Zoology **106** (2003): 159–168

http://www.urbanfischer.de/journals/zoology

ZOOLOGY

Quantification of flow during suction feeding in bluegill sunfish

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Received December 10, 2002 · Accepted April 27, 2003

Summary

Nearly all aquatic-feeding vertebrates use some amount of suction to capture prey items. Suction prey capture occurs by accelerating a volume of water into the mouth and taking a prey item along with it. Yet, until recently, we lacked the necessary techniques and analytical tools to quantify the flow regime generated by feeding fish. We used a new approach; Digital Particle Image Velocimetery (DPIV) to measure several attributes of the flow generated by feeding bluegill sunfish. We found that the temporal pattern of flow was notably compressed during prey capture. Flow velocity increased rapidly to its peak within 20 ms of the onset of the strike, and this peak corresponded to the time that the prey entered the mouth during capture. The rapid acceleration and deceleration of water suggests that timing is critical for the predator in positioning itself relative to the prey so that it can be drawn into the mouth along with the water. We also found that the volume of water affected by suction was spatially limited. Only rarely did we measure significant flow beyond 1.75 cm of the mouth aperture (in 20 cm fish), further emphasizing the importance of mechanisms, like locomotion, that place the fish mouth in close proximity to the prey. We found that the highest flows towards the mouth along the fish midline were generated not immediately in front of the open mouth, but approximately 0.5 cm anterior to the mouth opening. Away from the midline the peak in flow was closer to the mouth. We propose that this pattern indicates the presence of a bow wave created by the locomotor efforts of the fish. In this scheme, the bow wave acts antagonistically to the flow of water generated by suction, the net effect being to push the region of peak flow away from the open mouth. The peak was located farther from the mouth opening in strikes accompanied by faster locomotion, suggesting faster fish created larger bow waves.

Key words: suction feeding, pressure wave, bow wave, flow, water velocity, DPIV

Introduction

Suction feeding is by far the most commonly used mechanism of prey capture by aquatic vertebrates (Lauder, 1985; Liem, 1980; Liem, 1990). A large body of literature has been produced with the central goal being to understand the musculo-skeletal functional morphology of suction feeding (Aerts and De Vree, 1993; Aerts and Verraes, 1987; Alfaro et al., 2001; Anker, 1978; Ferry-Graham and Lauder, 2001; Grubich and Wainwright, 1997; Lauder, 1980b; Lauder, 1983; Liem, 1993; Motta, 1982; Motta, 1988; Sanford and Wainwright, 2002). A smaller, mostly theoretical, literature focuses on the mechanics that characterize the flow of water that is generated (Alexander, 1967; Lauder, 1980a; Muller et al., 1982; Muller and Osse, 1984; Osse and Muller, 1980; van Leeuwen, 1984; van Leeuwen and Muller, 1984; Weihs, 1980). In spite of these efforts, empirical observations have been hampered by the difficulty in visualizing and quantifying water motion, and thus our understanding of several key issues remains elusive. In particular, we lack a comprehensive temporal and spatial picture of the pattern of flow that is generated by a suction feeder.

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0944-2006/03/106/02-159 $ 15.00/0

Understanding this flow pattern is important because the critical event during suction feeding is the interaction between the prey and the suction flow. Thus, we would like to know when the maximum flow velocities are generated as a result of suction production. How far in front of the mouth does a suction feeder effect suction flow? Further, where in the flow field is velocity highest, and how rapidly does water velocity decay with distance from this peak? Some of these questions have been addressed by models (Muller et al., 1982; van Leeuwen, 1984), but, as indicated previously, attempts to validate these models have been technologically limited to largely qualitative observations (Lauder and Clark, 1984; van Leeuwen, 1984).

It is well documented that fishes usually combine forward body motion with suction when attacking prey (i.e., ram and suction) and the relative use of these behaviors has been identified as a major axis of diversity in fish feeding systems (Norton and Brainerd, 1993; Wainwright et al., 2001). The body of the swimming fish will push a wave of water in front of it that has a maximum velocity equal to the swimming speed of the fish, but which slows with distance from the fish (Muller and Osse, 1984; van Leeuwen, 1984). In theory, this bow wave will partially cancel the suction-induced flow (in the prey's frame of reference) and must be overcome by the suction flow in order for a net movement of water toward the predator to occur. In practice the effect of this bow wave on suction flow has never been documented, although the role of "compensatory suction" has received increasing attention in the literature (Summers et al., 1998; van Damme and Aerts, 1997). The impact of the bow wave on suction will depend on the relative magnitude of the two flows. Disentangling these two flows during visualization studies is difficult because only the resultant of the two flows can be visualized. Here we attempt to infer the effect of the bow wave by making observations on strikes that vary in attack speed of the predator, and thus the magnitude of the bow wave that is generated.

In this study, we used Digital Particle Image Velocimetery (DPIV) to quantify patterns of water flow generated by suction feeding bluegill sunfish. The application of modern flow visualization techniques and computer-aided analysis has allowed us to measure several attributes of the suction flow that have not previously been quantified. In this paper we address four specific questions. (1) What is the temporal pattern of flow velocity entering the mouth with respect to major kinematic events during suction feeding? (2) At the time of peak flow, what is the spatial pattern of water velocity along a midline transect projecting from the open mouth? (3) At the time of peak flow, what is the spatial pattern of water velocity in the horizontal plane? (4) What is the effect of the larger bow wave produced during strikes with higher attack speed on the pattern of flow along the midline transect?

Materials and methods

We used DPIV to visualize water flow patterns created by four size-matched bluegill sunfish (*Lepomis macrochirus*, mean total length 20 cm) to quantify gen-

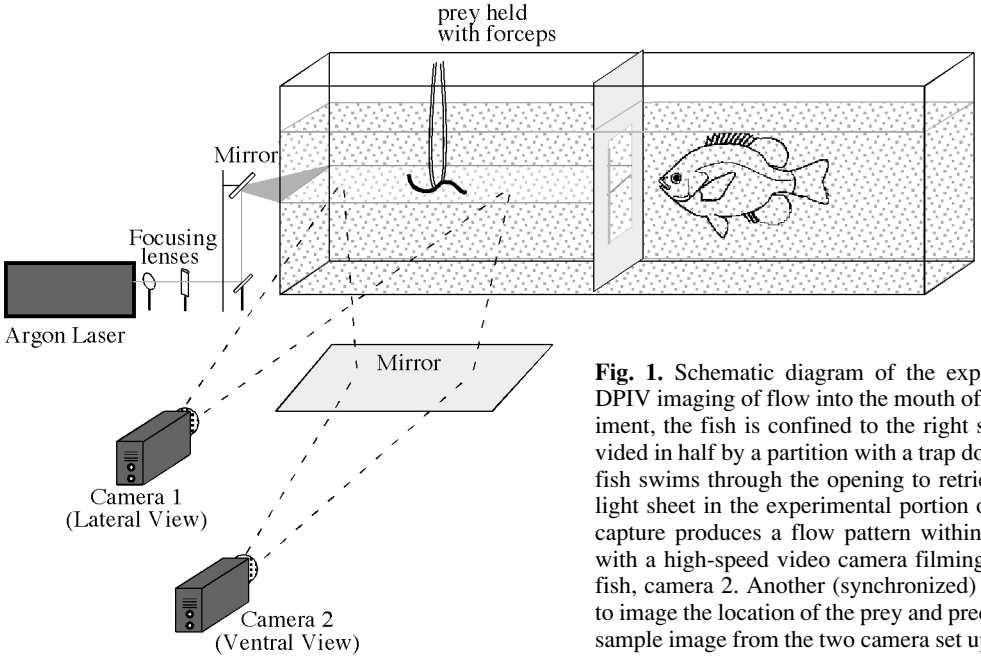


Fig. 1. Schematic diagram of the experimental arrangement used for DPIV imaging of flow into the mouth of bluegill sunfish. For each experiment, the fish is confined to the right side of an aquarium which is divided in half by a partition with a trap door. When the door is opened, the fish swims through the opening to retrieve a prey item held in the laser light sheet in the experimental portion of the aquarium on the left. Prey capture produces a flow pattern within the light sheet that is recorded with a high-speed video camera filming the ventral view of the feeding fish, camera 2. Another (synchronized) video camera, camera 1, is used to image the location of the prey and predator relative to the light sheet. A sample image from the two camera set up is shown in Figure 2.

eral flow parameters in the earth-bound frame of reference during prey capture (see also Ferry-Graham and Lauder, 2001). The prey used was 1–2 cm segments of earthworm (*Lumbricus* sp.). Each fish was placed into an experimental aquarium measuring 30 × 76 × 20 cm (Fig. 1). The water in the aquarium was seeded with 12 mm silver-coated glass beads at a density of 1.3 g cm^{-3}, and a 5 W argon-ion laser was used to create a horizontal planar light sheet following the methods described in (Drucker and Lauder, 1999). The plane of light was created by directing the laser beam through a series of focusing lenses that acted to spread the beam into a sheet of light approximately 10 cm wide and 0.1 cm thick. Mirrors placed at 45-degree angles served to direct the light sheet through the center of the experimental aquarium.

To ensure that the bluegill fed within the illuminated sheet, it was necessary to constrain the position of both the prey and the predator without actually interfering with the feeding event. Forceps were used to lightly hold the prey within the light sheet. To position the predator, a sliding trap-door was placed in the center of the aquarium dividing it into two chambers; a holding area and an experimental arena. Bluegill were trained to swim into the experimental arena by opening the door and offering food held on forceps in the center of the arena. All bluegill appeared to rapidly associate the raising of the door with the potential for food, and would readily swim through the open door regardless of whether or not the laser light sheet was illuminated. The trap door served to passively direct fish into the center of the light sheet where the prey was held.

Flow patterns within the light sheet were quantified by imaging the laser light reflected off the silver-coated glass beads with two synchronized NAC high-speed video cameras filming at 250 Hz with the shutter in the open position (Fig. 1). One camera was used to capture a ventral view of the feeding fish and surrounding water, and allowed for visualization of glass particle movement within the light sheet during the strike. A rule placed in the flow in this view was also filmed prior to feeding events for calibrating the measurements estimated from particle movement. The second camera was zoomed out relative to the first, and focused on a lateral view of the feeding fish to verify position and orientation within the light sheet. Images were combined on a split screen. Feeding sequences were analyzed if the predator and prey remained visible throughout the strike, remained perpendicular to the camera, and the laser light sheet intercepted the head at the midline. Four prey capture sequences from each of the four fish were subsequently analyzed.

From these sequences, we conducted a temporal analysis of flow during the strike. The flow of water around the mouth and jaws was quantified by downloading image pairs. Image pairs consisted of a given image and the image that followed it in time on the high-speed video tape (Δt = 4 ms). We viewed the entire strike sequence and collected image pairs corresponding with the following well-defined kinematic stages of the gape cycle: the onset of mouth opening (time zero), prey capture (when the prey item crossed the plane of the open mouth), peak gape (typically after prey capture), peak opercular expansion (when detectable), and mouth closure (the jaws were sometimes closed on the prey in a bite). Intervals just prior to mouth opening and immediately after mouth closure were also analyzed. The timing of strikes was remarkably consistent within and among individuals such that image pairs were separated by 20 ms intervals in all cases. This facilitated the estimation of means at each time interval (note that in this species prey capture is not particularly rapid; this resolution provided sufficient detail for inferring flow patterns throughout the gape cycle). Image pairs were analyzed using two-frame cross-correlation over a consistent 15 × 15 grid using the computer software Insight (v. 3.0, TSI Inc., St. Paul, MN). A two-dimensional array of vector profiles was generated corresponding to an area roughly 6–8 cm on a side and consisting of 225 uniformly distributed vectors (Fig. 2). The length of any vector represents the average magnitude of the velocity of the water within that grid space. Vectors were validated with a dynamic mean value algorithm (TSI Incorporated) and also visually validated. Vectors that grossly and obviously misrepresented the flow of water were deleted. Such errors typically occurred at the margins of the data field or on the fish body where laser light tended to be intensely reflected. In addition, vectors on the fish body were ignored for this analysis as they represented fish locomotion rather than water flow. Gaps in the vector flow field were filled by interpolation using a least squares estimate from neighboring particles in a 3 × 3 grid. From this mean flow data we extracted the maximum water speed in front of the fish. Maximum water speed, or velocity, was estimated by taking the value of the single largest vector directed towards the fish from the vector profile calculated at each time interval for each sequence. This parameter was simply used to approximate performance over time during prey capture. The peak value for maximum water velocity was extracted from each time series as an indication of the time of maximal performance during the prey capture event.

Velocity data from this analysis was further explored using regression analyses (SPSS 10 for Macintosh) to better understand patterns of increase or decrease in flow with the independent variable of time throughout the strike. Three separate models were fit to the data: linear, quadratic, and cubic. These three models should encompass all of the possible shape changes that we

might see in curves fit to our data. Adjusted R^2 values, which account for the extra explanatory power due solely to the addition of extra variables into the model, were used to determine model fit. Models were fit to average data (n = 16) as we were not interested in intra-strike variation among individuals.

We used the images from time of maximal performance for each strike to conduct a fine-scale spatial analysis of flow around the head of the feeding fish. We systematically analyzed discrete regions on and around the head of the fish by tracking both the fish and individual particles in the water from frame to frame during this 4 ms interval. This region of interest is at least partially within the region influenced by motion of the fish head, an area that cannot be accurately analyzed using a standard particle image velocimetry approach to computing velocity vectors (Nauen and Lauder, 2001). Using NIH Image 1b particles were digitized by hand at the margin of the fish, and then at 0.25 cm increments away from the fish for a minimum of 1.5 cm. Particles were easily identified from one frame to the next as they typically overlapped in position and often had subtle but distinguishing characteristics. This pattern was repeated along five transects in front of the fish: at the midline of the fish, 30º on either side of the midline (30° clockwise and 30° counter-clockwise), and again at 60º either side of the midline (60° clockwise and 60° counter-clockwise), for a total of at least 35 particles for each frame analyzed (Fig. 1). Transects were effectively ±1 mm in width. As described above, we used regression analysis to determine how flow patterns were affected by the independent variable of distance from the mouth opening

Finally, to relate these data to the behavior of the fish, we quantified both ram distance and average strike velocity. Ram distance (*sensu* Wainwright et al., 2001) is the distance moved by the predator during the strike, defined as the period starting with the onset of mouth opening (time zero) and ending with prey capture (when the prey crosses the plane of the open mouth). Movement of the predator was determined by digitizing a point on the tip of the lower jaw in the ventral view and measuring the displacement of that point over the duration of the strike in the earth-bound frame of reference. Our measure of ram distance includes any forward locomotory component of the strike as well as any contribution of lower jaw movement towards the prey item that occurs as the lower jaw is abducted into the open position. Average strike velocity was calculated as ram distance divided by strike duration (time from the onset mouth opening until prey capture). Lastly, we also quantified suction distance as this measure is frequently reported by other studies purporting to quantify suction production. We used correlation analysis to determine the relationships between these variables and our flow variables.

Results

In the temporal sense peak water velocities were generated on average 20 ms into the strike (20 ms after the start of mouth opening) and were about 8 cm s^{-1} at this time (Fig. 3). This was the time corresponding with prey capture and just prior to peak gape. Average

Table 1: Regression models fit to average water velocity data for understanding patterns in flow over time during the strike, and with distance from the mouth at any one position at the time of maximum velocity generation.

Independent variable	Adjusted R^2 of model (model)		
	Linear	Quadratic	Cubic
Time	0 ($y = 3.4E^{-3}x + 2.4$)	0.58* ($y = -1.2E^{-3}x^2 + 0.1x + 2.4$)	0.46 ($y = 3.9E^{-6}x^3 - 0.002x^2 + 0.1x + 2.6$)
Distance from mouth (60° ccw)	0.65** ($y = -5.2x + 12.1$)	0.78** ($y = 5.4x^2 - 13.2x + 13.7$)	0.75 ($y = -5.0x^3 + 16.6x^2 - 19.5x + 14.2$)
Distance from mouth (30° ccw)	0.92**** ($y = -6.1x + 13.2$)	0.90*** ($y = -0.6x^2 - 5.1x + 13.0$)	0.91** ($y = -5.5x^3 + 11.8x^2 - 12.1x + 13.5$)
Distance from mouth (midline)	0.51** ($y = -8.0x + 17.8$)	0.76** ($y = -12.0x^2 + 10.0x + 14.1$)	0.94*** ($y = 21.8x^3 - 61.1x^2 + 37.3x + 12.0$)
Distance from mouth (30° cw)	0.75*** ($y = -5.8x + 13.6$)	0.79** ($y = -3.9x^2 + 0.1x + 12.3$)	0.93*** ($y = 12.3x^3 - 31.6x^2 + 15.5x + 11.2$)
Distance from mouth (60° cw)	0.86*** ($y = -.91x + 17.4$)	0.95*** ($y = 6.4x^2 - 18.7x + 19.4$)	0.97*** ($y = -7.5x^3 + 23.3x^2 - 28.1 + 20.1$)

* $p = 0.08$ (NS), ** $p < 0.05$, *** $p < 0.01$, **** $p < 0.001$

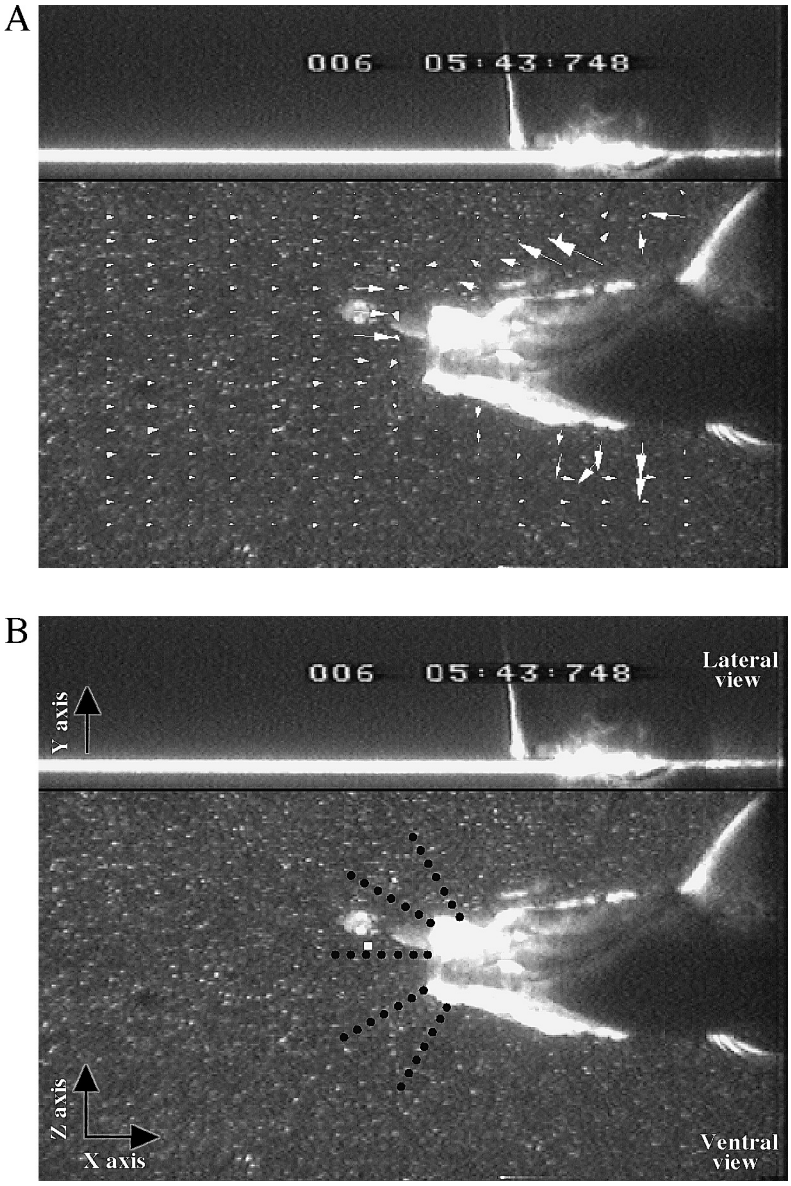


Fig. 2. Image from high speed video footage of a bluegill sunfish feeding on a worm piece held suspended by forceps within a horizontal laser light sheet. Each frame consists of a lateral and a ventral view, with real times shown (min:s:ms). The lateral view is to verify fish position relative to the laser light sheet and is not scaled equivalently to the ventral view. The ventral view is used for analysis of particle images and water flow patterns are calculated from these images. The water has been seeded with silver-coated glass beads (see text), the reflections of which can be seen in the ventral view. In **A**, vectors are shown that indicate the average magnitude of the water velocity in that area. Note that vectors on the fish body have been deleted, and that flow is averaged over relatively large areas of space. Water can be seen entering the mouth from both in front of and behind the head. This image is not the most dramatic example of flow being pulled from behind the open mouth (for more images see Ferry-Graham and Lauder, 2001); however, it was selected because it shows some of the finer scale patterns in water flow. Note that there are vectors oriented in both the + and - X directions immediately in front of the fish mouth. In **B**, the five spatial transects that were digitized to look at finer scale patterns in flow near the fish head are indicated.

mouth width at 20 ms was 1.96 cm (± 0.08 SE) and at peak gape it was 2.22 cm (± 0.10 SE). Some of the water entering the open mouth at this time was pulled from areas behind the mouth (see Fig. 2), but the largest flow vectors were always in the region in front of the open mouth in the area analyzed for this part of the study. A quadratic model fit to the flow data out-performed a linear model suggesting that the peak is an important component of the velocity generated over time (Table 1; $R^2 = 0.58$). Our more detailed spatial analysis of flow was therefore conducted at the 20 ms interval of the strike.

The five spatial transects revealed that flow in front of the mouth could reach higher velocities when quantified at smaller spatial scales than in the gross temporal analysis, with maxima on the fish midline transect averaging about 20 cm s^{-1} (Fig. 4). This flow was oriented towards the bluegill's mouth. Note that unlike the previous analysis, we did not decide *a priori* to measure flows only in the direction moving towards the fish mouth. The values determined here were based on tracking particles at certain positions in space, and could therefore potentially move in any direction in the horizontal plane. However, along each transect flow was consistently towards the open fish mouth. We rarely detected velocities imparted onto the water beyond 1.75 cm anterior to the open mouth, and in most cases flow was near zero within 1.5 cm of the plane of the open mouth for all flow profiles, both at and away from the midline.

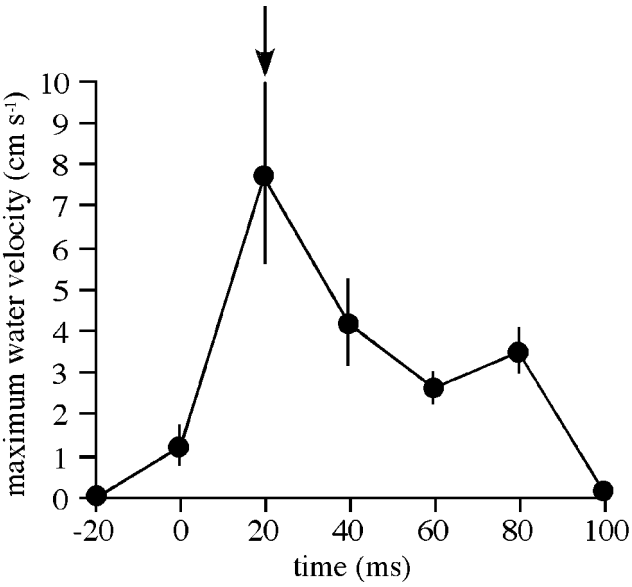


Fig. 3. Maximum flows generated in front of the mouth of the feeding bluegill at 20 ms intervals throughout the strike. The data shown indicate the velocity of the water flowing in a direction towards the fish mouth. Values are means of means for each individual (± SE). Notice that across all strikes the peak velocity was achieved at 20 ms into the strike, as indicated by the arrow, which typically corresponds to the time at which the prey begins to enter the mouth. Velocity is already much lower at the time of peak gape. Velocity was at or near zero 100 ms after mouth opening.

Velocity changed with distance from the open mouth (Fig. 4), and on the fish midline transect the highest water velocities were found 0.5 cm away from the open mouth (Fig. 4C). For the profiles away from the midline, maximum water velocities were found at or near the fish mouth (Fig. 4). Regression analyses further suggested that velocity did not decrease linearly with distance from the mouth at the midline of the fish. A highly significant cubic function best fit the data at the midline ($R^2 = 0.94$; Table 1). Away from the midline, linear regression generally did a better job of describing the change in velocity with distance from the mouth (Table 1), however, cubic or quadratic functions still performed well and occasionally outperformed the linear model. For example, the small velocity peak positioned at 0.25 cm from the mouth opening in Figure 4D suggests an asymmetry to the strike in these bluegill, with the jaws being protruded consistently to the right instead of directly anteriorly. Visual analyses confirmed this slight asymmetry in the direction of protrusion, and the regression analyses performed well at detecting differences in the flow patterns generated. The peak in water velocity located away from the mouth opening caused the cubic regression model to perform best for data measured at the midline and at position 30° clockwise (to the right of center). The equation for the midline, however, suggests a steeper transition from the velocity at the mouth opening to that at the peak (Table 1). Peak water velocity appeared to be affected by the behavior of the predator. Among strikes ram distance ranged from 0.34 cm to 0.95 cm. Accordingly, strike velocities ranged from approximately 17 to 47 cm s^{-1}, and averaged 29 cm s^{-1}, about five times greater than the peak water speed measured in the temporal analysis (Fig. 3) and only about 1.5 times greater than the peak water speed measured in the spatial analysis (Fig. 4C). Flow profiles from feedings with higher strike velocities showed peaks in water velocity that were farther away from the open mouth (Fig. 5). Across all feeding events, strike velocity was significantly correlated with the distance from the open mouth of the peak in water velocity ($r = 0.57$, $p = 0.02$; note that ram distance was also significantly correlated with distance from the open mouth of the peak in water speed as strike duration was nearly constant). However, despite the apparent trend visible in Figure 5, strike velocity was not significantly correlated with the actual magnitude of peak water velocity ($r = 0.09$, $p = 0.76$). Suction distance was not correlated with distance from the open mouth of the peak in water velocity ($r = –0.25$, $p = 0.37$), but was significantly negatively correlated with the magnitude of peak water velocity ($r = –0.59$, $p = 0.02$). This correlation did not hold when maximum water velocities extracted from our gross temporal analysis were used instead of those from the finer-scale spatial analysis ($r = –0.23$, $p = 0.43$).

Discussion

The use of DPIV allowed us to visualize the flow field that bluegill generated in the volume of water anterior to their mouth during suction feeding. This flow field was dynamic in time and space and was influenced by the attack velocity of the fish. Below, we focus on key results of our study and their implications for the understanding of suction feeding. First, peak suction velocities were achieved about 20 ms from the beginning of the strike, prior to the time when peak gape distance was reached and at or near the time when the prey entered the mouth. Second, suction feeding bluegill only influenced water in the immediate vicinity of their mouth, as water velocity usually fell to zero within 1.5 cm from the mouth. Third, flow varied in a non-linear fashion spatially and peak water velocity occurred 0.5 cm away from the mouth aperture, not at positions closest to the mouth. Fourth, the distance from the mouth that peak water velocity occurred was positively correlated with attack velocity of the fish. We interpret the third and fourth findings, in particular, as demonstrating the presence of a pressure wave or "bow wave" in front of the feeding fish.

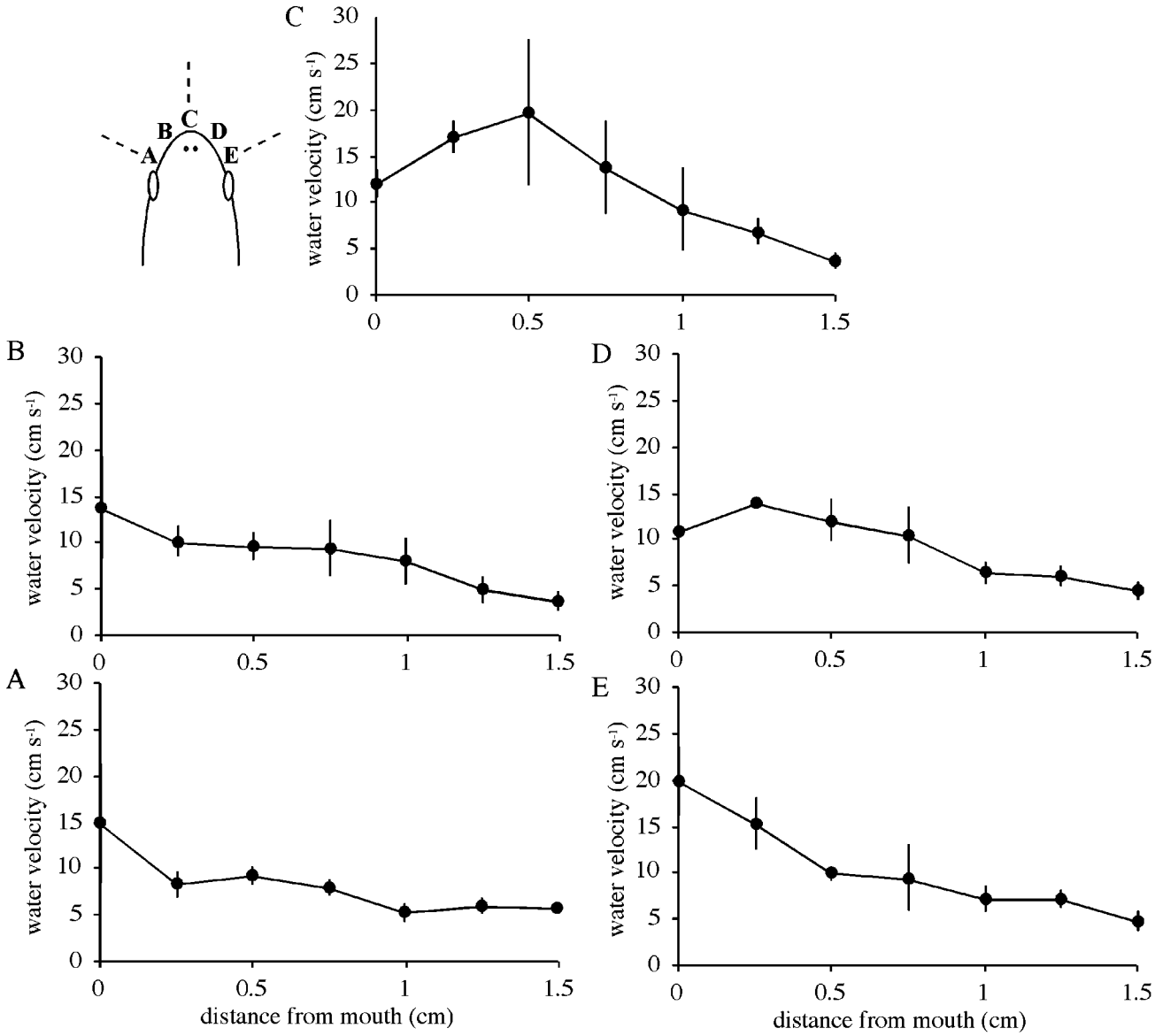
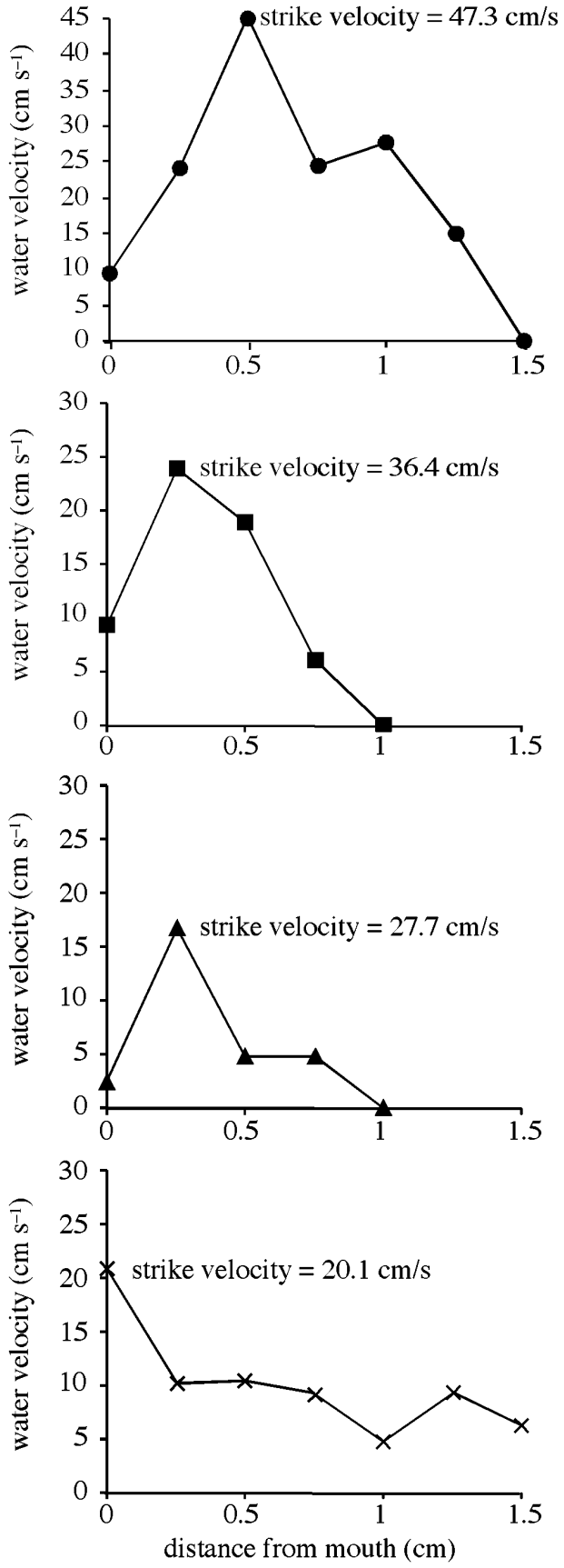


Fig. 4. Water velocities generated at 0.25 cm intervals from the bluegill's mouth. Velocities for each of the five spatial transects are shown in **A–E**, and correspond to the positions around the fish head as indicated in the key. The data are presented such that flow towards the bluegill's mouth has a positive value and flow away from the bluegill's mouth has a negative value at any position in space. Values are means of means for each individual (± SE). Notice that the net flow was towards the bluegill's mouth for all positions in space at this time (20 ms into the strike).

The temporal distribution of suction flow

The temporal pattern of flow was notably compressed during prey capture. Water velocity increased rapidly to its peak within 20 ms of the onset of the strike and quickly fell to about 50% of peak in another 20 ms (Fig. 3). The peak in velocity corresponded with the time of prey capture (see also Lauder and Clark, 1984). Suction feeders capture prey by drawing them into their mouth (or at least holding them still) with the flow of water that they generate. It appears that in order for bluegill to capitalize on peak flow rates for prey capture they must time their position relative to the prey such that the crucial interaction between the suction flow and the prey occurs during a brief window of a few milliseconds when flow rates are at, or near, their peak.

Suction feeders can exert two forces on prey with the flow of water that they generate. Drag will be propor-



tional to the square of water velocity surrounding the prey and the acceleration reaction will be directly proportional to the acceleration of the fluid relative to the motion of the prey (Denny, 1993). An important goal in future research will be to estimate and measure the relative contributions of these forces on the prey of suction feeders. Considering only drag, the expectation would be that forces peak at the time when water velocity is at its peak, in our study at about 20 ms into the strike. Acceleration will be highest prior to peak velocity and falls to zero as velocity peaks. Thus, while forces due to drag will reach their maximum when water velocity is at its highest, the contribution of acceleration reaction will be strongest at an earlier time, sometime between the onset of the strike and peak water velocity. It is therefore possible that maximum net forces occur prior to the time of peak water velocity.

Spatial distribution of suction flow

Not only was the generation of velocity temporally compressed, but the volume of water affected was quite small. Only rarely did we measure significant water velocity beyond 1.75 cm away from the mouth aperture. The average mouth diameter of the four bluegill in the study at the time of peak water velocity was 1.96 cm, indicating that suction flow did not even reach a full mouth diameter in front of the fish. Furthermore, within this restricted volume of water, velocity dropped rapidly with distance from the mouth (Figs 4 and 5). The restricted reach of suction flow (see also Lauder and Clark, 1984) and the rapid decline in suction velocity with distance from the mouth were both predicted by a quasi-steady model of fluid flow during suction feeding (Muller et al., 1982).

These results have major implications for the biology of suction feeding. The restricted distance over which suction feeders generate significant flow further emphasizes the importance of behaviors and mechanisms that permit predators to move the mouth into close proximity of the prey during the strike. The use of forward swimming during the attack is only one such mechanism. Jaw protrusion, a phenomenon that has evolved many times in teleost fishes (Alexander, 1967; Motta, 1984), is another mechanism that may quickly move the mouth opening within the critical proximity

Fig. 5. Water velocities generated at the midline of the fish for four strikes varying in predator effort. Effort is measured in this sense by fish attack velocity. Attack velocities are indicated in each profile. Ram distance for each profile is 0.95 cm, 0.73 cm, 0.56 cm, and 0.40 cm respectively. Note that strikes with higher attack velocities tended have peak water velocities farther from the mouth at point this time (20 ms into the strike).

of the prey (Ferry-Graham et al., 2001a; Ferry-Graham et al., 2001b; Waltzek and Wainwright, 2000).

Our fine-scale spatial analysis also revealed that the highest velocities towards the mouth were generated not immediately in front of the open mouth, but approximately 0.5 cm anterior to the mouth opening. We propose that this pattern is indicative of the presence of a pressure wave, a phenomenon resulting from the locomotion of the fish towards the prey (Muller and Osse, 1984; Osse and Muller, 1980). If suction into the buccal cavity were the only factor generating flow in this system, it is expected that the peak in water velocity would be located at the mouth opening (Muller et al., 1982). Depressed water velocity in the region nearest the mouth therefore suggests the presence of a phenomenon that is acting antagonistically to suction flow. A pressure wave would have the effect of pushing water in the same direction as the swimming fish, creating a 'bow wave'. The bow wave and suction represent flows in opposite directions and would sum to produce the net flow that was measured in our experiments. Our point-by-point spatial analysis suggested that net flow was towards the fish head everywhere in each transect, implying that suction velocities were of a larger magnitude than the bow wave velocities at each position along these transects.

For the profiles away from the fish midline, peak water velocities are found closer to the fish mouth, suggesting that there is less of a pressure wave in these regions. The magnitude of the velocity peaks are also smaller in the profiles away from the fish midline. This is as we would expect given a build up of water immediately in front of the moving fish that is then directed around the sides of the fish where it tapers off. Lauder and Clark (1984) were also able to show that the velocity imparted onto the water was highest at the center of the gape relative to the velocity generated dorsal and ventral to the margins of the maximally enlarged gape. However water velocity anterior to the fish jaws was not quantified, so it is not known if the velocity measured right at the mouth opening was the maximum velocity generated in the entire flow field. A maximum away from the open mouth would not have been detected by their analysis. Further, their analysis was conducted at time of peak or maximally enlarged gape, which is slightly later than the time of maximal velocity generation in both studies. The balance between the bow wave and suction may be different given that prey capture had already occurred.

The effect of behavioral variables on flow patterns

The size and velocity of the bow wave are expected to increase with strike velocity (Muller and Osse, 1984). Both attack velocity and ram distance were positively correlated with the distance from the mouth at which water velocity peaked. One explanation for this pattern is that a larger bow wave was created by faster approaching bluegill and that this bow wave canceled more of the flow generated by suction, pushing the increasing the distance from the fish at which suction velocity was highest. Attack velocity and ram distance were not correlated with the velocity of the fastest flowing water towards the mouth, however suction distance was significantly negatively correlated with this measure. This finding is intriguing given that several recent papers have specifically investigated suction distance and have failed to find that it is a good indicator of suction effort by the fish (Svanback et al., 2002; Wainwright et al., 2001). Despite the intuitive relationship that is apparent between water velocity and suction distance, there are many reasons why a tight correlation between the two may not exist. These are largely tied to fish behavior, such as timing of mouth opening relative to the distance from the prey at which the strike is initiated, and strike motivation. Indeed, we also failed to find a relationship between suction distance and our coarser measure of flow extracted from the temporal analysis. It may be that the relationship between suction distance and water velocity can be detected only at very fine scales. The larger temporal and spatial scales over which investigators tend to quantify suction distance may have the effect of introducing too many additional sources of variation and error into the measure so that the signal is swamped out.

Acknowledgements

The authors gratefully acknowledge the many colleagues and lab members who participated enthusiastically in lengthy discussions about hydrodynamics and prey capture in fishes. We are thankful in particular to M. McCay for providing insights on drafts of the manuscript as well as the thoughtful comments of two anonymous reviewers.

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