

Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes

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Summary

Locomotion is an integral aspect of the prey capture strategy of almost every predatory animal. For fishes that employ suction to draw prey into their mouths, locomotor movements are vital for the correct positioning of the mouth relative to the prey item. Despite this, little is known regarding the relationships between locomotor movements and prey capture. To gain insights into how fishes move during prey capture and the mechanisms underlying deceleration during prey capture, I measured the fin and body movements of largemouth bass, *Micropterus salmoides*, and bluegill sunfish, *Lepomis macrochirus*. Using a high-speed video camera (500 frames s⁻¹), I captured locomotor and feeding movements in lateral and ventral (*via* a mirror) view. Largemouth bass swam considerably faster than bluegill during the approach to the prey item, and both species decelerated substantially following prey capture. The mean magnitude of deceleration was significantly higher in largemouth bass (–1089 cm s⁻²) than bluegill (–235 cm s⁻²), and the timing of maximum deceleration was much later

for largemouth bass (30.3 ms after maximum gape) than bluegill (6.7 ms after maximum gape). Both species employed their pectoral, anal and caudal fins in order to decelerate during prey capture. However, largemouth bass protracted their pectoral fins more and faster, likely contributing to the greater magnitude of deceleration in the species. The primary mechanism for increased deceleration was an increase in approach speed. The drag forces experienced by the fins and body are proportional to the velocity of the flow squared. Thus, the braking forces exerted by fins, without any change in kinematics, will increase exponentially with small increases in swimming speed, perhaps allowing these fishes to achieve higher braking forces at higher swimming speeds without altering body or fin kinematics. This result can likely be extended to other maneuvers such as turning.

Key words: kinematics, braking, swimming, locomotion, prey capture, pectoral fin, anal fin, caudal fin, maneuvering, deceleration, suction, feeding, ram speed, accuracy.

Introduction

Feeding and locomotion are highly integrated among diverse groups of animals (e.g. Hoff et al., 1985; Gorb and Barth, 1994; Irschick and Losos, 1998; Iwaniuk et al., 1999; Dunbar and Badam, 2000; Budick and O'Malley, 2000; Domenici, 2001; Borla et al., 2002; Alfaro, 2003; Rice and Westneat, 2005; Higham et al., 2005a; Higham et al., 2007; Vincent et al., 2005; Walker et al., 2005). Because feeding is essential for growth and reproduction, the ability of the locomotor system to facilitate feeding contributes meaningfully to fitness. Fishes, in particular, capture prey by suction feeding, a rapid expansion of the mouth cavity to draw in water, but this can only be effective once the predator uses its locomotor system to position its mouth very close to the prey (Day et al., 2005; Higham et al., 2005a; Higham et al., 2006a). Although many fishes utilize suction to capture prey, the extent to which they rely on it depends on the ecology of the predator (Webb, 1984a;

Webb, 1984b; Carroll et al., 2004; Higham et al., 2006a). A commonly cited dichotomy separates 'ram feeders' from 'suction feeders', where the former relies predominantly on swimming speed to overtake evasive prey and the latter relies more on suction to draw non-evasive prey items towards them. These two scenarios, although very different, require a contribution from the locomotor system to be effective. While swimming speeds at the time of prey capture have been measured for many fishes (e.g. Nyberg, 1971; Rand and Lauder, 1981; Norton and Brainerd, 1993; Wainwright et al., 2001; Porter and Motta, 2004; Higham et al., 2005a; Higham et al., 2005b; Higham et al., 2006a; Higham et al., 2007), detailed interspecific examinations of locomotor movements throughout prey capture are rare (Rice and Westneat, 2005).

Fishes that rely predominantly on suction to capture prey tend to have small mouths, require a high level of accuracy during feeding, and feed on relatively non-evasive prey

(Higham et al., 2006a). By contrast, fishes that rely more on ram tend to have a larger mouth, require less accuracy and feed on relatively evasive prey. In both cases, braking during prey capture is likely to be important. For fishes relying predominantly on suction, braking will enhance accuracy by giving the predator more time to adjust the position of its mouth relative to the prey (Lauder and Drucker, 2004; Higham et al., 2006a) and will alleviate the negative effects of swimming speed on suction performance (Higham et al., 2005a). For fishes relying predominantly on ram, braking will enable the predator to be in a good position to follow a prey item that escapes (Webb and Gerstner, 2000; Webb, 2006). It remains unclear whether different species employ similar mechanisms of braking and whether the relative timing of braking is similar between species that employ different feeding strategies. Understanding how and when fishes decelerate is central to understanding predator-prey interactions.

Apart from feeding, deceleration is an integral component of animal movement and is ecologically important for intermittent locomotion (Higham et al., 2001; Kramer and McLaughlin, 2001), avoiding obstacles in the environment (Webb and Gerstner, 2000) and arriving predictably at a certain location (Higham et al., 2005b). Despite the pervasiveness of braking among almost all mobile animals, there is a paucity of studies that have addressed the mechanisms underlying deceleration (Drucker and Lauder, 2002; Drucker and Lauder, 2003; Higham et al., 2005b; McGowan et al., 2005). Fishes have multiple control surfaces that can contribute to braking, including the body, paired fins (pectoral and pelvic), median fins (dorsal and anal) and caudal fin. It is possible that certain fishes use a particular combination of fins to brake while other fishes use a completely different combination. This many-to-one mapping of form to function (Wainwright et al., 2005) could amplify the interspecific diversity of fin movements during braking. However, with the exception of Higham et al. (Higham et al., 2005b) and Rice and Westneat (Rice and Westneat, 2005), little is known about the integration of fin movements during deceleration in fishes.

During braking, fishes commonly protract their pectoral fins in order to increase the frontal area of the body (Breder, 1926; Harris, 1937a; Harris, 1937b; Bainbridge, 1963; Videler, 1981; Webb, 1984a; Geerlink, 1987; Webb and Fairchild, 2001; Borla et al., 2002; Drucker and Lauder, 2002; Drucker and Lauder, 2003; Higham et al., 2005b; Rice and Westneat, 2005). Pectoral fins likely enhance stability during braking since they limit side-to-side (yawing) movements by balancing each other if protracted together. In addition, perciform fishes such as centrarchids have pectoral fins that are located laterally on the body and generate a braking force such that the reaction force goes through the center of mass of the fish (Drucker and Lauder, 2002), thus limiting pitching movements. While the median fins can also contribute to braking, moving them to one side can lead to moments of yaw and roll (Drucker and Lauder, 2001; Standen and Lauder, 2005). By moving to the opposite side, the caudal fin might balance the forces from the median fins, possibly preventing a yawing maneuver. Whether species that rely more

heavily on the caudal and median fins become less steady during prey capture is not known. If this is the case, then the accuracy of the strike might be compromised since a yawing maneuver would likely shift the location of the mouth relative to the prey.

For aquatic vertebrates, centrarchid fishes have been a model group for studies dealing with feeding (e.g. Nyberg, 1971; Lauder, 1980; Lauder et al., 1986; Wainwright and Lauder, 1986; Norton and Brainerd, 1993; Grubich and Wainwright, 1997; Sass and Motta, 2002; Svanback et al., 2002; Ferry-Graham et al., 2003; Carroll, 2004; Carroll et al., 2004; Day et al., 2005; Higham et al., 2005a; Higham et al., 2006a; Higham et al., 2006b; Carroll and Wainwright, 2006) and locomotor (e.g. Jayne and Lauder, 1993; Jayne and Lauder, 1994; Jayne and Lauder, 1995; Jayne and Lauder, 1996; Jayne et al., 1996; Gibb et al., 1994; Johnson et al., 1994; Lauder and Jayne, 1996; Drucker and Lauder, 1999; Drucker and Lauder, 2000; Drucker and Lauder, 2001; Standen and Lauder, 2005; Higham et al., 2005b) function. The considerable diversity in both ecology and morphology makes centrarchids an excellent group for addressing questions regarding locomotor function during feeding. For example, species from the genus *Micropterus*, such as largemouth bass, have large mouths and are thought to rely heavily on high swimming speeds to capture large, relatively evasive prey (Higham et al., 2006a). By contrast, species from the genus *Lepomis*, such as bluegill, are deeper bodied, have relatively small mouths and are thought to rely heavily on suction to capture small, relatively non-evasive prey.

To gain insights into the mechanisms and timing of deceleration during prey capture, I studied the body and fin kinematics of largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*) during feeding. I addressed the following three specific questions in this study. (1) How do fishes decelerate? I predicted that both species will increase their frontal area by employing their pectoral, caudal and median fins in order to decelerate. (2) How do fishes modulate the magnitude of deceleration? I predicted that both species would increase the angular excursion of their fins in order to increase frontal area and the speed of the water relative to the fins. (3) How do fishes modulate swimming speed when capturing stationary prey? Because they typically feed on evasive prey, I predicted that largemouth bass would maintain a constant, relatively high ram speed until after the prey was captured. By contrast, I predicted that bluegill would decelerate considerably prior to capturing the prey item in order to maintain strike accuracy. Although comparing two species precludes conclusive interpretations of locomotor behavior based on feeding biology, I chose two closely related centrarchid species that exhibit extremely different morphological and ecological traits related to feeding. Thus, conclusions are likely related to feeding biology rather than other factors such as phylogenetic history.

Materials and methods

Experimental subjects

Largemouth bass (*Micropterus salmoides* Lacépède) and

bluegill sunfish (*Lepomis macrochirus* Rafinesque), both members of the freshwater family Centrarchidae, were studied. These two species have been the focus of several locomotor (Lauder and Jayne, 1996) and feeding (Higham et al., 2006a; Higham et al., 2006b) studies and are ideal for a comparative study since their ecology and morphology differ considerably (Lauder and Jayne, 1996; Carroll et al., 2004; Collar et al., 2005). Furthermore, these genera (*Lepomis* and *Micropterus*) are monophyletic and sister taxa with a most recent common ancestor estimated about 24 million years ago (Near et al., 2005). The fish were collected around Davis, CA, USA and were maintained in separate 38-liter aquaria. Data were analyzed from three individuals from each species of similar size. The mean body mass for largemouth bass and bluegill used in these experiments was 195.4 ± 20.9 g and 143.0 ± 24.7 g, respectively. Experiments complied with all guidelines for the use and care of animals in research at the University of California, Davis, where all experiments were conducted.

Morphology

Each fish used in this study was euthanized using an overdose of MS-222. The body was laid flat on its right side and the dorsal, anal and caudal fins were extended to their maximum position and pinned to a piece of Styrofoam. The left and right pectoral fins were removed carefully, extended to the natural maximum position and pinned to a small piece of Styrofoam. Each fin was brushed with formalin for preservation. With a ruler in the field of view, pictures were taken of each specimen and pectoral fins using a Kodak EasyShare CX7430 digital camera (1728×2304 pixels). The digital images were then imported into ImageJ version 1.33 (NIH, Washington, DC, USA) and the area of each fin was calculated (see Fig. 1). The aspect ratio (AR) of each pectoral fin was calculated by dividing the square of the length of the leading edge by the area.

Experimental protocol

Experiments were conducted in 200-liter tanks that were divided into two sections, which facilitated obtaining start–stop episodes with a standardized predator–prey distance. A very thin wire, angled away from the predator, was used to suspend small goldfish (approximately 5 cm long) or ghost shrimp (approximately 3–5 cm long). With the predator secured at one end of the tank with a trap door, the prey item was suspended approximately 40 cm from the door [see fig. 1 in Higham et al. (Higham et al., 2005b)]. Once the trap door was removed, the predator was free to swim towards the prey item and capture it. Although only sequences using tethered prey were filmed, freely moving prey were offered to the fish after every two trials involving tethered prey in order to maintain the fish's motivation and avoid any changes in behavior associated with capturing tethered prey. Locomotion and feeding were recorded from each fish using a high-speed NAC Memrecam ci digital system (Tokyo, Japan) operating at $500 \text{ images s}^{-1}$. Lateral and ventral (*via* a mirror underneath the prey oriented at 45°) views of the feeding event (Fig. 2) were obtained.



Fig. 1. Representative photographs of a pectoral fin from bluegill (A) and largemouth bass (B). Both fins are from the left side of the animal. Note that bluegill exhibit a significantly higher ($P < 0.05$) pectoral fin aspect ratio than largemouth bass (1.82 *versus* 1.34).

A picture was taken of a ruler that was placed inside the tank at the location of the prey to scale measurements. Two floodlights (600 W) on either side of the camera illuminated the experimental tank. The fish were not fed for a minimum of two days prior to the day of testing and the time between successive trials of a single individual within a single day was approximately 5–10 min. Only those sequences were analyzed in which the fish started from 40 cm away from the prey, the prey was completely consumed and there were no pauses during the prey capture event.

Kinematic measurements

For the 120 ms prior to and the 60 ms following maximum gape, frames were digitized at 250 Hz, since this provides a reliable estimate of acceleration during locomotion (Walker, 1998). For each frame, the forward displacement of the fish was calculated by digitizing the anterior margin of the eye in lateral

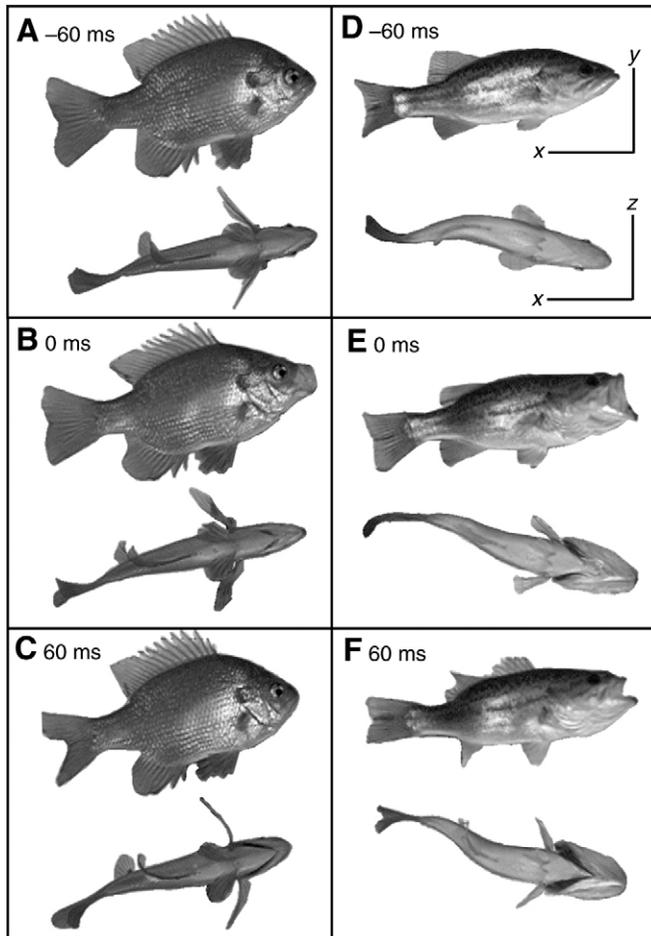


Fig. 2. Representative sequences for bluegill sunfish (A–C) and largemouth bass (D–F) decelerating during prey capture. The top two panels (A,D) are at 60 ms prior to maximum gape, the middle two panels (B,E) are at the time of maximum gape and the bottom two panels (C,F) are at 60 ms after maximum gape. Within each panel, the lateral view is above and the ventral view is below. The prey item is not shown because it is quite far in front of the fish 60 ms prior to maximum gape and it is inside the mouth at maximum gape and 60 ms after maximum gape. Note that the excursion of the pectoral fins is greater in largemouth bass than bluegill sunfish. Also note that both species employ their caudal, medial and pectoral fins during braking.

view. Using Igor Pro 5.01 (WaveMetrics Inc., Lake Oswego, OR, USA), the displacement data were smoothed using a cubic spline interpolation (smoothing factor=1, s.d.=0.001) and then the first and second derivative were calculated to obtain velocities and accelerations, respectively. In addition to this measure of instantaneous acceleration, the mean deceleration over the last 60 ms of prey capture was calculated by dividing the change in velocity over this time interval by 60 ms. From the lateral view, gape was the vertical distance between the tip of the lower jaw and the tip of the upper jaw, and maximum gape (MG) occurred when this distance was maximal.

From ventral view coordinates, instantaneous two-

dimensional fin angles were calculated every 20 ms starting from 120 ms before MG and ending 60 ms after MG. The pectoral fin and anal fin angles were calculated between lines from the anterior margin of the base of the fin to the distal tip of the fin and a point on the body posterior to the fin. The caudal fin angle was calculated between lines from a point on the body posterior to the base of the fin to the base of the fin and the tip of the fin.

Pectoral fin drag

The methods of Geerlink (Geerlink, 1987) were used to calculate a theoretical value of maximal drag created by the pectoral fins (D_{pec}) of bluegill and largemouth bass. The following equation was used: $D_{\text{pec}} = \frac{1}{2} \rho S_{\text{pec}} U^2 C_D$, where ρ is the density of the surrounding water (1026 kg m^{-3}), S_{pec} is the summed frontal area of the two pectoral fins if they are fully extended in a vertical position, U is the velocity of the fish at the time of MG, and C_D is the drag coefficient [1.17 as in Geerlink (Geerlink, 1987)].

Statistical analyses

To determine whether the species differ morphologically, an analysis of variance (ANOVA) was performed using species (fixed) as the independent variable. The dependent variables, which were analyzed separately, were pectoral fin aspect ratio (AR), and the \log_{10} -transformed residuals from a least-squares regression of body mass and the area of each fin (pectoral, anal and caudal). For pectoral fin area and AR, the average of the left and right fin was used for each individual in the ANOVA. In order to correct for multiple statistical tests, α (0.05) was adjusted using a sequential Bonferroni test (Rice, 1989).

In order to determine how deceleration was modulated, multiple regressions were performed on each species separately, with the mean deceleration over the last 60 ms of prey capture as the dependent variable. The independent variables were ram speed at the time of MG, maximum pectoral fin angle, maximum anal fin angle and maximum caudal fin angle. Additional least-squares regressions were performed in order to determine the correlation between continuous variables. All variables in these analyses were \log_{10} transformed to normalize variances, and in each case this allowed the variables to meet the assumptions of the parametric procedures.

Nine variables were included in a principal components analysis (PCA) to reduce dimensionality and search for axes of correlated kinematic variation: magnitude and timing of maximum caudal, anal and pectoral fin angles, maximum average deceleration, angular excursion of the body along the z-axis, and swimming speed at MG. The resulting principal components (1 and 2) became the axes of a multidimensional locomotor kinematic space, and were visualized in graphical form. To determine if the two species occupied different regions of kinematic space, an ANOVA was performed with species (fixed) and individual (nested within species; random) as the independent variables and the PC scores from a particular axis as the dependent variable. In order to properly account for

the replication of observations within individuals, the denominator in the F -test for the main effect of species was individual (nested within species) (Zar, 1996). SYSTAT version 9 (SPSS Inc., Chicago, IL, USA) was used for all statistical analyses.

Results

After accounting for body size, bluegill sunfish have significantly larger pectoral ($P<0.001$) and anal ($P<0.001$) fins than largemouth bass (Table 1). The two species did not differ in the size of their caudal fins. Bluegill sunfish exhibit a significantly higher pectoral fin aspect ratio ($P<0.05$) than largemouth bass (1.82 *versus* 1.34; Table 1).

Throughout the approach to the prey, largemouth bass swam at a much higher speed than bluegill sunfish (Fig. 3; Table 2). Between 120 ms and 40 ms prior to MG, largemouth bass decelerated. During the 40 ms prior to MG, largemouth bass accelerated. Following MG, largemouth bass decelerated continually and substantially. Bluegill exhibited a similar sequence of events, although the acceleration before MG occurred during the 20 ms, rather than 40 ms, prior to MG (Fig. 3).

Ram speed, at the time of MG, was positively correlated with MG for largemouth bass (Fig. 4; $r^2=0.58$; $P<0.001$). Although both species decelerated maximally following prey capture, the timing of maximum deceleration was much later for largemouth bass (30.3 ms after MG) than bluegill (6.7 ms after MG). Because the magnitude of deceleration was much higher for largemouth bass than bluegill, both species had similar ram speeds 60 ms after MG (Fig. 3A).

Both largemouth bass and bluegill protracted their pectoral fins as they approached the prey item (Fig. 5A). During the 60 ms following MG, largemouth bass protracted their pectoral fins, on average, over 40° . Pectoral fin protraction over the final 60 ms of the strike was significantly greater in bass than bluegill (ANOVA; $P<0.05$), who first retracted their pectoral fins and then protracted them between 40 and 60 ms after MG (Fig. 5A). Both species abducted their anal fin over 10° during the 60 ms after MG (Fig. 5B). The caudal and anal fins were almost always abducted in opposite directions during braking in both species (Fig. 2).

For both bluegill ($r^2=0.43$; $P<0.0001$) and largemouth bass ($r^2=0.31$; $P<0.01$), increased ram speeds 120 ms prior to MG resulted in increased magnitudes of deceleration following prey

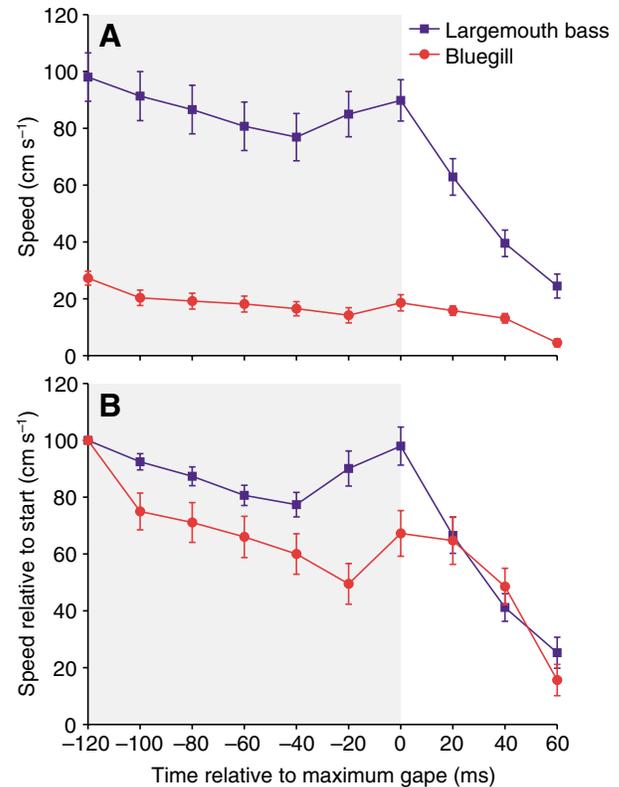


Fig. 3. Mean (\pm s.e.m.) swimming speeds (A) in 20 ms bins from 120 ms prior to maximum gape to 60 ms after maximum gape for bluegill sunfish (red circles) and largemouth bass (blue squares). The instantaneous value of speed was extracted at each time, rather than averaging the speed over the interval between bin durations. (B) Mean swimming speeds (\pm s.e.m.) shown in A scaled to the initial swimming speed 120 ms prior to maximum gape. Shaded areas indicate the time prior to maximum gape, and the unshaded areas indicate the time following maximum gape. Largemouth bass exhibit much higher swimming speeds prior to and during prey capture than do bluegill. While both species decelerate considerably following prey capture, largemouth bass exhibit a greater magnitude of deceleration. Note that, for both species, there is an increase in swimming speed immediately before maximum gape.

capture (Fig. 6A). In addition, increased ram speeds 120 ms prior to MG resulted in greater angular excursions (in the z -axis) of the body over the final 80 ms of the feeding event for largemouth bass ($r^2=0.52$; $P<0.001$) but not bluegill ($r^2=0.005$; $P>0.5$) (Fig. 6B). The model consisting of maximum fin angles and ram speed at the time of MG explained 84% ($P<0.001$) and 77% ($P<0.001$) of the variation in mean deceleration in largemouth bass and bluegill, respectively. However, maximum fin angles alone explain 37% ($P>0.05$) and 15% ($P>0.05$) of the variation in mean deceleration in largemouth bass and bluegill, respectively. Thus, ram speed accounts for a substantial amount of variation in mean deceleration. For largemouth bass, the maximum angle of the pectoral fin was also increased in order to increase the magnitude of

Table 1. Mean values for morphological features of the fins

Variable	Bluegill	Largemouth	F
Pectoral fin aspect ratio	1.82 \pm 0.1	1.34 \pm 0.09	11.9*
Pectoral fin area (cm ²)	10.1 \pm 1.3	6.4 \pm 1.0	37.8**
Caudal fin area (cm ²)	18.9 \pm 0.7	17.8 \pm 3.5	1.7
Anal fin area (cm ²)	11.4 \pm 1.3	6.1 \pm 0.7	38.2**

Values are means \pm s.e.m. (* $P<0.05$, ** $P<0.001$ following a sequential Bonferroni correction).

Table 2. Mean values for locomotor and feeding variables

Variable	Bluegill sunfish	Largemouth bass
Speed at maximum gape (cm s^{-1})	18.6±2.9	89.8±7.3
Relative speed at maximum gape (% of S_{-120})*	67.2±8.0	98.0±6.7
Maximum pectoral fin angle (deg.)	66.5±2.0	83.6±6.4
Maximum caudal fin angle (deg.)	52.6±3.1	45.7±1.5
Maximum anal fin angle (deg.)	29.5±1.3	33.9±1.7
Maximum deceleration (cm s^{-2})	-1299.2±87.4	-1922.1±136.9
Mean deceleration over final 60 ms (cm s^{-2})	-234.7±37.1	-1089.1±79.7
Change in body angle over final 80 ms (deg.)**	-0.4±0.5	9.7±2.9
Maximum gape (cm)	1.6±0.02	3.6±0.14
Time to peak gape (ms)***	11.1±0.9	22.7±0.8

Values are means ± s.e.m.

* S_{-120} =swimming speed 120 ms prior to maximum gape.

**This body angle refers to yawing movements of the fish.

***Time to peak gape was measured from 20% of peak gape to 95% of peak gape.

deceleration. Using the equation from Geerlink (Geerlink, 1987) (see above), largemouth bass and bluegill had theoretical values of maximum drag (D_{pec}) equal to 0.62 and 0.04, respectively.

From the PCA, swimming (ram) speed at the time of MG, mean deceleration during the final 60 ms, and angular excursion of the body in ventral view were the most highly correlated variables with principal component 1 (PC 1; Fig. 7; Table 3). I will refer to this axis as the 'ram speed' axis. Variables describing the angles of the fins loaded strongly on PC 2, and I will refer to this axis as the 'fin' axis (Fig. 7; Table 3). Largemouth bass had significantly higher scores on PC 1 than bluegill ($P=0.002$), but there was no difference between species on PC 2 ($P>0.05$).

Discussion

Both largemouth bass and bluegill employ their pectoral,

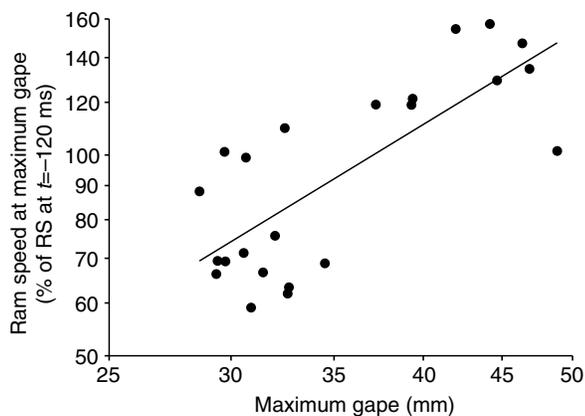


Fig. 4. Log-log plot of maximum gape *versus* ram speed (measured at the time of maximum gape), which is scaled to the ram speed 120 ms prior to maximum gape, for largemouth bass. Maximum gape during prey capture is positively correlated with ram speed ($y=3.7719x-37.135$; $r^2=0.58$; $P<0.001$).

anal and caudal fins during deceleration, although largemouth bass protract their pectoral fins more than bluegill. In addition, largemouth bass decelerate at a much greater magnitude than bluegill and achieve this by swimming faster prior to the onset of deceleration. Both species modulate the magnitude of deceleration by altering swimming speed rather than significantly altering fin kinematics. The greater magnitude of deceleration arises from the exponential increase in drag generated by the fins as swimming speed increases. Largemouth bass swim much faster than bluegill during prey capture and decelerate much later than bluegill. This behavior is likely to be associated with the decreased need for accuracy (because of the larger mouth) and the diet (largely comprised of evasive fishes) of largemouth bass.

Fin function during deceleration

Protraction of the pectoral fins during prey capture is a mechanism of deceleration employed by largemouth bass and bluegill (Fig. 5A). However, largemouth bass protract their fins faster and to a greater extent (Fig. 5A), suggesting that they generate more reverse thrust with their fins (Higham et al., 2005b). Although largemouth bass have significantly smaller pectoral fins than bluegill (Table 1), the drag force exerted by a fin is proportional to its velocity squared. Thus, a smaller fin, if protracted at a faster rate, has the potential for generating comparable or greater forces than a larger fin. Using the methods of Geerlink (Geerlink, 1987), the maximum drag forces exerted by the pectoral fins are much greater in largemouth bass than bluegill. Thus, despite having smaller pectoral fins, the swimming speed of largemouth bass appears to result in much higher drag forces from pectoral fins. When the area of the pectoral fins of bluegill sunfish is reduced, the fish compensate by protracting their fins at a higher speed in order to maintain a similar level of deceleration (Higham et al., 2005b). This behavioral modulation, combined with the results in the current study, suggests that fin morphology might not be the only factor that defines braking ability. For example, for a given pectoral fin (shape and size), the ability of the fish to hold

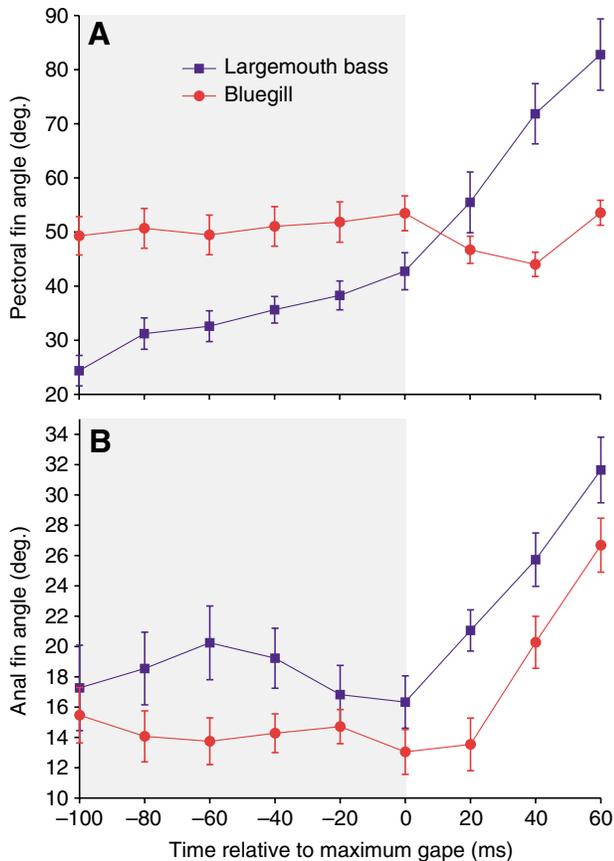


Fig. 5. Mean (\pm s.e.m.) pectoral (A) and anal (B) fin angles in 20 ms bins from 100 ms prior to maximum gape to 60 ms after maximum gape for bluegill sunfish (red circles) and largemouth bass (blue squares). Shaded areas indicate the time prior to maximum gape and unshaded areas indicate the time following maximum gape. Note that largemouth bass protract their pectoral fins more than bluegill during braking. Both species abduct their anal fins greatly after prey capture.

that fin against the flow of water would depend largely upon the ability of the abductor muscles to generate and sustain the necessary forces. A fish might then reach a threshold swimming speed where the fin muscles would no longer generate forces great enough to match the force exerted by the water on the fin. Thus, the ability of the pectoral fin abductor muscles to protract the pectoral fins to a position where drag is maximal could potentially limit the forces generated by fins, and ultimately braking performance.

Few studies have quantified pectoral fin angles during prey capture in fishes (Higham et al., 2005b; Rice and Westneat, 2005). Rice and Westneat examined the pectoral fin angles of two herbivorous species of parrotfish, *Sparisoma radians* and *Scarus quoyi*, during feeding (Rice and Westneat, 2005). As in largemouth bass and bluegill, both parrotfish species sweep their pectoral fins forward to initiate a braking maneuver as they approach the prey item. However, the braking maneuvers by the parrotfishes resulted in a large drop in swimming speed prior to contact with the prey item. This is quite different from the results of the present study in which largemouth bass and

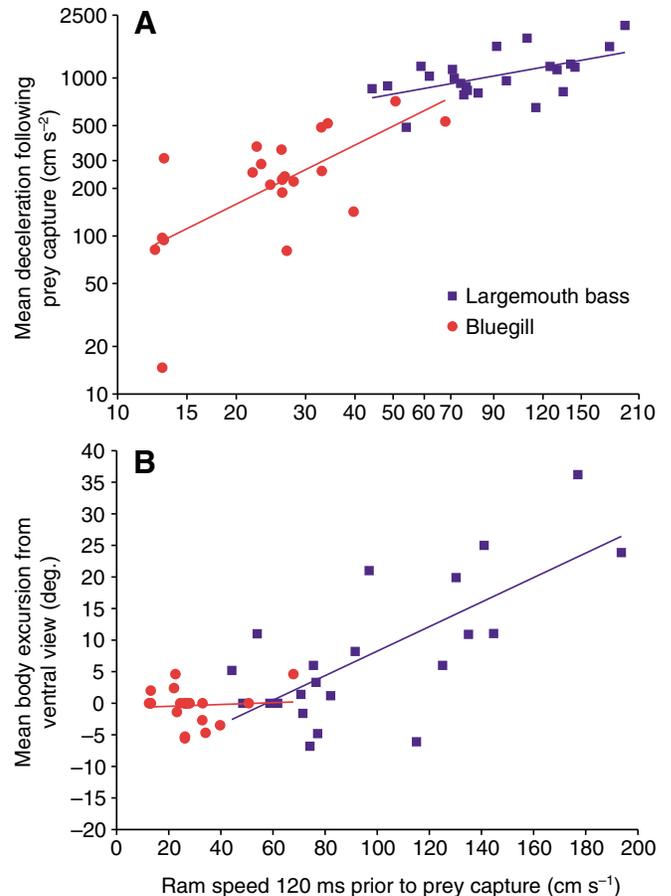


Fig. 6. Ram speed 120 ms prior to maximum gape *versus* average deceleration for 60 ms after maximum gape (A) and mean change in body angle along the z -axis for the final 80 ms of prey capture (20 ms prior to maximum gape plus 60 ms after maximum gape) (B) for bluegill sunfish (red circles) and largemouth bass (blue squares). Note that A is a log-log plot. For both bluegill ($y=9.2776x-17.049$; $r^2=0.43$; $P<0.0001$) and largemouth bass ($y=5.8397x+516.67$; $r^2=0.31$; $P<0.01$), an increase in ram speed 120 ms prior to maximum gape resulted in a significantly higher magnitude of deceleration following prey capture (A). For largemouth bass ($y=0.1941x-11.158$; $r^2=0.52$; $P<0.001$), but not bluegill ($y=0.0027x-0.4328$; $r^2=0.005$; $P>0.5$), an increase in ram speed 120 ms prior to maximum gape resulted in a greater change in body angle over the last 80 ms of prey capture (B).

bluegill both showed a large increase in swimming speed prior to prey capture. One explanation is that the parrotfishes studied by Rice and Westneat commonly feed from substrate, and braking after prey capture, as in bluegill and largemouth bass, would result in a collision with the substrate and potential injury. Future studies that examine the locomotor kinematics of largemouth bass and bluegill feeding from substrate would provide further insight into the differences between these groups of fishes.

When a fish generates suction, the flow enters the mouth and exits the posterior opercular slits. This allows the fish to ingest water at the same time that water is expelled, resulting in a volume of ingested water far exceeding the volume of the

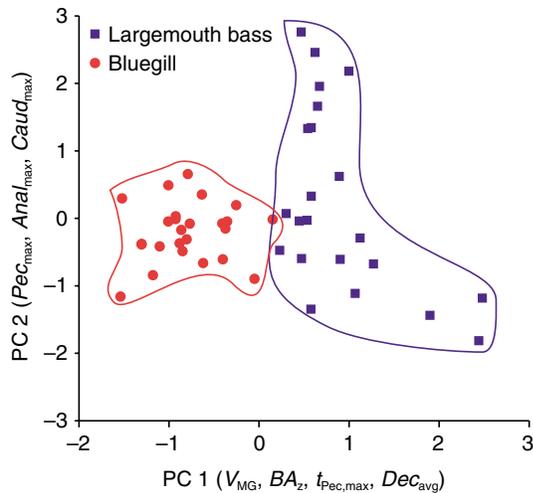


Fig. 7. Results (factor scores) from a principal components analysis (PCA) using nine locomotor variables from bluegill sunfish (red circles) and largemouth bass (blue squares). The parentheses located at each axis indicate the variables in which loadings were >0.5 . The negative signs indicate a negative loading. Note that largemouth bass and bluegill differed significantly with respect to PC 1 but not PC 2. PC 1 and PC 2 explained 33.6% and 20.8% of the total variance, respectively. See Table 3 for component loadings. Pec_{max} =maximum angle of the pectoral fin; $Anal_{max}$ =maximum angle of the anal fin; $Caud_{max}$ =maximum angle of the caudal fin; BA_z =angle of the body in the z -axis 60 ms after maximum gape; V_{MG} =swimming velocity at maximum gape; $t_{pec,max}$ =time of maximum pectoral fin angle; Dec_{avg} =magnitude of deceleration averaged over the last 60 ms of prey capture.

buccal cavity (Day et al., 2005; Higham et al., 2006a). The water that exits the opercular cavities during the feeding event is in close proximity to the anterior surfaces of the abducted pectoral fins (Fig. 2F). Thus, the speed of water passing the pectoral fins might be increased by this added flow out of the opercular cavities, resulting in a further increase in drag generated by the pectoral fins. This might enable fishes that have laterally placed pectoral fins to take advantage of suction feeding for deceleration. Largemouth bass and bluegill might take advantage of this, but bass have a much higher volumetric flow rate during feeding, so their benefit would likely be greater. Future studies that measure the flow exiting the opercular cavities around pectoral fins during feeding would provide insight regarding this potential method of enhancing deceleration.

The caudal and anal fins of both bluegill and largemouth bass were abducted, increasing the frontal area of the body and enhancing deceleration (Fig. 2). The use of caudal and median fins during braking has been observed in many species of fishes (e.g. Videler, 1981; Higham et al., 2005b). The median fins are capable of generating yawing and rolling movements of the body (Jayne et al., 1996; Drucker and Lauder, 2001; Webb, 2004; Standen and Lauder, 2005). During braking, however, both median fins are abducted to a common side (Higham et al., 2005b), thus reducing the possible rolling movement from

Table 3. Loadings from principal components analysis including nine locomotor variables

Variable	PC 1*	PC 2*
V_{MG}	0.912	-0.197
Dec_{avg}	0.961	-0.052
BA_z^{**}	0.717	-0.488
Pec_{max}	0.309	0.757
$Caud_{max}$	0.205	0.512
$Anal_{max}$	0.113	0.721
$t_{pec,max}$	0.697	0.193
$t_{caud,max}$	0.328	0.22
$t_{anal,max}$	0.123	-0.385

*PC 1 and PC 2 explained 33.6% and 20.8% of the total variance, respectively.

** BA_z refers to body angular excursion along the z -axis (ventral view).

V_{MG} , swimming velocity at maximum gape; Dec_{avg} , average deceleration over final 60 ms of the strike; Pec_{max} , maximum pectoral fin angle; $Caud_{max}$, maximum caudal fin angle; $Anal_{max}$, maximum anal fin angle; $t_{pec,max}$, the time of maximum pectoral fin angle; $t_{caud,max}$, the time of maximum caudal fin angle; $t_{anal,max}$, the time of maximum anal fin angle.

Loadings with a magnitude of >0.5 are marked in bold type.

one of the median fins. In almost all cases, the caudal fin moved to the opposite side of the median fins, which likely limits the yawing movements that might be caused if they were abducted to the same side. However, largemouth bass did exhibit an overall yawing movement during feeding (Table 2), and it was positively correlated with ram speed (Fig. 6B). The caudal fin of largemouth bass is approximately three times the size of the anal fin and is larger than the summed area of the pectoral fins (Table 1). Thus, the yawing movement of largemouth bass likely stems from the disproportionately large caudal fin. The caudal fin of bluegill is less than twice the size of the anal fin and is smaller than the summed area of the pectoral fins (Table 1). This suggests that the pectoral fins are generating more force than the caudal fin, which would help prevent yawing movements. Future studies that quantify the forces, using digital particle image velocimetry (DPIV), generated by the caudal and median fins during braking would provide further insight into their relative contributions to the overall braking force.

Mechanisms for modulating deceleration

The ability of a predator to modulate deceleration is imperative for arriving at a prey item at a predictable speed. I predicted that the angular excursions of the fins would increase in order to increase the magnitude of deceleration. The increased excursions would increase the speed of the surrounding water relative to the fin and thus result in higher drag forces. In addition, I thought that largemouth bass, because they exhibit greater deceleration, would exhibit greater fin excursions compared with bluegill. Given that the magnitude of deceleration of largemouth bass is approximately

four times that of bluegill (Table 2), it is surprising that largemouth bass only exhibit greater pectoral, and not other, fin excursions than bluegill during braking. What are largemouth bass doing to achieve this level of deceleration? Within each species, the only variable positively correlated with magnitude of deceleration was ram speed. Since the speed of largemouth bass prior to, and at the time, of prey capture is much greater than that of bluegill (Fig. 3), the drag force (proportional to velocity squared) from the body is much greater in largemouth bass. Given the nature of the aquatic environment, this mechanism for modulating deceleration might be very common among aquatic animals.

Swimming speed and prey capture

Largemouth bass approach their prey at much higher speeds than bluegill (Fig. 3). This result supports the notion that largemouth bass rely more heavily on ram, and bluegill rely more on suction to capture prey (Carroll et al., 2004; Higham et al., 2006a). While both largemouth bass and bluegill decrease their ram speed as they approach the prey item, they both accelerate immediately prior to MG (Fig. 3). This might allow the predator to adjust its location relative to the prey item and then lunge forward at the last moment. Because largemouth bass commonly feed on relatively evasive prey such as fish, it is not surprising that they accelerate more than bluegill immediately preceding MG. This might enhance their chances of capturing a prey that has the potential for initiating an escape response. Alternatively, this acceleration might be a passive result of ingesting water during suction feeding. This is supported by the fact that largemouth bass have a much larger MG and ingest a much larger volume of water than bluegill (Higham et al., 2006a). Given that suction feeding naturally draws the predator forward (Muller et al., 1982), the higher volume flow rate exhibited by largemouth bass might result in higher accelerations of the body than for bluegill. In addition, MG was positively correlated with ram speed at the time of MG (Fig. 4). Given that MG is positively correlated with volume and volumetric flow rate in largemouth bass (Higham et al., 2006a), the correlation between ram speed and MG might simply be a result of increased forces pulling the fish forward. This passive increase in swimming speed due to suction generation might obscure interspecific comparisons of ram speed if the species differ in the size of the ingested volume of water. Future studies that measure ram speed should thus be cautious when interpreting ram speeds as solely reflecting the motivation of the predator.

Largemouth bass typically feed on evasive prey such as fishes, and these prey items likely require higher ram speeds in order to be caught. Largemouth bass decelerate maximally much later than bluegill, supporting the idea that bass maintain speed until the prey item is in the mouth. However, largemouth bass do decelerate following prey capture, suggesting that overshooting the prey item too much might be disadvantageous. Webb and Gerstner suggest that predators feeding on evasive prey benefit from not overshooting the prey in case the prey manages to escape (Webb and Gerstner, 2000).

Not overshooting would put the predator in a good position to continue the chase and perhaps capture the prey item. Bluegill also decelerate during prey capture, but the reasons are likely to be different than for largemouth bass. Bluegill are more likely to feed in cluttered habitats or from substrate, and decelerating would prevent a collision in the environment. In addition, bluegill have much smaller mouths and likely depend more on accurately positioning their mouth relative to the prey item (see below for discussion), which might be compromised by swimming fast (Higham et al., 2006a).

An alternative explanation for why largemouth bass swim faster than bluegill during prey capture is that they are simply better swimmers than bluegill. This would suggest that bluegill are relegated to suction feeding as a result of their relatively poor ability to swim. However, several studies have shown that bluegill are morphologically specialized for suction feeding (Carroll et al., 2004; Collar and Wainwright, in press) and are better at generating a suction-induced flow of water than largemouth bass (Higham et al., 2006a; Higham et al., 2006b). In addition, bluegill can reach swimming velocities that are comparable to those of largemouth bass (Domenici and Blake, 1997). These lines of evidence strongly suggest that the locomotor behavior of bluegill and largemouth bass during prey capture is strongly related to their feeding ecology rather than their swimming capabilities.

The prey item in this study was tethered rather than freely moving. While tethering prey could potentially confound the experimental results, it also reflects an ecologically relevant prey capture situation for largemouth bass and bluegill. Both of these species feed on prey that is commonly located on or close to substrate, such as crustaceans (Collar et al., 2005). In addition, capturing prey prior to the initiation of an escape response (i.e. prior to prey movement) has been advocated as an advantage of ram feeding (see Nemeth, 1997) and is common in studies of fish feeding. Future studies that examine locomotor behavior of fish attacking a moving prey item would provide insight into the flexibility of locomotor behavior and whether differences between species persist regardless of prey presentation.

Braking and strike accuracy

Strike accuracy is imperative for successful prey capture and is an often overlooked aspect of suction feeding performance (Higham et al., 2006a). The constraints imposed by accuracy likely diminish with an increased MG because the ingested volume of water increases considerably with an increase in MG (Higham et al., 2006a; Higham et al., 2006c). Because increases in swimming speed decrease strike accuracy (Webb and Skadsen, 1980; Higham et al., 2006a; Higham et al., 2006c), it is possible that only those species with larger mouths are able to maintain high swimming speeds and still successfully capture prey. Indeed, largemouth bass swim faster and have a much larger MG than bluegill. This idea is corroborated by a study of 18 species of cichlid fishes in which MG was significantly and positively correlated with ram speed (Higham et al., 2006c). Future studies that directly measure

accuracy through ontogeny, and over a large range of ram speeds, could provide insight into the relationships between ram speed, MG and strike accuracy. Largemouth bass became increasingly unsteady (increased yawing movements during prey capture) with an increase in ram speed (Fig. 6B). This is probably an additional mechanism for decreased strike accuracy with an increase in ram speed. It is possible that, if bluegill swam faster, they would suffer a reduction in strike accuracy, which might significantly reduce the rate of successful prey capture.

Implications for turning maneuvers

Turning maneuvers are commonly executed using pectoral fins (Breder, 1926; Drucker and Lauder, 2001; Lauder and Drucker, 2004; Walker, 2004; Drucker et al., 2006). One mechanism of turning is to extend the pectoral fin on one side of the body while keeping the other fin against the body. The drag generated by the extended fin on the inside of the turn acts as a pivot and contributes to the rotational torque on the center of mass, resulting in yawing rotation (Breder, 1926; Drucker and Lauder, 2001; Walker, 2004; Drucker et al., 2006). Even with a smaller pectoral fin, an increased rate of fin protraction will result in an exponential increase in the drag force, and ultimately the yawing rotation. Given the relationship between fluid speed and drag, the swimming speed of a fish will likely also have profound effects on turning performance. In addition, the morphology of pectoral fins is likely linked to the swimming behavior of a fish. For example, fishes that typically swim fast, such as largemouth bass, might benefit from having smaller pectoral fins because less muscle power would be required to extend one of them during a turning maneuver.

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References

- Alfaro, M. E. (2003). Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophiine snakes. *J. Exp. Biol.* **206**, 2381-2392.
- Bainbridge, R. (1963). Caudal fin and body movement in the propulsion of some fish. *J. Exp. Biol.* **40**, 23-56.
- Borla, M. A., Palecek, B., Budick, S. and O'Malley, D. M. (2002). Prey capture by larval zebrafish: evidence for fine axial motor control. *Brain Behav. Evol.* **60**, 207-229.
- Breder, C. M. (1926). The locomotion of fishes. *Zoologica N. Y.* **6**, 159-297.
- Budick, S. A. and O'Malley, D. M. (2000). Locomotor repertoire of the larval zebrafish: swimming, turning and prey capture. *J. Exp. Biol.* **203**, 2565-2579.
- Carroll, A. M. (2004). Muscle activation and strain during suction feeding in the largemouth bass *Micropterus salmoides*. *J. Exp. Biol.* **207**, 983-991.
- Carroll, A. M. and Wainwright, P. C. (2006). Muscle function and power output during suction feeding in largemouth bass, *Micropterus salmoides*. *Comp. Biochem. Physiol.* **143A**, 389-399.
- Carroll, A. M., Wainwright, P. C., Huskey, S. H., Collar, D. C. and Turingan, R. G. (2004). Morphology predicts suction feeding performance in centrarchid fishes. *J. Exp. Biol.* **207**, 3873-3881.
- Collar, D. C. and Wainwright, P. C. (in press). Discordance between morphological and mechanical diversity in the feeding mechanism of centrarchid fishes. *Evolution*.
- Collar, D. C., Near, T. J. and Wainwright, P. C. (2005). Comparative analysis of morphological diversity: does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution* **59**, 1783-1794.
- Day, S. W., Higham, T. E., Cheer, A. Y. and Wainwright, P. C. (2005). Spatial and temporal patterns of water flow generated by suction feeding bluegill sunfish *Lepomis macrochirus* resolved by Particle Image Velocimetry. *J. Exp. Biol.* **208**, 2661-2671.
- Domenici, P. (2001). The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comp. Biochem. Physiol.* **131A**, 169-182.
- Domenici, P. and Blake, R. W. (1997). The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* **200**, 1165-1178.
- Drucker, E. G. and Lauder, G. V. (1999). Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J. Exp. Biol.* **202**, 2393-2412.
- Drucker, E. G. and Lauder, G. V. (2000). A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *J. Exp. Biol.* **203**, 2379-2393.
- Drucker, E. G. and Lauder, G. V. (2001). Wake dynamics and fluid forces of turning maneuvers in sunfish. *J. Exp. Biol.* **204**, 431-442.
- Drucker, E. G. and Lauder, G. V. (2002). Wake dynamics and locomotor function in fishes: interpreting evolutionary patterns in pectoral fin design. *Integr. Comp. Biol.* **42**, 997-1008.
- Drucker, E. G. and Lauder, G. V. (2003). Function of pectoral fins in rainbow trout: behavioral repertoire and hydrodynamic forces. *J. Exp. Biol.* **206**, 813-826.
- Drucker, E. G., Walker, J. A. and Westneat, M. W. (2006). Mechanics of pectoral fin swimming in fishes. In *Fish Biomechanics* (ed. R. E. Shadwick and G. V. Lauder), pp. 369-423. San Diego: Academic Press.
- Dunbar, D. C. and Badam, G. L. (2000). Locomotion and posture during terminal branch feeding. *Int. J. Primatol.* **21**, 649-669.
- Ferry-Graham, L. A., Wainwright, P. C. and Lauder, G. V. (2003). Quantification of flow during suction feeding in bluegill sunfish. *Zoology* **106**, 159-168.
- Geerlink, P. J. (1987). The role of the pectoral fins in braking of mackerel, cod and saithe. *Neth. J. Zool.* **37**, 81-104.
- Gibb, A. C., Jayne, B. C. and Lauder, G. V. (1994). Kinematics of pectoral fin locomotion in the bluegill sunfish *Lepomis macrochirus*. *J. Exp. Biol.* **189**, 133-161.
- Gorb, S. N. and Barth, F. G. (1994). Locomotor behavior during prey-capture of a fishing spider, *Dolomedes plantarum* (Araneae, Araneidae) – galloping and stopping. *J. Arachnol.* **22**, 89-93.
- Grubich, J. R. and Wainwright, P. C. (1997). Motor basis of suction feeding performance in largemouth bass, *Micropterus salmoides*. *J. Exp. Zool.* **277**, 1-13.
- Harris, J. E. (1937a). The mechanical significance of the position and movements of the paired fins in the Teleostei. *Pap. Tortugas Lab.* **31**, 173-189.
- Harris, J. E. (1937b). The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins. *J. Exp. Biol.* **14**, 32-47.
- Higham, T. E., Davenport, M. S. and Jayne, B. C. (2001). Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of *Anolis* lizards. *J. Exp. Biol.* **204**, 4141-4155.
- Higham, T. E., Day, S. W. and Wainwright, P. C. (2005a). Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. *J. Exp. Biol.* **208**, 2653-2660.
- Higham, T. E., Malas, B., Jayne, B. C. and Lauder, G. V. (2005b). Constraints on starting and stopping: behavior compensates for reduced pectoral fin area during braking of the bluegill sunfish *Lepomis macrochirus*. *J. Exp. Biol.* **208**, 4735-4746.
- Higham, T. E., Day, S. W. and Wainwright, P. C. (2006a). Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *J. Exp. Biol.* **209**, 2713-2725.
- Higham, T. E., Day, S. W. and Wainwright, P. C. (2006b). The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. *J. Exp. Biol.* **209**, 3281-3287.
- Higham, T. E., Hulsey, C. D., Rican, O. and Carroll, A. M. (2007). Feeding with speed: prey capture evolution in cichlids. *J. Evol. Biol.* doi:10.1111/j.1420-9101.2006.01227.x.
- Hoff, K. S., Lannoo, M. J. and Wassersug, R. J. (1985). Kinematics of midwater prey capture by ambystoma (Caudata: Ambystomatidae) larvae. *Copeia* **1985**, 247-251.
- Irschick, D. J. and Losos, J. B. (1998). A comparative analysis of the

- ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219-226.
- Iwaniuk, A. N., Pellis, S. M. and Winshaw, I. Q.** (1999). The relationship between forelimb morphology and behaviour in North American carnivores (Carnivora). *Can. J. Zool.* **77**, 1064-1074.
- Jayne, B. C. and Lauder, G. V.** (1993). Red and white muscle-activity and kinematics of the escape response of the bluegill sunfish during swimming. *J. Comp. Physiol. A* **173**, 495-508.
- Jayne, B. C. and Lauder, G. V.** (1994). How swimming fish use slow and fast muscle fibers: implications for models of vertebrate muscle recruitment. *J. Comp. Physiol. A* **175**, 123-131.
- Jayne, B. C. and Lauder, G. V.** (1995). Are muscle fibers within fish myotomes activated synchronously? Patterns of recruitment within deep myomeric musculature during swimming in largemouth bass. *J. Exp. Biol.* **198**, 805-815.
- Jayne, B. C. and Lauder, G. V.** (1996). New data on axial locomotion in fishes: how speed affects diversity of kinematics and motor patterns. *Am. Zool.* **36**, 642-655.
- Jayne, B. C., Lozada, A. F. and Lauder, G. V.** (1996). Function of the dorsal fin in bluegill sunfish: motor patterns during four distinct locomotor behaviors. *J. Morphol.* **228**, 307-326.
- Johnson, T. P., Syme, D. A., Jayne, B. C., Lauder, G. V. and Bennett, A. F.** (1994). Modeling red muscle power output during steady and unsteady swimming in largemouth bass. *Am. J. Physiol.* **267**, R481-R488.
- Kramer, D. L. and McLaughlin, R. L.** (2001). The behavioral ecology of intermittent locomotion. *Am. Zool.* **41**, 137-153.
- Lauder, G. V.** (1980). The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. Exp. Biol.* **88**, 49-72.
- Lauder, G. V. and Drucker, E. G.** (2004). Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE J. Oceanic Eng.* **29**, 556-571.
- Lauder, G. V. and Jayne, B. C.** (1996). Pectoral fin locomotion in fishes: testing drag-based models using three-dimensional kinematics. *Am. Zool.* **36**, 567-581.
- Lauder, G. V., Wainwright, P. C. and Findeis, E.** (1986). Physiological mechanisms of aquatic prey capture in sunfishes: functional determinants of buccal pressure changes. *Comp. Biochem. Physiol.* **84A**, 729-734.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A.** (2005). Joint work and power associated with acceleration and deceleration in tamar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **208**, 41-53.
- Muller, M., Osse, J. W. M. and Verhagen, J. H. G.** (1982). A quantitative hydrodynamical model of suction feeding in fish. *J. Theor. Biol.* **95**, 49-79.
- Near, T. J., Bolnick, D. I. and Wainwright, P. C.** (2005). Fossil calibrations and molecular divergence time estimates in centrarchid fishes (Teleostei: Centrarchidae). *Evolution* **59**, 1768-1782.
- Nemeth, D. H.** (1997). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J. Exp. Biol.* **200**, 2155-2164.
- Norton, S. F. and Brainerd, E. L.** (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11-29.
- Nyberg, D. W.** (1971). Prey capture in the largemouth bass. *Am. Midl. Nat.* **86**, 128-144.
- Porter, H. T. and Motta, P. J.** (2004). A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redbfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Mar. Biol.* **145**, 989-1000.
- Rand, D. M. and Lauder, G. V.** (1981). Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behavior. *Can. J. Zool.* **59**, 1072-1078.
- Rice, A. N. and Westneat, M. W.** (2005). Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae). *J. Exp. Biol.* **208**, 3503-3518.
- Rice, W. R.** (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223-225.
- Sass, G. G. and Motta, P. J.** (2002). The effects of satiation on strike mode and prey capture kinematics in the largemouth bass, *Micropterus salmoides*. *Environ. Biol. Fishes* **65**, 441-454.
- Standen, E. M. and Lauder, G. V.** (2005). Dorsal and anal fin function in bluegill sunfish *Lepomis macrochirus*: three-dimensional kinematics during propulsion and maneuvering. *J. Exp. Biol.* **208**, 2753-2763.
- Svanback, R., Wainwright, P. C. and Ferry-Graham, L. A.** (2002). Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiol. Biochem. Zool.* **75**, 532-543.
- Videler, J. J.** (1981). Swimming movements, body structure and propulsion in cod *Gadus morhua*. *Symp. Zool. Soc. Lond.* **48**, 1-27.
- Vincent, S. E., Herrel, A. and Irschick, D. J.** (2005). Comparisons of aquatic versus terrestrial predatory strikes in the pitviper, *Agkistrodon piscivorus*. *J. Exp. Zool. Part A Comp. Exp. Biol.* **303**, 476-488.
- Wainwright, P. C. and Lauder, G. V.** (1986). Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zool. J. Linn. Soc.* **88**, 217-228.
- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carrol, A. M., Hulsey, C. D. and Grubich, J. R.** (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039-3051.
- Wainwright, P. C., Alfaro, M. E., Bolnick, D. I. and Hulsey, C. D.** (2005). Many-to-one mapping of form to function: a general principle in organismal design? *Integr. Comp. Biol.* **45**, 256-262.
- Walker, J. A.** (1998). Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J. Exp. Biol.* **201**, 981-995.
- Walker, J. A.** (2004). Kinematics and performance of maneuvering control surfaces in Teleost fishes. *IEEE J. Oceanic Eng.* **29**, 572-584.
- Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N.** (2005). Do faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808-815.
- Webb, P. W.** (1984a). Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. *Can. J. Fish. Aquat. Sci.* **41**, 157-165.
- Webb, P. W.** (1984b). Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107-120.
- Webb, P. W.** (2004). Maneuverability – general issues. *IEEE J. Oceanic Eng.* **29**, 547-555.
- Webb, P. W.** (2006). Stability and maneuverability. In *Fish Biomechanics* (ed. R. E. Shadwick and G. V. Lauder), pp. 281-332. San Diego: Academic Press.
- Webb, P. W. and Fairchild, A. G.** (2001). Performance and maneuverability of three species of teleostean fishes. *Can. J. Zool.* **79**, 1866-1877.
- Webb, P. W. and Gerstner, C. L.** (2000). Fish swimming behaviour: predictions from physical principles. In *Biomechanics in Animal Behaviour* (ed. P. Domenici and R. W. Blake), pp. 59-77. Oxford: BIOS Scientific.
- Webb, P. W. and Skadsen, J. M.** (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462-1469.
- Zar, J. H.** (1996). *Biostatistical Analysis*. Upper Saddle river, NJ: Prentice Hall.