

Fish Locomotion: Biology and Robotics of Body and Fin-Based Movements

George V. Lauder and James L. Tangorra

Abstract The study of fish locomotion provides a rich source of inspiration for the design of robotic devices. Fish exhibit an array of complex locomotor designs that involve both diversity of structures used to generate locomotor forces, and versatile behaviors to engage with the aquatic environment. The functional design of fish includes both a flexible body exhibiting undulatory motion as well as numerous control surfaces that enable fish to vector forces and execute rapid maneuvers in roll, pitch, and yaw directions. Patterns of body undulation have often been misunderstood, and fish with propulsive mechanics as diverse as tuna and eels can display similar patterns of body bending during swimming. Many of the often-cited classical locomotor categories are based on a misunderstanding of body and fin kinematics. Fish fins can exhibit remarkably complex conformational changes during propulsion, and do not function as flat plates but have individual mobile fin rays actuated by muscles at the fin base. Fin motion and surface bending in most fish is actively controlled. Even during steady horizontal locomotion, median fins such as the dorsal and anal fins function to balance torques and can contribute to thrust. Locomotion using body undulation is not achieved independently from fin motion, and the vast majority of fish locomotor patterns utilize both the body and fins. Robotic systems derived from fish templates can range from simple flexible plastic panels to more complex models of whole body and fin design. Experimental test platforms that represent individual fins or specific components of fish locomotor design allow for detailed testing of hydrodynamic and mechanical function. Actuating and controlling complex fish robotic systems involving both the body and multiple individual fins are a major challenge for the future.

Keywords Swimming · Hydrodynamics · Fish · Locomotion · Robotics

G.V. Lauder (✉)

Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge
MA 02138, USA

e-mail: glauder@oeb.harvard.edu

J.L. Tangorra

Department of Mechanical Engineering, Drexel University, Philadelphia, PA 19104, USA

e-mail: tangorra@coe.drexel.edu

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1 Introduction

The study of fish locomotion provides a rich source of inspiration for the design of robotic devices. Fish exhibit an array of complex locomotor designs that involve both diversity of structures used to generate locomotor forces, and versatile behaviors to engage with the aquatic environment which can range from calm stratified lakes to turbulent high-velocity rivers. The functional design of fish includes both a flexible body exhibiting undulatory motion as well as numerous control surfaces that enable fish to vector forces and execute rapid maneuvers in roll, pitch, and yaw directions. Designers of robotic systems that must deal with the unpredictable aquatic environment can turn to the mechanics and function of fish as a source of ideas for how to approach the construction of new mechanical devices that use flexible control surfaces and patterns of wave-like motion to produce thrust and maneuvering forces.

In this chapter we provide a general background and an overview of the mechanics of fish locomotion, and then explore some of the mechanical systems that we have constructed to better understand the function of both the body and fins of fish. Research on fish robotics has the potential not only to demonstrate novel designs for autonomous underwater vehicles that are not based on propellers, but also to use robotic systems and their control to better understand the biology of fish swimming. In our view, the potential for using mechanical systems to test biological hypotheses about how and why fish are designed the way they are is one of the most intriguing areas for future work.

Within the past 15 years, there have been many reviews and overviews of the topic of fish swimming and the increase in publication rate on this topic reflects the growing interest in understanding the functional design of fish and the implications for robotic system construction. In this chapter, we will not duplicate material from these previous articles, but will instead focus on summarizing key features of fish functional design; note several misunderstandings in some of the current literature on the mechanics of fish swimming; address specific fish systems that are of special relevance for the construction of fish-like mechanical devices; and finally illustrate some of the mechanical systems that we have developed ranging from simple to complex representations of fish functional design.

Readers interested in the literature review of one or more aspects of fish locomotor function can examine classical summaries such as [4, 47–49, 76, 131] as well as the more contemporary books [12, 27, 75, 86, 110, 127, 134, 139] and articles [36, 39–41, 60, 62, 73, 87, 106, 109, 122, 123, 130, 132, 133].

2 Overview of Fish Swimming Dynamics

2.1 General Background

Perhaps the most common image of fish as swimming objects is the often-published horizontal section through a fish body that resembles a NACA airfoil in shape. This view emphasizes the overall streamlined nature of fish bodies and allows for comparisons between fish and objects that are designed to minimize drag or to generate lift. But fish shapes are complex in three dimensions [125, 126] and have multiple projections (fins) and changes in geometry along the body length that are not well represented in a horizontal NACA-like section. Figure 1 illustrates some of the complexity in fish shape with transverse sections obtained using a micro-CT scanner of a bluegill sunfish *Lepomis macrochirus*. Toward the front of the body, fish often are thickest due to the head and gill region housing the brain, feeding and respiratory systems. This portion of the body is not symmetrical in the transverse plane, and the top is often more pointed while the bottom (ventral) region is rounded. Moving back along the body reveals increased dorsal–ventral symmetry and the median fins which project into the water above and below the fish body. The surfaces of these fins are not smooth, and instead have a roughened exterior due to the fin rays that support the thin fin membrane. Near the base of the tail (the region known as the caudal peduncle: sections d and e in Fig. 1) the body becomes more symmetrical with sharp edges that cause flow separation as the body and tail move from side to side during swimming [124]. The consequences of body asymmetry for the generation and control of locomotor torques has not been addressed, and remains an interesting area for future work.

2.2 Fish Locomotion Using Body Deformation

Although the notion of a gait is most common in studies of terrestrial locomotion (as when a horse moves from a walk to a trot to a gallop as speed increases), many fish have gaits too. As swimming speed increases, fish can change from a primarily pectoral fin-based swimming style in which the body remains relatively still, to body undulation with fin motion, to exclusively steady wave-like body motions for thrust generation. If speed increases still further, unsteady locomotion can occur with burst-and-glide swimming with intermittent high-frequency beating of the tail. These gait transitions are significant because they reflect the use of different muscular systems and a shift from steady swimming to high-speed unsteady locomotion caused by a change in muscle fiber activation from slower red fibers to the faster-contracting white fibers [14, 30, 108].

Figure 2 shows patterns of body bending in several species of swimming fish. In most species, the head oscillates relatively little until swimming speeds increase beyond two body lengths per second. Species as diverse as eels, sunfish, and clown

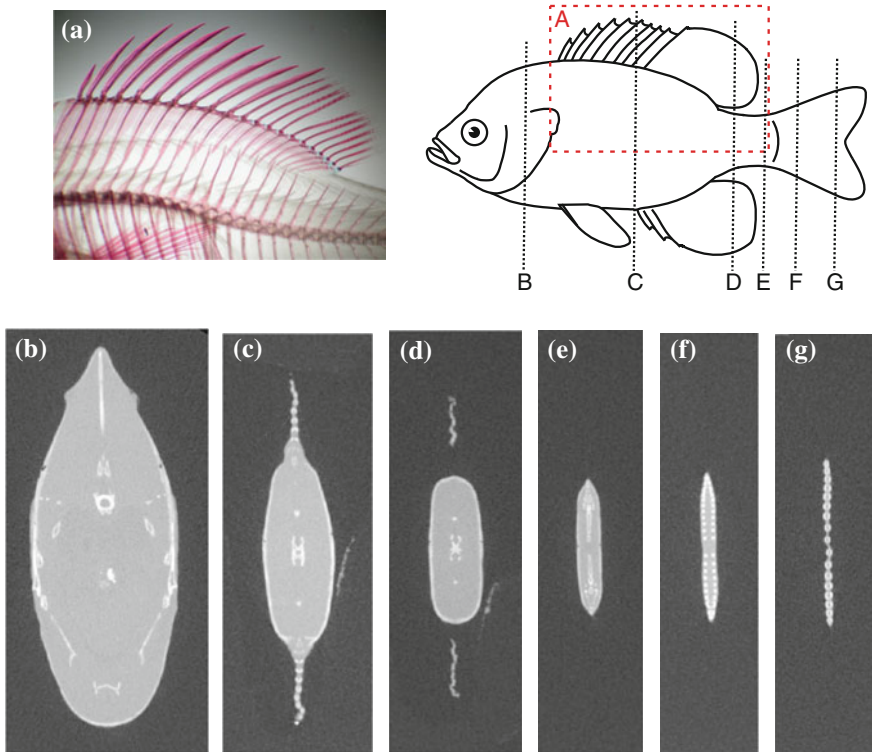


Fig. 1 Fish vary greatly in cross-sectional shape along the body. This figure illustrates shape cross-sections from micro-CT scans at several points (**b–g**) along the body of a 15 cm long bluegill sunfish, *Lepomis macrochirus*. Panel **a** shows the skeleton of this species (bones are stained red and the tissue has been enzymatically rendered transparent) to illustrate how fins such as the dorsal fin are supported by the axial skeleton. Panel **b** provides a guide to the location of the images below. Body shape changes from rounded anteriorly to the tail region where the *upper* and *lower* body surfaces have sharper edges. Fin surfaces are bumpy (see sections **c** and **g**) with projecting fin rays. All micro-CT images are shown at the same scale. From Lauder [61]

knifefish (Fig. 2) show remarkably similar patterns of body bending, and even quantitative analyses of tuna locomotion [29, 70] show similar patterns of head oscillation to other species. This result is not generally appreciated in the fish mechanics literature which suggests that tuna show reduced head oscillation amplitudes relative to other fish: the published quantitative analyses do not support this conclusion, although considerably more research needs to be done on tuna kinematics under controlled conditions.

Figure 3a shows an analysis of the amplitude of body bending as speed changes in largemouth bass [56]. At low speeds there is virtually no amplitude along the anterior third of the body, and even as speed increases considerably head oscillation does not increase greatly. There is a relatively sharp transition two-thirds of the way along the body where lateral body amplitudes begin to increase rapidly, reaching

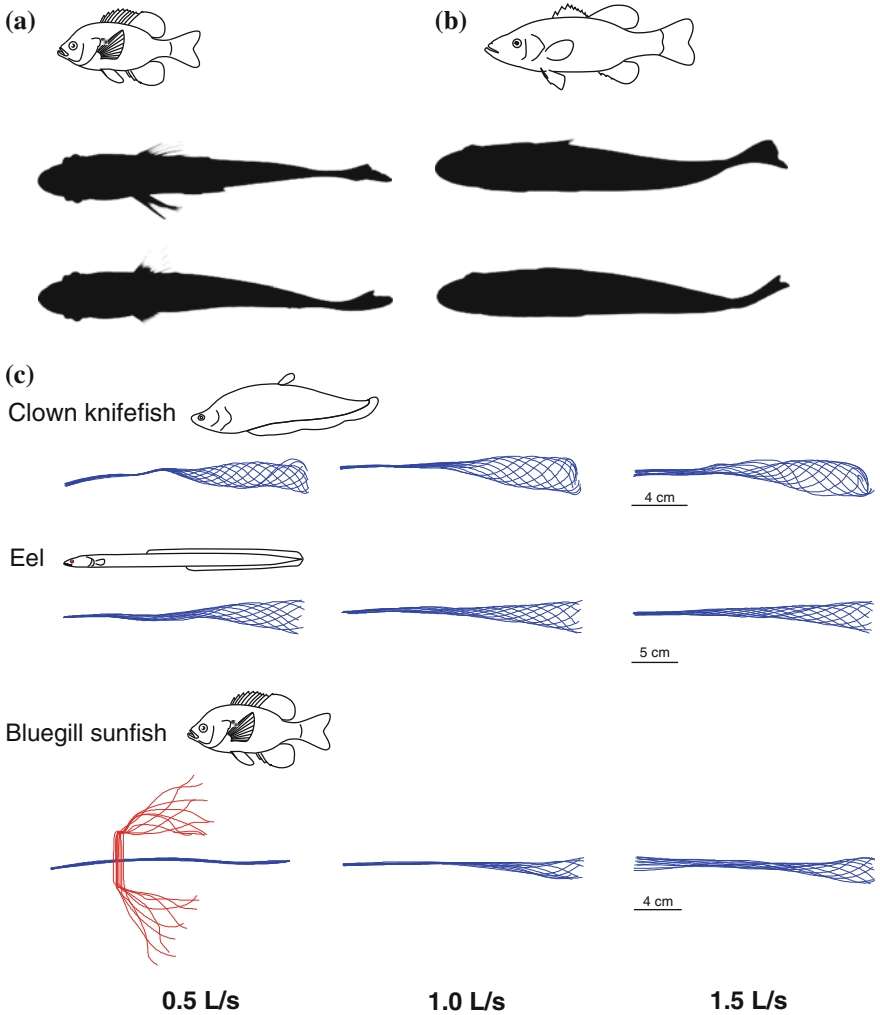


Fig. 2 Patterns of body motion in fish swimming with undulatory motion. During swimming, a traveling wave of bending passes down along the body. Panels **a** and **b** show body outlines at two different times in bluegill sunfish (*L. macrochirus*) and largemouth bass (*Micropterus salmoides*). Panel **c** shows how the pattern of body bending changes as fish increase swimming speed from slow (0.5 L/s) to moderate (1.5 L/s) speeds. At 0.5 L/s, bluegill sunfish use labriform locomotion and generate thrust only with their pectoral fin. Note the relatively low amplitude sideways (yaw) head motion and increasing amplitude along the body in most species. Panel **c** modified from Xiong and Lauder [140]

a maximum at the tail tip. Furthermore, graphs of amplitude versus length often have two inflection points (e.g., Fig. 3a), and are more complex than the relatively simple functions often used to program undulatory robotic devices.

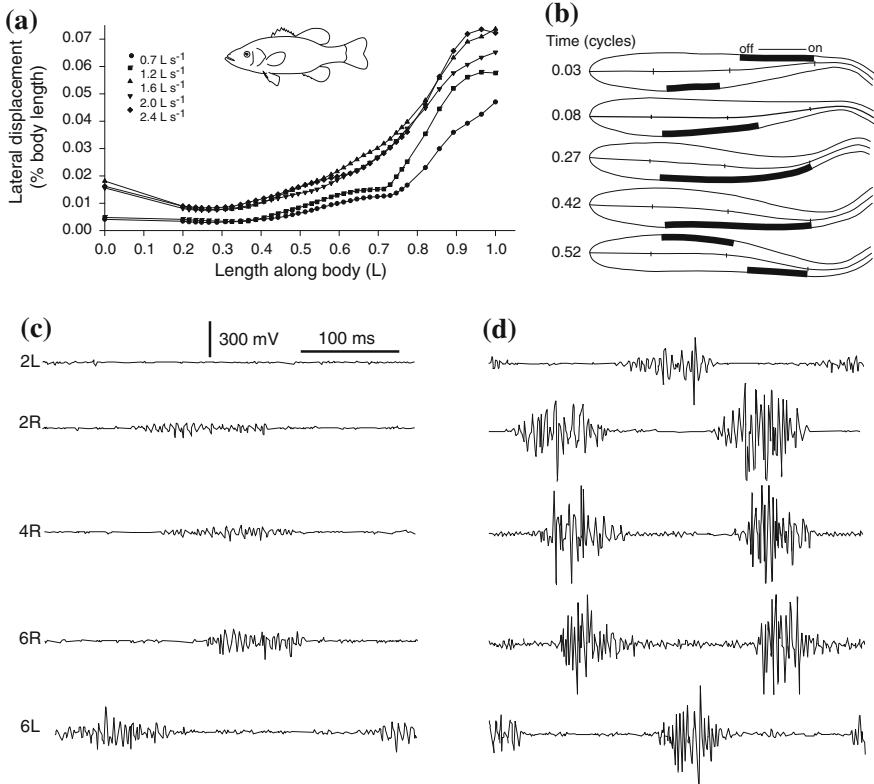


Fig. 3 Pattern of body bending during undulatory locomotion (a) and body muscle activity used to drive the bending wave (b and c). Body oscillation amplitude in swimming fishes increases with speed, and is minimal at a point approximately 30 % down the body from the tip of the snout. Waves of muscle activity (b, black bars) pass along the body to generate this wave, and muscle activity in the red fibers that power slow to moderate swimming increases as swimming speed increases (c, d). Labels in c refer to the positions down the body: positions 2, 4 and 6 correspond to 43, 57, and 72 % down the body. *R* and *L* refer to the Right and Left sides of the body. Modified from Jayne and Lauder [55, 56]

Fish kinematics in a wide diversity of species match this general pattern of reduced head oscillation with a wave-like pattern of body bending (Fig. 2). While fish species certainly differ in the number of waves and in specific details of the amplitude envelope [45], the differences in this two-dimensional view are minor, and recent quantitative comparisons of the midline kinematics of a diversity of species does not lend much support to the often-cited qualitative descriptions of fish swimming modes and simple graphical summaries that inaccurately depict patterns of body bending [76, 105].

Fish body undulations are caused by a wave-like pattern of muscle activation that sweeps from the head toward the tail (Fig. 3). During steady sustainable swimming, fish use almost exclusively red muscle fibers that have higher aerobic

capability even though these fibers usually form only a very small percentage of total fish muscle mass, often less than 5 %. The bulk of fish muscle mass is composed of larger white fibers that are used for rapid unsteady motions and escape responses [53, 54, 107, 108, 115]. Thus, the bulk of fish bodies are passive during slower, routine, steady swimming behaviors, and body wave motion is controlled actively only by a relatively small proportion of muscle fibers. Figure 3b illustrates that muscle electrical activity alternates between the left and right sides of a swimming fish, but due to the movement of the wave of electrical activity toward the tail and the relatively large extent of activation on one side, there is considerable co-activation of red muscle fibers on the right and left sides of the body at any one time. This may stiffen the body actively and reduce the amplitude of motion which could be tuned to particular swimming speeds based on the intensity of muscle activation. Figure 3c documents that the intensity of muscle activity increases with swimming speed as does the velocity of the muscle activation wave and frequency, while the overall pattern of red fiber activity remains similar until speeds increase to the point where white muscle fibers are activated. Fish certainly possess the capability of actively controlling body stiffness with their locomotor musculature, but the extent to which this alters locomotor function is largely unknown [81, 82, 88].

One area of fish swimming that has received relatively little attention but that has great promise for facilitating the comparison of fish swimming mechanics to that of robotic devices is the study of center of mass (COM) motion [135]. In contrast to biomechanical investigations of walking and flying animals, almost nothing is known about motion of the center of mass in swimming fish. One recent study of ours quantified the three-dimensional center of mass motion in several species of fish using different swimming modes [140], but much more remains to be done to better understand the pattern and magnitudes of fish center of mass movement during steady swimming behaviors. We propose that comparison of COM motion in live fish to that of robotic devices provides a useful performance metric by which autonomous robotic fish-like mechanical systems can be compared to the swimming performance of live fish. High COM oscillation amplitude during swimming would be expected to reflect high costs of transport, and autonomous robotic designs could be evaluated and compared based on the amplitude of COM oscillation in the three movement planes.

2.3 Fish Locomotion Using Fin Movements

Fish fins also play an important, and in many species a dominant, role in propulsion. Pectoral fins are commonly used for slower speed swimming and to generate thrust for steady swimming, and off-axis forces for maneuvering (e.g., [31, 34, 44, 128, 129, 137, 138]). Pectoral fin propulsion may involve complex conformational and wave-like motions (Fig. 4) [16, 28, 34, 68, 100], and both experimental and computational fluid dynamics of pectoral propulsion have shown that thrust can be

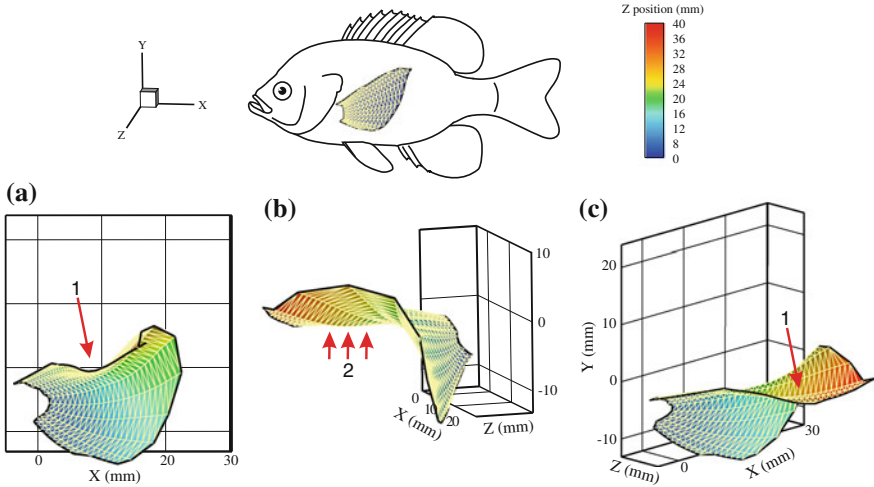


Fig. 4 Kinematics of the pectoral fins during locomotion in bluegill sunfish (*L. macrochirus*). Pectoral fins are often used by fish for slow to moderate speed locomotion, and can undergo complex conformational changes as the fin beats. This figure shows three views of a single time during the fin beat cycle; the three fin images are color coded by z-position, which indicates the distance of the fin element from the body. Note the bent and *cupped* shape of the fin at this time. Arrow #1 points to the wave of bending that travels from root to tip of the fin, while arrows labeled #2 point to the region of the fin surface that generates thrust during the outstroke. From Lauder [61]

generated on both the instroke and outstroke of fin motion, and that fin conformational changes may act to reduce vertical center of mass oscillations.

Fins such as median dorsal and anal fins (Fig. 5) are also important players in controlling fish body motion during undulatory swimming and these fins can also contribute thrust as they are actively moved by basal fin musculature [33, 35, 113, 114]. Dorsal and anal fins act to balance body torques during steady swimming (Fig. 5b) and to generate rolling moments during maneuvers. In addition, wakes from the dorsal and anal fins (and even the pelvic fins) can greatly alter incident flow on the tail [1, 112, 114]. Figure 5b shows the path of the caudal fin of a trout through the vortex wake shed by the dorsal fin and demonstrates that the tail of swimming fish does not move through undisturbed free-stream fluid, but instead encounters vortices that greatly alter the angle of attack of incident flow.

The fin rays of bony fish (but not sharks or rays) possess an interesting mechanical design that involves bilaminar jointed bony half-rays connected by collagen fibers and elastic tissue. The mechanical properties of these bilaminar fin rays have recently been studied in some detail [2, 42, 69, 116, 117] and represent a key evolutionary innovation in fish functional design that allows active curvature control of the fin propulsive surface and permits fish to resist fluid loading on their

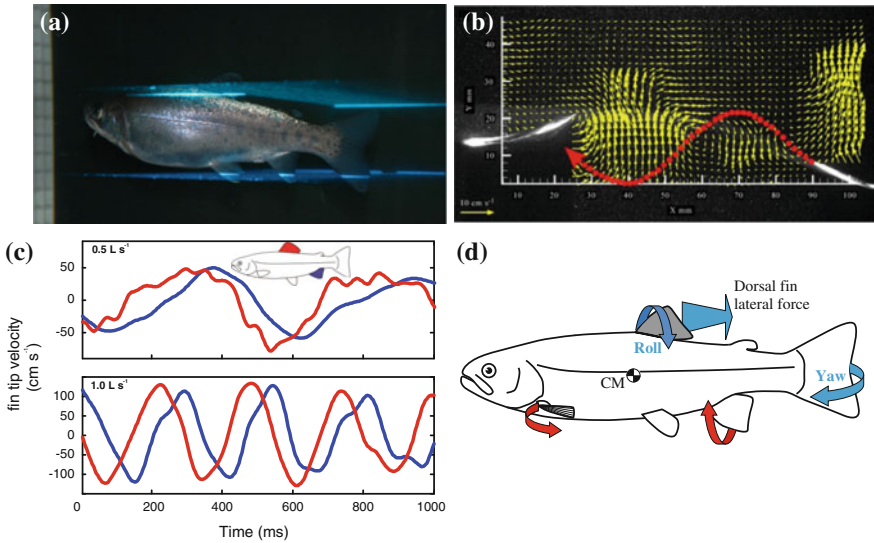


Fig. 5 Median fins such as the dorsal and anal fins play important roles during undulatory locomotion. **a** Trout (*Salvelinus fontinalis*) swimming in two horizontal laser light sheets to permit simultaneous imaging of flows generated by the dorsal and anal fins and the tail. **b** The dorsal fin (to the left) generates a clear vortex wake (yellow vectors) that the tail must pass through (red dots show the path that the tail will take through the dorsal vortex wake) during swimming rainbow trout (*Oncorhynchus mykiss*); free-stream flow has been subtracted. **c** Velocity through time of the dorsal and anal fins during locomotion at two speeds. These fins contribute significantly to both generating thrust and modulating body torques. **d** Schematic summary of the function of different median fins and their roles in controlling body position. Modified from Drucker and Lauder [35] and Standen and Lauder [114]

control surfaces [63]. Fin rays of sharks and rays are simpler collagenous rods that are not capable of active curvature control.

2.4 Multi-Fin and Body Locomotion Together: The Norm and not the Exception

Although in this chapter we have for the most part treated locomotion using body deformations separately from fin-based motions, in most fish species patterns of body deformation during undulatory propulsion occurs in concert with the active movements of fins. Two of the more common qualitative descriptive terms for fish swimming are “body and caudal fin” (BCF) and “median and paired fin” (MPF) locomotion. But dividing fish swimming into these two categories is entirely artificial and obscures the important fact that most species use the body *and* fins at the same time during swimming. And such coordinated use of the body and fins is

critical for maintaining control of body position and for effecting changes in body orientation.

As examples of the contribution of the median and paired fins, first consider swimming bluegill sunfish as speed increases [32]. At slow speeds below 1.0 L/s, the paired fins contribute 100 % of thrust, and the body provides no thrust. As speed increases to over 1.5 L/s, pectoral fins contribute approximately three-quarters of needed thrust, and body undulation occurs to complete the needed thrust to swim at this speed. At the highest steady swimming speeds, the pectoral fins contribute almost nothing to thrust, and the body nearly 100 %. And the bluegill dorsal fin contributes about 12 % of total thrust at speeds of 1.1 L/s [33].

Even in fish such as trout which are known for effective undulatory locomotion, the median fins make a contribution to controlling body position in roll and yaw, and we cannot consider undulatory locomotion without taking this into account. Standen and Lauder [114] estimated that for trout of 16 cm long swimming at 1.0 L/s, the dorsal and anal fins each add about 1 mN to thrust, which is nearly 10 % of total thrust required at this speed.

The use of both the fins and body together is particularly evident during maneuvering, and we recommend abandoning this artificial division of fish swimming modes as BCF versus MPF. Of course, this poses a considerable challenge for designers of whole fish robotic devices who must consider the possibility of adding active fin-like control surfaces to an already complex flexible body, and in the next section we consider a variety of mechanical models for fish fins and bodies.

3 Robotic Models of Fish Locomotion

3.1 Overview of Fish Robotic Systems

Recent years have seen greatly increased interest in robotic models of fish swimming and a wide diversity of approaches has been taken to the mechanical design of fish-like systems. One way of conceptualizing this variety is to consider a fish template and both relatively simple as well as more complex mechanical models derived from these templates (Fig. 6). Simple models have the advantage of more rapid construction and iteration times when changes are desired, and the ability to easily make modifications that represent basic abstractions of fish features. Examples of this approach include modifications of the trailing edge of a flexible flapping foil or panel to represent different fish tail shapes, or changes in body stiffness achieved by changing the panel material (Fig. 6). Examples of using simple mechanical models to understand the dynamics of propulsion include (but are certainly not limited to) the following studies [3, 9, 13, 17, 19, 25, 26, 50, 52, 64, 65, 74, 97, 98, 101].

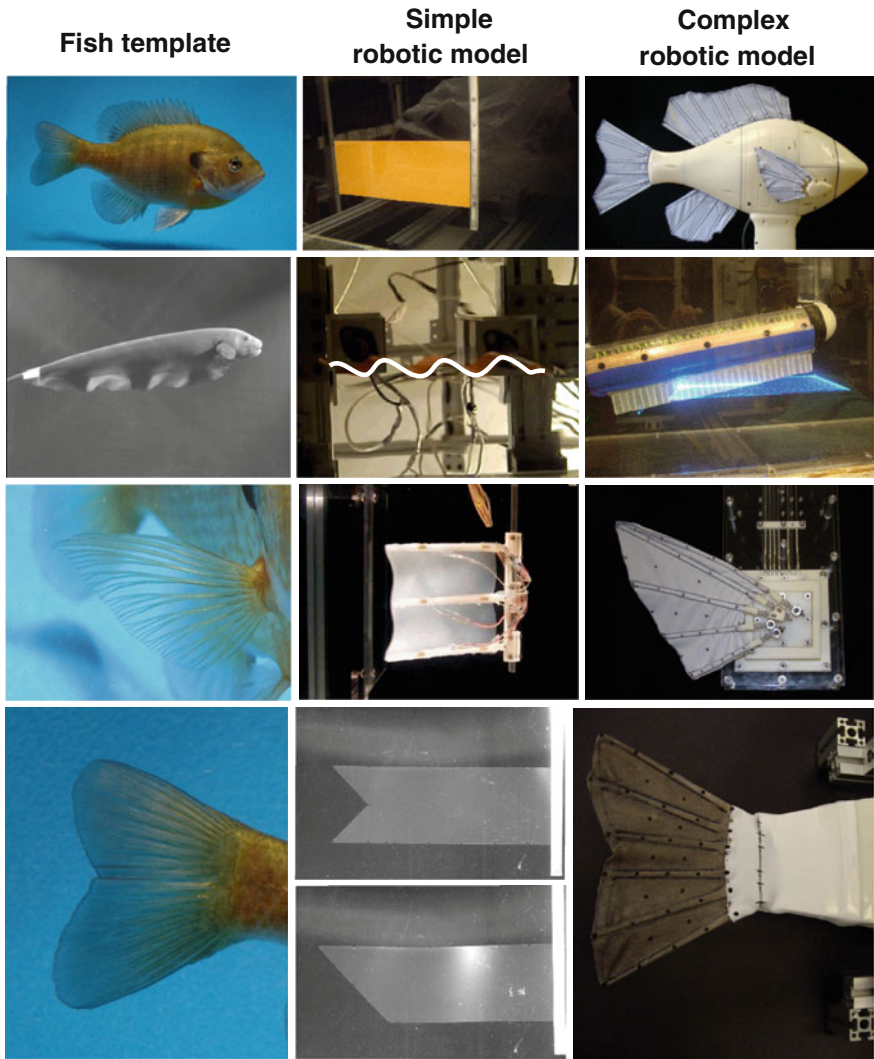


Fig. 6 Robotic approaches to studying fish locomotion can involve relatively simple flexible foil models of propulsion or more complex engineered devices. This diversity of approaches is based on fish templates, and can involve whole fish models (*top two rows*) or mechanical test platforms that represent individual fins such as the pectoral fin (*third row*) or caudal fin (*bottom row*). Individual panels show images from our collaborative work in fish robotics. Other chapters in this volume also present a diversity of fish robotic systems. Images are from research described in [3, 22, 23, 38, 65, 66, 96, 120, 121, 141]

Simple models are convenient but do not represent the complex behaviors inherent in biological systems. Thus, development of more complex mechanical devices that include active control of the body or fins is important for exploring

some of the behaviors seen in freely-swimming fish. Recent examples of using complex mechanical devices to understand whole-body or fin-based propulsion include the following studies: [5–8, 20–23], Epps et al. [37, 38, 51, 59, 71, 72, 77–80, 83–85, 90, 91, 93, 96, 104, 118–120].

Below we explore some of the benefits and drawbacks of using both simple and complex mechanical fish-like systems using examples from our previous research.

3.2 Simple Mechanical Models of Fish Locomotion

Simple flexible plastic strips or panels have proven to be useful passive models for flexible body propulsion in the water. These very basic propulsive systems are remarkably fish-like despite their simplicity, and exhibit a traveling wave of bending and self-propulsion at fish-like speeds and Strouhal numbers when actuated at frequencies of from 0.5 to 3 Hz in heave motion at their leading edge [111]. In order to effect propulsion of these simple flexible models of the fish body and tail region, the leading edge is attached to a rod controlled by heave and pitch motors (Fig. 7) and moved in a recirculating flow tank [64, 65, 98]. Flow speed is adjusted to achieve either self-propulsion when the net x-force (thrust) averages zero over a flapping cycle, or propulsive kinematics, forces, and hydrodynamics can be studied under conditions of net thrust or drag, measured with a force/torque sensor attached to the rod. These simple flexible strips (Fig. 7a, b) are convenient subjects for study because stiffness can be altered by changing the material, and different lengths and shapes can easily be attached to focus experiments on these parameters. The fish-like motions (Fig. 7c, d) produce interesting performance surfaces where thrust and efficiency of propulsion can be mapped over a range of heave amplitudes and frequencies for flexible foils of different stiffness (Fig. 7e, f). At low heaves and frequencies, efficiency is negative for the most flexible material as no net thrust is produced, but as stiffness and frequency increase, thrust is developed and efficiency approaches values of 0.2. Experiments like these also show that there can be a complex interaction between stiffness and frequency so that the material with the highest efficiency can depend on the frequency at which propulsion is occurring, and crossover points show where both flexible and stiff materials perform equally well (Fig. 7f).

Mechanical controllers that allow study of propulsion in flexible foils or panels are also convenient for the study of a number of fish structures, including the specialized skin structure in sharks. We have been using this approach to better understand how fish skin functions hydrodynamically, and to study the function of fish skin under conditions of self-propulsion. The vast majority of previous research on the skin of fish has been conducted using relatively simple models in constant velocity flow regimes. But fish bodies bend and flex during locomotion and the skin surface is thus subject to time-varying flows and changing angles of attack. It is our view that in order to understand the diversity of fish skin structures and how these surface structures function during locomotion, testing must be done under dynamic

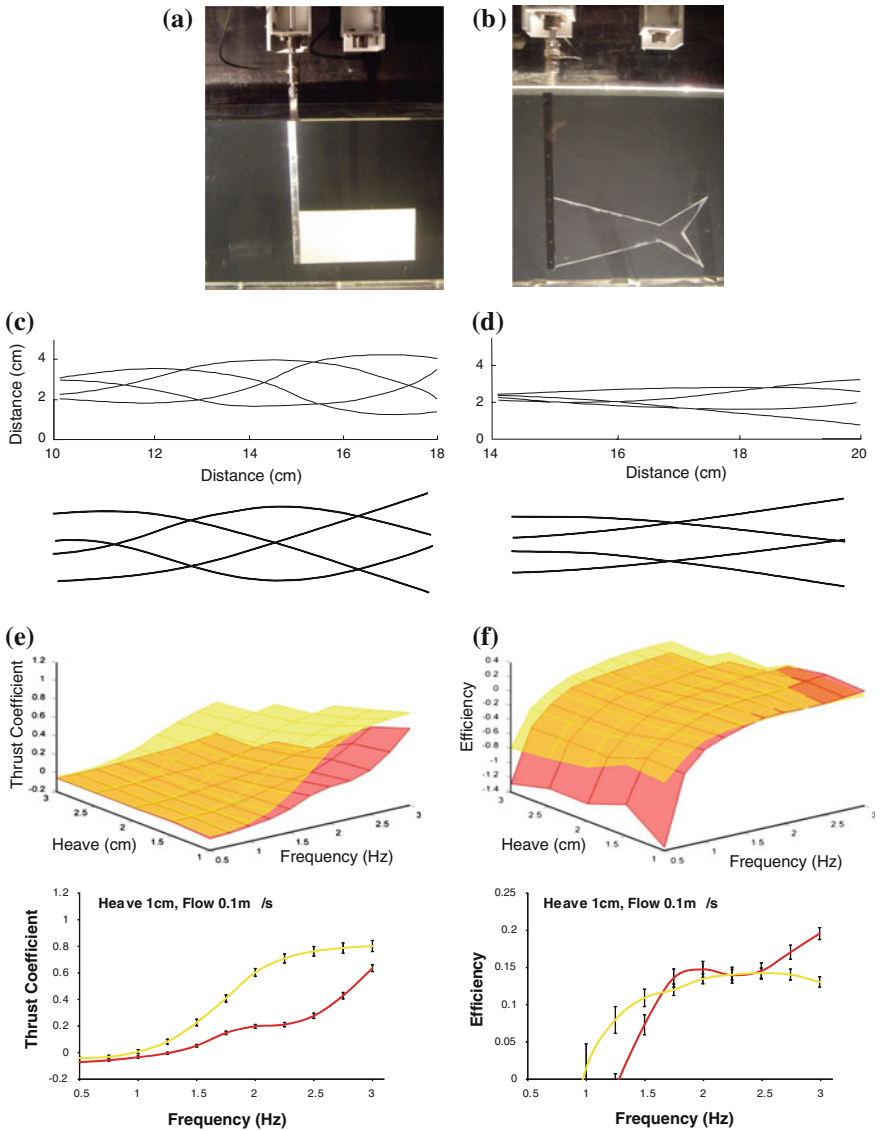


Fig. 7 Use of a flapping foil model system to study the dynamics of undulatory propulsion in fish. **a, b** A mechanical controller is used to oscillate flexible panels at the leading edge in heave and pitch motions while forces and torques on the shaft are measured (e.g., [64–66, 97, 98]). Flexible panels can be of any shape, and can be used as a simple model of fish caudal fins. **c, d** Motion of these flexible panels is similar to the undulatory body motion of the posterior half of the body of swimming fish and exhibits a range of dynamics that model both flexible (**c**) and stiff (**d**) fish bodies; midline data from clown knifefish and bluegill sunfish are shown on the *left* and *right*, respectively, with midlines from flexible and stiff swimming panels *below*. Use of a mechanical controller allows study of the full parameter space where heave (side to side) amplitude at the leading edge and frequency are used to explore the relationship of these parameters to thrust (**e**) and efficiency (**f**) for both flexible (*reddish* color) and stiff (*yellow*) flexible swimming foils. Plots below each surface show the relationship between thrust and efficiency and heave frequency for a particular heave and flow speed. Panels **c–f** modified from Shelton et al. [111]

self-propelled conditions. In addition, the frequencies, Strouhal numbers, and surface curvatures achieved by skin-like test membranes must match those exhibited by swimming fish.

Sharks have a remarkable structure to their skin. The surface of sharks is covered with millions of small tooth-like denticles that can range from 200 μm to 1 mm in size. Each denticle has a complex structure with a base embedded into the skin, and a stalk region that supports a flattened top containing ridges and valleys [58, 89, 92]. There is considerable variation in denticle structure among species of sharks [18], and equally substantial variation in denticle shape on different regions of the body [102, 103]. Adjacent denticles overlap, and changing the angle of the skin changes the angle of each denticle and hence the overlap between adjacent denticles. Previous work has suggested that shark skin functions to reduce drag, and may thus increase locomotor efficiency [10, 11, 24], but these analyses have been conducted under steady flow conditions in which the test surfaces were not moving.

In order to study the function of shark skin structures, we first assembled a flexible membrane composed of two pieces of fresh shark skin into a two-layer “sandwich” so that the skin surface denticles are exposed on each side (Fig. 8a). These membranes were then attached to a rod and moved by our mechanical flapper in a manner that matches the frequencies and surface curvatures of sharks swimming in vivo. By comparing the self-propelled speed of membranes with surface denticles intact and after they had been removed by careful surface sanding, we showed (Fig. 8a) that removal of the surface roughness reduced swimming speeds by an average of about 12 % [94]. Furthermore, the effect of surface roughness on self-propelled speed disappeared when rigid foils with shark skin on the surface are compared, indicating that the surface flexibility and motion of skin denticles is critical to their swimming performance advantage. Finally, particle image velocimetry of flow over the swimming shark skin membrane and the sanded control showed that removal of the surface alters the strength of the leading edge vortex, and suggests that the roughened shark skin surface may enhance leading edge suction and thus increase thrust. Shark skin surface roughness may thus enhance thrust on oscillating surfaces such as the tail where flow separation occurs [15] as well as reduce drag.

In order to better understand the function of shark skin, [136] designed a biomimetic shark skin membrane using additive manufacturing (Fig. 8b, c). Manufacture of shark-skin-like surfaces permits alteration of biological parameters, and controlled study of individual parameters of shark skin. Manufactured skin-like membranes were assembled into a two-layer sandwich and compared to a smooth control surface (Fig. 8b). These membranes consist of rigid denticles embedded into a flexible membrane and this allows the biomimetic skin membrane to bend and flex during swimming in a manner similar to real shark skin.

Testing under a wide range of parameters revealed improved swimming performance of the membranes with skin-like denticles compared to a smooth control. For example, Fig. 8d shows data from tests of self-propelled speed when the membranes are actuated at 1 Hz, heave values of ± 1.5 cm at the leading edge, and

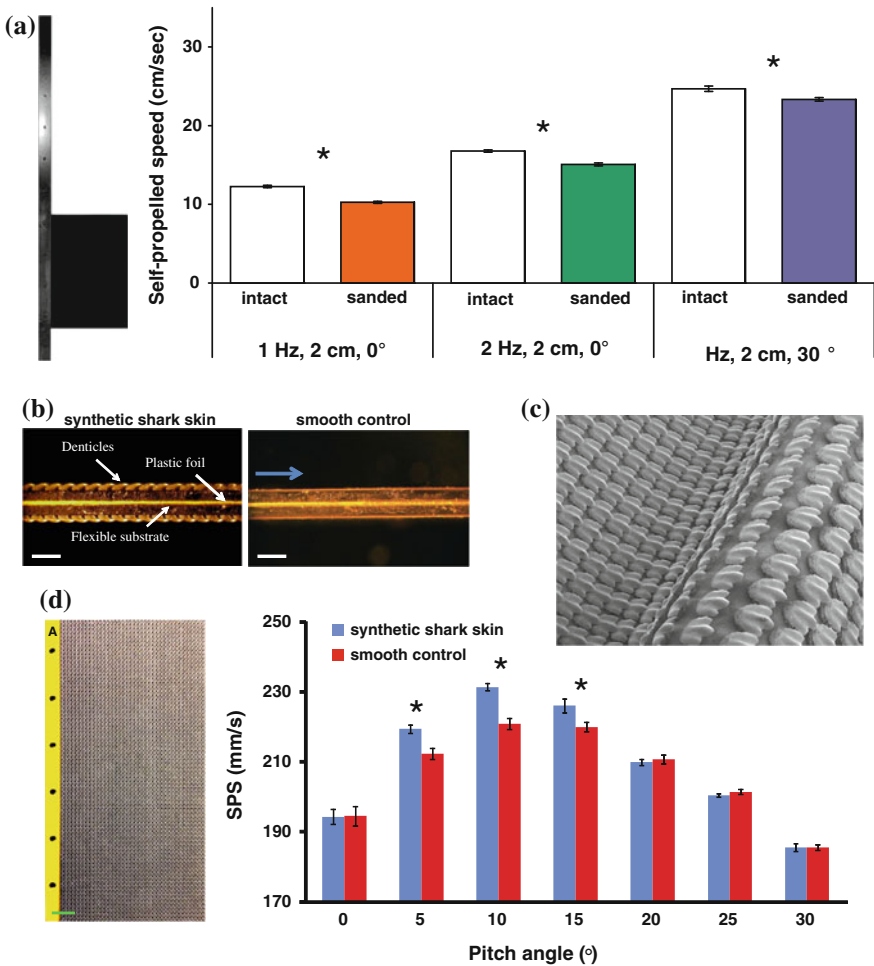


Fig. 8 Use of a mechanical flapping system to study the propulsive effect of shark skin. **a** Dynamic testing of the hydrodynamic function of shark skin denticles using pieces of shark skin that are attached to a flat support (shown on the left) which in turn is attached to a mechanical flapping foil device that allows controlled side-to-side and rotational motions of the shark skin membrane. Graph shows the self-propelled swimming speed of the shark skin membrane with intact denticles and after the denticles have been sanded off (to produce a relatively smooth surface) under three different motion programs. Note that in each case the swimming speed of the shark skin with denticles intact is significantly greater (*) than after the denticles have been removed by sanding. **b** Edge-on view of biomimetic shark skin assembled into a two-layer membrane compared to a smooth control of the same mass. White scale bars = 3 mm. **c** Scanning electron microscope view of biomimetic 3D-printed rigid shark skin denticles on a flexible membrane substrate. **d** Completed assembly of the tested flexible biomimetic shark skin foil (on left). Graph of the results from testing the self-propelled swimming speed of the biomimetic shark skin foil (blue bars) compared to the smooth control (red bars) at different pitch angles. At pitch angles of 5, 10, and 15° the biomimetic shark skin foils swim significantly faster (*) than the smooth controls. At the other pitch angles, the swimming speeds are similar. Modified from Wen et al. [136], Oeffner and Lauder [94], and Lauder [62]

a variety of pitch angles. Membranes with the roughened denticle-like surface swam faster for pitch angles of 5°, 10°, and 15°, but were not significantly different from controls at both higher and lower pitch values.

We believe that the manufacture of different fish-skin-like surfaces combined with dynamic testing that mimics conditions of fish swimming is a promising avenue for the future study of fish skin surface effects on locomotion.

3.3 Complex Robotic Models of Fish Locomotion

We have focused on bluegill sunfish (*Lepomis macrochirus*) as a model biorobotic system for studies of individual fin function, as well as for the development of more complex biorobotic models of the whole body and multi-fin function. Bluegill sunfish are particularly useful as they represent a generalized fish body shape and anatomy, and a substantial amount of three-dimensional kinematic, behavioral, and experimental hydrodynamic data on locomotor function exist that provide a useful baseline for both the design and analysis of biorobotic performance. The goals of our research using bluegill sunfish as a model system are (1) to better understand the locomotor performance of aquatic propulsive mechanical systems with flexible fish-like fins, (2) to develop manufacturing and assembly methods that allow construction of fins with fin rays having active control of the propulsive surface, (3) to conduct quantitative comparisons of data from mechanical devices to that of live fish, and (4) to use these biorobotic platforms to investigate complex swimming behaviors that are difficult to control in live fish such as multi-fin function during backward swimming and maneuvering.

We have developed several biorobotic models of the flexible fins of bluegill sunfish as experimental tools for investigating the mechanics and control of fin-based swimming. These systems include biorobotic pectoral and caudal fins that can execute the fin motions used during steady swimming, turn maneuvers, and hovering (Fig. 9, see [38, 121]); a freely swimming fish driven by paired pectoral fins [120]; and a model that integrates a moving peduncle with independently driven dorsal, anal, and caudal fins (our PDAC device, shown in Fig. 10). This biorobotic system is being used for investigating multi-fin swimming gaits which are common in fish when they stop, brake, swim backward, and maneuver through obstacles. The most recent of these systems incorporates distributed sensing within the fins (Fig. 9a, [57]), so that closed-loop control and navigation using object contacts can be explored. So that results from experiments conducted with these robotic systems have biological relevance, a priority of our design was to faithfully represent mechanical traits and to reproduce swimming characteristics of the biological fins. Physical features of the engineered fins were thus based on detailed studies of the bluegill sunfish biological system, and each model's dynamics, fin ray kinematics, and wake hydrodynamics were validated against those of the live fish (e.g., [31, 33, 44, 67, 68, 113]).

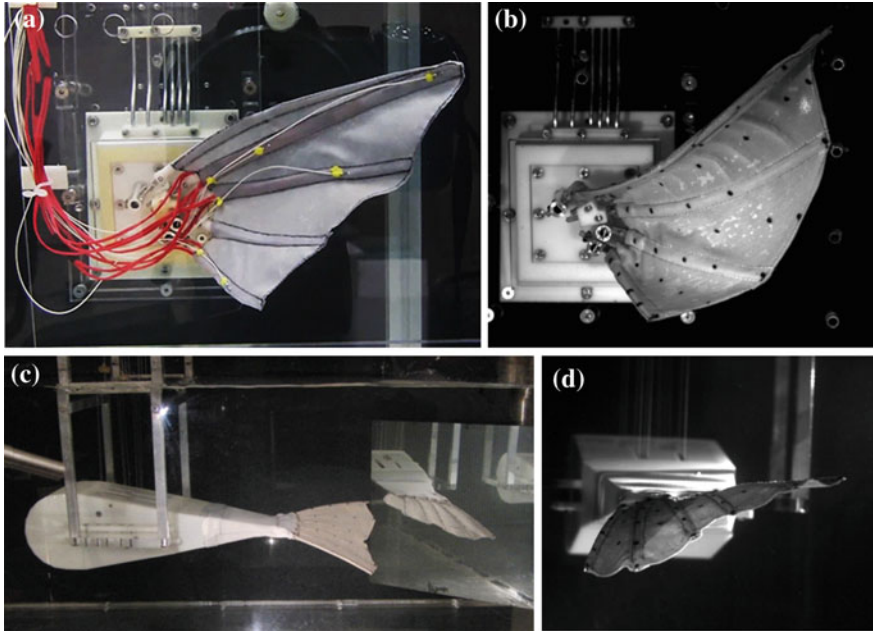


Fig. 9 Biorobotic pectoral (a, b) and caudal fins (c, d). Each of the rays of the pectoral fin has two actuated degrees of freedom which make them capable of executing a large repertoire of fin motions. In addition to steady swimming gaits such as that shown in (b), the pectoral fin can create the motions used during turns and hovering. The curvature of the fin rays seen in panel b is a result of the fluid loading on the compliant fin. Sensors within the pectoral fin (a) enable the curvature of the fin rays and the pressure across the fin webbing to be monitored for closed loop control. The rays of the caudal fin (c, d) are actuated through only one degree of freedom, but complex fin shapes can still be created by controlling phase relations between rays (d)

In order to produce good approximations of the complex fin kinematics used by the sunfish during swimming, each biorobotic fin uses multiple, independently actuated, compliant fin rays that are covered by a flexible fin webbing (elastane and polyester, latex, and/or urethane). The base of each fin ray is driven using servomotors (e.g., Maxon Precision Motors, Fall River, MA, USA) that are connected to the fin rays via nylon tendons. The fin rays are mounted to hinged bases which, with the servomotors, are designed to provide each fin ray with up to three degrees of actuated motion. In cases where the fin is designed to execute relatively simple kinematic patterns—such as steady swimming for caudal fins (Fig. 9c, d; [38]) bases with a single degree of freedom are sufficient. The fin rays move back and forth along an arc that is dictated by the orientation of the hinge within the base and complexity can be given to the fin shape by tailoring the compliance, phase relations, and the time course of individual rays. In cases where swimming gaits are more multifaceted such as pectoral fin maneuvering in sunfish, which involves complex motions of the fins and substantial conformational changes in the fin surface [46, 99], or where a single biorobotic model is used to investigate multiple

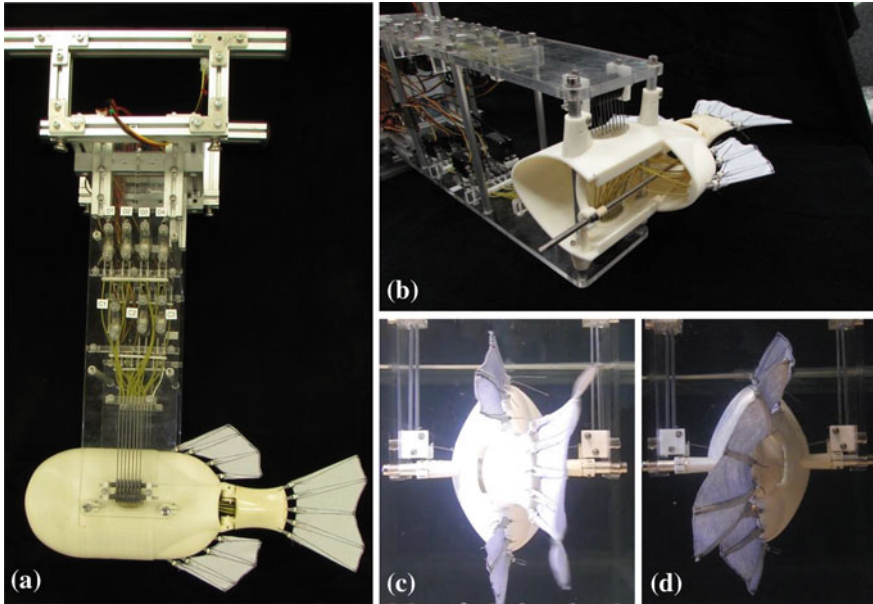


Fig. 10 Biorobotic model of the sunfish caudal peduncle (base of the tail) and the dorsal, anal, and caudal fins. The system provides independent control over the peduncle and 13 rays of the median fins for studies of multi-fin swimming. The location of the anal fin can be changed so that spatial relations among fins can be studied (b). Tendons, sheathed in housings, pass from the lateral sides of the fish to the fin ray bases (b). Fin motions and interactions are very different during steady swimming (c) and maneuvers, such as during backing (d) and this model is able to closely replicate the phasing and relative amplitudes of fin motions seen in live fish

kinematic patterns such as during maneuvering and steady swimming [96], the fin rays are also driven to rotate about the axis normal to the base (Fig. 9b). This, for example, enables a fin ray to follow different paths as it moves away from, or toward, the fish body. Active control over a fin ray's curvature, and thus over the fin's shape as it moves through the water, has been enacted in several biorobotic fins as a third degree of freedom using shape memory alloys, or a servomotor, to pull on a tendon that bends the rays shape [95]. In most cases, though, the fin rays are passive and curve only in response to fluidic loading. The cross sections of these passive fin rays are tapered from base to tip so that each ray's flexural rigidity scales to the flexural rigidity of the biological fin. This is key in allowing engineered fins to bend like a biological fin and to create appropriate wake and forces.

The nylon tendons that attach to the base of each fin ray are sheathed in a flexible, but non-collapsible, housing (Fig. 10), as is done for the cables of bicycle brakes. In addition to allowing the actuators to be located away from the fins, which benefits packing, these housings enable the tendons to follow curved paths within the robotic fins. In the PDAC robotic device, this permits the tendons of the robot's caudal fin to pass through the peduncle (Fig. 10), and for the peduncle to be actuated without causing the caudal fin's tendons to bind or to pull accidentally on the fin.

4 Conclusions

These devices based on bluegill sunfish, in addition to the wide variety of interesting complex fish robotic systems developed by other investigators, provide a solid foundation for future work in the area of fish biorobotics. Designing ever more complex fish-like systems will allow us to develop autonomous maneuvering robotic mechanisms that exhibit locomotor performance close to that of live fish. To accomplish this, biorobotic fish systems can make use of a diverse array of fins that allow force vectoring which will permit more complex behaviors than steady forward swimming alone. These devices will also be of great utility in testing biological hypotheses that are challenging to evaluate in living animals.

In the future, the use of simple mechanical systems to test specific hypotheses about the role of body shape, flexibility, and surface structure allows considerable control over experimental parameters, and will be of great value in investigating fundamental principles of aquatic propulsion. Researchers in fish biomechanics will benefit greatly from working with engineers to better understand how to construct a mechanical system that allows biological hypotheses to be tested. Similarly, engineers will continue to benefit from biological input which can provide insights into locomotor behaviors of the body and fins which may be unfamiliar to workers in design and manufacturing. We believe that one of the key challenges in the future is the control system needed to provide fish-like behavior and movement patterns in both steady and unsteady maneuvering propulsion. Developing an open-loop control will be challenging enough, but even more difficult is closed-loop control that integrates information from both the body and multiple fins. Closed-loop control is needed for navigation through complex habitats [43], and yet relatively few mechanical fish-like devices today incorporate such feedback.

Fish possess many interesting structural features of potential significance for locomotion that have yet to be studied, and the use of mechanical devices to explore the function of these features promises to help unlock some of the secrets of fish swimming performance.

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