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Flexible Fins and Fin Rays as Key Transformations in Ray-Finned Fishes

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The aquatic world has been home to a remarkable diversity of fishes for at least 600 million years. Although there is certainly enormous variation in the strategies used by fishes to feed and capture prey, there is at least an equal diversity of locomotor modes and associated morphologies that fishes use to navigate the three-dimensional aquatic realm. Locomotion is essential for reaching patchy prey resources, for reproduction and displaying to potential mates, for migration, for escape from predators, and for maneuvering through complex habitats.

These many functional demands on fish locomotor systems have given rise to considerable variation in the shapes of fishes and their fins, as well as to a variety of movement patterns that fishes use to swim and maneuver (Lauder 2006; Webb 1975). At least some of these functional demands may conflict with one another, so that fish body shapes may be a compromise between, for example, fin and shape patterns that enhance acceleration and those that increase steady swimming performance (Webb 1975). Fish fins are highly variable in shape, and movement of fins varies considerably among different swimming behaviors within a species. Also, evolutionary trends in the functional design of fish fins have been documented since the beginnings of scientific comparative anatomy and paleontology (Agassiz 1833–1843; Owen 1854), and a number of historical patterns of transformation in

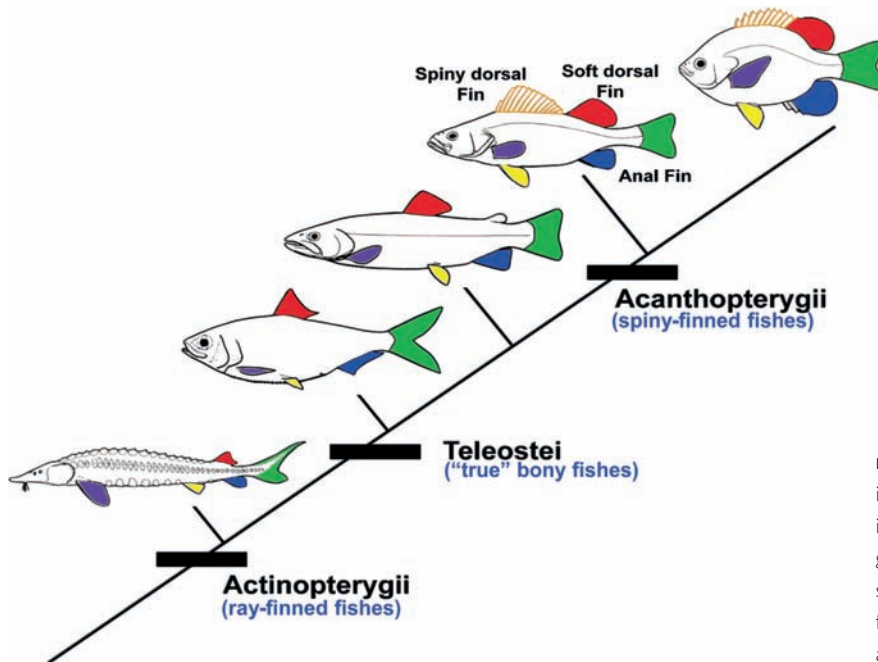* Department of Organismic and Evolutionary Biology, Harvard University

FIG. 2.1 Major patterns of fin position and shape in the evolution of ray-finned fishes. This diagram is a highly simplified phylogeny of selected major groups of ray-finned fishes to show changes in shape and position of the tail fin (green), pectoral fin (purple), pelvic fin (yellow), dorsal fin (red), and anal fin (blue).

fish locomotor design have been thoroughly discussed in the literature (Affleck 1950; Benton 1997; Breder 1926; Goodrich 1930; Lauder 1989; Lauder 2000; Romer and Parsons 1986; Rosen 1982).

This chapter will focus on a major transformation that characterizes the evolution of ray-finned fishes (Actinopterygii), the largest and most diverse clade of the general (non-monophyletic) group known as "fishes": functional design of fins. Ironically, the anatomy and function of fins is one of the least studied features of ray-finned fishes, despite being one of their most obvious characteristics and the one that gave the group its name! In particular, ray-finned fish fins have four key design features that are critical to locomotion in complex underwater habitats, and these four traits form an underlying theme to this chapter: (1) fins are flexible, (2) most fins in ray-finned fishes are collapsible, (3) fins are supported by flexible jointed fin rays with a unique bilaminar structure that allows active control of fin surface conformation, and (4) ray-finned fishes possess multiple sets of fins that allow them to take advantage of hydrodynamic interactions among fins, and to execute complex swimming behaviors requiring multifin control such as swimming backward.

Figure 2.1 summarizes schematically the overall pattern of ray-finned fish fin shape and position, although

within any individual clade different species may exhibit a variety of fin locations and shapes. The caudal fin in basal ray-finned fish clades such as sturgeon (as well as in many outgroup clades such as elasmobranchiomorphs) is heterocercal in shape, with an elongate upper lobe containing the vertebral column and a shorter lower lobe containing fin rays and some musculature but not vertebral elements. Most derived clades possess a homocercal tail in which the external shape of the upper and lower lobes is symmetrical around a horizontal axis, although the internal skeletal anatomy of the fin is somewhat asymmetrical in nature reflecting the ancestral heterocercal condition.

A general trend in pectoral fin placement is evident with basal clades typically possessing ventrally located fins with a predominant horizontal orientation (fig. 2.1). The pectoral fins of basal clades, while certainly mobile and used to adjust body position, display a considerably smaller range of motion than pectoral fins in more derived clades that are more wing-like and located on the lateral body surface.

The pelvic fins of ray-finned fishes (fig. 2.1) differ primarily in their location along the body and in their attachment to the axial skeleton and pectoral girdle. For the most part, the pelvic fins of basal clades are located posteriorly on the body in the tail region and have

skeletal supports that are embedded in the body wall, not attached to the axial skeleton. In derived clades, the pelvic fins are typically located more anteriorly, and may be attached to the pectoral girdle.

Dorsal and anal fins display a great variety of positions and shapes in ray-finned fishes, and broad evolutionary trends can be seen in fin position (fig. 2.1) as well as in changes in internal skeletal supports of these fins. In both basal and derived clades, dorsal and anal fin positions can mirror each other, with these fins having similar shapes and in similar longitudinal locations on the body. In other clades, the positions of dorsal and anal fins can be offset with the dorsal fin most commonly located more anterior to the anal fin. Dorsal and anal fins also can possess extremely elongate fin rays in some species of fishes, and show considerable variation in length and shape (fig. 2.1).

One general feature of fins in ray-finned fishes is so obvious that it often goes unstated: most fish fins are collapsible, or at least can undergo substantial active changes in surface area. This allows fish to adjust the area of fins that interacts with the water, and to fold fins against the body to minimize drag forces or to alter the balance of forces and torques on the body.

Another feature of ray-finned fish evolution that is relevant to understanding locomotor patterns is the swim bladder. Swim bladders (homologous to lungs) serve as organs that counter the weight of the skeleton and scales and allow for near-neutral buoyancy. Gas-filled inclusions in the body are present in the earliest fishes, and are retained as either lungs or swim bladders in the vast majority of ray-finned fishes (Brainerd, this volume; Liem 1989; Liem et al. 2001). By reducing the need to counter gravitational effects by producing lift forces, the swim bladder may have played a key role in permitting evolutionary diversification in locomotor modes and fin and body shapes in ray-finned fishes. Swim bladders have also become specialized in a number of clades and show an array of interesting functional designs that include oil-filled bladders and bladders encapsulated in bone, and have been lost in many benthic fish clades and deep-sea species where air bladders may be a liability. Studies of the correlated evolution of swim bladder function and fin and body shapes as fishes diversified into the three-dimensional aquatic habitat is an exciting area for future research.

Fin Rays of Ray-Finned Fishes: A Key Transformational Character

One would think that given a clade of over 30,000 species named for a key trait, the ray-fin, that this feature would have been studied in some detail, and the structural and mechanical properties of fin rays would be understood. But this is not the case. In fact, it is remarkable how little we know about both the structure and function of actinopterygian ray-fins.

Figure 2.2 illustrates a number of the features of ray-finned fish fin rays to provide an overview of the structural design of fin rays in this clade. The fin rays of sharks and living lungfish have a different design with a single rod-like element for each fin ray (Goodrich 1904; Goodrich 1906), and many of the features present in actinopterygian ray-fins are missing or greatly reduced in outgroup clades. For example, fin flexibility and collapsibility is greatly increased in most extant ray-finned fish clades as compared to most outgroups, although the contrast is greatest when teleost fish fins are compared to those of other extant outgroup taxa.

Perhaps most significant, however, is the bilaminar design of ray-finned fish fin rays, which contrasts with the organization of outgroup taxa. The fin rays of actinopterygians have a bilaminar structure with two halves (hemitrichia) comprising a single ray or lepidotrich (Alben et al. 2007; Geerlink and Videler 1987; Lauder, Madden, et al. 2011; Taft and Taft 2012). Fin rays may be fused into spines to support the anterior regions of dorsal and anal fins in some clades via a variety of developmental patterns, but the fin rays themselves are flexible structures that may branch toward their distal end (fig. 2.2). An unsegmented basal region of ray-finned fish fin rays is typical, while the middle and distal regions are segmented, which may increase the flexibility of rays (Alben et al. 2007; Taft and Taft 2012). The bilaminar and segmented design of actinopterygian fin rays has a particular functional significance: differential activity of muscles attaching at the base of these fin rays produces curvature of the fin ray surface (fig. 2.2F), allowing the fin to actively resist fluid loading. This feature can be of considerable importance during locomotion where fish may extend their fins into oncoming flow and stiffen the fin during a maneuver (Lauder and Madden 2006; Lauder and Madden 2007;
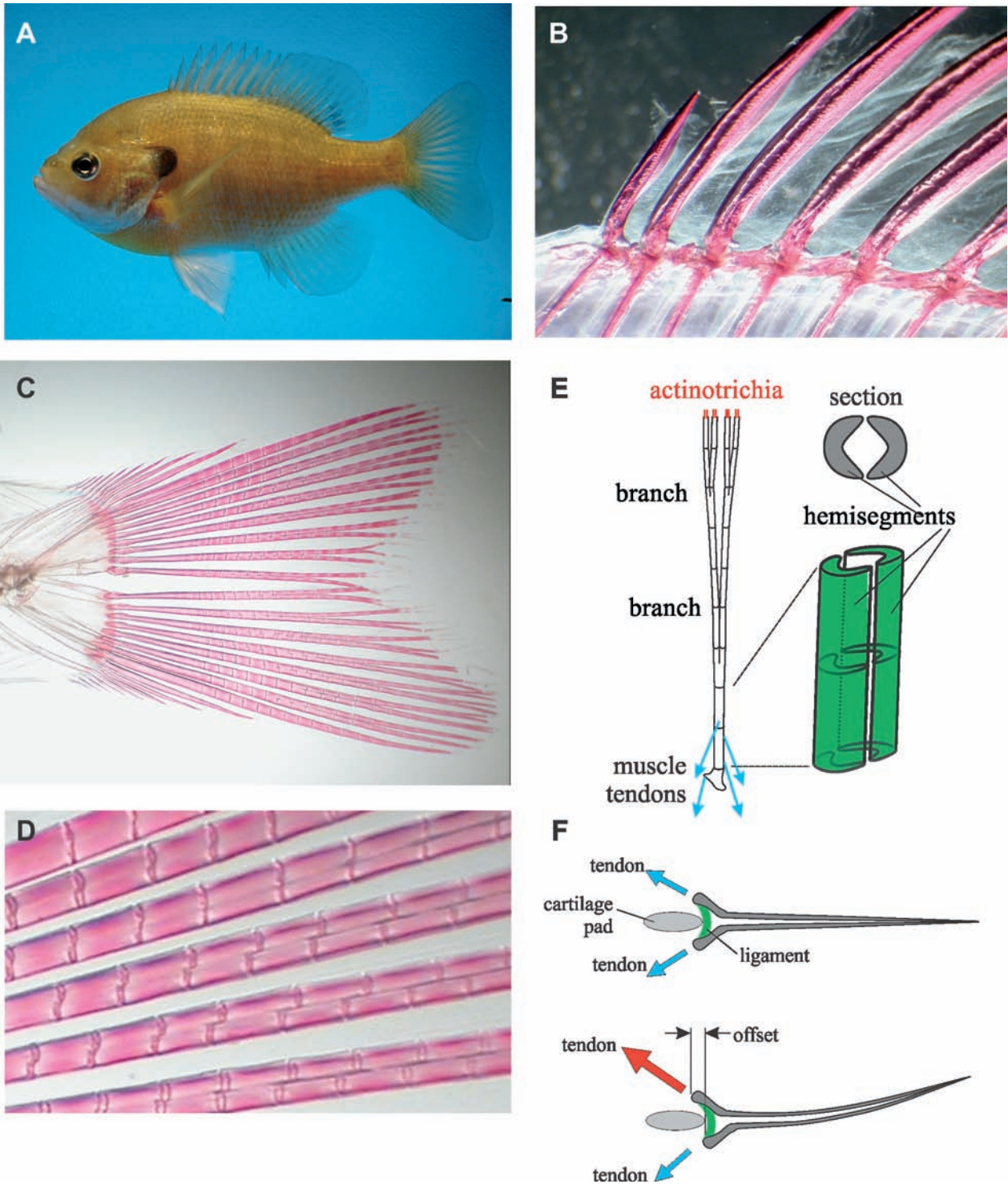
FIG. 2.2 Ray-finned fish fins (A) are supported by bony fin rays. In some clades rays are fused into spines supporting the anterior regions of the dorsal and anal fins (B). Fin rays (C) are composed of flexible jointed bony segments (D, E), each of which is itself divided into two hemisegments (E). Muscles at the base of each fin ray can produce a sliding motion (E, F) that allows fish to actively bend each fin ray and control the surface conformation of the fin. See Alben et al. (2007), Lauder et al. (2011b), and Lauder (2007).

Flammang et al. 2013). Active fin surface control is absent in outgroup taxa such as sharks and more basal groups like lamprey, placoderms, and acanthodians. These clades lack the bilaminar fin ray structure that is a prerequisite for active surface control.

The ability to actively control the conformation of a propulsive surface also contrasts with the functional design of propulsors such as bird feathers and insect wings that can be positioned as a whole in space, but cannot have their surface conformation altered actively by the animal.

Students wishing to make a simple model that illustrates the bilaminar design of ray-finned fish fin rays can use a commercial ziplock bag. Using scissors, cut off the bag just below the ziplock closure at the top to remove it, and then cut the remaining ziplock closure section in half transversely. Separate the two halves from one piece of the ziplock and you will see that the two halves are attached at the side. Zipping them together and then holding the open base between your thumb and forefinger will allow you to slide one half relative to the other half. When you do this, you will see the ziplock surface curve in space. With a little practice, considerable curvature of the ziplock closure can be achieved by sliding the two halves relative to each other. The ability to actively control the fin surface with muscles at the base of the fin has the additional advantage of not requiring the occurrence of muscles out along the fin length to achieve surface conformational changes. This in turn enables the fin to be thinner and lighter, and is a key innovation in the functional design of ray-finned fishes.

Recent functional studies of ray-finned fish fin rays have used techniques allowing control of individual hemitrichs as well as classical three-point bending and computational modeling to quantify mechanical properties of lepidotrichs (Alben et al. 2007; Flammang et al. 2013; Lauder, Madden, et al. 2011; Taft 2011; Taft and Taft 2012). At least for the relatively few species studied so far, actinopterygian fin rays vary in mechanical properties along the length of the ray with proximal regions being stiffer than distal (probably due to the unsegmented proximal region of the ray), and whole fin rays have an elastic modulus roughly equivalent to that of collagen. Actinopterygian fin rays are effective displacement transducers, with a small displacement at the base (0.1 mm) generating a large tip displacement of appoximately 4.0 mm.

We still understand very little about the functional diversity of fin rays within the actinopterygian clade. There is clearly substantial variation among species and among fins within any individual (Taft 2011), and yet study of the extent of this variation and its implications for locomotor function and habitat use have barely been considered.

Pectoral Fin Function

Pectoral fins in fishes show considerable diversity in both structure and function, with changes in fin area and shape, location on the body, and attachment angle all playing an important role in governing the effect of fin use on body position. Figure 2.3 schematically illustrates some of the changes in pectoral fin shape and position that occur during locomotion, and this flexibility is important for controlling the direction of forces generated by the fin during swimming and maneuvering (Drucker and Lauder 2003). Basal clades tend to have pectoral fin positions that are relatively ventral and with shallow attachment angles to the body (fig. 2.1). In many derived clades, especially those in which pectoral fins are used to generate thrust during swimming, the fin is larger in area, and the base of the fin is attached higher on the body at a greater angle.

The underlying anatomical basis of changes in attachment angle of pectoral fins has not been subject to detailed study, but certainly changes in the angles and connections between the radial bones that support pectoral fin rays and also between the radials and the scapula (fig. 2.3A) could allow for considerable variation among species in pectoral fin motion. Basal ray-finned clades have more numerous radial bones than derived clades and different patterns of skeletal connection between the radials and the pectoral girdle; this suggests that there may be differences in ability to reorient the pectoral fin among these groups of ray-finned fishes, although this issue has not been investigated. Most fish species can reorient the whole pectoral fin via changes in the angle of the base (fig. 2.3C), and reorientation of the fin base during different behaviors has the effect of altering the direction of pectoral fin forces.

In relatively basal actinopterygian clades such as salmoniform fishes with a relatively horizontal pectoral fin base, the pectoral fin generates considerable torque around the center of mass during braking. For example,
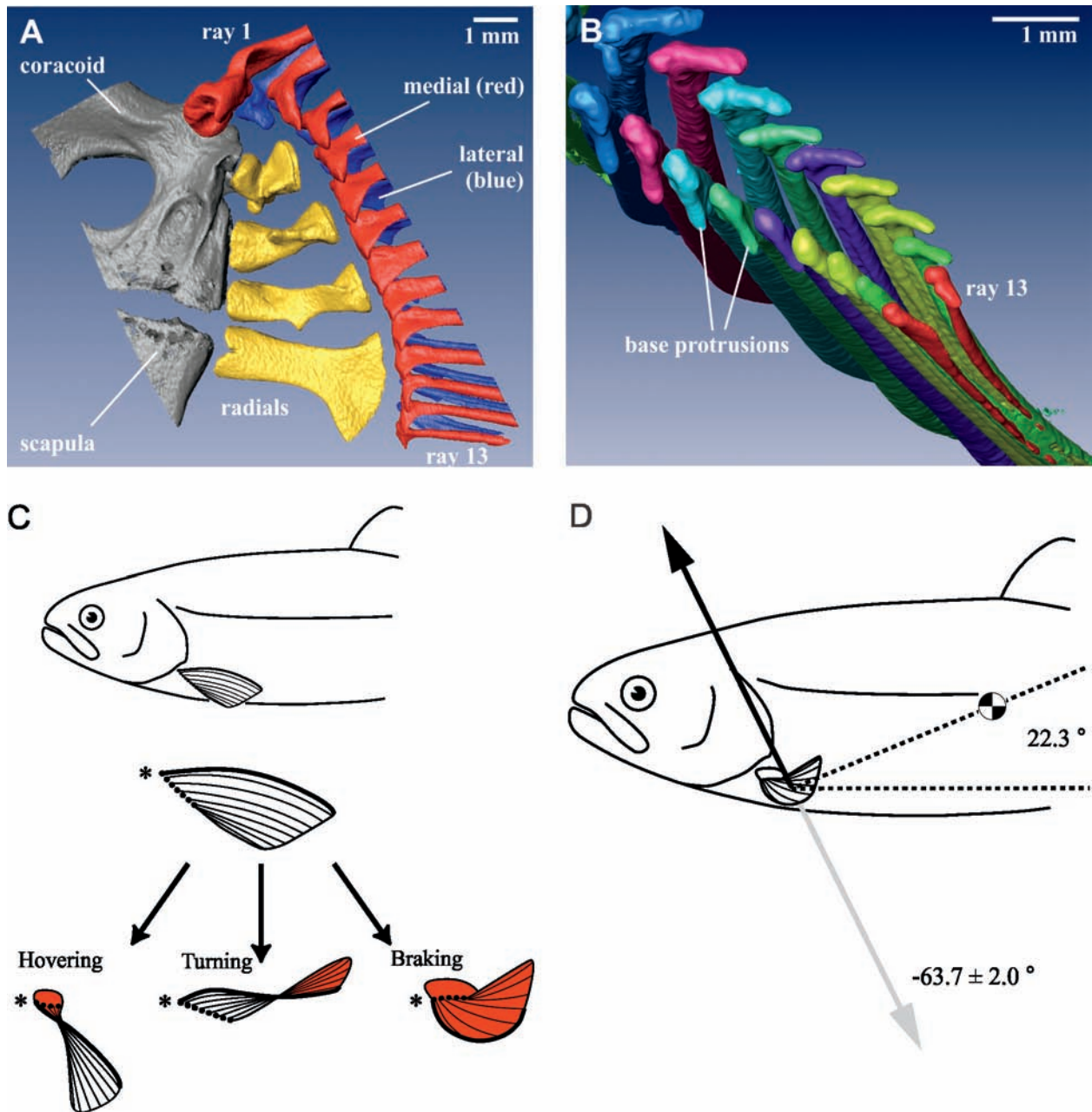
FIG. 2.3 A, The pectoral fin rays of ray-finned fishes articulate with rod-like radials that are attached to the scapula and coracoid of the pectoral girdle. B, Fin rays have small basal processes that serve as the locations of muscle attachment. C, The pectoral fin base can be actively reoriented and changes position during different locomotor behaviors. The asterisk marks the location of the base of the first fin ray for reference, and the dorsal surface is colored red. D, The pectoral fin of basal teleost fishes like trout generates forces during braking that generate torques around the center of mass: the gray arrow shows the direction of the reaction force that is almost orthogonal to the direction of the center of mass. See Drucker and Lauder (2003) and Lauder et al. (2011b).

in trout (fig. 2.3D), braking behavior to stop forward motion involves curling up the distal pectoral fin margin to generate force directed forward. But due to constraints on motion and shape of the pectoral fin, the direction of net force is anterodorsal, and hence the reaction force to this is directed posteroventrally. This results in con-

siderable torque around the center of mass (fig. 2.3D), and as a result trout move ventrally when braking and rotate counterclockwise around their center of mass (Drucker and Lauder 2003).

In other more basal clades such as sturgeon, experimental study of pectoral fin function has shown that the

ventrally located pectoral fins are used for maneuvering and to induce pitch moments to change body position, and have relatively little effect on flow during steady horizontal swimming (Wilga and Lauder 1999). Elevation and depression of the posterior fin margin generates a vortex wake that induces pitching moments that initiate swimming motions up or down in the water column.

In derived ray-finned fishes, there are a number of clades that use their pectoral fins as primary thrusters to generate locomotor forces and to maneuver and swim through the water (Drucker and Lauder 2000; Walker and Westneat 2002; Westneat 1996). Fishes such as bluegill sunfish, *Lepomis macrochirus*, are an excellent example of this type of pectoral fin use, and experimental work on the hydrodynamic function of the pectoral fins (Drucker and Lauder 1999) has shown that during slow swimming, each pectoral fin generates ring-like vortex structures in the wake that represent momentum added to the fluid and that propel the fish forward. The structure of the vortex wake changes with speed, and pectoral fin motion can generate more complex linked-ring configurations reflecting additional fluid momentum as swimming speed increases (Drucker and Lauder 2000). The structure of the vortex wake produced by fishes swimming with their pectoral fins has been the subject of a considerable number of both experimental and computational studies as biologists seek to use fish fins as a model for generating new types of underwater propulsors that might replace propeller systems for future small underwater vehicles (Bozkurttas et al. 2009; Dong et al. 2010; Drucker and Lauder 1999; Lauder and Madden 2007; Lauder et al. 2006; Mittal et al. 2006; Ramamurti et al. 2002).

Derived ray-finned fish clades have a pectoral fin base more vertically oriented and placed higher on the side of the body than in basal clades (fig. 2.1), and this has an important effect on the forces and torques generated during braking as compared to basal groups with horizontally oriented fins. For example, when bluegill sunfish execute a braking maneuver to stop swimming, they extend the pectoral fins from the body to increase drag and stop forward motion (Higham et al. 2005). The forces generated during this behavior are oriented anteroventrally and at such an angle that the reaction force passes through the center of mass (Drucker and Lauder 2002). This means that in bluegill sunfish the pectoral fins can be used in braking without generating pitch torques and thus altering body position, and stand in contrast to the function of more horizontally oriented pectoral fins where the body pitches as the fins are used in braking.

Caudal Fin Function

A very large literature exists on the anatomy and function of fish body (myotomal) musculature during swimming, but only recently has the important role of intrinsic tail musculature in fish locomotion been fully recognized. This is a key feature of the functional design of ray-finned fish fins: the fins possess intrinsic musculature distinct from the body muscles, which allows control over fin ray motion and position in space, and allows most ray-finned fishes to collapse their fins and reduce the surface area exposed to incident flow. Given the flexible surface of fins and the thin collagenous membrane that extends between adjacent fin rays, intrinsic fin musculature allows fish great control over fin posture and position.

Within the tail itself, and distinct from body musculature, are a series of intrinsic muscles that act to control tail conformation (fig. 2.4A–C). In derived ray-finned clades such as the Perciformes, there is an extensive complement of intrinsic tail musculature that controls adduction and abduction of individual fin rays (via the interradialis and supra- and infracarinalis muscles), motion of fin rays to each side of the tail (the flexor ventralis and dorsalis muscles), and movement of the upper tail lobe relative to the lower (the hypochordal longitudinalis) (fig. 2.4C). In basal ray-finned clades such as gar (*Lepisosteus*), intrinsic caudal musculature is much less extensive and consists only of a broad ventral flexor muscle on each side (fig. 2.4A). In bowfin (*Amia*), there is more extensive intrinsic musculature with most muscles focused on control of the dorsal portion of the tail (see fig. 2.4B; Flammang and Lauder 2008, 2009; Lauder 1989; Lauder et al. 2003).

These intrinsic tail muscles permit fine control of tail conformation and alteration of tail function during different locomotor behaviors. For example, the tail may be held in a relatively flat shape during steady swimming (fig. 2.4D), may assume an S shape during braking (fig. 2.4E), may be extended into a broad blade during acceleration (fig. 2.4F), or may be compressed during the glide phase following rapid forward motion (fig. 2.4G).
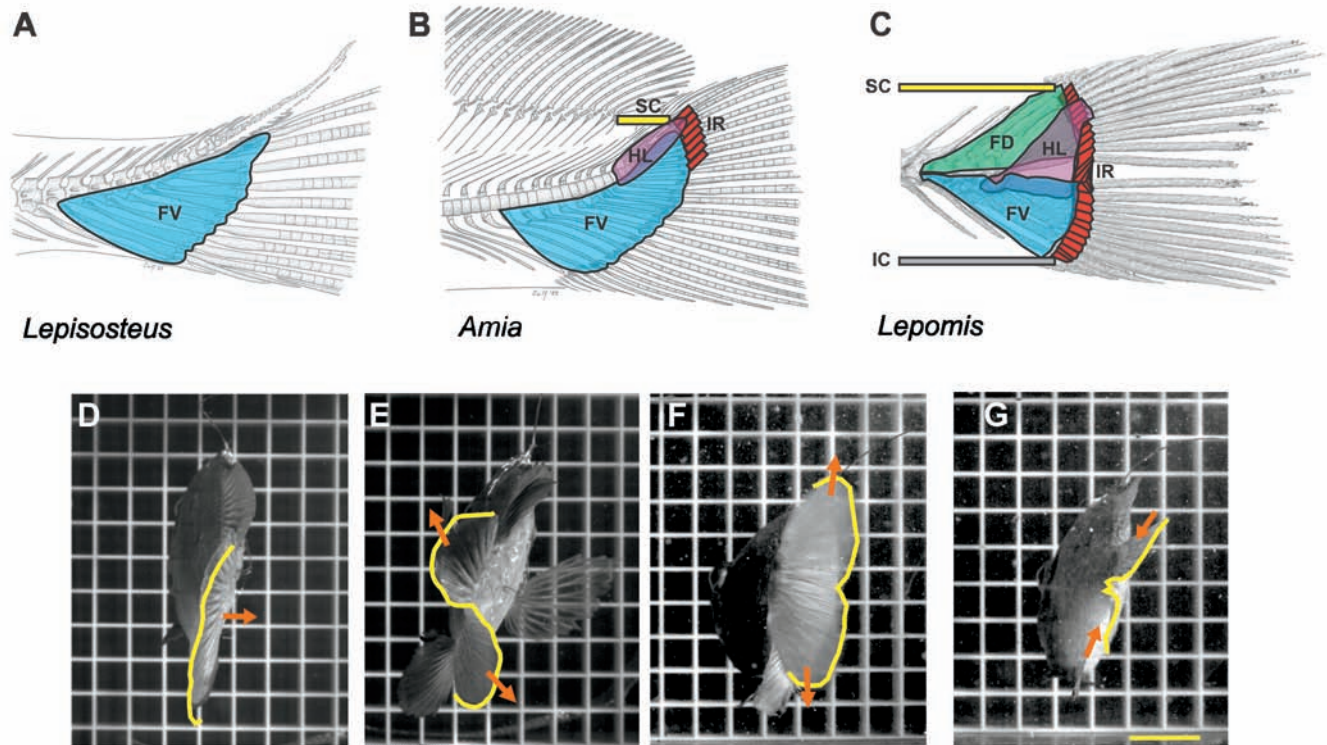
FIG. 2.4 Ray-finned fishes have control of tail conformation via intrinsic musculature that is distinct from the myotomal body muscles. Panels A, B, and C schematically diagram the diversity of intrinsic tail muscles in three ray-finned fish species, to show the diversity of intrinsic musculature and the substantial increase in muscular control of the tail in derived taxa such as bluegill sunfish (*Lepomis*) compared to basal clades such as gar, *Lepisosteus*. Intrinsic caudal muscles shown are the flexor dorsalis (FD, green), flexor ventralis (FV, blue), hypochordal longitudinalis (HL, purple), infracarinalis (IC, gray), interradialis (IR, red), and supracarinalis (SC, yellow). Note that *Lepisosteus* lacks all intrinsic caudal musculature except for a broad FV, and *Amia* lacks the FD, IC, and all ventral IR muscles. Panels D, E, F, and G show tail conformation in a bluegill sunfish from posterior view (the posterior tail margin is outlined in yellow) during steady swimming at 1.2 L/s (D), braking (E), and kick (F) and glide (G) behaviors. Red arrows illustrate the direction of tail motion during these behaviors. See Flammang and Lauder (2008, 2009).

The hydrodynamic function of the tail in ray-finned fishes has been studied as a means of understanding how different tail shapes influence patterns of momentum in the wake as reflected in vortex structure, to estimate the forces and torques generated by fish tails, and to evaluate how the wake from the dorsal and anal fins could influence the function of the caudal fin. Studies of caudal fin function using flow visualization with the particle image velocimetry technique have revealed the typical counterrotating centers of vorticity in the wake that reflect slices through caudal fin vortex rings, and enabled reconstruction of the vortex wake of fishes with homocercal tails. Particle image velocimetry has shown that the homocercal tail generates a largely symmetrical chain of linked rings during steady swimming in which side (lateral) forces are typically nearly double that of thrust force values (Standen and Lauder 2007).

Swimming by undulatory propulsion necessarily generates substantial side forces. The vortex wake of fishes with homocercal tails generates a central momentum jet that propels fish forward (Flammang et al. 2011b; Lauder and Tytell 2006; Nauen and Lauder 2001).

In basal ray-finned clades such as sturgeon, which have heterocercal tails, analysis of the vortex wake has shown that the sturgeon tail also produces a chain of linked vortex rings, and that the angle of the momentum jet is such that the reaction force passes through the center of mass (Liao and Lauder 2000). This means that the heterocercal tail of sturgeon does not generate body torques during steady horizontal locomotion, and that no rotational moments are produced by the heterocercal tail. This differs from the function of the shark heterocercal tail where both lift forces and pitch torques are produced by asymmetrical motion of the dorsal and

ventral lobes (Flammang et al. 2011a; Wilga and Lauder 2002).

Dorsal and Anal Fin Function

A key feature of ray-finned fish functional design is the presence of multiple fins that can produce interacting fluid flows. So far in this chapter we have treated fins as though they function independently, but this is clearly not always the case. In particular, the wake from the dorsal, anal, and pelvic fins passes downstream along the swimming fish and can at least potentially influence water flow over the tail and hence the vortex wake produced there. This process of wake interaction in fishes has been demonstrated both experimentally and computationally, as well as with simple robotic motels (e.g., Akhtar et al. 2007; Drucker and Lauder 2001; Flammang et al. 2011b; Lauder, Lim, et al. 2011; Standen 2008; Standen and Lauder 2007; Tytell 2006).

Figure 2.5A, B illustrates the motion of the dorsal fin relative to the tail in rainbow trout, *Oncorhynchus mykiss*, and shows the out-of-phase motion that the trailing edge of the dorsal fin exhibits relative to the leading edge of the caudal fin (Drucker and Lauder 2005). The flexible dorsal fin in trout is actively moved and generates a vortex wake that the tail moves through (fig. 2.5C). The wake can be quite dramatic, and substantially alters the fluid environment around the tail. For example, as shown in figure 2.5C, the dorsal fin produces a wake of strong alternating lateral jets, and the path taken by the tail goes through the vortex centers. One important consequence of the dorsal fin wake is that much of the time the tail experiences an incident flow direction that is nearly perpendicular to the free stream local flow that the fish is swimming through. Hydrodynamic models of fish tail function rarely consider the greatly altered flow environment experienced by the tail as a result of upstream fin action.

The production of strong lateral wake jets by the dorsal and anal fins of swimming fish has important consequences for the overall force balance during swimming. Figure 2.5D illustrates that these dorsal and anal fin fluid jets produce torques on the fish body that must be balanced for steady swimming, or can be modulated to induce maneuvers. Dorsal and anal fins produce opposite sign roll torques, and yaw moments produced by motion of the pectoral and tail fins must all be integrated to produce an overall stable force balance during steady swimming.

In the fish locomotion literature one often sees reference to the distinction between "body and caudal fin locomotion" and "median fin locomotion" as though these were two distinct locomotor modes. But in light of recent results showing that the median dorsal and anal fins are actively used even during steady swimming and that they generate significant hydrodynamic forces used to control the roll torque balance, this distinction seems artificial at best. Fish, even those swimming steadily without maneuvering, use their median fins actively, and use of median fins is integral to understanding the overall force and torque balance on fishes. The active use of multiple fins to control body posture during swimming is a hallmark of ray-finned fishes.

Median fins also play an important role in unsteady locomotor behaviors, and the ability of fishes to collapse and extend their fins during swimming behaviors is a critical feature of fin functional design. As fishes swim faster, the dorsal and anal fins are often depressed, which reduces their surface area (fig. 2.6A, B). But these fins are erected rapidly when an unsteady maneuver or a C-start escape response is initiated (fig. 2.6C, D). Median fins of fishes play an important role in unsteady locomotion, and perform numerous functions including increasing surface area near the center of mass, controlling roll and yaw torques, and adding momentum during escape responses (Chadwell et al. 2012a; Chadwell et al. 2012b; Tytell and Lauder 2008). Despite the recent increase in data on median fin function in fishes, there is much more to be learned about how these fins function during diverse locomotor behaviors, and how median fin function is integrated by the fish nervous system with input from the body and caudal fin musculature to control body position.

Fins as Sensors for Complex Locomotor Tasks

The median and paired fins characteristic of ray-finned fishes are also important when fish execute complex behaviors such as locomotion through obstacles, or move backward. The entire array of fins may move in concert to achieve complex locomotor behaviors. Although there is only very limited research on fish moving in
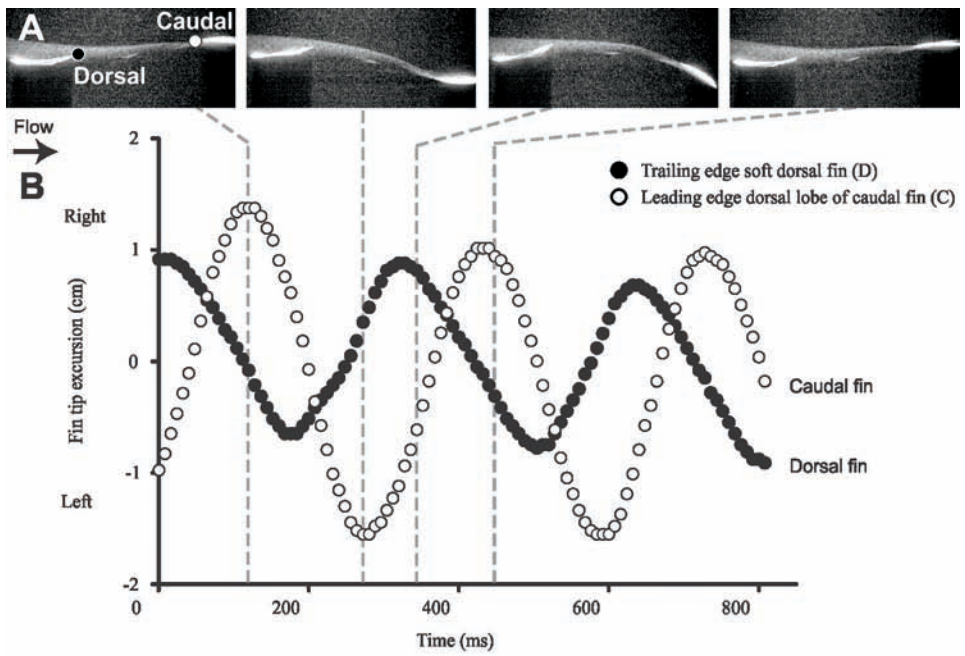
FIG. 2.5 Dorsal fin function in teleost fishes. Fin rays within the dorsal fin are under active control by muscles intrinsic to the fin, and generate an active wake flow that is encountered by the tail. A, Dorsal view video frames of the relative movement of the dorsal and caudal fin. B, Plot to show the out-of-phase motion of the dorsal and caudal fin. C, Path (red dots) taken by the tail through the wake generated by the dorsal fin (yellow arrows). Note the strong lateral jet flows generated by the dorsal fin. Data are from rainbow trout, *Oncorhynchus mykiss*. D, Both dorsal and anal fins are important for contributing to the balance of torques during locomotion, and movement of these fins (as well as the pectoral fin and tail) is controlled to balance roll, pitch, and yaw torques during steady swimming. See Drucker and Lauder (2003, 2005).
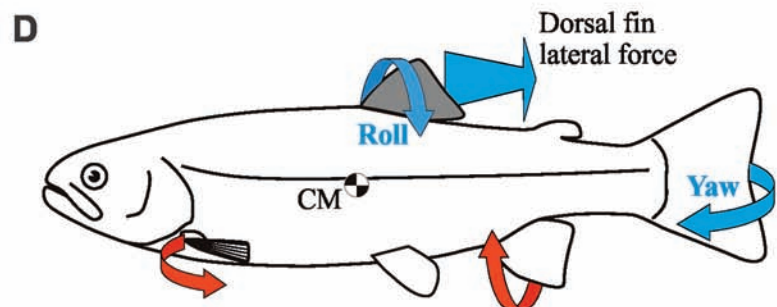
an obstacle-filled environment, such situations are very common for many fishes especially in lacustrine or riverine situations (Ellerby and Gerry 2011; Liao et al. 2003; Flammang et al. 2013). Study of fish moving through obstacles can also reveal unexpected functions for fish fins, and this is a rich area for future research.

A recent study of bluegill sunfish swimming through an array of posts (fig. 2.7) showed that fish did not avoid touching the posts as initially expected, but instead made contact with posts numerous times with their pectoral fins. Fish did not push off the posts, but instead used post contact as a means of sensing the obstacles and for
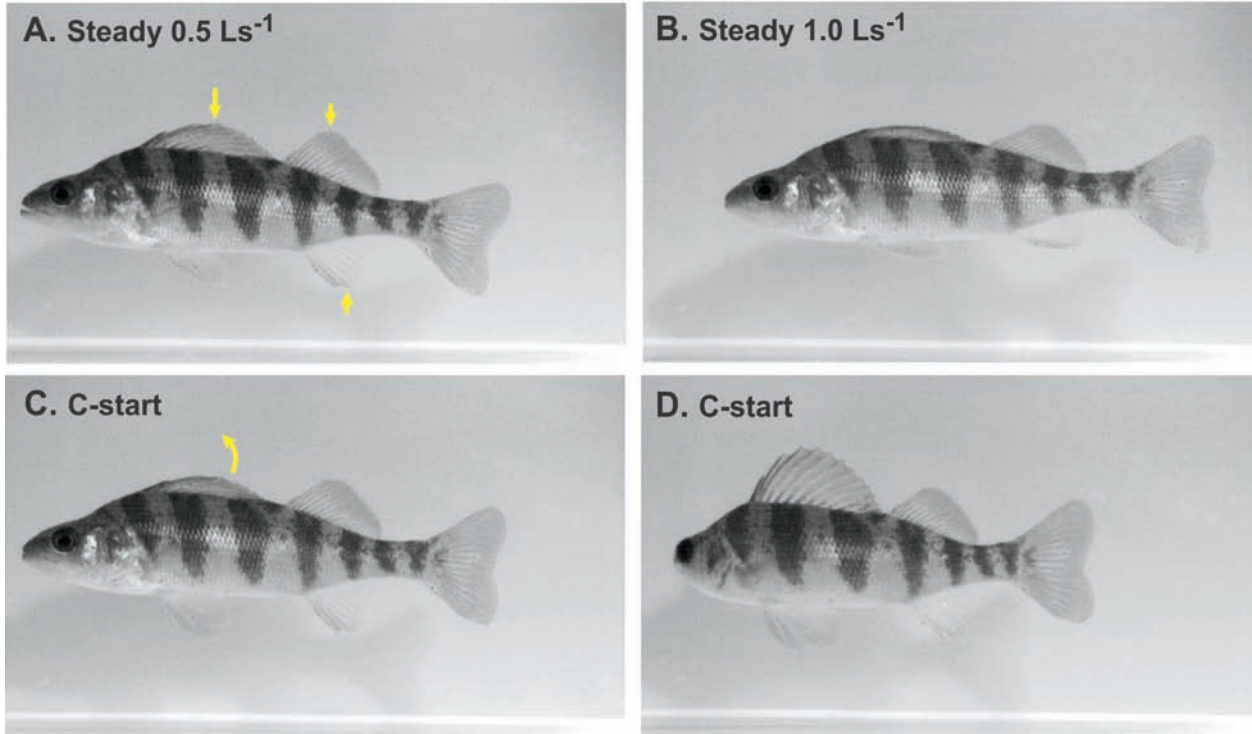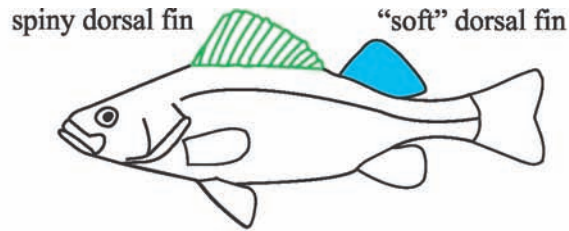
FIG. 2.6 The dorsal fin of many teleost fishes is separated into distinct anterior spiny and posterior "soft" or flexible regions, and the dorsal fin has important hydrodynamic functions during both steady swimming and rapid maneuvers. A, B, The dorsal and anal median fins are depressed (yellow arrows) and have a smaller surface area as steady swimming speed increases. C, D, During rapid escape behaviors such as a C-start response, the dorsal and anal fins are erected (yellow curved arrow). See Tytell et al. (2008) and Chadwell et al. (2012a, 2012b).

directing navigation through the array (Flammang et al. 2013). Study of post navigation in darkness (filmed using infrared light) and under conditions in which the lateral line sense has been eliminated (using a cobalt chemical treatment) showed that fish increased the number of fin taps on nearby posts. These data suggest strongly that ray-finned fishes use their fins for sensing the environment, and not just for propulsion (Flammang et al. 2013). Furthermore, recent physiological studies of ray-finned fish fin rays have shown that sensory nerves in the rays have the capability of acting as proprioceptors and generating action potentials in afferent fin ray nerves in response to both the amplitude and velocity of ray bending (Williams et al. 2013). The most important lesson from this recent work is that ray-finned fish fin rays can act as

both propulsors and sensors, and this additional role for flexible fins is potentially of considerable importance in allowing fish to navigate the aquatic realm.

Of course, most fish cannot only swim forward: fish frequently back up and reposition themselves in the water column. When fish back up, all fins are active at the same time in patterned motion to hold position, correct for unbalanced torques, and to generate backward thrust. In order to present a significant locomotor challenge to fish, we induced bluegill sunfish to move backward through an array of obstacles (fig. 2.7E, F). Backward thrust is generated with the pectoral, dorsal, and anal fins, and each of these fins in addition to the caudal fin makes contact with the posts. This suggests that all the fins are used as both sensors and propulsors
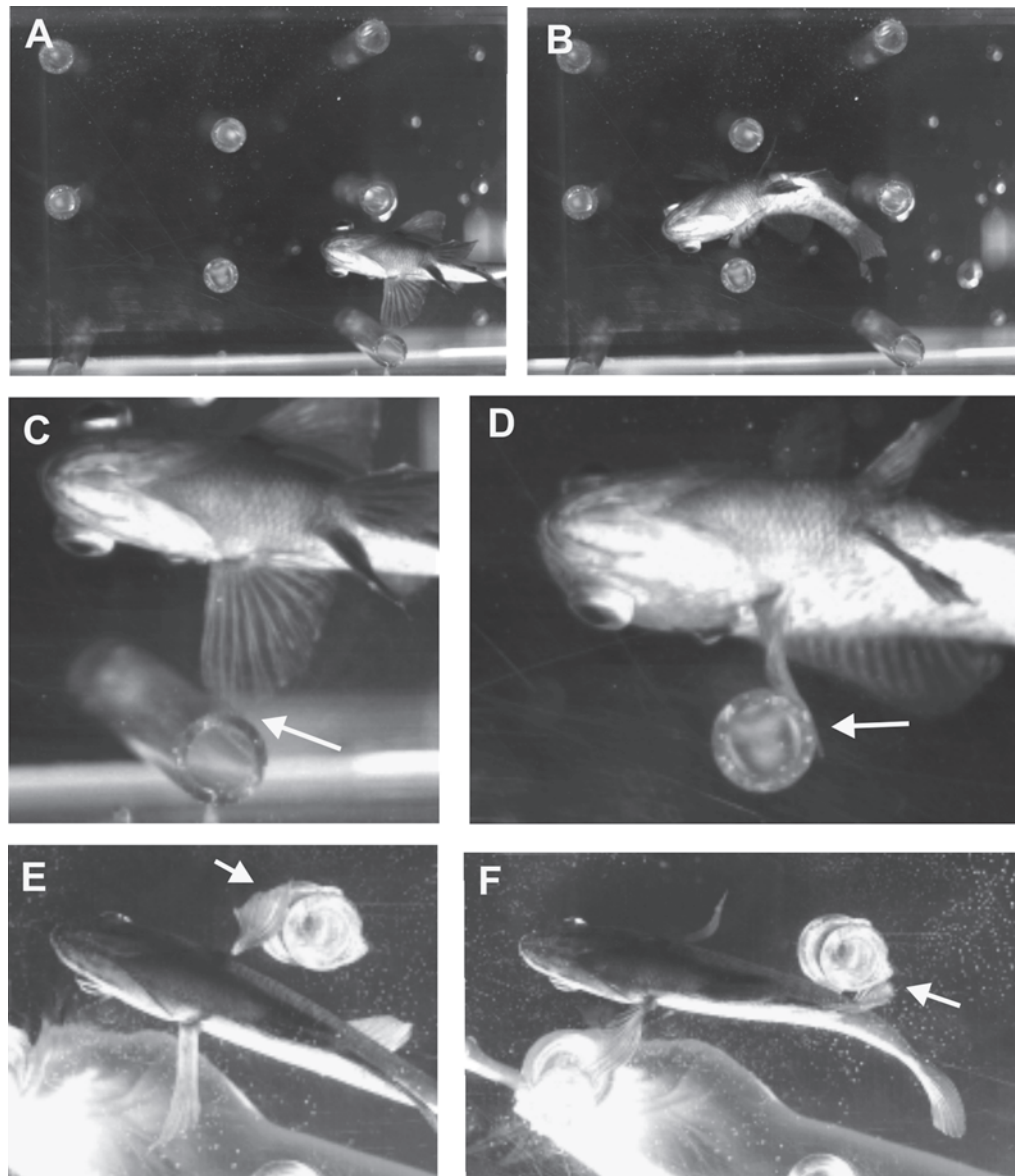
FIG. 2.7 Bluegill sunfish swimming through an obstacle course of posts in the forward direction (A) and (B), with enlarged views of the contact between the pectoral fins and posts (C) and (D). Panels (E) and (F) show bluegill swimming backward through the obstacles, with contact between the pectoral fins (E) and the dorsal and anal fins (F). These data suggest that ray-finned fishes can use their flexible fins for sensing the environment in addition to propulsion.

during the execution of complex swimming behaviors in cluttered environments.

Future Studies of Fish Fin Function

Although study of the kinematics and hydrodynamics of fish locomotion has revealed many aspects of how fishes interact with their fluid environment, there are inherent limitations to studies of live animals. Live fishes can be induced to perform only a relatively lim-

ited range of behaviors and movements, and there can be considerable variation among sequences. Many alterations of interest from a purely experimental and fluid dynamic perspective are difficult or impossible to perform in live fishes, such as changing the stiffness of fins or the body. And measuring three-dimensional forces during swimming and estimating the efficiency of swimming is extremely challenging if we are limited to working with live fish. Overall, when working on living animals, it is difficult to alter only one experimental

variable, while simultaneously maintaining control of all others (Lauder et al. 2012).

One area of research in fish biology that has recently seen considerable activity, in part due to an interest in escaping many of the limitations of working on live fishes, is the use of robotic models. Robotic models allow precise manipulation of movement patterns, ease in changing stiffness and shape of the swimming object, and direct measurement of forces and torques during locomotion. In addition, robotic models of morphology that exists now only in fossil taxa allow us to explore how fossils may have functioned. As a result of these advantages, research has progressed on robotic fish pectoral fins (Phelan et al. 2010; Tangorra et al. 2010) caudal fins (Esposito et al. 2012; Lauder et al. 2012), and on whole-fish robotic models, both simple (Alben et al. 2012; Flammang et al. 2011a; Flammang et al. 2013; Lauder et al. 2012; Lauder, Lim, et al. 2011) and complex (Long 2012; Long et al. 2006; Low and Chong 2010; Wen et al. 2012).

Another important approach that has played a key role in understanding how fishes swim and the effect of different movement patterns on swimming efficiency and patterns of force production is the use of computational models. Using a computer model of a swimming fish or their fins and computing three-dimensional flows and forces allows us to investigate how both fins and fishes of different shapes generate force on the fluid environment. Asking a computational eel to swim like a mackerel, for example, allows us to isolate the effect of movement pattern on swimming efficiency (Borazjani and Sotiropoulos 2010). Computationally dissecting fin kinematics allows us to ask which specific features of fin motion are responsible for components of force generation, and hence provides a deeper understanding of how fins generate locomotor forces (Bozkurttas et al. 2009; Dong et al. 2010; Mittal et al. 2006).

With both robotic and computational approaches as important components of future research on the locomotion of ray-finned fishes as well as a wide array of unsolved biological problems, future students of ray-finned fishes have much to look forward to as new techniques and comparative approaches reveal ever more intriguing aspects of locomotor diversity and fin function in this remarkable clade.

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Acknowledgments

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