

ADVANCED FISH PHYSIOLOGY (2)

A postgraduate course

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Feeding Behavior

For any fish, feeding is one of the main concerns of day-to-day living. Although many a luckless angler would swear otherwise, the fact is that a fish devotes more time and energy to eating, or searching for food to eat, than to anything else. Throughout the long evolution of fishes, there has been unrelenting selective pressure for those adaptations that enable a fish to come out on the better end of the eat-or-beaten contest. Certainly the most farreaching single event was the evolution of jaws. Their possessors were freed from a largely passive filterfeeding existence and could adopt a predatory mode of life. Improved means of capturing larger prey demanded stronger muscles, more agile movement, better balance, and improved special senses. More than any other aspect of its life habit, feeding behavior shapes the fish.

Most fishes are **carnivores** that prey on a myriad of animal foods from zooplankton and insect larvae to large vertebrates. Some deep-sea fishes are capable of eating victims nearly twice their own size—an adaptation for life in a world where meals are necessarily infrequent. Most advanced ray-finned fishes cannot masticate their food as we can because doing so would block the current of water across the gills. Some, however, such as the wolf eel (Figure 26-30), have molarlike teeth in the jaws for crushing their prey, which may include hard-bodied crustaceans. Others that do grind their food use powerful pharyngeal teeth in the throat. Most carnivorous fish almost invariably swallow their prey whole, using sharp-pointed teeth in the jaws and on the roof of the mouth to seize their prey. The incompressibility of water makes the task even easier for many largemouthed predators. When the mouth is suddenly opened, a negative pressure is created that sweeps the victim inside (Figure 26-31)



Figure 26-30

Wolf eel, *Anarrhichthys ocellatus*, feeding on a sea cucumber it has captured and pulled to the opening of its den.



Figure 26-31

Goosefish Lophius piscatorius awaits its meal. Above its head swings a modified dorsal fin spine ending in a fleshy tentacle that contracts and expands in a convincing wormlike manner. When a fish approaches the alluring bait, the huge mouth opens suddenly, creating a strong inward current that sweeps the prey inside. In a split second all is over.

A second group of fishes are **herbivores** that eat plants and algae. Although plant eaters are relatively few in number, they are crucial intermediates in the food chain, especially in freshwater rivers, lakes, and ponds that contain very little plankton.

Suspension-feeders that crop the abundant microorganisms of the sea form a third and diverse group of fishes ranging from fish larvae to basking sharks. However, the most characteristic group of plankton feeders are herringlike fishes (menhaden, herring, anchovies, capelin, pilchards, and others), mostly **pelagic** (open-sea dwellers) fishes that travel in large schools. Both phytoplankton and the smaller zooplankton are strained from the water with the sieve-like gill rakers (Figure 26-28). Because plankton feeders are the most abundant of all marine fishes, they are important food for numerous larger but less abundant carnivores. Many freshwater fishes also depend on plankton for food.

A fourth group of fishes contains **omnivores** that feed on both plant and animal food. Finally there are **scavengers** that feed on organic debris (detritus) and **parasites** that suck the body fluids of other fishes.

Digestion in most fishes follows the vertebrate plan. Except in several fishes that lack stomachs altogether, the food proceeds from stomach to tubular intestine, which tends to be short in carnivores (Figure 26-15) but may be extremely long and coiled in herbivorous forms. In the herbivorous grass carp, for example, the intestine may be nine times the body length, an adaptation for the lengthy digestion required for plant carbohydrates. In carnivores, some protein digestion may be initiated in the acid medium of the stomach, but the principal function of the stomach is to store the often large and infrequent meals while awaiting their reception by the intestine.

Digestion and absorption proceed simultaneously in the intestine. A curious feature of ray-finned fishes, especially the teleosts, is the presence of numerous **pyloric ceca** (Figure 26-15) found in no other vertebrate group. Their primary function appears to be fat absorption, although all classes of digestive enzymes (protein-, carbohydrate-, and fat-splitting) are secreted there.

Migration

Eel

For centuries naturalists had been puzzled about the life history of the freshwater eel *Anguilla* (an-gwil'la) (*L. eel*), a common and commercially important species of coastal streams of the North Atlantic. Eels are **catadromous** (Gr. *kata*, down, + *dromos*, running), meaning that they spend most of their lives in fresh water but migrate to the sea to spawn. Each fall, large numbers of eels were seen swimming down the rivers toward the sea, but no adults ever returned. Each spring countless numbers of young eels, called "elvers" (Figure 26-32), each about the size of a wooden matchstick, appeared in the coastal rivers and began swimming upstream. Beyond the assumption that eels must spawn somewhere at sea, location of their breeding grounds was completely unknown.

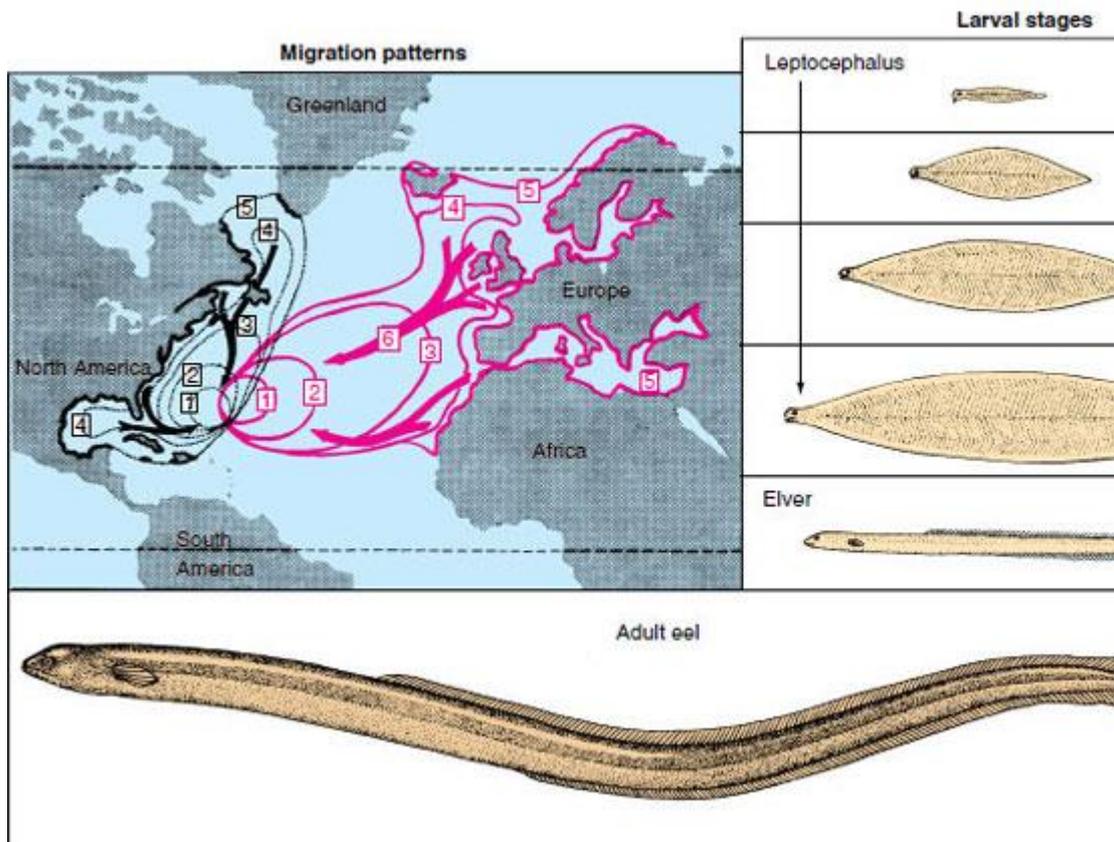


Figure 7
 Life histories of the European eel, *Anguilla anguilla*, and American eel, *Anguilla rostrata*. Migration patterns of European species are shown in pink. Migration patterns of American species are shown in black. Boxed numbers refer to stages of development. Note that the American eel completes its larval metamorphosis and sea journey in one year. It requires nearly three years for the European eel to complete its much longer journey.

The first clue was provided by two Italian scientists, Grassi and Calandruccio, who in 1896 reported that elvers were not larval eels but rather were relatively advanced juveniles. True larval eels, they discovered, were tiny, leaf-shaped, completely transparent creatures that bore absolutely no resemblance to an eel. They had been called **leptocephali** (Gr. *leptos*, slender, + *kephale*, head) by early naturalists, who never suspected their true identity. In 1905 Johann Schmidt, supported by the Danish government, began a systematic study of eel biology that he continued until his death in 1933. With cooperation of captains of commercial vessels plying the Atlantic, thousands of leptocephali were caught in different areas of the Atlantic with the plankton nets Schmidt supplied them. By noting where larvae in different stages of development were captured, Schmidt and his colleagues eventually reconstructed the spawning migrations.

When adult eels leave the coastal rivers of Europe and North America, they swim steadily and apparently at great depth for 1 to 2 months until they reach the Sargasso Sea, a vast area of warm oceanic water southeast of Bermuda (Figure 26-32). Here, at depths of 300 m or more, the eels spawn and die. The minute larvae then begin an incredible journey back to the coastal rivers of Europe. Drifting with the Gulf Stream and preyed on constantly by numerous predators, they reach the middle of the Atlantic after 2 years. By the end of the third year they arrive in the coastal waters of Europe where the leptocephali metamorphose into elvers, with an unmistakable eel-like body form (Figure 7). Here the males and females part company; males remain in the brackish waters of coastal rivers and estuaries while females continue up the rivers, often traveling hundreds of miles upstream. After 8 to 15 years of growth, the females, now 1 m or more long, return to the sea to join the smaller males; both return to the ancestral breeding grounds thousands of miles away to complete the life cycle.

Schmidt found that the American eel (*Anguilla rostrata*) could be distinguished from the European eel (*A. vulgaris*) because it had fewer vertebrae— an average of 107 in the American eel as compared with an average 114 in the European species. Since the American eel is much closer to the North American coastline, it requires only about 8 months to make the journey.



Figure 8
Migrating Pacific sockeye salmon (*Oncorhynchus nerka*).

Homing Salmon

The life history of salmon is nearly as remarkable as that of the eel and certainly has received far more popular attention. Salmon are **anadromous** (Gr. *anadromos*, running upward); that is, they spend their adult lives at sea but return to fresh water to spawn. The Atlantic **salmon** (*Salmo salar*) (L. *salmo*, salmon, *sal*, salt) and the Pacific salmon (six species in the genus *Oncorhynchus* [on-ko-rink'us] [Gr. *onkos*, hook, + *rhynchos*, snout]) have this practice, but there are important differences among the seven species. The Atlantic salmon may make repeated upstream spawning runs. The six **Pacific salmon species** (king, sockeye, silver, humpback, chum, and Japanese masu) each make a single spawning run (Figure 8), after which they die.

The virtually infallible homing instinct of the Pacific species is legendary: after migrating downstream as a smolt, a sockeye salmon ranges many hundreds of miles over the Pacific for nearly 4 years, grows to 2 to 5 kg in weight, and then returns almost unerringly to spawn in the headwaters of its parent stream. Some straying does occur and is an important means of increasing gene flow and populating new streams.

Experiments by A. D. Hasler and others have shown that homing salmon are guided upstream by the characteristic odor of their parent stream. When the salmon finally reach the spawning beds of their parents (where they themselves were hatched), they spawn and die. The following spring, newly hatched fry transform into smolts before and during the downstream migration. At this time they are imprinted with the distinctive odor of the stream, which is apparently a mosaic of compounds released by the characteristic vegetation and soil in the watershed of the parent stream. They also seem to imprint on the odors of other streams they pass while migrating downriver and use these odors in reverse sequence as a map during the upriver migration as returning adults.

How do salmon find their way to the mouth of the coastal river from the trackless miles of the open ocean? Salmon move hundreds of miles away from the coast, much too far to be able to detect the odor of their parent stream. Experiments suggest that some migrating fish, like birds, can navigate by orienting to the position of the sun. However, migrant salmon can navigate on cloudy days and at night, indicating that sun navigation, if used at all, cannot be the salmon's only navigational cue. Fish also

(again, like birds) appear able to detect and navigate to the earth's magnetic field. Finally, fishery biologists concede that salmon may not require precise navigational abilities at all, but instead may use ocean currents, temperature gradients, and food availability to reach the general coastal area where "their" river is located. From this point, they would navigate by their imprinted odor map, making correct turns at each stream junction until they reach their natal stream.



Figure 9
Rainbow surfperch *Hypsurus caryi* giving birth. All of the West Coast surfperches (family Embiotocidae) are ovoviviparous.

Reproduction and Growth

In a group as diverse as the fishes, it is no surprise to find extraordinary variations on the basic theme of sexual reproduction. Most fishes favor a simple theme: they are **dioecious**, with **external fertilization** and **external development** of the eggs and embryos (oviparity). However, as tropical fish enthusiasts are well aware, the ever-popular ovoviviparous guppies and mollies of home aquaria bear their young alive after development in the ovarian cavity of the mother (Figure 26-34). As described earlier in this section, some viviparous sharks develop a kind of placental attachment through which the young are nourished during gestation.

Let us return to the much more common oviparous mode of reproduction. Many marine fishes are extraordinarily profligate egg producers. Males and females come together in great schools and release vast numbers of gametes into the water to drift with the current. Large female cod may release 4 to 6 million eggs at a single spawning. Less than one in a million will survive the numerous perils of the ocean to

reach

reproductive

maturity.



Figure 10

Male banded jawfish *Opistognathus macrognathus* orally brooding its eggs. The male retrieves the female's spawn and incubates the eggs until they hatch. During brief periods when the jawfish is feeding, the eggs are left in the burrow.

Unlike the minute, buoyant, transparent eggs of pelagic marine teleosts, those of many near-shore bottomdwelling (benthic) species are larger, typically yolky, nonbuoyant, and adhesive. Some bury their eggs, many attach them to vegetation, some deposit them in nests, and some even incubate them in their mouths (Figure 10). Many benthic spawners guard their eggs. Intruders expecting an easy meal of eggs may be met with a vivid and often belligerent display by the guard, which is almost always the male.

Freshwater fishes almost invariably produce nonbuoyant eggs. Those, such as perch, that provide no parental care simply scatter their myriads of eggs among weeds or along the bottom. Freshwater fishes that do provide some form of egg care, such as bullhead catfishes and some darters, produce fewer, larger eggs that enjoy a better chance for survival.

Elaborate preliminaries to mating are the rule for freshwater fishes. The female Pacific salmon, for example, performs a ritualized mating "dance" with her breeding partner after arriving at the spawning bed in a fast-flowing, gravel-bottomed stream (Figure 26-36). She then turns on her side and scoops out a nest with her tail. As the eggs are laid by the female, they are fertilized by the male (Figure 26-36). After the female covers the eggs with gravel, the exhausted fish dies and drifts downstream.

Soon after the egg of an oviparous species is laid and fertilized, it takes up water and the outer layer hardens. Cleavage follows, and the blastoderm forms, sitting astride a relatively enormous yolk mass. Soon the yolk mass is enclosed by the developing blastoderm, which then begins to assume a fishlike shape. The fish hatches as a larva carrying a semitransparent sac of yolk, which provides its food supply until the mouth and digestive tract have developed. The larva then begins searching for its own food. After a period of growth the larva undergoes a metamorphosis, especially dramatic in many marine species such as the freshwater eel described previously (Figure 26-32). Body shape is refashioned, fin and color patterns change, and the animal becomes a juvenile bearing the unmistakable definitive body form of its species.

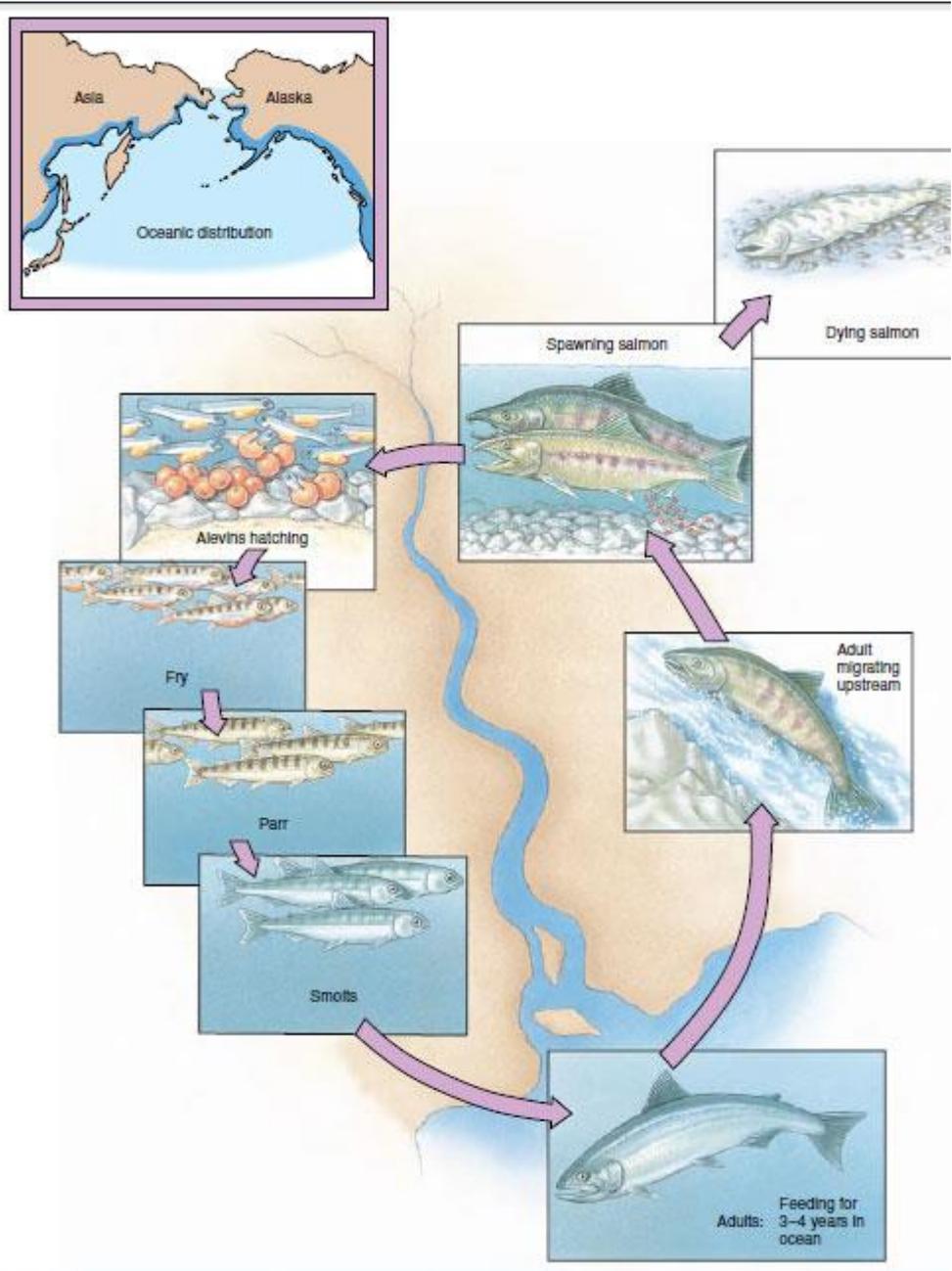


Figure 11
Spawning Pacific salmon and development of the eggs and young.

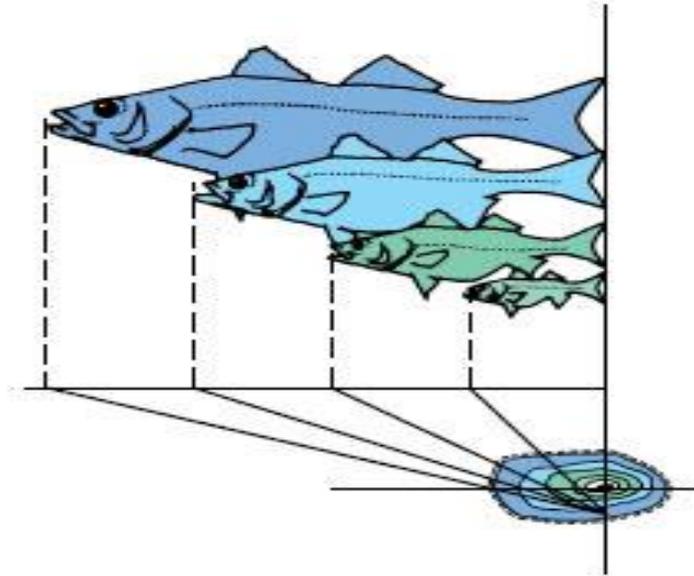


Figure 12

Scale growth. Fish scales disclose seasonal changes in growth rate. Growth is interrupted during winter, producing year marks (annuli). Each year's increment in scale growth is a ratio to the annual increase in body length. Otoliths (ear stones) and certain bones can also be used in some species to determine age and growth rate.

Growth is temperature dependent. Consequently, fish living in temperate regions grow rapidly in summer when temperatures are high and food is abundant but nearly stop growing in winter. Annual rings in the scales, otoliths, and other bony parts reflect this seasonal growth (Figure 12), a distinctive record of convenience to fishery biologists who wish to determine a fish's age. Unlike birds and mammals, which stop growing after reaching adult size, most fishes after attaining reproductive maturity continue to grow for as long as they live. This may be a selective advantage, since the larger the fish, the more gametes it produces and the greater its contribution to future generations.