Ecological and Evolutionary Principles of Marine Biology

Ecological Interactions

■ **Ecology is the study of interactions between organisms and their environment and the effects of these interactions on the distribution and abundance of organisms.**

Ecology is the study of interactions between organisms and their environment and how these interactions determine their distribution and abundance. **Biological interactions** occur between organisms, whereas **abiotic interactions** are effects of non-biological factors, such as seawater chemistry, on the functioning of organisms. In practice, the two kinds of interaction cannot be easily separated. For example, low temperature might prevent a cold-blooded creature from moving very rapidly (an abiotic interaction), and this limitation might in turn reduce its chances of escaping a predator (a biotic interaction).

■ **Resources are materials whose availability or abundance may limit population growth.**

A resource is any material whose availability or abundance in the natural environment can limit survival, growth, or reproduction. Food, space, and dissolved inorganic nutrients are all potentially limiting resources. Resources that can be depleted and are no longer available are **nonrenewable**. Resources that will continue to become available are **renewable**. The issue of renewability can be resolved by scaling against the life span of the organism that is exploiting the resource. Over the lifetime of some sessile organism, the space to which it attaches is a nonrenewable resource, but it will of course be renewed once the individual dies. Microorganisms such as bacteria as a food resource are renewable because they can often recover in population size even when grazed by larger and much longer-lived organisms such as sponges.

The Ecological Hierarchy

■ **Ecology is studied at many interacting hierarchical levels, including individual, population, species, community, and ecosystem.**

Ecological processes should be studied at many levels of a hierarchy, or a nested series of sets.

The Levels Defined

INDIVIDUAL LEVEL An individual is an organism that is physiologically independent from other individuals. Examples include a single snail and an interconnected colony of coral polyps.

POPULATION LEVEL A **population** is a group of individuals *of the same species* that respond to the same environmental factors and freely mix with one another—for example, in mating.

SPECIES LEVEL A **species** is a single population, or a group of populations, that is genetically isolated from other species; that is, it does not interbreed and reproduce with other species. An example of an appropriate question at this level of the hierarchy is: Will a change in sea temperature cause a species to become extinct? Although we do not include species per se in the ecological hierarchy, they are crucial in understanding the long-term evolutionary directions of ecosystems.

COMMUNITY LEVEL A **community** is a group of potentially interacting populations, each belonging to different species and all living in the same place—for example, all the barnacles, snails, seaweeds, starfish, and other species on a rocky shore that live together and interact, for instance, as predators and prey.

ECOSYSTEM LEVEL An **ecosystem** is an entire habitat, including all the abiotic features of the landscape or seascape and all the living species within it that interact—for example, an estuary and its inhabitants. The definition of the boundaries of an ecosystem can be somewhat arbitrary. For example, we can define a coral reef ecosystem, but we sometimes might want to define a coral-reef—open-ocean ecosystem if we want to understand the processes affecting the many species that broadcast larvae into the open sea. A salt-marsh ecosystem might be protected from wave damage by a nearby oyster reef system.

BIOSPHERE LEVEL The **biosphere** is the entire set of living things on the earth and the environment with which they interact. Interactions at the biosphere level may be crucial to human welfare—for example, the carbon budget and climate change.

INTERACTIONS AMONG THE LEVELS The various levels of the hierarchy cannot always be studied separately; hierarchical levels do interact. For example, changes in climate at the biosphere level may affect an individual snail's ability to escape a predator. Here, an upper level of the hierarchy has direct effects on a lower level. As another example, the efficiency of photosynthesis of individual phytoplankton may sum up to a major change in the nutrient cycling of a marine ecosystem. Such an effect involves the impact of changes at a lower level of the hierarchy on upper hierarchical levels.

Interactions on the Scale of Individuals

At the scale of individuals, both abiotic and biotic interactions are quite important. We can define **ecological niche** as the range of environments over which a species is found. The range of environments has both biological and physicochemical dimensions, such as interacting species, water depth range, and salinity range.

■ **Many ecological interactions occur between individuals and may be classified on a plus-minus-zero system depending on whether an individual benefits, suffers because of, or is not particularly affected by the interaction.**

A plus-minus-zero system may be used to characterize ecological interactions. Plus (+) interactions benefit a species. Minus (–) interactions harm it. Zero (0) interactions do not affect it in important ways. Table 4.1 summarizes the basic interactions and the plus-minus-zero classification for the organisms involved in each. Note that an interaction is generally classified using two symbols (e.g., + and –) to represent the effect on both kinds of organism involved in it.

Territoriality

■ **Territoriality is the maintenance of a home range that is defended.**

Territoriality is the maintenance of a home range and its defense against intruders. An individual may maintain a territory to protect (a) a feeding area, (b) a breeding area, or (c) a specific nest site. In most cases, territoriality is intraspecific. An example is the maintenance of nesting territories by many species of seabirds.

Predation

■ **Mobile and stationary predators search for prey using chemical, mechanical, and visual stimuli; some lure prey by using various "deceptions."**

Predators may be either stationary or mobile. **Stationary predators** include sea anemones (**Figure 4.1**) and other cnidarians; **mobile predators** include fishes, starfish (**Figure 4.2**), gastropods, birds, and crabs. Most swimming and crawling predators can move large distances to locate prey. Although fish are obvious, crabs and even starfish may move on the order of kilometers to locate new patches of prey. Within the sediment, mobile predators, such as polychaete annelids, sipunculids, and burrowing gastropods, move over smaller spatial scales. Despite the diversity, there are some organizing principles relating to prey handling and capture and to interactions between predators and prey.

TABLE 4.1 Types of Individual Interaction

TYPE	NATURE OF INTERACTION	PLUS-MINUS-ZERO CLASSIFICATION
Territoriality	Beneficial to one and detrimental to another or detrimental to both	+ – or – –
Competition	Beneficial to one and detrimental to another or detrimental to both	+ – or – –
Predation	Beneficial to one and detrimental to another	+ –
Commensalism	Beneficial to one but no effect on the other	+ 0
Mutualism	Beneficial to both individuals	+ +
Parasitism	Beneficial to one and detrimental to another	+ –

FIG. 4.1 A stationary predator, the anemone *Anthopleura xanthogrammica*, consuming a mussel. (Photograph by Jeffrey Levinton)
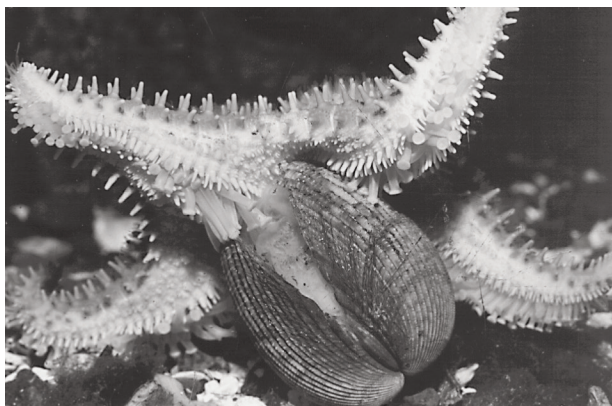

FIG. 4.2 A mobile predator, the starfish *Pisaster ochraceus*, consuming a cockle. Note the extended tube feet that are attached to the bivalve shell of the prey via suction (see Chapter 14). (Photograph by Paulette Brunner, with permission from Friday Harbor Laboratories)

■ **Mobile predators may adjust their hunting behavior to optimize the rate of ingestion of prey.**

Successful predators will consume more prey, which in turn will increase growth and reproductive output. Therefore, one might expect natural selection to optimize the organism's efficiency either in maximizing the amount of energy gained per unit time or in minimizing the time spent feeding so that there is more time to carry out other vital functions such as reproduction. **Optimal foraging theory** establishes the decision rules used by predators to optimize their food intake.

Many predators are able to consume a variety of prey items. Many drilling snails, for example, can consume a variety of barnacle and mussel species. Sea otters dive and retrieve urchins, abalones, and other large benthic invertebrates. Some species are of greater nutritional value than others, and the question is whether to specialize on the nutritionally valuable items or resort to feeding on the poorer items. When a predator encounters a prey item that is not very rewarding, should the predator feed on the item or pass it up to find something better? The **diet-breadth model** predicts that when overall food density is high, it pays to

specialize on the good items and to ignore the choices of lower food quality. As overall food density decreases, it pays to become less choosy and broaden the range of prey. This conclusion can be altered if there is some cost in learning to switch from one prey item to another. For example, a snail might develop olfactory imprinting on a given prey type. It might cost more to change this imprinting than to continue to hunt for the original prey item. Satiation, or the limits of digestive activities, may also be important. A predatory animal might pass up a prey item if the predator's gut is full and it can digest no more for the moment.

The time spent in a food patch is also an important area of decision that affects the predator's total intake of prey. The **time-in-patch model** predicts that *the time spent in a patch of prey should increase with an increase of travel time between patches*. This makes intuitive sense because an increase of travel time reduces the overall opportunity to gain food. It is not worth finding a new patch unless the food in it justifies the travel time. This adjustment has been found in blue whales, which feed on large zooplankton and small fish by trapping them on huge baleen plates (see Chapter 9). A study using sophisticated tracking methods showed that the whales fed for longer periods when they dived to great depths to patches of prey and required longer transit times to these depths and recovery at the surface. Foraging time periods were much shorter when the whales dived to relatively shallow depths (Doniol-Valcrose et al., 2011).

The choice of a best-sized prey is a good example of the optimal foraging approach. Prey organisms that are too large might take an inordinate amount of time to consume. Imagine a starfish spending 2 days to open and consume a large mussel. That time might be more profitably spent on somewhat smaller mussels, whose relative ease of opening would compensate for the reduced reward per mussel. It might also be relatively unprofitable to select very small mussels because too much time would be invested in handling and opening prey with little reward. **Figure 4.3**, which illustrates this argument graphically, shows the results of a study of crabs feeding on mussels. A large mussel provides a big meal for the crab, but the length of time required to crack such a mussel open makes it more profitable to select smaller mussels. Mussels that are too small are not worth the handling time. As a result, the crab selects intermediate-sized mussels.

Predator Avoidance

■ **Resistance to predators increases individual fitness and is therefore enhanced by natural selection.**

Many marine species have evolved a large variety of traits to deter predators. For example, the large majority of tropical sponges are highly poisonous. This might be expected of a sessile group with no ability to move to hide from predators.

Like other adaptations, antipredator defenses originate as variations in natural populations of prey. The presence of any deterrent behavior, morphology, or poison would enhance survival, and the survivors that possess such traits would contribute their genes to later generations.
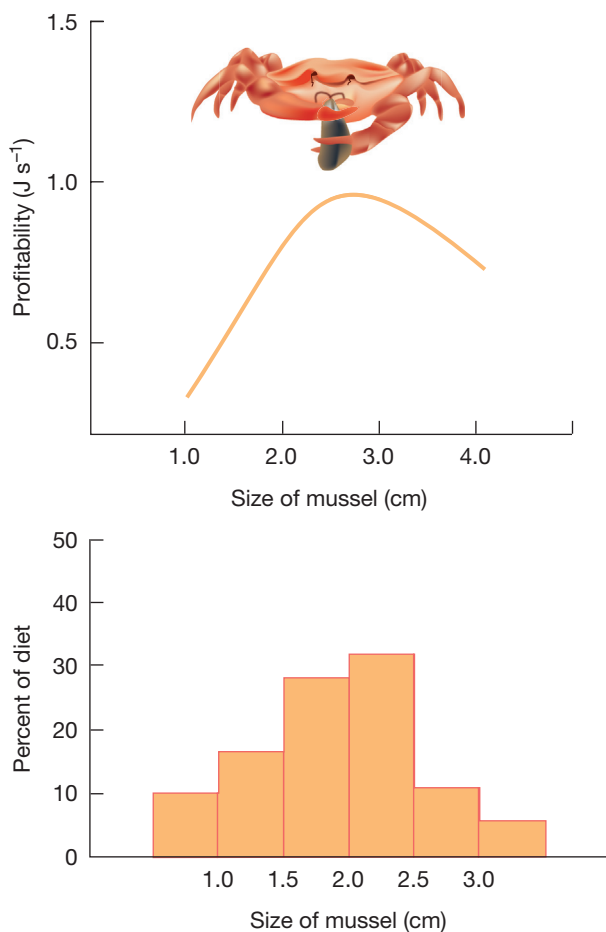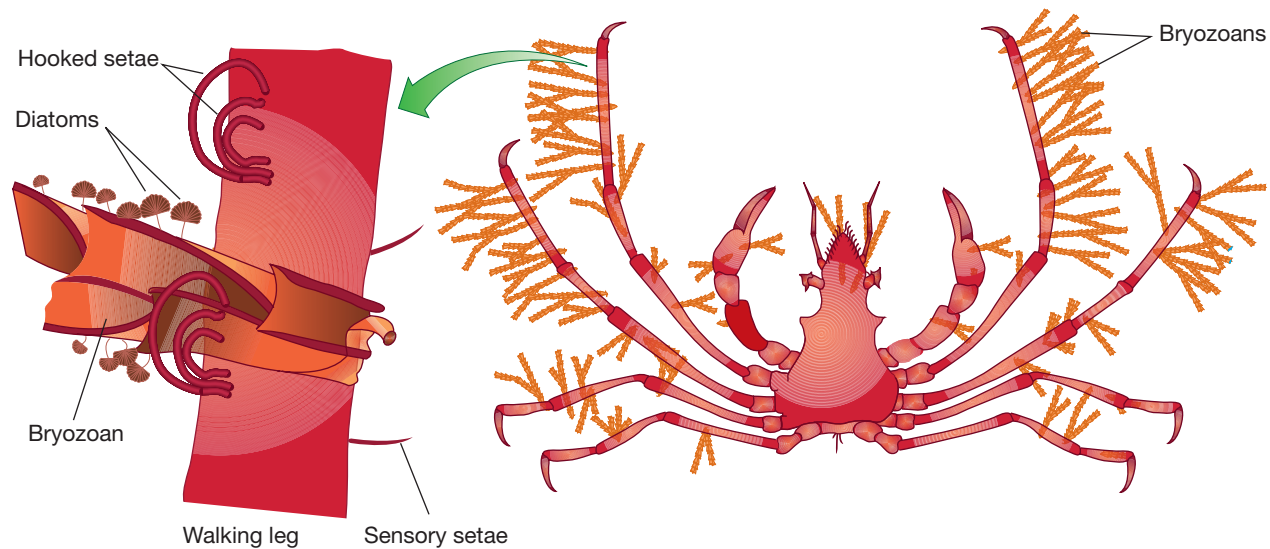
FIG. 4.5   Spider crabs have hooked setae on the sides and rostrum (anterior pointed section) and on the sides of the carapace. The California crab *Podochela hemphilli* may carry fragments of bryozoan colonies, which are ensnared in the hooked setae and camouflage the crabs from the view of predators. (After Wicksten, 1982)

change its shape and color pattern to mimic more than 15 species of nearby dangerous predators, including venomous sea snakes, jellyfish, and stingrays (Norman et al., 2001). To mimic a venomous sea snake, it buries in the sediment all of its body but two arms and uses photophores to adopt the color pattern and movement of a venomous sea snake by undulating above the bottom. Alternatively, **Müllerian mimics** may themselves be harmful and resemble other species that are also harmful. This type of mimicry is not well known in marine organisms.

■ **Many marine organisms can produce various morphologic features to discourage predator attacks (e.g., spines, strengthened skeletons, and other devices).**

Mechanical defense is one of the most common adaptations in defending against predators. In some cases, simple toughening of the body wall or stiffening by means of internal structures proves very effective. In many tropical seaweeds (e.g., *Halimeda* and *Pennicillus*), the thallus is strengthened with calcium carbonate. Many gastropods have a thickened shell that deters predatory fishes. A large number of fish species have spines, some of which are poisonous. For example, members of the family Scorpaenidae, including scorpion fishes and stonefishes, are armed with poisonous spines. In the case of the Pacific coral reef stonefish, the poison is quite virulent and can kill an adult human. The Caribbean urchin *Diadema antillarum* has long sharp spines with reversed barbs. These spines deter many predators, but some fishes bite at the urchin and apparently survive piercing by its spines.

An alternative strategy to fixed defense structures is to produce the defensive structure only when predators are present. Such **inducible defenses** provide an advantage to the prey, which might otherwise waste resources for growth or reproduction when predators are absent. Inducible defenses are especially useful for sessile species, which can deploy them in the direction of predator attack. For

example, the sessile bryozoan *Membranipora membranacea*, which lives as a sheet of individuals on hard surfaces, is often attacked by a specialized sea slug, *Doridella steinbergae*. An attack induces the production of a peripheral zone of colony members whose skeletons are armed with spines (**Figure 4.6**). The spines reduce predation by about 40 percent, but the whole colony grows more slowly than colonies not exposed to predators.

The trade-off for using an induced defense is illustrated well in the acorn barnacle *Chthamalus anisopoma*, which lives in the Gulf of California. This barnacle occurs in two forms: conical and bent (**Figure 4.7**). The conical form is typical of most acorn barnacles. In the case of the bent form, the barnacle grows with the rim of the aperture oriented perpendicular (rather than parallel) to its base. This protective growth form is induced by the presence of the carnivorous snail *Acanthina angelica*, which is spatially variable in abundance. One might ask why the barnacle does not always produce the bent form. Apparently, the bent form feeds less efficiently, with a reduction of somatic growth and fecundity. Thus, there is an advantage to being conical if predation is low. This situation stabilizes the coexistence of the two-form strategy.

An interesting change has occurred fairly recently in some Maine populations of the rocky-shore periwinkle *Littorina obtusata*. In locales where the snail has been exposed to the predatory crab *Carcinus maenas*, shells are lower spired and thicker, but shells are thinner where the crabs are rare or absent. Thus, the snails do not have to pay the price of making thicker shells when predators are absent (Trussell, 1996).

■ **Many marine organisms are defended chemically by toxic organic compounds, acid secretions, and toxic metals.**

Production of toxic compounds includes the secretion of acid by seaweeds and tunicates and the manufacture of toxic
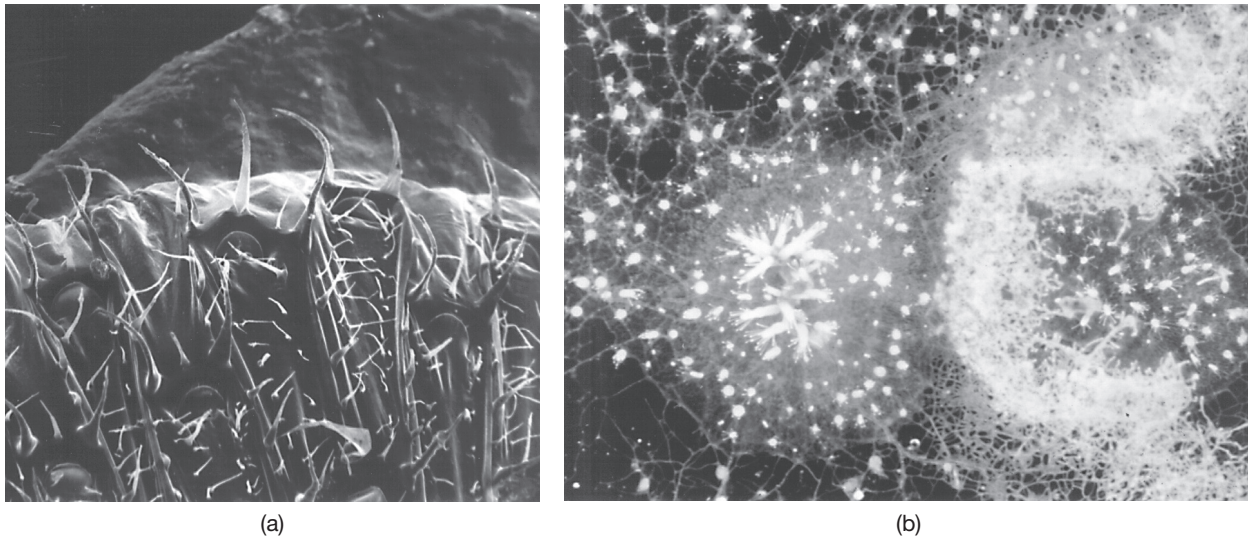
(a)   (b)

FIG. 4.6 Inducible defenses. (a) Spines induced by the predatory sea slug *Doridella steinbergae* on a colony of the bryozoan *Membranipora membranacea*. Scale is 1 mm. (Courtesy of Drew Harvell) (b) Stolons armed with nematocysts (light band) induced when unrelated colonies of the hydroid Hydractinia come into contact. (Photograph by Richard Grosberg)

FIG. 4.7 The (right) conical and (left) bent forms of the acorn barnacle *Chthamalus anisopoma*. The animal develops the bent form if predatory snails are present. (Courtesy of Curtis Lively)

organic compounds by many species of marine higher plants, seaweeds, and animals. The organism usually synthesizes these substances, although some animals can eat toxic plants and store the toxic substance. For example, the sea hare *Aplysia* can graze on the alga *Laurencia* and sequester this organism's highly toxic halogen-bearing terpenes. The sea hare is thus also toxic. See the discussion in Chapter 21 of how marine toxic substances may be useful in medical applications.

If a conspicuous color can be associated behaviorally with an unpleasant dining experience, a predator might avoid the prey on other encounters. Many of the most poisonous marine organisms are conspicuous rather than cryptic. Many free-living flatworms are highly toxic but brightly colored. One often sees bite marks on individuals, which suggests that the learning process that connects color and distastefulness is continuously reinforced. The poisonous black tunicate *Phallusia nigra* is conspicuous against its usual background: white coral reef or sand. Its

tunic can contain as much as 1 percent vanadium, a highly toxic metal, and the tunicate can also produce vacuoles of sulfuric acid.

Natural selection would increase genetic variants that have conspicuous coloration, but only if predation attempts largely failed and allowed the prey to escape. Otherwise, the conspicuous prey could not live to reproduce and spread the conspicuous color trait in the population. Such an association between a bad stimulus and conspicuous color is known as **aposematic coloration**.

The work of Joseph Pawlik (2011) demonstrated that many species of coral reef sponges have a wide variety of toxic compounds that can be detected by predatory fish with very generalized physiological sensors. Many of these compounds are not only toxic to predators but also poison fouling organisms that might smother the sponges. On the other hand, about 30 percent of the Caribbean sponges are not well defended at all. These species have adopted instead a strategy of rapid growth to allow survival against predation by fish, which rarely destroys the whole sponge.

■ **Mechanical and chemical defenses against predation change in frequency with latitude, habitat, and oceanic basin.**

Frequencies of species with toxic defenses trend with geography. The proportion of sponges and sea cucumbers that are toxic increases toward the tropics and can reach 100 percent on tropical coral reefs. Mechanical adaptations of snails to resist crushing by crabs also increase toward the tropics. These trends reflect greater predation pressure in the tropics, which enhances natural selection for increased defense. Although predation is also often intense at some high latitudes, the high diversity of predators in low latitudes may impose the greater selective force.

■ **Microhabitat can strongly affect a creature's vulnerability to predators.**

Marine animals may be able to avoid predators by simply retreating to inaccessible habitats. In some cases, the organism lives in a **spatial refuge** that is inaccessible to predators. Marine animals may also alternate between a microhabitat that provides a refuge from predators and one used for feeding or reproduction. Rocky intertidal shores have strong gradients of desiccation and temperature. This is a special problem for mobile predators such as asteroid sea stars and drilling gastropods, which require long periods of time to subdue and consume their prey. As a result, predation intensity is far less intense in the highest part of the shore, and prey such as mussels can escape predation in this zone. Mark Hay (1991) has noted that many small herbivorous invertebrates, such as amphipods, feed on seaweeds that are otherwise toxic to larger herbivores such as mobile fishes. They also nestle in the seaweed. The smaller herbivores may have evolved a preference for toxic algae, which escape removal by larger herbivores and thus provide a refuge and food source for the smaller animal species.

Commensalism

■ **Commensal relationships benefit one species only. The benefit usually relates to food, substratum, or burrow space.**

Commensal species acquire a benefit from another species but return no benefit or harm. Commensal relationships may be facultative or obligatory. A **facultative commensal** species does not completely depend on a certain single species but may live on one of a variety of species. Barnacles, for example, may settle and live on a variety of species of mussel or on other barnacles, seaweeds, or even rock. On the other hand, **obligatory commensals** can live only with certain other species. The western North Atlantic parchment worm *Chaetopterus* often contains a commensal crab *Pinnixa chaetopterans*, which settles and invades the worm tube as a larva. The crab eventually grows too large to leave the tube and eats material swept in by currents generated by the worm's parapodia. Burrows of the eastern Pacific echiurid worm *Urechis caupo* often contain a gobiid fish, a polynoid polychaete, and a pinnotherid crab (**Figure 4.8**). The polychaete feeds on some of the mucus bag constructed by the proboscis of the host *Urechis*, which the latter uses to capture organic particles for food. The fish and polychaete probably derive protection from predators and also probably feed on detritus and prey in the burrow.

Mutualism

■ **Mutualism is an evolved association among two or more species that benefits all participants.**

Mutualisms involve pairs of species that exchange crucial resources. Such relationships probably began as facultative interactions, but genetic variation allowed the evolution of interdependence, which might increase reproductive
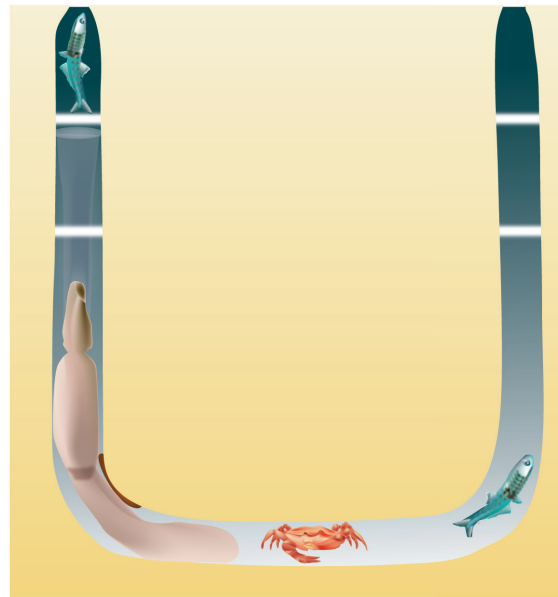
FIG. 4.8 Part of the burrow of the echiurid worm *Urechis caupo* showing the following commensals: the goby *Clevelandia* and the pinnotherid crab *Scleroplax*. (After Fisher and MacGinitie, 1928)

output of both partners in the mutualism. The obvious disadvantage of an obligatory relationship is the danger that one of the species will become locally extinct.

■ **Mutualism often reduces the risk of predation or disease or provides food for one member of the species pair.**

Many mutualisms are a trade-off between protection against predation on the part of one species and some other benefit on the part of the other participant. An association between species of the coelenterate genus *Hydractinia* and species of the hermit crab *Pagurus* is a good example. The coelenterate lives as a colony on hermit crab shells, and the relationship is species specific. The hermit crab is protected against predators and fouling by the *Hydractinia*. The hermit crab occupies a relatively fresh shell that serves as a substratum for the coelenterate. A number of crab species carry anemones on their claws, and some species have clearly defined rows of teeth on the claws, upon which the anemone holds on. The Chilean actiniarian anemone *Actiniloba reticulata* will move actively toward the legs of the crab *Hepatus chilensis*; on reaching its destination, it creeps along the crab's body and eventually comes to rest on the claws. In other cases, the crab collects the anemones. When disturbed, these anemone crabs wave their claws and threaten intruders with the stinging tentacles of the attached anemone.

One of the most remarkable mutualisms in coral reefs occurs between cleaner shrimp or cleaner fishes and a large number of fish species. Cleaner shrimp and fishes feed by picking ectoparasites off fishes, which approach them regularly (**Figure 4.9**). The Pacific cleaning fish *Labroides dimidiatus* maintains cleaning stations that are visited by about 50 species of fishes each day. "Customers" are attracted to the undulating movements of the

FIG. 4.9 Goatfish, *Mulloidichthys flavolineatus* at Kona, Hawaii, is being cleaned by two cleaner Wrasses, *Labroides phthirophagus*. (Brocken Inaglory)

cleaning fish. Interactions with cleaner fish result in reduced predatory attacks, and cleaner fish that compete tend to do a better job than when cleaner fish are less dense. The fish *Aspidonotus taeniatus* mimics the cleaner fish undulation, but instead of picking parasites, it attacks the approaching fish and takes a bite out of its fins. This "cheating" is likely a part of the cost and benefit that goes behind the development of the cleaner fish mutualism and whether a cleaner fish should pick parasites only or bite its client!

Parasitism

■ **Parasitism occurs when members of one species live at the expense of individuals of another species, without consuming the hosts totally as food and thereby killing them.**

Parasites live at the expense of other species and may get nutrients or shelter by damaging their hosts. **Ectoparasites** live attached to or embedded within gills, body walls, and other surfaces. **Endoparasites** live within the body and may occupy circulatory vessels or ramify within certain organs or tissues. If parasites are ineffective in utilizing their host, other parasites may enter and displace them by competition. If they are too effective, they may kill their host or even drive the host population to extinction. Because of this, parasitic species probably evolve through cycles of varying virulence. It is often difficult to draw an exact distinction between commensals and ectoparasites. Barnacles on fishes are probably harmless when sparse in density. In great numbers, however, they create sufficient projections to increase drag and thus impede the host's swimming.

Endoparasites have **highly modified morphologies** that adapted them to life within body cavities and to food uptake and absorption of fluids. Organs needed for free life, such as sensory structures and locomotory appendages, are usually lost. The life stage of the parasite that resides in the host can seem barely related to its actual relatives, which may be

typical free-living forms. In contrast to the overall degeneration, the reproductive organs of such parasites are usually hypertrophied and acquire a central importance.

■ **Parasites of invertebrates often affect the reproduction of the host.**

Some parasites seem to affect the reproductive organs of their hosts more than they affect any other organ. As a result, the hosts often survive but are sterile. The parasitic rhizocephalan barnacles, for example, have a typical crustacean-looking planktonic larva whose female settles, penetrates the body, and invades the fatty tissues of the reproductive organs of its crab hosts (**Figure 4.10**). The parasite uses the fat reserves for its own reproduction at the expense of the host, which may not have functional gonads as a result. Eventually, the barnacle tissue erupts through the crab's abdomen, allowing male barnacle larvae to settle, penetrate, and produce gametes that fertilize the female. The parasite, when invading a male crab, may cause its entire morphology to resemble a female and even induce mating behaviors characteristic of females.

Many animals are often in a race to grow and mature before the parasite load becomes too high for reproduction or even survival. This is a special problem for the eastern American mud snail *Tritia obsoleta*, which reproduces in its third year. By this time, females in many populations are densely parasitized by several species of trematodes and may not be able to reproduce.

■ **Parasites often have complex life cycles that depend on more than one host species.**

Because the host dies eventually or because its death may be accelerated by the presence of parasites, the parasites must have a means of dispersing to other hosts. As a result, parasites often have **complex life cycles**, with very different morphologies adapted to function in widely differing
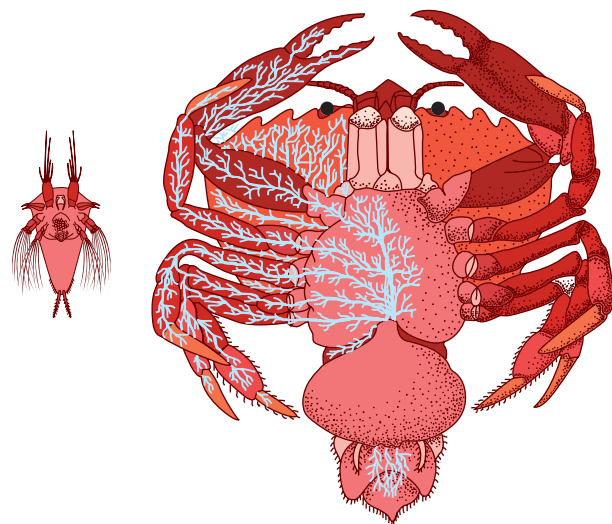

FIG. 4.10 Diagram of the extent of invasion of a rhizocephalan barnacle into the body of a crab. Swimming larvae (left, not to scale) invade a crab host and inject cells that reproduce and propagate a nutrient-absorbing tissue within the crab's body (right). (After Nicol, 1967)
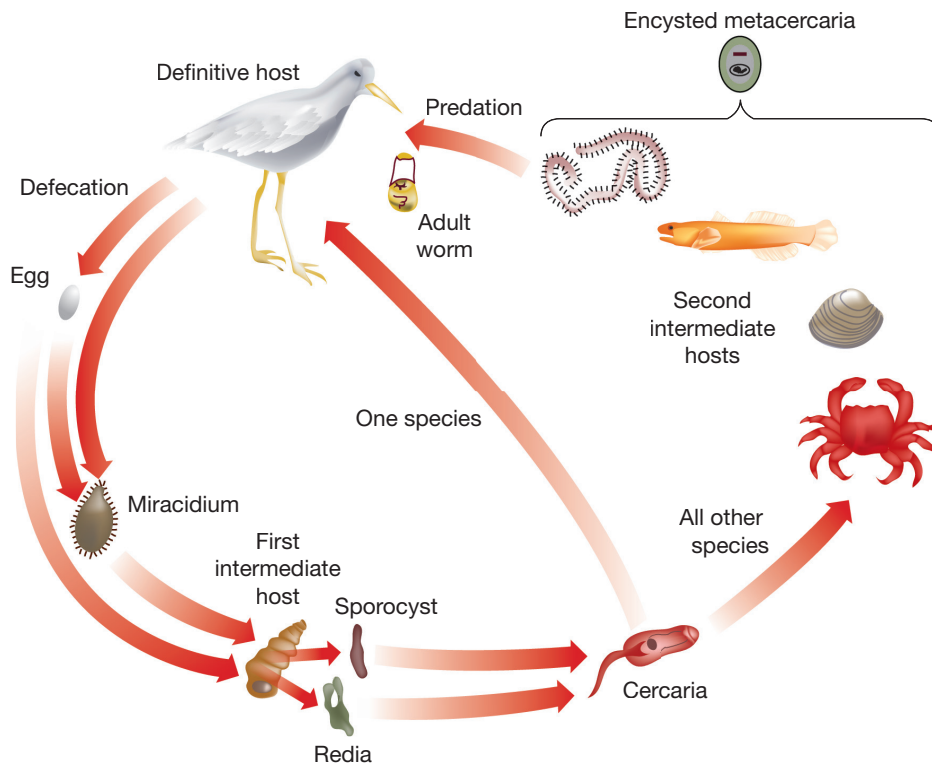
FIG. 4.11 Marine parasitic trematodes have complex life cycles with several intermediate hosts. (From Sousa, 1993)

microenvironments. There is a danger in depending on multiple hosts because one of the hosts might be absent or difficult to locate.

Many parasites have life stages suitable for specialized parasitic existence, for dispersal, and for location of hosts (**Figure 4.11**). Species of the crustacean isopod group Epicaridea may have two hosts. For example, the isopod parasite *Portunion maenadis* has a larval stage that attaches to the copepod *Acartia*; but it also has a free-swimming stage and a second parasitic stage, which lives in the visceral cavity of any of a number of crabs. The isopod parasite of the shore crab *Carcinus maenas* becomes a saclike sheath and bears no resemblance to a typical free-living isopod. In the phylum Platyhelminthes, or flatworms, a number of parasitic trematodes also have complex life cycles. Many species have a stage that inhabits mollusks, a free-swimming stage, and a terminal stage that invades fishes or birds. The fishes and birds often pick up the parasites while preying on the bodies of mollusks or even the siphons of clams.

The Population Level

■ **A population is a group of individuals that are affected by the same overall environment and are relatively unconnected with other populations of the same species.**

A species can be divided into a series of geographically localized populations. The individuals in a population share the same general influence of the physical and biological environment. Within the population, it is much more likely that individuals of a given species will breed with each other as opposed to members of other populations. Geographic barriers such as peninsulas or sudden breaks

in the environment might divide the species into a series of populations. For example, Cape Cod, Massachusetts, is a major barrier along the coast of the eastern United States, and many species do not have extensive dispersal across this barrier. Water temperature increases greatly from the north to the south of Cape Cod, and the same applies to Point Conception in southern California. The geographic ranges of many species end at such barriers.

Population size refers to the number of organisms in a defined area. **Population density** refers to the number of individuals per unit area (e.g., number of animals m^{-2}) or per unit volume (e.g., number of animals m^{-3}) and gives an idea of the degree of crowding or the degree of individual access to scarce resources, such as food or space.

■ **Population change stems from survival, birth, death, immigration, and emigration.**

Most marine populations are dynamic, and extensive change is the rule. Survival of adults is a major factor in population change. If survival is high, then the current population size plays a major role in explaining the population size in future time periods. **Generation time** is the mean time between birth and the age of first reproduction. The existence of more generations per unit time will produce more offspring and a greater potential rate of population increase. Many marine species are capable of producing hundreds of thousands of eggs per female. This is testimony to the low survival rate of adults and the extremely low survival typical of juveniles. Juveniles are often planktonic larvae, and the variability of ocean currents often dooms them to failure in that they never find the proper habitat in which to settle (see Chapter 7). Food limitation may also limit

reproduction. Immigration and emigration of adults can affect the change of population abundance.

We can chart the probability of survival of different-age classes by using a graph known as a **survivorship curve**. **Figure 4.12** shows an expected survivorship curve for a species (e.g., a crab) with a planktonic larval stage and a postsettling adult stage. We begin with a starting cohort and follow the mortality of these animals with increasing age. The survivors are plotted on a logarithmic abundance scale, and in this plot, the slope of the line gives the rate of mortality. As can be seen, the rate of mortality for the planktonic stage is far greater than that for the postsettling stage. Survival can be estimated by sampling a population repeatedly as long as immigration is slight and one can distinguish newly born individuals.

Reproduction is usually seasonal and corresponds to increases of food for reproducing adults and to environmental factors such as temperature and salinity. Because of this, birth is also seasonal. Different **year classes**, or sets of individuals born in the same year, can usually be identified by distinct sizes because animals of one year class have an entire year's head start on growth relative to the next year class. It is sometimes possible to determine the age of marine organisms whose date of birth is unknown. Growth rings can be found in the otoliths ("ear bones") of fishes, in the skeletons of corals, and in the shells of clams and snails.

Population size, fluctuation, and extinction are closely related. Most populations fluctuate greatly because of changing environmental conditions that affect reproduction and mortality. When population size is very small, relatively minor random changes may cause population extinction; low population density may prevent an individual from finding a mate, which is known as an **Allee effect**, named for a famous ecologist. For example, many marine species spawn eggs and sperm into the water, and if population density is very low, sperm from a male might not encounter eggs from a female. It is an important consideration in studying the conservation of rare and endangered species (see Chapter 20).

■ **Limiting resources may affect population growth.**

If resources were limitless and if there were no natural catastrophes, then a population could continue to increase indefinitely. In the real world, food or space will eventually
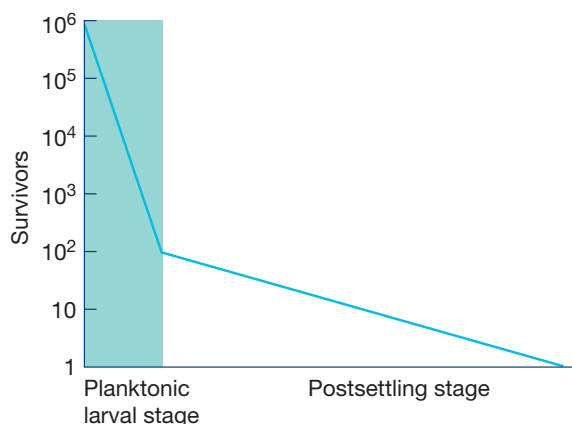
run out. As the resource becomes scarce, resource limitation of survival, growth, and reproduction will occur. **Figure 4.13** shows types of population change. In **exponential growth**, the population increases by the same proportion with the passing of a given amount of time, which might continue indefinitely if resources were limitless. In **resource-limited growth**, there is a limit, or **carrying capacity**, to the maximum population size that the environment's limited resources can sustain. As the population size approaches the carrying capacity, the rate of population growth decreases. When above carrying capacity, the population is too great for the available resources, and it declines. These situations involve intraspecific (within-species) competition for resources. In many cases, population change appears to be **random**. In this case, the factors regulating population size are too complex to show any simple pattern.

Many species occur together and require the same resources or at least overlap strongly in their resource use. This leads to **interspecific competition for resources**, and the carrying capacity of any one species is reduced owing to the similar resource requirements of other species. Competition is discussed later at the hierarchical level of the community.

■ **Populations are often metapopulations, which are a series of interconnected subpopulations, some of which may contribute disproportionately large numbers of individuals to the metapopulation as a whole.**

A group of populations that are living in discrete habitats but are nevertheless connected by dispersal are known as a **metapopulation** (**Figure 4.14**). A **source** is a subpopulation
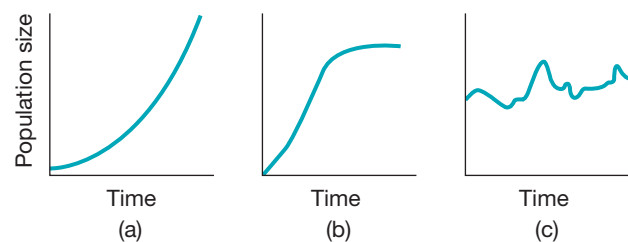
FIG. 4.13 Examples of population change. (a) Exponential growth, a continuing proportional increase. (b) Resource-limited growth, where a population's increase decelerates as carrying capacity K is approached. (c) Random change, where population-controlling factors are too complex to form any pattern.

FIG. 4.12 Expected survivorship curve for a marine invertebrate species with planktonic larvae.

FIG. 4.14 A metapopulation is a series of subequally sized subpopulations with locations that are interconnected by means of dispersal. The light-colored areas are source populations; the dark-colored areas are sinks.

that contributes individuals to the other subpopulations of the overall metapopulation. This may occur when reproduction and dispersal are unusually high in the local subpopulation. A **sink** is a location where a subpopulation may receive immigrants from other populations but does not contribute individuals to the metapopulation and cannot sustain a population on its own. An obvious example is when all immigrants in the sink subpopulation die upon arrival and local individuals fail to reproduce.

High dispersal rates among subpopulations of the metapopulation might work against adaptation to local environments. In the opposite extreme, dispersal might be very restricted between subpopulations, which would allow selection to cause local population differentiation. You can imagine, for example, an isolated population of snails that is exposed to a visual predator. In such a place, there might be strong selection for shell color that matches the background environment. In other sites, predators might be absent, and there would be no selection. If dispersal is high and homogeneous throughout the populations, the product of selection in the subpopulations with predators would be exported randomly to those in which no natural selection has occurred, and local differences in shell color would be absent.

Metapopulation thinking is very appropriate for marine systems, where dispersal of larvae between relatively isolated subpopulations is common. A fascinating example was discovered in a study of gastropods on mangroves of central Queensland, Australia. The intertidal arboreal snail *Littoraria filosa* (**Figure 4.15a**) occurs commonly on mangrove leaves and is obviously very resistant to desiccation. The snail has separate sexes, which copulate, and the planktotrophic dispersing larvae swim in the water for about a month. Stephen and Ruth McKillup (2000) followed populations for a number of years and found that the snail appeared to be an annual: Adults died during the period of larval dispersal and settling, and there was little temporal overlap between successive generations. They were surprised when they began to investigate individual mangrove trees (see Chapter 16 for a description of mangrove forests)
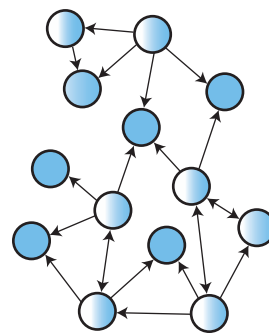
and found that snails on isolated trees only 10–15 m from the main mangrove forest were not annuals at all and continued to live after reproduction. It was apparent that the snails in the main mangrove forest were not "programmed to die." But why were they dying at all? As it turned out, a previously unknown species of flesh-eating fly was the main cause. After a female fly laid an egg near a snail shell, the hatching larva would crawl into the shell and consume the snail's body. In continuous mangrove forests, this process was so effective that no snails survived into a second year or even reproduced. The main population distributed within large patches of mangrove forest is actually a large sink. The settlement of larvae had to come from some other source.

The isolated mangrove trees, often out on the beach, apparently are the source. The fly rarely parasitizes snails there, perhaps because wind prevents flies from reaching the isolated trees. The snails there reproduce well. Larvae that arrive there will not reproduce. It is instead the series of "island" isolated trees (**Figure 4.16**) that constitute sources and may be responsible for supplying the entire population. Snails found on mudflats may also contribute to the larger metapopulation.

Along coasts, populations of a single marine species may extend for many thousands of kilometers. For example, the rocky-shore sea star *Pisaster ochraceus* extends from Baja California to Alaska. Planktonic larvae can potentially disperse over many kilometers, which creates a series of interconnected subpopulations over the entire range of the species. In Chapter 7, we discuss the role of such planktonic larvae and dispersal in creating **connectivity** between marine populations.

Spatial Variation

■ **Spatial distribution is a measure of the spacing among individuals in a given area.**

Spatial pattern is a useful feature of natural populations. The spatial distribution is the measure of the type of spacing among individuals. Consider a square meter of rock on a shoreline that has a population of barnacles. If a barnacle

(a)   (b)

FIG. 4.15   (a) *Littoraria filosa,* shell height approximately 2 cm. (b) An isolated mangrove island in Queensland, Australia, where the snail was collected.
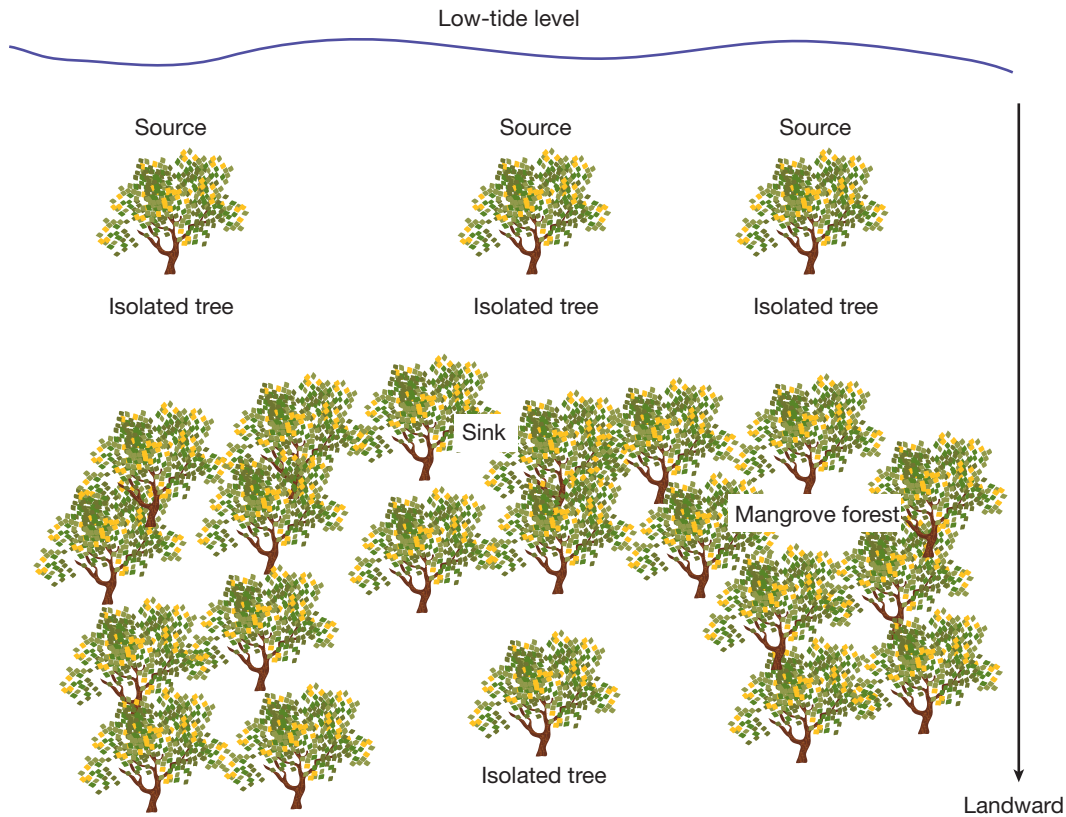
FIG. 4.16   Metapopulation structure in the mangrove leaf gastropod *Littoraria filosa*.
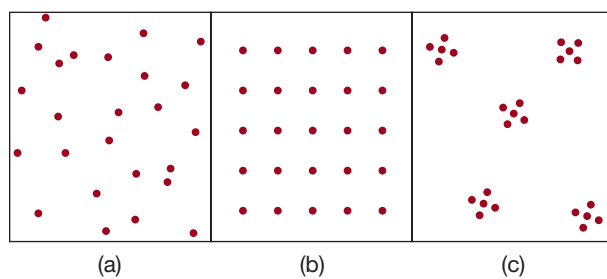
FIG. 4.17   Patterns of spatial distribution: (a) random, (b) uniform, and (c) aggregated.

has the same chance of being located in one spot as in any other spot, then the population has a **random spatial distribution**. **Figure 4.17a** shows such a distribution, which has the appearance of randomly sprinkled grains of salt. If every equal subarea contains a constant number of individuals, or at least a more uniform number than is expected by chance, then there is a **uniform spatial distribution** (**Figure 4.17b**). If more barnacles occur in a given subarea than are expected by chance, then other areas will be depleted of animals, giving an **aggregated** or **patchy** distribution of clusters and empty space (**Figure 4.17c**).

Spatial distributions are useful because they suggest hypotheses about the mechanisms affecting natural populations. It is rare for populations to have a random distribution. This usually occurs when larval settlement from the water column is random or animals are moving about randomly, as when mud snails move on a mudflat. Uniform

distributions occur when animals are maximizing the distance between neighbors, implying the establishment of territories or interference. For example, when larvae of the tube worm *Spirorbis borealis* settle on seaweed from the water column, they usually crawl away from other settled larvae before metamorphosing into adult worms. As a result, one eventually may see a uniform array of tiny spiral tubes on the seaweed frond. Aggregations usually imply some sort of patchiness about the environment, but organisms might be socially attracted to each other for mating or to form fish schools or other aggregations to protect against predators.

■ **A population may show a regular change in density along a sampling line.**

If sampling is done along a transect line, many populations change in a definable pattern. A population of plant-eating snails, for example, might decrease regularly with increasing water depth because the food source also declines with depth. If the density of a population at one site can be predicted from the density at neighboring sites, we speak of the population as having **spatial autocorrelation**. A spatial autocorrelation might occur if (a) there is a change in the environment that affects survival or causes differential subhabitat selection; (b) the population is moving in a defined direction (the change in density might reflect, e.g., the tail end of a migrating population of fish); or (c) a random process occurs, which occasionally can cause a nonrandom spatial pattern.

The Community Level: Structure and Interspecies Interactions

- **Many communities are organized around important structural aspects of the habitat or around foundation species that determine a great deal of the habitat structure.**

Ecological **communities** consist of a series of coexisting species. In many cases, the first level of explanation for the types of species that exist in a community is the **structural habitat**. The hard substratum of rocky shores usually precludes many species, especially those that depend on feeding on and living in soft sediment. Thus, the structural habitat is a major, if obvious, organizing force for marine communities. Equally important in many cases is the presence of **foundation species**, which contribute substantially to the structure of a local habitat and determine many of its physical and chemical properties. For example, the grasses we observe to dominate salt marshes are foundation species. They slow down water currents and increase the deposition of soft sediment, which creates the meadow-like soft-sediment environment that permits many species to dwell and burrow in the sediment among the grass blades. Mangrove trees have a similar effect on protected tropical shores and provide numerous habitats for animal and plant species on mangrove branches. These habitat-determining species are also called **ecosystem engineers**, as they alter substantially, sometimes even create, the structural habitat on which other species depend.

- **Distribution and abundance of species populations in a community are determined by the combined effects of the following processes: (a) dispersal of larvae, spores, and adults; (b) competition; (c) predation and herbivory; (d) parasitism; (e) disturbance; and (f) facilitation.**

Physical features of the environment, such as temperature, salinity, dissolved oxygen, and nature of substratum, may determine the maximum environmental range of a species. However, a series of dynamic community-level processes strongly affects distribution and abundance:

Larval Access

- **Larval recruitment patterns strongly affect the species composition of marine communities.**

Many marine fishes and invertebrates have planktonic larvae, which can disperse great distances. Interannual variation in larval settlement (recruitment) can determine the composition of marine communities. Some of this variation may result from the effects of local ocean currents, which may sweep larvae out to sea or keep them near the shoreline with strong variations among different species, which leads to different assemblages of species.

Interspecific Competition

- **Competition within and between species derives from the limiting resources of space and food.**

Competition occurs when two individuals of the same (intraspecific) or different (interspecific) species exploit a common

FIG. 4.18 Competition affects abundance where resources are limiting. In this example, the mussel *Mytilus californianus* competes for space with the barnacle *Balanus cariosus* on an intertidal rock near Bamfield, British Columbia. (Photograph by Jeffrey Levinton)

limiting resource (**Figure 4.18**). *The two prime limiting resources are space and food.* The study of competition must focus on these limiting resources. A **guild** is a group of species that exploit the same resource. Guilds need not include closely related species. In a typical rocky-shore site on the Pacific American coast, several hundred sessile species, including stalked barnacles, acorn barnacles, mussels, brown seaweeds, green seaweeds, and crustose coralline algae, share the same space resource. In a study of competition for space, it would make no sense to study mussels without also considering competing seaweeds.

- ◼ **Competition between species may involve direct displacement, preemption, or differential efficiency in the use of resources.**

Competition between species can proceed in several different ways. Often, when space is the limiting resource, one species may succeed through direct **displacement** of another. In such a case, we must assume that all encounters between species A and species B have the same outcome (e.g., A displacing B). By contrast, a species that holds space by colonizing a bare spot may then **preempt** invasion by another species, but only because it arrived first. Competition based on direct displacement of one individual by another is known as **interference competition**. Competitive success might involve one species overgrowing another, overtopping and shading another species if it depends on light, or a variety of other mechanisms. But if two species compete by virtue of requiring and exploiting the same resources, there might not be any direct behavioral interaction. In such **scramble** (or **exploitation**) **competition**, the more efficient species might gain more food and gradually increase in population size at the expense of the other. For example, one copepod species might be more efficient at grazing diatoms, a renewable resource, than a second copepod species and win in competition by producing more offspring, which increases the population of the first species at the expense of the second.

- ◼ **Competition has been demonstrated in marine communities by experimental removals of abundant species followed by expansions of competitors.**

One can be overwhelmed by the variety and complexity of nature. We often cannot explain patterns in marine communities very easily. If a species is absent, are predators the cause of its absence? Has the species lost out in interspecific competition? A similar problem arises when we examine zonation, the most common feature of rocky shores, where dominant species may occur in a series of horizontal bands.

One commonly observes, especially in quiet waters, a series of horizontal bands. Classically, they consist of, in order from high to low, intertidal, lichen, barnacles, limpets, and mussels. Why such dominance by single species? Marine ecologists, inspired principally by the pioneering works of Joseph Connell and Robert Paine, have approached the problem through systematic **manipulative field experiments**, which we have discussed in Chapter 1 as a means to test hypotheses. The experiments involve removals of hypothesized predators or competitors or by caging areas against predators with careful observation of the consequences. For example, for many years, Robert Paine removed the voracious starfish *Pisaster ochraceus* from a rocky shore off Cape Flattery, Washington. It was more than 10 years before a significant change took place in the distribution of beds of the mussel *Mytilus californianus*, which extended downward and overgrew several species of seaweed (see Chapter 16). The dominance of mussels resulted in a reduction of diversity of competing rocky-shore sessile species. The displacement of species by a superior competitor is known as **competitive exclusion**.

Field experiments may be prohibitively difficult because the organisms are microscopic or because the manipulation is difficult to interpret. Some field caging experiments, furthermore, change the experimental microenvironment in unacceptable ways. Cages built to protect soft bottoms from mobile predators also alter the depositional environment, and fine sediment settles within the cage. The experimenter is then altering two factors at once. This kind of situation may preclude field experiments, but **laboratory competition experiments** may be quite informative as long as some element of realism permits one to relate the laboratory results to field conditions.

Occasionally, so-called **natural experiments** are encountered. For example, we may discover that in most sites two species are found together. However, we might find that in some locations, one species is naturally absent and the other species has expanded in abundance. We might provisionally conclude that the first species normally affects the other's abundance. Although that is a fairly safe conclusion, we should remember that this is not a controlled experiment. The factor that removed one species may also have enhanced the other's abundance. For example, many fish species decline in estuaries, but mullets are often very abundant. One might be tempted to explain this set of circumstances on the basis of relaxed competition between mullets and other fish species. However, mullets are detritivores, and estuaries often have increased supplies of detritus. Reduced salinity may have independently eliminated the other fish while detrital supply increased the mullets independently.

- ◼ **Competition combined with differential success in different microhabitats results in niche structure.**

Niche structure is any predictable partitioning by coexisting species of a habitat into subhabitats or differential exploitation of resources. Ecologists have long believed that no two species can coexist on the same limiting resource. Although this is not always true theoretically, the presence of coexisting species using different resources has been used as evidence of the action of interspecific competition. Many of these studies are observational only. For example, species of the carnivorous snail genus *Conus* live associated with coral reefs throughout the Pacific. Alan J. Kohn (1967) found that species of *Conus* in subtidal coral reef habitats with high species numbers were highly specialized and tended to eat different foods. By contrast, the
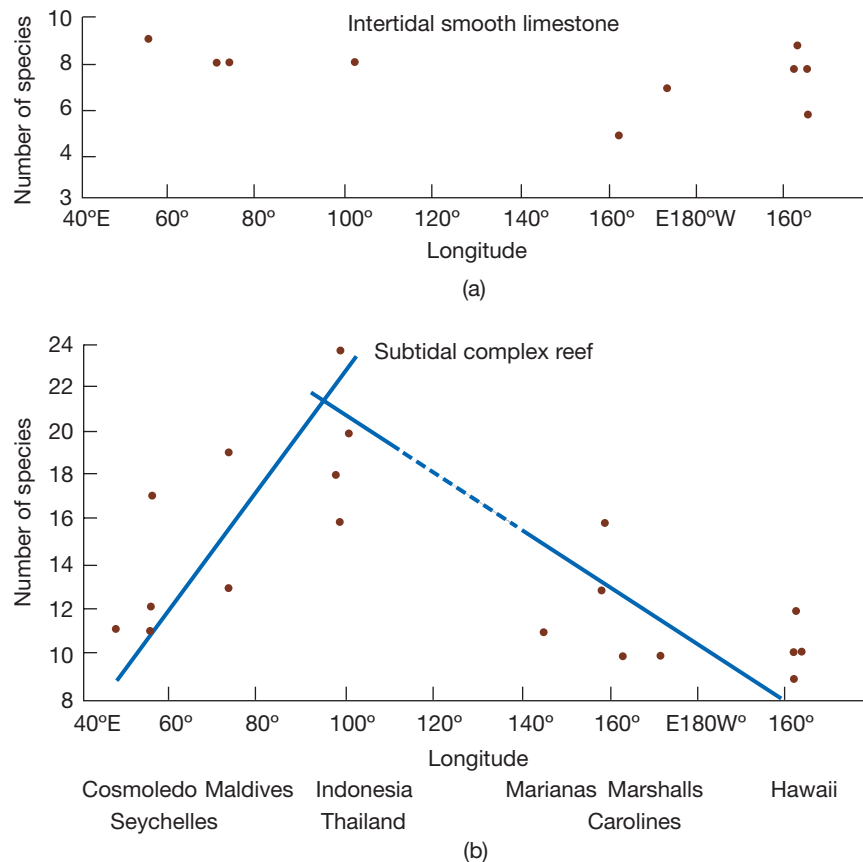
FIG. 4.19 Environmental heterogeneity promotes coexistence of many species by providing several distinct environments within which species may exploit unique resources. Diversity increases toward the southwest Pacific for the carnivorous gastropod *Conus* in complex subtidal hard substrata (b) but does not change in topographically simpler intertidal platforms (a). (After Kohn, 1967)

single species of *Conus* found on the coast of California has much more general food preferences. In the much more homogeneous intertidal smooth platform habitat, species diversity (number of species) does not increase toward the Indo-Pacific region (**Figure 4.19**). Although the evidence is circumstantial, it suggests that some niche structure exists and results from historical competition and the evolution of specialization among *Conus* species or prey.

■ **Some assemblages of natural species show extensive coexistence of presumed competitors despite apparent resource limitation.**

Unless there is an opportunity for niche displacement, one would expect a competitive dominant species to displace all other species. However, this **"law of competitive exclusion"** often does not seem to apply to all natural communities. For example, many species of phytoplankton coexist despite apparent resource limitation. In the open-ocean tropics, scores of species of phytoplankton coexist even though dissolved nutrients such as nitrogen are undetectable in the water column. Why have all inferior species not been outcompeted by species superior at taking up nutrients from the water? The great ecologist G. Evelyn Hutchinson termed this coexistence "the paradox of the plankton."

A number of processes can explain such a lack of competitive exclusion. These include the following:

1. *Competitive networks.* There may be complex competitive interactions combining multiple means of competitive superiority with no clear competitive dominant. It is possible that species A is competitively superior to species B but inferior to species C, leading to different outcomes of dominance depending on which species come into contact (**Figure 4.20**).

   In a simple hierarchy, one species might always win in competition. For example, intertidal mussels often smother all other competing species and win out in competition. But coral reefs appear to have network interactions. Sponge species A might be able to overgrow sponge species B, and B might be able to overgrow sponge C, but C might produce a poison that affects species A, which has poor chemical defense because it devotes it resources mainly to growth. Such complexities of competitive mechanisms delay competitive dominance by any one species.

2. *Lottery colonization.* Adult sites may be limited, but colonization is from a random larval pool in the water column. If an animal dies, a larva might settle from the water column and establish a territory, but currents
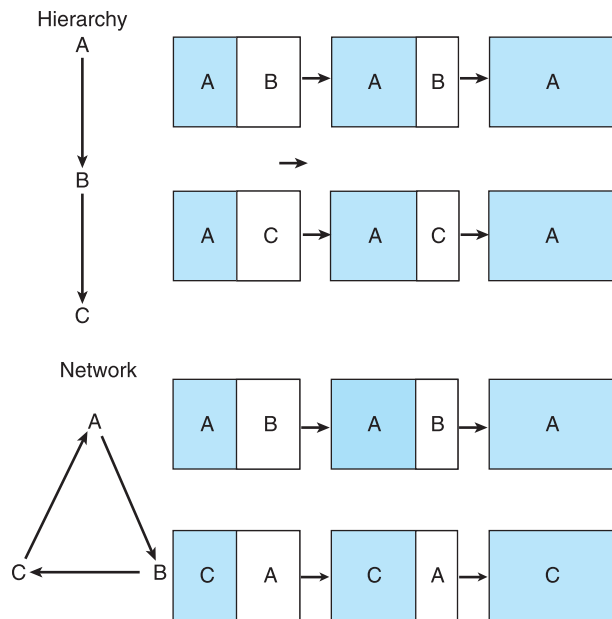
FIG. 4.20 In a simple competition hierarchy (top left), one species is superior to all others, and any given species is superior to another at a lower hierarchical level. In a network (lower left), however, species A may outcompete B, and B may outcompete C, but C may outcompete A. This can happen only if a distinctly different mechanism of competitive superiority for the C–A interaction exists to delay the eventual dominance of any particular species. The lower figure shows that networks create a variety of outcomes when the species are combined, perhaps by larval settlement of pairs of species.

and chance would determine the particular species of the colonist. The species composition of the community would be determined more by colonization than by interactions of the resident adults. Peter Sale (1977) explained the coexistence of several territorial fish species by means of the **lottery hypothesis**, which emphasizes random mortality and colonization by planktonic larvae. The fishes occupying any given site are the result of a random drawing from among the pool of planktonic fish larvae that happen to be in the water column when a benthic territory becomes open. Since gains made by a competitor are often lost because of random mortality, such random processes of adult extinction and recolonization delay or completely prevent the competitive displacement of one species by another. The **neutral theory of community ecology** states that such random interactions, combined with occasional extinctions and speciation events, result in indefinite coexistence of many species.

3. *Disturbance*. Complex patterns of disturbance may preclude the rise of any one species to dominance. Disturbance may be so common (as discussed shortly) that competitive dominance is prevented.

4. *Habitat complexity*. There may be habitat complexity, which permits the coexistence of many species. As discussed earlier, habitat differences may allow species to coexist by specializing on slightly different microhabitats.

Predation and Herbivory

■ **Predation may prevent domination by a superior competitor and may strongly affect species composition.**

The experimental removal of *Pisaster ochraceus* that resulted in the dominance of the mussel *Mytilus californianus* suggests a common effect—namely, that predation delays the competitive displacement of competitively inferior species by the competitive dominant. Herbivory can be considered a form of predation and often has the same effect on competing species of seaweeds. Experimental removal of sea urchins usually results in dominance by one rapidly growing seaweed species over the others.

■ **Seasonal influxes of predators in shallow water and in the intertidal zone may devastate local communities.**

Many habitats have a local permanent population of predators, but the spring and summer often bring on invasions of large populations of migratory predators with devastating consequences for prey populations. In the intertidal zone, the most prominent example of such predators consists of shorebirds, whose migrations may extend for thousands of kilometers. These birds often have favored feeding grounds on muddy or sandy beaches, which they visit successively during their migration. Fish often come inshore in summer and devastate local invertebrate populations.

Disturbance

■ **Disturbance opens up space in the community. Its frequency may regulate long-term aspects of species composition in a habitat.**

Marine populations suffer extensively from storms, continuous wave action, and unstable sediments. Intertidal populations often crash owing to large swings in temperature and humidity. Ice crushing (in high latitudes) and the bashing of floating logs are also major problems. Even in subtidal habitats, large swings in temperature may occur, as in the great increases in temperature during El Niño events. Any of these general physical effects is known as **disturbance**. Mobile animals may also cause mortality unrelated to predation. Such effects are known as biological disturbance. For example, while moving along rocky surfaces, limpets often bulldoze newly settled barnacle larvae from the rocks.

The effects of disturbance resemble those of predation because competitors are reduced in number. However, predation is usually a process that removes one individual at a time, although some predators come in devastating waves. Disturbance, by contrast, usually operates on larger spatial scales, removing patches of the community. Disturbance often initiates an orderly sequence of dominance by different species over time known as succession (discussed later).

■ **Species diversity may be maximized at intermediate levels of predation or disturbance.**

Let's consider first a gradient from very low to very high predation rates; we can apply the same set of causes and
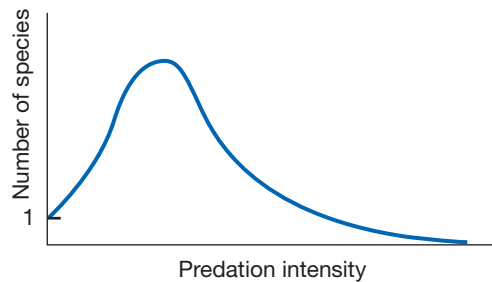
FIG. 4.21 When there are competing species and no predation, one superior species may take over. With predation that is random or targeted toward the competitively superior species, more species can coexist. With very high predation pressure, all individuals and species may decline. Thus, we might expect an intermediate graphical hump in the number of coexisting species as a function of increasing predation pressure. A similar effect is found for levels of disturbance.

effects to disturbance intensity. If there are no predators, we might expect a competitive dominant, if present, to displace all competitively inferior species. But as predation increases, resource space opens up, and more competing species may be allowed to coexist. As predation intensity increases further, however, nearly all individuals of all species will be removed, and the species diversity will decline relative to the intermediate disturbance levels. Thus, species diversity tends to be maximized at intermediate levels of predation.

Disturbance is likely to work in a similar way because it will most likely pare down the abundance of the competitive dominant. But if disturbance is very low, the competitively dominant species will displace all other competitors. If disturbance is extremely strong, all species, including the competitive dominant, will be eliminated. These combined effects are known as the **intermediate disturbance-predation effect** (**Figure 4.21**).

It is important to realize that this relationship is fueled by a large recruitment rate of new individuals into the area we are considering. With recruitment of all species low, co-existence might occur even at very low levels of disturbance because there would not be a sufficient influx of larvae of a competitive dominant to recruit to displace other species (Dial and Roughgarden, 1998).

Although the intermediate disturbance-predation hypothesis seems logical, it is not clear how often it works in nature, and some studies show that there are many departures. In some habitats, as we shall discuss, it is rare for a single competitive dominant to exist. Furthermore, inevitably, many species will not be eliminated by a competitively superior species. Finally, as disturbance increases, mortality may also increase, eliminating species faster than they might accumulate as competition is relaxed.

Parasites and Disease

■ Parasites are common and can affect their hosts by reduction in growth and reproduction or by enfeeblement.

As discussed earlier, parasites affect individual hosts by taking resources, interfering with reproductive output and

behavior, and enfeebling the host. On the population level, parasite load should reduce reproductive rate and cause the decline of population size. To examine population-level effects, we must know the percent infection (or prevalence) of the host population and the severity of parasite effects (or intensity). Lafferty (1993) was able to manipulate the prevalence and overall population density of trematode parasites on the California marsh snail *Cerithidea californica*. Snail populations with higher parasite prevalence had lower reproductive output and higher mortality rates. These results suggest that abundant and ecologically significant species may be greatly diminished by parasites in the strength of ecological interactions with other species in a community.

■ Diseases in marine organisms are poorly understood, but they can cause swift population declines.

Disease is a major cause of massive and widespread mortality. Infectious disease usually involves the invasion of an individual by a microorganism, such as a virus, bacterium, or protist. Unfortunately, our understanding of marine pathogens is very limited. For example, a marine protist is known to be the main cause of a disease that devastates populations of the eastern oyster *Crassostrea virginica*. This parasite caused the collapse of the very profitable oyster industry in Delaware Bay and has recently been a major cause of decline in Chesapeake Bay. Despite its obvious commercial importance, however, we still have no complete idea of the parasite's life cycle.

One of the most interesting issues of marine disease is the mechanism and rate of spread. In Chapter 18, we discuss coral reef and other tropical diseases, some of which can be interpreted as spreading by water currents. Such spread might cause a disease to invade an entire ocean basin in the time the surface currents spread the disease, which will often be less than a year. In other cases, disease vectors require direct contact. Disease organisms can be transported in hosts that are present in ballast water of ships. This means that the current use of untreated ballast water in many ships might be facilitating the spread of marine diseases throughout the ocean. Aquaculture facilities are also highly vulnerable to the spread of disease, and a virus causing white spot syndrome is responsible for enormous losses in shrimp farms throughout the world.

■ The role of disease must be verified by rigorous use of Koch's principles, which involve identification of the pathogen, isolation, and successful experimental infection of the target organism.

The role of a pathogen in a disease must be established by rigorous use of a set of principles named after disease biologist Robert Koch. First, the pathogen must be identified. This alone is a difficult process because a disease may be accompanied by the rapid increase of a number of microorganisms, but only one is likely the cause of the disease. Second, the pathogen must be isolated and raised in the laboratory. Finally, the pathogen in culture must be reintroduced into the target organism to confirm the cause of the pathogen of the disease. Given the difficulties of culture,

let alone reintroduction into wild species, these steps are difficult to achieve.

■ **Disease interacts strongly with changing environmental conditions and the increase of stressful physiological conditions of the host.**

Environmental factors may also be important in the spread of disease. First, an environmental shift might facilitate the geographic spread of a disease to new areas. The oyster disease Dermo, caused by an amoeboid protist species, has been increasing in occurrence toward higher latitudes in southern New England waters. This may be related to ocean warming, which seems to promote spread of the disease organism (Powell et al., 1999). Global warming of the past few decades may be facilitating the invasion of other disease organisms toward higher latitudes.

If the environment changes rapidly, physiological stress might make marine organisms more susceptible to disease. This was discovered in humans by physiologist Hans Selye, who demonstrated that those under psychological stress were more susceptible to disease. It is an interesting question whether global warming is sufficiently stressful that many marine organisms are becoming prone to disease. This may be the explanation behind the rapid spread of coral diseases in recent decades, as stressful warming events become more prevalent (see Chapter 17).

■ **Target organisms may evolve resistance to disease, resulting in cycles of virulence in marine populations, which are poorly understood.**

Disease is well known to undergo cycles of virulence and spread. In the worst case, a disease can drive an entire species to extinction or near extinction. Obviously, the rate of spread will then decline because the disease has no place to spread and perhaps no hosts to infect. But an alternative possibility is that the host population will have genetic variability for resisting the disease. When a new strain of the disease occurs, resistant genotypes will increase in frequency and reduce the impact of the disease. This can be demonstrated in the laboratory. Ford and Haskin (1987) were able to select populations of the eastern oyster *Crassostrea virginica* for resistance to the disease organism MSX. After a major mortality in Delaware Bay, surviving oysters were more resistant to infection. It is not known whether there is a physiological cost that is encumbered by the evolution of resistance.

Facilitation

The study of species interactions often involves negative interactions, as in predation and competition, but ecologists have found that positive interactions between species are often important in determining the species composition of marine communities (Bulleri, 2009). In some cases, species facilitate each other's presence. In stressful environments such as the rocky intertidal, associations of sessile species may result in retention of water at low tide, which enhances survival for all species. Some species, such as intertidal plants and seaweeds, increase moisture of the substratum, which attracts burrowing animals. But in turn, such burrowers may aerate the mud and increase the growth of plants. In soft sediments, several species might burrow and oxygenate the sediment, thus making it more hospitable for all burrowing species to live within the sediment (see Chapter 16 for more on the effects of burrowing species on sediment properties). **Foundation species** often alter the structural environment, which facilitates the presence of many other species. Sea grasses are good examples of this effect because they often make both the sediment and water column within the grass a suitable habitat for many quiet-water species.

Succession

■ **Succession is a predictable ordering of arrival and dominance of species, usually following a disturbance.**

Many people are familiar with the fate of small ponds in forests. The ponds fill in with sediment and are colonized by vegetation. Eventually, the soil and biota come to resemble those of the surrounding area. Succession comprises all the processes that are involved in such a progression. **Succession** is a predictable ordering of appearance and dominance of species, usually following an initial **disturbance**. A predictable final state, or **climax community**, may eventually develop. Succession is explained as either (a) a trend toward a stabler assemblage of species or (b) the simple sum of the colonization and persistence potentials of the species. Succession is not necessarily inevitable, and the rate of change is not predetermined. Much research on succession suggests that it is often more like a net trend than a closely integrated sequence of biological events.

Several factors are at work in varying degrees to determine the pattern of succession, even if the sequence is more or less predictable:

1. Differential rates of colonization might result in the early arrival of certain disturbance-dependent species. These species have high reproductive rates and short generation times. They are adapted to locate in newly disturbed environments, but such "weedy" species often are poor at holding on for very long.

2. Conditioning of the environment by resident species might facilitate the appearance of other species or prevent others from colonizing.

3. There may be monopolization of the habitat until some event (e.g., grazing) eliminates the dominant species and permits further colonization.

4. There may be irregularity in the time course of succession depending on events such as the arrival of predators or variation in recruitment to the site. On rocky shores, for example, filmy green algae often arrive first. They are frequently replaced by species with tougher holdfasts and compounds that deter herbivores. These species in turn often cannot colonize unless herbivores such as snails and urchins have eaten the green algae.

5. There may be an eventual dominance of species that are relatively resistant to predation and competitively superior to early succession species, at least under the conditions found late in succession.

■ **Succession may bring a community from one condition to another; however, other forces may also change community composition in a profound way, and local feedbacks may preserve the change.**

We usually think of the final state of succession as having a series of properties that deter a reversal to earlier stages of succession. Often in marine communities, however, major external disturbances or even differences in the time of year may cause major shifts from one community condition to another (**Figure 4.22**). Some habitats are continually disturbed with major habitat shifts. In Texas shallow bays, periods of rain and drought may drastically alter the salinity and favor very different groups of organisms adapted to differing salinity regimes. Continuing disturbance might guide the appearance of community types we see in such shifting regimes.

Dominance in marine communities might be determined by very local circumstances of disturbance and colonization. John Sutherland (1974) studied benthic colonization of ceramic plates and showed that the community composition of sessile animals depends strongly on the time of year the plates were placed in the water. For example, the colonial hydroid *Hydractinia*, would colonize and resist overgrowth by species that might settle later in the year. On the other hand, the tunicate *Styela* would colonize predictably, usurping space from colonial bryozoans. Therefore, communities do not fit the neat mold of succession as a predictable process of community condition *A* going to community condition *B* and so on. Sutherland termed the locally persistent assemblages of organisms multiple stable points, but we shall call them **alternative stable states**. The important requirement for alternative stable states is that the different community compositions arise as accidents of particular historical circumstances and manage to persist over time. If particular environmental conditions lead to a particular outcome, as in succession, we refer to the community so obtained as a new **phase shift**. For example, if the water becomes turbid and sea grasses disappear, leading to dominance of bare bottoms, we would call this a phase shift because it is predictably driven to a new state by a predictable environmental change. Alternative stable states are often preserved by feedback processes that preserve a given assemblage of species, once established. However, transitions between one stable state and another are often complex and the path of transition may differ forward and backward in transitions between states (see Petraitis, 2013, for more on this subject).

■ **The resilience of a community's ecological structure should increase with the diversity of species that have important ecological roles, such as grazers or top predators.**

Disturbance and large-scale population decline are common features of natural communities. In some cases, disturbance has large-scale random effects and removes many species. But in other cases, removals of top predators may occur simply because they are less abundant and more vulnerable to population reduction. Human effects such as overfishing might also focus disproportionally on some of the community, such as the top predators. It is therefore of great interest whether a community might return to its original state after a major disturbance. The capacity for such a return by a community is known as **resilience**.

Increased diversity appears to influence the resilience of a community. Why? First, some functional effects such as predation by top predators or grazing by herbivores might be retained if a diverse community exists. If one grazer is removed, another grazer might increase in abundance to replace it. Thus, community resilience is likely to decline as diversity declines. This is important in habitats where frequent disturbance allows only a few species to exist. A local extinction might have greater consequences than in another habitat where disturbance is less frequent and diversity is greater. It also means that a community will be more resilient when a massive disturbance or disease causes the local extinction of what might be the only top predator or grazer in a system, such as a coral reef. A removal under such circumstances might cause a major shift to an ecologically different regime with new patterns of dominance.
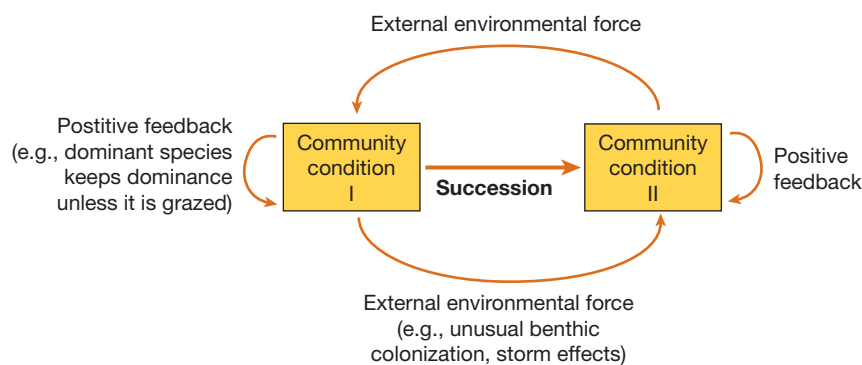

FIG. 4.22 Traditional models of succession would suggest that environments move through a series of community states. However, external changes or conditions, such as incursions of grazers, seasonal changes, or storms, may cause sudden shifts in community states. Positive feedbacks may keep the condition from changing.

Direct and Indirect Effects

■ **Ecological interactions may be direct or indirect.**

So far, we have discussed ecological interactions as direct effects between species. If a predator captures and consumes an individual of a prey species, the prey species is reduced in population size by one. By doing this, we are making a hidden assumption: The effect on a community is the sum of all instances of a direct effect between individuals of two species in a predation or other interaction event. But such effects may also be propagated through communities by **indirect effects** on other species. Here is a simple example. Consider a chain of interaction: Sea otters capture urchins, and urchins eat seaweed. If sea otters capture urchins, the urchin population will decline; that is a **direct effect**. But the decline of urchins would also result in the **indirect effect** of seaweeds being relaxed from grazing. Thus, the indirect effect would be that the removal of urchins causes an increase in seaweeds. From this we learn that removal of a species in an ecological system with strong species interactions will propagate throughout the community. One might imagine that if the seaweed population increases, there might be a decrease of dissolved nutrients required by the seaweed. The indirect effects will be very widespread.

■ **Indirect effects in communities can involve density-mediated indirect interactions (DMII) or trait-mediated indirect interactions (TMII).**

The indirect effect of predation on sea otters to seaweed abundance should be related to the density of sea otters mediated by sea urchins: The more otters, the more seaweed. This would be a **density-mediated indirect interaction**. But consider this possibility: Otters increase, and as a consequence, urchins change their behavior and start to hide in crevices, which keeps them from being spotted by the otters. This *behavioral trait* would not result in a decrease of urchins, but it would still result in less feeding by urchins on seaweeds. Therefore, *the presence of the trait of predator avoidance* would result in increased seaweed growth. As another example, dugongs are southwestern Pacific marine mammals that graze in sea grass meadows and can have major effects on grass diversity and abundance in Shark Bay, northwestern Australia. They prefer shallow sites where grass is abundant, but move to less productive deeper sites when tiger sharks are present. The dugongs are therefore modulating their use of foraging sites in proportion to the probability of attacks by sharks (Wirsing et al., 2007). These responses are known as **trait-mediated indirect interactions**. Because prey can often detect their predators by smell, feeling currents generated by the predators, or other means, indirect effects can propagate through communities without changes in density or direct consumption rates of one species by another. If an effect such as predator avoidance by reduction of activity in a species occurs, and the prey of this species is not reduced in population size or even grows as a result, this would also be known as a **nonconsumptive effect**.

The Ecosystem Level

■ **An ecosystem is a group of interdependent biological communities and abiotic factors in a single geographic area that are strongly interactive.**

An ecosystem consists of a group of communities that interact with the physical-chemical environment within a specific geographic area. Within the ecosystem, nutrients recycle between organisms and the environment, some of the species manufacture organic molecules using only solar energy and inorganic chemical sources (e.g., algae), and the interactions among species within the system are very strong. Under this definition, a large lake would comprise an ecosystem because the organisms, nutrients, and other environmental features interact within the lake. A coral reef and its immediate surrounding water also qualify as an ecosystem. An ecosystem is not necessarily independent of other ecosystems, but we can define the boundaries of an ecosystem. In reality, all ecosystems exchange nutrients and organisms with other ecosystems. It is crucial, therefore, to determine the boundaries of an ecosystem and the places where losses and gains may occur.

■ **Nearly all ecosystems have primary producers (mainly photosynthetic), which are consumed by herbivores, which in turn are eaten by carnivores. Material escaping this cycle passes through the saprophyte cycle.**

The manufacture of organic molecules is accomplished by **primary producers**. Phytoplankton, seaweeds, and sea grasses are the most familiar of these organisms, but many bacteria also manufacture organic substances with the aid of light or energy derived from inorganic chemicals. Plants are consumed by herbivores, and carnivores in turn consume these. In many marine ecosystems, most of the plant material produced is never consumed by herbivores; rather, much of it falls to the seafloor and is decomposed by bacteria and fungi, producing dissolved nutrients. The dissolved nutrients are then available for primary producers. This pathway is known as the **saprophyte (or detritus) cycle**.

Biomass, Productivity, Primary Productivity, and Secondary Productivity

Biomass (standing crop) is the mass of organisms present in a defined area or volume (expressed in units such as grams per square meter: $g\ m^{-2}$). Biomass is distinguished from **productivity**, *which is a rate*: the amount of living material or carbon produced per unit area per unit time (e.g., $g\ m^{-2}\ y^{-1}$).

In a natural environment, all organisms depend on primary producers, which use light energy, usually in the process of photosynthesis, to convert carbon dioxide and water into sugars and other essential compounds. A primary producer is also known as an **autotroph**, and consumers of autotrophs are known as **heterotrophs**. **Primary productivity** is the amount of living material produced in photosynthesis per unit area per unit time. In contrast, **secondary productivity** refers to the production of primary consumers, or herbivores, per unit area per unit time. The productivity

of carnivores, or consumers of herbivores, is **tertiary productivity**. A **food chain** is a set of connected feeding levels of primary, secondary, and tertiary (and so on) sources of productivity. An example of a simple food chain is

$$seaweed \rightarrow snail \rightarrow shorebird$$

Each organism (primary producer seaweed, secondary producer snail, tertiary producer shorebird) occupies a **trophic** (or food) **level**. In more complicated systems, a simple chain cannot be constructed, and a more complex **food web** is a better description. We discuss transfer through food webs in Chapter 12.

In general, primary production is greater than secondary production, which in turn is greater than tertiary production. Secondary production depends on consumption of primary producers, but this process is not perfectly efficient. Some material is never eaten, and even the eaten fraction may not be digested completely. Finally, not all the food that is digested is used for growth (i.e., production). In the case of carbohydrates, for example, a large fraction of the carbon content is respired in the form of carbon dioxide. As a result of such processes, material is lost between successive trophic levels (see Chapter 12 for further discussion).

■ **Some predatory species at the apex of food webs exert strong effects on the overall ecosystem.**

Predators at the top of food webs (often called top predators or **apex predators**) may exert strong effects not only on competitive interactions but also on entire ecosystems if there are strong interactions between the trophic levels. A predator at the top of a food web exerting such strong effects is known as a **keystone species**, a distinction first recognized by rocky-shore ecologist Robert T. Paine. When linkages among trophic levels are strong, changes in abundance of the top predator causes a **trophic cascade** through the trophic levels. In Pacific U.S. kelp forests, sea otter consumption of urchins has a cascading effect on kelps.

■ **Food webs may be controlled by top-down processes usually affected by prey on lower trophic levels or by bottom-up processes.**

The strong effect of fluctuations of apex predators, especially as indirect effects at lower trophic levels, is an example of **top-down effects** in ecological systems. These effects have often been noted when humans hunt an apex predator nearly to extinction, which initiates a trophic cascade down the food chain. Top-down effects clearly occur when predators consume their prey.

Changes in lower trophic levels may also exert strong effects on ecosystems. Such **bottom-up effects** might include a large-scale increase in phytoplankton productivity, which results in greater food input at the lower levels of a food chain and indirectly allows larger populations of apex predators to exist. There are even food webs where middle-level species are crucial determinants of food web dynamics. In Chapter 19 we discuss the central role of krill in Antarctic food webs.

■ **Ecosystem studies usually account for the processes that affect movement of materials and energy through food webs and through the nonliving part of the ecosystem.**

Studies at the ecosystem level attempt to account for the processes that control the system's **throughputs of materials or energy**. For example, an ecosystem study might focus on the control of movement of nitrogen through a marine planktonic ecosystem. Clearly, this is a biologically complex problem involving anything from microbial control of conversion among different forms of nitrogen to movement of nitrogenous materials from the water to plants, herbivores, and carnivores. Ecosystem studies involve a search for general features of material flow, and species are usually treated only as **functional groups** (e.g., herbivores).

Species, Genetic Variation, Evolution, and Biogeography
Genetic Basis of Organismal Traits

■ **Organism features can be explained based on a combination of genetic and nongenetic components.**

Marine organisms are universally variable in DNA sequence, form, color, and biochemistry. A **polymorphism** is any variation that can be identified in terms of a series of discretely different forms. In other cases, variation can be measured only as continuous variation, such as differences in body size or the proportional size of a fin. We must distinguish between genotype and phenotype. The **genotype** refers to the genes that characterize an individual or to those that control a particular trait, such as eye color. The **phenotype**, by contrast, is the form the organism takes. For example, it is possible that all the brown-haired individuals in a human population will not have the same genotype. By contrast, people with gray or brown hair may be of identical genotype. The gray-hair phenotype might be associated primarily with age.

Phenotypic variation in a population can be explained with a simple equation:

Phenotypic variation = variation explained by genetic factors + variation explained by environmental factors + an interaction between genetic and environmental factors

Much of the phenotypic variation we observe has nothing at all to do with genetic variation. Environmental effects such as nutritional status and microclimate alter the course of growth and development of animals with identical genotypes. *Both genetic and nongenetic components contribute to determine a trait*. Body size is a useful example. It is almost always controlled partially by genes, but the environment also exerts a large effect. Much of the variation we see in natural populations, however, exists because of the inheritance of different genes. Shell color is a conspicuous example of this in many mollusks.

It is extremely important to realize that having a given gene does not guarantee that the form of an organism will

always be the same. The same genotype may have a different phenotype when raised in different environments. This is known as a **genotype-by-environment interaction**.

In a few cases, variation is due to differences at a **genetic locus**, or single location on the genetic material, or DNA (see bonus chapter, "Molecular Tools for Marine Biology," online). In such a case, an individual has two genes for the trait, one inherited from the father and one from the mother.[1] The genes might be identical, or they may be different variants, or **alleles**. If there are two alleles *a* and *b*, then there are three possible genotypes: *aa*, *ab*, and *bb*. All three variants may look different, or one allele may be **dominant**. For example, if the *a* allele is dominant, then *aa* and *ab* genotypes may have identical phenotypes.

The mussel *Mytilus edulis* can be blue-black or brown owing to the control of a single genetic locus with two alleles (**Figure 4.23**). The brown allele is dominant over the blue-black, and the heterozygote, which inherits one brown allele and one blue-black allele, is therefore colored brown. In most traits, several or many genetic loci are in control. Body size, for example, is usually controlled by many loci. In such cases, the genetic component can be found by studying the degree of resemblance among relatives. The correlation of a trait between parents and offspring, for example, can give evidence of a genetic component. **Figure 4.24** shows the correspondence between number of vertebrae in mothers and in offspring of the eelpout *Zoarces viviparus*. The correlation is high, and we conclude that the variation in the trait is therefore controlled largely by genetic variation.

There are several types of common variation observed in marine populations. **Chromosome number** can be variable in natural populations. The Atlantic drilling snail *Nucella lapillus* is variable in chromosome number when found in different degrees of wave exposure. Many species have **color polymorphisms**. These polymorphisms may be explained mainly by genetic variation. Many **morphological characters** (e.g., body size and number of fin rays on a fish) are variable and are controlled, at least in part, by genetic variation. Variation in **biochemical and physiological traits** (e.g., presence of specific proteins and different levels of oxygen consumption) is common, and **enzyme polymorphisms** occur widely. **DNA sequences** also differ at genetic loci and, of course, give the most direct evidence of genetic differences among individuals.

What maintains genetic variability in populations? **Natural selection** is the process whereby individuals with certain genes survive and reproduce more successfully than others; this leads to dominance in the population by certain genetic variants. The relative survival and reproduction of a given genotype constitute its **fitness**. **Adaptation** occurs when natural selection causes evolutionary change in a population, which results in an increase in the ability of a typical member of the population to perform in that environment. We usually judge performance with respect to a given function, such as resisting heat shock.

[1] With the interesting exception of sex-determining chromosomes.

FIG. 4.23   External shell color of the marine mussel *Mytilus edulis* is genetically controlled by two alleles for *blue* or *brown*, as shown by these light brown and dark blue juveniles (shell length is about 1 cm). The allele for light brown is dominant, so the light-colored mussel may be a *brown-brown* homozygote or a *brown-blue* heterozygote. The dark blue mussel is a *blue-blue* homozygote. (Courtesy of David Innes)
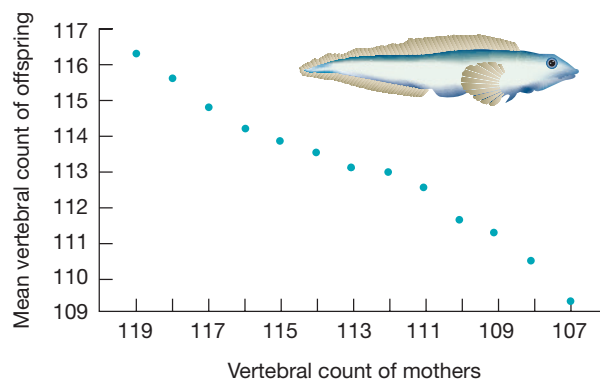

FIG. 4.24   The mean vertebral count of mothers and their offspring in the eelpout *Zoarces viviparus*. (Data from Schmidt, 1920)

Variation can be maintained by shifting of environments, which may favor one genetic variant, then another. Alternatively, a complex environment can favor several genetic variants but in different microhabitats. In some cases, a gene is favored simply because it is rare, which would cause a dynamic shifting back and forth of gene frequencies. This process, known as **frequency-dependent selection**, should work commonly when rare morphs are favored in mating. Finally, gene-level variation can be maintained if heterozygotes are favored in natural selection. This tends to keep alleles in the population because selection for a homozygote, or organism with identical alleles for a trait at a genetic locus, would favor one allele at the expense of others. Finally, immigration of different genetic variants from adjacent populations can increase variability in a local population.

Although natural selection is ubiquitous in natural populations, **random events** can also influence the genetics of marine populations. If the population is very small, chance events may cause the loss of certain variants from the population. This outcome, which is more likely when

there is little difference in fitness among genotypes, has been claimed especially for some biochemical variation in proteins.

■ **Single genotypes may have the capacity to develop into distinctly different morphologies.**

A given genotype may take different forms under different circumstances controlled strictly by environmental variation. This phenomenon is known as **phenotypic plasticity**, which is the ability of a single genotype to develop into different forms, usually as a response to environmental circumstances. One can rightly say that a population has evolved individuals that are plastic and capable of responding to individual circumstances. Every individual has the capacity to respond to local circumstances. We encountered such phenotypic plasticity in our discussion of inducible defenses. Many marine organisms can grow spines, increase shell thickness, or change morphology completely in response to predators. On the west coast of the United States, the intertidal snail *Nucella lamellosa* develops teeth in its shell aperture when predatory crabs are present, which helps deter the crab from attacking at the shell aperture. *N. lamellosa* will develop these teeth even if the crab is held in a cage upstream of the snail, allowing the snail to smell the crab's nearby presence (Appleton and Palmer, 1988).

It is of great interest to ask why some species show plasticity and can adapt to all circumstances whereas, in other cases, genetically distinct morphs coexist in natural populations, with each morph better suited to function under different circumstances. In both cases, you can imagine that there might be a great cost. If you were phenotypically plastic, you might be able to generate a range of morphologies with none of them quite right. That is, you would be a jack-of-all-trades but master of none (DeWitt et al., 1998). If the environment is very unpredictable and it is not clear that you will or will not encounter a given situation (e.g., predators), then phenotypic plasticity might be selected for. In a stable set of microhabitats, on the other hand, a genetic polymorphism for specialized individuals might be selected, assuming that the specialized morphs had greater efficiency than could be achieved by the phenotypically plastic form. Plasticity is to be expected when environmental change occurs within the life span of an individual. For example, some barnacles seasonally regenerate their penis in time for mating season but resorb it as winter approaches. Some species are capable of producing a longer penis if another individual is not within easy reach (barnacles are simultaneous hermaphrodites) or can strengthen the penis if there is high turbulence and it is difficult to extend the penis to a nearby barnacle.

■ **The geographic change in the frequency of genetic variants is called a cline.**

It is common for members of a species to differ from place to place in morphology, color, or size. For example, the color polymorphism in mussels, described earlier, shows
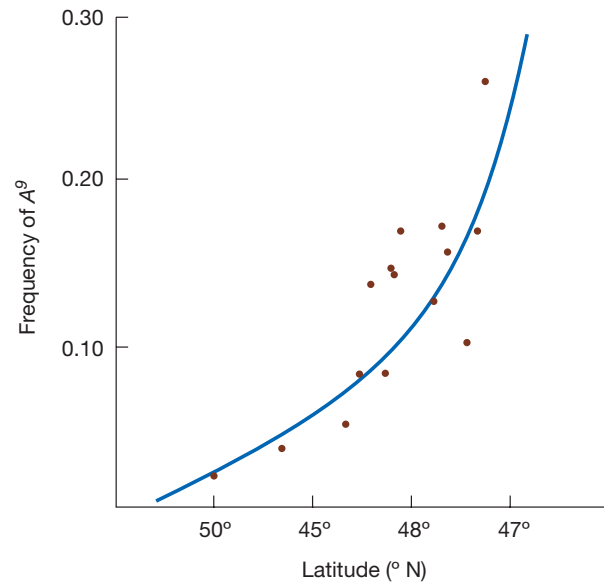

FIG. 4.25 Example of a cline: latitudinal variation of an allele, A^9, at a genetic locus coding for the enzyme lactate dehydrogenase in the crested blenny *Anoplarchus purpurescens* in Puget Sound, Washington. (After Johnson, 1971)

an increase in the brown form as one moves southward, which is related to the latitudinal gradient in solar input. Such geographic variation is also common in biochemical polymorphisms. Any directional change in frequency with geography is known as a **cline**. Figure 4.25 shows the change in frequency of an allele at an enzyme locus as one samples the crested blenny *Anoplarchus purpurescens* at different latitudes in the Puget Sound, Washington State, region.

■ **New species usually originate after a species is divided by a geographic barrier.**

For new species to originate, it is usually necessary for a geographic barrier to isolate a species into two or more populations. If the barrier is short lived, the populations will reconnect. If the barrier is longer lived, and especially if the populations diverge genetically, they may be relatively incompatible when reconnected. Offspring of population crosses between populations will be less fertile than crosses within populations. This would cause selection for mating with one's own kind and lead to further genetic differences between the populations, whereupon separate species would evolve. Such speciation involving geographic isolation is known as **allopatric speciation**. In some cases, we can see the recent effect of such barriers. Many pairs of closely allied species are found on either side of the Isthmus of Panama, which is only about 3 million years old. In many cases, newly evolved species are so similar that they are identical, or nearly indistinguishable, morphologically. Such species, known as **sibling species**, are very common among marine species (Knowlton, 1993). Although sibling species may have separate geographic ranges, many cases of co-occurrence have been discovered. For example, the
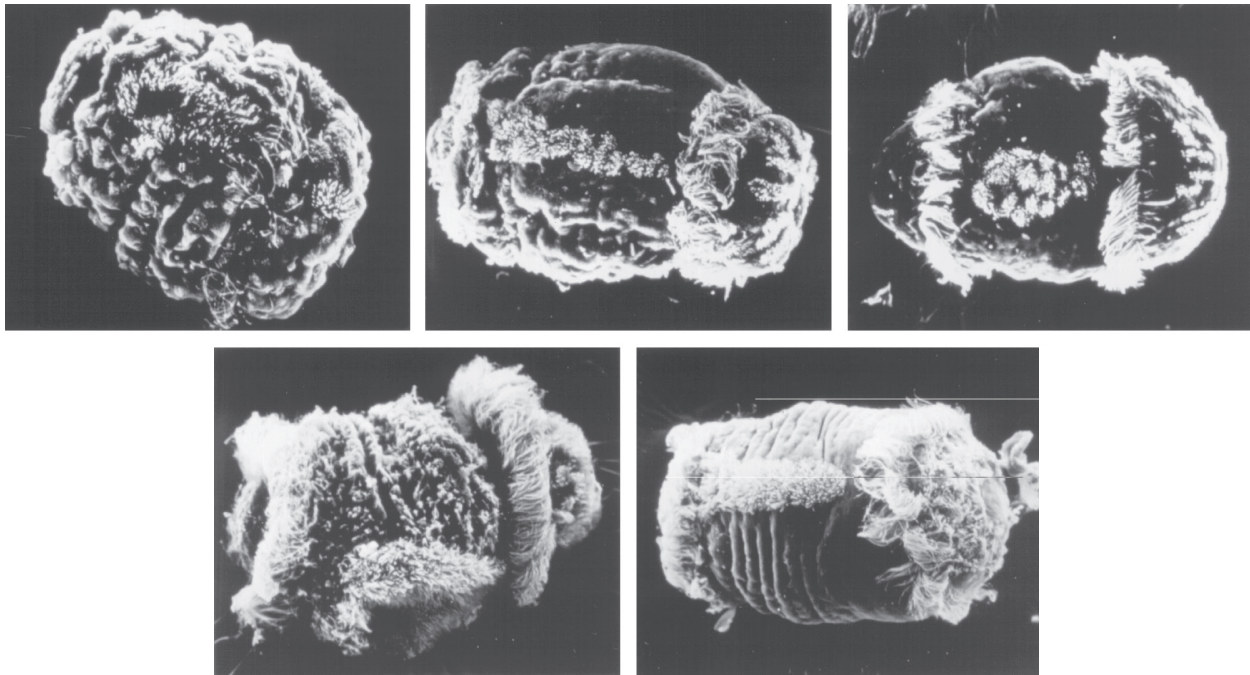
FIG. 4.26   Larvae of five sibling species of the polychaete worm genus *Capitella*, living in southern New England muds. (Courtesy of K. J. Eckelbarger and J. P. Grassle)

mud-dwelling polychaete annelid worm *Capitella capitata* is now known to consist of several closely related species that cannot be distinguished easily as adults but are quite different in the larval stage and also in chromosome number (**Figure 4.26**).

The **parapatric** model of speciation emphasizes the possibility of the origin of differentiation despite contact, as long as there are different natural selection pressures in the respective semi-isolated populations, allowing divergence even in the face of some gene flow from other populations. In effect, according to this model, natural selection is sufficiently strong to balance the influx of genes from another population, and reproductive incompatibility eventually develops between the two semi-isolated populations.

Identification of closely related species is accomplished primarily through unique DNA genetic markers that clearly identify one species from another.[2] Occasionally, some unique morphological trait may be found, as just mentioned for larvae of sibling species of the worm *Capitella.* **Figure 4.27** shows a DNA marker used to discriminate between two species of marine mussel, *Mytilus edulis* and *M. trossulus. M. trossulus* tends to occur in colder waters and has been found to occur in Newfoundland, eastern Canada, with *Mytilus edulis*, which is usually found farther south. Using a technique known as PCR to amplify DNA variants and separating them and visualizing unique bands (**Figure 4.27**) by a technique known

ITS DNA marker

Hybrid   *M. edulis*   *M. trossulus*

Internal shell color

Mytilus edulis   *Mytilus trossulus*
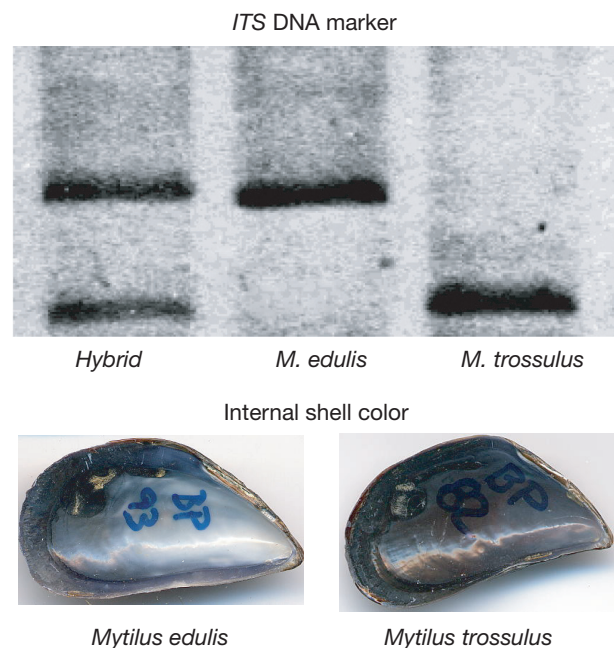
FIG. 4.27   Closely related or sibling species are often difficult to identify. Top: The *ITS* gene is used to diagnose sibling species of the mussel genus *Mytilus*, especially in locations like Newfoundland where hybrids are known to occur. DNA genes are isolated and run on an agarose gel for diagnosis. Bottom: Using the *ITS* gene for diagnosis, it was learned that internal shell color could be used also to tell the species apart. (Courtesy of David Innes; top photograph by J. Toro)

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[2] See discussion of barcode species identification in bonus chapter online.

as electrophoresis can readily pick up hybrids. As can be seen, the hybrids show up as double bands because the individual has inherited a copy of the gene that produces a different variant in each parent species. "Pure" species show single bands. In this case, Toro and colleagues (2002) discovered that all individuals with a unique DNA indicator band also had a specific shell color that differed between the two parent species.

Although most marine species probably arise from isolation across some sort of barrier, it is likely that some species arise within a population where males and females potentially have free contact. This could happen if there is a polymorphism for specificity for different microhabitats, which might lead to genetic variants mating and being located in the two different microhabitats, where selection reduces movement between the microhabitats. Such a mechanism is known as **sympatric speciation**, and has not been widely observed in the sea. Second, assortative mating might accelerate the division of two populations. If a polymorphism for color exists, it is possible that individuals of similar color and using visual mating cues might mate preferentially. This would possibly result in two differentiated species being formed if the assortative mating were continuous and without any crossing between morphs. For example, Barreto and McCartney (2007) investigated the blue hamlet and butter hamlet (genus *Hypoplectrus*), which are taken to be different species. But they used genetic markers known as amplified fragment length polymorphisms to show that these were not really different species at all but merely mated assortatively by strict color preference. No genetic variant they investigated could diagnose between these two forms. Rare matings between the color morphs seem sufficiently frequent to keep these two populations from becoming reproductively isolated true species.

As species are formed and genetic differences accumulate between closely related species, a series of isolating mechanisms develops between species. **Premating isolation** involves mechanisms that prevent members of two species from mating and producing zygotes in the first place. This is especially an interesting problem in the case of species with planktonic gametes. Even when gametes of different species are present together in the water column, the presence of different egg-sperm attractants, barriers to sperm penetration, and other mechanisms may have evolved to prevent crossing of species. In species that copulate, a series of behavioral mechanisms—including time of mating, location of mating, and mate recognition signals—may allow individuals to avoid mating with those of other species, even when very closely related. It is believed that newly formed species will evolve accentuated premating isolation mechanisms after they have reencountered each other, following a period of isolation. Even if two species cross and produce zygotes, **postmating isolation** might prevent successful production of offspring, as when gametes are incompatible. As two species are isolated and genetic differentiation occurs, a series of genetic incompatibilities might evolve that results in improper embryonic development or early death of embryos that arise from hybridization of newly formed species.

■ **Taxonomic classification involves successively nested grouping of species.**

Biologists universally accept the naming system devised by Linnaeus, which gives a species a binomial (two-name) description. Every species is described by its **genus** (plural: genera) plus **species** names. For example, the killer whale is named *Orcinus orca*. The genus is always capitalized; the species name never is. Note that species names are published in italics or written and then underlined. Some species are divided into subspecies, and three names are then used. One can abbreviate the genus portion of a species name (e.g., *O. orca*).

Organisms are classified into groups larger than the species level. Each high-ranking group is made up of a cluster of groups of the next lower level. The major taxa, or classification ranks, are as follows (from the lowest to the highest): species, genus, family, order, class, phylum, and kingdom. For example, the blue mussel on the east coast of the United States has the species name *Mytilus edulis*, belongs to the genus *Mytilus*, is a member of the family Mytilidae, the order Fillibranchia, the class Bivalvia, the phylum Mollusca, and the kingdom Animalia. Note that only the genus and species names are italicized.

Species are grouped by their overall evolutionary relationships. Species in the same genus are hypothesized to be more closely related by descent to each other than to species belonging to other genera. Genera within one family are usually believed to be more closely related to each other than to those in another family.

■ **Characters can be used to construct trees of relationship. Taxa are grouped by means of shared evolutionary derived characters.**

All members of a given group have shared evolutionary characters, which unite them by descent and distinguish them from other groups. Thus, mollusks have an external calcium carbonate shell, differing in that respect from members of other phyla. Arthropods, such as insects, horseshoe crabs, and shrimp, all have an external cuticle, a distinct segmentation, and jointed appendages. We argue that the more distinctive characters members of a group may share, the more likely it is that the group evolved from a common ancestor. This notion allows us to construct evolutionary trees of relationship, or **cladograms**, such as **Figure 4.28**, which shows the relationships of some purely hypothetical organisms. Note that we cannot be sure about the exact history, such as who the ancestors might be. In the figure, we take the simplest creature with fewest acquisitions to be the most ancestral, but this is based only on an assumption about the simplest being the most ancestral. From the characters, we can say only who is more closely related to whom. More direct evidence, such as a fossil record, might help determine ancestry.
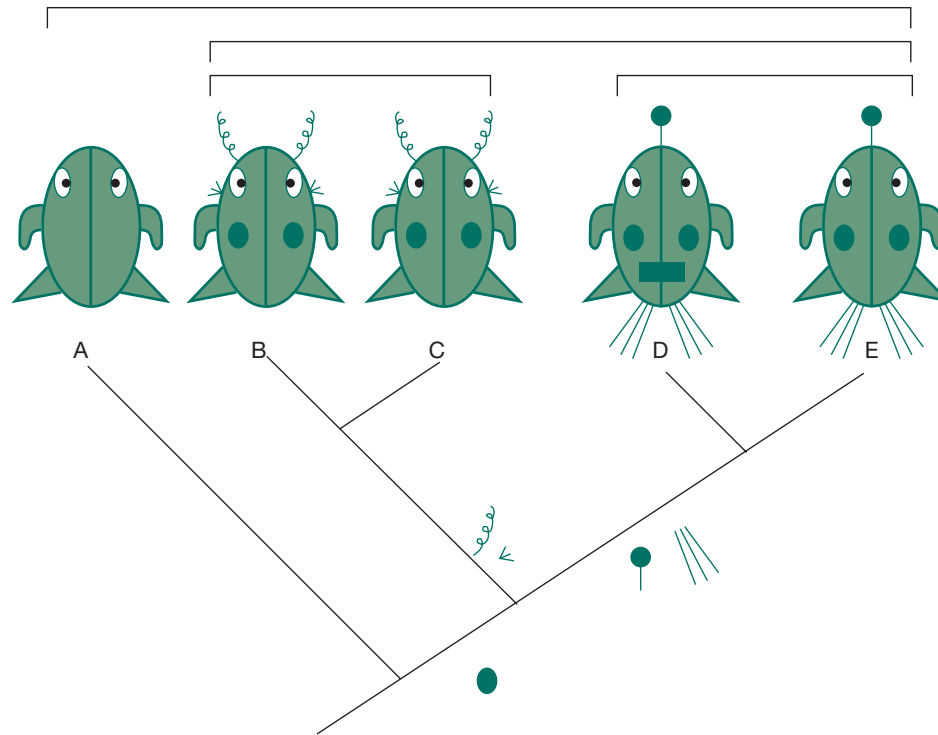
DNA nucleotide sequences

Species	n1	n2	n3	n4	n5	n6	n7	n8	n9	n10	n11	n12	n13	n14	n15
A	A	A	C	A	G	T	A	A	C	A	C	A	A	C	C
B	A	A	T	T	T	A	T	C	C	T	A	C	A	A	C
C	A	T	T	T	T	A	T	C	C	T	A	C	A	A	A
D	C	C	T	A	A	T	A	C	C	A	A	A	A	C	T
E	C	C	A	A	A	T	A	C	C	A	A	C	A	A	T

FIG. 4.28   Organisms that share a greater number of distinctive characters are likely to derive from common ancestors. Brackets on top indicate hierarchy of groups; morphological characters used to unite groups are shown along branches of the tree. Beneath the tree is a table of hypothetical DNA nucleotide sequences for the five groups. As can be seen by counting, groups B–C and D–E have the most nucleotides in common, which makes these data concordant with the morphological data. Evidence for grouping B–C and D–E groups is shown by colors of identical nucleotides.

An analysis of real critters may lead to a good deal of complexity (**Figure 4.29**) but also to an impartial analysis of evolutionary relationships. Groups are united by sets of uniquely shared evolved characters. Thus, as you go "upstream" to the base of the tree, you are encountering nodes in the tree with traits that unite all the downstream groups.

■ **DNA sequences are now used commonly to construct evolutionary trees.**

Although morphological characters may be very useful in understanding evolutionary relationships of species, DNA sequences are now commonly used for this purpose. Why? Because morphological characters often look alike only because natural selection has caused a form to evolve to converge on a single shape, which is directed by evolutionary adaptation to the local environment. For example, the presence of a predator might cause **convergent selection** in two distantly related snail species for the narrowing of a snail's aperture, which is a good adaptation to deter predators. Therefore, we cannot rely on that character to give evolutionary information about relationships. This could be true of some DNA sequences, but most are believed to be far less related to such simple cases of **convergence**. Using more genes and longer sequences of DNA will increase confidence. While it is not straightforward to quantify the difference, DNA sequences effectively give access to thousands of variable characters, many more than we can get from morphological characters. Of course, natural selection operates on DNA, and multiple mutations over time can mask the evolutionary relationships among species at any given nucleotide site, or exact location on the DNA that can vary as one of several genetic variants. But the large number of sites that are not controlled by natural selection and the large number of nucleotide sites that evolve slowly (and therefore, do not have the record of evolutionary relationships erased) should make up for these problems.
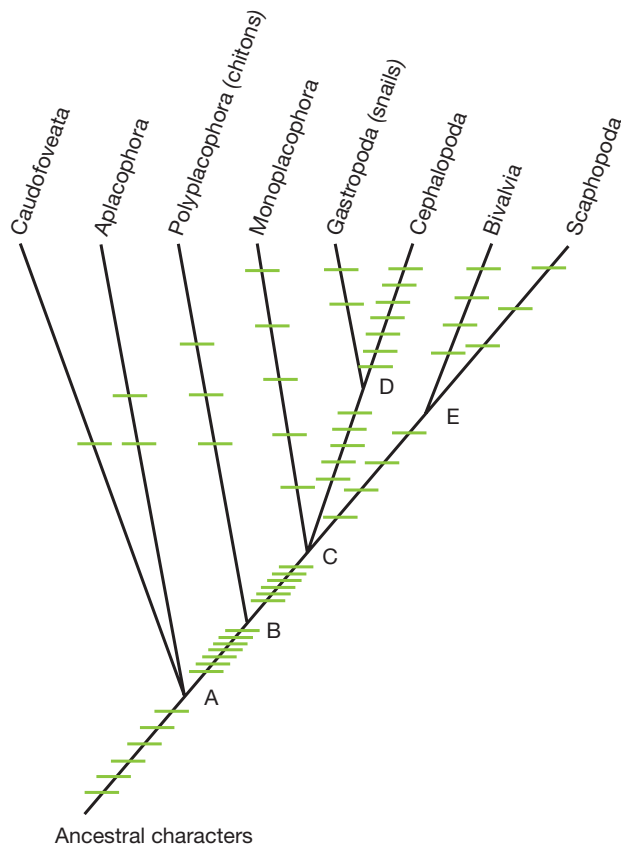
FIG. 4.29 A tree of evolutionary relationships for the phylum Mollusca. Traits (horizontal lines) between nodes unite all taxa downstream of the node higher on the page. On the stem of the tree, a number of characters unite the entire phylum, including reduction of the coelom, presence of an open hemocoelic circulatory system, and production of spicules or shell by a mantle shell gland. "Downstream" of every node (locations A–E) are traits that uniquely identify individual groups. Thus, the Bivalvia–Scaphopoda line is downstream of node E and the two groups are united by head reduction and decentralization of the nervous system, among other traits. (Modified from Brusca and Brusca, 1990)

The process of constructing phylogenies from DNA involves the following basic steps. First, DNA must be extracted from the individuals, and appropriate methods must be used to locate the specific genes to be sequenced and then to sequence those genes. This might lead to the sequences in **Figure 4.28**. Remember that each amino acid is coded by three nucleotides. We are using, for example, a DNA sequence that codes for amino acids in a protein of five amino acids. Note that one must choose the genes to sequence with care because some DNA may evolve far too slowly to obtain enough variation to analyze. In other cases, the rate of DNA evolution may be so fast that the record of evolutionary history is erased, making it impossible to relate one sequence to another. Following the sequencing step, two more steps are necessary:

1. Alignment of the DNA sequences so that individual nucleotide sites are evolutionarily related to each other

2. Construction of a tree based on the differences between evolutionarily related, or **homologous**, sites

A tree can be constructed by many methods, but the simplest is to join pairs of individuals whose sequences have the fewest differences. Then, in another round, these groups can be joined into larger groups on the same basis. Eventually, this will give a nested set of groups whose relationships arise from evolutionary transformation. The species that are most distant on the tree are most distantly related. The interested student will soon find that this is a very oversimplified representation, and many problems arise in calculating a tree (Felsenstein, 2004). In **Figure 4.28**, the DNA table is concordant with the morphology. As you can see, the groupings of B–C and D–E have the most nucleotide types in common and A is more distant, meaning that it has fewer nucleotides in common with the other two groupings.

■ CHAPTER SUMMARY

- Ecology is the study of biotic and abiotic interactions between organisms and their environment as they affect distribution and abundance. Biotic interactions such as competition are often affected by available resources.

- The ecological hierarchy consists of the individual, population or species, community, ecosystem, and biosphere. A population is a group of individuals that are affected by the same overall environment and are relatively unconnected with other populations of the same species.

- A species' ecological niche is its range of habitats. Interactions between individuals include territoriality, predation, commensalism, mutualism, and parasitism. Most populations are

dynamic, and limiting resources may affect population growth. Populations may become so rare that they have difficulty finding mates and will no longer increase.

- A population may be distributed randomly, more evenly, or in patches. A *metapopulation* is a series of interconnected subpopulations.

- Community ecology, or the interaction among species, helps determine their distributions. Often, one or more foundation species alter the habitat to allow others to live there. Other important processes are (a) dispersal of larvae, spores, and adults; (b) competition; (c) predation and herbivory; (d) parasitism; (e) disturbance; and (f) facilitation (or

positive interactions between species). The competition for resources involves space and food.

- Prey can survive by moving into refuges or escaping, evolving fixed or plastically responsive defenses, or outgrowing the predator's ability to subdue them. Still, seasonal influxes of predators in shallow water and in the intertidal zone may devastate prey populations. Disturbances such as storm damage can also greatly alter species abundances.

- Common parasites can reduce growth and reproduction as well as cause enfeeblement. Diseases can cause swift declines in marine populations.

- Succession is the ordering of species appearance, usually following a disturbance. Often, species may not be

able to colonize unless another species dies off either from disturbance or predators.

• An ecosystem is a group of interdependent communities in a single geographic area. Nearly all ecosystems have primary producers, which are consumed by herbivores and in turn are eaten by carnivores. The material that escapes passes through the saprophyte cycle. While primary productivity has a bottom-up effect on ecosystems, some predatory species at the apex of food webs exert top-down controls.

• Traits vary as a function of genetic polymorphism and plasticity in responding to environmental variation. Natural selection can lead to changes in the frequency of alleles, and a regular spatial change of allele frequency within a geographic area is called a cline. New species may arise when a barrier isolates two populations and they no longer interbreed.

• Every organism is described by its genus (plural: genera) and species. Evolutionary relationships can be used to construct trees of relationships. Taxa may be grouped by morphology or DNA sequences.

■ REVIEW QUESTIONS

1. Describe the ecological hierarchy.

2. Distinguish between a population and a community.

3. What is the difference between renewable and nonrenewable resources?

4. If the distance between exploitable patches increases, should the time spent by a forager in a patch increase or decrease? Explain your answer.

5. Under what conditions might a marine creature have color that matches the background? When might it have strongly visible coloration?

6. What is the advantage of an inducible defense as opposed to a fixed trait that is always available for defense?

7. Distinguish between commensalism and mutualism.

8. Why are parasites likely to have complex life cycles?

9. How might a resource limit population growth?

10. How might several genetic variants be maintained over time in a single population?

11. What is the main determinant of biogeographic provinces in coastal marine environments?

12. What is the major effect of predation in communities of competing prey species?

13. What are the major processes that contribute to determining the relative abundance of species in a community?

14. Define ecological succession.

15. Distinguish between biomass and productivity.

16. Some species consist of genetically identical individuals, all of which are very flexible in their ability to live in different subhabitats, whereas other species consist of individuals, each of which is distinctly different and specialized for a given subhabitat but inflexible. Under what conditions might each species be favored?

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