WATER FLOW PATTERNS DURING PREY CAPTURE BY TELEOST FISHES

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SUMMARY

Water flow into the mouth cavity during suction feeding in centrarchid sunfishes was studied by mapping the trajectories of small particles in the water during prey capture. In *Lepomis*, a circulation develops as the mouth opens, and water is drawn into the mouth from above, below and in front of the head. Water displaced by movement of the body as the prey is approached during the strike is entrained into the circulation towards the mouth. The parcel of water sucked into the mouth has a diameter approximately one-tenth that of the predator's length.

INTRODUCTION

The dominant mode of prey capture by teleost fishes is suction feeding, in which time-dependent flows displace the prey and surrounding fluid (Lauder, 1983). In this paper we analyse the pattern of water flow into the mouth cavity of two species of teleost fishes during prey capture. We contrast the flow patterns in two predators with different head shapes and attack speeds, and discuss the implications of these results for aquatic predator-prey interactions.

MATERIALS AND METHODS

Flow patterns into the mouth were observed in three species of sunfishes (Centrarchidae) collected locally: *Lepomis macrochirus* Rafinesque (one individual), *Lepomis gibbosus* (Linnaeus) (three individuals) and *Micropterus salmoides* (Lacepède) (four individuals). The average standard length (SL) of the four *Lepomis* was 11·6 cm and the average SL of the four *Micropterus* was 10·9 cm. Since we wished to compare flows for *Lepomis* and *Micropterus* of similar size, we chose individuals whose size variation was less than 2·0 cm total length. Each individual was separately housed in a 40-l aquarium. Suspended brine shrimp (*Artemia*) eggs were used as markers to reveal flow into the mouth during feeding. Approximately 3 g of eggs were placed in 500 ml of tap water for several hours. Positively buoyant eggs were discarded and only those neutral or slightly negatively buoyant were added to the aquarium prior to an experiment. The specific gravity of the particles was thus very near that of water.

During an experiment the particles were illuminated from a slit from above by two 600 W tungsten lamps. The light passed through a slit approximately 1·5 cm wide and 15 cm long just above the water surface. This arrangement provided a narrow beam of light so that only particles near the plane of camera focus were illuminated. Non-reflective black paper was placed in the background to enhance contrast. In front of the aquarium, another piece of black paper with an oval opening for filming blocked ambient light from entering the aquarium. Fish were filmed with Kodak 4X Reversal film and a Photosonics 16 mm 1PL camera at 24 frames per second, f 2·4 lens aperture to provide a narrow depth of field (0·5 cm), and 1/54th second exposure for each frame (a speed that produced adequate streak paths). Film exposures generally exceeded the feeding frequency by a factor of ten. A scale was filmed at the beginning of each experiment to provide a length calibration. Filming rates were subsequently calibrated using a pulse generator to verify the filming speed. The experimental approach used here represents a compromise between high-speed filming, which provides more temporal resolution with less detail per frame, and still pictures with sequential superimposed flashes (van Leeuwen, 1983). Fishes were trained to approach and consume small pieces of earthworm (*Lumbricus*) dropped through a tube into the beam of light in the aquarium. In later experiments, as much mucus as possible was rinsed from the worm pieces to prevent adhesion of particles to the prey.

Individual frames from feedings that occurred in the middle of the water column (at least 10 cm from the aquarium walls) were examined using a stop frame projector. For each frame the positions of the fish, prey, stationary particles and streak lengths were noted. Only particles in sharp focus and the narrowest, sharpest streaks were used as indicators of flow. The direction of particle movement could occasionally be determined by changes in the streak paths: streak lines narrowed and faded in the direction of movement as a result of particle acceleration. Because each feeding event contained only a limited number of particles in the proper position to indicate flow into the mouth, streaks from up to 15 feedings were superimposed onto templates of the appropriate stages of prey capture to provide summary flow diagrams (e.g. Fig. 1). One frame from the films is reproduced as Fig. 3 to provide an indication of the density of particles and the nature of the flow field as revealed in any one film frame. The particle speeds reported here probably underestimate the actual speeds of flow into the mouth; it is difficult to pinpoint the ends of indistinct streak tails of particles moving at high speeds. In addition, particle paths often disappeared into the mouth, preventing accurate measurement of the streak line tails, and movement normal to the film plane would cause an underestimate of speed.

Fig. 1. Pattern of flow into the mouth in the pumpkinseed, *Lepomis gibbosus* (A), and bass, *Micropterus salmoides* (B), during prey capture. The time between each frame in a sequence is 0·042 s. The short lines represent the paths of small particles in the water and indicate the general character of flow. Each sequence is depicted relative to a fixed background so that the relative positions of the predator and prey at each stage of the strike can be seen. Note the prominent circulations above and below the jaws at peak gape in the pumpkinseed (frame 3) and the pattern during the comparable stage in the bass. In frame 2, the prey is located between the upper and lower jaws and has been omitted for clarity. The dashed lines above the eye (frame 3 in *Lepomis* and frame 2 in *Micropterus*) mark the approximate dividing line between the dorsal circulation curving anteriorly towards the jaws and water moving dorsally and away from the gape. The thick arrows in (A) and (B) provide a fixed reference line in the background for each sequence.

Frame 1

Frame 1

2

2

3

3

4

5

1·0 cm

A *Lepomis*

B *Micropterus*
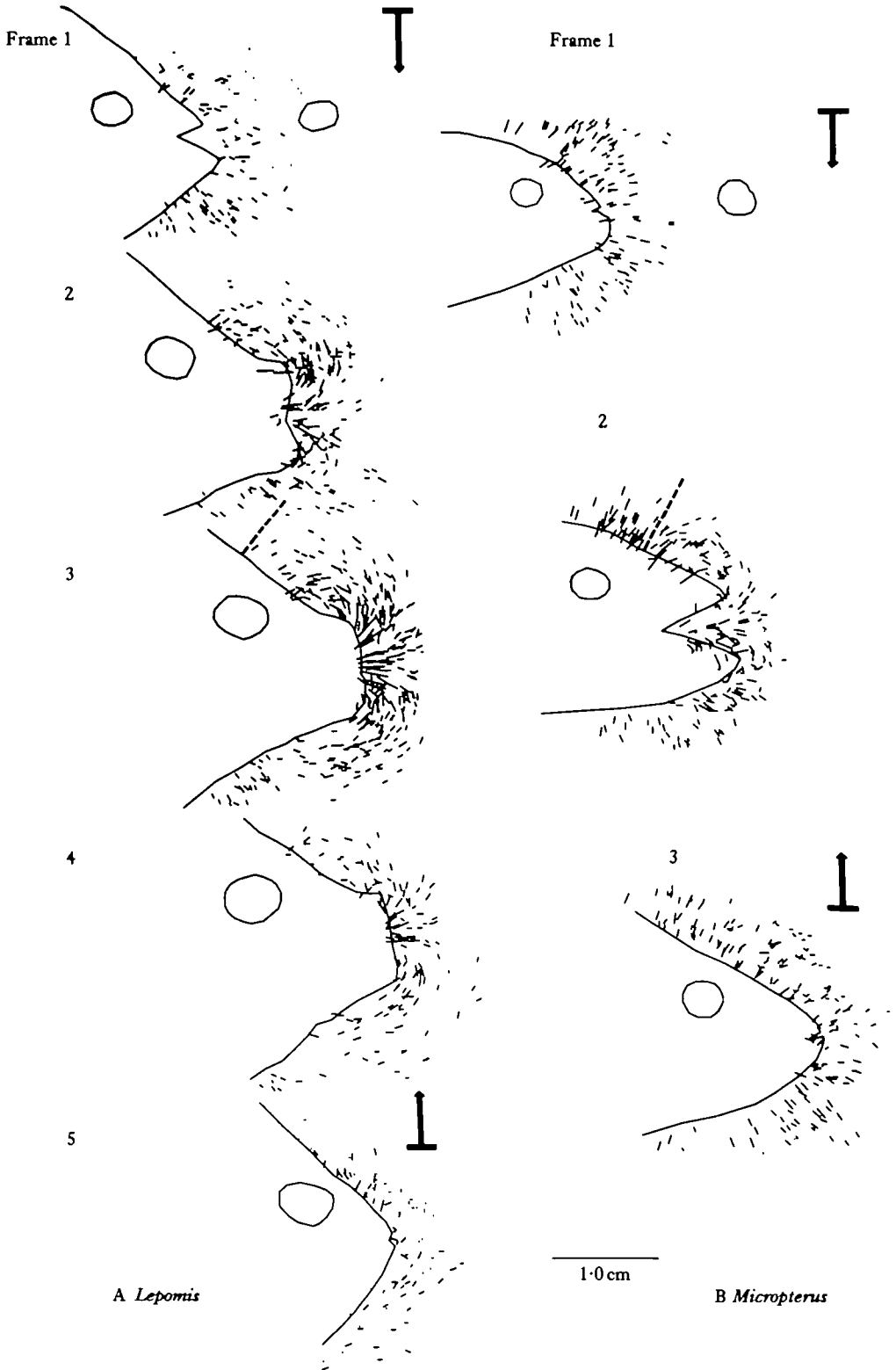
Both lateral and anterior views of prey capture were obtained, although the anterior views proved of limited utility because the reflective dorsal and ventral surfaces of the predator's head obscured particle movement. The flow patterns are thus described primarily as two dimensional. It is certain, however, that flow is not limited to the mid-sagittal plane, and likely that it approaches radial symmetry about the mouth opening.

RESULTS

Lepomis

The pattern of particle movement near the mouth during feeding is summarized in Fig. 1A, which also shows the positions of the predator and prey relative to a fixed background. As the prey is approached and the mouth begins to open, most particles near the predator are displaced anteriorly by body movement. Particles near the prey are stationary. One twenty-fourth of a second later (Fig. 1A, frame 2) the mouth has opened to peak gape (although the premaxilla and maxilla have not yet moved anteriorly to their peak excursion) and the prey is located near the mouth opening. (Gape is defined as the distance between the anterior margins of the premaxilla and mandible.) The particles anterior to the mouth have reversed direction from the previous frame and are moving caudally with an average speed of 4–5 cm s^{-1}. There is now a clear circulation above the head that curves anteriorly and ventrally towards the mouth so that particles in front of the eye move towards the upper jaw. Water dorsal to the eye (dashed line in Fig. 1, frames 2 and 3) continues to be displaced away from the body and mouth, while anterior to the eye, fluid displaced by body movement is entrained into the circulation towards the mouth. Ventral to the lower jaw, the particle paths continue to move away from the body, but anterior to it they are vertically oriented and are moving into the mouth (Fig. 3).

One-twelfth of a second after the mouth has begun to open, the prey has entered the buccal cavity (Fig. 1A, frame 3; Fig. 3) and flow speed in the centre of the mouth opening has reached a maximum. The circulation above the head is now well established, arching anteriorly over the upper jaw (Fig. 3). It is roughly mirrored by a well-developed circulation below the head, and water moved anteroventrally by body movement and opening of the mouth has been entrained into this ventral circulation. Anterior to both the upper and lower jaws, particles move perpendicularly to those flowing into the mouth within the central third of the gape. Peak flow speeds of about 25 cm s^{-1} are found in this central region. The vertical distribution of mean speeds in the plane of the gape is relatively uniform, decaying rapidly only at the extreme limits of the circulation around the jaws (Fig. 2A). Particle paths within the central third of the gape are all nearly horizontal (Fig. 2B). Only particles less than one gape diameter in front of the head are drawn toward the buccal cavity.

A flow pattern similar to that seen at peak gape is maintained in the next twenty-fourth of a second (Fig. 1A, frame 4). Peak speeds in the centre of the mouth are similar to those at peak gape. In the final stage (Fig. 1A, frame 5), the mouth has nearly closed and forward movement has stopped. Due to rapid abduction of the pectoral fins following peak gape, the predator's body may move posteriorly after the jaws close. Most of the particles anterior to the jaws are stationary, but those near the
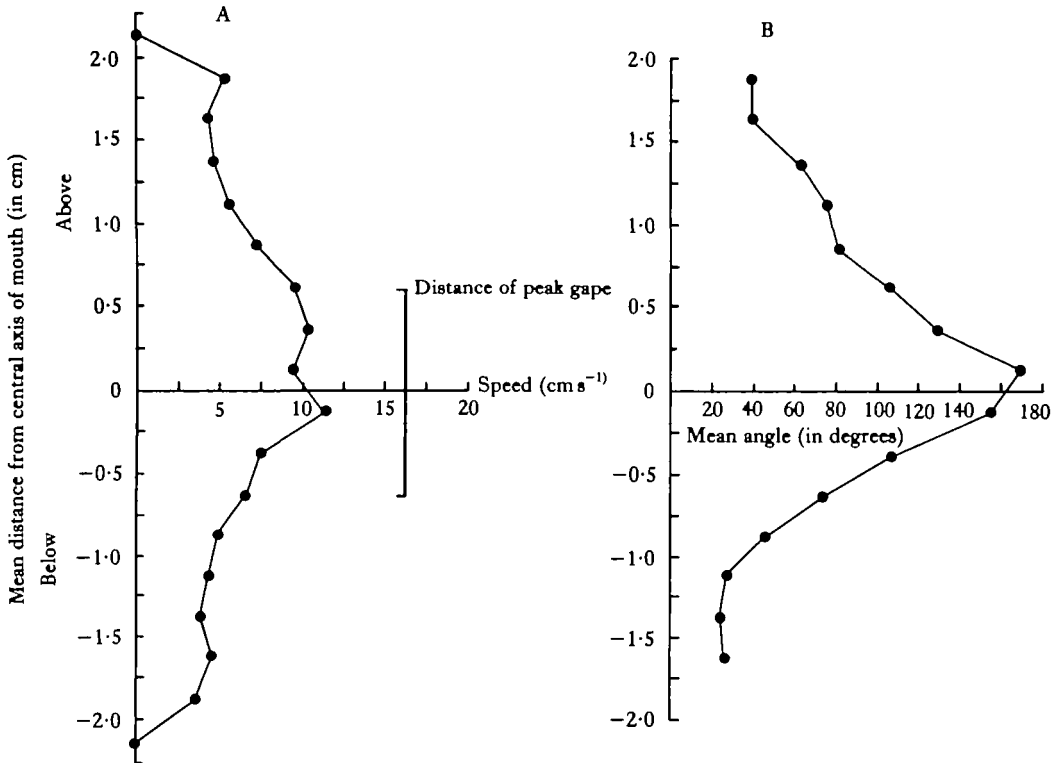
Fig. 2. (A) Graph of mean particle speed along the plane of the gape in *Lepomis gibbosus*. Average speeds were determined for areas of 125 mm² at 19 points along the plane of the gape. The actual gape distance is indicated on the right. Note that peak mean speed occurs in the centre of the mouth and that speeds fall off rapidly about 2·0 cm above and below the centre of the mouth. (B) Graph of mean particle path angle with respect to the horizontal along the plane of the gape in *Lepomis gibbosus*. Mean angles were determined for streak lines within 15 areas of 125 mm² along the plane of the gape. An angle of 0° indicates a path parallel to the horizontal, while a 90° angle represents a vertical path and 180° angles indicate particle paths parallel to the horizontal but in the opposite direction to those at 0°. Coefficients of variation for the mean values were smaller away from the centre of the mouth, and ranged from 0·26 at the periphery of the circulation to 0·6 at the centre of the gape.

upper and lower jaws move towards the head (posteriorly) as the mouth closes. Pectoral fin abduction is clearly shown by the large swirls of particles on either side of the head after peak gape. Peak particle velocities in fin-induced currents occur about 0·8 s after maximum gape.

Films of feeding in head-on view show that during the time that the mouth is open, particles move medially toward the centre line of the mouth from each side of the head. Water thus enters the mouth laterally as well as dorsoventrally (although we were unable to quantify flow parallel to the camera axis), and a single large three-dimensional circulation is probably present during feeding.

Micropterus

The basic pattern of particle movement seen during prey capture in the bass, *Micropterus*, is similar to that described for *Lepomis*, although the circulation during mouth opening is less pronounced and extensive. The bass approaches the prey with

a greater body velocity than either the bluegill or pumpkinseed sunfishes: $40\,\mathrm{cm\,s^{-1}}$, as compared to about $20\,\mathrm{cm\,s^{-1}}$ under these experimental conditions. An extensive flow away from the body is indicated by the numerous streaks extending anteriorly in front of the head (Fig. 1B, frame 1). One twenty-fourth of a second later (Fig. 1B, frame 2), the particles in front of the mouth have reversed direction and are moving into the mouth as a result of buccal cavity expansion. A loosely organized circulation is visible, although particle paths are less parallel and the central jet of fluid flowing into the mouth is weaker than during flow at peak gape in *Lepomis*. Unlike in *Lepomis*, particle speeds are highest above the head in the region where flow is directed away from the mouth. The line delimiting particle paths curving towards the mouth from those tracking dorsally is located anterior to the eye in the bass (Fig. 1B, dashed line in frame 2). In several sequences, the prey was positioned between the jaws at this stage and there were motionless particles in front of the prey, indicating that suction produced by buccal expansion was just enough to balance the tendency of forward body movement and premaxillary protrusion to push particles (and the prey) away from the head. Numerous particle paths at this stage of feeding show substantial changes of direction, especially near the margin of the lower jaw; their recurved paths illustrate the transition from anterior to posterior movement resulting from buccal suction.

In the final stage of prey capture, the mouth has closed and the anterior flow away from the body has redeveloped (Fig. 1B, frame 3). In most sequences the bass continues to move anteriorly and does not decelerate as rapidly as the bluegill or pumpkinseed sunfishes (Fig. 1).

DISCUSSION

Several investigators have recently emphasized the unsteadiness of high-speed suction feeding and the dangers of using steady-state models to predict flow patterns into the mouth (Lauder, 1980; Muller, Osse & Verhagen, 1982), although it is not apparent what effect assumptions of steady flow have on predictions of particle trajectories during relatively low speed suction feeding events such as those described in this paper. Weihs (1980), for example, modelled the mouth as a hydrodynamic sink, and assumed a constant rate of water intake. While this assumption is almost certainly violated, the predicted particle trajectories and the distributions of velocities around the mouth opening appear to agree qualitatively with those measured here.

The flow field described in this paper is closely similar to the situation described by van Leeuwen (1983) for flow into an expanding cylinder in the earth-bound frame. Bound vortices occur around the margins of the cylinder corresponding (in the two-dimensional section) to the dorsal and ventral circulations described here. In addition, we note that water displaced by body translation may, in the earth frame of reference, be entrained into these anterior circulations, as individual particles may be tracked moving into the ventral circulation. Vortices normally form at the edge of an accelerating body (see Weis-Fogh, 1975a,b; Maxworthy, 1981) and diffuse outwards at a characteristic rate (Batchelor, 1967). The jaws of a suction feeding fish can be considered as two flat plates rapidly accelerated away from each other during the mouth opening phase. Vortex formation will occur around the tips of the jaws
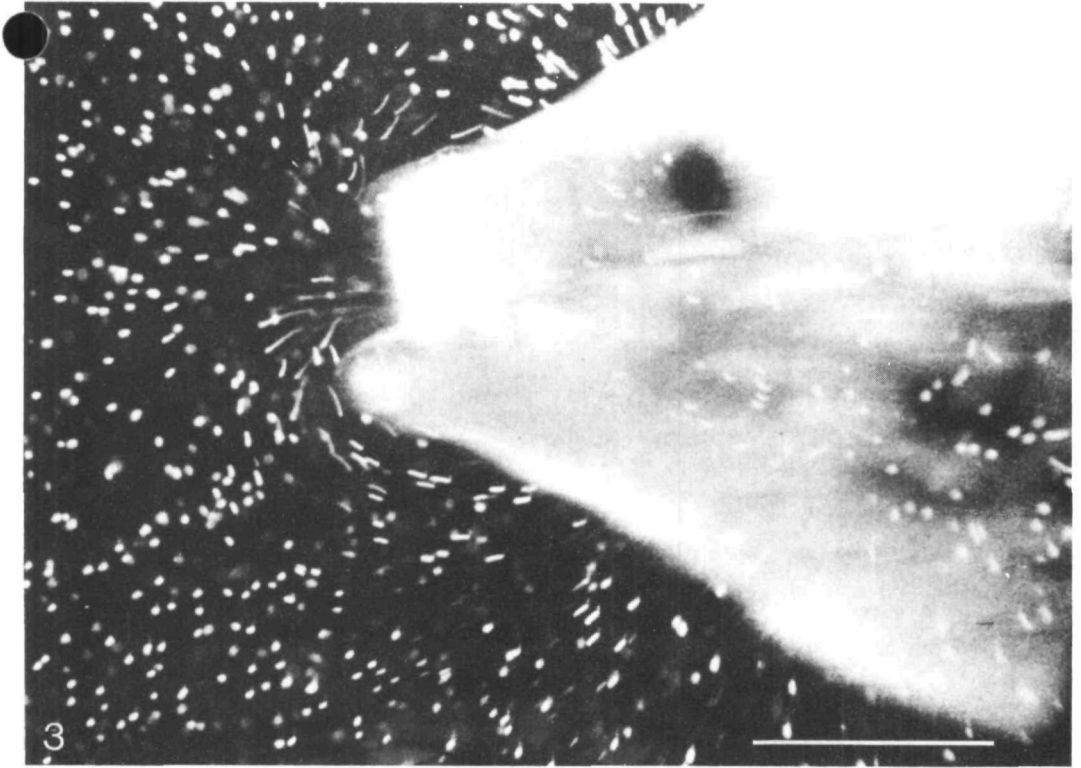
Fig. 3. One frame from a 16 mm film of prey capture in *Lepomis gibbosus* to show the pattern of particle distribution and movement at peak gape. The prey has just entered the buccal cavity and is not visible. Several of the streaks near the mouth opening taper in the direction of movement. This frame was exposed for 18·5 ms. While large circulations are evident around the mouth, the distance from which particles in front of the jaws are moving into the mouth is relatively small. Scale bar, 1·0 cm.

(Fig. 3). Diffusion of the vortex away from the jaw margin may be partially limited by the rapid reacceleration of the jaws back towards their initial position.

The flow pattern in *Lepomis* exhibits a number of differences from the bass *Micropterus*. The bass appears to generate relatively little suction when capturing nearly stationary prey, whereas in *Lepomis*, prey capture is always associated with a well-defined central jet of fluid into the mouth. Indeed, particles near the prey as the bass captures it are often not moving, indicating that negative pressure drawing water into the mouth cancels the anterior flow produced by locomotion. Another difference between the flow patterns of *Lepomis* and *Micropterus* concerns the distribution of particle velocities outside the central flow entering the mouth. In *Lepomis*, particle direction is predominantly vertical along the entire upper and lower borders of the axial flow. There is little tendency for streak lines outside this flow to become oriented into the mouth, while in the bass particles anterior to the upper and lower jaw margins are almost all moving posteriorly.

We have no data on the capture of elusive prey (minnows), where maximal suction pressures are generated (Lauder, 1980). The frequency of feeding (the time from the start of mouth opening to mouth closing) was only 3–5 Hz in these experiments, whereas *Lepomis* can feed at frequencies of 17–20 Hz. Anglerfishes can capture prey with a jaw movement frequency of 50 Hz (Grobecker & Pietsch, 1979) and flow patterns may differ at these high speeds.

The results of the experiments reported here on flow patterns in bass and pumpkin-seed sunfish have several implications for predator-prey interactions in fishes. By tracking the position of individual particles from frame to frame, it is possible to delimit roughly the volume of water that enters the mouth during suction feeding. For *Lepomis*, the measured diameter of the parcel sucked into the mouth (roughly circular in lateral view) is about 12 % of the total body length, while in the bass the volume is 8 % of body length in diameter. Although the bass begins the strike farther away from the prey than the sunfish and approaches the prey with nearly double the speed, the velocity distribution of particles around the mouth suggests that prey located above and below the jaws just before peak gape will be drawn toward the central flow into the buccal cavity. Since the highest speeds are recorded near the centre of the gape (in *Lepomis*), however, most of the water entering the mouth passes through the area anterior to the gape.

This paper provides experimental estimates of the size and position of the capture volume of fish predators, and provides the basis for future investigations (especially those using cinematography) to assess the relationships between prey position, escape ability and hydrodynamic aspects of predator feeding mechanisms.

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