

# Locomotion with flexible propulsors: I. Experimental analysis of pectoral fin swimming in sunfish

George V Lauder<sup>1</sup>, Peter G A Madden<sup>1</sup>, Rajat Mittal<sup>2</sup>, Haibo Dong<sup>2</sup>  
and Meliha Bozkurttas<sup>2</sup>

<sup>1</sup> The Museum of Comparative Zoology, 26 Oxford St, Harvard University, Cambridge, MA 02138, USA

<sup>2</sup> Department of Mechanical and Aerospace Engineering, George Washington University, Washington, DC 20052, USA

E-mail: [glauder@oeb.harvard.edu](mailto:glauder@oeb.harvard.edu)

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## Abstract

A full understanding of the mechanics of locomotion can be achieved by incorporating descriptions of (1) three-dimensional kinematics of propulsor movement, (2) material properties of the propulsor, (3) power input and control and (4) the fluid dynamics effects of propulsor motion into (5) a three-dimensional computational framework that models the complexity of propulsors that deform and change area. In addition, robotic models would allow for further experimental investigation of changes to propulsor design and for testing of hypothesized relationships between movement and force production. Such a comprehensive suite of data is not yet available for any flexible propulsor. In this paper, we summarize our research program with the goal of producing a comprehensive data set for each of the five components noted above through a study of pectoral fin locomotion in one species of fish: the bluegill sunfish *Lepomis macrochirus*. Many fish use pectoral fins exclusively for locomotion, and pectoral fins in most fish are integral to generating force during maneuvering. Pectoral fins are complex structures composed of jointed bony supports that are under active control via pectoral fin musculature. During propulsion in sunfish, the fin deforms considerably, has two leading edges, and sunfish can rotate the whole fin or just control individual sections to vector thrust. Fin material properties vary along the length of fin rays and among rays. Experimental fluid dynamic analysis of sunfish pectoral fin locomotion reveals that the fin generates thrust throughout the fin beat cycle, and that the upper and lower edges each produce distinct simultaneous leading edge vortices. The following companion paper provides data on the computational approach taken to understand locomotion using flexible pectoral fins.

## 1. Introduction

One of the most obvious aspects of the material design of organisms is that many of the structures and composite materials that interact with the environment are flexible. Tree branches and leaves bend in the breeze, bird wings flex during flight, insect cuticle deforms as the wings bend and fish fins and bodies bend during locomotion through the water. Given the many possible aspects of organismal design that might

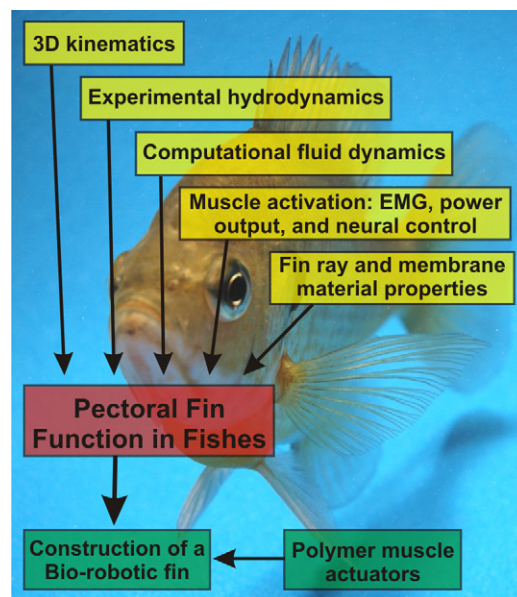
be viewed as inspiration for improving the functioning of man-made devices, the inclusion of flexible materials could be argued to be the most important. But incorporating flexible materials into human-engineered devices has proven to be an extremely challenging engineering problem. Almost without exception, man-made devices use rigid materials, gears and stiff linkages to achieve movement and interact with the environment. Materials that exhibit bending are most often considered to be near failure or are avoided due to the risk

of failure. In contrast, organisms rarely use rigid materials, and flexibility, deformation and twisting and bending are the rule both for applying forces to the environment, and for resisting loading imposed on organisms by the environment (Vogel 1988, Denny *et al* 1998, Koehl and Rosenfeld 2006).

Despite the obvious importance of flexibility for the functioning of biological materials, however, few studies have quantified the deformation of biological structures involved in locomotion, and even fewer have undertaken quantification of appendages bending during *in vivo* movement. The most extensive *in vitro* work to date is that by Combes and colleagues who studied the flexibility of insect wings (Combes and Daniel 2001, 2003a, 2003b, 2003c), but little is known about insect wing flexibility during flight as most analyses assume that the wing acts like a rigid flat plate. Theoretical analyses of the performance of flapping foils with flexibility have been undertaken (Ramamurti *et al* 1999, Katz and Weihs 1978, Liu and Bose 1997, Miao and Ho 2006, Triantafyllou *et al* 2004), although these studies typically involve relatively low levels of deformation.

Given the near ubiquity of deforming propulsive surfaces in animals, what type of information would be desirable to have about flexible biological propulsors? First, and arguably most importantly, data on the three-dimensional kinematics of propulsive surfaces are needed (figure 1). Without such data, the magnitudes of bending, twisting and curvature change during propulsion cannot be known. Three-dimensional kinematic data cannot just consist of tracking a few points in the  $x$ ,  $y$  and  $z$  dimensions: coordinate maps for the *surface* of the propulsor and how such maps change through time must be known in order to quantify both spanwise and chordwise bending and to calculate curvature changes through time. Also, without such three-dimensional coordinate data, computational fluid dynamic analysis (CFD) cannot be undertaken, as ideally three-dimensional kinematic data will serve as input into a computational model. Second, data are needed on the material properties and biomechanical design of propulsors (figure 1) so that active and passive components of deformation can be estimated. Third, control mechanisms for the propulsor need to be understood. How are propulsors activated and how extensive is the system for active control? Fourth, experimental hydrodynamic analyses of the effect of propulsors on the water or air are important for understanding how momentum is transferred to the fluid environment by propulsor movement. How does propulsor motion correlate with the production of vortices and momentum fluxes during locomotion? Fifth, having a fully three-dimensional computational fluid dynamic model of propulsor function (figure 1) allows both comparison with experimental flow patterns and calculation of surface pressure distributions, force production through time, and manipulation of surface geometry and motion that are not practical in experiments on living animals.

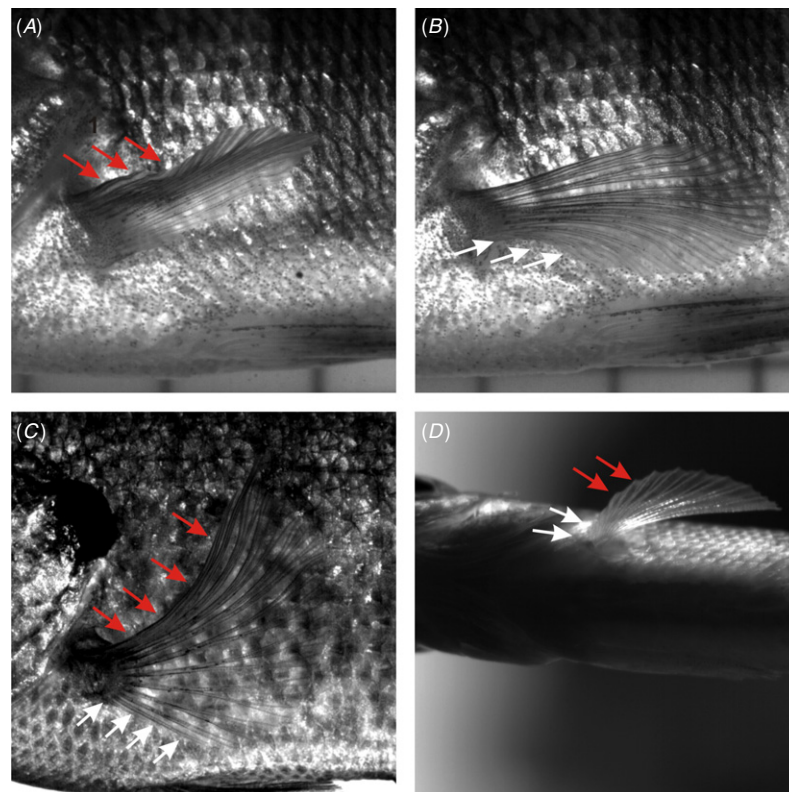
Finally, the construction of a robotic model of the propulsor is an extremely useful adjunct to the five experimental and computational approaches noted above as such models permit experimental modification and



**Figure 1.** Schematic overview of the major elements of research on flexible propulsors using the pectoral fin of sunfish as the main example discussed in this paper. A photograph of the bluegill sunfish with its left pectoral fin extended is shown in the background. A complete understanding of fin function involves each of the components shown in yellow boxes, as well as construction of robotic models to test functional hypotheses (green boxes). Further description in the text.

manipulation of design features not found in nature. Models can also be implemented with non-biological actuators such as conducting polymers (Madden *et al* 2004a, 2004b) with different properties and hence a different set of design constraints (figure 1) than either traditional or biological actuators. Robotic models can also be useful, as is widely acknowledged, for understanding how lessons learned from biology can be applied to the construction of a working representation (Long *et al* 2006). However, it is not often appreciated that such models can also be useful for testing biological hypotheses directly by modifying movement patterns and material properties.

Our goal in this paper is to provide a broad overview of the approach that we are taking to understanding locomotion achieved with flexible propulsors, using as our focal example the pectoral fin of bluegill sunfish, *Lepomis macrochirus* (figure 1). For each of the five major classes of data on flexible propulsors outlined above, we provide sample data and summarize selected recent research results. An extended discussion of the computational approach that we have taken to studying the flexible sunfish pectoral fin is detailed in the following companion paper (Mittal *et al* 2006), and other papers summarize additional aspects of this research program which is still in progress (Tangorra *et al* 2007, Lauder *et al* 2005, Lauder and Madden 2006, Fish and Lauder 2006, Bozkurtas *et al* 2006, Dong *et al* 2006). Additional recent papers provide a more general review of fish propulsor function from a biological perspective (Lauder 2006, Lauder and Tytell 2006, Shadwick and Gemballa 2006, Drucker and Lauder



**Figure 2.** Pectoral fins of fish undergo considerable deformation during locomotion, and the pectoral fin may have two simultaneous leading edges. (A) Pectoral fin motion in a yellow perch, *Perca flavescens*, showing the upper (dorsal) edge of the fin leading (red arrows) during propulsion. (B) Pectoral fin motion in a yellow perch, *Perca flavescens*, showing the lower fin edge leading during maneuvering (white arrows). (C) Pectoral fin motion during propulsion in the bluegill sunfish, *Lepomis macrochirus*, showing two simultaneous leading edges as the fin moves away from the body (red and white arrows). (D) Pectoral fin motion in the killifish, *Fundulus diaphanus*, also showing two simultaneous leading edges (red and white arrows).

2002a, Drucker *et al* 2006, Wilga and Lauder 2004, Westneat and Wainwright 2001, Westneat *et al* 2004).

## 2. Overview of methodology

There are a number of notable experimental challenges in studying a complexly deforming biological propulsor like fish pectoral fins. Quantifying the three-dimensional geometry of the fin throughout the fin beat cycle can be difficult due to the significant deformation which requires that multiple high-speed cameras be used. A minimum of two views is needed but we have found that three or more simultaneous cameras provide the best reconstructions of fin positions. In addition, high-resolution cameras ( $1024 \times 1024$  pixels minimum) are necessary to see structural details required for accurate reconstruction of surface geometry, and a sample rate of 500 Hz is ideal to provide sufficient time resolution of fin motion. Meeting these technical requirements also facilitates the generation of a kinematic data set that is appropriate as input for computational fluid dynamic analysis. A three-dimensional calibration (see Hsieh (2003), Standen and Lauder (2005), Hedrick *et al* (2002) and Lauder *et al* (2005)) allows quantification of  $x$ ,  $y$ , and  $z$  positions of points on the fin surface; for our three-dimensional fin reconstructions we

digitized 200–300 points on the fin surface at each of 20 time steps throughout the fin beat cycle. Reconstructed fin positions are illustrated in the following companion paper (Mittal *et al* 2006).

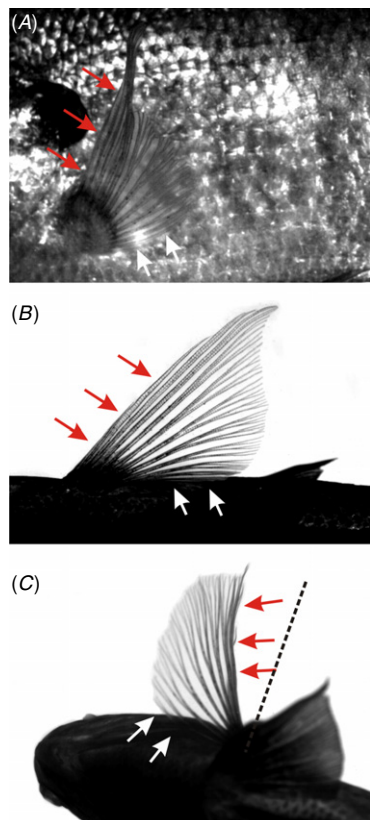
In addition, fish fins are composed of a diversity of composite materials arranged in a complex layout. This makes estimating active and passive properties of fin motion difficult, and especially so in the case of fish fins that have active curvature control (see below, and Lauder (2006)).

The data described below were obtained on bluegill sunfish, *Lepomis macrochirus*, swimming in a recirculating flow tank. Sunfish swam at  $20^\circ\text{C}$  and ranged in size from 15.0 to 18.5 cm in total length ( $L$ ). Locomotor speeds ranged from  $0.5$  to  $2.0 L s^{-1}$ . Comparative kinematic data were obtained from several other species (figure 2) to confirm that the fin motions observed in bluegill are not unique to that species.

Selected details on the techniques discussed below are provided in the relevant section.

## 3. Pectoral fin kinematics

High resolution digital videos of fish pectoral fin motion during locomotion reveal that the pectoral fins of most fish species are highly flexible (figure 2). Fish have active muscular



**Figure 3.** Pectoral fin motion in bluegill sunfish, *Lepomis macrochirus*, during turning and braking. (A) Pectoral fin on the inside of the turn in side view showing the twisted conformation of the fin with the upper (dorsal edge, red arrows) held away from the body. (B) Pectoral fin on the outside of the turn shown in bottom view, with the lower fin edge (white arrows) held against the body. (C) Pectoral fin position during braking, in bottom view. The lower fin edge (white arrows) has moved forward of the upper edge (red arrows), and the whole fin has been moved forward to an angle greater than  $90^\circ$  (the position of the body perpendicular is shown by the dashed black line).

control over the leading and trailing edges of their fins through adductor and abductor muscles and these muscle groups possess individual bundles that insert on the base of each individual bony fin ray that supports the fin. As a result, during locomotion fish pectoral fins exhibit changes in area, bending in both the chordwise and spanwise directions, distinct correlated movement of the upper (dorsal) and lower (ventral) edges (while the middle of the fin often lags behind) and waves of bending that pass out along the fin (figure 2). Two simultaneous leading edges are present on the sunfish pectoral fin during propulsion (figure 2(C)), and similar patterns of fin motion are observed during propulsion in perch and killifish (figure 2).

The pattern of pectoral fin motion during braking and maneuvering can be very different from that seen during propulsion (figure 3) (see also Drucker and Lauder 2001, 2002b, 2003, Higham *et al* 2005, Geerlink 1987). Fish that change vertical position during locomotion often bring the ventral pectoral fin edge away from the body prior to the

dorsal edge (figure 2(B)), generating upward fluid momentum and rotational torques on the body, sending the fish down. During yawing turns (figure 3), the fins on the inside and outside of the turn exhibit very different movement patterns (Drucker and Lauder 2001). Figure 3(A) shows a side view of the twisted conformation of the pectoral fin in a bluegill on the inside of the turn, while the fin on the outside of the turn (figure 3(B)) has the ventral rays held against the body. Braking involves bringing the pectoral fin forward, and the ventral rays have effectively reversed their anterior–posterior position compared to the fin conformation during braking.

#### 4. Fin anatomy and material properties

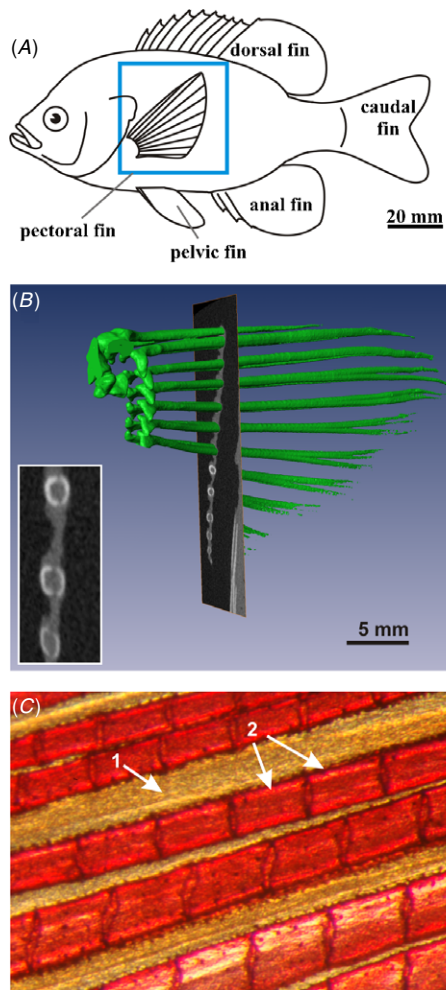
What is the structure of the pectoral fin in sunfish and what are the material properties of the fin components that produce such locomotor deformations? Each bluegill sunfish pectoral fin typically has 14 individual pectoral fin rays (figure 4) that support a thin collagenous membrane stretched between adjacent rays. Each fin ray, termed a lepidotrich, is composed of two semilunate half rays (hemitrichs), seen in the inset to figure 4(B), which are connected to each other by small collagenous and elastic fibers (Geerlink 1979, Geerlink and Videler 1987).

Each half ray has expanded sites at the base for the attachment of the fin ray muscles, and each hemitrich is itself composed of a series of small bony segments (figure 4(C)) attached end-to-end with short collagen fibers. Hemitrichs slide past each other when the two hemitrichs are moved differentially by the pectoral fin muscles at the base of the fin. Fish thus have active control over the curvature of their propulsive appendage since differential movement of the two fin ray hemitrichs causes the fin ray, and hence the fin surface, to bend (Lauder 2006, Lauder and Madden 2006, Geerlink and Videler 1987).

Three-point bending experiments on individual fin rays showed considerable differentiation in fin ray material properties depending on the location along the ray, and also changes in stiffness among rays. Figure 5 shows fin ray 8 in a bluegill undergoing three-point bending, and the results of one experiment showing that the proximal portion of the ray is considerably stiffer than the distal part. Calculation of fin ray Young's modulus (for the whole, composite, ray) gave values of about 1 GPa, and values of 0.3–1 MPa for the fin ray membrane (Lauder and Madden 2006, Tangorra *et al* 2007). These data will be used in future work to design a robotic flexible fin propulsor of comparable stiffness to the sunfish pectoral fin, and as a starting point for experimental explorations of the effect on varying fin stiffness on thrust generation.

#### 5. Muscular control of pectoral fin function

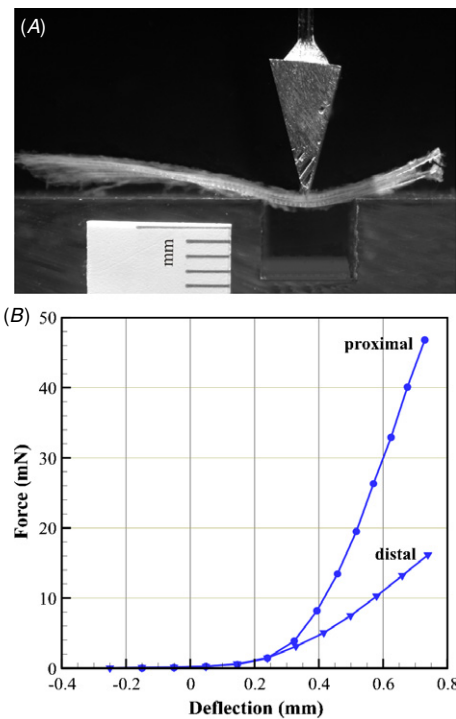
How do fish control the movement of individual fin rays? By implanting recording electrodes within the abductor and adductor muscles of the sunfish pectoral fin (figure 6), we measured muscle activity in the major muscle groups that move the pectoral fin rays, and recorded from individual muscle



**Figure 4.** Pectoral fin structure in bluegill sunfish, *Lepomis macrochirus*. (A) Position of the pectoral fins on the body. (B) Sunfish typically have 14 bony, jointed fin rays that support the fin membrane and form the pectoral fin. Micro CT scanning of fin ray structure shows that each fin ray is composed of two distinct curved elements (inset panel shows cross-sectional geometry—white indicates bone). (C) Photograph of pectoral fin rays with bone stained red (2, arrows); the collagenous membrane between the fin rays is shown in tan color (arrow 1).

bundles attaching to different regions of the pectoral fin. Such recordings demonstrate the pattern of muscle activation by the nervous system, and are particularly useful for investigating differential control and when anatomically antagonistic fin muscles are co-activated (Drucker and Jensen 1997, Westneat and Walker 1997, Jayne and Lauder 1994, 1995a, 1995b, Jayne *et al* 1996).

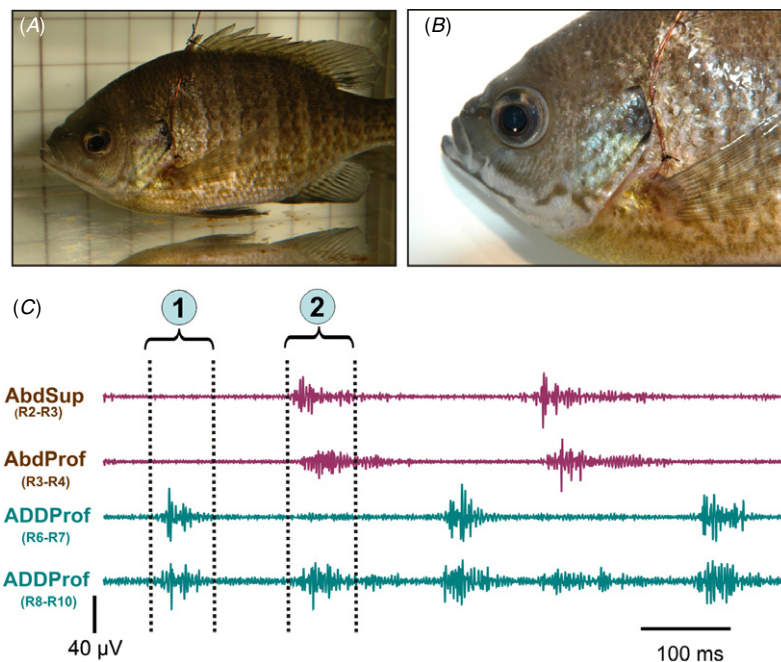
Figure 6 shows that during maneuvering (time 1), complete separation of adductor and abductor muscle activity can occur. Fish thus are able to activate the adductor muscles moving the fin toward the body completely independently of the abductor muscles that move the fin away from the body. Later in this same sequence, both adductor and abductor muscles are coactivated, but this time clear differential activity within the adductor muscle mass is observed: fin rays near the bottom of the fin (rays 8 to 10) are activated while those in the



**Figure 5.** Experimental measurement of fin ray material properties. (A) Three-point bending conducted on fin ray 8, removed from a bluegill sunfish pectoral fin. A triangular force probe is pressing on the fin ray. (B) Measurements of fin ray stiffness at two separate locations: one-third of total ray length from the base (proximal) and two-thirds ray length from the base (distal).

middle of the fin (rays 6 and 7) are not subject to muscular force. At this same time, the antagonistic abductor muscles also show differential activity among rays. Later in this same sequence, a clear alternating pattern of activity is observed between adductor and abductor muscle activity. Coactivation of the antagonistic muscle pairs during time 2 (figure 6) could reflect active bending of the pectoral fin rays by the controlled differential movement of the ray hemitrichs.

Sonomicrometry is a technique that allows quantification of muscle strain during natural behavior by measuring the time taken for sound to be transmitted between two small crystals implanted into the muscle (e.g., Donley and Shadwick (2003) and Shadwick *et al* (1999)). In order to construct a biomimetic robotic pectoral fin, it is useful to know values of strains experienced by the fin muscles; actuator materials could then be selected with good power output at the *in vivo* strains required by the fin to generate propulsive forces (Madden *et al* 2004a, 2004b). We implanted one pair of sonomicrometry crystals into the abductor superficialis pectoral fin muscle and measured muscle strain during steady swimming, yawing maneuvers and during backward swimming (figure 7). Muscle strains during steady swimming are relatively low, on the order of 6.3% (figure 7). But strains increase remarkably during maneuvers and backward locomotion using the pectoral fins, where strains range from 18% to 23% respectively. High strains during maneuvers may be a partial consequence of passive hydrodynamic loading on the fin, which forces the



**Figure 6.** Pectoral fin electrical activity patterns during locomotion at 2.0 body lengths ( $L$ ) per second. (A) Bluegill sunfish swimming in a recirculating flow tank with electrodes implanted into the musculature of the left pectoral fin to measure muscle motor patterns. The cable leading from the dorsal fin connects to recording amplifiers and a computer out of view. (B) Close view of the electrode cable sutured to the fish surface just anterior to the left pectoral fin. (C) Pectoral fin muscle electrical activity recordings during locomotion. Abductor muscles (AbdSup and AbdProf) move the fin away from the body in the outstroke, while adductor muscles (ADDProf, fibers attaching to two different groups of fin rays are shown) pull the fin back toward the body. Note that at time 1, there is no overlap in abductor and adductor muscle activity, while at time 2 electrical activity of these antagonistic muscle groups overlaps. Also note the differential activity within the adductor profundus muscle, as muscle bundles attaching to the different fin ray groups show different activity patterns.

fin surface away from the body, but high strain during steady backward pectoral fin locomotion is most likely a result of required stretching of the abductor muscle to generate thrust in the opposite direction to that of normal forward swimming.

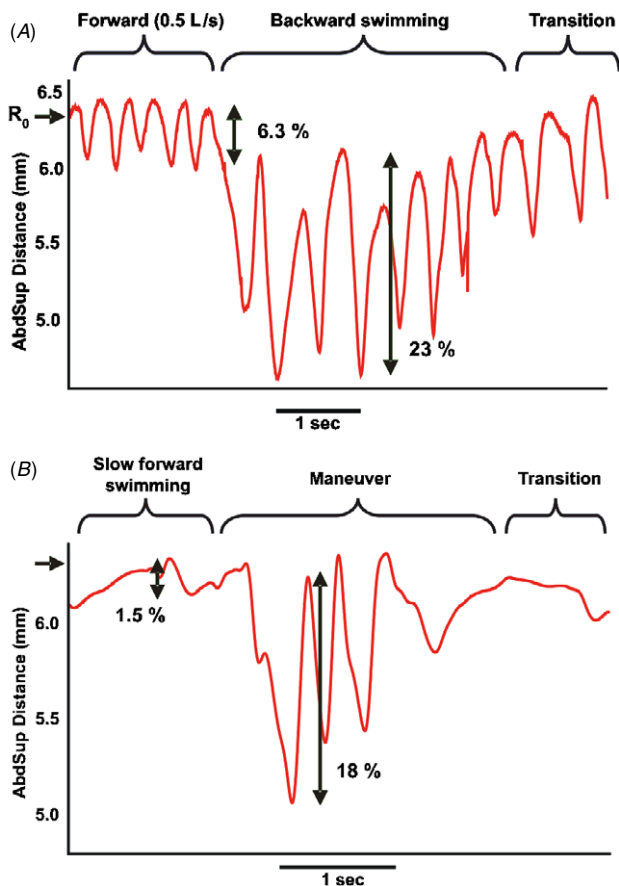
## 6. Experimental hydrodynamics

Experimental hydrodynamic analysis of pectoral fin function in bluegill sunfish during locomotion was conducted by injecting dye streams near the fin, and with particle image velocimetry (PIV) to quantify fin wake flow patterns.

Dye stream patterns were obtained by swimming bluegill in a recirculating flow tank. Fish were induced to swim near the ends of dye wands that released a steady stream of dye close to the base of the pectoral fin. High-speed video recordings were used to obtain image time series of the dye stream interacting with the pectoral fin during locomotion. Numerous trials resulted in a number of sequences showing a clear effect of pectoral fin motion on the dye stream. Figure 8 shows a series of frames from one sequence illustrating the effect of the pectoral fin on a dye stream as it passes over the upper edge of the fin during the fin beat. During fin abduction, dye can be seen moving over the upper fin edge, and curving back anteriorly in the upper fin edge vortex. In figure 6(B), a small amount of dye is trapped in the dimple just behind the leading edge formed in the spanwise wave that passes out the upper half of the fin during the transition from abduction to

adduction. As the fin retracts during adduction, vorticity that is shed by the upper portion of the fin is visible as a tightly rolled up dye region that continues to wrap up as the fin completes its stroke (figure 8(D)).

Digital particle image velocimetry (DPIV) on freely swimming fishes has been a technique that has proven very useful for understanding the hydrodynamic function of fish fins (Drucker and Lauder 1999, Nauen and Lauder 2001, 2002, Wilga and Lauder 2002, Drucker and Lauder 2002a, Lauder and Drucker 2002). We have recently modified our previous approach and used a transversely oriented laser light sheet to image flow in the wake of the sunfish pectoral fin (figures 9(A), 9(B)). This gives a good estimate of wake flows as the full wake can be imaged as it moves toward the camera. And with a rapid filming rate of 500 fps, an accurate reconstruction of time-dependent wake flow patterns can be obtained. Using two simultaneous high-speed cameras (figure 9(B)) makes it possible to obtain stereo-DPIV wake data (Nauen and Lauder 2002). Pectoral fin wake flow data obtained from the transverse plane clearly show the presence of two simultaneous, attached, leading edge vortices on both the upper and lower fin edges in the cupped configuration during the movement away from the body (figure 9(C)). Quantifying the momentum flux from the pectoral fin in the upstream–downstream direction using DPIV data indicates that the pectoral fin generates thrust throughout the fin beat cycle. Data from the horizontal light sheet plane (figure 9(D)) also

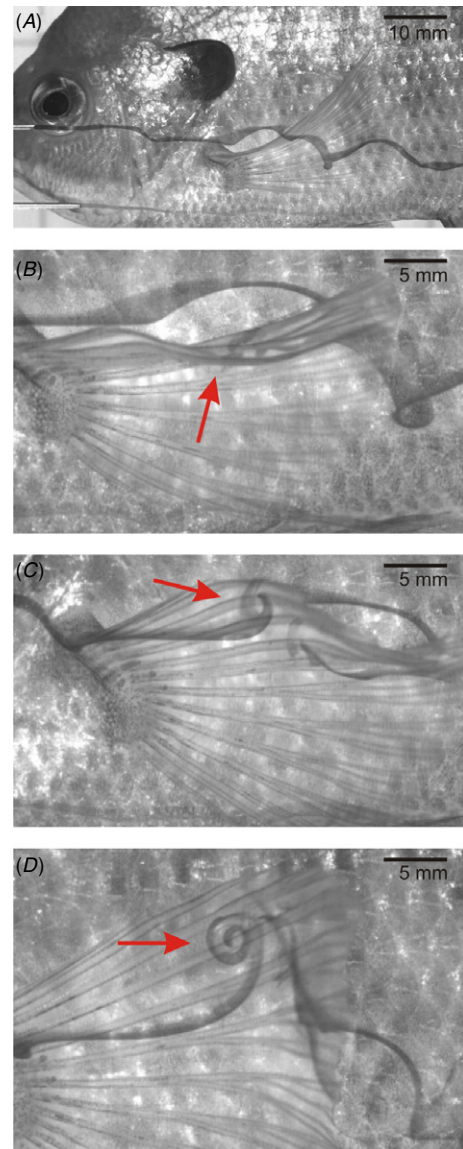


**Figure 7.** Sonomicrometry data showing muscle strain patterns from the abductor superficialis muscle during (A) steady forward swimming at  $0.5 L s^{-1}$ , with a transition to backward swimming, and (B) maneuvering locomotion following a period of slow forward swimming. The distance between sonomicrometry crystals is shown on the y-axis. Values of muscle strain during the various locomotor behavior are indicated on the graph. Note the dramatic increase in muscle strain during backward locomotion and maneuvering.

show that the fin, during abduction, generates downstream momentum, a point consistent with the forces calculated from the computational fluid dynamic model presented in the following companion paper (Mittal *et al* 2006).

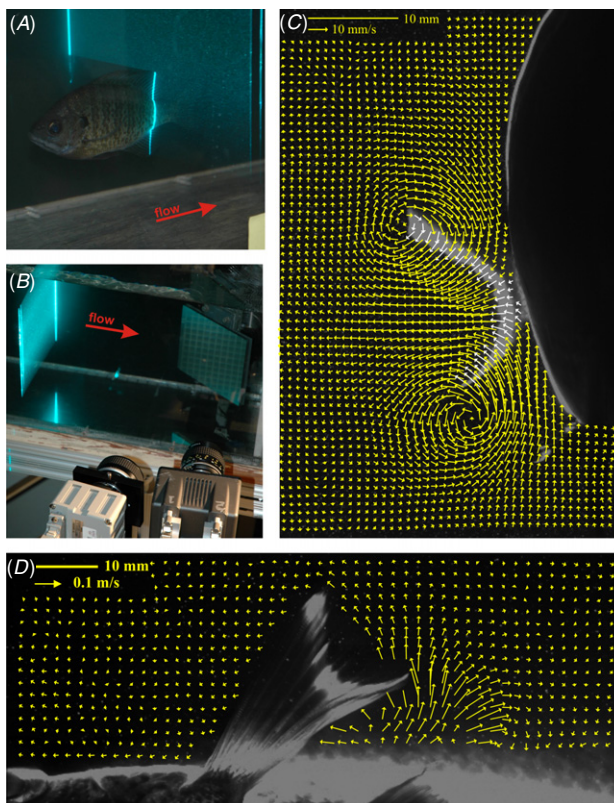
## 7. Discussion

The sunfish pectoral fin is a deformable propulsor of considerable complexity that has an extensive control system and hydrodynamic function that permits near continuous thrust throughout the fin beat cycle (see also Mittal *et al* (2006), Lauder *et al* (2005) and Bozkurtas *et al* (2006)). In many ways, the pectoral fin might be viewed as a special case of a heaving and pitching foil-based propulsor, and numerous experimental and computational studies have analyzed how flapping foils generate thrust and might be used to power underwater robotic vehicles (Dong *et al* 2006, Gopalkrishnan *et al* 1994, Guglielmini and Blondeaux 2004, Akhtar and Mittal 2005, Streitlein and Triantafyllou 1998, Blondeaux *et al* 2005, Long *et al* 2006, Triantafyllou *et al* 1993, 2004, Hover



**Figure 8.** Water flow patterns over the pectoral fin during unrestrained locomotion as revealed by dye. Images are frames from a high-speed movie (250 fps) of a dye stream impinging on the pectoral fin during a single fin beat cycle. In panel A the tips of two dye wands can be seen at the left with a strong dye stream emerging from the upper wand. The pectoral fin just starts to cut through the dye stream, which has been deflected slightly by motion of the head and body just anterior to the fin. (B) The pectoral fin moves away from the body and the upper edge has a characteristic 'dimple' which has trapped a small amount of dye (red arrow). (C) The upper fin edge moves back toward the body, revealing an attached upper edge vortex (red arrow). (D) the pectoral fin has moved back toward the body at the end of the fin beat, and the leading edge vortex has separated (red arrow).

*et al* 2004). A common result in these studies is that, as flapping foils reverse direction during the flapping stroke, drag forces momentarily exceed thrust, with a consequent loss of efficiency. In contrast, the flexible fish pectoral fin appears to avoid drag production by continuously generating at least low levels of thrust even during the stroke reversal.



**Figure 9.** Digital particle image velocimetry of pectoral fin locomotion in the bluegill sunfish. (A) A transverse light sheet (projected perpendicular to the body) was used to image flow from the pectoral fin. (B) Two high-speed cameras filming at 250 fps allowed time-resolved stereo particle image velocimetry. These cameras were aimed at a mirror located downstream in the flow, which generated views of water flow in the free-stream direction. (C) Water flow pattern around the sunfish pectoral fin at mid-outstroke. Note the cupped shape of the fin, and the development of two strong leading edge vortices simultaneously on both the upper and lower fin edges as the pectoral fin moves away from the body. (D) Other experiments used a horizontal light sheet with a ventral view camera. This image shows the accelerated flow resulting from fin movement away from the body as revealed by particle image velocimetry in the horizontal plane. Sunfish pectoral fins generate thrust both during motion away and toward the body.

Indeed, due to the considerable flexibility of the pectoral fin, it is difficult even to apply standard foil terminology to the fin beat cycle, because at no time does the entire fin surface move in one direction. Throughout the fin beat cycle, beginning at the start of the stroke, some portion of the pectoral fin is directing water downstream and adding momentum. As the fin moves away from the body, it bends in both chordwise and spanwise directions, and during the outstroke a wave of bending passes along the fin length (figure 2). Even as the fin reverses direction and begins to move back toward the body, portions of the fin continue to generate thrust (Mittal *et al* 2006) so that drag is never produced.

Control of this flexible foil propulsive system is a topic that remains largely unstudied, especially the control of individual fin ray motion and differential activity within larger muscle masses. However, the data presented here

point toward future studies in which multiple electrodes implanted within adductor and abductor muscle masses could provide data on the control of individual fin rays, and hence contribute to understanding how individual elements within the pectoral fin are moved under the control of the fish nervous system.

A key topic for future investigation is the extent to which the motion of the fin surface is passive. Certainly the motion of the whole fin surface will prove to be due to some combination of active and passive components. Future experimental work using precise motion control could move a freshly removed pectoral fin in the manner observed for the fish pectoral fin base in an effort to duplicate fin motion during locomotion. Differences between the movement observed under motion control and fin kinematics during locomotion could help determine which components of *in vivo* fin motion are active. Development of a fully coupled fluid-structure model could also contribute significantly to understanding the active and passive aspects of fin motion.

Finally, the design of a robotic pectoral fin would allow alteration of fin ray material properties and testing of different fin motions to examine the effect on fin kinematics and force production. Current robotic fin models based on the sunfish pectoral fin (Tangorra *et al* 2007, Lauder *et al* 2005) are a good step in this direction, but further development work is still needed to achieve the necessary flexibility for detailed examination of the active and passive components of fin function. A fully integrative research program (figure 1) that combines elements of robotic design and biological investigation will facilitate understanding the function of the remarkable biological propulsors that fish have evolved during the past 500 million years.

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## References

- Akhtar I and Mittal R 2005 A biologically inspired computational study of flow past tandem flapping foils *AIAA Paper* 2005-4760
- Blondeaux P, Fornarelli F, Guglielmini L, Triantafyllou M S and Verzicco R 2005 Numerical experiments on flapping foils mimicking fish-like locomotion *Phys. Fluids* **17** 113601
- Bozkurtas M, H D, R M, Madden P and Lauder G V 2006 Hydrodynamic performance of deformable fish fins and flapping foils *AIAA Paper* 2006-1392



- Combes S A and Daniel T L 2001 Shape, flapping and flexion: wing and fin design for forward flight *J. Exp. Biol.* **204** 2073–85
- Combes S A and Daniel T L 2003a Flexural stiffness in insect wings: I. Scaling and the influence of wing venation *J. Exp. Biol.* **206** 2979–87
- Combes S A and Daniel T L 2003b Flexural stiffness in insect wings: II. Spatial distribution and dynamic wing bending *J. Exp. Biol.* **206** 2989–97
- Combes S A and Daniel T L 2003c Into thin air: contributions of aerodynamic and inertial-elastic forces to wing bending in the hawkmoth *Manduca sexta* *J. Exp. Biol.* **206** 2999–3006
- Denny M, Gaylord B, Helmuth B S and Daniel J F 1998 The menace of momentum: dynamic forces on flexible organisms *Limnol. Oceanogr.* **43** 955–68
- Dong H, Mittal R and Najjar F M 2006 Wake topology and hydrodynamic performance of low aspect-ratio flapping foils *J. Fluid Mech.* **566** 309–43
- Donley J and Shadwick R 2003 Steady swimming muscle dynamics in the leopard shark *Triakis semifasciata* *J. Exp. Biol.* **206** 1117–26
- Drucker E G and Jensen J S 1997 Kinematic and electromyographic analysis of steady pectoral fin swimming in the surfperches *J. Exp. Biol.* **200** 1709–23
- Drucker E G and Lauder G V 1999 Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry *J. Exp. Biol.* **202** 2393–412
- Drucker E G and Lauder G V 2001 Wake dynamics and fluid forces of turning maneuvers in sunfish *J. Exp. Biol.* **204** 431–42
- Drucker E G and Lauder G V 2002a Experimental hydrodynamics of fish locomotion: functional insights from wake visualization *Int. Comput. Biol.* **42** 243–57
- Drucker E G and Lauder G V 2002b Wake dynamics and locomotor function in fishes: interpreting evolutionary patterns in pectoral fin design *Int. Comput. Biol.* **42** 997–1008
- Drucker E G and Lauder G V 2003 Function of pectoral fins in rainbow trout: behavioral repertoire and hydrodynamic forces *J. Exp. Biol.* **206** 813–26
- Drucker E G, Walker J A and Westneat M 2006 Mechanics of pectoral fin swimming in fishes *Fish Biomechanics (Fish Physiology vol 23)* ed R E Shadwick and G V Lauder (San Diego, CA: Academic) pp 369–423
- Fish F and Lauder G V 2006 Passive and active flow control by swimming fishes and mammals *Ann. Rev. Fluid Mech.* **38** 193–224
- Geerlink P J 1979 The anatomy of the pectoral fin in *Sarotherodon niloticus* Trewavas (Cichlidae) *Neth. J. Zool.* **29** 9–32
- Geerlink P J 1987 The role of pectoral fins in braking of mackerel and saithe *Neth. J. Zool.* **37** 81–104
- Geerlink P J and Videler J J 1987 The relation between structure and bending properties of teleost fin rays *Neth. J. Zool.* **37** 59–80
- Gopalkrishnan R, Triantafyllou M S, Triantafyllou G S and Barrett D 1994 Active vorticity control in a shear flow using a flapping foil *J. Fluid Mech.* **274** 1–21
- Guglielmini L and Blondeaux P 2004 Propulsive efficiency of oscillating foils *Eur. J. Mech. B* **23** 255–78
- Hedrick T L, Tobalske B W and Biewener A 2002 Estimates of circulation and gait change based on a three-dimensional kinematic analysis of flight in cockatiels (*Nymphicus hollandicus*) and ringed turtle-doves (*Streptopelia risoria*) *J. Exp. Biol.* **205** 1389–409
- Higham T E, Malas B, Jayne B C and Lauder G V 2005 Constraints on starting and stopping: behavior compensates for reduced pectoral fin area during braking of the bluegill sunfish (*Lepomis macrochirus*) *J. Exp. Biol.* **208** 4735–46
- Hover F S, Haugsdal O and Triantafyllou M S 2004 Effect of angle of attack profiles in flapping foil propulsion *J. Fluid Struct.* **19** 37–47
- Hsieh S T 2003 Three-dimensional hindlimb kinematics of water running in the plumed basilisk lizard (*Basiliscus plumifrons*) *J. Exp. Biol.* **206** 4363–77
- Jayne B C and Lauder G V 1994 How swimming fish use slow and fast muscle fibers: implications for models of vertebrate muscle recruitment *J. Comput. Physiol. A* **175** 123–31
- Jayne B C and Lauder G V 1995a Are muscle fibers within fish myotomes activated synchronously? Patterns of recruitment within deep myomeric musculature during swimming in largemouth bass *J. Exp. Biol.* **198** 805–15
- Jayne B C and Lauder G V 1995b Red muscle motor patterns during steady swimming in largemouth bass: effects of speed and correlations with axial kinematics *J. Exp. Biol.* **198** 1575–87
- Jayne B C, Lozada A and Lauder G V 1996 Function of the dorsal fin in bluegill sunfish: motor patterns during four locomotor behaviors *J. Morphol.* **228** 307–26
- Katz J and Weihs D 1978 Hydrodynamic propulsion by large amplitude oscillation of an airfoil with chordwise flexibility *J. Fluid Mech.* **88** 485–97
- Koehl M A and Rosenfeld A 2006 *Wave-Swept Shore: The Rigors of Life on a Rocky Coast* (Berkeley, CA: University of California Press)
- Lauder G V 2006 *The Physiology of Fishes* 3rd edn, ed D H Evans and J B Claiborne (Boca Raton, FL: CRC Press) pp 3–46
- Lauder G V and Drucker E G 2002 Forces, fishes, and fluids: hydrodynamic mechanisms of aquatic locomotion *News Physiol. Sci.* **17** 235–40
- Lauder G V and Madden P G 2006 Learning from fish: kinematics and experimental hydrodynamics for roboticists *Int. J. Autom. Comput.* **4** 325–35
- Lauder G V, Madden P G A, Hunter I, Tangorra J, Davidson N, Proctor L, Mittal R, Dong H and Bozkurtas M 2005 Design and performance of a fish fin-like propulsor for AUVs *Proc. 14th Int. Symp. Unmanned Untethered Submersible Technology (UUST)*. Autonomous Undersea Systems Institute, Lee NH USA
- Lauder G V and Tytell E D 2006 *Fish Biomechanics (Fish Physiology vol 23)* ed R E Shadwick and G V Lauder (San Diego, CA: Academic) pp 425–68
- Liu P and Bose N 1997 Propulsive performance from oscillating propulsors with spanwise flexibility *Proc. R. Soc. Lond. B* **453** 1763–70
- Long J H, Joseph S, Nicholas L and Mathieu K 2006 Four flippers or two? Tetrapodal swimming with an aquatic robot *Bioinspiration Biomimetics* **1** 20–9
- Madden J, Schmid B, Hechinger M, Lafontaine S, Madden P, Hover F S, Kinball R and Hunter I W 2004a Application of polypyrrole actuators: feasibility of variable camber foils *IEEE J. Oceanic Eng.* **29** 738–49
- Madden J, Vandesteef N A, Anquetil P, Madden P, Takshi A, Pytel R, Lafontaine S, Wieringa P A and Hunter I W 2004b Artificial muscle technology: physical principles and naval prospects *IEEE J. Oceanic Eng.* **29** 706–28
- Miao J M and Ho M H 2006 Effect of flexure on aerodynamic propulsive efficiency of flapping flexible airfoil *J. Fluid Struct.* **22** 401–19
- Mittal R, Dong H, Bozkurtas M, Lauder G V and Madden P G A 2006 Locomotion with flexible propulsors: II. Computational modeling and analysis of pectoral fin swimming in a sunfish *Bioinspiration Biomimetics* **1** S35–41
- Nauen J C and Lauder G V 2001 Locomotion in scombrid fishes: visualization of flow around the caudal peduncle and finlets of the Chub mackerel *Scomber japonicus* *J. Exp. Biol.* **204** 2251–63
- Nauen J C and Lauder G V 2002 Quantification of the wake of rainbow trout (*Oncorhynchus mykiss*) using three-dimensional stereoscopic digital particle image velocimetry *J. Exp. Biol.* **205** 3271–9

- Ramamurti R, Lohner R and Sandberg W C 1999 Computation of the 3-D unsteady flow past deforming geometries *Int. J. Comput. Fluid Dyn.* **13** 83–99
- Shadwick R and Gemballa S 2006 *Fish Biomechanics (Fish Physiology vol 23)* ed R E Shadwick and G V Lauder (San Diego, CA: Academic) pp 241–80
- Shadwick R E, Katz S L, Korsmeyer K E, Knowler T and Covell J W 1999 Muscle dynamics in skipjack tuna: timing of red muscle shortening in relation to activation and body curvature during steady swimming *J. Exp. Biol.* **202** 2139–50
- Standen E M and Lauder G V 2005 Dorsal and anal fin function in bluegill sunfish (*Lepomis macrochirus*): three-dimensional kinematics during propulsion and maneuvering *J. Exp. Biol.* **205** 2753–63
- Streitlein K and Triantafyllou G S 1998 On thrust estimates for flapping foils *J. Fluid Struct.* **12** 47–55
- Tangorra J L, Davidson S N, Hunter I W, Madden P G A, Lauder G V, Dong H, Bozkurtas M and Mittal R The development of a biologically inspired propulsor for unmanned underwater vehicles, in preparation
- Triantafyllou G S, Triantafyllou M S and Grosenbaugh M A 1993 Optimal thrust development in oscillating foils with application to fish propulsion *J. Fluid Struct.* **7** 205–24
- Triantafyllou M S, Techet A H and Hover F S 2004 Review of experimental work in biomimetic foils *IEEE J. Oceanic Eng.* **29** 585–94
- Vogel S 1988 *Life's Devices: The Physical World of Animals and Plants* (Princeton, NJ: Princeton University Press)
- Westneat M, Thorsen D H, Walker J A and Hale M 2004 Structure, function, and neural control of pectoral fins in fishes *IEEE J. Oceanic Eng.* **29** 674–83
- Westneat M and Wainwright S A 2001 *Tuna: Physiology, Ecology, and Evolution* ed B Block and E D Stevens (San Diego, CA: Academic) pp 271–311
- Westneat M W and Walker J A 1997 Motor patterns of labriform locomotion: kinematic and electromyographic analysis of pectoral fin swimming in the labrid fish *Gomphosus varius* *J. Exp. Biol.* **200** 1881–93
- Wilga C D and Lauder G V 2002 Function of the heterocercal tail in sharks: quantitative wake dynamics during steady horizontal swimming and vertical maneuvering *J. Exp. Biol.* **205** 2365–74
- Wilga C D and Lauder G V 2004 Biomechanics of locomotion in sharks, rays and chimeras *Biology of Sharks and Their Relatives* ed J C Carrier *et al* (Boca Raton, FL: CRC Press) pp 139–64