the **spinal cord,** which ends in a brain that is protected by a **skull** made of cartilage or bone. Vertebrates also are characterized by a bilaterally symmetrical body and the presence of an endoskeleton.

Vertebrates are chordates with a backbone that encloses a nerve cord, or spinal cord.

TYPES OF FISHES

Fishes are the oldest and structurally the simplest of all living vertebrates. They also are the most abundant vertebrates in terms of both species and individuals. About 24,000 of the at least 30,000 species of fishes are presently known to science. They make up about half of all species of vertebrates on Earth. Most species of fishes, so far around 15,300, are marine. Many new

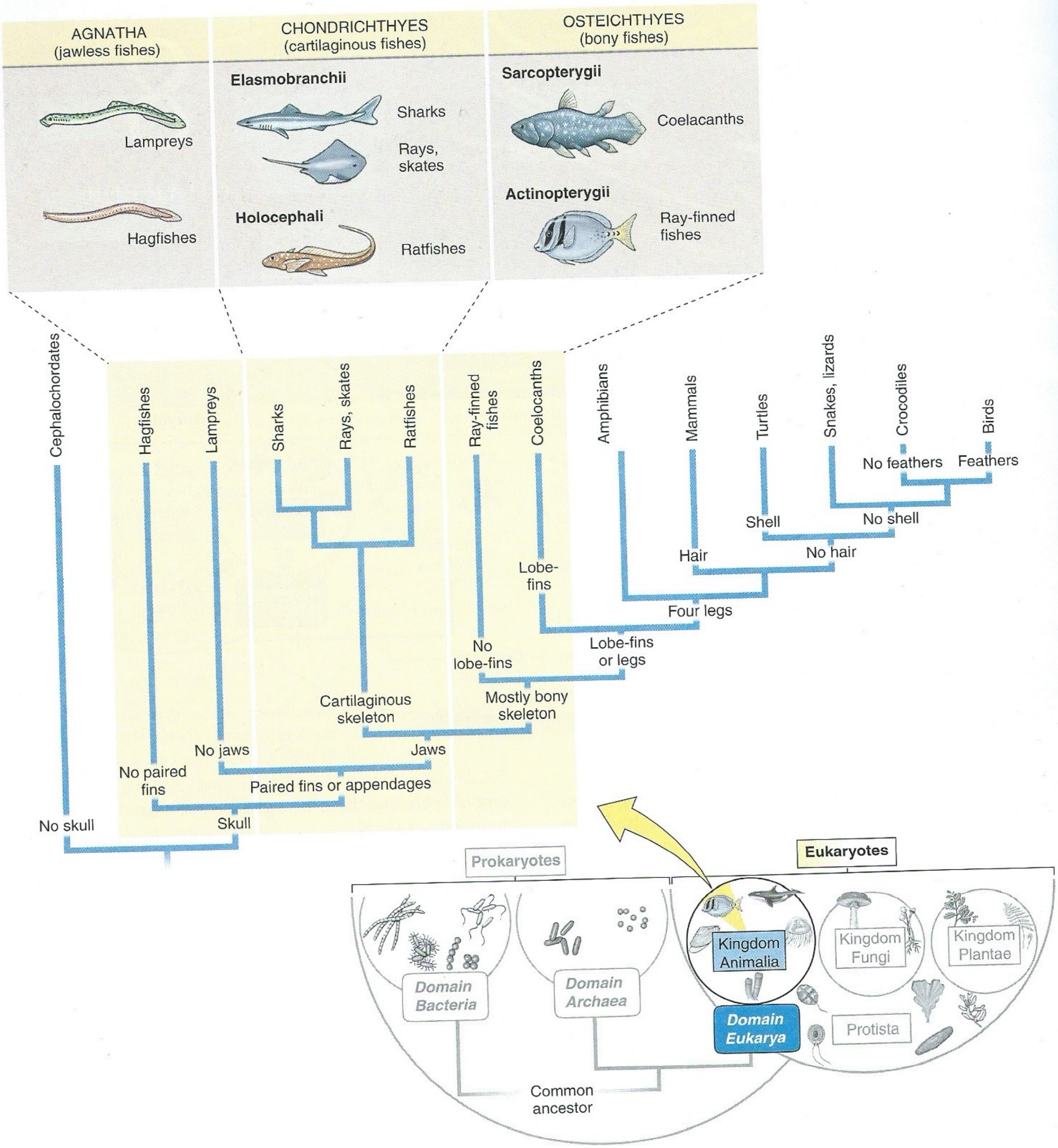


FIGURE 8.1 Classification scheme of fishes.

species are being discovered every year, but many are on the brink of extinction.

There is some disagreement as to how to classify the major groups of fishes. Three groups are traditionally recognized. One of the schemes proposed to show the relationships of these three groups with the rest of the vertebrates is given in Figure 8.1.

Jawless Fishes

The most primitive fishes living today are the **jawless fishes (Agnatha).** Because they lack jaws, they feed by suction with the aid of a round, muscular mouth and rows of teeth. The body is cylindrical and elongated like that of eels or snakes (Fig. 8.2). They lack the paired fins and scales of most fishes, but, like fishes and other vertebrates, the brain is protected by a skull. Some biologists do not even consider jawless fishes to be vertebrates because they lack true vertebrae.

Hagfishes, or **slime eels** (*Myxine, Eptatretus*), are jawless fishes that feed mostly on dead or dying fishes (see Table 8.1, p. 175). They sometimes bore into their prey and eat them from the inside out. Hagfishes live in burrows they dig in muddy bottoms, mostly at moderate depths in cold waters. Only about 20 species are known. They reach a maximum length of approximately 80 cm (2.6 ft). Their skin is used in the manufacture of leather goods, but they are mostly known for attacking bait or fishes on fishing lines, nets, and traps.

Lampreys (*Petromyzon*), found in most temperate regions, are primarily freshwater fishes. They breed in rivers and lakes, but some move to the sea as adults. They attach to other fishes and suck their blood or feed on bottom invertebrates. There are an estimated 30 species of lampreys.

Hagfishes and lampreys lack jaws and are the most primitive living fishes.

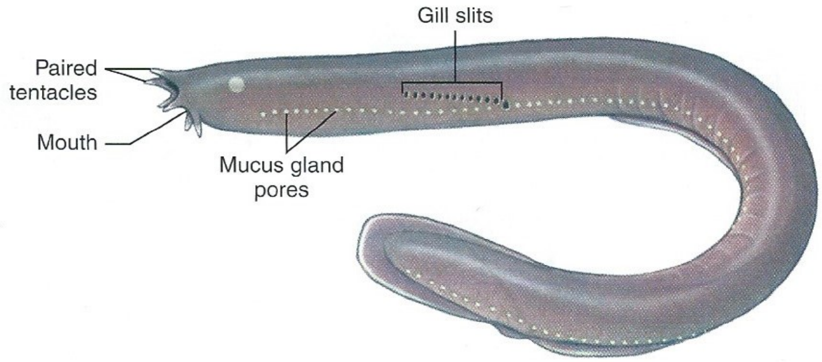


FIGURE 8.2 The Pacific hagfish (*Eptatretus stoutii*) has 4 pairs of sensory tentacles around the mouth and 12 pairs of gill slits. Hagfishes are also known as slime eels because of the abundant mucus produced by glands on the skin. The mucus is used by hagfishes to protect themselves while feeding with their heads buried in dead fishes and whales. Notice the absence of paired fins.

FIGURE 8.3 Shark jaws have several rows of triangular teeth. Individual teeth often have even smaller serrations, or denticles, along their edges. A tiger shark (*Galeocerdo cuvier*) may grow and discard 24,000 teeth in a 10-year period. These are the jaws of a sandtiger shark (*Carcharias taurus*). The small holes in the skin between the eye and the nostrils are the ampullae of Lorenzini (see Fig. 8.19*b*).

Cartilaginous Fishes

The **cartilaginous fishes (Chondrichthyes)** are a fascinating and ancient group that includes the sharks, rays, skates, and ratfishes. Cartilaginous fishes have a skeleton made of **cartilage,** a material that is lighter and more flexible than bone. Though the skeleton of jawless fishes is also cartilaginous, sharks and related fishes feature some significant advances. They possess movable jaws that are usually armed with well-developed teeth (Fig. 8.3). The mouth is almost always ventral—that is, underneath the head. Another important development is the presence of paired lateral fins for efficient swimming. Cartilaginous fishes have rough, sandpaper-like skin because of the presence of tiny **placoid scales.** These consist of a pointed tip that is directed backward (see Fig. 8.4*a*) and have the same composition as teeth.

Sharks, rays, skates, and ratfishes are characterized by a cartilaginous skeleton and a rough skin covered by minute placoid scales. They also have movable jaws and paired fins.

Sharks **Sharks** are magnificently adapted for fast swimming and predatory feeding. They are often described as "mysterious," "evil," or "formidable"—evidence of our fascination with sharks.

Sharks are sometimes referred to as "living fossils" because many of them are similar to species that swam the seas over 100 million years ago. Their fusiform, or spindle-shaped, bodies, tapering from the rounded middle toward each end, slip easily through the water. The tail, or **caudal fin,** is well developed and powerful. The tail is usu ally **heterocercal,** meaning that the upper lobe is longer than the lower lobe (see Fig. 8.4*a*). The upper surface of the body typically features two **dorsal fins,** the first of which is typically larger and nearly triangular. The paired **pectoral fins** are large

Four basic characteristics of chordates:
1. A single, dorsal, hollow nerve cord
2. Gill, or pharyngeal, slits
3. A notochord
4. A post-anal tail
• Chapter 7, p. 145

The term "fish" is used for a single individual or for more than one individual of the same species.

The term "fishes" is used to refer to more than one species of fish.

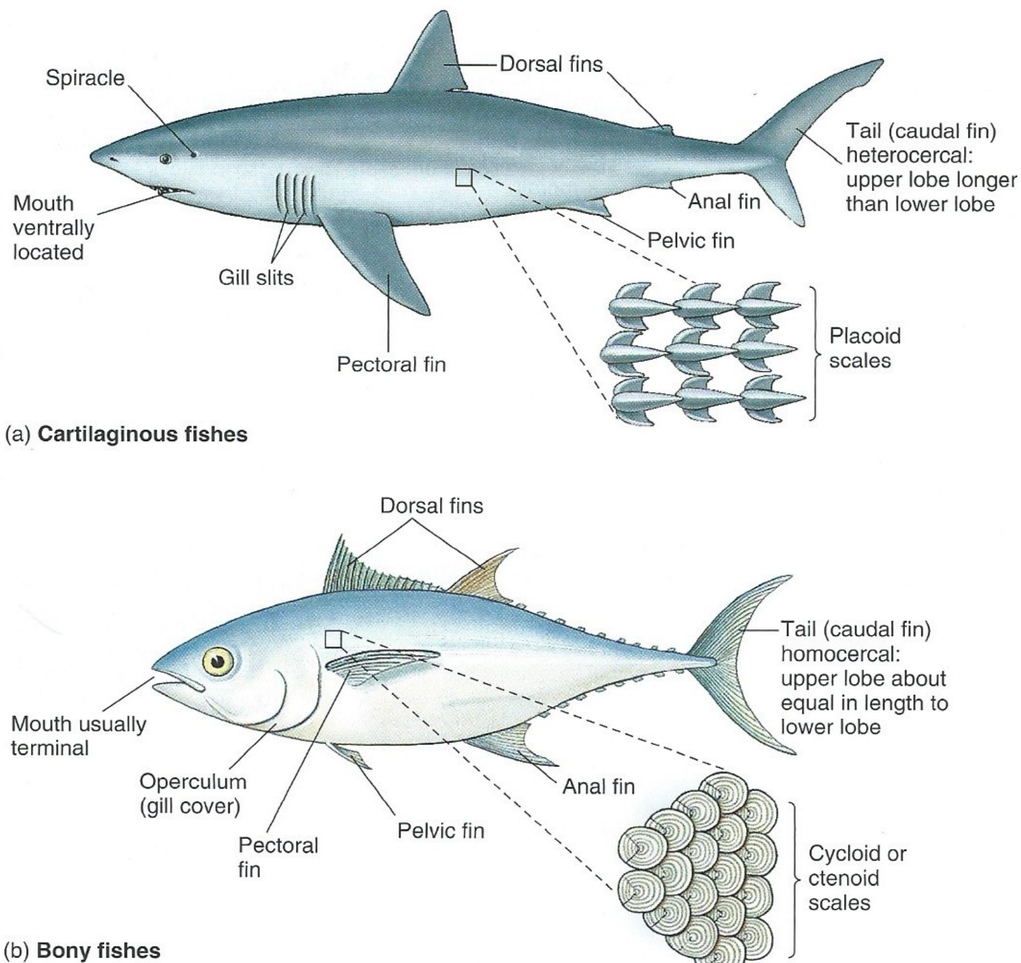


FIGURE 8.4 The most important external differences between (*a*) cartilaginous and (*b*) bony fishes. Also see Figure 8.12.

and pointed in most species. Five to seven gill slits are located behind the head (see Fig. 1.16) and are present on each side of the body.

The powerful jaws of sharks have rows of numerous sharp, often triangular teeth (Fig. 8.3). The teeth are embedded in a tough, fibrous membrane that covers the jaws. A lost or broken tooth is replaced by another, which slowly shifts forward from the row behind it as if on a conveyor belt.

Not all of the nearly 350 living species of sharks conform to this body plan. Hammerhead sharks (*Sphyrna*), for example, have flattened heads with eyes and nostrils at the tip of bizarre lateral extensions (Fig. 8.5*a* and photo on page 157). The head serves as a sort of rudder and separates the eyes and nostrils, which gives the shark binocular vision and sensory perception in practically all directions. The head of sawsharks (*Pristiophorus*) extends in a long, dorsoventrally flattened blade armed with teeth along the edges. The upper lobe of the tail is very long in the thresher sharks (*Alopias;* Fig. 8.5*k*). They use the tail to herd and stun schooling fishes, which they then eat.

The size of fully grown adults also varies. The spined pygmy shark (*Squaliolus laticaudus;* Fig. 8.5*l*) grows to no longer than 25 cm (almost 10 in). At the other extreme, the whale shark (*Rhiniodon typus;* Fig. 8.5*i* and 10.6) is the largest of all fishes. This huge animal, found in tropical waters around the world, may be as long as 18 m (60 ft), though specimens longer than 12 m (40 ft) are rare. Whale sharks pose no danger to swimmers; they are **filter feeders** that feed on plankton. Another giant, second in size only to the whale shark, is the basking shark (*Cetorhinus maximus;* Fig. 8.5*h*), also a plankton eater. There are reports of basking sharks 15 m (50 ft) long, but most do not exceed 10 m (33 ft). The great white shark (*Carcharodon carcharias;* Fig. 8.5*g*), which is considered the most dangerous to humans, may exceed 6 m (20 ft) in length.

Sharks are found throughout the oceans at practically all depths, but they are more prevalent in tropical coastal waters. Sharks are primarily marine, but a few species travel far up rivers. The bull shark (*Carcharhinus leucas;* Fig. 8.5*d*) may be permanently established in some rivers and lakes in the tropics. Several sharks are found mostly in deep water (Fig. 8.6*b*).

Shark meat is eaten around the world. Many people have tried shark without knowing because it is often illegally sold as "regular" fish or scallops. Our appetite for shark has led to disastrous overfishing. So many sharks are being caught that the number of these slow-growing and slow-reproducing fishes has sharply declined in many parts of the world. The number of whitetip sharks (*Carchirhinus longimanus*) in the Gulf of Mexico, for example, is only 1% of their number in the 1950s. Sharks are still fished for their oil, once used extensively in all kinds of products, and for their skin, which is processed into a leather called shagreen. The skin is also used as sandpaper.

Much more valuable are their fins, used for soup in the Orient. Sharks are caught, their fins cut off (a practice known as shark finning), and the wounded animals sometimes dumped in the sea to die. The mistaken belief that shark cartilage is a "joint nutrient" that may help in the treatment of arthritis has caused even more fishing pressure. Overfishing of sharks has led to a more stringent management of shark fishing, including a ban on shark finning in the United States and other countries and the establishment in 2011 of a shark sanctuary of nearly two million km^2 (750,000 mi^2) in the Marshall Islands, central Pacific. There is nevertheless a booming international trade in fins. Even deep-water sharks have not escaped overfishing. Fin sales of about 1.7 million tons a year around the world translate into 73 million sharks a year, more than four times the official shark catches.

Rays and Skates The 450 to 550 species of **rays** and **skates** have dorsoventrally flattened bodies and for the most part live on the bottom (Fig. 8.7). Fishes that live on the bottom are called

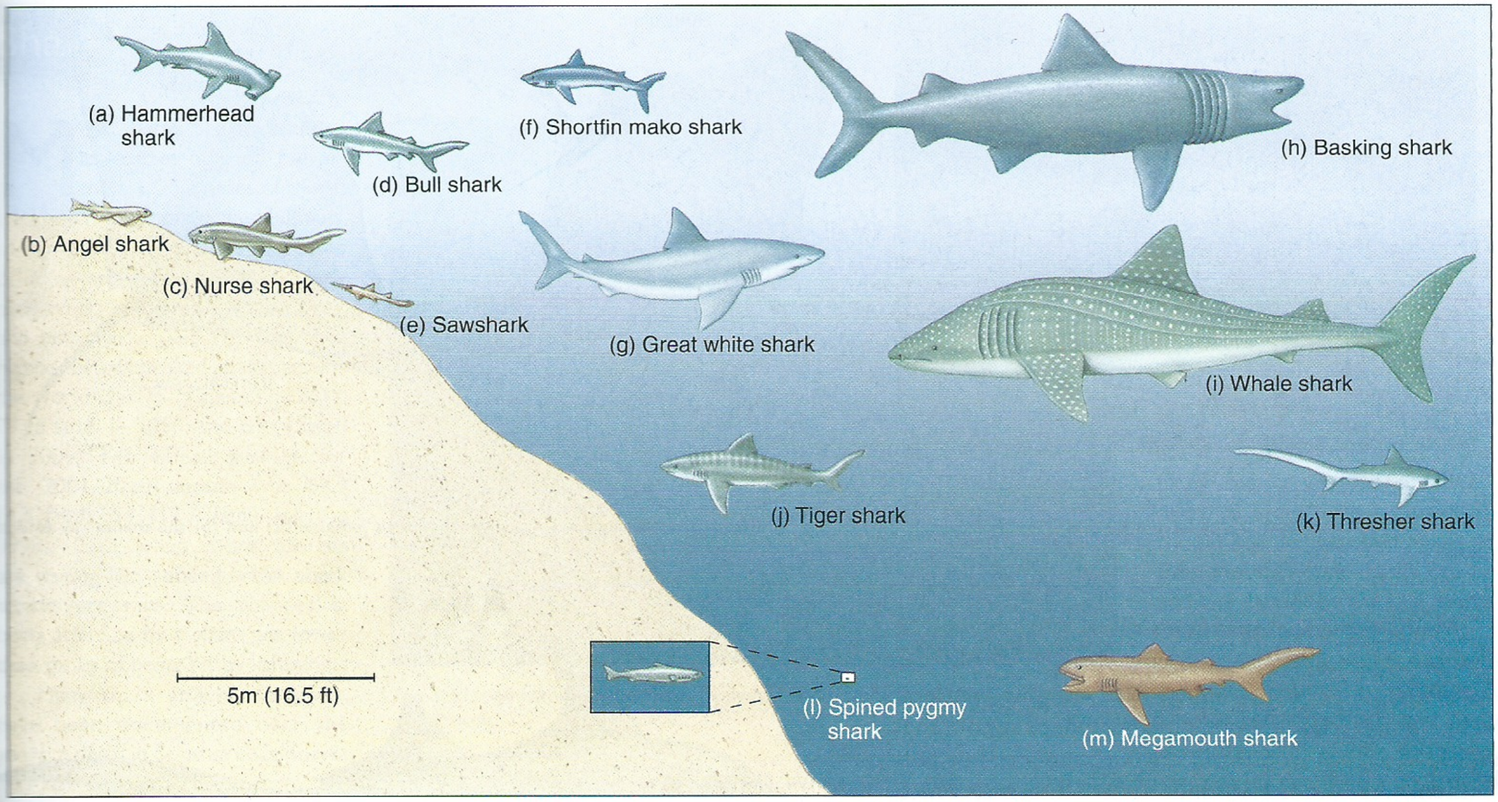
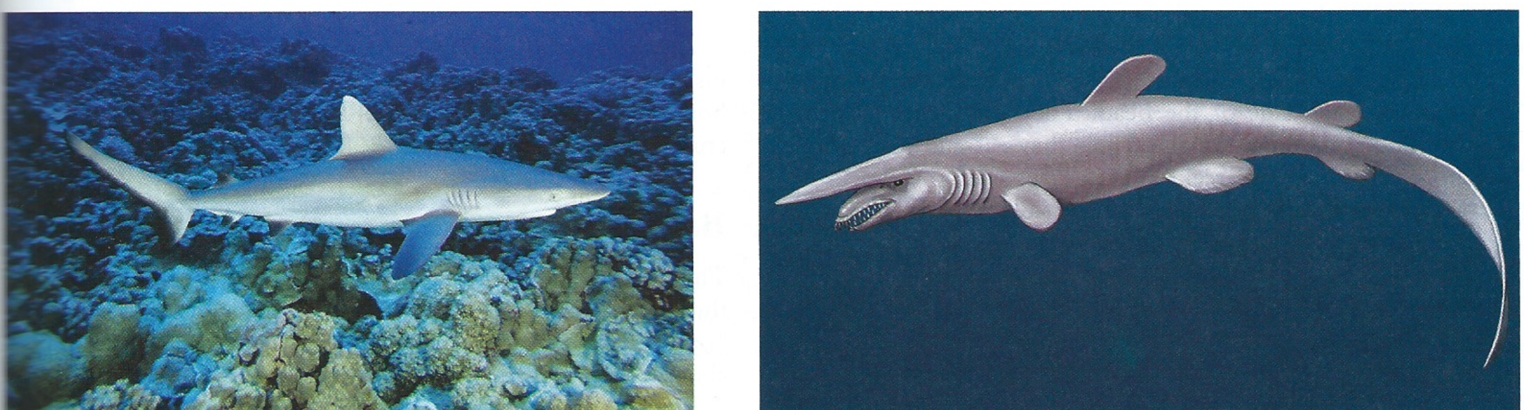


FIGURE 8.5 Sharks live practically everywhere in the ocean. Some of those mentioned in the text include (*a*) hammerhead shark (*Sphyrna zygaena*), (*b*) angel shark (*Squatina californica*), (*c*) nurse shark (*Ginglymostoma cirratum*), (*d*) bull shark (*Carcharhinus leucas*), (e) sawshark (*Pristiophorus cirratus*), (*f*) shortfin mako shark (*Isurus oxyrinchus*), (*g*) great white shark (*Carcharodon carcharias*), (*h*) basking shark (*Cetorhinus maximus*), (*i*) whale shark (*Rhiniodon typus*), (*j*) tiger shark (*Galeocerdo cuvier*), (*k*) thresher shark (*Alopias vulpinus*), (*l*) spined pygmy shark (*Squaliolus laticaudus*) (not drawn to same scale), and (*m*) megamouth shark (*Megachasma pelagios*).



(a) (b)

FIGURE 8.6 (*a*) The gray reef shark (*Carcharhinus amblyrhynchos*) is common in shallow waters of the tropical Indian and Pacific oceans. (*b*) The bizarre goblin shark (*Mitsukurina owstoni*) is usually found in deeper water.

demersal. Some sharks, like angel sharks (*Squatina*) and sawsharks (*Pristiophorus*), also have flattened bodies (Fig. 8.5*b* and *e*). To complicate things, some true rays, like the guitarfishes (*Rhinobatos*), have a body that looks very much like a shark's. Only rays, skates, and related fishes, however, have their gill slits (always five pairs) on the underside of the body—that is, located ventrally (Fig. 8.7*b*)—rather than on the sides. The pectoral fins are flat and greatly expanded, looking almost like wings. They are typically fused with the head. The eyes are usually on top of the head.

The tropical sawfishes (*Pristis*) look very much like sawsharks but have ventral gill slits and are therefore grouped with the rays and skates. They feed by swimming through schools of fish and swinging their blades back and forth to disable their prey. They are known to grow up to 11 m (36 ft) long.

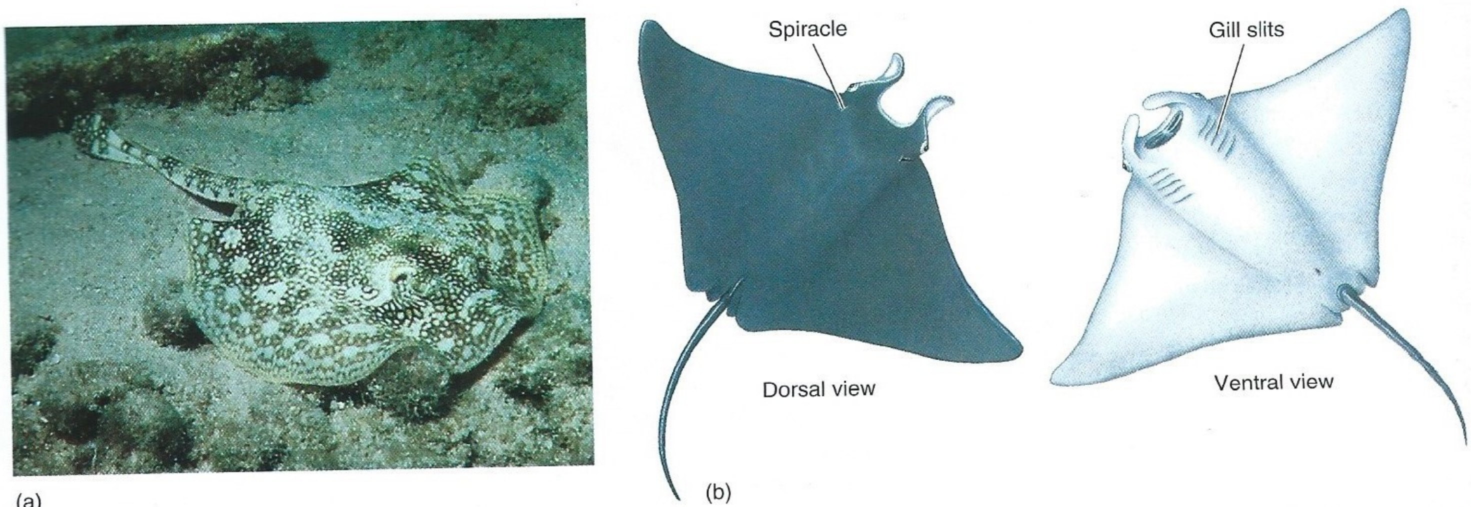


FIGURE 8.7 Rays and skates have a flattened body and ventral gill slits. Examples are (*a*) the yellow stingray (*Urolophus jamaicensis*) and (*b*) the manta ray (*Manta birostris*).

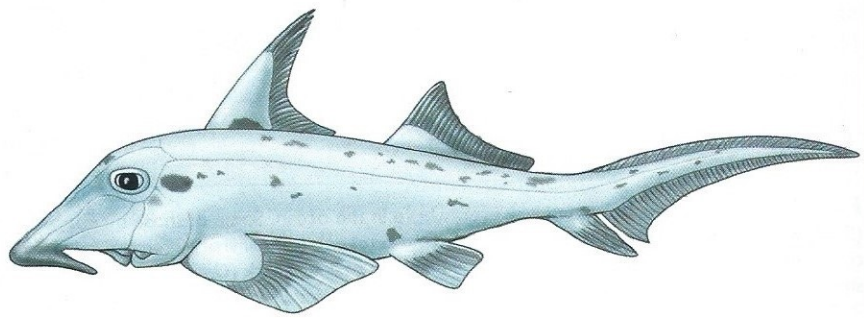


FIGURE 8.8 The elephant fish (*Callorhinchus*), an example of a ratfish, or chimaera. The elephant fish, which is caught commercially for food in the Southern Hemisphere, receives its name because of a snout that hangs down like an elephant's trunk.

Many species of **stingrays** (Fig. 8.7*a*) and their relatives—the eagle, bat, and cow-nosed rays—have a whip-like tail usually equipped with stinging spines at the base for defense. Poison glands produce venom that can cause serious wounds to anyone who steps or falls on them. Abdominal wounds from stingrays, which often occur when handling rays caught in nets, may result in death. Many stingrays cover themselves with sand, becoming nearly invisible. They feed on clams, crabs, small fishes, and other small animals that live in sediment. Stingrays have been known to damage valuable shellfish beds. They expose their food by excavating sediment with their pectoral fins. Their teeth are modified into grinding plates that crush their prey.

Electric rays (*Torpedo*) have special organs that produce electricity on each side of the head. They can deliver shocks of up to 200 volts that stun the fishes they eat and discourage predators. The ancient Greeks and Romans used the shocks of electric rays to cure headaches and other ailments, the original shock treatment.

Not all rays spend their lives on the bottom. Eagle rays (*Aetobatus*) and the spectacular manta and devil rays (*Manta, Mobula*) "fly" through the water, using their pectoral fins like wings. Eagle rays return to the bottom to feed. Mantas feed in midwater on plankton. Both have been observed leaping out of the water. The manta ray (*Manta birostris;* Fig. 8.7*b*) grows into a majestic giant. One individual was found to be almost 7 m (23 ft) wide.

Skates (*Raja*) are similar to rays in appearance and feeding habits, but they lack a whip-like tail and stinging spines. Some have electric organs. Skates lay egg cases, whereas rays give birth to live young. Skates can be extremely abundant, and the larger species are fished for food in some parts of the world.

Ratfishes About 30 species of strange-looking, mostly deep-water, cartilaginous fishes are grouped separately because of their unique features. The **ratfishes,** or **chimaeras** (Fig. 8.8), for instance, have only one pair of gill slits covered by a flap of skin. Some have a long, rat-like tail. They feed on bottom-dwelling crustaceans and molluscs.

Bony Fishes

The great majority of fishes are **bony fishes (Osteichthyes)**. As the name implies, they have a skeleton made at least partially of bone. There are approximately 23,000 species of bony fishes—about 96% of all fishes and almost half of all vertebrates. Between 75 and 100 new species are described every year. A little more than half of all bony fishes live in the ocean, where they are by far the dominant vertebrates.

The composition of the skeleton is not the only distinguishing feature of bony fishes. In contrast to the tiny, pointed placoid scales of cartilaginous fishes, bony fishes usually have **cycloid** or **ctenoid scales,** which are thin, flexible, and overlapping (see Fig. 8.4*b*). Cycloid scales are smooth, whereas ctenoid scales have many tiny spines along their exposed borders. The scales are made of bone and are covered by a thin layer of skin (see Fig. 8.19) as well as protective mucous. Some bony fishes, however, lack scales altogether. Another characteristic of bony fishes is the presence of an **operculum,** or **gill cover,** a flap of bony plates and tissue that protects the gills.

Shark!

Most sharks are harmless—at least to humans. Nevertheless, 25 species of sharks are known to have attacked humans, and at least 12 more are suspected of doing so. Three are particularly dangerous: the great white, tiger, and bull sharks (see Fig. 8.5). The number of unprovoked attacks around the world was 75 (12 fatal) in 2011, 79 (6 fatal) in 2010, and 63 (6 fatal) in 2009. The annual average for the 2001–2010 decade was 64.3 (4.3 fatal), 54 (12.7 fatal) for the 1990s. Even when more tourists are visiting less spoiled areas, shark attacks are rare. The chances of being attacked by a shark are lower than those of being hit by lightning.

The scalloped hammerhead shark (*Sphyrna lewini*) is not considered dangerous to humans.

Many shark attacks, however, have been documented over the years: a diver in Southern California was last seen protruding from the mouth of a shark, parts of arms and legs were found in the stomach of a tiger shark caught after a man had been mortally wounded in Australia, and a series of attacks by tiger sharks has occurred in Hawai'i. One of the authors knew a young man whose promising life ended horribly in the jaws of a tiger shark off Western Samoa.

World War II exposed the crews of torpedoed ships and downed airplanes to shark attacks. Many grim stories about bleeding bodies surrounded by sharks began to spread. They prompted research on the aggressive behavior of sharks and the circumstances leading to shark attacks.

Great white sharks typically inflict a massive wound on their prey (such as seals and sea lions) and then release it. The sharks wait until the bleeding prey is too weak to resist, then move in for the kill. White shark attacks on humans wearing wet suits may be cases of mistaken identity. Sometimes people are able to escape when sharks release them after the first bite. It has been discovered that before attacking, sharks may display distinctive aggressive behaviors—pointing downward of the pectoral fins, pointing upward of the nose with back hunched, or the shivering of the body. Displaying sharks may attack if someone approaches.

So far there is no absolutely guaranteed shark repellent. Copper acetate was used during World War II as a repellent but was eventually found to be ineffective. A black dye was used, but this helped only by obscuring the shark's vision. A chemical repellent is now available in the United States. Chain mail suits offer effective protection from sharks but are too expensive and cumbersome for widespread use. For someone like a downed flyer or shipwrecked sailor, perhaps the best protection is a black plastic bag large enough to float inside.

How can you decrease the risk of an attack? First, do not swim, dive, or surf in an area known to be frequented by dangerous sharks. Seal and sea lion colonies and coastal garbage dumps attract them. Blood, urine, and feces also attract sharks. Avoid murky water. Many sharks are more active at night, so avoid night swims. Sharks should not be provoked in any way. Even resting nurse sharks can turn and bite. Leave the water if fish suddenly appear in large numbers and behave erratically, which may be an indication that sharks are around. If you see a large shark, get out of the water with as little splashing as possible. If attacked, hit the shark's nose or gills with any object on hand, a spear or camera, but not with your bare hands! Do not panic.

Actually, we threaten the survival of sharks more than they threaten us. They reproduce slowly, and their numbers are being depleted by overfishing. This attitude toward sharks may be shortsighted, because they play an important role in marine communities. Overfishing of sharks in Caribbean coral reefs has triggered an increase in the number of groupers and other small predators, which prey on parrotfishes and other algal feeders. Algae then thrive, growing over and killing reef-building corals. Some catch shark only for the shark's fins or jaws. Others practice shark hunting for sport, leaving the meat to waste. A magnificent predator, the shark may soon be exterminated by humans, the fiercest predators of all.

The upper and lower lobes of the tail, the caudal fin, are generally the same size, or **homocercal** (see Fig. 8.4*b*). The fins of bony fishes generally consist of thin membranes that are supported by bony spines, or **fin rays,** in contrast to the stiff, fleshy fins of cartilaginous fishes. Fin rays may consist of rigid spines that act as rudders or are used for protection, sometimes associated with venom glands (see Fig. 8.10*a* and *c*). Some are flexible and used for propulsion and added maneuverability.

Whereas cartilaginous fishes have a ventral mouth, the mouth of most bony fishes is terminal—that is, located at the anterior end. Bony fishes have jaws with much more freedom of movement than those of sharks. The jaws of bony fishes are said to be protrusible because they can be projected outward from the mouth. The teeth are generally attached to the jawbones. Though they are usually replaced, the new teeth do not move forward in rows as do those in sharks.

Another important characteristic is the presence in many bony fishes of a **swim bladder,** a gas-filled sac just above the stomach and intestine (see Fig. 8.12*b*). It allows the fish to adjust its buoyancy to keep from sinking or rising (see "Increased Buoyancy," p. 342). This is a significant development that compensates for the relatively heavy bony skeleton.

Bony fishes are the largest group of living vertebrates. In addition to their bony skeleton, they typically have gills covered by opercula, highly maneuverable fins, protrusible jaws, and usually a swim bladder.

As we shall see in the section "Biology of Fishes," bony fishes are extraordinarily diverse in shape, size, color, feeding habits, reproductive patterns, and behavior. They have adapted to nearly every type of marine environment. All land vertebrates evolved from early bony fishes.

BIOLOGY OF FISHES

Discovering how fishes, cartilaginous and bony alike, have adapted to their environment so successfully is one of the objectives of **ichthyology,** the scientific study of fishes.

Body Shape

The body shape of a fish is directly related to its lifestyle. Fast swimmers like sharks, tunas (*Thunnus, Euthynnus*), mackerels (*Scomber, Scomberomorus*), and marlins (*Makaira*) have a streamlined body shape that helps them move through the water (Figs. 8.4 and 8.9*a;* also see "Swimming Machines," p. 347). Laterally compressed bodies are good for leisurely swimming around coral reefs, kelp beds, or rocky reefs but are still efficient enough to allow for bursts of speed to escape from enemies or capture food. This body form is seen in many inshore fishes like snappers (*Lutjanus*), wrasses (*Labroides, Thalassoma*), damselfishes (*Amphiprion, omacentrus*), and butterflyfishes (*Chaetodon;* see Fig. 8.28). Many demersal fishes, like rays, skates, and sea moths (*Pegasus;* Fig. 8.9*b*), are dorsoventrally flattened. Flatfishes such as flounders (*Platichthys*), soles (*Solea*), and halibuts (*Hippoglossus*) are flat and beautifully adapted to live on the bottom, but their bodies are actually laterally compressed (Fig. 8.9*c*). They lie on one side, with both eyes on top. They begin life with one eye on each side like other fishes, but as they develop one eye migrates up to lie next to the other one. Distinctly elongated bodies are characteristic of moray eels (*Gymnothorax*), trumpetfishes (*Aulostomus*), and pipefishes (*Sygnathus*), among others. Eel-like fishes often live in narrow spaces in rocks or coral reefs, or among vegetation (Fig. 8.9*d–f*). Many bony fishes, like seahorses (*Hippocampus;* Fig. 8.9*g*) depart from these generalized shapes. Trunkfishes (*Ostracion*) have truncate, or relatively short, bodies (Fig. 8.9*h*).

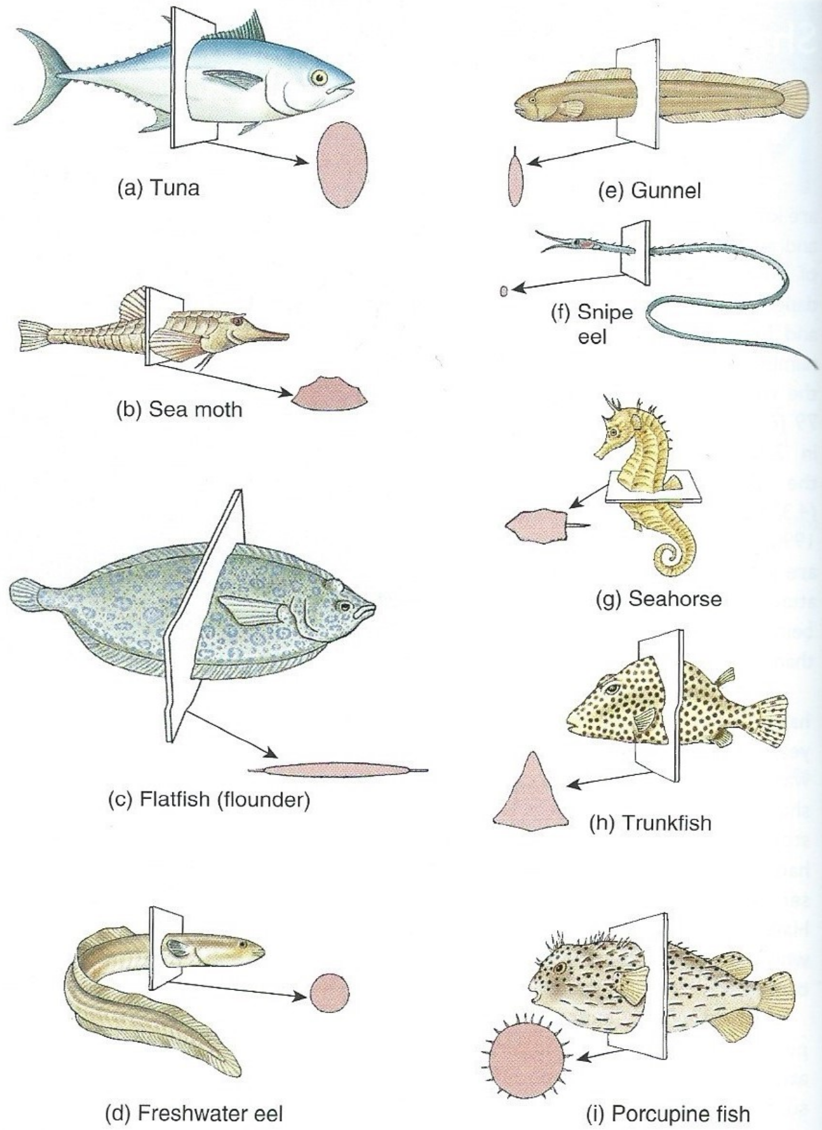


FIGURE 8.9 Body shape among bony fishes varies as an adaptation to habitat. It is streamlined for fast swimming in tunas (*Thunnus; a*); dorsoventrally flattened in bottom-dwellers such as the sea moth (*Pegasus; b*); or laterally flattened in bottom-dwellers such as the flounder (*Platichthys; c*). Fishes living among vegetation or rocks have eel-like bodies, as in the freshwater eel (*Anguilla; d*); ribbon-shaped, as in the gunnel (*Pholis; e*); or thread-like, as in the snipe eel (*Nemichthys; f*). Slow swimmers feature bodies that are elongated on a vertical plane, as in the seahorse (*Hippocampus; g*); triangular, as in the trunkfish (*Ostracion; h*); or round, as in the porcupine fish (*Diodon; i*).

Body shapes can be especially useful for camouflage. For example, some pipefishes live among the eelgrass they resemble. The long, thin trumpetfishes often hang vertically among gorgonian corals or tube-like sponges, or even sneak behind other fish when approaching prey. An irregular shape is often an excellent means of concealment. Bottom fishes such as blennies (*Blennius*) and sculpins (*Oligocottus*) have their outline broken up with irregular growths, particularly on the head, that resemble seaweeds. The body of the stonefish (*Synanceia verrucosa;* Fig. 8.10*a*) resembles a rock so closely that it is almost invisible to both potential prey and humans. Unfortunately for humans, this shallow-water fish from the tropical Indian and Pacific oceans possesses the most potent venom known in fishes. Stepping on a stonefish is excruciatingly painful and potentially fatal.

Coloration

Some bony fishes use color for camouflage, but others, particularly those living in the tropics, are among the most brightly colored animals in the sea. The colored pigments in bony fishes are mostly found in special cells in the skin called **chromatophores.** These cells are irregular in shape and have branches radiating from the center. The amazing variety of colors and hues observed among

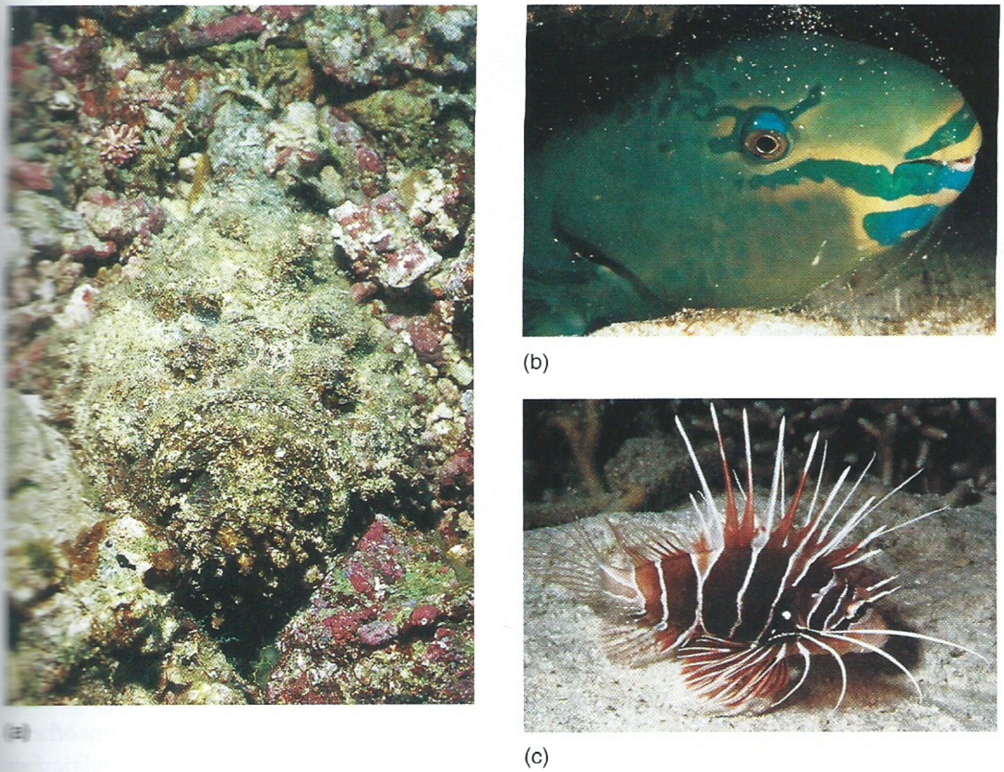


FIGURE 8.10 The variety of forms and habits among marine bony fishes is spectacular. (*a*) The stonefish (*Synanceia verrucosa*) does look like a stone, thus concealing its deadly venom. (*b*) The queen parrotfish (*Scarus vetula*) and other parrotfishes, so called because of their beak-like mouths, sleep at night by secreting a loose mucus envelope that surrounds the body, apparently as a protection against blood-sucking parasites. (*c*) A colorful bar-tailed lionfish (*Pterois radiata*) advertises spines that contain a powerful venom that sometimes kills humans.

marine fishes results from combinations of chromatophores with varying amounts of different pigments. Many fishes can rapidly change color by contracting and expanding the pigment in the chromatophores. Fishes may also have **structural colors** that result when a special surface reflects only certain colors of light. Most structural colors in fishes are the consequence of crystals that act as tiny mirrors. The crystals are contained in special chromatophores called **iridophores.** The iridescent, shiny quality of many fishes is produced by structural colors in combination with pigments (Fig. 8.10*b*).

Colors can tell us a lot about fishes. Some change color with their mood or reproductive condition. They may also use color to advertise the fact that they are dangerous, are poisonous, or taste bad—a phenomenon known as **warning coloration** (Fig. 8.10*c*). **Cryptic coloration,** blending with the environment to deceive predators or prey, is a common adaptation (Fig. 8.10*a*). Flatfishes and some blennies, sculpins, rockfishes (*Sebastes*), and others can change color to match their surroundings. Another use of color is **disruptive coloration,** the presence of color stripes, bars, or spots that help break up the outline of a fish. These and other uses of color are especially common among coral reef fishes (see Figs. 8.28 and 14.30).

Open-water fishes and many shallow-water predators, on the other hand, are rarely as colorful. Most of them have silver or white bellies in sharp contrast to dark backs (see Fig. 8.4). This distinctive color pattern, known as **countershading,** is a form of disguise in open water (see "Coloration and Camouflage," p. 344). Deep-water fishes also use color for concealment. They tend to be black or red, both of which are hard to see in the ocean depths (see "Coloration and Body Shape," p. 368).

Locomotion

Swimming is obviously a major part of the life of fishes. Fishes swim to obtain food, escape from predators, and find mates. Many cartilaginous and some bony fishes must also swim to flush their gills with water to obtain oxygen.

Most fishes swim with a rhythmic side-to-side motion of the body or tail. S-shaped waves of contractions moving from head to tail push against the water and force the body forward. Variations on this theme are illustrated in Figure 8.11.

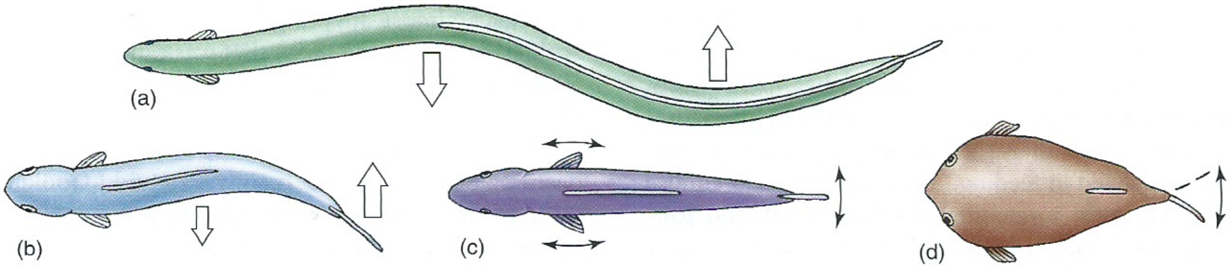


FIGURE 8.11 Locomotion in marine fishes. (*a*) Eels and other elongate fishes swim by undulating their bodies in lateral waves that travel from head to tail. (*b*) Fast fishes with shorter bodies—like tunas, snappers, and jacks—swim by flexing mainly the caudal (tail) portion of the body. (*c*) Surgeonfishes, parrotfishes, and others swim mainly by moving only the fins—that is, the caudal (tail), pectoral, anal, and/or dorsal fins. (*d*) Trunkfishes and porcupine fishes swim slowly by moving the base of the tail while the rest of the heavy body remains immobile.

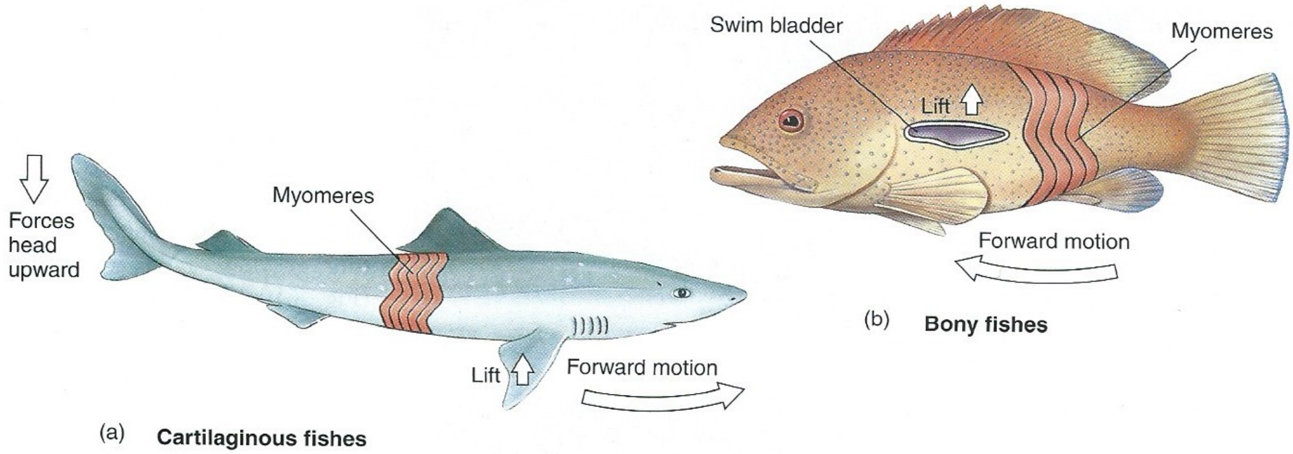


FIGURE 8.12 Cartilaginous and bony fishes use different adaptations to maintain their position in the water. (*a*) Sharks use their fins for lift. (*b*) Many bony fishes have evolved a gas-filled swim bladder to compensate for their heavier bony skeleton. This frees their fins for maneuverability, resulting in a much greater diversity of swimming styles (see Fig. 8.11).

The rhythmic contractions are produced by bands of muscle called **myomeres,** which run along the sides of the body (Fig. 8.12). The distinctive bands of muscle are easily seen in fish fillets. Myomeres are attached to the backbone for support. Muscles make up a large percentage of the body weight of a fish—as much as 75% in tunas and other active swimmers.

Sharks tend to sink because they lack the buoyant swim bladder of most bony fishes. To compensate, they have large, stiff pectoral fins that provide lift somewhat like the wings of a plane (Fig. 8.12*a*). The longer upper lobe of the tail tends to tilt the body upward, also generating some lift. The large amount of oil in the huge liver also provides buoyancy because it is less dense than water. In rays and skates the tail is greatly reduced and the pectoral fins are the main source of both thrust and lift, as in bird wings.

Because most bony fishes have a swim bladder, they do not have to rely on their pectoral fins to provide lift. The pectorals are thus free to serve other purposes. This gives bony fishes great maneuverability. Some can hover in the water or even swim backward, things that sharks cannot do. The other fins of bony fishes also help provide maneuverability. The dorsal and **anal fins** (see Fig. 8.4*b*) are used as rudders, at least part of the time, to steer and provide stability. The paired **pelvic fins** (see Fig. 8.4*b*) also help the fish turn, balance, and "brake."

The flexibility of their fins has allowed many bony fishes to depart from the standard undulating style of swimming. Some open-water bony fishes, such as tunas, emphasize sheer speed (see "Swimming Machines," p. 345). Many fishes, particularly those living around coral reefs, rocks, or kelp beds, swim mainly by moving their fins rather than their bodies, especially for the precise movements needed in feeding. Their tails are used almost solely as rudders. Wrasses, surgeonfishes (*Acanthurus*), and parrotfishes (*Scarus, Sparisoma*), which all live on coral reefs, and the California sheephead (*Semicossyphus pulcher*), common in kelp beds, swim mainly with their pectoral fins. Triggerfishes (*Balistes*) undulate their dorsal and anal fins to swim. This style is perfect for hovering over the bottom while hunting for crabs and sea urchins. Flying fishes (*Cypselurus*) have greatly expanded pectoral fins, which they use to glide through the air (see Fig. 15.21). A large variety of bottom fishes (gobies, sculpins, and many others) crawl or rest on the bottom on their pectoral and/or pelvic fins (see Fig. 8.9*b*). Clingfishes (*Gobiesox*) are small fishes that have their pelvic fins modified into part of a sucker that allows them to attach to rocks. Remoras, or sharksuckers (*Echeneis*), attach to sharks, whales, turtles, and many types of large fishes, using a large sucker on top of their heads. This sucker is derived from part of the dorsal fin.

Fishes usually swim with sideways undulations of the body and tail. The pectoral fins and tail of sharks have an important role in buoyancy control. The fins and tail of bony fishes are generally not used to control buoyancy and instead have become highly maneuverable and important in swimming.

Feeding

Most sharks are carnivores, but in contrast to typical carnivores, which capture smaller prey, some sharks feed by taking bites from prey larger than themselves. For this they use their formidable jaws coupled with shaking of the head. A few sharks are not particular; almost anything can be found in a shark's stomach. A tiger shark (see Fig. 8.5*j*) that was caught off South Africa was found to contain the front half of a crocodile, the hind leg of a sheep, three gulls, and two cans of peas. Nurse sharks feed mostly on bottom invertebrates, including lobsters and sea urchins. Some deep-water sharks subsist mainly on squids. Cookie-cutter sharks (*Isistius*) are small, slow-moving, deep-water sharks that attack larger fishes and dolphins and cut out chunks of flesh with their razor-sharp teeth and sucking lips. They also eat whole squids. Scientists have suggested that they use bioluminescence to lure their prey (see "Bioluminescence," p. 369). Even the rubber sonar domes of nuclear submarines have not escaped their bites.

Several species of cartilaginous fishes are filter feeders: the whale shark, the basking shark, the manta and devil rays, and the megamouth shark (*Megachasma pelagios;* see Fig. 8.5*m*), a gigantic deep-water shark discovered off the Hawaiian Islands in 1976 and soon after in Southern California and several other locations around the world. Like other filter-feeding fishes, basking sharks filter the water with their **gill rakers,** slender projections on the inner surface of the **gill arches** (see Fig. 8.17*b*). Whale sharks have filter plates made of modified placoid scales. The large mouths (see Fig. 10.6) of the three filter-feeding sharks have many small teeth and, excluding the megamouth, very long gill slits. The width of the spaces between the gill rakers or filter plates determines the size of the food captured. Water is strained through the gill rakers, and the shark swallows the food that is left behind. Whale sharks feed in warm water on small schooling fishes, squids, and planktonic crustaceans. Basking sharks, which live in colder water, feed on plankton by opening their mouths and slowly swimming through the water (see Fig. 8.5*h*).

Mantas feed on plankton and small fishes, filtering them from the water with their gill rakers. Two fleshy, horn-shaped projections on the sides of the manta's mouth help channel food into the cavernous mouth (see Fig. 8.7*b*).

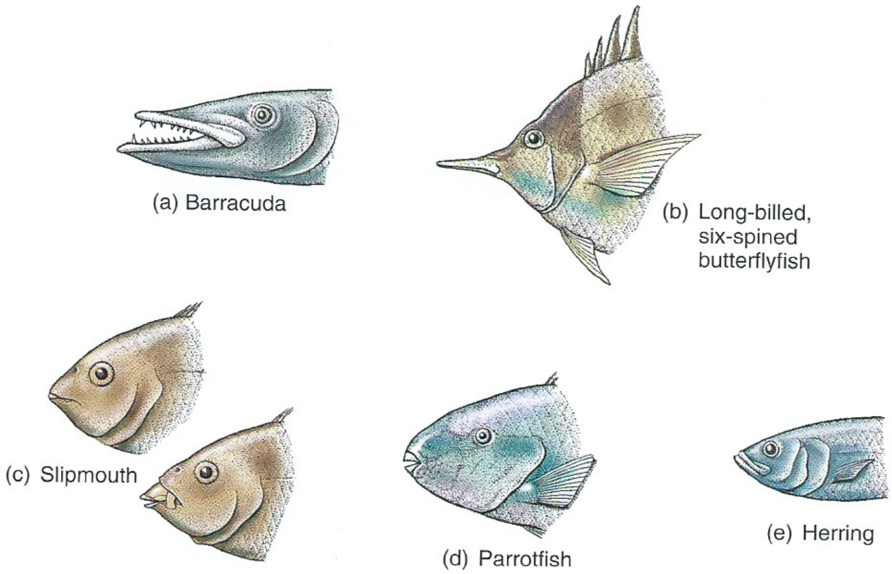


FIGURE 8.13 The shape of the mouth of bony fishes tells much about their diets. (*a*) The barracuda (*Sphyraena*) uses its large mouth to tear off chunks of prey. Most bony fishes, however, swallow their prey whole. (*b*) Many butterflyfishes (*Chaetodon*) use a long snout and small mouth to feed on very small prey. (c) The extremely protrusible mouth of the slipmouth (*Leiognathus*) is used for feeding on relatively small prey. (*d*) Parrotfishes (*Scarus*) use their beak-like mouths to graze on small algae and coral (see Fig. 8.10*b*). (*e*) Herrings (*Clupea*) and other filter feeders typically have large mouths.

Bony fishes are very diverse in the ways they feed. Their protrusible jaws allow them much more flexibility in feeding habits than sharks and rays have. Most bony fishes are carnivores; most groups of animals in the ocean are subject to being eaten by some bony fish. Bony fishes capture their prey from sediments, the water column, the surface of rocks, or other organisms, including other fishes, or combinations of these. Some chase their prey; others sit and wait.

Carnivorous bony fishes typically have well-developed teeth for catching, grasping, and holding their prey (Fig. 8.13*a*), which is usually swallowed whole. The roof of the mouth, gill rakers, and pharynx may also have teeth to help hold the prey. Deep-water fishes often have huge mouths and teeth (see Fig. 16.10), and a few capture and swallow prey larger than themselves.

Unusual food preferences have evolved in fishes. Some prefer sponges, infrequently touched by other carnivores. Others prefer sea urchins, sea squirts, or other seemingly tough-to-eat food items. Reef corals, skeleton and all, are eaten by several types of fishes including some butterflyfishes and parrotfishes, though only the living tissue is digested (Figs. 8.13*b* and 8.28). Many species, however, are non-specialists and capture a wide variety of prey. Some feed on small invertebrates and dead animal material from the bottom. These bottom feeders have a downward-oriented mouth adapted to suck food from the bottom. Frogfishes (*Antennarius*) and anglerfishes (*Gigantactis*; see Fig. 16.21) use a modified spine on the head to lure small fishes.

Fishes that feed primarily on seaweeds and plants are known as **grazers.** Parrotfishes, for example, graze on small algae growing on hard surfaces. Their front teeth are fused to form a beak-like structure (Fig. 8.13*d*). Some species use the beak to scrape off bits of live coral.

Fishes such as herrings (*Clupea*), sardines (*Sardinops*), anchovies (*Engraulis*), and menhadens (*Brevoortia*) filter plankton with their gill rakers. They typically strain their food by swimming with their large mouths (Fig. 8.13*e*) open. These plankton feeders are small, in contrast to the huge plankton-feeding sharks. They usually occur in large, often immense, schools. Plankton feeders are the most abundant fishes in the ocean, and they are an important food source for many types of carnivores. They also account for a large share of the world's fish catch (see "Major Food Species," p. 387).

Digestion

After being swallowed, food passes through the pharynx and a short tube called the **esophagus** into the **stomach** (Fig. 8.14). The stomach is where the process of digestion usually begins. It is typically J-curved or elongated but may be modified into a grinding structure or even lost altogether. The food passes from the stomach into the **intestine.** In most bony fishes the anterior portion of the intestine has many slender, blind tubes, the **pyloric caeca,** which secrete digestive enzymes. Other digestive enzymes are secreted by the inner walls of the intestine and the **pancreas.** Another organ important in digestion is the **liver,** which secretes **bile** needed for the breakdown of fats. The liver is particularly large and oil-rich in sharks, sometimes making up as much as 20% of their body weight.

A few fishes lack a stomach and tend to have a portion of the intestine expanded for the digestion of food. Carnivorous fishes have short, straight intestines. Fishes that eat seaweeds, which are more difficult to digest, have coiled intestines, which may be

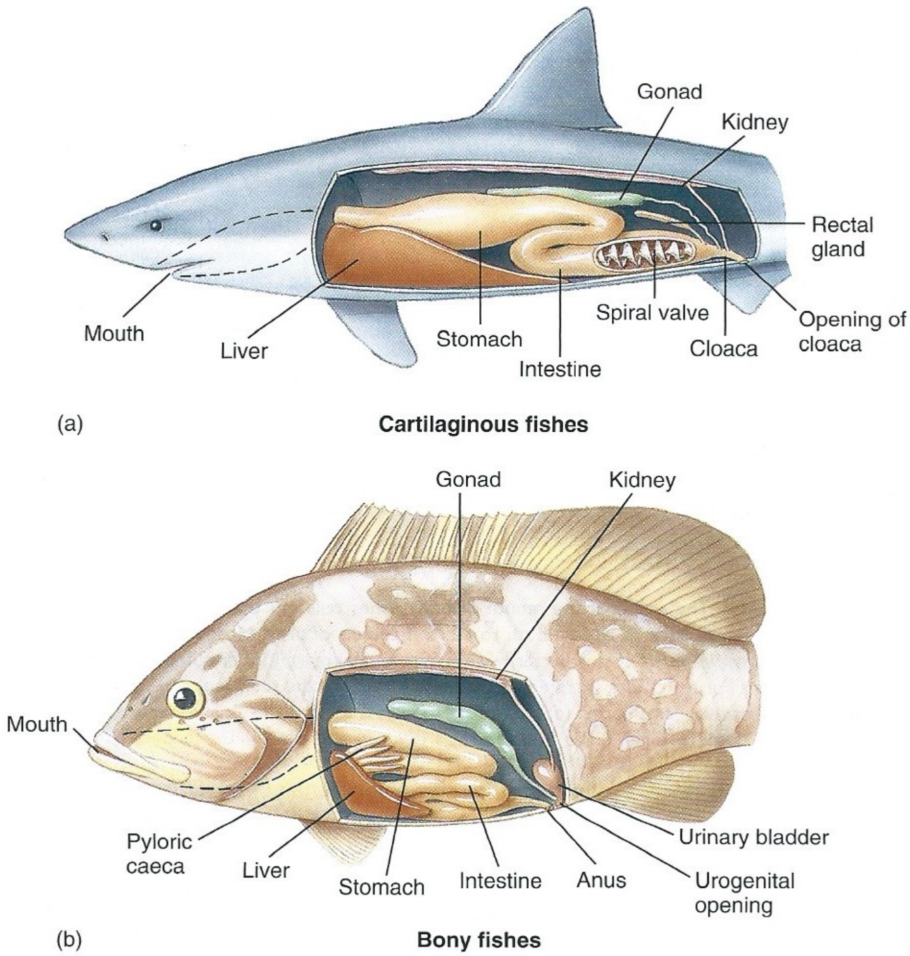


FIGURE 8.14 The digestive systems of (*a*) cartilaginous and (*b*) bony fishes display many of the basic features found in all vertebrates.

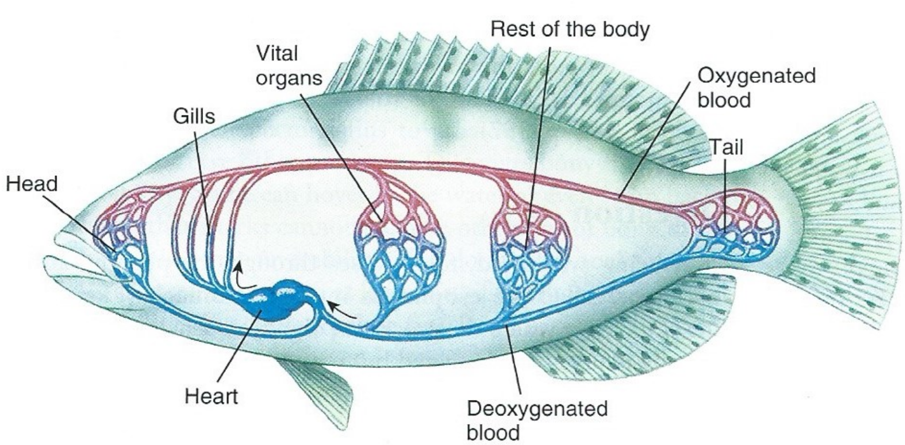


FIGURE 8.15 The circulatory system of fishes consists of veins that carry deoxygenated blood (in blue) from the body, a two-chambered heart that pumps blood to the gills for oxygenation, and arteries that carry oxygenated blood (in red) to the rest of the body.

much longer than the fish itself. The intestines of cartilaginous fishes and a few primitive bony fishes contain a spiraling portion called the **spiral valve,** which increases the internal surface area of the intestine (Fig. 8.14*a*). The intestine is responsible for absorbing the nutrients resulting from digestion. These nutrients pass into the blood to be distributed through the body. Undigested material exits through the anus, or the **cloaca,** the common passage for the digestive, excretory, and reproductive systems in cartilaginous fishes (Fig. 8.14*a*).

Circulatory System

All fishes have a two-chambered **heart** located below the gills (Fig. 8.15). Deoxygenated blood enters the first chamber of the heart from the body. The blood is then pumped to the second chamber, which then pumps it to the gills, where **gas exchange** takes place. The oxygenated blood is then carried back to the body by blood vessels called **arteries.** The arteries branch out into thin-walled **capillaries,** which allow oxygen and nutrients to reach every cell. Other capillaries then collect into larger blood vessels, **veins,** which carry deoxygenated blood, along with dissolved carbon dioxide, back to the heart to complete the cycle.

Respiratory System

Fishes obtain oxygen dissolved in water and release carbon dioxide from their blood through paired gills. The gills lie in the pharynx, a chamber just behind the mouth that represents the front part of the gut.

Irrigation of the Gills Fishes get the oxygen they need by extracting it from the water. To do this, they must make sure that water flows over the gills—that is, they must irrigate, or ventilate, the gills.

Most sharks swim continuously. Swimming, plus the opening and closing of the mouth, forces water through the mouth, over the gills, and out through the gill slits (Fig. 8.16*a*). When caught in fishing nets, sharks cannot swim to force the water in and therefore "drown." Not all sharks need to swim, however. Nurse sharks (*Ginglymostoma*) and several other sharks rest on the bottom during the day (see Fig. 8.5*c*). They force water over the gills by opening and closing the mouth.

Expansion and contraction of the walls of the pharynx and the gill slits assist in the irrigation of gills in sharks. Every gill lies in its own chamber, and each gill chamber opens to the outside by a separate gill slit. The first pair of gill slits of cartilaginous fishes is modified into **spiracles,** a pair of round openings just behind each eye. The spiracles are located on the dorsal surface of rays and skates (see Fig. 8.7*b*). They allow these fishes, many of which live on the bottom, to take in water even when the ventral mouth is buried in the sediment. When lampreys and other jawless fishes feed by sucking on other fishes, the passage of water through

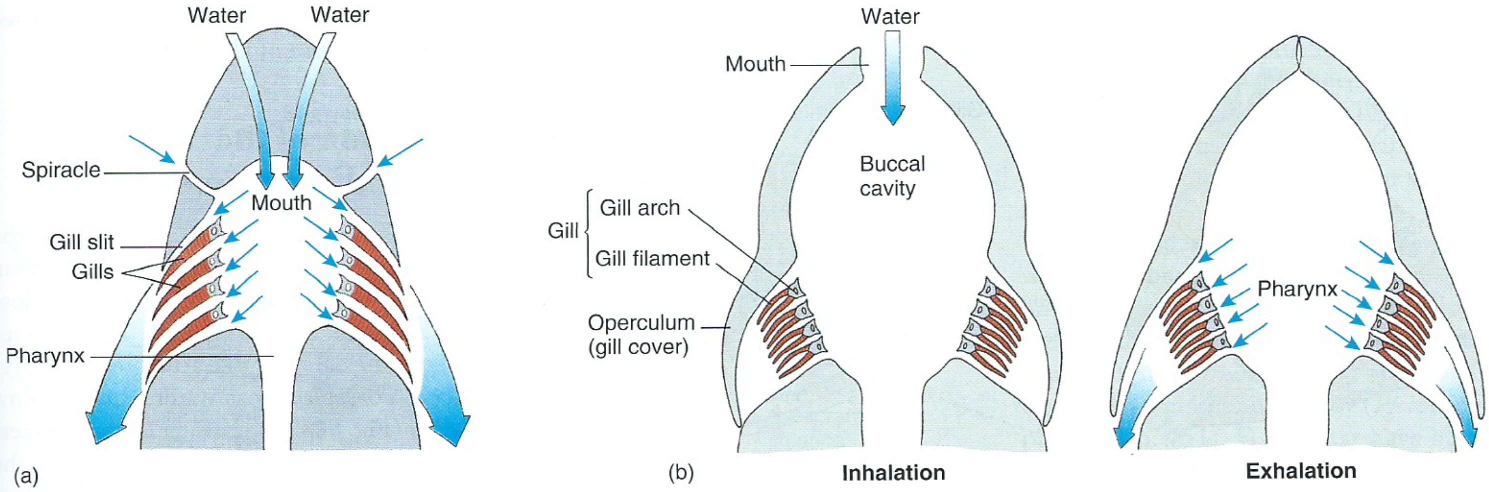


FIGURE 8.16 The mechanism behind the irrigation of the gills. (*a*) Cartilaginous fishes like sharks allow water in (path of water indicated by arrows) by opening the mouth, which is then closed. The rising of the floor of the mouth causes water to be pumped through the gills and out by way of the separate gill slits. The spiracles also allow water to move in; in rays and skates these play a crucial role. (*b*) Bony fishes are more efficient because of the presence of opercula, which close as the pharynx expands, sucking the water in. The closing of the mouth and the opening of the opercula force water through the gills and out.

their mouth is blocked and they pump water in as well as out through the gill slits.

Most bony fishes have a more efficient mechanism to bring in water to the gills. The gills on each side share a gill chamber, which opens to the outside through an opening on each side of the head. Each opening is covered by an operculum (Fig. 8.16*b*). When the mouth opens, the opercula close and the pharynx expands, sucking water in. The fish does the reverse to pump water out: the mouth closes, the pharynx contracts, and the opercula open. Some fast swimmers simplify things by just opening their mouths to force water into the gills.

Structure of the Gills Fish gills are supported by cartilaginous or bony structures, the gill arches (Fig. 8.17*b*). Each gill arch bears two rows of slender, fleshy projections called **gill filaments.** Gill rakers project along the inner surface of the gill arch. They prevent food particles from entering and injuring the gill filaments or may be specialized for filtering the water in filter-feeding fishes.

The gill filaments have a rich supply of capillaries (Fig. 8.17*c*), the oxygenated blood of which gives them a bright red color. Each gill filament contains many rows of thin plates or disks called **lamellae,** which contain capillaries. The lamellae greatly increase the surface area through which gas exchange can take place. The number of lamellae is greater in active swimmers, which need large supplies of oxygen.

Gas Exchange Oxygen dissolved in the water diffuses into the capillaries of the gill filaments to oxygenate the blood. **Diffusion** will take place only if oxygen is more concentrated in the water than in the blood. This is usually true because the blood coming to the gills has already traveled through the rest of the body and is depleted of oxygen (Fig. 8.15). As oxygen diffuses from the water to blood in the capillaries, the amount of oxygen in the water decreases and that in the blood increases. This can reduce the efficiency of gas exchange, which depends on the water having more oxygen than the blood. Fishes, however, have evolved a clever adaptation called a **countercurrent system of flow** to increase efficiency. The blood in the gills flows in the *opposite* direction to the water passing over them (Fig. 8.17*d*). When the water has passed over the gill and given up much of its oxygen, it meets blood that has just come from the body and is "hungry" for what oxygen remains in the water (Fig. 8.17*e*). By the time the blood has flowed most of the way through the gill, picking up oxygen, it encounters water that is just entering the gill chamber and is rich in oxygen. Thus, the oxygen content of the water is always higher than that of the blood. This system makes the gills very efficient at extracting oxygen. Without this countercurrent system, blood returning to the body would have less oxygen.

The blood disposes of its carbon dioxide using the same mechanism. Blood flowing into the gills from the body has a high concentration of carbon dioxide, a product of respiration. It easily diffuses out into the water.

Gas exchange in the gills of fishes is highly efficient. The surface area of gills is greatly increased by lamellae, and the flow of water through them is in a direction opposite to that of blood.

Gas Exchange The absorption of oxygen to be used in respiration (the breakdown of glucose to release energy) and the elimination of carbon dioxide that results from the same process.

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Diffusion The movement of molecules from areas of high concentration to areas of low concentration.

- Chapter 4, p. 72

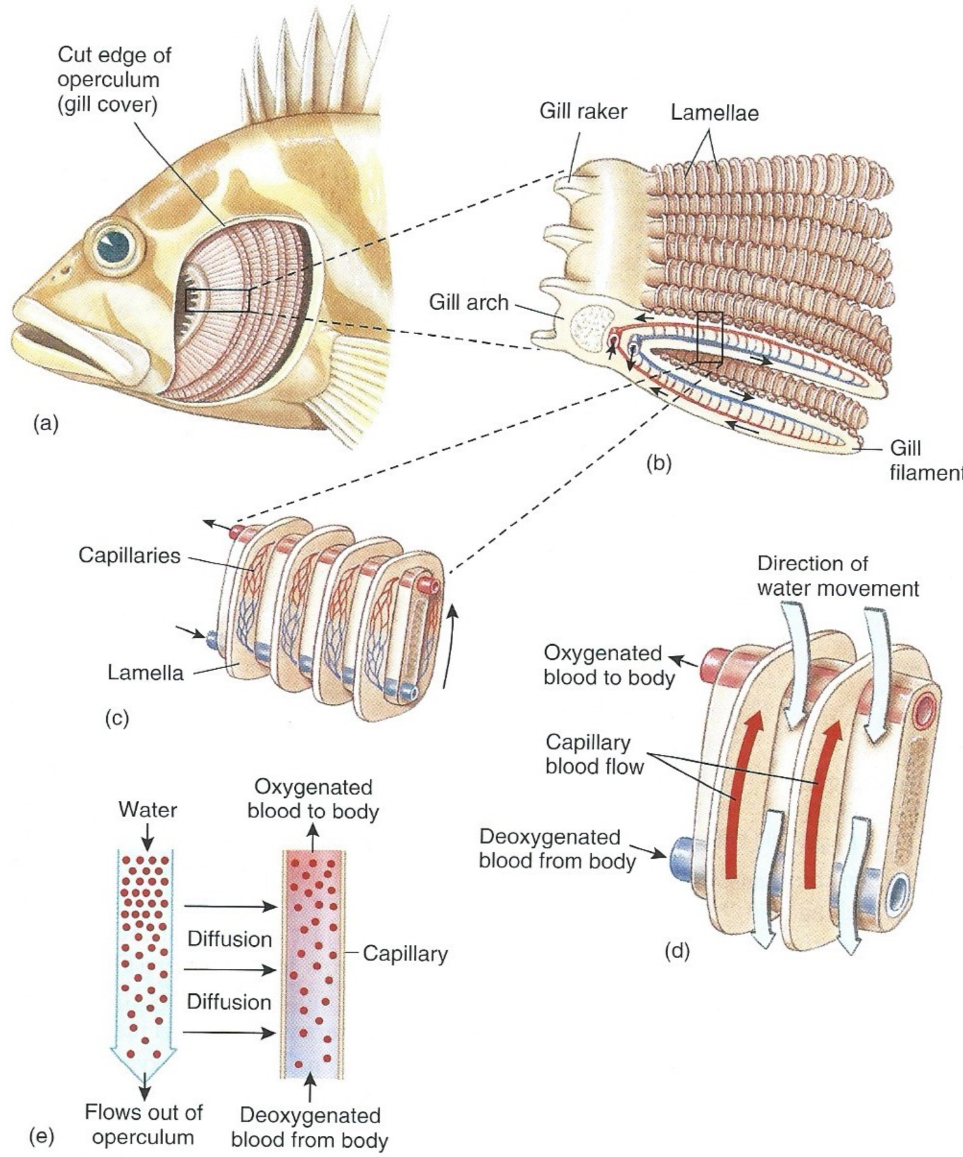


FIGURE 8.17 The gills of fishes are very efficient structures for gas exchange. Bony fishes have four pairs of gills (*a*), each containing two rows of numerous gill filaments (*b*). Lamellae in the gill filaments (*c*) increase the surface area of the gill filaments. (*d*) Diffusion of oxygen from seawater into the blood gets a boost because the water flows across the lamellae in the opposite direction to that of the blood. (*e*) The concentration of oxygen (indicated by dots) is always higher in the water than in the blood. If circulation were not reversed, blood to the body would have less oxygen.

Once oxygen enters the blood it is carried through the body by **hemoglobin,** a red protein that gives blood its characteristic color. Hemoglobin is contained in specialized cells called **erythrocytes,** or **red blood cells.** The hemoglobin releases oxygen to the tissues as it is needed. After it gives off its oxygen, the hemoglobin picks up carbon dioxide from the body and carries it to the gills, where it diffuses into the water.

Muscles use a lot of oxygen during exertion. They have a protein, called **myoglobin,** similar to hemoglobin, that can store oxygen. Hard-working muscles tend to have a lot of myoglobin, which makes them dark red. Strong swimmers, such as open-water sharks and tunas, have a high proportion of red muscle, as opposed to white muscle (see "Swimming: The Need for Speed," p. 345). Many other fishes have concentrations of red muscles at the base of heavily used fins.

Regulation of the Internal Environment

In contrast to most marine organisms, the blood of marine bony fishes is less salty than seawater (see Fig. 4.14). As a result, they lose water by **osmosis.** Marine bony fishes therefore need to **osmoregulate** to prevent dehydration. To replace lost water, they swallow seawater (Fig. 8.18*b*). Seawater contains excess salts, some of which pass straight through the gut without being absorbed. Salts that are absorbed are excreted by the **kidneys,** the most important excretory organs of vertebrates, and specialized **chloride cells** in the gills. The kidneys conserve water by producing only small amounts of urine.

Cartilaginous fishes use a different approach to salt balance (Fig. 8.18*a*). They reduce osmosis by increasing the amount of dissolved molecules, or **solutes,** in their blood, making the blood concentration closer to that of seawater. They do this by retaining a chemical called **urea,** a waste product that results from the breakdown of proteins. The amount of urea in the blood is controlled by the kidneys. In most animals urea is toxic and is excreted, but sharks and other cartilaginous fishes excrete only small amounts. Urea and related compounds are less toxic to cartilaginous fishes. They retain most of the urea in their blood; their gills help in this process by blocking the loss of urea.

Cartilaginous fishes also absorb water to prevent dehydration, mostly through the gills and from food. Excess salts are excreted by the kidneys, intestine, and a special gland near the anus called the **rectal gland** (Fig. 8.18*a*).

Marine fishes keep a constant internal environment and check water loss through the osmoregulatory activities of the kidneys, gills, and other mechanisms.

Nervous System and Sensory Organs

Vertebrates have the most complex and advanced nervous systems of any animal group. At the heart of the system is the **central nervous system,** consisting of the brain and spinal cord. The central nervous system coordinates and integrates all body activities and stores information. The brain is divided into several regions

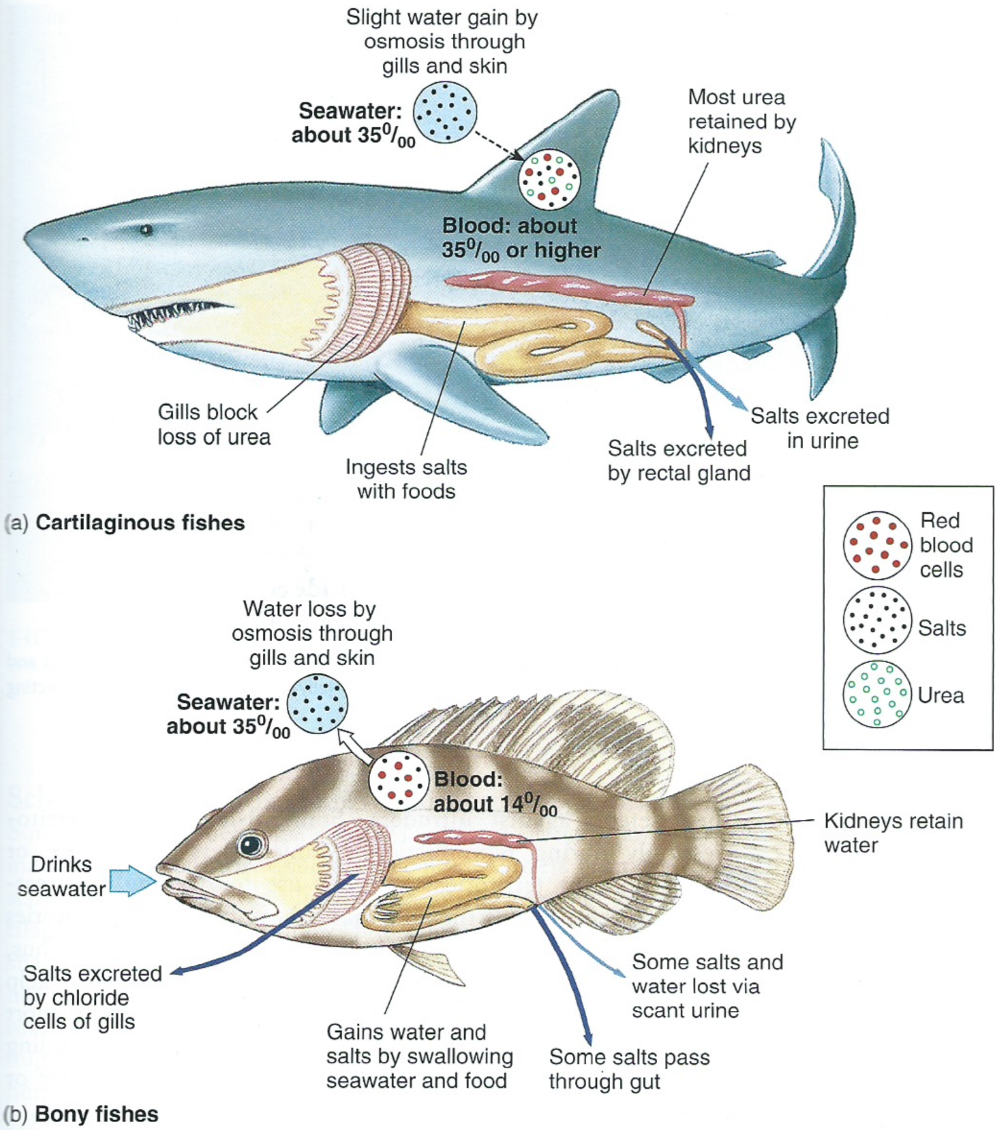


FIGURE 8.18 Marine fishes live in water that is saltier than their body fluids. For this reason, water tends to diffuse out of the body. (*a*) To prevent dehydration, sharks and other cartilaginous fishes concentrate urea, absorb seawater through their gills and skin, and excrete excess salts by way of the urine and feces. A special gland, the rectal gland, also excretes excess salts. Their blood ends up with a solute concentration almost equal to or even higher than that of seawater. (*b*) Marine bony fishes do not concentrate urea, which is toxic to them. Instead, their kidneys conserve water, and they drink seawater, excreting excess salts, as do cartilaginous fishes, but using different organs. Compare with Figure 4.14.

known to serve as centers for particular functions such as olfaction and vision. It is protected by a cartilaginous or bony skull. Nerves connect the central nervous system with various organs of the body and with sense organs that receive information from the surroundings. This information is sent to the brain in the form of nerve impulses.

Most fishes have a highly developed sense of smell, which they use to detect food, mates, and predators, and sometimes to find their way home. Fishes do this with special sensory cells located in **olfactory sacs** on both sides of the head. Each sac opens to the outside through one or two openings, the nostrils, or **nares.**

The sense of smell is particularly well developed in sharks. They can detect blood and other substances in concentrations as low as fractions of one part per million. Salmon (*Oncorhynchus*), which live as adults at sea but reproduce in fresh water, use olfaction to find the stream where they were born years earlier (see "Migrations," p. 167). They accomplish part of this remarkable feat by memorizing the sequence of smells on their way out to sea.

Fishes detect other chemical stimuli with **taste buds** located in the mouth and on the lips, fins, and skin. Taste buds also are found on **barbels,** whisker-like organs near the mouth of many bottom feeders such as marine catfishes (*Plotosus;* see photo on p. 151). Fishes that have barbels use them to detect food on the bottom.

Fish eyes are not very different from those of vertebrates that live on land. One important difference, though, is the way they focus. Whereas the eyes of most land vertebrates focus by changing the shape of the lens, the round lens of the fish eye focuses by moving closer to or farther away from the subject. This is partially why fish eyes tend to bulge. Bony fishes appear to rely on vision more than most cartilaginous fishes. Many bony fishes—particularly shallow-water species—have color vision, but most cartilaginous fishes have little or none. Some sharks have a distinct **nictitating membrane** that can be drawn across the eye to reduce brightness and to protect the eye during feeding.

Fishes have a unique sense organ called the **lateral line** that enables them to detect vibrations in the water. The lateral line consists of a system of small canals that run along the head and body (Fig. 8.19*a*). The canals lie in the skin and in the bone or cartilage of the head. They are lined with clusters of sensory cells, or **neuromasts,** that are sensitive to vibration. The canals usually open to the surface through pores that are quite visible.

The lateral line system picks up vibrations resulting from the swimming of other animals as well as water displacements caused by sound waves. It allows fishes to avoid obstacles and predators, detect prey, orient to currents, and keep their position in a school.

Osmosis The diffusion of water across a selectively permeable membrane, such as a cell membrane.

- Chapter 4, p. 72

Osmoregulation The active control by an organism of its internal *solute* concentration to avoid osmotic problems.

- Chapter 4, p. 74

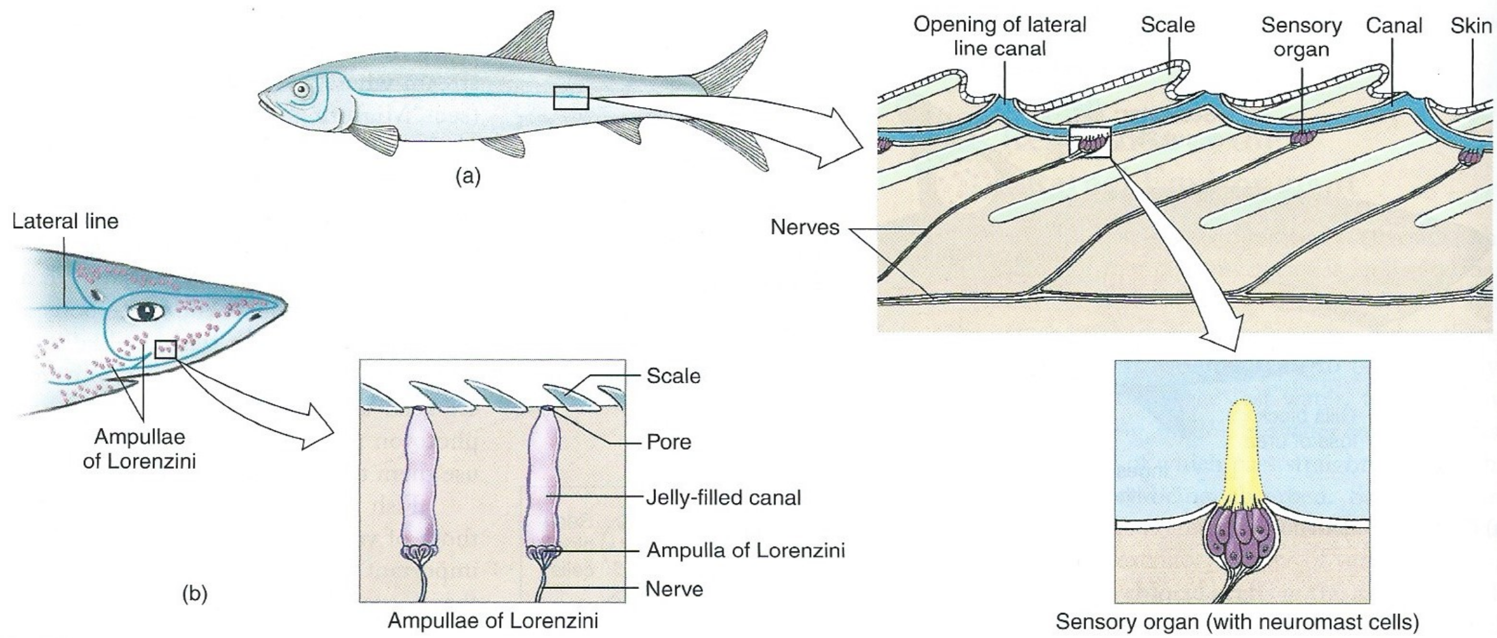


FIGURE 8.19 (*a*) Cross section through the skin of a fish, showing the lateral line sensory system. The nerves collect nerve impulses from the sensory organs and transmit the information to the brain. (*b*) In addition to the lateral line, cartilaginous fishes have ampullae of Lorenzini, a network of jelly-filled canals capable of detecting electrical fields in the water.

Cartilaginous fishes also have sense organs in the head called the **ampullae of Lorenzini** (see Figs. 8.3 and 8.19*b*) that can detect weak electrical fields. This system helps them locate prey. It may also help in navigation as a sort of electromagnetic compass or perhaps a detector of currents.

Fishes can also perceive sound waves with their **inner ears,** paired hearing organs located to the sides of the brain just behind the eyes. The inner ears are a set of fluid-filled canals that contain sensory cells similar to those in the lateral line canals. In some fishes the swim bladder amplifies sound by vibrating and transmitting sound waves to the inner ear. The inner ear is also involved in equilibrium and balance. Many fishes detect changes in body position from the movement of calcareous **ear stones,** or **otoliths,** that rest on sensory hairs, a mechanism similar to the **statocysts** of invertebrates.

The sense organs of fishes include eyes, olfactory sacs, taste buds, and inner ears, as well as a lateral line and other specialized organs that pick up vibrations or electrical stimuli from the water.

Behavior

Nearly all aspects of the lives of fishes involve complex behavior to adapt to light and currents, to find food and shelter, and to avoid predators. Behavior is also an important part of fish courtship and reproduction, which are described in the next section. This section provides only a glimpse of some aspects of fish behavior; some other highlights are discussed in other chapters.

Territoriality Many marine fishes, particularly open-water species, do not reside in any particular area. Others, however, are known to establish **territories,** home areas that they defend against intruders. Some fishes defend territories only during reproduction. Many others have more or less permanent territories that they use for feeding and resting or as shelter. It is thought that fishes often guard territories to ensure that they have enough food and other resources. Thus, territoriality is most common in crowded environments like kelp beds and coral reefs, where resources are most likely to be in short supply. Coral reef damselfishes are famous for fiercely defending their territories, often attacking fishes many times their size or even divers.

Fishes use a variety of **aggressive behaviors** to defend their territories. Actual fights are surprisingly rare. Instead, fishes usually prefer to avoid risking injury by bluffing. Raised fins, an open mouth, and rapid darting about are examples of such threatening postures. Territorial defense may also involve sound production. Marine bony fishes may make sound by grinding their teeth or rubbing bones or fin spines on another bone. Some fishes "drum" by pulling muscles on the swim bladder, and this sound is amplified by the air-filled bladder.

Sometimes a solitary individual defends a territory. In other species, like some butterflyfishes, territories are established by a male-female pair. Territories may also be inhabited by groups that belong to the same species. This is the case in many damselfishes, which inhabit spaces between the branches of corals (Fig. 8.20), and anemonefishes, or clownfishes (*Amphiprion;* see Fig. 14.35). Members of such groups often divide the territory into subterritories.

Statocysts Sense organs of many invertebrates consisting of one or more grains or hard bodies surrounded by sensitive hairs and used to orient the animal with gravity.

• Chapter 7, p. 122

FIGURE 8.20 Some damselfishes, such as the blue chromis (*Chromis cyanea*) from the Caribbean, live among corals. They dash into spaces between the coral whenever danger approaches.

Schooling Many fishes form well-defined groups, or **schools.** Some, including herrings, sardines, mullets (*Mugil*), and some mackerels, school throughout their lives. Others are part-time schoolers, especially as juveniles or during feeding. Most cartilaginous fishes are solitary, but a few, such as hammerhead sharks, mantas, and other rays, sometimes travel in schools. It has been estimated that around 4,000 species, including both marine and freshwater species, school as adults. Schools can be huge, as large as 4,580 million m^3 (161,720 ft^3) in the Atlantic herring (*Clupea harengus*). The members of a school are typically all about the same size. The stationary schools that are common around coral reefs, kelp beds, rocks, and shipwrecks, however, may include members of different sizes or even different species.

Schools function as well-coordinated units, though they appear to have no leaders (Fig. 8.21). The individual fishes tend to keep a constant distance between themselves, turning, stopping, and starting in near perfect unison. Vision plays an important role in the orientation of individuals within a school. In some species, though, blinded fish can school in a coordinated way. These fish probably use the lateral line, olfaction, and sound they emit to keep track of each other. The tight coordination of schooling fishes may break down when they are feeding or attacked by a predator.

Why do fishes school? One explanation is that schooling offers protection against predation. Predators may be confused if, for instance, the school circles a predator (Fig. 8.21*c*) or splits into several groups. It is also difficult for a predator to aim for just one fish in a cloud of shifting, darting individuals (Fig. 8.21*d*). On the other hand, some predators, such as jacks (*Caranx*), are more efficient when they attack schools of prey rather than individuals. It also has been suggested that schooling increases swimming efficiency because the fish in front form an eddy that reduces water resistance for those behind. There is experimental evidence, however, that this is not always the case and that fish do not always align in a hydrodynamically efficient way. In at least some fishes, schooling is advantageous in feeding or mating. There is probably no single reason that fishes school, and the reasons probably vary from species to species.

Migrations Another fascinating aspect of the behavior of marine fishes is **migration,** regular mass movements from one place to another once a day, once a year, or once in a lifetime. Schools of parrotfishes and other fishes migrate daily onshore and offshore to feed. Many open-water fishes migrate several hundred

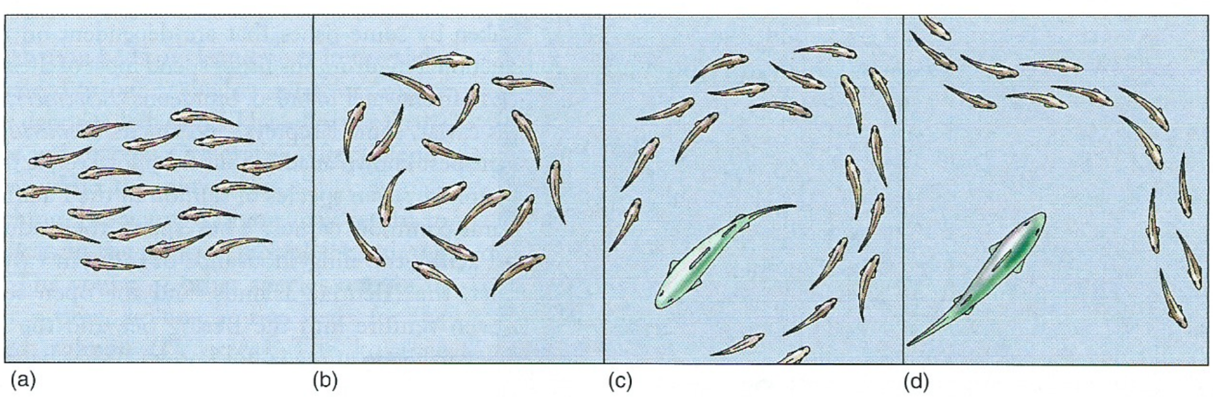


FIGURE 8.21 Fishes follow different recognizable patterns when schooling. Some common patterns include (*a*) traveling, (*b*) feeding on plankton, (*c*) encirclement of a predator, and (*d*) streaming to avoid a predator.

EYE ON SCIENCE

Great White Shark Migrations

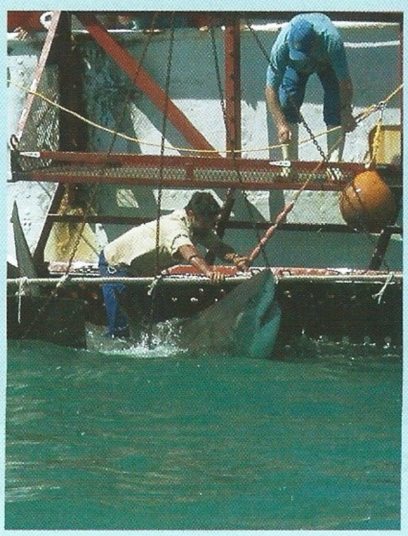
It was long thought that great white sharks (*Carcharodon carcharias*) spend a good part of their lives prowling along coasts hunting sea lions, seals, and large fishes. Current research in several parts of the world has nevertheless shown a new insight: great white sharks surprisingly travel long distances in regular, frequent migrations across the open ocean.

Electronic tags and satellite technology (see "Observing the Oceans," p. 6) have permitted recording the long-term movements of large marine animals such as the great white shark. Individual sharks are tagged by using a long pole while they swim along a boat, and photos of the dorsal fin are taken to record notches and other markings for individual identification. Photos are also taken to determine size and sex. The use of "pop-up" tags is a major advantage. They remain attached to a shark before being released at a pre-programmed time and float to the surface to transmit data on location, depth, and water temperature at previously determined intervals along the route. The data are sent to an Argo environmental monitoring satellite, which relays the information to a lab on land.

Great whites tagged with pop-up tags off the central California coast were tracked to an area 2,400 km (1,500 mi) east of the Hawaiian Islands. The migratory route from California to the central Pacific followed a similar route during five years of tracking. The start of the migration was timed with a decrease in the abundance of sea lions and seals along the coast, suggesting that food was a factor in triggering migrations. Individual sharks remained in the central Pacific for as long as four months before returning to California. It is speculated that sharks gather in the area to feed on marine mammals such as sperm whales and large fishes; some suggested sharks feed on deep-water squids. A different study tracked great whites from off northern Baja California, Mexico, to the same central Pacific location where the California sharks gathered. Sharks returned to the same areas in California and Mexico, thus showing homing behavior (see "Migrations," p. 167).

A similar study recorded the transoceanic migration of a shark (called "Nicole" after actress Nicole Kidman, known for her love of sharks) from South Africa to western Australia and back, a total of about 20,000 km (nearly 12,500 mi), a trip that took under nine months to complete. The estimated minimum speed of this migration was 4.7 km/hr (2.9 mi/hr), not much different from the fastest tunas. Tagging has also shown that great whites undertake long migrations along the coasts of Australia as well as patrolling along the coast.

One unanswered question is the role of long-distance migrations in the reproduction of great whites. So far there does not seem to be a connection with reproduction, but DNA analysis should help identify the genetic makeup of great white populations in different continents for determining the genetic parentage of individuals. How great whites orient during



their transoceanic migrations without any clues from landmasses or islands is another provocative question. Of particular importance is that the discovery of long-distance migrations in the great white shark reveals that the species, which is listed as vulnerable in the IUCN Red List of threatened species (see Table 18.1, p. 420), is particularly menaced while away from coasts where it is legally protected.

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

meters up and down the water column every day (see "Vertical Migration," p. 346). The most spectacular migrations, however, are the transoceanic journeys made by tunas, salmon, and other fishes. We still know little about why fishes migrate, but most migrations seem to be related to feeding or reproduction.

Feeding is one reason behind the migration of open-water species like tunas. Recaptures of tagged fish have provided much information on how far, how fast, and when tunas migrate (see "Swimming: The Need for Speed," p. 345). Though essentially tropical, some species migrate long distances to feed in temperate waters. Such is the case in the skipjack tuna (*Katsuwonus pelamis;* Fig. 8.22) and other tunas. Some sharks are now known to undertake long migrations (see "Great White Shark Migrations," above).

Also amazing are the migrations between the sea and fresh water undertaken by some fishes that are dependent on fresh water for reproduction. **Anadromous** fishes spend most of their lives at sea but migrate to fresh water to breed. Sturgeons (*Acipenser*), whose eggs are eaten as caviar, some lampreys, and smelts (*Osmerus*) are examples. By far the best known anadromous fish, however, is the salmon.

There are seven species of salmon in the Pacific, each known by several common names. They spend their adult lives in the North Pacific, traveling thousands of miles in vast sweeps along the coast, the Aleutian Islands, and the open sea (Fig. 8.22). Some even venture into the Bering Sea and the Arctic Ocean. How they navigate at sea is not known. It has been hypothesized that they use land features at least part of the way. Currents, salinity, temperature, and other water characteristics might

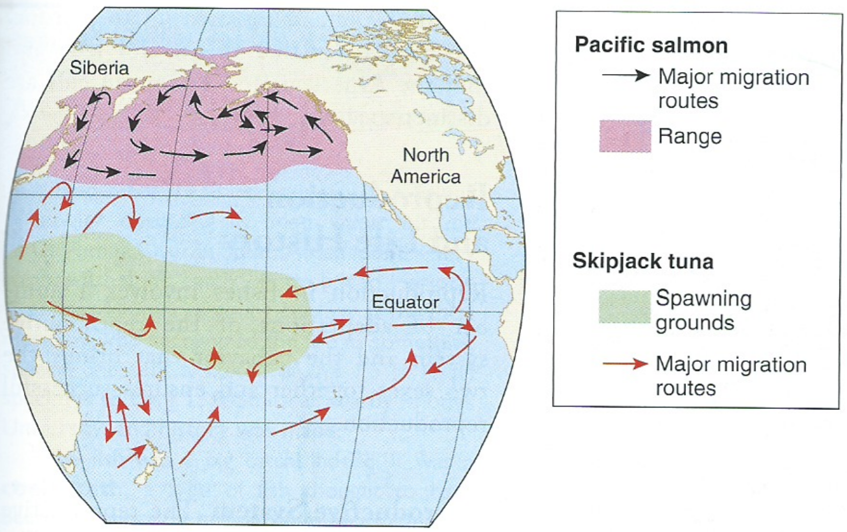


FIGURE 8.22 The skipjack tuna (*Katsuwonus pelamis*), the leading commercial catch among tunas, undertakes extensive migrations that every year take it almost halfway across the globe. The Pacific salmon (*Oncorhynchus*) migrates to spawn only once in a lifetime. Approximate limits of distribution and migration routes indicated are for all seven species of salmon.

provide clues. Other possibilities include orientation to polarized light, the sun, or the earth's magnetic field.

After several years at sea, salmon mature sexually and start migrating into rivers. They are probably guided at first by the earth's magnetic field. They do not feed once they enter fresh water, living instead on stored fat. Their kidneys must adjust to the change from salt to fresh water. Eventually, they reach the exact stream of their birth, sometimes far upstream (Fig. 8.23). The king, or chinook, salmon (*Oncorhynchus tschawytscha*) and chum, or dog, salmon (*O. keta*) reach as far inland as Idaho and the headwaters of the Yukon River.

Salmon find their home streams with remarkable accuracy, using a type of chemical memory. They recognize not only the "smell" of their own stream but also those of other streams they pass along the way. There also is evidence that they respond to chemicals released by other members of their own species. The ability of an animal to find its way back to a home area is known as **homing behavior.**

Salmon spawn on beds of clean gravel in the shallows. The female digs out a shallow nest, or "redd," into which she deposits her eggs. The eggs are fertilized by the male and covered with gravel. After defending the nest for a while, the salmon die.

After hatching, the young salmon may return to sea immediately, as in the pink, or humpback, salmon (*O. gorbuscha*). The young of other species remain in fresh water for a time, as long as five years for the sockeye, or red, salmon (*O. nerka*). The kokanee salmon, a race of this last species, is landlocked and does not migrate to sea at all. This is also the case of the rainbow trout, the landlocked variety of the steelhead salmon (*O. mykiss*). Unlike other salmon, the steelhead and rainbow trout can spawn many times before dying.

One of the biggest hazards Pacific salmon endure is the destruction of their natural environment by humans. Migration routes have been blocked by dams, spawning grounds filled with silt as a result of logging and cattle grazing, and rivers polluted by pesticides (which, among other toxic effects, are suspected of disrupting salmon's sense of smell), fertilizers, and animal waste. Around 11 to 15 million salmon once spawned in the Columbia River system in the northwestern United States. The number has now decreased by 90%, and most of the returning adults were born in hatcheries. Some species, like the sockeye, king, and chum salmon, have been declared endangered in some rivers. Sharp restrictions were imposed on the harvest of salmon along the Pacific coast of the United States, and in 2008 a total ban for the year was imposed in California and Oregon.

The Atlantic salmon (*Salmo salar*) breeds on both sides of the North Atlantic. It migrates across the ocean, mostly off Greenland, before returning to rivers from New England to Portugal. Atlantic salmon sometimes survive after spawning and return to the ocean. Some females have made as many as four round trips. Like their Pacific cousins, populations of the Atlantic salmon in the wild are in serious decline, though they are farmed for food in some temperate regions besides the Atlantic (see Table 17.3, p. 399).

FIGURE 8.23 The journey of Pacific salmon such as these sockeye salmon (*Oncorhynchus nerka*) is an arduous one, indeed. The fish have to swim far upstream, often leaping over rapids and waterfalls. Many fall prey to hungry predators or to the nets and lines of fishers.

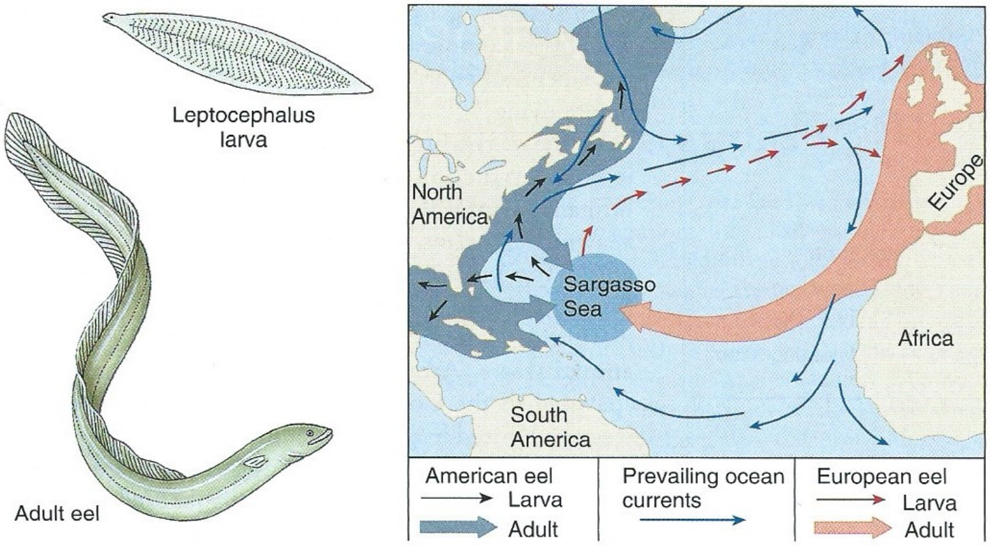


FIGURE 8.24 Two species of freshwater eels, the American (*Anguilla rostrata*) and European (*A. anguilla*) eels, breed in the Sargasso Sea and migrate to rivers in North America and Europe. The return trip of larvae is not precisely known, so the arrows indicate only the most likely routes.

Catadromous fishes have a migratory pattern opposite that of salmon. They breed at sea and migrate into rivers to grow and mature. Several catadromous fishes are known, but the longest migration of any of them is that of freshwater eels (*Anguilla*). There are at least 16 species, including the American (*A. rostrata*) and European (*A. anguilla*) eels.

Both American and European eels spawn in the **Sargasso Sea** at depths of at least 400 to 700 m (1,300 to 2,300 ft) and then die (Fig. 8.24). They spawn at different, though overlapping, periods and locations in the sea. The eggs hatch into tiny, transparent larvae that gradually develop into elongated, leaf-shaped **leptocephalus larvae.** American eel larvae drift in the plankton for at least a year. The juveniles then move into rivers along the Atlantic coast of North America. The leptocephalus larvae of the European eel are believed to spend at least an extra two or three years drifting in the Gulf Stream to reach rivers throughout western Europe. Adults of both species eventually grow to more than 1 m (40 in) in length. Both juveniles and adults are highly valued as food, particularly in Europe. After 10 to 15 years in fresh water, adults turn silver and their eyes become larger. Soon after this, they head out to sea.

The migration of eels back to the Sargasso Sea is not completely understood. There is experimental evidence that they use the earth's magnetic field as a cue for navigation. It has been assumed that European eels follow favorable currents that take them first along the coast of northwest Africa (Fig. 8.24), much like the Portuguese navigators of old (see "Tall Ships and Surface Currents," p. 51).

Some biologists once suggested that the adults of the European eel did not return to the Sargasso Sea at all but died at sea. According to this view, American and European eels were really the same species. Larvae that remained too long at sea simply ended up drifting to Europe. We now know that this is not true and that the American and European eels are distinct species.

Reproduction and Life History

Reproduction in fishes involves a number of adaptations of the reproductive system and the behavior that brings the two sexes together and ensures successful reproduction.

Reproductive System The reproductive system of fishes is relatively simple. The sexes are usually separate. Both sexes have paired gonads located in the body cavity (see Fig. 8.14).

In cartilaginous fishes, ducts lead from the ovaries and testes into the cloaca, which opens to the outside (see Fig. 8.14*a*). Jawless and bony fishes have a separate opening for urine and gametes, the **urogenital opening,** which is located just behind the anus (see Fig. 8.14*b*).

In many marine fishes the gonads produce gametes only at certain times. The timing of gamete production is crucial. Both sexes must be ready to spawn at the same time. Spawning, as well as larval development, must take place during the period with the most favorable conditions. The exact timing of reproduction is especially critical for fishes that make long migrations to breed.

The timing of reproduction is controlled for the most part by **sex hormones.** Sex hormones are produced in the gonads and released in small amounts into the blood. They stimulate the maturation of gametes and may cause changes in color, shape, and behavior before breeding.

The release of sex hormones is triggered by environmental factors such as day length, temperature, and the availability of food. Fishes can be artificially induced to spawn when these environmental factors are controlled or when hormones are injected. This technique is used to increase reproduction in fishes grown for food (see "Aquaculture," p. 396).

A few marine fishes are **hermaphrodites.** Some, like the hamlet (*Hypoplectrus*), are called **simultaneous hermaphrodites** because they can produce sperm and eggs at the same time. Though able to fertilize their own eggs, simultaneous hermaphrodites usually breed with one or more other individuals, ensuring cross-fertilization. One member of a pair of mating hamlets, for example, acts as a male and its sperm fertilizes the eggs released by the other individual. Roles are reversed after fertilization, and the "female" releases sperm to fertilize eggs released by the "male." Hermaphroditism also is found among several deep-water fishes, an adaptation to the depths of the ocean where it may be difficult to find members of the opposite sex (see "Sex in the Deep Sea," p. 374).

EVOLUTIONARY PERSPECTIVE

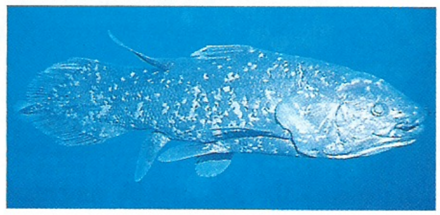
A Fish Called *Latimeria*

In December 1938 the skipper of a fishing trawler operating in deep water off the Chalumna River in South Africa found a very strange fish in his catch. He took it to Marjorie Courtnay-Latimer, a young curator at the local museum, who recognized the fish as something special. She sent a sketch of the 1.5 m (5 ft) specimen to Dr. J. L. B. Smith at nearby Rhodes University, and history was made.

The fish was a big catch, indeed. It was a **coelacanth,** a type of fish thought to have become extinct 60 million years ago. Extinction is not a rare event in evolution, and coelacanths were previously known only from fossils, some at least 400 million years old. They belong to the crossopterygian fishes, a group of fishes that might have given rise to the first land vertebrates. About 375 million years ago a crossopterygian fish with **lobe-fins,** paddle-like bony fins, crawled out of the water and changed life on Earth forever. There is ample evidence that all present-day land vertebrates evolved from crossopterygian fishes (see "When Fishes Stepped on Land," p. 80).

Dr. Smith officially described the fish and named it *Latimeria chalumnae* in honor of its discoverer and the river near which it was caught. Unfortunately, the internal organs of the fish had been discarded by the time Dr. Smith got to it, so nothing was known of its internal structure. A reward was offered for more specimens of the incredible "living fossil," so called because it is similar to no known species other than fossils. It was not until 1952 that a second specimen was caught near the Comoro Islands, between Madagascar and mainland Africa. Ironically, the fish is well known to the natives of the islands. They eat its oily flesh after drying and salting it, and they use its rough skin for sandpaper!

The coelacanth (*Latimeria chalumnae*), a living fossil.



A live Indonesian coelacanth (*Latimeria menadoensis*).

The fish, which is nocturnal in habits, is still very rare. None of the captured specimens has survived more than 20 hours; so little is known about their habits. In 1987 a small submersible was used for the first time to film and observe a live *Latimeria* in its natural environment at depths of 117 to 200 m (386 to 660 ft). Divers have filmed live *Latimeria* off the northeastern coast of South Africa from depths of only 104 m (320 ft) since 2000.

Latimeria is a large fish, up to 1.8 m (6 ft) in length and weighing as much as 98 kg (216 lb). The body is covered by large scales. It feeds on fishes, squids, and octopuses. This living fossil is unique in many ways. It has heavy, stalked fins that have bones as land vertebrates do. The fish appears to stand on the fins, but not to crawl over the bottom with them, as once thought. The pectoral fins can rotate nearly 180 degrees, allowing the fish to swim slowly over the bottom, sometimes standing on its head or with its belly up. Jelly-filled organs on the head may be used to detect electrical fields and thus help in prey location. Little is known about its reproduction. Females bear live young, as many as 26, and the huge eggs (about 9 cm, or 3.5 in in diameter) develop in the reproductive tract, apparently for at least a year.

Latimeria remains a priceless catch, and several aquaria around the world would like very much to capture live specimens. As their value in dollars soars, so do the concerns about the 200 individuals that may still survive in the Comoros. International trade has now been officially outlawed. More recent catches along the Indian Ocean coast of East Africa as far north as Kenya, however, indicate a wider distribution than originally thought. The South and East African specimens are genetically similar, so they are members of the same species.

In 1997 *Latimeria* surprised everybody by turning up in a fish market in Sulawesi, one of the islands of Indonesia, almost 10,000 km (6,200 mi) from the Comoros! A live specimen was taken off the same island in 1998. Though very similar in appearance to the Indian Ocean specimens, DNA evidence showed that the Indonesian coelacanth belonged to a species different from that in the Indian Ocean. The discoverer, Dr. Mark Erdmann, and the Indonesian team that had studied the specimen planned to formally describe the new species in a scientific publication. But a group headed by French scientists went ahead and officially described the Indonesian coelacanth as a new species, *Latimeria menadoensis*. Additional Indonesian coelacanths were filmed in deep water in 2006.

Are there any new coelacanths waiting to be discovered somewhere else?

A variation of hermaphroditism among fishes is **sex reversal,** or **sequential hermaphroditism,** in which individuals begin life as males but change into females **(protandry)** or females change into males **(protogyny).** These changes are controlled by sex hormones but triggered by social cues such as the absence of a dominant male. Sex reversal occurs in several groups of marine fishes, but it is most prevalent among sea basses and groupers (*Serranus, Epinephelus*), parrotfishes, and wrasses. Some rather complicated reproductive strategies have been discovered among these fishes.

In at least some species of anemone-fishes (*Amphiprion*), all individuals begin as males. Each sea anemone is inhabited by a single, large female that mates only with a large, dominant male. All the other fishes that live on the anemone are small, non-breeding males. If the female disappears or is experimentally removed, her mate changes into a female and the largest of the non-breeding males becomes the new dominant male. The new

Sargasso Sea The area of the Atlantic Ocean north of the West Indies that is characterized by masses of drifting Sargasso weed, a brown seaweed.

• Chapter 6, p. 104

Hormones Molecules that act as chemical messengers within the body.

• Chapter 4, p. 65

female can start spawning as soon as 26 days after her sex change. Males of some wrasses form harems of many females. If the male disappears, the largest, dominant female immediately begins to act as a male and within a relatively short period of time changes color and transforms into one that is capable of producing sperm.

Reproductive Behavior Potential mates must get together at the right time to breed. Many species migrate and congregate in specific breeding grounds, as in the salmon and freshwater eels previously discussed. Sharks are usually loners but may come together during the breeding season. Some of them appear to stop feeding at spawning time.

Many bony fishes change color to advertise their readiness to breed. Most salmon undergo dramatic changes. Both sexes of the sockeye salmon turn from silver to bright red, giving rise to another of its common names, the red salmon. In male sockeye and pink, or humpback, salmon, the jaws grow into vicious-looking hooks. Males of the latter species also develop a large hump. Color changes also can be observed in tropical fishes. Many male wrasses, colorful all the time, appear even more spectacular before breeding.

The first step in reproduction is **courtship,** a series of behaviors that attract mates. These behaviors involve an exchange of active displays such as "dances," special postures that display colors, and upside down swimming (Fig. 8.25). Each species has a unique courtship behavior. This is thought to help keep fishes from mistakenly mating with members of the wrong species.

Reproduction in fishes involves many adaptations that help individuals get together for mating. These include migrations, the display of particular colors as sex signals, and courtship behavior.

Some fishes have **internal fertilization** of the eggs, in which the sperm is directly transferred from males to females through the act of **copulation. External fertilization,** the release of gametes into the water, or **broadcast spawning,** is more common in fishes, however.

Internal fertilization occurs mainly in cartilaginous fishes. Unfortunately, not much is known about their sex life. Male sharks, rays, and skates have a pair of copulatory organs, called **claspers,** located along the inner edge of the pelvic fins (Fig. 8.26). The typical approach of a romantic male shark consists of biting his potential mate on the back. The male copulates by inserting his claspers into the female's cloaca. He bites and hangs from her or partly coils around her middle. Some skates mate after the male bites the female's pectoral fins. He presses his ventral surface against hers and inserts the claspers.

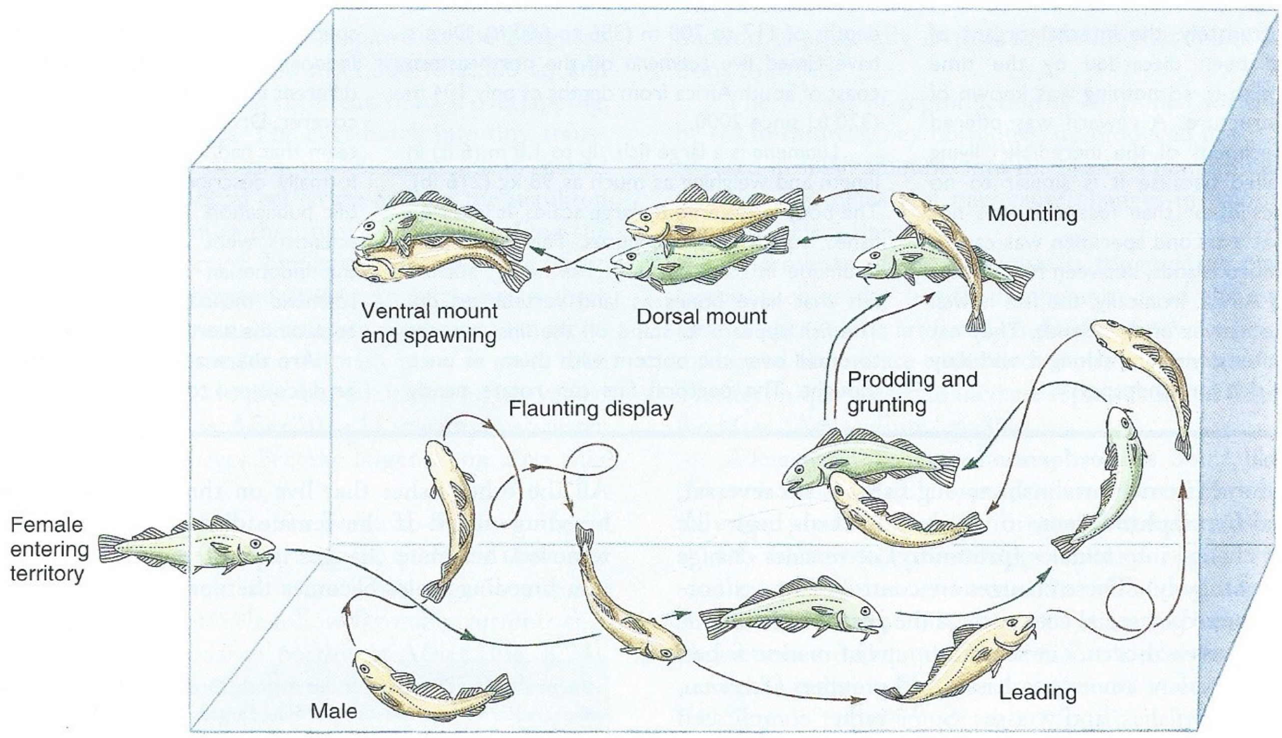


FIGURE 8.25 The Atlantic cod (*Gadus morhua*), once one of the most important food fishes in the world, spawns in large aggregations in the North Atlantic. The two sexes do not spawn indiscriminately but follow a strictly choreographed series of behaviors. The male establishes a territory, and the action starts after an interested female enters his territory. Most of the display is made by the male, which uses fully spread fins, grunting sounds, and a series of swimming behaviors. If the female does not follow the male, he has to start all over again to try to attract another female. The spawning of gametes into the water thus climaxes a series of behaviors that includes visual, sound, and tactile signals.

FIGURE 8.26 Fertilization in cartilaginous fishes is internal, so males must possess some type of copulatory organ. This is the function of the claspers, which are located on the inner edge of the pelvic fins. They are provided with a groove for the passage of sperm. Only one clasper is inserted into the female at a time. The photo shows a male silky shark (*Caracharhinus falciformis*); the claspers of a scalloped hammerhead shark (*Sphyrna lewini*) are shown in the inset.

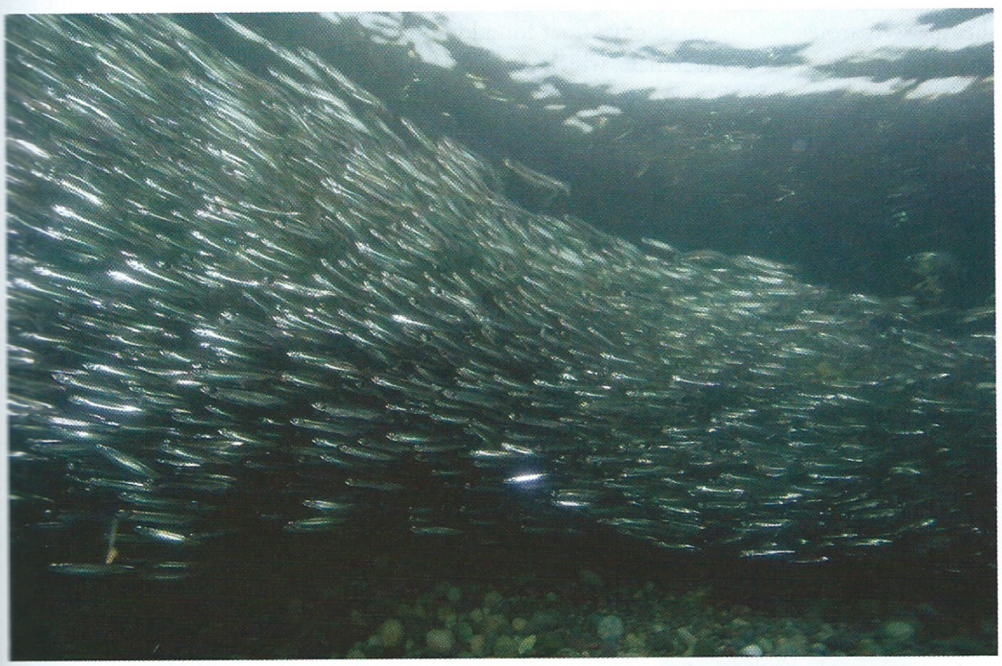


FIGURE 8.27 The capelin (*Mallotus villosus*), from temperate and polar waters of the North Atlantic, comes inshore to spawn in swarms. It typically spawns on gravel beaches.

Open-water fishes (sardines, tunas, jacks, and others) and those living around coral reefs and other inshore environments (such as surgeonfishes, parrotfishes, and wrasses) spawn directly into the water after courtship (Fig. 8.27). Females typically release many eggs. In the Atlantic cod (*Gadus morhua*), for example, a female 1 m (40 in) long can release up to 5 million eggs. The Atlantic tarpon (*Megalops atlanticus*) releases more than 100 million eggs every time it spawns.

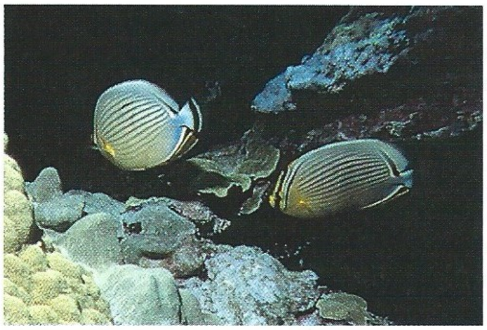
Some fishes, like butterflyfishes, spawn in pairs (Fig. 8.28), others in groups. Individual males may establish territories or aggregate into groups. Groups of males may be approached by single females or by females in groups. Usually, males seek out the females and entice them to spawn via courtship. Two individuals may pair only during spawning time, as in butterflyfishes, or may establish long-lasting bonds.

Eggs fertilized in the water column drift in currents and develop as part of the plankton. Most eggs contain oil droplets and are buoyant. Other eggs sink to the bottom. Herrings deposit their eggs on the surface of seagrasses, seaweeds, and rocks. Lampreys and salmon bury their eggs after spawning. The California grunion (*Leuresthes tenuis*) buries its eggs on sandy beaches during high tides; they don't hatch until the next high tide (see Fig. 3.30).

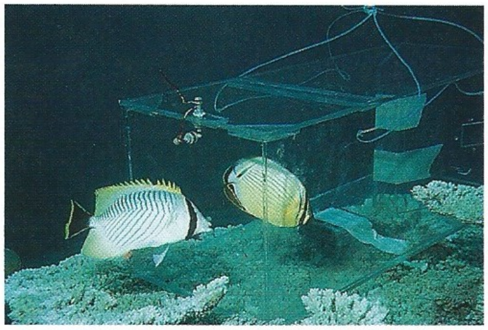
Most of the eggs that are released into the plankton don't survive. Fishes and other marine animals that spawn into the plankton are broadcast spawners that release as many eggs as possible to ensure that at least some hatch and make it to adulthood. Eggs require a lot of energy to produce because they must contain enough yolk to nourish the young until they hatch and can feed.

Fishes that spawn fewer and larger eggs have evolved ways to take care of them. In many damselfishes males establish and defend breeding sites or nests (Fig. 8.29) in holes among rocks or coral, empty mollusc shells, and other shelters—even discarded tires. After spawning, the eggs are retained in the nest and guarded by the males; the females leave after spawning. Males are promiscuous and will guard eggs they have fertilized from different females. Nests also are guarded by males in some gobies, blennies, and sculpins. In the Antarctic plunderfish (*Harpagifer bispinis*), the female prepares a breeding site and guards it for four to five months after spawning. If she disappears or is removed, her job is taken over by another plunderfish, usually a male.

Some fishes go even further and physically carry the eggs after they have been fertilized. Male pipefishes carry the eggs attached in neat rows to their bellies. A male seahorse literally becomes pregnant after the female deposits eggs in a special pouch on his belly. In some cardinalfishes, marine catfishes, and other groups, males brood the fertilized eggs in their mouths (see Fig. 4.21*b*).



(a)



(b)

FIGURE 8.28 Butterflyfishes are among the most colorful of coral reef fishes. Some species use their tiny mouths (see Fig. 8.13*b*) to feed on coral. Adults of some species occur in male and female pairs. (*a*) In the oval butterflyfish (*Chaetodon trifasciatus*) pairs establish territories around coral colonies. (*b*) Experiments using transparent plastic cages provide valuable information on their behavior. Here, a caged oval butterflyfish elicits an aggressive response from an individual chevron butterflyfish (*Chaetodon trifascialis*), an indication that the caged fish has intruded in the territory of the latter. This technique can be used to map the boundaries of territories. Territorial butterflyfishes that live in pairs, like *C. trifasciatus,* fight with other pairs, but fighting occurs only between individuals of the same sex in each pair. Therefore, by using a caged fish of known sex, experimenters can determine the sex of the wild fish, which is normally impossible in the field.

FIGURE 8.29 The yellow tail damselfish (*Stegastes arcifrons*) from the Galápagos Islands, like many other damselfishes, establishes and actively defends breeding sites where females lay their eggs.

Early Development Most fishes spawn eggs and are known as **oviparous.** In oviparous sharks, skates, and other cartilaginous fishes, the embryo is enclosed by a large, leathery egg case (the "mermaid's purse" of skates) that drops to the bottom after spawning (Fig. 8.30). About 43% of all cartilaginous fishes are oviparous. The egg cases are rather large and often have thin extensions that attach them to surfaces. Only a few are laid at a time. The eggs have a large amount of yolk in a **yolk sac** that is attached to the embryo's belly (see photo on page 64). Yolk provides energy for several months of development, a long time by fish standards. As a result, the pup is well developed when it finally hatches.

FIGURE 8.30 An egg of the swell shark (*Cephaloscyllium ventriosum*) containing a one-month-old embryo. The large, white structure is the yolk sac. The egg case has been cut open to show the embryo. The complete egg case of another shark is shown in the inset.

In some cartilaginous fishes the female retains the eggs inside her reproductive tract for additional protection. The eggs develop inside the female, which gives birth to live young. The young are larger than in oviparous species. Such fishes are known as **ovoviviparous.** Most ovoviviparous fishes are cartilaginous. A total of 300 embryos, still in egg cases, were found ready to emerge inside the reproductive tract of a female whale shark. Some rockfishes are among the few marine bony fishes that can be classified as ovoviviparous. Most bony fishes are oviparous and spawn their eggs for external fertilization.

In some ovoviviparous sharks, the embryos rely on other sources of nutrition once they have consumed the yolk. In the sandtiger shark (*Carcharias taurus;* see Fig. 8.3) only two pups, which are large (up to 1 m or 3.3 ft) and active, are born. Each survived in one of the two branches of its mother's reproductive tract by eating its brothers and sisters. When that source of food is gone, they consume unfertilized eggs produced by their mother's ovaries.

Some sharks and rays have embryos that actually absorb nutrients from the walls of the mother's reproductive tract. These sharks are said to be **viviparous.** The surfperches (*Embiotoca*), which are bony fishes, are also viviparous. Their young have large fins that absorb nutrients from the walls of the mother's uterus. Some sharks go further and have evolved to possess what some call a **placenta,** tissue that provides nourishment to the embryo. It is not a true placenta, however, because it develops from the walls of the mother's uterus rather than from the embryo as in the case of the true placenta of practically all mammals, including humans. All viviparous fishes are therefore said to show **aplacental viviparity**.

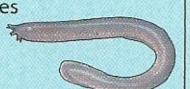
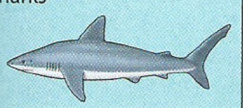
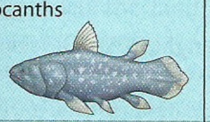
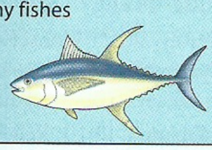
There is now evidence of yet another method of reproduction among sharks. A female bonethead shark (*Sphyrna tiburo*), a small hammerhead shark, gave birth to a pup after three years in an aquarium together with two females of the same species but no males. Though it was possible that the female had stored sperm in her body as the result of sex with a male shark prior to capture, the DNA of the pup matched the DNA of one of the three females with no evidence of DNA from a male. Though very rare among vertebrates, **parthenogenesis,** the development of an egg into a normal embryo without fertilization by sperm, has also been reported in a few bony fishes.

Development of the embryo proceeds rather quickly in most bony fishes. The transparent outer envelope of the eggs, the chorion, is thin, allowing oxygen to diffuse through. The eggs are usually spherical.

The embryo is supplied with nutrient-rich yolk. After one or more days of development, the eggs hatch into free-swimming larvae, or fry. When they first hatch, the larvae still carry the yolk in a yolk sac. The yolk is eventually consumed, and the larvae begin feeding. Many larvae, like the leptocephalus larvae of eels (see Fig. 8.24), do not resemble their parents at all and undergo metamorphosis to a juvenile stage that resembles the adult.

Most marine fishes are oviparous and release eggs into the water. Internal fertilization leads to ovoviviparous or viviparous conditions in some, especially cartilaginous fishes.

Table 8.1 Most Important Characteristics of Marine Fishes

Group	Distinguishing Features	Skeleton	Feeding	Reproduction	Significance in the Marine Environment
Hagfishes 	No paired fins, no scales, exposed gill slits, marine	Cartilaginous skull, no vertebrae, no jaws	Suction by round, muscular mouth with teeth	Oviparous	Predators of dead or dying fishes and bottom invertebrates
Lampreys 	Two dorsal fins only, no scales, exposed gill slits, fresh water or anadromous	Cartilaginous skull, no vertebrae, no jaws	Suction by round, muscular mouth with teeth	Oviparous	Suckers of fish blood or predators of bottom invertebrates
Rays, skates 	Paired fins, placoid scales, pectoral fins greatly expanded, five ventral gill slits, mostly marine	Cartilaginous	Grinding plates to feed on bottom animals or gill rakers to filter plankton	Oviparous, viviparous	Predators of bottom animals or filter feeders
Sharks 	Paired fins, placoid scales, 5–7 exposed and lateral gill slits, mostly marine	Cartilaginous	Teeth in jaws to capture prey or gill rakers to filter plankton	Oviparous, ovoviviparous, viviparous	Predators or filter feeders
Ratfishes 	Paired fins, placoid scales, one pair of gill slits covered by flap of tissue, deep water	Cartilaginous	Grinding plates to feed on bottom invertebrates	Oviparous	Predators of bottom invertebrates
Coelocanths 	Paired lobe-fins, large scales, gills covered by operculum, deep water	Bony	Teeth in jaws to capture prey	Ovoviviparous	Predators
Bony fishes 	Paired fins, cycloid or ctenoid scales (absent in some), gills covered by operculum, marine and fresh water	Bony	Teeth in jaws to capture prey or graze or gill rakers to filter plankton	Oviparous, ovoviviparous, viviparous	Predators, grazers, or filter feeders