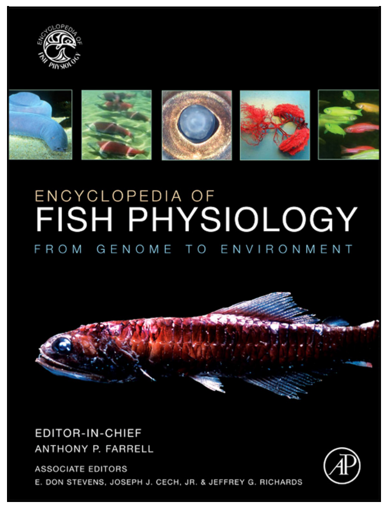

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Experimental Hydrodynamics

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Glossary

Acceleration reaction A synonym for the added mass effect. See added mass.
Added mass The effect in which accelerating bodies in a fluid appear to have additional mass. It is also called the acceleration reaction. The body can be a solid immersed in the fluid, or a coherent region of the fluid itself (see Lagrangian coherent structure).
Added mass coefficient The amount of added mass relative to the body's own mass (units: dimensionless).
Circulation A measure of the total amount of vorticity in an area of fluid bounded by a loop (units: $m^2\ s^{-1}$).
Flow tunnel Also called a flume. A device that produces a constant, even fluid motion. It is often used for studying steady swimming in fishes, so that a fish can swim at a steady speed against the flow, but remain stationary relative to a camera or other measuring devices.
Impulse The total force applied over a time period. The integral of force with respect to time (units: $kg\ m\ s^{-1}$).
Kinematic viscosity The ratio of viscosity and density (μ/ρ) (units: $m^2\ s^{-1}$). At 20 °C, water's kinematic viscosity is $1.004 \times 10^{-6}\ m^2\ s^{-1}$.
Lagrangian coherent structure A region of fluid that tends to remain together. There may be fluid motion inside and outside of the region, but fluid moving inside the region tends to stay inside, while fluid outside tends to stay outside.
Laminar flow Flow in which parallel portions of the fluid (laminae) move steadily past each other. Laminar flow does not preclude the presence of vortices (see turbulent flow).
Particle image velocimetry A technique for revealing complex patterns of flow in a fluid by automatically tracking the motion of suspended particles.
Reynolds number The ratio of inertial to viscous forces in a flow.
Shear Differences in parallel flow velocity between two points. For example, if fluid is moving from left to right parallel to a wall at one speed and at a different speed (but still parallel to the wall) further from the wall, then there is shear between those two points.
Turbulent flow Complex, disordered flow that contains eddies or vortices of many different sizes and structures. Vortex flow is not necessarily turbulent (see laminar flow).
Viscosity The ease with which a liquid will flow under an applied pressure; molasses is more viscous than water.
Vortex A mass of fluid in whirling or circular motion. Vortices always appear where hydrodynamic lift is being generated.
Vortex filament An imaginary line around which fluid rotates, produced by tracing along the vorticity vector. Vortex filaments cannot have free ends; they must terminate on solid boundaries or loop around back onto themselves.
Vortex ring A three-dimensional fluid structure in which a vortex forms a loop.
Vorticity A point measure of how much the fluid at a point is rotating. In three dimensions, vorticity is a vector that defines the axis around which the fluid is rotating; the length of the vector is proportional to the angular velocity. Generally, vorticity is only produced when a force is applied to a fluid (units: s^{-1}).
Wake The moving fluid left behind after an object moves through a region of fluid. It is only present at high Reynolds number. Flow patterns in wakes can be used to estimate forces and power around an object.

Introduction

Fish physiologists use experimental hydrodynamics techniques to visualize and quantify the way water moves around swimming fishes. The water motion provides information about the forces that fishes generate as they interact with their environment, for instance, during locomotion (**see also Buoyancy, Locomotion, and Movement in Fishes**: Undulatory Swimming) and feeding (**see also Buoyancy, Locomotion, and Movement in**

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Fishes: Feeding Mechanics). These flows and associated pressure waves also provide information to other aquatic animals (**see also Hearing and Lateral Line**: The Ear and Hearing in Sharks, Skates, and Rays), and are therefore important for group behaviors such as schooling and for predator–prey interactions. Finally, environmental flows, such as eddies in a stream or wave motions around reefs, also produce forces to which fishes must adjust, either compensating for them or, in some cases, extracting energy from them (**see also Buoyancy, Locomotion, and Movement in Fishes**: Stability and Turbulence). This article introduces basic principles of fluid dynamics, some standard techniques for measuring fluid flows, and several methods for interpreting flow fields (**See also Buoyancy, Locomotion, and Movement in Fishes:** Buoyancy, Locomotion, and Movement in Fishes: An Introduction).

Basic Fluid Dynamic Principles

A fluid is different than a solid because it has no defined shape. Consider a block of rubber. If the bottom was fixed and a force was applied parallel to the top (called shearing the block), the block would resist the force, and the force would be proportional to how far you sheared it (θ in **Figure 1(a)**). Now imagine doing the same thing to a block of fluid. The fluid can be deformed forever, so the amount of shear is irrelevant, but the speed at which you shear the block matters. The fluid velocity would vary throughout the block from 0 at the bottom to V at the top (**Figure 1(b)**). The amount a fluid resists shear rate is called its viscosity, denoted μ. Fluids such as honey and motor oil are highly viscous, while water and alcohol are less viscous.

Thus, viscosity tends to make fluids stick together. If two blobs of fluid (1 and 2 in **Figure 2**) are moving at different speeds, viscosity will resist the shear between them and tend to equalize their speeds. The opposite effect is inertia, the mass of the blobs of fluid. If the blobs are relatively large or moving quickly, then the viscous forces on them will have a small effect, and they will carry on moving at their separate velocities. The relative importance of inertia and viscosity is called the Reynolds number Re (the symbols used in this article are explained in **Table 1**):

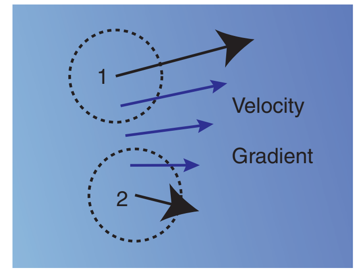

Figure 2 Definition of Reynolds number. Two blobs of fluid with different velocities (black arrows labeled 1 and 2). Viscosity will tend to equalize the velocity gradient between them (blue arrows), while the blobs' inertia will tend to keep their velocities different. Reynolds number is the ratio of inertial forces to viscous forces.

$$Re = \frac{\rho l U}{\mu} \quad (1)$$

where ρ is the density of the fluid, l a length, and U a velocity. The length and velocity are intentionally vague. The proper choice depends on the specific situation, but, in general, high Reynolds number ($Re >> 1$, which, in practice, means greater than 100 or so) means that viscosity is not very important. Reynolds number is also often written using the kinematic viscosity ν as

$$Re = \frac{lU}{\nu} \quad (2)$$

Re is only useful as an order of magnitude. One must choose an approximate length l and velocity U that are representative of lengths and velocities of interest. For instance, for a 10-cm fish swimming at 1 body length (L) per second, the scale of fluid motions is approximately the length of the fish and velocities are near the swimming speed. Re is thus $[(1000\ \mathrm{kg\ m^{-3}}) \times (0.1\ \mathrm{m}) \times (0.1\ \mathrm{m^{-1}\ s})]/(1 \times 10^{-3}\ \mathrm{Pa\ s}) = 10\ 000$. If the fish were swimming at $1.5\ L\ \mathrm{s}^{-1}$, it would not be much more informative to write $Re = 15\ 000$, because the order of magnitude is still the same.

High Reynolds number flow has several important consequences, listed as follows:

1. Fluid motions persist for some time. If a force starts a blob of fluid moving, then the inertia of the blob will keep it moving for a while, even after the force has stopped. Thus, at high Re, one can learn about forces on

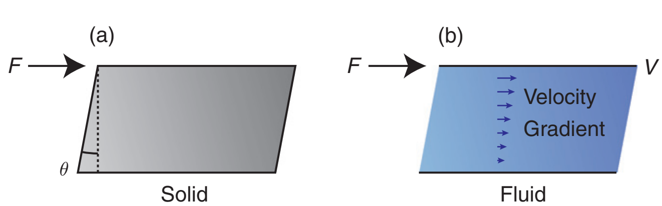

Figure 1 Differences between solids and fluids. Solids resist the amount of shear (θ), while fluids resist the shear rate ($\dot{\theta}$), which sets up a velocity gradient between the top and bottom.

Table 1 Symbols used in the article

Γ,	Circulation
δ,	Spacing between fluid velocity measurements
μ,	Viscosity
ρ,	Density
Σ,	A surface in a fluid
ω,	Vorticity vector
ω_z,	Component of the vorticity vector in the *z*-direction
a,	The thickness of a vortex ring along its central axis
A,	An area, usually the wetted surface area or the cross-sectional area
C,	A contour surrounding a vortex along which velocity is integrated to calculate circulation
d,	Diameter of a vortex loop in the horizontal plane
$\mathbf{C}_A$,	Added mass coefficient tensor
C_A,	Added mass coefficient for acceleration and force along the same axis
C_F,	Force coefficient. Normalized force relative to the swimming speed and body size
I,	Impulse vector
F,	Force vector
$\mathbf{F}_{mean}$,	Mean force vector
h,	Height of a vortex loop or a wake in the vertical plane
l,	Length (generally body length)
l,	Tangent vector along the contour *C*
L,	Body length of a fish
P_{thrust},	Thrust power
P_{wake},	Wake power; change in kinetic energy in the wake
Re,	Reynolds number
S,	Volume of an LCS
T,	Time period, usually half the tail beat period
u,	Velocity vector
U,	Speed (generally swimming speed)
U_V,	Velocity of an LCS as a group
u,	Component of the velocity vector in the *x*-direction
v,	Component of the velocity vector in the *y*-direction
w,	Component of the velocity vector in the *z*-direction
Wa,	Wake vortex ratio; ratio of unsteady effects to steady forces for an LCS

a body, such as a fish, by studying its wake, the moving fluid left behind after the body has moved past. In contrast, at low *Re*, any fluid motion requires force, and as soon as the force stops, the fluid stops too.
2. Vortices may be present. A vortex is a rotating piece of fluid that usually places shear stress on the fluid. Vortices are directly related to force in a fluid, and, at the limit of infinitely high *Re*, they persist forever. Thus, they are useful for studying forces produced in a fluid.
3. Flow may be turbulent. Turbulence is a poorly understood phenomenon in which flow becomes complex and irregular. Turbulence changes many of the standard rules of thumb of fluid dynamics, such as drag and lift coefficients, so one must be careful when studying turbulent flows.

Vorticity

Vorticity is a measure of how much a very small blob of fluid is rotating. Rotation is important because it is strongly related to force. In general, a force must be applied to a fluid to produce vorticity.

Vorticity is a point measure. Imagine putting a very thin rod into a fluid, and consider whether it will rotate, independently of its translational motion. Vorticity is non-intuitive: a vortex usually, but not always, has vorticity, and vorticity may be present in flow that does not appear to be rotating, such as a shear flow (Figure 3). Mathematically, vorticity ω is the curl of the velocity field:

$$\omega = \nabla \times \mathbf{u} \tag{3a}$$

$$= \left(\frac{\partial u_z}{\partial y} - \frac{\partial u_y}{\partial z}, \frac{\partial u_x}{\partial z} - \frac{\partial u_z}{\partial x}, \frac{\partial u_y}{\partial x} - \frac{\partial u_x}{\partial y} \right) \tag{3b}$$

written concisely using the curl operator in eqn (3a), or explicitly in eqn (3b). Vorticity ω is itself a vector, and defines the axis around which fluid is rotating, according to the right-hand rule. For example, the vorticity vector in Figure 3(a) is pointing out of the page toward the reader, while the vector in Figure 3(c) is pointing into the page away from the reader. For two-dimensional (2D) flows, such as those pictured in Figure 3, the first two components of ω are 0; figures therefore often depict only the *z*-component as a contour map.

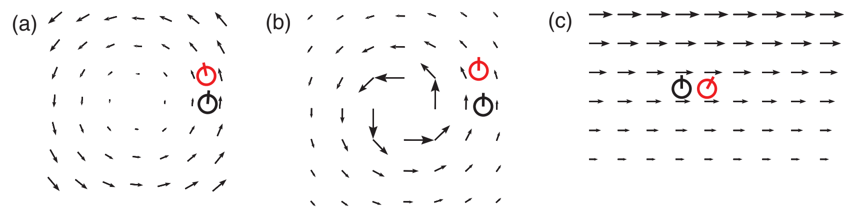

Figure 3 Examples of flow patterns with and without vorticity. In each case, the black circle represents an imaginary rod inserted into the **flow**, and the red circle indicates its position and orientation after some time has passed. (a) Swirling flow with vorticity. The red circle is rotated relative to the black circle. (b) Swirling flow without vorticity. The flow velocities decrease with radius so that the imaginary rod translates around, but does not rotate. Vorticity is zero at all points in this flow except for single point at the center. (c) Shear flow with vorticity. The imaginary rod translates and rotates, indicating vorticity.

One must remember, though, that real vorticity is 3D. In particular, if one follows the vorticity vectors, they define a vortex filament – a line around which fluid rotates. Vortex filaments cannot have free ends; they must either loop back on themselves or end at a solid boundary. The most common real 3D vortex structure, therefore, is a vortex ring, a circular vortex filament (**Figure 4**).

Added Mass

Fluids have one more strange effect that is prominent at high *Re*: the phenomenon of added mass, also termed the acceleration reaction. Accelerating bodies in a fluid behave as if they have some additional mass. In essence, added mass is the consequence of the fact that the fluid itself has mass. Accelerating a body in a fluid requires force to accelerate the body, and also some additional force to accelerate some fluid that surrounds the body. The acceleration reaction does not only affect solid bodies; it can also become important in unsteady flows without any solid bodies. If a blob of fluid accelerates, it also has added mass, which must be accounted for if one wants to estimate the force required to accelerate the blob.

Measuring Fluid Velocities

At any point in a moving fluid, the fluid has a speed and a direction in three dimensions. Generally, the motion at that point is represented by a vector (u, v, w), where u, v, and w are the speeds of the motion along the x, y, and z axes, respectively. The (u, v, w) vector is defined at every (x, y, z) coordinate in the fluid; therefore, the flow velocity is called a vector field. The magnitude of the vector $\left(\sqrt{(u^2 + v^2 + w^2)}\right)$ is the flow speed.

Techniques used for experimental hydrodynamics experiments fall into several classes, based on whether they make measurements at a single point or at many points in a plane or a volume, and what they measure at the point or points (i.e., the speed of the flow, or two or three components of the velocity vector). 1D techniques include hot wire anemometry and acoustic Doppler velocimetry, but neither of these are commonly used for studying fish. The most common technique is particle image velocimetry (PIV), a planar (2D) technique. Several fully volumetric (3D) methods are becoming more common.

Once velocities are estimated, derivative quantities such as vorticity can be estimated using standard

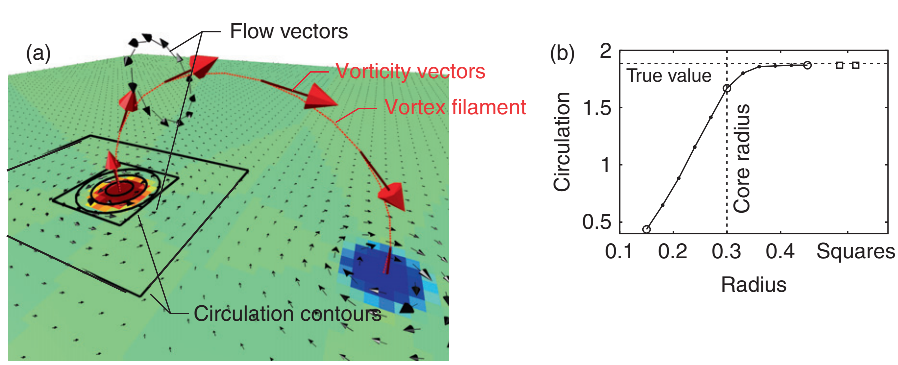

Figure 4 (a) 3D view of a vortex ring. Velocity vectors are shown in black and vorticity vectors are shown in red. Velocity vectors are shown only in the horizontal plane and in one example loop. The horizontal colored plane shows the z-component of the vorticity vector ω; red and blue indicate positive and negative values for ω_z, respectively. The central vortex filament is a red dashed line and it continues in a loop around under the horizontal plane. Several contours for estimating circulation are shown with thick black lines. (b) Circulation calculations. Circles show estimates for increasingly large circular contours, while squares indicate square contours. Open symbols indicate contours shown in (a).

numerical techniques. For planar measurements, such as PIV, with evenly spaced measurements of u and v on a grid with spacing δ between the measurements, out-of-plane vorticity can be approximated using a standard central difference technique as

$$\omega_z^{i,j} = \frac{1}{2\delta}\left[\left(v^{i,j+1} - v^{i,j-1}\right) - \left(u^{i+1,j} - u^{i-1,j}\right)\right] \qquad (4)$$

where $\omega_z^{i,j}$ is the z-component of vorticity at point (i, j), with i being the index that varies over the y values and j being the index that varies over the x values.

Particle Image Velocimetry

The technique called PIV is the most important experimental technique used for hydrodynamic measurements. It is a planar (2D) technique that can resolve the two components of the velocity vector that are in the plane. An important extension of the technique, called stereo PIV, can resolve all three velocity components but is still restricted to a planar measurement region.

Figure 5 shows a drawing of a typical PIV configuration. The water is seeded with small, reflective particles, and a strong light source, usually a laser, is used to illuminate a plane. A laser beam can be spread out to produce a plane using a cylindrical lens (shaped like half a cylinder) or a Powell lens (shaped like a house). One or more cameras are used to film the motion of the particles, and a computer algorithm is used to estimate the distance the particles have moved between two frames of the video.

For PIV to estimate fluid velocities accurately, the particles must not move too little or too much between frames. For a given average flow velocity, there are two main methods to ensure that the particle displacement is appropriate.

1. Use a continuous laser and adjust the frame rate of the camera (Figure 6(a)). Often this method requires a high-speed camera to achieve high-enough frame rates so that the particles do not move too far between frames. Because of the constant laser illumination, particle images may blur if the camera exposure time is too long. This is the most common method used for biological flows.
2. Use a pulsed laser and adjust the time between pulses (Figure 6(b)). Many of these systems use a double-pulsed laser, which can emit two pulses in rapid succession, but then have a relatively long delay before the next pair of pulses can be emitted. Pulsed lasers can often deliver large amounts of light in short amounts of time, which can be helpful to prevent particle blur. This method is more often used in engineering situations in which the flow is highly repeatable.

In recent years, a new generation of high-speed pulsed lasers have been developed, which combine the advantages of the two types of PIV systems.

Once the images are acquired, they must be processed to estimate the vector fields. The PIV algorithm does not track individual particles, because there are typically too many particles to identify specific ones reliably. Instead, it uses a technique called cross-correlation to estimate the average displacement of groups of particles (Figure 7). Each image is divided up into a grid of many small interrogation windows, and those windows are compared between two frames. The cross-correlation matrix indicates how well the images in the two windows match up when there is a slight offset between them (Figure 7(b)). The offset with the strongest correlation represents the

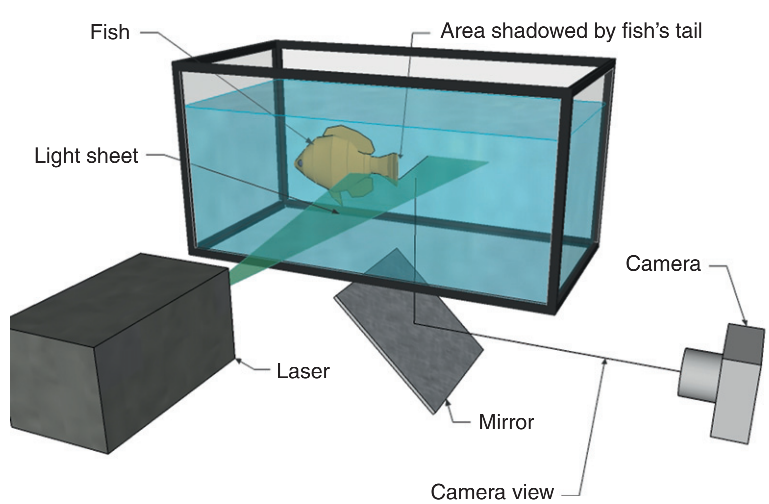

Figure 5 Schematic of a typical particle image velocimetry setup. A laser produces a horizontal light sheet, and a camera films the light sheet and fish from below. When the fish's tail is in the light sheet, it results in a shadow. These experiments are often performed in a flow tunnel, so that the fish swims against a flow (from left to right in this image), maintaining position in the laboratory frame of reference.

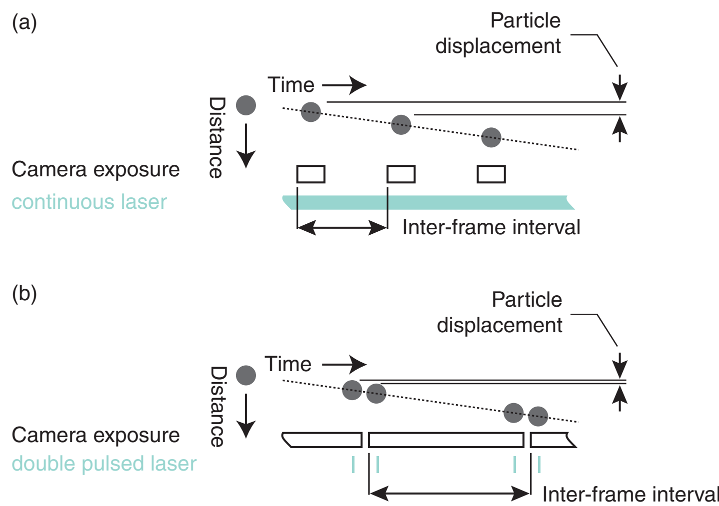

Figure 6 Schematic of the timing for two different PIV configurations. Panels show a particle (gray circle) as it moves over time along the dotted line. The open boxes indicate the camera exposure and the green bars indicate when the laser is on. Particles are shown only when the camera shutter is open and the laser is on. (a) With a high-speed camera and a continuous laser, the particle displacement may be relatively large, but the time between frames (inter-frame interval) is short. (b) With a normal camera and a double-pulsed laser, the particle displacement can be very small, but the inter-frame interval is often large.

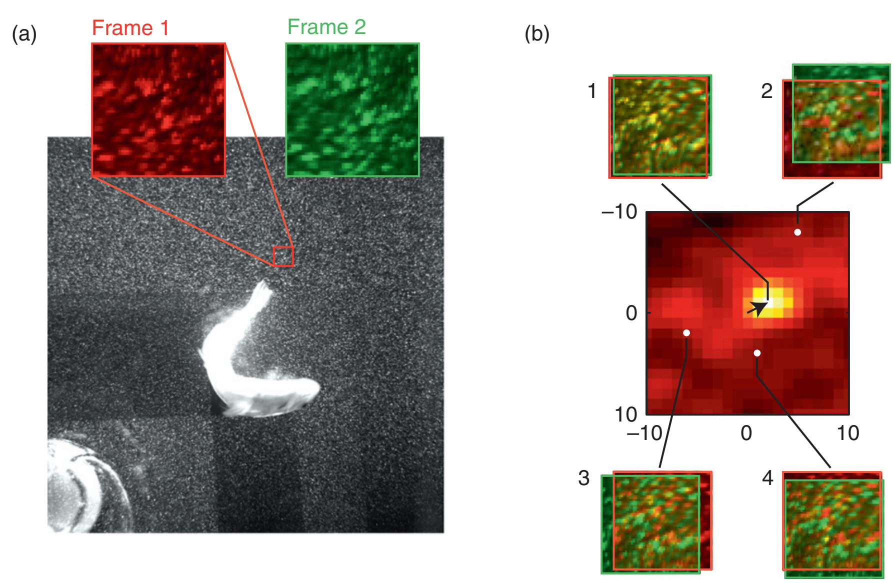

Figure 7 Example of the cross-correlation technique used to estimate velocity vectors for PIV. (a) Typical PIV image, with an interrogation window identified in red. The same window from the next frame is shown in green. (b) Example cross-correlation of the two windows. The center image shows the cross-correlation matrix, where hotter colors indicate greater correlation. The peak correlation is offset from the center by 3 pixels right and 2 pixels up, which is the best estimate of the average motion of particles in that window between frames. Around the cross-correlation are examples of the overlap between the two interrogation windows at different offsets. The windows are again in red and green, and regions where they overlap well show up as yellow.

average displacement of the particles (Figure 7(b1)). Most modern PIV systems now use a technique called super-resolution PIV, in which the cross-correlation technique runs several times, starting first with a fairly coarse grid, then repeating the algorithm with a finer grid that uses the previous results as a starting estimate. In this manner, very large numbers of vectors can be estimated.

An extension to the standard PIV technique is stereo-PIV, which uses two cameras at an angle to the light sheet to estimate the two in-plane velocity components, as well as the through-plane component. Besides the fact that it produces 3D velocity estimates, stereo-PIV has several other advantages. First, it is often able to correct errors better than normal PIV. Second, stereo-PIV calibration usually implicitly corrects lens distortion from the cameras.

Because fluid moves in three dimensions, planar PIV techniques require measurements in multiple planes or assumptions about the flow structure to generate 3D approximations of the flow. For example, counter-rotating vortex pairs are often assumed to be parts of the same vortex ring (**Figure 4**). **Figure 8** shows two examples of horizontal planes behind a swimming American eel (*Anguilla rostrata*) and a bluegill sunfish (*Lepomis macrochirus*), along with the simplest possible 3D reconstruction. Wakes of American eels are consistent with two unlinked vortex rings shed per tail beat (Fig. 8C), while the wakes of bluegill sunfish appear to have two linked loops per tail beat (Fig. 8D). One must be careful about these simple reconstructions. The bluegill sunfish's wake does have two linked vortex loops, as hypothesized in Fig. 8D, but the loops are not circular, and they interact in a complex way with vortices shed off the dorsal and anal fins. **Figure 9** shows a reconstruction of the bluegill sunfish's wake based on measurements made in multiple transverse planes.

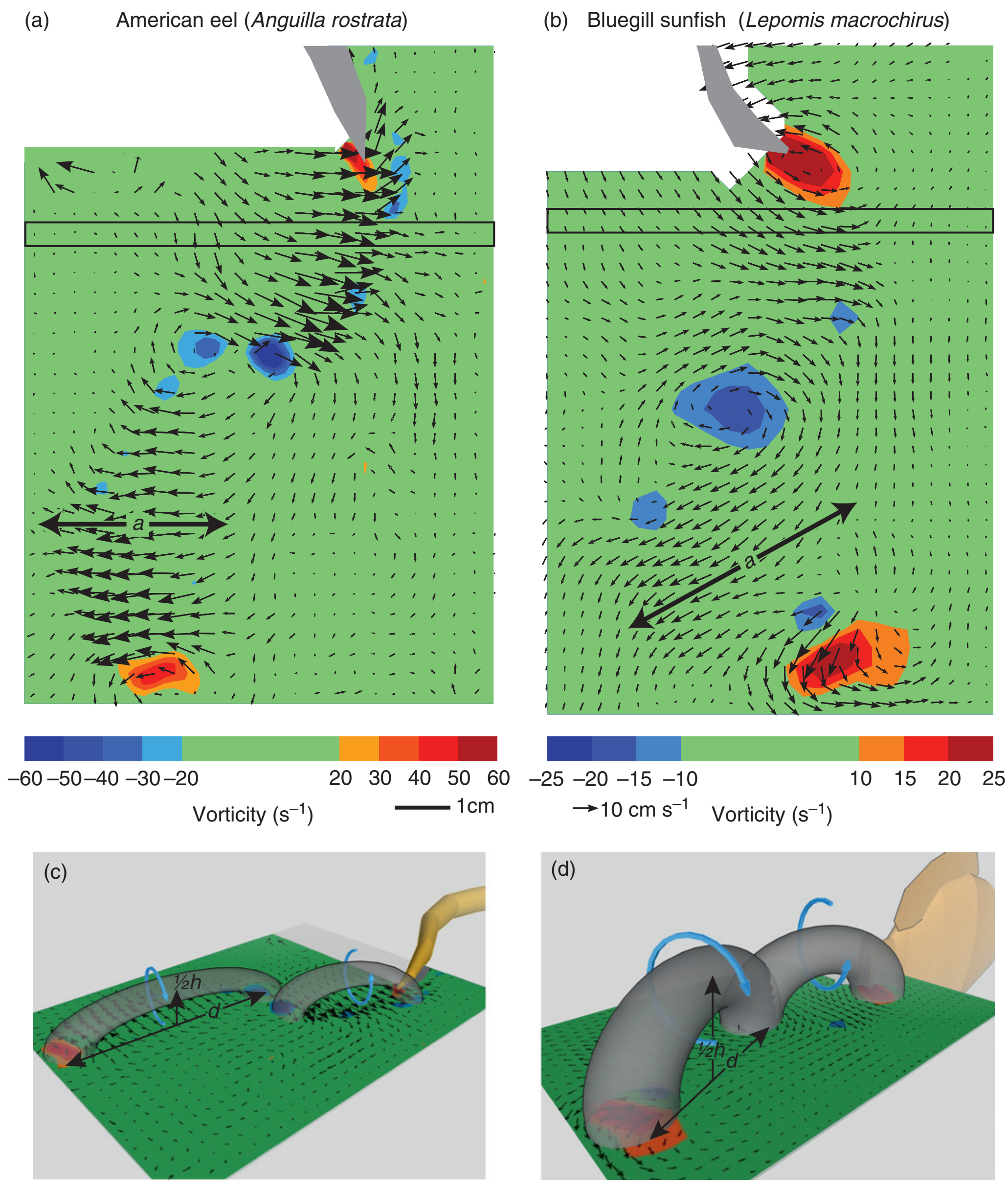

Figure 8 Examples of wake flow in horizontal planes behind an American eel and a bluegill sunfish, each swimming at approximately 1.9 Ls^{-1}. (a, b) Flow patterns near the end of a tail beat cycle. Velocities are given with black arrows, and vorticity is shown in color. Note that length and vector scales are the same, but the vorticity scales are different. The black box indicates the region used for power calculations. (c, d) Simplest 3D flow structure consistent with the wakes shown. Transparent gray tubes indicate vortex loops, and light blue arrows show 3D flow. Thick arrows show the diameter and half height of the vortex loops. (a, b) Modified from Tytell ED (2007) Do trout swim better than eels? Challenges for estimating performance based on the wake of self-propelled bodies. *Experiments in Fluids* 43(5): 701–712.

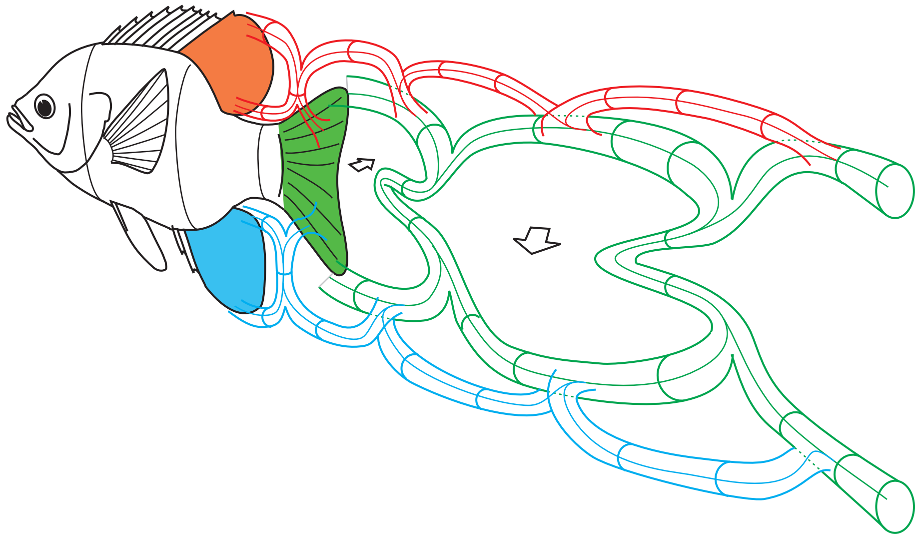

Figure 9 Schematic of 3D flow in the wake behind a bluegill sunfish, while the fish is swimming at 1.2 Ls^{-1}. Green loops show vortices shed off the caudal fin, while red and blue show those shed off the dorsal and anal fins, respectively. Note that the green loops are not circular. Modified from Tytell E (2006) Median fin function in bluegill sunfish. *Lepomis macrochirus*: Streamwise vortex structure during steady swimming. *Journal of Experimental Biology* 209: 1516–1534.

Volumetric Techniques

The oldest technique, dye flow visualization, is a volumetric technique, meaning that it resolves flow structures in a volume. Dye is injected into the flow and filmed as it follows the local fluid motion. Generally, dye tends to become concentrated near the center of vortices, but not always, which means that results need to be interpreted carefully. Dye images provide qualitative results about flow structure; for quantitative measurements of flow velocity, one must use other techniques. In addition, the fact that dye can move in three dimensions throughout a volume can make it challenging to interpret the images, particularly if only one camera is used. Some groups have used a planar light source, like those used for PIV, to illuminate a single plane of dye, which simplifies interpretation, but means that measurements are only available in that plane. Despite these limitations, dye can be quite useful for identifying the general structure of a flow or showing how two regions of flow mix.

Recently, two quantitative volumetric techniques, holographic PIV and defocusing PIV, have become feasible for biological fluid dynamics. Both of these techniques require a laser or lasers to illuminate a volume brightly and evenly. Holographic PIV relies on the interference between two beams of light to reconstruct 3D images of particles or bodies in the fluid. From these images, flow velocities can be estimated in a variety of ways. One method is to use computational techniques to estimate planar slices of the volume, which can then be analyzed using similar methods as 2D PIV. One form of defocusing PIV uses a single camera with a special lens with three apertures aligned in a triangle. A single particle thus produces three images in a triangle; the center of the triangle represents the position of the particle parallel to the camera, and the size of the triangle represents the particles distance away from the camera. The equipment and software necessary to implement defocusing PIV is now available commercially.

Interpreting Flow Fields

Force

In most cases related to fish locomotion, researchers who study fluid flow are interested in using their measurements to estimate forces on the fish's body. There are two general ways to estimate forces in a fluid, one based on fluid momentum that is best suited to rapidly changing or unsteady flows, and one based on fluid vorticity that is best for steady flows and time-averaged forces.

In both cases, one first estimates impulse **I**, the integral of force **F** applied to the fluid over time, or, more usefully, the mean force $\mathbf{F}_{\text{mean}}$ applied to the fluid multiplied by the total time T over which it was applied:

$$\mathbf{I} = \int_0^t \mathbf{F}\,\mathrm{d}t \tag{5}$$

$$= \mathbf{F}_{\text{mean}}\,T \tag{6}$$

One can then divide **I** by T to obtain mean force, or take the derivative to estimate instantaneous force:

$$\mathbf{F} = \partial\mathbf{I}/\partial t \tag{7}$$

Forces can be compared across different size or shape animals by estimating a force coefficient C_{F}:

$$C_F = F/[\frac{1}{2}\rho A U^2] \quad (8)$$

where A is the area of the body, usually either the wetted surface area or the cross-sectional area, and U the swimming speed. This normalization takes into account the fact that larger or faster animals generally produce more force, and allows one to ask the question, "If the body shapes and swimming speeds were the same, would these two animals produce the same forces?"

Vortex analysis

The amount of vorticity in an animal's wake is also related to the impulse on the animal. To estimate impulse, researchers often do not use vorticity directly, but use circulation, another measure of rotation strength. It is the total vorticity within an area circumscribed by a closed loop, such as the black loops shown in **Figure 4**.

For a steadily moving vortex ring, the procedure to estimate the force that generated it is quite straightforward. Any sufficiently large loop that passes through the center of a vortex ring has a constant circulation (**Figure 4(b)**) that is proportional to the force required to generate the ring:

$$F_{\text{mean}} = \frac{1}{4}\frac{\pi\rho\Gamma d h}{T} \quad (9)$$

where ρ is the density of the fluid, Γ the circulation, d the distance between the two vortex centers in the plane, and h an estimate of the out-of-plane height of the loop (see **Figure 8** for examples of h and d). For example, a good rough estimate for h for a ring shed by the caudal fin is the height of the fin itself. T is the time over which the two counter-rotating vortices were shed, generally half of the tail or fin beat cycle. Mathematically, circulation Γ can be written in two equivalent ways:

$$\Gamma = \int_{\Sigma} \omega \cdot \mathrm{d}\Sigma \quad (10)$$

$$= \oint_C \mathbf{u} \cdot \mathbf{dl} \quad (11)$$

where $\sum$ is a surface in the fluid, C the closed contour around the edge of the surface (thick black lines in Fig. 4), and l the tangent vector along the contour. The second form of the expression for circulation is important experimentally, because it allows one to estimate circulation without taking any derivatives of the velocity field. Taking derivatives tends to introduce numerical error, so the second form (eqn (11)) is often more accurate.

Momentum analysis

Newton's laws tells us that force is equivalent to change in momentum, and that, for any force on the body, there is an equal and opposite force on the fluid. Thus, in principle, one could simply measure the change in momentum in the fluid, which should be equal and opposite to the force on the animal.

For a solid body whose mass is not changing, this procedure is the familiar $F = ma$. In a fluid though, the volume of fluid affected may change, and thus m is not constant. To estimate change in fluid momentum, therefore, one must use three steps: (1) determine the volume of fluid affected by the force, (2) find the mean fluid velocity in that volume, and (3) include the effect of added mass.

1. Determine the volume. Some analyses have performed this step manually, but recently, a technique has been developed to identify what are called Lagrangian coherent structures (LCSs): volumes of fluid that tend to stay together. For example, if a fish's fin accelerated some fluid, one can track the volume of accelerated fluid as it grows and moves over time by using an LCS analysis.
2. Mean LCS velocity. Once the volume **S** has been determined, estimate the velocity U_v that the LCS itself is moving. Note that this velocity is not necessarily equal to the mean velocity of the fluid in the volume.
3. Added mass. Estimate the added mass coefficient tensor $\mathrm{C_A}$ for the volume, which will depend on the shape of the fluid volume, but not its velocity. For linear forces, the added mass tensor is a 3×3 matrix giving the added mass effect along each axis for acceleration along the same or a different axis. For complex bodies, the acceleration reaction may produce counter-intuitive forces, not necessarily parallel to the acceleration itself. However, we will simplify and consider only force and acceleration along the same axis, giving a scalar added mass coefficient C_A. For symmetric bodies or volumes of fluid, this approximation is appropriate.

The force on the animal corresponding to the changing fluid momentum is thus the opposite of the time derivative of the impulse required to produce the motion of the volume S:

$$F = -\frac{\partial}{\partial t}[\rho S(1 + C_A)U_V] \quad (12)$$

Figure 10 shows an example of this force calculation. The LCS around the bluegill sunfish's pectoral fin is estimated during one fin beat (**Figure 10(a)**). The vertical (lift) force is estimated, and the relative importance of the changes in velocity, volume, and added mass of the LCS are given (**Figure 10(b)**). Early in the cycle, changes in U_v are the dominant effect, while later in the cycle, the added mass coefficient C_A decreases, reducing the force.

Choosing vortex or momentum analyses

Since the tail and fins move back and forth, swimming is inherently unsteady; nevertheless, for swimming at a

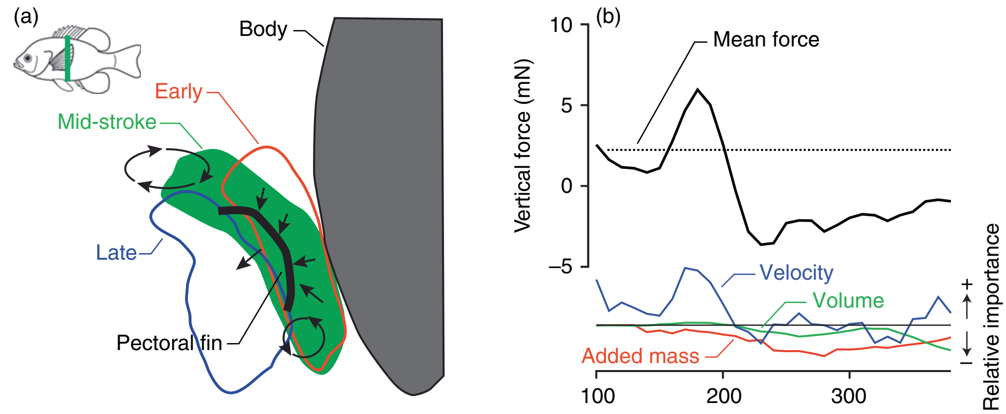

Figure 10 Example of a momentum analysis for the bluegill sunfish's pectoral fin beat. (a) Cross section through the fish body and pectoral fin. Schematics of the fin and flow are shown at mid-stroke with a thick black line and black arrows, respectively. The volume of fluid affected by the fin is shown in green for mid-stroke (same time as the fin and flow schematic), red for early in the stroke, and blue for late. Inset shows the position of the cross section. (b) Force estimates. Top panel shows the instantaneous force estimate based on the LCS calculations in (a), along with a mean force estimate (dotted line). Bottom panel gives the relative importance of the changes in LCS velocity, volume, and added mass to the force estimate. Early in the stroke, changes in velocity are the most substantial effect, contributing to positive force, whereas later in the stroke, changes in added mass become more influential, decreasing the total force. Modified from Peng J, Dabiri JO, Madden PG, and Lauder GV (2007) Non-invasive measurement of instantaneous forces during aquatic locomotion: A case study of the bluegill sunfish pectoral fin. *Journal of Experimental Biology* 210(4): 685–698 and Drucker EG and Lauder G (1999) Locomotor forces on a swimming fish: Three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *Journal of Experimental Biology* 202: 2393–2412.

steady average velocity, the vortex analysis described above is often sufficient and is much simpler to apply. For instance, in **Figure 10(b)** the time-averaged mean force matches the vortex analysis.

The relative importance of unsteady effects can be determined by the wake vortex ratio *Wa* as described by Dabiri:

$$Wa = \frac{C_A S U_V}{\Gamma} \tag{13}$$

which relates the observed vortex motion to the motion that one would expect if there were no unsteady forces. When *Wa* is very large or very small, the added mass forces are either speeding up or slowing down the vortex and an unsteady, momentum-based analysis is best. When *Wa* is near a critical value, either approach is correct, but the time-averaged vortex analysis may be simplest. For a vortex analysis (eqn. (9)) to be valid, the following condition serves as a rule of thumb:

$$Wa_{\text{crit}} = \frac{C_A}{1 + C_A} \tag{14}$$

If *Wa* is substantially above or below Wa_{crit}, then the momentum-based analysis is most appropriate.

For the purposes of estimating *Wa*, the added mass of a vortex ring can be approximated by that of a solid prolate spheroid. Choose the largest diameter $d_{\max}$ (*b* or *d* in **Figure 8**, whichever is larger) and estimate the thickness of the loop (*a* in **Figure 8**). **Figure 11** shows added mass as a function of the thickness/diameter ratio $a/d_{\max}$. Then estimate the mean circulation of the two vortex cores and the speed U_v that the whole loop is moving along its axis and use eqns (13) and (14) to determine the importance of unsteady effects. For

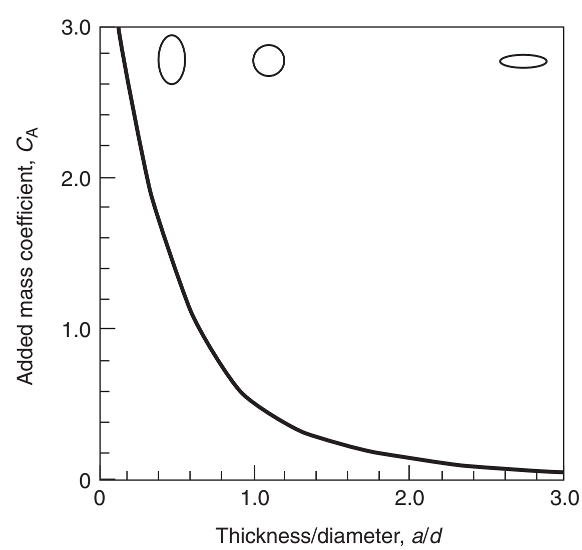

Figure 11 Theoretical added mass coefficients as a function of the thickness/diameter ratio of prolate spheroids, which approximate those of the LCS surrounding a vortex ring. Thickness *a* is the axis parallel to the motion of the ring, while diameter *d* is the largest diameter between vortex cores. Reproduced form Daniel TL (1984) Unsteady aspects of aquatic locomotion. *American Zodogist* 24: 121–134.

example, in Figure 10. Wa is between 0.2 and 0.4, while $C_A/(1+C_A)$ is about 0.4. Thus, the vortex analysis is appropriate.

Power

Another useful metric for analyzing a wake is the hydrodynamic power contained in the wake, P_{wake}. This power is one component of the total propulsive power, $P_{total} = P_{thrust} + P_{wake}$. A perfectly efficient swimmer would somehow manage to devote all of its power to thrust and would leave no wake. Real swimmers are not perfectly efficient, and therefore they leave a wake. The thrust power P_{thrust} is difficult to estimate, particularly for steadily swimming fishes, but P_{wake}, which can be quantified in a fairly straightforward manner, can be used as a proxy measure for inefficiency. Higher P_{wake} values are indicative of low efficiency, though they are not conclusive.

Because power is change in kinetic energy; wake power is estimated by adding up the kinetic energy of the fluid that enters and leaves a volume that surrounds the fish. For a wake measurement, such as those in Figure 8, one must have a sufficiently wide cross section across the wake that the fluid momentum added by the animal decreases to zero at the edges. The large width means that we can assume that there is no flow through planes parallel to the swimming direction of the fish. Ideally, one would also have a cross section upstream of the fish, although this can usually be estimated from the mean swimming speed (equal to the flow speed in a flow tunnel). The planes form a control volume. The net power that the fish adds to the fluid is the rate kinetic energy enters the upstream cross section, minus the rate it leaves the downstream cross section.

$$P_{wake} = \frac{1}{2}\rho h U \int (2Uu + u^2 + v^2)\,dy \qquad (15)$$

where h is the approximate height of the wake (usually equal to the height of a fin or the body), U the mean swimming speed or mean flow speed, u and v the fluid velocities added by the fish in the x and y directions, and where it is assumed that the upstream flow has a constant velocity U. Power can be normalized in a similar way as force (eqn (8)):

$$C_P = P/[\frac{1}{2}\rho A U^3] \qquad (16)$$

Figure 12 shows an example comparing wake power coefficients for American eels, rainbow trout (*Oncorhynchus mykiss*), and bluegill sunfish. Note that sunfish have the most costly wake, suggesting low swimming efficiency compared with American eels swimming slowly (0.5 Ls^{-1}) or rainbow trout swimming rapidly (~2 Ls^{-1}).

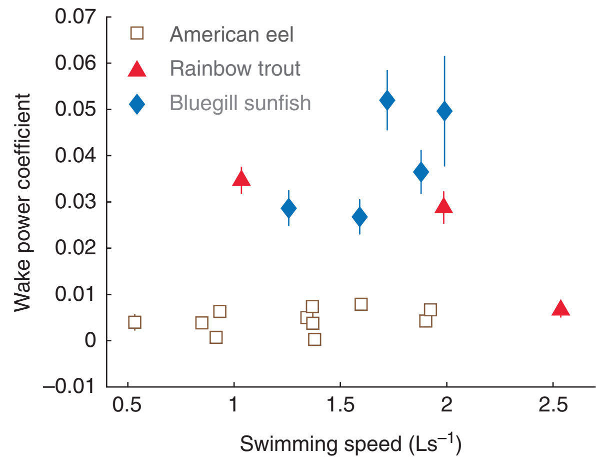

Figure 12 Wake power coefficients plotted against swimming speed for American eels, rainbow trout, and bluegill sunfish. Error bars indicate standard error; where they are not visible the symbol is larger than the error range. Modified from Tytell ED (2007) Do trout swim better than eels? Challenges for estimating performance based on the wake of self-propelled bodies. *Experiments in Fluids* 43(5): 701–712.

Future Developments

Much of this article has dealt with 2D flow fields, because these are currently the most common and easiest to measure. In the future, 3D measurements will become more common. Techniques such as defocusing PIV and holographic PIV are starting to be available commercially. In interpreting 3D flow fields is substantially more difficult than 2D fields. Nevertheless, the force and power analyses detailed above are applicable to 3D flows. In some ways, they are simpler to apply with 3D data, because one does not need to make assumptions about the 3D structure of the flow (e.g., the wake height h). At the same time, the flow data become much harder to visualize and understand. To help with this problem, it is likely that a class of techniques called dimensionality reduction methods will become much more important. These include principal orthogonal decomposition (POD) and biorthogonal decomposition (BOD), both of which are similar to principal components analysis, a technique commonly used to compare many different morphological measurements across fish species. Both techniques produce estimates of flow patterns that are the most coherent and energetically strongest. Then understanding the flow becomes easier, in that one can examine just these coherent modes.

See also: **Buoyancy, Locomotion, and Movement in Fishes**: Buoyancy, Locomotion, and Movement in Fishes: An Introduction; Feeding Mechanics; Stability and Turbulence; Undulatory Swimming. **Hearing and Lateral Line**: The Ear and Hearing in Sharks, Skates, and Rays.

Further Reading

Adrian R (1991) Particle-imaging techniques for experimental fluid dynamics. *Annual Review of Fluid Mechanics* 23: 261–304.

Batchelor G (1973) *An Introduction to Fluid Dynamics*. Cambridge: Cambridge University Press.

Dabiri JO, Colin SP, and Costello JH (2006) Fast-swimming hydromedusae exploit velar kinematies to form an optimal vortex wake. *Journal of Experimental Biology* 209(11): 2025–2033.

Daniel TL (1984) Unsteady aspects of aquatic locomotion. *American Zodogist* 24: 121–134.

Denny MW (1993) *Air and Water: The Biology and Physics of Life's Media*. Princeton, NJ: Princeton University Press.

Drucker EG and Lauder G (1999) Locomotor forces on a swimming fish: Three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *Journal of Experimental Biology* 202: 2393–2412.

Epps B and Techet A (2010) An error threshold criterion for singular value decomposition modes extracted from piv data. *Experiments in Fluids* 48(2): 355–367.

Faber T (1995) *Fluid Dynamics for Physicists*. Cambridge: Cambridge University Press.

Fish FE and Lauder GV (2006) Passive and active flow control by swimming fishes and mammals. *Annual Review of Fluid Mechanics* 38: 193–224.

Holmes P, Lumley J, and Berkooz G (1996) *Turbulence, Coherent Structures, Dynamical Systems, and Symmetry*. Cambridge: Cambridge University Press.

Katz J and Sheng J (2010) Applications of holography in fluid mechanics and particle dynamics. *Annual Review of Fluid Mechanics* 42: 531–555.

Peng J and Dabiri JO (2008) An overview of a Lagrangian method for analysis of animal wake dynamics. *Journal of Experimental Biology* 211(2): 280–287.

Peng J, Dabiri JO, Madden PG, and Lauder GV (2007) Non-invasive measurement of instantaneous forces during aquatic locomotion: A case study of the bluegill sunfish pectoral fin. *Journal of Experimental Biology* 210(4): 685–698.

Tytell ED (2006) Median fin function in bluegill sunfish. *Lepomis macrochirus*: Streamwise vortex structure during steady swimming. *Journal of Experimental Biology* 209: 1516–1534.

Tytell ED (2007) Do trout swim better than eels? Challenges for estimating performance based on the wake of self-propelled bodies. *Experiments in Fluids* 43(5): 701–712.

Vogel S (2003) *Comparative biomechanics: Life's Physical World*. Princeton, NJ: Princeton University Press.