

# Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry

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## Summary

It is well established that suction feeding fish use a variable amount of swimming (ram) during prey capture. However, the fluid mechanical effects of ram on suction feeding are not well established. In this study we quantified the effects of ram on the maximum fluid speed of the water entering the mouth during feeding as well as the spatial patterns of flow entering the mouth of suction-feeding bluegill sunfish *Lepomis macrochirus*. Using Digital Particle Image Velocimetry (DPIV) and high-speed video, we observed the flow in front of the mouth of three fish using a vertical laser sheet positioned on the mid-sagittal plane of the fish. From this we quantified the maximum fluid speed (measured at a distance in front of the mouth equal to one half of the maximum mouth diameter), the degree of focusing of water flow entering the mouth, and the shape of the ingested volume of water.

Ram speed in 41 feeding sequences, measured at the time of maximum gape, ranged between 0 and 25 cm s<sup>-1</sup>, and the ratio of ram speed to fluid speed ranged from 0.1% to 19.1%. In a regression ram speed did not significantly affect peak fluid speed, but with an increase in ram speed the degree of focusing of water entering the mouth increased significantly, and the shape of the ingested volume of water became more elongate and narrow. The implications of these findings are that (1) suction feeders that employ ram of between 0% and 20% of fluid speed sacrifice little in terms of the fluid speeds they generate and (2) ram speed enhances the total body closing speed of the predator.

Key words: DPIV, suction feeding, ram feeding, Centrarchidae, sunfish, *Lepomis macrochirus*, locomotion, swimming.

## Introduction

Many aquatic feeding vertebrates swim toward their prey while using suction to draw the prey into their mouth. This combination of 'ram' and suction allows the predator to rapidly close the distance to the prey item, and because the volume of water that is influenced by a suction feeder is restricted to a very small distance in front of the mouth, ram also allows the predator to position the mouth aperture close enough to the prey that suction can be effective. The relative use of ram and suction has been recognized as a major axis of behavioral diversity in aquatic feeders and several attempts have been made to quantify their relative contribution in predator–prey interactions (e.g. Norton and Brainerd, 1993; Svanbäck et al., 2002; Sass and Motta, 2002).

One important issue about the combined use of ram and suction concerns how the two behaviors may hydrodynamically combine (Weihs, 1980; Muller et al., 1982; Muller and Osse, 1984). How does the attack velocity of the predator influence the spatial pattern of fluid flow entering the mouth? The influence of ram speed on the water ingested during suction feeding was estimated by Weihs (1980) using a hydrodynamic sink model. In this model, the ingested volume

of water became focused in front of the mouth as ram speed increased. The shape of the ingested volume of water appears to be related to the ratio of ram speed to fluid speed, such that higher values will result in the capture of narrower and more elongated parcels of water (Weihs, 1980).

One metric of suction performance is the maximum fluid speed moving towards the mouth of the fish. While it may be possible that ram and suction work in concert to increase overall prey capture performance (Wainwright et al., 2001), it has also been suggested that swimming can decrease suction performance (Nyberg, 1971). The idea is that fluid flow is determined by the rate of buccal expansion, and if swimming speed approaches that of the suction-induced flow, net flow in the absolute reference frame could be negligible because most of the water flow into the mouth will be passive (Nyberg, 1971; van Leeuwen, 1984). Additionally, a swimming fish produces water movement in front of it, termed a bow wave, and it is possible that this could negatively influence the suction flow (Nyberg, 1971; Lauder and Clark, 1984; Muller and Osse, 1984; Van Damme and Aerts, 1997; Summers et al., 1998; Ferry-Graham et al., 2003).

In the present study we visualized the flows generated by suction-feeding bluegill sunfish using digital particle image velocimetry (DPIV; Fig. 1; e.g. Drucker and Lauder, 2002, 2003), and we measured the effect of bluegill swimming speed on aspects of the induced suction flows. Depending on the question, we measured fluid speed  $FS$  in either the earth-bound, or absolute, frame of reference ( $AFS$ ) or the fish's frame of reference ( $FFS$ ). We focused on the following three questions: First, does ram speed affect the maximum fluid speed entering the mouth during suction feeding, as measured in the absolute frame of reference? We hypothesize that, if the fish is stationary, fluid speed in the absolute frame of reference ( $AFS_{stationary}$ ) will result exclusively from buccal cavity expansion. However, if the fish is swimming at a ram speed  $RS$ , then fluid speed at the mouth aperture in the absolute frame of reference ( $AFS_{swimming}$ ) will equal the predicted fluid speed if the fish were not moving ( $AFS_{stationary}$ ) minus the magnitude of  $RS$ . This is because when the buccal cavity expands, water will enter the mouth passively at a speed equal to the swimming speed of the fish. We therefore expected that increases in ram speed would result in decreasing fluid speed as long as buccal expansion rate is identical.

Second, does ram speed affect the 'degree of focusing' of the water that has potential to enter the mouth, as measured in

the fish's frame of reference? The degree of focusing (Fig. 2) characterizes the directionality of flow towards the mouth. A low degree of focusing indicates water is being drawn from every direction, whereas a high degree of focusing indicates water is being drawn predominantly from in front of the mouth. We expected that, with increasing ram, the degree of focusing would increase (Drost et al., 1988; Weihs, 1980).

Lastly, does ram speed affect the shape of the ingested volume of water, as measured in the absolute frame of reference? If water flow into the mouth becomes more focused with increasing ram speed, this should influence the dimensions of the parcel of water that is captured during a suction feeding event. Modeling studies (Drost et al., 1988; Weihs, 1980) and limited empirical work (van Leeuwen, 1984) have indicated that this will be the case, with higher ram speeds resulting in the ingested parcel of water becoming elongate in the direction of swimming and reaching farther away from the mouth aperture.

## Materials and methods

### Experimental subjects

We studied the bluegill sunfish *Lepomis macrochirus* Rafinesque, a member of the freshwater family Centrarchidae. Bluegill have been the focus of considerable work on the

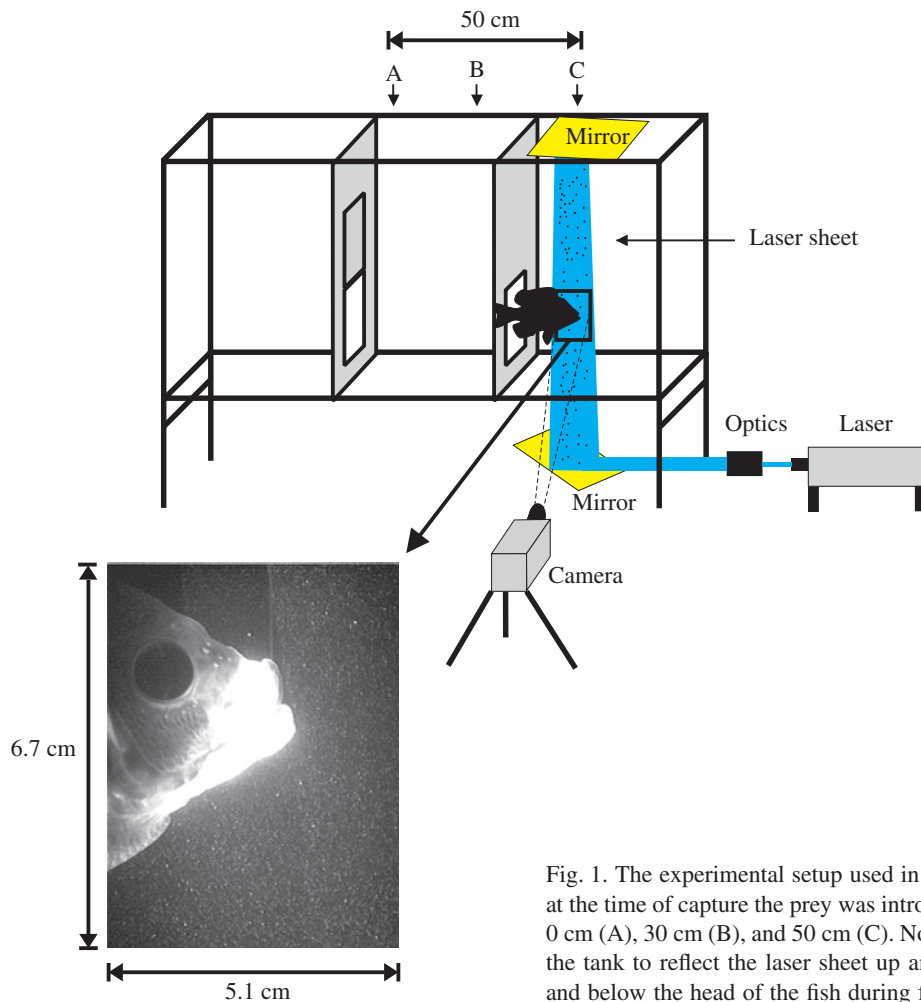


Fig. 1. The experimental setup used in this study. In order to elicit varying ram speeds at the time of capture the prey was introduced at one of three distances from the sunfish: 0 cm (A), 30 cm (B), and 50 cm (C). Note that mirrors were positioned below and above the tank to reflect the laser sheet up and then down in order to illuminate both above and below the head of the fish during feeding.

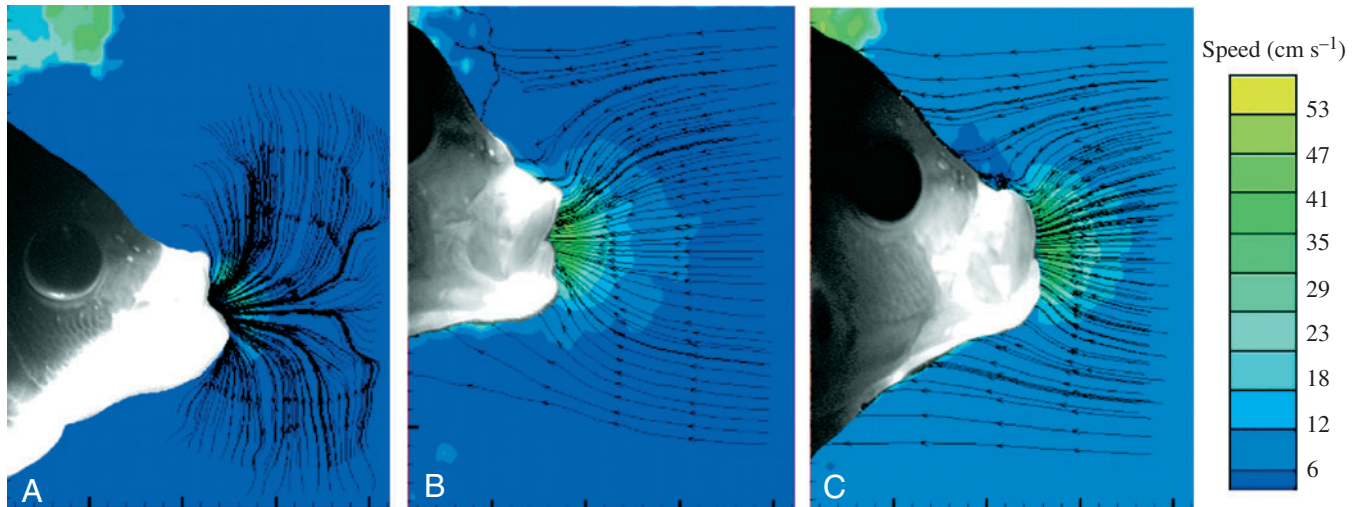


Fig. 2. Representative images, with streamlines and contours of fluid speed in the fish's frame of reference at the time of maximum gape for a low ram case (A;  $RS/AFS_{\text{aperture}}=0\%$ ), a medium ram case (B;  $RS/AFS_{\text{aperture}}=6\%$ ), and a high ram case (C;  $RS/AFS_{\text{aperture}}=14\%$ ). Note that the streamlines do not indicate the area of water ingested, but rather the instantaneous direction of movement of water at each location in space.

functional morphology and biomechanics of suction feeding (for example Lauder, 1980; Lauder and Clark, 1984; Ferry-Graham et al., 2003) and have been shown to be one of the highest performing suction feeders among centrarchid species (Carroll et al., 2004). 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 fed daily with cut squid (*Loligo* 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 fish with standard lengths of 15.3 cm, 15.0 cm and 15.4 cm.

#### Experimental protocol

Each bluegill 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 (Fig. 1). A tubifex worm (~1.0 cm) or a ghost shrimp (*Palaemonetes* sp., about 2 cm), was then dropped through a 0.3 cm diameter plastic tubing or attached to a thin wire, held within the laser light sheet and within the camera field of view, and the door was lifted. Varying locomotor speeds were elicited by introducing the prey items at one of three distances from the fish (Fig. 1A–C). Previous work indicates that bluegill will capture prey with relatively high ram speeds when traversing distances within the range used in this set-up (T. E. Higham, B. Malas, B. C. Jayne and G. V. Lauder, manuscript submitted for publication). Each individual was fed at every location and the order of locations for each fish was arbitrarily chosen.

#### Digital Particle Image Velocimetry (DPIV)

We used DPIV to quantify a number of parameters describing the flow of water into the mouth during suction feeding. Willert

and Gharib (1991) provide a detailed description of this technique for measuring fluid flow. 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 (Fig. 1). The aquarium was seeded with silver coated, neutrally buoyant glass spheres (12  $\mu\text{m}$ ) in order to visualize the flow of water. Mirrors above and below the tank were used to illuminate both above and below the head of the fish during feeding (Fig. 1). Lateral-view video sequences were recorded using a NAC Memrecam ci digital system (Tokyo, Japan) operating at 500 images  $\text{s}^{-1}$  (Fig. 1) with a field of view of  $5.1 \times 6.7$  cm. Additionally, a Sony CCD camcorder (Tokyo, Japan), operating at 30 images  $\text{s}^{-1}$ , 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 generated by bluegill is radially symmetrical about the long axis of the fish (Day et al., 2005).

An adaptive mesh cross correlation algorithm created by 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 with dimensions of  $0.9 \times 0.9$  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. Two-dimensional ( $x$  and  $y$ ) velocity vector profiles were visualized using Tecplot version 10 (Amtec Engineering, Inc., Bellevue, Washington, USA).

In order to determine the validity of the vector measurements, a two-step validation scheme was implemented. Only vectors with a signal-to-noise ratio (SNR) of 2 or greater were included in the analyses, and no smoothing was applied to the final

velocity field. Some spurious measurements passed the SNR validation criterion, and the second part of the validation scheme accounted for these measurements. Measurements both directly on the transect ( $i,j$ ) and at two grid points above ( $i,j+2$ ) and two grid points below ( $i,j-2$ ) were considered at each horizontal position along the transect. Measurements located two grid points away from the primary measurement location were used, because these do not overlap the primary measurement region. If at least two of the three measurements considered had not been removed, based on the SNR criterion (step one of the validation scheme), then the mean of the remaining measurements was used as the value of speed for that position along the transect. Finally, for several sequences we confirmed that measurements with an SNR of 2 were accurate by tracking particles manually for several sequences using IMAGE J version 1.33 (NIH, Washington, DC, USA).

A transect extending forward from the center of the fish's mouth was studied to measure the speed of the fluid as a function of distance from 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 equal to one half of the peak gape diameter (PG) of the fish for the feeding sequence. The accuracy at this position was validated in every trial. All vector velocities reported in this paper are at this distance and the term ' $AFS_{1/2 PG}$ ' refers to the speed of the fluid at this position.

#### Data analysis

The statistical analyses were performed only on those feedings that met the following criteria: (1) successful prey capture occurred, (2) the laser sheet intersected the mid-sagittal plane of the fish (verified with the anterior view camera), (3) the fish was centered on the filming screen in lateral view, and (4) maximum gape followed prey capture. The last point is important because the prey item can interfere with the DPIV measurements, which were made at maximum gape.

Using IMAGE J, the  $x$  and  $y$  coordinates of the tip of the upper and lower jaw were digitized for each image (2 ms intervals) starting before the onset of mouth opening and ending after the mouth was closed. These points were used to quantify changes in gape and to calculate maximum gape for every

feeding sequence. Time to peak gape ( $TTPG$ ) was measured as the time from 20% to 95% of maximum gape. This method for measuring  $TTPG$  reduced 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 achieved in an asymptotic relationship.  $TTPG$  was measured as an indication of the rate of buccal expansion that is used by the fish to generate suction (Sanford and Wainwright, 2002). The  $x$  and  $y$  coordinates of the anterior margin of the eye were digitized and used to quantify ram speed throughout the strikes. Although ram speed usually varied during the course of the strike, 'ram speeds' reported in this study were measured at the time of 95% of maximum gape, the same time that flow speed was measured.

Depending on the question being addressed, we either measured variables in the absolute frame of reference (AF; maximum suction speed and the shape of the ingested volume of water) or in the fish's frame of reference (FF; the degree of focusing). For the latter, we subtracted the ram speed of the fish from each speed vector in order to visualize the flow relative to the fish's mouth and body (Fig. 2).

To determine the degree of focusing (DF) of water flow that was directed towards the mouth, the streamlines in the fish's frame of reference were visualized using Tecplot, and we determined the most dorsal and ventral streamlines that entered the fish's mouth. At a distance anterior to the fish equal to the fish's maximum gape, we measured the maximum vertical distance between these outermost streamlines (Fig. 2) and then scaled this value by the maximum gape of the fish. The reciprocal of this value is defined as DF such that larger values of DF indicate a smaller vertical distance between streamlines and a flow pattern that is more focused in front of the fish.

To determine the shape of the ingested volume of water, we visually tracked particles going into the mouth using IMAGE J and drew a boundary around the outer limit of particles that entered the mouth (Fig. 3). We measured the maximum height and the length of this boundary and converted the measurements to a ratio that described the aspect ratio of the ingested volume in lateral view.

We used SYSTAT version 9 (SPSS Inc., Chicago, IL, USA) for all statistical analyses. All variables were first  $\log_{10}$  transformed to normalize variances, and in each case this

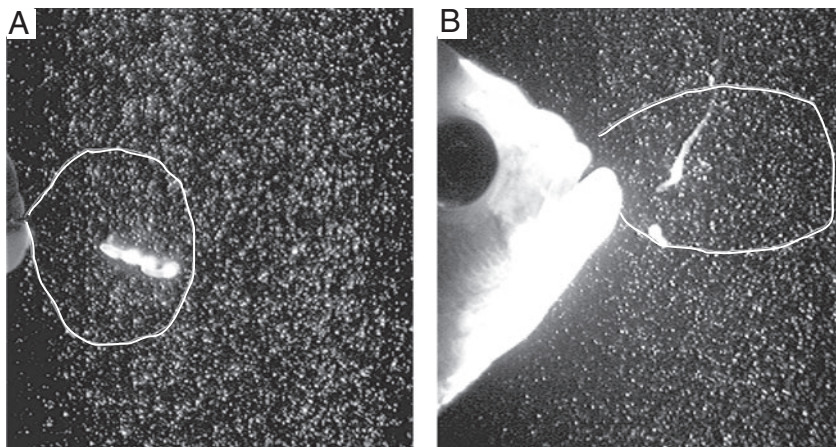


Fig. 3. Sample images illustrating a large height-to-length ratio of the ingested volume (A) and a trial with a small height/length ratio (B). Both images are taken at the time of 20% of peak gape and the white outlines indicate the volume of water that was captured during the feeding event. The fish in (A) was moving at  $0 \text{ cm s}^{-1}$  and the fish in (B) was moving at  $17.5 \text{ cm s}^{-1}$  at the time of peak gape.

Table 1. *P* values from multiple regressions performed separately on each variable

Variable	Peak		Height/ length ratio
	$AFS_{1/2 PG}$	DF	
Individual (2)	–	–	–
<i>TTPG</i> (1)	0.00009	0.001	–
Ram (1)	0.10	0.0004	0.001
Individual $\times$ <i>TTPG</i> (2)	–	–	–
Individual $\times$ Ram (2)	–	–	–
<i>TTPG</i> $\times$ Ram (2)	0.077	0.00002	–
Individual $\times$ <i>TTPG</i> $\times$ Ram (2)	–	–	–

*TTPG*, Time to peak gape;  $AFS_{1/2 PG}$ , absolute fluid speed at a distance equal to  $\frac{1}{2}$  peak gape; DF, degree of focusing.

Degrees of freedom for each factor in the model are noted in parentheses. Variables with  $P > 0.5$  in the initial regression were subsequently eliminated during the running of a reduced model.

allowed the variables to meet the assumptions of the parametric procedures. We performed mixed-model multiple regressions with individual (categorical, random), *TTPG* (continuous), and ram speed (continuous) as the independent variables and all two-way and the three-way interaction terms, with the following dependent variables: (1) maximum fluid speed ( $AFS_{1/2 PG}$ ), (2) the degree of focusing (DF) of the water moving towards the mouth of the fish, and (3) the height-to-length ratio of the ingested volume of water. *TTPG* was included as a variable in the analyses because it strongly affects the suction speed in bluegill sunfish (Day et al., 2005). Each complete multiple regression model was first run and all variables with  $P > 0.5$  were removed from the model, and the reduced models were re-run in a final analysis. All *P* values from this second analysis are presented in Table 1. Unless stated otherwise, all results are presented as mean  $\pm$  S.E.M.

## Results

A detailed description of the spatial and temporal patterns of suction flow in bluegill is presented elsewhere (Day et al., 2005). In almost all feeding events, regardless of ram speed, the bluegill decelerated during prey capture and stopped shortly after the time of peak gape (Fig. 4). As the mouth started opening, fluid movement was initiated and continued as long as the mouth of the fish was open (Fig. 4).

The average time to peak gape was  $32.0 \pm 2.1$  ms, with a range of 12.0 to 58.0 ms, and the average ram speed at the time of maximum gape was  $8.4 \pm 0.8$  cm s<sup>-1</sup> with a range of 0 to 24.6 cm s<sup>-1</sup>. Higher values of *TTPG* resulted in significantly lower values of  $AFS_{1/2 PG}$  (Table 1; Fig. 5A). Even when as high as 25 cm s<sup>-1</sup>, ram speed did not significantly affect  $AFS_{1/2 PG}$  (Table 1, Figs 4, 5B). Maximum fluid speed typically slightly preceded maximum gape or coincided with it (Fig. 4). The average  $AFS_{1/2 PG}$  for all trials ( $N=41$ ) was  $30.0 \pm 2.2$  cm s<sup>-1</sup> with a range of 14.1 to 67.7 cm s<sup>-1</sup>.

Water was drawn into the mouth from every direction for bluegill feeding without ram (Fig. 2A). As ram speed

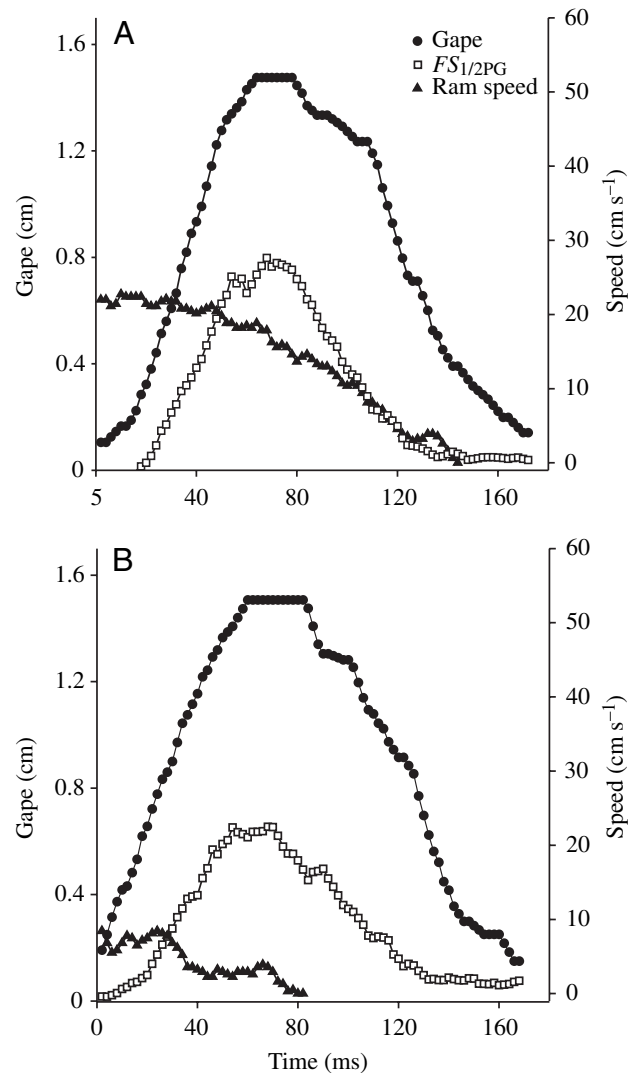


Fig. 4. Representative sequences from a high ram case (A;  $RS/AFS_{aperture}=19\%$ ) and a low ram case (B;  $RS/AFS_{aperture}=3\%$ ) showing the similarity in timing of events. Note that maximum suction speed coincided with peak gape or slightly preceded it. *RS*, ram speed; *AFS*, fluid speed.

increased, the water being drawn into the mouth was more focused in front of the mouth (higher DF values) at the time of maximum gape (Table 1; Figs 2B,C and 6). This effect was considerable; for example, there was more than a twofold increase in the degree of focusing with an increase in ram speed from 2 cm s<sup>-1</sup> to 10 cm s<sup>-1</sup> (Figs 2, 6).

As ram speed increased, the height-to-length ratio of the ingested volume of water decreased significantly, indicating that a more elongated volume of fluid was captured (Table 1, Figs 3, 7). While we only quantified the dimensions of the water parcel that entered the mouth during the strike, water outside this boundary was also moved by the suction.

## Discussion

Our study empirically quantified the effects of ram speed on

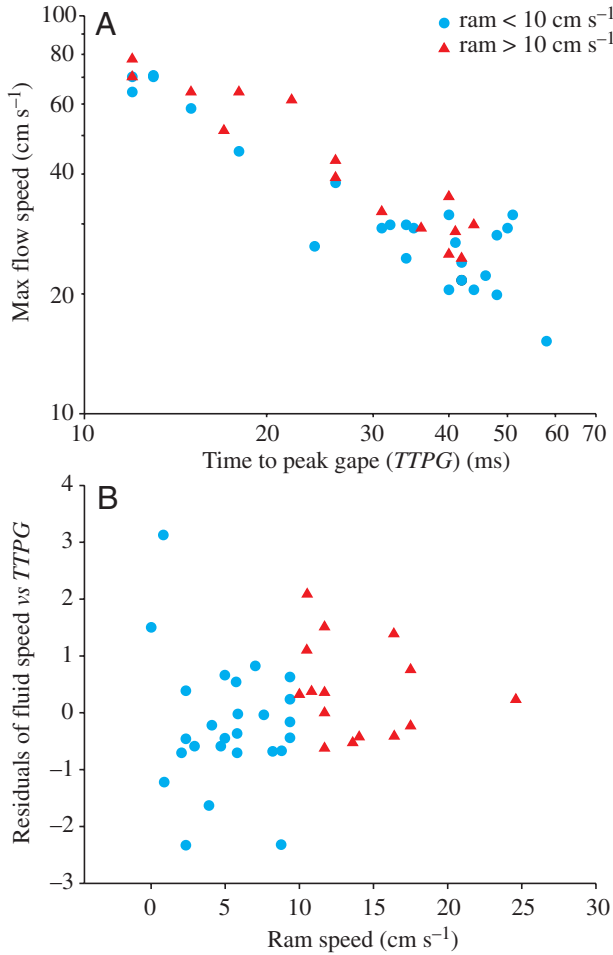


Fig. 5. (A) Time to peak gape ( $TPPG$ ) vs  $AFS_{1/2 PG}$  for all trials separated into ram speeds below and above  $10 \text{ cm s}^{-1}$ . (B) Residuals from the regression of maximum suction speed and  $TPPG$  vs ram speed. There was a significant effect of  $TPPG$ , but not ram speed, on maximum flow speed.

the flow speed ( $AFS_{1/2 PG}$ ), the degree of focusing (DF), and the shape of the ingested volume of water during suction feeding in bluegill sunfish. An increase in ram speed did not affect  $AFS_{1/2 PG}$ , but substantially increased DF and altered the shape of the ingested volume of water.

#### Swimming and suction performance

In contrast to our expectation, bluegill sunfish did not forfeit suction fluid speed when using forward swimming during feeding. Overall body closing speed was therefore enhanced by incorporating both suction and ram. For a bluegill using relatively high amounts of suction, the effect of moderate increases in ram speed is additive and results in increasing closing speed of the predator. This insensitivity of suction speed to moderate amounts of ram has not previously been recognized or predicted (Muller and Osse, 1984; van Leeuwen, 1984), and we suggest that it may be biologically significant for suction feeding predators, like bluegill and many other species, that feed on prey that have some capacity to escape

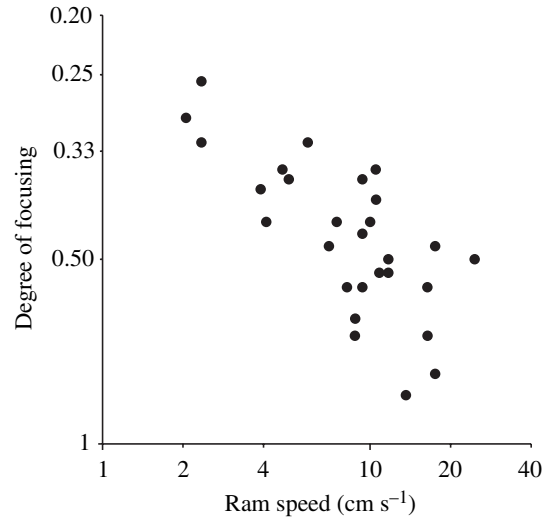


Fig. 6. Ram speed vs degree of focusing (DF) of water entering the mouth (log-log plot). Note that values of DF for ram speeds equal to  $0 \text{ cm s}^{-1}$  are not shown because they are equal to infinity.  $r^2=0.81$ ,  $P<0.05$ .

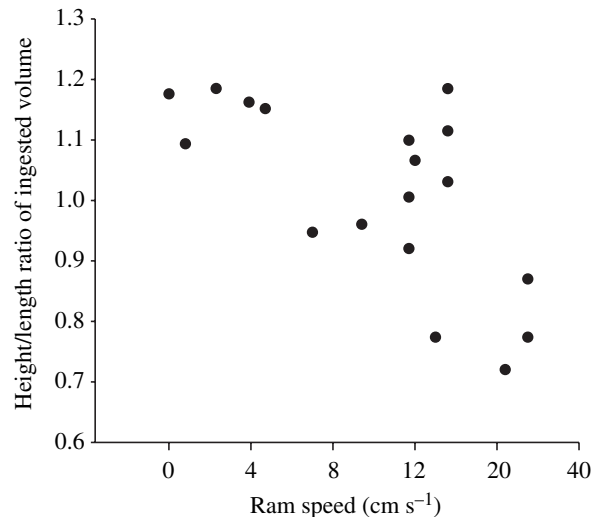


Fig. 7. The relationship between ram speed and the shape of the ingested volume of water. Only feedings using worm as prey are shown. Points with lower values of height/length ratio have a more elongated, narrow shape of ingested water.  $r^2=0.44$ ,  $P<0.05$ .

suction flows. Thus, there was no apparent hydrodynamic trade-off between ram and peak fluid speed over the range of values observed in this study.

In feeding bluegill the fluid speed generated during suction decays rapidly with distance from the mouth aperture such that  $AFS_{1/2 PG}$  is approximately 25% of that at the mouth aperture ( $AFS_{\text{aperture}}$ ) (Fig. 8; Day et al., 2005). Using this proportionality, we can estimate  $AFS_{\text{aperture}}$  using our measurements of  $AFS_{1/2 PG}$ . We find that the ram speeds were approximately 0–20% of maximum  $AFS_{\text{aperture}}$ . For a hypothetical  $AFS_{\text{aperture}}$  of  $100 \text{ cm s}^{-1}$ , a ram speed of  $20 \text{ cm s}^{-1}$  would reduce  $AFS_{\text{aperture}}$  to  $80 \text{ cm s}^{-1}$  in the absolute frame of

reference. This 20% decrement in fluid speed should then apply to all positions from the fish's mouth because the scaled shape of the relationship between flow speed and distance is uniform across the range of fluid speeds and ram speeds observed in our study (Day et al., 2005). If  $AFS_{1/2 PG}$  is 25% of  $AFS_{aperture}$ , a ram speed of  $20 \text{ cm s}^{-1}$  would reduce  $AFS_{1/2 PG}$  by  $5 \text{ cm s}^{-1}$ . However, body closing speed, or the speed that the predator and prey are moving towards each other, would actually be predicted to increase from  $25 \text{ cm s}^{-1}$  (only suction) to  $40 \text{ cm s}^{-1}$  ( $20 \text{ cm s}^{-1}$  of ram +  $AFS_{1/2 PG}$  of  $20 \text{ cm s}^{-1}$ ). Since the ratio  $RS/AFS_{aperture}$  was commonly less than 10% (27 of 41), the expected decrease ( $<3 \text{ cm s}^{-1}$ ) in  $AFS_{1/2 PG}$  is not as great as subtracting the complete ram speed. Thus, like fluid speed, the effect of ram speed decays rapidly with distance away from the mouth. Nevertheless, we did not see any tendency for ram speed to reduce suction speed (Fig. 5).

Since mechanical arguments all suggest that ram speed should negatively affect suction speed, one possible explanation for the lack of an effect in our study is that bluegill modulated some unmeasured aspect of buccal expansion to compensate for the effects of ram. Given that time to peak gape

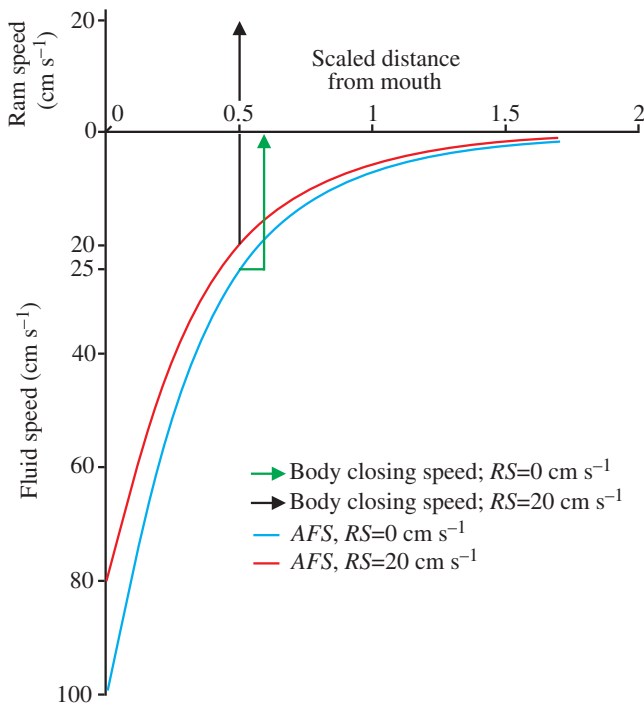


Fig. 8. The relationship between fluid speed  $AFS$  and distance from the mouth aperture (scaled to maximum mouth diameter) and the predicted effects of ram speed  $RS$  ( $RS/AFS_{aperture}=20\%$  in this case) on this relationship. The blue line represents  $AFS$  for a stationary fish and the red line  $AFS$  for a fish with a  $RS$  of  $20 \text{ cm s}^{-1}$ . Note that  $RS$  has a much greater effect on  $AFS_{aperture}$  than  $AFS_{1/2 PG}$ . The length of the green arrow represents the magnitude of body closing speed of a stationary fish ( $25 \text{ cm s}^{-1}$ ) and the length of the black arrow represents the magnitude of body closing speed of a fish with a  $RS$  of  $20 \text{ cm s}^{-1}$  ( $40 \text{ cm s}^{-1}$ ). Note that overall body closing speed is increased with moderate levels of  $RS$ . The relationship between fluid speed and distance from the mouth is from Day et al. (2005).

statistically explains 87% of the variation in fluid speed among feeding events in bluegill sunfish (Day et al. 2005), other forms of kinematic modulation likely exist. For example, the timing and magnitude of opercular expansion is thought to be decoupled from buccal expansion in some species (Norton and Brainerd, 1993). Future studies that measure the movements of several anatomical features (e.g. operculum, hyoid, suspensorium) at the same time as fluid flow will provide further insight into the mechanism for modulating the speed of fluid entering the buccal cavity.

Bluegill sunfish exhibit fine temporal control of their velocity prior to, and during, prey capture (T. E. Higham, B. Malas, B. C. Jayne and G. V. Lauder, manuscript submitted for publication). For example, in a laboratory setting bluegill decelerate to approximately 30% of their maximum approach speed at the time of prey capture, and then maximally decelerate until stopping (T. E. Higham, B. Malas, B. C. Jayne and G. V. Lauder, manuscript submitted for publication). One benefit of decelerating to 30% of the maximum approach speed could be to lower the ram speed-to-fluid speed ratio ( $RS/AFS_{aperture}$ ) to between 0–20%, since it is possible that larger ratios have a negative effect on suction performance. Two potential strategies that high performance suction feeders can employ to achieve a low  $RS/AFS_{aperture}$  include decelerating prior to prey capture or maintaining a low ram speed throughout the predator–prey interaction. The question of whether predators that rely predominantly on suction always exhibit a low  $RS/AFS_{aperture}$  ratio requires further investigation.

#### Degree of focusing

In our study, the degree of focusing (DF) during suction feeding increased with an increase in ram speed (Figs 2, 6). Focusing the flow of water enables the predator to draw water from in front of its mouth where the prey is positioned rather than drawing water from a wider space around the fish's head. The largest gain in DF seems to occur when values of  $RS/AFS_{aperture}$  are between 2 and 10%, whereas there is less of an increase in DF for values between 10 and 20%. At very high values of  $RS/AFS_{aperture}$ , the degree of focusing would approach 1, where the distance between streamlines is equal to the diameter of the mouth at maximum gape. Thus, increases in DF might become increasingly subtle as ram speed approaches suction speed.

By increasing DF, the accuracy required to capture a prey item also increases. Thus, swimming slowly, or slowing down prior to feeding, might enable the fish to maintain accuracy (more time for steering and positioning) and not forfeit suction performance. Decelerating prior to prey capture has been suggested as a way to increase accuracy during feeding (T. E. Higham, B. Malas, B. C. Jayne and G. V. Lauder, manuscript submitted for publication; Lauder and Drucker, 2004), but our observations provide a hydrodynamic basis for how braking can increase accuracy.

#### Shape of ingested water volume

When bluegill sunfish attacked the prey item at a high

velocity, they ingested a more elongated volume of water (Fig. 3). In the example shown in Fig. 3, the length of the ingested water along the  $x$ -axis is 50% greater in the case with high ram ( $17.5 \text{ cm s}^{-1}$ ) than in the case with no ram ( $0 \text{ cm s}^{-1}$ ). The shape of the ingested fluid volume is likely to be an important factor in determining whether a prey item is captured. For example, by extending the distance from the mouth that water is ingested, a predator might be able to limit the ability of the prey to escape.

With an increase in ram speed, the more elongate parcel of ingested water enables the bluegill to capture more fluid from the space in front of the mouth, corroborating several modeling studies (Weihs, 1980; van Leeuwen, 1984; de Jong et al., 1987; Drost et al., 1988). Drost et al. (1988) used a model to predict the shape of the ingested volume of water by suction-feeding carp larva swimming at  $3.5 \text{ cm s}^{-1}$ . Although all of the water drawn into the mouth originated from in front of the carp larva, the shape of the ingested volume of water is notably different from that of bluegill. For example, the maximum vertical height of the ingested volume in bluegill is typically centered (Fig. 3) while the volume ingested by the carp was predicted to be 'trumpet' shaped with the maximum vertical height occurring distally to the central axis (fig. 5 in Drost et al., 1988). We never observed this shape in bluegill feeding events. In another modeling study, de Jong et al. (1987) determined that the shape of the ingested volume of water would become more elongated as swimming speed increased, and our results confirm this. Additionally, the overall shape of the ingested volume of water predicted in the study by de Jong et al. (1987) more closely resembled the shapes that we observed.

Weihs (1980) developed a term that was the ratio of ingestion distance directly forward to that in the orthogonal direction, and predicted that it would increase with greater ram speed, and our results support this. Weihs (1980) also suggests that with increased swimming speed, a fish can minimize the amount of wasted ingested volume and thus maximize their efficiency. Another implication of narrowing and elongating the ingested volume of water is that the predator must increase attack accuracy as the region of influence in front of the predator will become more focused (Drost et al., 1988). Thus, it is likely that a trade-off exists between accuracy and efficiency in high-performance suction-feeding fish.

The hydrodynamic interactions between suction and ram are complex and it seems that, depending on their morphology and ecology, fish can modulate their ram speed in order to achieve a balance between the several interrelated factors that result from changes in ram speed. For example, bluegill sunfish have relatively small mouths and thus accuracy may be a relatively important factor. Moderate to low ram speeds increase their closing speed without forfeiting peak fluid speed, but a relatively low ram speed allows them to maintain accuracy (lower degree of focusing). Additionally, their efficiency increases with a moderate amount of ram speed by ingesting a narrower volume of water where the prey is located.

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