was considered. Here we put it all together to develop

a dynamic coherent picture of how marine primary productivity patterns change over seasonal time scales and oceanic distances. The numbers needed for this summary are difficult to come by and are changing as new techniques for measuring marine primary productivity are developed. Since the first edition of this text was written, estimates of global marine primary productivity have approximately doubled, thanks in large part to satellite monitoring systems such as the sea-viewing wide field-of-view sensor (SeaWiFS) described in Chapter 3. Globally, the marine plants described in this chapter account for only about 2% of each year's total marine primary productivity; phytoplankton take care of the rest. Thus, again, the emphasis of the following discussion is on phytoplankton.

The spatial patchiness of marine primary production described in Chapter 3 is related on large scales to areas of nutrient abundance and on much smaller scales to the local influences of grazers, near-surface turbulence, and nutrient patches. Seasonal variations, or patchiness in time, occur in response to changes in light intensity, nutrient abundance, and grazing pressure. The underlying pulse for these time changes is the predictable seasonal variation in the intensity of sunlight reaching the sea surface. **Figure 4.27**

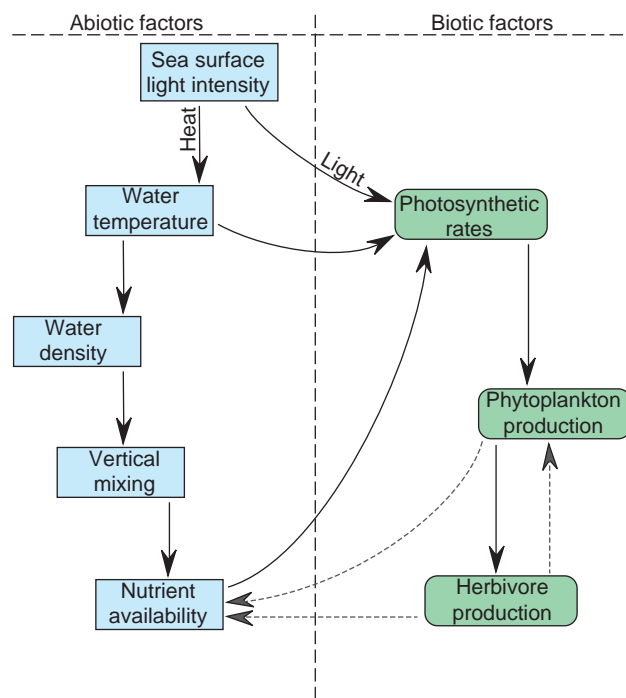


Figure 4.27

The seasonal variation of light intensity at the sea surface sets in motion a cascading series of changes in the photic zone. Eventually, these factors influence primary production, either directly (solid arrows) or through feedback links (dashed arrows).

outlines the major links between factors involved in defining the actual pattern of net primary production (NPP) through time. With these in mind, we can develop some general pictures of the seasonal pattern of primary production for several different marine production systems.

Temperate Seas

Figure 4.28 depicts a somewhat idealized graphic summary of major physical, chemical, and biological events in temperate oceanic areas well away from the influences of coastlines. These areas include broad swaths of midlatitude open ocean as well as locally defined areas such as the Grand Banks of the North Atlantic Ocean. These temperate oceanic systems are characterized by wintertime convective mixing between surface and deep layers.

A prominent feature in the production cycle of temperate seas is a spring diatom population explosion, or diatom bloom. Diatom blooms are the result of combined seasonal variations of water temperature, light and nutrient availability, and grazing intensity. In early spring, water temperature and available light increase, nutrients are abundant in near-surface waters, and grazing pressure is diminished. As soon as the minimum threshold level of sunlight needed for photosynthesis is achieved, conditions are ideal for rapid and abundant growth of primary producers. If the bottom of the mixed layer extends below the compensation depth (determined by light penetration, see Fig. 3.20), near-surface turbulence will distribute the phytoplankton cells randomly throughout the mixed layer, and primary production will remain low. Cells in the deeper portions of the mixed layer receive insufficient light, and no net production will occur. The spring bloom will commence only after the thermocline thins the mixed layer to a level above the compensation depth. In general, bloom conditions in the open ocean occur as a broad band of primary production sweeping poleward from midlatitudes in both hemispheres with the onset of spring. The standing crop of diatoms increases quickly to the largest of the year and begins to deplete nutrient concentrations. The grazers respond to the additional forage by increasing their numbers.

As spring warms into summer, sunlight becomes more plentiful, but the now strongly developed seasonal thermocline effectively blocks nutrient return from deeper water. The now warmer waters are “older” surface waters, with most of their dissolved nutrients depleted. Coupled with increased grazing, the diatom population peaks and then declines and remains low

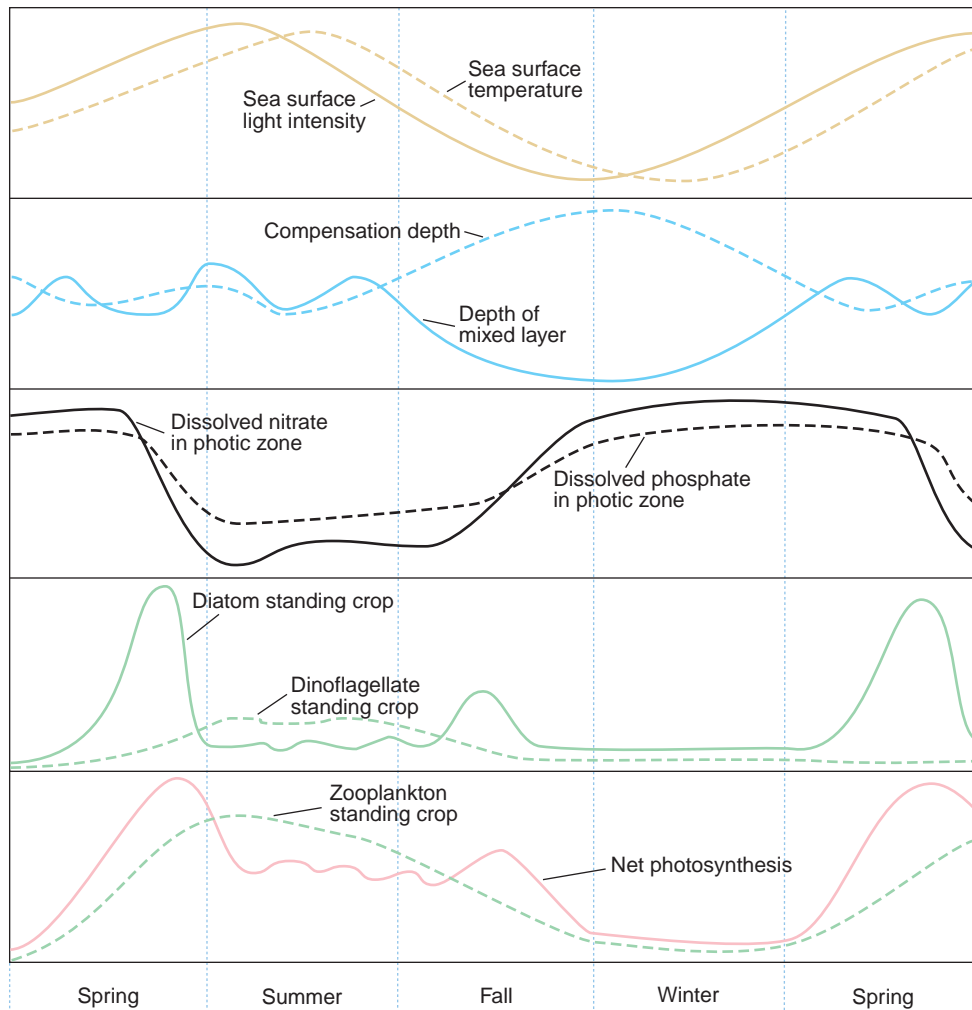


Figure 4.28

Seasonal fluctuations in the major features of a primary production system in temperate latitudes of the sea.

throughout the summer. With food more scarce, the summer zooplankton population also drops. Unlike diatoms, dinoflagellate populations increase slowly during the spring, remain healthy throughout the summer (although not as abundant as diatoms are in spring), and decline in autumn because of diminished light intensity.

This replacement of diatoms by dinoflagellates is a form of seasonal succession resulting from some basic ecological differences between the two principal groups of phytoplankton. Recall that diatoms lack flagella, cannot swim, are more readily inhibited in high-light intensities, perform better in low-light intensities, and have a nutrient need for silicate. These features give diatoms a competitive advantage in less-well-lit, colder, denser, nutrient-rich waters and dinoflagellates the advantage in warmer better-lit waters that may be deficient in silicate. Some dinoflagellates

deeper in the photic zone may supplement their meager nutrient supply by migrating downward a few meters during night hours to soak up additional nutrients from slightly deeper water.

Cooler autumn air temperatures begin to break down the summer thermocline and allow convection to renew nutrients in the photic zone. The phytoplankton respond with another bloom, which, although not as remarkable as the spring bloom, is often sufficient to initiate another upswing of the zooplankton population. As winter approaches, the autumn bloom is cut short by decreasing light and reduced temperatures. As production goes down, resistant overwintering stages of both phytoplankton and zooplankton become more abundant. Convective mixing continues to recharge the nutrient load of the surface waters in readiness for a repeat of the entire performance the following spring. It is now estimated that, on average,

about 206 g C/m² per year is produced in oceanic temperate and subpolar areas, with most of that total occurring during the spring diatom bloom.

Warm Seas

The production characteristics of tropical and subtropical oceanic waters closely resemble those of continuous summer in temperate regions, as outlined in Figure 4.28. Sunlight is available in abundance, yet NPP is low (about 55 g C/m² per year) because a strong permanent pycnocline blocks vertical mixing of nutrients from below. The low rate of nutrient return is partially compensated for by a year-round growing season and a deep photic zone. Even so, NPP and standing crops are low (Fig. 4.29), and dinoflagellates are usually more abundant than diatoms.

Regions of upwelling in the equatorial Pacific and, to a lesser extent, the equatorial Atlantic are more productive than tropical open ocean areas, but they are very limited in geographic extent (see Fig. 3.37). So too are coral reef communities, with annual NPP rates up to 5000 g C/m² per year. Upwelling is described in the next section, and the reasons for exceptionally high productivity rates on coral reefs are discussed in Chapter 10.

Coastal Upwelling

Coastal upwelling in temperate seas alters the generalized picture presented in Figure 4.28 by replenishing nutrients during the summer, when they would otherwise be depleted. As long as light is sufficient and upwelling continues, high phytoplankton production occurs and is reflected in abundant local animal populations (Fig. 4.30). In some areas, the duration and intensity of coastal upwelling fluctuate with variations in atmospheric circulation. Along the Washington and Oregon coasts, the variability of spring and summer wind patterns produces sporadic upwelling interspersed with short periods of no upwelling and lower NPP. Coastal upwelling zones have average NPP rates approaching 1050 g C/m² per year (Fig. 4.31). In the Peru Current, upwelling is massive year round and is interrupted only by major disturbances such as El Niño events.

El Niño is a phenomenon that represents a strong departure from the more typical current patterns in the central Pacific Ocean (see Fig. 1.37) that drive coastal and equatorial upwellings. El Niño is characterized by a prominent warming of the equatorial Pacific surface waters. El Niño occurs irregularly every few years, and each occurrence lasts from

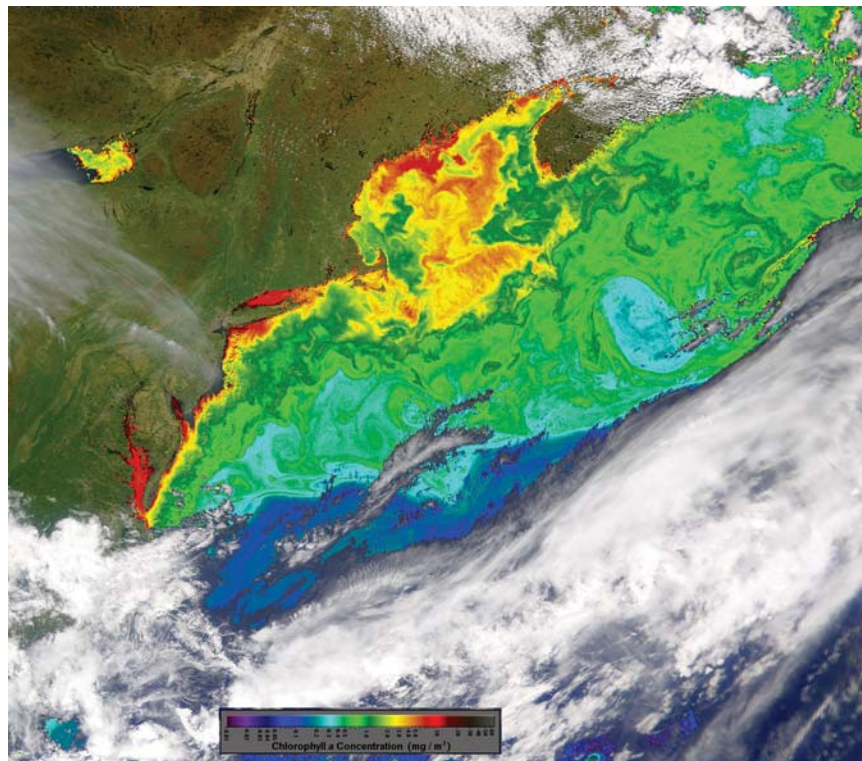


Figure 4.29

SeaWiFS image of chlorophyll *a* concentrations in the area off the U.S. East Coast, taken on May 11, 2002. The color bar is the same as those shown in other SeaWiFS images in Chapter 3. Note the increase in net primary production (NPP) with latitude.

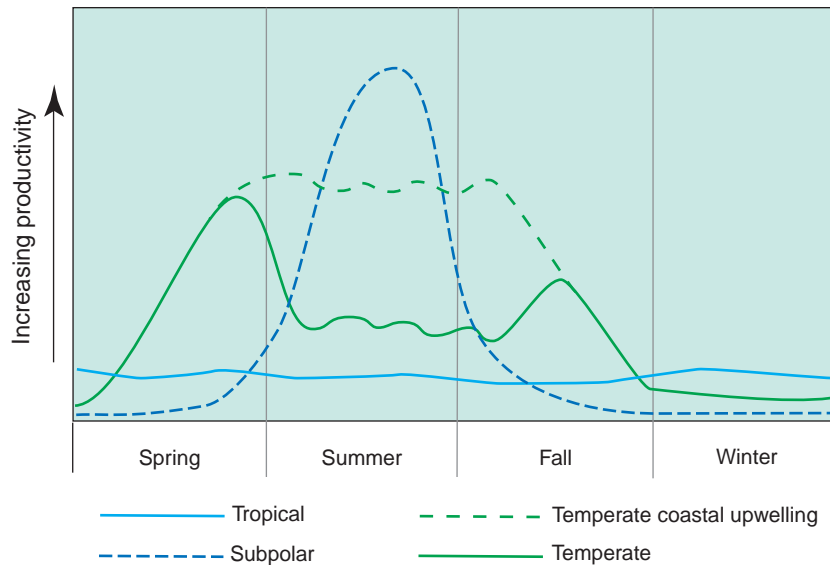


Figure 4.30

Comparison of the general patterns of seasonal variations in primary productivity for four different marine production systems.

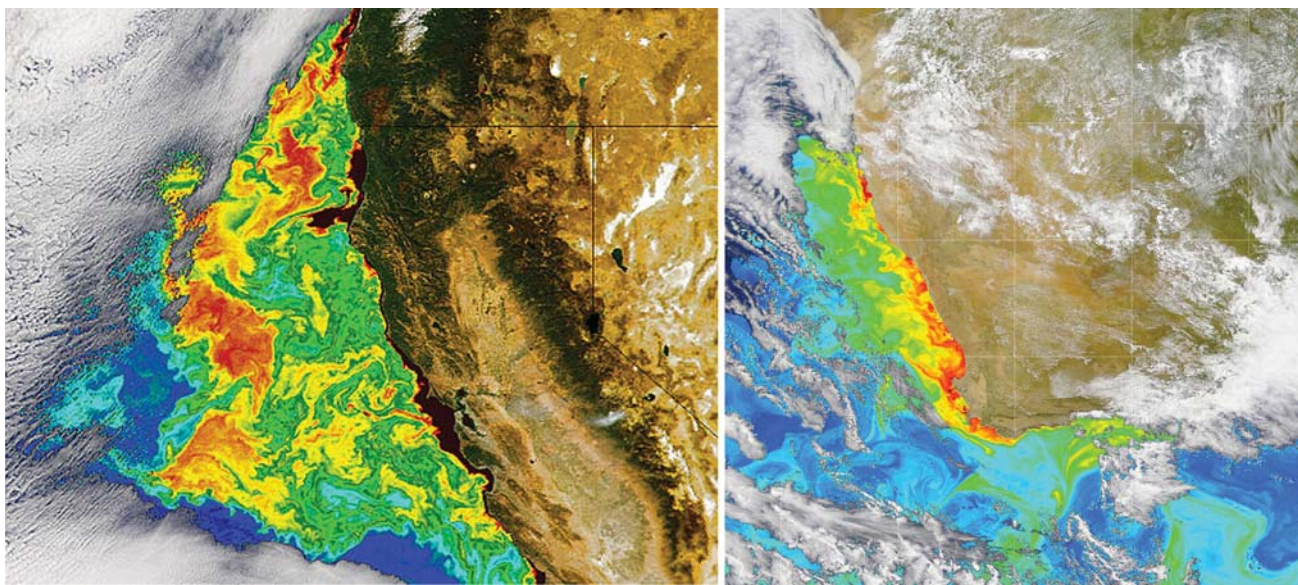


Figure 4.31

SeaWiFS image of chlorophyll *a* concentrations in the upwelling area of the California Current (left) and the Benguela Current off South Africa and Namibia (right). Note the pulse of high phytoplankton production off California being transported well offshore. The color designation is the same as that in other SeaWiFS images in this chapter and Chapter 3.

several months to well over a year. The El Niño phenomenon is associated with the Southern Oscillation, a trans-Pacific linkage of atmospheric pressure systems, and the climatic anomaly has come to be known collectively as El Niño/Southern Oscillation, or ENSO. Normally, the trade winds blow around the South Pacific high pressure center located near Easter Island and then blow westward to a large Indonesian low-pressure center. As these winds move

water westward, the water is warmed, and the thermocline is depressed from about 50 m below the surface on the east side of the Pacific to about 200 m deep on the west side. ENSOs occur, for reasons not yet understood, when this pressure difference across the tropical Pacific relaxes and both surface winds and ocean currents either cease to flow westward or actually reverse themselves. Although the effects of an ENSO event are somewhat variable, they are

usually global in extent and occasionally severe in impact.

The 1982–1983 ENSO event, for example, was associated with heavy flooding on the West Coast of the United States, intensification of the drought in sub-Saharan Africa and Australia, and severe hurricane-force storms in Polynesia. Surface ocean water temperatures from Peru to California soared to as much as 8°C above normal. The 1997–1998 ENSO event caused similar disruptions but was even more severe (Fig. 4.32). These strong El Niño events and the associated buildup of warm, less-dense water blocks upwelling of nutrient-rich waters, and coastal marine populations decline. During severe El Niño years, some fishes and fish-eating seabird populations almost completely disappear. Eventually, the area of warm tropical water dissipates, and El Niño conditions are replaced by cooler eastern tropical Pacific surface temperatures, low rainfall, and well-developed coastal upwelling along Peru and northern Chile.

Unfortunately, ENSO events continue to recur. The 2002–2004 episode is ranked in the top 10 El Niño events of the last 50 years. A similar El Niño event appeared in 2006 but it had an unusually short duration, collapsing in early 2007. As this edition is being prepared, the most current El Niño event

(2009–2010) is gaining strength and very well may replace the 2002–2004 episode on the top 10 list of ENSO events during the last half century.

Polar Seas

The two polar ends of the Earth share several environmental characteristics that distinguish them from other marine environments. Both experience long winter nights without sunlight. Low levels of sunlight keep sea surface temperatures hovering around 0°C, even in summer. Large parts of both polar marine environments remain perpetually covered by permanent sea ice known as **fast ice**. Even larger areas freeze over in winter to form **pack ice** that thaws and disappears each summer. Polar seas are defined as those areas of the ocean characterized by a cover of either permanent fast ice or seasonal pack ice. The approximate geographic extent of fast and pack ice is shown in Figure 4.33. Sea ice is a solid physical structure encountered in no other marine ecosystem. It acts as a barrier to insulate seawater from continued chilling effects of the atmosphere in winter, and thus, sea ice never more than a few meters thick forms in even the most extreme winter temperature regimes. Sea ice also provides a stable and nearly predator-free platform on which

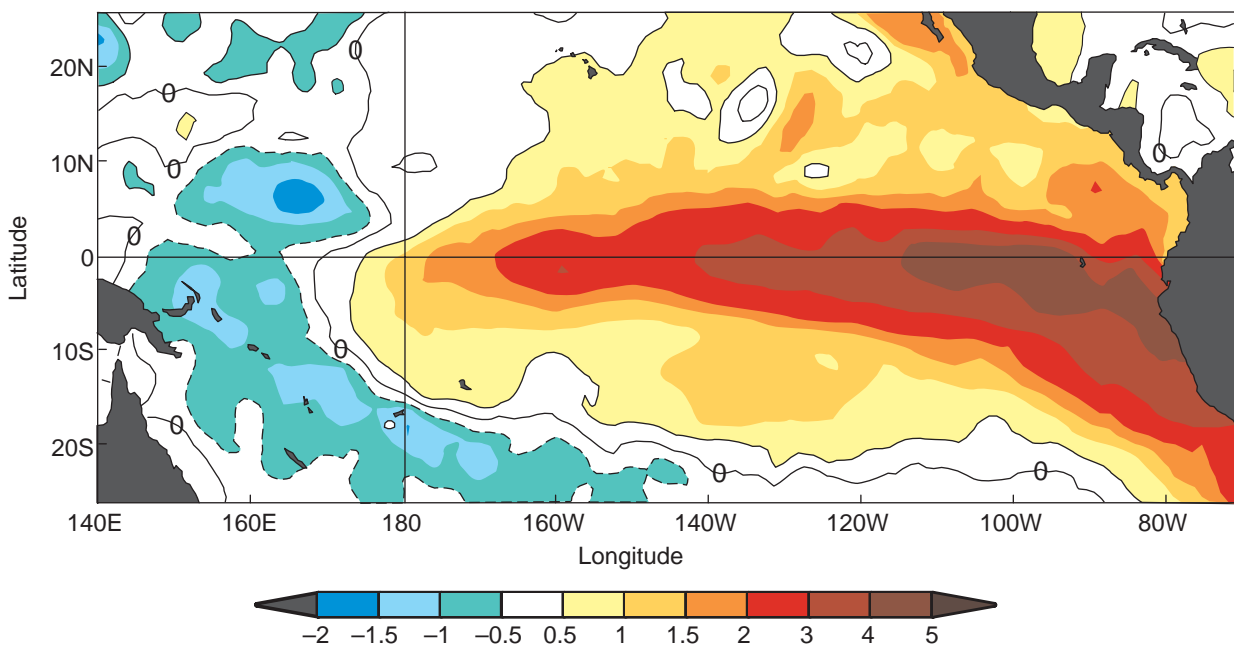


Figure 4.32

Observed sea surface temperature anomaly, in degrees Celsius, in the Equatorial Pacific Ocean based on a 7-day average in mid-September 1997. Notice the tongue of unusually warm water extending westward from the coasts of Ecuador and Peru.

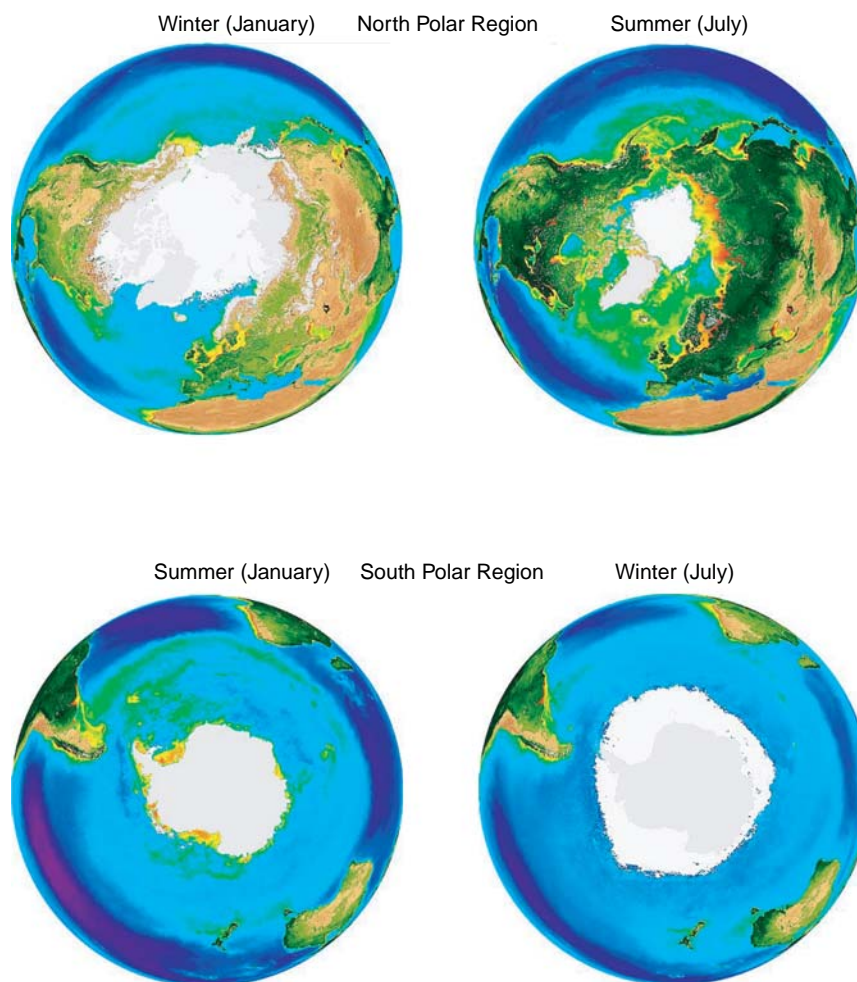


Figure 4.33

Approximate distribution of fast ice (summer) and pack ice (winter) in the north and south polar regions.

some birds and mammals can raise their young (see Chapter 7), yet it also effectively bars many of those same animals from moving easily from the ice surface to forage the water below. The thermocline, if one exists at all, is poorly established and its associated pycnocline is not an effective barrier to vertical movements of water and nutrient regeneration in the photic zone. Light, or more correctly the lack of it, is the major limiting factor for plant or phytoplankton growth in polar seas. Sufficient light to sustain high phytoplankton growth rates lasts for only a few months during the summer. Even so, photosynthesis can continue around the clock during those few months to produce huge phytoplankton populations quickly. As the light intensity and day length decline, the short summer diatom bloom declines rapidly. Winter conditions closely resemble those of temperate regions, except that in polar seas the conditions endure much longer. There,

the complete cycle of production consists of a single short period of phytoplankton growth, equivalent to a typical spring bloom immediately followed by an autumn bloom and decline that alternates with an extended winter of reduced net production. In both the Arctic Ocean and around the Antarctic continent, the seasonal formation and melting of sea ice play a central role in shaping patterns of primary productivity. As ice melts in the spring, the low salinity meltwater forms a low-density layer near the sea surface. This increases vertical stability, which encourages phytoplankton to grow near the sunlit surface. The melting ice also releases temporarily frozen phytoplankton cells, or ice algae, into the water to initiate the bloom. The individual phytoplankton cells produced in these summer blooms tend to be much larger than those in lower latitudes. These in turn feed relatively large planktonic copepods and benthic consumers, particularly amphipod crustaceans and

Table 4.2

Comparison of Arctic and Antarctic Oceanographic Features

Feature	Arctic	Antarctic
Shelf	Broad, two narrow openings	Narrow, open to all oceans
River input	Several	None
Nutrients in photic zone	Seasonally depleted	High throughout year
Icebergs	Small, irregular, not in arctic basin	Abundant, large, tabular
Pack ice		
Maximum area ($\times 10^6$ km ²)	13	22
Age	Mostly multiyear	Mostly 1 year
Thickness	3.5 m	1.5 m

Adapted from Hempel, 1991.

bivalve mollusks. As the sea ice continues to melt toward the poles in early summer, the zone of high phytoplankton productivity follows, and the stage is then set for short food chains supporting a very productive, seasonal, migrating ice-edge community of diatoms, krill, birds, seals, fishes, and whales. Animals that do exploit this production system must be prepared to endure long winter months of little primary production. Common responses of homeotherms to cope with the seasonal variability in their food supplies include extended fasting periods and long migratory excursions to lower-latitude waters in winter (see Chapter 7).

In addition to these similarities, some strong contrasts exist between north and south polar marine environments, and so do some of their productivity patterns. The Arctic is a frozen ocean surrounded by continents; the Antarctic is a frozen continent surrounded by ocean. Much of the Arctic Ocean is permanently covered by fast ice, and because so much of the year passes in darkness with almost no phytoplankton growth, the annual average productivity rate there is low (about 25 g C/m² per yr). Around the Antarctic continent, however, upwelling of deep nutrient-rich water supports very high summertime NPP rates and annual average rates of about 150 g C/m² per year. In these regions, water that sank in the Northern Hemisphere returns to the surface in an uninterrupted zone of upwelling that extends around the entire continent to support a band of high phytoplankton productivity from the ice edge north to the Antarctic Convergence between 60° S and 70° S latitude (see Fig. 3.40), bringing with it a thousand-year accumulation of dissolved nutrients. The extraordinary fertility of the Antarctic seas stands in sharp contrast to the barrenness of the adjacent continent. Consequently, almost all Antarctic life,

whether terrestrial or marine, depends on marine food webs supported by this massive upwelling. Comparable latitudes in the Arctic are interrupted by land masses to form the small regional Bering, Baffin, Greenland, and Norwegian Seas. Some important features of the two polar regions are compared in Table 4.2.

SUMMARY POINTS

Seasonal Patterns of Marine Primary Production

- Spatial and temporal variations in available sunlight, nutrients, and grazers cause significant seasonal and global differences in marine production. A diatom bloom during the spring, followed by the successional appearance of less-numerous dinoflagellates during the summer, is the prominent scenario of production in temperate seas.
- Tropical and subtropical waters exist in eternal stratification, with low rates of production and year-round plankton communities that resemble those of temperate regions during summer months.
- Rates of net primary production in areas of coastal upwelling are among the highest in the sea; however, they are very limited in geographic extent, and some of the most important ones are interrupted by El Niño events.
- The seasonal formation and melting of sea ice and tremendous variations in availability of sunlight greatly influences production in polar seas, yet photosynthesis can continue around the clock during a few summer months to create dense populations of phytoplankton.

4.5 Global Marine Primary Production

Obtaining accurate estimates of primary productivity from the ocean on a global scale is no easy task, even with the help of satellite technology as described in Chapter 3. Perhaps the most difficult aspect of production estimation is the development of a model that will transpose satellite-imagery data into reliable estimates of marine productivity. Proposed algorithms typically attempt to integrate many data sets simultaneously, such as surface wind stresses, vertical profiles of ^{14}C -based carbon fixation, precipitation, variable fluorescence data collected using a Fast-Repetition-Rate fluorometer, sea level pressure, depth-integrated carbon fixation, sea surface temperature, relative humidity, wavelength-integrated surface photosynthetically active radiation (or PAR), ice cover, surface chlorophyll concentration, aerosol optical depths, daily photoperiod, depth of the photic zone, and the vertical distribution of chlorophyll. As if this is not complicated enough, model-generated estimates of marine production using these data sets are greatly influenced by assumptions and data corrections made by researchers; for example, scientists at Rutgers University have estimated annual global ocean production to be between 40.6 and 50.4 billion metric tons of carbon per year. The variation in these estimates is due to iterations of their model when surface irradiance is corrected for cloudiness or not, when surface photoinhibition of photosynthesis is assumed to be present or absent, or when the optimal rate of

daily carbon fixation within the water column is estimated (by using the relationship between temperature and maximum phytoplankton-specific growth rates) or assigned a constant value. Since 1994, the Ocean Primary Productivity Working Group, a NASA-sponsored team of oceanographers, has been comparing the performance of various productivity algorithms in an attempt to establish a NASA-resident “consensus model” for routine estimation of marine production. We view these databases, production models, and “consensus algorithms” as continuously evolving entities that become better refined each year, and we present current best estimates of ocean primary productivity in the following paragraphs.

Mid- and high-latitude regions, shallow coastal areas, and zones of upwelling generally support large populations of marine primary producers, but most of this production is accomplished during the warm summer months when light is not a growth-limiting factor. Open-ocean regions, especially in the tropics and subtropics, where a strong thermocline and pycnocline are permanent features, and in polar seas, where light is limited through much of the year, have low rates of NPP (55 g C/m^2 per year).

Table 4.3 lists and compares the annual rates of marine NPP in several different regions (see Fig. 4.34 for a visual representation). Total NPP estimates included in syntheses such as this have been revised upward nearly 75% with the use of satellite-derived observations. About 76% of the total NPP occurs in the open ocean, spread thinly over 92% of the ocean’s area.

Rates of Net Primary Production for Several Ocean Regions

Table 4.3

Region	Area ($\times 10^6 \text{ km}^2$)	Percentage of Ocean	Average ($\text{g C/m}^2/\text{yr}$)	Total NPP (10^9 tonnes C/yr)
Open ocean				
Tropics and subtropics	190	51	55	10.45
Temperate and subpolar (including Antarctic upwelling)	100	27	206	20.60
Polar	52	14	27	1.40
Continental shelf				
Nonupwelling	26.6	7.2	290	7.71
Coastal upwelling	0.4	0.1	1050	0.42
Estuaries and salt marshes	1.8	0.05	975	1.76
Coral reefs	0.1	—	1410	0.14
Seagrass beds	0.02	—	937	<u>0.02</u>
				42.50

Data from Longhurst et al., 1995; Pauly and Christensen, 1995; Field et al., 1998; and Gregg et al., 2003.

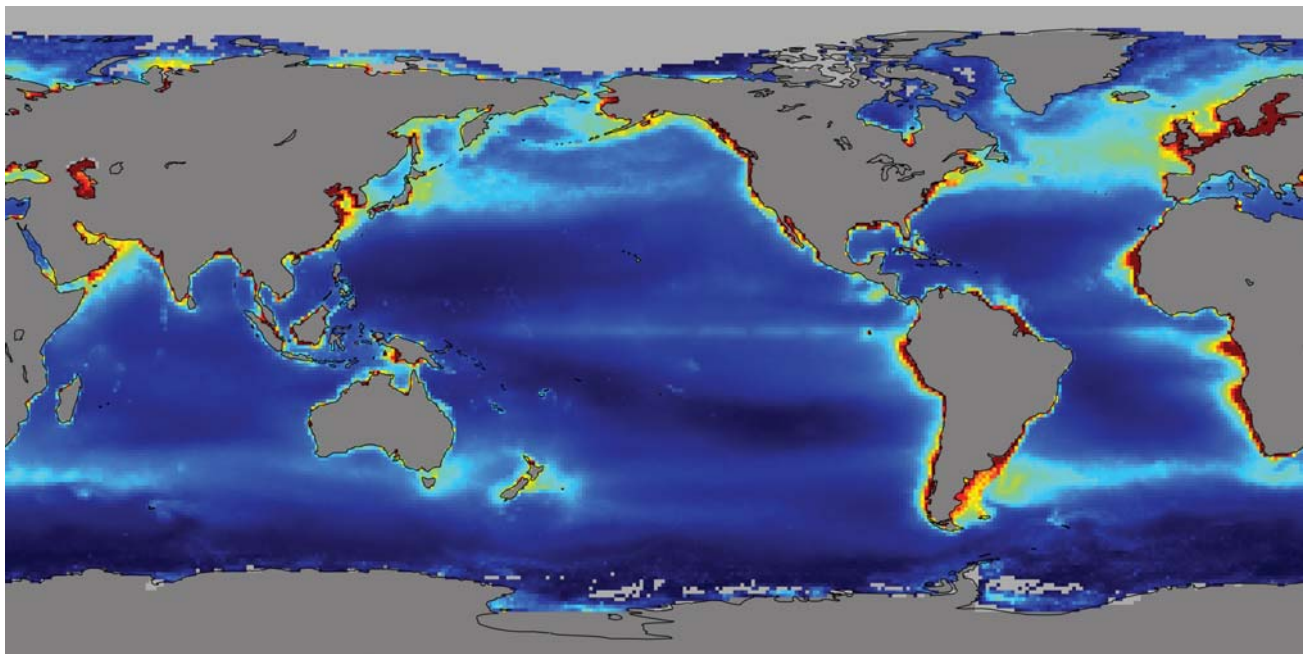


Figure 4.34

The geographic variation of marine primary production, composed from over 3 years of observations by the satellite-borne coastal zone color scanner. Primary production is low (less than 50 g C/m²/yr) in the central gyres (magenta to deep blue), moderate (50–100 g C/m²/yr) in the light blue to green areas, and high (greater than 100 g C/m²/yr) in coastal zones and upwelling areas (yellow, orange, and red).

The more productive regions are very limited in geographic extent. Collectively, estuaries, coastal upwelling regions, and coral reefs produce only about 2.3 billion of the 42.5 billion tonnes of carbon produced each year.

The productivity numbers of Table 4.3 indicate that a total of nearly 42.5 billion tonnes of carbon are synthesized each year in the world ocean, and all but 1.92 billion tonnes (95.5%) are from phytoplankton. That number is equivalent to a bit more than 90 billion tonnes of photosynthetically produced dry biomass, or about 15 tonnes of phytoplankton dry biomass for each person on Earth.

When compared with land-based primary production systems, NPP on land is slightly higher (about 56.4×10^9 tonnes C/yr), even though oceans cover more than twice as much of the Earth's surface as does land. The reason for this is that terrestrial areas do not suffer a significant loss of nutrients as does the photic zone, and thus, land production is 426 g C/m² per year (not including permanently iced areas). In contrast, marine production is 140 g C/m² per year. Although marine primary producers account for almost half of the total global NPP each year, at any one time phytoplankton represent only about 0.2% of the standing stock of primary producers because of their very rapid

turnover rates. About 25% of ice-free land areas supports NPP rates over 500 g C/m² per year; in the ocean, this value is less than 2%.

The entire human population on Earth currently requires about 5 billion tonnes of food annually to sustain itself, about 12% of the total annual marine NPP. Yet for several reasons to be discussed in Chapter 13, this abundant profusion of marine primary producers will probably never be used on a scale sufficient to alleviate the serious nutritional problems already rampant in much of our population. Instead, this vast amount of organic material will continue to do what it has always done: fuel the metabolic requirements of the consumers occupying higher marine trophic levels.

SUMMARY POINTS

Global Marine Primary Production

- Spatial variations in primary production are common, with mid- and high-latitude regions, shallow coastal areas, and upwelling zones being the most prolific, but only during warm summer months when sufficient sunlight is available.

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Topics for Discussion and Review

1. Terrestrial flowers are pollinated by a variety of insects, birds, and bats. How are the flowers of subtidal seagrasses pollinated?
2. Why are manatees and dugongs restricted to tropical and subtropical waters even though their preferred food (seagrass) occurs commonly at most latitudes?
3. The seeds of red mangroves germinate while their fruit still hangs from the parent tree. Summarize this unusual form of sexual reproduction.
4. *Sargassum* contains numerous small pneumatocysts to buoy the plant toward the sunlit surface and hosts a complex community of fishes and invertebrates that are uniquely adapted to living on this pelagic seaweed. Consider this paradox.
5. A life cycle consisting of alternating gametophyte and sporophyte generations is characteristic of almost all plants. How do the basic features of that life cycle differ among the different divisions of seaweeds?
6. What characteristics of green algae (Chlorophyta) support the hypothesis that they are ancestral to flowering plants (Anthophyta)?
7. How do local assemblages of kelp plants, seagrasses, and mangals influence and alter the physical characteristics of the shoreline on which they live?
8. Draw a generic graph of diatom concentrations in a temperate sea during the course of a single year, and then explain the factors that cause the observed peaks and valleys in this annual cycle.
9. What is the El Niño phenomenon, and how does it interrupt the massive upwelling of the Peru Current?
10. Describe how the formation and thawing of sea ice affect primary production in the Arctic and Antarctic.
11. Why are tropical waters usually as clear as gin, whereas the temperate ocean often seems as cloudy as soup?

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