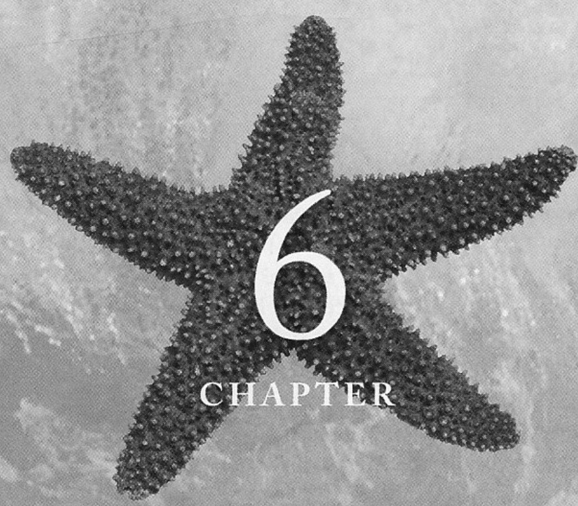
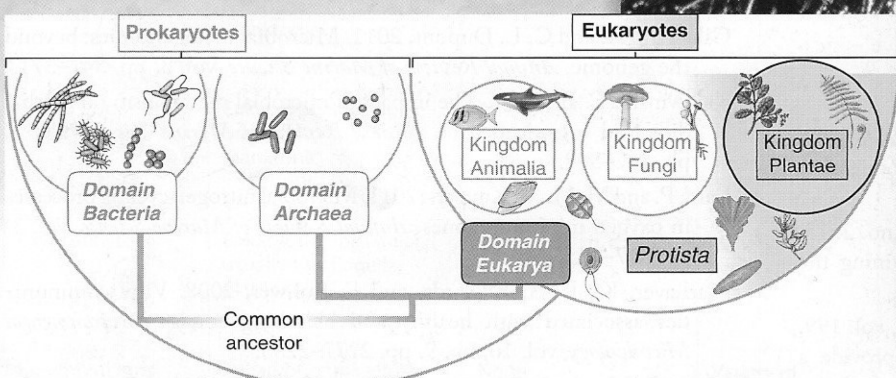


6

CHAPTER

# Multicellular Primary Producers: Seaweeds and Plants




Rocky-shore seaweeds, Nova Scotia, Canada.

As inhabitants of land, our perception of the world of photosynthetic organisms is based mostly on plants such as trees, ferns, and mosses. Many fascinating photosynthetic organisms populate the oceans, but for the most part they are very different from the land plants that surround us. Most, in fact, are not considered plants at all and therefore are not members of the kingdom Plantae. Non-plant photosynthetic organisms include photosynthetic bacteria and unicellular algae (both described in Chapter 5) and the seaweeds covered here. Some biologists, however, consider some or all seaweeds to be plants.

What makes practically all the organisms covered in this chapter "plant-like" is that they are **primary producers** capable of using light energy to perform photosynthesis, like photosynthetic bacteria and the unicellular algae. In other words, these organisms are **autotrophs.** There are always exceptions, and there are a few seaweeds that are not primary producers but parasites of other seaweeds.

Seaweeds play an important role in many coastal environments. Seaweeds transform solar energy into chemical energy in the form of organic matter and make it available to a long list of hungry creatures, which may include humans. Other organisms live on or even in the tissues of seaweeds. Seaweeds also produce oxygen for organisms both on land and in the ocean.

## MULTICELLULAR ALGAE: THE SEAWEEDS

The most familiar types of marine algae are those popularly known as **seaweeds,** which is a rather unfortunate term. For one thing, the word "weeds" does not do justice to these conspicuous and often elegant inhabitants of rocky shores and other marine environments. Some biologists opt for the more formal name of **macrophytes** or **macroalgae.** On the other hand, the term "seaweeds" is useful in distinguishing them from the unicellular algae surveyed in Chapter 5 and the seagrasses and salt-marsh grasses described later in this chapter. By definition, seaweeds are all multicellular; unicellular green and red algae are therefore not considered seaweeds. The classification of seaweeds takes into consideration not only structure but also other features, such as the types of pigments and food products they store (see Table 6.1, p. 113).

Like unicellular algae, seaweeds are eukaryotic. The structures of seaweeds, however, are far more complex than those of unicellular algae. Reproduction is also more elaborate. Though more complex than unicellular algae, seaweeds nevertheless lack the highly specialized structures and reproductive mechanisms of the mostly terrestrial plants.

The range of variation observed among seaweeds is spectacular. Those we see on rocky shores at low tide are usually small and sturdy as an adaptation to withstand waves. Some small, delicate ones live on other seaweeds. Kelps found offshore in cold waters are true giants that form dense underwater forests (see Fig. 6.8*b*).

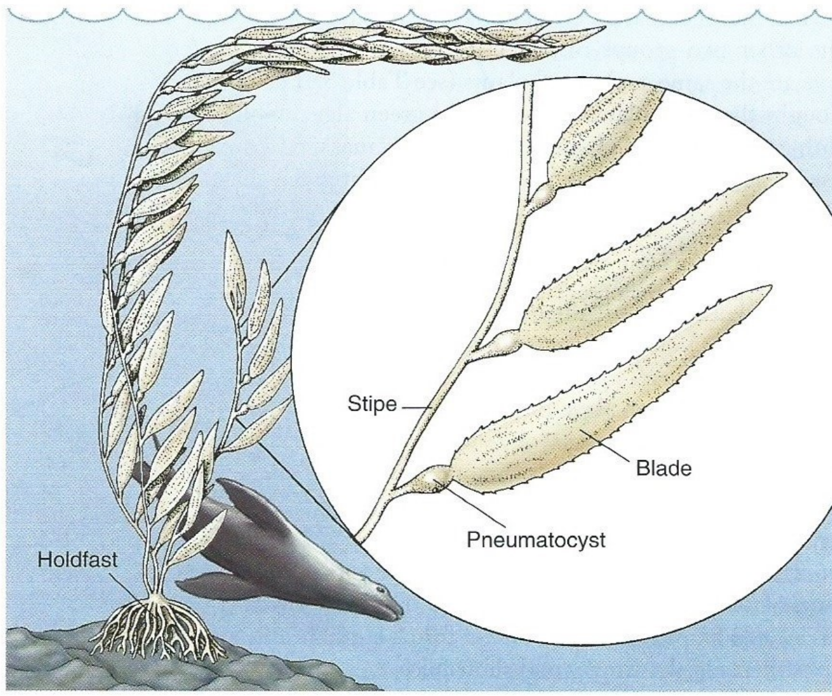



**FIGURE 6.1** The giant kelp (*Macrocystis*).

The multicellular condition of seaweeds allows many adaptations not available to unicellular forms. The ability of seaweeds to grow tall and rise off the bottom provides new opportunities as well as challenges, particularly that of wave action.

## General Structure

Seaweeds show a wide range of growth forms and complexity of structures. Nevertheless, several unifying features are worth mentioning. Seaweeds lack the true leaves, stems, and roots of plants. The complete body is known as the **thallus** (plural, **thalli**) whether it is a filament, a thin leafy sheet, or a giant kelp.

The leaf-like, flattened portions of the thallus of many seaweeds are known as **blades** (Fig. 6.1). They have a large surface area and are the main photosynthetic regions, though all portions of the thallus are able to photosynthesize in light as long as they have chlorophyll. Blades are technically not true leaves because they have no veins. Another difference is that, in contrast to true leaves, the upper and lower surfaces of blades are identical to each other. Gas-filled bladders known as **pneumatocysts** (Fig. 6.1) sometimes keep the blades close to the sea surface, thereby maximizing their exposure to the sunlight. The mixture of gases in the pneumatocysts of some seaweeds includes carbon monoxide, a gas that is toxic to humans.

Some seaweeds have a distinct, stem-like structure to provide support, the **stipe,** from which blades originate. It is long and tough in the large kelps. A structure that looks like roots, the **holdfast,** attaches the thallus to the bottom. Holdfasts are particularly well developed in the kelps (Fig. 6.1). They are not involved in any significant absorption of water and nutrients and do not penetrate through the sand or mud, as true roots do. Most seaweeds cannot anchor in soft sediments and are therefore restricted to hard bottoms. Water and nutrients, which bathe the entire thallus, are picked up directly across the surface without the need of roots. Also, in contrast to the leaves and stems of plants, the stipe and holdfast usually lack tissues specialized for water and nutrient transport.

Seaweeds typically consist of a thallus, which is sometimes provided with leaf-like blades, and a root-like holdfast. They lack true leaves, stems, or roots.

## Types of Seaweeds

There are three types of seaweeds: the green, brown, and red algae. It is not always easy to recognize the groups by their color in nature because the proportion of chlorophyll and other pigments (see Table 6.1, p. 113) can vary. Chemical analysis, however, reveals the characteristic pigments of each group.

**Green Algae** Most **green algae** (division, or phylum, **Chlorophyta**) live in freshwater and terrestrial environments. Only around 10% of the estimated 7,000 species are marine; many of these marine species are unicellular. This, however, does not mean that multicellular green algae are uncommon in the sea. Certain species dominate in environments with wide variations in salinity, such as bays and estuaries and isolated tide pools on rocky coasts.

**Primary Producers** Organisms that manufacture organic matter from carbon dioxide ($CO_2$), usually by photosynthesis.
- Chapter 4, p. 68

**Autotrophs** Organisms that can use energy (usually solar energy) to make organic matter.
- Chapter 4, p. 67

Most multicellular green algae have a simple thallus compared to the other two groups of seaweeds. Their pigments and food reserve are the same as those in plants (see Table 6.1, p. 113), so it is thought that land plants evolved from green algae. Chlorophyll in both green algae and plants is not normally masked by any other pigments, and green algae typically have a bright green thallus.

Multicellular green algae are common in some marine environments. They are typically bright green because chlorophyll is not masked by other pigments.

**FIGURE 6.3** The dead man's fingers (*Codium fragile*) form branched clumps on rocky shores. Its chloroplasts remain alive, and still photosynthesize, in sea slugs (shell-less gastropods) that feed on the seaweed.

Filamentous green algae may be common on rocks in shallow water and other seaweeds, as well as in rocky shore tide pools. The filaments of these species may be branched or unbranched. Species of *Enteromorpha* have a thin thallus in the form of a hollow tube. They sometimes flourish in polluted areas. Sea lettuce (*Ulva;* Fig. 6.2) forms paper-thin sheets whose shape varies depending on environmental factors. Different species of *Ulva* are widespread, from polar to tropical waters. *Valonia* forms large spheres or clusters of spheres in the tropics and subtropics.

Several other green algae consist of thin filaments or tubes (siphons) formed by a single giant cell with many nuclei. Such is the case in *Caulerpa*, which is restricted to the tropics and subtropics. Its many species show a great variety of shapes. Dead man's fingers (*Codium;* Fig. 6.3) is a green alga that extends from tropical to temperate waters, including both coasts of North America. It consists of multinucleated filaments woven into a spongy, often branching thallus. The thallus of *Halimeda,* a **calcareous green alga,** consists of numerous segments with deposits of calcium carbonate (see Fig. 14.10). The accumulation of its dead, calcified segments plays an important role in the formation of coral reefs (see "Other Reef Builders," p. 311).

**Brown Algae** The color of the **brown algae** (division, or phylum, **Phaeophyta**), which actually varies from olive green to dark brown, is due to a preponderance of yellow-brown pigments, particularly **fucoxanthin,** over chlorophyll. (See Table 6.1, p. 113). Almost all the approximately 1,500 known species are marine. Brown algae are often the dominant primary producers on temperate and polar rocky coasts and include the largest and most complex seaweeds.

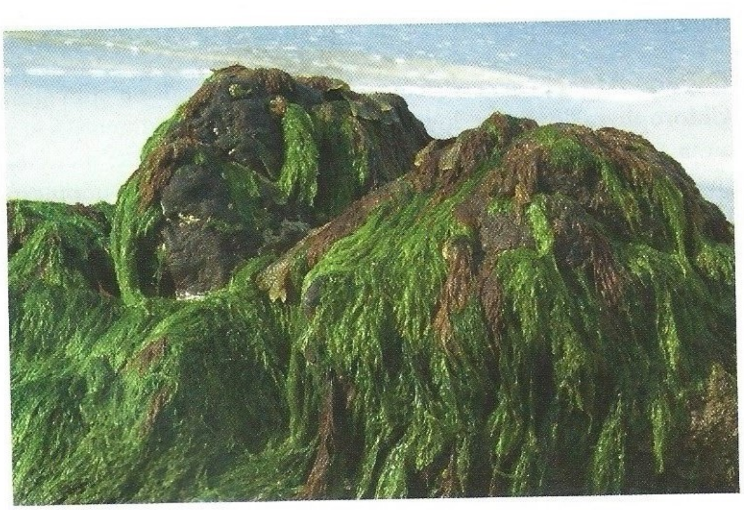


**FIGURE 6.2** *Ulva,* or sea lettuce, is a green alga that is common on rocks where fresh water, often containing high amounts of nutrients, reaches the sea.

The brown algae have yellow-brown pigments in addition to chlorophyll. They include the largest and structurally most complex seaweeds.

The simplest brown algae have a finely filamentous thallus, as in the widely distributed *Ectocarpus.* The thallus is flat and branched in *Dictyota* and fan-shaped and lightly calcified in *Padina* (Fig. 6.4). Both are tropical and subtropical. The thallus of most species of *Desmarestia* is branched in many ways. *Desmarestia* is found in cold waters. It ranges from the Antarctic, where it is one of the dominant species, to temperate shores elsewhere.

Some of the most conspicuous of all brown algae are those exposed at low tides at the middle and upper levels of rocky shores. Their thick, leathery thalli can withstand exposure to air (see "Exposure at Low Tide," p. 245). Many species have gas-filled floats. Known locally as **rockweeds,** or **wracks,** *Fucus* (Fig. 6.5) is found on the Atlantic and Pacific coasts of North America and other temperate shores. The knotted seaweed (*Ascophyllum;* Fig. 6.6) is found along temperate Atlantic coasts. In warm waters, including the Gulfs of Mexico and California, these temperate species are replaced by sargasso weed (*Sargassum*). Sargasso weed has spherical air bladders that keep the small, leaf-like blades afloat at the sea surface. Most species grow on rocks, but at least two float offshore in huge masses. The **Sargasso Sea,** an area in the Atlantic north of the West Indies (see Fig. 8.24), takes its name from sargasso weed. The seaweed drifts in other regions of the world as well. It is particularly common in the Gulf of Mexico.

The **kelps** are the most complex and largest of all brown algae. Most kelps are found below the low tide level in temperate and

**FIGURE 6.4** *Padina,* a brown alga, consists of clusters of flat blades that are rolled into circles. This species is from the Hawaiian Islands.

subpolar latitudes. In these environments they can occur in great abundance, providing food and shelter for many other organisms.

Some kelps consist of a single large blade, up to 3 m (almost 10 ft) in length, as in the many species of *Laminaria* (see Figs. 13.21 and 13.26). Their blades are harvested for food in several parts of the world (see "Seaweeds for Gourmets," p. 109). Several blades may grow from a single holdfast. In some species of *Laminaria* the blade is split or branched. In *Agarum* and *Alaria* (see Fig. 13.21), a conspicuous rib runs along the middle of the single blade. The blade of *Alaria* can be as long as 25 m (82 ft). *Postelsia,* commonly known as the sea palm because of its appearance (Fig. 6.7), grows on intertidal rocks exposed to heavy waves. It occurs in thick clusters from central California to British Columbia. Two branched forms, the feather-boa kelp (*Egregia;* see Fig. 13.26) and the southern sea palm (*Eisenia*), are also common on Pacific rocky shores.

In the Pacific the largest kelps are found in deeper water just below the lowest tide level. The bull kelp, *Nereocystis,* consists of a whip-like stipe up to 30 m (almost 100 ft) long with a large, spherical pneumatocyst at the upper end (see Fig. 13.26). Another large kelp is *Pelagophycus* (see Figs. 13.23 and 13.26). It is similar to the bull kelp, but it has impressive antler-like branches.

*Macrocystis* (see Fig. 6.1), the giant kelp, is the largest of the kelps and the world's largest bottom-dwelling organism. Its massive holdfast is attached to hard bottoms from the intertidal to depths of 25 m (83 ft) or more. Several long stipes grow from the holdfast, from which elongated blades develop (Fig. 6.8*a*). At the base of each blade a gas-filled pneumatocyst eventually develops, which helps keep the blades close to the surface. Individuals as long as 100 m (330 ft) have been recorded. It has been estimated that such kelps can grow as much as 14 cm (5.5 in) per day in optimal conditions. Many individuals, each with many fast-growing and intertwined stipes, form dense and very productive **kelp beds,** or **forests** (Fig. 6.8*b*), in the colder waters of the North and South Pacific (see the map in Fig. 13.22). Kelp beds are harvested by chopping off the tops for the extraction of several natural products (see "Economic Importance," p. 108). Kelp beds are among the richest, most productive environments in the marine realm. They show very high **primary production,** the rate of production of organic matter. The ecological significance and other aspects of the biology of kelp beds will be discussed under "Kelp Communities" (p. 300).

**FIGURE 6.5** The spiral rockweed (*Fucus spiralis*) is common on rocky shores on the Atlantic coasts of temperate North America and Europe. Its thallus lacks the air bladders that characterize a similar species, the bladder rockweed (*Fucus vesiculosus*).

**Red Algae** There are more species of marine **red algae** (division, or phylum, **Rhodophyta**) than of marine green and brown algae combined. Among other features, they have red pigments called **phycobilins,** which mask chlorophyll (see Table 6.1, p. 113). Most species actually are red, though some may have different colors depending on their daily exposure to light. The group is essentially marine; only a few of the approximately 4,000 species live in fresh water or soil. Red algae inhabit most shallow-water marine environments. Some are harvested for food and for the extraction of various products (see "Economic Importance," p. 108).

The red algae are the largest group of seaweeds. Their chlorophyll is typically masked by a red pigment.

**FIGURE 6.6**
The knotted rockweed (*Ascophyllum nodosum*) occurs on the North American and European coasts of the North Atlantic.

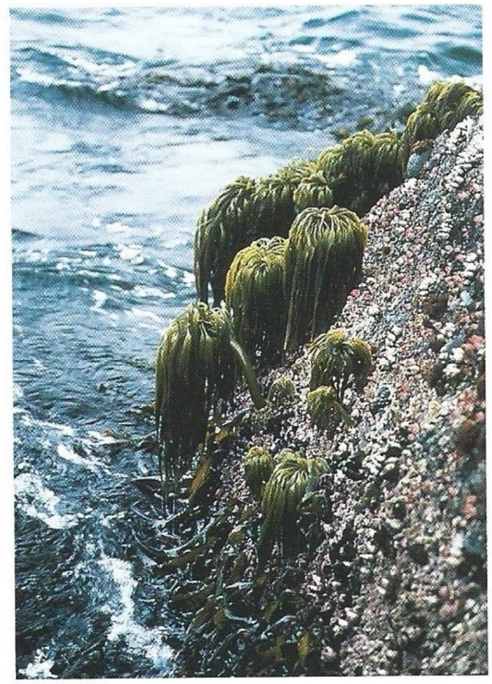


**FIGURE 6.7**
Stands of the sea palm (*Postelsia palmaeformis*) are common on rocky shores exposed to heavy wave action on the Pacific coast of North America (also see Figs. 11.12 and 11.16).

The structure of the thallus of red algae does not show the wide variation in complexity and size seen in brown algae. Some reds have become greatly simplified, at least in their structure, by becoming parasites of other seaweeds. A few have lost all trace of chlorophyll and have become heterotrophs, depending entirely on their host for nutrition. Most red algae are filamentous, but the thickness, width, and arrangement of the filaments vary a great deal. Dense clumps are more common on the upper levels of rocky shores that are exposed at low tide; longer and flatter branches predominate in areas less exposed to air and in deeper water. These variations are observed among the many species of *Gelidium* and *Gracilaria* that are found worldwide. *Endocladia* forms wiry clumps on rocky shores from Alaska to Southern California.

Some species of *Gigartina* have large blades as long as 2 m (6 ft). These are among the most massive of the red algae. Numerous species of *Porphyra* are common on rocky shores above the lowest tide marks from polar to tropical coasts (Fig. 6.9). The most common growth form is a thallus with thin, large blades. *Rhodymenia* is common in the North Atlantic. Its blades may reach 1 m (3 ft) in length. Irish moss (*Chondrus*) is another North Atlantic red alga. It can tolerate wide ranges of temperature, salinity, and light, and its shape varies greatly in response to these physical factors.

The **coralline algae** are red algae that deposit calcium carbonate within their cell walls. They are important in several marine environments. The calcified thallus takes a variety of shapes: thin disks growing over other seaweeds, branches with many joints (*Corallina;* Fig. 6.10), smooth or rough **encrusting** growths on rocks. The color of live coralline algae typically varies from light to intense reddish-pink; dead ones are white. Warm-water coralline algae are actively involved in the formation and development of Coral reefs (see "Other Reef Builders," p. 311). Other species thrive in temperate and polar waters, often attaining a large size.

(a) (b)

**FIGURE 6.8** (*a*) The growing end of a stipe of the giant kelp (*Macrocystis pyrifera*). (*b*) A kelp forest in California (also see Figs. 13.24 and 13.26).

## Life History

Reproduction is a complex affair in seaweeds. **Asexual,** or vegetative, reproduction is common. It may be more important than **sexual** reproduction in most species. Fragments of the thallus can often grow into new individuals, as occurs in the floating masses of *Sargassum* of Sargasso Sea fame. Some seaweeds produce **spores,** which

**FIGURE 6.9** Many species of *Porphyra*, a red alga, inhabit temperate, polar, and tropical rocky shores around the world. Some are of economic importance.

are cells specialized for dispersing to new locations or persisting through unfavorable conditions. Some spores are protected by resistant cell walls; others have flagella for movement and are known as **zoospores.**

The production of **gametes** is a key event in sexual reproduction. Gametes from two different individuals fuse, so that the new generation contains genetic information from both parents. Genetic variation is thus ensured generation after generation. Gametes produced by all members of a seaweed species may be similar in appearance or may consist of larger, non-motile eggs and smaller sperm that can swim by means of flagella. Male gametes in the red algae lack flagella and are non-motile. They may be released in strands of slime. Male and female gametes may be formed in the same thallus, but the chances are good that fusing gametes will be from separate thalli.

Cells of seaweeds (and of us all—clam, fish, or human) divide and produce identical cells by **mitosis.** Seaweeds may also produce haploid spores or gametes by **meiosis.** The existence of diploid and haploid cells is fundamental in understanding the often complex life histories of seaweeds. Their life histories can be divided into four basic types.

The first type (Fig. 6.11*a*) is the most common among all three groups of seaweeds, and it involves two types of thalli. The first is a diploid ($2n$) **sporophyte** generation that through meiosis produces not gametes but haploid ($n$, or $1n$) spores. Except in the red algae, these spores are typically motile. They divide and develop into the second kind of thallus, a haploid ($n$) **gametophyte** generation. The gametophyte is the one that produces haploid gametes. In some species there are separate male (sperm-producing) and female (egg-producing) thalli; in others, both types of gametes are produced by every thallus. The gametes are released and, on fertilization, produce a diploid ($2n$) zygote that develops into the diploid sporophyte. A life history with two generations, a sporophyte and a gametophyte, is an example of the phenomenon of **alternation of generations.** In some algae, such as sea lettuce (*Ulva*) and the brown *Dictyota*, the sporophyte and gametophyte are structurally identical, or **isomorphic.** On the other hand, in kelps (*Laminaria, Macrocystis,* and others) the large plant we see is the sporophyte, whereas the gametophyte is minute and barely visible (see Fig. 13.25), thus being **polymorphic** because there are at least two different-looking generations. A similar type of alternation of generations takes place in flowering plants, when a sporophyte dominates over a minute gametophyte.

The second type of life history, unique to the red algae, is more complex, involving alternation of three generations (Fig. 6.11*b*). It is similar to the life history illustrated in Figure 6.11*a*, but a third generation,

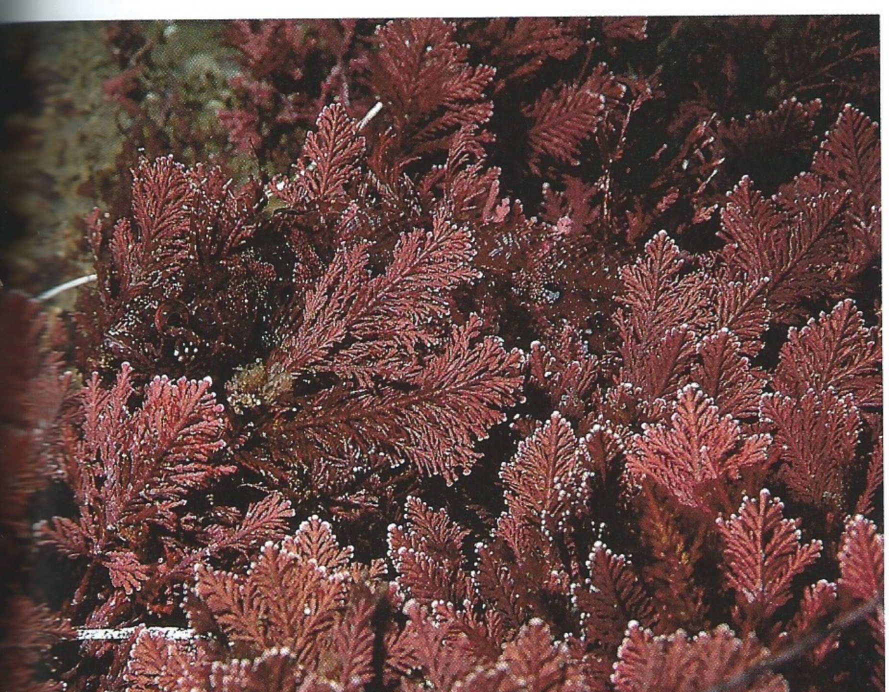


**FIGURE 6.10** *Corallina*, a coralline alga.

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

• Chapter 4, p. 68

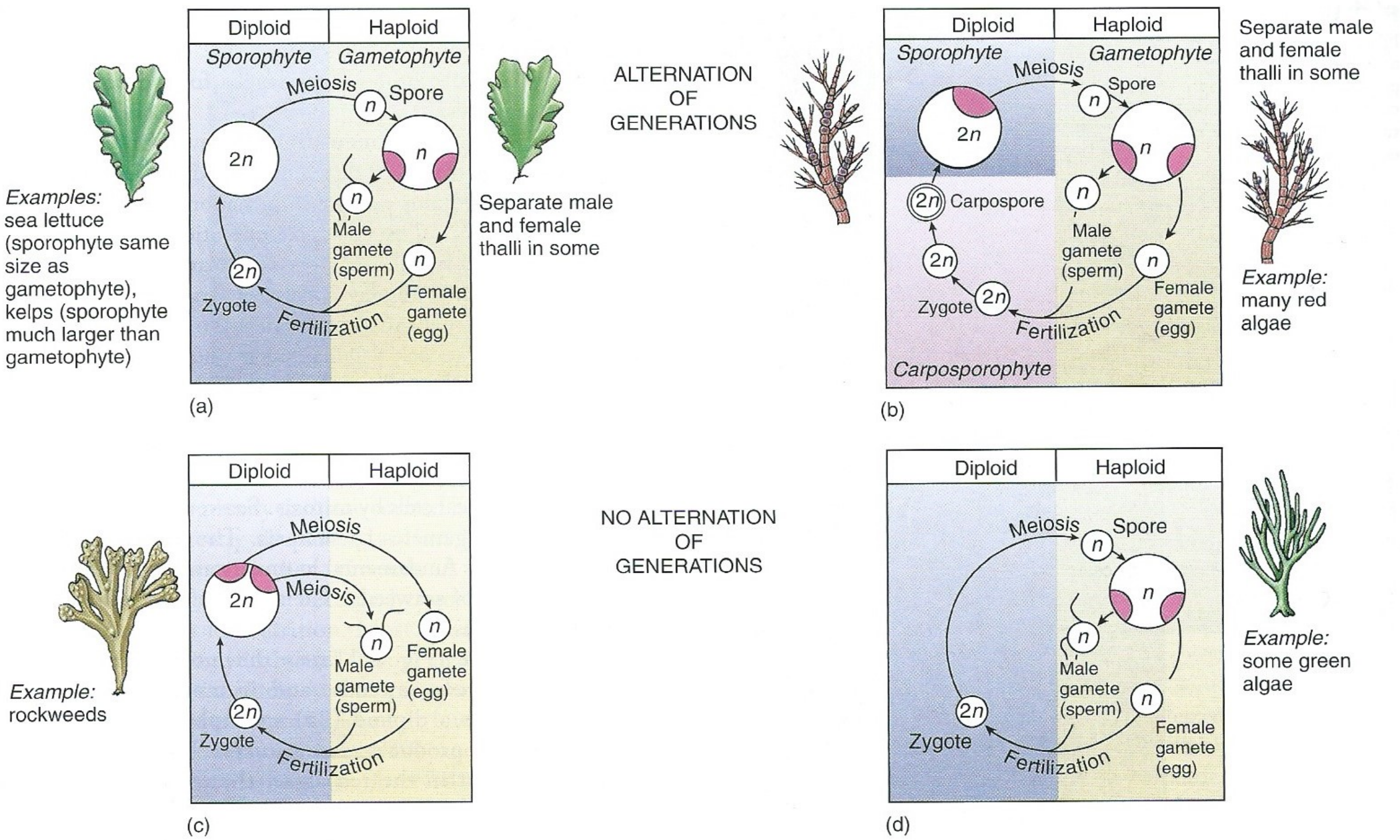



**FIGURE 6.11** Basic patterns of sexual reproduction in the life histories of seaweeds. These patterns are not absolute, and many modifications have been described. In some groups certain reproductive stages have different names.

a diploid **carposporophyte,** results from the fusion of gametes. **Carpospores,** diploid spores produced by the carposporophyte, develop into sporophytes.

The third type of life history (Fig. 6.11*c*) is perhaps the easiest to understand because it is similar to that of animals, including humans. There is no alternation of generations. Thus, there is only one thallus, and it is diploid. The thallus produces haploid gametes by meiosis. After fertilization the resulting zygote develops into a new diploid thallus. This type of life history is observed in some brown algae (*Fucus* and other rockweeds) and in some green algae (*Codium, Halimeda*).

In the fourth type of life history, which occurs in some green algae (Fig. 6.11*d*), the dominant thallus is haploid and produces haploid gametes. On fertilization the gametes form a diploid zygote. It is in the zygote where meiosis takes place, resulting in haploid spores. Each of these spores develops into a haploid individual, the only kind of thallus in the cycle.

Reproduction in seaweeds is by asexual and sexual means. Sexual reproduction may involve an alternation of a haploid (or gametophyte) and a diploid (or sporophyte) generation.

There are many known variations on these basic life history schemes, and probably others waiting to be discovered. Other aspects of the life history of seaweeds are also interesting. For example, the development of gametes or spores can be influenced by the amounts of nutrients in the water, by temperature, or by day length. High levels of nitrogen nutrients in the water cause the development of asexual spores in sea lettuce, but low levels stimulate the development of gametes instead. The release of gametes and spores can be triggered by the splashing of water in an incoming tide (and therefore by the cycles of the moon) or by chemical messengers received from cells of the opposite sex. In some seaweeds the release of male and female gametes is timed to take place at about the same time.

## Economic Importance

People have used seaweeds since time immemorial. Samples from the oldest human settlement in the Western Hemisphere, in southern Chile, show that the first Americans probably used seaweeds as food and medicine. People around the world still harvest seaweeds to be used in many ways. The most obvious use is as a food source. People from different cultures have discovered that many seaweeds are edible, especially some of the red and brown algae. They are consumed in a variety of ways (see "Seaweeds for Gourmets" p. 109). The farming, or **aquaculture,** of seaweed is big business in China, Japan, Korea, and other nations (see Table 17.3, p. 399).

## Seaweeds for Gourmets

Seaweeds, raw, cooked, or dried, are used as food in many cultures. Seaweeds are good sources of some vitamins (particularly $B_{12}$), minerals, fiber, and antioxidants. Seaweeds can add variety and taste to bland foods and may be used to wrap such foods as *sushi*. Mariculture of edible seaweed is a growing business in many parts of the world (see Table 17.3, p. 399). Seaweeds are harvested by hand, rinsed in water, dried on lines, and sold at health food stores or on the Internet. Connoisseurs use seaweed in salads, soups, omelettes, casseroles, and sandwiches. Cookbooks and websites containing seaweed recipes are available to whet the appetites of the most demanding gourmets.

*Ulva* is not called sea lettuce for nothing. It can be eaten fresh in salads. Seaweeds (or *limu*), including *limu 'ele 'ele* (the green *Enteromorpha prolifera*) and *limu manauea* (the red *Gracilaria coronopifolia*), are beloved by the Hawaiians. Purple laver (a species of *Porphyra,* a red alga) prepared in various ways is still eaten in some parts of the British Isles. It is washed and boiled, then formed into flat cakes, rolled in oatmeal, and fried; it is then called laverbread. Purple laver is also eaten as a hot vegetable or fried with bacon. Irish moss (*Chondrus,* a red alga and a source of carrageenan) is dried and used in preparing *blancmange* and other desserts in eastern Canada, New England, and parts of northern Europe. *Rhodymenia,* another red alga, is dried and eaten, mostly by those living along the Atlantic coasts of Canada and northern Europe. Called *dulse,* it is sometimes still used in making bread and several types of desserts. For those on a diet, dulse can also be chewed like tobacco (of course it's nicotine-free).

Pickled bull kelp (*Nereocystis*) tastes like pickled cucumbers, and another type of bull kelp (*Durvillea*) is widely used in salads and other dishes in Chile. Chileans also use dried sea lettuce in soups and stews. Sea palm (*Postelsia*), also known as "sea noodles," is reported to be excellent when sautéed in honey or stir-fried in sesame-seed oil and soy sauce. Coastal North American Indians in the Pacific cooked it in ovens and made it into cakes. Its indiscriminate collection is unfortunately endangering its survival, which is also true for other edible seaweeds.

Harvesting kelp (*Laminaria japonica*) in Japan.

It is in the Orient, however, that preparing seaweed for food has reached the level of an art. Several species are carefully cultivated, supporting multimillion-dollar operations. Seaweed culture is a very old tradition in Japan, and Japanese cuisine uses seaweed extensively. Species of *Laminaria* and *Alaria* are dried and shredded, then prepared in various ways. *Laminaria japonica* is heavily cultivated in Japan and when processed is known as *kombu.* The seaweeds are even used to make tea and candy. *Undaria,* or *wakame,* is another edible kelp that is best when fresh or cooked for a very short time. *Porphyra,* a red alga, is used to make thin sheets of *nori,* widely used in soups and to wrap *sushi* (see Fig. 17.7). Are you ready for feather-boa burgers, French-fried sea palm, and *wakame* shakes?

### Seaweed Cake*

1 1/2 cups salad oil

2 cups sugar

3 eggs

2 cups grated or chopped seaweed: bull kelp (*Nereocystis*), *ogo* (*Gracilaria coronopifolia*), *Eucheuma* (local species from Hawai'i), or local equivalent

2 cups grated carrots

1 cup crushed, drained pineapple (or 1 cup grated coconut, preferably fresh)

2 1/2 cups flour

1 teaspoon baking soda

1 teaspoon salt

1 teaspoon cinnamon

1 cup chopped walnuts (optional)

*Mix well the sugar and salad oil. Add the eggs, one at a time, beating well after each egg is added. Add the seaweed, carrots, and pineapple (or coconut). Sift together the flour, baking soda, salt, and cinnamon and add to mixture; mix well. Add the chopped walnuts if desired. Bake in oblong or bread-loaf pan at 160 °C (350 °F) for 45 to 50 minutes. Cake may be covered with buttercream frosting. Enjoy.*

*Adapted from I. A. Abbot, *Limu, An Ethnobotanical Study of Some Hawaiian Seaweeds,* 4th edition, National Tropical Botanical Garden, Lawa'i, Kauai'i, Hawai'i, 1996.

Seaweeds produce several types of gelatinous chemicals, called **phycocolloids,** that are used in food processing and in the manufacture of different products. These phycocolloids are valuable because of their ability to form viscous suspensions or gels even at low concentrations.

One important phycocolloid, **algin** (which comprises alginic acid and its salts, the alginates), is used extensively as a stabilizer and emulsifier in the manufacture of dairy products such as ice cream, cheese, and toppings, which need to be smooth and not likely to separate. Algin is also used in the baking industry to

# EYE ON SCIENCE

## Marine Algae as Biofuels

Land plants such as corn and soybeans are currently used as sources of **biofuels,** alternatives to oil, the increasingly scarce—and polluting—fossil fuel. Biofuels help offset the effects of global warming because the plants used to produce biofuels take up carbon dioxide ($CO_2$) from the atmosphere (see "Rolling the Dice: Climate Change," p. 231). Biofuels still release $CO_2$ when burned but they return back to the atmosphere at best the same amount of $CO_2$ without any long-term increase in $CO_2$ as in fossil fuels. Biofuels are also cleaner than fossil fuels. Most importantly, biofuels, unlike fossil fuels, are renewable resources that can be naturally replaced.

Marine unicellular algae are for some the most promising sources of biofuels. Fast-growing microalgae are among the most efficient primary producers, typically more efficient than land plants. Instead of transforming solar energy into organic matter that is fermented into ethanol, the biofuel most commonly obtained from land plants, many marine algae transform the glucose produced by photosynthesis (see Fig. 4.6) into lipids, which are stored as energy-rich oils that can be used as biofuels. The algae can be grown in arid or desert areas along the coast, thus avoiding the use of valuable agricultural land in competition with food crops. The use of seawater rather than fresh water, already a scant resource in many parts of the world, is another advantage of marine algae over land plants or freshwater algae. Some microalgae are heterotrophs so they can be grown in the dark and thus are able to grow around the clock. Furthermore, in contrast to land-based biofuels, marine biofuels do not increase food prices, as has happened with corn and soybeans. Nutrients from polluting wastewater can be used as fertilizer, whereas the use of reactive-nitrogen compounds as fertilizers to grow land plants is a major cause of eutrophication in marine environments (see "Overwhelming the Nitrogen Cycle," p. 237). Organic waste obtained after the extraction of lipids can be fermented to obtain ethanol.

$CO_2$, a greenhouse gas that makes up roughly 10% of emissions from fossil-fuel power plants, helps the growth of algae. $CO_2$ can be separated from other gases by the use of chemicals, "captured," and buried on land or under the sea floor, an expensive process. Pumping this $CO_2$ into ponds or tanks used to grow the algae is therefore another advantage of marine biofuels, that of **carbon capture.**

There are nevertheless some drawbacks in the production of marine biofuels. The algae must be grown in quantities large enough to make the process economically feasible. The right algae must be grown under very particular conditions, and they should not be affected by toxic substances accumulating in the water, water pollutants, or even eaten by contaminating grazers. Extractions of lipids must be efficient enough in order not to get other chemical components in the process. Production cost is also high, so far higher than costs for producing gasoline and other fuels.

Solutions to these problems involve the expertise of marine biologists, engineers, and other professionals. Numerous pilot plants around the world are at work aiming to produce marine biofuels in a sustainable way. Sources include oils from marine unicellular green algae (such as some species of *Chlorella* and *Dunaliella*) and marine diatoms (species of *Navicula*). Biofuels from genetically engineered algae are already added to jet the fuel used by several airlines. Fast-growing seaweeds such as kelps and some of the red algae are also being considered as producers of biofuels in the form of ethanol. Floating "seaweed farms" for biofuel production have been envisioned in Japan, Europe, and elsewhere, which together with other marine biofuels will help power the road vehicles and planes of the future.

*For more information, explore the links provided on the* Marine Biology *Online Learning Center.*

prevent frostings and pies from becoming dry. As a thickener and emulsifier it is used in the pharmaceutical and chemical industries and in the manufacture of various products, from shampoo and shaving cream to plastics and pesticides. Algin also has uses in the making of rubber products, paper, paints, and cosmetics. One of its biggest applications is in the textile industry, where algin thickens the printing paste to provide sharper prints. A major source of algin for commercial uses is the giant kelp (*Macrocystis*). The west coast of temperate North America, particularly California, is home to extensive giant kelp forests, making this an important algin-producing area. The forests are leased from the state of California, and large barges equipped with rotating blades cut and collect the stipes and fronds to a depth of 1 to 2 m (up to 6 ft) below the surface (Fig. 6.12). The stipes quickly grow back toward the surface. Another source of algin is *Laminaria,* which is harvested in the North Atlantic.

A second phycocolloid, **carrageenan,** is obtained from red algae such as Irish moss (*Chondrus*) in the North Atlantic and *Eucheuma* in the tropics. Several species of *Eucheuma* are farmed in the Philippines. Carrageenan is especially valued as an emulsifier. It is used to give body to dairy products and an amazing variety of processed foods, including instant puddings.

**FIGURE 6.12** The *Kelstar,* a kelp harvester based in San Diego, California. It (180 ft) long and has a capacity of 600 tons.


**FIGURE 6.13** Some common seagrasses.

Another phycocolloid extracted for its ability to form jellies is **agar.** Agar is used to protect ham, fish, and meats during canning, in low-calorie foods (because it is not digestible by humans), and as a thickener. It is also used in laxatives and other pharmaceuticals and in cosmetics. Biologists use agar as a medium in which to grow bacteria and molds. It is also widely used in research involving the analysis of proteins and DNA. Agar is obtained commercially from several red algae, especially from species of *Gelidium, Gelidiella,* and *Pterocladiella.*

Seaweed can also be used for fertilizer, food additives in animal feeds, and wound dressings in hospitals. Coralline algae are sometimes used in Europe to reduce the acidity of soils, and some red seaweeds are marketed as nutritional supplements. Seaweeds are also being investigated as a source of **biofuels** (see "Marine Algae as Biofuels," p. 110).

# FLOWERING PLANTS

The 250,000 species of **flowering plants,** or **angiosperms** (division **Magnoliophyta**), are the dominant plants on land, but few live in the ocean. Like other land plants (ferns, conifers, and other groups), they have true leaves, stems, and roots, all provided with specialized tissues to transport water, nutrients, and the food manufactured by photosynthesis. As such, they are grouped in the kingdom Plantae. Reproduction involves a dominant sporophyte that features an elaborate reproductive organ, the flower.

Few of these "higher" plants are successful in the oceans. Of all flowering plants, only the seagrasses are truly marine. They often live submerged by seawater, rarely exposed at low tide. Salt-marsh grasses and mangroves inhabit estuaries and shores protected from wave action. They are not completely at home in the ocean, and usually only their roots are covered by water at high tide. There are also many flowering plants adapted to colonize coastal areas exposed to salt-laden winds and occasional sea spray, though they do not tolerate immersion in seawater. Such plants may be found on sand dunes or living along the edges of salt marshes.

## Seagrasses

**Seagrasses** superficially resemble grass but actually are not grasses at all. The closest relatives of certain seagrasses seem to be members of the lily family, so we know that seagrasses evolved from land plants.

Seagrasses have adapted to life in the marine environment. They have horizontal stems called rhizomes that commonly grow beneath the sediment (Fig. 6.13). Roots and erect shoots grow from the stems (see Fig. 4.19*b*). Seagrass flowers are typically very small and inconspicuous (see Figs. 6.13*b* and 4.21*d*) because there is no need to attract insects for pollination. The **pollen,** which contains the sperm, is carried instead by water currents. It is often released in strands. In some seagrasses the pollen grains are long and thread-like instead of tiny and round, as in land plants. Tiny seeds, which in some species develop inside small fruits within the flower, result from successful fertilization. These seeds are dispersed by water currents and perhaps in the feces of the fish and other animals that browse on the plants.

**Types of cell division:**
**Mitosis** Cell division wherein the resulting cells are identical to the original cell, having their chromosomes in pairs (diploid cells, or $2n$), as in the case of our body cells.
**Meiosis** Cell division wherein the resulting cells are haploid ($n$, or $1n$), as in the case of gametes (spores in seaweeds), because they contain only half the number of the parent's chromosomes.
• Chapter 4, p. 77

Eelgrass (*Zostera*) is the most widely distributed of the nearly 60 species of seagrasses known. It is found in many temperate and tropical regions of the world, where it inhabits shallow, well-protected coastal waters such as bays and estuaries (see Fig. 13.15). It has distinctively flat, ribbon-like leaves (see Figs. 6.13*b* and 13.17). It is common in oxygen-poor sediments. Thick *Zostera* beds are highly productive and provide shelter and food to a variety of animals, some of considerable economic importance. Several species of *Posidonia*, which are found in the Mediterranean and along the southern coast of Australia, also play an important role in shallow coastal waters. The Mediterranean beds of *Posidonia*, sometimes known as Neptune grass, are threatened by pollution and fishing trawls.

Surf grass (*Phyllospadix;* see Fig. 6.13*e*) is an unusual seagrass because it is an inhabitant of rocky coasts exposed to wave action, as its common name implies. Some species may become exposed at low tides. It is found on the Pacific coast of North America.

More information on the biology and ecological significance of seagrasses is given in "Seagrass Beds," p. 294.

## Salt-Marsh Plants

**Cordgrasses** (*Spartina;* see Fig. 12.7) are true members of the grass family. At least 14 species are known. They are not really marine species but, rather, land plants tolerant of salt. Unlike seagrasses, which are true marine species, cordgrasses do not tolerate total submergence by seawater. They live in salt marshes and other soft-bottom coastal areas throughout temperate regions worldwide (see Fig. 12.17). Cordgrass salt marshes show a high primary production and provide habitat and breeding grounds for many species important to fisheries. They also offer protection against erosion, the result of the network of horizontal stems that extends under the sediment, and provide natural water purification systems (see Fig. 18.6). Flowers, and to a much lesser extent leaves, provide food to insects and other grazers. Most organic matter is made available to other organisms in the form of **detritus** (see Fig. 12.23).

Cordgrasses inhabit the zone above mudflats that becomes submerged by seawater only at high tide, so their leaves are always partly exposed to air. Salt glands in the leaves excrete excess salt. Other salt-tolerant plants, or **halophytes,** such as pickleweed (*Salicornia;* see Fig. 12.8), salt grasses (*Distichlis*), and rushes (*Juncus*) may be found at higher levels on the marsh. Salt-marsh plants and their adaptations to the estuarine environment along the mouths of rivers are discussed in "Salt Marshes" (p. 277).

## Mangroves

**Mangroves** are trees and shrubs adapted to live along tropical and subtropical shores around the world (see Fig. 12.17). They are essentially land plants that can tolerate salt to varying degrees. Luxuriant and very productive mangrove forests, or **mangals,** flourish along muddy or sandy shores protected from wave action (Fig. 6.14).

Mangroves include around 70 mostly unrelated species of flowering plants. They are adapted in various ways to survive in a salty environment where water loss from leaves is high and sediments are soft and poor in oxygen. Adaptations become more crucial in mangroves living right on the shore, such as species of the red mangrove (*Rhizophora;* Figs. 6.14 and 6.15), which are found throughout the tropics and subtropics. The extreme northern and southern limits of the red mangrove are those areas in which killing frosts begin (see Fig. 12.17). Salt marshes replace red mangrove forests in areas exposed to frosts. Other important species of mangroves include the black (*Avicennia*) and white (*Laguncularia*) mangroves. Most species of these and other mangroves are found along the shores of the tropical Indian and Pacific oceans.

The leaves of the red mangrove are thick, an adaptation to reduce water loss. As in several other mangroves, seeds germinate while still attached to the parent tree (Fig. 6.15*a*). They develop into elongated, pencil-shaped seedlings as long as 30 cm (1 ft) before falling from the parent. Successful seedlings stick in the soft, muddy sediment like a knife thrown into a lawn, or float in the water to be carried by currents to new locations (Fig. 6.15*b*).

**FIGURE 6.14** The red mangrove (*Rhizophora mangle*) forms lush forests along shores in Florida, the Caribbean, the Gulf of California, and other tropical regions of the Western Hemisphere and West Africa. Notice the long roots extending into the mud, exposed here at low tide. Other species of mangroves can be found farther inland (see Fig. 12.18).


**FIGURE 6.15** A seedling of the red mangrove (*Rhizophora mangle*) (*a*) as it appears in the tree and (*b*) one that has taken root in the soft sediment.

Many species of marine and terrestrial organisms live among the roots or branches of mangroves. Like seagrasses and salt-marsh plants, mangroves show high primary production, but relatively few animals graze on the leaves, with most organic matter being consumed as detritus (see Fig. 12.23). The most important species of mangroves, their distribution, the ecological significance of mangrove forests, and human impact are discussed in "Mangrove Forests" (p. 279).

Flowering plants, dominant on land, have few marine representatives. Seagrasses, which are true marine species, and salt-tolerant plants like salt-marsh plants and mangroves are exceptions. They have successfully adapted to soft-bottom coastal regions, developing as highly productive meadows and, in the case of mangroves, forests along the shore.

**Detritus** Particles of dead organic matter.
• Chapter 10, p. 223

## Table 6.1 Most Important Characteristics of Seaweeds and Marine Plants

| Group | Distinguishing Features | Photosynthetic Pigments | Major Food Reserves | Major Cell-Wall Components | Significance in the Marine Environment |
|---|---|---|---|---|---|
| Green algae  | Eukaryotic, unicellular and multicellular; mostly bottom-dwelling | Chlorophyll *a*, *b*, carotenoids | Starch | Cellulose, calcium carbonate in calcareous algae | Primary producers; calcareous algae are important sources of calcareous deposits in coral reefs |
| Brown algae  | Eukaryotic, multicellular; bottom-dwelling | Chlorophyll *a*, *c*, carotenoids (flucoxanthin and others) | Laminarin, oil | Cellulose, alginates | Primary producers; dominant components of kelp forests |
| Red algae  | Eukaryotic, multicellular; bottom-dwelling | Chlorophyll *a*, phycobilins (phycocyanin, phycoerythrin), carotenoids | Starch | Agar, carageenan, cellulose, calcium carbonate in coralline algae | Primary producers; coralline algae are important sources of calcareous deposits in coral reefs |
| Flowering plants (seagrasses, salt-marsh plants, mangroves)  | Eukaryotic, multicellular; bottom-dwelling | Chlorophyll *a*, *b*, carotenoids | Starch | Cellulose | Dominant primary producers in seagrass beds, salt marshes, and mangrove forests; nursery grounds for many species; help stabilize soft bottoms, protect coast from turbulence |