Learning from Fish: Kinematics and Experimental Hydrodynamics for Roboticists

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Abstract: Over the past 20 years, experimental analyses of the biomechanics of locomotion in fishes have generated a number of key findings that are relevant to the construction of biomimetic fish robots. In this paper, we present 16 results from recent experimental research on the mechanics, kinematics, fluid dynamics, and control of fish locomotion that summarize recent work on fish biomechanics. The findings and principles that have emerged from biomechanical studies of fish locomotion provide important insights into the functional design of fishes and suggest specific design features relevant to construction of robotic fish-inspired vehicles that underlie the high locomotor performance exhibited by fishes.

Keywords: Fish locomotion, robotics, fin, hydrodynamics, kinematics.

1 Introduction

With over 28 000 species and half a billion years of evolutionary history, it is not surprising that fishes have diversified into nearly every possible aquatic habitat and display remarkable adaptations for locomotion in the three-dimensional underwater environment[1~3]. So it is certainly natural for engineers to turn to fishes as inspiration for understanding how to move underwater, as a source of new ideas on propulsive systems, and to understand basic principles of unsteady motion that are not common in current human-designed systems which emphasize rigid elements and stability.

In last twenty years, biologists, increasingly interested in the mechanics of living organisms[4~6], have undertaken many biomechanical studies of living fishes and the mechanical properties of their tissues. Just this year, two books providing an overview of fish biomechanics and physiology have appeared[7,8] and a number of recent review papers describe new results on the biomechanics of fishes relevant to locomotion through water[3,9~18]. At the same time, engineers have increasingly begun to fashion underwater robotic vehicles based on inspiration from living fishes[19~22]. As the communities of researchers interested in engineering robotic underwater vehicles and biologists who have studied the biomechanics of living fishes begin to come together[23,24], this seems like a propitious time to summarize many of the findings from recent research on living fishes in a succinct form that will be useful to robotic designers.

In this paper we present 16 key results that we hope will be useful for roboticists interested in understanding the biomechanics of locomotion in fishes. These 16 aspects of fish locomotion represent, in our view, the most important general results that would be useful to researchers who want to use some of the most recent data from experimental studies of living fishes to design the next generation of robotic fish. For each of the 16 results, we summarize major findings and provide a sampling of the recent literature that addresses the topic as well.

Our primary goal is to have this paper serve as a primer to key recent biomechanical findings in fish locomotor mechanics that have resulted from experimental studies on living fishes. Such an overview cannot be comprehensive, but hopefully will serve as an introduction to current research on the biomechanics of fishes and to key results from recent experimental studies.

2 Sixteen key results from recent studies of fish locomotor biomechanics

2.1 Fish are statically unstable: the center of buoyancy is below the center of mass

A hallmark of the functional design of fishes is the presence of multiple fins positioned around the body (see Fig. 1). While many studies of fish locomotion have focused on the pattern of body bending, fish locomotor design is characterized most notably by the presence of fins which act as control surfaces. Fish fins are actively controlled by muscles and as is discussed

Fig. 1 Bluegill sunfish, *Lepomis macrochirus*, showing the characteristic fin positions common to most bony fishes (see Fig. 2A for labels): the pectoral fins on the side of the body (the left fin is visible here), the midline dorsal, anal and tail fins, and the paired pelvic fins below the body. The dorsal and anal fins have spines located in front of soft fin rays. In this photo, the soft dorsal fin is curved to the right side of the fish to maintain stability during hovering

below in more detail, active fin movement is central for the maintenance of fish posture and for locomotion.

Active fin control even during hovering is needed because fish are statically unstable. In most bony fish, the center of buoyancy is below the center of mass (see Fig. 2) resulting in a net rolling moment if the fish is perturbed even slightly. In addition, most fish are slightly negatively buoyant, despite having a swim bladder which can be actively filled or emptied of gas[25,26]. When fish are first anesthetized, they slowly turn upside down and sink to the bottom. Some open ocean fishes such as sharks achieve near neutral buoyancy by incorporating low-density fats into their livers[26~28], but the vast majority of fishes are slightly negatively buoyant. For example, the bluegill sunfish (*Lepomis macrochirus*) is a commonly-studied model bony fish species that has been the subject of numerous experimental studies of locomotor hydrodynamics (see Fig. 1). Drucker and Lauder[29] found that bluegill approximately 20 cm in total length had a submerged body weight of 3.4 mN, a force that was balanced by the downwards momentum of vortex rings shed by the pectoral fins during swimming.

This instability of fishes may contribute to their maneuverability, as momentary imbalances in forces can be used to increase maneuvering capabilities and rapid changes in body position and direction[30~32]. But there is most likely an energetic cost to this instability which requires near constant activity of fins to hold position.
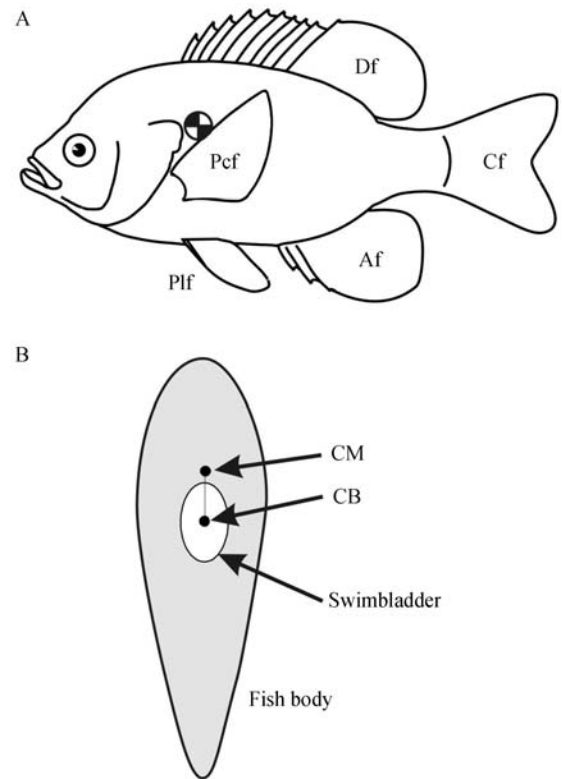

Fig. 2 The center of mass (CM) is located above the center of buoyancy (CB) for many fishes due to the swim bladder, a gas-filled buoyancy organ in the body cavity. The vertebral column, located, in the upper portion of the body, also contributes to shifting the CM above the CB. In panel A, the CM is marked by the symbol. Fin abbreviations Af, anal fin; Cf, caudal fin; Df, dorsal fin; Pcf, pectoral fin; Plf, pelvic fin. Modified from [37]

2.2 Fish fins are flexible

Fish fins are typically divided into two major classes: median, which are along the body center line, and paired (see Figs. 1 and 2)[12], and both types of fins play an important and active role during locomotion[33~35]. Although many models of fish fin function treat the fins as rigid flat plates with constant area, fish fins are anything but rigid and their flexibility is important for vectoring forces and for thrust production. Fig. 3 illustrates a variety of pectoral fin conformations in rainbow trout[34]. During steady swimming, the fins are held near the body, but during hovering, turning, or braking the fin is twisted into a variety of conformations. In addition, the base of the fin can be rotated by musculature in the body wall which reorients the entire fin surface. Fig. 4 shows deformation in the sunfish pectoral fin during steady locomotion: sunfish pectoral fins exhibit considerable change in area and shape as the fins beat.
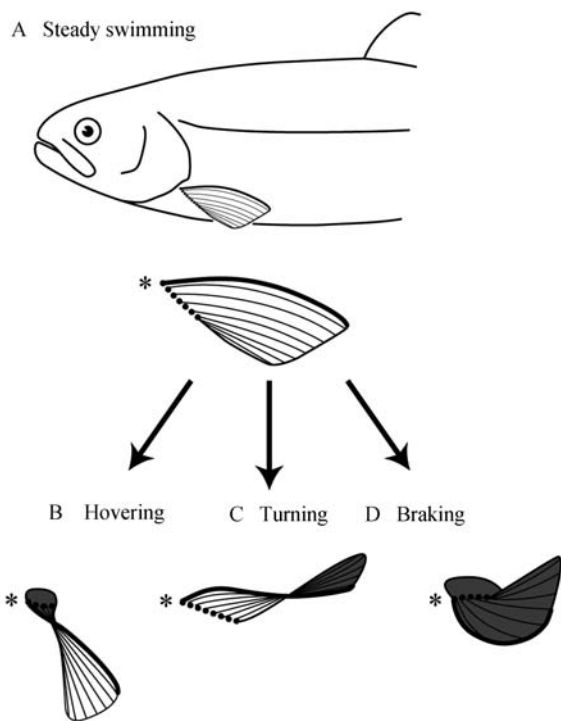
Fig. 3 Pectoral fin conformations in rainbow trout. Fish fins are flexible and are actively moved into a variety of conformations depending on the locomotor behavior. The grey color shows the dorsal surface of the fin. The asterisk indicates the location of the front fin base shown by the dotted line. Note how the fin base can be rotated by the fish to a nearly horizontal position and the considerable changes in fin surface orientation. Modified from [34]

2.3   Fish can actively control propulsive surface conformation

A little-known property of fish fins, and one that distinguishes them from insect wings and bird feathers, is that fish fins are supported by fin rays which display a remarkable structure allowing fish to actively control the curvature of the fin propulsive surface[3,36]. Fig. 5 shows the dorsal fin of a sunfish (*Lepomis*) which has a series of rigid spines in front of flexible fin rays, termed lepidotrichs. These flexible fin rays have a bilaminar structure with musculature attaching to the bases of the two halves. Differential muscle activity at the bases of the fin ray halves (hemitrichs) causes a curvature of the fin ray. This allows fish to curve their fins into oncoming flow and to actively resist hydrodynamic loading. The Young's modulus for fish fin rays is on the order of 1 GPa. A thin collagenous membrane connects adjacent fin rays, and has a Young's modulus of 0.3~1 MPa.
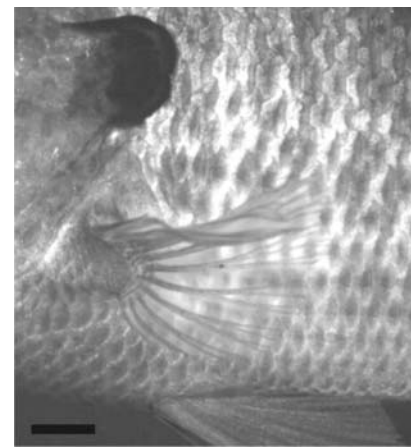

Fig. 4 Pectoral fin deformation during locomotion in bluegill sunfish, Lepomis macrochirus. One frame from a high-speed (250 Hz) digital video is shown illustrating the left pectoral fin approximately mid-way through the fin beat cycle. Note that the upper fin edge is twisted in the spanwise direction. There is a wave of bending that passes along the fin from base to tip during the fin beat.
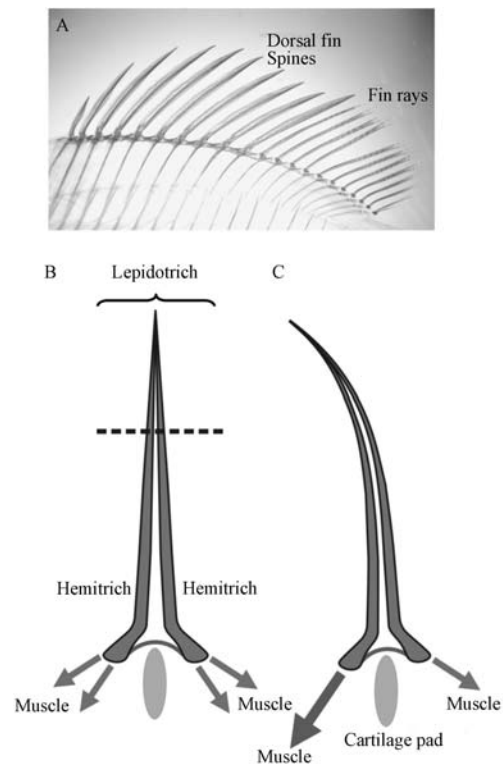Scale bar = 1 cm

Fig. 5 Structure of fish fin rays: fish have active control of fin surface conformation. Panel A shows the dorsal fin in a bluegill sunfish, with the front spines and the back soft rays. Panels B and C schematically show the bilaminar structure of fish fin rays and their muscular control, described further in the text. Modified from [3].

2.4 Fish fins move in a complex three-dimensional manner

Fish fins not only are flexible, but are moved in a three-dimensional manner during locomotion, as is evident from Figs. 3 and 4. This complexity of motion extends to the caudal fin or tail, which is often treated as a flat plate in theoretical models of fish propulsion or simply included in models as an undulating portion of the body. But the caudal fin, as well as other fins, moves in a complex manner even during steady swimming behaviors[10,37~39]. The tail of sharks is particularly noteworthy in this regard, and experimental three-dimensional studies of shark pectoral and caudal fin motion demonstrate that two-dimensional analyses are not adequate to understand fin function[40~42].

2.5 Patterns of 2D body undulation are very similar among fishes

The traditional categories that have been used to describe patterns of body undulation in fishes include terms such as "anguilliform" and "carangiform" which apply to "eel-like" and "mackerel-like" locomotion respectively[3,13,43~47]. A diversity of other names have been applied to swimming fishes to associate patterns of fin and body use with the exemplar species that exhibit these modes of swimming. But recently these terms have come under considerable criticism[3,13,48] as it has become increasingly clear that these categories obscure important differences among species in kinematics and hydrodynamic function, and are a two-dimensional approach that ignores the three-dimensional structure of fishes and the flows generated during locomotion. Fig. 6 shows body outlines taken from movies of fish swimming that illustrate three important facts: 1) a wave of bending passes down the fish from the head toward the tail during steady locomotion and the speed of this wave is greater than swimming speed, 2) the amplitude of this wave increases dramatically near the tail, and 3) the lateral (side-to-side) motion of the head is very small at low swimming speeds, but increases at higher swimming speeds. Even for eel locomotion (see Fig. 6), there is little movement of the front half of the body during slow and moderate swimming speeds[48~52], a point that has not been appreciated in much of the current literature on fish swimming. Body undulatory kinematics in swimming fishes are summarized in [3, 13], and representative recent analyses of body bending kinematics and the muscle activity that produces body bending during locomotion are provided in [53~60].

Two-dimensional analyses of fish locomotion (see Fig. 6) have shown that even fishes of very different body types such as eels, trout, mackerel, and tuna show
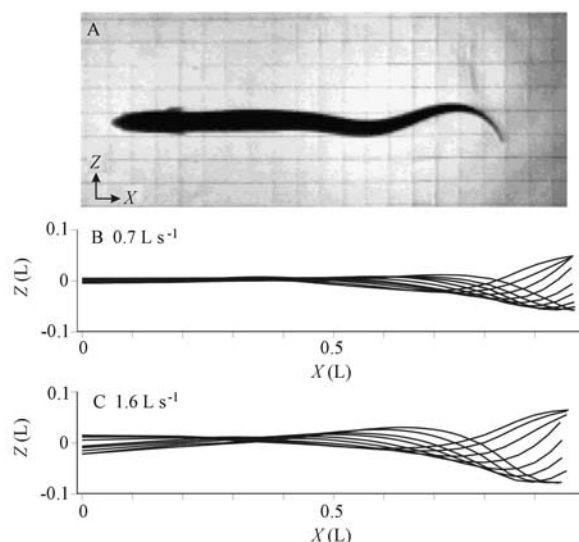

Fig. 6 Patterns of body undulation in eels (A) and largemouth bass (B, C). Oscillation of the front half of the body is minimal at slow swimming speeds and increases only slightly with speed during steady swimming. The y-axis shows side-to-side motion of the body, while the x-axis indicates position down the body. Both axes are in % total body length. Modified from [3]

extremely similar patterns of body movement when viewed in a horizontal section during steady undulatory locomotion[13]. All fish appear to move in a very similar undulatory manner ignoring the labels placed on them by biologists!

At the moment, relatively little is known about the diversity of force transmission systems in fishes and how forces generated during body bending are passed to the skeleton and connective tissue. In particular, there is little understanding of the diversity of force transmission systems in fishes that differ in body shape and fin placement, although recent work has begun to clarify many of these issues (see papers in [7] and [16]).

2.6 Fish vary greatly in 3D shape with important hydrodynamic consequences

Two-dimensional analyses ignore the three-dimensional effects of fish shape on hydrodynamic patterns, and recent work has shown just how critical consideration of the three-dimensional shape and kinematic effects are[13,35,37,61,62]. Fig. 1 clearly shows the complex body form exhibited by most fish, with dorsal and anal fins projecting above and below the midline. These fins are actively moved during swimming, and recent estimates from experimental studies of wake hydrodynamics (see below) indicate that the dorsal and anal fins of bony fishes may contribute as much to thrust as the tail itself during steady swimming[61,62]:

dorsal and anal fin thrust in bluegill sunfish is equal to the thrust generated by the tail. These data suggest strongly that future analyses need to take into account three dimensional effects, and that the differences observed among species of fish in their locomotor patterns may largely be a consequence of differing three-dimensional shapes and fin use.

2.7 Fish shed vortex rings or loops into the water to generate thrust

The past seven years have witnessed a flourishing of experimental studies of fish hydrodynamics, and a major result of these studies is the demonstration that fish fins generate thrust by producing vortex rings or loops. Studies documenting vortex production by swimming fishes include research on pectoral fins[29,32,34,63], the caudal fin[3,38,42,49,64~68], and dorsal fins[61,62,69]. Fig. 7 shows the pattern of vortex ring production in bluegill sunfish swimming at a slow swimming speed (0.5 L/s) with their pectoral fins alone, and the pattern of vortex production by the tail of sharks. The fish tail appears to function like a propeller, generating a localized thrust wake with an observable momentum jet in fish such as trout and mackerel, while eels generate primarily lateral momentum jets in the wake[49,50,70] and lack a well defined downstream momentum jet unless they are accelerating[70]. Eels lack a well-defined tail and show little morphological variation along their length, suggesting that the different wake pattern they exhibit may result from differences between eels and other fishes in the structure of the tail and the lack of a well-defined propeller.

Common to all fishes studied to date is the presence of large lateral momentum in the wake of the dorsal fin and tail[66,71] (see Fig. 8). Such large side forces may be a necessary consequence of the undulatory wave that passes down the body during locomotion (e.g., Fig. 6), or may be necessary for maintaining stability.

2.8 Fish tail shape influences vortex formation patterns

Comparative analyses of the vortex wakes in fishes with symmetrical tails (such as bluegill sunfish) and fishes such as sharks or sturgeon with asymmetrical tails shows differences in the vortex wakes shed by the tail into the trailing fluid (see Fig. 7). The vortex wake generated by tails that are externally symmetrical about a horizontal axis (such as the sunfish shown in panel A of Fig. 7) are typically mostly symmetrical ring-like loops, representing a series of linked rings[12,13,38,71]. In contrast, sharks have asymmetrical tails, with an inclined trailing edge, which has the effect of causing the rollup of a second vortex ring, gen-
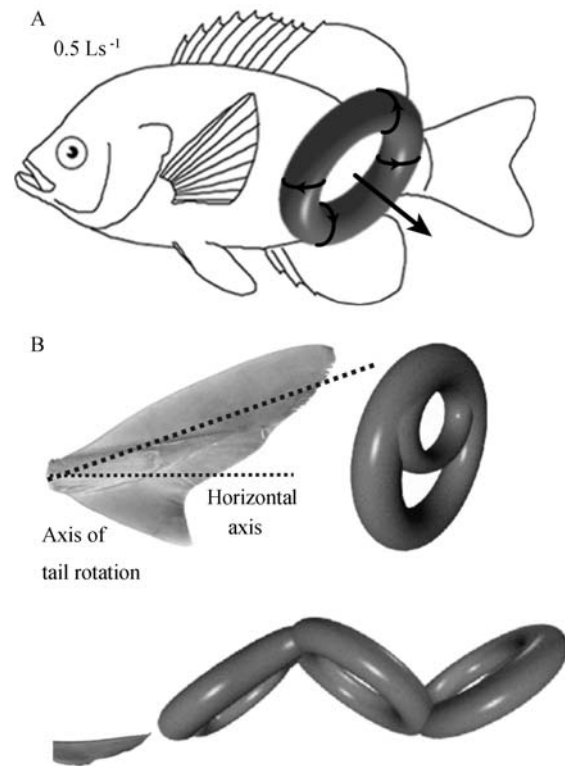

Fig. 7 Vortex rings generated by the pectoral fins in bluegill sunfish (A) and the tail of leopard sharks (B), seen from the side and top. The side view of the shark vortex wake shows the wake from a single tail beat, while the top view shows the whole chain of vortex rings produced as the shark swims. The inclined dotted line shows the axis around which the tail beats compared to the horizontal. Modified from [18, 29]

erating a ring-within-a-ring structure (see panel B in Fig. 7)[18,42]. Sturgeon have asymmetrical tails, and their vortex wake has also been analyzed[68]. Sharks and sturgeon swim with a significant body tilt and thus a positive body angle of attack to oncoming flow[18,68].

2.9 Median fins are under active control and generate substantial locomotor force

Many studies of fish locomotion ignore the median dorsal and anal fins to focus on patterns of body movement. But the dorsal and anal fins can generate substantial locomotor force (see Fig. 8). Bony fishes have special intrinsic muscles that attach directly to the dorsal and anal fin rays, and thus can move the fins actively[72]. Drucker and Lauder[35,62] studied the hydrodynamic wake of the dorsal fin in bluegill sunfish and trout, and found that even during rectilinear steady locomotion the dorsal fin generates substantial locomotor force with a strong side momentum component (see Fig. 8). Interestingly, in trout, the wake of

the dorsal fin decreases as swimming speed increases, while the opposite pattern was observed for bluegill sunfish. Tytell[61] estimated that the dorsal and anal fins together produce as much thrust as the tail in bluegill sunfish. The tail also possesses a diverse array of musculature that allows fine control of tail fin ray motion independent of the action of the major body muscles[10,73,74].

2.10 Fins in series can interact hydrodynamically

A glance at Fig. 1 shows that the dorsal and anal fins are located just in front of the tail, which thus could move through flow that has been significantly altered by the action of these forward median fins. Drucker and Lauder[37,62] and Tytell[61] showed experimentally that there is a substantial vortex wake shed by the dorsal and anal fins, and quantified wake flow incident to the tail (see Fig. 8). A key result of these studies is the demonstration that the tail does not move through undisturbed free-stream flow. Drucker and Lauder suggested that the dorsal and anal fin wake could generate increased thrust at the tail if the tail encounters flow altered to increase leading edge suction by modification of boundary layer flow at the appropriate time. Aktar and colleagues[75], in a computational fluid dynamic analysis using the dorsal fin and tail kinematics from the Drucker and Lauder[62] study, showed just such a substantial thrust enhancement when the tail moves through the wake of the dorsal fin. This shows that the presence of fins in series on the body of fishes could have significant effects on locomotor hydrodynamics and that fishes are very likely taking advantage of this arrangement to increase thrust at the tail.
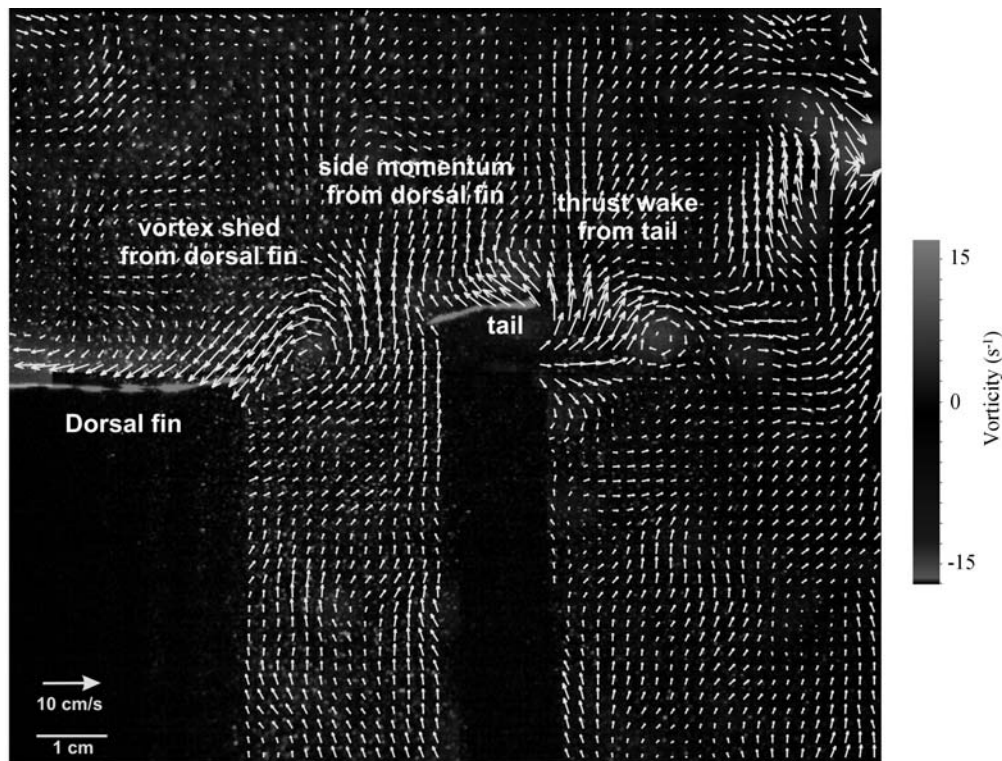

Fig. 8 Image from a digital particle image velocimetry (DPIV) analysis of water motion around the dorsal fin and tail of a bluegill sunfish swimming at 1.1 Ls^{-1}. 17 cm/s free-stream flow speed was subtracted to reveal vortical structures. This image in the horizontal plane was obtained with a high-speed video camera aimed down on a swimming sunfish from above. A laser light sheet aimed at the dorsal fin and tail illuminated particles in the flow. The dorsal fin and tail cast shadows where they intercept the light sheet. White velocity vectors show the pattern of water flow, and the vorticity scale on the right shows centers of fluid rotation. The dorsal fin is moved actively during swimming and sheds a vortex wake that moves downstream where it encounters the tail. The dorsal fin generates large side momentum. The tail generates its own thrust wake. The tail of swimming fishes does not encounter free-stream flow. Incident flow at the tail is highly modified by upstream fins

2.11   Many fish swim using their pectoral fins alone

Some fishes do not use their body during locomotion, and a number of recent studies have documented fishes that swim, often at high speeds, using their pectoral fins alone[14,15,17,29,32,75~80]. Analysis of pectoral fin "flapping" kinematics have compared "rowing" and "flying" or lift-based modes of moving the fins, and have documented the extensive use of the pectoral fins as primary locomotor devices.

In many fishes, the pectoral fins are used exclusively for locomotion only at slower speeds, and fishes shift locomotor modes and use other fins as described in the next section.

2.12   Fish have locomotor gaits

Although we often associate gaits in locomotion with terrestrial movement, as when horses change from a walk to a trot to a gallop[81,82], fish have locomotor gaits too[83~90]. Bluegill sunfish nicely demonstrate the phenomenon of gait change in fishes[29,91,92]. At slow swimming speeds of less than about 1.1 L/s, bluegill use their pectoral fins alone to generate thrust. Small motions of the dorsal, anal, and caudal fins might also be observed at slow swimming speeds to adjust body position. Above speeds of 1.1 L/s, bluegill recruit the red fibers only in their body musculature to power undulatory locomotion. As speed increases further to speeds above 2.5 L/s, bluegill recruit white muscle fibers in their body musculature to power unsteady locomotion. At these speeds and higher, bluegill use a "burst-and-glide" gait which is unsteady and is characterized by rapid bursts of swimming using only one or two tail beats, followed by a glide during which no locomotor movements are made[55,72,93]. Fish gaits thus differ from terrestrial locomotion where different gaits typically use the same muscles in different ways as speed increases. In fish, entirely different muscles or populations of muscle fibers are used as speed increases, and muscle fibers used for slower speed swimming are turned off and not activated at higher speeds[93].

2.13   Stability is a significant biomechanical problem for fish, especially at low speeds

Due to their generally elongate shape and the instabilities that arise from the locations of the center of mass and buoyancy noted above, maintaining body position and controlling low speed swimming and maneuvering postures are significant problems for fishes[30]. The fins and body of fishes have recently been shown to generate large lateral forces and these are useful for maintaining stability. Webb[94] has noted that studies of the energetics of fish swimming show that fish have elevated costs of maintaining body position at slow swimming speeds, but the reasons for this increased metabolism at slow speeds above what would be predicted are still not clear. Very few studies of fish locomotion have considered locomotor torques and no study has yet generated an overall quantitative dynamic force balance for swimming fishes. As a result, we still have only a vague understanding of the stability problem for swimming fishes.

2.14   Fin and body motion can change radically during acceleration and maneuvering

In contrast to studies of insect wings where differences between right and left side wing movements during turning are minor[95], fish fins exhibit dramatic changes in fin kinematics during maneuvering compared to steady swimming. There are relatively few studies of maneuvering kinematics in fishes, despite the importance of maneuvering in the locomotor repertoire of fishes[30,96], but studies of fin motion during maneuvering that have been published demonstrate substantial fin deformation not seen during steady swimming. Standen and Lauder[37] showed nearly right-angle bending of the dorsal fin when sunfish maneuver, and Drucker and Lauder[32,35,62] compared hydrodynamic function in pectoral and dorsal fins during maneuvering and steady swimming. The right and left side pectoral fins show dramatically different kinematic and hydrodynamic functions to vector flow momentum as fish execute turning maneuvers. Hovering can also be considered a type of maneuver, and fin conformations during this behavior also vary considerably from steady swimming (e.g., Fig. 3).

In addition, fish can use their whole body as a control surface to vector thrust in steering turns. By holding their body in a curved conformation, redirection of heading occurs. Powered turns are effected by differential right/left beating of the tail. And more extreme rapid maneuvers such as the c-start escape response[53,97,98] involve rapid bending of the body into a "C" or "S" like shape, before the propulsive phase moves fish away from the threat stimulus.

2.15   Fish body kinematics change in response to environmental hydrodynamic stimuli

The vast majority of research on fish locomotion has taken place in relatively low turbulence environments, either with fish in still water tanks or in recirculating flumes. But many fish swim naturally in flowing waters of high turbulence. Liao et al.[86,99,100] studied fishes swimming in the Karman vortex wake behind cylinders

placed in flowing water and demonstrated that trout can greatly alter their locomotor kinematic pattern to tune the pattern of body bending to the wavelength between oncoming vortices. Remarkably, fish swimming in a Karman street can completely shut off body muscle activity and generate thrust passively by adjusting the angle of their body airfoil in the vortex street to generate thrust as vortices pass by. The physical basis for this mechanism of passive thrust generation was confirmed by experimental studies of a heaving and pitching foil moving in the Karman wake of a cylinder[101].

A great deal more work remains to be done on fishes swimming in turbulence, and it is likely that fishes have much greater ability than currently recognized to extract energy from the hydrodynamic environment in which they live.

2.16 Control of fish body and fin motion is complex but still poorly understood

Fish possess remarkable muscular control over body and fin movements, and yet we are just at the beginning of understanding how the nervous system of fish controls motion, what the sensory inputs are that provide fish with positional information on their body and fins, and how fish sense and interpret their hydrodynamic environment. For example, there are no data on the sensory information available to fishes from the surface of fins. Can fish sense the position of their fins and the extent of deformation during locomotion? We have no idea at present, although we suspect that such information is not only available to the fish central nervous system, but that fishes use this information to modulate locomotor performance. By far the best-studied fish sensory system is the lateral line, which forms sensors on the surface of fishes and in canals that extend down each side of the body[102,103]. The lateral line system of fishes has recently been shown to sense vortices that impact the body[104]. Input from lateral line sensors presumably is also important for fish schooling behavior[105,106].

A number of studies have recorded electrical activity in the body and fin muscles of fishes, and this work gives a good indication of the nature of the motor output from the central nervous system to fish fins and the body[15,17,53,55,56,93,107~111]. But further work is badly needed that links motor output and sensory input with specific fin and body kinematic patterns.

3 Conclusions: toward a closer synergy of robotics and studies of living fishes

Given the considerable progress in studies of the biomechanics of living fishes over the past twenty years, and the increasing integration of techniques from engineering into studies of fish locomotion, the time seems ripe for roboticists and investigators analyzing the biomechanics of living fishes to enjoy greater collaborative efforts than is common at present. While there has been some exchange of ideas and results, relatively few collaborative projects have been undertaken in which the contributions from both biologists and roboticists are evident in the final product, be it a robotic vehicle or research on fish swimming. Such collaborative research and design can only enhance the excitement currently so evident in the papers and robotic vehicles that are appearing with increasing frequency.

Acknowledgments

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