Function of pectoral fins in rainbow trout: behavioral repertoire and hydrodynamic forces

Eliot G. Drucker* and George V. Lauder

Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

*Author for correspondence (e-mail: edrucker@uci.edu)

Summary

Salmonid fishes (trout, salmon and relatives) have served as a model system for study of the mechanics of aquatic animal locomotion, yet little is known about the function of non-axial propulsors in this major taxonomic group. In this study we examine the behavioral and hydromechanical repertoire of the paired pectoral fins of rainbow trout *Oncorhynchus mykiss*, performing both steady rectilinear swimming and unsteady maneuvering locomotion. A combination of kinematic analysis and quantitative flow visualization (using digital particle image velocimetry) enables identification of the propulsive roles played by pectoral fin motions. During constant-speed swimming (0.5 and 1.0 body length s^{-1}), the pectoral fins remain adducted against the body. These fins are actively recruited, however, for a variety of maneuvering behaviors, including station holding in still water (hovering), low-speed (i.e. non-fast-start) turning, and rapid deceleration of the body during braking. Despite having a shallow pectoral-fin base orientation (the plesiomorphic teleost condition), trout are capable of rotating the fin base over 30° during maneuvering, which affords the fin an impressive degree of kinematic versatility. When hovering, the pectoral fins are depressed beneath the body and twisted along their long axes to allow anteroposterior sculling. During turning and braking, the fins undergo spanwise rotation in the opposite direction and exhibit mediolateral and dorsoventral excursions. Water velocity fields and calculated momentum flows in the wake of the pectoral fins reveal that positive thrust is not generated during maneuvering, except during the retraction half-stroke of hovering. Relatively large laterally directed fluid force (mean 2.7 mN) is developed during turning, whose reaction powers yawing rotation of the body (4–41 ° s^{-1}). During deceleration, the wake-force line of action falls below the center of mass of the body, and this result supports a long-standing mechanical model of braking by fishes with ventrally positioned paired fins. Despite its traditional categorization as a propulsor of limited functional importance, the salmoniform pectoral fin exhibits a diverse locomotor repertoire comparable to that of higher teleostean fishes.

Key words: swimming, maneuvering, locomotion, pectoral fin, vortex wake, flow visualization, digital particle image velocimetry, rainbow trout, *Oncorhynchus mykiss*.

Introduction

Teleost fishes of the order Salmoniformes have historically received much attention from experimentalists interested in aquatic animal locomotion. Many salmoniforms, such as trout and salmon, are capable of high-speed burst swimming, and undergo long-distance spawning migrations. Such high-performance swimming has stimulated both field and laboratory investigation of the locomotor biology of these fishes. Of the extensive literature on salmoniform swimming, most studies have focused on axial locomotion (i.e. propulsion by body undulation). This work has shed light on the mechanics of both fast-start acceleration (reviewed by Domenici and Blake, 1997; Hale, 1999; Ellerby and Altringham, 2001) and constant-speed rectilinear swimming, with emphasis on body kinematics (Bainbridge, 1958; Webb, 1971a, 1988; Webb et al., 1984; McLaughlin and Noakes, 1998), muscle physiology (Hudson, 1973; Bone et al., 1978;

Eugène and Barets, 1982; Williams et al., 1989; Hammond et al., 1998; Coughlin, 2000), energetics (e.g. Brett, 1964, 1965; Webb, 1971b; Facey and Grossman, 1990) and locomotor performance (recent work includes Wilson and Egginton, 1994; McDonald et al., 1998; Peake and McKinley, 1998).

One important aspect of salmoniform locomotion, however, remains poorly understood: the role of non-axial propulsors during steady and unsteady swimming. Although the primary source of mechanical power for locomotion indeed is supplied by the myotomal musculature, ancillary propulsors, including the paired fins, are commonly recruited to supplement body undulation. During routine swimming (low-speed volitional locomotion, as defined by Webb, 1991), trout and salmon have been observed to use their pectoral fins, in particular, for fine control of body position. However, aside from measurements of pectoral-fin beat frequency (McLaughlin and Noakes,

1998), information on pectoral fin function in such fishes has been strictly qualitative (e.g. the pectoral fins exhibit 'swimming movements' or 'paddling movements'). There is little detailed, quantitative information about pectoral fin use during locomotion by salmoniform fishes, and virtually nothing is known about the hydrodynamic functions served by active pectoral fin movement in this major taxonomic group.

The objective of the present study was to investigate the function of the pectoral fins in a representative salmoniform fish, the rainbow trout *Oncorhynchus mykiss*, during both steady and unsteady locomotion. Specifically, we first characterized the behavioral repertoire of trout pectoral fins by documenting patterns of use during constant-speed swimming and during three maneuvering behaviors: hovering, turning and braking. Second, we employed quantitative flow visualization to record pectoral-fin wake dynamics. Empirical measurement of wake momentum flux and of resulting fluid force enabled identification of the propulsive roles played by various pectoral fin motions. Of the several maneuvering behaviors exhibited by trout, we focused in particular on the mechanics of braking. Using experimental data on the orientation of pectoral fin forces during deceleration of the body, we evaluated a long-standing yet previously untested functional hypothesis (Breder, 1926) regarding braking in plesiomorphic ray-finned fishes.

Materials and methods
Fish
Rainbow trout (*Oncorhynchus mykiss* Walbaum) were obtained from Red-Wing Meadow Hatchery, Montague, MA, USA, and housed in circular 1200 liter tanks at 15°C. Animals were fed a maintenance ration of commercial trout chow three times weekly and acclimated to laboratory conditions for 2 weeks before experimentation. Six animals of similar size (total body length, BL=24.7±0.8 cm, mean ± S.D.) were selected for swimming trials, which were conducted at 15°C.

Anatomical measurements
Trout were anesthetized using tricaine methanesulfonate (MS-222) to allow morphological measurements of the pectoral fin. Digital photographs were taken of fish in left lateral aspect, from which pectoral-fin base angle and surface area were measured (ImageJ software, National Institutes of Health, USA). Fin base angle was taken as the angle of inclination of the axis connecting the bases of the leading- and trailing-edge fin rays, and was measured both with the pectoral fin adducted, as when at rest, and abducted, as during maneuvering locomotion. Surface area was measured with the fin in an adducted and fully expanded position. After experimentation, animals were killed by overdose of MS-222 and frozen with their bodies straight. The location of the center of mass of the body was then estimated by suspending fish from needle-tipped probes inserted bilaterally into the flank. Probes were moved along the longitudinal body axis until the

fish balanced; at that anteroposterior position, the same procedure was then performed along the dorsoventral axis. The center of mass of the body was assumed to lie at the midpoint of the transverse axis intersecting the anteroposterior–dorsoventral balance point.

Behavioral observations and wake visualization
Trout swam individually in the center of the working area (28 cm×28 cm×80 cm) of a variable-speed freshwater flow tank under conditions similar to those described in our previous research (Drucker and Lauder, 1999, 2000, 2001a,b). Three current speeds were used to elicit a range of steady and unsteady swimming behaviors. Relatively low-speed swimming was selected for study, since such behavior commonly involves use of the pectoral fins to generate locomotor forces, and comprises the majority of the time-activity and energy budgets of many fishes including salmonids (reviewed by Webb, 2002). Rectilinear axial locomotion was induced at $0.5\,BL\,s^{-1}$, the lowest speed at which fish consistently oriented upstream and held station in the current, and at $1.0\,BL\,s^{-1}$. Low-speed maneuvering locomotion was performed by trout in response to a visual and auditory stimulus. A small-diameter wooden dowel was directed into the water and toward the floor of the working area approximately 20 cm away from trout swimming steadily at $0.5\,BL\,s^{-1}$ (cf. Drucker and Lauder, 2001b). Introducing the dowel upstream of or lateral to the head elicited braking or low-speed (non-fast-start) turning, respectively. The fish's immediate response to the stimulus precluded any interaction between the pectoral fin wake and the wake shed by the dowel. In still water (i.e. with the flume current turned off), trout used slow fin motions to maintain a stable orientation and to hold body position in the water column; this behavior we termed hovering. To characterize patterns of movement of the pectoral fins and body during both steady swimming and maneuvering, fish were imaged simultaneously in lateral and ventral aspect using synchronized digital high-speed video cameras (Redlake MotionScope PCI 500) operating at 250 frames s^{-1} (1/500 s shutter speed). Review of these light video recordings (39 sequences from three fish) allowed each swimming behavior to be defined kinematically.

In separate swimming trials the wake of the pectoral fin was visualized using digital particle image velocimetry (DPIV). This technique provides empirical data on patterns of water flow in two-dimensional sections of a swimming fish's wake (as described in detail by Willert and Gharib, 1991; Drucker and Lauder, 1999; Lauder, 2000). For our DPIV experiments with rainbow trout, an 8 W continuous-wave argon-ion laser (Coherent Inc., Santa Clara, CA, USA) was focused into a thin light sheet (1–2 mm thick) which illuminated reflective microparticles suspended in the water. Particle motion induced by pectoral fin activity was recorded by imaging the laser sheet with one of the Redlake video cameras (250 frames s^{-1}, 1/1000 s shutter speed); the second camera synchonously recorded a perpendicular reference view showing the position of the fin relative to the visualized transection of the wake. In

separate experiments, the laser was oriented to reveal two perpendicular flow planes: frontal (horizontal) and parasagittal (vertical) (cf. fig. 2 in Drucker and Lauder, 1999). In this study we focused our analysis on laser planes that maximized the image of within-plane flow for each swimming behavior. During steady swimming, hovering and yawing turns, wake flow was studied within the horizontal plane; for braking, the vertical flow plane was examined.

Kinematic and hydrodynamic analysis

Unsteady maneuvers induced by the experimental stimulus involved three-dimensional body movements. To define these swimming behaviors quantitatively, continuous variation in body velocity in the X, Y and Z directions (see reference axes in Fig. 1) was partitioned into discrete ranges. The distance traveled by an anatomical reference point visible in both lateral and ventral views (the proximal end of the pectoral fin's leading edge) was measured over the course of the fin stroke duration (i.e. abduction + adduction time) using ImageJ software. These excursion and timing data allowed calculation of mean body velocities $\mathbf{X}$, $\mathbf{Y}$ and $\mathbf{Z}$ (cm s^{-1}). Such body velocities are expected to differ slightly from those obtained by tracking motion of the fish's center of mass, a landmark whose position could not be consistently imaged in our relatively high-magnification video field. For the purpose of distinguishing turning from braking, the following kinematic criteria were applied: a turning event was defined as a maneuver involving translation of the body away from the given stimulus ($\mathbf{Z}>0$) without backward displacement of the body ($\mathbf{X}\geq0$); braking was defined as maneuvers with $\mathbf{X}<0$. In addition to linear velocity, the average angular velocity of the body was calculated by measuring the degree of rotation of the

longitudinal body axis over the pectoral-fin stroke period. From ventral and lateral video views, respectively, yawing rotation during turning and pitching rotation during braking were measured ($N=22$ events per behavior).

In total, 83 DPIV video sequences of steady and unsteady locomotion from five fish were reviewed to establish general wake flow patterns. Of these, detailed quantitative analysis was restricted to scenes in which the fish swam at a constant speed, either during prolonged rectilinear locomotion or immediately before maneuvers, and the pectoral fin intersected the light sheet at approximately mid-span ($N=15$ each for turning and braking; $N=12$ for hovering; $N=5$ for steady straight-ahead swimming). Water velocity fields in the wake of the pectoral fin were calculated from consecutive digital video images (480 pixels×420 pixels, 8-bit grayscale) by means of spatial cross-correlation (Willert and Gharib, 1991). To study the relatively weak vortices shed by trout pectoral fins, we employed a new image processing algorithm that greatly improved the accuracy and spatial resolution of DPIV flow analysis. With InsightUltra software (TSI Inc., St Paul, MN, USA), which utilizes recursive local-correlation (Hart, 2000), we measured velocity fields 8–9 cm on each side that contained nearly 2300 vectors (i.e. 52 horizontal×44 vertical or 30 vectors cm^{-2}). For all swimming behaviors except hovering in still water, the average free-stream flow velocity of the flume was subtracted from each vector matrix to reveal vortical structures in the wake and to allow measurement of flow structure and strength (for details, see Drucker and Lauder, 1999). Vortex circulation was calculated using a custom-designed computer program. Jet flow induced by pectoral fin motion was quantified as follows: (i) jet velocity was measured as the mean magnitude of velocity vectors comprising the
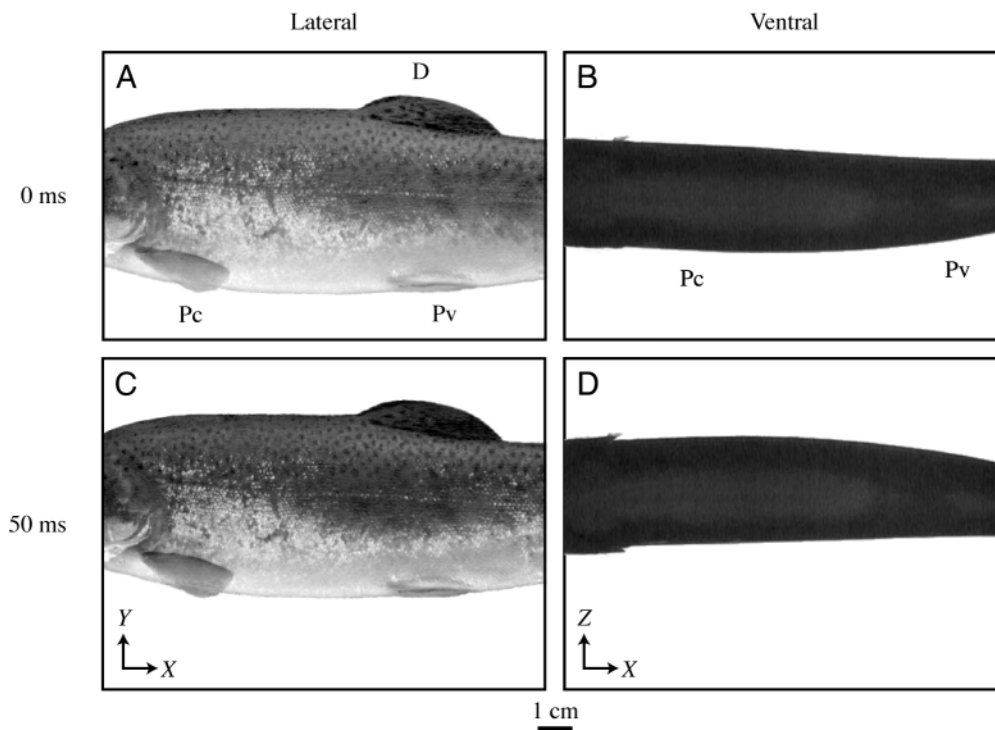

Fig. 1. Light video images of steady swimming by rainbow trout at $1\,BL\,\text{s}^{-1}$, recorded simultaneously in lateral and ventral views. As a traveling wave of bending passes posteriorly along the body from time 0 (A,B) to time 50 ms (C,D), the paired fins remain at rest in an adducted position. Pc, position of the left pectoral fin; Pv, position of the left pelvic fin. The dorsal fin (D) is relatively depressed during constant-speed straight-ahead locomotion.

region of accelerated flow; (ii) jet angle was taken as the average orientation of these vectors, measured relative to the longitudinal axis of the fish at the onset of the pectoral fin stroke. Both jet measurements were made at the end of pectoral fin adduction, at which time vortices and associated jet flow were fully developed.

Estimating the fluid force exerted by the pectoral fin involved measuring the rate of change in wake momentum over the stroke duration. On the basis of observed planar flow patterns (see Results), the three-dimensional shape of the wake generated by each fin stroke was taken as a vortex ring (cf. Drucker and Lauder, 1999, 2000, 2001b). Ring momentum was calculated as the product of water density, vortex circulation and ring area (the latter two measurements made at the end of the fin stroke). Ring area was taken as πR^2, where R is half the distance between paired vortex centers. Following earlier work (Milne-Thomson, 1966), time-averaged wake force was then computed as the total momentum divided by the period of propulsive fin motion. Total force exerted by the pectoral fin was resolved geometrically into perpendicular components within the frontal plane (thrust and lateral force) and parasagittal plane (thrust and lift) according to the mean jet angle. Further details of the calculation of wake force by this method can be found in earlier studies (Spedding et al., 1984; Dickinson, 1996; Dickinson and Götz, 1996; Drucker and Lauder, 1999). The accuracy of wake force estimates provided by the DPIV technique has previously been demonstrated by the measurement of a hydrodynamic force balance on steadily swimming fishes (Drucker and Lauder, 1999; Nauen and Lauder, 2002a).

Results

Behavioral and kinematic patterns

Recruitment and kinematics of the pectoral fin varied markedly with the mode and speed of locomotion. During steady straight-ahead swimming, the pectoral fins showed no movement, remaining in a fully adducted position on both sides of the body (Fig. 1). Both at 0.5 and $1.0\,BL\,s^{-1}$, rectilinear locomotion was powered solely by axial undulation. By contrast, during all maneuvering behaviors examined in this study, the paired fins were invariably active. While hovering at $0\,BL\,s^{-1}$, trout maintained a stable, horizontal orientation in the water by sculling the left and right pectoral fins beneath the body. These fin motions were bilaterally symmetrical in excursion, but out of phase temporally such that protraction of one fin coincided with retraction of the contralateral fin. Throughout the hovering stroke period, the pectoral fins were held in an abducted position while moving fore and aft (Fig. 2).

Low-speed turning maneuvers elicited from trout were submaximal escape responses involving excursions of both pectoral fins. At the onset of a turn, as the experimental stimulus was issued (Fig. 3A,B), the pectoral fin on the same side of the body as the source of the stimulus (the 'strong-side' fin) rapidly abducted and the body rotated toward the contralateral or 'weak' side (Fig. 3C,D). As the fish translated away from the stimulus, the strong-side fin returned toward the body while the weak-side fin, delayed in its movements, reached a position of maximal abduction. This turning maneuver in trout involved both yawing rotation (mean $13\,^{\circ}\,s^{-1}$) and bending of the anterior trunk (Fig. 3E,F; Table 1). Rapid deceleration of the body, unlike turning, was
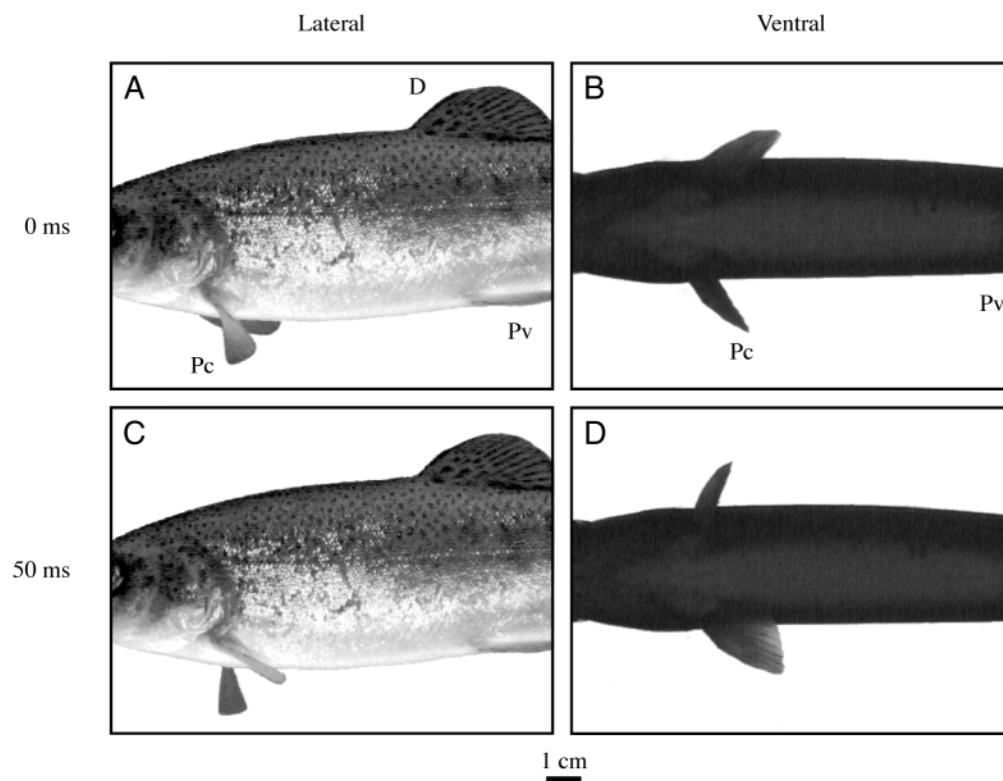

Lateral   Ventral

Fig. 2. Hovering in still water ($0\,BL\,s^{-1}$) at 0 (A,B) and 50 ms (C,D). This behavior involves maintenance of both horizontal and vertical body position, and is characterized by moderate erection of the dorsal fin and low-speed sculling of the pectoral fins beneath the body. The left and right pectoral fins move out of phase with each other such that when one fin is protracted the contralateral fin is retracted. Abbreviations as in Fig. 1.
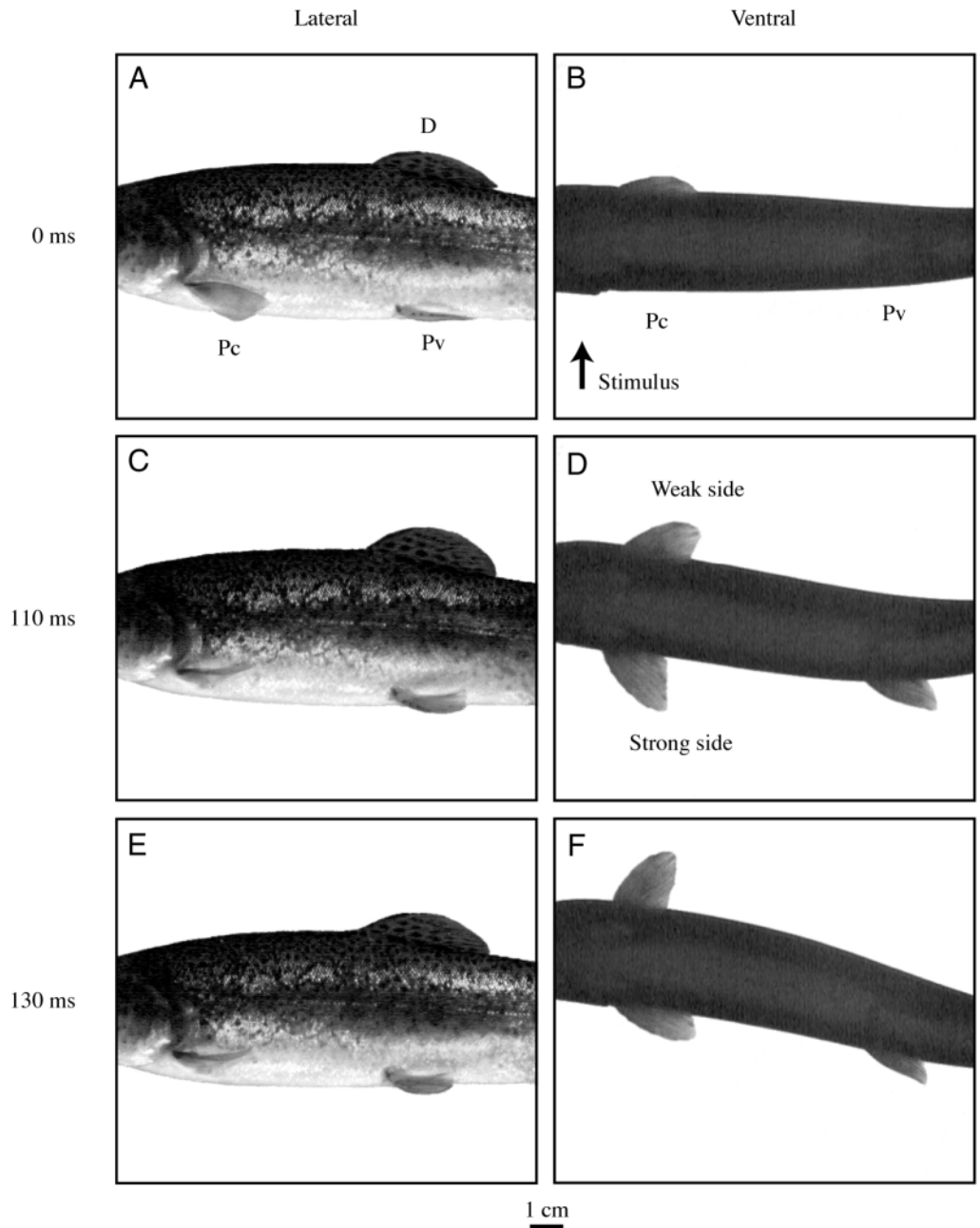
1 cm

Lateral   Ventral

Fig. 3. Low-speed turning (non-fast-start escape response). While swimming steadily at $0.5\,BL\,s^{-1}$, trout are exposed to a visual and auditory stimulus (at 0 ms; A,B), which elicits rapid abduction of the strong-side pectoral fin (i.e. the fin closer to the source of the stimulus). The weak-side pectoral fin shows slower and delayed abduction. These propulsor motions are accompanied by slight dorsal fin erection and abduction of the strong-side pelvic fin (at 110 ms; C,D). During the turning maneuver, the body of the fish yaws and translates toward the weak side (at 130 ms; E,F). Abbreviations as in Fig. 1.

characterized by temporally and spatially symmetrical excursions of the left and right pectoral fins. When trout were stimulated to brake, the fins were synchronously abducted and flexed along their long axes so that the trailing edges were elevated and protracted (Fig. 4A–D). These fin motions caused the fish to move posteriorly and to pitch nose-downward (mean $11\,^{\circ}\,s^{-1}$) (Fig. 4E,F; Table 1).

Pectoral-fin stroke timing and linear velocity of the body during maneuvering also varied significantly with behavior. During turning and braking, the fin stroke generating the strongest wake flow, and hence greatest fluid force, was abduction. The duration of pectoral fin abduction (T_{AB}) was 127 ± 8 and $207\pm13\,ms$ (mean ± S.E.M.), respectively, for these two maneuvers (unpaired t-test, d.f.=28; $P<0.01$). By

definition, turning and braking differed in the direction of body motion along the X-axis. For the former, the body moved anteriorly over the course of the pectoral-fin stroke cycle ($\mathbf{X}=+0.9\,cm\,s^{-1}$ on average); for the latter, body motion was posteriorly directed (mean $\mathbf{X}=-3.5\,cm\,s^{-1}$) (Fig. 5). In addition, turns involved significantly faster body translation toward the weak side (mean difference=$1.6\,cm\,s^{-1}$; t-test, d.f.=28; $P<0.001$). Both maneuvering behaviors were characterized by sinking in the water column ($\mathbf{Y}<0$), with braking exhibiting a greater downward body velocity than turning by $1.6\,cm\,s^{-1}$ on average (Fig. 5).

Wake dynamics and locomotor force

Pectoral fin motions exhibited during maneuvering generate

Table 1. *Kinematic and hydrodynamic measurements for pectoral fin maneuvers by rainbow trout*

				Wake force (mN)		
Maneuver	Angular velocity of body (degrees s^{-1})	Mean jet angle (degrees)	Mean jet velocity (cm s^{-1})	Lateral	Anterior	Dorsal
Hovering						
Protraction	–	118.5±5.4	3.6±0.3	–	–	–
Retraction	–	32.2±3.8	4.8±0.4	–	–	–
Turning	13.5±2.4	121.4±5.0	5.9±0.4	2.7±0.9 (0.8±0.3)	1.1±0.2 (0.4±0.1)	–
Braking	11.4±2.4	116.3±2.0	6.1±0.3	–	2.5±0.6 (0.7±0.1)	4.7±1.5 (1.5±0.2)

Values are means ± S.E.M. (N=12–22 events from two individuals per measurement).

Measurements for hovering and turning were made in ventral view (frontal-plane velocity field, *XZ*), and for braking in lateral view (parasagittal-plane velocity field, *XY*).

Angular velocity of body data report the rate of yawing rotation and nose-down pitching of the longitudinal body axis during turning and braking, respectively (not measured for hovering). For turning and for the protraction half-stroke of hovering, tabulated jet angles indicate wake flow oriented anterolaterally; for the retraction half-stroke of hovering, the average jet angle represents posteromedial flow; and for braking, the jet is directed anterodorsally.

Wake forces are stroke-averaged measurements reported per fin. Laterally, anteriorly and dorsally oriented components of force are reported for turning and braking, with force per unit pectoral fin area (mN cm^{-2}) in parentheses.
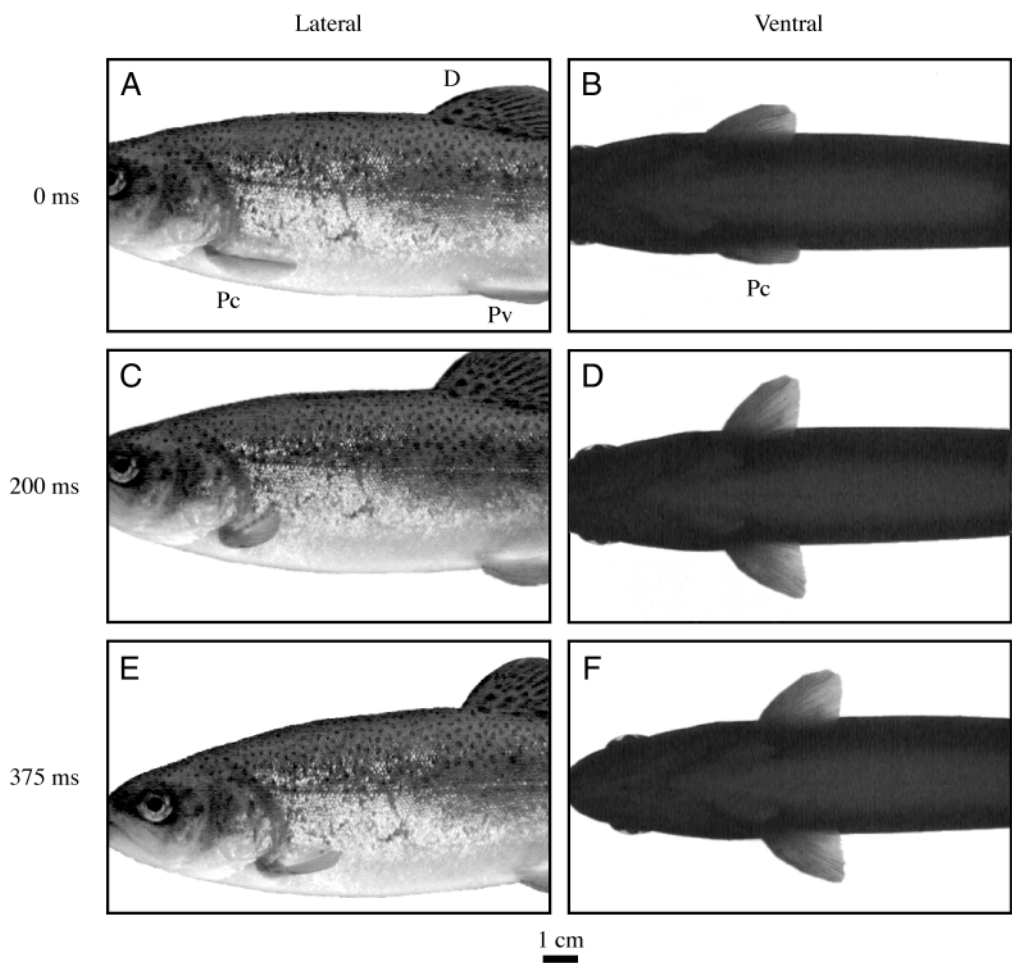

Fig. 4. Braking maneuver. Trout swimming steadily at 0.5 *BL* s^{-1} (at 0 ms; A,B) react to an upstream stimulus by abducting the left and right pectoral fins simultaneously and erecting the dorsal fin (at 200 ms; C,D). The pectoral fins' trailing edges are elevated and protracted resulting in a characteristic 'cupping' of the fins along their longitudinal axes. These fin motions decelerate the body and cause the snout to pitch ventrally (at 375 ms; E,F). Abbreviations as in Fig. 1.
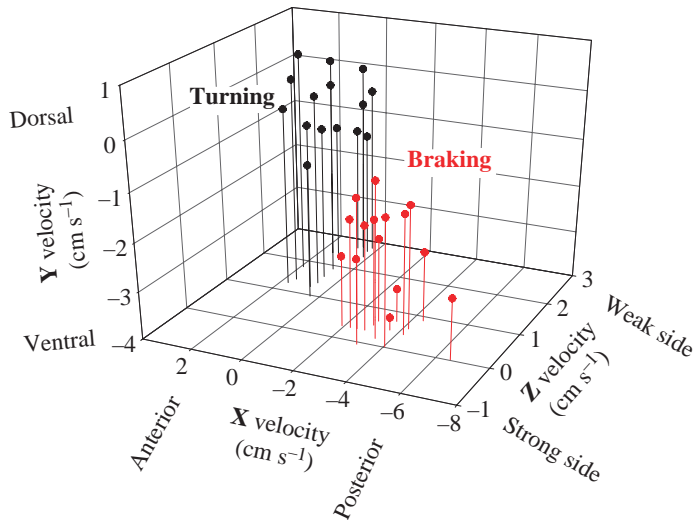
Fig. 5. Velocity of body excursions in three dimensions during turning and braking maneuvers. Text labels on the *X*, *Y* and *Z* reference axes (cf. Fig. 1) signify the direction of body movement. Each plotted point reflects the distance traveled by a reference point on the pectoral fin base over the entire fin stroke duration. Turning is characterized by anterior body movement and significantly faster translation toward the weak side than braking. Both maneuvers involve sinking in the water column (i.e. **Y** velocity<0).

distinctive wake flow patterns. While maintaining a stationary body position in still water, trout use asymmetrical left- and right-side fin strokes to produce alternating anterior- and posterior-directed jet flow. During this hovering maneuver, fin protraction results in the entrainment of water behind the propulsor; flow around the lateral and medial margins of the fin takes the form of paired attached vortices with opposite-sign circulation (Fig. 6, left side). These vortices remain bound to the fin at the end of the protraction half-stroke, and are not shed anteriorly as free vorticity. At the end of the retraction half-stroke, the pectoral fin is feathered and sheds attached flow posteriorly into the wake (Fig. 6, right side). Because contralateral fin strokes are out of phase with each other, wake flow is generated in opposite directions on opposite sides of the body at once (velocity range=1.1–7.5 cm s^{-1}; Table 1). During turning, by contrast, the dominant wake flow is generated unilaterally. Abduction of the strong-side fin results in the appearance of a single free vortex within the horizontal plane of analysis. This flow structure contains a region of relatively high-velocity jet flow oriented anteriorly and laterally (Fig. 7B). Braking maneuvers are characterized by the production of paired counterrotating vortices by each pectoral fin. Each half-stroke generates a single vortex, with abduction typically creating stronger rotational flows than adduction (cf. clockwise and counterclockwise vortices in Fig. 7D). For braking and turning, the velocity of the central region of accelerated flow ranged from 2.5 to 11.3 cm s^{-1} (mean 6 cm s^{-1}; Table 1).

The paired-vortex flow pattern observed for trout during deceleration of the body is similar to that noted previously for

other fishes swimming by pectoral fin propulsion (Drucker and Lauder, 1999, 2000, 2001b), and we assume that centers of opposite-sign rotation within planar flow fields represent transections of a roughly symmetrical, three-dimensional vortex ring (see also Spedding et al., 1984; Spedding, 1986; Nauen and Lauder, 2002a). Vortex circulation generated by fin abduction (Γ_{AB}) exceeded that produced by fin adduction (Γ_{AD}) by nearly twofold on average (mean ± S.E.M.=19.9±1.4 and 11.4±0.9 cm^2 s^{-1}, respectively). This pattern contrasts with results of earlier DPIV studies of fishes swimming by pectoral fin propulsion, in which Γ_{AB} and Γ_{AD} were comparable (e.g. Drucker and Lauder, 1999). In perfect cross sections of a symmetrical vortex ring, opposite-sign paired vortices have circulations of equal magnitude, according to Helmholtz's theorem (Fung, 1990). In our studies with trout, to avoid underestimating total vortex ring circulation due to possible out-of-plane flow on adduction, or by non-transverse sectioning of the vortex ring, we calculated stroke-averaged wake momentum during braking using Γ_{AB} only, rather than the mean of Γ_{AB} and Γ_{AD}. Pectoral fin force then was taken as this momentum value divided by T_{AB}. For turning, during which only one vortex appears on abduction, momentum and force were calculated similarly by modeling 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). In this case, 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.

Turning maneuvers were characterized by the production of anterolaterally directed wake force, with the lateral component exceeding the anterior component by a factor of 2.5 on average (Table 1). Braking involved the exertion of significantly greater anterior force than turning (unpaired *t*-test, d.f.=28; *P*<0.05), and a substantial dorsally oriented component of force. When corrected for interindividual variation in pectoral fin area (mean ± S.D.=3.18±0.34 cm^2, *N*=4 fish) swimming forces ranged from approximately 0.5 to 1.5 mN cm^{-2} (Table 1). Since the three-dimensional morphology of the wake was not well defined for hovering, locomotor forces were not estimated for this behavior.

Discussion
Kinematic repertoire of the trout pectoral fin

Despite its traditional categorization as a propulsor of limited functional importance as compared to the relatively larger and more laterally positioned pectoral fin of perciform fishes, the salmoniform pectoral fin exhibits a diverse locomotor repertoire that complements the swimming functions served by steady axial undulation. The range of motion of the fin observed during locomotion by *Oncorhynchus mykiss* is summarized in Fig. 8. When at rest, as during steady swimming (cf. Fig. 1A), the pectoral fin remains fully adducted with the first (leading edge) fin ray defining the dorsal margin of the fin surface (Fig. 8A). During hovering in still water (cf. Fig. 2A), the fin is abducted,

depressed and twisted along its long axis so that the surface which before the maneuver faced medially becomes
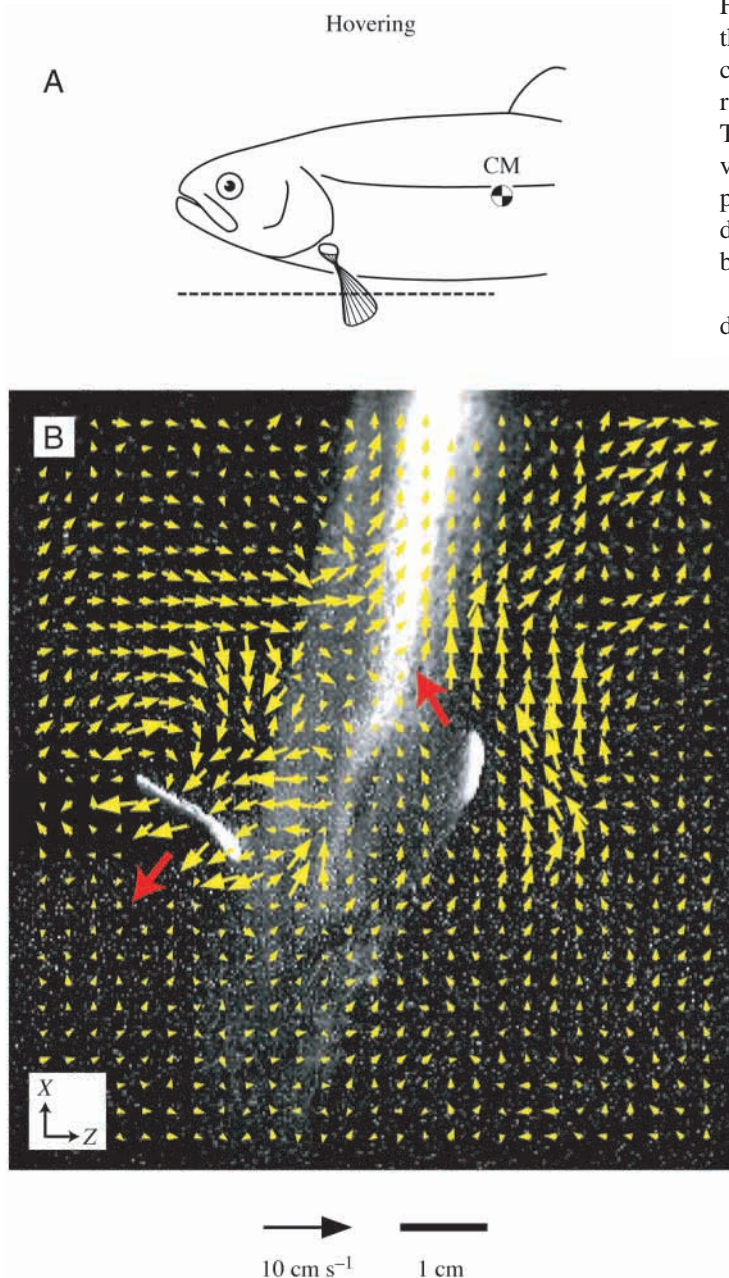

Fig. 6. Visualization of pectoral-fin wake flow during hovering. (A) Schematic illustration of the left pectoral fin in a protracted position (cf. Fig. 2A) intersecting a horizontal laser plane (broken line). High-speed video images of this plane (*XZ*) recorded from below were used to calculate velocity vector fields, an example of which is shown in (B). The fish maintains its position in still water using asymmetrical left–right pectoral fin motions (direction indicated by red arrows). As the fin at left protracts, fluid behind the fin is entrained and drawn anteriorly. At the same time, the fin at right retracts and sheds attached flow posteriorly. These momentum flows are balanced on the following half-stroke as each fin assumes the other's position. The center of mass of the body (CM) of trout used in this study was located at a longitudinal position $39\pm2\%\,BL$ (mean $\pm$ S.D.) posterior to the snout.

posteriorly oriented (Fig. 8B). Low-speed turning involves similar spanwise rotation but in the opposite direction and with the fin above rather than below the ventral body margin (cf. Fig. 3C). This fin motion causes the initially medial surface of the fin to face dorsally (Fig. 8C). Braking maneuvers are characterized by elevation of the fin's trailing edge, which results in a 'cupped' appearance of the fin blade (cf. Fig. 4C). The leading edge is substantially depressed to define the ventral margin of the fin. During deceleration of the body, the pectoral fin undergoes more extreme longitudinal rotation than during turning such that the originally medial-facing surface becomes laterally and dorsally oriented (Fig. 8D).

The impressive kinematic versatility of the trout pectoral fin during maneuvering may be facilitated by the mobility of the fin base. In previous studies of paired fin function in fishes, the angle of inclination of the fin's insertion on the body (δ) has been viewed as influencing the propulsor's kinematic range of motion (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 primarily anteroposterior (fore-and-aft) motions within a horizontal plane, whereas more horizontally oriented bases dictate a primarily dorsoventral (up-and-down) motion within a vertical plane (see Drucker and Lauder, in press). In rainbow trout, the insertion of the pectoral fin on the body is a flexible hinge joint, which defines a primary dorsoventral kinematic axis but also allows additional degrees of freedom of motion. When the pectoral fin is adducted (e.g. at rest during steady swimming), the base of the fin lies at a moderate angle to the horizontal (mean $\pm$ S.D.$=42\pm5°$, $N=4$ fish) (Fig. 8A). However, when the fin is abducted (i.e. in a position relevant for propulsion), the anterior fin base is depressed, which markedly reduces δ (Fig. 8B–D; mean $\pm$ S.D.$=10\pm3°$). Similar mobility of the pectoral fin base is visible in trout and salmon performing agonistic displays (see fig. 7 in Kalleberg, 1958). In salmoniform fishes, contraction of the arrector ventralis ('Marginalmuskel' of Jessen, 1972), which inserts on the proximal end of the first fin ray, may play an important role in causing this fin rotation.

With a nearly horizontal pectoral fin base during maneuvering, coupled with spanwise fin rotation, trout can achieve fore-and-aft fin movements that are critical for the generation of anteroposterior wake flows (Figs 6, 7). In general, fin base angle cannot be considered a fixed meristic for a given species, but rather a variable whose value depends on propulsor motion. Fin base angle as measured externally may be influenced by changes in position of the bases of pectoral fin rays relative to internal skeletal elements such as the radials, scapula and coracoid supporting the fin. Each of these elements is mobile, although magnitudes of pectoral girdle excursion during locomotion are not known. For relating fin design to locomotor kinematics and function (e.g.

Drucker and Lauder, 2001a, in press), the most appropriate measure may be the 'functional fin base angle' — the degree of inclination of the fin in a position used for swimming.

The absence of pectoral fin motion during steady swimming by the fish examined in this study conflicts with the results of an earlier report of the swimming behaviors of
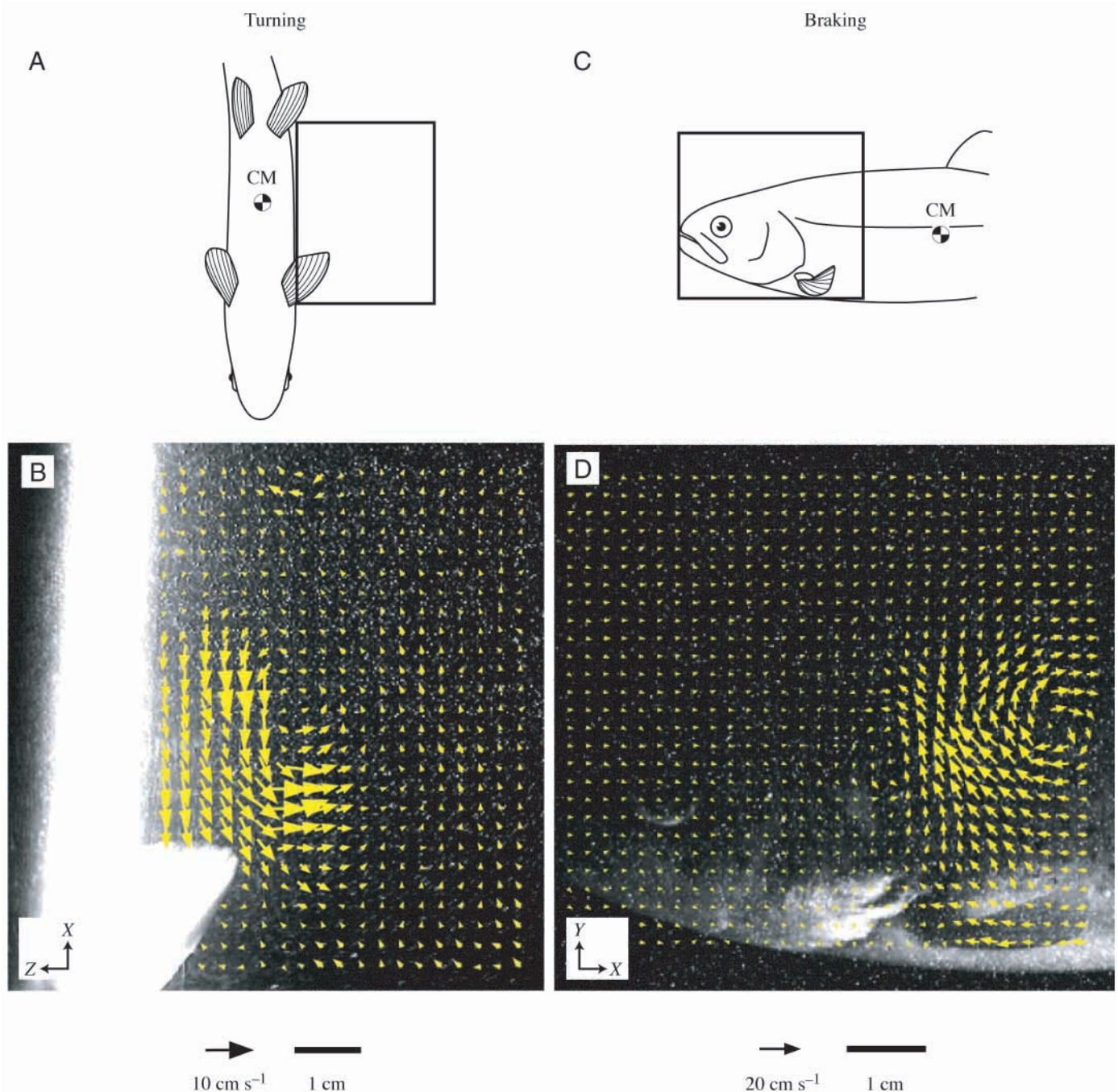

Fig. 7. Representative wake flow patterns during pectoral-fin turning and braking maneuvers. (A,C) Line drawings (not to scale) depict trout in ventral view during turning with the strong-side pectoral fin abducted (A) (cf. Fig. 3D) and in lateral view during braking with the fin 'cupped' (C) (cf. Fig. 4C). Boxed regions indicate areas within the laser light sheet for which velocity vector fields were calculated. (B) During slow turning, pectoral fin abduction generates a single vortex within the horizontal plane with an anterolateral-facing fluid jet. Fin adduction on the following half-stroke contributes no additional vorticity within this plane of analysis. (D) During braking, elevation and abduction of both pectoral fins at once generates a strong vortex on each side of the body visible in the vertical plane (clockwise flow at right side of panel); subsequent depression and adduction of the fins produces weaker counterrotating vortices (counterclockwise flow centered above base of fin). The central fluid jet between paired rotational centers is oriented anterodorsally. In B and D, the mean free-stream flow velocity ($0.5\,BL\,s^{-1}$ in the X direction) has been subtracted from each velocity vector. CM, center of mass of the body.

trout in their natal streams (McLaughlin and Noakes, 1998). For young-of-the-year brook trout *Salvelinus fontinalis*, the relationship between pectoral-fin beat frequency and swimming speed was highly variable, but the frequency of oscillation decreased significantly as speed increased. However, a majority of the fish observed during steady locomotion (approximately 65%) beat their pectoral fins at all swimming speeds (fig. 1C in McLaughlin and Noakes, 1998). This fin activity observed in the field may not be directly comparable to that documented under more controlled laboratory conditions. When swimming against a current with large-scale turbulence, as in natural streams, trout are likely

required to use their paired fins for correcting heading and attitude in response to local flow disturbance. Such stabilizing behavior is not expected when fish swim against a microturbulent current, as in the present flow tank study. Our results indicate for trout that corrective pectoral fin motions may not be necessary during steady swimming if the flow environment is sufficiently homogeneous. Further investigation of propulsor motions used in the field, in particular involving quantitative kinematic analysis, will improve our understanding of the diverse behavioral repertoire of the salmoniform pectoral fin.

Pectoral fin function during maneuvering locomotion

The use of quantitative flow visualization to study the wake of freely swimming fish provides insight into the functional roles played by the fins during locomotion. Previous studies have collected empirical data on wake flow generated by rainbow trout, but this work has focused on the mechanics of the axial propeller during straight-ahead constant-speed swimming (Blickhan et al., 1992; Lauder et al., in press; Nauen and Lauder, 2002b). The present application of DPIV to investigate wake dynamics in trout has revealed that the paired fins also serve important locomotor functions, in particular during unsteady maneuvering.

For negatively buoyant fishes (e.g. *Synchropus picturatus*; Blake, 1979) as well as for flying animals (insects and birds; Weis-Fogh, 1973; Rayner, 1979; Ellington, 1984), hovering involves the generation of relatively large lift forces with the paired appendages to balance body weight. For rainbow trout, which are only slightly negatively buoyant (Webb, 1993), 'hovering' motions of the paired fins undoubtedly generate some lift, but serve primarily to maintain a stationary and stable body position in still water. Unlike many other fishes that undulate large, broad-based pectoral fins along their anteroposterior axes (e.g. Blake, 1978), trout possess relatively small pectoral fins, which oscillate about narrow bases in a fore and aft motion during hovering. The broadside orientation of the fin during the protraction half-stroke results in an induced jet flow behind the propulsor directed anteriorly (left side of Fig. 6; Table 1); this momentum flow toward the surface of the fin reflects the production of drag. During the retraction half-stroke of hovering, the pectoral fin is feathered slightly, allowing attached fluid to be shed away from the fin and into the wake posteriorly (right side of Fig. 6; Table 1), a thrust-producing flow pattern (cf. Drucker and Lauder, 2002). When hovering, therefore, each pectoral fin serves the alternating functions of braking and propulsion. Playing these roles simultaneously on opposite sides of the body, the fins exert a rotational moment around the center of mass of the body during each half-stroke. Over the course of two consecutive half-strokes opposite-sign moments are balanced, as evidenced by the lack of discernible yawing of the body during this maneuver.

Unlike fast-start turning, which is characterized by extreme and rapid axial bending (e.g. Domenici and Blake, 1997), the turning behavior examined in this study was a low-speed startle
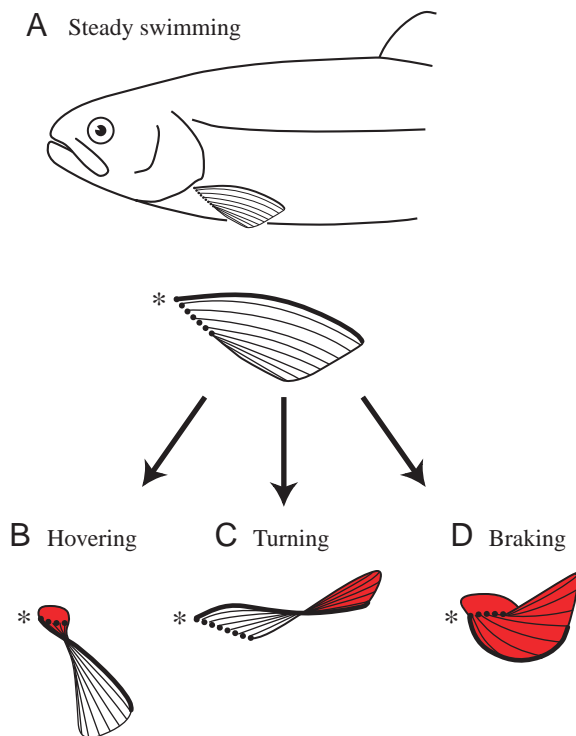

Fig. 8. Kinematic repertoire of the pectoral fin of rainbow trout. (A) During steady swimming, the fin remains adducted against the body (cf. Fig. 1A). The enlarged image of the fin below the body illustrates the angle of inclination of the fin base (dotted line) and the first fin ray (thick line), whose proximal end is indicated by an asterisk. During the maneuvering behaviors examined in this study, pronounced rotation and flexion of the pectoral fin was observed. In B–D, white and red areas indicate fin surfaces that face laterally and medially, respectively, when the fin is at rest in an adducted position (as in A). (B) While hovering, trout twist the fin along its spanwise axis (cf. Fig. 2A) to enable fore-and-aft sculling beneath the body. (C) Turning is characterized by rotation of the fin in the opposite direction above the ventral body margin (cf. Fig. 3C). (D) Braking involves fin rotation in the same direction as during turning, but to a greater degree such that the fin surface which faces medially at rest becomes dorsolaterally oriented (cf. Fig. 4C). Note that the pectoral fin base rotates to a nearly horizontal orientation during maneuvering locomotion. The considerable kinematic versatility of the trout pectoral fin permits a range of locomotor functions comparable to that of more derived teleost fishes.

reaction powered primarily by the pectoral fins. In response to the experimental stimulus, trout used strong-side pectoral fin abduction to yaw the body (angular velocity range=4–41 ° s^{-1}; Table 1) and to translate it toward the weak side (linear velocity range=1.0–2.8 cm s^{-1}; Fig. 5). These body velocities are comparable to those measured in bluegill sunfish *Lepomis macrochirus* performing the same maneuver (Drucker and Lauder, 2001b). In trout, pectoral fin abduction during turning generates anterolaterally directed wake flow (Fig. 7B). The fluid force acting to move the fish away from the turning stimulus arises in reaction to the dominant laterally oriented component of momentum added to the wake. Despite the production also of an anterior component of pectoral fin force (mean 1.1 mN, Table 1), whose reaction resists forward motion of the body, trout were consistently observed to travel anteriorly during turning (**X**>0, Fig. 5). One explanation for this phenomenon is that turning forces are not generated solely by the pectoral fins. In addition to strong-side pectoral fin motion, turning trout exhibited low-amplitude axial bending and abduction of the pelvic fin posterior to the center of mass (Fig. 3), as well as abduction of the dorsal fin toward the strong-side of the body (not figured; fin obscured by body in ventral view, Fig. 3). These propulsive fin motions may contribute to the forward translation of the body observed during the maneuver. The simultaneous use of multiple fins by fishes is well documented (e.g. Arreola and Westneat, 1996; Gordon et al., 2000). However, the partitioning of swimming force among these propulsors as yet has received very little experimental study (see Drucker and Lauder, 2001a, 2002).

The pattern emerging from analysis of wake dynamics in trout is that the pectoral fins do not function primarily as thrust-generating surfaces. Although the fins can indeed generate posteriorly oriented fluid flow, this function is limited to the retraction stroke of hovering during which jet velocities are relatively low. For the other maneuvers examined here, the largest component of locomotor force was oriented either laterally (turning) or anteriorly and dorsally (braking) (Table 1). The regulation of body posture and position by the paired fins of trout provides a clear example of active stability maintenance in fish to control both external (i.e. turbulence-induced) and self-generated (i.e. locomotor) perturbations (cf. Weihs, 1993; Webb, 1993, 2002).

Hydrodynamics of braking: testing Breder's hypothesis

In an effort to decelerate their bodies, ray-finned fishes (Actinopterygii) commonly extend the pectoral fins bilaterally to produce a retarding drag force (Breder, 1926; Harris, 1938; Bainbridge, 1963; Videler, 1981; Geerlink, 1987; Jayne et al., 1996; Webb and Fairchild, 2001). One influential model proposed in the early part of the twentieth century attempts 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. 9A). Since the center of pressure of the pectoral fin (taken as the centroid of the fin surface) lies below the center of mass
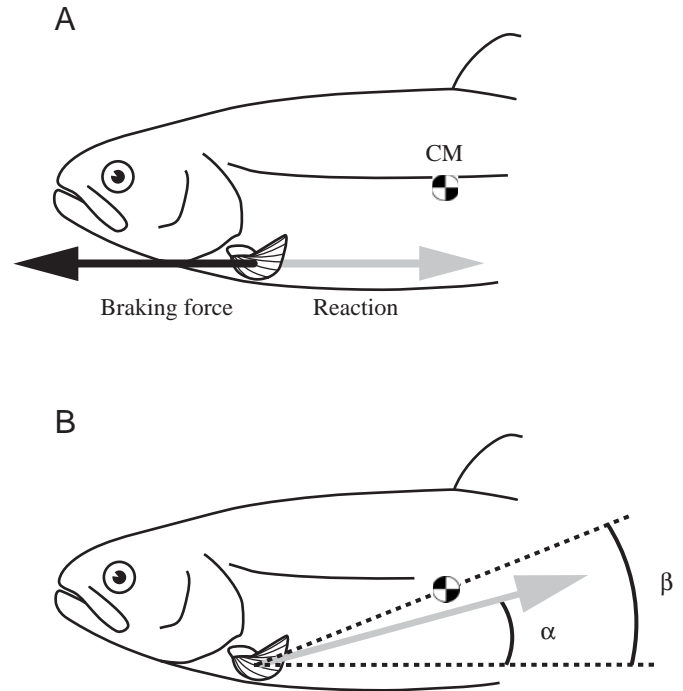

Fig. 9. Experimental evaluation of the braking hypothesis of Breder (1926). (A) Fishes such as trout possessing pectoral fins located ventrally on the body are predicted to exert an anteriorly directed braking force (black vector). The reaction to this horizontal momentum flow (gray vector) decelerates the body. We tested Breder's hypothesis that the line of action of the braking force lies below the center of mass of the body (CM) using anatomical and hydrodynamic measurements from *Oncorhynchus mykiss*. (B) An arbitrarily oriented braking reaction force (stroke-averaged) is shown to illustrate two angles within the parasagittal plane: (i) the angle α between the longitudinal axis of the fish and the line of action of the braking force acting on the fin; (ii) 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.

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. Although much-cited since its introduction, the model of Breder has persisted untested in the literature.

We used rainbow trout as a representative plesiomorphic actinopterygian taxon possessing anteriorly and ventrally positioned pectoral fins to evaluate the following hypothesis: during paired-fin braking, the line of action of the braking force lies below the center of mass of the body (Breder, 1926) (Fig. 9A). The experimental measurements required to test this hypothesis are illustrated in Fig. 9B: using parasagittal-plane DPIV we compared the angular inclination of the stroke-averaged reaction force vector to that of the CM. Breder's model was considered supported if the former is significantly less than the latter.

Although rainbow trout have a more limited ability to extend

the pectoral fins from the body than do many derived fishes (e.g. Gibb et al., 1994; Westneat, 1996; Drucker and Jensen, 1997; Walker and Westneat, 1997; Drucker and Lauder, in press), this species can nevertheless generate an anteriorly directed component of force for decelerating the body. During braking, trout rapidly bend the pectoral fin along its
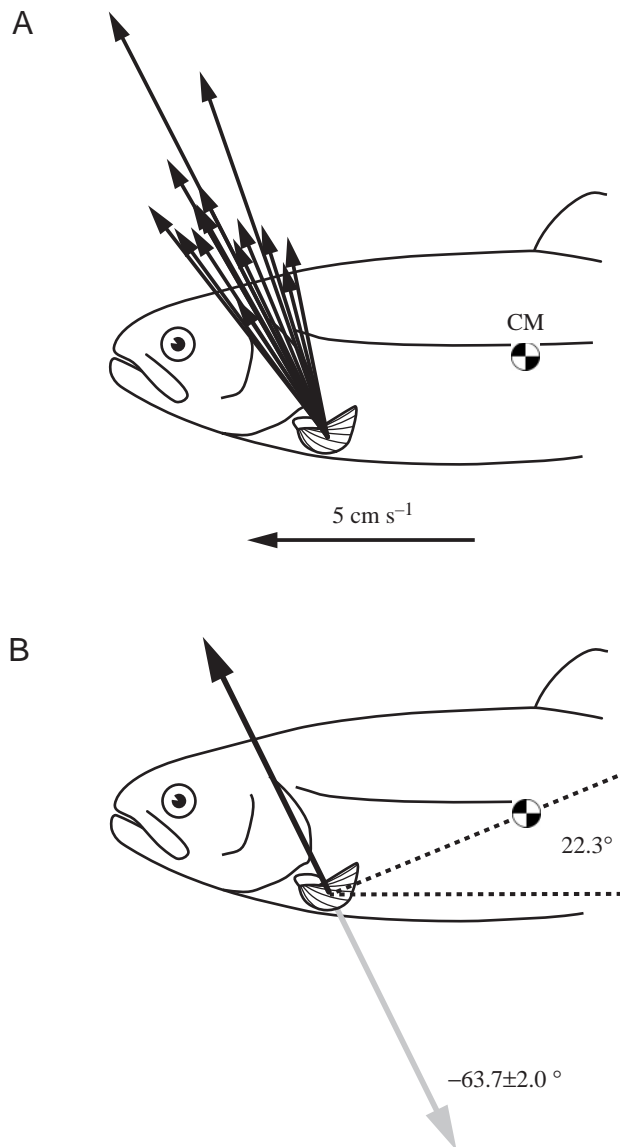

Fig. 10. Jet velocity vectors measured from the braking wake of trout. (A) Each arrow originating from the centroid of the pectoral fin signifies the mean magnitude and orientation of multiple velocity vectors (N=32–116) comprising the central wake jet for a single braking maneuver (cf. Fig. 7D). (B) Average orientation of the braking-force line of action (± S.E.M.), defined by the mean momentum jet angle (N=15 braking events). Black and gray vectors represent braking force and reaction force, respectively. Broken lines indicate the angle of inclination of the center of mass of the body (CM) above the horizontal (22.3°). The orientation of the braking force reaction relative to the CM supports a previously untested hypothesis (Breder, 1926) for fishes with ventrally positioned pectoral fins.

longitudinal axis so that the trailing edge is elevated and protracted (Fig. 4). A similar pectoral fin motion has been observed in juvenile salmonid fish during benthic station-holding (e.g. Kalleberg, 1958; Keenleyside and Yamamoto, 1962; Arnold et al., 1991). The function of this fin motion is to direct a central wake jet (i.e. relatively high-velocity fluid flow between counterrotating vortices) in an anterodorsal direction (Figs 7D, 10A; Table 1). The average orientation of the braking-force line of action, defined by the mean momentum jet angle, is summarized in Fig. 10B. In trout, the braking reaction force is inclined on average at an angle of 64° below the horizontal. This angle α is significantly less than the angle of inclination of the center of mass of the body (one-sample comparison of α to hypothesized mean β of 22.3°: d.f.=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. 9A) indicates that ventrally positioned pectoral fins may have larger than expected moment arms for exerting torque around the CM. During braking we observed 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 erected and 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 (Fig. 4C). In spite of these simultaneous fin motions to control the braking maneuver, however, trout exhibit pronounced pitching of the body during deceleration (Fig. 4A,C,E; ventral rotation of the longitudinal body axis anterior to the CM, range: 1–13°; pitching rate: 2–44 ° s^{-1}).

The potential importance of multiple fin surfaces in controlling braking is revealed through a comparison of forces derived from wake velocity fields and from the dynamics of body motion. From analysis of DPIV data, we estimate the anteriorly directed braking force generated by the left and right pectoral fins together as 5 mN (i.e. 2 fins × 2.5 mN, Table 1). Following Newton's second law, we can calculate the total force required to decelerate the body using mean kinematic measurements from *Oncorhynchus mykiss*. During braking, trout decrease their forward velocity by 3.5 cm s^{-1}, on average (Fig. 5), over the duration of the pectoral-fin stroke cycle (the period of abduction + adduction, mean 430 ms), and therefore experience a mean body deceleration of 8 cm s^{-2}. For trout of the length studied (body mass approximately 160 g; Webb, 1991), such a deceleration requires a total braking force of 13 mN. We conclude that the two- to threefold discrepancy between pectoral fin force and total braking force reflects a significant contribution of the median fins (tail, dorsal and anal fins) and pelvic fins to body deceleration.

It is noteworthy that Breder (1926) selected *Esox* sp. as a representative long-bodied fish for modeling pectoral fin braking. In such fishes, the paired fins are protracted beneath the body to generate anteriorly directed force (fig. 57A in Breder, 1926). Although *Oncorhynchus mykiss* is fully capable

of such excursions (e.g. during hovering, Fig. 2A,C), our experimental population never used them in this way in response to the braking stimulus offered. Empirical flow visualization work with additional taxa is required to define better the range of fin kinematics involved in different hydrodynamic functions.

Evolutionary patterns in pectoral fin mechanics

The paired fins of fishes are characterized by both structural and functional evolutionary transformations. Within ray-finned fishes, the pectoral fins exhibit distinct trends of change in their position and orientation on the body (Breder, 1926; Greenwood et al., 1966; Rosen, 1982; Parenti and Song, 1996; Drucker and Lauder, in press). The inclination of the pectoral fin base, for example, is typically horizontal in plesiomorphic taxa; in its apomorphic condition the fin base is more vertically oriented. An expected consequence of differences in pectoral-fin base angle is taxonomic variation in both the range of motion and functional repertoire of the fin (Drucker and Lauder, in press). Recent work on pectoral fin function in a basal actinopterygian (white sturgeon; Wilga and Lauder, 1999) and chondrichthyan outgroups (leopard and bamboo sharks; Wilga and Lauder, 2000, 2001) confirms that a horizontally oriented fin base restricts fin excursions to a primary dorsoventral kinematic axis. Despite their phylogenetic distance from salmoniform fishes, sturgeon and sharks are capable of 'cupping' the trailing edge of the pectoral fin in a manner generally similar to that observed in trout (Fig. 4) to generate forces for maneuvering.

Unlike these basal taxa with comparatively rigid paired fins, however, rainbow trout can rotate the pectoral fin base more than 30° during locomotion (Fig. 8). Correspondingly, trout exhibit a greater range of motion of the fin despite having a relatively shallow fin base inclination. Although not as mobile as the vertically oriented pectoral fins of many perciform fishes, the salmoniform pectoral fin does exhibit a diverse range of locomotor activities. Use of the pectoral fins for hovering, turning and braking constitutes a behavioral repertoire comparable to that of higher teleostean fishes (cf. Aleev, 1969; Geerlink, 1987; Drucker and Lauder, 2001b). The functional data presented in this study for salmoniform fish, representative of the plesiomorphic teleost condition, illuminates a trend of increasing kinematic and functional versatility of the pectoral fins within Actinopterygii. Future study of additional clades using quantitative flow visualization techniques will further our understanding of the relationship between propulsor design and locomotor function in swimming fishes.

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