Wake Dynamics and Locomotor Function in Fishes: Interpreting Evolutionary Patterns in Pectoral Fin Design[1]

Eliot G. Drucker[2,3] and George V. Lauder

Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, Massachusetts 02138

Synopsis. The great anatomical diversification of paired fins within the Actinopterygii (ray-finned fishes) can be understood as a suite of evolutionary transformations in design. At a broad taxonomic scale, two clear trends exist in the morphology of the anteriorly situated pectoral fins. In comparing basal to more derived clades, there are general patterns of (i) reorientation of the pectoral fin base from a nearly horizontal to more vertical inclination, and (ii) migration of the pectoral fin from a ventral to mid-dorsal body position. As yet, the functional significance of these historical trends in pectoral fin design remains largely untested by experiment. In this paper we test the proposal that variation in pectoral fin structure has an important influence on the magnitude and orientation of fluid forces generated during maneuvering locomotion. Using digital particle image velocimetry for quantitative wake visualization, we measure swimming forces in ray-finned fishes exhibiting the plesiomorphic and apomorphic pectoral fin anatomy. Our experiments focus on rainbow trout (*Oncorhynchus mykiss*), a lower teleost with pectoral fins positioned ventrally and with nearly horizontally inclined fin bases, and bluegill sunfish (*Lepomis macrochirus*), a relatively derived perciform fish with more vertically oriented pectoral fins positioned mid-dorsally on the body. In support of hypotheses arising from our prior wake studies and previously untested models in the literature, we find that the pectoral fins of sunfish generate significantly higher forces for turning and direct braking forces closer to the center of mass of the body than the pectoral fins of trout. These results provide insight into the hydrodynamic importance of major evolutionary transformations in pectoral fin morphology within the Actinopterygii.

Introduction

The enormous evolutionary radiation of bony fishes is characterized by pronounced morphological diversification of the paired fins. In both living and fossil forms, the pectoral and pelvic fins are prominent characteristics of the locomotor anatomy (Breder, 1926; Harris, 1937; Zug, 1979; Carroll, 1988; Janvier, 1996). The anteriorly situated pectoral fins of fishes, in particular, play important roles both in controlling body position and in propelling the body during steady and unsteady swimming behaviors. The greatest diversity of pectoral fin design occurs among the Actinopterygii, or ray-finned fishes (Fig. 1). Within this clade, historical transformations in the shape, orientation and position of the pectoral fins have been well-documented (Greenwood *et al.*, 1966; Rosen, 1982; Webb, 1982). To elucidate the functional consequences of this evolutionary variation, biomechanical researchers have examined the mechanism of action of the pectoral fins in a variety of ray-finned fishes. Important work in the nineteenth and early twentieth centuries involved inference of fin function from muscle architecture and qualitative observations of swimming behavior (*e.g.,* Williamson, 1893; Osburn, 1907; Schmalhausen, 1916; Magnan, 1930; White, 1939). More contemporary efforts have focused on hydrodynamic modeling (Blake, 1983*a, b*; Walker and Westneat, 2000, 2002; Combes and Daniel, 2001) and quantitative experimental analyses of pectoral fin motion and its neuromuscular control (Webb, 1973; Geerlink, 1983; Gibb *et al.*, 1994; Lauder and Jayne, 1996; Westneat, 1996; Drucker and Jensen, 1997; Westneat and Walker, 1997; Hove *et al.*, 2001; Walker and Westneat, 2002).

Despite a century of active investigation into the mechanism of pectoral fin function, there remains a critical area of study in which experimental zoologists are only now making initial progress: analysis of the physical interaction between the locomotor anatomy of freely swimming fishes and the aquatic medium. In the past several years, the use of new flow visualization techniques has, for the first time, enabled collection of quantitative data on the effect of motion of fish fins on the surrounding water (*e.g.,* Stamhuis and Videler, 1995; Müller *et al.*, 1997; Drucker and Lauder, 1999; Wolfgang *et al.*, 1999; Lauder, 2000). Empirical hydrodynamic analyses of the wake of swimming fishes have improved our understanding of how momentum is transferred from a moving animal to its fluid environment, and how propulsive fluid forces arise.

The purpose of this paper is to illustrate how modern tools for visualizing biological fluid flow can provide new insights into the relationship between propulsor structure and hydrodynamic function during aquatic locomotion. Using direct measurements of fluid dynamic quantities from the wake of freely swimming ray-finned fishes, we interpret the functional significance of observed variation in pectoral fin design. The general goal of our research in this area is to contribute to an understanding of the functional conse-

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[2] E-mail: edrucker@uci.edu

[3] Present mailing address: Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697.
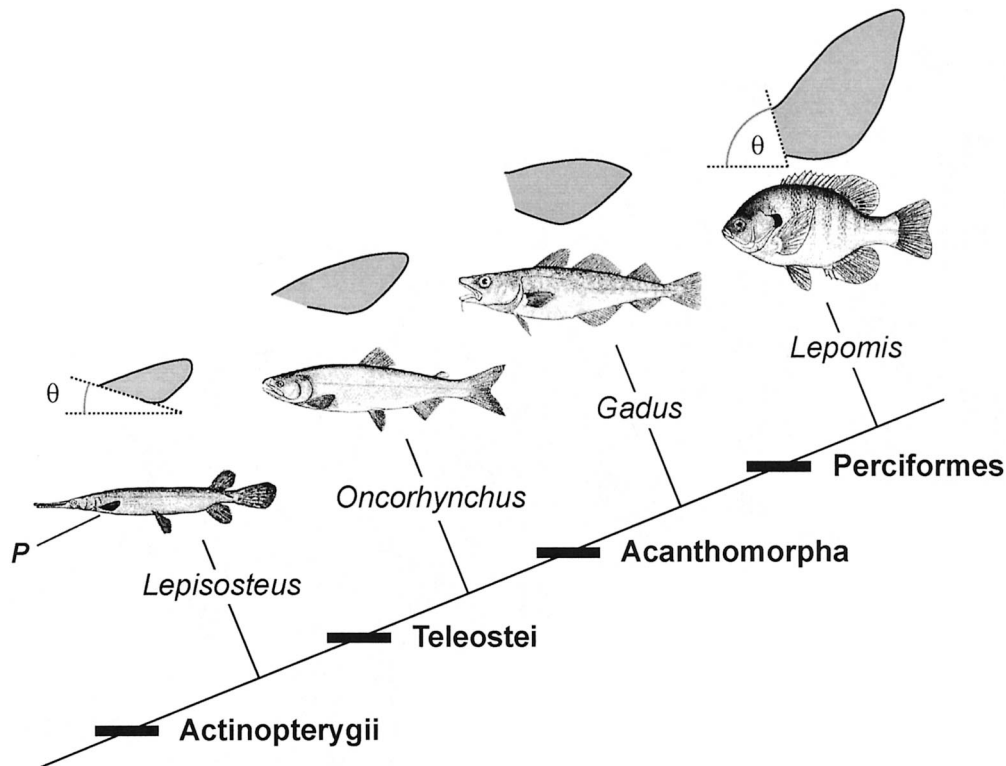
Fig. 1.   Phylogenetic relationships of selected genera of ray-finned fishes to illustrate two major evolutionary trends in the design of pectoral fins. First, the pectoral fin (labeled *P*) migrates from a ventral body position (shown by basal taxa such as *Lepisosteus* as well as lower teleosts including *Oncorhynchus*) to a derived dorsolateral position (as in *Gadus* and *Lepomis*). Second, the base of the pectoral fin is reoriented from a primarily horizontal to more vertical inclination. Enlarged images of the pectoral fin shown above each clade have been scaled to the same proportion of body length. In this study, we compare wake forces during maneuvering in two taxa exemplifying the plesiomorphic and apomorphic conditions of the pectoral fin: rainbow trout (*Oncorhynchus mykiss*) and bluegill sunfish (*Lepomis macrochirus*). θ, angle of inclination of the pectoral fin base measured relative to the longitudinal body axis. Images of fishes modified from Hart (1973), Moyle (1976), McGinnis (1984), and Romer and Parsons (1986).

quences of major evolutionary transformations in pectoral fin morphology within the Actinopterygii. In this paper, we focus on two historical trends in pectoral fin design, and test hypotheses regarding the implications of variation in fin structure for the generation of locomotor forces.

Evolutionary Trends in Pectoral Fin Design

Despite the great diversification of pectoral fin anatomy within the Actinopterygii, much of the observed variation in structure can be understood as a suite of evolutionary trends in design. Figure 1 shows a simplified cladogram of ray-finned fishes in which representative taxa from selected major groups are highlighted. Actinopterygii is an extremely speciose class of fishes; for the purposes of this paper, we restrict our focus to key clades illustrating discrete anatomical transformations of the pectoral fins. Among advanced ray-finned fishes, one recurring anatomical pattern concerns the external morphology of the pectoral fin. Within the order Perciformes, for instance, clear intrafamilial variation has been observed in the shape of the pectoral fin surface (described in terms of its aspect ratio, a morphological index defined as the square of fin length divided by fin area). Recent work provides

evidence that relatively low aspect-ratio fins are plesiomorphic and higher aspect-ratio fins are apomorphic within certain perciform families (Lauder and Jayne, 1996; Wainwright *et al.*, 1999, 2002). Consistent patterns of variation in pectoral fin shape are less apparent in comparisons among distantly related lineages.

Inspecting pectoral fin morphology at a broad taxonomic scale within the Actinopterygii does, however, reveal clear trends in other aspects of design, which serve as the experimental focus of this paper. Previous workers have shown that during actinopterygian evolution major transformations have occurred in (i) the anatomical position of the pectoral fin and (ii) the orientation of the pectoral fin base (Schmalhausen, 1916; Breder, 1926; Harris, 1937, 1938; Greenwood *et al.*, 1966; Gosline, 1971; Alexander, 1974; Rosen, 1982; Webb, 1982). The first design trend we examine here is in the orientation of the pectoral fin base, defined externally as the angle of inclination of the insertion of the pectoral fin on the body. In basal actinopterygians (*e.g.,* Fig. 1, *Lepisosteus*), as well as in basal teleost fishes (*e.g.,* Fig. 1, *Oncorhynchus*), the pectoral fin base typically has a nearly horizontal orientation (*i.e.,* the fin base lies at a shallow angle relative to the longitudinal body axis). In contrast, more derived taxa

(including acanthomorphs such as *Gadus* and *Lepomis*; Fig. 1) commonly show pectoral fins with more vertically inclined bases. In addition to this reorientation of the pectoral fin, there is also a trend of change in pectoral fin position. Primitively, the pectoral fin is located low on the body, positioned near the ventral body margin (*e.g.,* Fig. 1, *Lepisosteus* and *Oncorhynchus*). In acanthomorph fishes (Fig. 1), the pectoral fin is located higher on the body, at an approximately mid-dorsal position and closer to the center of mass of the fish.

At present, the functional significance of these observed historical trends of reorientation and dorsal migration of the pectoral fin remains largely untested by experiment. Our objective is to investigate how such general and widespread patterns of anatomical variation are related to fluid force production during locomotion. To initiate study in this area, we focus on two ray-finned fish species that exemplify the plesiomorphic and apomorphic conditions of the pectoral fin: rainbow trout (*Oncorhynchus mykiss*), a basal teleost with pectoral fins positioned ventrally with nearly horizontally inclined fin bases, and bluegill sunfish (*Lepomis macrochirus*), a perciform fish with more vertically oriented pectoral fins positioned mid-dorsally on the body (Fig. 1).

EXPERIMENTAL APPROACH

Study of the fluid forces generated by freely swimming animals is facilitated by an experimental hydrodynamic approach based on quantitative flow visualization (reviewed by Lauder, 2000; Drucker and Lauder, 2002). In recent work, we have utilized such an approach to investigate fin forces in a variety of actinopterygian fishes undergoing a range of locomotor activities (*e.g.,* Drucker and Lauder, 1999, 2000, 2001*a, b,* 2003; Liao and Lauder, 2000; Wilga and Lauder, 2000; Nauen and Lauder, 2001). We characterize wake dynamics using digital particle image velocimetry (DPIV), a flow visualization technique originally developed for the study of non-biological flow (Willert and Gharib, 1991), but which in recent years has been adopted by zoologists interested in flow within and around organisms. Recent advances in DPIV technology enable instantaneous measurements of water velocity within the wake in three dimensions (Raffel *et al.*, 1998; Stanislas *et al.*, 2000; see also papers by Gharib *et al.* [2002] and Lauder *et al.* [2002] in this volume). To obtain the necessary wake measurements for estimating swimming force, we employ in this study traditional two-dimensional DPIV but with significant methodological improvements to the experimental system used in our prior work.

Briefly, our DPIV experiments involve using a continuous-wave laser light sheet to illuminate small reflective particles seeded into the water within a recirculating flow tank in which a fish swims. High-speed video images of the laser plane are recorded to allow visualization of fluid motion within thin slices (1–2 mm thick) of the fish's wake. In separate experiments, the light sheet can be imaged in different orthogonal orientations to provide information about wake velocity in three dimensions. In the present paper, we analyze flow data for parasagittal (vertical) and frontal (horizontal) sections of the pectoral fin wake (see Drucker and Lauder, 1999, Fig. 2). Digitized video images are processed computationally by dividing the flow plane into a grid of subsample areas, each of which is assigned a velocity vector on the basis of cross-correlation (*i.e.,* analysis of the displacement of particle images in consecutive video fields). The result of a complete DPIV analysis is a two-dimensional matrix of velocity vectors that describes the average magnitude and orientation of flow over the course of the video framing period. For the experiments described in this study, a new image processing algorithm was employed that greatly improved the accuracy and spatial resolution of DPIV analysis, especially for the relatively weak vortices shed by trout pectoral fins. We used the recursive local-correlation technique of Hart (2000) to calculate velocity fields 8–9 cm on each side containing more than 2200 vectors from consecutive digital video images (480 horizontal × 420 vertical pixels) recorded at 250 Hz (as described by Lauder *et al.*, 2002).

To investigate the relationship between pectoral fin morphology and locomotor force production, we used DPIV to measure the structure and strength of the wake produced by trout and sunfish. Fishes of similar size were studied to establish general patterns of pectoral fin motion and associated wake flow (trout: $N = 6$; total body length, $L,$ 24.7 ± 0.8 cm, mean ± SD; sunfish: $N = 4$; $L,$ 22.0 ± 0.6 cm); two individuals of each species were used for detailed quantitative analysis. The average pectoral fin force F exerted by a fish over the course of the fin stroke period T was calculated from Milne-Thomson (1966) as the rate of change in wake momentum. For oscillating pectoral fins, a recurring pattern within planar flow fields is the production of paired counterrotating vortices with a central high-velocity fluid jet (Drucker and Lauder, 1999, 2000, 2001*b*). When the distance between vortex centers is not significantly different in perpendicular planes of analysis, we assume the three-dimensional shape of the wake is a toroidal vortex ring, whose momentum M is given by the product of water density, mean vortex strength (*i.e.,* circulation), and ring area. Inter-vortex distance D in both rainbow trout and bluegill sunfish does not show a significant dependence upon light sheet orientation (unpaired *t*-tests comparing D in parasagittal and frontal planes: df = 53, 11; $P = 0.11, 0.06$, respectively), and therefore F for these species is calculated as M/T (see Spedding *et al.*, 1984 and Dickinson and Götz, 1996 for other applications of this method for estimating wake force). Within each plane of analysis, the force exerted by the pectoral fin is geometrically resolved into two perpendicular components according to the orientation of the central fluid jet. After subtracting mean free-stream velocity from the flow field, the jet angle is measured
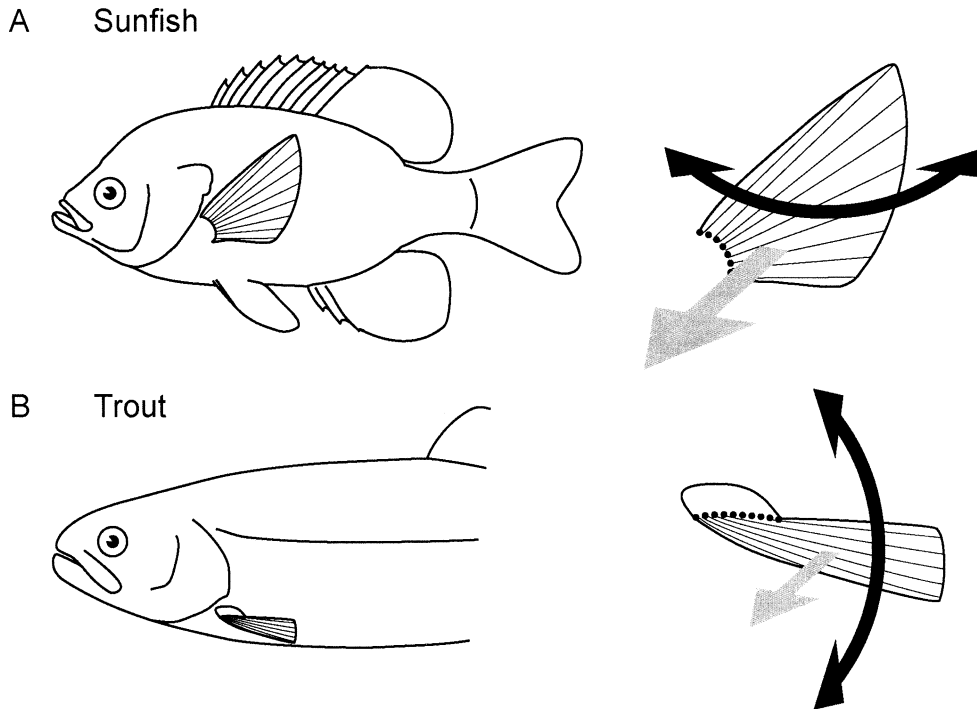
A Sunfish

B Trout

FIG. 2. Pectoral-fin base orientation and implications for turning force. Enlarged images of fins at right are scaled to the same leading-edge length. In both species, the orientation of the pectoral fin's insertion on the body is indicated by a dotted line. Double-headed arrows schematically represent the fin's stroke plane; gray arrows denote the relative magnitudes of predicted laterally oriented force vectors. Sunfish, possessing a more vertically inclined fin base (mean $\theta = 74°$), show anteroposterior fin motions within a horizontal plane (A), while trout, with a more horizontally oriented fin base (mean $\theta = 10°$), exhibit primarily dorsoventral fin excursions within a vertical plane (B). On the basis of this interspecific difference in fin range of motion, we hypothesize that sunfish will generate significantly larger laterally directed forces than will trout during pectoral-fin turning maneuvers. θ, angle of inclination of the pectoral fin base measured relative to the longitudinal body axis.

relative to the longitudinal body axis as the average angle of inclination of vectors comprising the region of accelerated flow between paired vortex cores (see Drucker and Lauder, 2000, Fig. 6). Data on the magnitude and orientation of wake force permit empirical study of the locomotor function of divergent fin designs.

FIN DESIGN AND LOCOMOTOR FORCE: TESTING FUNCTIONAL HYPOTHESES

To address experimentally the question of whether pectoral fin structure is related to swimming force, we focus in trout and sunfish on unsteady maneuvering behaviors. During turning (yawing rotation of the body) and braking (rapid deceleration of the body) in these species, we use DPIV to examine the extent to which fin base orientation and fin position on the body influence the magnitude and orientation of wake forces. Our investigation is centered upon the evaluation of three functional hypotheses. The first hypothesis, regarding the locomotor significance of pectoral-fin base orientation, has arisen from unexpected findings of our recent flow visualization research with perciform fishes. The second two hypotheses, concerning the hydrodynamic consequences of pectoral fin location in actinopterygian fishes, have persisted untested

in the literature since their proposal in the early part of the twentieth century.

FIN BASE ORIENTATION AND FORCE FOR TURNING MANEUVERS

The base of the pectoral fin can be modeled as a flexible hinge joint defined by the articulation between the elongated skeletal elements of the fin itself (fin rays) and the basal bony elements of the pectoral girdle (radials). Previous workers have examined the functional significance of variation in the angle of inclination of the fin base relative to the longitudinal axis of the body. In particular, fin base orientation has been viewed as influencing the kinematic range of motion of the pectoral fin (Geerlink, 1989; Lauder and Jayne, 1996; Drucker and Jensen, 1997; Wainwright et al., 2002; Walker and Westneat, 2002). More vertically oriented fin bases restrict fin oscillation to anteroposterior (fore-and-aft) motions within a horizontal plane, whereas more horizontally oriented bases dictate dorsoventral (up-and-down) motions within a vertical plane (Fig. 2). The use of DPIV to visualize flow patterns in the wake of pectoral fins has provided an intriguing result that suggests a possible hydrodynamic consequence of fin base inclination in the Actinopterygii. Bluegill sunfish, possessing a nearly vertically
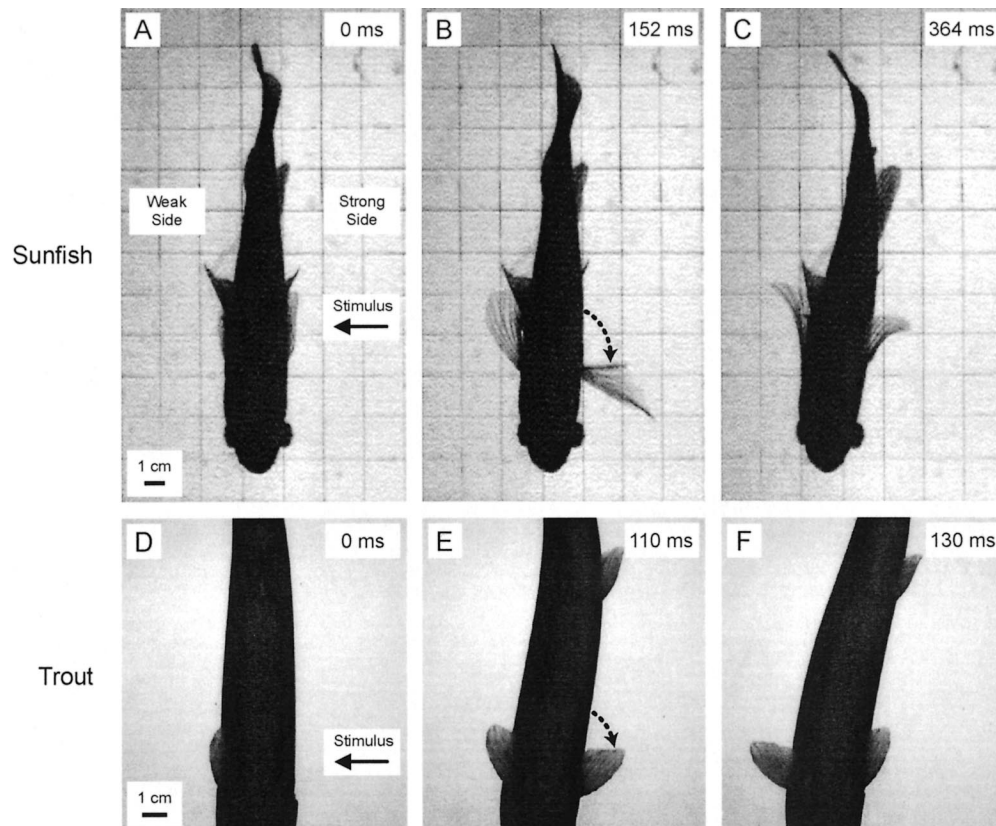
FIG. 3. Ventral-view video images of sunfish and trout performing low-speed yawing turns in response to a visual and auditory stimulus. The pectoral fin on the same side of the body as the turning stimulus is termed the 'strong-side' fin, while the contralateral fin is termed the 'weak-side' fin. Dashed-line arrows indicate the direction of pectoral fin abduction. In sunfish, issuance of the stimulus (A) results in rapid and pronounced protraction of the strong-side fin (B). In the depicted turn, the leading edge of this fin subtends an angle of 119° as measured relative to the longitudinal axis of the body. Body rotation, with minimal body bending, continues as the pectoral fins adduct (C). In trout, a similar response is elicited by the stimulus (D), but strong-side pectoral fin protraction is limited (41° for this turn) and pectoral fin motion is accompanied by body bending (E–F). Video images from Drucker and Lauder, 2001b, 2003.

oriented fin base (Fig. 2A), generate surprisingly large laterally or sideways-directed wake forces during steady swimming, even at the highest speeds sustainable by pectoral fin oscillation. In the face of increasingly rapid currents in the experimental flow tank, sunfish do not reorient wake vortex flow from a primarily lateral to primarily downstream direction. In contrast, the black surfperch (*Embiotoca jacksoni*), a perciform fish with a more horizontally oriented fin base, increases its speed by augmenting downstream-oriented thrust, but maintains only a very small component of lateral force at all speeds (Drucker and Lauder, 2000). The implication is that the angle of inclination of the pectoral fin base may represent an anatomical constraint on the magnitude and orientation of wake forces that can be developed.

On the basis of these observations during steady swimming, we predict that differences in lateral wake force among ray-finned fishes will be accentuated during turning maneuvers, which require the generation of laterally directed momentum flows to exert a yawing moment around the body's center of mass. We expect that vertically oriented pectoral fins such as those of bluegill sunfish that sweep fore and aft through the

horizontal plane (Fig. 2A) will have a greater capacity to generate lateral turning force than horizontally oriented fins like those of rainbow trout that beat primarily up and down (Fig. 2B). It is important to note, however, that flapping a fin along either an anteroposterior or a dorsoventral stroke axis can result in a sideways-oriented component of force. The latter stroke, however, as used by fishes with more horizontally oriented fin bases, also generates a substantial vertically oriented component of force which can lead to destabilizing rolling moments of the body during turning. Our first hypothesis is that, for turns involving a minimum of rolling of the body, *vertically oriented pectoral fins, by virtue of a greater range of motion within the horizontal plane, will generate significantly larger laterally directed forces than will horizontally oriented fins.* Since force magnitude depends not only on stroke kinematics but also on propulsor size, we evaluate this hypotheses for sunfish and trout by making interspecific comparisons of both absolute lateral force and force corrected for differences in pectoral fin area.

Turning maneuvers were elicited by exposing steadily swimming fishes to a visual and auditory stimulus on one side of the body (Fig. 3A, D). With this
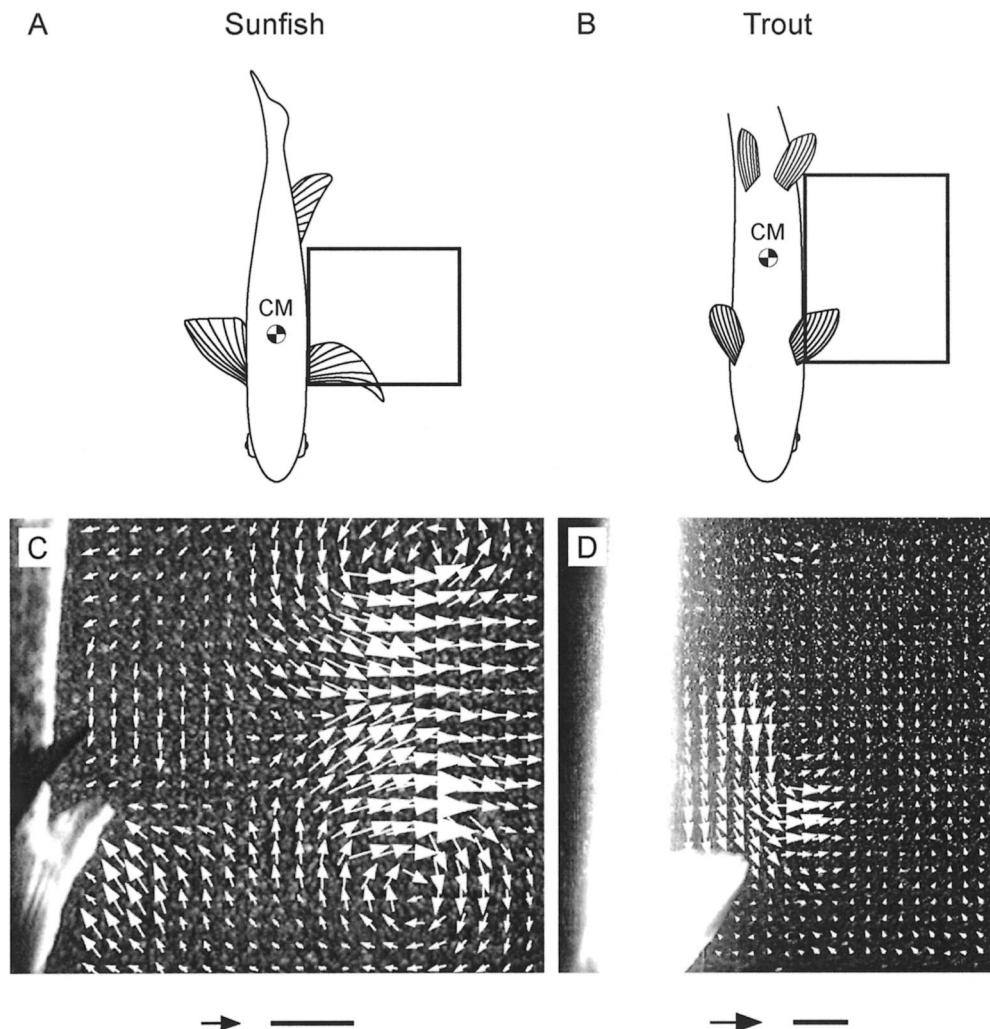
FIG. 4. Representative frontal-plane wake flow patterns during pectoral-fin turning maneuvers by sunfish and trout. (A, B) Ventral-view line drawings (not to scale) depict the pectoral fin in a protracted position during abduction (*cf.* Fig. 3B, E). Boxed regions indicate areas within the horizontal laser plane for which velocity vector fields were calculated at the end of the stroke period (C, D) (*cf.* Fig. 3C, F). Note that both fishes produce sideways-directed fluid flow during turning (vectors pointing to the right), but that sunfish (C) generate a much stronger laterally oriented wake jet than trout (D) for yawing the body around its center of mass (CM). Scales for C and D: arrow, 10 cm sec^{-1}; bar, 1 cm. Flow fields from Drucker and Lauder, 2001*b,* 2003.

technique we induced submaximal escape responses from both sunfish and trout (*i.e.,* relatively slow yawing turns powered by the pectoral fins, as opposed to fast-start turns driven primarily by body flexion). At the onset of a turn, the pectoral fin on the same side of the body as the source of the stimulus (the 'strongside' fin) rapidly abducts and the body begins to rotate toward the contralateral or 'weak' side (Fig. 3B, E). Body rotation within the horizontal plane continues as the strong-side pectoral fin strokes back toward the body (Fig. 3C, F). During turning, there are two notable interspecific differences in locomotor kinematics. First, the relatively short-bodied sunfish exhibits minimal axial bending during yawing rotation (Fig. 3B–C), while the elongate trout undergoes marked undulation of the trunk (Fig. 3E–F). Second, the pectoral fin's range of motion within the horizontal plane differs substantially between species. Sunfish are capable

of protracting the pectoral fin to a much greater degree than trout, a result consistent with the difference in fin base orientation measured for these species (Fig. 2). For the turns depicted in Figure 3, for instance, the angle through which the leading edge of the pectoral fin sweeps during abduction is approximately 80 degrees larger for sunfish than for trout. In the course of abducting and adducting the strong-side pectoral fin, however, both fishes generate measurable momentum flows in the wake.

Water velocity fields for turning maneuvers by sunfish and trout show marked differences in the structure and strength of the pectoral fin wake. Low-speed turning by sunfish involves the generation of paired counterrotating vortices by the strong-side pectoral fin (Fig. 4C). Each fin half-stroke (*i.e.,* abduction and adduction) contributes to the production of a single free vortex. These vortices, visible within the frontal plane of

TABLE 1. *Kinematic and hydrodynamic measurements for pectoral-fin turning by bluegill sunfish and rainbow trout.*

Measurement	Sunfish	Trout	t
Angular velocity of body rotation (degrees sec^{-1})	10.9 ± 2.0	13.5 ± 2.4	-0.75 (34)
Wake jet angle (degrees)	91.6 ± 5.5	121.4 ± 5.0	$-3.15*$ (27)
Wake momentum, lateral component (g cm sec^{-1})	$1{,}151.7 \pm 245.0$	42.6 ± 8.8	$4.25*$ (15)
Force, lateral component (mN)	20.9 ± 6.5	2.7 ± 0.9	$2.61*$ (15)
Lateral force/fin area (mN cm^{-2})	2.9 ± 0.9	0.8 ± 0.3	$2.07*$ (15)

Data tabulated as mean $\pm$ S.E.M. (sunfish: $N = 7$–14 pectoral fin beats per measurement; data from Drucker and Lauder, 2001*b*; Trout: $N = 15$–22; data from Drucker and Lauder, 2003). Interspecific comparisons made with unpaired *t*-tests (asterisks indicate significant differences at the Bonferroni-adjusted $\alpha = 0.01$; degrees of freedom shown in parentheses).

Wake measurements are from frontal-plane velocity fields. Jet angle is measured relative to longitudinal body axis. Wake forces are stroke-averaged measurements reported per fin. Dividing lateral force by fin area corrects for interspecific variation in propulsor size (mean pectoral fin area in sunfish and trout: 7.2 and 3.2 cm², respectively).

analysis, represent sections through a three-dimensional vortex ring with a central momentum jet (Drucker and Lauder, 2001*b*). In trout, rapid pectoral fin abduction results in the appearance of a single vortex and associated fluid jet in the frontal plane (Fig. 4D). The subsequent fin adduction does not cause a second vortex with opposite-sign rotation to appear as in sunfish. On the basis of wake visualization of oscillating pectoral fins in other species (Drucker and Lauder, 1999, 2000), however, we assume that a second vortex is in fact produced: the trout's pectoral fin, having a dorsoventral kinematic axis (Fig. 2B), likely produces out-of-plane flow as it strokes through the horizontal light sheet, shedding a second vortex on adduction that lies above the laser plane imaged with DPIV. To estimate the momentum of wake flow produced by the trout's pectoral fin, we modeled the wake as a vortex ring whose medial portion remains attached to the fin at the end of abduction (*cf.* Fig. 8 in Drucker and Lauder, 1999). Vortex ring circulation for trout, therefore, was taken not as the average from two free vortices in the wake, as in sunfish (Fig. 4C), but rather as the strength of the single shed vortex seen in the horizontal plane (Fig. 4D), which during rapid fin abduction is equal in magnitude to circulation that remains bound to the pectoral fin (according to Kelvin's Law; Milne-Thomson, 1966). Vortex ring diameter was approximated by measuring the distance between the centroid of the pectoral fin and the center of the shed vortex at the end of abduction (Drucker and Lauder, 2003).

Despite a large interspecific difference in the range of motion of the pectoral fin within the horizontal plane (*cf.* Fig. 3B, E), both species studied are capable of turning the body by shedding laterally directed wake flow. During turning, the angular velocity of the body, in yaw, showed a comparable range in both species (sunfish: 2–32 degrees sec^{-1}, $N = 14$ turns; trout: 4–41 degrees sec^{-1}, $N = 22$ turns). The average orientation of velocity vectors comprising the central wake jet differed by approximately 30 degrees (Table 1), but in both cases, the jet had a predominantly lateral orientation (Fig. 4). The laterally directed component of wake momentum in sunfish exceeded that in trout by a factor of nearly 30 (Table 1). Laterally exerted force arising from this momentum jet showed a large and significant interspecific difference: on av-

erage, sunfish generated eight-times as much lateral force for turning than did trout (Table 1). Correcting for interspecific variation in pectoral fin size, we find that the lateral force generated per unit fin area is also significantly greater in sunfish. These force comparisons provide support for the hypothesis that fin base orientation can influence the magnitude of turning force in the Actinopterygii.

FIN POSITION AND FORCE FOR BRAKING MANEUVERS

In order to decelerate their bodies, many ray-finned fishes extend the left and right pectoral fins simultaneously to produce a retarding drag force (Breder, 1926; Harris, 1938; Bainbridge, 1963; Videler, 1981; Geerlink, 1987; Jayne *et al.*, 1996; Webb and Fairchild, 2001). Two models proposed in the early part of the twentieth century attempt to explain the physical mechanism by which such braking is achieved. Breder (1926) proposed for elongate fishes with the pectoral fins low on the body that braking forces are oriented horizontally without a vertically oriented lift component (Fig. 5A). Since the center of pressure of the pectoral fin (taken as the centroid of the fin surface) lies below the center of mass of the body (CM), the reaction to this braking force exerts a substantial pitching or 'somersaulting' moment which must be opposed by action of the posterior fins to avoid an uncontrolled maneuver. For fishes whose pectoral fins extend higher up on the body, Harris (1938) proposed that the braking force is comprised of both a horizontal and vertical component so that the reaction force vector intersects the CM (Fig. 5B), thereby eliminating this destabilizing pitching moment. Although much-cited since their introduction, the models of Breder and Harris have not before been tested. The potential influence of fin position on maneuvering performance has been discussed previously (Gerstner, 1999; Webb and Gerstner, 2000; Webb and Fairchild, 2001), but there are presently very few experimental data on the fluid dynamic consequences of having the plesiomorphic *versus* apomorphic pectoral fin distribution.

Using rainbow trout and bluegill sunfish, respectively, we explicitly tested the hypotheses that (a) *for ventrally positioned pectoral fins, the line of action of the braking force lies below the center of mass of the body* (Breder, 1926) (Fig. 5A), and that (b) *for mid-*
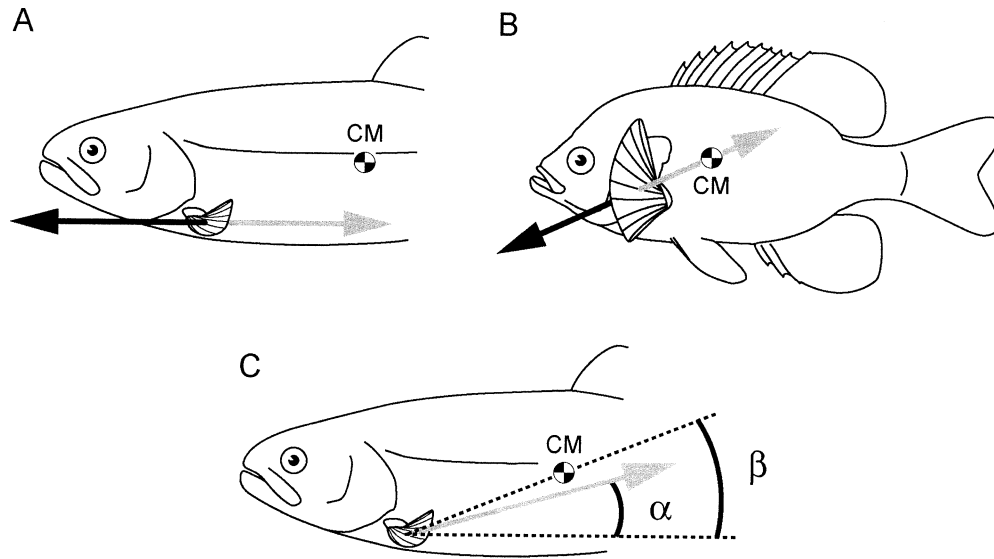
FIG. 5. Pectoral fin location on the body and implications for braking force. In all panels, the pectoral fins are depicted in their maximally extended positions. Black vectors represent braking forces exerted by the pectoral fin; gray vectors signify the reaction forces experienced by the fin. (A) Previously untested model of pectoral-fin braking proposed by Breder (1926). Species with the paired fins located ventrally are predicted to orient wake momentum horizontally; the braking-force line of action falls below the CM. (B) Proposed braking model of Harris (1938). Species whose pectoral fins extend more dorsally are predicted to direct the braking force such that the reaction force intersects the CM. (C) Experimental measurements made to evaluate these hypotheses. An arbitrarily oriented braking reaction force is shown to illustrate two angles within the parasagittal plane: (a) the angle α between the longitudinal axis of the fish and the line of action of the braking force acting on the fin; (b) the angle β between the longitudinal axis of the fish and the line connecting the center of mass of the body with the centroid of the pectoral fin in its fully extended position during braking. Breder's hypothesis is supported if α is significantly less than β; Harris' hypothesis is supported if α is not significantly different from β. CM, center of mass of the body.

dorsally positioned pectoral fins, the braking force re- action falls in line with the center of mass of the body (Harris, 1938) (Fig. 5B). Pectoral-fin braking maneuvers were elicited in both species by providing visual stimuli in the upstream region of the flow tank's working area. Braking was repeatedly induced in steadily swimming trout by directing a narrow wooden dowel into the water in front of the head; in sunfish, braking followed the capture of a small prey item introduced into the free-stream flow. To evaluate braking hypotheses experimentally, we compared the orientation of the stroke-averaged reaction force vector to the angle of inclination of the CM (Fig. 5C).

To generate an anteriorly directed component of force for decelerating the body, bluegill sunfish strongly protract the entire surface of the pectoral fin oriented broadside to the incident flow (Fig. 6A) (see also Jayne *et al.*, 1996). Although rainbow trout have a much more limited ability to extend the pectoral fin from the body (*cf.* Fig. 3B, E), this species can nevertheless also generate anteriorly directed momentum flow. During braking, trout rapidly bend the pectoral fin along its longitudinal axis so that the trailing edge is elevated and protracted (Fig. 6B). A similar pectoral fin motion has been observed in juvenile salmonid fish during benthic station-holding (Kalleberg, 1958; Arnold *et al.*, 1991). Despite differing fin kinematics, both species shed a braking wake comprised of paired counterrotating vortices with central jet flow. In sunfish, both vortices were consistently well-developed in the vertical plane of analysis (Fig. 6C), while in trout, the

vortex shed on fin elevation was often stronger than that produced during the following fin depression (Fig. 6D). Within each species, the orientation and magnitude of the central wake jet developed for braking showed relatively little variability. Sunfish consistently oriented wake momentum downward and forward, while trout oriented this momentum flow upward and forward (Fig. 7A). The species showed no significant difference in jet velocity (sunfish: 6.9 ± 0.6 cm sec^{-1}, mean $\pm$ S.E.M.; trout: 6.1 ± 0.3 cm sec^{-1}; unpaired *t*-test: df $= 31$; $P = 0.17$).

The average orientation of the braking-force line of action, defined by the mean momentum jet angle, is summarized in Figure 7B for the two species. In sunfish, the braking reaction force is inclined on average at a 28 degree angle above the horizontal. To test the hypothesis of Harris (1938), we compared in sunfish the reaction force angle (Fig. 5C: angle α) for multiple braking events to the angle of inclination of the center of mass of the body (Fig. 5C: angle β). This comparison revealed no significant difference (one-sample comparison of α to hypothesized mean β of 23.7 degrees: df $= 17$; $P = 0.26$), providing support for the idea that fish with more dorsally positioned pectoral fins can indeed direct the braking reaction through the CM. Consistent with this finding is the observation that, during braking, sunfish undergo very little pitching of the body. In trout, by contrast, the braking reaction force vector lies at an angle significantly less than the angle of inclination of the CM (Fig. 7B) (one-sample comparison of α to hypothesized mean β of
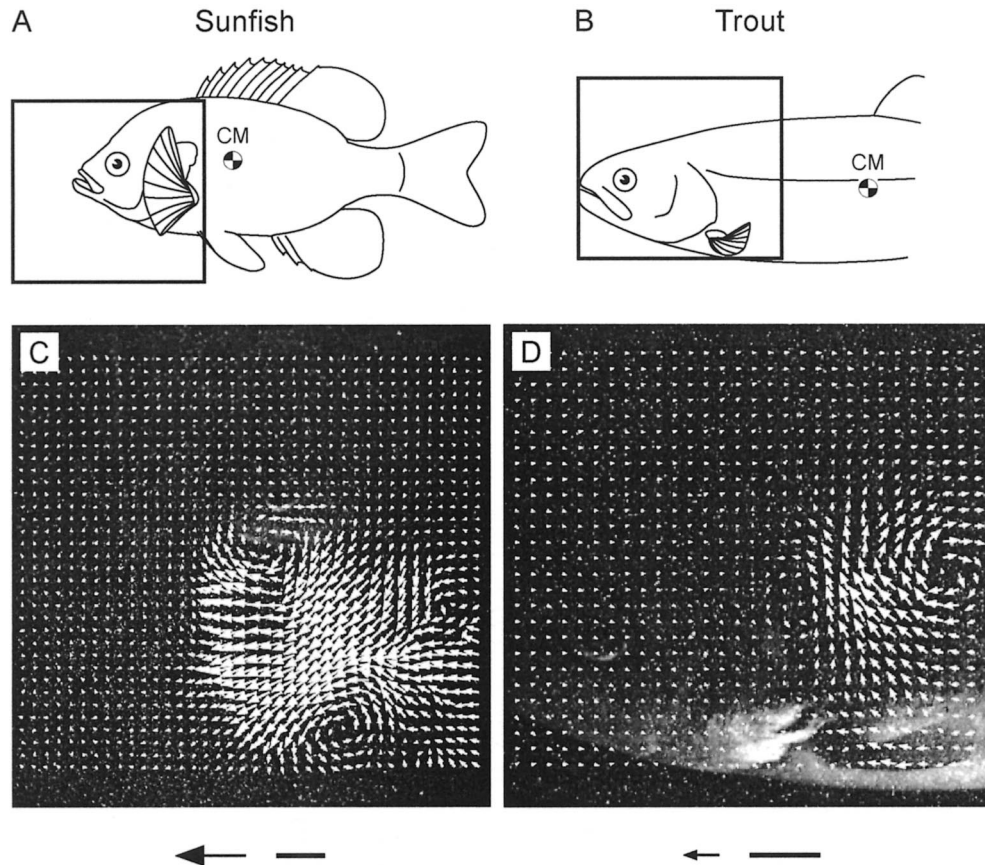
FIG. 6. Representative parasagittal-plane wake flow patterns during pectoral-fin braking maneuvers by sunfish and trout. (A, B) Lateral-view line drawings (not to scale) depict the pectoral fin in a fully extended position during deceleration of the body. Boxed regions indicate areas within the vertical laser plane for which velocity vector fields were calculated (C, D). Strong protraction of the entire pectoral fin surface by sunfish as shown in A generates a momentum jet oriented ventrally and anteriorly (C). In contrast, the relatively slight protraction of the pectoral fin's trailing edge in trout (B) results in a braking jet directed dorsally and anteriorly (D). Scales for C and D: arrow, 20 cm sec^{-1}; bar, 1 cm. CM, center of mass of the body.

22.3 degrees: df $= 14$; $P < 0.001$), a result supporting the hypothesis of Breder (1926). The fact that the braking-force line of action in trout lies far below the horizontal orientation postulated by Breder (1926) (Fig. 5A) indicates that ventrally positioned pectoral fins may have larger than expected moment arms for exerting torque around the CM. During braking, we observe trout to recruit fins posterior to the CM, presumably to counter the 'somersaulting' moment induced by pectoral fin extension. Specifically, the soft-rayed dorsal fin is abducted to one side, and the trailing edges of the pelvic fins are protracted and elevated in a manner similar to that of the pectoral fins anteriorly. In spite of these simultaneous fin motions to control the braking maneuver, however, trout exhibit pronounced pitching of the body during deceleration (ventral rotation of the longitudinal body axis anterior to the CM: range, 1–13 degrees; mean $\pm$ S.E.M., 4.4 $\pm$ 0.8 degrees; pitching rate: range, 2–44 degrees sec^{-1}; mean $\pm$ S.E.M., 11.4 $\pm$ 2.4 degrees sec^{-1}; $N = 22$).

CONCLUSIONS

The results presented in this paper serve to aid the interpretation of locomotor function from external fin morphology in ray-finned fishes. For the selected study species, which differ markedly in pectoral fin design, large and significant differences in locomotor force magnitude and orientation exist during maneuvering. Experimental hydrodynamic study of additional taxa, however, will undoubtedly improve our understanding of the relationship between pectoral fin structure and function. In a clade as large and diverse as Actinopterygii, taxonomic exceptions to the general anatomical trends described here are easily found. Polypteriforms (bichirs and ropefish), for instance, exhibit highly derived pectoral fins with nearly vertically inclined fin bases, despite the basal position of these taxa within Actinopterygii. Similarly, certain advanced ray-finned fishes (including, for example, members of the perciform families Embiotocidae and Labridae) have much more horizontally oriented pectoral fin bases than those in closely allied clades (Drucker and Jensen, 1997; Wainwright *et al.*, 2002; Walker and Westneat, 2002). Measuring locomotor forces in such exceptional taxa, as well as in additional species following the anatomical trends illustrated in Figure 1, will provide increased statistical power for testing functional hypotheses of fin design.
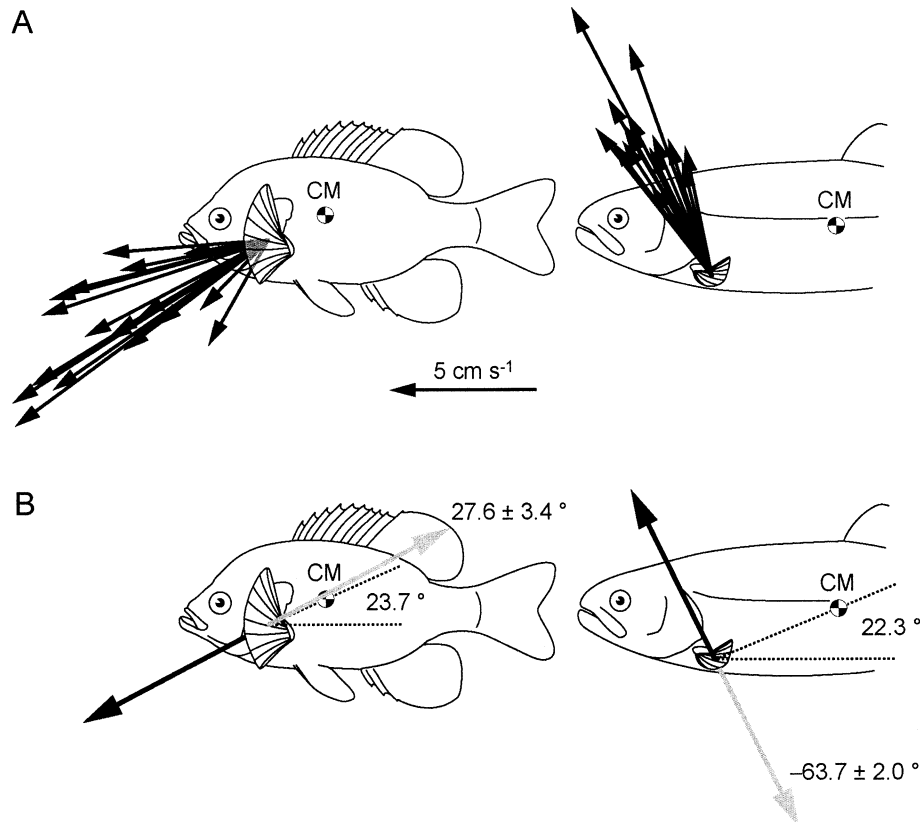
FIG. 7. Interspecific comparison of braking jet velocity and force orientation. (A) Jet velocity vectors measured for a representative individual of each species during braking. Each arrow originating from the centroid of the pectoral fin signifies the mean magnitude and orientation of multiple velocity vectors ($N = 18–116$) comprising the central wake jet for a single braking maneuver (*cf.* Fig. 6C, D). (B) Average orientation of the braking-force line of action (with standard error of the mean), defined by the mean momentum jet angle ($N=18$ and 15 braking events by sunfish and trout, respectively). Black vectors represent braking forces; gray vectors denote reaction forces. Dashed lines indicate the angle of inclination of the center of mass of the body (CM) above the horizontal. The orientation of the braking force reaction relative to the CM supports the previously untested hypotheses of Harris (1938) and Breder (1926) for fishes with mid-dorsally and ventrally positioned pectoral fins, respectively (see text).

The relationship between pectoral fin morphology and swimming performance also warrants further study. Recent investigations have examined the influence of pectoral fin shape on maneuverability (Gerstner, 1999; Webb and Fairchild, 2001), swimming speed (Wainwright *et al.*, 2002; Walker and Westneat, 2002) and propulsor efficiency (Combes and Daniel, 2001), but for other aspects of pectoral fin design the relationship between locomotor anatomy and performance is largely unknown. During low-speed yawing turns, we found that sunfish and trout exhibit a large difference in the magnitude of laterally oriented fluid force, yet show very similar turning performance, defined as the angular velocity of body rotation (Table 1). The performance comparison in this case is confounded by the fact that sunfish power body rotation primarily with the pectoral fins, while trout, having an elongate body like many other lower teleosts, supplement pectoral fin motion with axial bending to turn the body (Fig. 3D–F). We expect pectoral-fin base orientation to show a more direct relationship to turning performance in taxa with similar body forms (*e.g.,* short-bodied perciform fishes). At present, the rela-

tionship between pectoral fin position and braking performance is less clear. On the basis of our comparison between trout and sunfish, we predict that actinopterygians with pectoral fins in proximity to the center of mass of the body will have a greater ability to control body rotation during braking maneuvers than taxa with paired fins far from the CM. Yet in species with the latter fin distribution higher rates of body deceleration have been measured than in fish with the former fin arrangement (Webb and Fairchild, 2001). Continued study of the interrelationships among propulsor anatomy, locomotor force and swimming performance in taxonomically diverse ray-finned fishes will provide further insight into the functional consequences of evolutionary variation in fin design.

Acknowledgments

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