

THE DIVERSITY OF FISHES

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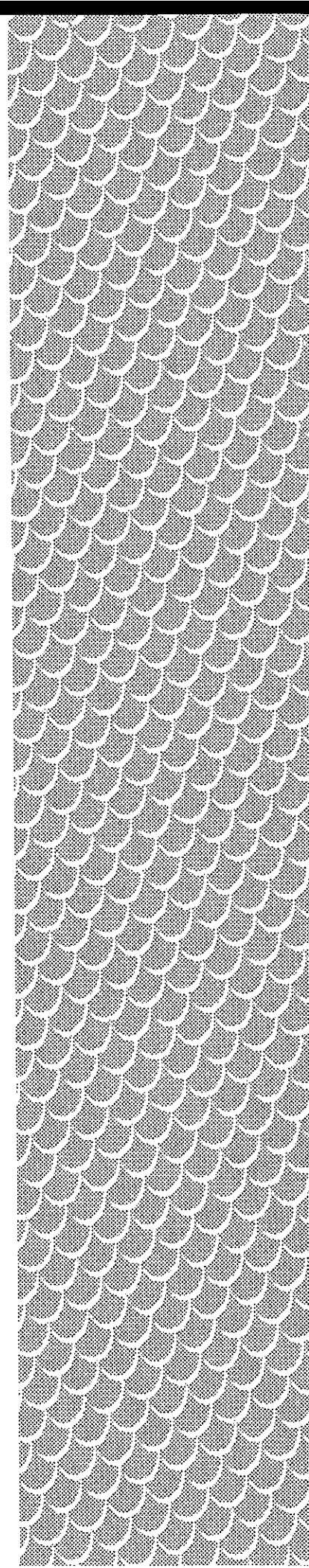
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Functional Morphology of Locomotion and Feeding

"Structure without function is a corpse and function without structure is a ghost."

(Vogel and Wainwright 1969, 93)

Structure and function are inseparable. In the preceding five chapters, we have characterized the anatomy of fishes and described the function of various physiological systems. Such anatomic and physiological descriptions only make evolutionary sense when we understand their function, and function has not been ignored in the preceding introductory material. But structure-function relationships deserve more in-depth exploration. The study of how parts operate and how environmental selection pressures have influenced their construction and operation is variously referred to as functional morphology, physiological ecology, ecomorphology, and ecological physiology. These closely interrelated topics draw heavily on many disciplines besides anatomy and physiology, including physics, biomechanics, biochemistry, ultrastructure, structural engineering, developmental biology, population ecology, behavior, paleontology, and of course evolution.

Our goals in this chapter are to explore further the anatomic and physiological challenges that arise from living in water and to bring together and expand upon the subject matter introduced in the preceding chapters. We will focus on two general tasks in this chapter—locomotion and feeding—for examples of the intimacy and intricacy of structure and function; additional discussions that emphasize functional morphology can be found in several other chapters (e.g., see Chaps. 9 and 17 through 19). We can literally only skim the surface of this fascinating, interdisciplinary topic, and we strongly encourage interested readers to pursue the additional and more detailed information available in the cited references and suggested readings at the end of the chapter.

LOCOMOTION: MOVEMENT AND SHAPE

"... [T]he gap between the swimming fish and the scientists is closing, but the fish is still well ahead."

(Lindsey 1978, 8)

Body shape and locomotory behavior in fishes are determined by the extreme density of water. Locomotory ad-

aptations in terrestrial and flying animals strongly reflect a need to overcome gravity. In contrast, body and appendage shape in fishes reflects little influence of gravity, because gas bladders or lipid-containing structures make most fishes neutrally buoyant (see Chap. 5, Buoyancy Regulation). Fish locomotion is more constrained by the density of water and the drag exerted by it (Videler 1993).

Water is about 800 times more dense and 50 times more viscous than air. Locomotion through this dense, viscous medium is energetically expensive, a problem exacerbated by the 95% reduction in oxygen-carrying capacity of water as compared to air (see Chap. 5, Water as a Respiratory Environment). The chief cause of added energetic cost is drag, which has two components: **viscous or frictional drag**, involving friction between the fish's body and the surrounding water; and **inertial or pressure drag**, caused by pressure differences that result from displacement of water as the fish moves through it.

Viscous drag is not affected greatly by speed but more by the smoothness of a surface and by the amount of surface area, which is linked to body and fin shape; production of mucus reduces viscous drag. Inertial drag increases with speed and is therefore also intimately linked to body shape. Most fast-swimming fishes have a classic streamlined shape that minimizes both inertial and viscous drag. A streamlined body is round in cross section and has a maximum width equal to 25% of its length. The width-length ratio is 0.26 in some pelagic sharks, 0.24 in swordfish, and 0.28 in tunas. The thickest portion of a streamlined body occurs about two-fifths of the way back from the anterior end, another rule followed by large pelagic predators.

Interestingly, these same streamlined fishes are also slightly negatively buoyant and hence sink if they cease swimming. They often have winglike pectoral fins that are extended laterally at a positive attack angle, thus generating lift. They minimize drag by retracting paired and median fins into depressions or even grooves in the body surface; a sailfish houses its greatly expanded dorsal fin "sail" in a groove on its dorsal surface during fast swimming (Hertel 1966; Hildebrand 1982; Pough et al. 1984).

Most fishes swim by contracting a series of muscles on one side of the body and relaxing muscles on the other.

The muscle blocks, called myomeres, attach to collagenous septa, which in turn attach to the backbone and skin (Fig. 8.1). Depending on the swimming form involved (see below), contractions may progress from the head to the tail or occur on one side and then the other. The result of the contractions is that the fish's body segments push back on the water. Given Newton's third law of motion concerning equal and opposite forces, this pushing back produces an opposite reactive force that thrusts the fish forward. Forward thrust results from combined forces pushing forward and laterally; the lateral component is canceled by a rigid head, by median fins, and in some cases by a deep body that resists lateral displacement.

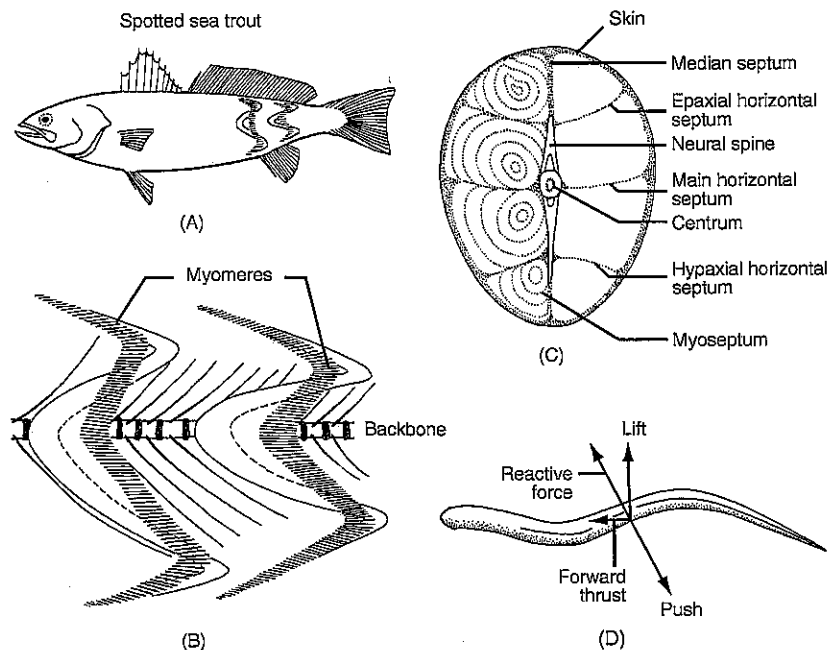
Locomotory Types

A general classification of swimming modes or types among fishes has been developed, building on the work of Breder (1926), Gray (1968), Lindsey (1978), and Webb (1984; Webb and Blake 1985). The chief characteristics of the different types are how much of and which parts of the body are involved in propulsion and whether the body or the fins undulate or oscillate. **Undulation** in-

volves sinusoidal waves passing down the body or a fin or fins; **oscillation** involves a structure that moves back and forth (Table 8.1). About 10 general types are recognized: anguilliform, subcarangiform, carangiform, modified carangiform (= thunniform), ostraciiform, balistiform, rajiform, amiiform, gymnotiform, and labriform; some of these are additionally subdivided. The names apply to the basic swimming mode of particular orders and families, although unrelated taxa may display the same mode, and many fish use different modes at different velocities.

The first four types involve sinusoidal undulations of the body. **Anguilliform** swimming—seen in most eels, dogfishes, other elongate sharks, and many larvae—occurs in fishes with very flexible bodies that are bent into at least one-half of a sine wave when photographed from the dorsal view (see Table 8.1). All but the head contributes to the propulsive force. As a wave proceeds posteriorly, it increases in amplitude. The speed (frequency) of the wave remains constant as it passes down the body and always exceeds the speed of forward movement of the fish because of drag and because of energy lost to reactive forces that are not directed forward (see above). To swim faster, faster waves must be produced. Anguilliform swim-

FIGURE 8.1. How fishes swim. (A) Lateral view of a spotted sea trout, *Cynoscion nebulosus*, with the skin dissected away to show the location of two myomeres on the left side. (B) The same myomeres as they appear relative to the backbone in a sea trout. The hatched region is the part of the myomere located closest to the skin; the dotted line shows the interior portion of the myomere where it attaches to the vertebral column. The anterior and posterior surface of each myomere is covered by a myoseptum made of collagen fiber in a gel matrix, shown as a slightly thickened line. (C) Cross section of a generalized teleost near the tail, showing the distribution of the various septa and their relationship to the backbone. Myosepta join to form median and horizontal septa. (D) How contractions produce swimming in a generalized fish. Progressive, tailward passage of a wave of contractions from the head to the tail **push** back on the water, generating **forward thrust** as one component of the **reactive force**. Sideways slippage (**lift**) is overcome by the inertia of the large surface area presented by fish's head and body.



(C) From Wainwright 1983; used with permission.

Table 8.1. Form, function, and locomotion in fishes. About 12 generalized types of swimming are recognized among fishes. The body part providing propulsion is indicated by cross-hatching; density of shading denotes relative contribution to propulsion. These locomotory patterns correlate strongly with body shape, habitat, feeding ecology, and social behavior. Convergence among unrelated fishes in terms of body morphology, swimming, and ecology demonstrates the evolutionary interplay of form and function. See Lindsey (1978), Beamish (1978), Webb and Blake (1985), Pough et al. (1984) for details.

	Swimming Type					
	Via Trunk and Tail			Via Fins		
	Anguilliform	Subcarangiform ^a Carangiform Thunniform	Ostradiform	Tetraodontiform Balistiform Diodontiform	Rajiform ^c Amiiform Gymnotiform	Labriform ^d
Representative taxa	eels, some sharks, many larvae	salmon, jacks, mako shark, tuna	boxfish, momyrs, torpedo ray	triggerfish, ocean sunfish, porcupinefish	rays, bowfin, knifefishes	wrasses, surperch
Propulsive force	most of body	posterior half of body	caudal region	median fin(s)	pectorals, median fins	pectoral fins
Propulsive form	undulation	undulation	oscillation	oscillation ^b	undulation	oscillation
Wavelength	0.5 to >1 wavelength	<1 (usually <0.5) wavelength			≥1 wavelength	
Maximum speed b.l./sec	slow to moderate 2	very fast to moderate 10-20	slow ?	slow ?	slow to moderate 0.5	slow 4
Body shape:						
lateral view	elongate	fusiform	variable	variable	elongate	variable
cross section	round	round		often deep	often flat	
Caudal fin aspect ratio	small	medium to large	large	small to medium	variable	large
Habitat	benthic or suprabenthic	low to high	low	low	low	low
		pelagic, w.c., schooling	variable	w.c.	suprabenthic	structure associated

b.l./sec - body lengths per second attainable; w.c. - up in water column.
^aIn subcarangiform types (salmons, cods), the posterior half of the body is used; carangiform swimmers (jacks, herrings) use the posterior third; and thunniform or modified carangiform swimmers (tunas, mako sharks) use mostly the caudal peduncle and tail (see text).
^bBalistiform and diodontiform swimming is intermediate between oscillation and undulation; porcupinefishes use their pectoral fins.
^cRajiforms (skates, rays) swim with undulating pectoral fins; amiiforms (bowfin) undulate their dorsal fin; gymnotiform swimmers (South American knifefishes, featherfins) undulate their anal fin.
^dLabriform swimmers use pectorals for slow swimming but use the subcarangiform or carangiform mode for fast swimming.
 Line drawings from Lindsey 1978; used with permission.

mers are comparatively slow because of their relatively long bodies and the involvement of anterior regions in propulsion; the same segments that push back on the water waste energy by pushing laterally and also create drag, because water pushes on these bent sections as the fish moves forward.

Anguilliform swimming has its compensating advantages, including greater ability to move through dense

vegetation and sediments and to swim backward. Anguilliform swimming in larval fishes, including species such as herrings that use carangiform swimming as adults, probably occurs because the skeleton of early larvae is unossified and the fish is exceedingly flexible and anatomically constrained from employing other modes (see Chap. 9, Larval Behavior and Physiology).

To get around the self-braking that occurs in anguilli-

form swimmers, faster-swimming fishes involve only posterior segments of the body in wave generation, using ligaments to transfer force from anterior body musculature to the caudal region. The progression of types from **subcarangiform** (trout, cod) through **carangiform** (jacks, herrings) to **modified carangiform** or **thunniform** (mackerel sharks, billfishes, tunas) entails increasing involvement of the tail and decreasing involvement of the anterior body in swimming.

One major advance in the carangiform and thunniform swimmers is the existence of a functional hinge that connects the tail to the caudal peduncle. This hinged coupling allows the fish to maintain its tail at an ideal attack angle of 10° to 20° through much of the power stroke. In anguilliform and subcarangiform swimmers, this angle changes constantly as the tail sweeps back and forth, producing less thrust at low angles and creating more drag at greater angles.

Thunniform swimmers also typically have a tail that originates from a narrow peduncle (= **narrow necking**) that is often dorsoventrally depressed and may even have lateral keels that streamline it during side-to-side motion. Narrow necking creates an overall more streamlined shape to the body and also reduces viscous drag and lateral resistance in that region of the body where they tend to be highest. The tail itself is stiff and sickle-shaped, being very narrow while quite tall. Such a large height-width ratio tail, referred to as a **high aspect ratio** tail, experiences minimal drag and is ideal for sustained swimming. The shape reduces viscous drag by reducing surface area and reduces inertial drag by having pointed tips that produce minimal vortices at their tips. The efficiency of the system is increased by tendons that run around joints in the peduncle region and insert on the tail, the joints serving as pulleys that increase the pulling power of the muscle-tendon network.

The thunniform mode of propulsion, involving a streamlined shape, narrow-necked and keeled peduncle, and high aspect ratio tail, has evolved convergently in several fast-swimming, pelagic predators, including mackerel sharks, tunas, and billfishes, as well as porpoises, dolphins, and the extinct reptilian ichthyosaurs. The fish and mammalian groups are also endothermic to some degree (Lighthill 1969; Lindsey 1978; Pough et al. 1989). Higher-speed, sustained swimming in the mackerel sharks and tunas is also made possible by the large masses of red muscle along the fish's sides (see Chap. 4, Red Muscle Versus White Muscle). Location of the red muscle close to the fish's spine allows the body to remain fairly rigid and also permits the retention of heat generated by muscle contraction. Hence thunniform swimming and endothermy are tightly linked.

Low aspect ratio, broad, flexible tails, such as those found in subcarangiform minnows, salmon, pikes, cods, and barracudas, are better suited for rapid acceleration from a dead start and can also aid during hovering by passing undulations down their posterior edge. Intrinsic muscles associated with the tail in low aspect ratio species help control its shape. Rainbow trout are able to increase the depth and hence produce a higher aspect ratio tail during high-speed swimming. **Fast-start** preda-

tors, such as gars, pikes, and barracudas, hover in the water column and then dart rapidly at prey. These unrelated fishes have converged on a body shape that concentrates the propulsive elements in the posterior portion of the body: Dorsal and anal fins are large and placed far to the posterior, the caudal peduncle is deep, and the tail has a relatively low aspect ratio. Maximum thrust from a high-amplitude wave concentrated in the tail region allows for rapid acceleration from a standing start (see Fig. 17.1).

Ostraciiform swimming, as seen in boxfishes and torpedo rays, is extreme in that only the tail is moved back and forth while the body is held rigid; the side-to-side movement of the tail is an oscillation more than an undulation. Boxfishes have a rigid dermal covering that extends back to the peduncle area. In the weakly electric elephantfishes, body muscles pull on tendons that run back around bones in the caudal peduncle region and insert on the tail, causing the fish to swim with jerky tail beats. Such an arrangement is thunniform in anatomy but more ostraciiform in function. Weakly electric fishes, such as the elephantfishes and South American knife-fishes mentioned below, often have devices for keeping their bodies straight while swimming. This relative inflexibility probably minimizes distortion of the electrical field they create around themselves (see Chap. 6, Electroreception).

The last five swimming types employ median and paired fins rather than body-tail couplings. **Tetraodontiform** swimmers (triggerfishes, ocean sunfishes) flap their dorsal and anal fins synchronously; their narrow-based, long, pointed fins function like wings and generate lift (forward thrust) continuously, not just during half of each oscillation. **Rajiform** swimmers hover and move slowly via multiple undulations that pass backward or forward along the pectoral fins of skates and rays. In **amiiform** swimmers, undulations pass along the dorsal fin (bowfin, African osteoglossomorph *Gymnarchus*, seahorses), whereas in **gymnotiform** swimming, undulations pass along the anal fin (South American and African knifefishes or featherfins). Rajiform and related swimming modes are slow but allow for precise hovering, maneuvering, and backing. The frequency with which waves pass along a fin can be very high, reaching 70 Hz in the dorsal fin of seahorses.

Labriform swimmers (chimaeras, surfperches, wrasses, parrotfishes, surgeonfishes) row their pectoral fins, pushing back with the broad blade, then feathering it in the recovery phase. As some negative lift is generated during the recovery phase, these fish often give the impression of bouncing slightly as they move through the water. If rapid acceleration or sustained fast swimming is needed, labriform swimmers, as well as many other fin-based locomotors, shift to carangiform locomotion.

Three final aspects of locomotory types deserve mention. First, the distinctiveness of the different locomotory types suggests that they are specializations, and specialization for one function usually produces compromises in other functions. Fishes that specialize in efficient slow swimming or precise maneuvering usually employ undulating or oscillating median fins. The long fin bases nec-

essary for such propulsion (e.g., bowfin, knifefishes, pipefishes, cutlassfishes) require a long body, which evolves at a cost in high-speed, steady swimming. Low-speed maneuverability can also be achieved with a highly compressed (laterally flattened), short body that facilitates pivoting, as found in many fishes that live in geometrically complex environments such as coral reefs or vegetation beds (e.g., freshwater sunfishes, angelfishes, butterflyfishes, cichlids, surfperches, rabbitfishes). These fishes typically have expanded median and paired fins that are distributed around the center of mass of the body and can act independently to achieve precise, transient thrusts, a useful ability when feeding on attached algae or on invertebrates that are hiding in cracks and crevices. But a short, compressed body means reduced muscle mass and poor streamlining, whereas large fins increase drag. Again, such fishes achieve maneuverability but sacrifice rapid starts and sustained cruising. Relatively poor fast-start performance may be compensated for by deep bodies and stiff spines, which make these fishes difficult to swallow (see Chap. 19, Discouraging Capture and Handling); they also typically live close to shelter. At the other extreme, thunniform swimmers have streamlined bodies, large anterior muscle masses, and stiff pectoral and caudal fins that are extremely hydrodynamic foils. They trade off exceptional cruising ability against an inability to maneuver at slow speeds.

Although specialists among body types can be identified, optimal design for one trait—sustained cruising, rapid acceleration, or maneuverability—tends to reduce ability in the other traits. Because most fishes must cruise to get from place to place and must accelerate and maneuver to eat and avoid being eaten, “the majority of fishes are locomotor generalists rather than locomotor specialists” (Webb 1984, 82).

Second, this generalist strategy means that few fishes use only one swimming mode. Many fishes switch between modes depending on whether fast or slow swimming or hovering is needed. In addition, most fishes have median fins that can be erected or depressed, adding a dynamic quality to their locomotion. A largemouth bass can erect its first dorsal and anal fins to gain thrust during a fast-start attack, then depress these fins to reduce drag while chasing a prey fish, then erect them to aid in rapid maneuvering. Most groups, with the exception of the thunniform swimmers, are capable of hovering in midwater by sculling with their pectoral fins or by passing waves vertically along the caudal fin. When hovering, some forward thrust is generated by water exhaled from the opercles; this force is countered by pectoral sculling. The fin movement involved in hovering may be difficult to detect, both by human observers and potential prey, because fishes that use these techniques often possess transparent pectoral fins.

Finally, note that not all fishes fit neatly into one of these categories (e.g., Box 8.1) and that many additional categories can and have been erected to accommodate variations among taxa (for more complete and alternative categorizations, see Lindsey 1978; Webb and Blake 1985; Videler 1993).

Specialized Locomotion

Certain highly derived forms of locomotion exist among fishes and do not fall into any of the general categories. A number of species walk along the bottom of the sea or leave the water and move about on land; these fishes have bodies that depart from a streamlined shape. Sea robins move lightly across sand bottoms using modified pectoral rays that extend out from the fin webs. They give the appearance of someone tiptoeing on many moving fingers. Antennarioid frogfishes and batfishes pull themselves along the bottom with movements of their modified pectoral and pelvic fins; their forward motion is aided by jet propulsion of water out their backward-facing, constricted opercles (Pietsch and Grobecker 1987).

Terrestrial locomotion is accomplished in a variety of ways. Climbing gouramies (*Anabantidae*) use paired fins and spiny gill covers to ratchet themselves along, whereas snakeheads (*Channidae*) row with their pectoral fins. So-called clariid “walking catfishes” move across land by lateral body flexion combined with pivoting on their stout, erect pectoral spines. Mudskippers (*Gobiidae*) swing their pectoral fins forward while supporting their body on the pelvic fins. They then push forward with the pectoral fins, like a person on crutches. Rapid leaps of 30 to 40 cm are accomplished by coordinated pushing of the tail and pectoral fins. Their unique pectoral fins are roughly convergent with the forelimbs of tetrapods, including an upper arm consisting of a rigid platelike region and a fanlike forearm and plantar surface (Gray 1968). Some species with anguilliform movement (moray and anguillid eels) are able to move across wet land employing their normal locomotion, which is analogous to the “serpentine” terrestrial and aquatic movements of most snakes (Chave and Randall 1971; Lindsey 1978).

Aerial locomotion grades from occasional jumping to gliding to actual flapping flight. Many fishes jump to catch airborne prey (trout, largemouth bass); meter-long arowanas (*Osteoglossidae*) can leap more than a body length upward and pluck insects and larger prey from overhanging vegetation. Other fishes take advantage of the greater speeds achievable in air: Needlefishes, mackerels, and tunas leave the water in a flat trajectory when chasing prey, and salmon leap clear of the water when moving through rapids or up waterfalls. Hooked fish jump and simultaneously shake their heads from side to side in an attempt to throw the hook; such oscillation is less constrained by drag in air than in water and therefore allows more rapid and forceful to-and-fro movement. Prey such as minnows, halfbeaks, silversides, and mullets jump when being chased.

Fishes capable of flight include gliders such as the exocoetid flyingfishes and pantodontid butterflyfishes, as well as gasteropelagic hatchetfishes, which purportedly vibrate their pectoral wings to generate additional lift (Davenport 1994; see Chap. 19, Evading Pursuit). The anatomy of the marine flyingfishes is highly modified for flying. The body is almost rectangular in cross section, the flattened ventral side of the rectangle providing a planing surface that may aid during takeoff. The ventral lobe of the caudal fin is 10%

BOX
8.1

Swimming in Sharks: The Alternative Approach

Different fish lineages have evolved a variety of solutions to the challenges of locomotion in water. In the process, mutually exclusive specializations for cruising, rapid starts, or maneuverability have arisen (see above). The fossil record indicates that similar body morphologies and an apparent trend toward increasing concentration of activity in the tail region have appeared repeatedly during osteichthyan evolution (Webb 1982; see Chap. 11). These patterns and trends all capitalize on the substantial stresses that can be placed on a rigid, bony skeleton and the forces achievable by muscle masses attached directly or indirectly to bony structures. Elasmobranchs are phylogenetically constrained by a relatively flexible and comparatively soft cartilaginous skeleton. Evolution of locomotion in chondrichthyans has, not surprisingly, taken a different albeit parallel path.

Most elasmobranchs swim via undulations, either of the body (sharks) or of the pectoral fins (skates and rays). Most sharks swim using anguilliform locomotion, although the amplitude of each wave in the caudal region is greater in swimming sharks than in eels. This exaggerated sweep of the posterior region probably capitalizes on the increased thrust available from the large heterocercal tail of a shark. Exceptions to anguilliform swimming include the pelagic, predatory mackerel sharks, which have converged in body form and swimming type with tunas, dolphins, and ichthyosaurs (see above). Skates and rays also undulate, passing undulations posteriorly along their pectoral fins while the body is held relatively rigid. The exception in this group is the torpedo rays, which differ in that they have an expanded tail fin and swim via ostraciiform oscillations. In these strongly electrogenic rays, the pectoral region is unavailable for swimming because it is modified for generating electricity.

The mechanics of swimming in sharks are fascinating and somewhat controversial. Three topics have received the most attention, involving the functions of the median fins, skin, and tail during locomotion. Despite anguilliform locomotion, most sharks are active, cruising predators with relatively streamlined bodies. This would seem anomalous given the relatively low efficiency of the anguilliform mode and the apparent incompatibility of a fusiform body bent into long propulsive waves. However, sharks enhance the

efficiency of their swimming mode in several ways.

Most sharks have two dorsal fins, the first usually larger than the second, separated by a considerable gap. The dorsal lobe of the pronounced heterocercal tail may be thought of as a third median fin in line with the dorsal fins, again separated from the second fin by a considerable gap. The distances between the three fins are apparently determined by the size of the fins, their shapes, and the waveform of swimming of the fish. Each fin tapers posteriorly, leaving behind it a wake as it moves through the water. This wake is displaced laterally by the sinusoidal waves passing down the fish, so the wake itself follows a sinusoidal path that moves posteriorly as the fish moves through the water. This wave is slightly out of phase with the fish's movements by a constant amount.

Calculations of the phase difference and wave nature of the wake suggest an ideal distance between fins that would maximize the thrust of the second dorsal and particularly of the tail. If timed correctly, the trailing fins can push against water coming toward them laterally from the leading fins. Such an interaction between flows would enhance the thrust produced by the trailing fin. Measurements of swimming motions and fin spacing in six species of sharks indicate just such an interaction (Webb and Keyes 1982; Webb 1984). Unlike bony fishes that use their median fins for acceleration and braking but fold them while cruising to reduce drag, sharks use their median fins as additional, interacting thrusters.

The energy provided with each propulsive wave of muscular contraction is additionally aided by an interaction between the skin and the body musculature of a shark. The skin includes an inner sheath of two layers of collagen fibers that are mechanically similar to tendons. The fibers in one layer lie at about a 60° angle to the fibers in the adjacent layer, thus creating a cylinder reinforced with a double helix of wound fibers, an exceptionally strong and incompressible—but readily bendable—structure (S. Wainwright 1988).

Inside the skin, hydrostatic pressure varies as a function of activity level. The faster the shark swims, the higher the internal hydrostatic pressure. Pressure during fast swimming is about 10 times what it is during slow swimming, ranging between 20 and 200 kilopascals. Internal hydrostatic pres-

BOX
8.1*(Continued)*

sure develops from unknown sources, probably due to changes in the surface area of contracting muscles relative to skin area and to changes in blood pressure in blood sinuses that are surrounded by muscle. The shark's body is therefore a pressurized cylinder with an elastic covering.

During swimming, the higher the internal pressure, the stiffer the skin becomes, which increases the energy stored in stretched skin. Body muscles attach via collagenous septa not just to the vertebral column but also to the inside of the skin (for this reason, it is exceptionally difficult to remove the skin from the muscle of a shark). As the muscles on the right side of the body contract, muscles and skin on the left side are stretched. The stretched skin is very elastic, but stretched muscle is less so. As muscles on the right side relax, the energy stored in the skin on the left side is released, aiding muscles on the left side at a point when they can provide relatively little tension. Therefore, the skin may act in initiating the pull of the tail across the midline and increase the power output at the beginning of the propulsive stroke.

The faster the shark swims, the greater the elastic recoil from the stretched skin. Muscles attach to the relatively narrow vertebral column of calcified cartilage but also attach to the much larger surface area of stiff, elastic skin that encompasses the shark from head to tail and in essence forms a large, cylindrical external tendon. Muscles pulling on the skin provide propulsive energy that probably exceeds the thrust derived from muscles attached to the vertebral column (Wainwright et al. 1978; Wainwright 1983).

Most of the power in shark swimming comes from the tail, but this tail is not symmetrical as it is in most bony fishes. The heterocercal tail, with its expanded upper lobe, would seem to provide a lifting force to the posterior end of the body. This lift should cause the body to rotate around its center of mass, plunging the anterior end in a perpetual dive (Fig. 8.2A).

One long-held explanation is that the flat underside of the head and particularly the broad stiff pectoral fins create lift at the anterior end to counteract the downward force. However, it seems inefficient for the tail and the pectoral fins to function against each other, the tail propelling and the pectoral fins continually braking the shark's progress. Given the 400-million-year success of elasmobranchs and the

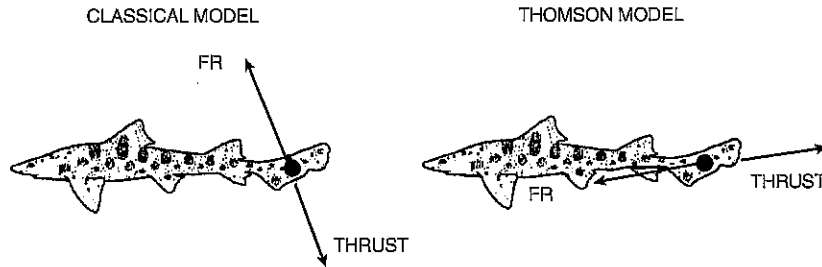
widespread occurrence of heterocercal tails in many previously speciose lineages of both bony and cartilaginous fishes, it is hard to imagine that heterocercal tails are inherently inefficient. This apparent dilemma has prompted an ongoing search for mechanisms that promote relatively straight forward propulsion.

The search has turned into something of a debate. The classic model, as described above, indicates that the tail pushes back and down on the water, creating an equal and opposite resulting force up and forward, which is counteracted by paired fins and head shape to produce forward movement. The classic model is supported by video analysis and dye-tracer studies (Ferry and Lauder 1996). These more recent findings refute earlier interpretations of photographs and selective amputation of fin parts of tails held in a test apparatus (Fig. 8.2B; Simons 1970; Thomson 1976, 1990), which suggested that forward thrust is generated by differential movements of the upper and lower lobes of the tail.

The answer to how sharks climb, dive, and turn—rather than pivoting around their center of balance—probably lies in their ability to continually adjust the relative angles of attack not only of their tail fin parts but also of their pectoral and other fins. Maneuverability in bony fishes usually involves deep, compressed bodies and use of median and pectoral fins; to accelerate, bony fishes increase the frequency of their tail beats. Sharks, with their streamlined bodies and relatively rigid fins, have taken a different evolutionary path to achieve maneuverability that may involve tail lobe dynamics and paired fin adjustments. Sharks change speed by altering tail beat frequency, but they also vary tail beat amplitude and the length of the propulsive wave passing down their body (Webb and Keyes 1982).

Sharks have taken the relatively inefficient anguilliform swimming mode imposed by their flexible bodies, and combined elastic skin, rigid but carefully spaced median fins, and a dynamic heterocercal tail to achieve an efficient compromise among cruising, acceleration, and maneuverability. The actual mechanics of swimming in sharks and bony fishes are still a matter of debate and research, but our growing understanding underscores the intricacies and importance of locomotory adaptations in fishes.

FIGURE 8.2. The two competing models that explain how forward locomotion is accomplished in sharks. The classical model interprets the shape of the heterocercal tail as generating a downward and backward thrust, which has a resultant force (FR) that is upward and forward. The resultant force would then cause the head of the shark to be pushed downward, but this motion is countered by the planing surfaces of the pectoral fins and head. In the alternative Thomson model, upper and lower lobes of the tail provide counteracting forces that drive the fish directly ahead.



From Ferry and Lauder 1996; used with permission of the authors.

to 15% larger in surface area than the dorsal lobe and is the only part of the body in contact with the water during taxiing. The pectoral fins are supported by enlarged pectoral girdles and musculature. The pectoral fins differ from normal teleost fins in the shape of and connections between the lepidotrichia, and the pectoral fin rays are thickened and stiffened, giving the leading, trailing, dorsal, and ventral surfaces more of a winglike than a finlike construction. In some flyingfishes, pelvic fins also contribute lift and are appropriately modified.

Some other atheriniform fishes such as needlefishes and halfbeaks also propel themselves above the water's surface by rapidly vibrating their tail, the lower lobe of which is the only part still in the water. Some halfbeaks have relatively large pectoral fins and engage in gliding flight. Gradations of pectoral fin length and lower caudal lobe strengthening and lengthening among atheriniforms provide a good example of apparent steps in the evolution of a specialized trait, namely flying (Lindsey 1978; Davenport 1994).

FEEDING: BITING, SUCKING, CHEWING, AND SWALLOWING

Adaptations concerned with feeding clearly involve structures used in food acquisition and processing, such as jaw bones and muscles, teeth, gill rakers, and the digestive system. Less obvious, but also important, are morphologic adaptations in eye placement and function, body shape, locomotory patterns, pigmentation, and lures. The functional morphology of feeding deserves detailed exploration because of its intimate linkage to all aspects of fish evolution and biology.

For many fishes, a simple glance at jaw morphology, dentition type, and body shape allows accurate prediction of what a fish eats and how it catches its prey. Small fishes with fairly streamlined and compressed bodies, forked tails, limited dentition, and protrusible mouths that form a circle when open are in all likelihood zooplanktivores. This

generalization holds for fishes as diverse as osteoglossomorph mooneyes, clupeomorph herrings, ostariophysine minnows, and representative acanthopterygian groupers (e.g., *Anthias*), snappers (*Caesio*), bonnetmouths (*Inermia*), damselfishes (*Chromis*), and wrasses (*Clepticus*).

Large, elongate fishes with long jaws studded with sharp teeth for holding prey, and with broad tails adjoined by large dorsal and anal fins set far back on a round body are piscivores that ambush their prey from midwater with a sudden lunge (see Chap. 18). An alternative piscivorous morphology includes a more robust, deeper body, fins distributed around the body's outline, and a large mouth with small teeth for short chases and engulfing prey; this is the "bass" morphology of many acanthopterygian predators such as kelp basses, striped bass, sea basses, black basses, and peacock bass, all in different families.

Generalized body shapes in predators do not exclude highly successful specialists that have arrived at very different solutions to catching mobile prey. Examples include lie-in-wait and luring predators (goosefishes, frogfishes, scorpionfishes, stonefishes, flatheads, death-feigning cichlids), cursorial predators that run down their prey (needlefishes, bluefish, jacks, mackerels, billfishes), electrogenic predators that shock prey into immobility (torpedo rays, electric eels), or fishes with either an elongate anterior or posterior region for slashing and incapacitating prey (thresher sharks, sawfishes, billfishes).

A strong correspondence between morphology and predictable foraging habits exists in most other trophic categories, including herbivores (browsers, grazers, phytoplanktivores), scavengers, mobile invertebrate feeders, sessile invertebrate feeders, and nocturnal planktivores, to name a few. Convergent solutions to similar selection pressures are a striking characteristic of the foraging biology of fishes (Keast and Webb 1966; Webb 1982).

Our emphasis here will be on the functional morphology of structures directly responsible for engulfing and processing food. Moderate detail is provided, but we can only superficially discuss the diversity in structure, action, and interconnection among the 30 moving bony ele-

ments and more than 50 muscles that make up the head region of most fishes.

Jaw Protrusion: The Great Leap Forward

Jaws evolved in fishes. The major difference between vertebrates and invertebrates is not so much the development of an ossified and constricted backbone; coelacanths, lungfishes, and sturgeons all lack distinct vertebral centra. The real advance that undoubtedly drove vertebrate evolution was the assembly of closable jaws used in feeding. The mechanics of jaw function and adaptive variation in jaw elements tell us a great deal about both how fishes feed and how fishes evolved.

As will be discussed in Chapter 11, one of the major advances made by, but not exclusive to, higher teleosts is the ability to protrude the upper jaw during feeding. Jaw protrusion makes possible the **pipette mouth** of the higher teleosts. Pipetting creates suction forces that can pull items from as far away as 25% to 50% of head length. Jaw protrusion also functions to overtake a prey item, extending the food-getting apparatus around the prey faster than the predator can move its entire body through the water. Attack velocity may thus be increased by up to 40%. As many as 15 different functions and advantages have been postulated for the protrusible jaw of teleosts. These advantages generally involve increased prey capture ability and efficiency but also suggest that antipredator surveillance and escape ability may be enhanced (Lauder and Liem 1981; Motta 1984).

The elements involved in jaw protrusion include the bones of the jaw (premaxilla, maxilla, mandible), ligamentous connections of these bones to the skull and to each other (premaxilla to maxilla, ethmoid, and rostrum; maxilla to mandible, palatine, and suspensorium; mandible to suspensorium), and several muscles, notably the epaxials, levator operculi, hypaxials, adductor mandibulae, and levator arcus palatini (Fig. 8.3).

During jaw protrusion, the entire jaw moves forward and slightly up or down. Protrusion in a generalized percomorph occurs as the cranium is lifted by the epaxial muscles and the lower jaw is depressed by muscles associated with the opercular and hyoid bone series. Movement of the mandible causes the maxillary to pivot forward, the suspensorium (the hinge joint that suspends the lower jaw from the cranium) contributing to maxillary rotation. The descending process of the premaxillary is connected to the lower edge of the maxillary, so the premaxillary is pushed forward, its ascending process sliding forward and down the rostrum.

The jaw is closed through the actions of the adductor mandibulae muscle on the mandible, the levator arcus palatini on the suspensorium, and the geniohyoideus on the hyoid apparatus. Many variations on this simplified description exist, differing among taxa in terms of twisting of jaw bones, points of attachment and pivot between structures, inclusion of other small bony elements, and actions of muscles and ligaments on particular elements (Motta 1984).

Jaw protrusion creates rapid water flow that carries edible particles, both small and large, into the fish's

mouth. Suction velocity increases from 0 to as much as 12 m/sec in as little as 0.03 second (Osse and Muller 1980). Fishes that feed on such different prey as phytoplankton, zooplankton, macroinvertebrates, and other fishes utilize suction to capture prey; the larger the object, the more suction pressure must be produced to capture it. Suction feeding, also known as **inertial suction**, results from rapid expansion of the buccal (mouth) cavity, which creates negative pressure in the mouth relative to the pressure outside the mouth. Particles in the water mass ahead of the fish are carried into the mouth along with the water. The jaws then close, pushing the water out the gill covers but retaining the prey in the mouth. Gill rakers, jaw teeth, and teeth on various nonmarginal jaw bones (palate, vomer, tongue) act as mechanical barriers to escape out the opercular chamber.

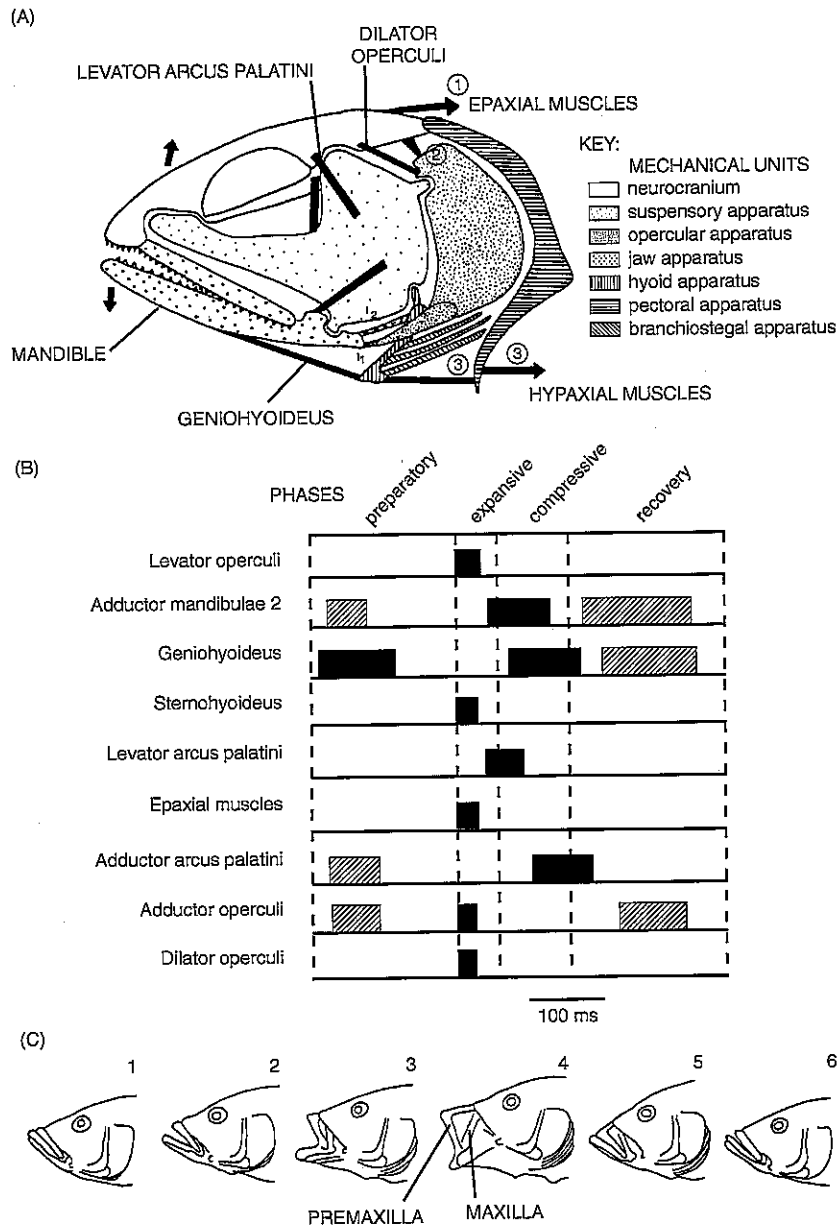
Suction pressures vary during a feeding event in advanced percomorphs, increasing and decreasing four times. The four phases of suction feeding are preparation, expansion, compression, and recovery (Lauder 1983a, 1985). During **preparation**, as the fish approaches its prey, pressure in the buccal cavity increases as a result of inward squeezing of the suspensorium and lifting of the mouth floor.

The **expansion** phase is when maximal suction pressure develops; the mouth is opened to full gape via lower jaw depression, premaxillary protrusion, and expansion of suspensory, opercular, and mouth floor (hyoid) units. Expansion is the shortest phase during jaw activity, requiring only 5 milliseconds in some anglerfishes. The negative pressures generated during expansion can reach -800 cm H₂O (0.7 atmospheres) in bluegill sunfish, approaching the physical limits imposed by fluid mechanics. Such rapidly achieved low pressures cause cavitation, which involves water vapor suddenly coming out of solution and forming small vapor-filled cavities (the bubbles produced behind an accelerating boat propeller result from cavitation) (Lauder 1983a). The popping noise made during feeding by bluegill may result from the collapse of cavitation bubbles.

The **compression** phase occurs and pressure increases as the mouth is closed by reversing the movements of cranial bones, an activity that requires contraction of a different set of muscles (see Fig. 8.3B). The opercular and branchiostegal valves at the back of the head open up after the jaws close, which allows water but not prey to flow out of the buccal and opercular cavities. **Recovery** involves a return of bones, muscles, and water pressure to their preparatory positions.

Modifications of this basic plan underscore some rather spectacular derivations that allow specialized feeding activities. In cichlids, the suspensorium and maxilla are mechanically decoupled. Jaw protrusion occurs as a result of movement of the suspensorium, independent of the maxilla. The consequence of this decoupling of suspensorium and maxilla is that the jaw can be protruded via four different pathways: lifting the neurocranium, abducting the suspensorium, lowering the mandible, or swinging the maxilla. Cichlids make use of different combinations of jaw elements and protrusion pathways to feed on different prey types or in different habitats. High-speed motion picture analysis of jaw action indicates that

FIGURE 8.3. Opening, protrusion, and closing of the jaw in most percoids. (A) Jaw opening involves three major couplings of muscles, ligaments, and bones: 1) epaxial muscles that lift the cranium; 2) levator operculi muscles that move opercular bones up and out and help depress the mandible; and 3) hypaxial muscles that depress the mandible via actions of the hyoid apparatus. (B) Electrical activity of different muscle groups as measured during four phases of jaw opening and closing. Blackened bars represent major muscle activity; cross-hatched bars indicate occasional activity. Abductors move bones outward; adductors move bones inward. (C) The sequence of events during opening and closing of the jaw of a cichlid, *Serranochromis*: 1 = preparatory; 2-4 = expansion; 5-6 = compression.



(A), (B) slightly modified from Lauder 1985; (C) from Lauder 1985 after Liem 1978; used with permission.

some cichlids may use eight different feeding patterns in which they vary their gape, biting force, and amount of jaw protrusion depending on the prey type, location, and behavior. The cichlid jaw is the closest that fishes have come to a prehensile feeding tool. Cichlids show a diver-

sity of foraging types unequalled in any other fish family (see Chap. 15). It is likely that the derived trait of a decoupled suspensorium and resulting trophic versatility have contributed greatly to their success (Liem 1978; Lauder 1981; Motta 1984; Liem and Wake 1985).

Fishes other than cichlids have reworked the basic elements of jaw protrusion and have evolved dramatic specializations that increase attack velocity or suction. As mentioned in Chapter 11, the pikehead, *Luciocephalus pulcher*, shoots its jaw out, increasing its attack speed from 1.3 m/sec to 1.8 m/sec. Little suction is generated during a strike. Extreme and rapid jaw protrusion in this species involves modified anterior vertebrae and massive epaxial muscles and tendons that run from the vertebrae to the posterior part of the cranium. Upward flexion of the head, made possible by a highly bendable neck, leads to extreme jaw protrusion. Other predators have converged on analogous neck-bending abilities to increase prey capture efficiency, including a characin and two cyprinids (Lauder and Liem 1981).

Suction pressure is produced via expansion of the buccal cavity. A generalized perciform such as the yellow perch increases its mouth cavity volume by a factor of six, creating a negative pressure capable of supporting a water column about 15 cm high. The apparent record for volume increase is held by a small (30 cm long), bizarre, elongate midwater fish, *Stylophorus chordatus*. *Stylophorus*, among its other oddities, has a tubular mouth and a membranous pouch that stretches dorsally from its mouth to its braincase. During feeding, the fish throws its head back and thrusts its tubular mouth forward. The mouth becomes separated from the braincase by a distance of about 1 cm, the intervening space being filled by the now expanded membranous pouch. Mouth volume increases almost 40-fold, creating pressures three times greater than in the generalized perch. The fish engulfs copepods as water rushes in at a calculated velocity of 3.2 m/sec, from as far away as 2 cm (Pietsch 1978).

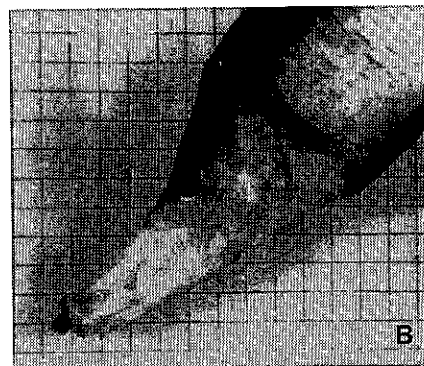
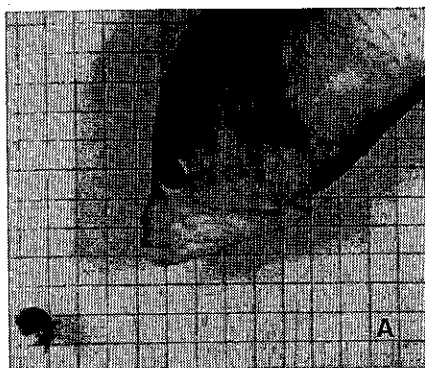
Another extreme of jaw protrusion occurs in the tropical sling-jaw wrasse, *Epibulus insidiator* (Westneat and Wainwright 1989). Sling-jaws protrude their jaws up to 65% of their unextended head length, which is twice the

extension found in any other fish (Fig. 8.4). This extreme protrusion is accomplished via a major reworking of many jaw elements. Several bones in the sling-jaw's head have unique sizes and shapes, including the quadrate, interopercle, premaxilla, and mandible. Ligaments connecting these bones are unusually large, and a ligament found in no other fish links the vomer to the interopercle.

The modified bones undergo extreme and in some cases unique rotations during jaw protrusion; the lower jaw actually moves forward during protrusion, a departure from the depression movement seen in all other fishes. The sling-jaw shoots its mouth out at small fishes and crustaceans on coral reef surfaces, suctioning them into its mouth. It achieves a strike velocity of 2.3 m/sec, but all of this speed is contributed by the jaw, because the fish hovers almost still in the water while attacking prey. Extreme jaw protrusion in sling-jaws involves the evolution of unique bones and ligaments, but the muscles of the jaw and skull have shapes, functions, and sequences of activity that differ little from generalized perciforms. Novel jaw function is therefore accomplished by drastic modification of some structures and retention of primitive condition in others. The sling-jaw exemplifies a widely made observation about the evolutionary process: that every species represents a mosaic of ancestral and derived traits.

Suction feeding has evolved repeatedly during fish evolution and occurs in many nonteleosts as well as in primitive and specialized teleosts that are unable to protrude their jaws. Elasmobranchs, including skates, rays, and such sharks as nurse sharks, can generate suction forces as strong as 1 atmosphere (about 1 kg/cm²) for feeding on buried mollusks or lobsters in reef crevices (Tanaka 1973). Lungfishes and bowfin among nonteleosts, and anguillid eels, salmon, pickerels, and triggerfishes among teleosts do not protrude their jaws but use inertial suction for feeding; sturgeons have independently evolved jaw protrusion and suction feeding.

FIGURE 8.4. Extreme jaw protrusion in the sling-jaw wrasse, *Epibulus insidiator*. The sling-jaw has novel bone shapes and extreme bone and ligament rotations, and has even invented a new ligament involved in jaw protrusion. (A) A 15-cm-long wrasse approaches its crustacean prey with its mouth in the retracted condition. Note that the posterior extension of the lower jaw, involving the articular and angular bones, extends as far back as the insertion of the pectoral fin. (B) During prey capture, the wrasse protrudes both its upper and lower jaws forward, extending them a distance equal to 65% of its head length. Jaw expansion creates suction forces that draw the prey into the mouth. Positions (A) and (B) are separated by about 0.03 second.



Suction in the nonprotruding species is often accomplished by rapid depression of the floor of the mouth. Triggerfishes and other tetraodontiform fishes such as boxfishes can reverse this flow and forcefully expel water from their mouths (Frazer et al. 1991). Alternate blowing and sucking are used to manipulate food items in the mouth during repositioning for biting. Blowing is also used for uncovering invertebrate prey buried in sand or for manipulating well-defended prey items. A Red Sea triggerfish, *Balistes fuscus*, feeds on long-spined sea urchins. The only spine-free region of the urchin is the oral disk around the mouth. Triggerfishes swim up to an urchin sitting on sand and blow a powerful jet of water at the urchin's base. The water stream lifts the urchin off the substrate and rolls it over, at which point the triggerfish bites through the now-exposed oral disk, killing the urchin (Fricke 1973). Triggerfishes also use blowing to uncover buried prey such as sand dollars. Blowing involves compression of the mouth via actions of muscles associated with the opercular, mandibular, and hyoid bones (Frazer et al. 1991; Turingan and Wainwright 1993).

Pharyngeal Jaws

Depression of the mouth floor also creates water flow toward the throat, thereby helping push food items posteriorly. Here the prey encounter a second set of jaws, the pharyngeal apparatus (see Chap. 11, Division Teleostei). Pharyngeal jaws evolved from modified gill arches and their associated muscles and ligaments. The lower pharyngeal jaws are derived from the paired fifth ceratobranchial bones, whereas the upper jaws consist of dermal plates attached to the posterior epibranchial and pharyngobranchial bones. Both jaws bear teeth that vary depending on the food type of the fish (see below). Dentition not only varies functionally among species that eat different food types but also may develop differently among individuals of a population as a function of the food types encountered by the growing fish. In the Cuatro Ciénegas cichlid of Mexico, *Cichlasoma minckleyi*, fish that feed on plants develop small papilliform pharyngeal dentition, whereas those that feed on snails develop robust molariform dentition (Kornfield and Taylor 1983).

In their simplest action, pharyngeal jaws help rake prey into the esophagus. They may additionally reposition the prey, immobilize it, or actually crush and disarticulate it. These actions involve at least five different sets of bones and muscles working in concert, including 10 different muscle groups and bones of the skull, hyoid region, lower jaw, pharynx, operculum, and pectoral girdle. The main action is the synchronous occlusion (coming together) of the upper and lower pharyngeal jaws. In cichlids, the prey is crushed between the anterior teeth of both pharyngeal jaws, pushed posteriorly by posterior movement of both jaws, and then bitten by the teeth of the posterior region of the jaws (Lauder 1983a,b; 1985).

Pharyngeal pads and their function as jaws influence feeding in another important manner. Gape limitation, the constraint on prey size imposed by mouth size (see Box 18.2), is in part determined by oral jaw dimensions: A fish cannot eat anything it cannot get into its mouth.

But gape limitation is also influenced by pharyngeal gape. If a prey item is too large to pass through the pharyngeal jaws, it is also unavailable to the predator. Hence many predators can capture but not swallow a prey item because of pharyngeal gape limitation.

In small-mouthed species, such as the bluegill sunfish, oral and pharyngeal gape differ only by 20% to 30%. But in piscivores that use oral protrusion for prey capture, such as the largemouth bass, oral jaws may be twice the size of the pharyngeal jaws, which means that usable prey size is considerably smaller than what can be engulfed by the mouth. Posterior to the pharyngeal jaws is the throat, the width of which is determined by spacing between the cleithral bones of the pectoral girdles. Thus a predator can only eat prey that can pass through its oral jaws, pharyngeal jaws, and intercleithral space (Lawrence 1957; Wainwright and Richard in press).

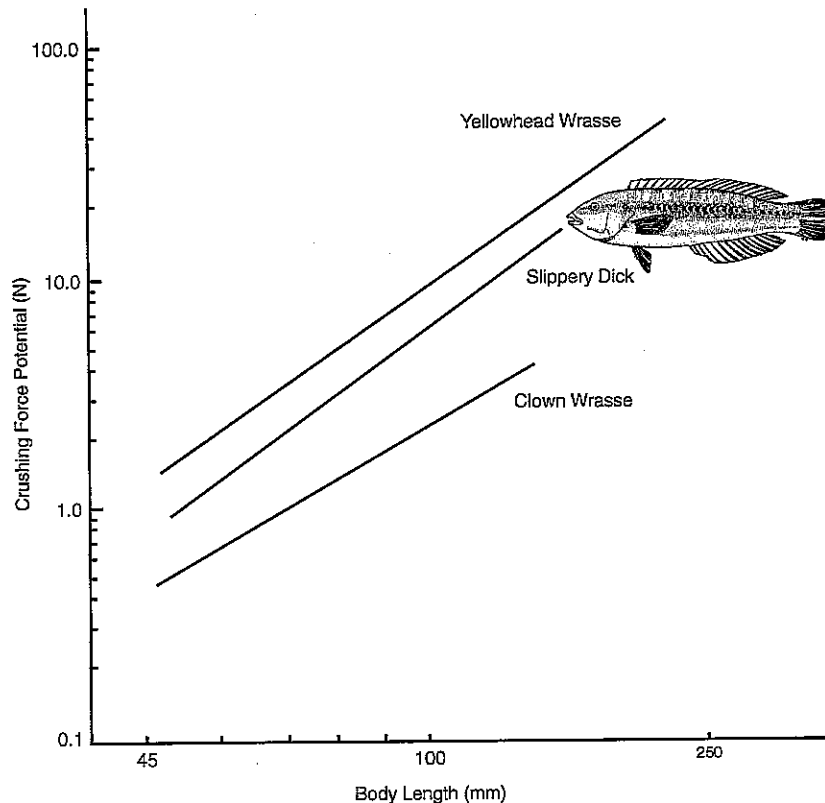
A crucial function of the pharyngeal apparatus in many species is therefore to crush prey to a size small enough to pass through the throat. Here prey morphology comes into play, because prey that is just small enough to fit between the pads may be too hard to crush and is thus unavailable to the predator. This interplay of structure, function, and the constraints created by the pharyngeal apparatus is shown nicely in Caribbean wrasses that feed on hard-bodied prey (P. Wainwright 1987, 1988). Wrasses, along with other "pharyngognath" fishes such as parrotfishes and cichlids, have a highly modified pharyngeal apparatus that can crush hard-bodied prey. The size of the muscles that move the pharyngeal jaws differs among three species, the clown wrasse (*Halichoeres maculipinna*), slippery dick (*H. bivittatus*), and yellowhead wrasse (*H. garnoti*). In all three species, muscle mass and pharyngeal gape increase with increasing body size (Fig. 8.5).

At any size, clown wrasses have smaller pharyngeal musculature than do the other two species. Small slippery dicks and yellowhead wrasses can crush and eat snails that are unavailable to larger clown wrasses. Small clown wrasses cannot crush even small snails. These abilities are reflected in the natural feeding preferences of the species. Small clown wrasses feed preferentially on relatively soft-bodied crabs and other invertebrates; they shift to snails only after attaining a body length of 11 cm, when they eat hard-bodied prey that are smaller than those taken by equal-sized fishes of the other two species. Slippery dicks and yellowhead wrasses feed extensively on snails beginning at a relatively small fish body length of 7 cm. Pharyngeal crushing strength accounts for inter- and intraspecific differences in feeding habits in these fishes; competitive interactions and optimal prey characteristics other than shell strength have little if any influence.

Dentition

The prey a fish eats and how those prey are captured are often predictable from the type of teeth the fish possesses. Even within families, species differ considerably in their dentition types as a function of food type and foraging mode (e.g., butterflyfishes, Motta 1988; cichlids, Fryer and Iles 1972; surgeonfishes, Jones 1968). Here we focus

FIGURE 8.5. *Crushing ability in three related wrasses as a function of body size. Larger wrasses can crush larger snails because of their stronger pharyngeal jaws, but differences among species also affect feeding preferences. Clown wrasses have relatively weak jaws and feed on relatively soft-bodied prey, particularly when the fish are younger. Slippery dicks and yellowhead wrasses have strong jaws and feed on shelled prey throughout their lives.*



From P. Wainwright 1988; used with permission of The Ecological Society of America. Slippery dick drawing from Gilligan 1989.

on general groups of foragers and how their dentition corresponds to food type.

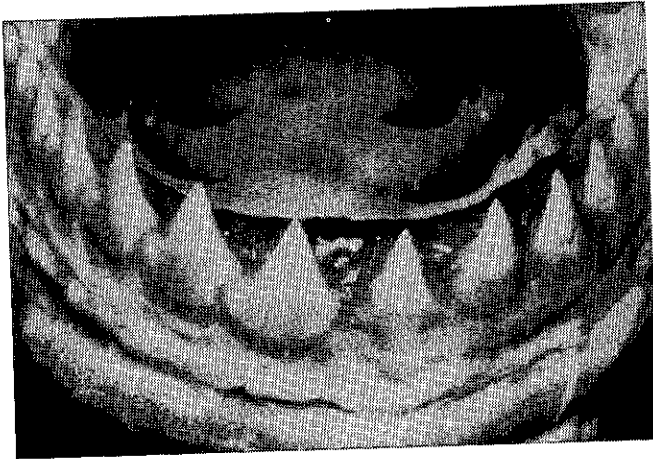
Piscivores and feeders on other soft-bodied, mobile prey such as squid show five basic patterns of marginal (= oral or jaw) teeth.

1. Long, slender, sharp teeth usually function to hold fish (mako, sandtiger, and angel sharks, moray eels, deep-sea viperfishes, lancetfishes, anglerfishes, goosefishes). In some groups (e.g., goosefishes, anglerfishes; also esocid pikes), elongate dentition is repeated on the palatine or vomerine bones. These medial teeth point backward and may have ligamentous connections at their base, which allows them to be depressed as prey is moved toward the throat but prevents escape back through the anterior jaws.
2. Numerous small, needlelike **villiform** teeth occur in elongate, surface-dwelling predators such as gars and needlefishes, as well as more benthic predators such as lizardfishes and lionfishes.
3. Flat-bladed, pointed, **triangular** dentition is usually used for cutting off prey and is found in such

fishes as requiem sharks, piranhas, barracudas, and large Spanish mackerels. Piranhas have teeth that are remarkably convergent in shape with those of many sharks (Fig. 8.6). In sharks, the lateral margins of blade-like teeth are often serrated, which enhances their cutting function when the head is shaken or the jaws are opened and closed repeatedly. Sharks and piranhas, as well as other characins, have also converged on replacement dentition. Tooth replacement occurs in a few other teleostean groups, including some salmon, wrasses, filefishes, and triggerfishes (Roberts 1967; Shellis and Berkowitz 1976; Tyler 1980).

4. Recurved, conical **caniniform** teeth with sharp points characterize such piscivores as bowfin, cod, snappers, and some sea basses. Sharp, conical dentition serves to grasp and hold. It reaches its extreme form in the almost triangular, fanglike, slightly flattened teeth of the African tigerfish, *Hydrocynus*.
5. Surprisingly, many highly predaceous piscivores have limited marginal **cardiform** dentition that has a rough sandpaper texture and consists of nu-

FIGURE 8.6. Convergence in dentition among predatory fishes. The triangular, razor-sharp teeth of a piranha, *Pygocentrus nattereri*, are remarkably similar in shape and action to those of many sharks. Note the small lateral cusps at the base of the teeth, a feature also shared with many sharks. Piranhas also replace their teeth as do sharks, but piranhas alternately replace all teeth in the left or right half of a jaw, rather than replacing individual teeth or rows of teeth. The teeth in the left side of the jaw (= right side of photo) have recently erupted.



From Sazima and Machado 1990; used with permission.

merous, short, fine, pointed teeth (e.g., large sea basses, snook, largemouth bass, billfishes). The former species rely on large, protrusible mouths for engulfing prey fishes, whereas billfishes immobilize their prey by slashing or stabbing with the bill (see Box 18.1).

Often, a predator will have a mixture of dentition types, such as anterior canines followed by or intermixed with smaller, needlelike teeth (e.g., the pike-characin *Hepsetus*), or long canines intermixed with smaller conical teeth (some wrasses). Ultimately, and regardless of location in the mouth and whether teeth are of one or several types, primary dentition type reflects food characteristics. The primary biting teeth of arid marine catfishes are palatine, not marginal, in location. Among 10 Australian species, piscivores have sharp, recurved palatine teeth; worm feeders have small, sharp recurved palatine teeth; and molluscivores have globular, truncated palatine teeth (Blaber et al. 1994).

Fishes that feed on hard-bodied prey, such as mollusks, crabs, and sea urchins, often have teeth and jaw characteristics that represent a separation of the activities of capturing versus processing prey. Many such fishes have strong conical dentition in the anterior part of their jaws for plucking mollusks from surfaces. The prey are then passed posteriorly to flattened, molariform teeth in marginal or pharyngeal jaws. Convergence is apparent when comparing mollusk-eating fishes from different taxa. Horn sharks (*Heterodontus*) have small conical teeth anteriorly that grade posteriorly into broad, rounded pads for crushing and grinding. Wolf-eels have strong, conical canines anteriorly and rows of rounded

molars posteriorly in each jaw. Similar anterior-posterior differences occur in freshwater drum, sheepshead, cichlids, and wrasses.

A suction versus chewing arrangement occurs in many fishes that feed on sand-dwelling mollusks. Suckers such as the river redhorse, *Moxostoma carinatum*, are ostariophysans in which the molarlike teeth occur on the pharyngeal arches. In ostariophysans, only the lower arch develops dentition, which usually occludes against horny pads in the roof of the mouth. In higher teleosts, the pharyngeal teeth are composed of both dorsal and ventral pharyngeal arch derivatives, such as in the redear or "shellcracker" sunfish, *Lepomis microlophus*. Analogously, stingrays suction mollusks off the bottom and then crush them in pavementlike dentition. Fishes that remove invertebrate prey such as sponges, ascidians, coelenterates, and chitons that are attached to surfaces tend to have powerful oral jaws either with incisor-like dentition (triggerfishes) or with teeth fused into a parrotlike beak (parrotfishes, pufferfishes). In parrotfishes, the beak bites off algae or pieces of coral that are then passed to the pharyngeal mill for grinding.

In addition to marginal, medial, and pharyngeal teeth, fishes have one other mouth region where hard structures aid in the capture or retention of prey. These are the gill rakers, which are bony or cartilaginous projections that point inward and forward from the inner face of each gill arch. As with the various teeth, gill raker morphology corresponds quite closely with dietary habits.

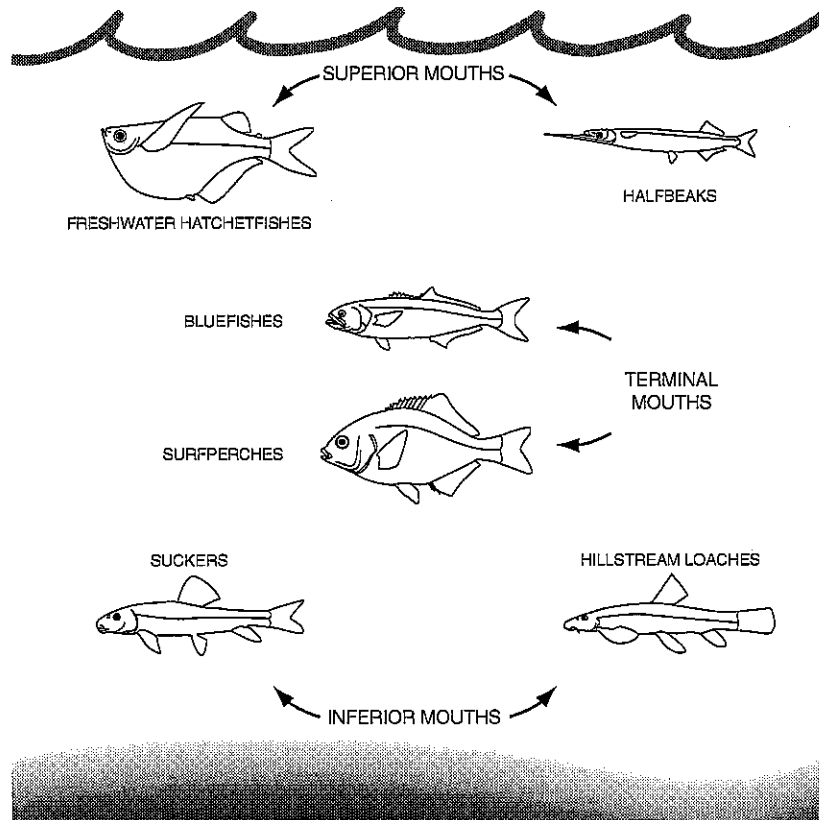
Piscivores and molluscivores, such as sea basses, black basses, and many sunfishes, tend to have short, widely spaced gill rakers that prevent escape of large prey out the gill openings. Fishes that eat zooplankton of large and intermediate size, such as bluegill sunfish and black crappie, have longer, thinner, and more numerous rakers. Feeders on small zooplankton, phytoplankton, and suspended matter have the longest, thinnest, and most numerous rakers; menhaden, *Brevoortia* spp., filter phytoplankton, detritus, and small zooplankters and have more than 150 rakers just on the lower limb of each gill arch.

Among related species, gill rakers differ according to diet. In North American whitefishes (Coregoninae), the inconnu (*Stenodus leucichthys*) feeds on small fishes and has 19 to 24 rakers; the shortnose cisco (*Coregonus reighardi*) feeds on mysid shrimp, amphipods, and small clams and has 30 to 40 rakers; whereas the cisco (*C. artedii*) eats small zooplankters, midge larvae, and water mites and has 40 to 60 rakers (Scott and Crossman 1973). In most filter-feeding fishes, particles are captured by mechanical sieving, whereby large particles cannot pass through narrow spaces between gill rakers. Electrostatic attraction, involving capture of charged particles on mucus-covered surfaces, is also suspected (Lauder 1985).

Mouth Position and Function

Mouth position, in terms of whether the mouth angles up, ahead, or down, also correlates with trophic ecology in many fishes (Fig. 8.7). The vast majority of fishes, regardless of trophic habits, have **terminal** mouths, which means that the body terminates in a mouth that

FIGURE 8.7. Correspondence among mouth position, feeding habits, and water-column orientation in teleosts. Fishes with supraterrinal mouths frequently live near and feed at the surface, whereas fishes with subterminal mouths often scrape algae or feed on substrate-associated or buried prey. Fishes with terminal mouths often feed in the water column on other fishes or zooplankton but are also likely to feed at the water's surface, from structures, and on the bottom. See also Fig. 23.3



Fish drawings from Nelson 1994; used with permission.

opens forward. Deviations from terminal location usually indicate habitat and feeding habit. Fishes that swim near the water's surface and feed on items at the surface often have mouths that open upward, termed **superior** or **supraterrinal** (e.g., African butterflyfishes, freshwater hatchet or flyingfishes, halfbeaks, topminnows). Some predators that lie on the bottom and feed on prey that swim overhead also have superior mouths (stonefishes, weeverfishes, stargazers).

Mouths that open downward, termed **subterminal** or **inferior**, characterize fishes that feed on algae or benthic organisms, including suckers, some North American minnows, suckermouth armored catfishes, Chinese algae eaters, some African minnows and cichlids, clingfishes, and loach gobies. Upside-down catfishes feed on the undersides of leaves but do so while swimming upside down; not surprisingly, they have inferior mouths. Fishes that do not have to visually fix on their prey (e.g., algae-scraping clingfishes, catfishes, loaches, some cichlids), or that take somewhat random mouthfuls of sediments that are then sifted orally (suckers, mojarras), may gain an antipredator advantage by having an inferior mouth. A terminal mouth in such fishes would require that they angle head

down each time they scraped or sampled the benthos, which would make them less able to escape rapidly if surprised by a predator.

Specialized suctorial mouths characterize unrelated fishes that scrape algae from rocks, particularly if they also live in high-energy environments. This ecological grouping includes hillstream loaches, suckermouth armored catfishes such as the familiar *Plecostomus* of the aquarium trade, Southeast Asian algae eaters, and the loach gobies of Australia. The gyri-nocheilid algae eaters live in swift streams where they rasp algae from rocks with their lips while remaining attached with their suctorial mouth. Gyri-nocheilids have evolved an additional incurrent opening dorsal to the operculum that opens into the gill chamber. They breathe in through the dorsal opening and out through the operculum. Drawing water in through the mouth in the more normal manner would require the fish to detach from the substrate, at which moment it might risk being swept downstream. Mouths are not the only way for algae feeders to remain attached in wave-swept habitats. Gobiesocid clingfishes accomplish this via pelvic fins modified into a suction disk (Wheeler 1975; Nelson 1994).

SUMMARY

1. Functional morphology focuses on how structures work in the context of the daily tasks and interactions experienced by organisms. Locomotion and feeding offer many intriguing examples of the structure-function relationship. Locomotion in water presents very different physical challenges than are experienced by terrestrial animals. Density and drag are much greater in water, making locomotion energetically expensive and leading to the general hydrodynamic, streamlined shape of most fishes.
2. Swimming in fishes usually involves alternating contractions and relaxations of muscle blocks on either side of the body that result in the fish pushing back against the water and consequently moving forward. Many variations on this basic theme exist, and about 10 different modes of swimming have been identified that involve either undulatory waves or oscillatory back-and-forth movements of the body or fins. Body and fin shape correlate strongly with locomotory mode and habitat, the most extreme examples being the rapid-swimming, highly pelagic mackerel sharks, tunas, and billfishes with streamlined bodies and lunate, high aspect ratio tails.
3. Locomotory adaptations create trade-offs. Maneuverability is often achieved at a cost in fast starts and sustained speed and vice versa. Versatility is achieved by using different modes for different purposes (fin sculling for positioning, body contractions for fast starts and cruising), which causes most fishes to evolve generalist rather than specialized swimming traits. Highly specialized locomotion includes fishes that can "walk" across the bottom or on land, climb terrestrial vegetation, leap, glide, and even fly.
4. Sharks, being cartilaginous, cannot rely on muscles attached to a rigid bony skeleton for propulsion. They instead undulate via contractions of their body muscles, which are firmly attached to a relatively elastic skin; the skin functions as an external tendon and provides propulsive force by rebounding. Some propulsive force comes from changing hydrostatic pressure inside the cylinder of the shark's body. The spacing of the two dorsal fins aids the tail in propulsion, and both lobes of the tail work to provide forward thrust via mechanisms that are incompletely understood.
5. Food getting in fishes involves adaptations of the jaw bones and muscles, teeth, pharyngeal arches, gill rakers, and digestive system, as well as modifications in body shape, sensory structures, and coloration.
6. Food type can often be predicted from jaw and body shape and dentition type, regardless of taxonomic position. Zooplanktivorous fishes are usually streamlined, with compressed bodies, forked tails, and protrusible mouths that lack significant teeth. Lurking, fast-start piscivores are generally elongate, round in cross section, with broad tails, posteriorly placed median fins, and long, tooth-studded jaws that grab prey. Alternatively, many piscivores that pursue prey for short distances are more robust, with fins distributed around the body outline, and with large mouths for engulfing prey. Many specialists that depart from these norms can be found.
7. An important food-getting innovation among modern fishes, particularly in teleosts, was the development of protrusible jaws and the pipette mouth. Modifications to jaw bones, ligaments, and muscles allow a fish to shoot its upper jaw forward and increase the volume of the mouth cavity, both creating suction forces and increasing the speed with which a fish overtakes its prey.
8. In addition to anterior, marginal jaws and dentition on the roof of the mouth and tongue, teleosts have their gill arches modified into a second set of posterior, pharyngeal jaws. Pharyngeal jaws help move prey toward the throat and in many fishes serve to reposition prey for swallowing and for processing via crushing, piercing, and disarticulation. Pharyngeal teeth facilitate the eating of hard-bodied prey (mollusks, arthropods) and plant material.
9. Dentition type corresponds strongly with food type and is often repeated on the marginal jaws, vomer, palate, and pharyngeal pads. Piscivores and other predators on soft-bodied prey variously possess long, slender, sharp teeth; needlelike villiform teeth; flat-bladed triangular teeth; conical caniniform teeth; or rough cardiform teeth. Mollusk feeders have molariform teeth. Gill rakers also capture prey and may be numerous, long, and thin in plankton feeders, or widely spaced, stout, and covered with toothlike structures in predators on larger prey.
10. Mouth position also correlates with where a fish lives and feeds in the water column. Water-column feeders typically have terminal mouths that open forward, whereas surface feeders often have superior or subterminal mouths that open upward. Fishes that feed on benthic food types have subterminal or inferior mouths that open downward and that may generate suction forces that allow a fish to attach to hard substrates while feeding.

SUPPLEMENTAL READING

Alexander 1983; Duncker and Fleischer 1986; Gerking 1994; Gray 1968; Hildebrand 1982; Hildebrand et al. 1985; Hoar and Randall 1978; Pough et al. 1989; Videler 1993; Vogel 1981; Wainwright et al. 1976; Webb and Weihs 1983.