Animal Locomotion
Animal Locomotion
Preface

The physical principles of swimming and flying in animals are intriguingly different from those of ships and airplanes. The study of animal locomotion therefore holds a special place not only at the frontiers of pure fluid dynamics research, but also in the applied field of biomimetics, which aims to emulate salient aspects of the performance and function of living organisms. For example, fluid dynamic loads are so significant for swimming fish that they are expected to have developed efficient flow control procedures through the evolutionary process of adaptation by natural selection, which might in turn be applied to the design of robotic swimmers. And yet, sharply contrasting views as to the energetic efficiency of oscillatory propulsion – especially for marine animals – demand a careful assessment of the forces and energy expended at realistic Reynolds numbers. For this and many other research questions, an experimental approach is often the most appropriate methodology. This holds as much for flying animals as it does for swimming ones, and similar experimental challenges apply – studying tethered as opposed to free locomotion, or studying the flow around robotic models as opposed to real animals.

This book provides a wide-ranging snapshot of the state-of-the-art in experimental research on the physics of swimming and flying animals. The resulting picture reflects not only upon the questions that are of interest in current pure and applied research, but also upon the experimental techniques that are available to answer them. Doubtless, many new questions will present themselves as the scope and performance of our experimental toolbox develops over the coming years.

While there has been great progress in identifying the principles and role of vorticity shedding and control in fish swimming, much remains to be done in terms of understanding the three-dimensional structure of the vortical patterns and the energetics of the flow. These developments will also drive work on sensing and control. Observations and flow visualization with living fish and experimentation with robotic fish-like swimming devices are unique tools in exploring the properties of the flow structures produced by fish. Some of the more pertinent questions in this regard are addressed in the opening article by George Lauder *Swimming hydrodynamics: ten questions and the technical approaches needed to resolve them*. The field of micro-organism swimming is equally intriguing and is a field that will grow rapidly in the near future. Hence, while they fall outside the strict scope of “animal locomotion”, bacteria find a place in this book – not least because of the insight they yield into the effects of collective behaviour in swimming micro-organisms more generally.

Turning now to flying, the emphasis in experimental research has shifted in recent years from an exploratory quest to identify “novel” mechanisms of unsteady lift production - clap and fling, leading-edge vortices, rotational mechanisms, wake capture - to more detailed examinations of the underlying flow physics. This shift has been enabled in large part by the widespread availability of Particle Image Velocimetry (PIV), which has allowed new questions to be asked, for example, about the detailed wake structures of birds and bats, or of the importance of tandem wing interactions and aeroelastic deformation in insects. This aspect of the field is addressed directly with a review article from Geoff Spedding and Anders Hedenström *PIV Based Investigations of Animal Flight*. Other more classical techniques, such as smoke visualization and direct force or pressure measurements retain an important role in cases where PIV is impractical or uninformative, and all feature in this book accordingly.

Many fundamental questions remain, and many more will doubtless arise, as an ever wider range of species and systems is studied. Here in a single volume are measurements from multiple species of swimming and flying organisms – from bacteria to fish, and from insects to birds and bats. This presentation offers a glimpse of the future possibilities opened by comparative experimental approach which asks not only how the fluid dynamic principles operate, but also how they vary systematically with fluid medium, scale, form and function.

(Vol. 45, No. 4, May 2009) with the addition of a review article contributed by George Lauder (DOI: 10.1007/s00348-009-0765-8, October 2009). The editors hope that this condensed version of the current state-of-the-art in the field will be appreciated by the readers and, of course, we welcome any feedback or suggestions for future publishing efforts.

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# Table of Contents

## Part I: The Hydrodynamics of Swimming

Swimming Hydrodynamics: Ten Questions and the Technical Approaches Needed to Resolve Them  .......................................................... 3
  *George V. Lauder*

A Potential-Flow, Deformable-Body Model for Fluid–Structure Interactions with Compact Vorticity: Application to Animal Swimming Measurements ........................................ 17
  *Jifeng Peng, John O. Dabiri*

Wake Visualization of a Heaving and Pitching Foil in a Soap Film  ............................................. 27
  *Florian T. Muijres, David Lentink*

A Harmonic Model of Hydrodynamic Forces Produced by a Flapping Fin  ........................................ 37
  *David N. Beal, Promode R. Bandyopadhyay*

Flowfield Measurements in the Wake of a Robotic Lamprey  .................................................. 45
  *Marcus Hultmark, Megan Leftwich, Alexander J. Smits*

Impulse Generated during Unsteady Maneuvering of Swimming Fish  ........................................ 53
  *Brenden P. Epps, Alexandra H. Techet*

Do Trout Swim Better Than Eels? Challenges for Estimating Performance Based on the Wake of Self-propelled Bodies  ........................................... 63
  *Eric D. Tytell*

Time Resolved Measurements of the Flow Generated by Suction Feeding Fish  ........................................ 75
  *Steven W. Day, Timothy E. Higham, Peter C. Wainwright*

Powered Control Mechanisms Contributing to Dynamically Stable Swimming in Porcupine Puffers (Teleostei: *Diodon Holocanthus*)  ............................................. 87
  *Alexis M. Wiktorowicz, Dean V. Lauritzen, Malcolm S. Gordon*

Fluid Dynamics of Self-propelled Microorganisms, from Individuals to Concentrated Populations  .................................................. 99
  *Luis H. Cisneros, Ricardo Cortez, Christopher Dombrowski, Raymond E. Goldstein, John O. Kessler*

Swimming by Microscopic Organisms in Ambient Water Flow  ........................................... 117
  *M.A.R. Koehl, Matthew A. Reidenbach*

Water-Walking Devices  .................................................. 131
  *David L. Hu, Manu Prakash, Brian Chan, John W.M. Bush*

Flapping Flexible Fish: Periodic and Secular Body Reconfigurations in Swimming Lamprey, *Petromyzon marinus*  .................................................. 141

Vortex Dynamics in the Wake of a Mechanical Fish  ........................................... 161
  *Christoph Brücker, Horst Bleckmann*

Investigation of Flow Mechanism of a Robotic Fish Swimming by Using Flow Visualization Synchronized with Hydrodynamic Force Measurement  ........................................ 173
  *Guang-Kun Tan, Gong-Xin Shen, Shuo-Qiao Huang, Wen-Han Su, Yu Ke*
# Table of Contents

**Part II: The Physics of Flying**

<table>
<thead>
<tr>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>PIV-Based Investigations of Animal Flight</td>
<td>187</td>
</tr>
<tr>
<td>Geoffrey R. Spedding, Anders Hedenström</td>
<td></td>
</tr>
<tr>
<td>Wing–Wake Interaction Reduces Power Consumption in Insect Tandem Wings</td>
<td>203</td>
</tr>
<tr>
<td>Fritz-Olaf Lehmann</td>
<td></td>
</tr>
<tr>
<td>Experimental Investigation of Some Aspects of Insect-Like Flapping Flight Aerodynamics for Application to Micro Air Vehicles</td>
<td>215</td>
</tr>
<tr>
<td>Salman A. Ansari, Nathan Phillips, Graham Stabler, Peter C. Wilkins, Rafal Zbikowski, Kevin Knowles</td>
<td></td>
</tr>
<tr>
<td>Design and Development Considerations for Biologically Inspired Flapping-Wing Micro Air Vehicles</td>
<td>237</td>
</tr>
<tr>
<td>Kevin D. Jones, Maz F. Platzer</td>
<td></td>
</tr>
<tr>
<td>Smoke Visualization of Free-Flying Bumblebees Indicates Independent Leading-Edge Vortices on Each Wing Pair</td>
<td>249</td>
</tr>
<tr>
<td>Richard James Bomphrey, Graham K. Taylor, Adrian L.R. Thomas</td>
<td></td>
</tr>
<tr>
<td>The Influence of Airfoil Kinematics on the Formation of Leading-Edge Vortices in Bio-inspired Flight</td>
<td>261</td>
</tr>
<tr>
<td>David Rival, Tim Prangemeier, Cameron Tropea</td>
<td></td>
</tr>
<tr>
<td>Wake Patterns of the Wings and Tail of Hovering Hummingbirds</td>
<td>273</td>
</tr>
<tr>
<td>Douglas L. Altshuler, Marko Princevac, Hansheng Pan, Jesse Lozano</td>
<td></td>
</tr>
<tr>
<td>Characterization of Vortical Structures and Loads based on Time-Resolved PIV for Asymmetric Hovering Flapping Flight</td>
<td>285</td>
</tr>
<tr>
<td>T. Jardin, Laurent David, A. Farcy</td>
<td></td>
</tr>
<tr>
<td>Unsteady Fluid–Structure Interactions of Membrane Airfoils at low Reynolds Numbers</td>
<td>297</td>
</tr>
<tr>
<td>P. Rojratsirikul, Z. Wang, I. Gursul</td>
<td></td>
</tr>
<tr>
<td>Aerodynamic and Functional Consequences of Wing Compliance</td>
<td>311</td>
</tr>
<tr>
<td>Andrew M. Mountcastle, Thomas L. Daniel</td>
<td></td>
</tr>
<tr>
<td>Shallow and Deep Dynamic Stall for Flapping Low Reynolds Number Airfoils</td>
<td>321</td>
</tr>
<tr>
<td>Michael V. Ol, Luis Bernal, Chang-Kwon Kang, Wei Shyy</td>
<td></td>
</tr>
<tr>
<td>High-Fidelity Simulations of Moving and Flexible Airfoils at Low Reynolds Numbers</td>
<td>341</td>
</tr>
<tr>
<td>Miguel R. Visbal, Raymond E. Gordnier, Marshall C. Galbraith</td>
<td></td>
</tr>
<tr>
<td>High-Speed Stereo DPIV Measurement of Wakes of Two Bat Species Flying Freely in a Wind Tunnel</td>
<td>361</td>
</tr>
<tr>
<td>Time-Resolved Wake Structure and Kinematics of Bat Flight</td>
<td>371</td>
</tr>
<tr>
<td>Tatjana Y. Habel, Nickolay I. Hristov, Sharon M. Swartz, Kenneth S. Breuer</td>
<td></td>
</tr>
<tr>
<td>Experimental Investigation of a Flapping Wing Model</td>
<td>383</td>
</tr>
<tr>
<td>Tatjana Y. Habel, Cameron Tropea</td>
<td></td>
</tr>
<tr>
<td>Aerodynamics of Intermittent Bounds in Flying Birds</td>
<td>401</td>
</tr>
<tr>
<td>Bret W. Tobalske, Jason W.D. Hearn, Douglas R. Warrick</td>
<td></td>
</tr>
</tbody>
</table>
Experimental Analysis of the Flow Field over a Novel Owl Based Airfoil
Stephan Klän, Thomas Bachmann, Michael Klaas, Hermann Wagner, Wolfgang Schröder
413

The Aerodynamic Forces and Pressure Distribution of a Revolving Pigeon Wing
James R. Usherwood
429

Author Index
443
PART I

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

George V. Lauder

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.
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 2010, 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.
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.
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; Bozkurttas et al. 2006; Shen et al. 2003; Shoele 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 2010) 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 (Shoele and Zhu 2009; Zhu and Shoele 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.
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 (Brucker 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

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)
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...
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.
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 (Bozkurttas 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 (Bozkurttas 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.

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Hoerner SF (1965) Fluid-dynamic drag. Hoerner Fluid Dynamics, Bakersfield, California
A potential-flow, deformable-body model for fluid–structure interactions with compact vorticity: application to animal swimming measurements

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Abstract  This paper presents an approach to quantify the unsteady fluid forces, moments and mass transport generated by swimming animals, based on measurements of the surrounding flow field. These goals are accomplished within a framework that is independent of the vorticity field, making it unnecessary to directly resolve boundary layers on the animal, body–vortex interactions, or interactions among vortex lines in the wake. Instead, the method identifies Lagrangian coherent structures in the flow, whose dynamics in flows with compact vorticity are shown to be well approximated by potential flow concepts, especially the Kirchhoff and deformation potentials from deformable body theory. Examples of the application of these methods are given for pectoral fin locomotion of the bluegill sunfish and undulatory swimming of jellyfish, and the methods are validated by analysis of a canonical starting vortex ring flow. The transition to a Lagrangian approach toward animal swimming measurements suggests the possibility of implementing recently developed particle tracking (vis-à-vis DPIV) techniques for fully three-dimensional measurements of animal swimming.

1 Introduction

A distinguishing feature of animal swimming in real fluids is the generation of vorticity and the shedding of vortices into the wake. It is for this reason that much of the experimental work on animal swimming has been approached from a perspective that aims to quantify vorticity dynamics (e.g. Drucker and Lauder 1999, 2001; Wilga and Lauder 2004; Bartol et al. 2005; Dabiri et al. 2005; Stamhuis and Nauwelaerts 2005). The standard tool for flow field measurements is digital particle image velocimetry (DPIV), which quantifies the velocity field of the flow in an Eulerian frame of reference, i.e. instantaneously and at fixed locations in space. The vorticity field is then immediately deduced by numerically taking the curl of the measured velocity field.

These wake studies have been complemented by theoretical tools that, in principle, enable the quantification of instantaneous forces and moments created by the animal, given knowledge of the surrounding flow field. However, with the exception of purely steady flows, these methods require either measurement of the boundary layers on the animal, the replacement of the animal body with an equivalent system of image vorticity, or measurements on the surface of a control volume with length scales an order of magnitude larger than the animal itself (Wu 1981; Noca 1997, 1999). Each of these options is difficult to achieve in practice. Therefore, the state-of-the-art in the field is the calculation of time-averaged forces, in which unsteady effects like added-mass tend to cancel when integrated over a swimming cycle (Daniel 1984).

The study of body–vortex interactions, such as those occurring due to incident vortices from upstream or generated by the head of the animal (e.g. Gopalkrishnan et al. 1994; Liao et al. 2003; Beal et al. 2006), is also...
limited by practical obstacles to quantitative flow visualization. The velocity and vorticity fields cannot usually be well resolved at the interface between the animal and the surrounding fluid while maintaining a full-field view of the flow (see Anderson et al. 2001, for a notable exception). Together these limitations represent a potential show-stopper to more detailed and quantitative analyses of animal swimming.

In general, the challenge of analyzing flow measurements is related to the need to identify consistent boundaries in the flow on which to evaluate the equations of motion. The aforementioned theoretical tools rely on either the fluid–solid boundary represented by the animal surface, or a virtual, fluid–fluid boundary used to define a control volume. Recent applications of Lagrangian, particle-tracking flow analyses have demonstrated that in many unsteady flows there exist physically meaningful, fluid–fluid boundaries that act as barriers to fluid transport. The Lagrangian coherent structures (LCS) defined by these real fluid–fluid boundaries are currently studied for their kinematic properties and have been used primarily to better understand transport and mixing processes or to identify fluid structures in turbulence (e.g. Haller 2000, 2001, 2002; Green et al. 2006).

This paper examines the dynamic properties of LCS and shows that these properties can be used to deduce the forces and moments on a swimming animal. A distinguishing feature of this approach is that it does not appeal to the vorticity dynamics in the flow. Instead, it is shown that potential flow concepts from deformable body theory can be used to approximate the LCS dynamics when the vorticity field is sufficiently compact (i.e. bounded spatially). The LCS tend to appear away from the surface of the animal body but not at prohibitively large distances away. Together these properties make it possible to determine instantaneous, unsteady forces and moments created by swimming animals without the need to resolve boundary layers on the animal, to construct equivalent image vorticity systems, or to use far-field control volume analyses. In addition, the known transport properties of LCS enable quantification of mass transport that is induced by the animal during locomotion.

Recent implementation of these methods in studies of the bluegill sunfish pectoral fin and the entire body of a free-swimming jellyfish are highlighted to demonstrate the capabilities and limitations of the present approach. To be sure, the methods presented here are more generally applicable than animal swimming. However, the study of animal swimming provides a robust test of the method in flows characterized by unsteady fluid–structure interactions and complex vorticity dynamics. Validation using direct numerical simulations of a starting vortex ring formed by a piston-cylinder apparatus demonstrates the capabilities of the method in a more canonical flow and helps to put these results in the context of traditional fluid mechanics analyses.

Section 2 presents the experimental and analytical methods that constitute this vorticity-free approach to the study of animal swimming. Examples of the resulting measurements, taken from recent contributions by the authors and coworkers, are presented in Sect. 3 along with a validation of the method using direct numerical simulations of vortex ring formation by a piston-cylinder apparatus. Finally, Sect. 4 suggests a path forward that addresses issues such as three-dimensional flow, in situ animal measurements, and measurement validation.

2 Experimental and analytical methods

2.1 Identification of Lagrangian coherent structures

The first step in the vorticity-free approach to swimming measurements is to identify the LCS from which fluid dynamic forces and moments will be deduced. Haller (2001) and Shadden et al. (2005, 2006) identify LCS as ridges of local maxima in the finite-time Lyapunov exponent (FTLE) field of a given flow. The FTLE measures the maximum linearized growth rate of the distance between initially adjacent fluid particles. To determine this quantity, fluid particles are tracked over a finite time interval. Since the available information regarding the velocity field \( \mathbf{u} \) is typically given in an Eulerian frame (e.g. DPIV), the particle trajectories \( \mathbf{x}(t) \) are determined by numerical solution of the ordinary differential equation

\[
\dot{\mathbf{x}}(t) = \mathbf{u}(\mathbf{x}(t), t),
\]

with the initial position of the fluid particle used as the initial condition. The flow map, which maps fluid particles from their initial location at time \( t_0 \) to their location at time \( t_0 + T \) can be expressed as

\[
\phi_{t_0}^{t_0+T}(\mathbf{x}) : \mathbf{x}(t_0) \to \mathbf{x}(t_0 + T),
\]

where \( \phi_{t_0}^{t_0+T}(<x>=\mathbf{x}(t_0 + T) \) describes the current location of a fluid particle advected from the location \( \mathbf{x}(t_0) \) at time \( t_0 \) after a time interval \( T \). A given infinitesimal perturbation \( \delta \mathbf{x}_{t_0} \) (i.e. fluid particle separation) at time \( t_0 \) is transformed to \( \delta \mathbf{x} \) by the relation

\[
\delta \mathbf{x} = \nabla \phi_{t_0}^{t_0+T}(\mathbf{x}) \delta \mathbf{x}_{t_0},
\]

where \( \nabla \phi_{t_0}^{t_0+T}(\mathbf{x}) \) is the deformation gradient tensor and defined by
\[ \nabla \psi_{t_0}^{+T}(x) = \frac{d\psi_{t_0}^{+T}(x)}{dx}. \] (4)

The magnitude of the mapped perturbation is defined by the symbol \( \|\delta x\| \) and given by

\[ \|\delta x\| = \sqrt{\langle \delta x_0, [\nabla \psi(x)]^* \nabla \psi(x) \delta x_0 \rangle}, \] (5)

where \([ ]^*\) denotes the transpose of matrix \([ ]\). The inner product can be written in summation form as

\[ \langle \delta x_0, [\nabla \psi(x)]^* \nabla \psi(x) \delta x_0 \rangle = \sum_{i} \sum_{j} \sum_{k} (\delta x_0)_i (\nabla \psi(x))_{ik} (\nabla \psi(x))_{jk} (\delta x_0)_j. \] (6)

Let the symmetric matrix \( \Delta \) be defined as the Cauchy–Green deformation tensor:

\[ \Delta = [\nabla \psi_{t_0}^{+T}(x)]^* \nabla \psi_{t_0}^{+T}(x), \] (7)

and let \( \lambda_{\text{max}}(\Delta) \) be the maximum eigenvalue of the Cauchy–Green deformation tensor. Note from Eq. 5 that \( \sqrt{\lambda_{\text{max}}(\Delta)} \) gives the maximum stretching of \( \delta x_0 \) (i.e. the maximum separation of fluid particle pairs initially located at \( x(t_0) \)) when \( \delta x_0 \) is aligned with the eigenvector associated with \( \lambda_{\text{max}}(\Delta) \); hence

\[ \|\delta x\|_{\text{max}} = \sqrt{\lambda_{\text{max}}(\Delta)}\|\delta x_0\|. \] (8)

The finite-time Lyapunov exponent \( \sigma_T^f(x) \) is then defined as:

\[ \sigma_T^f(x) = \frac{1}{T} \ln \sqrt{\lambda_{\text{max}}(\Delta)} = \frac{1}{T} \ln \|\delta x(T)\| / \|\delta x(0)\|. \] (9)

Shadden et al. (2005) showed that the ridges of local maxima in the FTLE field act as material lines in the flow and, furthermore, are nearly perfect barriers to fluid transport when computed in the limit as \( T \) becomes very large. Shadden et al. (2005) also derived an estimate for the fluid flux across an LCS that is deduced from finite-time data (i.e. finite \( T \) in Eq. 9) and showed that, for practical purposes, this quantity is often negligible. Hence, the LCS are treated as ideal material lines in practice. The absolute value \(|T|\) is used instead of \( T \) in Eq. 8 because FTLE can be computed for \( T > 0 \) and \( T < 0 \). The material line is called a repelling LCS (\( T > 0 \)) over the time interval if infinitesimal perturbations away from this line grow monotonically under the linearized flow. The material line is called an attracting LCS (\( T < 0 \)) if it is a repelling LCS over the interval in backward time. In the parlance of dynamical systems, repelling and attracting LCS reveal stable and unstable manifolds, respectively.

The FTLE field can be calculated from a time-series of discrete velocity field data typical of DPIV measurements. The flow map is determined by integration of the velocity field and the FTLE can be calculated from the flow map. There are currently at least two software packages available for the calculation of FTLE fields from DPIV-type velocity field data. MANGEN, a package developed by F. Lekien and C. Coulliette, is a C-language program previously implemented by Shadden et al. (2005, 2006) and is available for download at http://www.lekien.com/~francois/software. A MATLAB package for FTLE calculation has been developed by the authors (Peng and Dabiri 2007) and is available for download at http://dabiri.caltech.edu/software.

The extraction of LCS curves from FTLE fields can be accomplished by a variety of ad hoc methods including thresholding or gradient searches of the FTLE field to identify local maxima. Shadden (2006) derives more rigorous criteria than these; however, for practical purposes, identification of LCS boundaries from well-resolved FTLE fields is relatively insensitive to the implemented method of extraction.

Figure 1 shows the forward-time and the backward-time FTLE fields computed for a steadily propagating vortex ring generated by a piston-cylinder apparatus (Shadden et al. 2006). The corresponding repelling and attracting LCS identified by the ridges of high FTLE values are shown in Fig. 2. The increasingly sinuous nature of the repelling (attracting) LCS near the front (rear) of the vortex ring is the result of perturbations from an ideal, unperturbed vortex.

![Fig. 1](image-url) Contour plot of forward-time (left) backward-time (right) FTLE fields for vortex ring propagating from left to right. LCS are identified by the ridge of high FTLE values (red).
potential flow field. We make direct use of these equations presently, where the LCS structure is treated as a deformable body. It is important to note that there exist no a priori restrictions on which segments of the repelling and attracting LCS can be used to construct the deformable body, as long as (1) the segments form a closed curve and (2) the aforementioned potential flow hypothesis is satisfied. Nonetheless, certain combinations of the LCS provide more information regarding the fluid dynamics than others; hence, the choice should be made judiciously (see next section).

Let $\mathbf{U}_1 = \nabla \phi_1(\mathbf{X}, t)$ represent the ambient flow field surrounding the LCS, where $\phi_1$ is the velocity potential of the ambient flow and $\mathbf{X}$ is the position vector measured relative to the laboratory frame of reference. The outward-facing unit normal to the LCS is denoted $\mathbf{n}$; the position vector relative to the LCS centroid, $\mathbf{x}$; and the instantaneous surface of the LCS, $\mathbf{S}(\mathbf{x}, t) = 0$. The velocity potential that arises due to the presence of the LCS in the flow is given by

$$\phi_2 = \mathbf{U}_2 \cdot \mathbf{\Phi} + \mathbf{\Omega} \cdot \mathbf{\Psi} + \phi_d + \phi_0$$

where $\mathbf{U}_2$ is the linear velocity of the LCS centroid in the laboratory frame and $\mathbf{\Omega}$ is the angular velocity of the principal axes of the LCS. The harmonic functions $\mathbf{\Phi}, \mathbf{\Psi}, \phi_d$, and $\phi_0$ represent, respectively, the translational Kirchhoff potential, rotational Kirchhoff potential, deformation potential, and additional potential associated with the ambient flow. These potentials satisfy the boundary conditions listed below:

$$\frac{\partial \phi}{\partial n} = \mathbf{n}; \quad \frac{\partial \mathbf{\Psi}}{\partial n} = \mathbf{x} \times \mathbf{n}; \quad \frac{\partial \phi_d}{\partial n} = -\frac{\partial \Omega / \partial \mathbf{n}}{\nabla \phi_1 / \partial \mathbf{n}}; \quad \frac{\partial \phi_0}{\partial n} = -\mathbf{U}_1 \cdot \mathbf{n}$$

where each is evaluated on the LCS surface $\mathbf{S}(t)$. In addition, $\phi_2 \to 0$ as $|\mathbf{x}| \to \infty$. The fluid dynamic force $\mathbf{F}$ and moment $\mathbf{M}$ (per unit fluid density) acting on the LCS are given by

$$\mathbf{F} = \frac{d}{dt} \int_\mathbf{S} \phi \mathbf{n} d\mathbf{S} = \int_\mathbf{S} \nabla \phi (\nabla \phi \cdot \mathbf{n}) d\mathbf{S} + \frac{1}{2} \int_\mathbf{S} (\nabla \phi)^2 \mathbf{n} d\mathbf{S}$$

$$\mathbf{M} = \frac{d}{dt} \int_\mathbf{S} \phi \mathbf{x} \times \mathbf{n} d\mathbf{S} + \mathbf{U}_2$$

$$\times \int_\mathbf{S} \phi \mathbf{n} d\mathbf{S} - \int_\mathbf{S} \mathbf{x} \times \mathbf{U}_1 (\nabla \phi \cdot \mathbf{n}) d\mathbf{S}$$

$$+ \frac{1}{2} \int_\mathbf{S} (\nabla \phi)^2 (\mathbf{x} \times \mathbf{n}) d\mathbf{S}$$
where \( \phi = \phi_1 + \phi_2 \). The following sections consider the application of these governing equations to two common classes of animal swimming measurements in which we will assume that ambient flow and LCS rotation are negligible, i.e. \( \mathbf{U}_1 = \mathbf{\Omega} = \phi_0 = 0 \).

2.3.1 Inertial frame; single appendage measurements

When studying the dynamics of single appendages in an inertial frame, we must account for the combined dynamical effect of the appendage and the vorticity that it generates. The LCS captures this by delineating an ‘effective appendage’ boundary that interacts with irrotational fluid surrounding the appendage–vortex system. Specifically, the effective appendage is given by the closed boundary formed by the intersection of the forward- and backward-time LCS curves (cf. Figs. 1 and 2). If the deformation of the effective appendage is small relative to its translation through the fluid, i.e. \( \phi_d \ll \mathbf{U}_2 \cdot \Phi \), then Eq. 12 reduces to

\[
\mathbf{F} = \frac{d}{dt} \int_S (\mathbf{U}_2 - 2\Phi) \mathbf{n} \, dS
\]

(14)

The balance of this fluid dynamic force and the external force \( \mathbf{F}_{\text{ext}} \) applied by the animal to the appendage leads to a temporal change in the momentum of the effective appendage:

\[
\mathbf{F} + \mathbf{F}_{\text{ext}} = \frac{d}{dt} (V_{\text{LCS}} \mathbf{U}_2)
\]

(15)

or, equivalently,

\[
\frac{d}{dt} (V_{\text{LCS}} (\mathbf{I} + \mathbf{A}_{\text{LCS}}) \mathbf{U}_2) = \mathbf{F}_{\text{ext}}
\]

(16)

where \( V_{\text{LCS}} \) is the volume of fluid displaced by the LCS, \( \mathbf{I} \) is the identity matrix, and \( \mathbf{A}_{\text{LCS}} \) is the added-mass tensor of the LCS (i.e. \( \mathbf{A}_{\text{LCS}} = -\int_S \Phi \cdot \mathbf{n} \, dS \); Lamb 1932). Since the external force \( \mathbf{F}_{\text{ext}} \) is applied by the animal, an equal and opposite locomotive force \( \mathbf{F}_L \) is exerted by the fluid on the animal, i.e. \( \mathbf{F}_L = -\mathbf{F}_{\text{ext}} \).

2.3.2 Non-inertial frame; whole animal measurements

It is often necessary to measure animal swimming in a non-inertial frame; for example, when tracking free-swimming animals over distances longer than a stationary measurement window will permit. In these cases, the LCS centroid velocity \( \mathbf{U}_2 \) in Eq. 10 cannot be determined by visual inspection. However, if a closed curve surrounding the entire animal body can be constructed from the measured LCS, then the locomotive force generated at the animal–fluid interface becomes an internal force in the system and Eq. 12 reduces to a simplified expression for \( \mathbf{U}_2 \):

\[
\frac{d}{dt} (V_{\text{LCS}} (\mathbf{I} + \mathbf{A}_{\text{LCS}}) \mathbf{U}_2 - \int_S \phi_d \mathbf{n} \, dS) = 0
\]

(17)

The deformation potential \( \phi_d \) can be determined by using a standard boundary value problem solver (e.g. MATLAB) with the boundary condition specified in Eq. 11. The problem then becomes purely kinematic, in which the animal body velocity \( \mathbf{U}_{\text{body}} \) can be deduced from its weighted contribution to the velocity of the LCS centroid, i.e.

\[
\mathbf{U}_{\text{body}} = \frac{\mathbf{U}_2 V_{\text{LCS}} - \mathbf{U}_{\text{fluid}} V_{\text{fluid}}}{V_{\text{body}}}
\]

(18)

where \( V_{\text{body}} \) is the volume of the animal body (assumed neutrally buoyant), and the subscript fluid refers to properties of the fluid enclosed by the LCS.

It is important to note that, unlike the previous section in which deformation of the effective appendage was neglected, whole body calculations based primarily on either the repelling or attracting LCS can have a substantial contribution from the deformation potential \( \phi_d \) in Eq. 17. This is because the lobular portions of the LCS may be included in the deformable body in these cases. In the previous section, the deforming, lobular portions of both the repelling and attracting LCS were eliminated from the analysis when the LCS were intersected to determine the effective appendage boundary.

3 Results

3.1 Bluegill sunfish pectoral fin locomotion

The analysis presented in Sect. 2.3.1 was applied by Peng et al. (2007) to DPIV measurements of the bluegill sunfish pectoral fin. The animals were swum in a flume so that they could be observed in an inertial frame of reference. Since measurements were taken in a transverse plane, i.e. with ambient flow normal to the measurement plane, Eq. 16 could be used to deduce the lateral and lift components of the locomotive force \( \mathbf{F}_L \) (but not the thrust component). Figure 3 shows a snapshot of the computed forward- and backward-time FTLE fields and the resulting LCS structure that comprises the effective appendage boundary. These FTLE fields are not resolved as sharply as the vortex ring calculations shown in Fig. 1. This is due to the shorter integration time \( T \), the result of a shorter duration of available DPIV measurements. Nonetheless, the effective appendage is reconstructed without much difficulty.
Figure 4 plots the measured lateral and lift forces deduced from the vorticity-free analysis. For comparison, the steady force level determined using the vorticity method of Drucker and Lauder (1999) is also plotted. The time-averaged force computed using the vorticity method is sensitive to the time at which the vorticity field is evaluated and the vorticity threshold used to identify the spatial extent of the shed vortex. We selected an instant near the end of the fin downstroke and included all vorticity above the background noise level in the calculation. The result is provided for qualitative comparison with the present vorticity-free method. As shown in Fig. 4, the present method provides detailed information regarding the transient fluid dynamic forces, in addition to the time-averaged dynamics. To be sure, this particular data set is limited by a lack of measurement data before the start of the fin downstroke at time $t = 0$. Hence, at the beginning of the fin motion there is insufficient data to compute the backward-time FTLE and the corresponding repelling LCS, which locates the front boundary of the effective appendage. Since it is not possible to evaluate the locomotive forces until this portion of the effective appendage geometry is revealed, the peak force generation during the early downstroke is not captured in the analysis and the corresponding time-averaged force over the downstroke may be underestimated. Nevertheless, the transient force dynamics that are captured agree with observations of instantaneous animal body kinematics (Peng et al. 2007).

3.2 Jellyfish undulatory locomotion

The analysis presented in Sect. 2.3.2 was applied to DPIV measurements of free-swimming Aurelia aurita medusae.

![Fig. 3 FTLE fields and LCS for the flow generated by a bluegill sunfish pectoral fin.](image)

![Fig. 4 Measured locomotive forces in a horizontal and b vertical directions.](image)
This species of jellyfish swims via full body undulations that create vortex rings of alternating rotational orientation during the swimming cycle (Dabiri et al. 2005). The animals were observed in an inertial frame in order to validate the non-inertial analytical methods. Figure 5 shows a snapshot of the forward-time LCS structure. Deformation of the lobular portions of the LCS (i.e., the two elongated lobes) upstream of the animal makes a substantial contribution to Eq. 17. Figure 6 compares the measured LCS centroid velocity $U_2(t)$ to that predicted by Eq. 17; the agreement is reasonable, and it appears that the discrepancies are due to three-dimensional flow effects that cannot be captured by the two-dimensional DPIV measurements.

3.3 Validation of the potential flow hypothesis

To test the potential flow hypothesis and associated analytical method, we analyzed direct numerical simulations of vortex ring formation by a piston-cylinder apparatus. Details of the numerical model, which is similar to the experiment shown in Fig. 2, are described in a separate study (Shadden et al. 2007). The forward-time FTLE fields are shown for four frames in Fig. 7. The LCS extracted from the forward- and backward-time FTLE fields are plotted in Fig. 8, showing the temporal evolution of the flow. As in the case of the bluegill sunfish pectoral fin data, the backward-time LCS structure could not be identified until a finite time after flow initiation, since no data exists before that time. In Fig. 9, the total fluid momentum determined by the present vorticity-free method (i.e. spatial integration of the fluid potential in Eq. 12) is compared with a direct evaluation of this quantity from the DNS over the time interval $0.4T_S < t < T_S$, where $T_S$ is the duration of the piston stroke. The agreement is very good. Since the numerical data set provides a vorticity field that is well resolved even near the solid boundaries, we can also compute the instantaneous first moment of vorticity in the flow in order to determine the fluid momentum by a vorticity approach (Wu 1981). This result is also close to the DNS calculation, as expected since the effect of nozzle exit overpressure, which may not be captured by the vorticity approach, has decayed by the time $t = 0.4T_S$.

As mentioned previously, the vorticity-free analyses implemented presently rely on the assumption that there is no vorticity on or external to the LCS boundary, so that the shear stresses on the LCS surface are negligible. This hypothesis can be tested directly based on the measured velocity field data, by integrating the shear stress tensor $\tau$ on the surface $S(t)$ of the LCS and comparing this with the computed locomotive force $F_L$. The ratio $\frac{\int_{S(t)} \tau \cdot n \, dS}{F_L}$ is evaluated in Fig. 10 for DPIV measurements of the pectoral fin.
and the free-swimming jellyfish from the previous sections. Figure 10 shows that in both cases the shear on the LCS is small relative to the locomotive force, consistent with the potential flow hypothesis. The local peak in the pectoral fin data is attributable to vorticity outside the dorsal edge of the LCS, as seen in Fig. 3c. This vorticity external to the LCS causes the potential flow hypothesis to break down locally. The quantitative effect of non-compact vorticity on the validity of the potential flow hypothesis is an issue of ongoing study.

4 Discussion

The ability of the present methods to deduce unsteady fluid forces and moments makes them a valuable complement to existing techniques for quantitative studies of animal swimming. The vorticity-free approach can benefit from the wealth of theoretical tools developed for the study of potential flows, such as Hamiltonian formulations for optimization (e.g. Galper and Miloh 1995). From the perspective of an experimentalist, these methods possess the practical advantage that vorticity dynamics need not be resolved exactly. Furthermore, Haller (2002) showed that the geometry and kinematics of the LCS are robust to localized measurement errors (which will appear in the computed fluid particle trajectories), whereas the integrals that must be evaluated in common vorticity formulations are not.

To be sure, the present approach requires the extraction of fluid particle trajectories, data that we have derived here from Eulerian, DPIV data. In principle, it would be more efficient to extract these trajectories empirically, as in particle-tracking velocimetry (PTV) techniques. However, PTV methods are most effective in flows with relatively low seeding densities, typically at least an order of magnitude less than DPIV. Computing the FTLE fields would then require substantial interpolation of the measured fluid particle trajectories. One potential advantage of this approach, however, is that three-dimensional PTV can be implemented with substantially greater ease than an equivalent DPIV technique. Furthermore, PTV has experienced significant refinements recently (Pereira et al. 2006; Ouellette et al. 2006). The extraction of three-dimensional fluid