

Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water

Timothy E. Higham^{1,*}, Steven W. Day² and Peter C. Wainwright¹

¹*Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA and*
²*Department of Mechanical Engineering, Rochester Institute of Technology, 76 Lomb Memorial Drive, Rochester, NY 14623-5604, USA*

*Author for correspondence (e-mail: thigham@ucdavis.edu)

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Summary

Suction feeding fish draw prey into the mouth using a flow field that they generate external to the head. In this paper we present a multidimensional perspective on suction feeding performance that we illustrate in a comparative analysis of suction feeding ability in two members of Centrarchidae, the largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*). We present the first direct measurements of maximum fluid speed capacity, and we use this to calculate local fluid acceleration and volumetric flow rate. We also calculated the ingested volume and a novel metric of strike accuracy. In addition, we quantified for each species the effects of gape magnitude, time to peak gape, and swimming speed on features of the ingested volume of water. Digital particle image velocimetry (DPIV) and high-speed video were used to measure the flow in front of the mouths of three fish from each species in conjunction with a vertical laser sheet positioned on the mid-sagittal plane of the fish. From this we quantified the maximum fluid speed (in the earthbound and fish's frame of reference), acceleration and ingested volume. Our method for determining strike accuracy involved quantifying the location of the prey relative to the center of the parcel of ingested water. Bluegill sunfish generated higher fluid speeds in the earthbound frame of reference, accelerated

the fluid faster, and were more accurate than largemouth bass. However, largemouth bass ingested a larger volume of water and generated a higher volumetric flow rate than bluegill sunfish. In addition, because largemouth bass swam faster during prey capture, they generated higher fluid speeds in the fish's frame of reference. Thus, while bluegill can exert higher drag forces on stationary prey items, largemouth bass more quickly close the distance between themselves and prey. The ingested volume and volumetric flow rate significantly increased as gape increased for both species, while time to peak gape had little effect on the volume. However, peak gape distance did not affect the maximum fluid speed entering the mouth for either species. We suggest that species that generate high fluid speeds in the earthbound frame of reference will commonly exhibit small mouths and a high capacity to deliver force to buccal expansion, while species that ingest a large volume of water and generate high volumetric flow rates will have larger buccal cavities and cranial expansion linkage systems that favor displacement over force delivery.

Key words: volume, Centrarchidae, *Lepomis*, *Micropterus*, swimming, ram, kinematics, prey capture, feeding, DPIV, ingested volume, accuracy, suction feeding, performance.

Introduction

Performance testing has become a prominent tool among functional morphologists interested in the consequences of natural variation in organismal design. Understanding the basis of the ability of animals to perform key tasks helps establish the link between phenotypic variation and ecological patterns such as resource use and fitness. One example of where our understanding of performance remains imperfect is with feeding in fishes. Prey capture by fishes offers excellent potential for a unified view of performance across a large slice of vertebrate life because most fish species use the same basic

suction feeding mechanism to capture their prey, and yet there is tremendous diversity in size and shape of the feeding apparatus and a complete understanding of the implications of this diversity for suction feeding ability is still lacking (Carroll et al., 2004; Muller and Osse, 1984; Norton and Brainerd, 1993; Van Wassenbergh et al., 2005; Wainwright et al., 2001).

One commonly cited metric of suction feeding performance is the maximum speed of the water entering the mouth cavity. Fluid speed is attractive as a metric of suction feeding performance because the drag experienced by a prey item in the suction flow will be proportional to the square of fluid

speed relative to the prey (i.e. difference between the speed of the prey and the speed of the fluid surrounding the prey) and because a rapid flow presumably limits the time for prey escape. Variation in fluid speed has been inferred indirectly by tracking the prey movement towards the predator (Norton and Brainerd, 1993; Cook, 1996; Van Leeuwen, 1984; Wainwright et al., 2001; Waltzek and Wainwright, 2003) or by measuring the magnitude of subambient pressure in the buccal cavity (Lauder, 1980; Lauder, 1983; Lauder et al., 1986; Nemeth, 1997; Sanford and Wainwright, 2002; Carroll et al., 2004). A few studies have directly quantified the flow speeds generated by suction feeders (Muller and Osse, 1984; Van Leeuwen, 1984; Ferry-Graham et al., 2003; Day et al., 2005; Higham et al., 2005a), but to date there has been no attempt to measure the peak fluid speeds that an individual or species is capable of generating. Acceleration of the fluid may also contribute to the effectiveness of suction feeding because of the acceleration reaction force that it generates and exerts on the prey in the flow. Although Drost et al. estimated the acceleration of fluid during suction feeding in larval fish (Drost et al., 1988), the potential importance of fluid acceleration has been ignored in most recent considerations of suction feeding performance (e.g. Carroll et al., 2004; Van Wassenbergh et al., 2005; Wainwright et al., 2001).

While the speed and acceleration of the fluid entering the mouth generate forces and generally limit the time available to the prey for escape, there are several features of the ingested volume of water that could influence performance of the strike (Wainwright et al., 2001). The larger the volume of water ingested by a fish during the strike, the less chance the prey item has of escaping the flow. While the flow of water entering the mouth can be modulated by swimming speed (Muller and Osse, 1984; Higham et al., 2005a) and how fast the buccal cavity is expanded (Day et al., 2005), little is known regarding the modulation of the shape, size and flow of the ingested volume of water. For example, although it is clear that an increase in swimming speed will result in a narrower and more elongate ingested volume of water (Weihs, 1980; Higham et al., 2005a), it is not clear how ram speed influences the total volume of ingested water or the flow rate of this volume. Most studies have either measured volume indirectly from morphology (Cook, 1996; De Visser and Barel, 1998; Viladiu et al., 1999; Van Wassenbergh et al., 2005) or from geometric estimates of volume change of the head during the strike (Van Leeuwen, 1984). With fishes, these methods underestimate the total volume of water ingested during the strike, because while fish ingest water through their buccal cavity they expel water out a caudal valve located at the posterior end of the opercular cavity. This ability to expel water while ingesting more enables fish to circumvent the constraints of buccal cavity volume, which would otherwise limit the ingested volume (Muller and Osse, 1984; Van Leeuwen, 1984; Day et al., 2005). In fact, fish species such as rainbow trout and bluegill sunfish can ingest a volume of water much greater than the volume of their buccal cavity (Van Leeuwen, 1984; Day et al., 2005). In addition, fish are able to maintain a flow of water until the mouth is almost

closed (Day et al., 2005; Higham et al., 2005a) which likely decreases the chances of the prey escaping. Understanding how fish can manipulate this ingested volume of water may give new insights into suction feeding performance.

An understudied aspect of suction feeding performance is the ability to accurately direct the flow of water that is generated external to the fish's mouth. Accurate positioning of the mouth relative to the prey item is essential for prey capture. Further, the suction flow is ephemeral, requiring the fish to time its placement to maximize the effectiveness of the flow. Several factors including approach speed, timing of mouth opening and mouth size are likely important for determining the accuracy of prey capture. The accuracy of a predator is typically quantified as the number of successful attempts relative to the number of failed attempts (e.g. Nyberg, 1971; Drost, 1987; McLaughlin et al., 2000). This approach is designed to compare the ability of different species to feed on a particular prey type. However, it would be useful to design a metric of accuracy that relates to the ability of fish to position prey within the flow of water that they generate during suction feeding.

In this study we adopt a multidimensional view of suction feeding performance in a comparative analysis of two species that have been the focus of a tremendous amount of research on feeding functional morphology and ecology, the largemouth bass, *Micropterus salmoides* and the bluegill sunfish, *Lepomis macrochirus*. Using digital particle image velocimetry (DPIV) we measure the peak fluid speeds and local acceleration generated by these species feeding on elusive prey in both the earthbound and fish's frames of reference. We measure the volume of water captured during feeding and the rate of volume flow entering the mouth. Finally, we introduce a new method for quantifying strike accuracy and use this method to compare the two species. Based on the fluid speeds calculated in the earthbound frame of reference, our results strongly confirm previous interpretations of feeding performance in these species. We find that bluegill generate higher fluid speeds and accelerations, and are more accurate with their strike. Largemouth bass ingest a larger volume of water during the strike and generate higher volumetric flow rates. Because of their higher swimming speed, largemouth bass actually generate higher fluid speeds than bluegill sunfish in the fish's frame of reference, allowing them to close more quickly on the prey item.

Materials and methods

Experimental subjects

We studied largemouth bass (*Micropterus salmoides* Lacépède) and bluegill sunfish (*Lepomis macrochirus* Rafinesque), both members of the freshwater family Centrarchidae. These species were selected for this study because they differ considerably in their morphology and ecology. Bluegill feed predominantly on small planktonic crustaceans and benthic insect larvae, whereas largemouth bass feed predominantly on large evasive prey, including fish and

crayfish (Keast, 1978; Collar et al., 2005). 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 in Yolo County, California, USA, brought back to the University of California, Davis and housed individually in 100-liter aquaria at 22°C. Fish were maintained on a diet of cut squid (*Loligo* sp.), goldfish (*Carassius auratus*), ghost shrimp (*Palaemonetes* sp.), and/or small annelid ‘tubifex’ worms. All maintenance and experimental procedures used in this research followed a protocol that was reviewed by the University of California, Davis Institutional Animal Care and Use Committee. We analyzed data from three bluegill sunfish with standard lengths of 15.3 cm, 15.0 cm and 15.4 cm, and from three largemouth bass with standard lengths of 16.6 cm, 17.7 cm and 18.0 cm. We emphasize that the comparisons we draw between the two species are therefore restricted to fish in a narrow size range. It is likely that many of the parameters we measured will change with body size in these species (Carroll et al., 2004).

Experimental protocol

Each fish was placed in the experimental tank and trained to feed in the laser sheet (see below). At the onset of experiments, the individual was kept at one end of the tank and restrained behind a door [see fig. 1 in Higham et al. (Higham et al., 2005a)]. A tubifex worm (about 2 cm), ghost shrimp (about 2 cm) or goldfish (about 2–3 cm) was then introduced *via* plastic tubing or attached to a thin wire. The prey was held within the laser light sheet and within the camera field of view, and the door was lifted. Although the tubifex worms were not attached to something, they were barely moving in the field of view.

Digital Particle Image Velocimetry (DPIV)

We used DPIV to quantify maximum fluid speed and a number of parameters describing the ingested volume of water during suction feeding. The details of this method are described elsewhere (Willert and Gharib, 1991; Day et al., 2005; Higham et al., 2005a). An Innova-90 5 W argon-ion continuous wave laser (Coherent, Inc., Santa Clara, CA, USA) was used in combination with a set of focusing lenses and mirrors to produce a vertical laser sheet that was approximately 10 cm wide and 1 mm thick in the aquarium. To visualize the flow of water, the aquarium was seeded with 12 µm silver-coated, hollow glass spheres (Potter Industries, Inc., Carlstadt, NJ, USA) with a specific gravity of 1.05. Mirrors above and below the tank were used to illuminate both above and below the head of the fish during feeding. Lateral-view video sequences were recorded using a NAC Memrecam ci digital system (Tokyo, Japan) operating at 500 images s⁻¹. The field of view ranged from 5.1×6.7 cm to 8.4×11 cm, depending on the species. Additionally, a Sony CCD camcorder (Tokyo, Japan), operating at 30 images s⁻¹, was used to capture anterior view images for each sequence in order to determine the orientation and position of the fish relative to the laser sheet. While we only analyzed sequences recorded in lateral view in

this study, we have found that the flow pattern is approximately radially symmetric about the long axis of the fish (Day et al., 2005).

An adaptive mesh cross correlation algorithm (Scarano and Riethmuller, 1999) was used to calculate velocities from image pairs. The distance that particles traveled between image pairs (2 ms interval) was determined within interrogation windows of varying dimensions, depending on the species (e.g. bluegill=0.9×0.9 mm, bass=0.13×0.13 mm), with 50% overlap between interrogation windows. The algorithm then returned a two-dimensional grid of two components of measured velocity for each image pair that was processed.

The instantaneous velocity measurement at a single measurement point contains a random error that we measured using published methods (Day and McDaniel, 2005). Assuming adequate density of seed particles, uncertainty due to random errors is a function of the interrogation window size and the diameter of an individual particle’s images. The conditions in our experiments lead to a random error of approximately 5%.

A transect extending forward from the center of the fish’s mouth was studied to measure the speed of the fluid entering the mouth. The closest position to the mouth where accurate measurements of velocity vectors were made in 100% of the sequences was at a distance away from the mouth aperture equal to one half of the peak gape diameter (*PG*) of the fish for the feeding sequence. The measurement at this position was validated in every trial. All velocities reported in this paper are at this distance and on the centerline, and we refer to the magnitude of these velocities as ‘fluid speeds’.

Frames of reference

The frame of reference is an important factor when quantifying fluid speeds during suction feeding (Muller and Osse, 1984; Higham et al., 2005a). An increase in ram velocity will increase the fluid speed relative to the fish. Thus, we measured the fluid speeds in the earthbound frame of reference directly and then calculated fluid speed in the fish’s frame of reference. To calculate the latter, we added the magnitude of the forward velocity of the fish to the fluid speed generated by suction. The forward velocity of the fish was always calculated in a direction towards the prey item. We note that this method of changing frame of reference is appropriate for fluid velocity measurements on the centerline, where all water movement is in this axis, but it would not generalize to positions away from the centerline where water movement also has a *y* and *z* component. As explained below, certain variables are expressed in both frames of reference while others are only calculated in one of them.

Data analysis

Only those sequences in which the laser sheet intersected the mid-sagittal plane of the fish (verified with the anterior view camera) and in which the fish were centered on the filming screen in lateral view were used for analyses. Using IMAGE J version 1.33 (NIH, Washington, DC, USA), the *x* and *y*

coordinates of the tip of the upper and lower jaws were digitized for each image (2 ms intervals) starting prior to the onset of mouth opening and continuing until the mouth was closed. These points were used to calculate gape distance as a function of time and to determine the value of peak gape for each sequence. Time to peak gape (*TTPG*) was measured as the time from 20% to 95% of maximum gape (Sanford and Wainwright, 2002; Day et al., 2005; Higham et al., 2005a). This method reduces errors that are related to a variable rate of early mouth opening and the difficulty in clearly identifying the point where the peak value is reached in an asymptotic relationship. *TTPG* was measured as an indicator of the rate of buccal expansion (Sanford and Wainwright, 2002). In order to determine the ram velocity during feeding, we first digitized the x and y coordinates of the anterior margin of the eye for each frame. Ram velocity was the first derivative of the displacement of the eye. Ram velocity varied throughout the strike and the speeds reported in this paper, with the exception of the volumetric flow rate calculation (see below), are those measured at the time of 95% of maximum gape, which approximates the time of maximum fluid speed. The temporal pattern of kinematic events and fluid speeds was investigated as was done previously for the bluegill sunfish (Day et al., 2005). The relative timing of key kinematic events was determined manually from the graphed profiles of each feeding and the mean and standard deviation of timing of these was calculated as a percentage of *TTPG*.

To determine the volume of the ingested parcel of water (V), we manually tracked particles going into the mouth using IMAGE J. Any particle that entered the mouth between mouth opening and mouth closing was considered ingested. We then defined a boundary around the outer limit of particles (in the

frame at the onset of mouth opening) that entered the mouth and digitized several points (>20) along this boundary (Fig. 1). Assuming the flow field was symmetric about the long axis of the fish (Day et al., 2005), we calculated the total volume of ingested water by integration of the two-dimensional boundary.

To determine the rate of volume ingestion (dV/dt), we initially employed the methods described above in a stepwise fashion to determine the volume at several times throughout the gape cycle. For the same sequences, we calculated dV/dt by multiplying the area of the mouth aperture by the speed of the fluid (at the mouth aperture) entering the mouth at intervals of 2 ms. Although we measured fluid speeds at a distance equal to $\frac{1}{2}$ maximum gape away from the aperture, we converted these values to fluid speed at the mouth aperture by multiplying by 3.6 (bluegill) and 4.6 (bass), which follows the methods employed in earlier work (Day et al., 2005; Higham et al., 2005a). The volumetric flow rate was only calculated in the fish's frame of reference, so the fluid speeds described above were added to the magnitude of the forward velocity of the fish to determine the fluid speed for the calculation of dV/dt relative to the mouth aperture. The forward velocity of the fish was the average of the velocity at the onset of the strike and the velocity at the time of maximum gape. From the relationship of dV/dt versus time, we determined the maximum dV/dt value and the time of this maximum for a comparison with the timing of kinematic variables. The two methods for calculating dV/dt generated similar results so we employed the latter method for the remainder of the sequences.

The methods for determining the shapes of the ingested volume of water are discussed in greater detail elsewhere (Higham et al., 2005a). In short, we measured the maximum height and the length of the boundary described above and converted the measurements to an aspect ratio of the ingested volume in lateral view. The ingested volume was more narrow and elongate as values of this ratio decreased.

To determine the accuracy of the strike, we digitized points along the edge of the ingested volume and used these to determine the center of the parcel of water (COP; Fig. 1). For the shrimp and tubifex worms, the center of mass (COM) was the best-approximation of the center of the body. For the goldfish prey, the COM was located slightly dorsal and posterior to the pectoral fin insertion site on the body. All measurements of the COM of the prey were made at the onset of the strike prior to any movement. We then calculated the straight-line distance from the COP to the edge of the ingested volume, with the line passing through the estimated center of mass (COM) of the prey item. In order to determine where along this line the prey was, we calculated the straight-line distance from the COP to the

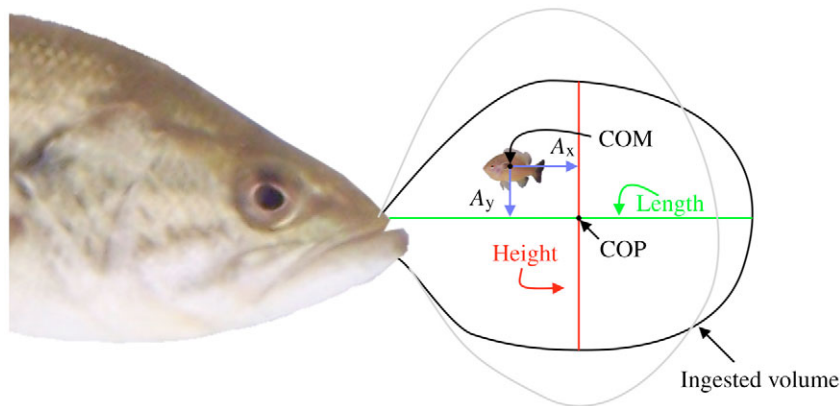


Fig. 1. A schematic diagram of the measurements made to characterize strike accuracy. The boundary, which surrounds the ingested volume of water in lateral view, shows a typical shape for a largemouth bass (dark line). The lighter boundary shows a typical shape of the ingested volume of water for a bluegill sunfish. The aspect ratio of the parcel of ingested water was calculated from its length and height. Strike accuracy was determined by measuring the distance from the center of the parcel (COP) to the center of mass of the prey (COM) and then dividing this by the distance between the COP and the boundary of the ingested volume, intersecting the COM of the prey. The vertical (A_y) and horizontal (A_x) components of accuracy were determined by measuring the distance between the COM of the prey and each axis.

COM of the prey. The accuracy index (AI) was defined as $AI=1-(\text{distance to prey}/\text{distance to volume boundary})$ such that higher values of AI indicate the prey item was closer to the COP. Values of 1 indicate the prey is located at the COP (i.e. the value within the parentheses above would be zero). If the prey were located on the boundary of the ingested volume, the AI would equal zero (i.e. the value within the parentheses above would be one).

In addition to this overall metric of accuracy, we measured the vertical (relative to the x -axis) and the horizontal (relative to the y -axis) accuracies for each strike (Fig. 1). We first calculated the distance between the COM of the prey item and either the x -axis (A_y) or the y -axis (A_x) (Fig. 1). We then calculated the straight-line distance from the boundary of the ingested parcel of water to the axis of interest (going through the COM of the prey). The accuracy relative to the axis of interest was defined as $A_{x \text{ or } y}=1-(\text{distance to prey from axis}/\text{distance to boundary from axis})$. Values of 1 indicate the prey item is located on the axis of interest and values of zero indicate that the prey is located on the boundary of the ingested parcel of water.

Maximum fluid speed, measured at a distance of $\frac{1}{2}$ of maximum gape away from the center of the mouth, was quantified for a large number (96) of sequences for bluegill sunfish and largemouth bass. The purpose of this was to determine the average maximum fluid speed for each species under a variety of feeding situations.

In a separate analysis to characterize maximum suction feeding performance, we selected the maximum value for fluid speed and fluid acceleration for each individual using fluid speeds in the earthbound and fish's frames of reference. The acceleration we are measuring is the local acceleration of the fluid since our measurements are at a single location. Thus, acceleration in our study refers to the local acceleration of the fluid. We also selected the maximum value for dV/dt , which was only calculated in the fish's frame of reference. The local acceleration of the fluid in the earthbound frame of reference was calculated by dividing the maximum fluid speed by the

time to peak fluid speed ($TTPFS$), which is the time from 20% of peak gape to the time of maximum fluid speed. To calculate local fluid acceleration in the fish's frame of reference, we added the average ram speed of the strike to the maximum fluid speed and then divided this by $TTPFS$. To characterize the accuracy for the maximum performance strikes, we first selected the three sequences per individual that exhibited the highest fluid speeds. For each individual, we then averaged the three values of accuracy for these strikes.

Statistical analyses

Prior to performing any statistical analyses, we \log_{10} transformed all of the variables (with the exception of the accuracy index) in order to normalize variances. For the accuracy index, we used an arcsin transformation. For each species separately, we performed mixed-model multiple regressions in order to determine the effects of $TTPG$, ram speed and maximum gape on the following dependent variables: (1) total volume of ingested water, (2) maximum rate of volume flow (dV/dt), and (3) the accuracy index (AI). We performed analyses of variance (ANOVAs) in order to determine the effects of species on several variables. For these analyses, the independent variables were species (fixed) and individual (nested within species; random). In order to correct for multiple statistical tests, α (0.05) was adjusted using a sequential Bonferroni test (Rice, 1989). We used SYSTAT version 9 (SPSS Inc., Chicago, IL, USA) for all statistical analyses.

Results

A detailed description of the hydrodynamics during suction feeding in bluegill has been presented elsewhere (Day et al., 2005; Higham et al., 2005a). Largemouth bass had an average maximum gape twice that of bluegill sunfish (Table 1). The average swimming velocity at the time of prey capture was substantially higher in largemouth bass than bluegill sunfish (Table 1). The average time to peak gape ($TTPG$), however,

Table 1. Mean values for several variables examined in this study

Variable	Largemouth bass	Bluegill sunfish	P value
Maximum gape (cm)	2.6±0.1	1.3±0.1	<0.0001*
$TTPG$ (ms)	22.4±1.4	28.3±3.2	0.70
Ram speed (cm s ⁻¹)	48.0±5.7	8.1±2.0	<0.0001*
Ingested volume (cm ³)	27.8±3.3	4.5±0.5	<0.0001*
Accuracy index (AI)	0.46±0.03	0.80±0.02	<0.0001*
Height-length ratio of ingested volume	1.01±0.04	1.09±0.04	0.47
Average maximum dV/dt (cm ³ s ⁻¹)	1389.2±133	214.5±40.4	<0.0001*
Average EFS (cm s ⁻¹)	31.7±1.1	38.4±2.8	0.005*
Average FFS (cm s ⁻¹)	83.3±3.5	46.5±3.4	<0.0001*

$TTPG$, time to peak gape; EFS , fluid speed at a distance of $\frac{1}{2}$ maximum mouth diameter in the earthbound frame; FFS , fluid speed in the fish's frame; dV/dt , change in volume per unit time.

Values are means ± s.e.m. The P values reflect the results of ANOVAs performed separately on each variable with species as the independent variable. *Significant ($\alpha=0.05$) following a sequential Bonferroni correction.

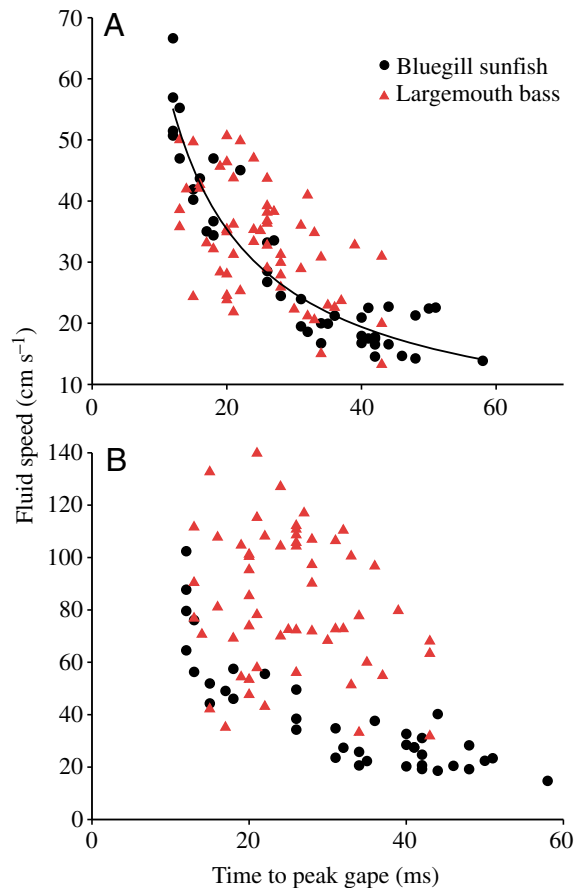


Fig. 2. Time to peak gape (*TTPG*) versus fluid speed for both bluegill sunfish (black circles) and largemouth bass (red triangles) using fluid speeds calculated in the earthbound frame of reference (A) and the fish's frame of reference (B). The curve in A is fit to the bluegill sunfish data to show how largemouth bass exhibit a similar relationship. For both species, fluid speed (measured at $\frac{1}{2}$ peak gape in front of the fish on the center line) increases with a decrease in *TTPG*. Note that the variation in fluid speed for a given *TTPG* is higher for bass than bluegill in both A and B. Also note that the variation in fluid speed for a given *TTPG* is much greater when accounting for the ram speed of the fish (B). The data for bluegill are from Day et al. (Day et al., 2005).

did not differ significantly between the two species. For both species, fluid speed *FS* (in both the earthbound and fish's frame of reference) decreased as a function of *TTPG*, although there was more variation in *FS* independent of *TTPG* for bass than for bluegill (Fig. 2). Bluegill sunfish generated higher average peak fluid speeds than largemouth bass in the earthbound frame of reference, but the opposite result was observed for fluid speeds in the fish's frame of reference.

As was done for bluegill sunfish (Day et al., 2005), a mean scaled velocity profile was found by fitting a fourth order polynomial to 58 pooled feedings from all bass ($r^2=0.985$), as shown in Fig. 3. The s.d. of residuals of scaled fluid speeds *SFS* about the mean scaled velocity profile are shown as error bars in the figure, $SFS_{\text{pooled-bluegill}}=0.348x^4-2.49x^3+6.61x^2-7.78x+$

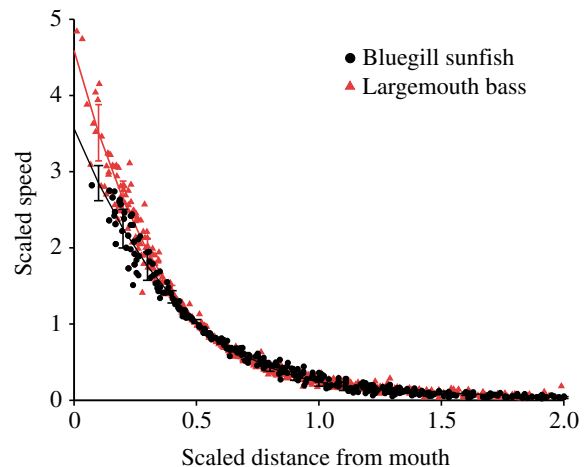


Fig. 3. Mean profiles of scaled speed along the centerline transect for bluegill sunfish (black circles) and largemouth bass (red triangles). The lines correspond to the polynomial fit to each pooled dataset. For each feeding in these pooled datasets, the profile at the time of peak fluid speed was scaled by dividing spatial distances by gape at this time and the magnitude of speed by the measured speed located at a distance of $\frac{1}{2}$ gape in front of the fish. The speed at this location is used throughout as a reference, because at this location fluid speed is substantial and the *PIV* measurements meet the validation criteria (see Materials and methods). The error bars represent the s.d. of the residuals about the fit lines. Fluid speed at the mouth aperture is approximately 3.5 times (bluegill) and 4.5 times (bass) that at $\frac{1}{2}$ gape. The data for bluegill are from Day et al. (Day et al., 2005).

3.56 (see Day et al., 2005), $SFS_{\text{pooled-bass}}=0.986x^4-5.80x^3+12.53x^2-12.07x+4.59$.

Characteristics of the ingested volume

Largemouth bass ingested a significantly larger volume of water (*V*) than bluegill sunfish (Table 1), and ingested the volume of water at a faster rate as indicated by the rate of volume change (dV/dt ; Table 1; Fig. 4). For both largemouth bass and bluegill, approximately 50% of the total *V* was ingested by the time of maximum gape (Fig. 4). Furthermore, maximum dV/dt occurred at approximately the time of maximum gape. This is almost coincident with the timing of peak fluid speed, as measured at a distance of $\frac{1}{2}$ peak gape (Figs 4, 5). In general, the temporal pattern of key kinematic and fluid mechanical events is very similar for the two species (Fig. 5), with one exception being that bass tend to ingest their prey relatively later in the mouth opening sequence than bluegill sunfish. The time of peak fluid speed is nearly simultaneous with the onset of peak gape for both species (Figs 4, 5).

For both species, larger values of peak gape resulted in a significantly greater volume of ingested water, and a faster rate of volume ingestion (Fig. 6). In contrast, neither species exhibited a significant relationship between time to peak gape (*TTPG*) and the volume of water ingested (Fig. 7A). For bluegill, and not largemouth bass, the rate of volume flow into

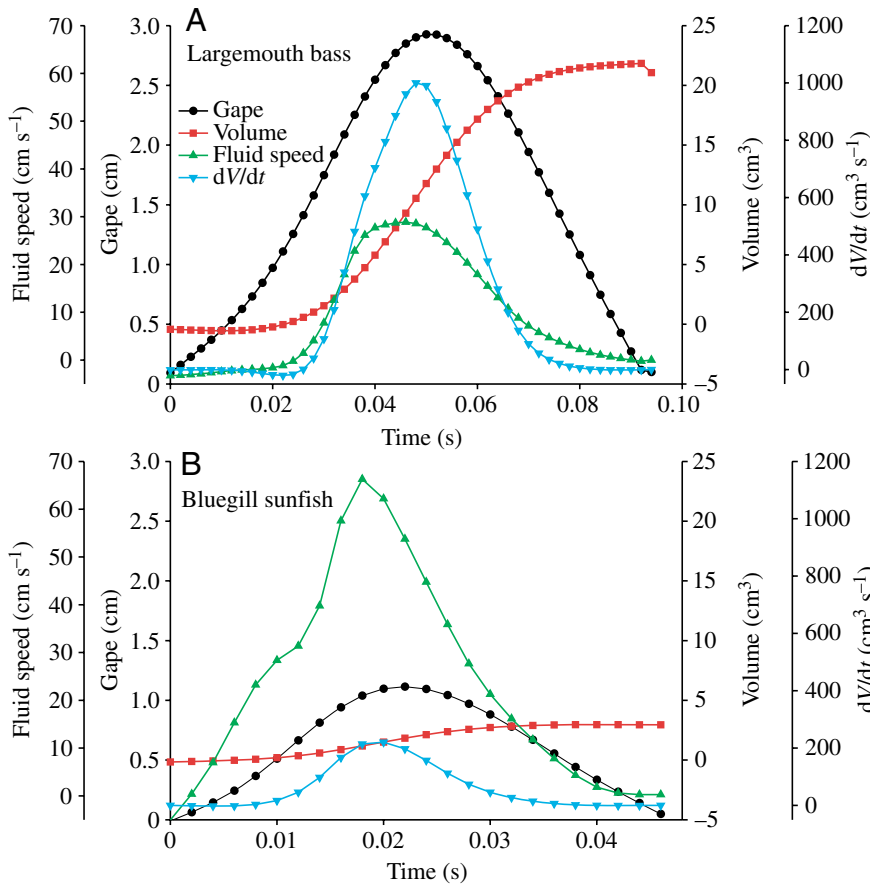


Fig. 4. Representative sequences of gape (black circles), volume (red squares), fluid speed in the earthbound frame of reference (green upward triangles), and the change in volume per unit time (dV/dt ; blue downward triangles) for (A) largemouth bass and (B) bluegill sunfish. Positive values of fluid speed indicate that the water is flowing towards the fish's mouth. Note that the volume ingested by largemouth bass is substantially greater than the volume ingested by bluegill. Also note that maximum gape of largemouth bass is approximately twice that of bluegill. For this figure, we applied a smoothing spline with a smoothing factor of 1 or 2 to each of the variables using Igor Pro 5.01 (WaveMetrics Inc., Lake Oswego, OR, USA).

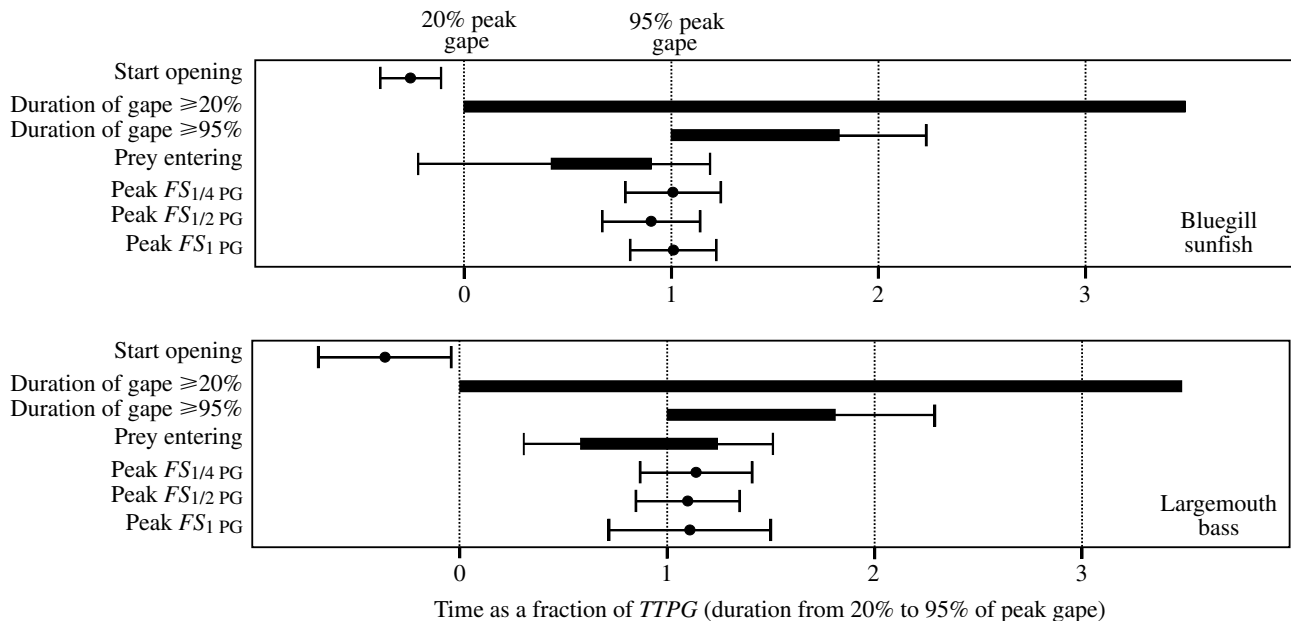


Fig. 5. Relative timing of kinematic events and peak fluid speeds for bluegill (top) and bass (bottom). To account for variation in absolute speed of the event, all times are shown normalized to $TTPG$. Because of the definition of $TTPG$ used (see Materials and methods), the kinematic events of 20% PG and 95% PG are necessarily located at 0 and 1, respectively. All other symbols and error bars show the mean \pm s.e.m. for all feedings analyzed. Note that peak fluid speed occurs at approximately the same time as 95% mouth opening for bluegill, but slightly after 95% opening for bass. Events that have some duration (duration of gape and prey entering) are represented as filled bars with error bars to show the s.e.m. for the start and finish of these events. The three values of the time of peak fluid speed (FS) represent three locations in front of the mouth of the fish relative to peak gape (PG). The data for bluegill are from Day et al. (Day et al., 2005).

the mouth was significantly higher when the *TTPG* was reduced (Fig. 7B). Finally, for both species, an increase in ram velocity resulted in a significantly greater ingested volume of water (Fig. 8).

The average height to length ratio of the ingested volume of water was similar in the two species (Table 1; Fig. 9). The height and length were, on average, approximately equal. With an increase in ram velocity, the ingested volume of water became significantly more elongate and narrow in largemouth bass (Fig. 9). This relationship was also found in bluegill sunfish, and is presented elsewhere (Higham et al., 2005a).

Bluegill sunfish were more accurate than largemouth bass during feeding (Table 1; Fig. 10A). The primary difference between the two species was the vertical accuracy (Fig. 10B) such that bluegill ingested a volume of water where the prey was situated closer to the *x*-axis of the ingested volume (see Fig. 1 and Fig. 10B). Bluegill and largemouth bass were equally accurate at positioning the prey item along the horizontal axis extending from the fish's mouth. Although bluegill exhibited a nearly significant relationship between ram

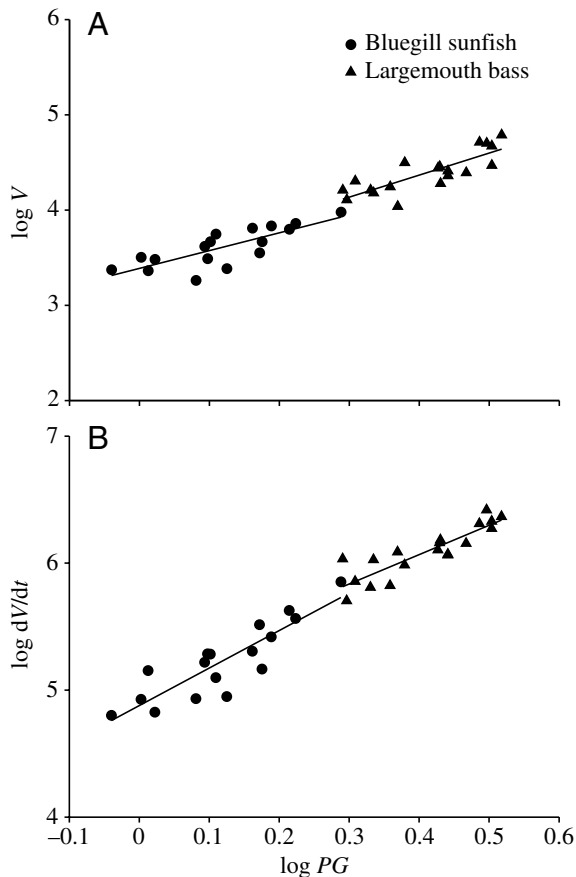


Fig. 6. Log-log plot of peak gape (*PG*; cm) versus (A) volume (*V*; mm³) and (B) the change in *V* per unit time *t* (*dV/dt*; mm³ s⁻¹) for bluegill sunfish (circles) and largemouth bass (triangles). *PG* had a significant effect on *V* for both bluegill ($r^2=0.63$; $P<0.01$) and bass ($r^2=0.67$; $P<0.01$). Additionally, peak gape affected maximum *dV/dt* for both bluegill ($r^2=0.74$; $P<0.01$) and bass ($r^2=0.67$; $P<0.01$).

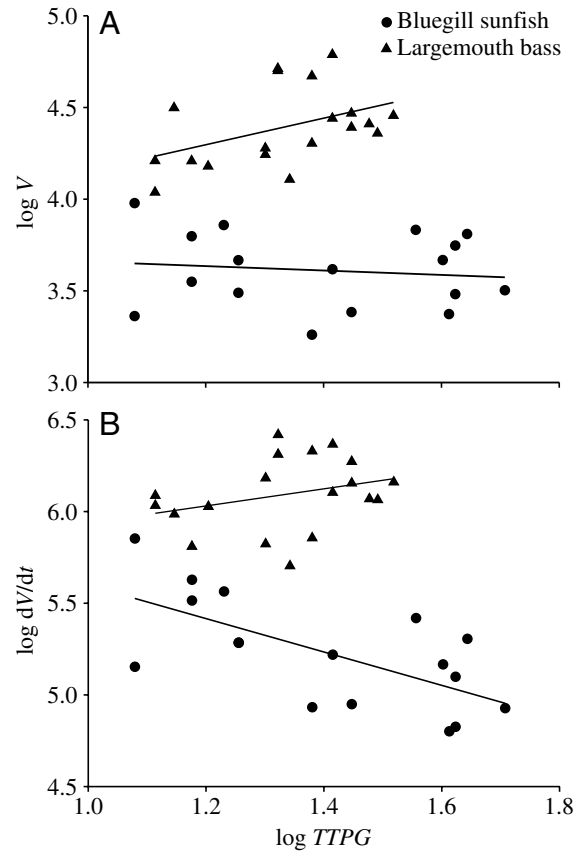


Fig. 7. A log-log plot of time to peak gape (*TTPG*; ms) versus (A) volume (*V*; mm³) and (B) the change in volume per unit time (*dV/dt*; mm³ s⁻¹) for bluegill sunfish (circles) and largemouth bass (triangles). *TTPG* did not affect *V* significantly in bluegill ($r^2=0.02$; $P=0.6$) or bass ($r^2=0.19$; $P=0.06$). Additionally, *TTPG* was significantly negatively related to maximum *dV/dt* in bluegill ($r^2=0.45$; $P<0.01$) but not bass ($r^2=0.25$; $P=0.08$).

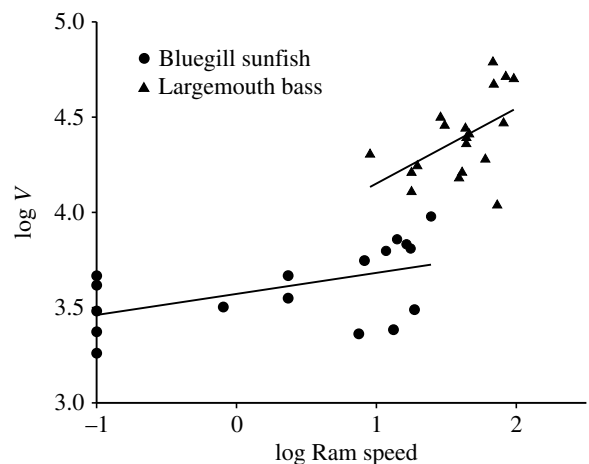


Fig. 8. A log-log plot of ram speed (cm s⁻¹) versus ingested volume (*V*; mm³) for bluegill sunfish (circles) and largemouth bass (triangles). Ram speed significantly affected ingested volume for bluegill ($r^2=0.27$; $P=0.03$) and bass ($r^2=0.26$; $P=0.03$).

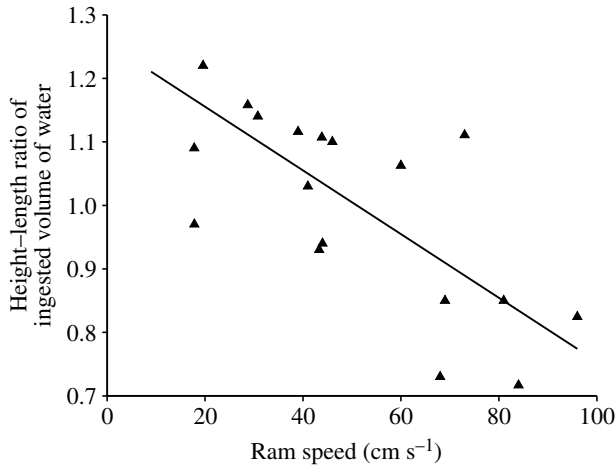


Fig. 9. A plot of ram speed *versus* the height to length ratio of the ingested volume of water for largemouth bass. As ram speed increased, the ingested volume of water became significantly more elongate and narrow ($r^2=0.57$; $P<0.01$). This relationship, showing a similar trend, is published elsewhere for bluegill sunfish (Higham et al., 2005a).

speed and overall accuracy (Fig. 10A), neither species exhibited a significant decline in accuracy with an increase in ram speed.

Suction feeding performance

From the sequences used for these analyses, bluegill sunfish generated significantly higher fluid speeds and higher magnitudes of acceleration in the earthbound frame of reference, and exhibited significantly greater strike accuracy compared to largemouth bass (Table 2; Fig. 11). However, largemouth bass generated higher, but not significantly different, fluid speeds in the fish's frame of reference (Table 2;

Table 2. Peak values for suction feeding performance variables in largemouth bass and bluegill sunfish

Variable	Largemouth bass	Bluegill sunfish	<i>P</i> value
<i>EFS</i> (cm s ⁻¹)	46.1±1.0	71.0±3.9	0.003*
<i>FFS</i> (cm s ⁻¹)	116.3±11.9	85.8±10.2	0.12
<i>dV/dt</i> (cm ³ s ⁻¹)	2605.8±379.9	442.8±150.2	0.005*
Accuracy index	0.39±0.03	0.82±0.05	0.002*
<i>EFA</i> (m s ⁻²)	4.5±0.2	6.6±0.4	0.009*
<i>FFA</i> (m s ⁻²)	6.3±0.5	7.9±0.9	0.18

EFS, fluid speed in earthbound frame of reference; *FFS*, fluid speed in fish's frame of reference.

dV/dt=Change in volume per unit time; *EFA*, fluid acceleration in earthbound frame of reference; *FFA*, fluid acceleration in fish's frame of reference.

Values are means ± s.e.m. across three specimens per species of the best values achieved by each fish in this study. The *P* values indicate results of ANOVAs on the species effect. *Significant ($\alpha=0.05$) following a sequential Bonferroni correction.

Fig. 11A). The maximum volumetric flow rate was significantly higher for bass compared to bluegill (Table 2; Fig. 11B).

Discussion

Several properties of the water flow generated by suction feeding fishes can potentially influence the likelihood of successful capture in a particular feeding event and we have tried to depict this multidimensional nature of suction feeding performance in a comparison of largemouth bass and bluegill. In the earthbound frame of reference, bluegill generated higher

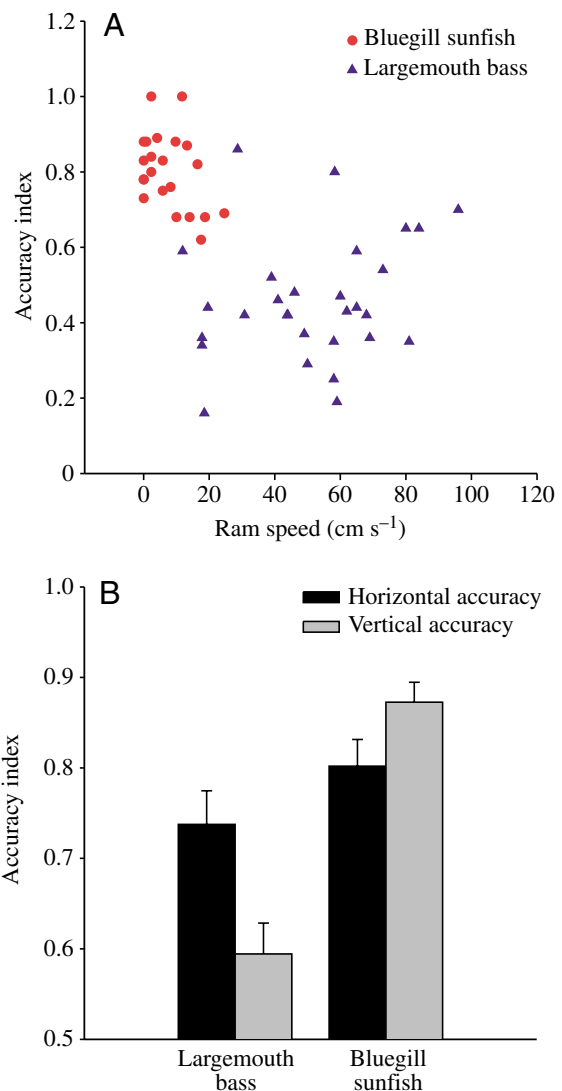


Fig. 10. (A) Plot of ram speed *versus* the accuracy index (AI) for largemouth bass (triangles) and bluegill sunfish (circles). Note that bluegill were more accurate than largemouth bass but that accuracy did not decrease significantly with ram speed for either species. (B) Graph of horizontal (black bars) and vertical (gray bars) accuracy for largemouth bass and bluegill sunfish. Note that bluegill sunfish were significantly more accurate than largemouth bass in the vertical plane ($P<0.01$) but not the horizontal plane.

fluid speeds than bass, higher magnitudes of acceleration and showed greater accuracy with their strikes. In contrast, largemouth bass ingested a greater volume of water and had higher rates of volume flow during the strike. However, when viewed in the fish's frame of reference, largemouth bass approached the prey faster and achieved higher fluid speeds than the bluegill due to the higher swimming speed. Higher fluid speeds by the bluegill in the earthbound frame of reference imply a higher capacity to generate drag forces on stationary prey items, while the higher fluid speed of bass in the fish frame of reference imply a faster rate of closing the distance between the predator and prey. These results generally confirm expectations from previous studies with these species

of their feeding ecology, feeding behavior and functional morphology. Bluegill are known to have a greater capacity to generate suction pressure inside the buccal cavity (Carroll et al., 2004), a fact that has been interpreted as reflecting a greater scope for fluid speed. The larger mouth and buccal cavity of bass has been suggested to be well-suited to feeding on the larger and more elusive fishes, crayfish and shrimp that dominate their diet (Werner, 1977; Norton and Brainerd, 1993).

Fluid speed and acceleration

The speed of the water entering the mouth has generally been considered the most important measure of suction feeding performance (Muller et al., 1982; Van Leeuwen and Muller, 1984; Ferry-Graham et al., 2003; Higham et al., 2005a), but the technical difficulty associated with measuring fluid speed directly has slowed progress in this area. This study represents the first direct measurement and comparison of maximum fluid speeds between species. Bluegill sunfish generated higher fluid speeds in the earthbound frame of reference than largemouth bass (Table 1), confirming the interpretation made previously that the greater capacity for subambient buccal pressure in bluegill indicated a greater scope for fluid speed (Carroll et al., 2004). However, in the fish's frame of reference, largemouth bass actually generated higher fluid speeds than bluegill sunfish. Largemouth bass achieve this by exhibiting higher ram speeds than bluegill (Table 1). Thus, it seems that bass would benefit from feeding in open areas where they could maximize their approach speed and thus maximize the fluid speeds they generate during suction feeding. In a habitat that precludes high attack speeds, bluegill will likely be able to generate higher fluid speeds (relative to the fish).

Bluegill accelerate the fluid faster than largemouth bass regardless of the frame of reference (Table 2). In the case of a prey item moving as if it were a particle of water, greater fluid speed and acceleration will minimize the time that prey have to initiate an escape response. If prey are not moving along with the suction flow, such as when prey are sucked off a holdfast, higher flow velocities will generate larger drag forces and higher accelerations will generate a larger acceleration reaction, which resists changes in velocity and thus prevents the deceleration of fluid (Daniel, 1984). High velocity and high acceleration of the fluid should both result in improved suction feeding performance.

Muller and Osse describe strategies of suction feeding that are defined, in part, by the timing of the opening of the opercular valves (Muller and Osse, 1984). Largemouth bass and bluegill sunfish both open their opercular cavities after the prey is captured and after the time of maximum gape (T. E. Higham, unpublished). However, largemouth bass open this valve earlier in the strike sequence than bluegill sunfish (approximately 3 ms after maximum gape for bass *versus* 19 ms for bluegill). Muller and Osse suggest that it is beneficial for a fish to combine early opening of the opercular valve with swimming (Muller and Osse, 1984). Given that the ram velocities of largemouth bass are much greater than bluegill

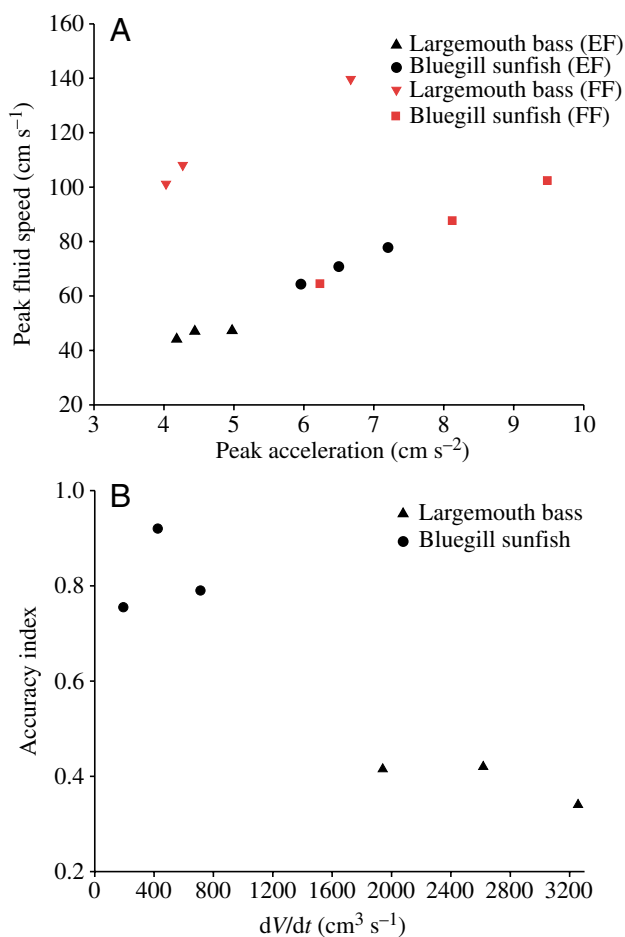


Fig. 11. Plots of (A) peak fluid speed *versus* peak acceleration, and (B) accuracy *versus* the volumetric flow rate, for largemouth bass (triangles) and bluegill sunfish (circles). In A, the red symbols indicate measures of peak fluid speed and acceleration in the fish's frame of reference (FF), whereas the black symbols indicate values in the earthbound frame of reference (EF). Peak fluid speed, peak acceleration and volumetric flow rate (dV/dt) were calculated using the single maximum value for each variable for each individual. Thus, each point represents the single highest value for each individual. Accuracy was calculated by selecting the three sequences per individual that had the highest peak fluid speed and then averaging the accuracy for those three strikes.

sunfish (Table 1), it seems that the two species in our study follow this trend. Assuming that ram speed does not affect mouth expansion, it is interesting to note that for either species it does not seem that an increase in ram speed results in earlier opercular opening, which contradicts the hypothesis by Muller and Osse (Muller and Osse, 1984).

Ingested volume

For each species, the primary correlate of increases in the ingested volume was increasing gape distance, measured here as an indication of overall buccal expansion. Time to peak gape (*TTPG*) had little influence on the ingested volume, despite its considerable effect on the peak fluid speed entering the mouth in bluegill sunfish (Day et al., 2005). Although fluid speed was faster with a shorter *TTPG*, this was countered by a shorter duration of the suction flow that resulted in little net change in volume. By increasing the ingested volume of water, the distance from the prey (if centered in this volume) to the edge of the parcel of fluid increases and thus the chance of the prey escaping may be less likely.

Largemouth bass ingested a much larger volume of water than did bluegill (Table 1). Bass are piscivorous ram-suction feeders that eat primarily evasive prey including fish, crayfish and penaeid shrimp (Nyberg, 1971; Huskey and Turingan, 2001). Thus, the larger ingested volume may be an adaptation to feeding on evasive prey. Based on measured buccal volumes of these two species (D. C. Collar, unpublished), bluegill can ingest up to 2.5 times the size of the buccal volume (max. ingested=9510 mm³) while bass ingest up to 3.2 times the size of the buccal volume (max. ingested=61337 mm³). Both species are able to maintain a unidirectional flow of water that is expelled from the opercular cavity at the same time that more water is being ingested. The ability of largemouth bass to ingest more water relative to their buccal volume than bluegill could be related to the observation that they swim faster during prey capture, which will generate a greater passive flow of water through the buccal cavity (Table 1).

Based on unpublished values of buccal lengths for largemouth bass and bluegill sunfish, the individuals in our study had buccal lengths of 2.29 cm (bluegill) and 2.81 cm (bass) (D. C. Collar, unpublished). If one assumes that the shape of the expanding buccal cavity is similar in the two species, then differences in buccal length should result in differences in elevation of the regressions of gape diameter on ingested volume (Fig. 6A). We found no difference between species in this scaling pattern, suggesting that minor differences in buccal shape may counter the effects of a difference in buccal length (analysis of covariance, $P_{\text{species} \times \text{gape}}=0.42$, $P_{\text{species}}=0.06$).

Volumetric flow rate

For both bluegill and largemouth bass the primary mechanism for modulating the volumetric flow rate was to modulate the extent of buccal expansion during the strike, as indicated by maximum gape (Fig. 6). Shorter times to peak gape (*TTPG*) resulted in higher volumetric flow rates in

bluegill, but did not affect the volumetric flow rate for largemouth bass (Fig. 7). This difference between the two species suggests that largemouth bass are modulating another kinematic variable to regulate the flow of water through the buccal cavity in a different way than bluegill. This could be accomplished with a greater decoupling of jaw rotation and buccal expansion in bass, or by modulation of the opercular opening. Interestingly, bass exhibit a greater amount of variation in fluid speed for a given *TTPG* (Fig. 2), supporting the idea that other kinematic variables are being modulated by bass.

Accuracy during feeding

Our study presents a novel method for quantifying accuracy during the feeding event by measuring the location of the prey relative to the center of the ingested parcel of water (Fig. 1). We suggest that this may be an important, understudied aspect of suction feeding performance. It is well known that proper timing of the strike is essential to a successful outcome. A fish will not capture prey if the strike occurs too early, when the prey is not in range, and strikes will be unsuccessful when the mouth of the predator is too close to the prey item prior to mouth opening (Nyberg, 1971; Webb and Skadsen, 1980; Coughlin, 1991). Our observations indicate that bluegill have a superior ability to position the suction flow field on the prey item. This has not been previously demonstrated and may reflect some level of compensation for the fact that bluegill generate a smaller flow field than bass. Bluegill often feed on midwater zooplankton, such as cladocera, as well as small benthic chironomid larvae and vegetation dwelling insect larvae (Keast, 1978; Mittelbach, 1981; Mittelbach, 1984; Brown and Colgan, 1984; Collar et al., 2005). Their ability to generate small, well-directed regions of high-speed suction flow may be a key factor in their well-documented ability to rapidly remove large numbers of these small prey from a feeding arena (Mittelbach, 1981).

One explanation for why bass were less accurate than bluegill could be that the average ram speed of bass was higher than bluegill ($48.0 \pm 5.7 \text{ cm s}^{-1}$ versus $8.1 \pm 2.0 \text{ cm s}^{-1}$). It has been shown for other species that accuracy decreases with an increase in attack velocity (Webb and Skadsen, 1980). Whether largemouth bass are less accurate because they swim at higher speeds or whether they swim faster because they rely less on accuracy is not fully understood. Higham et al. found that bluegill sunfish developed a narrower, more elongate, and more focused ingested volume of water with an increase in ram speed (Higham et al., 2005a). Having the area that is influenced by suction generation directed more in front of the fish could make accuracy a more important factor. It has been suggested that braking could increase the accuracy of a suction-feeding fish (Lauder and Drucker, 2004; Higham et al., 2005a; Higham et al., 2005b), and this might be more important for fish that ingest a relatively small volume of water. Future studies that relate braking during suction feeding to mouth size (indirect measure of ingested volume) would provide further insight into this issue.

Interestingly, while the species were equally good at positioning the prey horizontally, bluegill were better at positioning the prey vertically. With an increased ram velocity, the height to length ratio of the ingested volume of water decreased for both bluegill sunfish (Higham et al., 2005a) and largemouth bass (Fig. 9). Given that bluegill ingest a smaller volume of water, the vertical dimension of this volume at maximal ram speeds would be much smaller than that of bass at a comparable ram speed. Thus, if the attack strategy involves swimming at a speed that reduces the vertical height of the ingested volume of water, then the vertical accuracy of bluegill would be especially significant. The length of the ingested volume of water increases with an increase in swimming speed (Higham et al., 2005a), suggesting less of a constraint along the horizontal axis with changes in ram speed.

In studies of larval fishes, accuracy was quantified by the perpendicular uptake distance (*PUD*) between the centroid of the prey and the longitudinal axis of the fish (extending outward from the fish to the location of the prey) (Drost, 1987; Coughlin, 1991). In these cases, measurements were dependent on the orientation of the predator, both in ventral and lateral view. Without measuring the area of water influenced by suction, these studies lacked a scaleable metric that could be applied to a variety of morphologically distinct species. Our measures differ since they are relative to the *x*-axis of the ingested volume rather than the central axis of the mouth. Additionally, our measures are scaled to the dimensions of the ingested volume rather than just a distance from the axis of interest.

Suction feeding performance

Successful prey capture using suction depends on several aspects of predator behavior and the pattern of water flow that is generated during the strike, including a fluid speed high enough to draw the prey towards the predator, ingesting a volume of water great enough to entrain the prey, and accurate positioning of the suction flow field. Given this multidimensional nature of suction feeding performance it is interesting to ask how different species are distributed in the suction feeding performance space. Without taking ram velocity into account, our results suggest the possibility that a trade-off exists between the ability to generate high fluid speeds and the volumetric flow rate. Bluegill generate higher fluid speeds than bass, but bass overcome a slower fluid speed and are able to move more water per time into the mouth. It is known from previous work that bluegill are able to generate greater suction pressure magnitudes than largemouth bass, and this has been attributed to bluegill having a greater force capacity of the epaxial musculature that elevates the cranium during the strike and a higher mechanical advantage for the transfer of force from this muscle to the expansion of the buccal cavity (Carroll et al., 2004). At a given body size they also have a lower area of the buccal cavity across which the expansive epaxial forces are distributed. In comparison with bluegill, largemouth bass are modified to achieve greater volume of expansion for a given amount of epaxial contraction.

Thus, the basic trade-off in biological musculoskeletal lever systems between transfer of force and displacement may underly a trade-off in design of the fish suction feeding mechanism that results in a contrast between species modified to generate high fluid speeds and accelerations (i.e. high force transfer) *versus* other species that generate high volume and volumetric flow rate (i.e. large displacements). As additional comparative data are generated it will be instructive to see how morphological variation maps onto the distribution of fish species in this performance space. We predict that a common pattern will be that species that generate high fluid speeds will commonly exhibit small mouths and a high capacity to deliver force to buccal expansion, while species that ingest a large volume and generate high values of dV/dt will have larger buccal cavities and more efficient buccal expansion.

The underlying basis of differences between species in strike accuracy may simply be that accuracy decays with increasing approach speed of the predator (Fig. 10). If this proves to be the case generally, then a second trade-off is identified that may influence the distribution of species in the suction feeding performance space.

In the fish's frame of reference, largemouth bass generate higher fluid speeds than bluegill sunfish. Although bluegill sunfish are capable of exerting greater drag forces on the prey during suction feeding (due to higher flow speeds in the earthbound frame), largemouth bass close the distance to the prey faster. This suggests that bluegill might be specialized for drawing relatively non-evasive prey into their mouths either from the water column or from substrate, whereas bass are adept at overtaking highly evasive prey. The strategy employed by largemouth bass requires that the prey not be close to substrate or the high swimming velocity might result in a collision, suggesting that a trade-off exists between feeding performance and the habitat in which they feed.

List of symbols and abbreviations

<i>AI</i>	accuracy index
A_y, A_x	distance between the prey's COM and either the <i>x</i> -axis or the <i>y</i> -axis, respectively
COM	center of mass
COP	center of the parcel of water
DPIV	digital particle image velocimetry
dV/dt	rate of volume ingestion
EF	earthbound frame of reference
FF	fish's frame of reference
<i>PG</i>	peak gape diameter
<i>PUD</i>	perpendicular uptake distance
<i>FS</i>	fluid speed
<i>SFS</i>	scaled fluid speed
<i>TTPFS</i>	time to peak fluid speed
<i>TTPG</i>	time to peak gape
<i>V</i>	volume

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