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Functional morphology and hydrodynamics of backward swimming in bluegill sunfish, *Lepomis macrochirus*

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ABSTRACT

Most teleost fishes, like the bluegill sunfish *Lepomis macrochirus*, have multiple flexible fins that are used as modifiable control surfaces. This helps to make fish highly maneuverable, permitting behaviors like reversing direction of motion and swimming backwards without having to rotate body position. To answer the question of how fish swim backwards we used high–speed videography and electromyography to determine the kinematics and muscle activity necessary to produce reverse-direction propulsion in four bluegill sunfish. We found that, in contrast to slow forward swimming, low-speed backward swimming is a multi-fin behavior, utilizing the pectoral, dorsal, anal, and caudal fins. The pectoral fins alternate beats, each fin broadly flaring on the outstroke and feathered on the instroke. The dorsal fin and dorsal portion of the caudal fin move out of phase as do the anal fin and ventral portion of the caudal fin. Electromyography of muscles in the pectoral, dorsal, anal, and caudal fins demonstrated bilateral activation when these fins changed direction, suggesting that fins are stiffened at this time. In addition to backward propulsion by the pectoral fins, particle image velocimetry revealed that the dorsal and anal fins are capable of producing reverse momentum jets to propel the fish backward. Because teleost fishes are statically unstable, locomotion at slow speeds requires precise fin control to adequately balance torques produced about the center of mass. Therefore, the kinematics of backward swimming may be the result of compensation for rolling, pitching, and yawning instability. We suggest that asymmetric pectoral fin activity with feathering during adduction balances rolling instability. The ventral to dorsal undulatory wave on the caudal fin controls pitch instability and yaw instability encountered from pectoral-driven backward locomotion. Thrust generation from the dorsal and anal fins decreases the destabilizing effect of the long moment arm of the tail in backward swimming. Thus, backward locomotion at slow speed is not simply the reverse of slow forward swimming.

1. Introduction

The flexible fins of ray-finned fishes allow them to achieve complex fin conformations that redirect fluid and offer hydrodynamic performance advantages (Lauder et al., 2006; Tytell, 2006; Lauder and Madden, 2007; Flammang et al., 2013). Because of this fine motor control of fin shape, ray-finned fishes are highly maneuverable and able to change heading and control their position without having to swim for any appreciable distance to do so. This ability to maneuver in a confined space permits many ray-finned fishes to take advantage of habitat niches in cluttered environments (Flammang and Lauder, 2013; Flammang, 2014).

Our current understanding of locomotion in ray-finned fishes is based on a wealth of information on the motor control, kinematics, and fluid dynamics that permit forward swimming, hovering, and turning (Gibb et al., 1994; Drucker, 1996; Drucker and Jensen, 1997; Drucker and Lauder, 1999; Ramamurti et al., 2002; Standen and Lauder, 2005; Lauder et al., 2006; Lauder, 2010). More recently, a few studies have investigated how ray-finned fishes, specifically the bluegill sunfish (*Lepomis macrochirus*), navigate a cluttered environment while swimming forward (Ellerby and Gerry, 2011; Flammang and Lauder, 2013). However, one area in which there is a notable lack of information is the analysis of backward locomotion: how are fish able to swim backward? Previous research has focused on eels (*Anguilla anguilla*), which swim backward by undulation of their entire body (Long et al., 1997; D'Aout and Aerts, 1999), and on knifefish (*Apteronotus albifrons*), which use undulations of their elongate anal fin to move backward (Nelson and MacIver, 1999; Youngerman et al., 2014). Both these fishes have elongate bodies and reverse the direction of muscle activation controlling the body or fin to change from forward to backward swimming.

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Many fishes that have a less elongate and higher aspect ratio body shape use a combination of median and paired fin activity to swim forward and execute stopping and turning maneuvers (Arreola and Westneat, 1996; Jayne et al., 1996; Drucker and Jensen, 1997; Gerstner, 1999; Drucker and Lauder, 2003; Higham et al., 2005). And many of these species also have the ability to swim backward without body undulation, despite significant anteroposterior asymmetry, because they are able to use flexible fins to redirect flow and generate reverse thrust (Webb and Gardiner, 2001; Flammang and Lauder, 2009). Bluegill sunfish can swim backward, but nothing is known of how this behavior is controlled, the overall gait or movement pattern exhibited by the different fins arranged around the body, and the hydrodynamic effects of fin motion.

The main goal of the research described here is to document the pattern of muscle activity in the pectoral, dorsal, anal, and caudal fins of bluegill sunfish during slow backward locomotion for comparison to activity in these muscles during forward swimming at similar speeds. Secondary goals are to provide a kinematic gait diagram showing the overall pattern of fin use during slow backward swimming, and to document a novel hydrodynamic feature of fin function observed during backward locomotion. Bluegill sunfish possess a relatively stiff body (compared, for example, to eels), and hence rely on paired and median fin motions to move backward. We used high-speed video to analyze the amplitude and relative timing of median and paired fin kinematics, electromyography to record patterns of fin muscle electrical activity, and particle image velocimetry to analyze selected fluid flow patterns produced by median fins.

At least in theory, backward swimming could be accomplished by simply reversing the pattern of fin motion used during forward locomotion. But because the location of the center of mass (COM) in bluegill is not in the geometric center of the fish (Drucker and Lauder, 1999; Tytell and Lauder, 2008), torques generated by fins with respect to the leading edge (head during forward swimming, the caudal fin tip during backward locomotion) differ depending on the direction of motion. We thus hypothesized that backward swimming would *not* be the reverse of forward swimming, and that in order to swim backward and maintain body orientation and posture, fish would require recruitment and active coordination of median and paired fins not seen in forward swimming at slow speeds.

2. Materials and methods

2.1. Fish

Four bluegill sunfish (*Lepomis macrochirus*; mean total length (L) = 16.5 cm ± 0.5 s.d.) were used in these experiments. Fish were kept in individual 40 l tanks and fed earthworms three times weekly. All fish were handled ethically according to Harvard University Institutional Animal Care and Use Committee guidelines, protocol 20-03.

2.2. Kinematic protocol

Experiments were performed in a 600 l recirculating flow tank with a 28 cm x 28 cm x 80 cm working area, as in previous research (Standen and Lauder, 2005; Tytell, 2006; Flammang and Lauder, 2008). Three synchronized high-speed video cameras (Photron USA, Inc., San Diego, CA, USA) simultaneously recorded the fish swimming in the lateral, posterior, and ventral views. Backward swimming maneuvers were filmed at 250 frames s^{-1} with 1024×1024 pixel resolution.

Backward swimming behavior was performed unsolicited or elicited by positioning a wooden dowel 1–2 cm in front of the fish's rostrum, without contacting the fish. Fish readily swam backward when the dowel was positioned in front of the head. We only recorded swimming at voluntary speeds; these ranged from 0.20 to 0.71 L/s (mean = 0.34 ± 0.11 s.d.) and were averaged across individuals for statistical analysis. Attempts to induce higher backward swimming speeds resulted in bluegill turning around to swim away from the stimulus. These backward swimming velocities were very similar to those used by bluegill during slow forward swimming using the pectoral fins, and studied previously by Gibb et al. (1994), Jayne et al. (1996), and Drucker and Lauder (1999). Data are compared to the forward swimming speed of 0.5 L/s from Flammang and Lauder (2008). Also, in the present paper we do not address hovering motions of fins: detailed kinematics for hovering were previously presented by Flammang et al. (2013). Each fish was recorded swimming backwards before electrode insertion (fish A = 8 sequences; B = 11; C = 11; D = 11) and several weeks later with electromyography (EMG) electrodes implanted (A = 10; B = 10; C = 8; D = 8; see Section 2.3 for details on EMG recordings). Electromyographic data were recorded during forward swimming at comparable speeds to those observed for backward locomotion in order to enable statistical comparisons of muscle activity patterns between forward and backward locomotion (see Table 1). In many of the sequences when fish swam slowly forward, we slowly inserted the dowel in front of the head, and fish then reversed direction, swimming backwards at an equivalent speed.

2.3. Electromyographic protocol

Fish were anaesthetized using tricaine methanesulfonate (MS222, trade name Finquel; Argent Labs, Redmond, WA, USA) and ventilated during electrode placement, as in previous studies (Jayne and Lauder, 1993; Jayne et al., 1996; Tytell and Lauder, 2002; Flammang and Lauder, 2008). Electromyography electrodes were

Table 1

Mean ± standard error of muscle activity duration and intensity during forward (F; $n = 100$) versus backward (B; $n = 95$) swimming behaviors in all individuals. Intensity is measured as both the root-mean-square (RMS) and integral of mean activity because statistical differences were not consistent between the two measures.

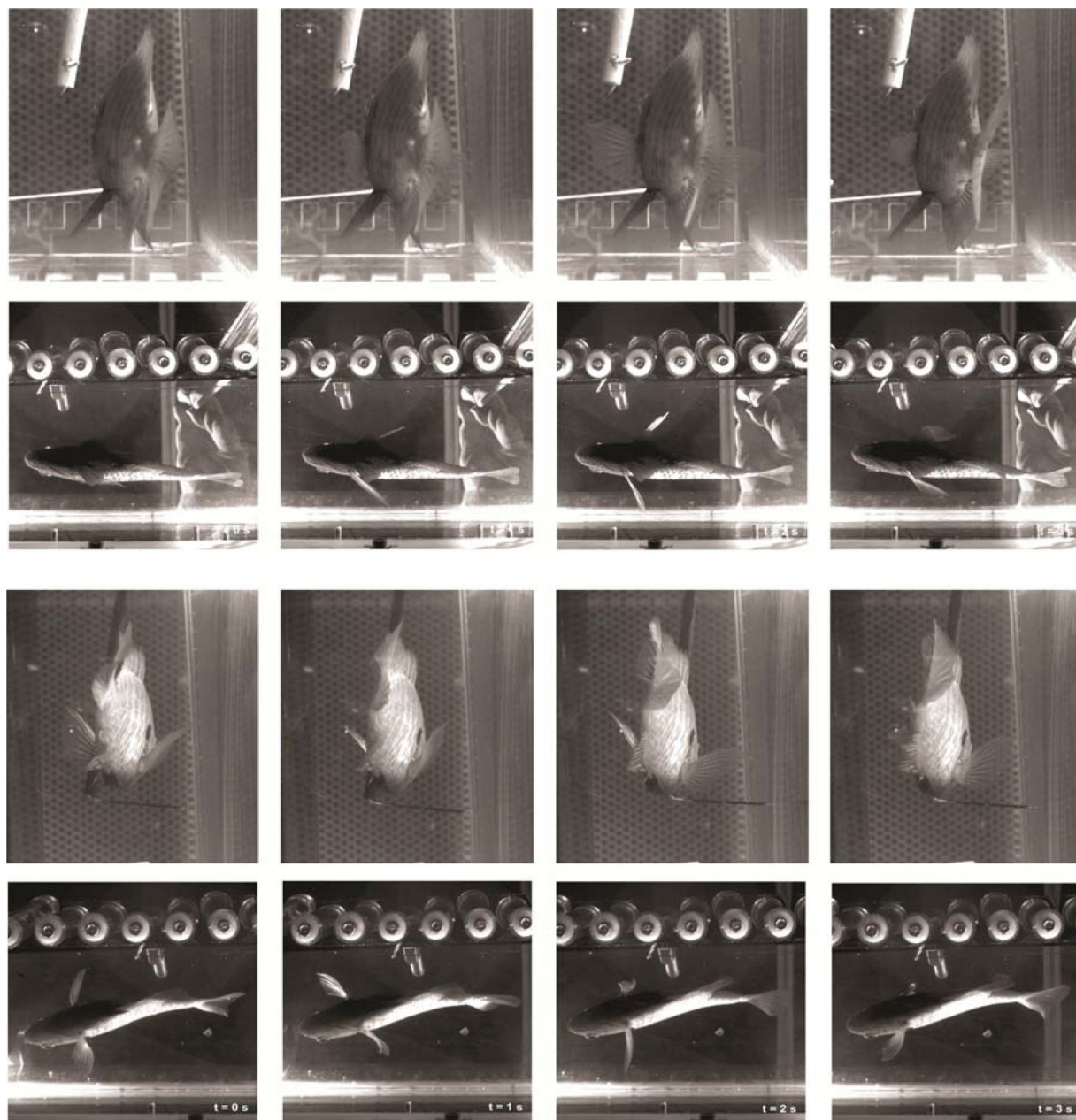| Muscles	Direction	Duration (s)	Intensity (V) RMS	Integral
Pectoral adductors	F	0.294 ± 0.008	0.010 ± 0.000	0.002 ± 0.000
	B	0.259 ± 0.010	0.012 ± 0.001	0.002 ± 0.000
Pectoral abductors	F	0.276 ± 0.008	0.007 ± 0.000	0.001 ± 0.000
	B	0.297 ± 0.011	0.017 ± 0.001	0.003 ± 0.000
Dorsal inclinators	F	0.207 ± 0.016	0.004 ± 0.000	0.001 ± 0.000
	B	0.290 ± 0.011	0.022 ± 0.002	0.004 ± 0.000
Anal inclinators	F	0.118 ± 0.015	0.001 ± 0.000	0.000 ± 0.000
	B	0.244 ± 0.012	0.012 ± 0.001	0.002 ± 0.000
Hypochordal longitudinalis	F	0.294 ± 0.013	0.003 ± 0.000	0.001 ± 0.000
	B	0.228 ± 0.019	0.006 ± 0.001	0.001 ± 0.000
Interradialis at mid-tail (IR9)	F	0.718 ± 0.072	0.006 ± 0.001	0.003 ± 0.000
	B	0.280 ± 0.041	0.036 ± 0.012	0.006 ± 0.001

Fig. 1. Bluegill sunfish swimming forward (top two rows) and backward (bottom two rows), seen in both the posterior and ventral views.

made from 2 m lengths of 0.05 mm bifilar Teflon-coated steel with 0.5 mm of the tips bared of insulation and split apart so as not to be in contact. Subcutaneous implantation of each electrode into muscle was performed using a sterile 26 g needle. Electrodes were placed in the adductor profundus muscles of the left and right pectoral fins, the abductor superficialis of the left and right pectoral fins, the fourth from posterior dorsal inclinator, the fourth from posterior anal inclinator, the left and right hypochordal longitudinalis, and the ninth interradialis muscle (at the base of the fork) of the caudal fin (Flammang and Lauder, 2008, 2009).

Fish recuperated under observation in a recirculating flow tank for at least twice as long as the surgery had lasted before experiments began. EMG signals were amplified 5000 times through Grass model P511 K amplifiers (Grass Technologies, Warwick, RI, USA) set to filter at high bandpass (100 Hz) and low bandpass (3 kHz), with a 60 Hz notch filter. Digital recordings of EMG signals were captured in LabChart 7.3.7 software using an ADInstruments

PowerLab/16SP analog-to-digital converter (ADInstruments, Inc., Colorado Springs, CO, USA). Following the experiments, fish were euthanized using an overdose of MS222 and fixed in formalin and preserved in 75% ethanol. Electrode tips were dissected post-experiment to verify placement.

2.4. Particle image velocimetry

Flow patterns generated by the dorsal and anal fins were quantified using standard particle image velocimetry (PIV) techniques as in our past research (e.g., Drucker and Lauder, 1999; Tytell and Lauder, 2008). Laser light height was adjusted to provide a two-dimensional view of flows from the middle of either the dorsal or anal fins, and fish were induced to perform backward locomotion while the fins were illuminated by the horizontal light sheet. It was not possible to simultaneously image flows from the pectoral fins during backward swimming, and our analysis here is restricted to
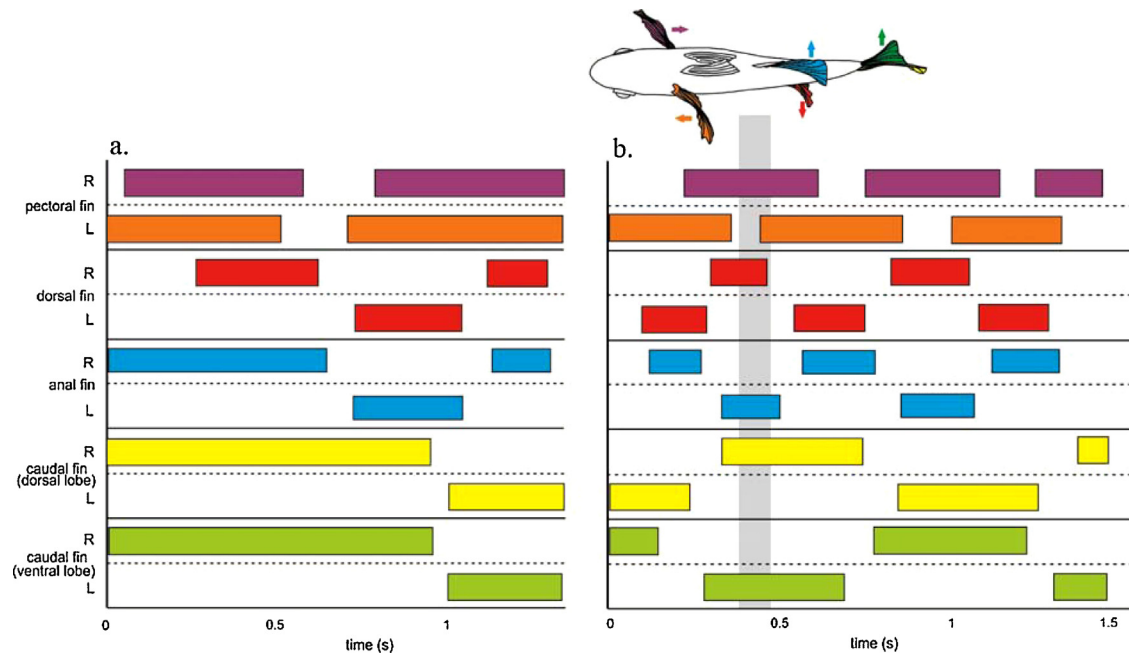
Fig. 2. Kinematic pattern during (a) forward and (b) backward swimming of bluegill sunfish at equivalent speeds of approximately 0.5 L/s on average. Each panel shows a representative gait diagram from one sequence of a bluegill sunfish swimming in a straight line. The colored bars indicate the duration of each fin's motion away from the midline of the body, from onset of abduction through return to the resting or midline position. (b) Graph at the top: illustration drawn from high-speed video of the ventral view of the body and fin position at the time indicated by the grey bar on the gait diagram. Bars are color-coded to match the fin colors and directional arrows in the image above.

the dorsal and anal fin wakes. Particle motions were analyzed using DaVis 7.3 software (LaVision Inc., Ypsilanti, MI, USA) to generate velocity vector fields and to calculate the fluid flow magnitudes and angles resulting from dorsal and anal fin motion.

2.5. Data analysis

High-speed video and EMG recordings were synchronized by a trigger signal through the ADInstruments PowerLab/16SP analog-to-digital converter. The three video views were calibrated in three dimensions using direct linear transformation of a custom 40-point calibration frame and digitized using a program written for MATLAB R2011a (MathWorks, Inc., Natick, MA, USA) by Hedrick (2008). A total of 12 points were digitized in each of the 77 back-

ing sequences: (1) the tip of the third most dorsal (longest) left pectoral fin ray; (2) the tip of the third most dorsal right pectoral fin ray; (3) the center of the pelvic girdle; on the dorsal fin, the (4) tip and (5) base of the fourth from caudal-most fin ray; on the anal fin, the (4) tip and (5) base of the fourth from caudal-most fin ray; (8) the tip of the third caudal fin ray; (9) the base of the ninth caudal fin ray; (10) the tip of the fifteenth caudal fin ray; (11) the tip of the ninth caudal fin ray (the fork of the caudal fin); and (12) the COM. Points 8–11 were chosen specifically to correlate with previous, more detailed investigations of the action of the bluegill caudal fin in backward swimming maneuvers (Flammang and Lauder, 2009). LabChart 7.3.7 software (ADInstruments, Inc.) was used to rectify, integrate, and digitize the onset, duration, and intensity of the EMG recordings (measured as both the root mean

Table 2

Statistical analysis comparing muscle activity duration and intensity during forward ($n = 100$) versus backward ($n = 95$) swimming behaviors in all individuals. Intensity is measured as both the root-mean-square (RMS) and integral of mean activity because statistical differences were not consistent between the two measures. Kruskal–Wallis (KW) ANOVA on ranks was performed to identify if the difference in activity measures for forward and backward swimming for any muscle was statistically different. If statistically different, a post-hoc multiple comparison using Dunn's method was performed. The test statistics H (Kruskal–Wallis) and Q (Dunn's method) were compared to critical values at $\alpha = 0.05$.

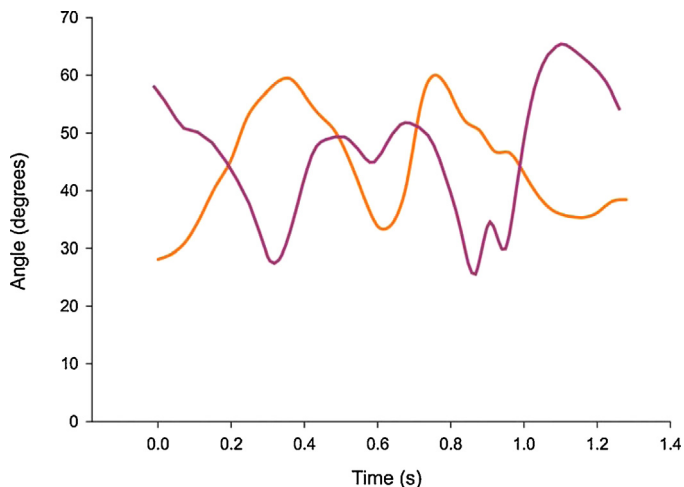| Muscle activity	Duration		Intensity (RMS)		Intensity (Integral)	
	KW	Dunn's	KW	Dunn's	KW	Dunn's
Pectoral adduction	$P < 0.001$ ($H = 11.56$)	$P < 0.05$ ($Q = 3.40$)	$P = 0.938$ ($H = 0.006$)	ns	$P < 0.001$ ($H = 8.83$)	$P < 0.05$ ($Q = 2.97$)
Pectoral abduction	$P = 0.217$ ($H = 1.52$)	ns	$P < 0.001$ ($H = 54.0$)	$P < 0.05$ ($Q = 7.35$)	$P < 0.001$ ($H = 50.45$)	$P < 0.05$ ($Q = 7.10$)
Dorsal inclinator	$P = 0.003$ ($H = 8.70$)	$P < 0.05$ ($Q = 2.94$)	$P < 0.001$ ($H = 110.91$)	$P < 0.05$ ($Q = 10.51$)	$P < 0.001$ ($H = 109.89$)	$P < 0.05$ ($Q = 10.45$)
Anal inclinator	$P < 0.001$ ($H = 31.77$)	$P < 0.05$ ($Q = 5.53$)	$P < 0.001$ ($H = 119.63$)	$P < 0.05$ ($Q = 10.74$)	$P < 0.001$ ($H = 95.89$)	$P < 0.05$ ($Q = 9.59$)
Hypochordal longitudinalis	$P = 0.224$ ($H = 1.48$)	ns	$P < 0.001$ ($H = 17.97$)	$P < 0.05$ ($Q = 4.23$)	$P = 0.231$ ($H = 1.43$)	ns
Interradialis at mid-tail (IR9)	$P < 0.001$ ($H = 18.25$)	$P < 0.05$ ($Q = 4.27$)	$P < 0.001$ ($H = 14.15$)	$P < 0.05$ ($Q = 3.76$)	$P = 0.099$ ($H = 2.72$)	ns

Fig. 3. Pectoral fin angles during backward swimming of bluegill sunfish. Angle of left (orange) and right (purple) pectoral fins during backward swimming. Angles are measured relative to the frontal plane.
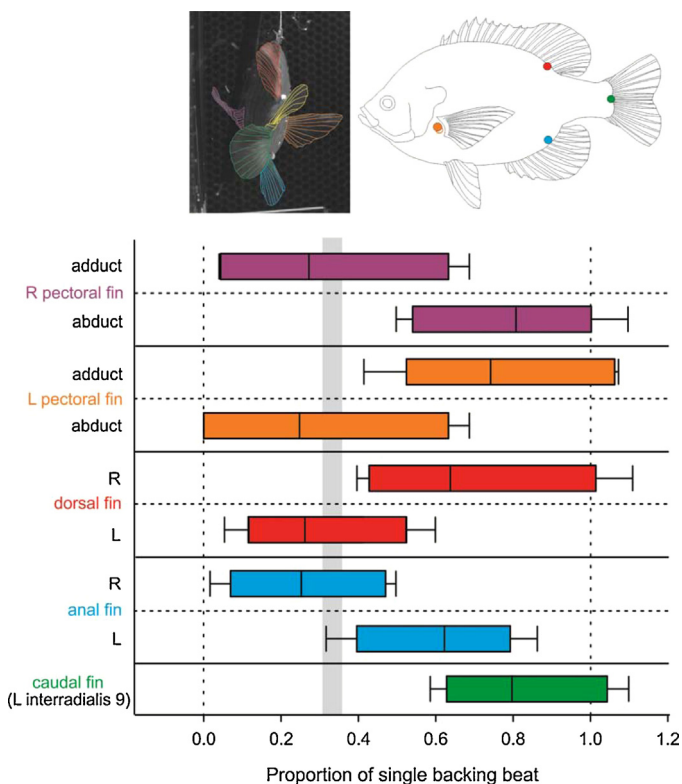

Fig. 5. Particle image velocimetry (PIV) analysis of the jet produced by the anal fin of a bluegill sunfish swimming backward. Note that the anal fin momentum jet is aimed anteriorly, toward the head. White arrow points toward the jet produced by the anal fin.

Fig. 4. Summary of muscle activity during backward locomotion of bluegill sunfish. Mean muscle activity duration as proportion of one backing fin beat (relative to the onset of left pectoral fin abduction). Mean of horizontal bar plots is designated as a vertical bar, error bars represent 95% confidence intervals. Data shown are for all backing sequences from all fish (n = 65 sequences, four fish). The grey vertical band designates the point in time at which the fish was in the position of the top image (posterior view, through a mirror). Bars are color-coded to match the fin colors above. Fish outline at upper right shows the positions of inserted electrodes.

square and the integral of the rectified EMG burst). Both measures of intensity are commonly used in biomechanical analyses, but generally only one method is reported. We chose to include both tests here because they differed in statistical outcomes and there was no way to justify using one over the other. Data of duration and intensity of EMG activity of all muscles combined did not pass the Shapiro–Wilk normality test for analysis of variance, so the non-
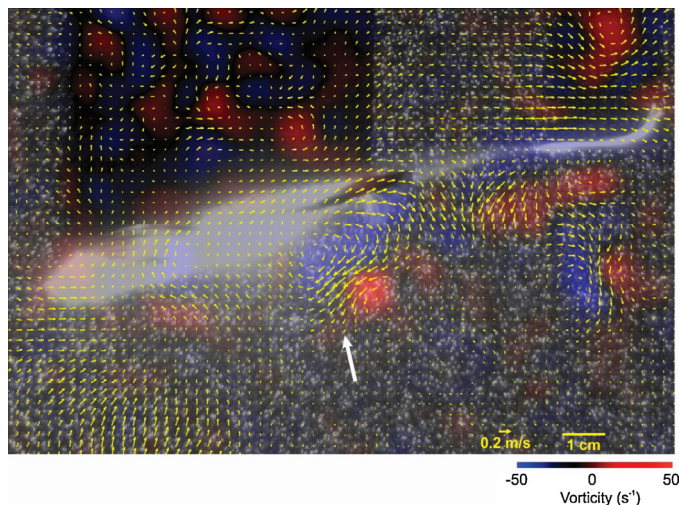
parametric Kruskal–Wallis ANOVA on ranks was used to test for statistically significant differences in fin muscle activity between forward and backward swimming behaviors (SigmaPlot 12.0; SYS-TAT Software, Inc., San Jose, CA, USA). To isolate groups that differed from others, Dunn's pairwise multiple comparison procedure was used.

3. Results

77 sequences of four fish swimming backwards were analyzed (Fig. 1). Throughout each backing sequence, pectoral, dorsal, anal, and caudal fins were in motion at approximately 2 Hz but the fish body was held in a relatively straight position. This contrasts with forward locomotion where at the slow speeds of less than 1.0 L/s only the pectoral fins are used to generate thrust.

The backward swimming gait of bluegill sunfish was characterized by a repeated pattern of alternating left and right pectoral fin motion with synchronized median fin activity; conversely, in forward swimming, the pectoral fins were adducted and abducted at the same time and there was no synchrony with the posterior median fins (Fig. 2). During backward swimming, as the pectoral fin on one side of the body was adducted, the pectoral fin on the other side of the body was abducted (Fig. 3): left and right pectoral fin motions were thus asynchronous. During the outstroke of the left pectoral fin, the dorsal fin was inclined to the left and the anal fin was inclined to the right. During abduction, the pectoral fin was broad and flat in the transverse plane, reaching a maximum angle of approximately 70° to the frontal plane (Fig. 3). After reaching maximum anterior excursion, the pectoral fin rotated anteriorly and was then adducted in a feathered orientation (approximately 25° to the frontal plane). The dorsal and anal fins were in phase with each other as they undulated to the left and right sides of the fish. The dorsal and anal fins reached maximum lateral excursion to one side of the fish as the contralateral pectoral fin reached maximum anterior excursion and the ipsilateral pectoral fin was close to the body. The caudal fin was oscillated vertically in a wave-like pattern that originated in the ventral lobe of the caudal fin and progressed dorsally. Backward locomotion thus involved movement of the pectoral, dorsal, anal, and caudal fins.

EMG recordings of fin muscles demonstrated a considerable degree of temporal overlap between antagonistic muscles (Fig. 4). For example, pectoral fin adductor and abductor muscle activity
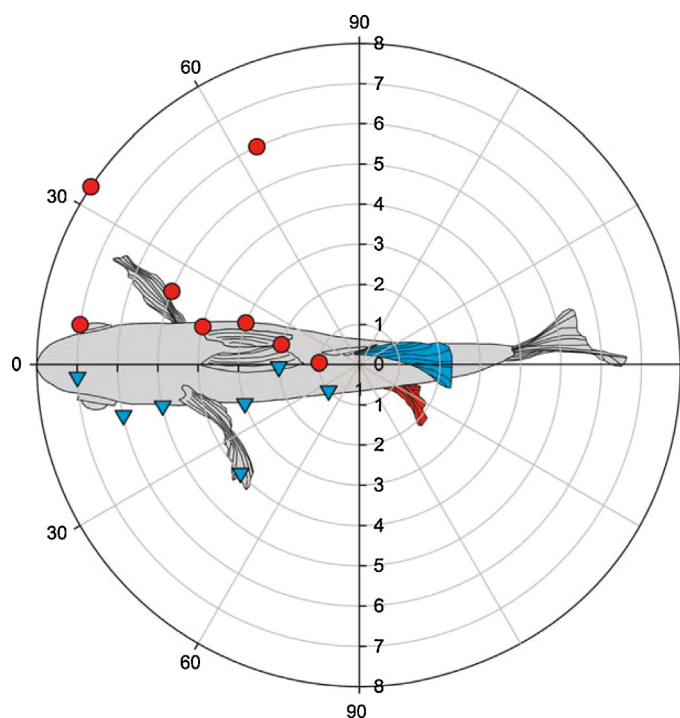
Fig. 6. Reverse momentum jets produced by the dorsal and anal fins of bluegill sunfish swimming backward. Polar plot of jet angle of the dorsal (top, red circles, n = 8) and anal (bottom, blue triangles, n = 7) fin jets relative to the body midline (x-axis, 0°, relative to ventral view of fish for orientation). Numbers on the central y-axis indicate each sequence analyzed. Both anal and dorsal fin momentum jets during backward locomotion are directly anteriorly, toward the head.

Table 3
Measurements of reverse momentum jet angle and magnitude from particle image velocimetry (PIV) data on bluegill sunfish swimming backward. Table values are means (±one standard error (SE)). Angles <90° indicate that the momentum jet is directed toward the head.

	Dorsal fin		Anal fin	
	mean	±SE	mean	±SE
Jet angle from fish midline (°)	22.29	6.93	21.14	8.82
Average jet magnitude (m/s)	0.045	0.007	0.055	0.013
Maximum jet magnitude (m/s)	0.083	0.014	0.126	0.041

frequently occurred simultaneously during outstroke of the fin. A similar pattern was observed in the dorsal and anal fins as they passed the body midline to reach to the opposite side.

Comparison of fin muscle EMG activity between forward and backward swimming behaviors (Tables 1 and 2) revealed a statistically significant difference in the duration of pectoral fin adduction activity, but not in pectoral fin abduction motor patterns. The duration of dorsal and anal inclinator muscle activity, as well as that of the interradialis muscles in the caudal fin, were also significantly different between the two behaviors. However, the hypochordal longitudinalis, an intrinsic caudal muscle, showed no difference in activity duration.

During backward swimming, we observed that bluegill sunfish produced reverse momentum jets from motion of the dorsal and anal fins (Fig. 5). These jets were angled at an average of 22.3° and 21.1° from the midline of the fish, respectively (Fig. 6 and Table 3), indicating that these fins generated momentum aimed forward (toward the head), and contributed to negative thrust moving fish backward. Mean and maximum magnitudes of the jet produced by the dorsal fin were 4.5 and 8.3 cm s^{-1}, respectively and, for the anal fin, 5.5 and 12.6 cm s^{-1}.

4. Discussion

Backward swimming in bluegill sunfish is accomplished by alternating motions of the pectoral, dorsal, anal, and caudal fins; it is not accomplished by reversing the fin motions used for forward swimming. While forward swimming at slow speeds (less than 1 L/s) in bluegill sunfish is typically accomplished using only the pectoral fins (Gibb et al., 1994; Drucker and Lauder, 1999), backward locomotion at slow speeds involves recruitment of the dorsal, anal, and caudal fins (the latter exhibiting a vertical wave) in addition to the pectoral fins. We found numerous differences between forward and backward locomotion in patterns of muscle activity (Table 2), and also documented a novel pattern of dorsal and anal fin use during backward swimming which allows these fins to generate reverse momentum to assist in powering backward swimming.

For fish to travel forward and backward along the same linear path, at the same speed, but not use reciprocal fin motions for the two behaviors, suggests that additional physical forces underlie the difference between motions in the two directions. In particular, the kinematic patterning of backward swimming may be explained by three basic phenomena: rolling stability, pitching stability, and yawing stability.

Many fish are statically unstable because their COM is located dorsal to their center of buoyancy (Alexander, 1967; Webb, 1975; Standen and Lauder, 2005; but see Webb and Weihs, 1994 for counterexamples). They gain dynamic stability and counterbalance roll torques using fin position and inertial motions, and at higher swimming speeds the fluid forces exerted on fins make controlling body position easier. At slow swimming speeds, maintaining body position is more difficult, and this has been adduced as one reason that the cost of transport for fishes may increase at low speeds (Korsmeyer et al., 2002). Swimming backward slowly produces additional instability in that the feathering adduction stroke likely does not produce thrust, whereas in forward swimming the bluegill generates thrust on both the outstroke and instroke of the pectoral fin (Lauder and Madden, 2007), which may explain the significant difference in adductor EMG activity between the two behaviors (Table 2). The pattern of fin motion during backward movement, such as alternating feathered instroke and powered outstroke by the pectoral fins, may act to balance rolling torques about the COM. Contralateral activation of the pectoral fin adductor and abductor muscles was recorded using EMG, suggesting that on the outstroke the pectoral fin required stiffening against hydrodynamic loading to maintain a broad, flat orientation. Thus, fish pushed back against the water with the abducting pectoral fin while the opposite pectoral fin was adducted in a feathered orientation. In backward swimming, pectoral fin rowing appears to involve more drag-based dynamics as the fin surface is relatively flat during (reverse) thrust generation, whereas in forward swimming, modulation of pectoral fin shape results in lift-based forces and complex vortex generation mechanisms (Lauder and Madden, 2007).

As part of the coordinated fin kinematics seen during backward swimming, we observed a ventral to dorsal wave of activation in the caudal fin, visible in the posterior view (Fig. 4.). This undulatory wave is in the reverse direction to that seen during forward swimming in bluegill sunfish (Flammang and Lauder, 2009). When swimming forward, the dorsal to ventral wave of caudal fin undulation produces lift in addition to thrust (Flammang and Lauder, 2008, 2009; Esposito et al., 2012). Undulation in the reverse direction would produce force directed dorsally, resulting in the caudal end of the fish being pushed ventrally. We hypothesize that this reverse lift maintains the pitch of the fish body by balancing torques generated by the pectoral fins which are anterior to the fish COM. Volumetric flow visualization techniques (Flammang et al., 2011) would be a useful future approach to summarize the fluid dynamics acting on the whole fish body during backward swimming and test

this hypothesis. Ting and Yang (2008) proposed a similar role for the caudal fin wave in a cichlid fish that swims with a significant pitch orientation.

Yawing instability during backward swimming stems from the majority of thrust production coming from pectoral abduction. During forward swimming, the long moment arm of the tail behind the COM is a source of self-correcting stabilization for any destabilizing yaw produced by the short moment arm of the head anterior to the COM. As bluegill sunfish swim backward, the tail is a source of large destabilizing torques and little self-correcting stabilization is produced by the short moment arm of the head. Therefore, during backward swimming, reverse momentum is generated not only from the abducting pectoral fins, but also from the dorsal and anal fins (Figs. 5, 6, and Table 3), shifting thrust production towards the direction of travel, thus reducing yawing instability.

Finally, we were surprised at the extent to which the dorsal and anal fins could vector locomotor forces. Previous research on bluegill fin hydrodynamics has shown that the dorsal and anal fins are capable of generating force at angles up to 90° to the body (Drucker and Lauder, 2001; Standen and Lauder, 2005). We did not anticipate that these fins would exhibit the level of deformation that they did, and that both the dorsal and anal fins would be capable of generating reverse thrust and contributing to backward propulsion. This is accomplished by significant and rapid curvature of the posterior regions of these fins so that a fluid jet is directed toward the head (Fig. 5). Backward locomotion in bluegill provides yet another example of the diverse functional capabilities of the flexible fins of teleost fishes.

Backward locomotion in fishes is poorly studied and so it is not clear how general the results presented here for bluegill are with respect to fishes with differing dorsal and anal fin designs. Other species with similar median fin placement may be able to utilize comparable fin deformation patterns to effect reverse thrust, while other species (such as trout, or carangid fishes with elongate but thin median fins) may not be able to generate reverse thrust with these fins. In such cases, other fin or body-based mechanisms of backward locomotion may be used, or backward swimming capability may be limited.

Acknowledgements

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