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Pelvic fin locomotor function in fishes: three-dimensional kinematics in rainbow trout (*Oncorhynchus mykiss*)

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SUMMARY

The paired pelvic fins in fishes have been the subject of few studies. Early work that amputated pelvic fins concluded that these fins had very limited, and mainly passive, stabilizing function during locomotion. This paper is the first to use three-dimensional kinematic analysis of paired pelvic fins to formulate hypotheses of pelvic fin function. Rainbow trout (*Oncorhynchus mykiss*) were filmed swimming steadily at slow speeds (0.13–1.36 *BL* s^{-1}) and during manoeuvres (0.21–0.84 *BL* s^{-1}) in a variable speed flow tank. Two high-speed cameras filmed ventral and lateral views simultaneously, enabling three-dimensional analysis of fin motion. During steady swimming, pelvic fins oscillate in a regular contralateral cycle. This cyclic oscillation appears to have active and passive components, and may function to dampen body oscillation and stabilize body position. During manoeuvres, pelvic fins move variably but appear to act as trimming foils, helping to stabilize and return the body to a steady swimming posture after a manoeuvre has been initiated. Fins on the inside of the turn move differently from those on the outside of the turn, creating an asymmetric motion. This paper challenges the understanding that pelvic fins have a limited and passive function by proposing three new hypotheses. First, pelvic fins in rainbow trout have complex three-dimensional kinematics during slow-speed steady swimming and manoeuvres. Second, pelvic fins are moved actively against imposed hydrodynamic loads. Third, pelvic fins appear to produce powered correction forces during steady swimming and trim correction forces during manoeuvres.

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Key words: swimming, manoeuvring, locomotion, pelvic fin, evolutionary fin function, stability, rainbow trout, *Oncorhynchus mykiss*.

INTRODUCTION

Most fishes have two sets of paired fins, the pelvics and pectorals, and three median fins, the dorsal, anal and caudal fin. Early fish locomotion research determined that undulatory body and caudal fin motions produce thrust during swimming (Lighthill, 1971). More recently, paired pectoral, and median dorsal and anal fins in fishes have been shown to have locomotory function (Arnold et al., 1991; Jayne and Lauder, 1996; Webb et al., 1996; Westneat and Walker, 1997; Schrank et al., 1999; Drucker and Lauder, 2002; Walker and Westneat, 2002; Standen and Lauder, 2005; Standen and Lauder, 2007; Tytell et al., 2008). Paired pelvic fin function, however, remains largely unstudied. This paper is the first to study detailed three-dimensional movements of pelvic fins in fishes and to evaluate hypotheses for how these fins might function.

Early work amputated pelvic fins and detected no change in body motion during swimming, suggesting that pelvic fins had little or no locomotive function (Monoyer, 1866; Grenholm, 1923; Harris, 1936). Elegant work by Harris (Harris, 1937; Harris, 1938) later refined our ideas of pelvic fin function. He concluded that fish with basal fin morphologies, such as sharks (Fig. 1; ventral pectoral fins and ventral pelvic fins posterior of the centre of mass), had extremely limited pelvic fin function, whereas more derived fishes, such as perch (Fig. 1; lateral pectoral fins and ventral pelvic fins anterior of the centre of mass) had pelvic fins with limited trimming function to reduce pitching and upward body displacement during braking. Regardless of body position, pelvic fins were thought to be held fairly still, acting as static trimming foils rather than dynamic moving structures. Researchers concluded that pelvic fins had limited locomotor function during steady swimming.

This paper tests three main hypotheses put forth in the early literature on pelvic fin function in fishes. First, that pelvic fins have a very limited three-dimensional motion during slow-speed steady swimming and during manoeuvres. Second, that pelvic fin motion is primarily passive, questioning the role of intrinsic fin musculature. Third, that pelvic fins are used primarily in static trim movements rather than dynamic thrust movements during swimming. These hypotheses were tested by using three-dimensional analysis of pelvic fin motion in rainbow trout (*Oncorhynchus mykiss* Walbaum 1792). I challenged trout to swim at very slow speeds, forcing them to balance their body position without the aid of dynamically stabilizing fast flow, and I enticed fish to perform natural yawing manoeuvres while foraging for non-evasive food, to determine how pelvic fins are used in unsteady locomotor behaviours.

MATERIALS AND METHODS

Fish

I collected data on ten rainbow trout (*Onchorynchus mykiss* Walbaum 1792) and analyzed in detail the seven animals that had the most complete data sets. Fish had been raised at Blue Stream Hatchery, West Barnstable, MA, in natural bottom stream channels. Fish were maintained in the laboratory in a 1200 litre circulating tank and kept on a 12h:12h L:D photoperiod with a mean water temperature of 16°C (±1°C). The seven individuals analyzed in this study had a mean total length (*BL*) of 21.24±1.24 cm (mean ± s.e.m.; range 18.5–26.9 cm) and a mean total mass of 102.3±16.58 g (range 59.1–165.4 g).

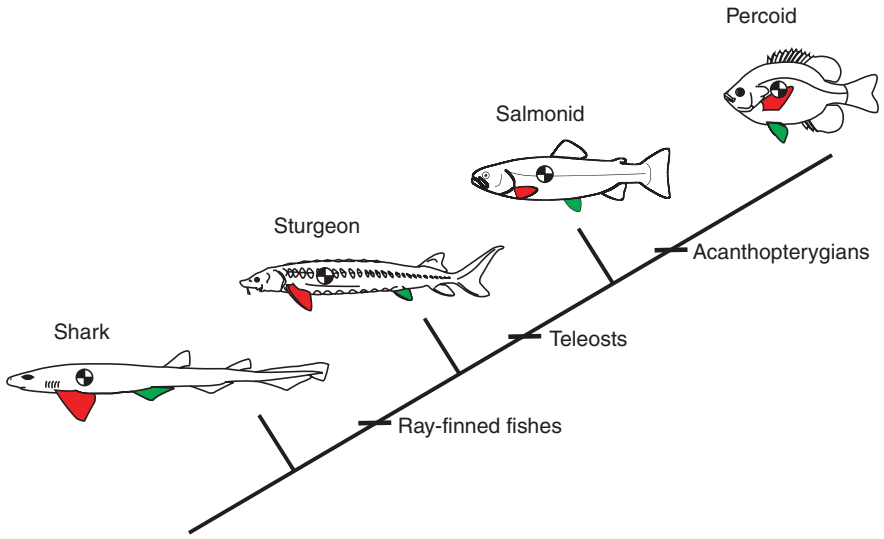

Fig. 1. An evolutionary transformation: paired fin position throughout fish evolution. A representative cladogram of selected fish groups. In the basal condition, paired pectoral fins (red) are ventrally located and paired pelvic fins (green) are located behind the centre of mass. In the derived condition, pectoral fins are located laterally on the body and the pelvic fins are located directly below or even in front of the centre of mass. Black and white circles represent the estimated location of fish centre of mass.

Behavioural observations

Trout swam in the centre of the working area (28 cm wide, 28 cm deep, 80 cm long) of a variable speed flow tank under conditions similar to those described in previous hydrodynamic work (Standen and Lauder, 2007). A mirror was placed parallel to the flow inside the right side of the flow tank to visualize the right pelvic fin (Fig. 2). The mirror lay 2.5 cm inside the working area of the flow tank wall at its base and was flush with the tank wall roughly 14 cm up the right tank side. The mirror only minimally reduced the working area of the flow tank and fish swimming behaviour did not visibly change with the presence of the mirror. Fish were recorded swimming steadily at speeds from 0.13 to 1.36 $BL\,s^{-1}$. Fish also performed yawing turns while swimming at speeds from 0.21 to 0.84 $BL\,s^{-1}$. Turns were not elicited but occurred as spontaneous feeding behaviours as fish foraged for particles in the flow tank. I used two synchronized high-speed video cameras (Photron Fastcam 1280×1024 pixels, Photron, San Diego, CA) operating at 250 frames s^{-1} (1/250 s shutter speed) to visualize the movement patterns of the pelvic fins (Fig. 2).

Camera calibration

Lateral and ventral kinematic cameras were calibrated using a three-dimensional cube-like object with 20 known point locations (Standen and Lauder, 2005). Each of these points could be seen from both cameras and were digitized in both views. By using direct linear transformation, the 2D location of these points in both views were used to calculate the camera locations relative to each other and to predict the three-dimensional location of the known points (Ty Hedrick custom Matlab DLTcalibration program, The Mathworks, Natick, MA, USA). This calibration allowed the calculation of three-dimensional motions of fish fins during locomotion.

Kinematic measurements

To quantify the temporal and spatial patterns of fin movement, video sequences were analyzed using a custom digitizing program in Matlab (Ty Hedrick DLTdataviewer, Matlab version R2006a). For each fish, left and right pelvic fin motion was tracked by digitizing four points per fin. Points marked the four fin corners of each fin. Two points marked the lateral-most fin ray: one point at the base where the ray attaches to the body and one at the ray tip. Two other points marked the medial most fin ray: again, one point at the base and one point at the tip. These points clearly described the motion of lateral and medial pelvic fin edges, as well as a relative approximation of the fin area (the area within the four digitized points). Video sequences were three to five consecutive contralateral fin beats in duration. The three-dimensional motion of paired pelvic fin oscillation was quantified at 20 ms intervals.

Both fin tip velocity and body velocity were calculated for each fin. Body motion is dominated by the mediolateral (ML) oscillation of the propulsive wave moving along the fish. For the purposes of

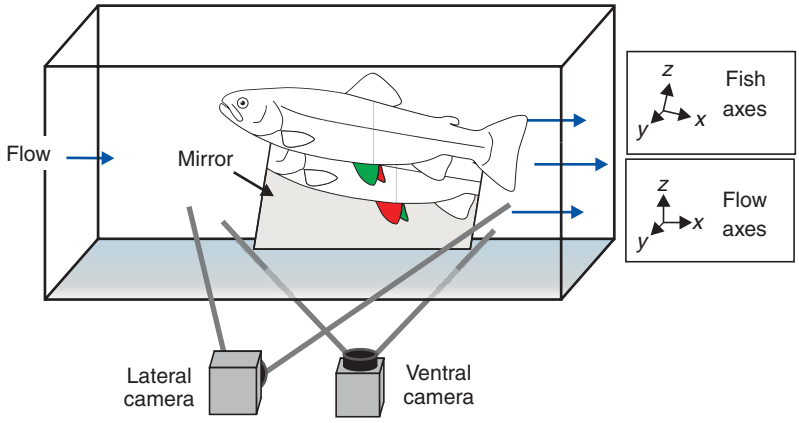

Fig. 2. Experimental apparatus. Fish swam in a multi-speed flow tank. High-speed cameras filmed ventral and lateral views simultaneously, enabling three-dimensional analysis of fin motion. A mirror slightly angled along the right side of the fish allowed full visualization of the right pelvic fin. Fin motion was measured relative to the water flow (flow axes) and relative to the fish body position (fish axes, which change as the fish turns during manoeuvres).

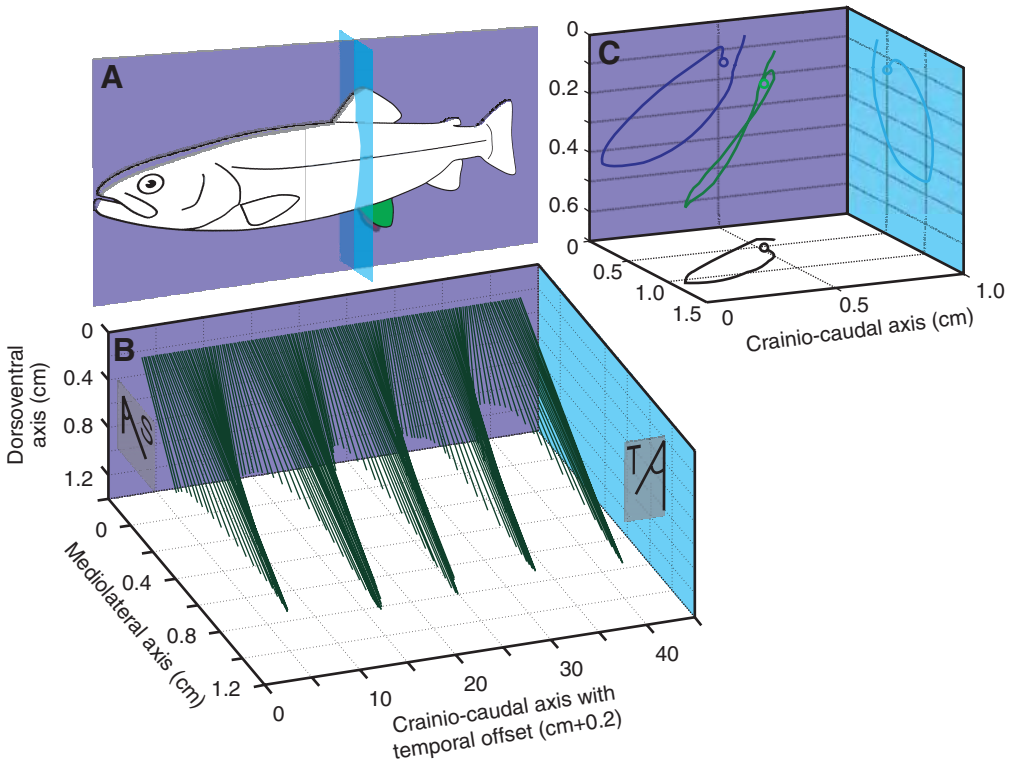

Fig. 3. Motion of lateral edge of left pelvic fin. The motion of each pelvic fin is described as the change in angle of the fin's lateral edge with the mid-sagittal plane and the transverse plane of the fish. The fin's lateral edge is defined as the line between where the base of the most lateral pelvic fin ray attaches to the body and the tip of the same lateral-most fin ray. (A) Purple represents the fish's mid-sagittal plane; cyan represents the fish's transverse plane. (B) Representative angles are labeled S (sagittal) and T (transverse) to depict the angle measured. Black lines represent the left pelvic fin lateral edge as it moved through its oscillating cycle over four fin beats. (C) Plot of the three-dimensional motion of the lateral pelvic fin-ray tip over one fin beat. Axes dimensions are the same as in B with all units in cm and no temporal offset in the crainio-caudal axis. The circles represent the start of fin stroke when the angle between the fin edge and the transverse plane was minimal. The green line represents the three-dimensional motion of the fin tip. Blue, cyan and black lines represent the motion of the fin tip projected on the three axial planes.

this paper, lateral body velocity was calculated as the time derivative of the displacement of the left medial fin attachment point along the mediolateral axis. Fin tip velocity was calculated by taking the time derivative of the three-dimensional lateral pelvic fin tip motion (body motion subtracted). This paper focuses on the magnitude and timing of the oscillation motion of the paired fins during slow-speed swimming and lateral yawing manoeuvres.

Describing fin motion

Axial coordinates

During steady swimming, fish oriented their anteroposterior (AP) axis along the axis of flow; therefore, the coordinates of the fish and flow axes were the same. The *x*-axis runs anterior to posterior along the fish. The *y*-axis runs mediolaterally from the right to the left side of the fish, and the *z*-axis runs dorsoventrally. Data gathered during steady swimming can then be related to both fish body and flow direction simultaneously. When fish manoeuvre, however, fish axial planes move relative to the flow and must be defined using a local set of axes that move with the fish's body (Fig. 2).

For manoeuvring data, the axial planes that describe the fish body position were calculated by digitizing the fish's AP axis. The AP axis was defined from the nose tip to a clear mid-ventral point just anterior of the pelvic fins. The ML and dorsoventral (DV) fish axes were calculated using the flow axis in combination with the digitized AP axis. This was done by projecting the AP axis onto the plane perpendicular to the flow *z*-axis. The flow *y*-axis was then projected onto the plane perpendicular to this projected AP axis. This makes the AP and ML fish axes perpendicular and aligned with the fish's true heading. This system did not take into consideration any roll the fish may have experienced during its manoeuvre. After much testing, however, body roll was so slight that the error associated with calculating roll from off-axis camera views was larger than the measured roll itself. The DV fish axis was calculated by taking the cross product of the projected AP axis and the projected ML axis. This transforms all digitized coordinates into a right-hand rule system for easy identification of angular direction. These fish axes were used to calculate lateral pelvic fin ray tip position relative to the body (see description below).

During steady swimming trout oscillated their pelvic fins both mediolaterally and anteroposteriorly. These two motions are most easily conceived relative to the animal's mid-sagittal plane (ML motion; Fig. 3A, purple plane) and to the animal's transverse plane (AP motion; Fig. 3A, cyan plane). The terms abduct and adduct are used to describe fin motion relative to the body and within the sagittal plane; angles between the fin and the transverse plane oscillated during abduction and adduction. The terms pronate and supinate are used to describe fin motion relative to the body and within the transverse plane; angles between the fin and the sagittal plane oscillated during pronation and supination. Fin oscillation motion is described relative to the transverse and sagittal planes (for example, fins were abducted when moving towards the transverse plane).

Large angles between the fin edge and each plane occurred when the fin was close to the body (adducted in the mid-sagittal plane and suppinated in the transverse plane; Fig. 4A,B, respectively). Small angles, sometimes negative in the case of the mid-sagittal plane, were observed when the fin was away from the body (abducted in the mid-sagittal plane and pronated in the transverse plane; Fig. 4C,D, respectively). The magnitude of the angles between the fin edge and the mid-sagittal plane were corrected for the contralateral, parasagittal location of the left and right pelvic fins. This means, for both left and right fins, large angles occur at suppination and small angles at pronation. By defining the oscillation of each pelvic fin using these angles, the ML motion during the fin oscillation can be partially separated from the cranial-caudal fin motion, allowing for a discussion of possible force production by fins and resulting fin function.

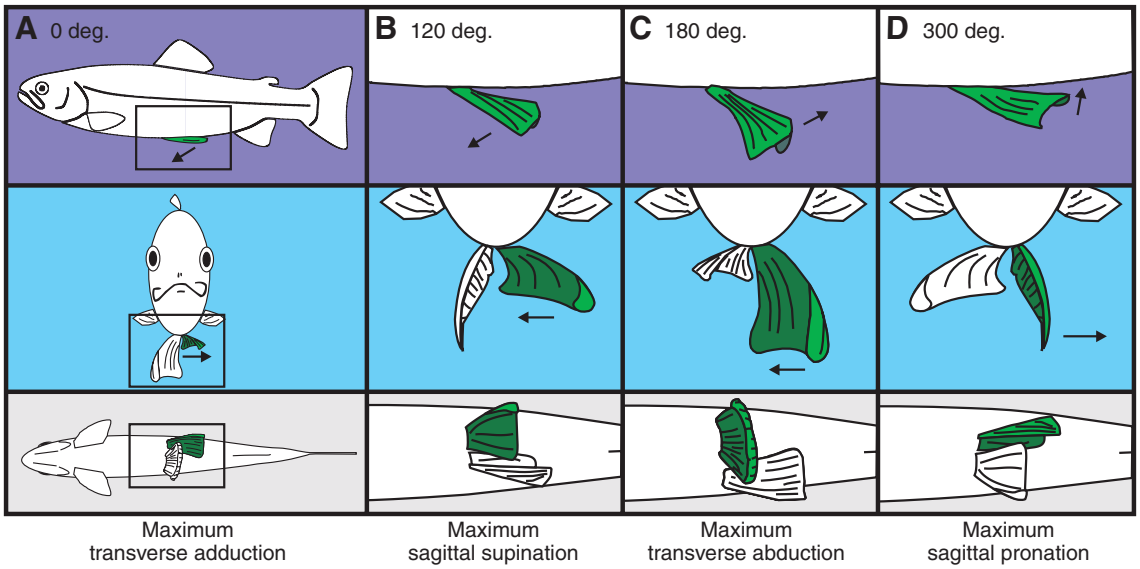

Fig. 4. Pelvic fin motion. Paired pelvic fins oscillated in a regular contralateral cycle. (A–D) Four stages of left pelvic fin oscillation are drawn in lateral, transverse and ventral views. The left fin is coloured green, the dorsal side of the fin in light green and the ventral side of the fin in dark green. (A) Column A is arbitrarily assigned as the start of the oscillating cycle when the fin is adducted against the body relative to the transverse plane (phase=0 deg.). (B) As the fin started its cycle the fin's lateral edge began abducting toward the transverse plane and supinated away from the sagittal plane where it reached maximum lateral excursion (phase=120 deg.). (C) As the fin continued abducting toward the transverse plane, the fin's lateral edge started pronating medially toward the fish's mid-sagittal plane (phase=180 deg.). (D) The fin began adducting away from the transverse plane as the fin's lateral edge was pronated maximally toward the mid-sagittal plane (phase=300 deg.). Finally, the fin made its return stroke back to a fully adducted, partially supinated starting position (A, phase=360 deg./0 deg.). Arrows in each of the images note the direction in which the fin is moving or about to move. Background colours of each panel correspond with those in Fig. 3.

Timing

Paired pelvic fins have a complex three-dimensional oscillation when trout swim at slow speeds. For steadily swimming fish, the beginning of the fin stroke cycle was arbitrarily chosen as the point at which the lateral pelvic fin ray tip was fully adducted against the body, roughly at right angles to the fish's transverse plane. The stroke cycle was considered to be at mid-stroke when the lateral pelvic fin tip was maximally abducted away from the body towards the transverse plane. Polar coordinates were used to define the timing of the stroke cycle. A complete fin beat cycle occurred over 360 deg.; the fin beat cycle started with maximal adduction at phase cycle 0 deg., moved through maximal abduction (mid-stroke) at phase cycle 180 deg., and returned to maximal adduction at phase cycle 360/0 deg. All variables were plotted relative to these polar coordinates, allowing analysis of the phase relationships and timing.

I observed no regular fin oscillation cycle during manoeuvres. In lateral yawing manoeuvres, however, the body moved in a consistent S-shaped pattern. Left and right turns were grouped, and manoeuvres are described by IN/towards and OUT/away sides relative to fish turning direction. Based on the consistent S-shaped body movement pattern, manoeuvres were divided into three stages: the first stage starts with the original body position and ends with maximum excursion of the body away from the turn; the second stage starts with maximum excursion away from the turn to maximum excursion in the direction of the turn; finally, the third stage continues from maximum excursion in the direction of the turn to the final steady body position, most often slightly away from the turning direction. An example trace of the change in body excursion can be seen in the blue line of Fig. 8A.

Statistics

Statistical analysis was divided into two sections: timing and magnitude. Cycle timing of maximum and minimum values was calculated for each variable and each fin. Because timing was calculated in polar coordinates, it was analyzed using standard circular data analysis. Mean timing angles and 95% confidence intervals were calculated according to Zar (Zar, 1999), with angular variance calculated according to Batschelet (Batschelet, 1965; Batschelet, 1981).

Velocity data measurements during steady swimming were treated as diametrically bimodal distributions, as they peaked twice in a single fin beat (Zar, 1999). A Rayleigh's test for circular uniformity was conducted on all maximum and minimum values for each variable and fin to determine whether variables occurred at predictable times in the oscillation cycle. The approximation:

$$P = \exp\left(\sqrt{1+4N+4N(N^2-R^2)}-1+2N\right),$$

where N is the sample size and R is the Rayleigh's test statistic, was used to calculate the support for R. If variables proved to have directionality based on the Rayleigh's test, a two-sample testing of mean timing angles was performed using an F-statistic according to Zar (Zar, 1999). The timing of all variables was tested first between maximum and minimum values within one fin and then compared between fins. Timing between steady swimming and manoeuvring data was not compared statistically to avoid inferring meaning from differences that might be found between non-comparable data sets.

Magnitudes of maximum and minimum values for all variables, fins and behaviours were calculated using standard statistical procedures to calculate mean and standard error. For each fin, maximum and minimum values were compared for each variable. Maximum and minimum values were also compared between fins to assess the symmetry of the paired fin strokes. Simple two-sided t-tests were conducted on variables with equal variance. When a

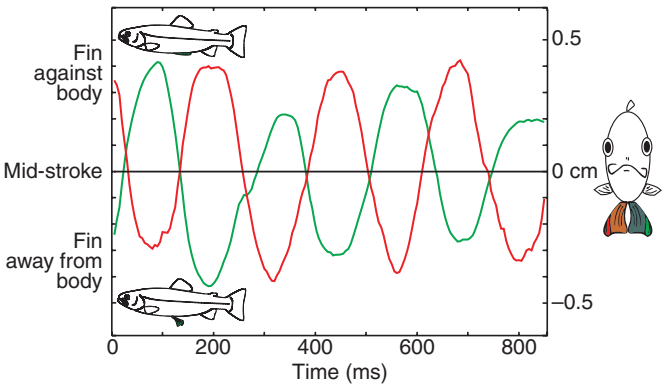

Fig. 5. Paired pelvic fin oscillation during steady swimming. Oscillation of the pelvic fin's lateral ray tip in the *x*-dimension (motion in the sagittal plane along the cranio-caudal fish axis) over time. Green line represents the left pelvic fin; red represents the right pelvic fin.

two-sided *F*-test determined that samples had unequal variance, the Welch ANOVA was used to test for equal means.

Significance levels for all tests were based on initial *P*-values of <0.05, and all linear statistical tests were completed using JMP (version 7.0, 2007, SAS Institute, Cary, NC, USA). Circular statistical tests were conducted using a custom-made program within Matlab (Matlab version R2006a). Measurements noted in the text are expressed as mean ± s.e.m.

RESULTS

Fin morphology

Average fin area differed among fish (0.78–2.04 cm^2, $P<0.0001$) and, as expected, was positively correlated with body size (18.5–26.9 cm). A simple linear regression of area of $-1.44+0.13$(length) describes the relationship ($R^2=0.89$, $P<0.0001$, d.f.=6). Left and right fin area did not differ significantly (left fin mean area=1.07±0.03; right fin mean area=1.13±0.04; *t*-test, mean area $P=0.88$, *t*-ratio=0.15, d.f.=12).

Fin kinematics: steady swimming

Two major oscillations overlapped during a fin beat cycle (Figs 3, 4): (1) oscillations relative to the transverse plane (initiated first), where, from roughly 0 to 180 deg., the fin moved towards the transverse plane (abduction, Fig. 4A–C), and where, from 180 to 360 deg., the fin moved away from the transverse plane (adduction, Fig. 4C,D,A) and (2) oscillations relative to the sagittal plane (initiated 120 deg. after transverse plane oscillations), where, from roughly 120 to 300 deg., the fin moved toward the sagittal plane (pronation, Fig. 4B–D), and where, from 300 to 120 deg., the fin moved away from the sagittal plane (supination, Fig. 4D,A,B). Right and left fins oscillate 180 deg. out of phase with each other (Fig. 5).

The majority of fin motion was driven by the fin's lateral edge. Plotting the fin's lateral edge over time shows the regular fin oscillation relative to the mid-sagittal and transverse planes (Fig. 3B). Following the lateral pelvic fin tip over one oscillation cycle shows the fin path was oval when projected in all three planes (Fig. 3C). The fin's path for the first half of the stroke was different from the return path, possibly due to functional partitioning of fin motion throughout the stroke.

During steady swimming, left and right pelvic fins did not differ significantly in oscillation kinematics (relevant statistics reported in timing and magnitude results below). Left and right fins oscillated roughly 180 deg. out of phase, this means that when the left fin was maximally abducted towards the transverse plane, the right fin was maximally adducted (Fig. 5; circular test for equal means, left fin abduction angle equals right fin adduction angle, $F_{0.05(1),1,95\text{-}2}$calc=0.1288, $P=0.7205$).

Six variables were used to describe fin motion (Fig. 6; see also Table S1 in the supplementary material). Body amplitude was symmetrical around the midline; body excursion to the left did not differ from body excursion to the right. There were significant differences between maximum and minimum values for all variables ($P=0.0001$ for all comparisons; Fig. 6). Left and right fins were not statistically different for all variables, with the exception of the angle of the fin with the mid-sagittal plane; in this case the left fin supinated more than the right fin ($P=0.0083$). Body and fin velocity oscillated

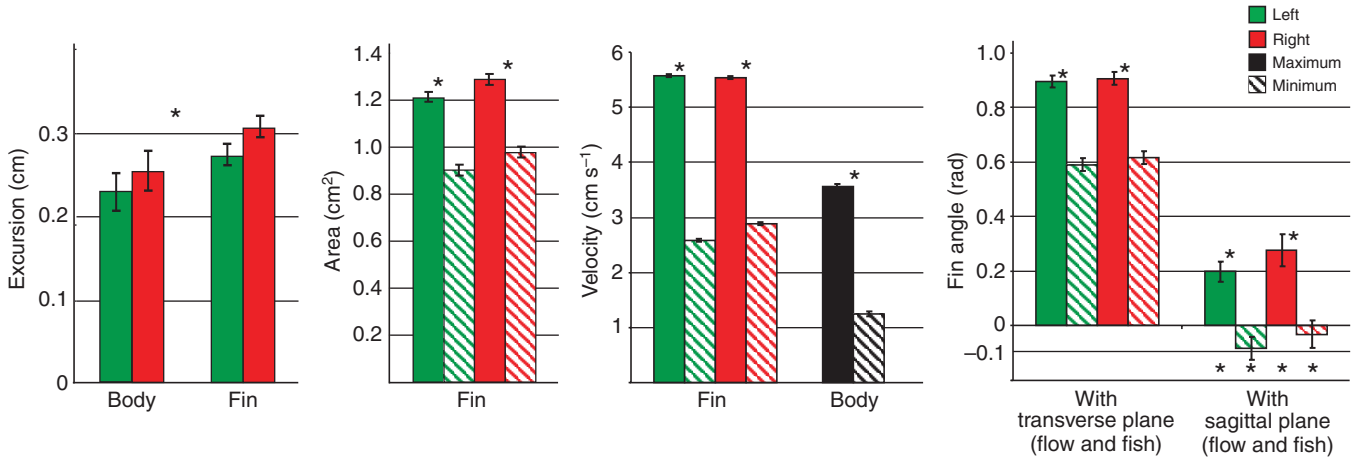

Fig. 6. Magnitude of kinematic variables for body and fins during steady swimming. Green bars represent the left fin and red bars represent the right fin. Body and fins moved symmetrically around the midline of the fish [excursion to the left (cm)=excursion to the right (cm), $P>0.07$]. Fin excursions (body motion subtracted) were larger than body excursions ($P=0.0011$). For all remaining variables, maximum values were significantly larger than minimum values for each fin ($P<0.0001$). Right and left fins did not differ in fin area, fin or body velocity (black bars), or fin angle with the transverse plane ($P>0.05$). Left and right fins did differ in angle with the sagittal plane; right fins had larger pronation angles than left fins ($P=0.0001$). Large angles (rad) represent fin adduction/supination and small angles represent fin abduction/pronation. Asterisks above the bars denote significantly different values within fins ($P<0.0001$). Asterisks below the bars denote significantly different values between fins ($P<0.001$). Fin excursion, fin area and fin angle with the sagittal plane had significant interaction between fish and fin ($P<0.0001$). The subtle variation in these variables between animals suggests a fine-tuned adjustment of fin area and kinematics to maintain a steady gait.

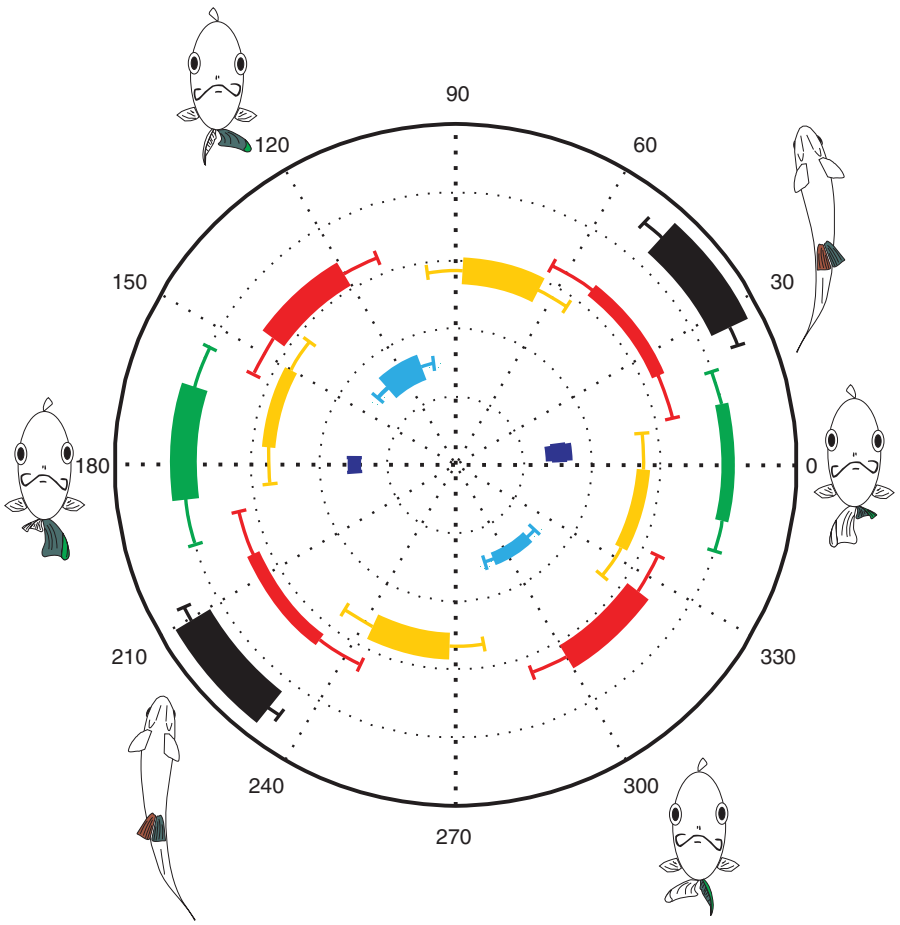

Fig. 7. Pelvic fin kinematic timing during steady swimming. Complete pelvic oscillation cycle of left fin represented in a polar plot. 0 deg. arbitrarily represents the start of the stroke when fin is held against body. 180 deg. represents mid-stroke when the pelvic fin's lateral tip is maximally abducted. Each rectangle represents the 95% confidence interval around the mean peak kinematic variable with error bars depicting angular variance s^2 (Batschelet, 1965; Batschelet, 1981). Bar colours define the following: black, maximum amplitude of body at fin attachment site; green, fin area; red, body velocity; yellow, fin velocity; dark blue, fin angle with transverse plane; light blue, fin angle with sagittal plane. Thick bars represent maximum values for each variable and thin bars represent minimum values. The data represent left pelvic fins of all fish during all swimming trials.

between maximum and minimum values in a diametrically bimodal distribution caused by the side-to-side fish body motion.

Fin timing: steady swimming

The timing of each variable during the fin stroke cycle is represented using polar coordinates (Fig. 7; see also Table S2 in the supplementary material). All variables had angular directionality, meaning their maximum and minimum values occurred at predictable times in the fin oscillation cycle (Raleigh's test $P<0.0001$ for all comparisons). The beginning of the fin beat was arbitrarily assigned at maximum fin adduction with respect to the transverse plane (Fig. 4A); this point in the cycle corresponds with 0 deg. and 360 deg. This system applies to both right and left fins; variables were measured relative to their respective fin's oscillation.

Left and right fins did not differ in timing (Fig. 7). All variables had discreet maximum and minimum peaks (abduction/adduction and supination/pronation in the case of angles), which occurred roughly 180 deg. out of phase from one another. Variation in the timing of adduction and abduction was due to the calculation of angles using three-dimensional variables rather than the two-dimensional location of fin's lateral tip oscillation, which was used to define arbitrary phase timing (Fig. 5). Fin area was minimal at the start of the cycle, and maximal at mid-stroke. Body excursion is discussed relative to the fin of interest. Maximum body excursion towards the fin side occurred just after cycle start (at roughly 40 deg.) and maximum body excursion toward the non-fin side occurred roughly 180 deg. later, just after mid-cycle (at roughly 220 deg.). Minimum body velocity was diametrically bimodal in its distribution, and occurred near maximum body excursion (roughly 40 and 220 deg.); maximum body velocity, also bimodal, occurred roughly 180 deg. later, halfway between peak body excursions. Maximum fin supination away from the sagittal plane occurred after maximum fin-side body excursion (at roughly 120 deg.), pronation occurring roughly 180 deg. later, just after maximum non-fin side body excursion, at roughly 300 deg. Fin velocity was also diametrically bimodal in its distribution. Maximum and minimum fin velocity occurred at roughly 35 deg. and 120 deg., respectively, after peak body excursions.

Fin kinematics: manoeuvres

None of the variables measured during manoeuvres, including heading change, showed consistent timing with respect to fin motion (Raleigh's test, $P\geq0.0767$ for all comparisons). Body motion and the fish's heading, however, were relatively consistent between manoeuvres and can be used to define manoeuvre stages, thereby providing a template for discussing fin motion (Fig. 8). Manoeuvres resulted in a lateral displacement of the fish's body. During manoeuvres, fish bodies traced an s-shaped path. Manoeuvres began with a change in heading in which the fish's nose moved in the direction of the turn while its pelvic girdle was forced away from the turn. The maximum change in heading corresponded with the maximum body excursion away from the turn. Usually the maximum heading remained relatively constant for some time as the body surfed across the flow in the direction of the yawing turn. Both the duration and the distance of the sideways body displacement were determined by the length of time the fish held its maximum change in heading. Just before the body was half way through its maximum lateral displacement the heading began to return to the centre,

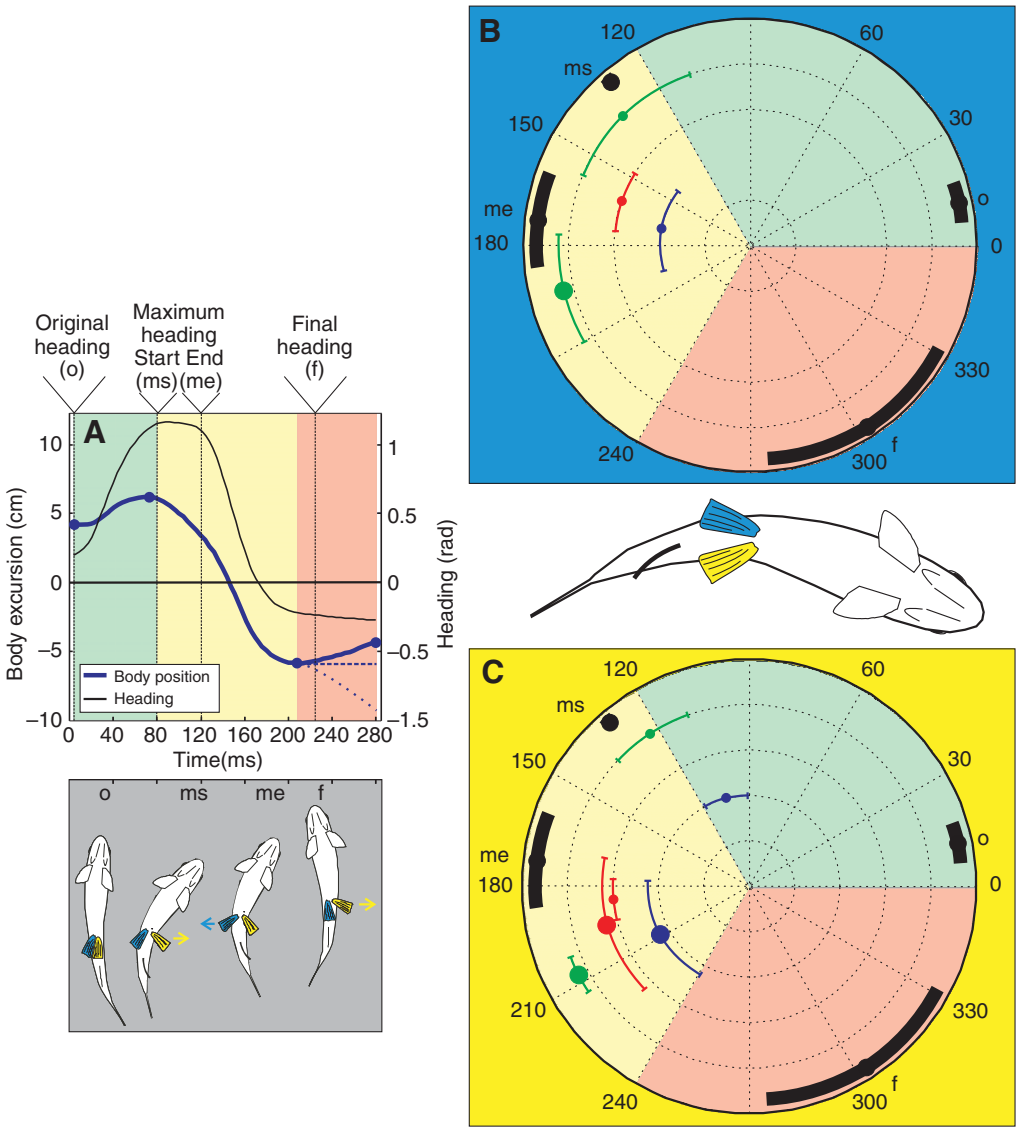

Fig. 8 Kinematic and timing data for manoeuvres. (A) Representative example of a single manoeuvre. The thick blue line represents the change in lateral body position (left *y*-axis); the blue dots on the line represent the starting position, the maximum body excursion to the outside of the turn, the maximum body excursion to the inside of the turn and the final body position. Three alternate final body positions are displayed with solid, dashed and dotted lines. Each manoeuvre is divided according to body excursion: stage one (green) is the start of the manoeuvre until the maximum excursion to the outside; stage two (yellow) is the maximum outside excursion to the maximum inside excursion; and stage three (pink) is the maximum inside excursion until the final body position. The black line represents heading over time (right *y*-axis). The timing of original heading (o), the start and end of maximum heading (ms and me, respectively), and the final heading (f) are noted by dashed vertical black lines. The diagram of fish below represents the general motion of the fish body at the time of original heading, the maximum heading start and end, and the final heading (f). (B,C) Polar plots of mean timing for all manoeuvres color coded to the three stages of the manoeuvre. Black bars represent the timing of heading changes and correspond with A. Only variables with directionality (Raleigh's test $P<0.05$) are represented on the polar plots. Small dots represent minimum/abduction mean values and large dots represent maximum/adduction mean values. (B) The outside fin had directionality in fin area (green), and fin abduction with fish transverse (blue) and flow transverse (red) planes. (C) The inside fin had directionality in fin area (green), and both fin abduction and adduction with fish transverse (blue) and flow transverse (red) planes. All variables that had consistent timing peaked well after the fish had started turning, suggesting that pelvic fins are not used to initiate manoeuvres but possibly to stabilize and control body position while returning it to a forward heading.

reaching final heading sometime after the body reaches maximum excursion in the direction of the yaw. The final stage of the turn was somewhat variable; the body did one of three things (Fig. 8A): (1) it remained at maximum yawing excursion; (2) it returned slightly towards its original position; or (3) it continued drifting in the direction of the yaw. These outcomes were determined by heading changes and might be the result of variation in fin motion throughout stage two of the yawing manoeuvre.

The six variables used to describe fin motion during steady swimming were also used to describe fin motion during manoeuvres (Fig. 9; see Table S3 in the supplementary material). Angles relative to fish body axes were also included for manoeuvres, as fish heading was no longer equal to that of the flow. In addition, fins were divided according to their location relative to the turning manoeuvre. Fins located on the side toward which the fish turned were considered inside fins and those located on the side from which the fish turned

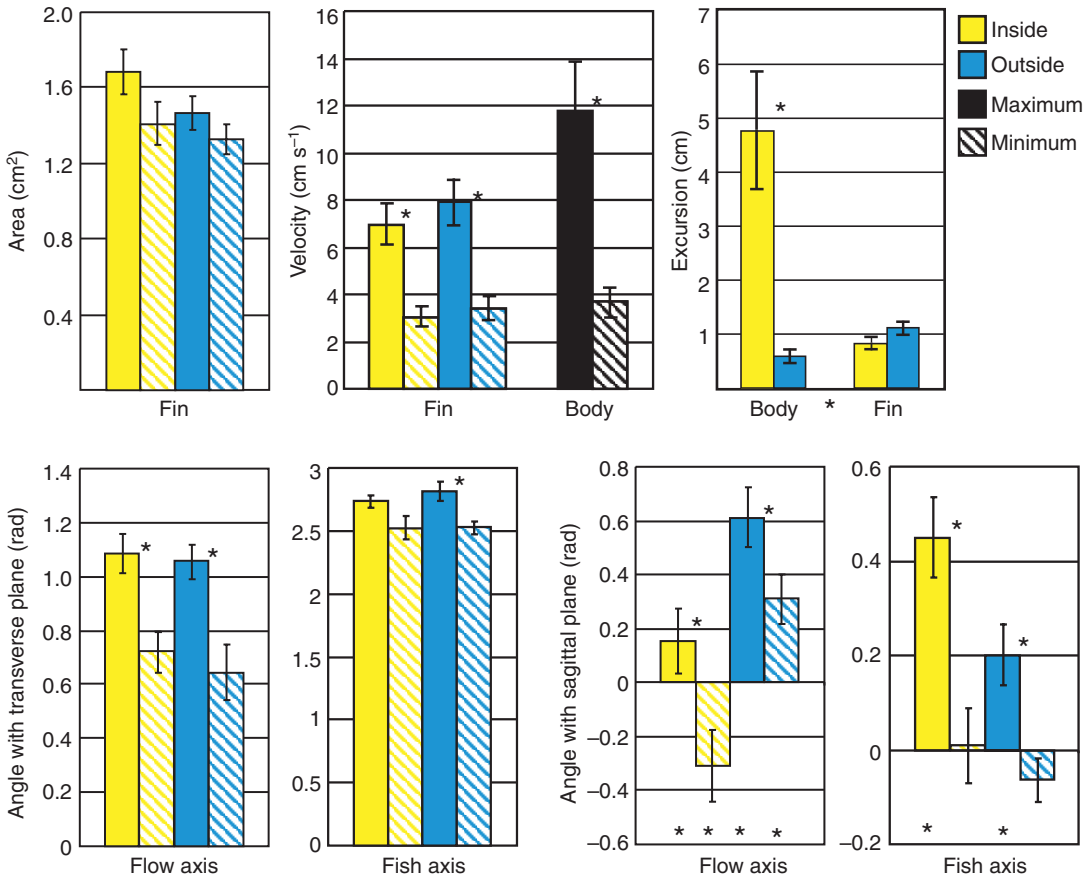

Fig. 9. Magnitude of kinematic variables for body and fins during manoeuvres. Fish body sides, and their respective fins, are defined as inside (the side closest to the direction of the turn, yellow) and outside (the side farthest from the direction of the turn, blue). Fin area was measured in cm^2, angles were measured in radians, and velocities were measured in $cm\,s^{-1}$. Asterisks above bars denote significantly different values within fins ($P<0.05$). Asterisks below bars denote significantly different values between fins ($P<0.05$). Solid colours represent maximum values and diagonal lines represent minimum values. All between fin comparisons were not significant, with the exception of fin angle with the flow sagittal plane (abduction and adduction) and with the fish sagittal plane (adduction only, $P<0.05$). Fin area, and fin angle with the sagittal plane (fish and flow axes) had significant interaction between fish and fin ($P<0.03$). The differences in these variables between individuals suggest fine-tuned adjustments of fin surface area and mediolateral motion during manoeuvres, which possibly affect roll stabilization.

away were outside fins. All comparisons were made between inside and outside fins.

As expected, body amplitude was not symmetrical around the body midline during manoeuvres. Body excursion in the turning direction was larger than the initial excursion away from the turn (Fig. 9). Body velocities also showed distinct maximum and minimum values. Kinematics were similar between inside and outside fins with two distinct differences (Fig. 9); inside fins had a far greater pronation and a much smaller supination relative to the flow compared with outside fins, and the adduction and abduction angles of the inside fin to the fish's body did not differ (Fig. 9).

Fin timing: manoeuvres

The timing of each variable during manoeuvres is represented using polar coordinates (Fig. 8; see Table S4 in the supplementary material). Manoeuvres were divided into three stages (Fig. 8A). The first stage bounded by angles 0 deg. to 120 deg. represented the period from the original heading until the body reached the maximum excursion away from the turn. The second stage bounded by angles of 120 deg. to 240 deg. was the period between maximum body excursion away from the turn and maximum body excursion towards the turn. Finally, the third stage, angles 240 to 360 deg., was variable and represented the period between maximum body excursion towards the turn until the body position stabilized. Sometimes this occurred immediately (Fig. 8A, dashed line), and sometimes the body continued on a regular drift towards one side or the other (Fig. 8A, solid and dotted lines).

Manoeuvres were variable but a general pattern emerged among trials. This pattern consisted of several steps. The fish's heading changed, the inside pelvic fin abducted and supinated away from the body, the rate of heading change slowed and the outside pelvic fin abducted and supinated, the body straightened and both fins weakly adducted and pronated but remained fairly extended. This pattern happened quickly and with temporal variability between manoeuvres making it difficult to find statistical significance between trials. To clarify the timing data, a single value for each variable was used during each manoeuvre to calculate timing. For example, fin area peak timing was determined by the largest maximum peak area and smallest minimum peak area for each manoeuvre.

During manoeuvres not all variables had directionality when plotted onto the stages of body motion as described above. Timing varied considerably for many variables, meaning there were no significant calculations of mean timing angle during a manoeuvre. The variables that did have angular directionality were inconsistent between fins. For the outside fin, fin area and abduction angles

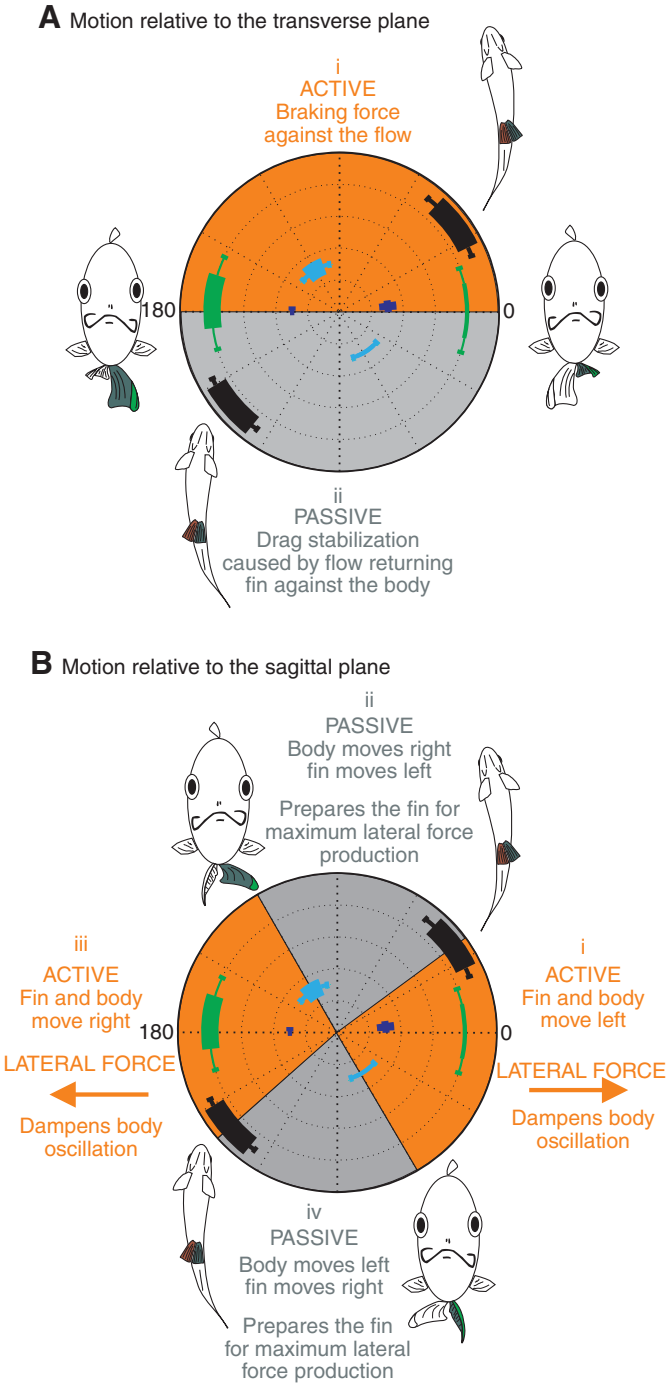

Fig. 10. Pelvic fin steady swimming functional hypotheses. The complete pelvic oscillation cycle of left fin is represented in two identical polar plots. Body excursion (black), fin area (green), fin angle with transverse plane (dark blue), and fin angle with sagittal plane (light blue) are represented on the plots. 0 deg. arbitrarily represents the start of the stroke when the fin is held against the body. 180 deg. represents mid-stroke, when the outside fin tip is maximally abducted. Thick bars represent maximum values for each variable and thin bars represent minimum values. Data represent the left pelvic fins of all fish during all swimming trials. Widened areas on bars represent the mean and 95% confidence interval; thin lines represent the angular variance s^2 (Batschelet, 1965; Batschelet, 1981). (A) Motion relative to the transverse plane. (i) As the pelvic fin supinates towards the transverse plane it actively pushes against the oncoming flow producing a braking force. (ii) The fin passively adducts away from the transverse plane owing to water drag, stabilizing and straightening the body in the flow. (B) Motion relative to the sagittal plane. (i) As the pelvic fin adducts away from the sagittal plane it moves in the same direction as the body, actively pushing against the induced flow and producing a lateral force in the direction the body is oscillating. This force may act to dampen body oscillation, helping to slow and reverse body motion. (ii) As the body changes direction the fin continues supinating away from the sagittal plane, passively moved by body induced water flow. This motion maximally supinates the fin, preparing for the next active cycle. (iii) The fin begins pronating towards the sagittal plane, in the same direction as body oscillation, against body induced flow. This produces a lateral force in the direction of body motion with maximum fin area dampening the body oscillation and helping to reverse the body direction. (iv) Body oscillation changes direction while the fin continues pronation. Induced flow due to body motion passively moves the fin to maximize pronation towards sagittal plane, preparing for the lateral force production of the next stroke.

between the fin's lateral edge and the transverse plane of the fish and the flow had direction, or predictable timing. For the outside fin, all other variables were evenly distributed throughout the manoeuvre cycle and had no significant directionality (Raleigh's test, $P \geq 0.0647$ for all variables). Inside fin area, fin abduction and fin adduction (relative to both fish and flow) were directional. For the inside fin, all other variables were evenly distributed throughout the manoeuvre cycle (Raleigh's test, $P \geq 0.1245$ for all variables).

Almost all variables with significant directionality peaked during the second stage of manoeuvring. Peaks in fin area occurred at similar times for inside and outside fins: minimum fin area occurring just before maximum heading and maximum fin area occurring just after (Fig. 8). Inside fin abduction relative to the fish occurred before maximum heading was reached and adduction occurred after maximum heading ended. Outside fin abduction relative to the fish occurred after inside fin abduction and concurrently with the end of maximum heading. Fin abduction and adduction relative to the flow did not differ in timing, occurring at the start of heading reduction during manoeuvres.

Comparing manoeuvres with steady swimming

Slow-speed steady swimming in trout was accompanied by remarkably predictable and regular pelvic fin oscillations (Fig. 7). Manoeuvres, by contrast, showed a large variation in pelvic fin motion. Inside and outside fins did not have a clear phase relationship relative to the body or to each other (Fig. 8). I used average body excursion (left and right sides pooled for steady swimming; in and out sides relative to turning pooled for manoeuvres) to make a conservative comparison of body motion between steady swimming and manoeuvring behaviours. Body excursion during manoeuvres (mean excursion=2.68 cm) was far greater than during steady swimming (mean excursion=0.24 cm; *t*-test for unequal variance, d.f.=1, 11.004, P=0.0133). Fin area during manoeuvres (max 1.57±0.11, min 1.36±0.10) was also greater than during steady swimming (max 1.25±0.04, min 0.94±0.03; manoeuvres *vs* steady swimming *t*-test for unequal variance: max, d.f.=1, 95.061, P=0.0003; min, d.f.=1, 85.999, P=0.0001). Angles between the fin's lateral edge and the flow axes were similar between manoeuvres and steady swimming (*t*-test for unequal variance for all comparisons, $P \geq 0.084$; see Tables S1 and S3 in the supplementary material), with the exception of fin abduction toward the flow transverse plane, which was smaller for manoeuvres (*t*-test for unequal variance, d.f.=1, 59.129, P=0.0341). Fin's lateral edge pronation and supination relative to the fish's sagittal plane did not differ between manoeuvres and steady swimming (*t*-test for unequal

variance: supination, d.f.=1, 54.603, P=0.6313; pronation, d.f.=1, 51.991, P=0.3096). By contrast, fin's lateral edge adduction and abduction relative to the fish's transverse plane was significantly higher during manoeuvres than during steady swimming. This difference in peak adduction/pronation and abduction/supination angles between behaviours may be due to the slight tilting behaviour of trout when swimming steadily at slow speeds. The angular difference between adduction/pronation and abduction/supination was roughly the same for manoeuvres and steady swimming. Although minimum fin velocity does not differ between steady swimming and manoeuvres, maximum fin velocity is greater during manoeuvres (t-test for unequal variance: min, d.f.=1, 55.043, P=0.1377; max, d.f.=1, 58.791, P=0.0067). The maximum and minimum body velocity was greater during manoeuvres than during steady swimming (t-test for unequal variance: min, d.f.=1, 41.372, P=0.0001; max, d.f.=1, 41.033, P=0.0001).

DISCUSSION

This paper describes pelvic fin kinematics, providing strong inferential data that suggest pelvic fins have an active and complex three-dimensional motion, which appears to produce forces using both static and dynamic processes.

Paired pelvic fin motion during steady swimming

Of the few studies previously done on pelvic fins, Harris provides the most complete description of pelvic fin function (Harris, 1936; Harris, 1937; Harris, 1938). For Harris (Harris, 1938), pelvic fin function depended on a phylogenetic context (Fig. 1); fish such as sharks, with a basal fin morphology (ventral pectoral fins and pelvic fins located posterior to the centre of mass), showed little to no pelvic fin function, whereas more derived teleosts (lateral pectoral fins and pelvic fins directly below or in front of the centre of mass) had pelvic fins with limited elevating and depressing functions. These hypotheses were supported by earlier research in which pelvic fins had been amputated and little to no effect on fish stabilization had been found (Monoyer, 1866; Grenholm, 1923). The most definitive pelvic fin function proposed by Harris, was that pelvic fins counteracted the upward drift of the body caused by lateral pectoral fins during braking in derived perciform fishes (Harris, 1938). Excluding fishes with highly unique and specialized pelvic fin structures, Harris described pelvic fin motion as a limited abduction and adduction directly below the body, resulting mainly in static trimming forces (Harris, 1938). In this paper, I show that trout – a member of the actinopterygian sub-class of fishes, with pelvic fins located well behind the centre of mass – have an active and complex three-dimensional pelvic fin motion, suggesting that pelvic fins have a stabilizing and locomotor function beyond the limited scope proposed by Harris.

During slow-speed swimming (0.13–1.36 $BL\,s^{-1}$) trout moved their pelvic fins in contralateral oscillations. Each individual pelvic fin moved in two major oscillations that overlapped during the fin beat cycle (left and right fins act 180 deg. out of phase): (1) oscillations relative to the transverse plane (initiated first); and (2) oscillations relative to the sagittal plane (initiated 120 deg. after the transverse plane oscillations). Both the direction and timing of these oscillations suggested that pelvic fin motion is, at least partially, the result of active muscle use, and not due to body and water motion alone. For example, fish swam head into the flow; therefore, as pelvic fins oscillated towards the transverse plane, they moved against the downstream current. This motion would require muscle activation, particularly as the fin area increased as they were presented to the flow. Fin oscillation relative to the sagittal plane also appeared to be active. There were two points in the sagittal oscillation cycle at which, instead of moving with the lateral flow caused by body motion, the fin tips moved with the body against the local flow pattern. Pelvic fins do have a complex musculature: two sets of abductors and adductors control each pelvic fin surface (Grenholm, 1923), suggesting that fins can be used dynamically to produce forces in many directions. The contralateral pelvic fin oscillation suggested that fin musculature is active over 75% of the stroke cycle, although future studies that record electrical activity in pelvic fin muscles will be needed to confirm and demonstrate the pattern of pelvic fin muscle use.

Hypothesized pelvic fin function during steady swimming

Based on kinematic analysis it appears that pelvic fin oscillation produced a series of forces (Fig. 10). During the stroke phases when the fin was actively pushing against flow, one can assume the fin produced hydrodynamic force. There were also points in the oscillation cycle when fins seemed to move with the flow, and were not necessarily powered actively; these phases may also be hydrodynamically functional.

As the fin oscillated on approaching the transverse plane, its surface area increased against the oncoming flow, possibly causing a drag-based force. This braking force might: (1) help to slow the fish's forward speed [trout are fast endurance swimmers, comfortable swimming at speeds of 2.5 $BL\,s^{-1}$ (Bainbridge, 1960; Webb, 1971a; Webb, 1971b), they may use their fins at slow speeds to control forward velocity (Webb, 2006)]; (2) act as a pitch control (providing a drag surface well behind the fish's centre of mass forces the tail up); and (3) act to pivot the fish around the pelvic fin base, providing yawing stabilization, which helps to change the fish's heading and start the next body wave oscillation. The second half of pelvic oscillation with the transverse plane appears to be passive; oncoming flow pushes the fin into an adducted position along the body. Although this phase of the stroke may not require muscle activity, the drag on the fin by the flow, which adducts the fin, might act as a stabilizing force. The fin, like a dihedral foil, may produce roll- and yaw-stabilizing lift in much the same way feathers on an arrow act to straighten the trajectory of the shaft (Fish, 2002; Weihs, 1993; Weihs, 2002).

Fin oscillation with the sagittal plane should produce lateral jet forces during the part of the cycle in which the fin is moved actively against local flow. Dorsal and anal fins that oscillate relative to the fish's sagittal plane have been shown to produce clear lateral jets (Standen and Lauder, 2007). I would expect the pelvic fin sagittal oscillation to produce similar hydrodynamics. For example, the left fin, supinating while moving left with the body, should produce a left lateral force with the fin's dorsal side. This force would dampen the leftward body oscillation preparing for the body's return to the right. Later in sagittal plane oscillation, the fin pronates towards the right as it moves rightward with the body. This motion should produce a rightward lateral force with the fin's ventral surface, again helping to dampen rightward body oscillation. During the portion of the sagittal oscillation that appears to be passively driven by flow, the pelvic fin may have two functions: (1) the fin might again be acting as a passive stabilizing foil as it moves first into maximum supination and later into maximum pronation away from the body; and (2) the fin might be reducing energy expenditure by passively allowing water pressure to move the fin into maximum supination and then pronation positions. This passive motion would prepare the fin for maximum lateral force production when it begins its active movement against the flow.

In summary, when both fins are oscillating 180° out of phase, three major forces appear to always be in effect. (1) A powered braking force (as one fin or the other abducts into the oncoming flow). (2) A passive stabilization force (fins producing static drag and possibly lift, like a dihedral foil, as they are adducted by the flow). And (3), lateral thrust forces that combine to dampen body oscillation (when the left fin is pushing with its dorsal side towards the left, the right fin, 180° out of phase, is also pushing towards the left but with its ventral side). Finally, the phase lag between individual fin oscillations ensures that pelvic fins never lie directly along the fish's belly. When either fin is fully adducted relative to the transverse plane it is partially supinated relative to the sagittal plane and vice versa, providing a stabilizing roll reducing foil at all points in the cycle. During slow-speed steady swimming in trout, pelvic fins have a complex, active motion that appears to have both a dynamic-powered and a static-trim force producing function.

Manoeuvring

Pelvic fin kinematics were highly variable during manoeuvres. Fish voluntarily manoeuvred while feeding on food pellets moving through the flow tank. Consequently, the distance of pellets from the fish's original position varied. Moreover, the pellet's drifting speed varied depending on its position in the flow tank. Judging the distance and speed of target food particles, fish actively modulated pelvic fin kinematics to help control body position during food capture.

Despite these differences between manoeuvres, a general movement pattern existed. Manoeuvres began with a change in the fish's heading followed by inside fin abduction. Next, there was a reduction in heading change with abduction of the outside fin. Finally, fish heading returned close to the original heading and often was accompanied by a secondary inside fin abduction (Fig. 8). Fish use their pectoral fins and body musculature to initiate heading changes when turning (Drucker and Lauder, 2003). Peak pelvic fin oscillation occurs well after the initiation of heading change (Fig. 8), suggesting that pelvic fins contribute to body posture control after turn initiation.

The timing patterns of fin motion during manoeuvres suggested that two mechanisms of control are used by pelvic fins: variable and consistent. Peaks in pronation and supination of fins occurred irregularly throughout manoeuvres, suggesting that pelvic fins are capable of fine tuning their motion and timing to offset perturbations. Conversely, peaks in abduction, adduction and fin area have consistent timing, and can be predicted to occur at particular points during a manoeuvre, suggesting coordinated function. Consistent pelvic fin motion during manoeuvres implies asymmetric functions between inside and outside pelvic fins.

The motion of the fin on the inside of the turn suggests two main functions. (1) Abduction just before and during maximum heading increases inside fin drag. Because pelvic fins are located behind the centre of mass, this may pivot the body into the turn, helping to maintain and stabilize maximum heading amplitude. And (2), rapid fin adduction as the fish heading returns to centre, again, might pivot the body in the reverse direction, allowing the body to realign behind the centre of mass, ultimately returning the fish heading to centre. Maximal fin area at this point also provides a larger stabilizing foil surface.

Concurrently, the outside fin motion also suggests two unique functions. (1) Just prior to maximum heading change, the outside fin has minimal area, possibly reducing deleterious drag and thereby reducing the turn angle and (2) at the end of maximum heading, the outside fin abducted with maximal fin area; this may increase drag on the outside of the turn, continuing to pivot the body around the centre of mass, bringing the heading to centre and completing the turn.

Steady swimming and manoeuvres compared

Webb defines two types of correction forces that aquatic organisms use to maintain stability: powered corrections and trimming corrections (Webb, 2002). Powered correction forces are active motions of fins, independent of body motion, to produce forces. Trimming correction uses induced flow over a relatively stationary fin to produce forces as the body is moving through the fluid. Trout pelvic fins appear to produce powered correction forces during slow-speed swimming when the body is not moving fast enough to produce trimming forces over the fins, and trimming correction forces during manoeuvres when the lateral speed of the body is increased.

Conclusions

Harris (Harris, 1938) concluded that pelvic fins, at best, produced weak trimming forces; fish with basal morphologies having less functional pelvic fins than those with derived morphologies. The data from this paper clearly show complex three-dimensional motion in trout pelvic fins, which suggests complex pelvic fin function in an actinopterygian with relatively basal fin morphology (Fig. 1). Future electromyographic and flow visualization experiments will clarify the activation pattern of muscles driving the pelvic fins and the resultant hydrodynamic forces produced, testing the hypotheses of fin function set forth in this paper.

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