Pectoral Fin Locomotion in Fishes: Testing Drag-based Models Using Three-dimensional Kinematics[1]

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SYNOPSIS. Paired fin propulsion in fishes has classically been divided into two categories which represent biomechanical extremes in the use of appendages for propulsion: lift-based and drag-based mechanisms of thrust production. Theoretical models predict that fishes using drag-based propulsion should have wedge-shaped fins with relatively blunt distal edges, a fin beat cycle that is oriented along the anteroposterior (x) axis, feathering of the fin to reduce drag during the protraction phase, and maximal fin area during the retraction phase as the fin sweeps posteriorly perpendicular to the body. In this paper we use a three-dimensional analysis of pectoral fin propulsion in the largemouth bass, *Micropterus salmoides*, to (1) evaluate the extent to which bass pectoral fin kinematics fit predictions of drag-based propulsion, and (2) demonstrate the complexity of fin movement when the traditional two-dimensional analysis is extended into three dimensions. We attached small markers to visualize the diaphanous distal fin edge, and we videotaped lateral and ventral views from which we could measure x, y, and z coordinates from the fin and body. We divided the fin into two triangular elements for which we calculated planar (three-dimensional) angles relative to each of three reference planes (XY, YZ, and XZ) during the fin beat cycle. We show how angles of attack based only on two-dimensional data may result in gross errors that severely compromise understanding of the mechanics and hydrodynamics of pectoral propulsion. Furthermore, three-dimensional analysis revealed that bass fin kinematics are much more complex than expected on a rowing model of drag-based propulsion, and that the pectoral fins may produce drag-based thrust even during protraction. Three-dimensional kinematic data are critical to understanding the hydrodynamics of aquatic animal propulsion. Such data are a necessary foundation for reconstructing patterns of movement, modeling (both theoretical and empirical), and for assessing the extent to which motion is under active control or a passive consequence of fluid resistance.

INTRODUCTION

Although the study of aquatic locomotion has involved numerous taxa ranging from protozoa to mammals and a consequent wide diversity of hydrodynamic environments and modes of propulsion (Gray, 1968; Lighthill, 1975; Wu *et al.*, 1975; Maddock *et al.*, 1994; Vogel, 1994), fishes have played a prominent role in our attempts to understand how animals generate propulsive forces in the aquatic medium (Webb, 1975; Hoar and Randall, 1978;

Blake, 1983; Videler, 1993). Two facts account for much of this focus on fishes. First, fishes exhibit a considerable diversity of interspecific locomotor morphology. Differences in external body shape and axial musculo-skeletal structure, such as those found in eels, trout, and tuna underlie different hydrodynamic mechanisms of generating propulsive forces and facilitate investigating alternative locomotor methods at moderate to high Reynolds numbers. Second, individual fish possess both a variety of body surfaces that interact with the surrounding water and a concomitant array of locomotor behaviors. Any one fish may use the body surface and caudal fin for steady undulatory locomotion at moderate to high speeds, pectoral fins for low speed movement or hovering, caudal and median fins during rapid escape (c-start) responses, and caudal, pectoral, and median fins for braking and maneuvering. This array of body surfaces and behaviors provides an excellent system for investigating mechanisms of aquatic propulsion over a variety of speeds and conditions while controlling for inter-individual variation.

Given the broad interspecific and intraspecific diversity in fish locomotor structures and behaviors, it is not surprising that many investigators have focused on a relatively few components of this variation in order to conduct more thorough analyses of physiology and mechanics: myotomal muscle structure and function, swimming kinematics of steady undulatory swimming, and a few phylogenetically diverse "exemplar" taxa such as eel, trout, carp, and scup (e.g., Wardle et al., 1995). One consequence of this approach is that many aspects of fish locomotor mechanics, such as those of low speed swimming, remain poorly understood from an experimental perspective. Many fishes swim slowly by using the pectoral fins, and although some experimental data have been obtained (Webb, 1973; Blake, 1979a, Blake, 1980; Geerlink, 1983, 1989; Archer and Johnston, 1989; Gibb et al., 1994; Drucker and Jensen, (1996); Westneat, 1996), much of the progress in understanding this form of locomotion has occurred by theoretical modeling of fin movements (Blake, 1981a, b; Daniel,

1984, 1988; Webb and Blake, 1985; Daniel and Webb, 1987; Vogel, 1994). Blade element theory (Blake 1979a, 1981b), actuator disc theory (Blake, 1979b), and unsteady airfoil theory (Daniel, 1988) have all been used to estimate force production by pectoral fins in fishes. In addition, while the analysis of phylogenetically disparate taxa has been helpful in understanding basic features of pectoral propulsion, to date no single clade of fishes has been studied to provide an historical perspective on fin function.

In this paper we provide kinematic data on pectoral fin propulsion for taxa within a monophyletic clade of fishes, the sunfish family Centrarchidae, with the overall goal of examining the biomechanics of this mode of fish locomotion in detail. We present three-dimensional kinematic data to demonstrate the complexity of fin movements even in a "simple" case of low speed swimming using the pectoral fins. We also evaluate the extent to which theoretical models of pectoral propulsion are applicable to sunfishes and discuss the value of detailed kinematic data for understanding the diversity of locomotor modes in fishes.

Thrust Production by Pectoral Fins

Paired fin propulsion in fishes has classically been divided into two categories which represent biomechanical extremes in the use of appendages for propulsion: lift-based and drag-based mechanisms of thrust production (Blake, 1981b; Daniel, 1984, 1988; Webb and Blake, 1985; Vogel, 1994). In lift-based propulsion the pectoral fins are used as wings (Westneat, 1996) and move primarily along a dorsoventral axis. The angle of attack of the fin is adjusted during the fin beat cycle so that positive thrust is produced during both the upstroke and downstroke, and this requires reorienting the fin at the upper and lower limits of its excursion. As noted by Vogel (1994, p. 285), lift-based propulsion generates positive thrust throughout most of the fin beat so that the duty factor is effectively 100%, and this mode of propulsion is most efficient at moderate to high swimming speeds. Lift-based propulsion is relatively ineffi-
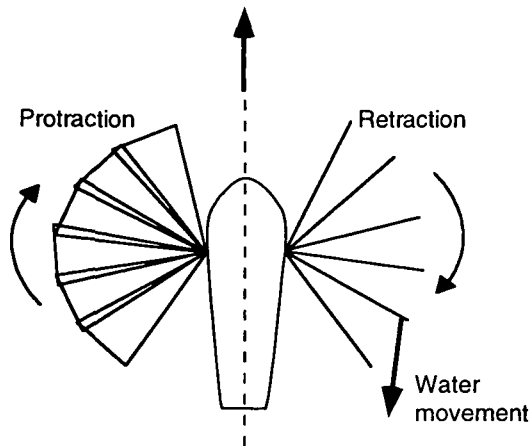
FIG. 1. Schematic diagram of model drag-based propulsion in fishes. During retraction (shown on the right side), the fin is vertical (at a 90° angle to the bottom) and water is pushed posteriorly generating thrust and moving the fish anteriorly in the direction of the solid arrow shown at the midline. The fin is thus drawn as a line during retraction as it would appear in dorsal view. During protraction (shown on the left side) the fin is feathered to a 0° angle relative to the axis of forward travel and hence experiences relatively little drag. During retraction the fin appears as a wedge-shaped plate in dorsal view. The direction of water movement resulting from fin retraction is schematically indicated by the posteriorly-pointing arrow attached to the fin element. Modified from Blake (1981b).

cient at very low speeds due to the low incident fluid velocity over the appendage (wing) and hence a greatly reduced magnitude of the lift force on the fin.

In drag-based propulsion the pectoral fins move primarily along an anteroposterior axis in a "rowing" mode of propulsion (Fig. 1). The fins are retracted posteriorly while oriented perpendicular to the frontal plane and impart momentum to the water if the velocity of fin retraction is greater than the velocity of water movement. At the start of the recovery (protraction) stroke, the fin is tilted so that it is parallel to the frontal plane and brought forward to begin the fin beat cycle again. Feathering the fin during protraction greatly reduces drag on the fin, but there is no positive thrust generated during this return stroke: hence the duty factor of this locomotor mode is about 50%. Drag-based propulsion is most efficient at low speeds and decreases in efficiency as body

velocity approaches the velocity of fin retraction.

The acceleration reaction is also a potentially important aspect of pectoral fin propulsion as changes in fin velocity may impart additional thrust in a direction parallel to the direction of fluid motion over the fin and reduce the magnitude of lift forces (Daniel, 1984; Daniel and Webb, 1987). The acceleration reaction depends on unsteady (time dependent) movement of the fins, and becomes significant when the reduced frequency parameter σ ($=\omega \cdot L/U$, where ω is the frequency of oscillation, L is the length of the fin, and U is the speed of fin movement through the water) is greater than about 0.1 (Daniel, 1984). Deceleration of the fin at the end of both protraction and retraction will result in thrust due to the change in velocity of the added mass of water associated with the pectoral fin. For example, as the fin decelerates at the end of the retraction stroke (Fig. 1), water accelerated by the fin will tend to keep moving posteriorly as fin velocity decreases. The magnitude of this thrust will depend on the rate of change of fin velocity, the shape of the fin, and the stroke angle (Daniel, 1984). Gibb et al., (1994) estimated that for the pectoral fin of bluegill sunfish operating at a Reynolds number of 5 × 10³, σ may be as high as 0.85 suggesting that unsteady effects might be quite important in contributing to thrust production during pectoral locomotion.

The shape of the fin may also affect thrust production during pectoral locomotion. Blake (1981a) has modeled the effect of pectoral fin geometry on thrust production and concluded that a wedge-shaped blunt fin (with the apex of the wedge attached to the body and the blunt edge forming the distal fin margin; as in Fig. 1) is a hydrodynamically more efficient fin shape for drag-based propulsion than a rectangular shape due to reduced interference drag near the body. Within the sunfish family Centrarchidae, such blunt-edged fins characteristic of drag-based propulsion are present in primitive clades such as Micropterus (bass) and Pomoxis (crappie) (Fig. 2). Outgroup taxa to the Centrarchidae also possess relatively short blunt fins suggesting
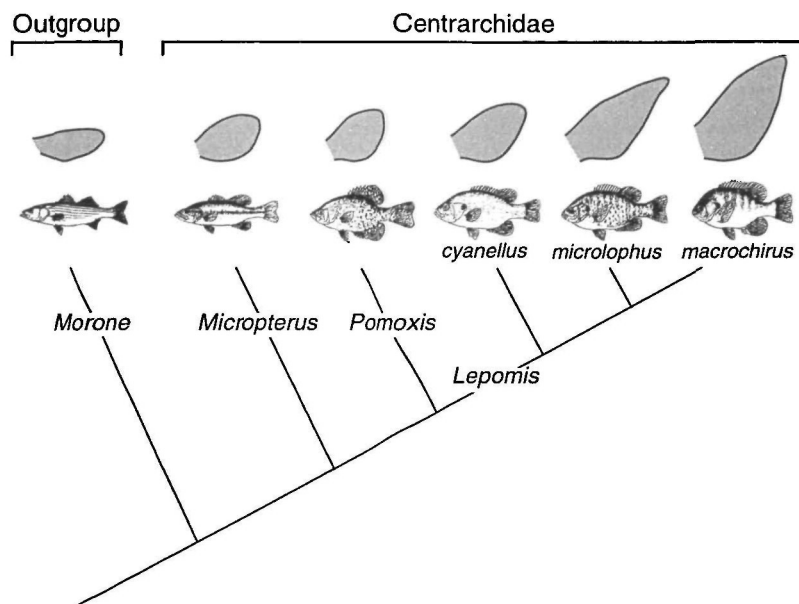
FIG. 2. Phylogenetic relationships of representative taxa within the North American teleost fish family Centrarchidae (following Mabee [1993, 1995] and Wainwright and Lauder [1992]) and an outgroup clade (Percichthyidae: *Morone*) to show evolutionary patterns to pectoral fin shape within this clade. Images of the left pectoral fin above each clade have been scaled proportionally to the size of the fin in that clade, and all taxa are drawn to the same total length. Note the trend in the Centrarchidae from a primitive short and blunt fin (suggested to be characteristic of drag-based propulsion) to the longer wing-like fin used in lift-based propulsion. Images of fishes modified from McGillis (1984), Freshwater Fishes of California, © 1984 by the Regents of the University of California.

that this condition is primitive for sunfishes as a clade.

Lift-based propulsion is associated with more "wing-like" fin shapes where the distal tip is tapered and the fin as a whole is more "diamond-shaped." Species within the sunfish genus *Lepomis* possess more wing-like pectoral fins (Fig. 2) with greater relative area than the blunt fins characteristic of basal groups in this clade.

Methods for Three-Dimensional Analysis

The most basic data needed for an analysis of pectoral fin locomotion in fishes are kinematic. Without an understanding of how the fin moves in three-dimensional space we lack the ability to conduct accurate modeling (either empirical or theoretical), estimate thrust production, or understand the extent to which fin movements are under active muscular control. Fin motion is inherently three-dimensional as the pectoral fin typically moves in both dorsoventral and anteroposterior directions during swimming due to the oblique orientation of the base of the fin with the body. Therefore, it is essential that kinematic data be measured in three-dimensional space and that specific marked points on the fin be followed through time. Tracking the movement of individual markers allows both the visualization of parts of the fin that can not normally be seen due to the diaphanous nature of the fin membrane, and also permits division of the fin surface into smaller units that can be analyzed individually. A full three-dimensional analysis also allows calculation of 3D angles of attack of different portions of the fin surface, rather than restricting angular calculations to their projection onto one plane. As we will show below, two-dimensional analyses can result in gross errors that severely compromise understanding the mechanics and hydrodynamics of pectoral propulsion.

In order to analyze movement of the pectoral fin, it is useful to visualize the fin
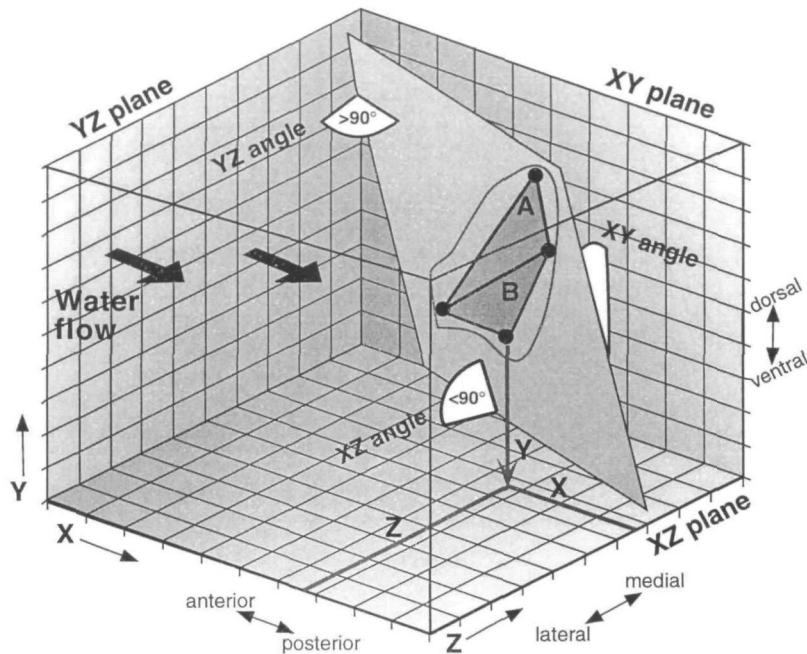
FIG. 3. Schematic representation of the three-dimensional space used to analyze pectoral fin kinematics in largemouth bass. Movements of the fin are defined with respect to three planes: YZ, XY, and XZ. The base of the pectoral fin is located on the XY plane, and the pectoral fin surface is shown lying within a plane that makes a three-dimensional angle with each of the three reference planes: YZ, XY, and XZ angles. The fin surface is divided into two triangles (A and B). The planar angles of intersection are reflected by the pie wedges shown for the YZ, XZ, and XY angles. These angles are measured orthogonally to the reference planes and are *not* projections of one plane onto the other. Note that as this figure is drawn, the fin plane intersects the XZ and YZ planes. The XY planar angle is shown for completeness, but would actually lie behind the fin plane as drawn. See text for further explanation.

in three-dimensional space. Figure 3 illustrates a left pectoral fin oriented within a schematic cube defined by three reference planes: YZ, XY, and XZ. In anatomical terminology, YZ is equivalent to the transverse plane, XY the sagittal plane, and XZ the frontal plane. If these reference planes are viewed as part of a flow tank in which a fish is swimming by pectoral fin propulsion, then water is moving from anterior to posterior perpendicular to the YZ plane as indicated by the solid black arrows, and parallel to the XY plane. The XZ plane would then correspond to the bottom of the flow tank. The base of the pectoral fin is drawn as being located just lateral to the XY plane with the fin extending at an angle into the flow, and the fish would be oriented with its long axis parallel to the XY plane facing into the YZ plane. For graphical conve-

nience the surface of the pectoral fin is indicated as lying entirely within a plane extending out from the fin base toward each of the three reference planes (Fig. 3). The outer edge of the fin is indicated by a thin line and surface of the fin lying within this line has been divided into two triangles, A and B, by a three markers (indicated by black dots). These markers are on the distal edge of the fin while a single point defines the base of the fin. While the fish is anesthetized, it is possible to attach small pieces of black plastic to mark the distal fin allowing visualization of specific points on this otherwise largely invisible region of the fin (Fig. 4; also see Gibb *et al.,* 1994).

The location of each of the points on the fin is specified by x, y, and z coordinates (Fig. 3). The values of these coordinates are obtained experimentally by us-
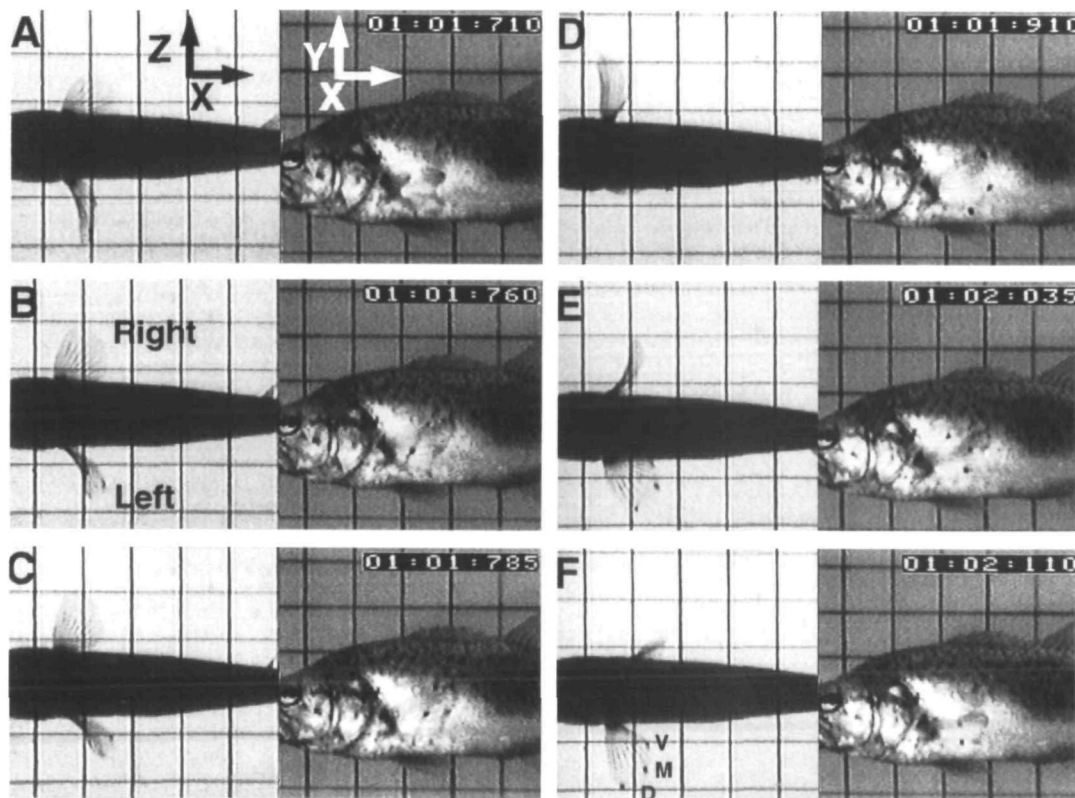
FIG. 4. Video images showing the pectoral fin beat cycle in largemouth bass. The last three digits at the top of each panel indicate elapsed time in ms. Each panel contains two views obtained simultaneously with separate cameras: the ventral mirror-image view is on the left and shows movement in the Z and X dimensions, while the lateral view is on the right and shows movement in the Y and X dimensions. Three small markers have been placed on the left pectoral fin: Left and Right labels in panel B indicate the respective fins, and the D, M, and V labels in panel F indicate the Dorsal, Middle, and Ventral markers respectively. The background grids in both views are 2 × 2 cm. In this figure the three markers on the left fin are most easily seen in lateral view (D) and ventral view (F), although during data acquisition all markers generally could be followed throughout the fin beat cycle. The original video images have been cropped and contrast-enhanced for clarity using Adobe Photoshop.

ing two synchronized high-speed (200 fs⁻¹) video cameras (Fig. 4) that provide lateral (XY plane) and ventral (XZ plane) views of the fin. These two orthogonal images (Fig. 4A) allow measurements of the three-dimensional position of each marker: the XZ view provides the z coordinate, while the XY view provides the x and y coordinates. All coordinates were initially measured in the earth frame of reference, although many of the movements illustrated in this paper are presented relative to the position of the fin base. The fin base showed minimal oscillation in the X, Y, and Z planes through the fin beat cycle,

and the XY plane was thus assumed to be parallel to the anatomical sagittal plane. The video cameras showing both views have equal magnification and are aligned to minimize parallax errors.

The x, y, and z coordinates for each point allow calculation of the surface area of the two triangular elements of the fin (Fig. 3) which may change throughout the fin beat as the spacing among adjacent fin rays is altered cyclically by the fin musculature and water pressure. Most importantly, the three-dimensional planar angle that each triangle makes with each of the three reference planes can be calculated. Each fin el-

ement defines a plane which extends beyond the borders of the fin to intersect the three reference planes. For, example, the plane defined by triangle B makes an XZ angle with the frontal (XZ) plane and a YZ angle with the transverse (YZ) plane. As the fin beats all three angles will change with time, and Figure 3 illustrates the conventions used to define these angles. The XZ angle is 90° when the fin triangle is perpendicular with the XZ plane, less than 90° (acute) when the triangle is tilted to the left (as shown in Fig. 3), and greater than 90° (obtuse) when the triangle is tilted to the right. We use a similar convention for the YZ plane. If fin triangle B stays perfectly vertical throughout the fin beat cycle, it will always form a 90° angle with the XZ plane but the YZ angle will oscillate from about 90° when the fin is against the body to a value of about 40° at peak abduction. Values of 0° for the XY angle indicate when a triangular fin element is parallel to the XY plane, negative values (between 0° and −90°) indicate that the fin markers are lateral to the fin base (as shown in Fig. 3), while positive values (between 0° and +90°) indicate that the distal fin markers are located medial to the fin base (this latter condition does not occur for the left pectoral fin which sweeps through an XY angle ranging from 0° to about −75° during the fin beat cycle). Note that these planar angles are measured orthogonally to each plane, and do not represent projections of the fin edge onto each plane. Also, these planar angles measure the orientation of the surface of the fin, and hence are not equivalent to fin angles estimated by projection of line segments located on the fin onto orthogonal reference planes.

We also calculated an instantaneous movement vector for each triangle and each time increment of movement (see Fig. 8). Movement vectors were oriented perpendicular to the triangle surface with their base located at the triangle centroid. Vector orientation may thus be used as a visual guide to the orientation of the surface of that triangle. Vector magnitude was scaled in proportion to the area of the triangle times the component of squared velocity of centroid movement along the normal to the

triangle surface. Longer vectors in Figure 8 thus reflect either greater triangle area, greater velocity, or both.

3D KINEMATICS OF THE BASS PECTORAL FIN

The shape of the pectoral fin of largemouth bass, *Micropterus salmoides,* is characteristic of fishes that presumably use drag-based propulsion (Fig. 2). First we present kinematic data to document the complexity of movement of the pectoral fin in bass, and then we provide comparisons to other taxa.

Three-dimensional excursions of fin markers

Video images of one fin beat cycle in bass are shown in Figure 4. Markers on the distal fin edge are labeled dorsal, middle, and ventral. Movements of the fin in the negative and positive directions of the x, y and z axes are designated as: protraction and retraction, depression and elevation, and abduction and adduction, respectively.

Beginning with the fin maximally abducted (Fig. 4A), the fin sweeps posteriorly and medially during adduction (Fig. 4C) until the fin surface is oriented nearly parallel to the body (effectively a 90° angle to both the XZ and YZ planes). At the end of adduction (Fig. 4D), the three markers on the distal fin edge are clearly visible in lateral view. Fin abduction then begins and the fin moves anteriorly and ventrally (Fig. 4F) prior to starting a new cycle. Fin beat frequencies range from 1.8 to 2 Hz and do not change significantly over a speed range of 0.3 to 0.75 Lsec⁻¹.

The complexity of the fin movements is illustrated by a plot of the displacement of the dorsal marker in each of the three dimensions (Fig. 5) relative to a fixed point on the bass. During early adduction the dorsal marker moves dorsally and posteriorly, whereas after maximal adduction of this marker, it moves anteriorly while continuing to move dorsally (Fig. 5). Ventral movement begins during abduction and anterior movement. A consequence of the phase differences among the three-dimensional movements is that quantifying movement in any one dimension will not allow
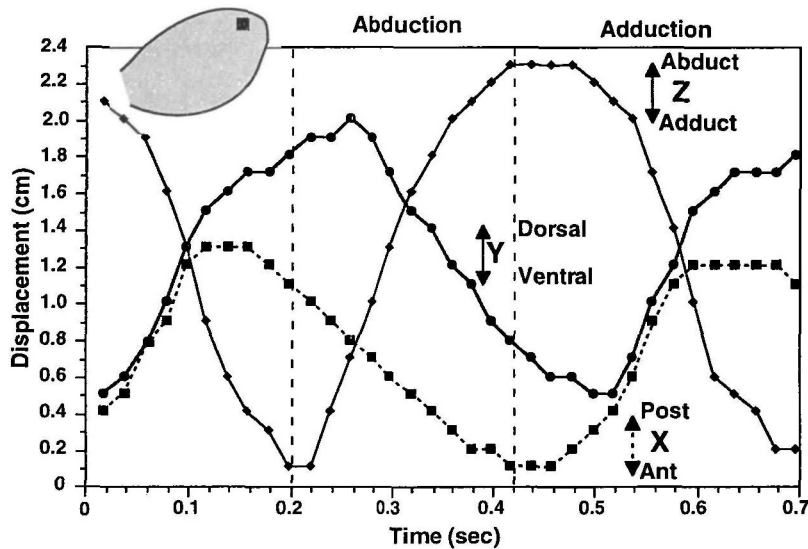
FIG. 5. Displacement in three dimensions of the most dorsal marker on the bass pectoral fin relative to the body during locomotion at 0.5 Lsec⁻¹ (equivalent to 10.5 cmsec⁻¹). Abduction and adduction phases of fin movement are defined by extreme displacements in the Z dimension. Negative slopes for plots of Y (●), Z (♦), and X (■) indicate, fin depression, adduction, and protraction respectively. Z-values are measured relative to a fixed point on the fish; hence, decreasing z-coordinates reflect fin adduction. Note that the maximal speed of fin retraction (X dimension) exceeds the speed of fish movement.

inference of movement in the other two dimensions. The maximal speed of fin retraction exceeds the speed of the bass (Fig. 5) suggesting that a drag-based mechanism is one of the thrust production mechanisms used during locomotion.

Movement of all three markers in the fish frame of reference is illustrated in Figure 6. All markers move in a loop with an axis oriented anteroventrally, and this contradicts expectations of a simple rowing pattern during which the fin would retract along the anteroposterior axis, feather while protracting, and then expand anteriorly prior to retraction. Instead, these complex movements include a counter-clockwise loop of the dorsal marker and a clockwise loop for the middle and ventral markers. This movement pattern at 0.3 Lsec⁻¹ is consistent with a relatively passive ventral portion of the fin following actively controlled leading dorsal rays. This hypothesis is corroborated by electromyographic analyses of fin muscles (Lauder and Jayne, unpublished). At higher speeds (e.g., 0.5 Lsec⁻¹), all markers move in counter-clockwise loops.

Three-dimensional angles of fin elements

Analysis of the three-dimensional orientation of fin triangular elements A and B (Fig. 7B, C, D) shows that at the start of fin adduction, both fin elements make an acute angle with the XZ plane indicating that they are oriented with their most dorsal vertex located anterior to the ventral vertices. As the fin moves posteriorly, triangle B reorients to achieve nearly a 90° angle to the XZ plane and maintains a value close to 90° until the fin is fully adducted. Triangle A, however, moves through the 90° angle to reach nearly a 120° angle to the XZ plane. In this orientation, triangle A would be expected to exert a force on the fluid in a posterior and ventral direction. When the fin is against the body at midbeat, both triangles are oriented at 90° to the XZ and YZ planes and at a nearly 0° angle to the XY plane. During abduction, both triangles maintain nearly a 90° angle to the YZ plane (Fig. 7B, C) while forming increasingly acute angles to the XZ (horizontal) plane.
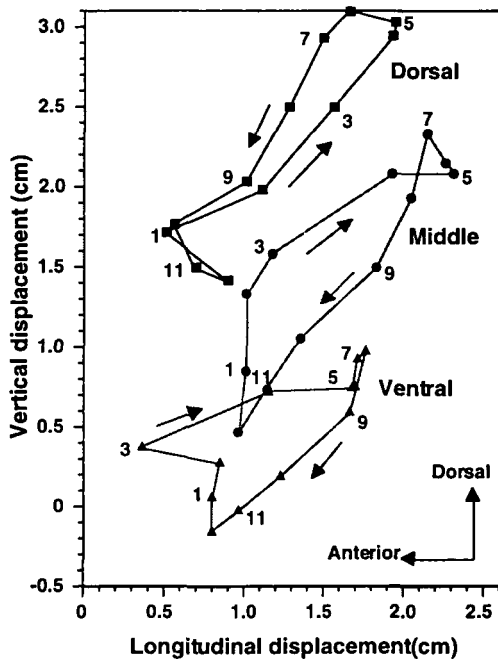
Three-dimensional planar angles pro-

FIG. 6. Loop plot for swimming at 0.3 Lsec⁻¹ (equivalent to 6.3 cm/sec) showing the vertical (Y) and longitudinal (X) displacements of three markers on the bass pectoral fin (■ dorsal, ● middle, and ▲ ventral) relative to a fixed point on the fish. Arrows show the direction of marker movement during one fin beat cycle within each loop. Numbers next to selected points indicate homologous times on each marker loop. Time between successive points is 0.05 sec.

vide an indication of the orientation of each fin element with respect to reference planes, and hence measure a geometrical angle of attack. However, nearly all previous analyses of fish swimming have used single camera views that preclude such three-dimensional calculations. To what extent could two-dimensional methods be in error? For pairs of markers on the distal edge of the fin of a bluegill, Gibb *et al.*, (1994) compared angles calculated from a two-dimensional (lateral) view versus angles derived the intersection of the XY plane and the plane containing a three dimensional triangular fin element (similar to triangle A in Fig. 3). Table 1 shows the large discrepancies in angles (ranging from 22° to 83°) resulting from these different methods. These errors are so large as to suggest that serious misinterpretation of fin function is likely

if only two-dimensional data are used as a basis for estimating the hydrodynamic environment of the pectoral fin. Furthermore, even the signs of various angles may be in error. For example, early in the fin beat cycle at 1.1 Lsec⁻¹, a line segment formed by a (two-dimensional) projection of the fin edge onto the XY plane forms a positive 58° angle relative to the path traveled by the fin, whereas the intersection of the planar fin element and XY plane forms an angle of −11° relative to the direction of fin movement in the XY plane (Table 1).

The excursions, angles of the triangular fin elements discussed above, and movement of the triangle centroids are visualized in a three-dimensional reconstruction of fin position shown in Figure 8. During mid-adduction (T_1), fin elements A and B move dorsally, posteriorly, and medially as reflected by the direction of triangle centroid motion. At mid-abduction (T_2) both fin elements are moving ventrally, anteriorly, and laterally. Movement vectors attached to the centroid of each triangle show that during protraction (time T_2) the lateral surface of both triangles is facing posteriorly (Fig. 8): the distal tip of the vector attached to the centroid of triangle A is located posterior (along the x dimension) to the centroid of that triangle. The surface of triangle B has a slightly less posterior orientation, with the result that the entire fin is slightly concave downward at this time. Thus, the fin is "feathered" to some extent during protraction, and this configuration of the fin may provide lift-based propulsive force during this portion of the fin beat cycle. Note that the lateral fin surface is not oriented anteriorly during protraction as would be expected if the fin were exhibiting a primarily translational motion.

Figure 8 also illustrates the important result that the bass fin may produce drag-based thrust even during protraction. At time T_2, as triangle A centroid is moving anteroventrally, there is still a positive component of centroid velocity that projects onto a line perpendicular to the fin surface. Hence, triangle A is capable of pushing water posteriorly at this time even though the centroid is moving anteroventrally, due to
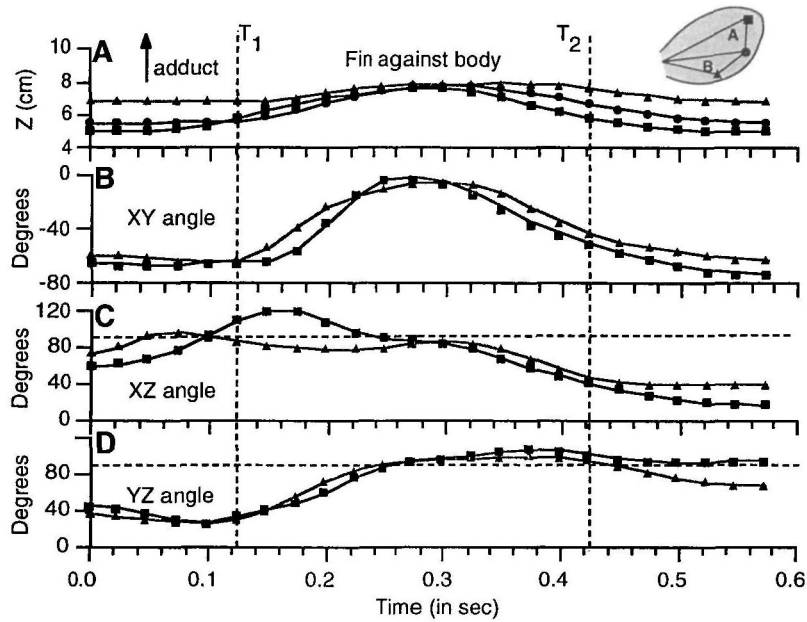
FIG. 7. Plots of three-dimensional kinematic parameters for the bass pectoral fin during a single fin beat cycle from locomotion at 0.6 Lsec⁻¹ (equivalent to 12.6 cm/sec) relative to the earth frame of reference as shown in Figure 3 (hence increasing Z values reflect adduction). A, lateral (z) excursion of the three distal fin markers; B, C, D three-dimensional angles of the two triangular components of the bass pectoral fin with the XY, XZ, and YZ planes. In C and D, horizontal dashed lines mark the 90° angle to each plane. Note that when the fin is fully adducted against the body, both triangles make nearly a 90° angle to the XZ and YZ planes. The ■ and ▲ symbols indicate kinematic parameters for the upper (A) and lower (B) fin triangles respectively. T₁ and T₂ refer to times during adduction and abduction of the fin for which three-dimensional reconstructions of fin position are presented in Figure 8.

the orientation of the line of centroid motion relative to the fin surface. This result may at first appear counterintuitive, but is in fact analogous to a sailboat tacking upwind. A sailboat can sail into the wind via the judicious orientation of the sail surface relative to wind velocity. In a similar manner, the bass can generate positive drag-

TABLE 1. Comparison of angles derived from two-dimensional methods versus three-dimensional methods for the two most dorsal markers on the bluegill (Lepomis macrochirus) pectoral fin.*

Swimming speed	Phase within fin beat cycle	Two-dimensional angle	Three-dimensional angle
0.3 Ls⁻¹	5–10%	86°	3°
0.3 Ls⁻¹	65–75%	43°	65°
1.1 Ls⁻¹	11–16%	58°	−11°
1.1 Ls⁻¹	58–63%	23°	−1°

*Note how poorly the two-dimensional calculations estimate the actual three-dimensional angle. Data from (Gibb et al., 1994.) See text for more detail.
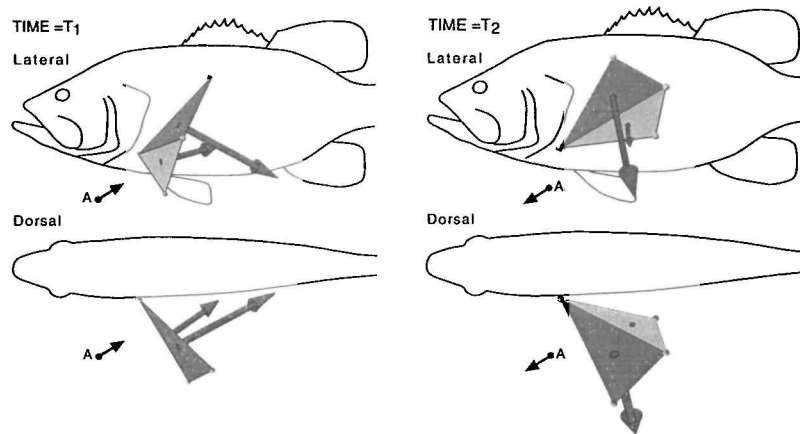
based thrust during fin protraction by an appropriate orientation of the fin surface relative to its path of motion.

The difficulty in appreciating the three-dimensional configuration of the fin derives in part from our tendency to view movement in two dimensions only. Even though Figure 6 depicts motion only in the XY plane, the anteroventral orientation of the movement loop is clear. The major axis of pectoral fin movement is not oriented horizontally, and during protraction, the fin is moving ventrally to the same extent that it is moving anteriorly (Figs. 5, 6). Furthermore, the orientation of the surface of fin element A is an essential parameter to consider when attempting to visualize movement. Note that in Figure 8 (time T₂) the base of triangle A is located medial and anterior to the distal fin markers while the most dorsal marker is located laterally to the middle marker. At time T₂, the surface

FIG. 8. Three-dimensional reconstruction of the position and movement of the bass pectoral fin during adduction and retraction (times T_1 and T_2 see Fig. 7). Note that the fin has been enlarged relative to the body to illustrate triangle and vector orientations. This reconstruction is based on the X, Y, and Z coordinates of the three fin markers and a point at the base of the pectoral fin; small spheres indicate the location of fin markers and the base of the fin used for three-dimensional calculations of triangle position. Vectors originating at the centroid of each of the two fin triangles show the orientation of the triangular surface: each vector is oriented perpendicular to the fin triangle plane. The length of each vector is proportional to the squared velocity of the triangle centroid in the direction normal to the triangle surface (see text for further discussion). Note that at time T_2 the surface of the upper triangle (A) is oriented posteriorly. Triangle B is not visible in dorsal view at time T_1 because it is hidden beneath triangle A. The direction of triangle A centroid movement in shown by the arrow below each fish image. At time T_2 the centroid of triangle A is moving anteriorly and ventrally as seen in lateral view.

of triangle A is moving laterally, ventrally and anteriorly, folding the fin along the border between triangles A and B.

One likely cause of the complexity of fin movements in bass is the oblique articulation of the fin with the body. The axis of the fin base is inclined from anterodorsal to posteroventral (Fig. 2) and the path of fin motion may thus be largely determined by anatomy. The orientation of the fin ray bases, their attachment to the underlying radial elements, and the lines of action of abductor and adductor muscles may render purely translational motion along any one axis impossible.

COMPARISONS TO OTHER TAXA

While three-dimensional kinematic data of this kind are not yet available for any other fish taxon, a basic three-dimensional description of fin movement in bluegill, *Lepomis macrochirus*, with marked pectoral fins was presented by Gibb *et al.*, (1994). A comparison between bluegill and bass is instructive because although both species are members of the same sunfish clade, they

possess patterns of fin structure that would be expected *a priori* to conform to lift-based and drag-based kinematic patterns respectively (Fig. 2). In addition, both species were studied under the same experimental conditions and are size-matched by total length: bluegill averaged nearly 18 cm in total length (Gibb *et al.*, 1994) while the bass used for the experiments reported in this paper had a mean length of about 21 cm.

At a similar total length, bluegill possess pectoral fins of greater maximum length and area than bass: the distance from the most dorsal marker to the fin base is 4.3 cm in bluegill compared to 2.8 cm in bass, while the respective total fin areas are 6.5 cm^2 and 4.0 cm^2.

Bass show little change in fin beat frequency with speed, and over a speed range of 0.3 to 0.75 Lsec^{-1} use significantly higher frequencies than bluegill. For example, at 0.5 Lsec^{-1}, bluegill pectoral fin beat frequencies average about 1.35 Hz, while bass beat frequencies reach almost 2 Hz. Bluegill beat frequencies are strongly speed de-

pendent (Gibb *et al.*, 1994) while those of bass are not. In addition, the percent of cycle spent in protraction is much greater for bass (55%) than for bluegill (35%) at a speed of 0.5 Lsec⁻¹.

For bluegill and bass swimming at 0.3 Lsec⁻¹, one similarity in the movement of the pectoral fin (as seen in the XY plane) is that the most dorsal marker moves in a counterclockwise fashion whereas the ventral markers move clockwise [Fig. 6; Gibb *et al.*, (1994)]. This suggests that for both species the ventral fin rays are passively following the leading dorsal rays at slow speeds. In both species, the path traveled by dorsal and ventral fin markers in the XY planar projection becomes counter-clockwise at speeds above 0.5 Lsec⁻¹ suggesting the recruitment of additional muscles controlling the ventral fin rays. Previous work by Webb (1973) and Geerlink (1983) also has indicated that the dorsal fin rays may lead fin movement during the beat.

Compared to bluegill at the same relative speed, bass have greater phase lags among dimensional excursions for a single marker, and this is most easily seen by comparing the anteroventral and posterodorsal movements of the dorsal marker. In bluegill, maximal depression of the dorsal fin marker (minimum y) is nearly synchronous with maximum abduction (maximum z) of the fin, whereas in bass maximum depression is reached approximately 20% cycle later than maximum abduction (Fig. 5). In bass, phase lags approach 30% cycle for maximal posterior movement compared to maximal dorsal fin movement, whereas in bluegill these phase lags are much less, ranging from 0% at 0.3 Lsec⁻¹ to about 11% at 1.1 Lsec⁻¹.

Both bluegill and bass pectoral fins possess a reduced frequency parameter σ of about 0.33 at a speed of 0.5 Lsec⁻¹, but bluegill swim at significantly higher speeds up to 1.1 Lsec⁻¹ prior to switching gait to include undulation of the body and caudal fin. At these highest speeds bluegill reduced frequencies approach 0.85. The transition to body and caudal fin undulation in bass occurs at about 0.8 Lsec⁻¹ in a fish of 20 cm total length.

CONCLUSIONS

Models of drag-based propulsion

The development of theoretical models of fish fin hydrodynamics has been a major stimulus to the field and has provided experimentalists with an extremely useful framework for interpreting descriptions of fish fin kinematics. The models of Blake [(1979a, 1980, 1981a, b), also see Webb and Blake (1985), Webb (1988), Daniel (1984), and Vogel (1994)] have been particularly fruitful in defining precisely the theoretical extremes of lift- and drag-based propulsion. For example, modeling drag-based propulsion (Fig. 1) provides a well-defined extreme against which the kinematics of the bass fin can be compared. Does the bass fin function in a drag-based manner? Bass possess fin shapes and a general locomotor mode that qualitatively appears to be drag-based, especially when compared to taxa that seem to more closely approach the lift-based end of the propulsive spectrum such as *Coris* and *Cymatogaster* (Webb, 1973; Geerlink, 1983).

However, the results of three-dimensional kinematic analyses in both bass and bluegill show that it is very difficult to characterize pectoral fin locomotion in these taxa as fitting either a drag- or lift-based model. Our data show that the fin movements are extremely complex and defy both simple characterization and easy inference of hydrodynamic regime or thrust production mechanism. This conclusion is based on four points.

First, the pectoral fin does not correspond to rigid plate-like element. Triangles A and B move along different paths and they make different planar angles with the three reference surfaces. The division of the pectoral fin into these two elements represents a minimal level of analysis in which the fin is divided into a section that is controlled primarily by the leading (dorsal) fin rays (element A) and a section that is increasingly passive with decreasing speed (element B). For a more complete analysis relevant to hydrodynamic modeling, the fin could be divided into spanwise strips, but there are considerable practical difficulties with achieving this.

Second, even our division of the fin into two triangles assumes that these triangles themselves do not bend. This is clearly an oversimplification as fin rays are flexible (Arita, 1971) and bend along their length during locomotion. This flexibility may be important in thrust generation. For example, as the fin is abducted early during protraction, the proximal ends of the fin rays move laterally before the distal ends because the abductor musculature attaches to the base of the rays. As the distal portions of the fin follow, they make an obtuse angle to the YZ plane (Fig. 3) which will generate positive thrust as the distal portions of the fin rays move laterally. In addition, bending of the fin rays may result in more posteriorly directed thrust than would be possible without ray bending. For example, in Figure 8, at time T_1, if the fin rays bend as the fin is retracted, the movement vectors would be more posteriorly oriented than shown in Figure 8, enhancing thrust. To date, no study has quantified fin ray bending during locomotion and discussed the potential impact that bending may have on fin hydrodynamics, but this is clearly an area for future investigation.

Third, the pattern of fin movement described here for bass does not match the motions expected of a fish swimming under a drag-based hydrodynamic regime. The fin is not protracted and retracted with a major axis of movement oriented in the x dimension. Instead, motion of the fin is extremely complex in three dimensions with an anteroventrally inclined axis of motion.

Fourth, the value of the reduced frequency parameter (about 0.35) suggests that unsteady effects are important but of unknown impact. Undoubtedly during deceleration of the fin at the end of protraction and retraction the acceleration reaction does play an important role in providing additional thrust. However, the changing area of the fin, the oblique and changing orientation of the fin to the flow, and the difficulty in calculating an added mass coefficient for the fin under these conditions, make it very difficult to experimentally assess the importance of unsteady effects. Given the increasing amount of data that implicate unsteady effects as having a significant impact

on moving appendages (Daniel, 1984, 1988; Dickinson and Götz, 1993), it seems unlikely that simple vector analyses of lift and drag components under a quasi-steady model of locomotion will accurately describe the hydrodynamic environment of the fish pectoral fin.

Three-dimensional kinematic analysis in fish locomotion

The vast majority of kinematic analyses of fish locomotion have been conducted in two dimensions. For many purposes such as determining the frequency of the tail beat and lateral (z) excursion of points along the body, a two-dimensional approach is fully appropriate. However, in some cases the two-dimensional approach may prove extremely misleading. Analysis of pectoral fin movement provides one such case in which three-dimensional data are essential. Even for determining such basic hydrodynamic parameters such as the angle of attack, three-dimensional data are critical as shown by Table 1. Furthermore, determining the orientation of the *surface* of the body or appendage (crucial to understanding how force is exerted on the water) depends on obtaining three-dimensional coordinates for points on that surface so that planar angles may be calculated.

The value of three-dimensional data extends to influencing how we choose to characterize basic locomotor patterns. Relying on two-dimensional data to characterize movements that occur in three dimensions will give an inaccurate characterization of fin motion and imprecise inferences of function. Such errors are likely to be particularly consequential in comparative studies where differences in three-dimensional motion among taxa may be critical to understanding evolutionary diversification in function.

Finally, although kinematic studies alone may not possess the cachet of analyses of muscle physiology, studies of flow dynamics, or the production of mathematical models of function, the value of detailed kinematic data for studies of locomotor function cannot be overestimated. Without such data we are unable to estimate the hydrodynamic environment of locomotor structures, and

we will not be able to construct accurate mathematical models because the input to such models (patterns of movement) will not be available. Kinematics derived from a two dimensional view only are likely to contain gross errors. Resolving a fundamental problem of aquatic locomotion, explaining how a moving body generates force on the fluid medium, is critically dependent on understanding how movement occurs and the extent to which such motion is under active control.

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