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The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes

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Summary

Suction feeding fish rapidly expand their oral cavity, resulting in a flow of water directed towards the mouth that is accompanied by a drop in pressure inside the buccal cavity. Pressure inside the mouth and fluid speed external to the mouth are understood to be mechanically linked but the relationship between them has never been empirically determined in any suction feeder. We present the first simultaneous measurements of fluid speed and buccal pressure during suction feeding in fishes. Digital particle image velocimetry (DPIV) and high-speed video were used to measure the maximum fluid speed in front of the mouth of four largemouth bass and three bluegill sunfish by positioning a vertical laser sheet on the mid-sagittal plane of the fish. Peak magnitude of pressure inside the buccal cavity was quantified using a transducer positioned within a catheter that opened into the dorsal wall of the buccal cavity. In both species the time of peak pressure preceded the time of peak fluid speed by as much as 42 ms, indicating a role for unsteady flow effects in shaping this relation. We parameterized an existing model of suction feeding to determine whether the relationship between peak pressures and fluid speeds that we observed could be predicted using just a few kinematic variables. The model predicted much higher fluid speeds than we measured at all values of peak pressure and gave a scaling exponent between them (0.51) that was higher than observed (0.36 for largemouth bass, 0.38 for bluegill). The scaling between peak buccal pressure and peak fluid speed at the mouth aperture differed in the two species, supporting the recent conclusion that species morphology affects this relation such that a general pattern may not hold.

Key words: volume, Centrarchidae, *Lepomis*, *Micropterus*, kinematics, prey capture, feeding, DPIV, suction feeding, buccal pressure, fluid speed, hydrodynamics.

Introduction

Suction feeding is the most common feeding mode among fishes (Lauder, 1980; Muller et al., 1985; Carroll et al., 2004) and is frequently observed in other vertebrates (Lauder, 1985). Suction feeding involves a rapid expansion of the buccal cavity, which generates a flow of water directed towards the predator's mouth (Day et al., 2005; Higham et al., 2005; Higham et al., 2006) that is mechanically linked to a drop in pressure inside the oral cavity (Van Leeuwen and Muller, 1984; Lauder, 1980). The maximum induced fluid velocity achieved during a suction feeding event has been identified as a useful index of suction feeding performance (Ferry-Graham and Wainwright, 2002; Higham et al., 2006; Van Wassenbergh et al., 2006), but because fluid speed has historically been difficult to measure, researchers have sometimes relied on peak buccal pressure as an indicator of peak fluid speed (e.g. Carroll et al., 2004; Nemeth, 1997). This has seemed a reasonable approach because peak fluid speed and buccal pressure are linked through the relationships specified in the fundamental equations of fluid motion (i.e. conservation of momentum) (Vogel, 1994).

There is reason to believe, however, that the relationship between peak fluid speed and buccal pressure may not be universal. A recent modeling study indicated that the quantitative relationship between peak buccal pressure and peak fluid speed is altered by differences in cranial morphology between species (Van Wassenbergh et al., 2006). These authors concluded that because the relation between peak fluid speed and peak buccal pressure differed in model output for morphologically different species, one cannot infer relative magnitudes of fluid speed from pressure alone. It is important to note, however, that this reasoning (Van Wassenbergh et al., 2006) was based on a model (Muller et al., 1982) that simplifies the complex movements and water flow patterns of suction feeding and has not been validated with simultaneous direct measurements. Indeed, simultaneous measurements of suction pressure and fluid speed have never been made in any suction feeding predator. Such measurements, the focus of the present study, would allow a test of the often held, but recently challenged (Van Wassenbergh et al., 2006), assumption that peak buccal pressure accurately reflects peak fluid speed (Carroll et al., 2004), and would permit the first empirical validation of this aspect of the existing model of suction feeding (Muller et al., 1982).

The suction feeding model (Muller et al., 1982) calculates both pressure and fluid speed given buccal cavity dimensions and a mouth expansion profile. The expanding head was modeled as a single truncated cone with an anterior (gape) and posterior height, and a number of parameters describing how the buccal cavity expands. Van Wassenbergh et al. used a modification of this model, involving three truncated cones connected in series (Van Wassenbergh et al., 2006). The ability to generate values for peak fluid speed and buccal pressure using only kinematics is desirable given the technical challenges required to measure either directly, and an accurate model would be particularly useful for interpreting interspecific morphological diversity. But, the utility of a model for use in studying diversity depends upon the successful validation of the model by experimental results.

In this study we simultaneously measured peak fluid speed (using DPIV) and buccal pressure in two fish species that have been the focus of extensive research on feeding functional morphology and ecology: the largemouth bass *Micropterus salmoides* and the bluegill sunfish *Lepomis macrochirus.* These species exhibit different morphology, in terms of head shape, mouth size and buccal cavity shape (Carroll et al., 2004). The specific objectives of this study are to (1) quantify the relationship between peak values of pressure and fluid speed in these two species of centrarchids, so that we can (2) determine whether a common scaling relationship exists between fluid speed and pressure in these two morphologically different species (Van Wassenbergh et al., 2006), and (3) determine whether the expanding cone model of suction feeding (Muller et al., 1982) accurately reflects the relationship between buccal cavity kinematics, peak buccal pressure and peak fluid speed.

Materials and methods

Experimental subjects

We studied largemouth bass *Micropterus salmoides* Lacépède and bluegill sunfish *Lepomis macrochirus* Rafinesque, both members of the freshwater Centrarchidae. These species were selected for this study because they differ considerably in cranial morphology and the capacity to generate buccal pressures (Carroll et al., 2004) and suction flow-speeds (Higham et al., 2006). 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 each monophyletic and sister taxa with a most recent common ancestor estimated about 24 million years ago (Near et al., 2005). Specimens 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 tubificid 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 (*SL*) of 17.0 cm, 17.4 cm, and 18.0 cm and from four largemouth bass with standard lengths of 18.0 cm, 18.5 cm, 19.1 cm, and 19.4 cm.

We utilized data from D. C. Collar (D. C. Collar, unpublished observations) regarding the shapes and sizes of the buccal cavities of bluegill sunfish and largemouth bass. Buccal cast measurements were made by injecting commercial silicon sealant into the mouths of freshly killed fish (Carroll et al., 2004). The anterior–posterior length and dorsal–ventral height of each cast were determined using oral landmarks imprinted on the silicon casts. Least-squares regressions were fit to log-transformed data from 14 bluegill (ranging from 52 to 155 mm *SL*) and 23 largemouth bass (ranging from 122 to 365 mm *SL*), using log *SL* as the independent variable.

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., 2005)]. A ghost shrimp (about 2 cm) was attached to a thin wire and placed in the tank. The prey was held within the laser light sheet and within the camera field of view, and the door was lifted permitting the fish to move across the aquarium and capture the shrimp while in lateral view to the camera.

Digital Particle Image Velocimetry (DPIV)

We used DPIV to quantify maximum fluid velocity during suction feeding. The details of this method are described in greater detail elsewhere (Willert and Gharib, 1991; Day et al., 2005; Higham et al., 2005; Higham et al., 2006). 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. The aquarium was seeded with silver coated, near-neutrally buoyant 12 μm glass spheres (specific gravity=1.05) 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. Lateral-view video sequences were recorded using a NAC Memrecam ci digital system (Tokyo, Japan) operating at 500 images s^{-1}. 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 generated by bluegill is 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 distances that particles traveled between image pairs (2 ms interval) were determined within variably sized (e.g. 16×16 pixels for bluegill sunfish) interrogation windows with 50% overlap. The algorithm then returned a two-dimensional grid of two components of measured velocity for each image pair that was processed. The velocities used for further analyses were extracted at a distance equal to ½ of maximum peak gape away from the mouth aperture. Because all fluid velocities in this study were measured along the midline of the fish at this distance from the mouth aperture, and the direction of fluid velocity was always towards the fish, we refer to the magnitude of these measurements and use the term ‘fluid speed’ henceforth.

Pressure

Fish were anesthetized by exposure to 0.3 g l^{-1} of buffered MS-222 and placed in a surgical tray containing freshwater (Carroll et al., 2004). Once anesthetized, a biopsy needle was forced through the neurocranium of the fish caudal to the ascending process of the pre-maxilla but rostral to the braincase. The needle emerged within the buccal cavity just lateral to the midline. A plastic cannula was constructed from PE-90 tubing and threaded into the needle. The end of the cannula that was inside the buccal cavity had been flared prior to the procedure, enabling the cannula to be pulled up against the dorsal surface of the cavity with its opening positioned about 1–2 mm away from the buccal wall. A small sleeve of Tygon tubing (Cole-Parmer, Vernon Hills, IL, USA) was pushed over the cannula where it protruded from the head of the fish and served to prevent the tube from sliding into to the skull.

A Millar SPR-407 microcatheter-tipped pressure transducer (Millar Instruments, Inc., Houston, TX, USA) was threaded into the cannula and held in place by inserting the tip of the cannula into a piece of silicon that was allowed to set around the pressure transducer cable. The tip of the pressure transducer was positioned such that it was flush with the buccal cavity or slightly dorsal to the opening of the cannula. Thus, the sensing element was physically shielded by the plastic cannula, but exposed by a short fluid path to pressure in the buccal cavity. Surgery took no more than 15 min, and all fish recovered from the procedure. Experiments began within 2–4 h after surgery. Pressure transducers were calibrated prior to the surgery by placing them into a sealed flask. The pressure within the flask was varied over a range of –60 to 0 kPa using a vacuum pump and was measured with a commercial (World Precision Instruments, Sarasota, FL, USA) pressure transducer that came with an NIST (National Institute of Standards and Testing) certificate of calibration. The voltage output of the transducer is a linear function of pressure (r^2=0.99).

Pressure data were amplified 10 times, digitized and recorded at 5000 Hz on a PC running a custom LabView program using a DAQpad 6070E data acquisition system (National Instruments, Austin, TX, USA). Maximum buccal pressure was measured from each pressure trace by inspecting the values of pressure through time in a computer file. By doing this, erroneous maxima resulting from noise were avoided. Since the baseline pressure varied depending on the depth of the fish, we refer to pressure in this paper as the difference between the maximum pressure and the baseline value prior to the strike. Values of maximum pressure refer to this difference between peak pressure and the baseline preceding that pressure pulse. The measurements of fluid speed and pressure were synchronized using a manual switch that delivered an analog voltage to simultaneously trigger both the video camera and the pressure data acquisition system.

Comparisons between our data and the existing model

We parameterized the expanding cone model (Muller et al., 1982) with kinematic data that we obtained for both bluegill sunfish and largemouth bass. To do this, we recorded additional video of fish capturing shrimp held on a wire, and we obtained simultaneous lateral and ventral (*via* a mirror situated underneath the tank oriented at 45°) views to the NAC Memrecam camera. From this footage, we quantified the anterior height of the buccal cavity (gape) and the posterior width at the posterior margin of the opercula throughout the strike in order to determine the buccal expansion kinematics used in the expanding cone model [h_1 and h_2, respectively (from Muller et al., 1982)]. By varying time-to-peak gape (*TTPG*) in the model, we established the relationship (for each species) between $\log_{10}$ of predicted peak fluid speed and $\log_{10}$ of peak pressure. Using these relationships, we found the model’s estimate of peak fluid speed corresponding to each value of measured peak pressure from the first set of experiments. Because we measured fluid speed at a distance equal to ½ peak gape away from the mouth aperture along a central axis, we also converted the values of peak fluid speed from the model (at the mouth aperture) to speeds at a distance equal to ½ peak gape away from the mouth aperture, using established relationships between fluid speed and distance from the mouth aperture for both bluegill sunfish (Day et al., 2005) and largemouth bass (Higham et al., 2006). We divided the values from the model by the conversion factors for bluegill sunfish (3.6) and largemouth bass (4.6). We then compared these values of peak fluid speed from the model with those measured with DPIV using one-sample *t*-tests. In order to test the sensitivity of the model to the kinematic profile, we altered the shapes of the kinematic profiles and inspected the relationship between peak pressure and peak fluid speed. The shape of the kinematic profile refers to the shape of the curve describing how the heights of the anterior and posterior valves change with time. The shape is defined using six terms (from Muller et al., 1982). We also altered the shapes of the kinematic profiles to determine if the kinematics measured from video provided the closest predictions to those values actually measured. Ultimately, the kinematic profiles measured from video resulted in the closest predictions of fluid speed to those actually measured from DPIV, and it was these values that were used in subsequent analyses.

Data analysis

Only those DPIV 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 jaw 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., 2005; Higham et al., 2006). 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). The displacement of the fish's body was determined by digitizing the anterior edge of the eye. Ram speed (velocity in the anterior direction) was the first derivative of displacement, and the ram speeds used in this study were calculated at the time of maximum fluid speed.

Statistical analyses

We used SYSTAT version 9 (SPSS Inc., Chicago, IL, USA) for all statistical analyses. Prior to performing any statistical analyses, we $\log_{10}$-transformed all of the variables in order to normalize variances. For each species separately, we performed linear regressions to determine the effects of *TTPG* and pressure on peak fluid speed. A multiple regression, with pressure and ram speed as the independent variables and peak fluid speed as the dependent variable, was used to determine whether ram speed, after accounting for pressure, affected peak fluid speed. An analysis of covariance (ANCOVA) was used to compare the slopes and *y*-intercepts between largemouth and bluegill sunfish. One-sample *t*-tests were used to test whether the slopes of the empirical data for each species were different from the model slope of 0.51. Results are presented as mean ± s.e.m. unless otherwise stated. P=0.05 was taken as the level of significance.

Results

Detailed descriptions of the hydrodynamics during suction feeding in bluegill sunfish and largemouth bass have been presented elsewhere (Day et al., 2005; Higham et al., 2005). Bluegill sunfish generated higher fluid speeds and lower subambient buccal pressures than largemouth bass (Fig. 1). Time to peak gape (*TTPG*) was significantly, and negatively, correlated with the magnitude of pressure generated by bluegill (r^2=0.95; P<0.001; slope=–1.29) and more weakly in bass (r^2=0.29; P=0.001; slope=–0.68) (Fig. 2). In the multiple regression, only peak pressure had a significant effect on peak fluid speed (model r^2=0.74). There was no effect of ram speed on peak fluid speed (P=0.92).

For largemouth bass, peak pressure preceded maximum fluid speed by an average of 18.0±2.8 ms and 95% gape by an average of 14.2±3.0 ms (also see Fig. 3). For bluegill sunfish, peak pressure preceded maximum fluid speed by 9.6±1.7 ms and maximum gape by 5.2±1.1 ms (also see Fig. 3). The magnitude of peak pressure was positively correlated with peak fluid speed in both bluegill and bass, and the species exhibited a similar relationship between these variables (Fig. 4). The equation of the regression for largemouth bass was y=0.356x+1.2245, and y=0.3803x+1.1904 for bluegill sunfish. The value of r^2 was higher for bluegill sunfish (r^2=0.79; P<0.001) than largemouth bass (r^2=0.56; P<0.001), but this was a result of bluegill having a larger range of values of peak

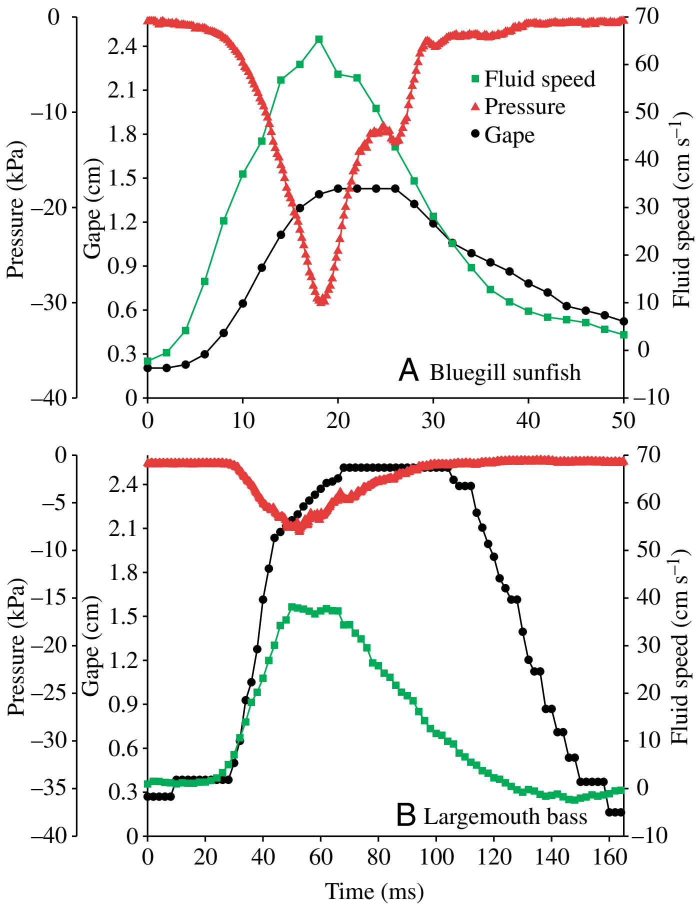

Fig. 1. Representative sequences of gape (black circles), fluid speed (green squares), and pressure (red triangles) for bluegill sunfish (A) and largemouth bass (B). Note that the magnitudes of subambient pressure and fluid speed are both greater in bluegill sunfish than largemouth bass.

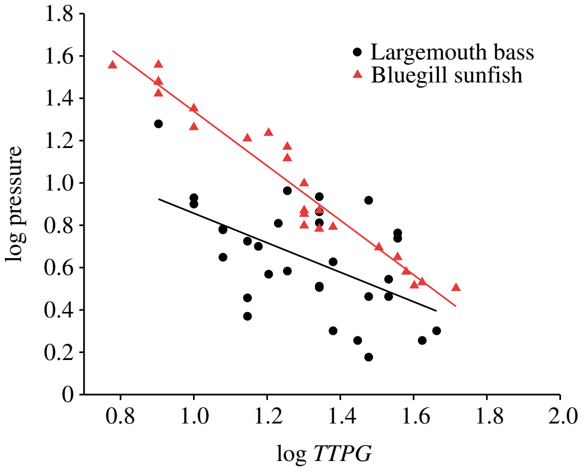

Fig. 2. A log–log plot of time to peak gape (*TTPG*, ms) *versus* peak buccal pressure (kPa) for largemouth bass (black circles) and bluegill sunfish (red triangles). For this plot, the absolute value of pressure was used. Note that as the duration of time to peak gape gets longer, the magnitude of pressure decreases. The relationship between these variables is much stronger for bluegill (r^2=0.95) than for bass (r^2=0.29).

pressure since the average residuals were identical for both species (both=0.05). An ANCOVA found no significant difference between bluegill (0.38) and bass (0.36) in the slope of this relationship (F=0.45, P=0.5).

The values of peak fluid speed calculated with the model (Muller et al., 1982) are shown in Fig. 4. The model overestimated peak fluid speed throughout the range of peak pressure values observed in this study. The slope of the predicted values (0.51) was not significantly different from the slopes of the empirical data (0.36 for bass; 0.38 for bluegill), using one-sample t-tests (bass: t=1.30, P>0.1; bluegill: t=0.89, P>0.1).

Using buccal cast measurements (D. C. Collar, unpublished), the lengths of the buccal cavities for bluegill sunfish and largemouth bass in our study were 19.8 mm and 26.2 mm, respectively. The average heights of the buccal cavities were 16.1 mm for bluegill and 28.2 mm for bass.

Discussion

Bluegill sunfish and largemouth bass both exhibit strong relationships between peak pressure and peak fluid speed (Fig. 4). Thus, with a reasonable degree of accuracy, pressure can be used to predict peak fluid speed within each species (bluegill: r^2=0.79; bass: r^2=0.56). However, the similarity in the relationship between pressure and fluid speed in the two species (Fig. 4A) is sensitive to the location that fluid speeds are measured (compare Fig. 4A with 4B). While it appears that largemouth bass and bluegill sunfish exhibit almost identical relationships between pressure and fluid speed at a distance equal to ½ peak gape away from the aperture (Fig. 4A), this is not the case when fluid speed is evaluated at the mouth aperture (Fig. 4B). Our previous empirical results indicated that, in bass, fluid speed drops off more steeply between the mouth aperture and ½ peak gape than in bluegill (Higham et al., 2006). When the fluid speed values shown in Fig. 4A are transformed into estimates at the mouth aperture (Fig. 4B), the species regressions separate, with the bass showing a higher elevation than the bluegill, indicating higher fluid speeds for a given pressure in bass. This difference between the two species when using fluid speeds at the mouth aperture supports the insight (Van Wassenbergh et al., 2006) that the relationship between peak buccal pressure and peak fluid speed can differ between species with different buccal morphology. We therefore concur with the cautionary message that the magnitude of peak buccal pressure should not generally be used to infer the exact magnitude of induced fluid speeds when making comparisons across species, and possibly across ontogenetic stages within species (Van Wassenbergh et al., 2006). We note, however, that the magnitude of the difference between species is greater than predicted by the model (Fig. 4B) so we cannot recommend that this model be used to generate quantitative predictions of pressure and fluid speed (e.g. Van Wassenbergh et al., 2005a; Van Wassenbergh et al., 2006). A new, more complete model of suction feeding fluid mechanics is needed before reliable generalities can be made about how skull morphology and movement affect the relationship between buccal pressure and velocity of the induced flow of water.

The existing model of suction feeding (Muller et al., 1982) uses an expanding truncated cone to represent the opening buccal cavity and the model can be used to estimate pressure and fluid

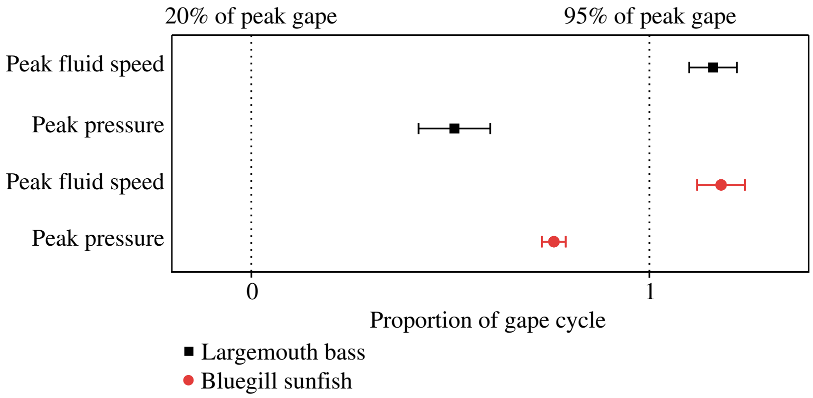

Fig. 3. The relative timing of peak pressure and peak fluid speed with respect to 20% of peak gape (dotted vertical line on the left) and 95% of peak gape (dotted vertical line on the right) for largemouth bass (black squares) and bluegill sunfish (red circles). Each value is scaled to the duration of time to peak gape where 0 is 20% and 1 is 95% of peak gape. Note that peak fluid speed follows peak gape in both largemouth bass and bluegill sunfish. The timing of peak pressure is earlier, relative to 95% of peak gape, in bass (0.51) than in bluegill (0.76).

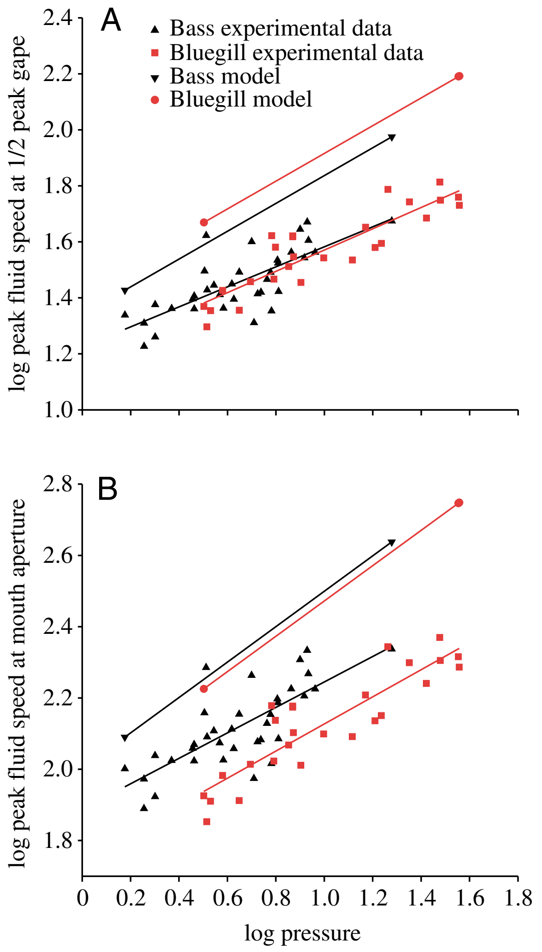

Fig. 4. Measured values of peak fluid speed (cm s^{-1}) and peak buccal pressure (kPa) for largemouth bass (black upward triangles) and bluegill sunfish (red squares), and the fluid speeds predicted from the model (Muller et al., 1982) for largemouth bass (black downward triangles) and bluegill sunfish (red circles). As in previous plots, the absolute value of buccal pressure is shown. The lines designated as 'model' are based on values of peak fluid speed calculated using the model (Muller et al., 1982) for the pressures that we measured. This was done separately for each species. See text for additional explanations. The slopes of the linear regressions fit to the model output (0.51) are higher than the slopes of the empirical data for largemouth bass (0.36) and bluegill sunfish (0.38), and the values for fluid speed predicted by the model are well above the measured values. Note that pressure explains more of the variation in fluid speed for bluegill (r^2=0.79; P<0.001) than bass (r^2=0.56; P<0.001). (A) Fluid speeds where we measured them are shown, at a distance equal to ½ peak gape away from the mouth aperture; (B) fluid speeds at the mouth aperture. In order to transform the measured values of fluid speed to values at the mouth aperture, we multiplied the bass values by 4.6 (Higham et al., 2006) and the bluegill values by 3.6 (Day et al., 2005), based on empirical relationships of the drop in fluid speed with distance from the mouth aperture. Note that the two species exhibit different relationships between pressure and fluid speed for fluid speeds measured at the mouth aperture, whereas the two species are similar for fluid speeds measured at ½ peak gape away from the mouth.

speed for a given profile of buccal expansion and ram velocity. The poor fit of our measured values of peak fluid speed and peak buccal pressure to output from this model raises some concerns about the usefulness of the model for studying this relationship. When parameterized with morphology and kinematic profiles of largemouth bass and bluegill sunfish we found the estimates of fluid speed for a given value of peak pressure to be higher than those actually measured (Fig. 4). For example, at a peak pressure of 10 kPa, the model (using bluegill sunfish) calculates a peak fluid speed of 89 cm s^{-1} as compared to the observed 37 cm s^{-1} (at a distance equal to ½ peak gape away from the mouth). Of additional concern is that the scaling relationship between peak pressure and peak fluid speed was not accurately estimated by this model, resulting in a bigger gap between predicted and observed values at higher values of suction pressure (Fig. 4).

We can suggest several features of a suction-feeding fish that are not explained in this model that may help account for its inadequate performance. First, modeling the oral cavity as a truncated cone may be too much of an oversimplification of the shape of the teleost buccal cavity. Our preliminary work with a double truncated cone model similar to one used recently (Van Wassenbergh et al., 2006) indicates that adding this complexity results only in extremely small changes to the model estimates, so this may not be the major factor leading to the poor fit of our data to the model. In addition, although our studies have confirmed that the expanded buccal cavity is approximately circular in cross-section along most of its length, neither the mouth nor the buccal cavity begin the feeding event with a circular cross-sectional shape. Measurements from largemouth bass using sonomicrometry indicate that the buccal cavity begins the strike sequence as an ellipse with a high, laterally oriented aspect ratio that changes to approximate a circle at full expansion (Sanford and Wainwright, 2002). This issue was partially addressed in a study of catfish that used a model of an expanding elliptical cross-section (Van Wassenbergh et al., 2005a). While this should help more accurately reflect the shape change during buccal cavity expansion, relatively little progress has been made in refining the modeling of the shape or role of the expansion of the opercular region or determining its real contribution to suction feeding mechanics (Lauder, 1983; Van Leeuwen and Muller, 1985).

Flow patterns within the buccal cavity may not be realistically represented by the existing model (Muller et al., 1982) of suction feeding. Although the model allows for unsteady flow, this flow is unidirectional, caudal and parallel to the long axis of the fish everywhere within the mouth cavity, and a uniform fluid speed is prescribed at any given axial position. These assumptions appear to be violated during the expansive phase of the strike, at which time the buccal walls, and therefore the fluid at these walls, are moving normal to this axis. We anticipate that consideration of this outward expansion could contribute to increased magnitude of suction pressure at the inner walls of the buccal cavity in addition to that associated with the fluid speed and acceleration, consistent with our placement of the pressure transducer near the buccal wall.

Finally, the model assumes a stiff inner wall of the buccal cavity. This is clearly not reasonable in some regions of the buccal cavity where only a thin layer of collagen-reinforced connective tissue is all that separates the anterior buccal cavity from the external space. Accounting for compliance in the walls of the buccal cavity would tend to reduce the model estimates of volume expansion rate, and may complicate the relationship between pressure and fluid speed.

Successful prey capture using suction depends on the predator generating a water flow that can capture the prey. For an individual fish, higher fluid speeds are generated when the mouth and buccal cavity are opened more quickly (Fig. 2) (Day et al., 2005; Higham et al., 2006). Interestingly, while the pressure–fluid speed relationships for the two species broadly overlap, the *TTPG*-pressure relationships are only slightly overlapping (Fig. 2). In addition, the strength of the relationship between *TTPG* and peak pressure differed considerably between species, with bass showing a relatively weak pattern (r^2=0.28) while in bluegill 95% of variation in peak pressure was accounted for by *TTPG* (Fig. 2). *TTPG*, with eight other kinematic variables, accounted for 79.7% of the variation in minimum subambient pressure generated by largemouth bass (Svanbäck et al., 2002). Furthermore, 99% of the variation in pressure generated by largemouth bass has been accounted for (Sanford and Wainwright, 2002), but that required 19 independent variables. One potential explanation for the weaker relationship between *TTPG* and pressure in largemouth bass is that suction feeding kinematics may be less tightly integrated in this species, resulting in more independent modulation of skull movements posterior to the jaws. For example, opercular expansion and hyoid depression might be modulated somewhat independently of *TTPG* in bass, resulting in more variable patterns of buccal expansion and pressure generation. This possibility has not yet been explored in the literature.

In both bluegill and largemouth bass, peak pressure occurs prior to the time of peak fluid speed. This temporal disconnect between peaks indicates the possibility of an important role for unsteady flow effects, which is not surprising given that accelerations of the fluid are frequently above 8 m s^{-2} for bluegill (Higham et al., 2006). The timing of peak pressure in largemouth bass is almost coincident with the peak rate of percentage change in buccal area, determined using sonomicrometry (Sanford and Wainwright, 2002). Since the timing of peak pressure is later in bluegill (76% of *TTPG*) than in bass (50.6% of *TTPG*) (Fig. 3), this suggests that the peak rate of percent change in buccal area might also occur later, relative to 95% peak gape, in bluegill. Future comparative studies that measure the dynamics of buccal cavity expansion, using either sonomicrometry (e.g. Sanford and Wainwright, 2002) or high-speed cineradiography (e.g. Van Wassenbergh et al., 2005b), will provide insight into the consequences of variable buccal expansion kinematics and the relationships between pressure, fluid speed and buccal expansion.

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