

Dynamics and Energetics of Animal Swimming and Flying: Introduction¹

MALCOLM S. GORDON,² JAY R. HOVE,³ AND IAN K. BARTOL

Department of Organismic Biology, Ecology, and Evolution, University of California, Box 951606, Los Angeles, California 90095-1606

SOME GENERAL ISSUES

A few broad general questions have been central to the study of the dynamics and energetics of animal swimming and flying since the field began. A partial list includes:

1. What are the biomechanical bases for swimming and flying in the various groups of animals?
2. What are the kinematic and kinetic bases for swimming and flying? How do the shapes and movements of involved body parts generate thrust, drag, lift, dynamic stability, and maneuverability?
3. What are the energy costs of swimming and flying?

This symposium approaches answers to these questions from multiple directions.

Four primary sets of technological developments have come together in the past decade to make it possible to revisit each of these questions in innovative, quantitative ways. These developments are: a) high-speed digital video photography; b) algorithms for rapid analysis of digital images; c) laser based quantitative flow visualization techniques (DPIV: digital particle imaging velocimetry); and d) algorithms for computational fluid dynamics (CFD).

Interdisciplinary collaborative investigations using these technologies, involving physiologists, functional morphologists, mathematical and physical modelers, and engineers, are producing refined and elegant analyses of the dynamics and energetics of animal movements through both compressible and incompressible fluids. This symposium presents state of the art reports from active participants in this work.

In recent years four important research-related trends have converged:

a) The technical developments cited have made possible many kinds of measurements that were previously obtainable only with great difficulty, if at all. Many of the papers included here are based upon use of these new techniques.

b) The field has been enriched by the recruitment of a substantial number of new, creative, active younger researchers. Many of these people are represented here.

c) There has been an increase in the availability of

research funds for these studies. As is often the case, this circumstance has resulted from the prospect of a range of significant new applications. A number of the papers included here refer to some of these interesting applications.

d) There is a trend toward increased openness on the parts of both some universities and some support agencies to new kinds of interdisciplinary or multidisciplinary collaborations. Most of the papers included here result from such collaborations.

RECENT BACKGROUND

This symposium highlights the rapid progress made recently in studies of animal swimming and flying, and the variety and significance of the new information obtained. It updates, complements, and supplements the proceedings of two other recent symposia.

A symposium entitled “Designs for life: the science of biomechanics” was presented at the March 1999 annual meeting of the Society for Experimental Biology (Altringham and Ellington, 1999). That symposium includes eight papers relating to topics also considered here.

A symposium entitled “Unifying principles in locomotion: water, land, and air,” was presented at the August 1999 5th International Congress of Comparative Physiology and Biochemistry (Boggs and Frappell, 2000). That symposium also includes eight papers relating to topics considered here.

THIS SYMPOSIUM

The papers presented here are grouped into three subject matter categories: quantitative flow visualization (6 papers); modeling and computational fluid dynamics (5 papers); and other issues, other approaches (3 papers).

QUANTITATIVE FLOW VISUALIZATION

The first six papers consider recent developments in DPIV technology and a sampling of applications of those methods. A particularly challenging aspect is that of visualizing flows in three dimensions (3-D). Three different approaches to achieving this goal are represented here: i) synthesis from multiple 2-D images; ii) visualizations of small volumes using stereo photographic methods; and iii) larger volume, whole field visualizations, using defocusing DPIV (DDPIV).

Gharib *et al.* (2002) describe the principles underlying DDPIV and provide several examples of its use in engineering studies. At its present stage of development the method has tremendous promise for help-

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² E-mail: msgordon@ucla.edu

³ Present address: Option of Bioengineering, California Institute of Technology, Pasadena, California 91125.

ing to definitively resolve a wide range of biologically important questions relating to animal swimming and flying. Efforts at making biological applications are just beginning.

The next four papers all use syntheses of multiple 2-D DPIV images to derive what may be called averaged or synoptic visualizations of fluid flows around and behind a variety of swimming animals, mostly fishes. The results are major advances over earlier studies using dye streams and other non-digital approaches to flow visualization. However, since they are syntheses of multiple serial sections of flow fields, averaging results from multiple events, they remain at best indications of the transient, non-steady state conditions that ultimately will be essential for full understanding.

Bartol *et al.* (2002) describe vortical flow patterns around dimensionally exact, rapid prototyped models of the bony carapaces (without fins) of four different groups of rigid-bodied, multi-propulsor ostraciid fishes. These fishes are primarily median and paired fin (MPF) swimmers. An unexpected result is that there are striking similarities between the flow patterns found and those that occur around the wings of delta-winged aircraft. This inference is supported by independent measurements on the models of both surface pressure distributions and force balance studies.

Muller *et al.* (2002) describe how body and caudal fin (BCF) swimming fishes, as exemplified by a species of mullet, vary thrust production in rectilinear swimming by varying slip ratios. Slip is the ratio between the swimming speed of the fish and the speed at which the undulatory waves powering swimming travel along the fish's body.

Videler *et al.* (2002) discuss scaling relationships between fluid flow patterns generated by moving animals of several kinds and the Reynolds numbers (Re) associated with the movements. They discuss two life history stages of a marine copepod, two early life history stages of a BCF swimming fish (zebrafish) using a burst and coast swimming mode, and a continuously swimming mullet. The range of Reynolds numbers represented is from less than 1 to above 10^4 .

Drucker and Lauder (2002) use visualizations of the wakes of BCF swimming rainbow trout and bluegill sunfish to begin estimating the hydrodynamic consequences of the differences between the two species in the positions and shapes of their pectoral fins. They find that the more dorsally located, more vertically oriented pectorals of the sunfish generate significantly higher forces for both turning and braking than do the more ventrally located, nearly horizontally oriented pectorals of the trout. The forces developed by the fins of the sunfish are also closer to the center of mass of the body than are those generated by the fins of the trout.

This section concludes with a description by Lauder *et al.* (2002) of early results of efforts at using high-resolution stereo-DPIV techniques for 3-D visualizations of flow fields in the wakes of median fins of BCF

swimming fishes. They present results from studies of rainbow trout, bluegill sunfish, and chub mackerel. Indications are that lateral forces generated are high relative to thrust forces and that the mechanical performance of median fins is relatively low. The soft dorsal of the sunfish also generates a thrust wake, and that wake may enhance thrust generation by the caudal fin when the wakes of the two fins interact.

MODELLING AND COMPUTATIONAL FLUID DYNAMICS

The next five papers use combinations of mathematical and physical models, including robotic models, and computational fluid dynamic approaches to consider a range of issues relating to energetics, dynamic control, and robotics.

Schultz and Webb (2002) revisit the perennial question of power requirements for swimming in fishes, especially BCF swimmers. The physical impossibility (at least to date) of directly measuring the forces generated by swimming fishes without substantially modifying either the fishes themselves or the hydromechanics of their swimming means that only indirect estimates of these forces are available. The best recent estimates of drag and thrust have not significantly reduced or eliminated the variability of those estimates with respect to equivalent rigid physical reference models. They suggest that the best measures of swimming performance are velocity and power consumption, and that 2-D inviscid simulations give realistic predictions. They estimate that steady swimming power is several times that required for towing an equivalent flat plate at the same speed.

Triantafyllou *et al.* (2002) discuss vorticity control as a major mechanism used by BCF swimming fishes and in fish-like robots to enhance performance in both rectilinear swimming and maneuvering. Experimental and numerical studies indicate that minimizing energy needed for BCF swimming involves mechanisms eliminating flow separations, reducing turbulence, and extracting energy from oncoming flows. They show that variation in fin flexibility is a basic mechanism for controlling vorticity.

Walker and Westneat (2002) consider important features of pectoral fin locomotion in labriform swimming fishes. They combine experimental and computational studies to investigate the dynamic, energetic, ecological, and evolutionary consequences of rowing using paddle-shaped fins as compared with flapping using wing-shaped fins in, respectively, the three-spine stickleback and the bird wrasse. The experimental results confirm some aspects of conventional wisdom relating to dynamics and energetics, but reject others. The computational results make several predictions relating to differences in maneuvering performance and swimming energetics between the two propulsive systems. These predictions imply certain things about the behavior and ecological distribution of fishes using the two systems. Laboratory and field studies of labrid swimming abilities and distributions support these predictions.

Daniel and Combes (2002) analyze an issue central to flight control in many animals using flapping flight. Significant bending and flexion of the wings accompany flight in these animals. To what extent is wing surface shape controlled by the mechanics of wing structure as compared with fluid dynamic loading? Using both computational and analytic methods they compare bending stresses arising from structural forces with those arising from fluid pressures within a widely varying parameter space. They conclude that fluid pressure stresses play a minor role in determining wing shape in almost all parameter combinations occurring in wings moving in air. They then show that modest changes in passive elasticity of wing structures can increase thrust for given levels of energy input.

In the last paper in this group Liu (2002) describes some of the results of a major research and development program in Japan that is based upon an integrated computational system for simulation-based biological fluid dynamics. That system has four primary subsystems: morphological modeling; kinematic modeling; CFD modeling; and post-processing for visualization. He presents results from two projects: a study of swimming by frog tadpoles and another of flapping flight in a hovering hawkmoth. He then briefly considers some implications of this work for the future development of micro air vehicles (MAVs).

OTHER ISSUES, OTHER APPROACHES

The final three papers consider a variety of other aspects of animal swimming and flying, focusing on a wider phylogenetic range of organisms.

Alexander (2002) discusses some elegantly simple models of the energetics of long distance migrations and of central place foraging, taking into account the speeds and energy costs of the journeys. He uses examples from the insects, fishes, birds, and mammals, involving a wide range of body sizes. Travel modes include flapping and soaring flight, swimming, and running. Conclusions are that, at least from the standpoint of energetics, long distance migrations are likely to be beneficial to only marine mammals and flying birds. These two groups are also the only ones likely to benefit from foraging over long distances. For the other groups observed migration and foraging ranges generally lie within the limits predicted by the models.

O'Dor (2002) summarizes major results from unique studies of the field energetics of cephalopod mollusks. He and his associates have developed transducer-transmitter combinations that fit within the mantle cavities of free-swimming cephalopods of several kinds. These transmitters have been calibrated against oxygen consumption in laboratory studies. They permit radio-acoustic positioning telemetry in the field of activity patterns and energy costs of wild animals behaving normally. Results indicate that cephalopods use their complex nervous systems to reduce high costs of jet propulsion by taking advantage of complex natural flow and density fields. A variety of life history adaptations are also important.

Weihers (2002) revisits an interesting question (which he first published on in 1980) relating to high-speed swimming in mammalian dolphins and their relatives. When travelling for longer distances these animals often porpoise—they alternate swimming under water close to the water surface with long, ballistic jumps. Field observations show that swimming bouts are about twice as long as the lengths of the leaps. Weihers calculates that, within certain ranges of speeds, it would be energetically more efficient for the animals to use burst and coast swimming, rather than continuous swimming, during the underwater stages.

FUTURE POSSIBILITIES

We are in the early days of a period that will see many different applications to studies of animal swimming and flight of the four technologies mentioned at the beginning of this introduction. How rapidly new knowledge will be acquired will depend heavily on several factors: a) cost—the new technologies involved are expensive both to acquire and maintain; b) user friendliness—the mathematical, engineering, and computer skills required to make effective use of these methods are not widely present in the biological research community; and c) existence of a supportive research climate for multidisciplinary, collaborative projects.

Success in these ventures will require recruitment of unconventionally trained, interdisciplinarily inclined scientists. These people will then be employed in research efforts that are likely to be structured more like large research groups in physics and chemistry, or molecular biology, rather than in the solo practitioner, small business-like entrepreneurial groups hitherto common in much of organismic biology.

The field is also likely to be dramatically further impacted by additional new technologies now emerging. The most obvious is that of nanotechnology. Applications of microscale detector and transmitter devices will surely make possible entire arrays of experiments and observations that are now impossible.

Another symposium on swimming and flying will be well justified within another few years. It will likely be as different from this one as this one is from the two other symposia cited earlier that took place in 1999.

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