

Linking Cranial Kinematics, Buccal Pressure, and Suction Feeding Performance in Largemouth Bass

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ABSTRACT

The rate and magnitude of buccal expansion are thought to determine the pattern of water flow and the change in buccal pressure during suction feeding. Feeding events that generate higher flow rates should induce stronger suction pressure and allow predators to draw prey from further away. We tested these expectations by measuring the effects of prey capture kinematics on suction pressure and the effects of the latter on the distance from which prey were drawn—termed suction distance. We simultaneously, but not synchronously, recorded 500-Hz video and buccal pressure from 199 sequences of four largemouth bass, *Micropterus salmoides*, feeding on goldfish. From the video, we quantified several kinematic variables associated with the head and jaws of the feeding bass that were hypothesized to affect pressure. In a multiple regression, kinematic data accounted for 79.7% of the variation among strikes in minimum pressure. Faster mouth opening and hyoid depression were correlated with lower pressures, a larger area under the pressure curve, and a faster rate of pressure reduction. In contrast, buccal pressure variables explained only 16.5% of the variation in suction distance, and no single pressure variable had a significant relationship with suction distance. Thus, although expected relationships between head kinematics and buccal pressure were confirmed, suction distance was only weakly related to buccal pressure. Three explanations are considered. First, bass may not attempt to maximize the distance from which prey are drawn. Second, the response of prey items

to suction-induced flow depends on prey behavior and orientation and is, therefore, subject to considerable variation. Third, previous theoretical work indicates that water velocity decays exponentially with distance from the predator's mouth, indicating that variation among strikes in flow at the mouth opening is compressed away from the mouth. These findings are consistent with other recent data and suggest that suction distance is a poor metric of suction feeding performance.

Introduction

Inertial suction feeding is the most widespread prey capture technique in fishes and other aquatic vertebrates (e.g., Alexander 1969; Liem 1979; Lauder 1980*b*, 1980*c*, 1985; Lauder and Shaffer 1985; Lauder and Reilly 1988; Lauder and Prendergast 1992) and is thought to be the basal feeding mechanism in gnathostomes (Lauder 1982). Suction feeding involves an explosive expansion of the buccal cavity that draws water and prey into the mouth, and it is used to capture a remarkable range of free-moving and attached prey items in the viscous aquatic medium (Alexander 1967, 1970; Osse 1969; Liem 1979; Nemeth 1997*b*).

Buccal expansion that characterizes suction feeding is caused by a series of linked movements of the highly kinetic fish skull, including depression of the lower jaw, depression and lateral expansion of the hyoid apparatus, cranial elevation, and lateral expansion of the suspensorium (Alexander 1967; Lauder 1980*a*, 1985). Because water is incompressible, continuity dictates that the initial expansion of the oral cavity causes water to rush into the opened mouth, creating a rapid drop in buccal pressure (van Leeuwen and Muller 1984; Muller 1989). This mechanical link between flow and pressure has allowed researchers to use buccal pressure as a metric of the magnitude of suction generated during prey capture (Norton and Brainerd 1993; Grubich and Wainwright 1997; Nemeth 1997*b*). During buccal expansion, pressure falls rapidly to values that may be as low as -70 to -1 kPa below ambient, depending on the predator species (Alexander 1969, 1970; Lauder 1980*c*; Lauder and Lanyon 1980; Muller et al. 1982; van Leeuwen and Muller 1983; Norton and Brainerd 1993; Nemeth 1997*a*, 1997*b*). Although water velocity will decrease rapidly with distance from the mouth of the predator (Muller et al. 1982), the higher the flow rate at the mouth opening, the greater the potential distance from which any given prey can be drawn.

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Changes in water velocity affect the suction feeding ability of fishes in three ways. First, the flow of water may directly entrain the prey. Second, drag forces will increase with the velocity of water flow (Denny et al. 1985; Lovvorn et al. 1991; Videler 1993). The drag force experienced by the prey is also influenced by prey size, shape, orientation, and behavior (Denny et al. 1985; Lovvorn et al. 1991; Videler 1993). Under steady flow conditions, the drag force is proportional to the square of the velocity of the medium passing by the prey. However, water velocity will decrease with distance from the source (Muller et al. 1982). Thus, the predator can increase the drag on the prey by increasing the velocity of the water and by positioning the source of the flow (i.e., the mouth) as close to the prey as possible. Finally, an almost completely unexplored force is that caused by the acceleration reaction caused by changing water velocity (Denny 1993). The greater the acceleration of water, the stronger this force will act to draw the prey item toward the predator. For an individual suction feeder, it is expected that variation among strikes in cranial kinematics will result in differences among strikes in the induced water velocity and acceleration. Strikes that exhibit greater velocity and acceleration at the mouth opening are expected to have greater suction pressure, and the higher flow rate should provide the potential to draw prey from further away.

Following this picture of how prey capture kinematics, water flow, suction forces, and prey capture are related, previous researchers have attempted to use the distance from which predators draw the prey into its mouth, termed suction distance, as a way to quantify suction feeding performance (Cook 1996; Gibb 1997; Lernell and Weisgram 1997; Nemeth 1997b; Ferry-Graham 1998). This metric, suggested initially by Norton and Brainerd (1993), is attractive because it is relatively easily measured from video and does not require invasive surgery or instrumentation. Our purpose in this study was to test the effectiveness of suction distance as an indicator of suction feeding performance. We simultaneously recorded buccal pressure and video from feeding largemouth bass. Using a multiple regression approach, we evaluate the strength of the relationships between cranial kinematics, suction pressure, and suction distance. In particular, we emphasize two specific predictions: stronger suction pressure will occur in strikes with more rapid opening of the mouth and expansion of the buccal cavity; and suction distance will be greater in strikes with stronger suction pressure.

Material and Methods

Study Animals

The largemouth bass (*Micropterus salmoides* Lacepede) is the largest member of the Centrarchidae, a group of predatory freshwater fishes endemic to North America. It was chosen for this study because of its aggressive feeding behavior when in captivity and because it has been the subject of numerous stud-

ies of feeding functional morphology that provide us with a baseline regarding prey capture behavior (Nyberg 1971; Lauder 1983; Lauder and Clark 1984; Wainwright and Lauder 1986; Richard and Wainwright 1995; Grubich and Wainwright 1997). During prey capture, the largemouth bass is known to employ a range of kinematic strategies through modulation of motor activity and buccal pressure (Wainwright and Lauder 1986; Grubich and Wainwright 1997). The specimens used in this study were obtained from a private fish farm in Sacramento County, California. Fish were housed separately in 100-L aquaria at 23°–25°C and fed a mixed diet of living fish (*Gambusia* and *Carasius*), earthworms (*Lumbricus*), and pieces of frozen squid (*Loligo*). The study individuals were numbered 1–4 and had standard lengths of 235, 224, 245, and 235 mm and weighed 376, 347, 422, and 364 g, respectively.

Before feeding experiments, the bass were starved for 2–3 d to increase hunger level. During experiments, live goldfish prey (*Carassius auratus*; 38.4 ± 0.6 mm SL) were presented at least 20 cm from the bass to permit an extended period of interaction between predator and prey. Experiments took place in the same aquaria where the bass were maintained and generally occurred over a 3- to 5-d period until approximately 50 sequences per fish were recorded for each individual. The bass were fed prey until satiation to capture a broad range of strike efforts.

Prey Capture Kinematics and Suction Distance

Feeding sequences were videotaped using a NAC Memrecam (Simi Valley, Calif.) ci high-speed video system at 500 frames s^{-1} in lateral view with a 1-cm background grid. For scale, a rule was placed in the field of view and also recorded for several frames. During filming, the tanks were illuminated with two 600-W floodlights. Sequences were stored digitally for analysis.

We only analyzed strikes that were performed approximately perpendicular to the camera and in which the outcome of the attack was successful. A total of 199 strike sequences from the four individuals were analyzed. For each sequence, nine landmarks were digitized at 2-ms intervals from the frame before the onset of mouth opening until the frame after the mouth began to close or until the prey was captured (estimated as the time when the approximate center of mass of the prey crossed the plane of the gape). The landmarks digitized were (1) center of mass of the prey (estimated as the point just dorsal and posterior to the insertion of the pectoral fin), (2) anterior tip of the premaxilla, (3) anterior tip of the lower jaw, (4) anterior-most point of the eye, (5) point of rotation of the lower jaw, (6) ventral-most point of the hyoid, (7) point of attachment of the opercle to the hyomandibula, (8) dorsal-most point of attachment of the pectoral fin, and (9) a fixed point on the background to account for camera movements (Fig. 1c). Time 0 was defined as the first field in the strike sequence when the mouth was fully opened. Because the initial mouth-opening stages were relatively gradual and highly variable, the onset of

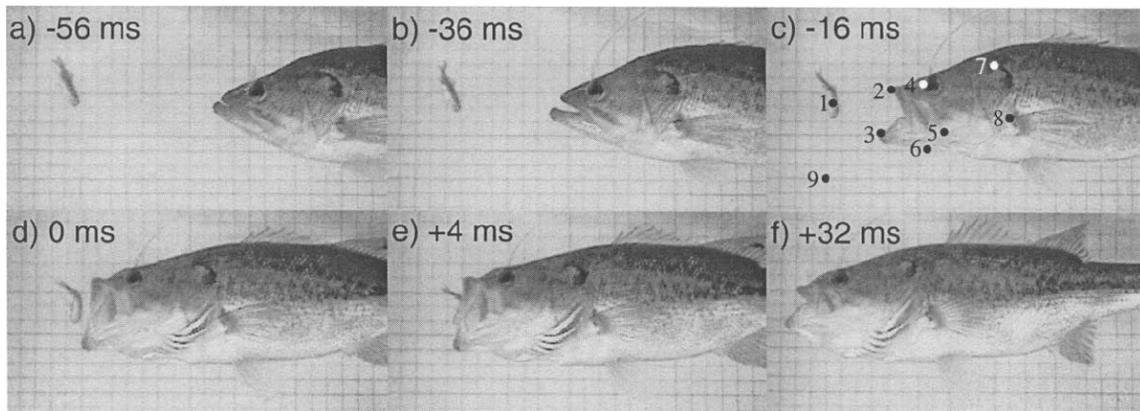


Figure 1. Composite video images of prey capture by largemouth bass. Time is indicated in upper-left corner of each image, and background grid contains 1-cm squares. The frames represent (a) beginning of the sequence, (b) onset of mouth opening, (c) frame with landmark configuration, (d) first frame in which peak gape was reached, (e) frame before prey was captured, and (f) mouth closing.

mouth opening was defined as the moment when the predator had opened its mouth to 20% of the maximum gape distance in the strike (distance between landmarks 2 and 3, Fig. 1c). The time to maximum gape was thus calculated as the time from the onset of mouth opening until maximum gape was reached.

We also measured the amount of hyoid depression, lower jaw rotation, and cranial rotation using the digitized landmarks. These variables were selected to characterize the major expansive actions of the head during suction feeding (Richard and Wainwright 1995). Hyoid depression was calculated as the distance between landmarks 4 and 6; the angle of the lower jaw was calculated as the angle between landmarks 4, 5, and 3; and the angle of cranial elevation was calculated from landmarks 4, 7, and 8. The latter angle could also receive some contribution from retraction of the pectoral girdle. Displacement variables were evaluated over entire sequences to determine peak hyoid depression, peak lower jaw angle, and peak cranial elevation. The times of peak lower jaw angle, peak hyoid depression, and peak cranial elevation were calculated relative to the time of peak gape. Displacement data were also used to calculate maximum velocities of hyoid depression, jaw rotation, and cranial elevation by taking the highest rate of displacement calculated between any two frames in a sequence after smoothing the data with a five-frame moving average. We calculated the attack velocity of the bass on the basis of movements of the eye (landmark 4) between the onset of mouth opening and the frame before the time when the prey crossed the plane of the gape (defined as the time of prey capture).

The effects of suction on the prey in each attack were measured both as the distance travelled by the prey toward the mouth and as the velocity of the prey entering the mouth of the bass. Suction distance was calculated as the net distance moved by the prey from the onset of mouth opening until the

frame before prey capture (Fig. 1). The velocity of the prey entering the mouth was calculated as an average velocity over the last three frames before prey capture. Ram distance, the distance moved by the predator, was measured from each feeding sequence by calculating the distance traveled by the anterior tip of the premaxilla between 20% of mouth opening and the frame before prey capture.

Pressure

The day before experimental recordings, the bass were anaesthetised with tricane methanesulfonate (MS-222), and a plastic cannula was implanted in the neurocranium near the dorsal midline just anterior to the eyes and into the dorsal roof of the buccal cavity just posterior to the vomer and lateral to the parasphenoid bone. This provided a path for positioning the transducer at the edge of the buccal cavity wall. The cannula was flanged on one end to hold it snugly against the interior surface of the buccal cavity. Shortly before recording sessions commenced, the pressure transducer (Millar SPR-407) was threaded through the cannula such that the tip of the transducer lay flush with the opening of the cannula into the buccal cavity. The cannula was sealed at the opposite end around the transducer cable using a piece of tight-fitting, flexible rubber tubing. Pressure changes relative to ambient levels were digitized using Sonosoft software (Sonometrics Corporation, London, Ontario) at a sampling rate of 500 Hz. Pressure recordings were not synchronized with the video.

From the pressure recordings we calculated the total duration of subambient pressure, the most negative pressure achieved during the strike (Fig. 2; minimum pressure), the rate of pressure reduction, and the area under the pressure curve (pressure area). Total duration of subambient pressure was calculated as the time between when the pressure in the buccal cavity during

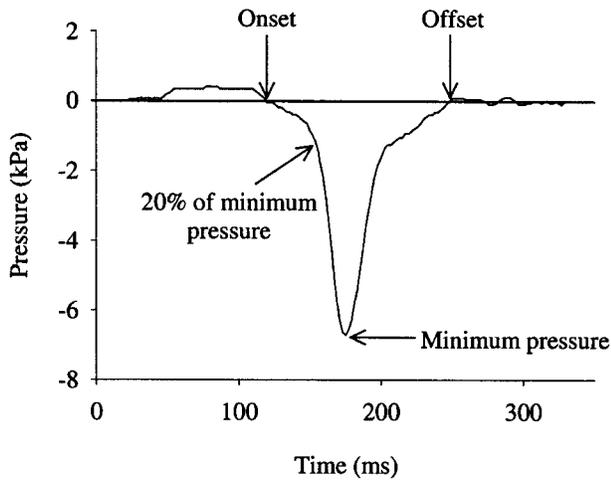


Figure 2. Typical pressure profile during a strike illustrating the pressure variables measured in this study.

a strike fell below ambient (onset) to when the pressure recovered to ambient (offset; Fig. 2). The rate of pressure drop was calculated as the average rate of pressure change from 20% of minimum pressure to minimum pressure. Time to minimum pressure was calculated from the onset of subambient pressure until minimum pressure was reached (Fig. 2). The pressure area was calculated as the area between ambient pressure and the pressure in the buccal cavity from the onset until the offset of subambient pressure.

Data Analysis and Statistics

We tested the strength of the relationship between prey capture kinematics and buccal pressure using a multiple regression approach. This allowed us to determine how much variation in buccal pressure could be explained by jaw and head kinematics. By adding a categorical factor for individual bass, the multiple regression became a complex analysis of covariance with numerous interaction terms. For all pressure variables, we built regression models in several steps. We began by including all dependent variables in the model and then removing kinematic variables and interaction terms one at a time from the model if their P value was larger than 0.4 (a conservative test of their significance), starting with the variable with the highest P value. We report only the final reduced models. This approach was also taken to analyze the effects of variation in pressure and kinematic variables on velocity of the prey entering the mouth and suction distance. In the first models with kinematic variables as independent variables, we used all kinematic variables from Table 1 except for time of prey capture. In the first model with pressure variables as independent variables, we used all pressure variables from Table 1 plus attack velocity. All data

were log-transformed before statistical analysis to make relationships linear and to meet assumptions of normality.

Results

Prey Capture Kinematics

Bass fed aggressively during the experiments, typically initiating the strike from one body length away from the prey, rapidly overtaking the prey, and capturing it with an explosive expansion of the mouth and buccal cavity. Peak gape was achieved as quickly as 24 ms, but time to peak gape varied across about a sixfold range (Table 1; Fig. 3). Peak jaw rotational velocity varied by about sixfold, whereas maximum speed of hyoid depression varied about ninefold (Fig. 3). A more detailed description of prey capture kinematics in this species is presented elsewhere (Richard and Wainwright 1995).

Buccal Pressure

The general pattern of change in pressure in the buccal cavity during strikes by bass was similar to that reported previously for this and other fish species (Alexander 1970; Lauder 1980*b*, 1983; van Leeuwen and Muller 1983; Norton and Brainerd 1993; Grubich and Wainwright 1997). A pressure pulse in a typical strike sequence began with a small increase in buccal pressure followed by a rapid decrease in buccal pressure and then by a return to ambient pressure with an occasional pulse of superambient pressure (Fig. 2). During a strike, pressure in the buccal cavity reached its minimum 8–211 ms following the onset of subambient pressure (Table 1; Fig. 3*E*). Minimum pressure ranged from -1.3 to -15.6 kPa below ambient (Fig. 3*A*, 3*B*), whereas the pressure area varied from around -60 to -600 kPa ms (Fig. 3*C*). The rate of pressure drop ranged from -0.02 to -0.55 kPa ms^{-1} (Fig. 3*D*). Minimum pressure was not significantly affected by the number of prey already eaten by bass during a recording session, indicating no satiation effect (ANCOVA: $F_{1,194} = 0.115$, $P = 0.735$).

Kinematic and Pressure Relationships

The final multiple regression models describing pressure based on kinematic variables explained 79.7% of the variation in minimum pressure, 68.7% for pressure area, 57.1% for the rate of drop, 37.5% for the time to minimum pressure, and 29.9% for the duration of subambient pressure (Table 2). Time to peak gape (Fig. 3*A*), time of peak cranial elevation, and time of peak hyoid depression were positively correlated with minimum pressure (Table 2). The maximum velocity of both hyoid depression (Fig. 3*B*) and jaw rotation was negatively correlated with minimum pressure (Table 2). Thus, lower values of buccal pressure occurred during strikes with more rapid motion. No interaction terms were significant in this model, although the individual effect was significant (Table 2).

Table 1: Basic statistics of variables measured from prey capture sequences in the largemouth bass

Variables	Mean	SD	Range
Kinematics:			
Peak gape (mm)	34.77	.55	1.5–5.53
Time to peak gape (ms)	54.21	5.24	24–144
Maximum velocity of hyoid depression (mm ms ⁻¹)	.40	.12	.082–.88
Peak hyoid depression (mm)	11.47	3.72	1.5–27
Time of peak hyoid depression (ms)	10.91	2.53	–6 to 50
Maximum velocity of jaw rotation (° ms ⁻¹)	1.20	.33	.4–3.32
Peak lower jaw angle (°)	43.11	10.41	14–86.32
Time of peak lower jaw angle (ms)	2.97	1.10	–4 to 18
Maximum velocity of cranial elevation (° ms ⁻¹)	.42	.085	.15–.97
Peak cranial elevation (°)	12.02	2.11	5.2–22.5
Time of peak cranial elevation (ms)	6.70	1.21	–20 to 52
Attack velocity (mm ms ⁻¹)	.72	.065	.013–1.48
Time of prey capture (ms)	4.98	2.89	–22 to 88
Pressure:			
Minimum pressure (kPa)	–5.20	.94	–1.33 to –15.60
Rate of pressure drop (kPa ms ⁻¹)	–.15	.035	–.02 to –.55
Pressure area (kPa ms)	–263	54	–59 to –585
Time to minimum pressure (ms)	69.29	18.92	8–211
Duration of subambient pressure (ms)	157	23	57–398
Distances:			
Suction (mm)	10.06	1.51	.42–26.57
Ram (mm)	44.79	5.55	13.54–97.67

Note. Means and standard deviations (SD) are calculated using the mean of each individual ($n = 4$), and the ranges include the minimum and maximum values measured in this study.

Pressure area was positively correlated with time to peak gape (Fig. 3C), peak gape, the time of peak hyoid depression, time of peak cranial elevation, and time of peak angle of the jaw (Table 2). Negative correlations with pressure area were found with peak lower jaw angle, maximum velocity of hyoid depression, and maximum velocity of jaw rotation (Table 2). Thus, greater pressure area was correlated with higher velocity kinematics and greater displacements. There were no significant interaction terms in this model, although the individual effect was significant (Table 2).

The rate of pressure drop was positively correlated with time to peak gape (Fig. 3D) and the time of peak cranial elevation (Table 2). The rate of pressure drop was also negatively correlated with the maximum velocity of jaw rotation (Table 2), indicating that a faster rate of pressure drop was correlated with higher velocities in the kinematic variables. There was neither a significant individual effect nor interaction terms in the analysis of the rate of pressure drop (Table 2).

Time to minimum pressure was positively correlated with time to peak gape and the time of peak lower jaw angle (Table 2). Time to minimum pressure was negatively correlated with maximum velocity of jaw rotation (Fig. 3E), maximum angle of the jaw, and peak gape (Table 2). Thus, a shorter time to

peak gape was correlated with higher velocity and increased displacements. There was no significant individual effect or interaction terms in the analysis of time to minimum pressure (Table 2). Attack velocity was not a significant part of the model accounting for minimum pressure (Table 2), although the overall pairwise relationship indicated that minimum pressure was lower in strikes with higher attack velocity ($r^2 = 0.421$).

The duration of the subambient pressure pulse was positively correlated with the time to peak gape, and peak cranial elevation (Table 2). The duration of subambient pressure was also negatively correlated with the maximum velocity of jaw rotation (Fig. 3F), peak lower jaw angle, and peak gape (Table 2). This indicates that a longer duration of subambient pressure was correlated with slower kinematics, a smaller mouth opening, and more cranial elevation. There were no significant interaction terms in this model, although the individual effect was significant (Table 2).

Pressure, Kinematics, and Suction Distance

The final multiple regression model describing suction distance based on pressure variables explained only 16.5% of the total variation (Table 2). The overall r^2 between minimum pressure

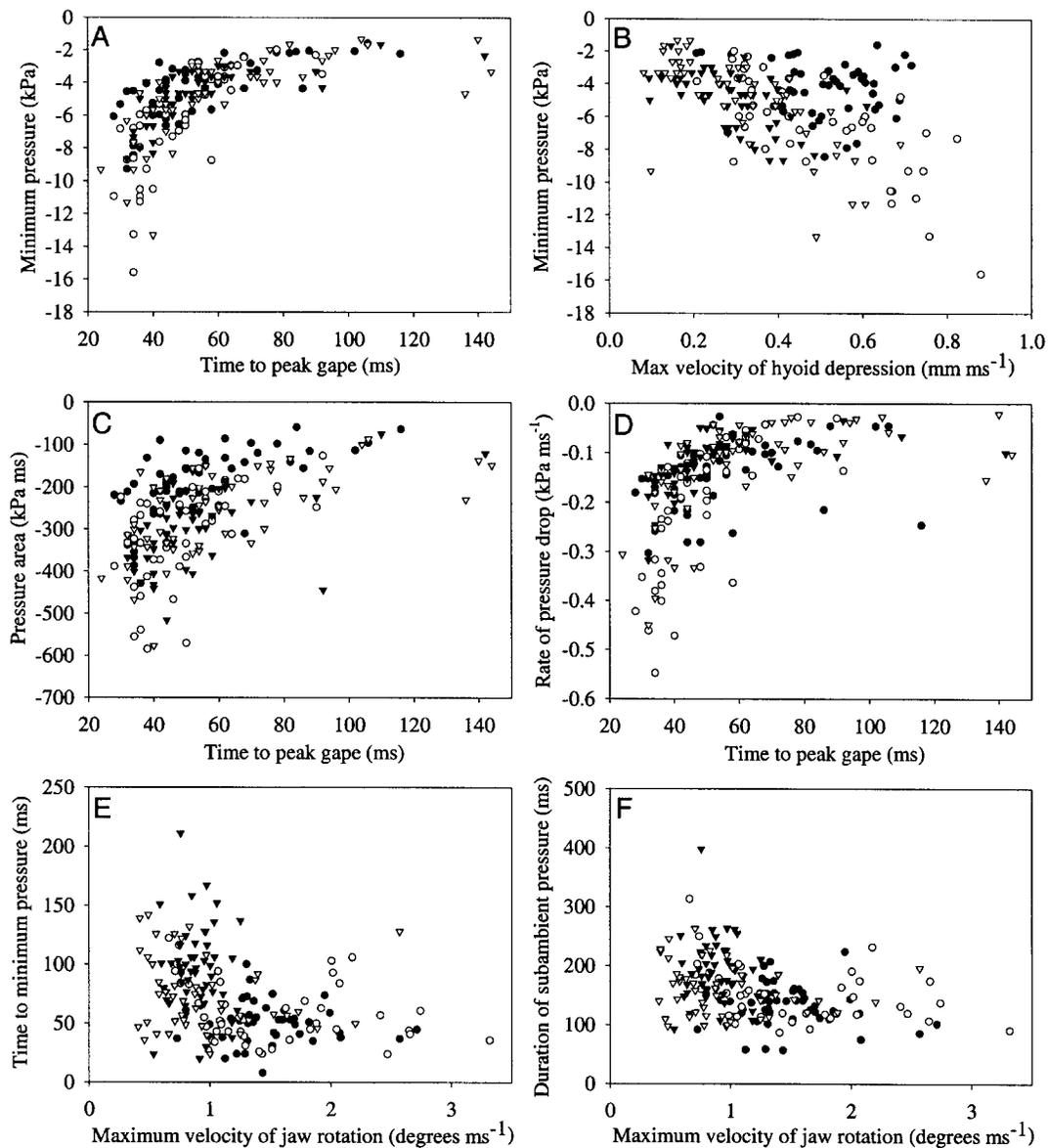


Figure 3. Bivariate plots of correlations between kinematic variables and pressure variables for the entire data set. The different symbols indicate the four individuals, where *filled circles* represent bass number 1, *open circles* represent bass number 2, *filled triangles* represent bass number 3, and *open triangles* represent bass number 4.

and suction distance was 0.0057, whereas it was $r^2 = 0.0178$ between pressure area and suction distance (Fig. 4). In both cases, the trends are opposite of our expectations. That is, strikes with lower pressure and greater pressure area tended to have the lower values of suction distance (Fig. 4). This surprising trend may have been related to the pattern of lower pressure in strikes with higher attack velocities ($r^2 = 0.421$, $P < 0.001$). No single variable alone was significantly correlated with suction distance, although there were significant differences among

individual bass in suction distance (Table 2). A significant interaction term was detected between pressure area and individual bass (Table 2; Fig. 4B) although no single bass showed a significant relationship between suction distance and pressure area (correlations: bass 1; $r = -0.154$, $n = 51$, $P = 0.280$, bass 2; $r = 0.075$, $n = 46$, $P = 0.620$, bass 3; $r = 0.184$, $n = 50$, $P = 0.202$, bass 4; $r = -0.139$, $n = 50$, $P = 0.336$). A significant interaction term was also detected between duration of subambient pressure and individual bass (Table 2), although

Table 2: Final ANCOVA models using kinematic or pressure variables as independent variables from prey capture sequences in largemouth bass

Dependent Variable	r^2	Independent Variables ^a
Minimum pressure ^b	.797	a ^{***} , c ^{***} (+), d ^{***} (-), k ^{***} (+), e [*] (+), f [*] (-), g, b, j
Pressure area ^b	.687	a ^{***} , c ^{***} (+), f ^{***} (-), d ^{***} (-), e ^{**} (+), f ^{**} (-), b [*] (+), k [*] (+), h
Rate of pressure drop ^b	.571	a, c ^{***} (+), f ^{***} (-), k ^{**} (+), g
Time to minimum pressure ^b	.375	a, f ^{***} (-), g ^{***} (-), c ^{***} (+), b ^{**} (-), h [*] (+), d, j, k, a × c
Duration of subambient pressure ^b	.299	a ^{***} , f ^{***} (-), g ^{**} (-), b ^{**} (-), c [*] (+), j [*] (+), k, d, h
Suction distance ^c	.293	a, a × n [*] , a × o [*] , l, n, m, a × m, o
Suction distance ^b	.177	a, b [*] (-), g [*] (+), e [*] (+), c, l, j, i, d

^a The independent variables are as follows: a = bass, b = peak gape, c = time to peak gape, d = maximum velocity of hyoid depression, e = time of peak hyoid depression, f = maximum velocity of jaw rotation, g = peak lower jaw angle, h = time of peak lower jaw angle, i = maximum velocity of cranial elevation, j = peak cranial elevation, k = time of peak cranial elevation, l = attack velocity, m = rate of pressure drop, n = pressure area, and o = duration of subambient pressure. Variables and interaction terms producing P -values $\geq .4$ were removed from a larger model including all kinematic or pressure variables and interaction terms. See text for description of this analysis. The independent variables after individual bass (a) are listed in order of importance for the model. A plus or minus sign in parentheses after significant variables indicates the direction of the slope of correlation between the independent variable and the dependent variable.

^b Models using kinematic variables as independent variables.

^c Model using pressure variables as independent variables.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

no single bass showed a significant correlation between suction distance and duration of subambient pressure (correlations: bass 1; $r = 0.046$, $n = 51$, $P = 0.751$, bass 2; $r = -0.143$, $n = 46$, $P = 0.344$, bass 3; $r = -0.032$, $n = 50$, $P = 0.826$, bass 4; $r = 0.063$, $n = 50$, $P = 0.665$).

The multiple-regression model constructed using kinematic variables instead of pressure variables explained only 17.7% of the total variance in suction distance (Table 2). Peak gape was negatively correlated with suction distance, whereas peak lower jaw angle and time of peak hyoid depression were positively correlated with suction distance.

When velocity of the prey entering the mouth was used as the dependent variable in the model instead of suction distance, both pressure and kinematic variables were found to be important. The velocity of the prey entering the mouth of the bass was affected by minimum pressure, pressure area, and the attack velocity of the bass (ANCOVA, bass: $F_{3,185} = 2.53$, $P = 0.059$; minimum pressure: $F_{1,185} = 14.17$, $P < 0.001$; pressure area: $F_{1,185} = 8.23$, $P = 0.005$; attack velocity: $F_{1,185} = 5.22$, $P = 0.024$; time to minimum pressure: $F_{1,185} = 1.43$, $P = 0.233$; bass × attack velocity: $F_{3,185} = 1.98$, $P = 0.118$), but the

model only explained 23.8% of the total variation in the velocity of the prey. Minimum pressure, pressure area, and attack velocity were all negatively correlated with the velocity of the prey, indicating that higher prey velocity was correlated with more negative pressure, larger pressure area, and a slower attack velocity.

The cumulative r^2 for the models describing variation in minimum pressure, pressure area, and rate of pressure drop (Table 2) revealed that the first two kinematic variables included in each model accounted for most of the variation explained by the models (Fig. 5). Less redundancy in the independent variables was seen in the models describing variation in time to minimum pressure and duration of subambient pressure (Fig. 5). In these five models, the individual bass accounted for most of the variation explained by the models.

Ram Distance

There was a weak, positive correlation between ram distance and minimum pressure, although this relationship differed among bass (ANCOVA, $r^2 = 0.150$, bass: $F_{3,187} = 5.234$, $P =$

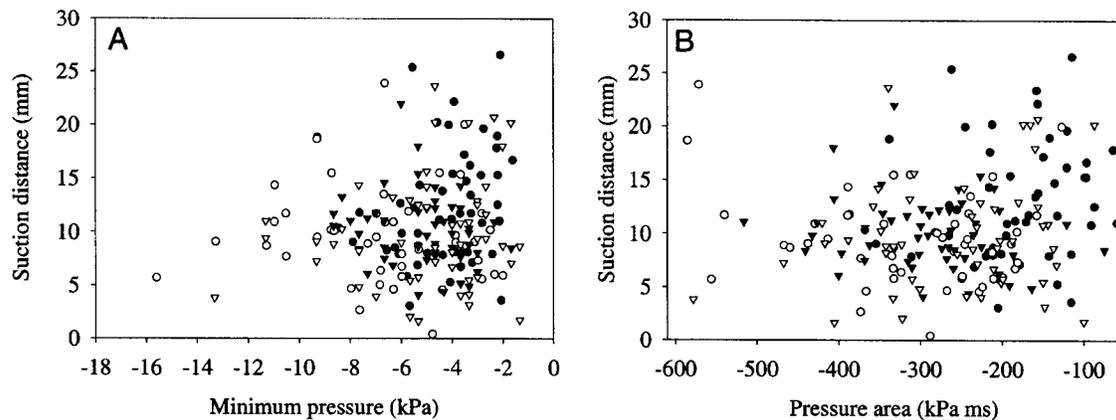


Figure 4. Bivariate plots of suction distance and (A) minimum pressure and (B) pressure area; symbols are the same as in Figure 3

0.002; ram distance: $F_{1,187} = 4.240$, $P = 0.041$; bass \times ram distance: $F_{3,187} = 4.005$, $P = 0.009$). There was also a weak positive correlation between ram distance and suction distance (Fig. 6; ANCOVA, $r^2 = 0.116$, bass: $F_{3,189} = 0.329$, $P = 0.804$; ram distance: $F_{1,189} = 9.471$, $P = 0.002$; bass \times ram distance: $F_{3,189} = 0.394$, $P = 0.758$).

Discussion

It has been recognized for some time that fish are able to alter their feeding behavior in response to prey type and satiation level (e.g., Lauder 1980c; Wainwright and Lauder 1986; Grubich and Wainwright 1997; Nemeth 1997b), but it is less clear what the functional implications of this modulation are. The approach used in this study allowed us to determine the consequences of variation in kinematics for buccal pressure and suction distance, providing tests of the expected links between musculoskeletal function, forces exerted on the water, and prey capture. We found a strong relationship between the movement patterns of head structures and the pattern of buccal pressure but a surprisingly weak relationship between either pressure or kinematics and suction distance. Our best model explained only about 17% of the variation in suction distance, casting doubt on the utility of suction distance as a measure of suction feeding performance.

Kinematics and Pressure

The kinematic variables provided strong predictive power for minimum pressure, pressure area, and rate of pressure drop, with r^2 values of the models reaching as high as 0.8 (Table 2). The data revealed that faster strikes produced the largest and fastest drops in pressure. The time to peak gape and maximum velocity of jaw rotation were the strongest predictors of suction pressure. Strikes with faster time to peak gape and faster jaw

rotation had lower values of minimum pressure, higher pressure area, faster pressure drop, shorter subambient pressure pulses, and faster times to minimum pressure. Strong patterns of correlation among the kinematic variables also produced considerable redundancy in the regression models, such that most of the explanatory power in these models was accomplished by the first two independent variables in the model (Fig. 5).

The pressure that is generated during suction feeding occurs in response to the initial expansion of the mouth and buccal cavity (Muller et al. 1982; van Leeuwen and Muller 1984). It can be expected mechanically that the magnitude of the pressure drop will be related to the rate of change in volume of the buccal cavity (van Leeuwen 1984) and the acceleration of the water (Alexander 1967; van Leeuwen and Muller 1983). Thus, the magnitude of the pressure gradient should be related to kinematic measures of the rate of buccal expansion. We suggest that mouth opening and jaw rotation may have performed best in our analysis because these movements were the most clearly seen and accurately measured among those movements that we quantified. Because the kinematic variables are highly correlated, the multiple regression results should not be taken as a strong test of whether specific movements are more causally linked to pressure than any others. Measures of maximum displacement rarely made significant contributions to these models. These findings corroborate electromyographic results from this and related species that show that strikes with greater synchrony of muscle activity onset tend to have lower pressure and faster times to minimum pressure (Lauder et al. 1986; Grubich and Wainwright 1997). We note that during prey capture events, greater synchrony of activity in muscles does not imply a shorter overall cycle time, because more synchronized strikes also have longer bursts of muscle activity (see discussion in Grubich and Wainwright 1997). Thus, shorter relative onset times in these strikes reflected muscles that were more in phase with each other.

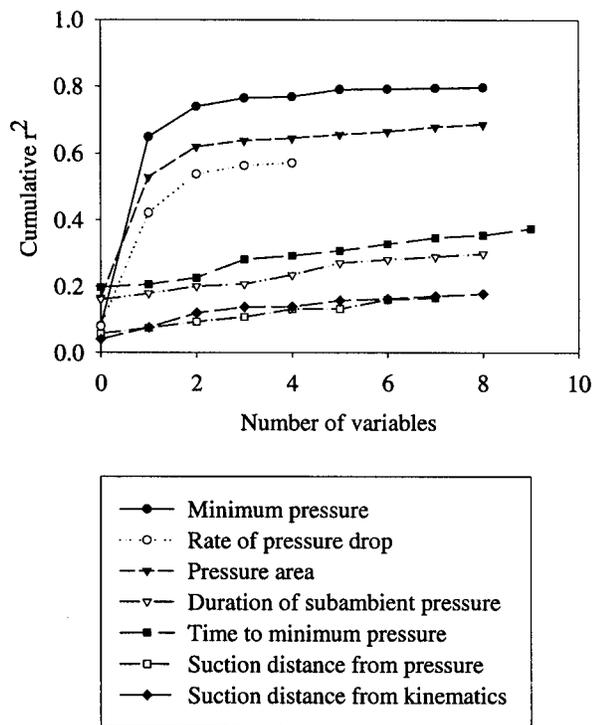


Figure 5. Plot of cumulative r^2 of the different models describing pressure variables with kinematic variables and of the two models describing with pressure variables or kinematic variables. Proportion of variance explained with zero variables are from ANOVAs without any covariate and, thus, only includes the categorical variable "bass" in the model.

The regression models describing the time to minimum pressure and duration of subambient pressure performed more poorly than the models for pressure magnitude, with r^2 values of 0.38 and 0.3, respectively (Table 2). Even the timing of kinematic events was only weakly predictive of these two variables. Because the subambient pressure pulse is completed during the earliest stages of the strike, it may be that many kinematic events occur after the suction pressure pulse.

Our results indicate a stronger relationship between cranial kinematics and minimum buccal pressure (overall $r^2 = 0.8$) than previously observed in studies that related minimum pressure to muscle activity in this species (Grubich and Wainwright 1997; mean $r^2 = 0.55$) and other centrarchids (Lauder et al. 1986; mean $r^2 = 0.5$). A strong relationship is expected between kinematics and pressure because the rate of water flow into the mouth, and hence buccal pressure, is a function of the rate of oral and buccal expansion. The connection between muscle EMG and speed of muscle contraction is less clear (Basmajian and De Luca 1985).

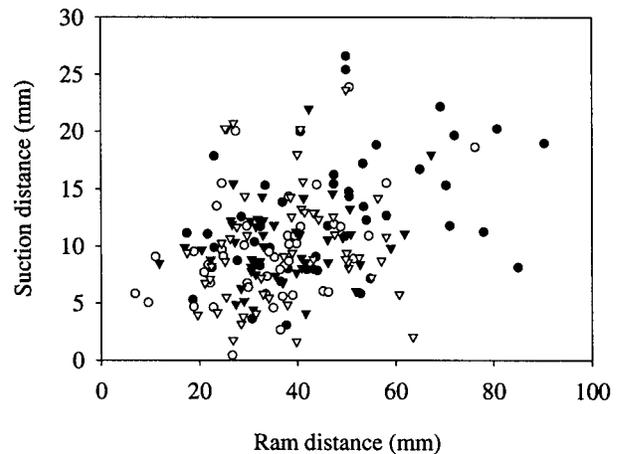


Figure 6. Bivariate plot of correlation between ram distance and suction distance for all four bass. Symbols are the same as in Figure 3.

Pressure and Suction Distance

As the buccal cavity expands during suction feeding, water flows into the mouth to fill the new space, and a pressure gradient is generated that is proportional to the rate of flow (Muller et al. 1982). A strike that generates greater flow rates can be expected to also result in lower buccal pressure. The velocity of this flow will decline as a function of distance from the predator's mouth (Fig. 7), but it can be expected that a strike that induces a greater flow velocity at the mouth opening will result in proportionally greater velocity at some distance in front of the fish. If the ability to capture the prey is a function of the velocity of flow, it is expected that strikes that extend that critical velocity further in front of the mouth should be capable of higher values of suction distance. Interestingly, we found that bass showed only a weak tendency to extend suction distance in strikes with greater suction pressure (Table 2). We see three factors that could work to decrease the strength of the relationship between buccal pressure and suction distance.

First, even if the potential for greater suction distance exists in strikes with greater buccal pressure, it is possible that the bass did not take advantage of that potential. Ultimately, the predator determines suction distance by timing the strike relative to the position of the prey. It may be that bass modulate the onset of mouth opening such that the distance between predator and prey at this moment is constant across strikes. Thus, individual fish may not capitalize on existing potential for greater suction distance.

The second possibility is that a number of factors introduce error into measuring suction distance and will act to decrease the r^2 in statistical models. The effort made by the prey to evade capture appeared to vary among strike sequences in our study. This, coupled with variation among strikes in the ori-

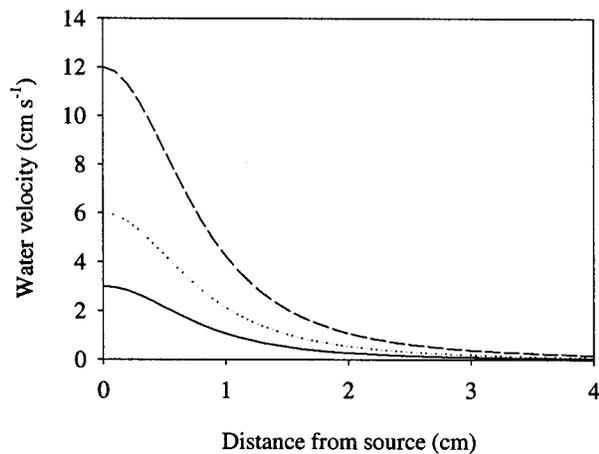


Figure 7. The relationship between instantaneous water velocity, in the earthbound frame of reference, and distance from the mouth aperture in a suction strike along the central axis extending rostrally in front of the predator. Three different instantaneous flow speeds at the mouth aperture are modeled, 3 cm s⁻¹ (full drawn line), 6 cm s⁻¹ (dotted line), and 12 cm s⁻¹ (hatched line), as expressed by the formula $u(x) = u_0 h^3 / (x^2 + h^2)^{3/2}$, where u_0 is instantaneous water velocity at the mouth aperture and h is the radius of the mouth opening. Both u_0 and h are time-dependent variables. In the plots shown, no forward body velocity was assumed and h was arbitrarily set to 1 cm (formula from Muller et al. 1982).

entation of the prey relative to the bass, introduces variation in the mechanical response of the prey to the suction-induced flow. Thus, suction distance is an inherently variable and indirect metric of the flow entering the mouth of the predator.

The third factor that may weaken the relationship between buccal pressure and suction distance is the pattern of water flow in front of the mouth of a suction feeder. The primary point here is that the speed of water being sucked toward the mouth is expected to be inversely proportional to x^3 , where x is the distance from the mouth aperture. The full equation for instantaneous speed of water in the earthbound frame, along a midline axis projecting out from the mouth, developed in a quasi-steady flow model of suction feeding by Muller et al. (1982) is

$$u(x) = \frac{u_0 \times h^3}{\sqrt{(x^2 + h^2)^3}},$$

where h is the radius of the mouth, x is the distance from the mouth apparatus along the midline axis, and u_0 is the instantaneous velocity of water at the mouth aperture. Note that both h and u_0 are time-dependent parameters in this model as they change during the course of the strike and that u_0 depends on flow caused by suction as well as by forward body motion and jaw protrusion. Velocity of the water directly in front of the

mouth will fall exponentially with distance from the mouth (proportional to x^{-3}). Thus, the magnitude of variation among strikes in peak values of u_0 will be greatly compressed as distance from the mouth increases (Fig. 7).

A major implication of the relationship between flow and distance from the mouth is that suction feeding will be effective only over a limited distance (Alexander 1967; van Leeuwen and Muller 1984; Wainwright et al. 2001). Because flow decays so rapidly, suction feeders will be acutely constrained to capturing prey that lie in close proximity to the mouth opening. Mechanisms of rapidly moving the mouth aperture close to the prey, such as rapid locomotion and jaw protrusion, may be viewed as strategies that permit suction feeders to get close enough to their prey such that suction feeding can be effective. However, we note that the model of Muller et al. (1982) has not been fully explored empirically and that, in general, there are few direct measurements of flow patterns in front of suction feeding fishes (Lauder and Clark 1984; van Leeuwen and Muller 1984; Ferry-Graham and Lauder 2001). Quantification of flow patterns may be a powerful approach to understanding the mechanical constraints on suction feeding performance and the implications of trophic diversity.

The weak relationship between buccal pressure and suction distance found in this analysis fits a pattern in recent studies that have failed to document substantial variation in suction distance among closely related species feeding on a common prey item. Five species of butterfly fishes that varied considerably in their expected suction feeding abilities did not differ significantly in suction distance when feeding on living adult *Artemia* (Ferry-Graham et al. 2001). Similarly, Wainwright et al. (2001) found no significant difference in suction distance across seven species of cichlids representing forms as diverse as large-mouthed piscivores and midwater zooplankton specialists. Although refined methodologies may permit future studies to resolve slight differences in suction distance, it appears that variation will be subtle and absolute values severely constrained. We suggest that a fruitful area for future research on suction feeding performance will be to focus on the velocity of flow in close proximity to the mouth opening and the volume of water drawn. These two factors may be difficult to routinely measure, but understanding how individual fish modulate flow and how evolution modifies skull mechanics to produce diversity in suction feeding performance may require the insights provided by these parameters.

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