CHAPTER 14

Marine Ecology

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CRITICAL CONCEPTS USED IN THIS CHAPTER
CC14 Phototrophy, Light, and Nutrients
CC17 Species Diversity and Biodiversity

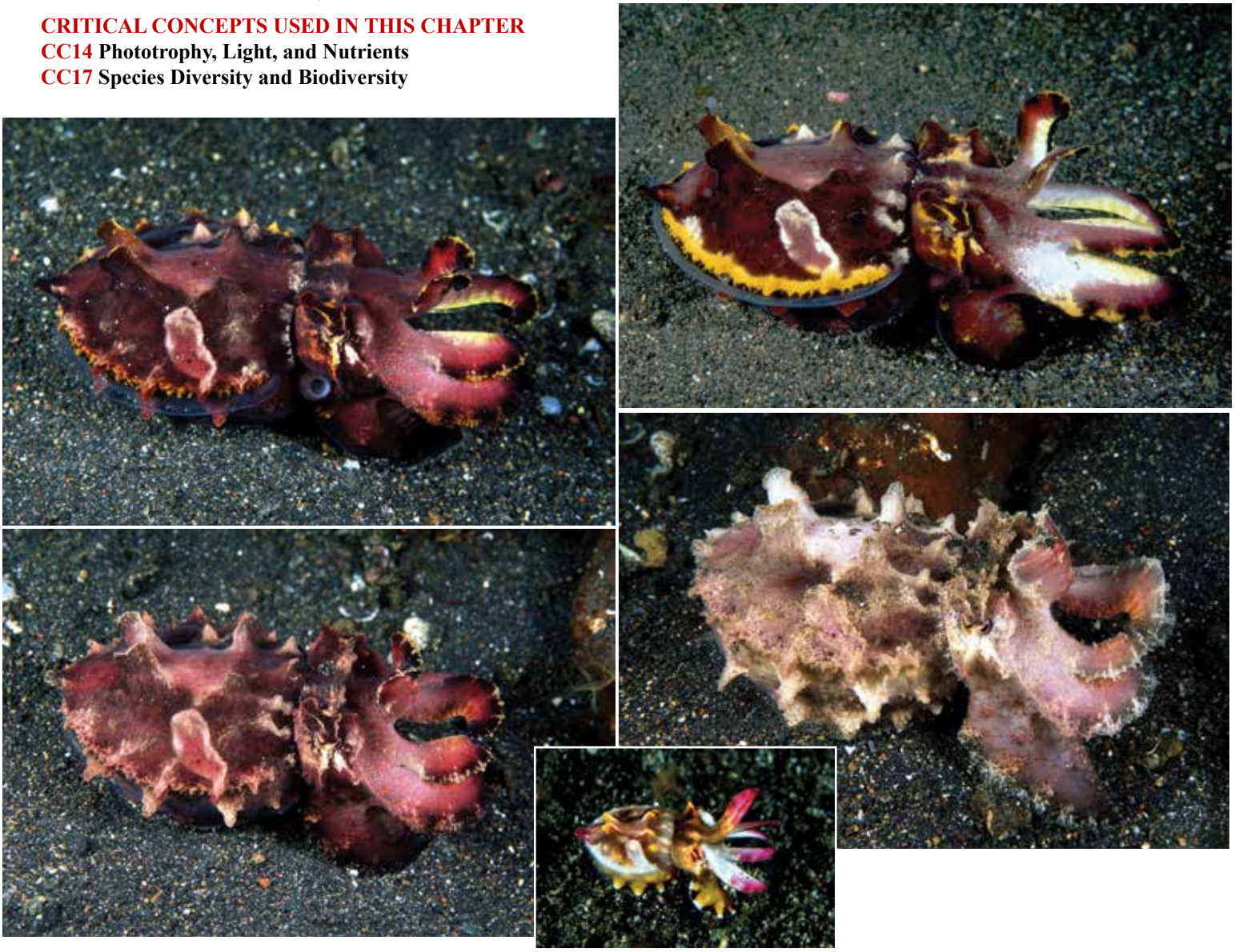


FIGURE 14-1. Each of these images show the flamboyant cuttlefish (Metasepia pfefferi), which can grow to about 10 cm long. The four larger images illustrate the mastery that this species has with changing its colors. These four photos, all of the same cuttlefish, were taken in succession over a period of less than one minute. Unfortunately, the full startling range of its color cannot be captured in photographs, it can only be seen properly in person. The smaller image in the bottom left corner is a young cuttlefish, which is only about one centimeter long. It is no more than a few days old, but is already capable of the same color changing artistry that the adults of its species possess. In fact, the cuttlefish can alter their colors even before hatching from their transparent egg cases, as seen later in this chapter in **Figure 14-28**.

The oceans are populated by uncounted millions of **species**, most of which have not yet been identified. Marine ecology is the study of relationships between species and between species and their **environment**.

Because each species has a unique relationship to the ocean environment and to other species, marine ecology is a complex discipline. This chapter describes the environmental factors that govern the distribution of marine organisms, and the types of adaptations that have evolved in marine species to meet the challenges of living in the ocean.

ECOLOGICAL REQUIREMENTS

A fundamental imperative of life is survival of the species. Hence, all species must meet two requirements. First, an adequate food supply must be ensured for each life stage. Second, enough individuals of the species must survive until they reproduce successfully. The principal challenges are

- Where to live
- What food to eat and how to obtain it
- How to avoid predators
- Where, how, and when to reproduce

In meeting these challenges, marine species have adopted an extraordinary variety of life cycles to take advantage of the vari-

ous attributes of the marine environment.

HABITATS

The major **habitats** available to marine organisms are in the water column, on the seafloor surface, and in seafloor **sediment** (Chap. 12). For **photosynthetic** organisms (CC14), only the first two habitats are suitable, and only within the **photic zone**. Consumer and **decomposer** species are present in each of the three habitats: **pelagic** species in the water column, **benthic epifauna** and epiflora on the seafloor, and benthic **infauna** within the sediment.

The three habitats offer different advantages and challenges. Each species has selected its own unique balance between those opportunities and challenges. Many species take advantage of different balances at successive stages of their life cycle by changing their habitat between stages.

In shallow water, photosynthesis may take place at the seafloor if it is within the photic zone, and **chemosynthetic communities** are present at least in restricted areas of the seafloor below the photic zone. In both locations, **primary production** by benthic organisms creates some food. This primary production can be substantial locally, particularly in coastal waters and at **hydrothermal vents**, but in most of the ocean the food supply is produced by photosynthesis by phytoplankton that include algae and cyanobacteria. Some archaea utilize light energy to supplement their energy needs, so they are **phototrophs**, but they use a mechanism other than photosynthesis and may use simple organic compounds instead of carbon dioxide. In the deep ocean, nutrient depleted, high oxygen waters and deep sea sediments, certain species of **archaea** are the dominant "primary producers" (Chap. 12, CC14).

Pelagic Habitat

Phytoplankton and other phototrophic microorganisms in the pelagic environment are effectively **grazed** by **zooplankton** and single-celled **protists** that, in turn, are eaten by **carnivores** or omnivores. During this process, most of the **biomass** produced by primary producers is used by photic-zone pelagic consumers to fuel their energy needs (Chap. 12). Consequently, only a small fraction of primary producer biomass eventually sinks or is transported below the photic zone, and food is scarce in the environments below the photic zone.

Most pelagic organisms must actively seek food and avoid or fight off predators at the same time. Whatever strategy an organism uses for these activities, it uses up energy that must be obtained from food. Hence, one penalty for living in the pelagic habitat is that more food must be consumed than is needed for growth and reproduction. The need to avoid sinking also carries an energy penalty for pelagic organisms. **Buoyancy** can be maintained by swimming, which uses energy directly, or with pockets of gas or low-**density** oil in the body structure, each of which requires energy to produce.

All pelagic organisms must evade predators, compete for food, and counteract the tendency to sink. Below the photic zone, predators are less abundant and easier to avoid because they cannot hunt visually in the darkness. Offsetting this advantage is the scarcity of food below the photic zone. Many species, especially of zooplankton and squid, migrate between the photic zone and the **aphotic zone** to take advantage of this trade-off between the zones. These organisms feed in the photic zone at night and then descend to the darkness below in the day, in a strategy known as **diel** vertical migration. Nevertheless, even this behavior has an energy cost, because energy must be expended to move vertically between layers.

Benthic Epifaunal Habitat

Organisms that live on the seafloor do not need to expend energy to control buoyancy and generally require less energy to find and capture food than pelagic organisms require. Hunting is reduced to a two-dimensional problem, and because many benthic prey are sedentary or nearly so, hunting movement can be slow and energy-efficient. Even more energy is saved by **benthos** that remain sedentary and wait for prey to walk, swim, or drift by.

The energy savings of living in the benthic epifaunal environment may be offset by the scarcity of food and the difficulty of evading predators. Organisms that move slowly and sit on the sediment may be easy to find and capture. Hence, many benthic epifaunal species have developed defensive mechanisms such as poisons, spines, and shells or tubes into which they withdraw. Such mechanisms require energy that otherwise could be used for growth and reproduction. Where food is readily available, epifauna may be abundant and the competition for available space may be a significant disadvantage. Finding living space is a problem, particularly for epifauna that attach to rocks, because most of the seafloor is covered by sediment and rocky substrates are very limited.

Although the benthic epifaunal environment in shallow water is similar to that in deeper water, benthic algae enhance the food supply in many shallow areas. Coral reefs sustain exceptionally diverse (CC17) and abundant encrusting algae communities. Also, in some shallow areas the kelp in kelp forests (Fig. 15-8) provides abundant hiding places for predator avoidance.

Benthic Infaunal Habitat

Even though food is scarce in most of the benthic infaunal environment, some organic **detritus** accumulates continuously in sediments. Many animals, such as worms and certain **crustaceans**, feed by sifting sediment grains to obtain organic particles or by digesting organic matter as sediment is passed through the gut. Other benthic infaunal species live in the sediment primarily for protection from predators and feed on particles in the water above or prey on passing animals.

The relatively poor supply of food available to benthic infauna is offset by the energy savings of relatively sedentary lifestyles, by the lack of need for buoyancy control, and by the reduced need for defenses against predators. In **estuarine** and other coastal environments, much of the **salinity** and temperature variation that can occur in overlying waters does not occur in the sediment, so infauna are not subject to these environmental stresses. Intertidal benthic infauna also avoid exposure to air during low **tides**.

Benthic infauna must expend energy to dig into or move through sediments or rock. They must also cope with an environment that varies because of **biochemical** and chemical processes within the substrate. The most important of these processes consume dissolved oxygen and produce toxic hydrogen sulfide, so most infaunal species can live only in the oxygenated surface layer of sediment. In areas where detritus inputs are high and water movements slow, the oxygenated layer is thin or absent, but elsewhere it ranges from a few millimeters to several meters in thickness. Where sulfide is present, the **biota** consists primarily of **bacteria**, archaea, and **fungi** adapted to the sulfide environ-

ment and animals that build burrows or tubes through which they can obtain oxygenated water from above.

Other Ocean Habitats

Special challenges and opportunities are also found in other ocean habitats, including the **surface microlayer**, the **intertidal zone**, and hydrothermal vents. The surface microlayer, which is only a few molecules thick, concentrates a variety of natural and **contaminant** organic compounds. A few species attach themselves to the surface microlayer to keep from sinking. **Surface tension** tends to prevent small particles within the microlayer from sinking, even if their density is higher than that of seawater. Many species distribute their eggs and **larvae** by placing them in the surface microlayer, where **currents** distribute them until they grow large enough to feed and swim independently. Placement in the surface microlayer reduces the need to use energy to provide the eggs and larvae with oils or other means of buoyancy control.

Although the intertidal zone and hydrothermal vents are sites of very high **primary productivity** and food is abundant, each of these habitats imposes substantial offsetting challenges due to variations in environmental conditions. These two unique environments are discussed in **Chapter 15**.

FEEDING

With the exception of organisms that obtain their energy needs through **phototrophy** or chemosynthesis, all marine species must obtain energy from organic compounds that they obtain as food. The food can consist of another living organism, nonliving organic particles, or dissolved organic compounds.

Because concentrations of dissolved organic compounds in seawater are extremely low, few marine species are known to rely on dissolved organic matter as their principal source of sustenance. Nevertheless, this source of food may be important to some species, including bacteria and other decomposers, and a few higher animals. To use dissolved organic matter, an organism must take up individual dissolved molecules through its membrane surface. This process is very slow if dissolved compounds are transported to the membrane by **diffusion**, but it can be enhanced if water flows over the membrane.

In terrestrial **ecosystems**, animals feed in three basic ways: by grazing the abundant macroscopic (large) plants that cover much of the Earth's surface, by consuming detrital organic particles in leaf litter and soils, and by hunting and eating other animals. Similarly, in the oceans many species graze on the seafloor, eat detritus in the sediment, and hunt and eat other animals. However, because most autotrophs and detritus in the oceans consist of small particles dispersed in the water column, many marine species are **suspension feeders** that feed on particles.

Suspension Feeding

Suspension feeders must be able to efficiently gather the phytoplankton, zooplankton, and detritus particles that constitute their food. They do so in several different ways. Many suspension feeders are **filter feeders** that have a web-like or mat-like structure to capture particles as water flows through it. This simple method works efficiently for suspension feeders that filter out and eat large particles, but filter feeding becomes more difficult as the size of the filtered particles becomes smaller. Zooplankton that eat small phytoplankton and detritus particles would need a filter mesh so small that **viscosity** would restrict the flow of water through the filtering apparatus. Consequently, these zooplankton generally have evolved hairlike appendages, called "setae," on their mouths. As water passes through the mouth, particles are captured by the setae.

As an alternative or sometimes an addition to filter feeding, many suspension feeders secrete mucus to which particles adhere

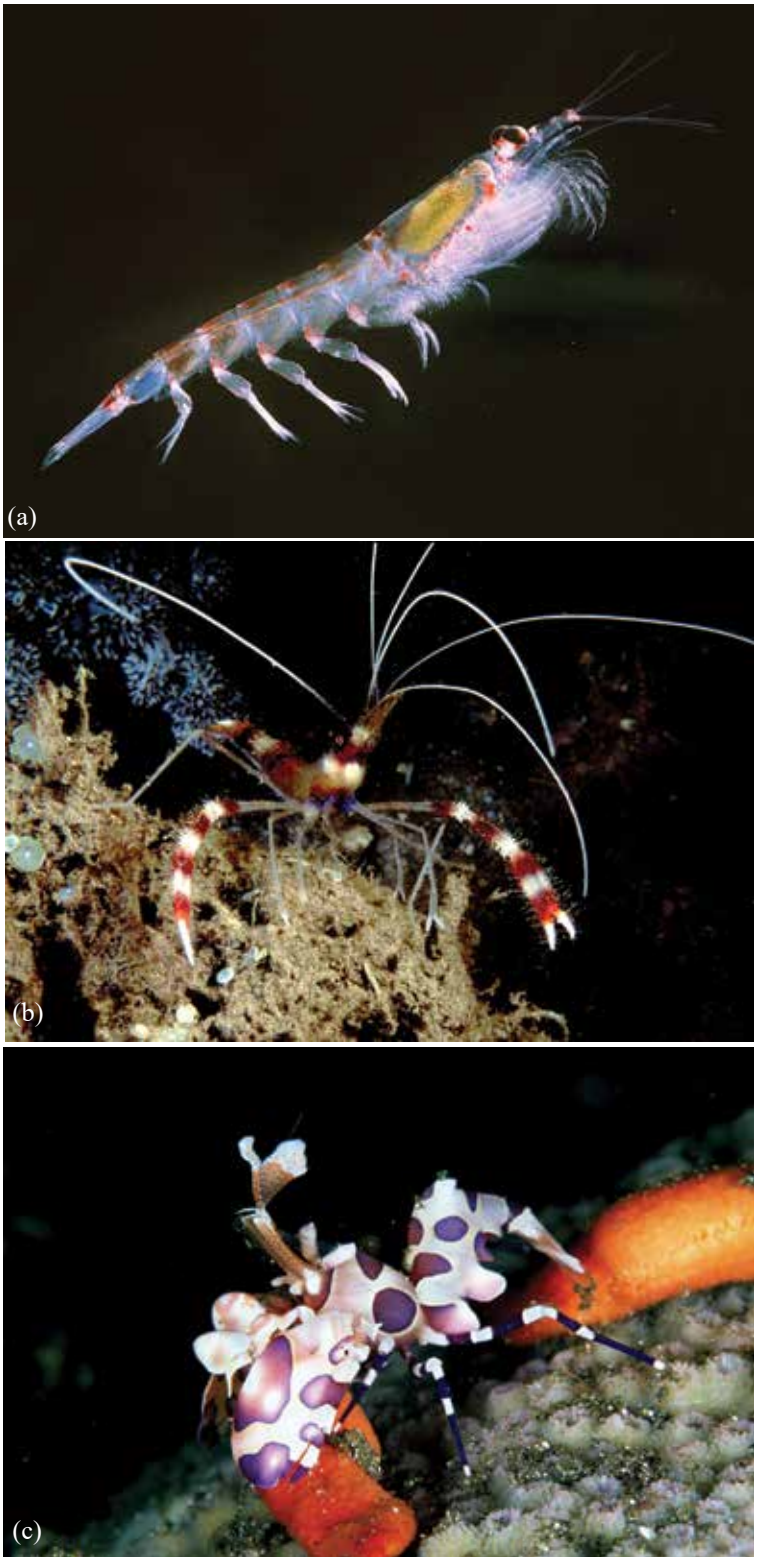


FIGURE 14-2. Forelimb use in crustaceans. (a) A deep-sea euphausiid or krill. (b) Banded coral shrimp (*Stenopus hispidus*, Papua New Guinea). (c) Harlequin shrimp (*Hymenocera elegans*, Papua New Guinea). The forelimbs of the krill are adapted for filter feeding. Compare these with the forelimbs of the coral shrimp, which eats larger food particles than the krill does, and the massive forelimbs of the harlequin shrimp, which feeds on tough sea star bodies.

as water flows past. The organism then ingests the mucus and the food that it contains. Many other suspension feeders capture particles that come in contact with appendages designed to grab or grasp a particle and transfer it to the mouth. A number of zooplankton species feed on relatively large prey by capturing them in this way with setae on their appendages. When this mechanism is used to capture live prey, it can be considered a hunting method and the organism can be considered a predator.

Many suspension feeders ingest particles selectively, most often by size. Particles smaller than a certain size are not captured by the filtering or other feeding apparatus, and particles larger than a certain size cannot be captured or passed into the mouth. Different species have evolved to collect different size ranges of particles. Certain zooplankton species that are adapted for capturing large phytoplankton, such as **diatoms**, tend to be most abundant where and when diatoms are the dominant phytoplankton. Other zooplankton species are better adapted to capture smaller phytoplankton, such as **flagellates**, and therefore are most abundant when flagellates dominate. Because different species of carnivores feed on different **herbivorous** zooplankton species, the size of food particles available to suspension feeders can affect the entire food web.

Many suspension feeders selectively ingest only certain species within a selected size range of particles. For example, herbivores consume only living phytoplankton cells and reject detritus particles of similar size. Such selective feeding requires the feeding organism to expend energy to sort its food supply. The benefit gained is that the selected food has higher nutritional value than non-selected species or detritus has. In contrast, many suspension feeders are nonselective omnivores that ingest bacteria, archaea, algae, animal, and detritus particles of appropriate size without discrimination.

Suspension-feeding species inhabit both pelagic and benthic environments. Pelagic suspension feeders include zooplankton and **nekton**. Some **planktonic** suspension feeders simply drift through the water, capturing food particles brought to them by turbulence and diffusion. The chance of encountering a food particle in this way is low because of the low concentrations and slow movement of the particles in the water, so filter feeders generally have evolved methods of ensuring a flow of water through their feeding apparatus. The three basic methods are:

- Actively pumping water through the filtering apparatus
- Moving the filtering apparatus through the water
- Keeping the filtering apparatus stationary and allowing ocean currents to move water through it

Marine organisms have developed numerous physiological variations and apply one or a combination of these methods to capture food.

Pelagic Suspension Feeders

Many pelagic suspension feeders have evolved mechanisms to move or pump water past or through their feeding apparatus as they drift through water. Crustaceans such as **copepods** and **euphausiids** (**Fig. 12-19a,b**) have long, slender forelimbs or appendages surrounding their mouths (**Fig. 14-2a**), with which they grasp or direct suspended food particles toward the mouth. In contrast, the equivalent mouthparts of most shrimp, also crustaceans, are designed to cut or crush, reflecting the shrimp's hunting or **scavenging** feeding habits (**Fig. 14-2b,c**). Suspension-feeding crustaceans and many other zooplankton can swim weakly through the water to increase their chances of encountering food particles.

Pteropods, which are **mollusks** related to slugs and snails, have adapted to suspension feeding by evolution of their foot (like the foot on which a snail crawls) to be a membrane that extends from the body (**Fig. 14-3**). The pteropod uses this sail-like membrane as a paddle to propel itself slowly through the water. This action moves water past the mucus-covered membrane, which captures suspended food particles that brush against it.

Salps, a type of **tunicate**, evolved in aquatic environments to take advantage of suspended particulate food. Many salps have a simple body resembling an elongated barrel (**Fig. 12-20e**) with an opening at either end. Within the barrel, the salp is coated with a continuously moving mucous sheath, which captures food particles from water pumped continuously through the salp's body by sequenced contractions of bands of muscles. There are also colonial salps, which are composed of individual members joined to form the outer wall of a sac-like structure. Each individual's **incurrent** opening faces outward, and each **excurrent** opening discharges into the common open space inside the sac (**Fig. 14-4**). This arrangement enables the colony to "swim" as water is forced out of the relatively narrow sac opening by the combined pumping efforts of its members. As a result, each individual is more likely to encounter food particles than it would if it operated

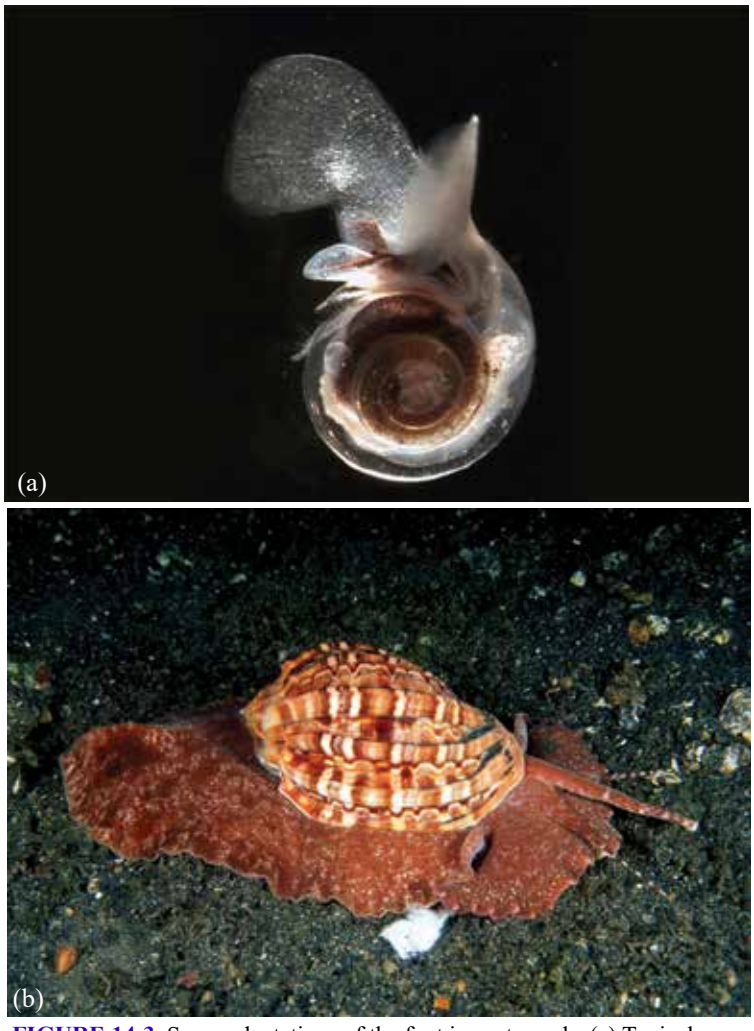


FIGURE 14-3. Some adaptations of the foot in gastropods. (a) Typical pteropod (Limacina helicina). (b) Marine gastropod, a harp shell (Harpa major, Indonesia). The transparent part of the pteropod is its foot, which is very different from that of other gastropods, such as the harp shell. The harp shell's foot is extended from its shell flat onto the seafloor and allows it to "walk."

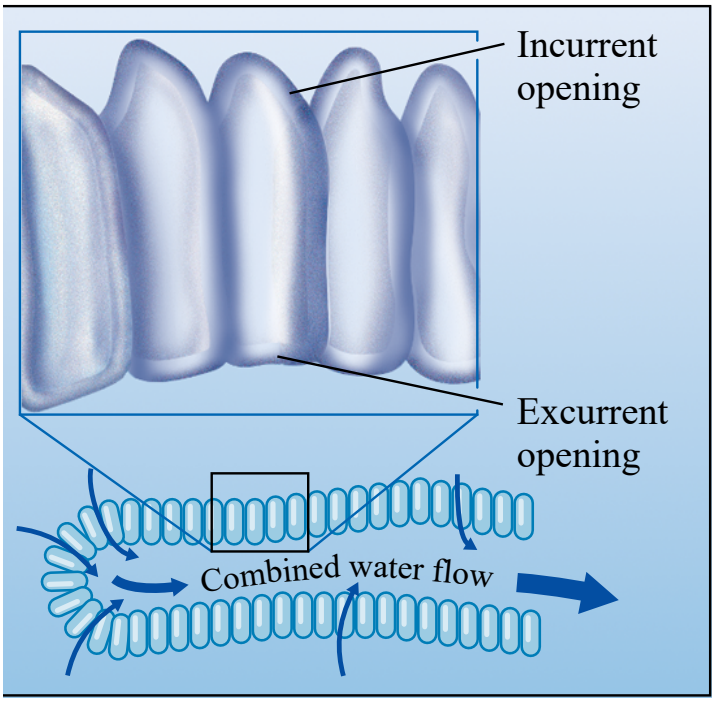
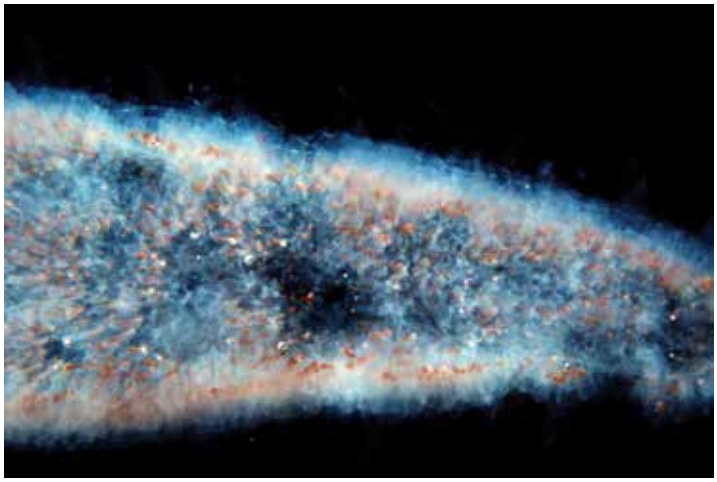


FIGURE 14-4. Salps. Each individual of a salp colony draws water into its body and filters it for food. The combined water flow from all individuals is passed out of the open end of the saclike colony, which slowly propels the colony through the water. If you look carefully in the inset photograph, you will see the individual members of the salp colony. Note that they resemble their relatives, the tunicates shown in **Figure 14-9**.



alone.

Most **jellies** and **ctenophores** (**Fig. 12-20d**) feed on suspended particles by extending long trailing tentacles that, in some species, have poisonous stinging cells and, in others, are covered with a sticky substance to capture food. These organisms are generally carnivores that feed selectively on zooplankton or small fishes, and many propel themselves by contracting rhythmically while trailing their tentacles through the water in order to increase their chances of encountering food. The Portuguese man-of-war achieves a similar increase in mobility and feeding efficiency by allowing winds to blow the colony across the ocean surface.

Although many jellies and ctenophores are suspension feeders, larger species of these organisms are clearly hunters that selectively seek, kill, and consume small fishes and other nekton. The distinction between suspension feeding and hunting is not precise. Some species are clearly suspension feeders and some are clearly hunters, but other species use elements of both approaches and feed on both suspended particles (plankton and/or detritus) and small nekton.

Benthic Suspension Feeders

Like other benthos, benthic suspension feeders benefit from the low energy needs of their sedentary lifestyle and the lack of a need to control buoyancy. They have the additional advantage that ocean currents bring food to them, which reduces the energy needed to hunt for food. Consequently, many benthic epifaunal and infaunal species are suspension feeders. Suspension feeders are especially abundant in coastal regions where suspended particulate food is plentiful.

In soft sediments that cover much of the seafloor, certain infaunal suspension feeders pump water into their feeding apparatus through tubes that they extend upward into the water (**Fig. 14-5**). This feeding method is particularly advantageous in intertidal mudflats because a buried mollusk can withdraw its siphon and close its shell for protection when the sediment is exposed at low tide. On mudflats or muddy sand **beaches** where cockles are abundant, buried cockles can be detected as the tide **ebbs** because they squirt a small fountain of water into the air as they close abruptly when the water recedes.

The sea pen is a benthic infaunal suspension feeder that extends a beautiful and intricate fanlike structure into the water column to feed (**Fig. 14-6a,b**). Suspended particles are captured as they drift with the current into the fan. The fan can be folded up and withdrawn into the sediment where the main body of the organism is buried. Many sea pens withdraw by day and open to feed only at night, when zooplankton are more abundant because many species migrate from below the photic zone and nocturnal zooplankton emerge from their daytime hiding places. Other types of **invertebrates**, including some species of tube worms, **sea cucumbers**, and **anemones**, live in soft sediment and extend feeding tentacles or webs into the water (**Fig. 14-6**).

Epifaunal suspension feeders are especially abundant and diverse in **continental shelf** regions, where there is a solid substrate to which they can attach without being covered by sediment.

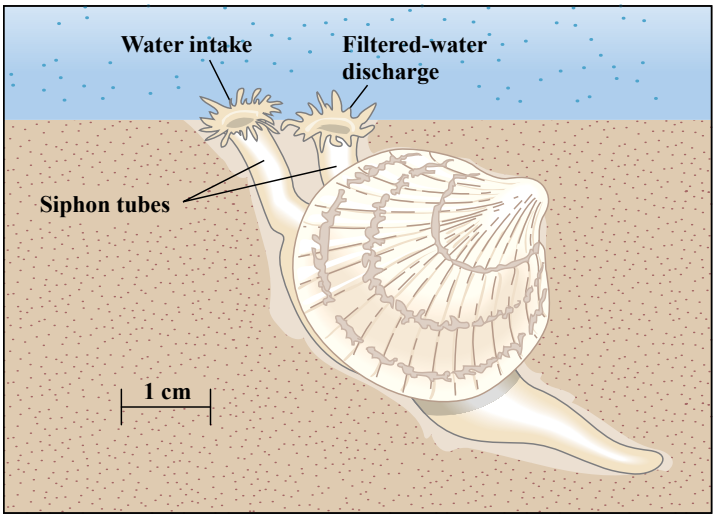


FIGURE 14-5. Some bivalve mollusk species, such as this cockle (family Cardiidae), live buried within the sediments but extend two tubes up into the water column just above the surface. They pump water in from one tube and out the other, and they filter food particles as the water passes through their bodies.

FIGURE 14-6. Examples of sand-dwelling benthic infaunal suspension feeders. (a) A sea pen (order Pennatulacea, Papua New Guinea) with its feeding polyps oriented into the current. (b) The reverse side of the same sea pen shown in (a). (c) This sand anemone (Papua New Guinea) feeds on large "suspended" matter such as small fishes. If it is threatened or when it captures prey, it can withdraw these tentacles almost instantly and completely into a hole in the sand, where the remainder of its body is hidden. (d) A tube worm (family Sabellidae, Papua New Guinea) with its netlike feeding apparatus extended into the water column. This worm, when it senses danger withdraws almost instantaneously and completely into its protective tube which is buried in the sand. It senses potential predators, by changes in lighting (e.g. shadows) and small pressure changes (vibrations) so getting close enough to photograph them open like in this image is not easy.

In temperate and high **latitudes** these areas are limited to a few rocky outcrops on the seafloor, but in tropical regions **coral reefs** provide extensive areas of suitable substrate. Suspension-feeding epifaunal invertebrates include species of mollusks, crustaceans, tunicates, **corals**, anemones, sea cucumbers, **sea stars**, and worms.

The most familiar epifaunal suspension-feeding mollusk is the mussel (**Fig. 14-7a**), which attaches itself to any available substrate and partially opens its shell to pump water through its body and feed. Other bivalve mollusks, such as the spiny oyster (**Fig. 14-7b**), use a similar method in coral reef communities, where they are firmly attached to the reef. Some scallop species in temperate latitudes do not attach to the seafloor, but instead live on coarse sand or gravel bottoms, from which they can "swim" up into the water column for short distances by snapping their shells shut to create propulsive jets of water.

Barnacles are suspension-feeding epifaunal crustaceans (**Fig. 14-7c**) that look nothing like their close relatives shrimp and crabs, because they have evolved an unusual feeding method. Barnacles, in essence, lie on their backs, strongly attached to rocks or other hard substrates such as ships' hulls, and are protected by hard plates and shells. They open the plates and extend their much altered legs as a weblike structure that sweeps through the water to grasp and capture suspended particles (**Fig. 14-7d**).

Most of us think of coral reefs as large, strangely shaped, hard, rocklike structures (**Fig. 14-8a,b**). However, reef-building

corals are actually extremely small suspension-feeding epifaunal organisms that grow in colonies, each of which may contain millions or even billions of individuals, called **polyps**. Some of the many species of corals have **hard parts** that are left behind when individuals die and thus serve as a base on which other polyps can grow.

The living coral individuals, or polyps, feed by extending tentacles that capture food particles, primarily zooplankton, and draw them down into the mouth (**Fig. 14-8c**). Most hard corals extend their tentacles to feed only at night, but many species of soft corals, which are found mostly in the Pacific and Indian Oceans, feed both day and night. Many of these spectacular soft corals (**Fig. 14-8d,f**) come out to feed (open their polyps) only when there is a strong current to bring abundant food supplies to the colony. Many corals,

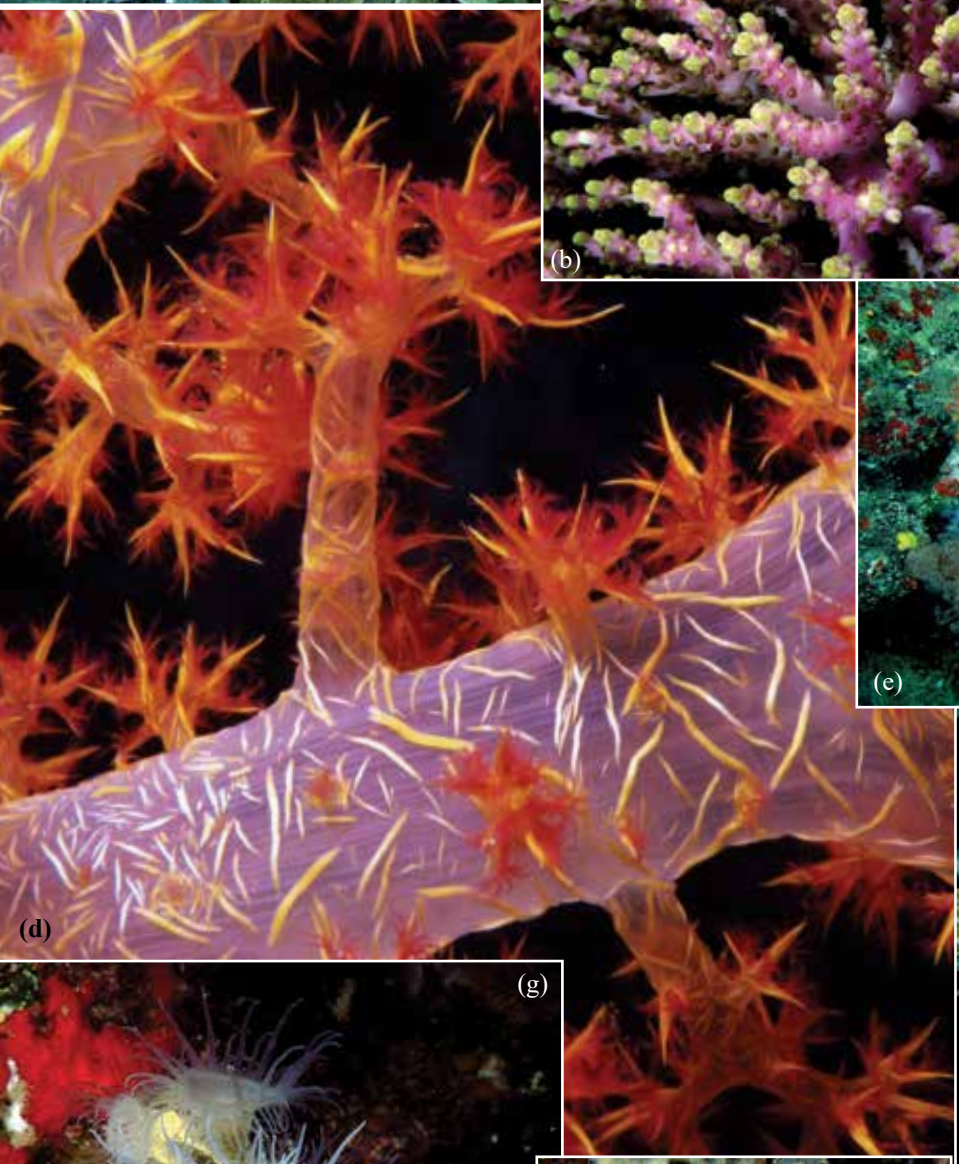
(d)

FIGURE 14-7. Examples of suspension-feeding invertebrates. (a) California mussels (*Mytilus californianus*, Monterey, California) grow in profusion in shallow waters. Other species of mussels are common in other areas. (b) A Pacific spiny oyster (*Spondylus varians*, Papua New Guinea) attaches to a coral reef wall and opens its shell so that it can feed by pumping water through its body. (c) A colony of barnacles in Monterey, California. The colony contains more than one species, in this case probably primarily *Balanus glandula* and Chthamalus sp. (d) Barnacles, including these coral barnacles (order Pyrgomatidae, Indonesia), use fanlike modified feet to sweep through the water and collect food particles.

(a)

(b)

(c)


(d)

(e)

(f)

(g)

(h)

(i)

both soft and hard, produce colonies that extend upward or outward into the water from their attachment point (**Fig. 14-8b,d,e**). This spreading maximizes the volume of water that passes over the colony and, thus, the amount of particulate food that passes within reach. Many species of zooanthids and anemones, close relatives of corals, are also suspension feeders that eat plankton and detritus (**Fig. 14-8g,h**), but larger anemones (**Fig. 14-8i**) are primarily carnivorous hunters that eat fishes and invertebrates.

There are many species of suspension-feeding epifaunal tunicates, particularly on coral reefs. They feed in the same way as salps but are attached to the substrate and have both their incurrent and excurrent openings on their upper bodies. Tunicate species include a variety of single and colonial forms (**Fig. 14-9**).

Certain species of sea cucumbers, sea stars, and worms sus-

FIGURE 14-8. (Previous page) Polypoid species (class Anthozoa) take many different forms. (a) A hard coral known as brain coral (Diploria sp., Papua New Guinea). (b) A hard coral often called staghorn coral (*Acropora sp.*, Papua New Guinea). (c) Close-up showing polyps of a hard coral species (*Tubastrea sp.*, Fiji) extended to feed at night. (d) Colony of a soft coral (*Dendronephthya sp.*, Fiji). Dendronephthya occur in many different colors. (e) Typical gorgonian sea fan (*Melithaea sp.*, Papua New Guinea). These fans can consist of millions of individual polyps and be several meters across. (f) Close-up of a soft coral colony (*Xenia sp.*, Papua New Guinea) showing individual polyps at different stages of feeding. The eight fingers surrounding each polyp's mouth open wide to capture suspended particles and then close like a fist to move the particles to the mouth. (g) A small suspension-feeding colonial anemone (Nemanthus annamensis, Fiji). (h) A colonial zooanthid (*Protopalythoa sp.*, Papua New Guinea). (i) A "magnificent sea anemone" (*Heteractis magnifica*, Fiji), here providing a home for a pink anemonefish (*Amphiprion perideraion*).

FIGURE 14-9. (Above) Tunicates (also called "ascidians") are among the most advanced invertebrates, although they appear very simple in structure. (a) Lightbulb tunicate (*Clavelina sp.*, Philippines). (b) The colonial tunicate species *Didemnum molle* (Papua New Guinea). Each of the rounded forms is a colony. (c) There are two species of tunicates in the photograph. The three tall, blue and blue-green individuals are *Rhopalaea sp.*, and the three smaller individuals with darker bodies and yellow markings around their incurrent and excurrent openings are *Clavelina robusta* (Indonesia). (d) A very different form of colonial tunicate that covers and encrusts the reef (*Botryllus sp.*, Indonesia).

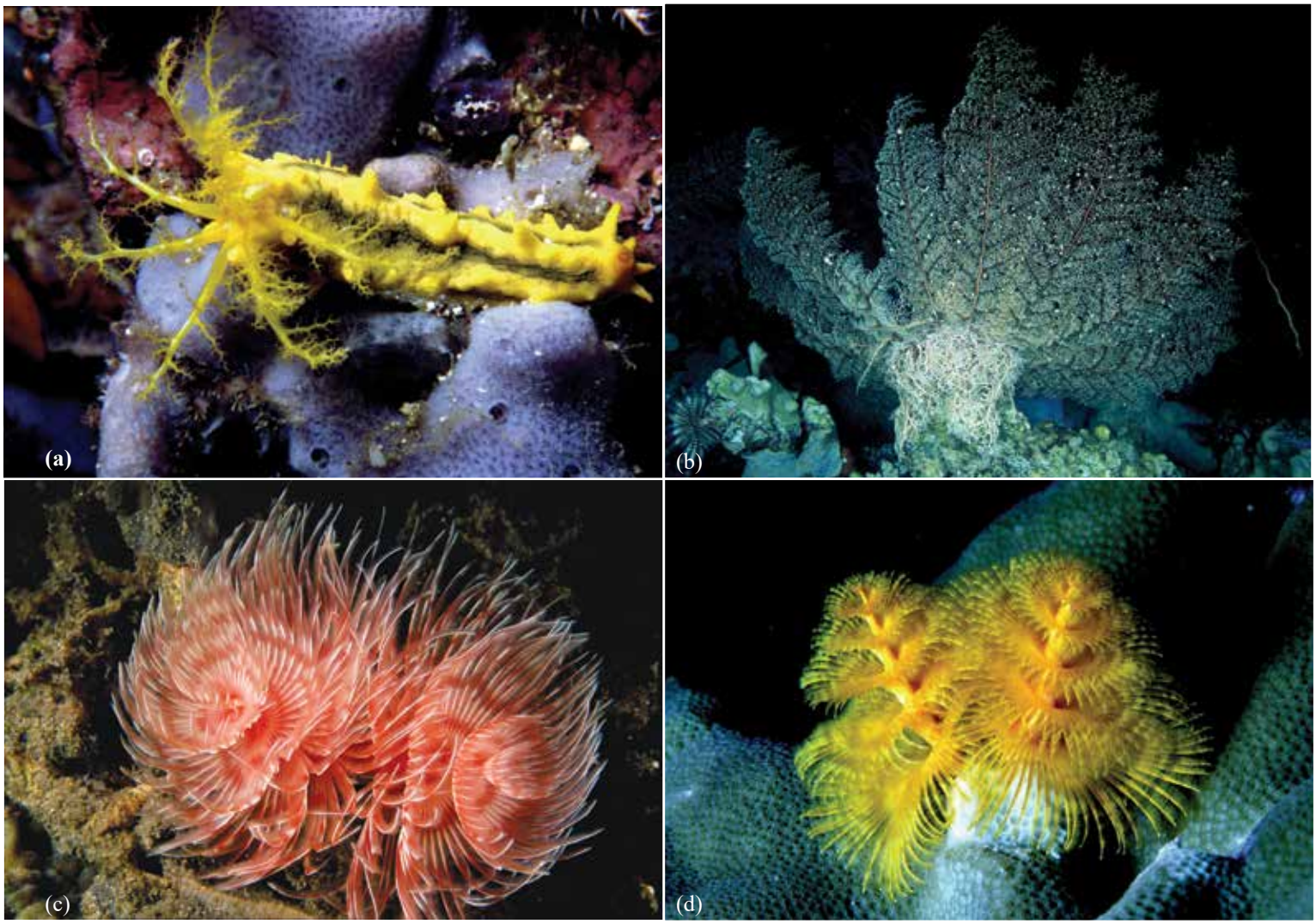


FIGURE 14-10. Examples of suspension feeders that employ weblike structures to capture food particles. (a) A creeping sea cucumber (*Cucumaria sp.*, Philippines) with its suspension-feeding apparatus extended. (b) A basket star (family Gorgonocephalidae, Papua New Guinea) with its arms extended into the current to feed at night. (c) A sabellid spiral fan worm (*Protula magnifica*, Indonesia). (d) A Christmas tree worm (*Spirobranchus giganteus*, Papua New Guinea).

pension feed by extending intricate tentacles or weblike structures into the water column (**Fig. 14-10**). The elaborate basket star (**Fig. 14-10b**) comes out to feed only at night and spreads its intricate arms, which can extend more than a meter, across the current to capture food efficiently from huge volumes of water. During the day, the basket star coils into a tiny ball and hides in crevices in the reef. Fan worms (**Fig. 14-10c**) and Christmas tree worms (**Fig. 14-10d**) live in tubes that are usually drilled into, or built with the surrounding growth of a hard coral colony. They feed by day but have an amazing ability to sense movement or shadows of moving objects and withdraw into their tubes instantaneously as divers or predators approach.

Surface Grazing

Although shallow seafloor areas with macroscopic algae that can be grazed by herbivores are rare, much of the seafloor provides sufficient, and in some areas abundant, food for grazers. This food supply varies in composition from location to location, but on most of the ocean floor it consists primarily of detritus and the bacteria and other decomposers associated with the detritus. The concentration of these foods generally decreases with ocean depth and is higher where the seafloor is below a region of high pelagic primary productivity.

Note that, in marine ecosystems, the term grazing includes feeding on detritus and animals and is not restricted to plant eating, its common terrestrial usage. On the seafloor within the photic zone, detritus and associated decomposer biomass are supplemented by other sources of grazer food, including benthic **microalgae** and **macroalgae**. Benthic microalgae, particularly diatoms, are abundant on shallow seafloor, where light and **nutrients** are abundant and where waves or other water motions rarely **resuspend** sediments to cause abrasive scour.

Many marine animals that live on the seafloor, especially species that live on hard substrates, are colonial forms whose individuals are small and immobile. The colonies can be grazed by other animals without significant harm to the colony because grazing removes only a limited proportion of the colony's individuals, which can be replaced relatively quickly by reproduction. Many colonial animal species thus provide a renewable food supply for grazers in much the same way that plants do for terrestrial grazers.

Numerous adaptations have evolved for surface grazing. Many species of surface grazers obtain food by sifting the upper layer of sediment and therefore can also be considered **deposit feeders**. Deposit feeders, which are species that obtain food from

within sediments, are described later in this chapter. Species that surface-graze may also suspension-feed or hunt larger prey.

Some surface grazers, such as **sea urchins** (Fig. 14-11a), have evolved such that their mouth is on their underside. These organisms crawl over sand and rocks, scraping off encrusting benthic **algae** and ingesting detritus as they move. Tiny allied cowries crawl across their favorite food, the **sea fan**, and ingest the individual polyps (Fig. 14-11b). Other surface grazers include **nudibranchs**, or sea slugs (Fig. 14-11c,d), that crawl across the substrate (including corals and other immobile animals that constitute or cover the hard surface of the substrate) to eat algae, detritus, or animals such as corals, **sponges**, **hydroids**, and tunicates.

Surface grazers do not necessarily live on the sediment surface. For example, some clams live buried in the sediment and extend long siphon tubes to the water above. They use the siphon tubes to select food particles and "vacuum" them off the sediment surface (Fig. 14-12a).

In some shallow areas, large concentrations of macroalgae (Fig. 13-4) are extensively grazed by many animal species. In extremely shallow water, the seafloor may be covered with the **sea grass** *Thalassia sp.* (Fig. 14-12b) or with other rooted plants, such as the marsh grass *Spartina* (Fig. 14-12c). These plants are not heavily grazed, because they are difficult to digest. The plants must be broken down by bacteria and fungi to detritus before they become a desirable and widely used food source. Small animals like the marsh periwinkle snail do not eat the tough grass itself, but instead graze on the nutritious film of diatoms, bacteria, and fungi that coat the surface of the plants. Some notable species, such as the manatee (Fig. 12-26) and the green sea turtle (Fig. 14-12d), are adapted to feed directly on sea grasses. Thalassia, the favorite food of green sea turtles, is commonly called "turtle grass."

Deposit Feeding

Organic detritus that falls to the sediment surface is used mostly by decomposers and surface-grazing benthic **fauna**, but some detritus is buried by **bioturbation** and by accumulating sediment, especially in areas of high **sedimentation rate** or **anoxic** bottom water.

Organic matter buried in sediments serves as food for decomposers and deposit-feeding animals (Fig. 14-13). As this food is depleted, the concentration of organic matter generally decreases with depth below the sediment surface, which is one reason that deposit feeders are concentrated in the upper layers of sediment. Some fish species that live in the water column hunt and feed on

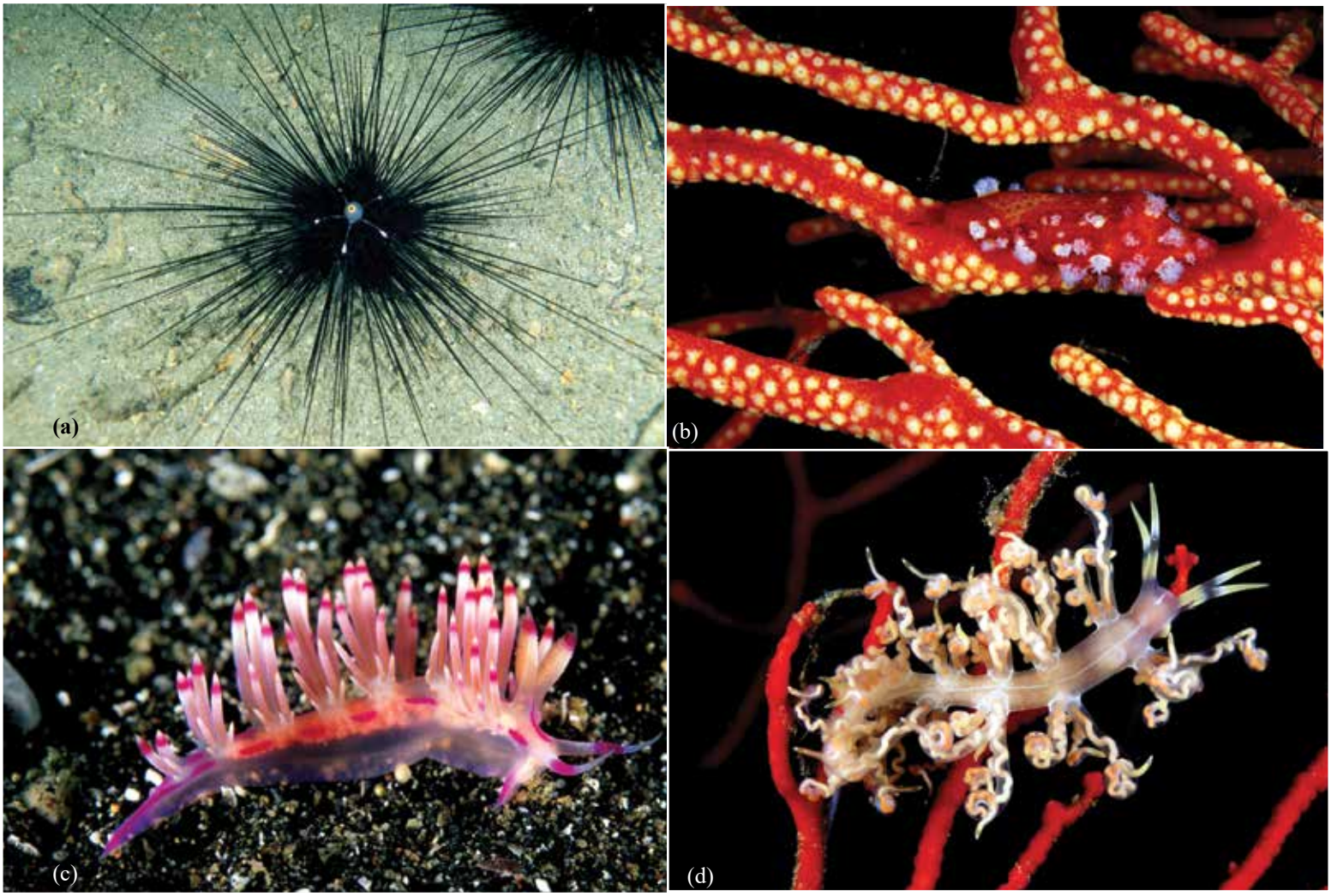


FIGURE 14-11. Examples of surface grazers. (a) Long-spined sea urchins (*Diadema savignyi*, Papua New Guinea), browsing across the seafloor. (b) An allied, or egg, cowrie (*Primovula sp.*, Indonesia) on a gorgonian sea fan. Notice that the gorgonian's polyps have been eaten on the areas of the sea fan along which the cowrie has moved. (c) A flabellina nudibranch (*Flabellina rubrolineata*, Indonesia). These shell-less gastropod mollusks advertise their toxic nature with their flamboyant coloration and body shapes. (d) This spectacular nudibranch (*Pyllodesmium undulatum*, Papua New Guinea) has a transparent body, like a number of other nudibranch species, so its internal organs are visible.

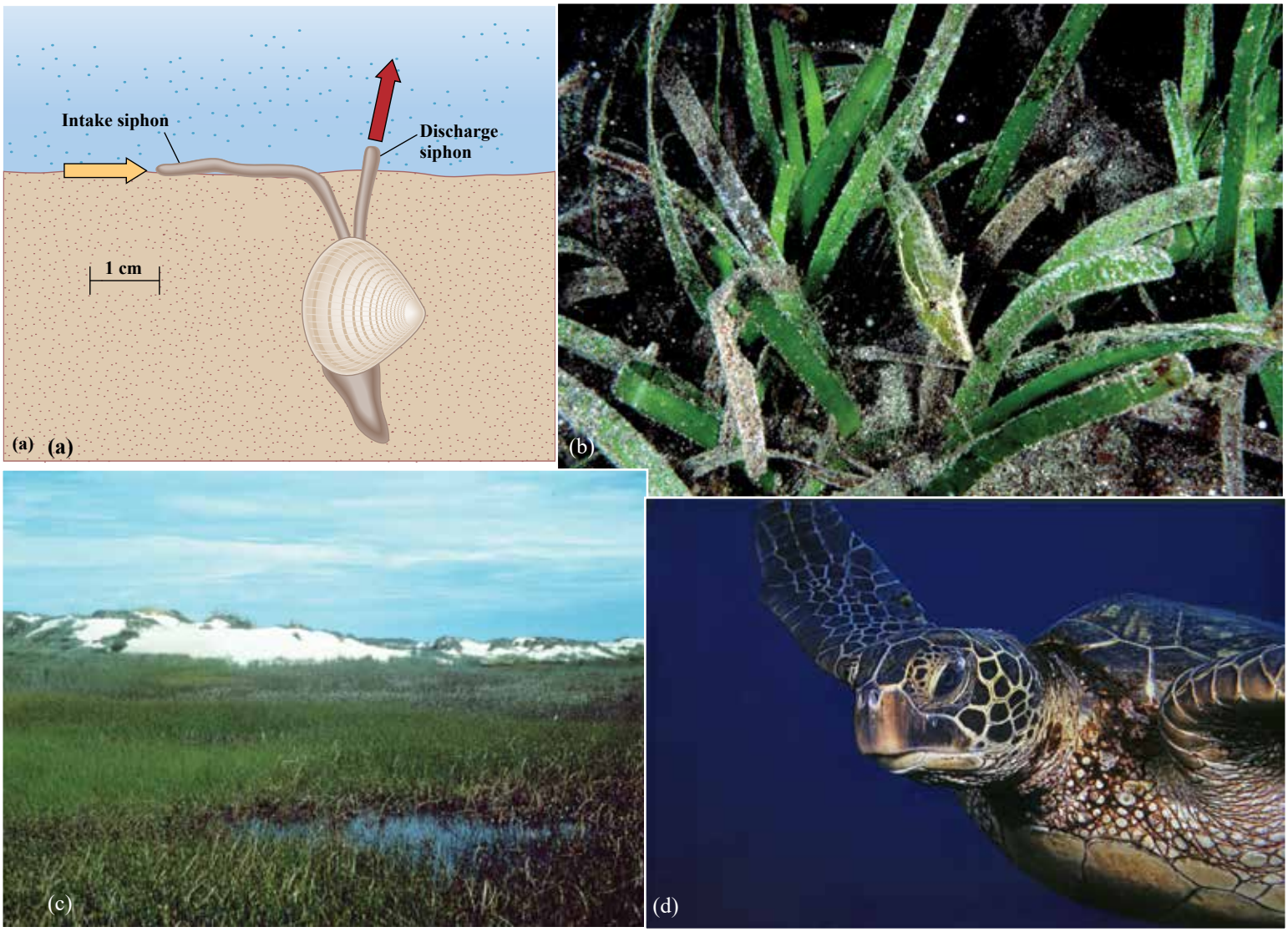


FIGURE 14-12. A benthic infaunal surface grazer, and seagrass communities. (a) The clam *Tellina sp.* feeds on the sediment surface. (b) Sea grass, especially turtle grass (*Thalassia sp.*), is a favorite food of the green sea turtle. Turtle grass beds are excellent places for animals such as this seagrass filefish (*Acreichthys tomentosus*, Papua New Guinea) to hide. (c) Rooted marsh grasses, primarily *Spartina sp*. (Aruba, Caribbean Sea), form dense beds in many coastal wetlands where the water is brackish. (d) Green sea turtle (*Chelonia mydas*, Hawaii).

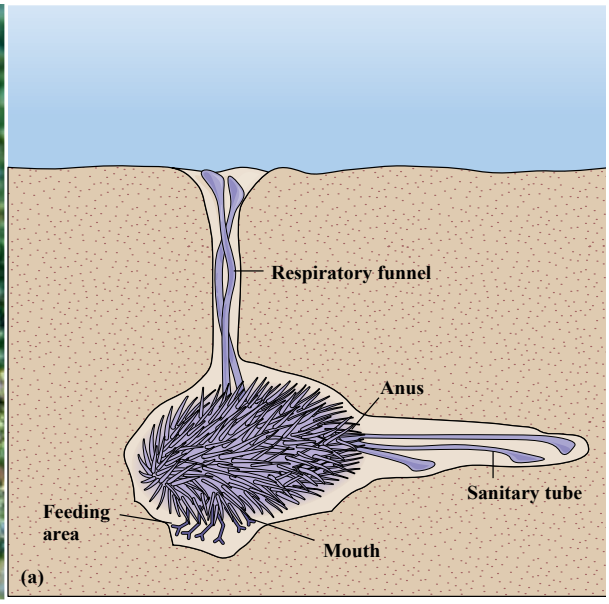
small animals, such as clams, that live below the surface of the sediments and are often considered to be a special category of deposit feeders.

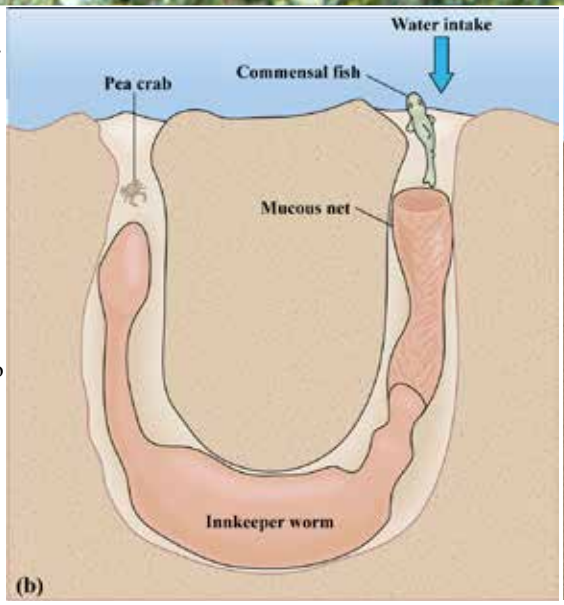
Deposit-feeding infauna generally eat their way through sediments, digesting organic particles or the organic matter that coats some particles in much the same way that earthworms eat their way through soil. Much of the detrital organic matter that survives decomposition to be buried in sediment is refractory (difficult to decompose) and has low food value. Consequently, many deposit-feeding infauna obtain most of their food by consuming bacteria and fungi, many species of which live within the sediment. Other deposit-feeding infauna have evolved means of decomposing refractory detritus.

Because detritus particles are generally small and have lower density than inorganic sediment particles, detritus tends to settle and concentrate in low-energy areas where fine-grained sediments also accumulate. Consequently, fine mud deposits tend to have higher organic matter concentrations than coarser sediments have, and they are more favorable habitats for deposit feeders. However, to live and feed in sediment, deposit feeders must have a supply of oxygen for **respiration**. In muddy sediment where organic matter is abundant, respiration by animals and decomposers quickly uses up the oxygen dissolved in **pore waters**. Oxygen is not readily replenished from the water column above, because downward diffusion of oxygenated water through the sediment is slow.

Many deposit feeders either are restricted to the near-surface oxygenated sediment layer or have evolved mechanisms to acquire oxygen from the water column above. For example, the heart urchin has adapted some of its tube feet to create a periscope-like breathing apparatus that it extends upward to the sediment surface (**Fig. 14-13a**). Deposit-feeding clams extend their siphons to the sediment surface for this same purpose. Many other infaunal deposit feeders form and live in a U-shaped or similar burrow and draw oxygenated water through the burrow as they feed. The innkeeper worm (**Fig. 14-13b**), lugworm (**Fig. 14-13c**), and many other species use variations of this method.

Muddy sediments tend to be dominated by **annelid** worm populations, whereas sandy substrates are more likely to be dominated by various species of deposit- or filter-feeding clams. Many deposit feeders pass sediment through the gut and discharge feces containing large volumes of processed sediment through





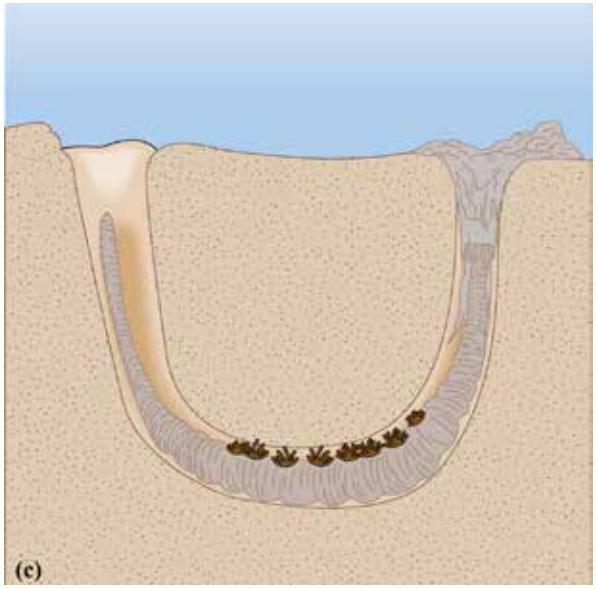


FIGURE 14-13. Examples of deposit feeders. (a) The heart urchin (*Echinocardium sp.*) feeds on detritus buried in the sediments and respires through long tubes extended to the surface of the sediment. (b) The innkeeper worm (*Urechis caupo*) builds a U-shaped tunnel through which it draws oxygen-containing water for respiration. The tunnel forms a perfect home for several associate species, sometimes including several gobies and two species of small crabs. Although it lives in the surrounding sediment, a small clam species also uses the burrow by extending its siphon tubes into the burrow to obtain oxygenated water. (c) Lugworms (*Arenicola brasiliensis*) use a similar U-shaped burrow. (d) Goatfishes such as this blackstriped goatfish (*Upeneus tragula*, Indonesia) use their barbells (the two yellow "whiskers" protruding from just under the mouth) to sense and smell out small invertebrates under the surface of the sediments. The goatfish digs into the sediments with the barbells to capture and eat these invertebrates, so it may be considered to be a deposit feeder, but it is also a hunter. Other fishes, especially some wrasses, often follow the goatfish to capture a free meal from among the invertebrates that the goatfish exposes as it digs.

the excurrent end of their burrow or breathing tube. In this way, food-depleted material is transported to the sediment surface, where it will not be reingested. Some species, particularly annelid worms, produce tightly packaged **fecal pellets** that accumulate on the sediment surface and protect it from **erosion**. Other species, especially certain clams, **excrete** their fecal material as a cloud of loose particles.

Clams may discharge their wastes as a cloud of particles for reasons other than to get rid of food-depleted sediment. This form of waste disposal may protect the clams' environment from invasion by other species. By working through the upper layer of sediment and continuously dispersing this material at the surface, clams prevent the silty sand in which they live from compacting and becoming firm enough for epifauna to attach to or lie on without being buried. In addition, the clouds of fine inorganic particles that the clams continuously create tend to clog the feeding apparatus of filter-feeding organisms with non-nutritious material.

HUNTING AND DEFENSE

All marine species must ensure that enough individuals survive predation to produce the next generation. Carnivorous species must also adopt a successful hunting method that can counter the defensive methods of their prey and provide adequate food. Although there are only a few basic approaches to either offense or defense, combining these approaches makes possible an incredible variety of offensive and defensive strategies. The situation is analogous to the game of chess, in which a few simple permitted moves of the chess pieces can be combined into an almost infinite variety of offensive or defensive strategies. Each species has its own unique combination of defensive and offensive strategies. In a chess game, the most successful strategy is usually one in which individual moves are combined in such a way that each contributes to both defense and offense. Similarly, marine species often use the same approach for both purposes.

Basic offensive and defensive approaches used by marine organisms are summarized in **Table 14-1**. The following sections

TABLE 14-1 Some General Approaches to Hunting and Defense

Behavior	*Offensive Uses*	*Defensive Uses*
Speed	Chase down prey	Escape predators
Lures	Attract prey	Confuse predators
Camouflage and mimicry	Ambush	Escape detection Confuse or deter predators
Concealment	Ambush	Escape detection Evade capture
Spines and armor	Overcome armor or other defenses	Deter predators
Poisons	Kill or disable prey	Reduce predator population Reduce competitor population Deter predators
Group cooperation	Overwhelm and confuse defenders	Confuse predators Minimize predation

describe and illustrate how these approaches are used by various species, and how fish species have evolved to optimize variations of them. The unusual sensing mechanisms that some marine species use to locate prey are discussed in a subsequent section.

Speed

The most familiar approach to hunting and defense in terrestrial ecosystems is speed. The predator chases the prey, and the prey tries to outrun the predator. For example, lions and tigers chase antelopes, but antelopes often escape by outrunning their pursuers. Speed is used in much the same way in the marine environment.

Predators that hunt by using their swimming speed include a variety of sharks, bony fishes, **marine mammals**, and squid. The prey are generally other species of fishes, marine mammals, or squid. In some cases the hunt is similar to the lion–antelope chase, but it occurs in three dimensions. Prey outnumber the predator and live uneasily in the predator's presence, always carefully monitoring its movements and maintaining a respectful distance. Suddenly the predator selects a potential victim and begins the chase. Unwary prey or prey that are weak or injured fail to elude the predator and are consumed. Stronger individuals and those that are more successful in avoiding predators preferentially survive to reproduce and pass on their more successful genes to future generations. The predatory species is subject to a similar natural selection process because stronger and more skillful predators outcompete weaker and less successful members of their species for the available food resources.

Only the largest predators and prey can invest the considerable energy required to overcome water resistance and swim long distances at high speed. These species must obtain large quantities of food to replace energy reserves used in the chase. Consequently, most ocean predators use speed in ways that ensure a quick kill, and prey species seek ways to escape their predators quickly.

Predators may use a short burst of speed as the final component of a hunting strategy in which stealth or other approaches are used to initially get within striking distance of the prey. A variety of fish species, including lizardfishes (**Fig. 14-14a**), frogfishes (**Fig. 14-14b**), and hawkfishes (**Fig. 14-14c**), lie quietly in wait on the seafloor until their prey passes nearby. Then a quick burst of speed is sufficient to capture the prey. Lizardfishes rely on their prey's mistake in approaching within half a meter or so, a distance across which a lizard-fish can make a very fast attack. Frogfishes are among the fastest-moving marine animals, but they can maintain their speed for only a few tens of centimeters and must be very close to their prey for a successful hunt. To ensure that its prey approaches close enough for such attacks, a frogfish uses two other approaches in its hunting strategy: camouflage and a lure, which are discussed below.

Speed is also used in a variety of ways as a component of defensive strategies. **Gobies** use short bursts of speed to retreat to their home, which is generally a hole in the sand or reef where they are safe from predators (**Fig. 14-14d**). Some invertebrates, such as the fan worm (**Fig. 14-10c**), Christmas tree worm (**Fig. 14-10d**), and some sand anemones (**Fig. 14-6c**), use a high-speed, almost instantaneous, retreat into a protected tube or burrow to avoid predation. Many fish species change direction quickly to evade an onrushing predator. For example, butterflyfishes (**Fig. 14-14e**) can evade predators by swimming quickly in and out of the tortuous nooks and crannies of a reef or by simply making tight turns.

Lures

Lures are used by ocean predators to attract fishes and other prey just as they are used in sportfishing. The lure is made to look like a tasty morsel of food to attract the prey species to the concealed predator (or fishhook). The best-known practitioners of this technique are frogfishes (**Fig. 14-14b**). Lying still and camouflaged, a frogfish wiggles a fleshy knob on the end of a stalk-like projection extending from above the mouth. When another fish approaches, this lure appears to be a small fish, shrimp, or other food morsel. By the time an unwary approaching fish is close enough to realize its mistake, it is within striking distance of the frogfish's lightning-quick, short-range attack. Because the predator uses little energy while lying in wait, it requires successful hunts only infrequently. In addition, the lure can attract more prey than would normally swim by. The deep-sea anglerfish (**Fig. 14-15**) uses the lure-based ambush strategy to perfection. Its **bioluminescent** lure appears as a tantalizing tiny point of light to prey that live in perpetual dark, although many potential prey species in this zone are sightless.

Ironically, lures can also be used for defensive purposes. They are used by many reef fish species, especially butterflyfishes, which have a dark spot near the tail (**Fig. 14-14e**) that resembles an eye. The real eye is often camouflaged in a vertical black line. When a predator makes its initial move toward a butterflyfish, it aims its attack toward the front of the fish to block its expected

FIGURE 14-14. Some fishes that employ speed for offense or defense. (a) A twospot lizardfish (*Synodus binotatus*, Indonesia) lying in wait for passing prey. (b) A striated frogfish (*Antennarius striatus*, Indonesia). The frogfish wiggles the lure, called an "esca," on the end of its illicium, a modified first ray of the dorsal fin located just above the eye. When wiggled, the esca looks like a small polychaete worm to the frogfish's unsuspecting prey. (c) A Falco, or dwarf, hawkfish (*Cirrhitichthys falco*, Indonesia) that has just been rewarded for its time spent lying in wait by capturing a favorite food item, a shrimp. (d) A fire goby or dartfish (*Nemateleotris magnifica*, Papua New Guinea) hovering above its hole in the reef, into which it is ready to dart and take refuge. (e) Bennett's butterflyfish (*Chaetodon bennetti*, Papua New Guinea). Note the large false eyespot near its tail.

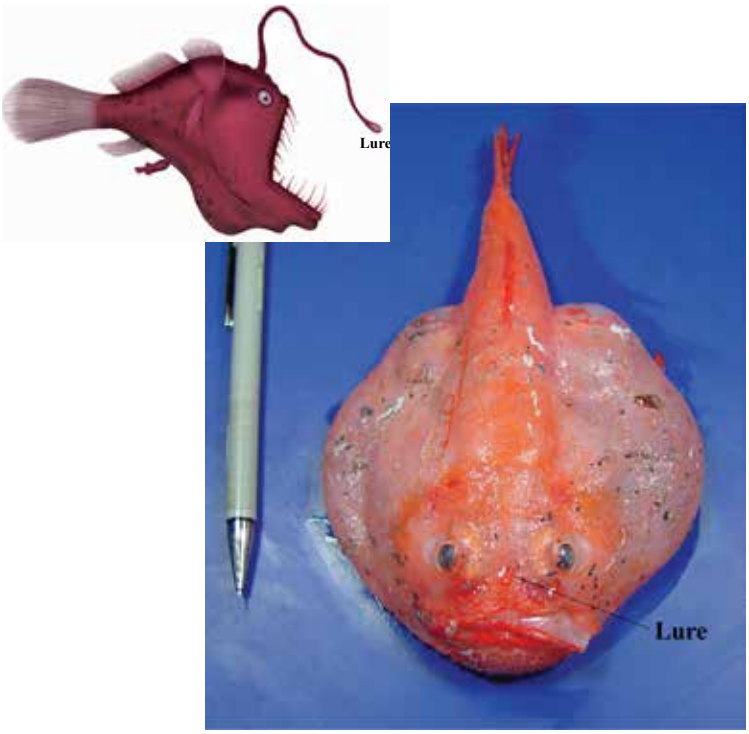


FIGURE 14-15. This deep-sea anglerfish (*Chaunax pictus*) is bloated from the pressure reduction as it was brought to the surface. Look carefully and you can see the angler's bioluminescent lure, a small black dot on the end of a stalk just between its eyes. The stalk is now lying limp on the fish's body. The inset shows how the lure is normally deployed.

escape route. If the predator is lured into orienting its attack to the false eye location, the butterflyfish gains valuable moments in which to swim in a direction other than that expected by the predator. The false eye may also be larger than the real eye to make the prey seem much bigger and thus more capable of retaliatory defense. You may have seen some of the many butterflies and moths that have false eyes for the same reason.

Camouflage and Mimicry

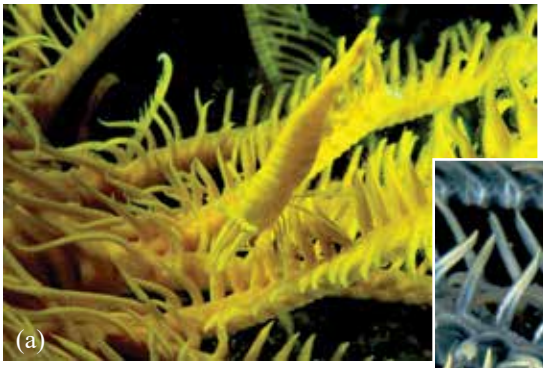
Camouflage (the art of making an object difficult or impossible to see against its background) and mimicry (the art of making an individual look like a completely different species or object) are practiced by many marine species. The principal use of camouflage is probably to enable an organism to escape detection by its predators, but it is also used by predators to enable them to get close to their prey without detection. In many cases, camouflage is extremely effective (**Fig. 14-16**). Countless times when my diving partner has pointed out an organism on a reef, I have needed many seconds of careful visual examination before I could suddenly see through the effective camouflage to discern the organism.

Marine animals take many different approaches to camouflage, but the predominant basic approach is to make texture, color, and pattern appear the same as those of the background. Some animals, such as octopuses and cuttlefish, can change their colors almost instantly to blend into their background. These species can also change their body texture to blend into a reef. Octopuses, cuttlefish, and many other species change color by using muscles to expand or contract pigment filled cells in their outer body surface called "chromatophores" under direct control of their nervous system. However, this is not the only way to match the color of a background. For example, some species of frogfishes (**Fig. 14-14b**) have a variety of colors and color patterns, and each individual finds itself a permanent or semipermanent home where it is surrounded by similarly colored sponges or sponge-encrusted rocks. The frogfish's body is lumpy and irregular, so its shape and texture do not instantly reveal its presence. In addition, the frogfish has small eyes surrounded by confusing decoration, again for camouflage. Scorpionfishes and many seahorses (**Fig. 14-16d,h,i**) use a very similar camouflage technique: a mixture of drab colors that blend into their background on a reef or rubble-covered bottom, and frilly appendages that disguise their body outline.

The differences in frogfish and scorpionfish camouflage reflect their different preferred habitats and habits. Frogfishes live in or on a reef and rarely move from one preferred location. Scorpionfishes live primarily on a coral rubble seafloor and move periodically from place to place to hunt. Scorpionfishes therefore need a more generalized camouflage than frogfishes do, to blend with the variety of backgrounds they encounter. Like frogfishes and scorpionfishes, the ghost pipefish (**Fig. 14-16e**) is a master of both color and body form camouflage. Some species live among algae or turtle grass (*Thalassia*) and even swim in a vertical orientation to parallel the algae or turtle grass blades.

Tiny shrimp, crabs, and other invertebrates that live on **crinoids** and soft corals make very effective use of camouflage (**Fig. 14-16a,b,g,j,k,l**). Many of these tiny and beautiful invertebrates spend their entire life cycle on a single host crinoid or soft coral that they perfectly mimic. These hosts have a wide variety of colors and color patterns, and the guest species often match the pattern. Many of the tiny invertebrate species that inhabit crinoids and soft corals have not been well studied, so we do not know how each of these species achieves its perfect camouflage. Some species of shrimp will change color within several days to match a new host perfectly when they are moved from one crinoid or

FIGURE 14-16. (Next page) Examples of camouflage. (a,b) Crinoid shrimp (*Periclimenes amboinensis*, Papua New Guinea and Indonesia) on their host crinoid. These two photographs show how the shrimp are camouflaged to hide in crinoids of different colors. (c) A spotted sole partially buried in the sand (*Phyllichths punctatus*, Indonesia). (d) This raggy scorpionfish (*Scorpaenopsis venosa*, Indonesia) is well camouflaged against the sand and rubble seafloor, but it even enhances its natural camouflage by allowing algae to grow on its body. (e) The algae ghost pipefish (*Solenostomus halimeda*, Papua New Guinea) is well camouflaged to look just like a frond of this green calcareous alga. The ghost pipefish even spends most of its time swimming slowly in a vertical position to look even more like the alga. The pipefish is on the left-hand side of the clump of algae in this photograph. (f) There are many species of decorator crabs, each of which covers itself in sponges and other epifauna and algae. This one is a decorator spider crab (*Camposa retusa*, Papua New Guinea). (g) A commensal spider crab (*Xenocarcinus conicus*, Palau) on a gorgonian coral. The crab is about 1 cm in length. (h) A pygmy (or gorgonian) seahorse (*Hippocampus bargibanti*, Indonesia) blends in with its host sea fan with coloration and body "bumps" that resemble the polyps of the fan when they are closed. (i) The spotted seahorse (*Hippocampus kuda*) is found in many colors, often to blend in with its background. This individual in Papua New Guinea, with its color and coating of algae and organic detritus, blends perfectly with the dead leaves and detritus of its home near the mouth of a stream. (j) The coral shrimp (*Dasycaris zanzibarica*, Indonesia) lives on a whip coral and is camouflaged by its body protuberances and perfect color to match the whip. (k) Like the coral shrimp, this tiny spider crab (*Xenocarcinus tuberculatus*, Indonesia) is camouflaged on its whip coral. (l) A tiny (3 to 5 mm long) rounded sea star shrimp (*Zenopontonia noverca*, Indonesia) is almost transparent, but it has flecks of color to match its sea star host. It can be seen in this photograph only because the lighting was just right to leave it a little shadowed.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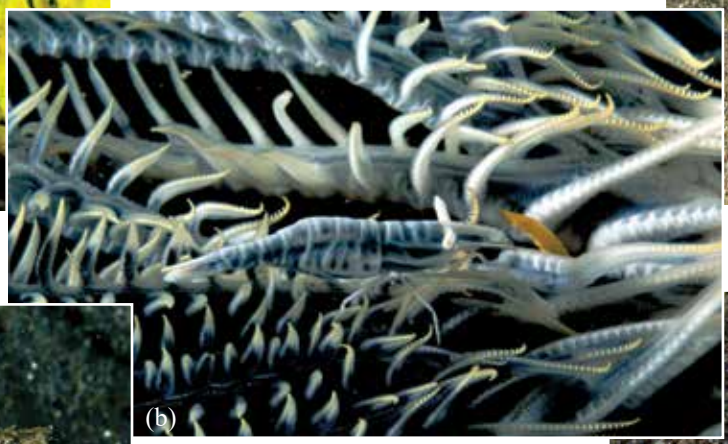
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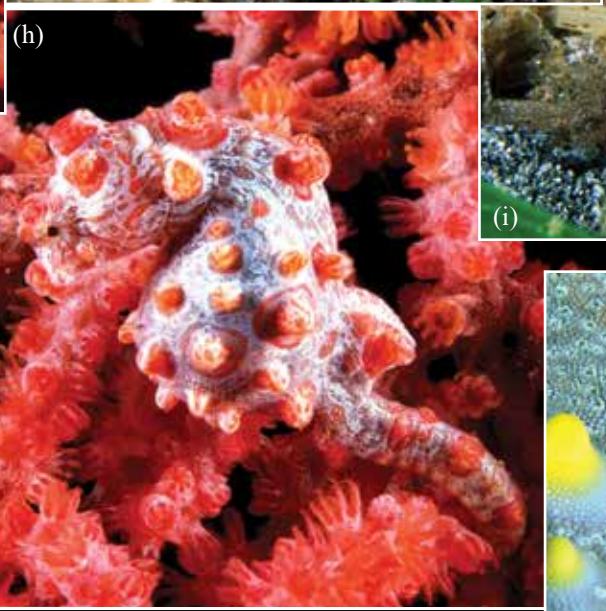
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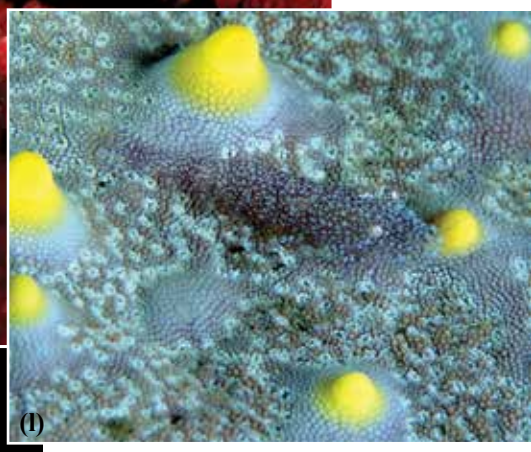
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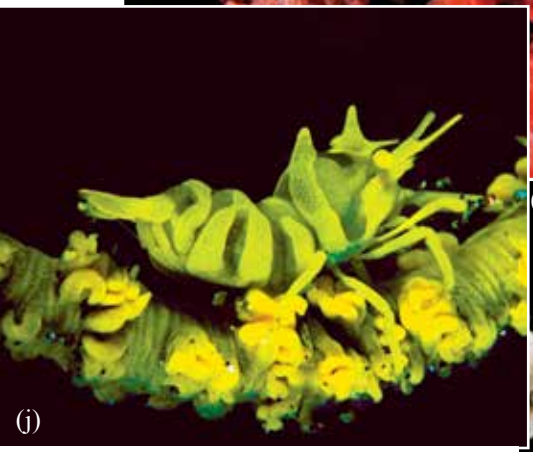
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soft coral to a differently colored individual or colony of the same species. The shrimp likely achieves this color change by using its chromatophores, or by eating small parts of its host and incorporating the host's colored pigments into its own body, or possibly by a combination of these techniques.

Sometimes even the perfect color-matching capabilities of crinoid and soft coral inhabitants appear to provide insufficient camouflage. Many invertebrates, particularly several species of tiny crabs, also have modified body shapes to match the structure of their host. In some cases, the crab's or other lodger's body is covered with spines and protuberances that mimic the appearance of the host or its individual polyps. In other cases, the lodger plucks off some of its host's polyps and places them on its shell or appendages (**Fig. 14-16g**). The technique of placing other organisms on one's own body for camouflage is practiced by many invertebrate species. For example, the decorator crab (**Fig. 14-16f**) covers its entire body with algae, sponges, and other invertebrates, beneath which the crab is not easily seen, particularly if it stays motionless when a predator nears. The polyps, sponges, and other species used for camouflage can live and reproduce while attached to the camouflaged crab. As will be discussed later in the chapter, the association may even be beneficial to both species.

Pelagic fishes and marine mammals that swim in the water column away from the seafloor take advantage of somewhat different camouflage. Many of these species have countershading that minimizes the contrast of their bodies against the background as viewed by predators from above or below. Species that rely on counter-shade camouflage have a white or silver and highly reflective underside (**Fig. 14-17a,b**) that efficiently reflects the ambient light downward and reduces the contrast between the fish's (or mammal's) body and the water surface as seen by a predator from below. The upper side of the countershaded species is dull, nonreflective, and often mottled gray or blue-gray to reduce upward reflection of light and soften the outline by providing variations in the light reflected. A predator looking downward must distinguish the dull and confusing shape of the countershaded prey seen against the murky, confused background of the seafloor or deep water below.

Some species conceal their identity by mimicking another species. Again, this approach can be used in either hunting or defense. The false cleaner wrasse is a small carnivorous fish that mimics a species of cleaner wrasse (**Fig. 14-17e**). Cleaner wrasses establish stations where they wait to eat **parasites** off larger fishes, and they advertise their services by their bright colors and a jerky dance that is similar for all cleaner species. The cleaner benefits from the food supply of parasites, and the cleaned fish benefits by being rid of the parasites. The false cleaner mimics not only the cleaner's coloration and body shape, but also its advertising dance. The unsuspecting parasitized fish moves in and lowers its defensive guard to the false cleaner, which simply takes a bite out of the fish. Often the fish is startled but stays and allows the false cleaner a second bite before realizing its mistake and scurrying away in complete confusion.

The black-saddled mimic filefish (also known as the mimic leatherjacket) uses mimicry for defensive purposes. The filefish (**Fig. 14-17c**) is virtually indistinguishable in size, shape, and markings from a pufferfish, the black-saddled toby (**Fig. 14-17d**). Because the puffer is poisonous and predators are unable to distinguish the two species, they ignore both the puffer and its mimic. The juvenile mimic surgeonfish (**Fig. 14-17f**) mimics both the looks and the behavior of the pearlscale angelfish (**Fig. 14-17g**), and it is about the same size as the angelfish, but the larger adult mimic surgeonfish (**Fig. 14-17f**) looks completely different from the juvenile. Angelfishes have sharp spines on their cheeks to deter predators, so the predators do not attack the juvenile mimic surgeonfish even though surgeonfishes do not have such a spine.

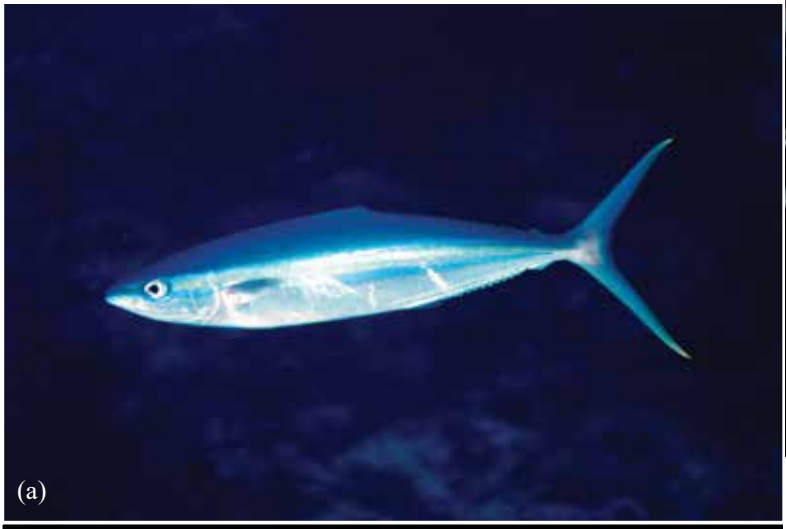
Concealment

Although many marine predators use senses other than vision to locate their prey, most marine predators in the photic zone hunt primarily by sight. Consequently, concealment is an excellent technique that is widely used for defensive purposes and also by certain predators to ambush their prey. Camouflage and concealment are often used together to prevent detection. For example, flounders and soles (**Fig. 14-16c)** are not only camouflaged, but also may partially bury themselves in sand to conceal their presence further.

Concealment is a very effective strategy for many invertebrates and fishes that bury themselves in sand or mud; hide in cracks, crevices, or caves of a reef or rubble-covered seafloor; or build and live in holes in a reef, sediments, or rocks. Most species that use concealment for defense against visual hunters remain concealed by day and come out to feed at night. Other species emerge during the day but seldom stray far from their hiding places. These species use concealment places in two ways: to hide in to escape detection when predators approach and as a refuge into which the usually much larger would-be predator cannot follow. For example, fire gobies (**Fig. 14-14d**) live in holes excavated in coarse sand or rubble areas around coral reefs. Some will dive into these holes, of which they may have several, when a predator is in sight. Others will stay out until the predator reaches a distance of a meter or two and then dive into their holes at lightning speed. Photographing these gobies, and many other reef fishes that have similar habits, requires the patience to lie quietly in wait until the fish re-emerges.

Nocturnal species that conceal themselves by day and hunt at night are often a deep red color and have big eyes (**Fig. 14-18a,b,e**) that enable them to hunt when light levels are very low. The red color aids concealment in caves or at night because red light is strongly absorbed by seawater. Consequently, these organisms appear dark gray or black unless seen near the surface in daylight or when illuminated with artificial light. In addi-

FIGURE 14-17. (Next page) Examples of countershading and mimicry. (a) This trevally, called a "rainbow runner" (*Elagatis bipinnulata*, Solomon Islands), lives mostly in the open water column. Note the light-colored underside and nonreflective upper surface that provide countershading. (b) Another trevally species, the bluefin trevally (*Caranx melampygus*, Solomon Islands), is also countershaded with a light underside and darker upper surface, but this species spends much of its life close to the reef and seafloor. Perhaps the spotting on the trevally's upper side helps it to visually blend in better with the seafloor when seen from above. (c) Blacksaddle mimic filefish or leatherjacket (*Paraluteres prionurus*, Philippines). (d) Black-saddled toby (*Canthigaster valentini*, Papua New Guinea). Can you tell the difference between this puffer (toby) and the leatherjacket in part (c)? The puffer lacks a first dorsal fin, and it has shorter dorsal and anal fins than the leatherjacket has. (e) A cleaner wrasse, similar to *Labroides pcthirophagus* (Hawaii), shown in the inset, is removing parasites from a Celebes sweetlips (*Plectorhinchus celebicus*, Papua New Guinea).(f) A juvenile mimic surgeonfish (*Acanthurus pyroferus*, Indonesia). The inset shows an adult (Papua New Guinea). (g) A pearlscale angelfish (*Centropyge vrolikii*, Papua New Guinea).


(a)

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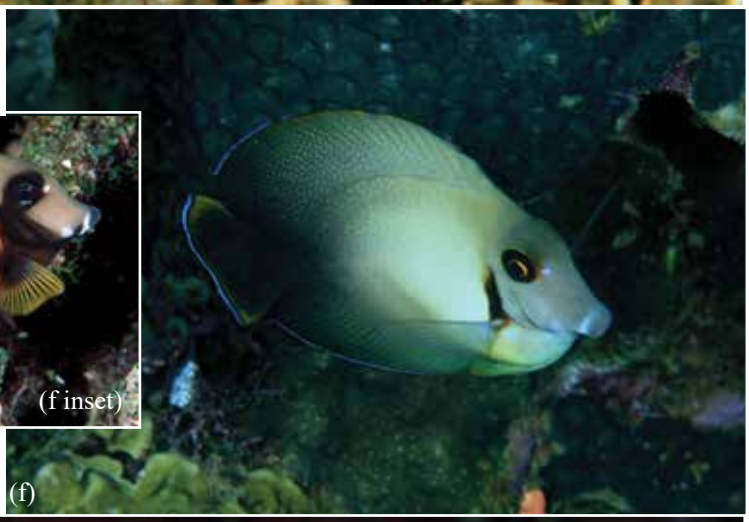
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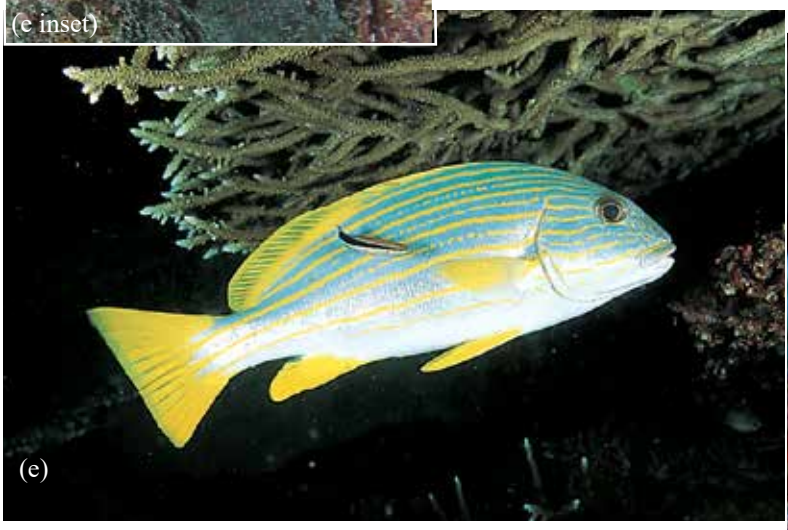
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tion, many marine species have eyes that are not sensitive to red **wavelengths**.

A wide variety of fishes, shrimp, crabs, sea urchins, octopuses, and many other invertebrate species conceal themselves by day and emerge at night (**Fig. 14-18**). In contrast, many species that hunt or feed during the day conceal themselves at night (**Fig. 14-19a**). Diving at night on a reef or rocky area reveals a community very different from the one seen during the day. Many invertebrates, including certain sea pens (**Fig. 14-6a,b**), shrimp, crabs, and mollusks (**Fig. 14-19b**), emerge only at night and bury themselves in the soft seafloor by day. Nocturnal predators use the cover of night as a form of concealment to ambush their prey.

Concealment would seem to be impossible for species that live in the water column. Nevertheless, squid and octopuses are able to conceal themselves by speeding off behind an opaque cloud of ink that they release when threatened.

In the open ocean, where there are no reefs or backgrounds to blend into, some pelagic animals use transparency as a means of concealment. By having bodies composed largely of water, animals like jellyfish, comb jellies (ctenophores) and salps allow

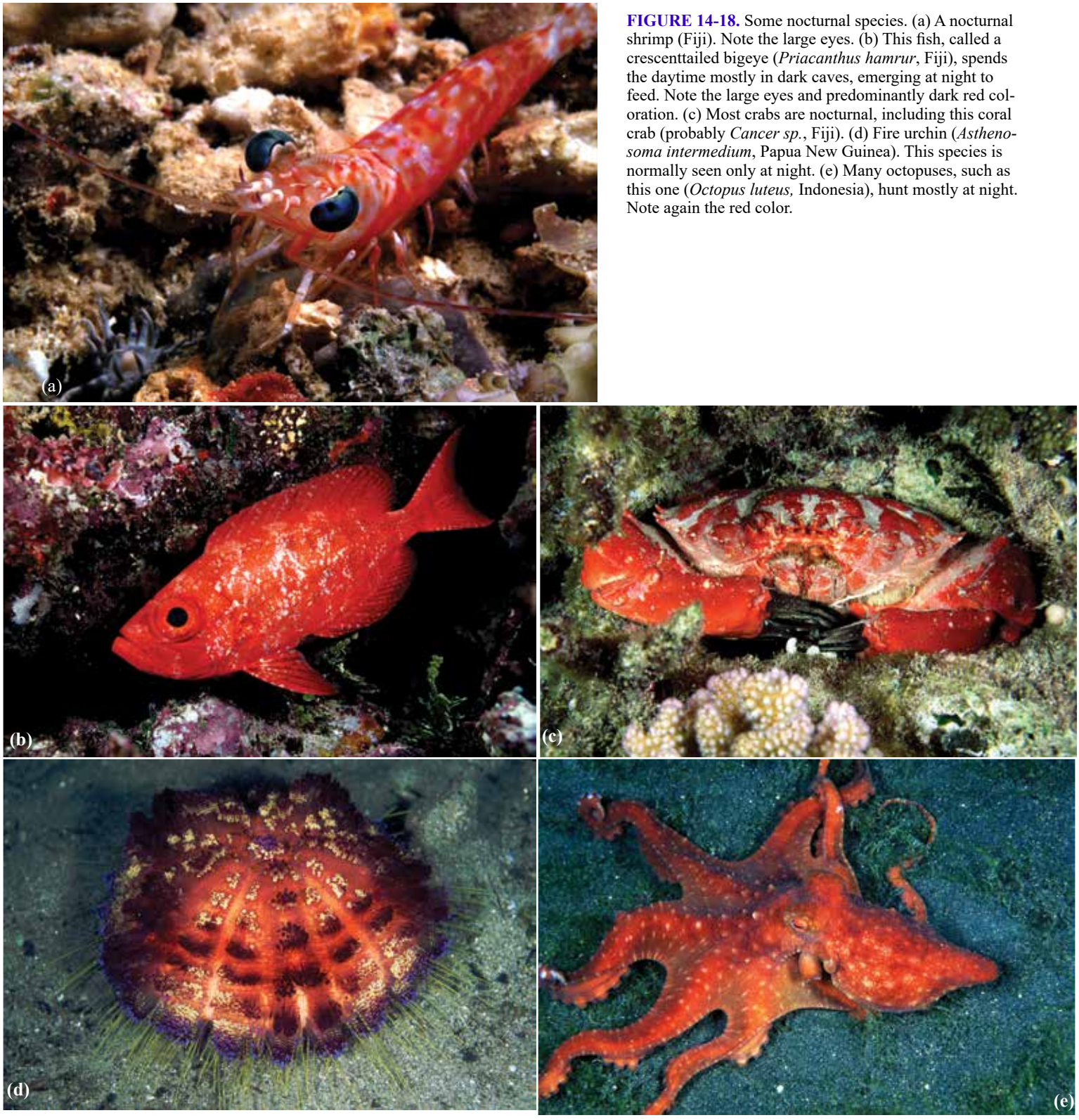


FIGURE 14-18. Some nocturnal species. (a) A nocturnal shrimp (Fiji). Note the large eyes. (b) This fish, called a crescenttailed bigeye (*Priacanthus hamrur*, Fiji), spends the daytime mostly in dark caves, emerging at night to feed. Note the large eyes and predominantly dark red coloration. (c) Most crabs are nocturnal, including this coral crab (probably *Cancer sp.*, Fiji). (d) Fire urchin (*Asthenosoma intermedium*, Papua New Guinea). This species is normally seen only at night. (e) Many octopuses, such as this one (*Octopus luteus,* Indonesia), hunt mostly at night. Note again the red color.

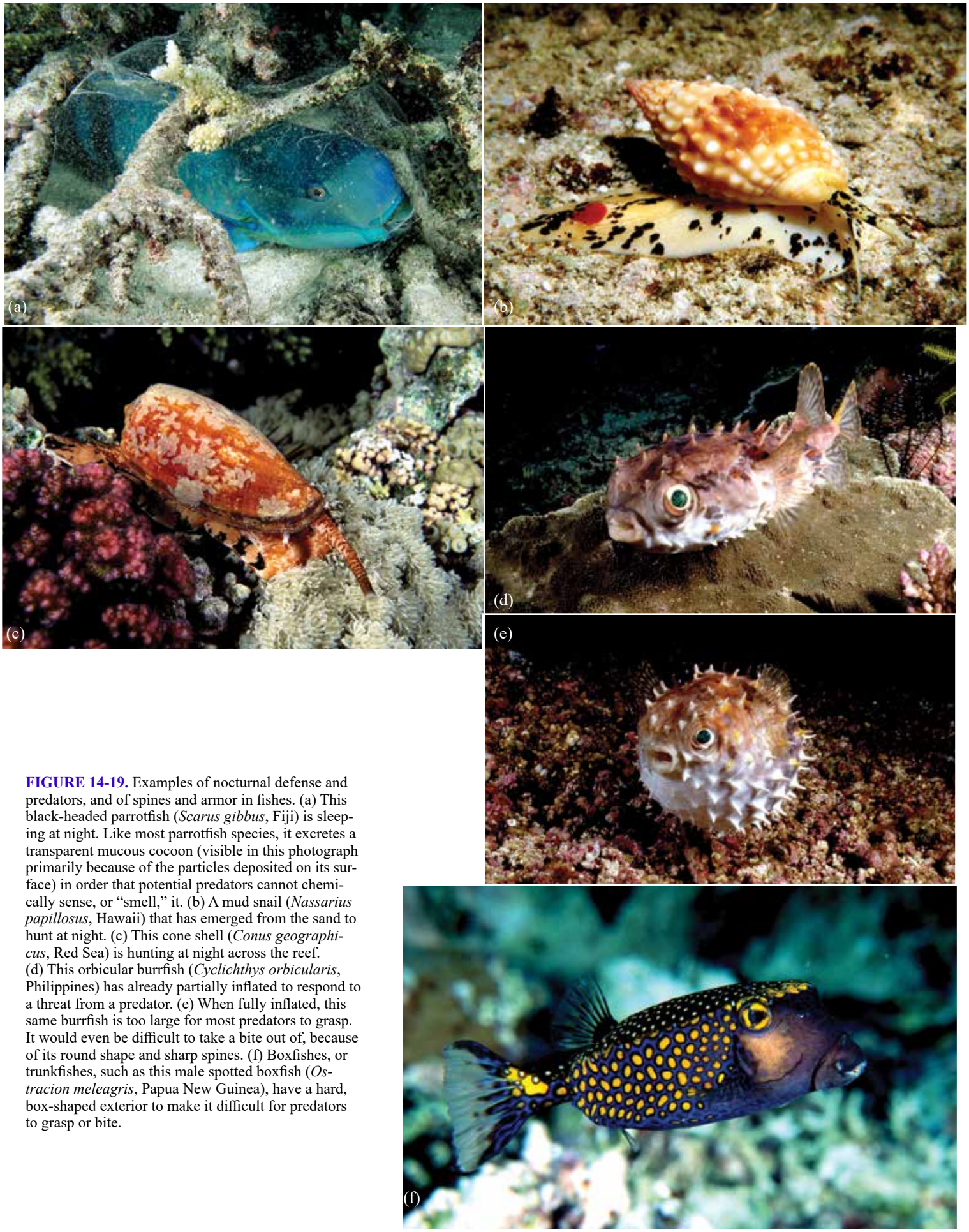


FIGURE 14-19. Examples of nocturnal defense and predators, and of spines and armor in fishes. (a) This black-headed parrotfish (*Scarus gibbus*, Fiji) is sleeping at night. Like most parrotfish species, it excretes a transparent mucous cocoon (visible in this photograph primarily because of the particles deposited on its surface) in order that potential predators cannot chemically sense, or "smell," it. (b) A mud snail (*Nassarius papillosus*, Hawaii) that has emerged from the sand to hunt at night. (c) This cone shell (*Conus geographicus*, Red Sea) is hunting at night across the reef. (d) This orbicular burrfish (*Cyclichthys orbicularis*, Philippines) has already partially inflated to respond to a threat from a predator. (e) When fully inflated, this same burrfish is too large for most predators to grasp. It would even be difficult to take a bite out of, because of its round shape and sharp spines. (f) Boxfishes, or trunkfishes, such as this male spotted boxfish (*Ostracion meleagris*, Papua New Guinea), have a hard, box-shaped exterior to make it difficult for predators to grasp or bite.

light to pass directly through them so they are nearly invisible to predators. Other organisms, like glass squid and certain larval fishes, have transparent tissues and organs, leaving only their eyes visible. This strategy makes it almost impossible to detect in the sunlit upper layers of the ocean.

Spines and Armor

Numerous invertebrates have evolved thickened shells or long spines to prevent predators from reaching their vital soft parts. Many mollusks have external shells that protect them after they retreat inside. Bivalve mollusks, including clams and scallops, have two hinged valves that they can close tightly together. Gastropod mollusks have a single shell (**Fig. 14-19c**) into which the animal's soft parts can be withdrawn. The entrance to the shell is closed off with a tough door called an "operculum." Some fishes, such as puffers and burrfishes (**Fig. 14-19d,e**), have developed special jaws to crush mollusk shells. Crabs have a large armored crushing claw for the same purpose. In turn, many mollusks have developed extremely thick and strong shells or armored spines. Spines increase the size of the shell and make it more difficult for a crab's claw or fish's jaw to grasp and crush it. Many mollusks conceal themselves during the day and hunt only at night to avoid predators, but some predators, particularly crabs, are also nocturnal. There is a perpetual contest between predator and prey as each evolves better adaptations for survival.

Many sea urchins (**Fig. 14-18d**) have evolved long sharp spines that cover their entire upper body. The spines are often tipped with reverse barbs or venom injectors. A direct approach by a predator to one of these sea urchins is likely to result in severe stab wounds or even paralysis and death. However, some triggerfishes will methodically pick off one spine at a time until they can attack the underlying external shell of its, then helpless, inhabitant. Other triggerfishes use a jet of water from the mouth to blow the sea urchin over, exposing the vulnerable underside that has no spines—an elegant means of circumventing the urchin's defenses. In addition to their formidable spines and, in some species, highly toxic venom, many sea urchins have become nocturnal to avoid daytime predators.

Crustaceans, including shrimp, crabs, and lobsters, have developed hard external shells that they must periodically shed and regrow as the soft animal within becomes larger. Worms, such as the fan worm and Christmas tree worm (**Fig. 14-10c,d**), use rocks, coral, or sand to build armored burrows into which they can withdraw. Sea cucumbers do not have hard shell armor, but they have developed thick leathery outer skins containing calcium carbonate that, although pliable, are almost impossible to bite through.

Certain fish species have also developed armor and spines. Boxfishes (**Fig. 14-19f**) have a hard, boxlike body that allows only slow and awkward swimming but makes them large in cross section to prevent a predator's jaw from grasping and crushing them. The armor also prevents the predator from taking small bites off a boxfish's body. When attacked, burrfishes (**Fig. 14-19d,e**) gulp large amounts of water and swell up, extending spines that normally lie flat on their body. Burrfishes reportedly may even inflate when already caught in a predator's jaws and simply wait for the predator to weaken or die from hunger before deflating and releasing themselves.

Toxins

A variety of invertebrate species, many marine algae, and certain fishes produce or concentrate from their food a wide spectrum of toxic substances. These substances are sometimes used to kill parasites and larval stages of other organisms that may settle on the toxin-producing species, but their main use is to discourage predators. Most of the myriad toxic substances synthesized by marine species have not been identified, and many thousands of these compounds are likely to be found. Because most toxic substances discourage predators, including bacteria and **viruses**, by interfering with their biochemistry, these substances hold the potential to be used as, or to lead to the development of, drugs that can treat human illness. Several drugs derived from marine toxins are already in routine use or are undergoing clinical trials. For example, a powerful painkiller derived from the venom of cone snails (**Fig. 14-19c**) that blocks nerve channels has been found to be more potent than morphine without being addictive.

Many species that produce toxins to make themselves inedible, notably nudibranchs (**Fig. 14-11c,d**), are brightly colored. The conspicuous color schemes of nudibranchs and similarly toxic tunicates, sponges, and other invertebrates warn predators of the poison defense. In response, many predators have evolved mechanisms to detoxify the poison produced by their prey species.

Numerous species inject toxins into the predator to repel its attack. Sea urchins inject such venom with the tips of their spines. Stonefishes and scorpionfishes (**Fig. 14-16d**) inject deadly venom with sharp spines along their dorsal (upper) fin. Anemones, corals, hydroids, and other invertebrates all inject venom by firing little poisonous darts called "nematocysts" from their tentacles. Some nudibranchs even steal these defenses by consuming anemones or hydroids and assimilating the undischarged nematocysts into their own body tissues to fire at their own predators.

Toxins are used for hunting as well as defense. For example, anemones (**Fig. 14-20a**) use toxin-laden nematocysts to attack and stun or immobilize invertebrates and small fishes that blunder into their trap. Once stunned, the prey is trapped by mucus-laden anemone tentacles that fold over and pass the prey toward the mouth or open stomach at the anemone's center. Anemonefishes (often called "clownfishes" or "clown anemonefishes") live in or near the anemone (**Fig. 14-20b-f**), retreating into its protective toxic folds and tentacles when threatened. The anemonefishes avoid being stung by developing a specialized mucus coating that prevents the anemone's stinging cells from firing, effectively camouflaging the fish as part of the anemone's own body, essentially a way of gaining immunity.

Other notable species that use toxins to immobilize their prey include cone shells (**Fig. 14-19c**), which inject their venom through a long, thin tube extended from their body, and blue-ringed octopuses (**Fig. 12-1**), which transmit their toxin in mucus as they bite their prey. A number of human deaths have been caused by cone shell toxin injected when people inadvertently stepped on a cone shell living just buried in the sand in shallow water near the beach. One species of blue-ringed octopus, which lives in tide pools and on shallow reefs around Australia, is not aggressive but will bite if threatened or stepped on. The venom injected by this species is especially toxic, and there is no known antidote. A bite often results in death.

Numerous species excrete poisons into the surrounding water to discourage competitors or potential predators. On the West Coast of the U.S., certain species of the diatom Pseudo-nitzschia produce a potent neurotoxin called domoic acid during large algal

FIGURE 14-20. Anemonefishes, also called "clownfishes" or "clown anemonefishes," live in family groups in association with a number of different species of large carnivorous anemones, such as the Haddon's sea anemone (*Stichodactyla haddoni*, Indonesia) shown in (a). There are a number of anemonefish species, including the examples shown here. (b) Tomato anemonefish (*Amphiprion frenatus*, Papua New Guinea). (c) Clown anemonefish (*Amphiprion percula*, Papua New Guinea). (d) Pink anemonefish (*Amphiprion perideraion*, Papua New Guinea). (e) Spinecheek anemonefish (*Premnas biaculeatus*, Papua New Guinea). (f) Clark's anemonefish (*Amphiprion clarkii*, Papua New Guinea). All anemonefish species are damselfishes of the subfamily Amphiprioninae, except the spinecheek, which belongs to another subfamily.

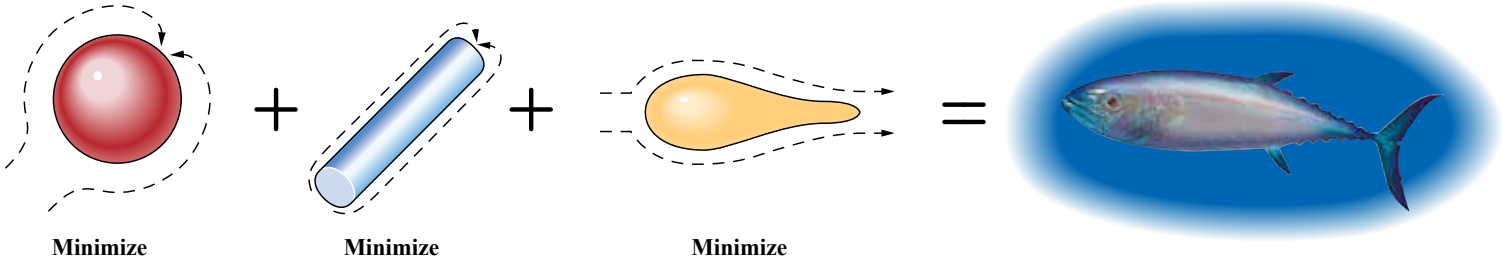


FIGURE 14-21. Three types of drag slow an object as it moves through water: surface drag, form drag, and turbulence drag. For each type, the magnitude of the drag varies with the shape of the moving object. This figure shows the optimum shape required to minimize each type of drag. Body shapes of most fish species are a compromise between the need to minimize drag and other needs of the animal, such as acceleration and turning speed. Fishes that swim constantly at high speed, like the tuna in this figure (*Thunnus sp*., Fiji), have a body shape that provides the best compromise for reducing the sum of the three types of drag: a rounded body that is narrow at the tail and thicker near the front. Nuclear submarines also are built in this general shape.

events. While these diatoms are the source, the toxin accumulates in the tissues of filter-feeders like sardines and anchovies. When larger marine mammals, such as California sea lions and whales, consume these fish, they ingest concentrated doses of the toxin, which causes seizures, brain damage, and often death. Domoic acid is also the cause of Amnesic Shellfish Poisoning which can cause persistent neurological symptoms in humans who consume filter feeding shellfish.

Group Cooperation

Both hunting and defense can be aided by cooperative approaches involving several or many individuals of the same species and sometimes between members of two different species. The Portuguese man-of-war is a good example (**Chap. 12**). Group cooperation is a common adaptation, but two special categories are of interest: colonial forms and **schooling** in pelagic animals.

Colonial species abound in the oceans and include many sponges and **cnidarians**. In some colonial forms, each individual feeds and reproduces separately, but the individuals cooperate to enhance each other's and the species' success. For example, individual polyps of sea fans and corals, by growing attached to each other, extend the colonies' reach into the water column. This extension gives each polyp a better chance of encountering food and reduces competition by other species that live on sediment or rock surfaces.

Pelagic species, including many fishes, squid, and marine mammals, congregate in schools. Similarly, phytoplankton and zooplankton often have patchy (clustered) distributions. Schooling and clustering behavior affords advantages. For example, a group of fish can often overcome the defenses of a single individual of an otherwise superior species. Damselfishes lay their eggs in clusters on a reef surface and then defend them aggressively. Wrasses and other fishes arrive in groups to feed briefly but voraciously on the eggs as the damselfishes frantically try to chase them off but fail because there are too many attackers.

Fish schools have no leader, but each fish precisely matches the seemingly random twists and turns of the school, maintaining a precise distance from each of its neighbors. Movements of the school may confuse predators by making the school appear to be a single large organism. In addition, predators may have difficulty singling out a victim from the moving school. Schooling may

FIGURE 14-22. Some fish shapes that minimize form drag. (a) The cornetfish (*Fistularia commersonii*, Red Sea) has a very long, needle-shaped body to minimize form drag. (b) Side view of Klein's butterflyfish (*Chaetodon kleinii*, Papua New Guinea). (c) Front view of the same species of butterflyfish. Note the lateral compression of the body (narrower across than vertically), which reduces form drag and enables the fish to execute turns quickly.

have benefits in reproduction as well. Finding a mate is easier in a school, and a high rate of fertilization is ensured if eggs and sperm are released to the water column simultaneously by many members of the school. Mass **spawning** can in fact be considered a form of "schooling" of the fertilized eggs and larvae.

When prey is concentrated in schools, the predator spends much of its time searching for the school. Once it encounters a school, it cannot consume the entire school, so most individuals will survive, even if the predator gorges itself. Predators are able to consume less food through periodic gorging than they could by continuous steady feeding. Schooling of the prey and mass spawning thus reduce the efficiency of predator feeding, and consequently more of the prey species survive. This outcome may be the principal advantage of schooling.

SELECTED ADAPTATIONS IN FISHES

Each marine species is adapted in different ways that enable it to survive. Fishes are adapted in many different ways to respond to such challenges as swimming in a manner that best supports their hunting and defensive strategies, the high osmotic pressure of seawater, the variability of **osmotic pressure** in estuarine waters, and control of their buoyancy.

Swimming Adaptations

Water is much denser than air, so it is much more difficult to travel through water than through air. The next time you go swimming, try running through knee-deep water and you will understand just how much more difficult it is to move through water. Fishes must overcome water resistance to swim. Therefore, the body shape of a fish must be optimized to facilitate its specific swimming habits.

While swimming, fishes must overcome three types of resistance or drag: surface drag, form drag, and turbulent drag. Surface drag is the **friction** between a fish's body surface and the water. Form drag comes about because water must be pushed out of the way, and turbulent drag is related to the smoothness of water flow past the swimming object.

Surface drag increases as the surface area in contact with the water increases. Consequently, surface drag is minimized if the swimming object is spherical because a sphere has the smallest surface area per unit volume of any solid object. Form drag increases in proportion to cross-sectional area (**Fig. 14-21**). The perfect shape to minimize form drag is needlelike, but this shape has a high ratio of surface area to volume and is subject to increased surface drag. A few fish species are needle-shaped (**Fig. 14-22a**), and others have an extremely thin platelike body (**Fig. 14-22b,c**) to minimize form drag. Most fish shapes are a compromise: rounded or oval in cross section, but elongated in the swimming direction. This shape tends to minimize total (form plus surface) drag (**Fig. 14-21**).

The third form of drag, turbulent drag, dictates the final refinement in fish body shape. The turbulent flow of water around the fish is reduced if the front is rounded and blunt and the rear tapers to form a teardrop shape (**Fig. 14-21**). This shape is similar to the cross section of an airplane wing, or the form of a blimp or submarine, all of which are designed to minimize drag.

The fastest and most continuously swimming fishes, such as tuna (**Fig. 14-21**), have a generally teardrop shape to minimize total drag and thus minimize energy used in swimming. Eyes that are flush and smoothly contoured against the body and a slimy coating are other adaptations that reduce surface drag. Fishes that do not swim continuously and fishes that are adept at fast turns rather than high speed have less need to reduce drag than fast swimmers have. Thus, these fishes often have body shapes that are greatly modified from the teardrop form to conform with their own special habits. Fishes that specialize in short bursts of speed with quick accelerations generally are somewhat

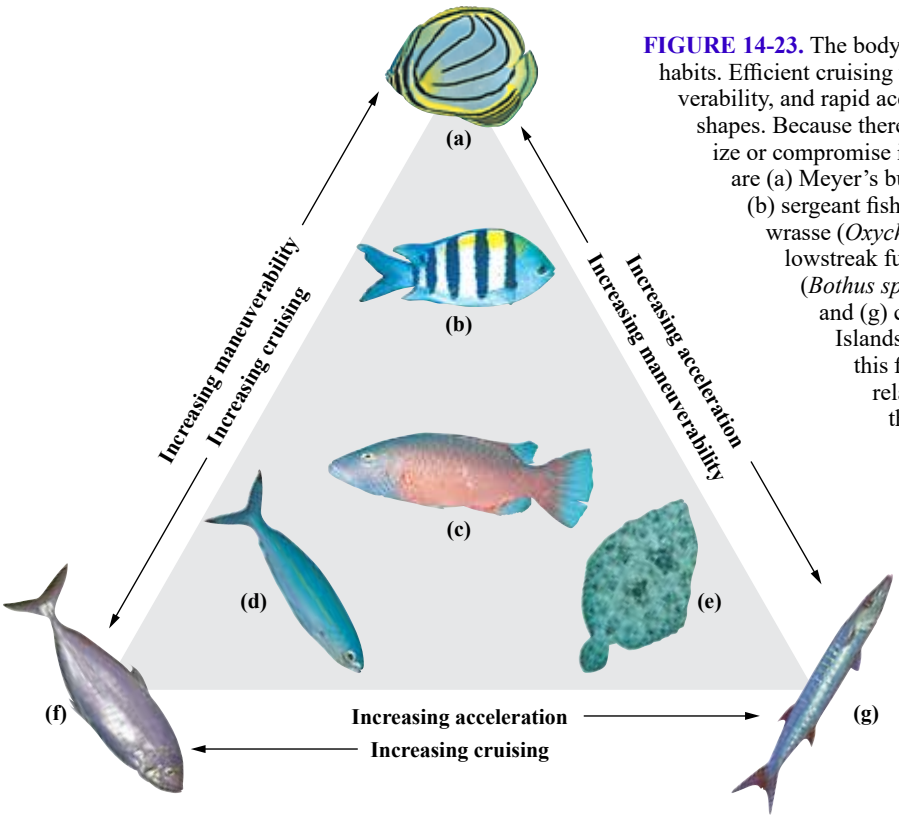


FIGURE 14-23. The body shapes of fish species are related to their swimming habits. Efficient cruising with minimal energy expenditure, maximum maneuverability, and rapid acceleration are all desirable but require different body shapes. Because there is no perfect shape, each species tends to specialize or compromise in a different way, as shown here. The species shown are (a) Meyer's butterflyfish (*Chaetodon meyeri*, Papua New Guinea), (b) sergeant fish (*Abudefduf sp.*, Papua New Guinea), (c) cheeklined wrasse (*Oxycheilinus digramma*, Papua New Guinea), (d) yellowstreak fusilier (*Pterocaesio lativittata*, Vanuatu), (e) flounder (*Bothus sp.*, Hawaii), (f) trevally (probably *Carangoides sp.*, Fiji), and (g) chevron barracuda (*Sphyraena putnamiae*, Solomon Islands). The relative sizes of the species are not preserved in this figure. Although most fish species follow the general relationships between shapes and behaviors depicted in this figure, some do not fit this pattern, because their behavior is highly specialized. For example, frogfishes (**Fig. 14-14b**) are sedentary, except for short bursts of rapid acceleration. Their thick bodies provide the musculature for these quick bursts, but they cannot sustain the movement as barracudas can.

thickened in the middle (**Fig. 14-23**) by the heavy musculature necessary for such maneuvers (similar to the difference between long-distance runners and weight lifters). Fishes that specialize in quick turns generally are somewhat flattened (**Fig. 14-22b,c**) so that the flat sides of their body can be used in turning in much the same way that a boat's rudder is used. Fishes that hunt mostly by stealth or feed on plankton and do not need to swim quickly often have bizarre body shapes (**Fig. 14-16e**). Fin shapes are also modified to accommodate different swimming habits.

Adaptations of Fins

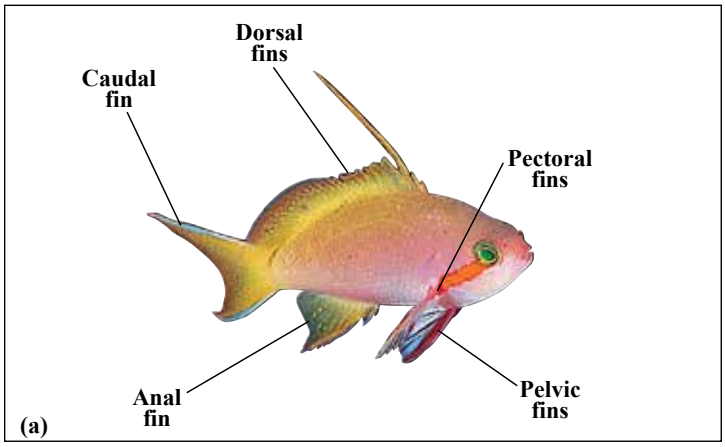
Fish fins are extremely important in swimming and executing turns, just as the tail fin, rudder, short rear wings, and wing flaps of an airplane are important in controlling course and stability. Fishes generally have a pair of pectoral fins (one on each side of the body behind the head), two dorsal fins along the center of the back, and an anal fin beneath the rear half (**Fig. 14-24a**). They also have a caudal fin at the posterior, and a pair of pelvic fins on either side of the lower body forward of the anal fin. These fins vary greatly among species in size, shape, and location, and some fins may be absent in certain species.

The pairs of pelvic and pectoral fins are used primarily to execute maneuvers, including turns and stops, and usually can be folded flat against the body when not in use. The vertical dorsal and anal fins serve primarily as stabilizers during swimming and, in some species, can be folded against the body when not needed. The caudal fin is the primary provider of propulsion in most species. Most fishes also alternately contract and relax muscles along their body to create a wavelike motion that travels along the body and produces a forward thrust (**Fig. 14-24b**). The caudal fin that provides the final thrust is flared out vertically to provide a large surface area and, consequently, strong thrust as it is moved from side to side. You can experience such a thrust increase if you use swim fins.

Increasing the caudal fin surface area increases thrust but also increases surface drag. Therefore, the caudal fin is modified to reflect the swimming habits of the species. These modifications are shown by the **aspect ratio** of the fin, which is defined as

$$\frac{(\text{fin height})^2}{(\text{fin area})}$$

Five major types of caudal fins are distinguished by different ranges of aspect ratio and fin shape (**Fig. 14-25**). Rounded fins (aspect ratio 1; **Fig. 14-25a**) are useful for maneuvering and quick acceleration by species such as butterflyfishes (**Figs. 14-14e; 14-22b,c; 14-23a**). Truncate fins (aspect ratio 3; **Fig. 14-25b**) and forked fins (aspect ratio 5; **Fig. 14-25c**) reduce drag in comparison with rounded fins, but they still provide substantial maneuvering assistance. Truncate and forked fins are used by many species that swim reasonably fast but also maneuver relatively quickly (**Fig. 14-23**). Lunate caudal fins (aspect ratio up to 10; **Fig. 14-25d**) are typical on fast and continuously swimming species, such as trevally (**Fig. 14-17a,b, 14-23f**), tuna (**Figs. 12-22a, 14-21**), marlin, and swordfish. Lunate caudal fins in these species are rigid and have little use in maneuvering, although they are very efficient in forward propulsion. Fast-swimming predatory species with lunate caudal fins can outrun other species with truncate, forked, or rounded caudal fins, but the prey species have an excellent chance of avoiding the predator by using their



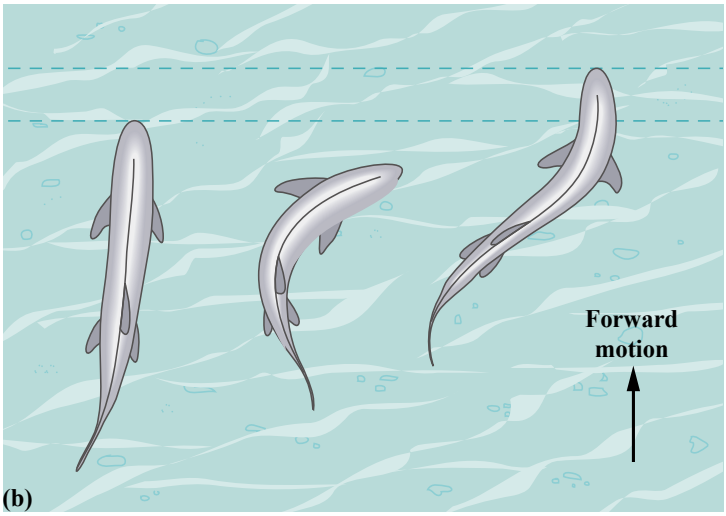


FIGURE 14-24. Fish fins and swimming motion. (a) Fishes have a dorsal fin or fins along the back, pectoral fins on either side of the body, a pair of pelvic fins under the forward half of the body, an anal fin under the rear half of the body, and a caudal fin at the tail. Each of these types of fins may be much modified for special purposes in different fish species. The fish shown here is a threadfin, or red-cheeked fairy basslet (*Pseudanthias huchtii*, Papua New Guinea). (b) Most fish species swim by using a series of undulating body motions. (c) Triggerfishes and their relatives, such as this barred filefish (also called an orange-fin filefish; *Cantherhines dumerilii*, Hawaii) swim not by undulating their bodies, but by back-and-forth motions of their specially adapted soft dorsal and anal fins. This movement gives them great maneuverability, but it is less efficient in providing acceleration than is the undulating body motion method of swimming.

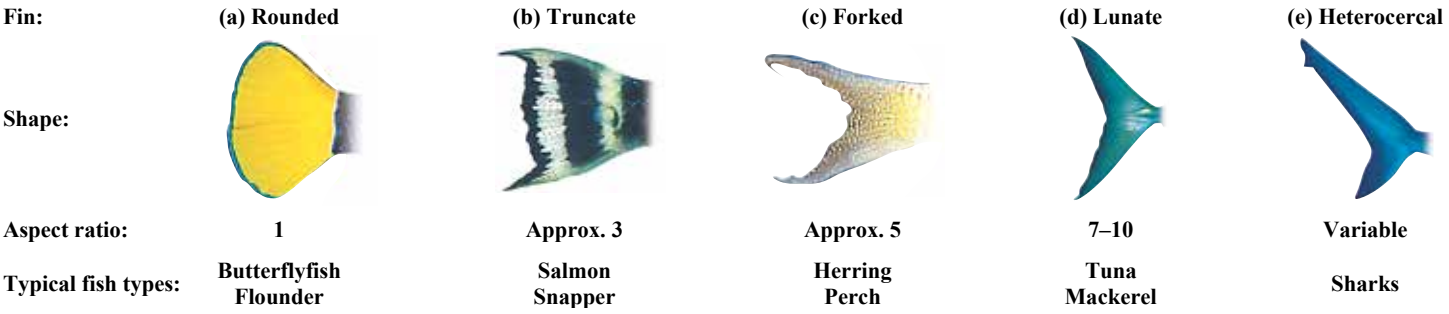


FIGURE 14-25. The shape of the caudal fin in fish species is related to their swimming behavior. There are five basic types of caudal fins, characterized by different aspect ratios, although caudal fins of many species have characteristics intermediate between these categories. The caudal fins shown here belong to (a) a blue-girdled angelfish (*Pomacanthus navarchus*), (b) a redbreasted Maori wrasse (*Cheilinus fasciatus*), (c) a male black-spot angelfish (*Genicanthus melanospilos*), (d) a trevally (*Carangoides sp.*)—all photographed in Papua New Guinea—and (e) a gray reef shark (*Carcharhinus amblyrhynchos*), photographed in Palau. Their relative sizes are not preserved in this figure.

greater maneuverability.

Heterocercal caudal fins are asymmetrical, the upper lobe being longer and taller than the lower lobe (**Fig. 14-25e**). This type of caudal fin is used primarily by sharks (**Fig. 12-23**). It is similar to the lunate caudal fin in that it provides very efficient forward thrust but little help in maneuvering. However, its asymmetrical shape also provides upward lift, which is important to sharks because they have no swim bladder and tend to sink if they stop swimming. Lift is also provided by the sharks' pectoral fins.

Unlike those of most other fishes, sharks' pectoral fins are large, flat, and relatively inflexible (**Fig. 12-23**), providing lift like aircraft wings. The pectorals are relatively far forward on the shark's body (**Fig. 12-23**) and lift the front of the shark, while the caudal fin lifts the tail. Although sharks are powerful swimmers, their fins are designed poorly for maneuvering, and they are not adept at capturing prey that can anticipate their charge and perform evasive maneuvers. Unfortunately, this knowledge is of little use to swimmers who may be attacked by sharks, because human body shapes do not allow for quick maneuvers in the water.

Although most fish species use their fins for swimming, numerous species have fins adapted to perform highly specialized functions. A number of species have dorsal fins modified to act as defensive, and perhaps offensive, weapons. In these species, the individual rays or spines of the dorsal fins, or parts of the dorsal fins, are needle-sharp and may contain a venom that is injected into any predator that challenges the fish. Species with this type of dorsal fin include stonefishes and scorpionfishes (**Fig. 14-16d**), which lie on a reef or the seafloor and use their dorsal defenses to protect against attacks from above. They also include lionfishes (**Fig. 14-26a**), which swim close to a reef, turning their backs toward any approaching predator and their more exposed undersides toward the reef. In some species, such as frogfishes (**Fig. 14-14b**) and anglerfishes (**Fig. 14-15**), the forward-most ray or rays of the dorsal fin are adapted to become lures that can be dangled in front of the fish's mouth to entice prey.

In triggerfishes (**Fig. 14-26b**), the forward dorsal fin consists primarily of a single strong, rigid spine that normally lies flush against the fish's body. This spine can be extended from the body to become a fearsome weapon that gives the triggerfish its name. Certain triggerfish species may also use this spine defensively. When chased, they swim headfirst into holes in the reef and extend their trigger to lock themselves in. Because of the way the trigger is hinged, almost no amount of tugging by a predator can pull the triggerfish out. Once the predator leaves, the trigger can be relaxed, allowing the triggerfish to back out of its refuge. Triggerfishes also use modified fins for swimming. The anal and dorsal fins are enlarged and undulate back and forth in wavelike motions that replace the body undulations used by other fishes. These fins enable triggerfishes to hover, turn, and swim slowly forward or backward to enter holes in the reef just wide enough for them to fit through.

Many species that live or rest frequently on the seafloor have pectoral and sometimes caudal fins that are elongated and have strong rigid spines on which the fish can rest. Sandperches (**Fig. 14-26c**) have this type of adaptation. In certain deep-sea species that inhabit areas where currents are generally weak, both the pectoral fins and the lower lobe of the caudal fins are elongated to an extent that can exceed the fish's body length. These fishes "walk" on the seafloor as if perched on a tripod.

Like triggerfishes, wrasses (**Fig. 14-26d**) do not normally swim by using body undulations for propulsion. Instead, they propel themselves with their pectoral fins, which they stroke back and forth in much the same way that an oar is used. The fin is moved backward while spread vertically to push the water back and the fish forward. Then it is rotated and moved forward while in a horizontal orientation that minimizes drag. Wrasses can also swim by using their caudal fin and body undulation in the same way that other fishes do, but the oar-like propulsion created by using the pectoral fins provides better control of movements at slow speeds. Such control is ideally suited to the wrasses' feeding habit of picking small crustaceans, algae, and individual coral polyps from cracks and crevices in reefs.

Many fishes spend most of their lives concealed in holes in a reef and do very little swimming. These fishes generally have greatly reduced fins, and their dorsal, caudal, and anal fins are often fused into one continuous fin extending around the fish. In extreme cases, the dorsal and anal fins may be missing entirely. Such fishes usually have an elongated body and swim by using sinuous body undulations. Swimming without the use of dorsal and anal fins is slow and inefficient, but it is perfectly suited to the lifestyles of these fishes. Snakelike flexibility and the lack of protruding fins enable them to swim easily through the narrow, tortuous passages of holes in the reefs where they live. Species adapted in this way include gobies (**Fig. 14-26e**) and moray eels (**Fig. 14-26f**).

Flyingfishes have some of the most bizarre fin adaptations. These warm-water fishes have elongated pectoral (and, in some species, also pelvic) fins that can be spread out from the sides to resemble bird wings. When they sense danger, flyingfishes swim

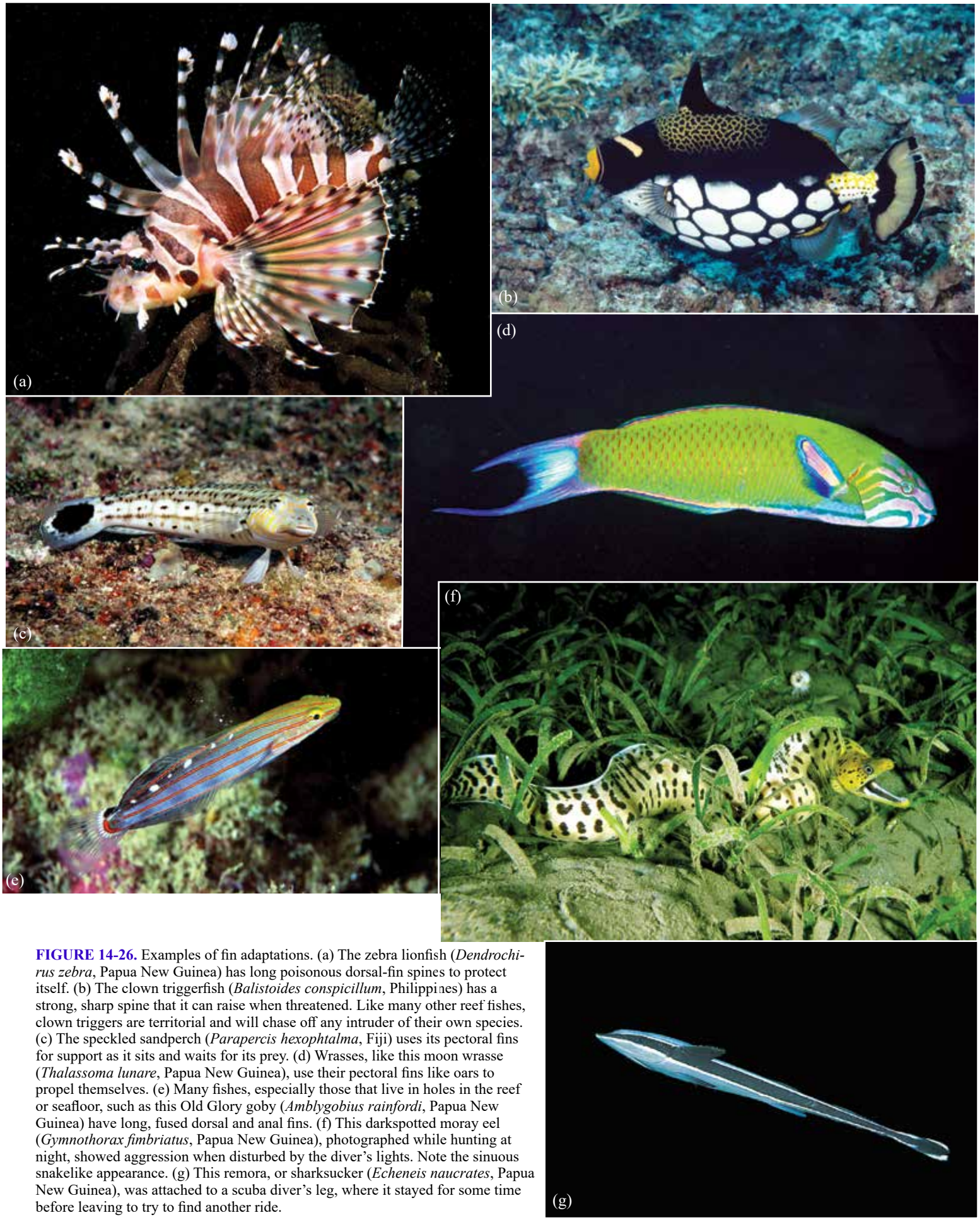


FIGURE 14-26. Examples of fin adaptations. (a) The zebra lionfish (*Dendrochirus zebra*, Papua New Guinea) has long poisonous dorsal-fin spines to protect itself. (b) The clown triggerfish (*Balistoides conspicillum*, Philippines) has a strong, sharp spine that it can raise when threatened. Like many other reef fishes, clown triggers are territorial and will chase off any intruder of their own species. (c) The speckled sandperch (*Parapercis hexophtalma*, Fiji) uses its pectoral fins for support as it sits and waits for its prey. (d) Wrasses, like this moon wrasse (*Thalassoma lunare*, Papua New Guinea), use their pectoral fins like oars to propel themselves. (e) Many fishes, especially those that live in holes in the reef or seafloor, such as this Old Glory goby (*Amblygobius rainfordi*, Papua New Guinea) have long, fused dorsal and anal fins. (f) This darkspotted moray eel (*Gymnothorax fimbriatus*, Papua New Guinea), photographed while hunting at night, showed aggression when disturbed by the diver's lights. Note the sinuous snakelike appearance. (g) This remora, or sharksucker (*Echeneis naucrates*, Papua New Guinea), was attached to a scuba diver's leg, where it stayed for some time before leaving to try to find another ride.

upward with a rapid burst of speed that carries them through the water surface and into the air. Once in the air, they spread their fins and, using these "wings," sail a few tens of centimeters above the waves. They can glide for as long as 30 s, and some species can prolong their glide by flailing an elongated lower lobe of the caudal fin at the sea surface as they descend close to the water. Although flying is a very effective strategy to escape from some predators, flyingfishes expose themselves to predation by seabirds.

A number of species, such as clingfishes and remoras (**Fig. 14-26g**), use fins as suction devices with which they can hold onto the seafloor or another organism. Clingfishes use modified pelvic fins to cling tenaciously to rocks in coastal areas where wave action is intense. Remoras use a modified dorsal fin as a suction cup to attach the top of their head to sharks, manta rays, other large ocean animals, and even boats and **scuba** divers. The remora's sucker looks so little like a fin that careful research was needed to identify its origin. Although remoras must swim rapidly to catch and attach to a host, they are then transported without having to expend energy. Remoras can detach themselves to feed on any nearby available food, particularly scraps of their host's meal if they are riding on a shark or other predator.

Ghost pipefishes (**Fig. 14-16e**) and seahorses (**Fig. 14-16h,i**) have perhaps the most extreme adaptation of body form and fins. Some species swim in a vertical head-down or head-up position and propel themselves slowly by rapid back-and-forth oscillations of their small dorsal fins. Because the fish is oriented vertically, the thrust from these fins is oriented perpendicular to the fish's body. Ghost pipefishes thus swim sideways, although they swim in a normal horizontal position when they need to swim rapidly to avoid danger.

Osmoregulation

The relative proportions of dissolved chemicals in body fluids of fishes, other **vertebrates**, and invertebrates are remarkably similar to their relative proportions in seawater. In most invertebrates, the salinity of internal fluids is also the same as the external seawater salinity. However, the internal fluids of fishes are less saline than seawater. The reason is that bony fishes are thought to have first evolved in freshwater. Because osmosis causes water to diffuse across cell membranes from lower salinity to higher salinity, fishes must be able to counteract osmosis.

Osmosis of water molecules across a semipermeable membrane (such as the cell surface) from lower to higher salinity is easy to understand. Because the "concentration" of water molecules is higher in the lower-salinity fluid, more water molecules are in contact with that side of the membrane. Thus, more water molecules diffuse through the membrane toward the higher-salinity fluid than diffuse in the opposite direction. In contrast, dissolved salt molecules would be more likely to diffuse from high to low salinity because of their higher concentrations, but ions of dissolved salts are generally much larger than water molecules and hence less likely to pass through the openings in a semipermeable membrane.

One way to counteract osmosis is to increase the pressure on the high-salinity side of the membrane, which forces more water molecules through the membrane to the lower-salinity fluid. The pressure needed to balance water migration across a membrane is called "osmotic pressure." Osmotic pressure increases as the difference in salinity between the fluids on either side of the membrane increases.

Marine fishes must have a mechanism for counteracting osmosis or they would continuously lose water to their surroundings and dehydrate. Fishes cannot maintain a pressure difference across their external membrane, because they would be able to do so only if they had an impermeable body surface, like the pressure hull of a submarine. With an impermeable body surface, feeding and excretion of waste products would be extremely difficult because they would have to take place through the equivalent of a submarine airlock. In addition, all aquatic organisms must exchange oxygen, carbon dioxide, and nutrients with seawater through a porous membrane. Consequently, fishes have adapted methods called **osmoregulation** to counteract osmosis in seawater.

Fishes that live in seawater osmoregulate by drinking seawater to replace water lost from their internal fluids by osmosis. The excess salt ions ingested with the seawater are excreted through specially adapted cells in the **gills** (**Fig. 14-27a**). Freshwater fishes osmoregulate by drinking almost no water and excreting large volumes of very dilute urine to discharge the water that enters their bodies by osmosis. They also must take up dissolved salts through their gills (**Fig. 14-27b**). Certain estuarine fish species or species that live in environments of variable salinity, such as **tide pools**, must be able to osmoregulate in both directions. Because few fish species have such ability, most estuarine fishes migrate within the estuary as river and tidal flows vary to remain at the same approximate external salinity.

Two special categories of fishes have evolved life cycles that require them to cross the salinity gradient between freshwater and seawater twice during their life cycles. These are the **anadromous** and **catadromous** fishes (**Chap. 13**).

Swim Bladders and Buoyancy

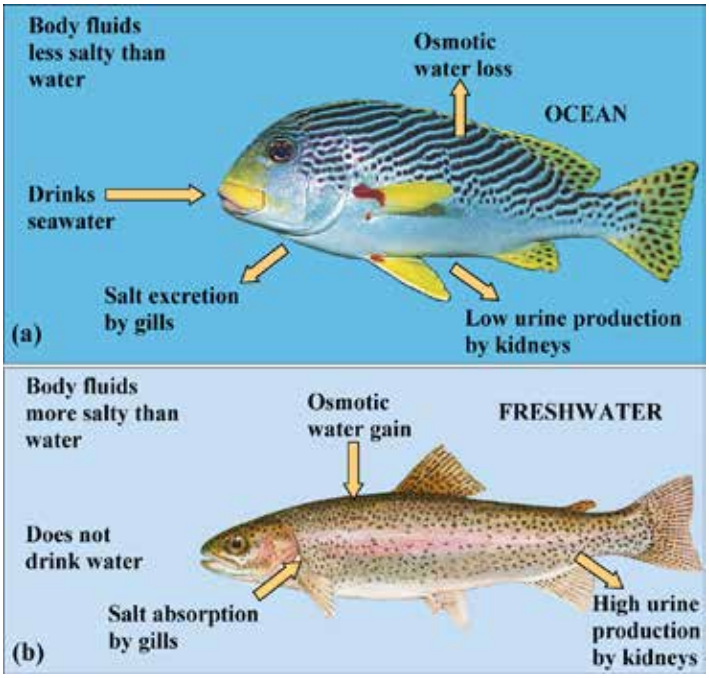


FIGURE 14-27. Osmoregulation. (a) Fishes that live in seawater, such as the Goldman's sweetlips (*Plectorhinchus goldmanni*, Vanuatu) illustrated here, lose water continuously by osmosis across their body surfaces and must drink seawater and excrete salt through specially adapted cells to replace the lost water. (b) Fishes that live in freshwater, such as Rainbow trout (*Oncorhynchus mykiss*), absorb water continuously by osmosis and get rid of the excess by producing copious amounts of very dilute urine.

Some fish species that live most of the time on the ocean floor can afford to be negatively buoyant (dense enough to sink) because they expend relatively little energy swimming against **gravity** during their limited excursions above the seafloor. Examples include most species of frog-fishes (**Fig. 14-14b**) and scorpionfishes (**Fig. 14-16d**). Most fishes live in the water column and cannot afford to expend energy by swimming continuously to counteract gravity and maintain their depth. Consequently, most pelagic fishes (and other vertebrates and some invertebrates) must find a way to adjust their buoyancy to be approximately equal to that of seawater. The two primary ways of doing this are to synthesize and retain low-density oils, or to develop a gas-filled bladder.

Many fish species that live in surface layers and mid depths achieve neutral buoyancy by filling an internal swim bladder with gas. The amount of gas within the swim bladder must be adjusted as the fish changes depth. Otherwise, the gas will expand or contract and change the buoyancy of the fish as it ascends or descends. Some fishes with swim bladders make only limited and slow vertical excursions because the exchange of gas between blood and swim bladders is slow. Such species often die if caught and brought rapidly to the surface, because the swim bladder expands faster than the fish can evacuate the gas (**Fig. 14-15**). Other species have a special duct that connects the swim bladder with the esophagus, and they can ascend rapidly by "burping" to release excess gas from the swim bladder. Moray eels (**Fig. 14-26f**) have this duct, allowing them to change depth rapidly while hunting prey.

In shallow-water fishes, the gases in the swim bladder are similar to the atmosphere in composition: about 20% oxygen and 80% nitrogen. Some shallow water fishes fill their swim bladder by surfacing and gulping air. Fishes that live at greater depths have higher oxygen concentrations in their swim bladders, in some species up to 90% oxygen. The oxygen concentration in swim bladder gas reflects the mechanism fishes employ to force gas from solution in their blood to a gas in the swim bladder which is more effective for oxygen than for other gases.

At a depth of 7000 m, the pressure is so great and gases so compressed that their density is approximately the same as that of fats. Consequently, many deep-water fishes have swim bladders filled with oil or fat instead of gases. These fishes do not need to adjust the amount of gas in the swim bladder as they change depth.

The largest and most active swimmers, such as mackerel and tuna (**Figs. 12-22a, 14-21**), have no swim bladder. These fishes can afford the relatively small energy penalty required to maintain their depth against their negative buoyancy because they expend much greater amounts of energy in swimming. Many of these species, especially sharks, have fins and body shapes designed to counteract their negative buoyancy as they swim. Sharks also have large livers with high concentrations of lighter-than-water oils to provide some compensation for their negative buoyancy.

REPRODUCTION

To reproduce successfully, each species must ensure that enough of its offspring survive to reproductive age and that these progeny in turn produce enough of their own offspring to continue the cycle. Reproductive cycles are poorly documented or poorly understood for all but a few marine species, but the basic elements of their diverse strategies are known.

Separate-Sex Reproduction

The majority of marine species reproduce by sexual interaction between male and female. Sexual reproduction increases **genetic** diversity (**CC17**), which improves the species' ability to survive and adapt to environmental change.

In sexual reproduction, sperm is transferred from male to female by a copulatory organ or directly from the male sexual organ to eggs laid previously by the female. Alternatively, sperm is either discharged into the water, where it fertilizes eggs retained by the female, or eggs released into the water, where fertilization occurs.

Direct transfer of sperm from male to female requires relatively few eggs and sperm to ensure sufficient fertilizations. Hence, this strategy minimizes the energy needed to produce eggs or sperm. However, it requires that males and females locate each other for breeding, which for many species is a major problem, especially if they are permanently attached to a surface. Many motile fishes and invertebrates find mates in mating congregations that assemble at a specific time of year and place. Mating congregations enable some fishes to select mates that have desirable characteristics.

The mate location problem has been solved in an unusual way by a number of species, including some barnacles and fishes that live at depth, in the dark. In these species, one sex is relatively small and resides either near or directly on the other. The smaller sex is usually the male because producing sperm requires less energy, and hence less body weight, than producing eggs does. The deep-sea anglerfish (**Fig. 14-15**) is a good example of a species that uses this strategy.

In pelagic reproduction, sperm and often eggs are released into the water (**Fig. 14-28a,b,c,l**). Sperm are attracted to eggs or females of their own species probably by chemotaxis ("tasting" or "smelling" of chemical clues released into the water by eggs or females). If sperm are released far from the eggs or females, or at a different time than the eggs, the probability of fertilization is very small. Consequently, pelagic spawning often occurs synchronously among all males and females of a given species in a specific region. Often this synchronous spawning occurs at a specific time of year or on a specific day. The timing is usually coordinated with a particular phase of the tides, such as high **spring tides** at full or new moon. Corals (**Fig. 14-28**a), many other benthic invertebrates, and many fishes spawn synchronously. In some fish species, a male and female pair will spin around each other or swim in contact with each other (**Fig. 14-28b**), simultaneously releasing and mixing a cloud of sperm and eggs. Other species form spawning congregations in which vast clouds of sperm and eggs are released simultaneously. Often the individuals swim in a school or swarm that spirals inward and upward toward the surface as sperm and eggs are released. This movement ensures that sperm and eggs are concentrated in an intensely mixed, dense cloud; keeps the eggs away from benthic predators; and probably reduces loss to pelagic predators.

Hermaphroditism

In many species, hermaphroditic life cycles have solved the problem of finding or ensuring the presence of a mate. Hermaphrodites are individuals that have both the sexual organ (gonad) necessary to produce sperm and the sexual organ necessary to produce eggs. In certain species, including most nudibranchs, the individual may perform either the male or female function, or both, at any time in its sexually mature stage (**Fig. 14-28d,f**).

The common acorn barnacle is also a hermaphrodite in which each individual has a penis that can be used to inject sperm into any other barnacle because each barnacle also has ovaries. Thus, although adult barnacles are permanently attached to a surface, a suitable mate is always present in any location where these barnacles are well established (**Fig. 14-7c**).

Sequential hermaphroditism is the ability of an individual to change from female to male or from male to female at an appropriate time in its adult life. The female-to-male sex change confers an advantage to species in which reproductive success is aided by the presence of a strong, experienced male during reproduction. For example, damselfishes (**Fig. 14-28k**), including anemonefishes (**Fig. 14-20**), lay their eggs on the reef surface (under the edge of the anemone in the case of anemonefishes). Reproductive success in these species depends on the successful defense of fertilized eggs against predators. For a given anemone, an anemonefish family may consist of a large aggressive male, a somewhat smaller female, and usually 4 to 10 smaller subadults or juveniles. The male defends the eggs from predation and defends his anemone from predation by butterflyfishes. If the male dies, the female grows and changes sex, and one juvenile grows to become a sexually mature female.

A male-to-female sex change is the preferred strategy of many species in which the female produces more eggs as it becomes larger. This strategy is common in invertebrates. For example, the common eastern oyster (*Crassostrea virginica*) is a male for several years as it grows, and then it transforms into a female. In transitional individuals, both sperm and eggs may be produced and the individual may even fertilize itself.

Asexual Reproduction

There are several different methods of asexual reproduction, including binary fission, fragmentation, and vegetative reproduction. In another form of asexual reproduction, unfertilized eggs develop into adults, but this reproductive strategy is rare in marine life.

In binary fission, a single-celled organism divides into two offspring. Diatoms reproduce by binary fission (**Fig. 12-17**). Fragmentation is a reproductive process of multicelled organisms that is similar to binary fission. For example, fragments of certain macroalgae and of some invertebrates, including various worms and sea stars, can break off and develop into new individuals. In some cases, fragmentation occurs through the production of special buds that are designed to break off the main individual. This budding process is common in macroalgae and sponges.

In vegetative reproduction, a single individual divides into many individuals that may or may not be physically connected. Vegetative reproduction is the most important marine asexual reproductive mechanism and occurs in many marine algae and invertebrate species, particularly colonial forms, including corals, sponges (**Fig. 14-28m**), and anemones. In benthic invertebrates, a single larva may settle on a substrate, **metamorphose**, and then reproduce vegetatively to cover a broad area of substrate.

Asexual reproduction produces many individuals that are genetically identical **clones**. Therefore, colonies of vegetatively reproduced anemones or encrusting sponges, for example, are all the same sex and color. Cloned colonies can occupy a substrate very densely because the cloned individuals do not have aggressive territorial responses toward each other as they would toward other individuals of their species. This lack of aggression may be important in colonial species, such as the Portuguese man-of-war, in which millions of cloned individuals must cooperate, each performing only one of a variety of separate and different functions needed to feed, defend, move, and reproduce the colony.

Asexual reproduction allows the successful colonization of suitable benthic microhabitats encountered by a single settling larva and avoids the difficulties of ensuring that sperm and eggs are united successfully. However, asexually generated populations have little genetic diversity, and hence the colony, and the species, may be poorly adapted to survive any unfavorable changes in its environment.

Egg Laying

Most marine fish and invertebrate species are oviparous and lay large numbers of eggs that hatch on the seafloor (**Fig. 14-28e-k**) or in the water (**Fig. 14-28a,b,c,l**) to become larvae that are **meroplankton**. In most cases, the vast majority of the eggs and larvae (sometimes more than 99.999%) are consumed by carnivores before they reach adulthood. For benthic species, many additional larvae may die because they settle on unsuitable substrates. Therefore, species that have pelagic eggs and/or larvae generally must produce very large numbers of fertilized eggs to ensure survival of the species. Species that spawn eggs to the water for fertilization must produce especially large numbers of eggs because many will not even be fertilized.

Production of very large numbers of pelagic eggs ensures the wide dispersal of larvae, which enables them to take advantage of the dispersed phytoplankton food resource. For benthic species, the dispersal of large numbers of larvae also facilitates the colonization of suitable substrate where this substrate is found only in isolated areas. Because this strategy carries a substantial energy cost, many species of oviparous fishes, such as anemone-fishes (**Fig. 14-20**) and other damselfishes (**Fig. 14-28k**), lay many fewer eggs on the substrate and protect the eggs from predators until they hatch. Other species, including many sharks, skates, and rays, octopuses and squid (**Fig. 14-28i,j**) lay only a very few eggs that are protected from predators in tough envelopes or encased in a gel (**Fig. 14-28d-h**). Finally, **ovoviviparous** fishes retain fertilized eggs within their reproductive tracts until they hatch. Seahorses (**Fig. 14-16h,i**) and some pipefishes (**Fig. 14-16e**) have an unusual **incubation** mode whereby newly fertilized eggs are deposited in a pouch on the male's abdomen, where they remain until they hatch. Some cardinalfishes incubate eggs in the male's mouth (**Fig. 14-28n**).

Although it would seem to be energy-efficient to produce fewer eggs and protect them until they hatch, energy must be expended to protect the eggs, and this strategy does little to reduce mortality during the larval stage. Larval mortality can be reduced if larvae can evade some predators, but to do so, the larvae must be relatively large. Remember, if larvae are small, they cannot swim effectively, because of the enhanced effect of viscosity (**Chap. 5**). If larvae must be large when hatched, eggs must have large yolks to provide the energy for growth. This requirement offsets any energy gained by producing fewer eggs.

Viviparous species are at the opposite extreme from the prolific pelagic spawners in the trade-off between egg numbers and protection. In viviparous animals, including mammals, offspring are nurtured inside the mother's body until they become fully developed and assume adult or nearly adult form. Some shark and ray species are viviparous, as well as all marine mammals. Only one or two offspring are produced at a time because of the

FIGURE 14-28. (Caption on p.393)

FIGURE 14-28. (Caption and part (n) are on the following page, p.393)

FIGURE 14-28 (Previous pages) Reproduction. (a) Synchronous spawning of a hard coral colony (*Acropora sp.*, Papua New Guinea). The eggs, the pinkish white globules, are all released within minutes of each other to float up and join the plankton where they hatch. (b) Mandarinfish (*Synchiropus splendidus*, Indonesia) male and female pair photographed almost exactly at the instant that they spawned. At dusk, they swim very rapidly upward about a meter from the rubble patch where they live, release their eggs and sperm at the same instant, and then return rapidly to safety. (c) This female Lembeh frogfish (A*ntennarius sp.*, Indonesia) is swollen with eggs. She and the much smaller male that was waiting close by swam upward and spawned near the surface a few hours later that night. (d) Although they are all hermaphrodites, nudibranchs exchange sperm through ducts in their side, seen connected in this image (*Hypselodoris bullocki*, Indonesia). Each individual retains and lays its own fertilized eggs. (e) Nudibranch laying eggs (*Kentrodoris rubescens*, Papua New Guinea). (f) On rare occasions, three nudibranchs may exchange eggs and sperm simultaneously (*Nembrotha rutilans*, Indonesia). (g) Nudibranch eggs are laid in a characteristic spiral ribbon pattern encased in a protective gel (species unknown, Hawaii). (h) Snails, although related to nudibranchs, nearly all reproduce sexually, but they also lay eggs encased in a protective gel (*Epitonium billeeanum*, Papua New Guinea). (i) Common reef squid eggs (*Sepioteuthis lessoniana*, Papua New Guinea) laid in rubbery gel casings in a seagrass bed. (j) Flamboyant cuttlefish eggs (*Metasepia pfefferi*, Indonesia) laid under a coconut shell half. The individual near the center of the image is close to hatching, and the unhatched cuttlefish can be seen through the transparent egg case. (k) Many species of damselfishes, including this Indo-Pacific sergeant (*Abudefduf vaigiensis*, Vanuatu), lay eggs on the reef surface and then stay to defend the eggs aggressively from potential predators until they hatch. The eggs are the tiny reddish brown dots covering the reef surface behind the sergeant. (l) Sea cucumbers that normally lie flat on the substrate (see inset) rear up as high as they can before releasing clouds of eggs or sperm. Fertilization takes place in the water column, where the sperm are attracted to the eggs by chemical sensing; but the fertilization rate is low, and large numbers of eggs and sperm must be produced (*Thelenota rubralineata*, Papua New Guinea). (m) Most of this burrowing sponge (*Oceanapia sagittaria*, Indonesia) lies buried under the sediments. It reproduces vegetatively by growing the round ball-like structure in the image, which is released to the currents. (n) Banggai cardinalfish (*Pterapogon kauderni*, Papua New Guinea). The male shown here is incubating eggs (the orange spherical objects) in his mouth. If you look closely you can see the eyes of some of the young that are almost ready to hatch.

large amount of energy needed to nurture the offspring during its prebirth development, but the large live-born offspring have a high rate of survival to reproductive age.

Timing

The timing of reproduction during the life cycle and during the year can be important. Spawning in some species takes place over a period of days or weeks at the same time each year. In other species, individuals may spawn several times a year; and in some species, spawning is almost continuous because at any given time, some individuals in the population are spawning. In middle and low latitudes, most pelagic spawning species spawn only once a year, in spring. This pattern synchronizes the production of larvae with the availability of abundant food supplies from the spring phytoplankton **bloom**.

In many species, the time of spawning may be determined by variations in light intensity and temperature, which also influence the timing of the phytoplankton bloom. Dramatic year-to-year variations in the reproductive success of many species can and do occur. They are due in part to annual variations in factors controlling the timing of the phytoplankton bloom and of spawning. In some years, spawning may occur at the wrong time or place, in which case larvae miss the phytoplankton bloom and their population incurs massive starvation losses. Omnivores and carnivores suffer in turn, and their populations decline.

In tropical latitudes and certain **upwelling** areas where plankton food supply varies relatively little during the year, pelagic spawners have a greater tendency to spawn year-round. However, this trend is not universal, because even in these areas, monthly, biannual, or annual synchronous spawning still provides many advantages for larval survival that are not afforded by continuous spawning.

In certain species, spawning is timed to provide the maximum protection of eggs from predators. The best-known users of this method are the small fish called grunion that spawn on southern and Baja California beaches, and the horseshoe crab that spawns along the Atlantic coast. These and other species deposit eggs to incubate in beach sands above the **high-tide line**. Thus, eggs are protected from the many predators that abound in coastal waters and sediments. Eggs must be placed in sand high enough up the beach to be free from wave action or they would soon be washed out and devoured.

Grunions cannot climb above the high-tide line, and both grunions and horseshoe crabs have pelagic larvae that cannot crawl across the beach to enter the water after they hatch. How do grunions and horseshoe crabs place their eggs in sand above the high-tide line and yet ensure that the sand is covered with water when the larvae hatch? Each species times its spawning to occur at or a little after some of the highest spring tides of the year. In the grunion's case, the high spring tides that occur on the Pacific coast during summer are perfect because the highest tide of the day (see the discussion of **mixed tides** in **Chapter 10**) occurs at night. At high tide in the darkness, when they are safe from air attacks by birds, grunions can move into very shallow water high up on the beach. There they lay eggs during a frenzied spawning that lasts about 30 min, until the tide recedes. After the eggs are laid, **tidal ranges** diminish as spring tides progress to **neap tides**, and then build back toward the next set of spring tides. Two weeks after the eggs are laid, the next set of spring tides oc-

curs (**Chap. 10**). By this time, the eggs have matured. When the overlying sand is resuspended by waves of the high spring tides, eggs are released to the water and the larvae hatch, becoming meroplankton.

The factors that determine the timing of spawning within a given year are relatively simple to understand. It is more difficult to understand why some species reproduce only once and then die while others reproduce repeatedly, and why some species mature rapidly while closely related species may take much longer to reach reproductive age. The average mortality rate of larval and adult stages, energy requirements of spawning, and year-to-year variability in larval mortality rate are believed to be important and interrelated explanatory factors.

In species with high adult mortality and relatively low larval mortality, natural selection will favor early and one-time reproduction. Because adult mortality is high, individuals that mature late will be selectively removed from the population because they are more likely to die before they produce offspring. Individuals that spawn more than once will also be selectively removed because they are likely to die before reaching a second or subsequent spawning cycle. Thus, for many species it is a successful strategy to reach maturity quickly, spawn only once, and then die. Salmon and eels are prime examples of species that use this strategy. Also, these fishes make long-distance migrations to spawn during which they stop feeding and deplete their own body tissues for fuel. This metabolic cost makes it evolutionarily more efficient to invest all remaining energy in a single reproductive event rather than attempting a return journey.

If egg or larval mortality is high in relation to adult mortality, natural selection will favor individuals that mature late and spawn more than once. Individuals that mature early and divert a large fraction of their food energy resources to reproduction, but relatively little to growth and predator avoidance, will be more likely to die early. An individual that matures late, devotes most of its energy to growth and survival, and diverts only a small amount each reproductive year or cycle to reproduction will produce more eggs in its lifetime. The late maturer is larger when reaching reproductive age, and thus it is capable of producing more eggs than a younger-maturing individual could, while expending the same amount of energy as a percentage of body weight. If this late maturer invests a relatively small proportion of its food energy in reproduction during each year, it can survive to spawn repeatedly, further increasing its lifetime egg production.

Selection for late maturity and multiple spawning cycles is further enhanced by great year-to-year variability in the survival of eggs and larvae. Survival through multiple spawning cycles enables a species collectively to outlast excessive variations in egg production or survival in successive spawnings. Because adults of several ages contribute to each year's total egg production, the effect of a small or missing year class (resulting, for example, from a poor year for larval survival) is minimized. Pelagic eggs and larvae are subject to intense predation and to ocean current and **climate** variations. Many fishes and benthic invertebrates with pelagic eggs and larvae have the relatively late-maturity and multiple-cycle reproduction that is associated with high and variable mortality of eggs and larvae.

Even closely related species can have very different reproductive timing. For example, the common mussel (*Mytilus edulis*) and California mussel (*Mytilus californianus*) are closely related and coexist in some areas. Because *M. edulis* has high mortality due to predation, it is outcompeted by *M. californianus* for living space in places where the larvae of both species settle. *M. edulis* invests a very large amount of energy in reproduction in comparison with *M. californianus* and spawns once a year in winter, whereas *M. californianus* spawns throughout the year.

Migration

Many marine animals migrate between different regions during their life cycles. The migrations can cross tens of thousands of kilometers, but typically they are much shorter in distance. Generally, one area on the species' migration route is its reproductive site, where eggs are fertilized, released, or deposited. The other end of the migration route (or other points on a complex migration pathway) is the main feeding ground for adults and/or juveniles. Hence, for most species, migration can be viewed as a strategy for ensuring appropriate habitat and food supply for each life stage of the species.

Migration may place larvae where appropriate food supplies are abundant and adults in another region where their different food supply is plentiful. However, migration is often not this simple, because adequate food supplies for each stage often are present throughout the migration route or at only a single location.

Why then do species not avoid the energy expenditure imposed by migration? There may be several answers. For example, the species might deplete available food in a specific region if it did not migrate to allow recovery of the food species populations. Migration may also place eggs, larvae, and/or the adult populations in locations where they are less subject to predation. Alternatively, migrations may enable species that are usually scattered widely across large ocean areas to congregate in one or more breeding areas, thus improving the chances of finding a mate and enhancing genetic mixing and diversity. Finally, adult migration to a spawning ground may ensure that pelagic eggs and drifting or weakly swimming larvae are carried by ocean currents to locations where food suitable for young adult stages is abundant.

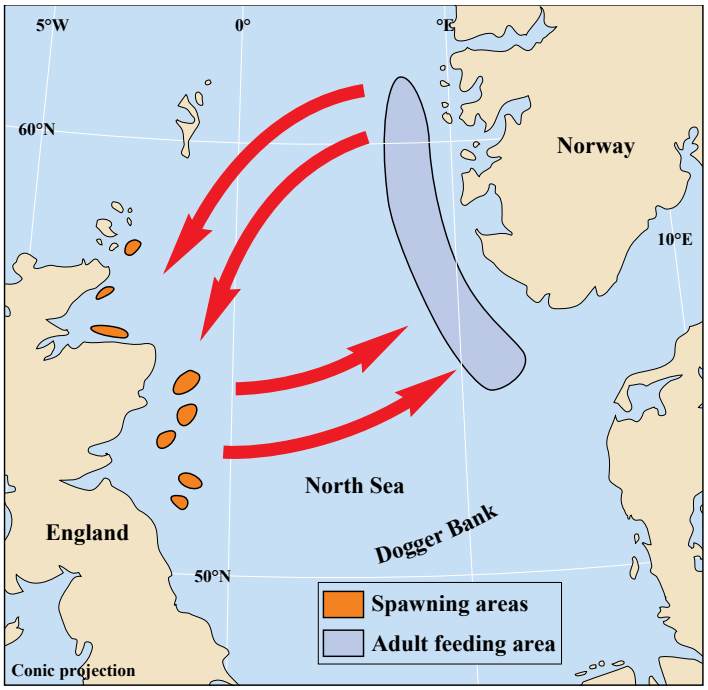
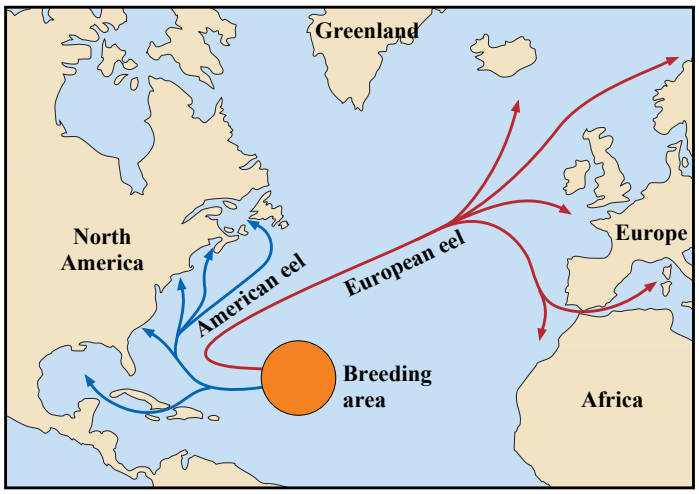
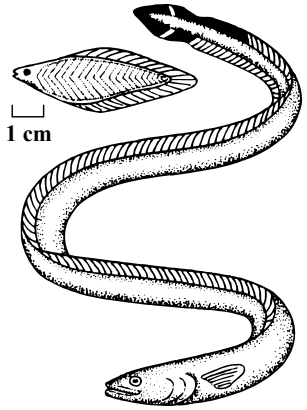
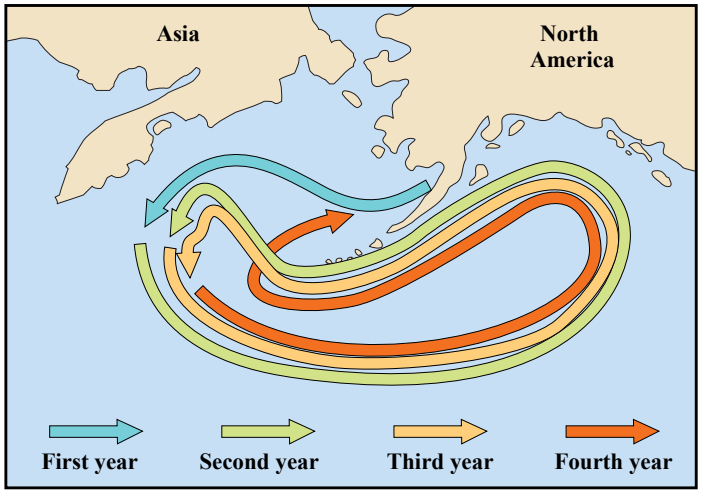


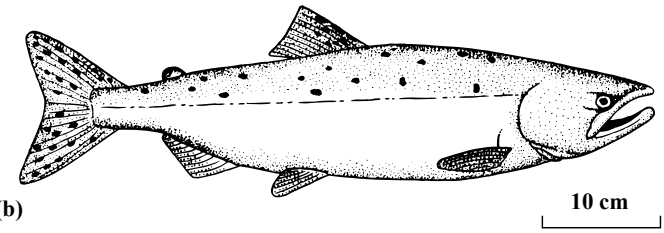
FIGURE 14-29. North Sea herring migrate from feeding areas off the coast of Norway to a number of localized areas off the Scottish coast to spawn.





(a)





(b)

After drifting to such feeding grounds, larvae can metamorphose to the adult stage. Each of these possible advantages of migration and probably others are important for some species.

The North Sea **herring** has a migration–reproduction pattern typical of many abundant coastal pelagic fishes. Adults feed for much of the year in areas of rich plankton production off Norway (Fig. 14-29). In spring, herring migrate across the North Sea to spawning grounds near the Scottish coast. There they breed and lay eggs, which attach to stones or gravel on the seafloor. After they hatch, the larvae are transported eastward by currents to the adult feeding grounds, where they assume adult form.

Anadromous and catadromous fish species have perhaps the most amazing migrations. For example, the catadromous Atlantic eel, *Anguilla*, spends its approximately decade-long adult life in freshwater rivers of North America, Europe, and the Mediterranean Sea. At the end of this period, the eels undergo changes that include exchanging their dull gray color for a silver hue and growing enlarged eyes typical of pelagic fish species that live below the photic zone. The eels then migrate down their home rivers and thousands of kilometers across the oceans to the southeastern part of the Sargasso Sea (Fig. 14-30a). There, the eels breed and then presumably die. Their leaf-shaped larvae (called leptocephali) are a few millimeters long when they begin their journey to the streams that will become their adult homes.

The American population drifts north with the Gulf Stream for 1 or 2 years before somehow sensing the proximity of the rivers of their ancestors, at which point the eels swim upstream to reach their new freshwater homes. European eels take 2 to 3 years to drift to their European homes. Mediterranean eels take an additional year to drift north with the Gulf Stream and then back to the south with the **eastern boundary current** of the North Atlantic Gyre until they can enter the Mediterranean. Although all Atlantic eels are considered the same species, the American, European, and Mediterranean eels are genetically distinct. These distinct populations may breed in slightly different areas of the Sargasso Sea so that larvae can join the Gulf Stream at the best point for the most efficient ride home.

In the Pacific Ocean, a similar species of catadromous eel that has adult populations in North America and Asia migrates to a spawning region in the southwestern part of the North Pacific Gyre that corresponds to the southwestern corner of the Sargasso Sea. Many details of the eel's migration, breeding behavior, and spawning locations are still unknown. In addition, as with all migrations, the chemical, magnetic, visual, or other clues that eels use to guide their migration to appropriate locations are unknown and subject to much research.

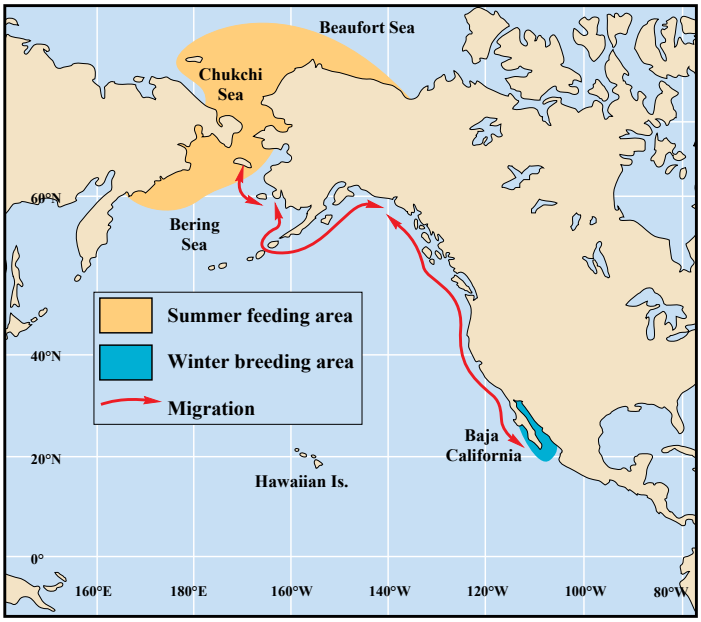
Pacific salmon are anadromous species that use a migration pattern almost opposite that of the eel (Fig. 14-30b). Salmon start life as eggs laid by the parent in gravel beds of rivers along the North Pacific coast. The eggs hatch 1 to 4 months later, and the resulting plankton-eating larvae grow quickly. During either their first or second year, juvenile salmon swim down the river to the ocean. By the time they reach the ocean, they are small but voracious predatory fishes. The salmon grow into adults and migrate across the Pacific Ocean to their selected feeding grounds, which

FIGURE 14-30. Migration routes. (a) Adult Atlantic eels migrate from their river homes in Europe and North America to the southwestern corner of the Sargasso Sea, where they spawn and die. Their larval offspring travel back to North America and Europe via the North Atlantic subtropical gyre currents and enter rivers (generally the home rivers of their parents), where they grow to maturity. (b) There are several species of North Pacific salmon, each of which has a somewhat different migration pattern. This figure shows a typical pattern in which the juvenile salmon migrate from their home streams to sea to spend 3 or more years migrating and feeding in the North Pacific Ocean between Alaska and Russia. The adults then return to rivers (usually to their home streams) to spawn and die.

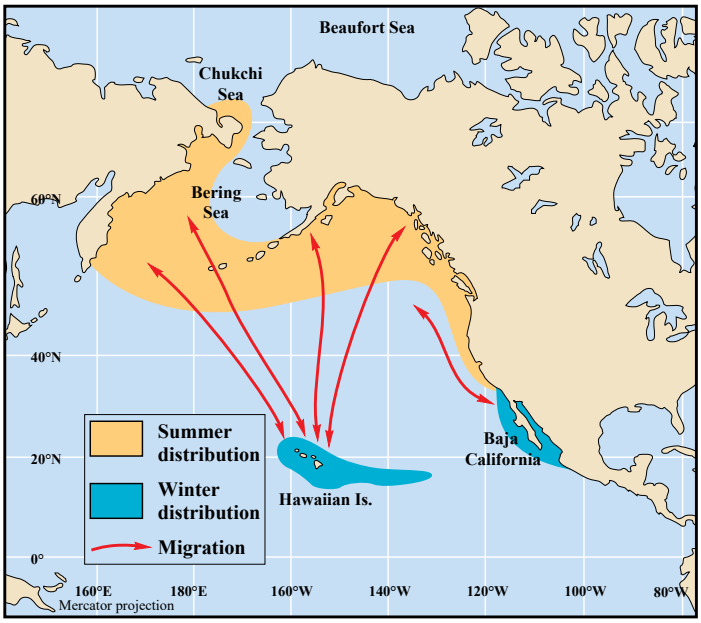
range throughout the North Pacific Ocean. After remaining in the ocean up to about 5 years, they return to their home streams to breed and then die.

Salmon usually lay only several thousand eggs, far fewer than many other fish species. However, the eggs and larvae have relatively low mortality because they are protected from the abundant ocean predators through the spawning migration. Hence, the features of the salmon reproductive cycle are comparatively low egg and larval mortality, a single relatively early reproductive cycle followed by death, enormous energy costs of spawning migration, and production of a relatively small number of eggs in a favorable habitat. These features constitute a stable and successful reproductive strategy, as described earlier.

Almost all salmon return to the stream in which they hatched.



(a) Gray whales



(b) Humpback whales

FIGURE 14-31. Some whale migrations. (a) California gray whales migrate annually between feeding areas in the Beaufort and Chukchi seas and breeding areas off the coast of Baja California. (b) Humpback whales feed in the far North Pacific Ocean and Bering Sea and migrate to breeding areas around Hawaii and Baja California.

They are thought to achieve this feat by "smelling" the distinctive chemical compositions of their home streams. However, contrary to popular misconception, not all salmon successfully migrate back to their home streams. As many as 10% to 20% are known to lose their way and migrate to streams other than their original home. Such "mistakes" are probably important to the maintenance of genetic diversity in the species and to the recolonization of streams where catastrophic events may have destroyed the spawning population.

The longest known ocean migrations are those of sea turtles and marine mammals, particularly the California gray whale. Sea turtles range far and wide throughout the oceans and return with great reliability to the beaches where they hatched.

All **baleen** whales, which, with the exception of the gray whale, are filter feeders, migrate seasonally. They feed in plankton-rich, high-latitude waters during spring and summer, and they return to warm tropical waters to breed in winter. California gray whales are unique among baleen whales because they feed by sifting sediment to eat small sediment-dwelling crustaceans called **amphipods** and they undertake one of the longest known seasonal migrations. In summer, they feed in the Bering and Chukchi Seas (**Fig. 14-31a**). When winter approaches, they migrate south along the North American coast, generally staying within sight of land. Their migration takes them some 11,000 km south to the shallow coastal **lagoons** of Baja California, where food is extremely limited and where adults must live off the fat reserves built up during summer. In the warm lagoon water, gray whales breed and females give birth 1 year later. Although young whales weigh about 2 tonnes, they have relatively thin layers of **blubber**, the fat that protects these warm-blooded mammals from losing body heat. If they were born in colder waters where the amphipod food supply is abundant, their mortality rate would be very high. The annual 22,000-km migration is therefore undertaken to ensure both adequate food for adults in summer and the high survival rate of offspring necessary to this species, which, like all other mammals, produces few young during its lifetime. Other whales, such as the humpback, also make long annual migrations (**Fig. 14-31b**).

ASSOCIATIONS

Until relatively recently, competition was viewed as the dominant force shaping marine ecosystems. According to this view, ecosystems sustain a number of species, each of which competes with all others for food and living space. However, we now know that many species enter into associations with other species as an essential part of their life cycles and that these associations are critically important to the functioning of marine ecosystems and species evolution.

Associations between species, called **symbiosis**, can take a bewildering variety of forms but are of three basic types: **parasitism**, whereby one species benefits from the association and the other is disadvantaged; mutualism, whereby both species (or all species if more than two species are involved) benefit from the association; and commensalism, whereby one species benefits and the other does not benefit but suffers no disadvantage from the association. It is often difficult to determine what, if any, advantage or disadvantage the partners receive in a given association. Many microbial species, including bacteria and archaea, are associates of other larger species but little is yet known about all but a very few of such associations so the examples of as-

FIGURE 14-32. Parasites of fishes. (a) This whip goby (*Bryaninops yongei*, Indonesia) has a large parasite, a copepod crustacean, on its body. (b) A large black isopod parasite (a crustacean of the family Cymothoidae commonly known as a "fish doctor") on a lemon damsel (*Pomacentrus moluccensis*, Papua New Guinea). There are two parasites. Look carefully and you might be able to see the much smaller male just under the large female. (c) Fish doctor parasites are common on many species of fishes, including this flasher scorpionfish (*Scorpaenopsis macrochir*, Indonesia). (d) This parasitic snail (*Thyca crystallina*, Indonesia) is apparently found only on this one sea star species (*Linckia laevigata*).

sociations in this chapter are but a tiny fraction of the very large number that exist in marine ecosystems. Indeed it is likely that all non-microbial species live with a variety of associated microbial species.

A parasite lives in or on, or frequently visits, another organism (the host) and feeds on the host's tissues or steals the host's food, thereby disadvantaging, without destroying, the host. A tremendous variety of parasitic species are present in the oceans, including marine worms, crustaceans, and snails. The majority are small and most live inside their host's body. Some, however, such as the fish and sea star parasites shown in **Figure 14-32**, are partly or fully external to their hosts. Fish parasites are abundant. As scuba divers can observe on a coral reef, several species of small fishes and shrimp make their living by eating parasites off larger fishes' bodies (**Fig. 14-17e**). The larger fishes seek out the cleaner, which often establishes a cleaning station to which its customers return for periodic service.

Because they live either in or on another organism, many parasitic species do not need sensory, locomotory, or skeletal organs. Consequently, many have become degenerate and lack such organs. Many species are little more than a digestive and reproductive system. The reproductive system is generally large because the parasite must normally produce enormous numbers of larvae so that a few of these larvae can encounter suitable hosts. Host location is a major problem for parasites, many of which are parasitic on only one host species. Accordingly, parasite life cycles are often very complex, with one or more intermediate hosts (**Fig. 14-33**).

Commensal or mutual associations can provide various benefits to the cooperating species. These include ready availability of food, avoidance of predators or parasites, easy transportation, and suitable living surfaces.

The association between anemonefishes and their anemones (**Fig. 14-20**) has major benefits for the anemonefishes. Hiding in the anemone's stinging tentacles protects an anemonefish from potential predators. In addition, laying eggs under the anemone where they are protected from predators reduces the numbers of eggs needed. Anemonefishes may use the anemone for food in

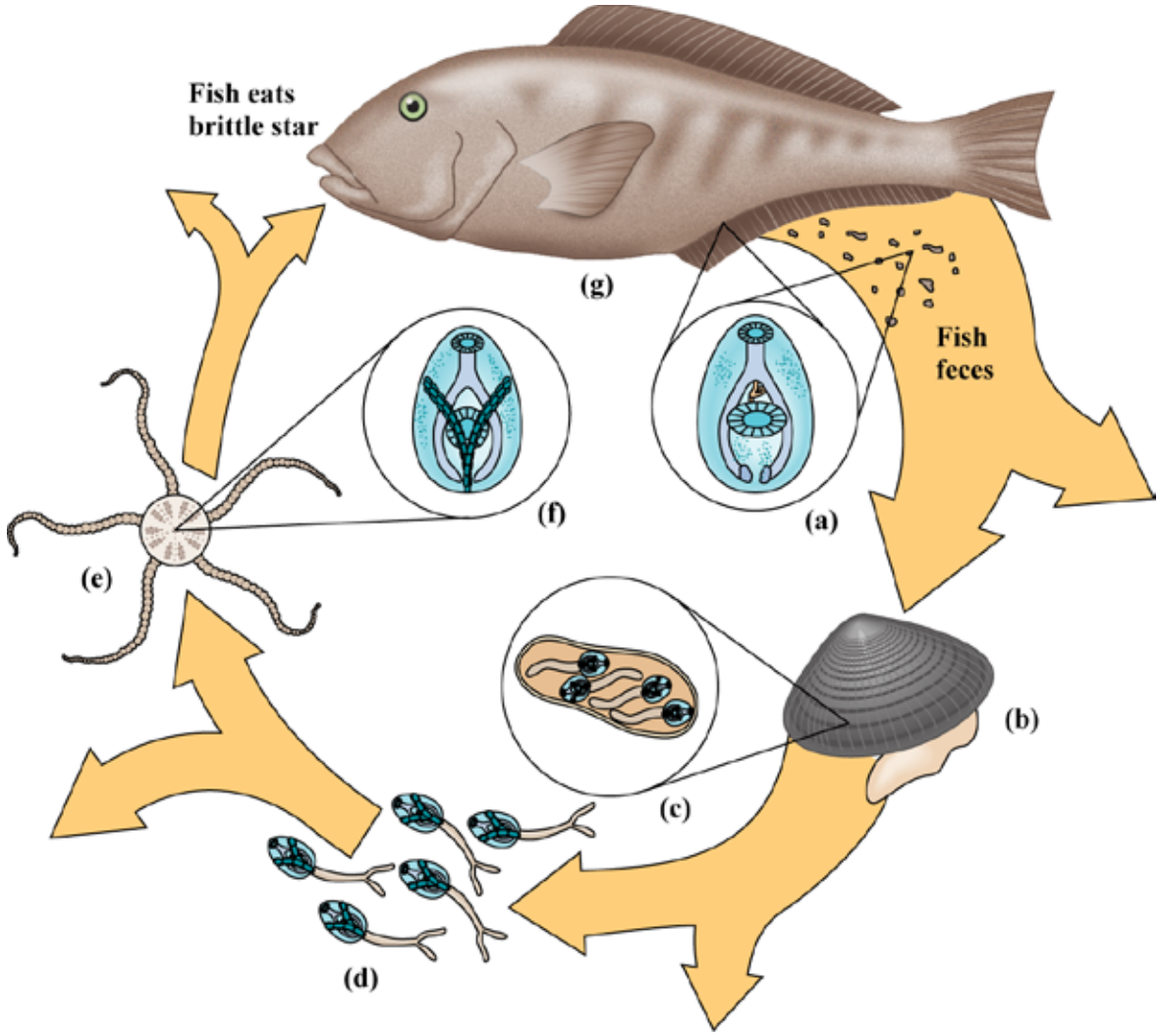


FIGURE 14-33. The life cycles of parasites are often complex. The adult fish fluke lives in the gut of its fish host (a). It produces very large numbers of eggs that are discharged with the host's feces and hatch into a juvenile stage called a "miracidium." Although most of the miracidia do not survive, a very small number enter a bivalve mollusk (b), which acts as an intermediate host for the parasite. While in the bivalve, the miracidium develops into a larval form (c), which in turn develops a large number of another life stage, called a "cercaria" (d). The cercariae are released to the water, and a very small number of these cercariae eventually enter a second intermediate host, a brittle star (e). Inside the brittle star, the cercariae develop into yet another life stage, the metacercaria (f). If this intermediate host is eaten by a fish (g), the metacercaria develops into an adult fish fluke parasite. At each stage in its life cycle, only an extremely small fraction of the individuals survive to reach the next host. This is true because many parasites, such as the fish fluke, can use only a single species or only a very small number of species as host for one or more of their life stages.

times of need, eating mucus, food scraps, and even anemone tentacles. They may also benefit by having external parasites stung to death and removed by the anemone.

Because many anemones are found without anemonefishes but anemonefishes are never found without an anemone, the benefits of the association to the anemone are less obvious. The anemone does benefit by being cleared of dead tissue, mucus, food wastes, and parasites by the anemonefish. The anemonefish also protect the anemone from its few predators. Without the anemonefish, the anemone could be consumed by certain butterflyfishes and might have to defend its delicate tentacles from such predators by closing up if the anemonefish were not present. Because the anemone cannot feed when closed, the freedom to remain open when predators are nearby is undoubtedly a benefit of the anemonefish association. In some cases, the anemone may benefit by being fed by the anemonefish, which, on occasion, have been seen to carry food to the anemone.

Many other associations also involve a mobile species that uses a nonmobile or less mobile host for protection and food. Examples are associations in which a variety of crabs (**Figs. 14-34a-e**), small fishes (**Figs. 14-34f,g**), shrimp (**Figs. 14-34h-q, 14-35e**), scale worms (**Fig. 14-34r**), and mollusks (**Fig. 14-34s**) live on crinoids (**Fig. 14-16a,b**), corals (**Fig. 14-16g,h,j,k**), sea stars (**Fig. 14-16l**), and sea fans (**Fig. 14-11b**). In most of these associations, the small lodger is well camouflaged or hidden within the host. The lodger eats mucus, dead tissue, parasites, the host's body parts or food supply, or any combination thereof. Generally, the host benefits by being cleaned of mucus, dead tissue, and/or parasites.

Even if it is eaten by its partner species, the host may gain. Many species that feed on their host are present as only a single pair on their much larger host. This pair nourishes itself from the host's tissues but eats the host only at a rate that can be replaced by normal growth. The resident pair aggressively protect their host against colonization by others of their species, parasites, and other species that would also consume the host. Thus, although it loses some tissue to the associate species, the host is better protected.

Many associations involve a normally nonmobile species that lives on a mobile host. Examples are the associations formed

(a)

(b)

(c)

(d)

(e)

(f)

(g)

(h)

(i)

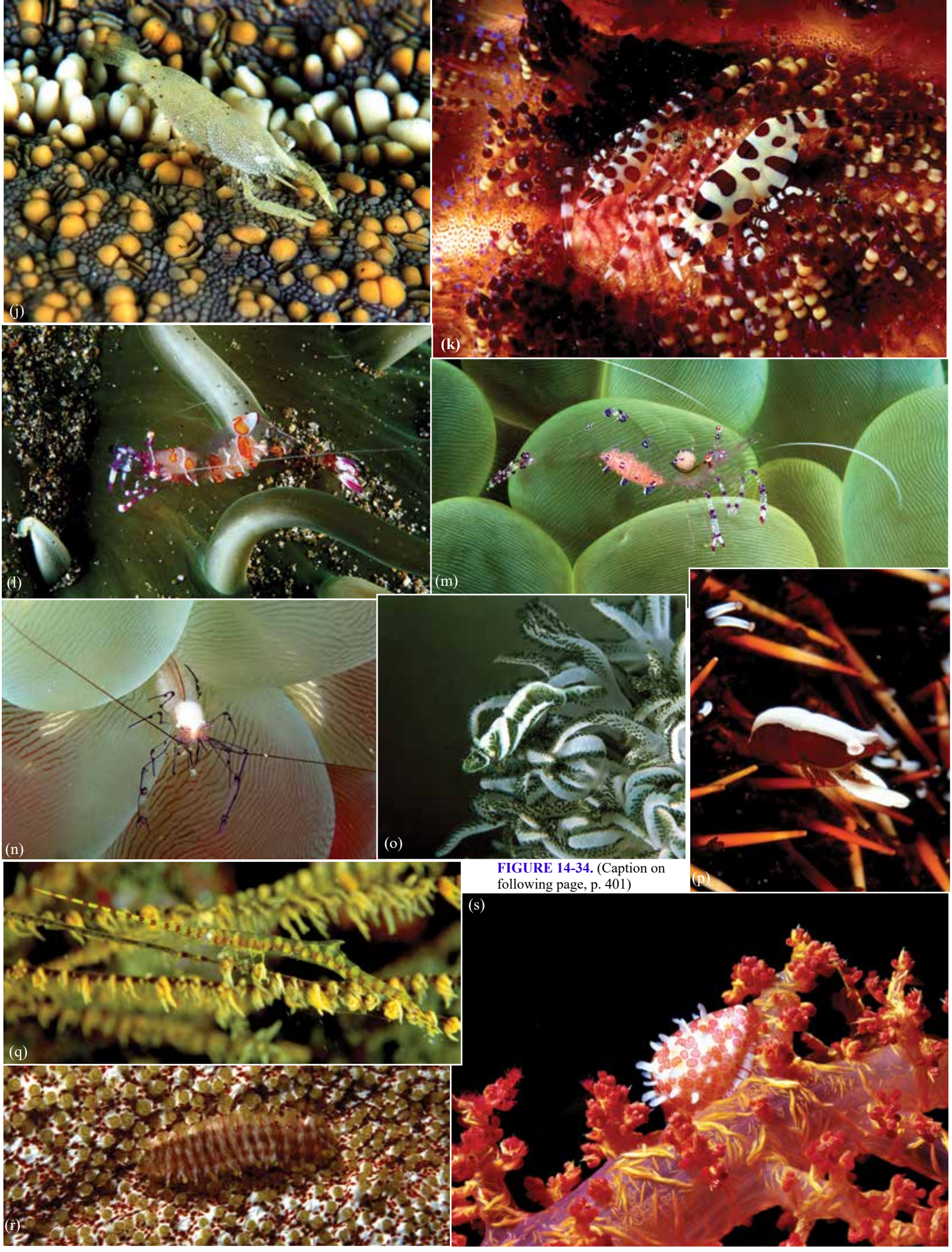


FIGURE 14-34. (Caption on following page, p. 401)

FIGURE 14-34. (Previous pages) Examples of the many associations between species. (a) The arrowhead crab (*Huenia heraldica*, Papua New Guinea) shown here not only blends into the algae (*Halimeda sp.*) that it lives on, but usually carries pieces of the algae around with it, as this one is doing, to further enhance its camouflage. (b) Many small crabs live in or on a larger invertebrate for camouflage, to hide and sometimes to steal the host's food or feed on the host itself. Many species, such as the Xenia swimming crab (*Caphyra sp.*) shown here on a soft coral, are poorly studied and difficult to identify (Indonesia). (c) This tiny spider crab (*Xenocarcinus tuberculatus*, Indonesia) lives on a coral whip, usually just one pair per whip. (d) The porcelain crab (probably P*orcellanella triloba*, Indonesia) lives on a sea pen, even when the sea pen withdraws into the sand for protection. (e) Another tiny porcelain crab (probably *Porcellanella sp.*, Indonesia) lives on a whip coral. (f) The weed cardinalfish (*Foa brachygramma*, Papua New Guinea) spends its life hidden in weeds or, as in this case, in a crinoid where it cannot be seen or reached by predators. (g) The crinoid clingfish (*Discotrema crinophila*, Papua New Guinea) lives and hides in a crinoid and usually has a body color that matches the crinoid. (h) Emperor shrimp (*Periclimenes imperator*, Papua New Guinea) like the pair shown here live on a variety of hosts, including nudibranchs and sea cucumbers. (i) Sea star shrimp (*Periclimenes soror*, Indonesia), live on sea stars and match their body color to blend in with the host's body. (j) This sea star commensal shrimp (*Zenopontonia noverca*, Indonesia) is partially transparent, and with its spots it blends in so well with its background when it is on some parts of the sea star's body that we had to wait for the shrimp to move before getting a photograph in which the shrimp is more visible. (k) A pair of Coleman's shrimp (*Periclimenes colemani*, Papua New Guinea) living protected on their venomous fire urchin host (*Asthenosoma varium*). (l) Many species of shrimp, like this one (*Ancylomenes cf. venustus*, Indonesia), live in anemones. (m) Many small commensal shrimp species, including this one (*Periclimenes cf. tosaensis*, Indonesia), have mostly transparent bodies, so they can blend in with several different hosts. This individual is living in a bubble coral, and the eggs that it's carrying can be seen as a pink egg mass through its transparent body. (n) This species of coral shrimp (*Vir philippinensis*, Indonesia) lives only in bubble corals. (o) A humpbacked shrimp (*Hippolyte commensalis*, Indonesia) can hardly be seen when it withdraws into its soft coral host. (p) This tiny urchin shrimp (*Gnathophylloides mineri*, Indonesia) is also virtually impossible to see when it hunkers down among the spines of its urchin host where it normally hides. (q) This saw blade shrimp (*Tozeuma armatum*, Indonesia) has an unusually elongated body so that it can lie flat against the strands of black coral on which it lives. (r) Scale worms, including this species (*Gastrolepidia clavigera*, Vanuatu), have flattened bodies and coloration to match their host, usually a sea cucumber, as seen here. (s) This egg cowrie (*Pseudosimnia sp*., Red Sea) lives on and probably eats soft corals such as the one shown here (*Dendronephthya sp.*).

by the decorator crab (**Fig. 14-16f**) and the anemone crab (**Fig. 14-35a**). The decorator crab gains camouflage and protection from its covering of algae, hydroids, and sponges, which are unpalatable and rarely attacked by predators. The immobile associates may gain by being transported through the water, which increases their chances of obtaining food or dissolved nutrients, and by using the host as a substrate on which to grow. In similar associations, the sponge may be an indifferent partner removed from its home on the reef and carried on the crab's back by a pair of specially adapted legs. The anemone **hermit crab** is well protected by the adopted mollusk shell in which it lives, but it is further protected by the stinging anemones that it attaches to the shell (**Fig. 14-35a**). The anemone gains by being transported through areas where food can be obtained, including scraps of food released as the hermit crab feeds by tearing apart its prey. This association, like many others, is highly specific. The association usually involves the same species of anemone and hermit crab, and the shell of the same species of mollusk. Some species of decorator crabs also cover themselves with sponges (**Fig. 14-16f**) or carry an urchin on their backs (**Fig. 14-35b**) to afford them protection.

The remora (**Fig. 14-26g**) is an example of a species that is mobile but hitches a ride on a larger swimming animal. In some cases, remoras gain by stealing food from their host. However, the major advantage to the remoras is probably transportation, since they often ride on manta rays, which feed on plankton. It is not clear whether sharks or manta rays gain anything from a remora's presence, but these hosts apparently are not harmed by carrying the passenger.

The association between gobies and shrimp is clearly beneficial to both partners. A goby and a shrimp live together in a common sand burrow, where they can retreat to safety from predators. The shrimp is blind, and the fish is incapable of digging its own burrow. The shrimp therefore digs and maintains the common burrow, but it is vulnerable to predators when it pushes excavated sand out of the hole. The goby repays the shrimp for its digging by sitting at the burrow entrance watching for predators (**Fig. 14-35c**). With one of its long, sensitive antennae, the shrimp maintains contact with the goby's caudal fin. If a predator approaches, the goby wiggles its fin to warn the shrimp, which immediately withdraws into the burrow. If danger increases, the goby itself darts into the burrow.

The few associations described here are all relatively easy to observe and study, but most associations are much more subtle. For example, coordinated feeding by two or more fish species that benefits both species does occur but may be infrequent and difficult to observe. In addition, many associations are difficult to study because one species is well hidden inside the other or because one or both partners are microscopically small. For example, the giant clam, *Tridacna* (**Fig. 14-35d**), has a mutually beneficial association with **zooxanthellae**. The algae live inside the soft **mantle** tissues of the clam and give this part of the clam its often brilliant coloration. The algae benefit from a secure location within the clam's tissues, where they also receive a steady supply of carbon dioxide and nitrogenous waste products from the clam, which the algae use for photosynthesis. There, the algal cells can obtain needed sunlight when the clam is open, and they are protected from settling of other benthic organisms that might otherwise overgrow them. In addition, the clam closes when threatened, protecting both itself and its algae. The clam benefits from the association by using the algae's by-products as a supplemental food supply. Thus, the algae are essentially a carefully cultivated garden that supplements the clam's food so that it does not have to filter extremely large volumes of water. This feeding arrangement is very energy-efficient and probably accounts for the giant clam's ability to grow to its huge 1- to 2-m size. Hard corals have a similar association with zooxanthellae (**Chap. 15**).

COMMUNICATION AND NAVIGATION

The majority of species must be able to communicate at least on a rudimentary level—for example, to provide an indication of sex and attract a mate. Most predators cannot rely on finding their prey by chance but must actively seek them out. Many marine species must navigate from place to place in migrations or to find suitable habitat, food, and mates. Humans and most other terrestrial animals use their five senses—vision, smell, hearing, touch, and taste—to perform these functions, with vision being the predominant sense. Light is absorbed and **scattered** in seawater, and most of the ocean is dark. In addition, when light is present, its path is distorted by **refraction**. Therefore, marine species rely

FIGURE 14-35. Additional examples of associations. (a) This anemone hermit crab (*Dardanus sp.*, Papua New Guinea) has found a strong gastropod mollusk shell to live in and has attached several anemones on the shell to further discourage potential predators. (b) This crab (*Dorippe frascone*, Indonesia) has a pair of legs that are modified to carry an urchin, in this case *Astropyga radiata*, on its back. The urchin's toxic spines protect the crab from predators. (c) This tiger pistol shrimp (*Alpheus bellulus*, Indonesia) lives in a single burrow with the yellow shrimp goby (*Cryptocentrus cinctus*). The shrimp digs and maintains the burrow. The goby warns the shrimp, which is blind, when a predator approaches, and they both disappear into the burrow. (d) A giant clam (*Tridacna gigas*, Papua New Guinea). (e) This small pistol shrimp (*Synalpheus sp.*, Papua New Guinea) lives in its host crinoid.

much less on vision than most terrestrial species do.

In the marine environment, hearing, chemical sensing that is equivalent to taste or smell, and touch have assumed much greater importance. Marine organisms have also developed other senses, including the ability to sense electrical fields and probably the Earth's magnetic field. Our knowledge of these unusual and different senses and even of how marine organisms use their greatly enhanced hearing, chemical sensing, and touch is still extremely limited.

Although vision is much less useful in the oceans than on land, it is still widely used by many marine species, and many adaptations of vision are found in species that live in the ocean environment. The most important adaptations are greatly enlarged eyes or multiple-lens eyes that can see in very low light levels and distinguish subtle changes in light intensity (**Fig. 14-18a,b**).

Most marine species do not see sharply focused images, and many, particularly some marine invertebrates, have bizarre-looking eyes (e.g., **Figs. 14-18a, 14-35a**). Some species have light-sensing organs that cannot be readily identified as eyes. For example, the giant clam (**Fig. 14-35d**) and many other benthic invertebrates are able to sense very small variations in light intensity, which enables them to withdraw into their shells, tubes, or other protective environments when predators approach.

Chemical sensing is very important in the marine environment, but very little is known about it. For example, anadromous and catadromous species are thought to use a well-developed

chemical sensing capability to detect and navigate to their home streams. They apparently can sense small differences in the composition of chemicals present in very low concentrations in these home streams. Sharks also appear to have an extremely keen sense for chemicals. They are attracted to blood even when they are kilometers away from its source and the concentration of blood chemicals is exceedingly small. Adventurous scuba divers deliberately attract sharks by dumping blood and shredded fish into the water.

Sound travels through seawater with relatively little loss of intensity. Consequently, sound sensing, or hearing, is well developed in many marine species, and sound is used extensively for communication. Many species, particularly **cetaceans** such as whales and dolphins, use sound not only for communication, but also to locate objects, including prey. Most cetaceans can generate sound pulses that bounce off objects in their path. They focus and process the resulting echoes, and thus are able to "see" the objects. This **echolocation** ability is extremely sophisticated and capable of high sensitivity and precision in at least some species. For example, the dolphin echolocates by emitting low-**frequency** clicks to scan objects at distances up to hundreds of meters. As it nears the object, the dolphin uses higher-frequency clicks to get a more detailed "picture." With their echolocation abilities, dolphins can identify specific objects that differ only slightly in shape, size, thickness, or material composition. Dolphins and other cetaceans can produce and sense an extraordinary range of sound frequencies far beyond human hearing at both high and low frequencies.

We do not know exactly how cetaceans produce sound pulses or how they focus and sense returning echoes. However, some species are believed to create the sounds by moving air within hollow bony structures in the head. The bulbous brow of most cetaceans (**Fig. 12-25**) contains oil- or fat-filled structures believed to be responsible for focusing sound pulses when they are generated. Returning echoes appear to be captured by the fat-filled lower jaw, which conducts the sound directly to the inner ear, allowing for precise navigation and hunting in total darkness.

In addition to cetaceans, many other marine species produce sounds thought to be used primarily for communication. For example, certain fishes are known to generate sound by using their swim bladders, and they may sense other fishes' sounds or echoes in the same way. Scuba divers, if they listen carefully, can hear a continuous cacophony of noises in the oceans that sounds like the static on a radio. Some species use sound for more sinister purposes. The pistol (or snapping) shrimp (**Fig. 14-35e**) has one very large, overdeveloped claw, which, when snapped closed, creates a loud noise that can be heard across a room if the shrimp is in an aquarium. The concussion of the shrimp's snapping sounds stuns its invertebrate or small fish prey, sometimes into unconsciousness. The stunned prey is then easy game for the shrimp. Other species, notably killer whales, also may generate and use intense sound pulses to stun or even to kill their prey.

Fishes can sense small changes in pressure through sensory organs located in a row along each side of their bodies that form what is called the "lateral line." Lateral-line sensors are apparently used by schooling fish to sense motions of their neighbors. Together with visual clues, these sensors may explain how schooling fish can turn in unison. Sharks also may be able to sense pressure variations, since they are attracted from long distances by the thrashing of a sick or dying fish. The low-frequency pressure variations caused by such a fish are transmitted through the water as very low-frequency sound waves, and the shark's ability to sense such pressure fluctuations may simply be an extension of its "hearing."

Evidence is steadily accumulating that many marine species are able to sense magnetic fields, including the Earth's magnetic field. This ability may be vital for migrating species such as sea turtles. In addition, some marine species are able to generate and sense electrical fields.

CHAPTER SUMMARY

Ecological Requirements.

The fundamental needs of all species are a place to live, food, safety from predators, and successful reproduction.

Habitat.

The water column, seafloor, and sediments are three fundamentally different habitats. Pelagic organisms must avoid sinking, and most pelagic animals must actively seek food. Benthic epifauna save energy because they do not have to control buoyancy, but they have difficulty avoiding predators and, in most areas, must rely on detrital food that rains down from above or on predation. Benthic infauna have some protection from predators and do not require buoyancy control, but because food in sediments is limited, they must expend energy to move or dig through the sediment, and they must obtain oxygen that is depleted in most sediments below the upper few centimeters. The surface microlayer, intertidal zone, and hydrothermal vents are special habitats that present unique problems and opportunities.

Feeding.

Suspension feeders eat particles suspended in the water column, including living phytoplankton and zooplankton, and detritus. Many suspension feeders are filter feeders that strain water through a mesh-like structure to capture food. Other suspension feeders use mucus to capture food particles, or they are able to grab or grasp particles with arm-like appendages. Many suspension feeders increase their feeding efficiency by pumping water through their collection apparatus, moving the apparatus through the water, or placing it in currents. Many suspension feeders are present among both pelagic fauna and benthic epifauna, and a few benthic infaunal species suspension-feed using a feeding apparatus that they extend above the sediment surface or by pumping water through their tubes or burrows.

Surface grazers consume algae, small sedentary animals, and detritus from the seafloor. Food is abundant only where the seafloor is within the photic zone, where the substrate may be covered with benthic microalgae, macroalgae, and sponges, tunicates, and other animals. In the deep sea, surface grazers eat primarily detritus or bacteria. Surface grazers may feed by using specially adapted mouths on the underside of the body that can either rasp off food organisms or grasp food as they sift through the surface sediment. Others suck off and sift surface sediment to obtain food particles. Some surface grazers also suspension-feed or hunt.

Most deposit feeders move through the sediment, taking sediment into the gut, where they digest organic matter from detritus or coatings. In sediments with anoxic pore waters, deposit feeders must obtain oxygen from the water above or remain in the oxygenated upper sediment layer.

Hunting and Defense.

Speed is used by both hunter and hunted; the hunter chases, and the potential prey seeks to escape. Prolonged movement at high speed in the oceans is energy-intensive because of water resistance. Consequently, all but a few of the largest ocean animals use speed in short bursts rather than in prolonged chases. Other strategies are used to get close to the prey, and then a short burst of speed over the remaining small distance is used to capture the prey. In defense, speed generally is used for immediate escape, followed by other strategies to ensure ultimate safety.

Many marine hunters use lures to attract prey. The lure is typically an appendage on or near the mouth that resembles a bite-sized meal to the prey. Some species use false markings such as eyespots to lure predators into attacking in the wrong direction or at the wrong place as the potential prey speeds off in the opposite direction.

Hunters use camouflage to lie in wait unseen by their prey, or they mimic species that clean other species so that they can approach unsuspecting prey. Many species use camouflage to conceal themselves from predators, or they mimic fiercer or poisonous species to deter predators. Concealment in sediment, within other species, or in holes in reefs and rocks is a much-used defensive strategy. Many species conceal themselves by day and emerge to hunt only at night. Hunters also conceal themselves to ambush prey.

Spines and armored bodies are used by many marine species as defensive mechanisms, and in some cases as weapons. Hunters use crushing claws and jaws to overcome the armor of prey species. Poisons are used by hunters that inject venom into their victims to stun or kill them, and by potential prey species that inject venom into attacking species or make themselves toxic to eat. Many species that are poisonous to predators are brightly colored to advertise their toxicity.

Schooling or cooperation can be used to overcome defenses of a confused prey species, and to confuse predators or frighten them off by creating the appearance of a target much larger than any one individual.

Selected Adaptations in Fishes.

Fish body shapes differ by species to reflect swimming habits. Species that swim continuously have teardrop shapes—a compromise that minimizes total drag, including surface, form, and turbulent drag. Fishes that make fast turns are flattened so that the flat sides can act like a rudder. Fishes that specialize in a quick burst of speed are thickened in the middle by the needed musculature.

Fin shapes also vary with swimming habits. The caudal fin is rounded in fast-maneuvering and -accelerating species, truncated and forked in faster-swimming species, and lunated in the fast, continuous swimmers. Heterocercal caudal fins and pectoral fins in sharks provide lift to maintain buoyancy. Fins are also adapted for special purposes, such as "walking," defense and venom injection, attachment to substrates or hosts, and even gliding through the air.

Unlike invertebrates, bony fishes have internal body fluids that have lower salinity than seawater, and therefore they must prevent the continual loss of water by osmosis. Marine fishes osmoregulate by drinking seawater and excreting salts through a special gland. Freshwater fishes gain water by osmosis and osmoregulate by producing large volumes of urine. Some species that live where salinity is variable must be able to osmoregulate in both ways.

Most fish species maintain buoyancy by producing and storing low-density oils or by filling a swim bladder with gas. Gas must be released from or added to the swim bladder as the fish changes depth. Oils are favored in abyssal species because gas compressed at depths below about 7000 m is more dense than oil. Some species have no swim bladders, must swim continuously to avoid sinking, and have fins and bodies adapted to provide lift.

Reproduction.

Many species reproduce sexually, either by the direct transfer of sperm from male to female or, more often, by the release of sperm, or of eggs and sperm, to the water column for fertilization. Mating congregations and synchronous spawning by all males and females of a species maximize the probability of egg fertilization, improve egg and larval survival, and maximize genetic diversity.

Because mates may be difficult to locate, many species are hermaphroditic, and some can even function as both sexes at the same time. Asexual reproduction is common in algae and in colonial invertebrates.

To ensure egg fertilization and survival, either very large numbers of eggs must be produced and released or smaller numbers of eggs must be defended against predators. Many fishes and invertebrates release large numbers of eggs to the water column, where they hatch to become meroplankton. Other species lay eggs on the substrate and protect them until they hatch, and still others retain fertilized eggs in or on their bodies until they hatch. Spawning often occurs at times and locations that match the availability of suitable food for larvae. Species with high adult mortality and relatively low larval mortality tend to reproduce early and only once. Species with high egg and larval mortality tend to mature late and spawn more than once.

Many species migrate during their life cycle. Most often they move from adult or seasonal feeding areas to mating or spawning areas. Anadromous and catadromous fishes migrate between freshwater and the ocean.

Associations.

Symbiosis between species is very common in the marine environment. In some associations, one species benefits and the other is disadvantaged (parasitism). In other associations, both species benefit (mutualism), or one species gains and the other is neither advantaged nor disadvantaged (commensalism). Benefits gained from associations include food, living space, camouflage, protection from predators, removal of parasites, and transportation.

Communication and Navigation.

Many marine species have and use vision, but other senses are often more important. These senses are used to locate prey, mates, and predators and for navigation. Sensing of dissolved chemicals, akin to smell or taste, is especially well developed in many species. Certain species generate sounds that are used for echolocation, to stun prey, or to communicate. Many species can sense small changes in pressure, electrical fields, and probably the Earth's magnetic field.

KEY TERMS

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

exams.

algae
amphipods
anadromous
anemones
annelid
anoxic
aphotic zone
archaea
aspect ratio
bacteria
baleen
barnacles
beaches
benthic
benthos
biochemical
bioluminescent
biomass
biota
bioturbation
bloom
buoyancy
carnivores
catadromous
cetaceans
chemosynthetic communities
climate
clones
cnidarians
contaminant
continental shelf
copepods
corals
crustaceans
ctenophores
currents
decomposer
density
deposit feeders
detritus
diatoms
diel
diffusion
eastern boundary current
ebbs
echolocation
ecosystems
environment
epifauna
erosion
estuarine
euphausiids
excrete
excurrent
fauna
fecal pellets
filter feeders
flagellates
incubation
incurrent
infauna
intertidal zone
invertebrates
jellies
lagoons
larvae
latitudes
macroalgae
mantle
marine mammals
meroplankton
metamorphose
microalgae
mixed tides
mollusks
neap tides
nekton
nudibranchs
nutrients
osmoregulation
osmotic pressure
ovoviviparous
parasites
parasitism
pelagic
photic zone
photosynthetic
phototrophs
phototrophy
planktonic
polyps
pore waters
primary productivity
protists
pteropods
reefs
refraction
respiration
resuspend
salinity
salps
scatter
scavenging
schooling
scuba
sea cucumbers
sea fan
sea grass
sea stars
sea urchins
sediment
sedimentation rate
spawning
species
sponges
spring tides
frequency
friction
fungi
genetic
gills
gobies
gravity
grazed
habitats
hard parts
herbivorous
hermit crab
herring
high-tide line
hydroids
hydrothermal vents
surface microlayer
surface tension
suspension feeders
symbiosis
tidal ranges
tide pools
tides
tunicate
upwelling
vertebrates
viruses
viscosity
viviparious
wavelengths
zooplankton
zooxanthellae

STUDY QUESTIONS

1. What are the four fundamental challenges that any species must meet to survive?
2. What are the advantages and disadvantages of the benthic infaunal habitat in comparison with the benthic epifaunal and pelagic habitats? Describe how these factors change with depth and substrate type.
3. How do suspension feeders obtain food, and why are there so many suspension feeders in the oceans?
4. Why do most deposit feeders live in only the upper few tens of centimeters of the sediment?
5. Why are some pelagic predators not able to swim fast? What other capabilities do they use to capture prey?
6. Why do many fish species congregate in schools?
7. What are the physical characteristics of a fish species that swims continuously at high speeds, and of a species that waits on the seafloor for prey to swim by?
8. What are the three ways in which different fish species maintain their buoyancy? Which of these is more common in abyssal species, and why?
9. For what reasons do many species migrate at some stage in their life cycles?
10. What aspects of their environment might marine species be able to detect with senses other than sight?

CRITICAL THINKING QUESTIONS

1. Most marine species are adapted to eat only food of a certain type, such as suspended particles, organic coatings on sediment particles, phytoplankton cells of a certain size range, zooplankton, or small fishes. Discuss the possible reasons why most species do not develop (or do not retain) the ability to feed on many different types of food.
2. Nudibranchs are snails that have no shell. They generally live on reefs and feed on algae, sponges, or corals. There are many holes in reefs that make excellent hiding places. Why do nudibranchs use poisons and bright coloration to warn off predators rather than just using the many available hiding places in the reef?
3. Discuss the advantages and disadvantages of a spawning strategy in which large numbers of eggs and sperm are released simultaneously to the water column.
   (a) Explain why you might expect this strategy to be more common in coral reef communities than in the polar regions.

(b) Are there any terrestrial species that employ a similar strategy? If so, what are they, and how does their strategy differ from the similar strategies of ocean species?

4. Describe the advantages and disadvantages that are experienced by species that live in association with other species.
(a) Explain why species associations are so common in the oceans.
(b) Do species live in associations in the terrestrial environment? If so, describe some of these associations.

CRITICAL CONCEPTS REMINDERS

CC14 Phototrophy, Light, and Nutrients: Phototrophy (which includes photosynthesis) and chemosynthesis are two processes by which simple chemical compounds are made into the organic compounds of living organisms and upon which all species are ultimately dependent. Phototrophy depends on the availability of light and can only take place in a shallow upper layer of water or on the shallow seafloor. Chemosynthesis does not use light energy but instead uses chemical energy from reduced compounds. Therefore, chemosynthesis can occur in all ocean environments in which oxygen is depleted, but these environments are very limited in extent in the present-day oceans.

CC17 Species Diversity and Biodiversity: Biodiversity is an expression of the range of genetic diversity; species diversity; diversity in ecological niches and types of communities of organisms (ecosystem diversity); and diversity of feeding, reproduction and predator avoidance strategies (physiological diversity), within the ecosystem of the specified region. Species diversity is a more precisely-defined term and is a measure of the species richness (number of species) and species evenness (extent to which the community has balanced populations with no dominant species). High diversity and biodiversity are generally associated with ecosystems that are resistant to change.

CREDITS

Figure 14-1a – Segar, D., and E. Stamman Segar, 1997: Flamboyant cuttlefish (*Metasepia pfefferi*).

Figure 14-1b – Segar, D., and E. Stamman Segar, 1997: Flamboyant cuttlefish (*Metasepia pfefferi*).

Figure 14-1c – Segar, D., and E. Stamman Segar, 1997: Flamboyant cuttlefish (*Metasepia pfefferi*).

Figure 14-1d – Segar, D., and E. Stamman Segar, 1997: Flamboyant cuttlefish (*Metasepia pfefferi*).

Figure 14-1e – Segar, D., and E. Stamman Segar, 1997: Young flamboyant cuttlefish (*Metasepia pfefferi*).

Figure 14-2a – Uwe Kils, 2011: Antarctic krill (*Euphausia superba*). Accessed 20 March 2026, https://en.wikipedia.org/wiki/File:Antarctic_krill_%28Euphausia_superba%29.jpg.

Figure 14-2b – Segar, D., and E. Stamman Segar, 1997: Banded coral shrimp (*Stenopus hispidus*, Papua New Guinea).

Figure 14-2c – Segar, D., and E. Stamman Segar, 1997: Harlequin shrimp (*Hymenocera elegans*, Papua New Guinea).

Figure 14-3a – Hopcroft, R., 2015: *Limacina helicina*, UAF/NOAA. Accessed 20 March 2026, https://oceanexplorer.noaa.gov/ocean-fact/acidification/.

Figure 14-3b – Segar, D., and E. Stamman Segar, 1997: Marine gastropod, a harp shell (*Harpa major*, Indonesia).

Figure 14-4b – Segar, D., and E. Stamman Segar, 1997: Individual members of the salp colony

Figure 14-6a – Segar, D., and E. Stamman Segar, 1997: A sea pen (order Pennatulacea, Papua New Guinea) with its feeding polyps oriented into the current.

Figure 14-6b – Segar, D., and E. Stamman Segar, 1997: A sea pen (order Pennatulacea, Papua New Guinea) with its feeding polyps oriented into the current.

Figure 14-6c – Segar, D., and E. Stamman Segar, 1997: Sand anemone (Papua New Guinea).

Figure 14-6d – Segar, D., and E. Stamman Segar, 1997: Tube worm (family Sabellidae, Papua New Guinea) with its netlike feeding apparatus extended into the water column.

Figure 14-7a – Segar, D., and E. Stamman Segar, 1997: California mussels (*Mytilus californianus*, Monterey, California).

Figure 14-7b – Segar, D., and E. Stamman Segar, 1997: Pacific spiny oyster (*Spondylus varians*, Papua New Guinea).

Figure 14-7c – Segar, D., and E. Stamman Segar, 1997: Colony of barnacles in Monterey, California.

Figure 14-7d – Segar, D., and E. Stamman Segar, 1997: Coral barnacles (order Pyrgomatidae, Indonesia).

Figure 14-8a – Segar, D., and E. Stamman Segar, 1997: A hard coral known as brain coral (*Diploria sp.*, Papua New Guinea).

Figure 14-8b – Segar, D., and E. Stamman Segar, 1997: A hard coral often called staghorn coral (*Acropora sp.*, Papua New Guinea).

Figure 14-8c – Segar, D., and E. Stamman Segar, 1997: Close-up showing polyps of a hard coral species (*Tubastrea sp.*, Fiji) extended to feed at night.

Figure 14-8d – Segar, D., and E. Stamman Segar, 1997: Colony of a soft coral (*Dendronephthya sp.*, Fiji). Dendronephthya occur in many different colors.

Figure 14-8e – Segar, D., and E. Stamman Segar, 1997: Typical gorgonian sea fan (*Melithaea sp.*, Papua New Guinea).

Figure 14-8f – Segar, D., and E. Stamman Segar, 1997: Close-up of a soft coral colony (*Xenia sp.*, Papua New Guinea) showing individual polyps at different stages of feeding.

Figure 14-8g – Segar, D., and E. Stamman Segar, 1997: A small suspension-feeding colonial anemone (*Nemanthus annamensis*, Fiji).

Figure 14-8h – Segar, D., and E. Stamman Segar, 1997: A colonial zooanthid (*Protopalythoa sp.*, Papua New Guinea).

Figure 14-8i – Segar, D., and E. Stamman Segar, 1997: A "magnificent sea anemone" (*Heteractis magnifica*, Fiji), here providing a home for a pink anemonefish (*Amphiprion perideraion*).

Figure 14-9a – Segar, D., and E. Stamman Segar, 1997: Lightbulb tunicate (*Clavelina sp.*, Philippines).

Figure 14-9b – Segar, D., and E. Stamman Segar, 1997: The colonial tunicate species *Didemnum molle* (Papua New Guinea).

Figure 14-9c – Segar, D., and E. Stamman Segar, 1997: Three tall, blue and blue-green Rhopalaea sp. and three smaller *Clavelina robusta* (Indonesia) with darker bodies and yellow markings around their incurrent and excurrent openings.

Figure 14-9d – Segar, D., and E. Stamman Segar, 1997: Colonial tunicate that covers and encrusts the reef (*Botryllus sp.*, Indonesia).

Figure 14-10a – Segar, D., and E. Stamman Segar, 1997: A creeping sea cucumber (*Cucumaria sp.*, Philippines) with its suspension-feeding apparatus extended.

Figure 14-10b – Segar, D., and E. Stamman Segar, 1997: A basket star (family Gorgonocephalidae, Papua New Guinea) with its arms extended into the current to feed at night.

Figure 14-10c – Segar, D., and E. Stamman Segar, 1997: A sabellid spiral fan worm (*Protula magnifica*, Indonesia).

Figure 14-10d – Segar, D., and E. Stamman Segar, 1997: A Christmas tree worm (*Spirobranchus giganteus*, Papua New Guinea).

Figure 14-11a – Segar, D., and E. Stamman Segar, 1997: Long-spined sea urchins (*Diadema savignyi*, Papua New Guinea), browsing across the seafloor.

Figure 14-11b – Segar, D., and E. Stamman Segar, 1997: An allied, or egg, cowrie (*Primovula sp.*, Indonesia) on a gorgonian sea fan.

Figure 14-11c – Segar, D., and E. Stamman Segar, 1997: A flabellina nudibranch (*Flabellina rubrolineata*, Indonesia).

Figure 14-11d – Segar, D., and E. Stamman Segar, 1997: Spectacular nudibranch (*Pyllodesmium undulatum*, Papua New Guinea)

Figure 14-12b – Segar, D., and E. Stamman Segar, 1997: Turtle grass (*Thalassia sp.*).

Figure 14-12c – Segar, D., and E. Stamman Segar, 1997: *Spartina sp.* (Aruba, Caribbean Sea), form dense beds in many coastal wetlands where the water is brackish.

Figure 14-12d – Segar, D., and E. Stamman Segar, 1997: Green sea turtle (*Chelonia mydas*, Hawaii).

Figure 14-13d – Segar, D., and E. Stamman Segar, 1997: Black-striped goatfish (*Upeneus tragula*, Indonesia).

Figure 14-14a – Segar, D., and E. Stamman Segar, 1997: Twospot lizardfish (*Synodus binotatus*, Indonesia).

Figure 14-14b – Segar, D., and E. Stamman Segar, 1997: Striated frogfish (*Antennarius striatu*s, Indonesia).

Figure 14-14c – Segar, D., and E. Stamman Segar, 1997: Falco, or dwarf, hawkfish (*Cirrhitichthys falco*, Indonesia).

Figure 14-14d – Segar, D., and E. Stamman Segar, 1997: Fire goby or dartfish (*Nemateleotris magnifica*, Papua New Guinea).

Figure 14-14e – Segar, D., and E. Stamman Segar, 1997: Bennett's butterflyfish (*Chaetodon bennetti*, Papua New Guinea).

Figure 14-15b – Adapted from SEFSC Pascagoula Laboratory, 2013: A large painted anglerfish (*Chaunax pictus*). NOAA NMFS SEFSC, Collection of Brandi Noble, accessed 20 March 2026, https://www.noaa.gov/media/digital-library-photo/pl23fish4157jpg.

Figure 14-16a – Segar, D., and E. Stamman Segar, 1997: Crinoid shrimp (*Periclimenes amboinensis*, Papua New Guinea) on their host crinoid.

Figure 14-16b – Segar, D., and E. Stamman Segar, 1997: Crinoid shrimp (*Periclimenes amboinensis*, Indonesia) on their host crinoid.

Figure 14-16c – Segar, D., and E. Stamman Segar, 1997: A peacockspoted partially buried in the sand (*Phyllichths punctatus*, Indonesia).

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Figure 14-19d – Segar, D., and E. Stamman Segar, 1997: Orbicular burrfish (*Cyclichthys orbicularis*, Philippines).

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– Adapted from Cushing, D. H., 1982: Recruitment. *Climate and Fisheries*. Academic Press, 61.
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– Adapted from Cushing, D. H., 1982: Recruitment. C*limate and Fisheries*. Academic Press, 68.
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