Chapter A2: Everything You Ever Wanted to Know about Fish

A2-1 Introduction

Fish are the most numerous and diverse of all vertebrate groups. They go back more than 400 million years and make up over half of all vertebrate species. About 24,600 species in 482 families live in the world today. Experts think that thousands more species are yet to be found.

Fifty-eight percent of the world's fish species live in the sea and 41 percent live in freshwater. This number is striking, since the volume of freshwater is only 1/7,500th that of the oceans. One percent, just over 200 species, move between freshwater and the sea. Most of these 200 species are ***anadromous***, i.e., they reproduce in freshwater but mature at sea. A few species are ***catadromous***, spawning in the sea but maturing in freshwater.

More than three quarters of marine species live on or along the shallow continental shelves. The deep waters beyond, which comprise most of the oceans, have only about 2,900 fish species.

This chapter provides general information on the distribution, anatomy, physiology, and ecology of fish based on information in Wetzel (1983), Nelson (1994), Ross (1995), Moyle and Cech (1996), and Helfman et al. (1997).

Chapter Contents

A2-2 Fish Diversity and Abundance

A2-2.1 Biological Diversity

The behavior, physiology, and morphology of fish are very diverse. Fish eat all conceivable plant or animal food items. Some species form large schools; others have territorial or solitary lifestyles. Fish migrate over short or long distances looking for food or areas to mate. Extreme examples are some species of Pacific salmon, which swim more than 1,880 miles (3,000 km) up the Yukon River to reproduce; or the giant blue tuna, which swims throughout the world's oceans seeking food. Some species can also walk on land or glide in the air.

Most fish are cold-blooded, but some are partially warm-blooded. Most species use gills to get oxygen, but some supplement gill breathing by gulping air. A few will drown if they cannot breathe air. Some fish make venom, electricity, sound, or light. Most fish release sperm and eggs into the water or the bottom with little parental care; others build nests, are live bearers, or mouth brooders. Most fish have fixed sexual patterns, i.e., they are either male or female for their entire lives. A surprising number switch sex at some point in their lives. The majority of species reproduce many times over a lifetime; some die after the first mating.

Fish live from one year to over a century. Adult fish range from a 0.4 inch (10 mm) marine goby to the giant 39.4 ft (12 m) whale shark. Fish shapes range from snake-like to ball-like, saucer-like, or torpedo-like, with many forms in-between. Some species are sleek and graceful; others are ungainly or grotesque. Fins may be missing or are changed for use as sexual organs, suction cups, pincers, claspers, lures, or to serve other functions. Fish can be highly-colored to drab grey. Finally, approximately 50 species lack eyes.

A2-2.2 Distribution and Zoogeography

Fish live in all possible aquatic habitats on the planet. Most are found in "normal" habitats, such as lakes, rivers, tidal rivers, estuaries, and oceans. Within those habitats, fish are found at elevations of up to 17,000 ft (5,200 m) in Tibet, and depths of over 3,300 ft (1,000 m) in Lake Baikal and 23,000 ft (7,000 m) below the ocean surface. Fish live in water ranging from essentially pure freshwater with salt levels close to that of distilled water, to hyper-saline lakes with salt levels over three times that found in the sea. Their habitats extend from caves or springs to the entire ocean, from hot soda lakes in Africa with water temperatures up to 44 ˚C (111 ˚F) to deep-sea hydrothermal vents in the eastern Pacific, and the Antarctic ocean where water temperatures drop to -2 ˚C (28 ˚F).

a. Freshwater

Freshwaters support most of the world's fish species, when one considers the volume of available water. This disparity arises from greater productivity, and isolation.

- Freshwaters are quite shallow on average. Sunlight, which stimulates photosynthesis and increases algal growth, can reach a relatively large part of their volume. In contrast, the oceans have a mean depth of 12,100 ft (3,700 m). Much of the water column is too deep and dark for photosynthesis and stays unproductive. The shallower continental margins, which support most marine species, are an exception.

- Freshwater habitats easily break up into isolated water bodies, creating many distinct "islands" of water over the terrestrial landscape. This isolation promotes the formation of new species over time. Droughts, volcanos, earthquakes, landslides, glaciation, and river course adjustments break up habitats. In contrast, marine habitats are unbroken over great distances and volumes. They are less likely to form barriers, except on a trans-oceanic scale.

In North America, from the Arctic to the Mexican Plateau, freshwaters belong to a zoogeographic region called the ***Nearctic***. This area has approximately 950 known fish species, classified into 14 families. The most species-rich families are the Cyprinids (minnows and related species), Catostomids (suckers and related species), Ictalurids (catfish and related species), Percids (darters and related species), and Centrarchids (sunfish and related species).

The Nearctic region in North America is divided into two subregions, each with many "provinces":

- The *Arctic-Atlantic subregion* includes the Mississippi-Missouri drainage basins, the Great Lakes-Saint Lawrence drainage basin, the rivers that drain the Atlantic seaboard, the Hudson Bay drainage basin, the rivers that drain into the Arctic Ocean, and the Rio Grande drainage basin.

- The *Pacific subregion* contains the Pacific drainages from the Yukon river to Mexico, and the interior drainages west of the Rocky Mountains.

b. Oceans

The distribution of marine fish in the world's oceans suggests four major marine regions, two of which are associated with North America:

- The *Western Atlantic Region* includes the ***temperate*** shores of the Atlantic seaboard, the Gulf of Mexico, the ***tropical*** shores of the Caribbean Sea, and the tropical and temperate shores of the Atlantic ocean along South America. Most of the 1,200 fish species in this region live in the West Indian coral reefs.

- The *Eastern Pacific Region* is split from the rest of the Pacific Ocean by the expanse of water between the continent and the Pacific islands. The fish diversity is less than that of the Western Atlantic, mainly because this region has fewer coral reefs. Several species in the Eastern Pacific Region are closely related to species in the Western Atlantic

Region, since these two regions were once connected until the Isthmus of Panama formed a barrier around 3 million years ago.

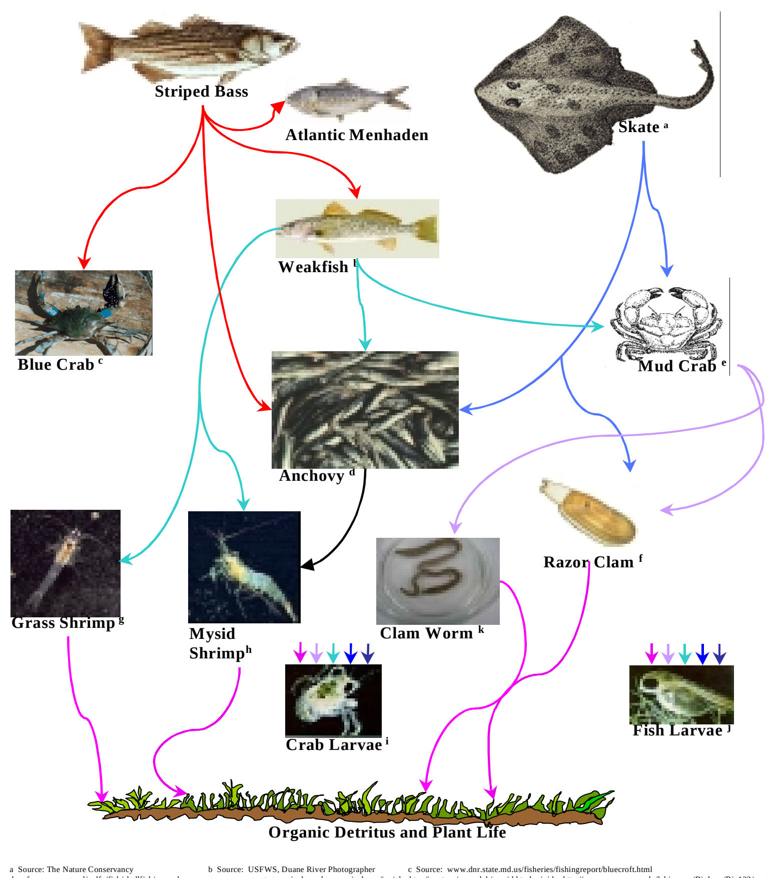
Most fish species live in coral reefs. ***Speciation*** drops in temperate or polar regions, even though the number of individual fish within a species may be quite high. Many species also have relatively small ranges, resulting in a high degree of ***endemism*** (i.e., confinement to relatively small geographic areas). Global distribution of marine fish is hampered by physical barriers (e.g., land and mid-ocean barriers). Distribution of freshwater fish is limited by land and salt water barriers.

A2-2.3 Habitat Diversity

Different variables determine where fish can live and reproduce. These variables include dissolved oxygen levels, water temperature, turbidity, salinity, currents, ***substrate*** type, competition, and predation. Lake-dwelling species may prefer deep, cold, nutrient-poor lakes versus shallow, warmer, nutrient-rich lakes. Species within lakes may seek out open water areas, the shallow or deep ***benthic zone***, or in-shore areas. A similar pattern exists in streams and rivers: some fish prefer swifter waters, whereas others seek pools or quiet backwaters. Regional species assemblages differ between the cooler, swifter, and clear headwaters and warmer, slower, more turbid low-land stretches.

Habitat use changes seasonally or throughout the life of a fish: a species may have eggs and larvae that are ***pelagic***, juveniles that seek inshore nursery habitat, and adults that live in deep, cool, open water. Some fish are flexible enough to thrive in different habitats: trout, sunfish, minnows, or smallmouth bass are equally successful in lakes and streams, as long as conditions are acceptable. Others, such as sculpins, are more selective, and only tolerate a relatively narrow range of conditions.

Figure A2-1: Simplified Food Web Associated with the Bay Anchovy



A2-3 Influence of Fish on Aquatic Systems

Fish are an intrinsic part of aquatic food webs due to their numbers and functional diversity, and their effects as competitors, predators, and prey. Studies show that fish have direct effects on the structure and function of aquatic ecosystems: their presence causes changes in habitat use, prey population structure, population dynamics, and nutrient flows. Large shifts can occur when fish are removed or eliminated.

A fish's lifecycle starts as a fertilized egg. The egg hatches in days, weeks, or even months, based on the species and on water temperature. Larvae are called sac fry for the first several days or weeks of their life until they consume all their yolk. In their first year, they are called yearlings or age 0+ fish. The term juvenile is more generic and refers to sexually immature fish. The age of first reproduction is species-specific: small, shorter-lived species such as minnows mature in one or two years. Larger or longer-lived species such as sharks, sturgeons, or tarpon can take ten or more years to reproduce.

Each fish plays a role in aquatic food webs based on its size, feeding habits, or habitat needs. The term "***game fish***" refers to species wanted by recreational fishers; these fish have high value in a benefits analysis because they are highly valued by mankind. The term, even though not based on biology, normally refers to fish that are predators near or at the top of aquatic food chains. Examples of game fish include pike, largemouth bass, salmon, bluefish, snook, or tarpon.

The term "***forage fish***" or "prey fish" is vague because all fish in their younger life stages are eaten by bigger fish and other organisms. Forage fish often refers mainly to smaller species that feed on plant material or small animals (***zooplankton***, fish eggs or ***sacfry***, small crustaceans, etc.) and are themselves eaten, even as adults. Examples of forage fish include anchovies, rainbow smelt, bluegill sunfish, and numerous minnow species. Their value to humankind in a benefits analysis is less than that of game fish, but their biological value to the ecosystem is even more important, because without them, there wouldn't be any game fish.

Many predators eat fish. Invertebrate predators include diving beetles, dragonfly larvae, jellyfish, sea anemones, squids, cone shells, crabs, and others. Amphibian predators include bullfrogs and other large frog species. Reptilian predators include water snakes, aquatic lizards, turtles, and crocodiles or alligators. Bird predators include albatrosses, auks, cormorants, eagles, egrets, gannets, goldeneye ducks, herons, kingfishers, loons, mergansers, murres, ospreys, pelicans, petrels, penguins, seagulls, skimmers, spoonbills, storks, terns, and many others. Finally, mammal predators include dolphins, seals, sea lions, bears, otters, mink, and raccoons, among others.

This great predatory pressure affects fish distribution. Wading birds, for instance, feed in shallows along weedy edges or quiet backwaters. Small fish measuring less than 1.6 inches (<4cm) are safe there, because they can hide among stems, leaves, rocks, debris, or other structures. In contrast, larger prey fish avoid shallows and seek deeper water out of the reach of wading birds. The deeper water is a relatively safe alternative, because the piscivorous fish that live there are usually ***gape limited*** (i.e., limited by the size of prey fish they can swallow because their mouths can open only so wide).

A2-3.1 Responses by Different Aquatic Receptors to Fish

❖ *Aquatic plants*

Grazing by fish (and other organisms) affects plants, by altering plant biomass and productivity, changing the species composition of the vegetation, and causing plants to invest energy in growth instead of reproduction to replace parts lost to grazing. Less than 25 percent of fish species in temperate streams are true herbivores, compared with 25 percent to 100 percent in tropical streams. In temperate seas, only 5 to 15 percent of species are herbivores, compared with 30 percent to 50 percent in coral reefs.

❖ *Zooplankton*

Fish predation in lakes, ponds, and reservoirs can affect zooplankton by forcing changes in their daily vertical migrations. During the day, zooplankters hide at depth, on the bottom, or in dense vegetation, to avoid being eaten by fish. The zooplankters rise to the surface at night to feed. These migration patterns become less pronounced when the number of planktivorous fish drops.

❖ *Benthic invertebrates*

Benthic invertebrates live on or in the substrate. The population dynamics and behaviors of the benthos can change in response to fish predators. Studies have shown that these changes are subtler than for the more exposed zooplankton. Aggressive benthic feeders, such as bluegill sunfish in lakes or creek chubs in streams, can depress local populations of benthic invertebrates. More often, the presence of benthic feeders causes behavioral changes in prey to reduce predation. For example:

- insect larvae move from the surface of rocks to less desirable (but more protective) spots underneath the same rocks;
- crayfish — a favorite bass prey — move less and hide over bottom types that match their colors and make them less visible when bass are present;

- the amount of benthic ***invertebrate drift*** drops when fish predators are present.

A2-3.2 Ecosystems are Complex — Fish Predation and Trophic Cascades

The effects described above show that predators and prey are linked. The next sections show that fish do not live in a biological vacuum, but interact at different levels with other organisms.

a. Trophic cascades and their effects on biological responses

- A ***trophic cascade*** is a kind of "ripple effect" that occurs when the numbers of organisms at different levels within a food web change as a result of the addition or deletion of predators or prey. For example, fewer zooplanktivores are consumed when top predators are removed, and therefore the number of zooplanktivores rises. In turn, the increased numbers of zooplanktivores deplete populations of zooplankton, reducing predation on phytoplankton and increasing algal blooms. The opposite response can occur if top predators are added (for example, by stocking) or zooplanktivores are removed (for example, by commercial fishing, disease, or I&E).

Such responses have been seen in freshwater systems, as shown by the following experiments:

- A lake contained the trophic cascade of redear sunfish — snails — epiphytes (i.e., algae that grow on submerged plants) - submerged plants. When the sunfish were removed from test plots in the lake, the snail population grew and ate more epiphytes. The absence of epiphytes afforded more light for the plants, which grew better than in areas of the lake where sunfish were present.

- A similar situation occurred in rivers. This trophic cascade included piscivorous fish (large roach and steel head trout) - predators of benthic invertebrates (damselfly nymphs and fish fry) — herbivorous benthos (midges) — filamentous algae. The number of nymphs and fish fry increased when roaches and steel head trout were removed from test plots. The predation rate on midges went up and reduced their population levels. The resulting growth of the filamentous algae was better than that seen in areas where the roaches and trout remained.

b. Trophic Cascades and their effects on physical parameters

Big changes in physical variables can result from the presence or absence of fish predators. Lakes or reservoirs with hard waters and high pH levels can have "whiting events" in the summer. Lake Michigan is such a lake. These events occur when photosynthesis by phytoplankton is very high in the warm surface layers. This activity removes dissolved CO_2, raises the pH of the water even further and causes calcium carbonate ($CaCO_3$) to precipitate (the solubility of $CaCO_3$ goes down as pH goes up) and turns water into a milky, white color. Whiting affects zooplankton feeding, decreases primary productivity, and causes nutrients to sink to the bottom.

In the 1970s, salmonids were stocked in Lake Michigan. By 1983, these fish ate so many zooplanktivorous alewives that predation pressures on zooplankton fell. The lower pressure increased the number of phytoplankton-eating cladocerans and led to more grazing on the phytoplankton. As a result, photosynthetic activity dropped, the rise in pH during the summer was lower than normal, little or no $CaCO_3$ precipitated out of solution, and no whiting event took place in 1983.

The absence of zooplankton-eating fish can affect temperature regimes in small lakes (<20 km^2). Compared to similar lakes with piscivorous fish, such lakes have many zooplankton, which keep the phytoplankton in check. The clarity of the water column increases, light goes deeper, and water temperatures are higher at greater depth. Trophic cascades have been used to control eutrophication in lakes because they can generate strong biological and physical responses. Piscivorous fish are stocked to lower the number of zooplanktivores, enhancing the populations of herbaceous zooplankters who control the algal blooms.

A2-3.3 Effects of Fish on the Cycling and Transport of Nutrients

Fish can affect nutrient cycling. Phosphorus (P) is generally the limiting nutrient for plants in lakes and reservoirs. Fish excrete P as soluble reactive phosphorus (SRP) through their gills or feces. SRP is easily taken up by algae. Studies show that fish excretion is an important source of SRP to lakes and reservoirs and may have direct impacts on primary productivity in those systems.

Fish are found in different trophic levels and feeding groups. They are highly mobile organisms that move nutrients among compartments. In lakes, bottom feeders such as suckers, carp, or catfish stir up sediments while looking for food. Nutrients are resuspended in the water and support algal growth. Some fish species that live in lakes make daily vertical migrations; they transport N and P from the deeper, colder layers to the surface, and release these nutrients through excretion and defecation in areas where most algal growth occurs.

Fish are also major nutrient reservoirs. In certain lakes, up to 90 percent of the P is tied up in bluegill sunfish. This value shows the importance of fish to primary productivity, at least in nutrient-deficient waters: nutrients in fish are released to the water by the gills or feces, or during fish decomposition after death. Studies in a clear, deep lake showed that P released by roaches represented around 30 percent of the P budget of the epilimnion during summer stratification. Fish removal experiments in lakes can also lead to drops in N and P in the water, presumably because the fish increase nutrient levels. Fish biomass loss from emigration, fishing, or other ways (including I&E) can affect nutrient balances, hence primary productivity.

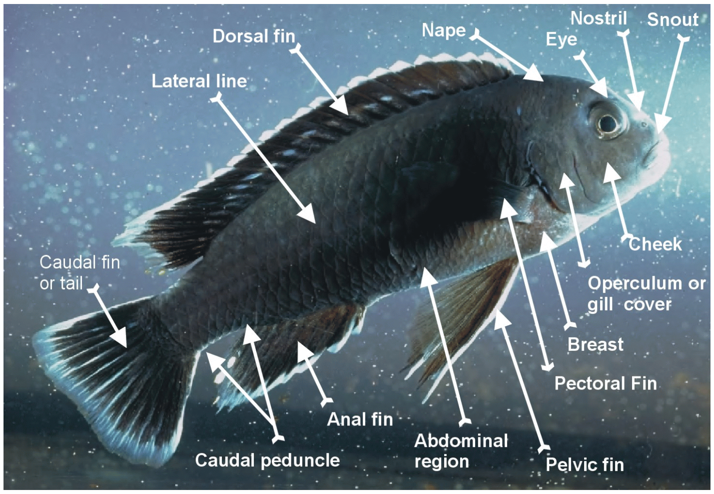
Fish tie different ecosystems together, particularly species that spend part of their lives in freshwater and part at sea. Such fish move large amounts of nutrients when they migrate between habitats. Prolific species, such as menhaden or herring, are prey for larger piscivorous fish in coastal areas and are major sources of nutrients. The gulf menhaden , an abundant species in Gulf estuaries, is a case in point. The fish spawn off-shore in late winter. Their larvae enter estuaries to feed. Juveniles grow by a factor of 80 over a nine-month period; they return to the Gulf in late fall to mature. Each year, an estimated 5 to 10 percent of the primary productivity in the salt marshes and estuaries is exported into the Gulf in the form of menhaden. Up to 50 percent of the total N and P lost annually from these habitats does so in the form of migrating menhaden. The loss in one habitat is a gain for another, because menhaden are a major source of prey. The carbon in these fish represents 25 to 50 percent of off-shore production in the Gulf. Other fish species with similar lifecycles all along our coastal habitats help move energy, nutrients, and carbon across aquatic ecosystems.

In conclusion, the links and feedback loops in aquatic food webs make it difficult to predict what effects could result from the loss of fish from such systems. The examples above remind us that every action leads to a reaction, some of which are unpredictable but can have large effects. Thus, losses of impinged and entrained organisms from the local population can have cascading effects throughout the food web.

A2-4 Exterior Fish Anatomy

Most people can recognize a fish. Its external shape, the structure and position of its mouth, the location of fins, or the presence of spines are a few of the characteristics that vary among species. The long evolutionary history of fish has led to many changes that help fish use all aquatic environment habitats. Some basic patterns are present in the exterior anatomy of most fish species. These are discussed below.

Figure A2-2: Exterior Fish Anatomy



The external shape of a fish reflects its lifestyle and habitat use. For example, the lifestyles of tuna and flounders have changed the "typical" fish body shape. Tuna migrate and hunt throughout the world's oceans. They have streamlined bodies with strong muscles and a specially-shaped tail to swim fast and catch prey. The largest members of this group, such as the bluefin tuna, are even partially warm-blooded to raise their endurance and speed. Flounders, on the other hand, are flat and move less: they spend much time on the ocean floor buried in the sand. They catch molluscs, worms, or fish that swim by.

Figure A2-2 details a fish's exterior anatomy and the rest of Section A2-4 describes the major elements of exterior fish anatomy. Green underlined words refer back to the corresponding figure. The section focuses on those elements that may be important to impingement or entrainment. A basic knowledge of scales, for example, may help in understanding survival in fish that have lost their scales from I&E.

A2-4.1 Fish Shapes

The "typical" fish is long and cigar-like. Six general body shapes have developed around this basic design depending on the species' lifestyle and habitat preferences:

- **Rover-predators** are streamlined, with well-spaced fins along the body to provide stability and maneuverability. These fish are always mobile looking for prey. Examples include bluefin tuna and ***pelagic*** sharks.

- **Lie-in-wait predators** have long bodies, flattened heads, and large mouths. Their ***dorsal fins*** and ***anal fins*** are located far back on the body and their ***caudal fin*** is large. The size and place of most of their fins provide quick, forward thrust needed to catch prey. Their colors and secretive behavior make them blend into their surroundings. These fish lie in ambush and capture prey by quick-burst swimming. A typical example of a lie-in-wait predator is the pike.

- **Surface-oriented fish** are smaller, with an upward-pointing mouth, a flattened head, large eyes, and a dorsal fin located toward the tail. Their shape lets them capture small prey living below the water surface. Examples of surface-oriented fish include mosquito fish and brook silversides.

- **Bottom-dwelling fish** generally have a small or nonexistent ***air (e.g. swim) bladder***. They spend much time foraging or resting on the bottom. Examples are rays and skates, which are flattened dorso-ventrally; and flounders, which lie on their sides.

- **Deep-bodied fish** are usually flattened sideways, with a body depth measuring at least one-third of their length. Their dorsal and anal fins are long and the ***pectoral fins*** are placed high on the body, directly above the ***pelvic fins***. Deep-bodied fish tend to have a ***protrusible*** mouth, large eyes, and a short snout. Many have spines that increase their ability to escape predators, but at the expense of speed. Sunfish are examples of deep-bodied fish.

- **Eel-like fish** have long bodies, blunt or wedge-shaped heads, and tapered or rounded tails. Their pelvic fins are small or missing. Such fish are well adapted to entering small crevices and holes in reefs or rock formations. Examples include the American eel and the murray eel.

A2-4.2 Skin and Scales

Skin covers the entire body of a fish. It protects against micro-organisms and helps regulate water and salt balances. It also has the pigment cells that give fish their colors. The outer skin layer is the ***epidermis***: it is thin and lacks blood vessels but is replaced as it wears off. The ***dermis*** is the inner, thicker layer, from which the scales grow. Much mucus is released by mucus glands in the dermis. Mucus covers the fish with a protective layer: it cleans body surfaces, prevents the entry of pathogens, helps regulate salt balances, and reduces friction.

Most fish are covered with scales. Some fish are scaleless, others are partially covered. Differences may be big even in closely-related species: the leather carp is scale-less, the mirror carp is partly covered with scales, and the common carp is fully covered with scales. Scale-less species generally have a tough, leathery skin to compensate.

Scales are thin, calcified plates that grow out of the dermis and protect the skin. They usually overlap like roof shingles and are known as ***imbricate scales***. Another type of scale, ***mosaic scales***, fit closely together like a mosaic but do not overlap; adjacent scales may touch, or they may be separated by a small space. The scale structure also varies by fish group: sharks, skates, and rays are covered with ***placoid scales*** (or ***dermal denticles***), which give these fish the rough feel of sandpaper. Higher, bony fish, such as sunfish or minnows, are covered by smoother ***leptoid scales***. Scale and mucus loss make fish more vulnerable to infections.

Scales are colorless; color comes from cells called ***chromatophores*** found in the dermis. Some of these cells contain pigments that produce the bright colors seen in fish. Others create various color hues (such as the typical "metallic" coloration in some fish species) by scattering or reflecting light.

Mechanical injuries from impingement and entrainment can abrade the epidermis, dermis and scales, removing them. This causes increased susceptibility to infection and osmotic stress. Freshwater fish will suffer from excessive water uptake, while saltwater fish will lose water (Rottmann et al., 1992). Abrasion can also cause a reduction in the lethal shear threshold of a fish, creating a greater susceptibility to injury or mortality from the shear forces created by spatial differences in the velocity of moving water ([22024]).

A2-4.3 Fins

Swimming is a challenge because water is not a solid material, but flows upon impact. Deep-bodied fish tend to fall over on their side, because the water provides no support. The body of a fish also shifts sideways as it swims. Fish have developed several strategies, including fins, to lend stability and maneuverability for swimming more efficiently through the water. Fins are bony or ***cartilaginous rays*** projecting from the fish's body, and which are connected by a thin membrane. Some of those rays are articulated and are called ***soft rays***. Others are stiff and are known as ***spines***. Many fish incorporate soft rays and spines in their fins to provide flexibility and protection. Some species also have poison glands attached to the base of hollow spines to protect against predators.

Fins have many roles: they are used to swim and maneuver but also serve as rudders, balancers, defensive weapons, feelers, sexual structures, sucking disks, and prey or mate attractors. They have many shapes, colors, and lengths, and are found in different locations on the body. Fins come in two varieties: ***paired fins*** and ***vertical*** (or ***median***) ***fins***.

a. Paired fins

Paired fins include the ***pectoral fins*** and ***pelvic fins***, which are ***ventral fins*** found at the bottom of the body (compared to dorsal fins, found on top of the body). Pectoral and pelvic fins resemble the four limbs of the higher vertebrates: the pectoral fins are the forelimbs and are attached to the shoulders; the pelvic fins represent the hind limbs. Neither fin type plays a major role in locomotion; they prevent the body from pitching and rolling and to help to brake forward motion.

❖ ***Pectoral fins***

Pectoral fins are located behind the gill openings. They provide maneuverability, but also balance the body at low swimming speeds. Pectorals can have different shapes and functions: flying fish have large pectoral fins to help them soar in the air; mudskippers have modified pectoral fins for crawling on land; and sea robins use the three front rays of their pectoral fins as feelers.

❖ ***Pelvic fins***

Pelvic fins are located on the underside of the body but vary in their placement: they may be found in front of the pectorals (e.g., in cods, pollock, or winter flounder), below the pectorals (e.g., in largemouth bass, Atlantic croakers, or darter goby), or in the middle of the body (e.g., in salmon, American shad, herring, or striped mullet). The pelvic fin is used to stop, hover, maneuver, and balance. Pelvic fins can become specialized. Some species have fused pelvic fins, which form a suction disk for clinging to rocks and coral. In male sharks, the pelvic fins form claspers, which serve as sperm cell conduits.

Either one of these fin types may be absent in fish. Eels lack pelvic fins but have fused dorsal, caudal, and anal fins (see discussion below). Lampreys lack pectoral fins. Generally, however, pelvic fins are much more likely than pectoral fins to be absent.

b. Vertical fins

Vertical fins are found along the centerline of the body, at the top, bottom, and back of a fish. ***Dorsal fins***, ***anal fins***, and ***caudal fins*** are vertical fins found on most fish. Their roles include locomotion, protection, and balance.

❖ ***Dorsal fins***

Dorsal fins are found on top of the body and consist of one or two (and rarely three) separate fins. They help prevent the fish from turning over in the water. Many species incorporate stiff spines in their dorsals to protect against predators. The dorsal fin may be followed by the adipose fin, a fleshy outgrowth with no rays, typically found in salmonids and catfish. Mackerellike fish have small, detached finlets consisting of a single ray behind their dorsal (and anal) fins. Other species have highly modified dorsal fins: remoras have a sucker disk used for attaching to sharks, sea turtles, and other large marine animals. Angler fish have a modified dorsal fin ray that bears a fleshy, moving lure used for attracting prey.

❖ ***Anal fin***

The anal fin is found on the belly of the fish behind the vent, or anus. It is usually a single fin (rarely two) used in balance. Many species include stiff, sharp spines to protect against predators. The anal fin is absent in rays and skates, which move about and feed close to the bottom. (Contrary to rays and skates, which have a depressed body shape, flatfish actually lie on their sides and have normal anal fins.) Anal fins also serve other purposes; in male mosquitofish, the anterior rays of the anal fin have joined into a single structure used to transfer sperm to the female.

❖ ***Caudal fin***

The caudal fin is at the back of the fish and serves mainly to aid in locomotion. Swimming behavior shapes the caudal fin. Some rover-predators, such as tuna and marlin, have a stiff, quartermoon-shaped forked tail attached to a narrow ***caudal peduncle***. The deeper the fork, the more active the fish. Deep-bodied fish and most surface- and bottom-oriented fish have rounded, square, or only slightly-forked tails. A few fish, such as sea horses, lack a caudal fin.

A2-4.4 Mouth and Dentition

The shape, size, and position of the mouth and teeth reflect the fish's habitat and diet. The mouths of bottom-feeding fish, such as carps, suckers, or catfish, generally point downward. In extreme cases, the mouth is tucked underneath the fish, as in rays, skates, and sturgeons. The mouth of surface-oriented fish, such as killifish, mosquitofish, and Atlantic silversides, points upwards. Most fish, however, have a ***terminal mouth***. Mouths can become highly specialized, with shapes ranging from long, tube-like, probing structures to large, parrot-like beaks.

Fish do not chew their food; their teeth grab and hold prey until it can be crushed, torn apart, or positioned to be swallowed. Predators, such as sharks, barracudas, and piranhas, have rows of highly-developed teeth. Most species have teeth that look alike and are packed along the inner rim of the lower and upper jaw. Teeth typically point inward to prevent prey from fleeing after capture. Some predators, including pikes and pickerels, also have teeth on their tongues, gill arches, throats, and the roofs of their mouths. Fish that strain the water for plankton or eat plants have few well-developed teeth. Species that crush coral or clams have fused teeth in the form of a cutting edge, crushing plates, or broad, blunt teeth arranged like cobblestones. These species include parrot fish or skates and rays. The number of teeth in fish varies greatly and ranges from 0 to more than 10,000.

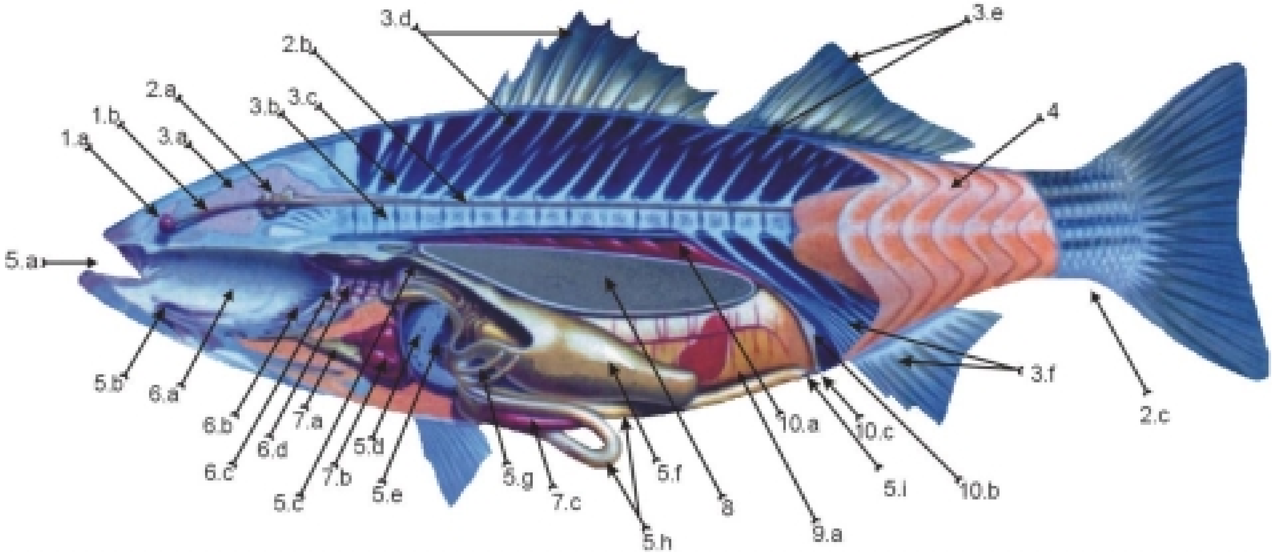
A2-5 Interior Anatomy

Section A2-5 discusses various components of the interior anatomy of a fish. Terms in this section that are green and underlined are glossary terms that also refer to Figure A2-3 which diagrams many of the internal organs of the striped bass.

The internal anatomy of fish varies less than their external anatomy. All vertebrates share many structures, such as a central nervous system or an internal skeleton. Other structures are unique to fish (e.g., ***air or swim bladders*** (Figure A2-3) for ***buoyancy*** control and internal gills for gas exchange and salt regulation). This section outlines basic features of the internal anatomy of fish. Rather than in-depth review , this section provides a basic understanding of the structure and function of the major organ systems in fish.

This knowledge is important because the systems discussed here may play a role during impingement or entrainment. For example, (1) impinged fish may suffocate if they cannot pass water over their gills due to high water pressures;
(2) anadromous fish adjusting to different salt levels in the water during migrations may be more vulnerable than resident species to the stresses of impingement; and (3) the air or swim bladder of larval fish may be damaged when they undergo rapid pressure changes within the cooling system.

Figure A2-3: Interior Fish Anatomy



Source: EPA, based on a drawing by Jack J. Kunz, National Geographic Society, 1969

1. Olfactory System
    - 1.a Nasal Capsule
    - 1.b Olfactory Nerve

2. Nervous System
    - 2.a Brain
    - 2.b Spinal Column
    - 2.c Lateral Line

3. Skeletal System
    - 3.a Cranium/Skull
    - 3.b Vertebra/Backbone
    - 3.c Neural Spines
    - 3.d 1st Dorsal Fin Spines & Pterygiophore
    - 3.e 2nd Dorsal Fin Spines & Pterygiophore
    - 3.f Anal Fin Spines and Support

4. Muscle Segment (myomere)

5. Digestive System
    - 5.a Mouth
    - 5.b Tongue
    - 5.c Esophagus
    - 5.d Liver
    - 5.e Gall Bladder
    - 5.f Stomach
    - 5.g Pyloric Caeca
    - 5.h Intestines
    - 5.i Anus

6. Respiratory System
    - 6.a Buccal Cavity
    - 6.b Gill Rakers
    - 6.c Gill Arches
    - 6.d Branchial Cavity

7. Circulatory / Cardiovascular System
    - 7.a Ventral Aorta
    - 7.b Heart
    - 7.c Spleen

8. Air Bladder

9. Reproductive System
    - 9.a Ovary

10. Excretory System
    - 10.a Kidney
    - 10.b Bladder
    - 10.c Urinary Duct/Urogenital Opening

A2-5.1 Skeletal System

The internal skeleton holds together and protects the soft, internal organs, helps maintain the proper body shape, and serves as an attachment or leverage point for ***striated*** (i.e., skeletal) ***muscles***.

a. Types of skeletons

Fish belong to three broad groups, based on skeletal differences:

❖ *Agnathans*

Agnathans, the jawless fish, are the most primitive of all fish. Most species became extinct 350 million years ago, except for the eel-like hagfish and lampreys. Hagfish live in the ocean and scavenge dead fish or other vertebrates. Lampreys live both in marine and freshwater environments; some species parasitize other fish. Agnathans lack jaws; they also lack a true vertebral column, ribs, scales, paired appendages, and other skeletal features typically found in more modern fish. Instead of true hollow ***vertebrae*** (Figure A2-3), hagfish and lampreys have a flexible ***notochord***, a long, cartilaginous rod that acts like a primitive backbone.

❖ *Chondrichthyes*

Chondrichthyes, the ***cartilaginous*** fish, include sharks, rays, skates, and the less familiar but striking Chimaeras. These fish do not have true bone; instead, their skeletons are made of cartilage combining hardness and elasticity. Unlike bone, cartilage usually does not mineralize (there are exceptions), but instead consists of a flexible matrix made of fibers meshed in a protein-like material. Typical Chondrichthyes are also distinct from bony fish for other reasons, including: (1) lack of a air/swim bladder; (2) presence of a solid braincase instead of one with many pieces of bone; (3) individual external gill openings instead of a single combined opening; (4) primitive fin structure; and (5) tooth-like scales.

❖ *Osteichthyes*

Osteichthyes, the bony fish, include all other living fish species. The Osteichthyes have a bony skeleton; notable exceptions include primitive bony fish, such as sturgeons or paddlefish, which have only partly ***ossified*** skeletons. Bony fish have gills in a common chamber covered by a movable bony ***operculum*** (see Figure A2-2), and fins supported by bony rays radiating from the fin base. They usually have a gas bladder to provide buoyancy. The ***teleosts*** are the most successful bony fish; most aquarium, commercial, and recreational species belong to this group. Teleosts comprise more than 30,000 species and subspecies.

b. Major components

The major components of the internal skeleton in modern fish include the following:

- The **backbone** replaces the notochord of the jawless fish and consists of interlocking hollow vertebrae that run from the back of the ***skull*** (Figure A2-3) to the tail. The ***spinal cord*** (Figure A2-3), which starts in the brain and runs through the backbone, is also protected by it. The number of vertebrae range from 16 to more than 400, depending on the fish species. Each vertebra has an upward-projecting spine called the ***neural spine*** (Figure A2-3). The vertebrae found behind the abdominal cavity may also have one or more downward-pointing spines (the ***haemal spines***).

- The **skull** is a complex structure in the head region. Its major part is the ***cranium*** (Figure A2-3), or braincase, which protects the brain and several sense organs. The skull is also an attachment point for the lower jaw, the backbone, and the shoulder and ***pelvic girdles***. In sharks and related fish, the skull does not have sutures. The skull of bony fish consists of many fused bones.

- The **ribs** or ***spines*** (Figure A2-3) are loosely attached to the vertebrae and surround the fish's abdominal cavity. They are small projections in cartilaginous fish, but are fairly well-developed in bony fish. Unlike in terrestrial vertebrates, fish ribs play no part in breathing. They instead transmit muscle contractions during swimming and frame the body. Fish also lack a breastbone to create a rigid rib cage.

- The ***fin spines*** (Figure A2-3) are spine-like bones not directly connected to the rest of the skeleton. They anchor both dorsal and ventral fins into the muscles through connecting structure called ***pterygiophores*** that reach toward or may intertwine with both the neural and haemal spines of the vertebrae.

A2-5.2 Muscle System

Muscles comprise one-third to one-half of the mass of an average fish. The activity of the nervous system has little consequence except through its action on muscles, which are used both to swim and to aid digestion, nutrition, secretion, and circulation. Muscles exert their force by contracting. If a muscle is attached to different places on the skeleton, the contraction creates a pull, resulting in movement. Two major types of vertebrate muscle tissue exist:

- **Smooth muscle**, the simpler of the two, is under involuntary control. It is found in the lining of the digestive tract, where it provides the slow contractions needed to advance food. It is also found in the ducts of glands connected to the gut and the bladder, as well as in blood vessels, genital organs, and other locations (the heart consists of highly modified smooth muscle). Although it plays a major role in the well-being of fish, smooth muscle is not involved in swimming.

- ***Striated muscle*** (Figure A2-3), forming the "flesh" of the fish, is under rapid, voluntary control. These muscles are large, well-formed structures; their main role is in swimming. Striated muscles are also used to move eyes, jaws, fins, and gill covers.

The biggest muscle mass in fish is the ***axial musculature***, which runs from head to tail on both sides of the body. It is arranged in repeating, W-shaped, overlapping segments called ***myomeres***. A tough membrane connects each myomere to its neighbor. An additional membrane, called the ***horizontal septum***, divides the myomeres into a dorsal and ventral half.

The fish creates a wave along its flanks by contracting opposite ***muscle segments*** (Figure A2-3). The wave gains speed as it travels backwards and causes the tail to thrust against the resistance of the water, thereby moving the fish forward. There is little specialization in the axial musculature. One exception are the muscles used for moving the pectoral and pelvic fins. Each fin has two opposing muscles: one extends the fin, the other depresses it.

A2-5.3 Major Sense Organs

The sense organs in fish have many uses, including orienting the animals and detecting electrical, mechanical, chemical, thermal, and electromagnetic signals from their surroundings. The nervous system is split into two main parts: the ***central nervous system*** (CNS) and the ***peripheral nervous system*** (PNS). The CNS includes the brain and spinal cord. The PNS consists of paired nerves that run outward from the CNS and connect to other areas in the body. One function of the nervous system is to tie ***receptor cells***, such as the eyes or lateral line, to ***effector cells***, such as the skeletal muscles. Receptor cells detect outside signals; effector cells create a response. Another part, the ***visceral nervous system***, serves the gut, circulatory system, glands, and other internal organs.

This section discusses the structure and function of the organs tied to olfaction, taste, equilibrium/hearing, vision, and the lateral line.

a. Olfaction

Many fish have a keen sense of smell. Certain shark species can detect the odor of blood over great distances in the ocean. The ***olfactory epithelium*** is found at the bottom of specialized holes called ***nasal pits*** located in the snout. Unlike the noses of terrestrial vertebrates, the pits do not open into the ***buccal cavity*** (Figure A2-3). Each ***olfactory cell*** connects to the ***olfactory bulb*** of the brain via nerves. The olfactory cells project rod-like extensions into the nasal pit. These extensions detect the odor molecules. Little is known about the exact processes that generate the sense of smell in fish.

b. Taste

The taste cells are grouped in clusters called ***taste buds***. Each cluster has 30 to 40 taste cells connected to nerve fibers. Taste buds are usually found in small depressions. Each sensory cell has a hair-like projection, which may extend to the surface of the epithelium via the ***taste pore*** and detect taste. Fish can detect sourness, saltiness, bitterness, and/or sweetness.

All fish do not experience taste in the same way. Most have taste buds in their ***mouth*** and ***pharynx***, and can therefore taste to one degree or another. Some, like the bullhead catfish, also have tastebuds over their entire body surface. Others, such as sturgeons and carp, have taste buds on oral feelers to facilitate finding food in mud or murky waters. Still others have taste buds covering their heads.

c. Equilibrium and hearing

Fish do not have the features of hearing found in terrestrial vertebrates (i.e., ear lobes, ear canals, ear drums, ear ossicles). The basic ear structure in fish and all higher vertebrates is the ***inner ear***, a paired sensory organ found in the skull. This structure originally evolved as an organ of equilibrium and is still used as such by all terrestrial and aquatic vertebrates. The ability to hear evolved later.

The inner ear in fish consists of sacs and canals that form a closed system containing a liquid called an ***endolymph***. Some of the internal surfaces of the sacs and canals are lined by a tissue called the ***macula***. The sensory cells that make up the macula resemble the neuromasts found in the lateral line system discussed below. These cells connect to auditory nerves in the brain. Calcium carbonate crystals are deposited on top of the macula and combine to form ear stones called ***otoliths***. Depending on the tilt of the head, the acceleration, or the rate of turning, the otoliths contact the sensory cells in different ways, causing specific patterns of nerve firings. The CNS interprets these signals and provides data to the fish on its orientation and movement through space.

The inner ear also captures sound waves. Sound waves carry farther in water than in air and are therefore a source of information to fish. Whereas cartilaginous fish (e.g., sharks, ray, skates) respond only to very low vibrations, most bony fish hear a range of sounds. Fish do not have external hearing structures; sound is believed to pass through the skull into the inner ear. The vibrations cause the otoliths to shake, generating the effect of hearing.

Sound must generate head vibrations for fish to hear. Some fish have "hearing aids" to better capture sounds. These aids rely on the gas in air/swim bladders to amplify the vibrations of sound in water. The swim bladder in herrings has an extension that reaches forward and carries vibrations directly to the inner ear. Catfish and carp use a different method: bony processes of the anterior vertebrae form a chain called the ***Weberian ossicles***, which connect the swim bladder to the head region. These modifications show the importance of sound to fish.

d. Vision

The basic anatomy of fish eyes resembles that of other vertebrates. The ***cornea*** is the outermost layer, through which light enters the eyeball. The cornea is followed by a ***lens***, which serves to bend and focus the light rays on the ***retina*** in the back of the eye. Muscles attached to the lens allow fish to focus on nearby or far away objects. ***Ocular fluid*** fills the interior of the eye and the space between the cornea and lens. Fish have evolved a ***tapetum*** to let the eye catch more light. This is a highly reflective tissue that mirrors the light back onto the eye. Unlike terrestrial vertebrates, fish lack a pupil to control the intensity of the incoming light.

The retina in fish is composed of ***rods*** and ***cones***, which are light-gathering cells containing ***visual pigments***. Rods have more pigments than cones and are more sensitive to dim light. Cones work only at higher light levels and are usually missing in fish that live in low-light habitats, such as the deep sea. Different pigments have distinct molecular structures and are sensitive to specific wavelengths. When light hits visual pigments, a chemical reaction is started that results in nerve impulses. These are carried by the ***optic nerve*** to the brain for processing.

Fish have adapted to deal with the unique optics of water and the different light conditions that exist in aquatic environments.

❖ *Refraction*

Refraction refers to the bending of light as it passes from one medium to another, such as from air to water or from water to tissue. The cornea and ocular fluids of fish do not refract light. Fish lenses are good at bending light, and make images free of aberrations or distortions by changing the refractive properties of the tissues within the lens. Light passing through the lens follows curved paths to form sharp images on the retina.

This arrangement is a problem when fish need to focus on nearby or far away objects. Mammals focus by changing the curvature of the lens. Fish cannot do that. Most fish move the lens toward or away from the retina along the optical axis. As a general rule, freshwater species accommodate less than do marine species; useful vision is more limited in the more turbid waters of lakes and rivers, compared to ocean water.

❖ *Light absorption*

Water's light absorption properties change with depth. Longer wavelengths (reds and greens) are quickly removed at the surface; only shorter wavelengths (blues) go farther down. Deep water fish have visual pigments sensitive to blue light. A change in spectral quality with depth affects fish that move between the seas and inland waters. Adult salmon in the ocean, for example, have rod pigments that best absorb in blue end of the spectrum. As the fish migrate into shallower freshwater, their pigments are gradually replaced by new ones that are more sensitive to the redder end of the spectrum.

❖ ***Color vision***

Fish can see colors if they live in relatively shallow or clear water. Consequently, numerous tropical fish species display brilliant colors.

e. Lateral line

Most fish have a "***lateral line***"(Figure A2-3) running along their flanks from head to tail. The lateral line provides spatial and temporal information. It is so sensitive that blinded fish can locate fish or other nearby objects. A fish can also feel the motion of its own body relative to the surrounding water: as it approaches an object, the pressure waves around the fish's body are slightly distorted. The lateral line detects these changes and enables the fish to swerve. Low frequency sound waves generate pressure waves in the water column, which are also detected by the lateral line.

The lateral line can be single, double, or forked, consisting of thousands of tiny sensory organs that lie on the skin surface within small pits. These sensory organs connect to the brain. At the bottom of each pit is a ***neuromast***, a small structure that detects vibrations and water movement around the fish. The neuromast consists of sensory hairs enclosed in a gel-filled capsule that protrudes into the water. The neuromasts send out electrical impulses to the brain. The enclosed sensory hairs bend when a pressure wave distorts the gelatinous caps. This movement either increases or decreases the frequency of nerve impulses depending on the bending. It is this change in frequency which is sensed by the fish.

A2-5.4 Circulatory System

The circulatory system transports and distributes various substances including oxygen, nutrients, salts, hormones, or vitamins to cells throughout the body; and removes waste products such as carbon dioxide, nitrogenous wastes, excess salt, or metabolic water. The circulatory system also maintains proper physiological conditions within the body, fights diseases, heals wounds, and serves as an accessory to the nervous system through the ***endocrine*** (i.e., hormone) ***system***.

The major parts of the circulatory system are the ***blood*** and the ***circulatory vessels***.

a. Blood

Blood fills the circulatory system vessels. Blood's liquid "matrix," called ***blood plasma***, contains several cell types:

- ***Red blood cells*** are packed with ***hemoglobin***, which contains iron atoms to carry oxygen to the cells and carbon dioxide away from the cells.
- ***White blood cells*** fight infections and other diseases.
- ***Thrombocytes*** help the blood to clot.

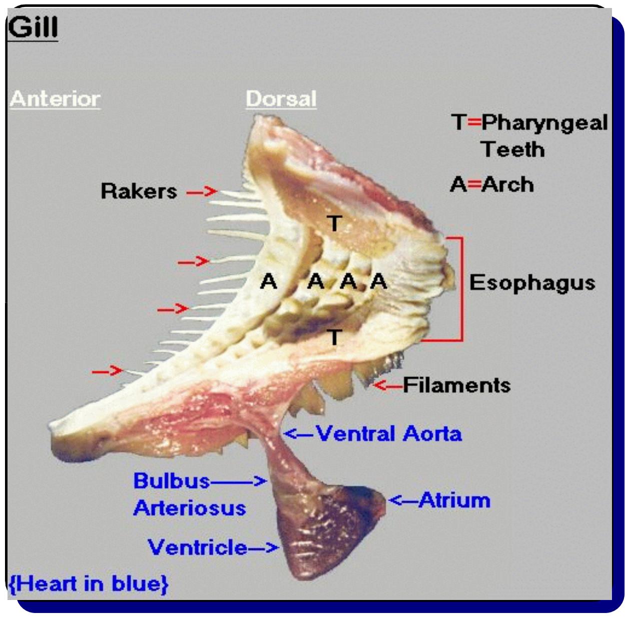
The life span of blood cells ranges from hours to months, depending on cell type. The body must therefore make new cells to replace old ones. Blood-forming tissue in fish is found in one or more of the: ***spleen*** (Figure A2-2), ***kidneys*** (Figure A2-3), ***gonads*** (sex organs), ***liver*** (Figure A2-3), and ***heart*** (Figure A2-3 and Figure A2-4). Bone marrow does not form blood cells in fish.

b. Circulatory vessels

The circulatory system includes the heart, ***arteries*** and ***veins***, ***capillaries***, and the ***lymphatics***.

The heart of a typical fish, a modified tube with four sequential chambers, is found close to the gills. Oxygen-poor blood enters the ***sinus venosus***, and is pumped through the ***atrium*** and ***ventricle*** into the ***bulbus*** (Figure A2-3) or ***conus*** arteriosus. From there, it is pumped out of the heart, into the ***ventral aorta***. The ventricle does most of the pumping. One-way valves prevent blood from flowing backward. The ventral aorta runs toward the gills and branches into parallel ***aortic arches*** that run through each gill. After the blood is re-oxygenated, the blood vessels rejoin into one large ***dorsal aorta***, which carries the blood to the organs.

Figure A2-4: Gill and Heart Anatomy



Arteries carry higher-pressure, oxygen-rich blood. When they reach their target organs, the arteries split into smaller branches called ***arterioles***. These enter the organ and continue to divide until they become so narrow that red blood cells can pass through them only single-file. At this point, the blood vessels are called ***capillaries***. The microscopic capillaries are the most important part of the circulatory system. Whereas blood is simply carried through the arteries and veins, blood in the capillaries releases oxygen and nourishment to the cells and picks up carbon dioxide and other wastes. The capillaries rejoin and form larger ***venules***. The venules merge into ***veins***, which carry the oxygen-poor blood out of the organs and back to the heart. The venous system is at a lower pressure than the arterial system because pressure is lost as blood passes through the capillaries.

Bony fish also have a lymphatic system, a network of vessels running parallel to the venous system, returning excess fluids from the tissues to the heart. The lymphatics are not connected to the arterial blood supply, but instead arise from their own dead-end capillaries within the tissues. The excess fluid is captured as ***lymph*** and returned to the venous system.

A2-5.5 Respiratory System

Fish are ***aerobic***, i.e., they must breathe oxygen. Most fish obtain their oxygen from the water. Extracting oxygen from water is difficult because (1) water is a thousand times denser and 50 times more viscous (at 68 ˚F [20 ˚C]) than air; (2) when saturated, water contains only 3 percent of the oxygen found in an equal volume of air; and (3) oxygen solubility in water decreases with increasing temperature. Fish expend much energy moving water over their gills; they have evolved efficient gills to maximize oxygen uptake while minimizing the cost of breathing.

a. Basic gill anatomy

Gills are similar among groups of fish. The paired gills are internal and located in the ***pharyngeal region***, specifically the ***branchial cavity***. They are supported by flexible rods called ***gill bars***. The number of gill bars ranges from four to six. On the side facing the pharynx, the gill bars carry stiff strainers called ***gill rakers*** (Figure A2-3 and Figure A2-4). Though not used in breathing, some species use gill rakers to strain out food particles. A typical gill bar has two large ***gill filaments*** (Figure A2-3 and Figure A2-4), which point outward (i.e., away from the pharynx and into the branchial cavity). Each gill filament supports many ***gill lamellae***, where the gases are exchanged.

An average of 20 lamellae are found on each mm of gill filament. Lamellae are covered by tissue one cell layer thick to optimize gas exchange. Those of adjacent gill filaments usually touch or mesh together, which favors contact between the gills and water. The gill surface area varies by a factor of 10 (on a per weight basis) and depends on the animal's activity. Active swimmers like white shark or tuna have larger gill surface areas than do sedentary fish like sunfish or carp. A fish such as a 44-pound sea bass has a respiratory surface of about 60 ft^2.

b. Gas exchange

When the fish opens its mouth to breathe, the branchial cavity is closed by a stiff ***operculum*** (in bony fish) or a series of flap-like ***gill septa*** (in cartilaginous fish) to prevent oxygen-depleted water from re-entering the branchial cavity. The operculum and septa also help keep a negative pressure in the buccal cavity when the mouth opens, forcing water to rush in. As the fish closes its mouth, the buccal cavity becomes smaller and water is forced backward over the gills.

Breathing water has drawbacks, partly due to its low oxygen content. Gills increase oxygen uptake using a ***countercurrent exchange*** mechanism. The gill lamellae face the incoming water, which always moves from the buccal cavity to the branchial cavity. Blood flows through the lamellae in the opposite direction. When blood first enters the lamellae, it encounters water low in oxygen (the "upstream" gill lamellae have already removed some oxygen). The blood entering the lamellae contains even less oxygen. This difference lets the small amount of oxygen still present in the water move into the blood. The oxygen content of blood flowing into the incoming water goes up, but so does that of the ever "fresher" water. A nonstop oxygen flow in favor of the blood all along the lamellae results. Oxygen keeps moving into the bloodstream until the blood leaves the lamella. Through this process, fish remove up to 80 percent of the oxygen from the water. Carbon dioxide moves in the opposite direction based on the same principle.

c. Other gill functions

The central role of gills is to take up oxygen and release carbon dioxide. Gills also have other functions due to their large surface area and close contact with water.

❖ *Osmoregulation*

Gills, together with kidneys, are used in ***osmoregulation***: the control of salt and water balances. The internal fluids of freshwater fish are "saltier" than the surrounding water. When blood moves through the gills, salt diffuses from the blood into the water, whereas water tends to move into the body. The kidneys release the extra water as dilute urine to keep a proper internal water balance. Freshwater fish also drink little or no water. Any salt loss is made up by ***chloride cells*** located in gill filaments and lamellae. These cells move salts from the water into the blood to make up for the loss. Mucus covers the gills, which protects them from injuries but helps in osmoregulation.

This situation reverses in marine bony fish: their internal fluids are less "salty" than their surroundings: water in the blood moves out of the body, but salts move in. These fish drink freely to make up for water loss. Drinking sea water brings salts into the body; these salts are excreted by both the gill chloride cells and the kidneys.

> ✤ Osmoregulation is a vital physiological need for fish and other aquatic organisms. This is particularly true for anadromous fish, which move from the ocean into freshwater habitats to spawn, and whose offspring migrate back into the ocean to mature. These species undergo profound physiological changes over relatively short periods of time to adapt to and survive in drastically different osmotic environments. Some species may be less able to survive physical shock or extreme stress during this transitional period, and could therefore be more susceptible to mortality from impingement.

Cartilaginous fish (and some primitive bony fish) also live in salt water but maintain their water balance differently. These fish keep high levels of urea in their blood, which causes their internal fluids to be saltier than seawater. Some water enters the gills, and the kidneys produce moderate amounts of urine. These fish need little or no additional water and drink infrequently.

❖ *Heat exchange*

Most fish are cold-blooded: their body temperature equals that of the water. Internal heat created by muscle activity is lost to the environment when the fish's blood passes through the gills to extract oxygen from water. Pelagic fish, such as certain tuna and sharks, are exceptions. These fish have countercurrent heat exchangers in their muscles to keep much of the heat inside and prevent it from being lost through the gills. Their body temperatures can be up to 20-25 ˚F (-6.7 to -3.9˚C) higher than that of the surrounding water.

❖ ***Excretion***
Freshwater and marine bony fish release their nitrogenous wastes through their gills. Blood moves the waste, in the form of ***urea***, to the gills. There, urea changes into toxic ammonia, which quickly diffuses into the water. Cartilaginous fish (i.e., Chondrichthyes) keep high levels of urea in their blood and lose very little of it through their gills to help in osmoregulation.

❖ ***Predation***
Gills have evolved to catch prey in plankton feeders, which swim with their mouths open. These fish have numerous, fine, and long gill rakers that strain plankton. Examples include the paddlefish (*Polyodon spathula*), the gizzard shad, and the Atlantic herring (*Clupea harengus*).

A2-5.6 Air/Swim Bladder

Buoyancy is the tendency of an object to float or rise in water, and depends on the object's density versus that of water. An aquatic organism with a density like water is weightless, neither rising or sinking. Less effort is needed to keep it from sinking or to move about. Most fish regulate their density to reach neutral buoyancy.

a. Strategies to increase buoyancy

Fat is less dense than water. One way to reduce body density, and increase buoyancy, is to increase body fat. About one-third of a fish's body weight needs to be fat to make the fish weightless in seawater. Several shark species increase buoyancy in this manner: they have huge livers full of ***squalene***, a fatty substance that provides buoyancy, being much less dense than seawater. Buoyancy is also attained by storing gases within the body. Many bony fish have an air/swim bladder for this purpose.

The amount of body volume that must be in the form of gas to achieve "weightlessness" depends on the saltiness of the water. Freshwater contains less salt than seawater; it is therefore less dense and provides less buoyancy. Swim bladders in freshwater fish range from 7 to 11 percent of body volume, while those of marine fish range from 4 to 6 percent of body volume.

b. Structure and function

Fish would be neutrally buoyant at only one depth, if air/swim bladders had a fixed amount of gas. Water pressure increases as water depth increases. When a fish swims to a lower depth, the increased pressure compresses the gas in the swim bladder, lowering its volume and increasing the density of the fish. The fish must swim more actively to compensate for this to prevent its denser body from sinking further. Water pressure decreases expanding the volume of gas in the swim bladder, when a fish swims toward the surface. Without the ability to change the amount of air in the swim bladder, a fish becomes less dense and rises to the surface like a cork.

The volume of gas in an air/swim bladder, and hence its pressure, needs adjusting as a fish changes depths. Most fish have an air/swim bladder that is isolated from the outside of the body and air pressure within the bladder varies when gas moves from the bladder to nearby blood vessels and back again. In some species, such as carp, a ***pneumatic duct*** joins the air/swim bladder with the ***esophagus***. This connection acts as a " valve" to release extra gas as the fish swims toward the surface, or to take up gas by gulping air at the surface before swimming toward the bottom.

It is simple to remove gas from an expanding air/swim bladder: the pressure forces the gas into the surrounding blood capillaries, which carry it away. Filling up a bladder is more difficult because it is done against the high pressures already in the bladder.

In most bony fish (i.e., Osteichthyes), gas enter the air/swim bladder through the ***red body***. The name comes from a structure known as the ***rete mirabile*** (the "marvelous net"), a dense bundle of capillaries arranged side by side in countercurrent fashion. Blood leaving the area carries gases at the same pressure found in the air/swim bladder. The gas pressure of blood coming into the area is much lower, similar to that in the surrounding water. Gases move from the outgoing blood to the incoming blood, not unlike the gas exchange process in the gills. The red body boosts the process by releasing compounds that raise the incoming blood's oxygen level. When the gas pressure in the red body exceeds that within the swim bladder, gas moves into the latter. Gas uptake and release is not immediate; swim bladders can burst when fish caught at great depth come to the surface too fast.

c. Effect of entrainment on the swim bladder

Changes in pressure can have a dramatic and often lethal effect on fish with swim bladders. Cooling water systems contain both positive and negative pressure differentials. A large positive pressure change will cause the swim bladder to implode. The effects of negative pressure changes appear to be more damaging. Negative pressure changes can cause the swim bladder to explode if the pressure across the membrane cannot be equalized fast enough. Pressure effects may be the leading cause of mortality in larvae of bluegill, carp, and gizzard shad. Gas disease may also result from a negative pressure change. Gas becomes more soluble in a negative pressure system, and following the release of pressure, hemorrhaging of blood vessel walls may occur around the eyes, gills, fins, and kidneys.

A2-5.7 Digestive System

The digestive system processes ingested food to meet the energy needs of fish.

The digestive system of fish has four major functions:

- **Transportation:** Swallowed food moves through the various gut sections for handling. Solid wastes must be removed at the end.
- **Physical treatment:** Food must be reduced in size by muscular action before it can broken down by digestive chemicals. Fluids are added to turn the food into a soft, pasty pulp.
- **Chemical treatment:** Food is turned into simpler compounds in the "digestive" phase.
- **Absorption:** The products of digestion are absorbed through the intestinal wall and either distributed as fuel or stored for later use.

The digestive system starts at the ***mouth*** (Figure A2-3), which captures prey. Food is passed through the ***buccal cavity*** into the muscular ***pharynx***, where it is swallowed into the tube-like ***esophagus*** (Figure A2-3). The esophagus uses smooth muscle to transport food to the ***stomach*** (Figure A2-3) (note that some fish such as chimaera, lungfish, and certain teleosts do not have a stomach; the esophagus connects directly to the ***intestine*** (Figure A2-3)). In many fish, a muscular ***sphincter*** exists where the esophagus meets the stomach. The stomach, when present, can be either a "U"- or "V"-shaped tube or a straight, cigar-shaped organ. Its internal wall is deeply folded and rich with mucus-secreting glands. Other glands release digestive acids, and enzymes such as pepsin and lipases, to break down protein and fats. At the end of the stomach, many bony fish have extensions called ***pyloric caeca*** (Figure A2-3), which may help digest and absorb food.

The ***pancreas*** is a major source of digestive enzymes, that form an "intestinal juice" to break down fats, proteins, and carbohydrates into simpler molecules. The intestine has glands which produce more digestive enzymes, or mucus to lubricate food passage. Intestinal contractions move the food along. The inner lining of the intestine is deeply folded to increase the surface area for absorption. All Chondrichthyes and some primitive bony fish have an intestinal ***spiral valve***, which looks like an auger enclosed in a tube. This valve increases the surface area of the gut because the food must twist through the intestine instead of moving straight through. The length of the intestine in bony fish varies: herbivores have long, coiled intestines, but carnivores have short, straight intestines. After digestion is complete, the wastes pass through the ***rectum*** and are excreted via the ***anus*** (Figure A2-3).

The ***liver*** (Figure A2-3) is not directly tied to digestion but is associated with it. This organ produces ***bile*** and bile salts, which help pancreatic enzymes split and absorb fats. Bile collects in the ***gall bladder*** (Figure A2-3) before it enters the intestine. The liver is a major storage organ. Blood leaving the intestines passes through the liver; fats, amino acids (building blocks for protein), and carbohydrates (simple sugars) are removed and stored there. The simple sugars are stored as ***glycogen*** and released to the blood when a burst of energy is needed.