

Swimming hydrodynamics: ten questions and the technical approaches needed to resolve them

George V. Lauder

Received: 10 September 2009 / Revised: 26 September 2009 / Accepted: 28 September 2009 / Published online: 11 October 2009
© Springer-Verlag 2009

Abstract Recent experimental and computational studies of swimming hydrodynamics have contributed significantly to our understanding of how animals swim, but much remains to be done. Ten questions are presented here as an avenue to discuss some of the arenas in which progress still is needed and as a means of considering the technical approaches to address these questions. 1. What is the three-dimensional structure of propulsive surfaces? 2. How do propulsive surfaces move in three dimensions? 3. What are the hydrodynamic effects of propulsor deformation during locomotion? 4. How are locomotor kinematics and dynamics altered during unsteady conditions? 5. What is the three-dimensional structure of aquatic animal vortex wakes? 6. To what extent are observed propulsor deformations actively controlled? 7. What is the response of the body and fins of moving animals to external perturbations? 8. How can robotic models help us understand locomotor dynamics of organisms? 9. How do propulsive surfaces interact hydrodynamically during natural motions? 10. What new computational approaches are needed to better understand locomotor hydrodynamics? These ten questions point, not exclusively, toward areas in which progress would greatly enhance our understanding of the hydrodynamics of swimming organisms, and in which the application of new technology will allow continued progress toward understanding the interaction between organisms and the aquatic medium in which they live and move.

1 Introduction

The study of swimming hydrodynamics has attracted considerable attention in recent years as engineers and biologists, both separately and together, have focused on the remarkable diversity in design and locomotor performance of aquatic organisms. A great deal of progress has been made, as evidenced by the chapters in this volume and by the number of review papers and books presenting our current understanding of how aquatic organisms interact with their fluid environment. Many of these recent overviews (e.g., Dabiri 2009; Fish and Lauder 2006; Fish et al. 2008; Lauder 2006; Lauder and Tytell 2006; Lauder and Madden 2007; Shadwick and Lauder 2006; Triantafyllou et al. 2005; Triantafyllou et al. 2000) have focused on the results from recent studies of aquatic locomotor dynamics, and present current information on swimming organisms. Here, I will take a different approach and structure this essay around a selection of the key questions that remain, and emphasize the techniques and approaches needed to address these questions going forward. I will present only limited data for each topic, and instead focus on discussing for each question the concepts and approaches relevant to broader issues in swimming hydrodynamics.

The ten questions presented below are certainly not the only possible ones that might be discussed, but these questions can serve as a starting point for thinking about new directions for the next years of research. For each question I first assess briefly the current state of research, and then address some of the technical approaches that are needed to address these questions. Some of the needed experiments or computations are feasible now, but others will require the development of new technologies or the further application of techniques just now becoming available to biologists and engineers studying aquatic locomotor systems.

G. V. Lauder (✉)
Museum of Comparative Zoology, Harvard University,
26 Oxford Street, Cambridge, MA 02138, USA
e-mail: glauder@oeb.harvard.edu

2 Ten questions for swimming hydrodynamics

2.1 What is the three-dimensional structure of propulsive surfaces?

Without an understanding of the three-dimensional shape of the propulsive surfaces of aquatic animals, and how these shapes can deform during propulsion (see Question 2 below), it is difficult to imagine how we will make substantial further progress in understanding the hydrodynamics of swimming organisms. While some organisms probably can be treated reasonably by two-dimensional analyses, either experimental or computational, in my view we have effectively reached the limit of progress using two-dimensional views and computational techniques (Lauder et al. 2007; Tytell et al. 2008). It is now important that we move to a full three-dimensional understanding of the shape of swimming animals, and to understand how deformation of propulsive surfaces takes place during locomotion.

One would think that numerous data files would be available on the three-dimensional shapes of animals such as jellyfish, fish, and marine mammals. And yet, until very recently, almost no data existed to document the geometry of complex biologic propulsive surfaces. Even now there are surprisingly few data sets with full three-dimensional shape information. Most studies of locomotion in fishes and marine mammals, e.g., treat the body two-dimensionally, either by considering a horizontal slice of a swimming animal, or a vertical plane through a flapping appendage.

This situation is beginning to change, and both computational fluid dynamics (Borazjani and Sotiropoulos 2009; Bozkurttas et al. 2009; Liu et al. 1997; Wolfgang et al. 1999; Zhu et al. 2002) and experimental fluid mechanical analyses (Bartol et al. 2005; Cooper et al. 2008; Lauder and Madden 2007; Lauder and Madden 2008; Weber et al. 2009) are beginning to incorporate a full three-dimensional animal geometry. A public database of such biologic geometries is still lacking, and would be a valuable resource for scientists. Such a database could be created through micro-CT (Computed Tomography) scanning of a diversity of whole organisms and individual propulsive surfaces, which would permit detailed reconstruction of body surface shape (as well as many internal bone and cartilage elements).

While the streamlined shape of marine mammal bodies and flukes in cross-section is well known (Fish 2004; Fish et al. 2008) and the streamlined shape of most fish bodies is well understood (Hertel 1966; Hoerner 1965; Webb 1975), it is not generally appreciated that the fins of fishes are often not at all streamlined, and in fact resemble the basic design of insect wings in forming a textured surface. In fact, textured surfaces are a prominent feature of the fins of

ray-finned fishes, and these propulsive surfaces are far from smooth (Fig. 1). The fins of most fishes consist of jointed bony or cartilage fin rays with a thin collagenous membrane extending between them. This results in a “bumpy” surface structure, the implications of which have never been investigated. The biomechanical properties of fish fin rays and the remarkable bilaminar design have been analyzed (Alben et al. 2007; Geerlink and Videler 1987; Lauder and Madden 2007), but the effect of the uneven fin surface (with fin rays that may extend as much as 1 mm above the membrane on each side) on flow control during swimming has not been studied. It is also noteworthy that different fins present the textured surface at different orientations to incoming flow. For example, the bumpy surface of fin rays in the caudal fin are oriented at a relatively low angle of attack to freestream flow, while the dorsal and anal fin rays can be nearly orthogonal to incoming flow depending on the extent to which fish erect these fins. Three-dimensional reconstructions of fin geometry would be a first step toward computational fluid dynamic analyses of the effects of surface structure.

There is also considerable variation in cross-sectional geometry along the body of fish when viewed in three dimensions, and this is another area that has received relatively little attention. Figure 1 shows a series of body cross sections resulting from a micro-CT scans of a bluegill sunfish (*Lepomis macrochirus*) where the change in sharpness of the upper and lower body margins is evident, and suggests the possibility of considerable change in flow separation along the body during undulatory locomotion. Also noteworthy in the posterior sections is the textured surface structure of the dorsal and caudal fins.

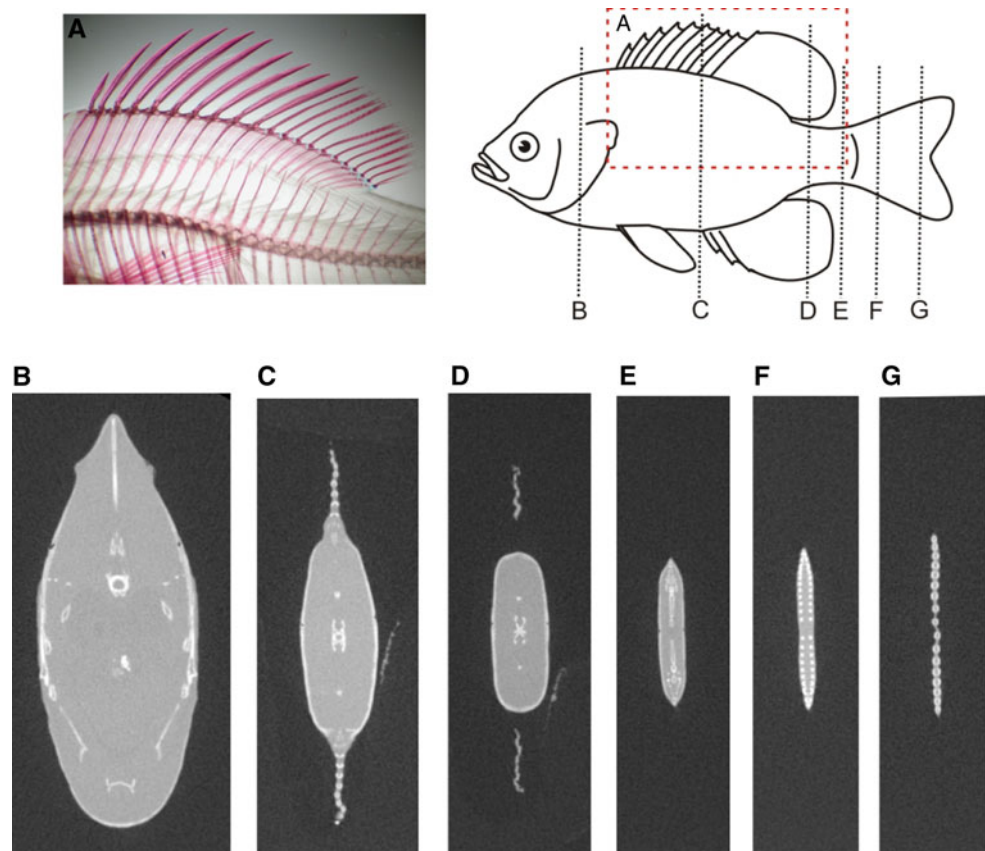
2.2 How do propulsive surfaces move in three dimensions?

If little is known about the three-dimensional structure of animal locomotor surfaces, then even less is known about how these control surfaces move in three dimensions.

Although it might seem, in the year 2009, that the three-dimensional motions of aquatic animal appendages or bodies should have been well studied, in fact there are extremely few papers in which the three-dimensional conformation of propulsive surfaces has been measured through time. The lack of data on the motion of appendages through time and space is a serious constraint on both computational and experimental analyses of animal locomotion in water, as without this information analyses are necessarily simplified into two dimensions.

Figure 2 shows three different views of one position of the pectoral fin of a bluegill sunfish at the mid-fin beat time (near the transition time from outstroke to instroke) during steady locomotion at one body length per second

Fig. 1 Anatomy of a bluegill sunfish to illustrate changes in cross-sectional shape down the body and the non-streamlined textured surfaces of the fins. Bluegill image in *upper right* shows the location of anatomic features. **a** cleared and stained image of the dorsal fin region of a bluegill sunfish (bones are stained *red*, and muscle and skin have been cleared) to show the bony spines and rays that support the thin fin membrane. **b–g** micro-CT sections through a bluegill sunfish to illustrate changes in shape down the body. Note the relatively rounded shape of the body until the tail region where sections are flat with sharp upper and lower edges. Fin surfaces are bumpy (see sections **c** and **g**) with projecting fin rays. All micro-CT images are shown at the same scale



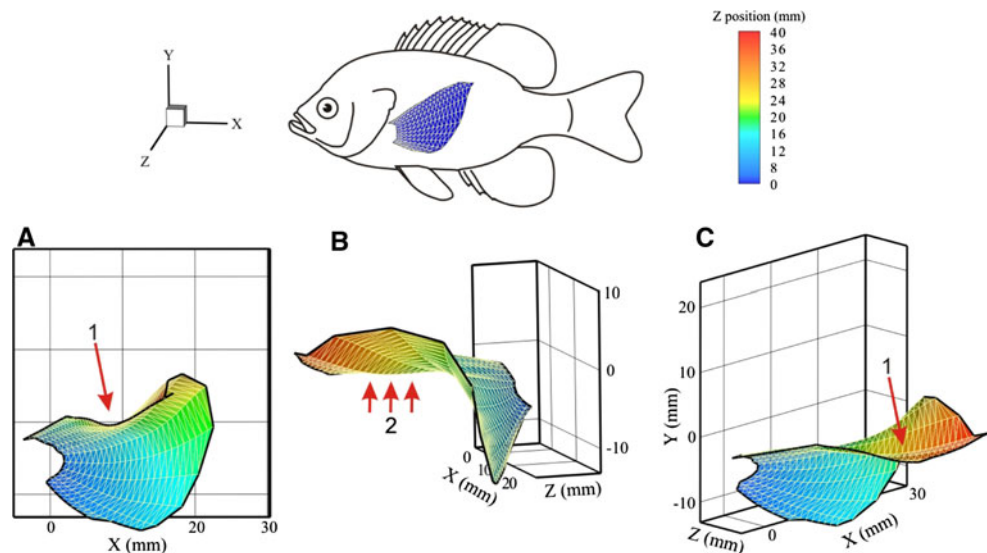
(approximately 10 cm/sec in this case). The conformation of the fin is complex and involves cupping of the upper and lower margins to form two simultaneous leading edges, a wave of bending that travels from root to tip, and chordwise deformation, which changes through time (Lauder et al. 2006; Lauder and Madden 2007). Given the complex kinematics of this pectoral fin, using a flat-plate model or a highly simplified representation of the fin that does not allow for changes in fin area through time or chordwise or spanwise dimensional changes is not likely to lead to advances in our understanding of pectoral fin propulsion. This accurate representation of the three-dimensional motion through time of a fish pectoral fin was critical to using computational fluid dynamics to understand the mechanism of thrust production by the sunfish pectoral fin (Bozkurtas et al. 2009). Accurate three-dimensional kinematic data of propulsor and body surface deformation through time are key elements of computational fluid dynamic modeling.

However, data such as those shown in Fig. 2 are difficult to obtain. Multiple synchronized high-speed cameras with reasonable resolution (1 K by 1 K at least) are needed to obtain three-dimensional kinematics when there is considerable deformation and folding of moving appendages. Often the propulsive surfaces of swimming animals are either not well marked naturally, or are difficult to place clear markers on to facilitate quantification of motion.

Ideally, up to several hundred points would be measured at each time step to give an accurate representation of surface deformation, and a measurement frequency of five to ten times the movement frequency will be needed to capture transient components of three-dimensional motion. And, once some system of identifying points has been developed, the job of digitizing the *x*, *y*, and *z* locations in space and through time begins. None of this is trivial. And although computer-assisted quantification techniques are increasingly being developed for insects (e.g., Fontaine et al. 2009; Wang et al. 2008) to reduce the manual work needed to reconstruct three-dimensional propulsor conformations, these approaches have not yet yielded a bounty of three-dimensional kinematic data for swimming animals.

The three-dimensional motions of swimming animal propulsors are the result of a complex fluid–structure interaction, complex in part due to the (mostly unstudied) non-linear material properties of biologic propulsors. The observed motion will be a function of the material properties of the body and appendages (which change along the chordwise and spanwise directions), interacting dynamically with fluid-generated forces. Quantification of three-dimensional motion could thus also be used to test fluid–structure interaction computational models which, if correct in a particular case, should be able to predict the resulting movement pattern.

Fig. 2 Three views of a single time during the fin beat cycle (just after the transition from fin outstroke to instroke) to illustrate bending and conformational changes in a fish pectoral fin. 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



For swimming fishes, examples of three-dimensional data on fins include efforts to quantify the curvature of fish fin rays in three dimensions during a variety of natural locomotor movements (Lauder et al. 2006; Standen and Lauder 2005; Standen and Lauder 2007; Standen 2008; Taft et al. 2008), and these data have proven very useful for understanding how the structure of fish fin rays (Alben et al. 2007; Lauder and Madden 2007) deforms under in vivo locomotor conditions. In addition, it is clear that fish propulsive surfaces frequently undergo substantial changes in area during both the movement cycle at one swimming speed, and also when compared across changes in speed or locomotor behavior (Tytell et al. 2008). So analyses of fish locomotion very much need to account for area changes in fins during motion. I am not aware of any three-dimensional experimentally obtained kinematic data for swimming mammals.

2.3 What are the hydrodynamic effects of propulsor deformation during locomotion?

Although quite a few papers have investigated the effects of flexibility on aquatic locomotor performance (e.g., Alben et al. 2004; Alben 2008; Blondeaux et al. 2005; Bozkurtas et al. 2006; Shen et al. 2003; Shoel and Zhu 2009), we still lack basic information on how flexible natural biologic systems are and hence on how much changes in flexibility affect locomotor parameters such as thrust generation and efficiency. Only limited three-dimensional data are available for swimming fishes, and some two-dimensional estimates of fluke camber changes through the tail stroke are available for marine mammals (Fish and Lauder 2006; Fish et al. 2008).

For example, one form of natural flexibility in motion is the cupping and bending motions of pectoral fins in

swimming fishes (e.g., Fig. 2). One possible benefit of this motion is the control of both positive and negative lift forces during the outstroke and instroke, as the production of simultaneous up and down forces could act to minimize center of mass oscillation (Lauder and Madden 2007). Another example of the control of propulsor deformation is the caudal fin (tail) of swimming fishes. Researchers as early as Bainbridge (1963) noticed the substantial change in fish fin shape during the tail beat (also see Lauder 1989; Lauder 2000), and this has been quantified for swimming fishes and related to the vortical flow patterns shed by the tail (Tytell 2006). In addition, Flammang and Lauder (Flammang and Lauder 2008; Flammang and Lauder 2009) showed that these conformational changes in tail shape are actively produced with intrinsic musculature, and caudal fin shape change varies greatly in concert with the type of maneuver being performed by the swimming fish.

Changes in fin area with swimming speed (Standen and Lauder 2005; Standen and Lauder 2007; Tytell et al. 2008) have obvious implications for hydrodynamic force production, and the evidence is now clear that swimming fishes actively adjust their fin area as speed changes. However, the pattern of fin area change with speed can differ considerably between species, with swimming trout and bluegill sunfish showing different patterns of fin area change as speed increases.

Radially symmetrical jellyfish greatly simplify the problem of quantifying body deformation, and recent studies of jellyfish hydrodynamics have shown in detail how the flexible body moves to produce thrust and generate specific wake vortex patterns (Dabiri et al. 2005; Dabiri et al. 2006).

The study of propulsor deformation and its possible hydrodynamic consequences is one area in which a robotic approach (see Question 8 below) can be extremely useful,

permitting controlled alterations in flexibility of elements scaled to the naturally observed bending of biologic tissues during movement. Study of a range of flexible propulsors in a flapping robotic apparatus allowing measurement of efficiency and energy consumption simultaneously with wake dynamics will allow more definitive statements about the hydrodynamic consequences of flexibility than is now possible.

Additionally, a computational fluid dynamic approach can be used to investigate models of varying flexibility to compute resulting changes in efficiency and wake dynamics. Examples of this approach applied to fish pectoral fins allowed the conclusion that structural flexibility of pectoral fin rays may increase both thrust and efficiency (Shoel and Zhu 2009; Zhu and Shoel 2008).

2.4 How are locomotor kinematics and dynamics altered under unsteady conditions?

Fish often move in an unsteady manner. And even when the time-averaged center of mass velocity is constant, the motion of individual propulsors is dynamic. So understanding the hydrodynamics of aquatic animal locomotion requires understanding how body motions and induced flows change with time. This in turn requires both time-resolved kinematics and experimental fluid dynamic data.

Only in the past ten years has there been increasing focus on investigating the fluid dynamics of unsteady locomotor behaviors such as maneuvering locomotion. There are still no experimental analyses of maneuvering fluid dynamics or changes in propulsor conformation during maneuvers by aquatic mammals. Most analyses of acceleration or other unsteady behaviors such as braking, stopping, or backing up have occurred in fishes, where particle image velocimetry and kinematic analysis have demonstrated the considerable changes in wake dynamics and the shape and area of propulsive surfaces that accompany maneuvers (Flammang and Lauder 2009; Shirgaonkar et al. 2008; Tytell 2004). The study of unsteady locomotor dynamics is an area of swimming hydrodynamics that is very much in need of further analysis.

One unsteady behavior in fishes that has received a great deal of attention from fish biologists and neurobiologists is the so-called c-start escape response. In this behavior, the fish rapidly (5–30 ms) bends its body into a c-like shape during stage 1, followed by a strong tail movement during stage 2 to move the center of mass away from the stimulus (Wakeling 2006). This behavior is controlled by a well-understood neuronal network, and has been the subject of nearly a thousand papers over the years. But virtually nothing is known about the fluid dynamics of this canonical unsteady locomotor behavior.

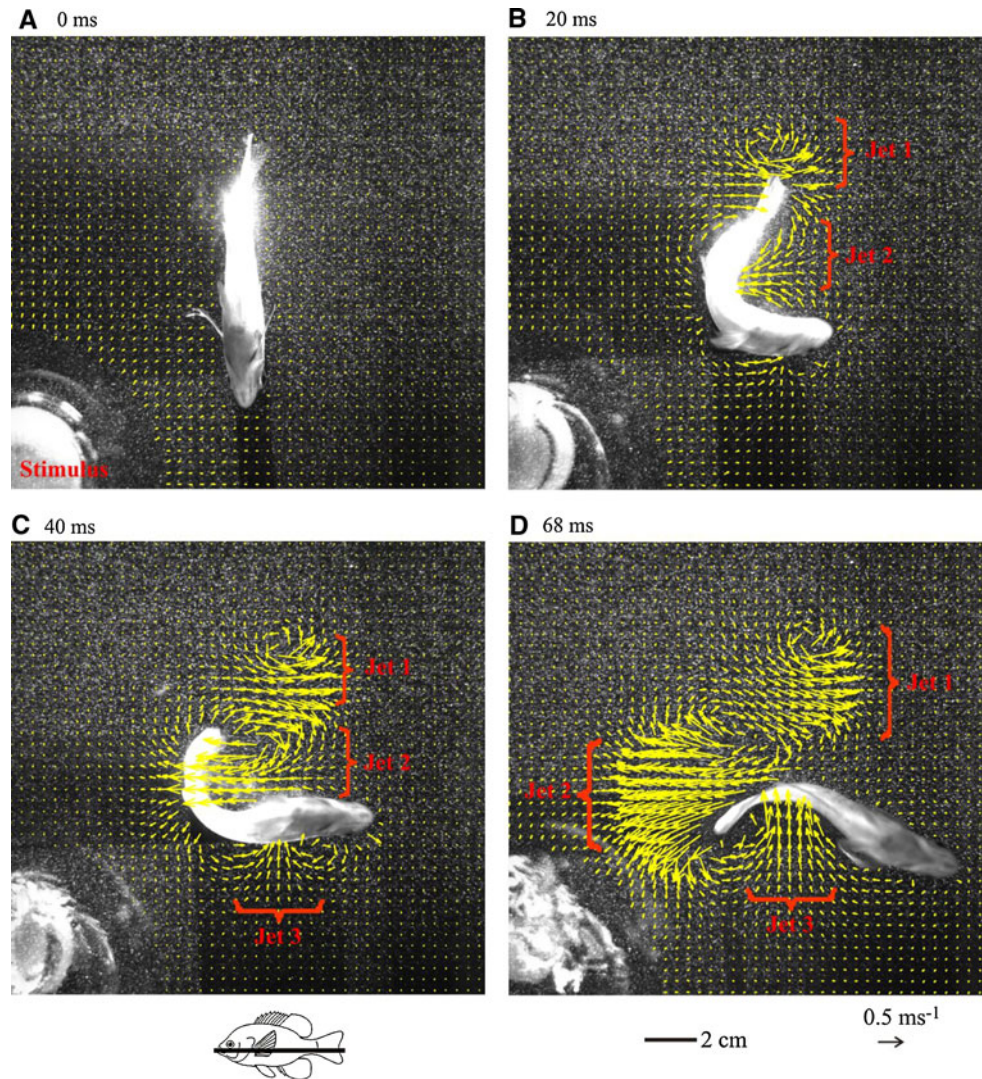
Figure 3 shows one result from the analysis by Tytell and Lauder (2008) who quantified the fluid dynamics of the escape response in bluegill sunfish. The rapid pattern of body bending during the c-start escape produces three distinct vortical flows, nearly orthogonal to each other. Summing the estimated forces along the direction of the escape response calculated from particle image velocimetry data produced an estimate for body momentum that was not significantly different from that calculated from the body motion itself. Generally similar flow patterns were also found by Epps and Techet (2007) in their study of rapid turning maneuvers. A great deal of more experimental study is needed on rapid locomotor behaviors, which are frequently exhibited by fishes and which form a very important part of their natural locomotor repertoire.

Another key area of unsteady swimming hydrodynamics is the behavior exhibited by fishes swimming in turbulent flows. Although natural turbulence in streams may be hard to replicate in a laboratory setting, it is possible to generate controlled turbulence using cylinders in a flow. Producing a Karman street and inducing fish to swim there reveals a number of novel locomotor modes (Liao et al. 2003a, b; Liao 2004) that had not previously been observed by fishes swimming steadily in the typical laboratory setting. The control system used by fishes to interact with turbulent flows is mostly unknown, although there is a great deal of information about individual fish sensory systems (Collin and Marshall 2003; Coombs and Van Netten 2006; Webb et al. 2008). Analyses of aquatic animals swimming in well-characterized unsteady flows is just in its infancy, and a great deal more research is needed in this area.

2.5 What is the three-dimensional structure of aquatic animal vortex wakes?

There are now numerous reconstructions, using data from two-dimensional planar particle image velocimetry, of the vortex wakes shed by swimming animals. Examples include simplistic views of the vortex wake produced by the tail of swimming fishes (Lauder and Drucker 2002; Nauen and Lauder 2002a; Videler 1993; Wilga and Lauder 2004), pectoral fin vortex rings (Drucker and Lauder 1999; Drucker and Lauder 2000), and more sophisticated estimates of the vortical patterns shed by the tail as well as dorsal and anal fins (Tytell 2006; Tytell et al. 2008) of swimming fishes. These data have been generated using time-resolved particle image velocimetry, with framing rates up to 1000 Hz, which gives good resolution of the evolution of the wake in a single plane. Some progress has also been made in understanding the vortical wake and patterns of wake momentum using stereo particle image velocimetry which results in three velocity components for a single plane (Nauen and Lauder 2002b; Sakakibara et al.

Fig. 3 Wake flow patterns (yellow velocity vectors) generated by a bluegill sunfish exhibiting a c-start escape response to show the unexpected hydrodynamic patterns that can emerge from unsteady locomotor behaviors. Each rapid c-start produces *three* nearly orthogonal jet flows (labeled Jet 1, Jet 2, and Jet 3) as the fish bends its body during the escape. The stimulus is visible in the lower left of each image, and the laser light sheet intersected the mid-body region. Image from Tytell and Lauder (2008)



2004; Willert 1997), but a key future goal should be to use more technically sophisticated methods to estimate the three-dimensional structure of wake vorticity.

There are unavoidable difficulties in using planar data to reconstruct three-dimensional structures, especially when freely swimming fishes are studied. Phase averaging is possible, although difficult, because each fin beat is slightly different both in the timing and excursion of fin and body motion, and fishes rarely swim in a constant absolute position (Lauder and Madden 2007; Lauder and Madden 2008). Extrapolating from data obtained in one plane to a three-dimensional vortex structure is also challenging. To some extent, these difficulties can be mitigated by using a scanning approach in which the laser light sheet is scanned rapidly through the moving fin (Brücker and Bleckmann 2007; Lauder and Madden 2007; Zhang et al. 2008), or reorienting the laser light sheet into orthogonal orientations to evaluate vorticity in multiple planes (e.g., Drucker and Lauder 1999). Such approaches have permitted

considerable progress in reconstructing vortex dynamics and analyzing momentum fluxes associated with the moving body and propulsors, and inaccuracies have been at least reduced by using time-resolved particle image velocimetry which provides a high-sample rate of flow dynamics (200–1000 Hz) relative to the frequency of body and appendage motion (typically 1–10 Hz).

Nonetheless, future advances in understanding locomotor dynamics would be greatly aided by the ability to reconstruct the full three-dimensional flow pattern generated by moving organisms. Technically, this is just now becoming feasible, but there are as yet no examples of volumetric data showing the full three-dimensional vortex wake structure behind a swimming body or moving animal surface. The technology to generate such data is just now available, with tomographic, holographic, or defocusing approaches becoming more common, and allowing the calculation of all three velocity components within a volume at an instant in time, thus providing a snapshot of the

full wake structure (Hain et al. 2008; Pereira et al. 2000; Svizher and Cohen 2006; Troolin and Longmire 2008; Wieneke 2008).

2.6 To what extent are observed body and propulsor deformations actively controlled?

The extent to which observed body and propulsive surface deformations are primarily active, passive, or a complex interaction between the two, is one of the most difficult questions facing investigators studying the locomotor dynamics of swimming organisms. This is a non-trivial question, and addressing this issue comprehensively requires not just approaches from fluid mechanics, but also the use of electrophysiological techniques such as electromyography to determine when muscles are active to power locomotion.

Because most swimming animals have bodies and/or moving propulsive surfaces with intrinsic muscles that can be activated to varying degrees, the stiffness of the body and surfaces can be altered from moment to moment. And, changes in body stiffness often accompany changes in speed of swimming animals (e.g., Long 1998; Long and Nipper 1996). Bony fish, in particular, possess fin architectures that allow them to control the stiffness of their appendages by activating muscles at the base of the fin, even though no muscle tissue resides within the fin itself (Alben et al. 2007; Geerlink and Videler 1987; Lauder 2006; Lauder and Madden 2006). This makes interpreting observed correlations between movement and wake-flow patterns very difficult.

There is at least one situation in which it is possible to conclusively state that animals are actively moving their bodies and appendages: if motion occurs into external flow so that body motion opposes the direction of flow. Alben et al. (2007: Fig. 8) show an example of this from the sunfish pectoral fin during a maneuver. But in almost all cases, the observed deformation will be neither clearly actively generated nor purely a passive result of flow-induced pressure on the surface.

At least two distinct approaches can be taken to the problem of determining the extent of active versus passive control of surface deformation. First, measurements can be made of muscle activity patterns during swimming to determine if the appendages or body regions under analysis are being activated by the animal's musculature as the appendages move into oncoming fluid. In addition, muscle activity recordings will show if an animal is resisting fluid loading on the body or appendages even though they are being deformed by fluid forces. Examples of such data for fishes are given in Flammang and Lauder (2008, 2009) for fish tail function, and muscular control of fish body deformation is reviewed in Shadwick and Lauder (2006).

Second, a computational approach is possible. Generating a coupled fluid–structure model for a particular

appendage will allow computing both flows and shapes of the appendage with a prescribed root movement pattern. The computed and predicted movement patterns can then be compared to the body and appendage motions observed during natural locomotion (Zhu and Shoele 2008).

Progress in addressing this question will depend in part on our ability to generate a much greater array of data on the material properties of biologic tissues, and data on how these properties can be actively controlled. Most important will be the development of new methods for determining the in vivo stiffness of tissues of swimming animals, and how stiffness changes during movement of the body and appendages.

2.7 What is the response of the body and appendages to external perturbations?

Despite the many analyses of propulsion in aquatic animals ranging from jellyfish to a diversity of fishes to marine mammals, very few papers have attempted to perturb directly the freely swimming animal with a controlled stimulus. And yet such perturbations could be exceptionally informative about the instantaneous mechanical properties of the moving body or fins, and also reveal many aspects of both the hierarchical locomotor control system and the dynamics of body stability.

Webb (2004b) conducted an exemplary study of the responses of fishes to jets of water impinging on their body, and showed that the fish species studied appeared to be more sensitive to roll disturbances and attempted to correct for roll torques more rapidly than for yaw or pitch torques; also see Webb (2006, 2004a) for more general discussions of fish stability. But further experiments are needed to assess how aquatic animals maintain stability and to understand the role that different sensory systems play in regulating stable body posture.

Figure 4 shows an example of an experimental arrangement used to perturb swimming bluegill sunfish. A synthetic jet vortex generator was used to produce a single vortex ring that propagated toward the swimming fish. This jet is visualized by filling the cavity in the vortex generator with dye, and jets can be aimed at both pectoral fins (Fig. 4a) and the caudal fin (Fig. 4b, c). If the impinging vortex ring is not too strong, fish do not attempt to escape, and fins exhibit a passive response to the vortex jet. In this case, the strength of the vortex ring impacting the swimming fish was determined to be in the range of forces generated by fish fins during locomotion: fin and vortex impulses ranged from 0.1 to 1.0 mNs.

Another type of perturbation can be achieved by altering the viscosity of the liquid in which animals move, either by altering viscosity directly by adding polymers or by changing the temperature (Horner and Jayne 2008; Hunt

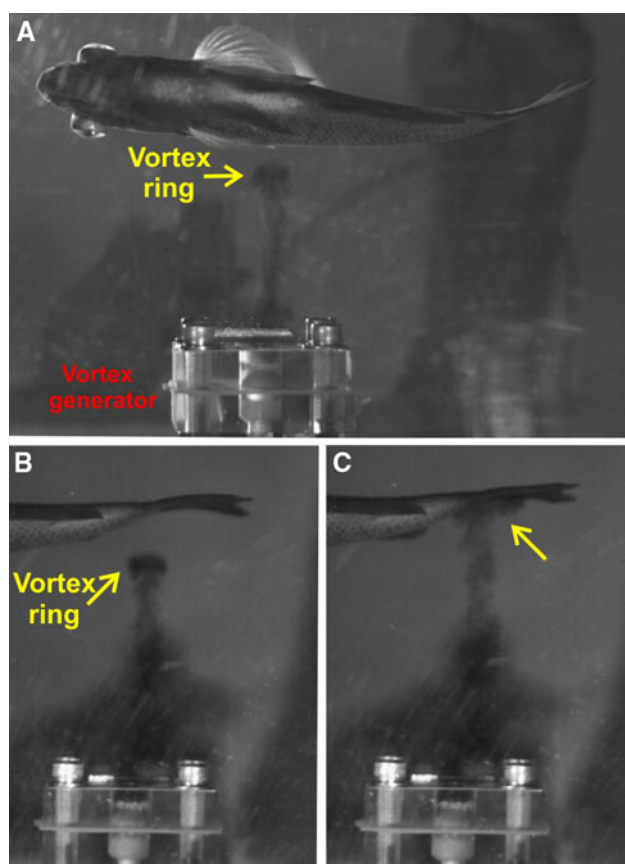


Fig. 4 Vortex perturbations of a freely swimming bluegill sunfish. Images are individual frames from 500-Hz digital videos of generated vortices impacting the fish during locomotion. **a** The sunfish (18 cm in length) and the vortex generator used to perturb the fish which is freely swimming in a recirculating flow tank at 0.5 L/s. A small vortex (48 mN impact force) is about to hit the fish just posterior to the center of mass. **b** A small vortex ring moving toward the fish near the tail fin. **c** Impact of this vortex ring 28 ms later on the tail. The original movie clearly shows rapid and passive deflection of the tail within 10 ms resulting from vortex impact

von Herbing and Keating 2003; Johnson et al. 1998). Studies of this kind promise new insights into the regulation of locomotor dynamics in swimming animals by greatly extending the parameter space within which animals must perform locomotor actions.

Perturbation studies of swimming animals are still in their infancy, and a great deal more remains to be done, especially in the development of controlled systems for generating appropriate stimuli that induce a response (either active or passive) in the swimming animal, and in methods of analyzing responses of animals to stimuli.

2.8 How can robotic models help us understand locomotor dynamics?

The last 10 years have seen a rapid increase in the development of robotic devices that can swim (e.g.,

Bandyopadhyay 2002; Kato 2000; Long et al. 2006; Tan et al. 2007; Triantafyllou and Triantafyllou 1995). In some cases, robotic animal-like swimmers are developed to answer engineering questions about underwater propulsion. But robotic models have an important role to play in helping biologists understand how aquatic animals function to move effectively. Robotics can inform biology in many useful ways. One key area in which robotic swimming devices are useful is in allowing isolation of individual factors that might influence propulsion. For example, comparative analyses of fish locomotion are hampered by the fact that species of fishes differ in many mechanical attributes. If one is interested in the effect of fish tail shape on propulsion, a comparison can be done between fish of different species that have different tail shapes, but there are many other features of these species that will differ also. Similarly, if one is interested in how changes in fish body or fin flexibility alter propulsive efficiency, a comparison could be made between different species that differ in flexibility, but these species will also differ in many other attributes, any of which could affect propulsion. The many ways in which species differ from each other make it very difficult to isolate individual components and thus to investigate key biomechanical questions to better understand aquatic locomotion.

Robotic models are a great advantage in allowing isolation of individual components of design, but this can also come at the cost of simplifying the biology to such an extent that key features of animal design are lost. However, it is possible to undertake a range of studies from simple physical models of propulsion to more highly biomimetic robotic devices that allow one to investigate fundamental questions about propulsion with much greater control than can be achieved using live animals.

As one example of this approach, an overview of a diversity of robotic approaches from our recent research on fish propulsion is shown in Fig. 5 (Lauder et al. 2007). We have attempted to range from the study of simple flexible plastic foils where we can easily change material properties and shapes (even though these systems are not as biologically realistic) to more highly biomimetic designs with fish pectoral fin robots that closely resemble the pectoral fins of live fishes (Tangorra et al. 2007). Even complex fish locomotor surfaces such as a ray wing can be modeled simply using a two-actuator system to understand basic properties of surface deformation and its effect on propulsion. One critical feature of these robotic test platforms is that they are self-propelling: they generate propulsive forces and swim against oncoming flow on a low-friction air carriage so that they can be studied easily using standard kinematic and fluid dynamic approaches (Lauder et al. 2007). The ability to study robotic models under conditions of self propulsion is critical to understanding the body and fin motions and how wake-flow patterns are produced.

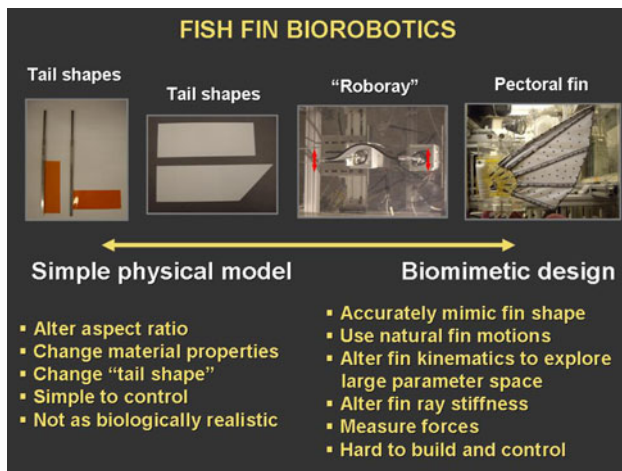


Fig. 5 Diagrammatic overview of one approach to fish biorobotics that includes both simple physical models (flapping flexible plastic foils—on the left) and more highly biomimetic models of fish and their fins (biomimetic pectoral fin—on the right). Simple physical models with one or two actuators allow easy alteration of flexibility and shape to model fish tail diversity, while more complexly actuated designs permit study of motion similar to that in freely swimming fishes. Some positive and negative aspects of each extreme approach are listed

Robotic test platforms have many advantages: control of specific structural parameters such as flexibility, precise motion control, direct measurement of force (difficult in freely swimming fishes), and exploration of a wider parameter space of motion than seen in live animals. Robotic devices also facilitate three-dimensional kinematic studies and correlated hydrodynamic analyses, as the location of the locomotor surface can be known accurately. And, individual components of a natural motion (such as outstroke vs. instroke of a flapping appendage) can be programmed separately, which is certainly difficult to achieve when working with a live animal.

2.9 How do propulsive surfaces interact hydrodynamically during natural motions?

One aspect of aquatic animal propulsion that is clearly evident in fishes, and to a lesser extent in marine mammals, is the possibility that the different control surfaces used for locomotion can interact with each other hydrodynamically. The idea of hydrodynamic interactions among propulsive surfaces is an old one, but recently this idea has received more attention. One aspect of this question is the extent to which flow encountered by the trailing edge of the swimming animal is altered by body motions upstream, and this has been a topic of some discussion for swimming fishes (Lauder and Tytell 2006; Müller et al. 2001; Tytell and Lauder 2004). But the possibility of hydrodynamic interactions between flapping appendages (acting as two individual foils) has also been a topic of interest, although most

research to date has been on insect wings during flight (Birch and Dickinson 2003; Lehmann et al. 2005; Lehmann 2008; Lehmann 2009; Usherwood and Lehman 2008). There is certainly a great deal more that could be studied on the interesting topic of hydrodynamic interactions among propulsive surfaces of swimming animals.

Experimental studies of live fishes have shown that upstream fins such as the dorsal and anal fins actively generate vortex wakes that travel downstream and encounter the tail (Drucker and Lauder 2001; Standen and Lauder 2007), and that the tail experiences greatly altered flows that are quite different from the free stream. This has clear implications for locomotor efficiency, as well as for the hydrodynamic mechanisms that are involved in lift and thrust production during swimming. One computational study (Akhtar et al. 2007) analyzed a range of phase relationships between the flapping dorsal fin and tail of swimming bluegill sunfish, and compared the biologic values to the values of thrust and efficiency calculated for a diversity of parameter values. Interestingly, the optimal computed phase difference of 48° is different than the observed 108° observed during swimming sunfish. This result is still unexplained, but suggests that fish are subject to constraints on fin shapes, location, and movement patterns that limit their ability to move propulsive surfaces in a hydrodynamically optimal fashion.

2.10 What new computational approaches are needed to better understand locomotor hydrodynamics?

There is only so much that can be learned from experimental studies of live animals. Data that are important for understanding hydrodynamic mechanisms and flow physics, such as surface pressure distributions, are extremely hard to obtain on freely swimming animals. Small localized transducers can be attached (see, e.g., the classic papers by DuBois et al. 1976; Dubois and Ogilvy 1978), but data from one point on the swimming animal gives only a very general impression of the forces exhibited by the surface as a whole.

A computational approach, particularly when married with experimental analysis of live animals and robotic devices, permits exploration of a large parameter space, alteration of movement patterns, and a focused investigation of hydrodynamic mechanisms underlying locomotor performance. And computational approaches are an excellent way to simplify biologic structures and movement patterns, and compare them to more canonical engineering solutions such as heaving and pitching foils.

There have been a number of recent computational fluid dynamic analyses of aquatic locomotion, which involve study of either whole body deformations (Borazjani and Sotiropoulos 2008; Borazjani and Sotiropoulos 2009;

Carling et al. 1998) or propulsive surfaces such as pectoral fins (Bozkurtas et al. 2009; Mittal et al. 2006; Ramamurti et al. 2002). To date no study that I am aware of has included both moving fish bodies and fins together. Since fish fins are actively moved by intrinsic musculature (Lauder 2006) and shed their own vortex wake, computational approaches to fish locomotion in the future could certainly be extended by incorporating both body and fin motions. The computational studies of Borazjani and colleagues (2008; 2009) in particular show how understanding difficult issues in comparative hydrodynamics can be greatly enhanced by a computational approach, as they were able to directly compare computationally fish swimming in an anguilliform versus carangiform locomotor mode, something that would not be possible to achieve by studying live fishes.

Computational approaches also have recently contributed considerably to the analysis of experimental data, as evidenced by recent work on a Lagrangian approach to wake dynamics and identification of an “upstream wake” (Dabiri 2005; Peng and Dabiri 2008a; Peng and Dabiri 2008b).

Future contributions of computational approaches are likely to be enhanced by the development of more sophisticated internal body models of swimming animals (e.g., Bowtell and Williams 1991; Bowtell and Williams 1994) and then coupling these to fluid dynamic model for a comprehensive analysis of body and control surface inputs and outputs during swimming. However bright the prospects for such an approach, this work will be challenging, as full three-dimensional analyses of all propulsive surfaces will be needed, as will knowledge of the dynamic material properties of the body and moving surfaces. As noted above, acquiring time-varying geometries on moving organisms is not a simple task, although recent techniques such as proper orthogonal decomposition (POD) allow simplification of the movement pattern, once acquired, for subsequent computational analysis (Bozkurtas et al. 2009). An additional challenge will be the ability to run computational analyses at Reynolds numbers high enough to reflect the speeds and sizes of most adult swimming organisms, in the range of 5,000 to 20,000.

3 Conclusions

There are many unresolved questions in the study of the swimming hydrodynamics of animals, and the papers collected in this volume exemplify many of the new avenues of research that will lead to future advances. In this contribution, I have gathered together ten key questions that in my view might, especially for students contemplating research in this area, guide plans for future studies of

swimming hydrodynamics. Addressing even a portion of one of these questions could form the basis for thesis research or even the focus of an entire research program for several years.

There are certainly many other possible questions that could be addressed, and in the interest of brevity I have omitted many interesting areas of research. But I believe that if, in the next decade, we are able to make as much progress as we have in the past one, the field of swimming hydrodynamics will have demonstrated remarkable innovation and growth that promises many new discoveries about how swimming animals interact with their fluid environment.

Acknowledgments This work was supported by an ONR-MURI Grant N00014-03-1-0897, and by ONR grant N00014-09-1-0352. We thank Drs. Rajat Mittal for many helpful discussions on bio-inspired propulsion. Many thanks to members of the Lauder and Tangorra Laboratories for numerous helpful discussions, and to Timo Gericke for constructing the vortex generator.

References

- Akhtar I, Mittal R, Lauder GV, Drucker E (2007) Hydrodynamics of a biologically inspired tandem flapping foil configuration. *Theor Comput Fluid Dyn* 21:155–170
- Alben S (2008) Optimal flexibility of a flapping appendage in an inviscid fluid. *J Fluid Mech* 614:355–380
- Alben S, Shelley M, Zhang J (2004) How flexibility induces streamlining in a two-dimensional flow. *Phys Fluids* 16:1694
- Alben S, Madden PGA, Lauder GV (2007) The mechanics of active fin-shape control in ray-finned fishes. *J Roy Soc Interface* 4:243–256
- Bainbridge R (1963) Caudal fin and body movements in the propulsion of some fish. *J Exp Biol* 40:23–56
- Bandyopadhyay PR (2002) Maneuvering hydrodynamics of fish and small underwater vehicles. *Int Comp Biol* 42:102–117
- Bartol IK, Gharib M, Webb PW, Weihs D, Gordon MS (2005) Body-induced vortical flows: a common mechanism for self-corrective trimming control in boxfishes. *J Exp Biol* 208:327–344
- Birch JM, Dickinson MH (2003) The influence of wing-wake interactions on the production of aerodynamic forces in flapping flight. *J Exp Biol* 206:2257–2272
- Blondeaux P, Fornarelli F, Guglielmini L, Triantafyllou MS, Verzicco R (2005) Numerical experiments on flapping foils mimicking fish-like locomotion. *Phys Fluids* 17:113601
- Borazjani I, Sotiropoulos F (2008) Numerical investigation of the hydrodynamics of carangiform swimming in the transitional and inertial flow regimes. *J Exp Biol* 211:1541–1558
- Borazjani I, Sotiropoulos F (2009) Numerical investigation of the hydrodynamics of anguilliform swimming in the transitional and inertial flow regimes. *J Exp Biol* 212:576–592
- Bowtell G, Williams TL (1991) Anguilliform body dynamics—modelling the interaction between muscle activation and body curvature. *Phil Trans R Soc Lond B* 334:385–390
- Bowtell G, Williams TL (1994) Anguilliform body dynamics—a continuum model for the interaction between muscle activation and body curvature. *J Math Biol* 32:83–91
- Bozkurtas M, Dong H, Mittal R, Madden P, Lauder GV (2006) Hydrodynamic performance of deformable fish fins and flapping foils. AIAA paper 2006-1392

- Bozkurttas M, Mittal R, Dong H, Lauder GV, Madden P (2009) Low-dimensional models and performance scaling of a highly deformable fish pectoral fin. *J Fluid Mech* 631:311–342
- Brücker C, Bleckmann H (2007) Vortex dynamics in the wake of a mechanical fish. *Exp Fluids* 43:799–810
- Carling JC, Williams TL, Bowtell G (1998) Self-propelled anguilliform swimming: simultaneous solution of the two-dimensional Navier–Stokes equations and Newton’s laws of motion. *J Exp Biol* 201:3143–3166
- Collin SP, Marshall NJ (2003) Sensory processing in aquatic environments. Springer Verlag, New York
- Coombs SA, Van Netten SM (2006) The hydrodynamics and structural mechanics of the lateral line system. In: Shadwick RE, Lauder GV (eds) *Fish biomechanics volume 23 in fish physiology*. Academic Press, San Diego, pp 103–139
- Cooper LN, Sedano N, Johansson S, May B, Brown JD, Holliday CM, Kot BW, Fish FE (2008) Hydrodynamic performance of the minke whale (*Balaenoptera acutorostrata*) flipper. *J Exp Biol* 211:1859–1867
- Dabiri JO (2005) On the estimation of swimming and flying forces from wake measurements. *J Exp Biol* 208:3519–3532
- Dabiri JO (2009) Optimal vortex formation as a unifying principle in biological propulsion. *Ann Rev Fluid Mech* 41:17–33
- Dabiri JO, Colin SP, Costello JH, Gharib M (2005) Flow patterns generated by oblate medusan jellyfish: field measurements and laboratory analyses. *J Exp Biol* 208:1257–1265
- Dabiri JO, Colin SP, Costello JH (2006) Fast-swimming hydromedusae exploit velar kinematics to form an optimal vortex wake. *J Exp Biol* 209:2025–2033
- Drucker EG, Lauder GV (1999) Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J Exp Biol* 202:2393–2412
- Drucker EG, Lauder GV (2000) A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *J Exp Biol* 203:2379–2393
- Drucker EG, Lauder GV (2001) Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. *J Exp Biol* 204:2943–2958
- Dubois AB, Ogilvy CS (1978) Forces on the tail surface of swimming fish: thrust, drag and acceleration in bluefish (*Pomatomus saltatrix*). *J Exp Biol* 77:225–241
- DuBois AB, Cavagna GA, Fox RS (1976) Locomotion of bluefish. *J Exp Zool* 195:223–235
- Epps B, Techet A (2007) Impulse generated during unsteady maneuvering of swimming fish. *Exp Fluids* 43:691–700
- Fish F (2004) Structure and mechanics of nonpiscine control surfaces. *IEEE J Oceanic Eng* 29:605–621
- Fish F, Lauder GV (2006) Passive and active flow control by swimming fishes and mammals. *Ann Rev Fluid Mech* 38:193–224
- Fish FE, Howle LE, Murray MM (2008) Hydrodynamic flow control in marine mammals. *Integr Comp Biol* 48:788–800
- Flammang BE, Lauder GV (2008) Speed-dependent intrinsic caudal fin muscle recruitment during steady swimming in bluegill sunfish, *Lepomis macrochirus*. *J Exp Biol* 211:587–598
- Flammang BE, Lauder GV (2009) Caudal fin shape modulation and control during acceleration, braking and backing maneuvers in bluegill sunfish, *Lepomis macrochirus*. *J Exp Biol* 212:277–286
- Fontaine EI, Zabala F, Dickinson MH, Burdick JW (2009) Wing and body motion during flight initiation in *Drosophila* revealed by automated visual tracking. *J Exp Biol* 212:1307–1323
- Geerlink PJ, Videler JJ (1987) The relation between structure and bending properties of teleost fin rays. *Neth J Zool* 37:59–80
- Hain R, Kähler C, Michaelis D (2008) Tomographic and time resolved PIV measurements on a finite cylinder mounted on a flat plate. *Exp Fluids* 45:715–724
- Hertel H (1966) Structure, form and movement. Reinhold, New York, NY
- Hoerner SF (1965) Fluid-dynamic drag. Hoerner Fluid Dynamics, Bakersfield, California
- Horner AM, Jayne BC (2008) The effects of viscosity on the axial motor pattern and kinematics of the African lungfish (*Protopterus annectens*) during lateral undulatory swimming. *J Exp Biol* 211:1612–1622
- Hunt von Herbing I, Keating K (2003) Temperature-induced changes in viscosity and its effects on swimming speed in larval haddock. In: Browman HI, Skiftesvik A (eds) *The big fish bang*. Institute of Marine Research, Bergen, pp 23–34
- Johnson TP, Cullum AJ, Bennett AF (1998) Partitioning the effects of temperature and kinematic viscosity on the c-start performance of adult fishes. *J Exp Biol* 201:2045–2051
- Kato N (2000) Control performance in the horizontal plane of a fish robot with mechanical pectoral fins. *IEEE J Oceanic Eng* 25:121–129
- Lauder GV (1989) Caudal fin locomotion in ray-finned fishes: historical and functional analyses. *Amer Zool* 29:85–102
- Lauder GV (2000) Function of the caudal fin during locomotion in fishes: kinematics, flow visualization, and evolutionary patterns. *Amer Zool* 40:101–122
- Lauder GV (2006) Locomotion. In: Evans DH, Claiborne JB (eds) *The physiology of fishes*, 3rd edn. CRC Press, Boca Raton, pp 3–46
- Lauder GV, Drucker EG (2002) Forces, fishes, and fluids: hydrodynamic mechanisms of aquatic locomotion. *News Physiol Sci* 17:235–240
- Lauder GV, Madden PGA (2006) Learning from fish: kinematics and experimental hydrodynamics for roboticists. *Int J Automat Comput* 4:325–335
- Lauder GV, Madden PGA (2007) Fish locomotion: kinematics and hydrodynamics of flexible foil-like fins. *Exp Fluids* 43:641–653
- Lauder GV, Madden PGA (2008) Advances in comparative physiology from high-speed imaging of animal and fluid motion. *Ann Rev Physiol* 70:143–163
- Lauder GV, Tytell ED (2006) Hydrodynamics of undulatory propulsion. In: Shadwick RE, Lauder GV (eds) *Fish biomechanics volume 23 in fish physiology*. Academic Press, San Diego, pp 425–468
- Lauder GV, Madden PGA, Mittal R, Dong H, Bozkurttas M (2006) Locomotion with flexible propulsors I: experimental analysis of pectoral fin swimming in sunfish. *Bioinsp Biomimet* 1:S25–S34
- Lauder GV, Anderson EJ, Tangorra J, Madden PGA (2007) Fish biorobotics: kinematics and hydrodynamics of self-propulsion. *J Exp Biol* 210:2767–2780
- Lehmann F-O (2008) When wings touch wakes: understanding locomotor force control by wake wing interference in insect wings. *J Exp Biol* 211:224–233
- Lehmann F-O (2009) Wing-wake interaction reduces power consumption in insect tandem wings. *Exp Fluids* 46:765–775
- Lehmann F-O, Sane SP, Dickinson M (2005) The aerodynamic effects of wing-wing interaction in flapping insect wings. *J Exp Biol* 208:3075–3092
- Liao J (2004) Neuromuscular control of trout swimming in a vortex street: implications for energy economy during the Karman gait. *J Exp Biol* 207:3495–3506
- Liao J, Beal DN, Lauder GV, Triantafyllou MS (2003a) Fish exploiting vortices decrease muscle activity. *Science* 302:1566–1569
- Liao J, Beal DN, Lauder GV, Triantafyllou MS (2003b) The Kármán gait: novel body kinematics of rainbow trout swimming in a vortex street. *J Exp Biol* 206:1059–1073
- Liu H, Wassersug RJ, Kawachi K (1997) The three-dimensional hydrodynamics of tadpole locomotion. *J Exp Biol* 200:2807–2819

- Long J (1998) Muscles, elastic energy, and the dynamics of body stiffness in swimming eels. *Amer Zool* 38:771–792
- Long JH, Nipper KS (1996) The importance of body stiffness in undulatory propulsion. *Amer Zool* 36:678–694
- Long JH Jr, Koob TJ, Irving K, Combie K, Engel V, Livingston N, Lammert A, Schumacher J (2006) Biomimetic evolutionary analysis: testing the adaptive value of vertebrate tail stiffness in autonomous swimming robots. *J Exp Biol* 209:4732–4746
- Mittal R, Dong H, Bozkurtas M, Lauder GV, Madden PGA (2006) Locomotion with flexible propulsors II: computational modeling and analysis of pectoral fin swimming in sunfish. *Bioinsp Biomimet* 1:S35–S41
- Müller UK, Smit J, Stamhuis EJ, Videler JJ (2001) How the body contributes to the wake in undulatory fish swimming: flow fields of a swimming eel (*Anguilla anguilla*). *J Exp Biol* 204:2751–2762
- Nauen JC, Lauder GV (2002a) Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae). *J Exp Biol* 205:1709–1724
- Nauen JC, Lauder GV (2002b) Quantification of the wake of rainbow trout (*Oncorhynchus mykiss*) using three-dimensional stereoscopic digital particle image velocimetry. *J Exp Biol* 205:3271–3279
- Peng J, Dabiri JO (2008a) An overview of a Lagrangian method for analysis of animal wake dynamics. *J Exp Biol* 211:280–287
- Peng J, Dabiri JO (2008b) The ‘upstream wake’ of swimming and flying animals and its correlation with propulsive efficiency. *J Exp Biol* 211:2669–2677
- Pereira F, Gharib M, Dabiri D, Modarress D (2000) Defocusing digital particle image velocimetry: a 3-component 3-dimensional DPIV measurement technique. Application to bubbly flows. *Exp Fluids* 29:S78–S84
- Ramamurti R, Sandberg WC, Lohner R, Walker JA, Westneat M (2002) Fluid dynamics of flapping aquatic flight in the bird wrasse: three-dimensional unsteady computations with fin deformation. *J Exp Biol* 205:2997–3008
- Sakakibara J, Nakagawa M, Yoshida M (2004) Stereo-PIV study of flow around a maneuvering fish. *Exp Fluids* 36:282–293
- Shadwick RE, Lauder GV (2006) Fish biomechanics. In: Hoar WS, Randall DJ, Farrell AP (eds) *Fish physiology*, vol 23. Academic Press, San Diego
- Shen L, Zhang X, Yue D, Triantafyllou MS (2003) Turbulent flow over a flexible wall undergoing a streamwise travelling wave motion. *J Fluid Mech* 484:197–221
- Shirgaonkar AA, Curet OM, Patankar NA, MacIver MA (2008) The hydrodynamics of ribbon-fin propulsion during impulsive motion. *J Exp Biol* 211:3490–3503
- Shoele K, Zhu Q (2009) Fluid–structure interactions of skeleton-reinforced fins: performance analysis of a paired fin in lift-based propulsion. *J Exp Biol* 212:2679–2690
- Standen EM (2008) Pelvic fin locomotor function in fishes: three-dimensional kinematics in rainbow trout (*Oncorhynchus mykiss*). *J Exp Biol* 211:2931–2942
- Standen EM, Lauder GV (2005) Dorsal and anal fin function in bluegill sunfish (*Lepomis macrochirus*): three-dimensional kinematics during propulsion and maneuvering. *J Exp Biol* 205:2753–2763
- Standen EM, Lauder GV (2007) Hydrodynamic function of dorsal and anal fins in brook trout (*Salvelinus fontinalis*). *J Exp Biol* 210:325–339
- Svizher A, Cohen J (2006) Holographic particle image velocimetry measurements of hairpin vortices in a subcritical air channel flow. *Phys Fluids* 18:014105–014114
- Taft N, Lauder GV, Madden PG (2008) Functional regionalization of the pectoral fin of the benthic longhorn sculpin during station holding and swimming. *J Zool Lond* 276:159–167
- Tan G-K, Shen G-X, Huang S-Q, Su W-H, Ke Y (2007) Investigation of flow mechanism of a robotic fish swimming by using flow visualization synchronized with hydrodynamic force measurement. *Exp Fluids* 43:811–821
- Tangorra J, Anquetil P, Fofonoff T, Chen A, Del Zio M, Hunter I (2007) The application of conducting polymers to a biorobotic fin propulsor. *Bioinsp Biomimet* 2:S6–S17
- Triantafyllou MS, Triantafyllou GS (1995) An efficient swimming machine. *Sci Amer* 272:64–70
- Triantafyllou MS, Triantafyllou GS, Yue DKP (2000) Hydrodynamics of fishlike swimming. *Ann Rev Fluid Mech* 32:33–53
- Triantafyllou M, Hover FS, Techet AH, Yue D (2005) Review of hydrodynamic scaling laws in aquatic locomotion and fish swimming. *Transactions of the ASME* 58:226–237
- Troolin D, Longmire E (2008) Volumetric 3-component velocity measurements of vortex rings from inclined exits. In: 14th international symposium on applications of laser techniques to fluid mechanics. Lisbon, Portugal, pp 1–11
- Tytell ED (2004) Kinematics and hydrodynamics of linear acceleration in eels, *Anguilla rostrata*. *Proc Roy Soc Lond B* 271:2535–2540
- Tytell ED (2006) Median fin function in bluegill sunfish, *Lepomis macrochirus*: streamwise vortex structure during steady swimming. *J Exp Biol* 209:1516–1534
- Tytell ED, Lauder GV (2004) The hydrodynamics of eel swimming. I. Wake structure. *J Exp Biol* 207:1825–1841
- Tytell ED, Lauder GV (2008) Hydrodynamics of the escape response in bluegill sunfish, *Lepomis macrochirus*. *J Exp Biol* 211:3359–3369
- Tytell ED, Standen EM, Lauder GV (2008) Escaping flatland: three-dimensional kinematics and hydrodynamics of median fins in fishes. *J Exp Biol* 211:187–195
- Usherwood JR, Lehman F-O (2008) Phasing of dragonfly wings can improve aerodynamic efficiency by removing swirl. *J Roy Soc Interface* 5:1303–1307
- Videler JJ (1993) *Fish swimming*. Chapman and Hall, New York
- Wakeling JM (2006) Fast-start mechanics. In: Shadwick RE, Lauder GV (eds) *Fish biomechanics volume 23 in fish physiology*. Academic Press, San Diego, pp 333–368
- Wang H, Ando N, Kanzaki R (2008) Active control of free flight manoeuvres in a hawkmoth, *Agrius convolvuli*. *J Exp Biol* 211:423–432
- Webb PW (1975) Hydrodynamics and energetics of fish propulsion. *Bull Fish Res Bd Can* 190:1–159
- Webb PW (2004a) Maneuverability—general issues. *IEEE J Oceanic Eng* 29:547–555
- Webb PW (2004b) Response latencies to postural disturbances in three species of teleostean fishes. *J Exp Biol* 207:955–961
- Webb P (2006) Stability and maneuverability. In: Shadwick RE, Lauder GV (eds) *Fish biomechanics volume 23 in fish physiology*. Academic Press, San Diego, pp 281–332
- Webb JF, Fay RR, Popper A (2008) *Fish bioacoustics*. Springer Verlag, New York
- Weber PW, Howle LE, Murray MM, Fish FE (2009) Lift and drag performance of odontocete cetacean flippers. *J Exp Biol* 212:2149–2158
- Wieneke B (2008) Volume self-calibration for 3D particle image velocimetry. *Exp Fluids* 45:549–556
- Wilga CD, Lauder GV (2004) Hydrodynamic function of the shark’s tail. *Nature* 430:850
- Willert C (1997) Stereoscopic digital particle image velocimetry for application in wind tunnel flows. *Meas Sci Technol* 8:1465–1479
- Wolfgang MJ, Anderson JM, Grosenbaugh M, Yue D, Triantafyllou M (1999) Near-body flow dynamics in swimming fish. *J Exp Biol* 202:2303–2327

- Zhang W, Hain R, Kähler C (2008) Scanning PIV investigation of the laminar separation bubble on a SD7003 airfoil. *Exp Fluids* 45:725–743
- Zhu Q, Shoen K (2008) Propulsion performance of a skeleton-strengthened fin. *J Exp Biol* 211:2087–2100
- Zhu Q, Wolfgang MJ, Yue DKP, Triantafyllou GS (2002) Three-dimensional flow structures and vorticity control in fish-like swimming. *J Fluid Mech* 468:1–28