

Integrating the determinants of suction feeding performance in centrarchid fishes

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SUMMARY

When suction-feeding vertebrates expand their buccal cavity to draw water into their mouth, they also exert a hydrodynamic force on their prey. This force is key to strike success, directly countering forces exerted by escaping or clinging prey. While the ability to produce high flow accelerations in front of the mouth is central to the predator's ability to exert high forces on the prey, several mechanisms can contribute to the disparity between the potential and realized performance through their effect on flow and acceleration as experienced by the prey. In the present study, we test how interspecific variation in gape size, mouth displacement speed and the fish's ability to locate prey at the optimal position affect variation in the force exerted on attached prey. We directly measured these forces by allowing bluegill sunfish and largemouth bass to strike at ghost shrimp tethered to a load cell that recorded force at 5000 Hz, while synchronously recording strikes with a 500 Hz video. Strike kinematics of largemouth bass were slower than that of bluegill, as were estimated flow speeds and the force exerted on the prey. This difference in force persisted after taking into account the faster suction flows and accelerations of bluegill, and was only accounted for by considering interspecific differences in gape size, mouth displacement speed and fish's ability to locate the prey at the optimal position. The contribution to interspecific differences in the force exerted on the prey was estimated to be 42% for flow speed, 25% for strike efficiency, 3% for gape size and 30% for mouth displacement speed. Hence, kinematic diversity results in substantial differences in suction performance, beyond those expected based on the capacity to generate a high flow velocity. This functional complexity, in the form of biomechanically independent mechanisms that are recruited for one function, can potentially mitigate performance trade-offs in suction-feeding fishes.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/211/20/3296/DC1>

Key words: teleostei, fish evolution, functional morphology, aquatic feeding, predator–prey interaction.

INTRODUCTION

Organismal performance is inherently complex, with underlying functional systems and their component parts typically working together to enhance the effectiveness of a behavior (e.g. Bauwens et al., 1995; James et al., 2007; Wainwright et al., 2007). This functional complexity can potentially mitigate performance trade-offs and, thus, support morphological and ecological diversification (Alfaro et al., 2005; Hulsey et al., 2006; Lynch and Conery, 2003; Wainwright, 2007). In aquatic suction feeding, force is transferred from the cranial muscles, through a system of linkages and levers expanding the buccal cavity, to the flow of water outside the mouth. The resulting water movement exerts hydrodynamic force on the prey, dragging it towards the mouth (Holzman et al., 2007; Van Wassenbergh et al., 2006b; Wainwright and Day, 2007; Wainwright et al., 2007). Suction forces are, therefore, key to strike success, directly countering forces exerted by escaping or attached prey.

The mechanisms that transfer mechanical force to hydrodynamic forces provide a good example of multiple factors that contribute to a performance outcome. A key element in the predator's ability to exert force on a prey that is outside its immediate reach is its capacity to manipulate the water around the prey (Holzman et al., 2007; Van Wassenbergh et al., 2006b; Wainwright and Day, 2007). Commonly, the ability to produce fast flows at the mouth aperture is measured as a metric of suction performance (Day et al., 2005; Ferry-Graham et al., 2003; Higham et al., 2006; Van Wassenbergh et al., 2006b). However, force exerted on the prey depends on the flows and accelerations at the location of the prey. Thus, in addition

to the fish's ability to produce fast flows and accelerations at the mouth aperture, there are a set of mechanisms and behaviors that potentially modify the flow at the frame of reference of the prey (Holzman et al., 2007; Holzman et al., in press; Nauwelaerts et al., 2007).

First, smaller mouth size causes a steeper flow velocity profile in front of the mouth so that, for a given flow speed at the mouth, the force exerted on prey due to this gradient is higher in small-mouth fishes (Wainwright and Day, 2007; Wainwright et al., 2007). Second, to efficiently translate the flow and acceleration at the mouth to water motion at the prey, the predator must time the strike so that the prey lies close to the mouth at the moment of peak flow speed and acceleration (Holzman et al., 2007). The exact positioning of the prey determines the strike efficiency, defined here as the proportion of force exerted on the prey from the maximal force exerted with a 'perfect' positioning of the prey (Holzman et al., 2007). However, the ideal strike initiation distance varies with strike kinematics and can be different for each strike (Holzman et al., 2007). Lastly, rapid displacement of the mouth (by jaw protrusion, fast cranial elevation or fast ram) towards the prey results in a more rapid change in flow velocity at the prey as the velocity profile is moved across the prey (Holzman et al., in press). As acceleration-based forces are the dominant forces exerted on the prey, rapid mouth displacement has been shown to enhance the force exerted on prey by over 35% in bluegill sunfish (Holzman et al., in press).

The integrated effects of swimming, mouth expansion and jaw protrusion on prey capture were previously investigated for prey

that behaves as an element of water, with no velocity differential between the prey and the surrounding fluid (Van Leeuwen and Muller, 1984). Here, we ask whether the simplified case of passive, free-floating prey can be generalized to the more realistic cases of attached and escaping prey, where a velocity differential exists between the prey and the accelerating water. The objectives of the present study were to measure the force exerted on attached prey in two species that markedly differ in mouth morphology and associated prey capture behavior (bluegill sunfish and largemouth bass), and to quantify the relative effects of mouth displacement speed, mouth size, the ability to accelerate fluid into the mouth and the ability to locate the prey at the mouth at the time of highest acceleration on the force exerted on prey (strike efficiency). Forces were measured directly by allowing the fish to feed on shrimp tethered to a small force transducer and were compared with forces predicted from a hydrodynamic model. This model was then used to assess how changing discrete parameters (mouth displacement speed, gape size and strike efficiency) in bass kinematics can explain the observed difference between species in the force exerted on the prey, and allowed us to partition the contribution of these factors to total force.

MATERIALS AND METHODS

Experimental subjects

Bluegill (*Lepomis macrochirus* Rafinesque 1819) and largemouth bass (*Micropterus salmoides* Lacepède 1802) were selected for the present study because they occupy extremes in the ecospace and morphospace for centrarchid fishes (Carroll et al., 2004; Collar and Wainwright, 2006) representing 'velocity' and 'volume' suction-feeding centrarchids, respectively (Osse and Muller, 1980). Bluegill feed predominantly on small planktonic prey and benthic insect larvae, whereas largemouth bass feed on larger evasive prey, including fish and crayfish (Flemer and Woolcott, 1966). Among centrarchids, bluegill produce the strongest suction pressure, exhibit a high suction index (a morphology-based predictor for the ability to produce suction forces) and are able to produce fast flows and accelerations (Carroll et al., 2004; Collar and Wainwright, 2006; Higham et al., 2006). However, bass are characterized by weak intra-oral suction pressure, have a much lower suction index and a high volumetric flow (Carroll et al., 2004; Collar and Wainwright, 2006; Higham et al., 2006).

Fish were collected locally in Yolo County, near the University of California Davis campus, CA, USA. The fish were housed in 100-liter aquaria at 22°C and fed daily with cut squid, ghost shrimp and krill. The fish were starved for 24 h before each experiment. Data were analyzed for four individuals from each species with standard lengths of 156, 167, 172, 178 mm for bluegill and 159, 166, 180, 190 mm for bass.

Measurements of the force exerted on attached prey

Measurements of the force exerted on attached prey as well as a framework for deducing this force from kinematic data are described elsewhere (Holzman et al., 2007; Holzman et al., in press) (see Fig. S1 in supplementary material and Appendix). For this study, measurements of the forces exerted on attached prey were made for 15 feeding events from each bluegill (total $N=60$) and 6–10 feeding events from each bass (total $N=33$). In brief, the force exerted on attached prey was measured by allowing the fish to feed on live ghost shrimp (length, 20 ± 1 mm) tethered to a load cell (Futek S-Beam Jr load cell 1 lb, Irvine, CA, USA). The output of the load cell (voltage) was recorded at 5000 Hz on a PC running a custom-written LabView script through a DAQpad 6070E data acquisition system (National

Instruments, Austin, TX, USA). Lateral sequences of the strike were filmed using a high-speed digital video camera (500 frames s^{-1} , NAC Memrecam Ci, Tokyo, Japan). The camera and the load cell were synchronized using an external trigger. Strikes were excluded from analysis if the predator's mouth touched the prey prior to gape closing or if the mouth did not fully open. Conversion of voltage data to force was based on factory calibration of the load cell, which was verified using a series of measured weights before each experimental day. The sensitivity of the load cell, combined with the data acquisition system, was 0.005 N in the range of 0 to 4.44 N.

Kinematic analysis

Video sequences were analyzed using DLTdataviewer2 (<http://www.unc.edu/~7ethedrick/software1.html>), a free toolbox for automated kinematic analysis in MATLAB (MathWorks Inc., Natick, MA, USA). A frame-by-frame analysis was conducted for each sequence, starting ~10 frames before the onset of gape expansion and ending ~10 frames after the fish had started closing its mouth. For each frame, the x and y coordinates of the anterior tip of the fish's upper and lower jaw, a landmark on the fish's body and the prey's eye were determined. These landmarks were used to calculate the following variables: gape distance, the distance between the center of the predator's mouth and prey's eye at the onset of the strike (hereafter strike initiation distance), and mouth displacement (defined as the forward displacement of the center of the mouth on the predator-prey axis). For each sequence, we also determined the time to peak gape (TTPG), defined as the time it took the fish to open its mouth from 20% to 95% of the maximal gape observed during the strike (as in Day et al., 2005), the distance between the center of the fish's mouth and the prey at the time of strike initiation (gape=20% of peak gape), the size of peak gape, prey length and prey height (maximal diameter). For each strike sequence used in this study, we calculated body ram, jaw protrusion and mouth displacement speeds (the sum of body ram and jaw protrusion speeds) by following the position of the body and mouth center through the mouth-opening phase of each strike. Speed was calculated as the slope for at least four consecutive measurements of mouth or body position. Only slopes spanning at least two-thirds of the mouth-opening phase and having a coefficient of determination (R^2) >0.9 were used ($>95\%$ of the strikes measured). Data acquisition typically spanned several days, and the number of consecutive feeding trials was limited to 12 trials per day to minimize satiation during a feeding session.

Use of strike kinematics to calculate the force exerted on attached prey

The framework for deducing the force exerted on the prey from the fish's strike kinematics is based on insights from Particle Image Velocimetry (PIV) studies on live fish, which link the speed of mouth opening (TTPG) to the magnitude of external flows, and relate the spatial patterns of the flow in front of the mouth to gape size (Day et al., 2005; Higham et al., 2006; Holzman et al., 2007) (Fig. S1 in supplementary material). The estimated flow speeds at the mouth and the observed distance between the prey and the predator are subsequently used to estimate the flow speed and acceleration of the water at the location of the prey (Day et al., 2005; Holzman et al., 2007; Holzman et al., in press) (Fig. S1 in supplementary material and Appendix). In brief, flow speed at the mouth was estimated using the relationship between TTPG and peak flow speed at the mouth (Day et al., 2005; Higham et al., 2006; Holzman et al., 2007). Hereafter, flow velocities and accelerations are given with respect to an earthbound frame of reference. Time of flow initiation was

equated to the time of 20% of peak gape, and peak flow speed was set to occur at 95% of gape cycle for bluegill and 120% for bass [based on observed patterns in Higham et al. (Higham et al., 2006)]. Axial fluid acceleration at the earthbound frame of reference at the aperture of the mouth (hereafter, acceleration at the mouth) was calculated as the first derivative of flow with respect to time. Flow speed at the location of the prey was calculated based on the flow speed at the mouth and the distance between the predator and the prey, using experimental data on the stereotypic decay of scaled flow speed as a function of scaled distance from the mouth (Day et al., 2005; Higham et al., 2006; Holzman et al., 2007). These flow speeds and accelerations at the prey were, in turn, used to calculate the forces exerted on the prey (Holzman et al., 2007; Holzman et al., in press) (see Fig. S1 in supplementary material and Appendix for a detailed explanation of our use of strike kinematics to deduce the force exerted on attached prey). To validate this approach, we compared the magnitude and timing of peak-simulated force with those of the measured forces (see Results).

Determination of strike efficiency

As the flow and accelerations in front of the fish's mouth are extremely ephemeral, the prey has to be positioned sufficiently close to the mouth at the moment of peak acceleration to maximize the force on the prey (Holzman et al., 2007). Starting the strike too far or too close to the prey will result in a relatively low force on the prey. The ability of the fish to position the prey at the optimal distance is reflected in the 'strike efficiency', defined as the ratio between the force exerted in the observed strike initiation distance and the force exerted at the optimal distance. To calculate strike efficiency, we determined the optimal initiation distance for each strike by systematically modifying the strike initiation distance from 0 to 40 mm (in 0.5 mm intervals) and recording peak calculated force at each distance. For each strike, the optimal distance was the distance resulting in the highest force.

Contribution of morphology and kinematics to force exerted on prey

The forces exerted on prey by bluegill were substantially higher than those exerted by bass (see Results). This difference could potentially be attributed to a number of differences in the morphology and behavior between the two species, including the ability of bluegill to produce faster flows and acceleration in the earthbound frame of reference (Higham et al., 2006), differences in mouth size (Wainwright et al., 2007), a possible difference in the strike efficiencies between the two species [their ability to time their strike so that they will produce the maximal force on their prey (Holzman et al., 2007)] and a difference in their mouth displacement speed (Holzman et al., in press). To account for the intraspecific variation in acceleration at the mouth, we initially regressed, for each species, the forces exerted on the prey against the acceleration of water at the mouth and compared the slopes of that regression for the two species. Thus, in the following analyses, the slope of the regression is our dependent variable for comparing interspecific performance. We chose to regress the force exerted on the prey against acceleration at the mouth (rather than peak flow speed) because acceleration-based forces account for <95% of the total force exerted on large prey (Holzman et al., 2007; Wainwright and Day, 2007). Our null hypothesis was that the slopes would not be significantly different, indicating that the differences in observed force are due to differences in the acceleration at the mouth alone.

If the slopes of the regressions were significantly different between species, it would indicate a contribution of other factors

to the difference in force. To quantitatively relate the observed differences in strike kinematics to the difference in force exerted on the prey, we sequentially changed discrete parameters or combinations of parameters (strike kinematics, mouth diameter, etc.) in our force model to test whether a change in one or more of these variables can account for the observed interspecific difference in the slope of the regression. For each case, we regressed the simulated force against acceleration at the mouth (to account for the observed intraspecific differences) and then tested whether the regression slopes for the two species were different. Specifically, we changed bass kinematics to include smaller gape, higher strike efficiency and faster mouth displacement. To re-parameterize bass with bluegill-like strike efficiency, we set strike initiation distance to a distance yielding 80% of the maximal peak force (corresponding to the efficiency of bluegill in the subset of slow strikes).

The contribution of each change in bass kinematics (smaller gape, higher efficiency, faster protrusion) to the overall force on the prey was evaluated as the difference in force, calculated using the updated kinematics and the previous model, divided by the force exerted on the prey in the 'mouth displacement' model (where bass were modeled to have small gape, high efficiency and fast mouth displacement). For example, the fractional contribution of strike efficiency was calculated as: $f_e - f_g / f_j$, where f_e, f_g, f_j are the forces exerted on the prey under the efficiency model (bass with small mouth and high efficiency), gape model (small mouth) and mouth displacement models, respectively. The fractional contribution of flow speed was calculated as $1 - (\text{the sum of fractional contributions for } f_e, f_g, f_j)$.

Statistical analysis

Because fish used in our experiments (four bluegill and four bass) were measured multiple times, the strikes of each fish were not independent. To test for the difference in strike kinematics between the two species, we used repeated-measures analysis of variance (ANOVA), with species as the categorical predictor (two levels), strike order as the repeated-measures factors (six and 15 levels for bass and bluegill, respectively) and TTPG as the dependent variable. A similar analysis was made to test the difference in gape size, mouth displacement speed, strike initiation distance and peak measured force exerted on the prey. A prerequisite for repeated-measures ANOVA is that the number of repeated measures in each cell is identical (Hill and Lewicki, 2006), therefore, we used six strikes for each bass and 15 strikes for each bluegill. For bass, this meant that only a subset of the strikes was used for statistical analysis based on the order in which they were recorded. We made sure that there was no correlation between strike order and the magnitude of acceleration at the mouth in any of the fish (Spearman correlation, $P > 0.05$ for all fish). Means for kinematic variables and measured forces are reported for the entire datasets for bass and bluegill throughout the manuscript.

To test the adequacy of our force model for bass, we used a mixed-model approach (Pinheiro and Bates, 2000). In essence, this model enables a regression-like analysis while accounting for the dependent errors due to repeated measurements on individuals. This framework was used to assess the correlation between the magnitude of peak measured force and the magnitude of peak calculated force (based on strike kinematics), and the correlation between the timing of peak measured force and peak calculated force. For these correlation analyses, we determined the fit of the model (R^2 ; see below) and the slope of the regression. We interpreted a good fit between the model and the measured force from a high R^2 as well as a slope similar to 1.

To assess how discrete kinematic variables may account for the discrepancy in forces exerted by bluegill and bass on their prey, we compared the slopes of the regression between their measured force with the acceleration at the mouth. Slopes were compared using a mixed-effect model, with acceleration at the mouth as a dependent variable, measured force as an independent variable, species as categorical predictor and the identity of individual fish as a random factor. After recalculating the force exerted by bass with modified kinematics, we re-tested to determine whether the slopes calculated for the two species are different.

To assure that our mixed-effects models account for the correlation structure that is due to the dependent samples, for each analysis, we built a series of mixed-effects models with increasing complexity and then selected the best model based on the Akaike's Information Criterion (AIC) score and a likelihood ratio test (Johnson and Omland, 2004; Pinheiro and Bates, 2000). The simplest model included fish as a random factor, while more complex models included a correlation structure in observation order, autocorrelated error and an error correlated with the independent variable. However, in all analyses, these models did not provide additional explanatory power, and only results from the simplest model are discussed in the present study. In analyses where significant effects were found, we calculated R^2 based on the log-likelihood results of the model using:

$$R^2 = 1 - \exp\left[-\frac{2}{N}(\log L_m - \log L_0)\right], \quad (1)$$

where N is the number of observations, $\log L_m$ is the log-likelihood of the model of interest and $\log L_0$ is the log-likelihood of an intercept-only model (Magee, 1990).

Statistical analyses were done using the free software R statistics (v. 2.5.0; <http://www.R-project.org>) after verifying that the residuals for mixed-effects models followed a normal distribution and that the data did not violate the sphericity assumption for the repeated-measures ANOVA.

RESULTS

Attached prey – strike kinematics

Bluegill and bass differed in their kinematics when striking attached prey (Fig. 1A,B; Fig. 2A–D). Largemouth bass strikes showed significantly slower mouth opening, with a mean TTPG of 25.1 ± 1.6 ms (\pm s.e.m.) compared with 14.3 ± 1.0 ms for bluegill (repeated-measures ANOVA; $F_{1,12}=11.1$, $P<0.002$ for species effect). Moreover, bass strikes were characterized by slower mouth displacement speeds, with a mean speed of 0.8 ± 0.1 ms^{-1} compared with 1.25 ± 0.05 ms^{-1} for bluegill (repeated-measures ANOVA; $F_{1,12}=3.2$, $P<0.05$ for species effect). Strike initiation distance was similar for the two species [12.5 ± 1.23 mm for bass and 10.9 ± 0.42 mm for bluegill (repeated-measures ANOVA; $F_{1,12}=0.4$, $P>0.5$ for species effect)]; however, these distances were less variable for bluegill (coefficient of variation of 0.3 for bluegill vs 0.55 for bass). Maximal gape size was not significantly different between the species [a mean of 20.5 ± 0.53 mm in bass vs 17.3 ± 0.27 mm for bluegill (repeated-measures ANOVA; $F_{1,12}=0.1$, $P>0.7$ for species effect)]. Whereas bluegill rapidly closed the distance on their prey using mainly jaw protrusion and cranial elevation (Fig. 1B), bass swam forward towards their prey and used slower yet longer ram to close the distance to their prey (Fig. 1A).

Attached prey – measured forces

The slower mouth opening speeds in bass translated to an estimated twofold difference in flow speed, with mean peak flow speeds

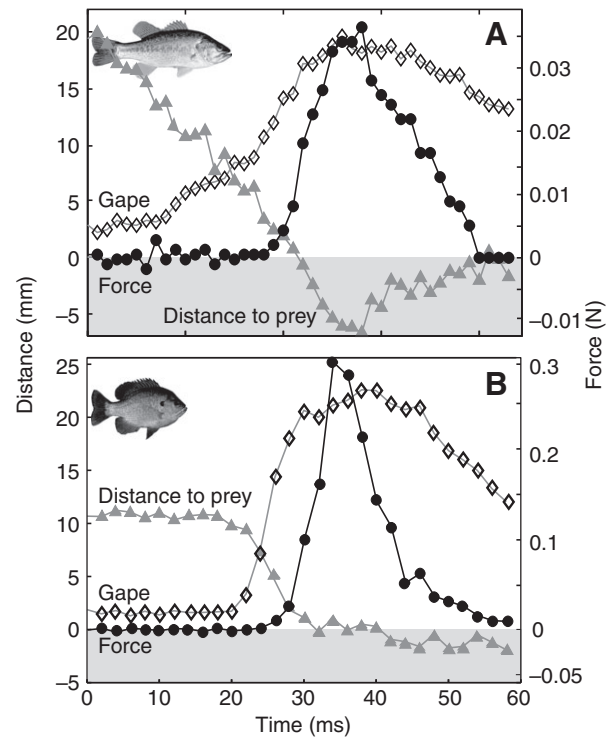


Fig. 1. Representative profiles of gape kinematics (open diamonds), the distance between the center of the predator's mouth and the prey (grey triangles), and the force exerted on the prey (closed circles) in largemouth bass (A) and bluegill (B). In largemouth bass, the distance between the predator and the prey is closed by swimming towards the prey from a distance. In bluegill, that distance is closed through jaw protrusion after a period of minimal ram (time 0–20 ms in B). Shaded area represents negative predator–prey distance, i.e. the prey is in the mouth. Note the different force scale in A and B.

estimated at 1.17 ± 0.07 ms^{-1} compared with 2.02 ± 0.1 ms^{-1} for bluegill (repeated-measures ANOVA; $F_{1,12}=14.7$, $P<0.001$ for species effect). The difference in flow speed corresponded to a twofold difference in the acceleration at the mouth, estimated as 86 ± 3.3 ms^{-2} for bass and 193 ± 16.6 ms^{-2} for bluegill (repeated-measures ANOVA; $F_{1,12}=6.6$, $P<0.011$ for species effect). Concomitantly, the force exerted on the prey by bluegill was much higher compared with that exerted by bass, with a mean peak force of 0.16 ± 0.017 N exerted by bluegill compared with 0.03 ± 0.003 N exerted by bass (repeated-measures ANOVA; $F_{1,12}=19.6$, $P<0.001$ for species effect) (Fig. 3). However, even after taking into account the faster accelerations in bluegill's strikes (by regressing the acceleration at the mouth against peak measured force), the slope of force against acceleration regression was significantly higher for bluegill [$8.63 \times 10^{-4} \pm 1.74 \times 10^{-4}$ Nms^{-2} compared with $2.33 \times 10^{-4} \pm 0.92 \times 10^{-4}$ Nms^{-2} for bass ($R^2=0.46$ and 0.19 , respectively; mixed-effects model; $F_{1,7}=2.1$, $P<0.05$ for species effect) (Table 1; Fig. 4) indicating that for a given acceleration of water at the mouth, the force exerted on bluegill prey was approximately 4× higher than that experienced by bass prey.

Attached prey – calculated forces

The forces calculated with the hydrodynamic model (based on observed strike kinematics) were in strong agreement with the forces measured with our force transducer. For bass, the timing of the

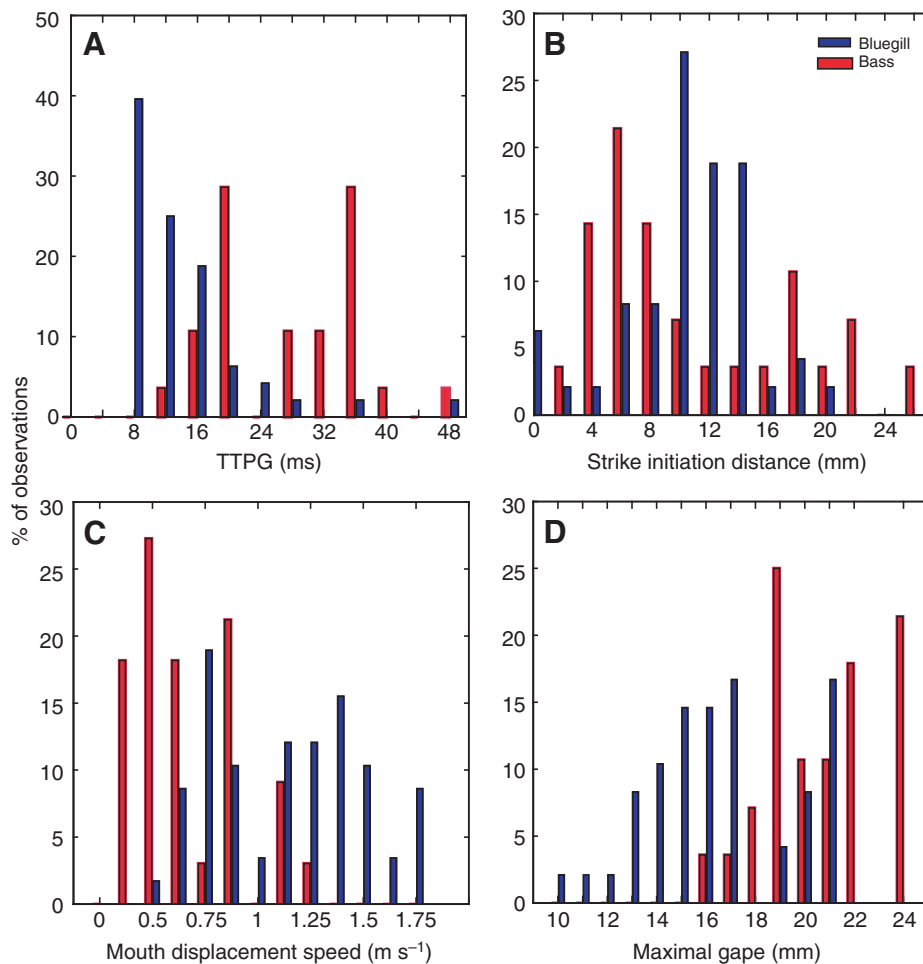


Fig. 2. Observed kinematic variation of largemouth bass (red bars; $N=4$ fish, 6–10 trials per fish) and bluegill sunfish (blue bars; $N=4$ fish, 15 trials per fish) while striking on attached prey. The two species were significantly different in their time to peak gape (A, TTPG) and mouth displacement speeds (C) (repeated-measures ANOVA; $P>0.05$ for both) but strike initiation distance (B) and maximal gape diameter (D) did not differ significantly (repeated-measures ANOVA; $P<0.1$ for both).

observed and calculated peak force were linearly correlated ($R^2=0.659$; mixed-effects model; $F_{1,23}=50.6$, $P<0.001$), with the timing for observed peak force preceding that of the expected force, as indicated by the slope=0.66 (Fig. 5A). Calculated as a fraction of the timing of the peak calculated force, peak observed force occurred at $83.2\pm 5\%$ of the timing of peak calculated force. The peak calculated force for bass was correlated with the observed force ($R^2=0.68$; mixed-effects model; $F_{1,23}=55.74$, $P<0.001$) with a slope of 1.02 (Fig. 5B). The magnitude of the observed force was $110\pm 22\%$ of the calculated force. Similar fits were previously observed for bluegill (Holzman et al., 2007). The strong fit between the observed and calculated forces enabled us to use the force model

as a predictive tool to determine the effects that changes in strike kinematics had on the force exerted on prey.

Effect of strike kinematics on force exerted on attached prey – simulations

By using the force model and systematically replacing aspects of bass kinematics with those of bluegill (Fig. 6), we asked whether the interspecific differences in gape size, mouth displacement speed and strike efficiency accounted for the differences in force exerted on the prey. In the following analyses, we regressed the simulated force against acceleration at the mouth to account for intraspecific variation in acceleration at the mouth and, for each iteration of the

Table 1. Effects of strike kinematics on suction feeding performance in two centrarchid species

Species	Force	N	R^2	Slope ($\times 10^{-4} \text{ N m s}^{-2}$)	Species effect (P)
Bluegill	Measured	60	0.49	$8.63\pm 1.74^{***}$	–
Largemouth bass	Measured	33	0.19	$2.33\pm 0.92^{**}$	0.04
	Gape simulation		0.16	$2.63\pm 0.93^*$	0.001
	Efficiency simulation		0.38	$5.07\pm 1.1^{***}$	0.01
	Mouth displacement simulation		0.46	$7.71\pm 3.0^*$	0.3

To examine the effect of discrete strike kinematics on the disparity in the measured force between the two species, we simulated largemouth bass strikes parameterized with the observed kinematics (Fig. 6A) with a gape similar to bluegill (gape simulation; Fig. 6B), with high strike efficiency and small gape (efficiency simulation; Fig. 6C), and a model including high strike efficiency, small gape and fast mouth displacement (mouth displacement simulation; Fig. 6D). In each case, first we regressed the simulated force against acceleration at the mouth (to account the observed intraspecific variation; Fig. 4) and then tested whether the slopes of the two species are different ('species effect'). R^2 and slope (columns 4,5) are statistics for the regression of force and acceleration at the mouth (mean \pm s.e.m.), significance level indicates a difference from slope of zero. 'Species effect' indicates whether the slope is different from that of bluegill. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

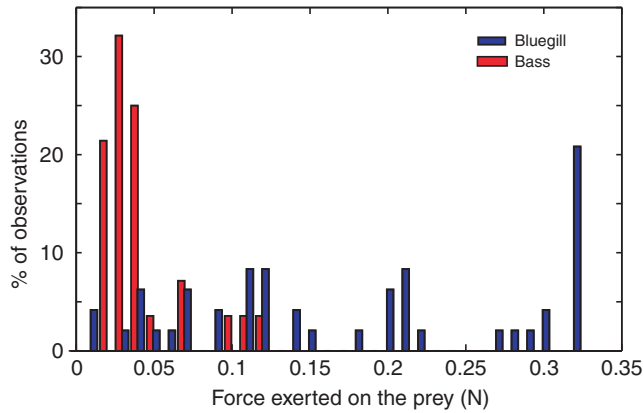


Fig. 3. The magnitude of peak force exerted on attached prey by largemouth bass (red bars; $N=4$ fish, 6–10 trials per fish; total $N=33$) and bluegill sunfish (blue bars; $N=4$ fish, 15 trials per fish; total $N=60$). The force measured for bluegill (0.16 ± 0.017 N); was much higher than the force measured for bass (0.03 ± 0.003 N; repeated-measures ANOVA, $P<0.001$). The difference in force was partly because bluegill's strike had, on average, twofold faster flow speeds and accelerations [estimated based on the relationship between TTPG and flow speed (Higham et al., 2006)].

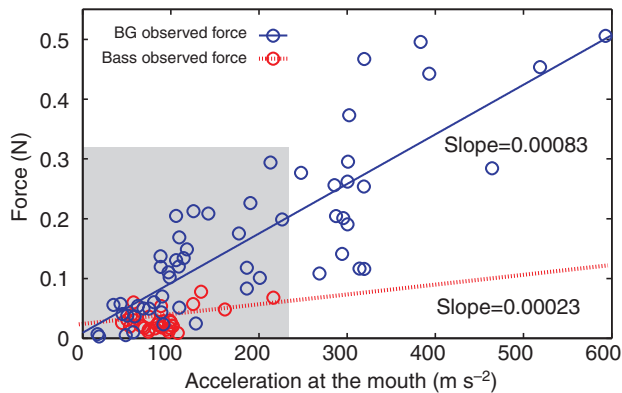


Fig. 4. Interspecific differences in the measured force exerted on attached prey. To take into account the intraspecific variation in the acceleration at the mouth aperture, we regressed the measured force against acceleration at the mouth and then compared the slopes for the two species. Similar slopes (and intercepts) would indicate that the differences in observed force are due to differences in the acceleration at the mouth alone. However, the slope of the regression was significantly different between species (mixed-effects model, $P<0.05$), indicating a contribution of other factors to the difference in force. Forces exerted by bluegill (BG) are indicated by blue open circles and blue regression lines, largemouth bass data are indicated by red open circles and red broken regression lines. Grey background represents the observed range of accelerations at the mouth for bass.

model, determined whether the slopes for the two species were different (Table 1).

First, we parameterized bass strikes with a small, bluegill-like mouth, which is expected to augment force on the prey by inducing a sharper spatial gradient in flow velocity (Wainwright and Day, 2007). The forces exerted by our simulated 'small mouth' bass were only ~13% higher than the measured forces under the observed bass kinematics, and were still significantly weaker than those measured for bluegill (slope of $2.63\times 10^{-4}\pm 0.93\times 10^{-4}$ N m s⁻²; mixed-effects model, $F_{1,7}=7.1$, $P<0.001$ for species effect) (Table 1).

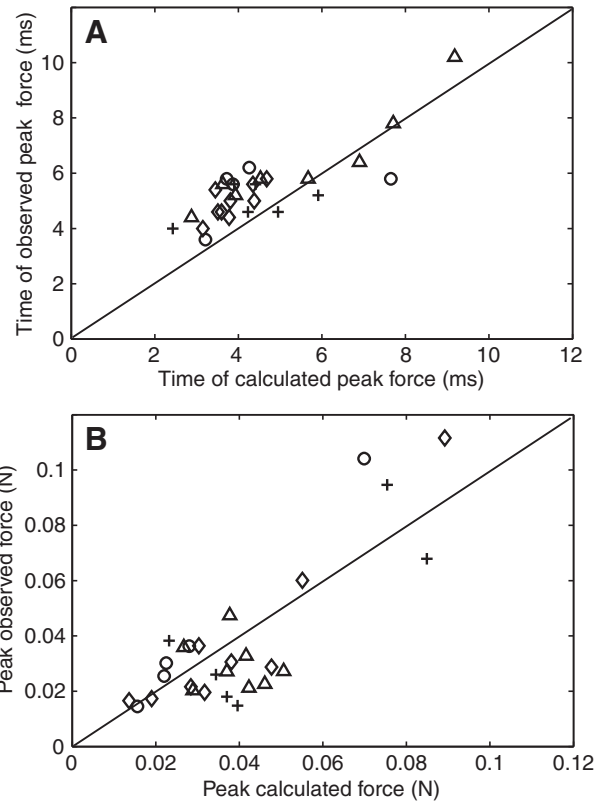


Fig. 5. Comparison of timing and magnitude of the observed and calculated forces exerted by largemouth bass on tethered prey. Time 0 (A) is the first frame digitized in the image sequence (~10 frames prior to the onset of gape, arbitrarily selected for each sequence). The timings of the observed and calculated peak force were linearly correlated (mixed-effects model, $R^2=0.659$; $F_{1,23}=50.6$, $P<0.001$), with the timing for observed peak force preceding that of the expected force (slope=0.66). Similarly, the peak calculated force was correlated with the observed one (mixed-effects model, $R^2=0.68$; $F_{1,23}=55.74$, $P<0.001$) and a slope of 1.02 (B). Different symbols represent data for the four fish studied, diagonal line represents the case of $x=y$.

Next, we simulated bass to strike from the distance that maximized force exerted on the prey (Holzman et al., 2007) by systematically varying strike initiation distance for each strike to find the highest peak force. The force exerted by the 'efficient' bass was doubled compared with the measured force (slope of $5.07\times 10^{-4}\pm 1.1\times 10^{-4}$ N m s⁻²; mixed-effects model, $F_{1,7}=7.28$, $P<0.01$ for species effect) (Table 1) but was still approximately half that exerted by bluegill.

However, we could account for the difference in force when simulated bass were parameterized with mouth displacement speeds equal to those of bluegill, in addition to similar mouth size and high strike efficiency. The 'bluegill-like bass' exerted ~53% more force than 'efficient bass' [slope of $7.71\times 10^{-4}\pm 3.0\times 10^{-4}$ N m s⁻² (mixed-effects model; $F_{1,7}=1.1$, $P>0.3$ for species effect)] (Table 1), indicating that differences between species in mouth displacement speed have a large influence on the forces exerted on their prey.

We partitioned the contribution of each change in bass kinematics by comparing the force exerted on the prey before and after the change, and dividing this difference by the force in the most inclusive model (bass with small mouth, high strike efficiency and fast mouth displacement speeds). The contribution of mouth size was $3\pm 0.9\%$ of the total force, whereas bluegill-like efficiency contributed

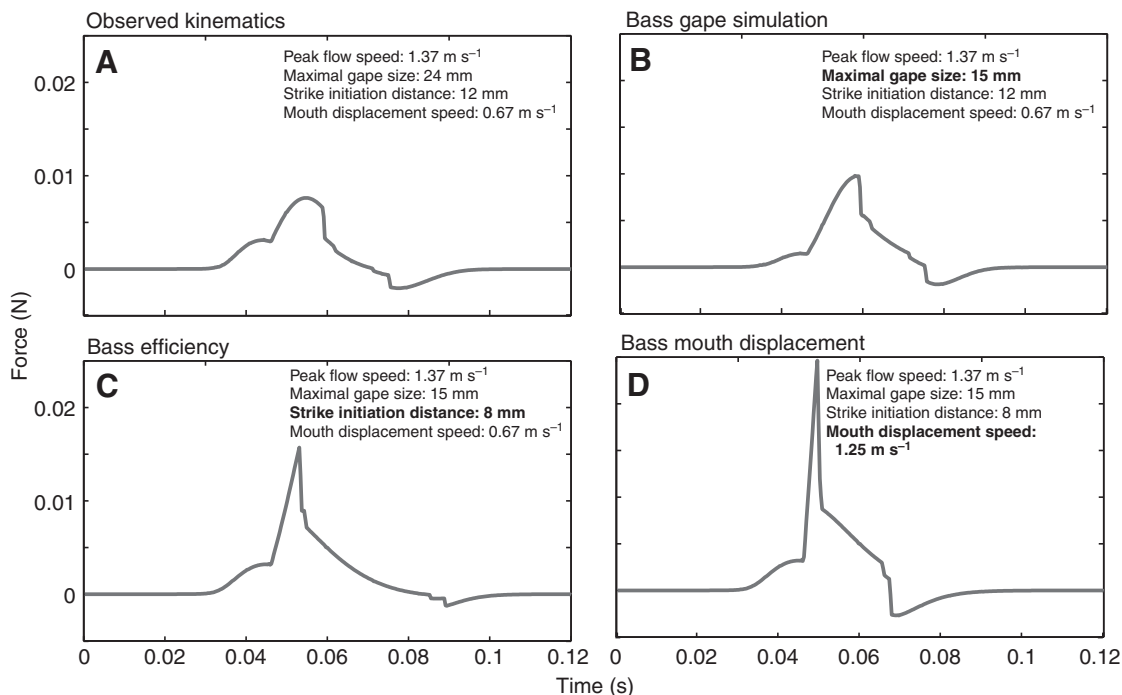


Fig. 6. The effects of discrete kinematic variables on the force exerted on the prey in a representative bass strike, illustrated using the force model. Firstly, the force model was first run with the observed kinematics, returning the expected force as a function of time (A). Peak force was recorded and the maximal gape was then changed to fit the mean bluegill gape, force was recalculated (B) and peak force recorded. Next, we changed strike initiation distance to increase strike efficiency (C) and finally we changed mouth displacement speed to fit the mean bluegill speed (D). The procedure (A–D) was repeated for each strike and peak force was recorded following each change. Note that changes to kinematics are cumulative so that each model retains the changes made previously. Each change to kinematics appears in bold font when first made.

25.1±4% and bluegill-like mouth displacement speed contributed 29.8±3.7% of the force. The remaining 42.1±3.5% was contributed by the acceleration at the mouth.

DISCUSSION

In this study, we investigated the factors contributing to interspecific differences in the force exerted on attached prey by suction-feeding fishes. In our experiments, strike kinematics of bass were slower than that of bluegill, leading to an estimated twofold difference in flow speeds and acceleration at the mouth between the two species. The overall force exerted on the prey by bluegill was much higher than the force exerted by bass. Surprisingly, this difference persisted in our model calculations even after taking into account the differences in flow speeds. Only after accounting for parameters, such as differences in strike efficiency, gape size and mouth displacement speed, were we able to explain the observed differences in the overall force exerted by the two species. While the difference in gape size contributed relatively little (3%) to the discrepancy in force exerted by the two species, the contribution of strike efficiency and mouth displacement speed was much higher (~25% and ~30%, respectively). Acceleration at the mouth was the primary contributor to the forces exerted on the prey, contributing 42% of the total force. None of the discrete changes was sufficient to explain the intraspecific differences in the force exerted on the prey.

In this study, we addressed some of the questions discussed by Van Leeuwen and Muller who quantified the separate contribution of swimming, mouth expansion and jaw protrusion to the speed of the prey relative to the predator (Van Leeuwen and Muller, 1984). Whereas their model treated the prey as an element of water, with

no velocity differential between the prey and the surrounding fluid, our work took advantage of recent theoretical developments (Wainwright and Day, 2007) and treated the aquatic predator–prey interaction as a hydrodynamic interaction between fluid and solid in an unsteady flow. Indeed, the conclusions of Van Leeuwen and Muller (Van Leeuwen and Muller, 1984) will, in general, be altered by consideration of the nature of the forces that are exerted on more realistic prey types. Whereas Van Leeuwen and Muller (Van Leeuwen and Muller, 1984) concluded that flow speed is the major factor contributing to strike success (estimated using the flow at the mouth), the results of the present study indicate that acceleration, rather than flow speed, is the most important factor in determining the force exerted on the prey (see also Wainwright and Day, 2007). As the two will usually be correlated within species (Holzman et al., 2008), this is not necessarily the case between different species (for example, if two species can generate the same flow speed but one does so with larger buccal cavity and slower expansion rate, acceleration will be slower for that species). Moreover, by not accounting for the effects of jaw protrusion and ram speed (together accounting for mouth displacement speed) on acceleration at the frame of reference of the prey, Van Leeuwen and Muller (Van Leeuwen and Muller, 1984) underestimate the contribution of rapid mouth displacement (swimming and jaw protrusion), which can substantially increase the force experienced by attached and escaping prey (Holzman et al., in press). Lastly, Van Leeuwen and Muller (Van Leeuwen and Muller, 1984) did not account for variation in strike efficiency, which had a substantial effect on our results. Note also that, for the same flow speed, gape size had a small effect in our calculations but would not have any effect on the calculations of Van Leeuwen and Muller (Van Leeuwen and Muller, 1984).

Functional morphologists interested in the relationship between structure and function often test hypotheses by comparing the performance of species located along an axis of morphological variation (e.g. Carroll et al., 2004; Gibb and Ferry-Graham, 2005; Van Wassenbergh et al., 2006a; Waltzek and Wainwright, 2003). In suction-feeding fishes, one primary axis of interest has been the ability to generate low pressure in the buccal cavity and the corresponding ability to produce flow speed outside the mouth (Carroll et al., 2004; Higham et al., 2006; Nauwelaerts et al., 2007; Van Wassenbergh et al., 2006a; Westneat, 2006; Wilga et al., 2007). However, the comparison outlined in the present study demonstrates that functional diversity in mouth displacement kinematics, strike efficiency and gape size all influence the ability of the fish to exert a suction force on the prey, given the velocity and acceleration of water they are able to generate (Holzman et al., 2007; Wainwright et al., 2007; Wilga et al., 2007). Although the effect of mouth size was modest in the case of the two species we examined, differences in gape size can be more important in other interspecies comparisons, where differences in mouth size are larger.

Importantly, the complexity underlying suction feeding morphology [the ability to produce strong suction flows, 'suction index' (Carroll et al., 2004)], jaw protrusion linkages and the ability to coordinate strikes to exert maximal force on the prey may permit independent evolution of musculoskeletal mechanisms that influence suction feeding performance (Alfaro et al., 2005; Collar and Wainwright, 2006; Wainwright et al., 2007). This functional complexity, in the form of skeletal, semi-independent mechanisms that can be recruited to enhance an overall function, can potentially mitigate performance trade-offs (Alfaro et al., 2005; Hulsey et al., 2006; Lynch and Conery, 2003; Wainwright, 2007). For example, an evolutionary change that limits the ability to produce buccal pressure can potentially be mitigated by any of the three mechanisms (increased mouth displacement speed, decreased mouth size and higher strike efficiency). However, to the best of our knowledge, no study has yet quantified the evolutionary integration or independence of suction feeding components. Independence of these mechanisms can result in a diversity of evolutionary transformations that can potentially result in similar levels of force being exerted on prey, another example of many-to-one mapping (Alfaro et al., 2005; Wainwright, 2007).

Faster mouth displacement speed is a major contributor to the higher forces exerted by bluegill on its prey (Holzman et al., in press). Jaw protrusion is recognized as a major innovation in the teleost feeding mechanism permitting fast mouth displacement speed (Motta, 1984; Schaeffer and Rosen, 1961; Westneat, 2004). Several hypotheses for the possible selective advantage of jaw protrusion for aquatic feeding have been proposed (Coughlin and Strickler, 1990; Lauder, 1982; Motta, 1984; Van Leeuwen and Muller, 1984), related either to the increase in speed of closing in on the prey due to protrusion (Lauder, 1982; Motta, 1984; Osse, 1985; Van Leeuwen and Muller, 1984) or explained in the context of specific feeding scenarios, such as feeding from a substratum or in a spatially complex habitat (Lauder, 1982; Motta, 1984). Whereas variation in jaw protrusion distance and speed across teleost species is considered an important axis of morphological and ecological diversification (Waltzek and Wainwright, 2003; Westneat, 2006; Westneat and Wainwright, 1989; Westneat et al., 2005), there has been little evidence for the functional consequences of this variation. This new insight into the role of mouth displacement speed in suction feeding provides an opportunity for larger-scale comparative studies on the evolution of jaw protrusion and ram as mechanisms for augmenting the force on the prey. Having established a functional link between the structure and function of jaw protrusion, it is possible to

formulate and test hypotheses on the origin and diversity of jaw protrusion linkages and levers, taking into account the hydrodynamic consequences of jaw protrusion.

In this study, we used two species located at the opposite extremes of the morphological potential for suction production among centrarchids, representing 'velocity' vs 'volume' suction feeders (Higham et al., 2006; Osse and Muller, 1980). Within centrarchids, bluegill produce the strongest measured suction pressure within their buccal cavity (Carroll et al., 2004), and they possess the highest morphologically based suction index (Collar and Wainwright, 2006) and fast suction flows (Higham et al., 2006). Bass are characterized by a poorer ability to produce intra-oral pressure and have a much lower suction index (Carroll et al., 2004; Collar and Wainwright, 2006). Bluegill, however, are characterized by a higher volumetric flow rate (Higham et al., 2006). Under our experimental design, the two species also differed markedly in strike kinematics, including the speed of mouth displacement and their ability to produce fast accelerations at their mouth aperture. Using a hydrodynamic model for calculating the force exerted on the prey, we could relate performance differences between the two species to those interspecific differences. The analysis of interspecific differences in mouth displacement speed could also be used to examine the consequences of mouth displacement speed in a broader phylogenetic context. Such a comparison should account for interspecific differences in suction capacity (the magnitude of external flows), morphology (gape size) and ram speed and jaw protrusion speed. These traits can be measured directly for the species or deduced from kinematics and morphological predictors. For example, the magnitude of external flows can be directly measured using flow visualization methods [PIV (Higham et al., 2006)] but for a large number of species it is probably more practical to predict that flow based on TTPG or buccal expansion rates [strike kinematics (Van Wassenbergh et al., 2006a)], pressure measurements or suction morphology [suction index (Carroll et al., 2004; Collar and Wainwright, 2006)]. Similarly, jaw protrusion can be measured directly but can also be deduced from jaw morphology based on jaw linkage geometry (Westneat, 1994). Other data, such as diet type and breadth, and habitat use can be added to the analysis. Variation in jaw protrusion speed and extension is also a conspicuous axis of diversification within elasmobranchs (Motta and Wilga, 2001; Wilga et al., 2001; Wilga et al., 2007). It would be interesting to evaluate the relative role of protrusion and ram in both sharks and rays and their contribution to suction feeding performance.

The two species used in this study represent extremes of the trophic diversity in Centrarchidae, with bluegill representing a planktivorous suction feeder and bass representing a specialized ram-suction feeding piscivore (Carroll et al., 2004; Collar and Wainwright, 2006; Gibb and Ferry-Graham, 2005; Higham et al., 2006; Norton and Brainerd, 1993). Although bluegill often feed on insect larvae that cling to their holdfast in response to feeding strikes (Flemer and Woolcott, 1966; Huish, 1957; Sadzikowski and Wallace, 1976; VanderKooy et al., 2000), the experimental setup used in the present study probably does not reflect a common scenario for bass [although the range of TTPG and strike initiation distances corresponds to previous observations (Higham et al., 2006; Svanback et al., 2002)]. However, direct measurements of the force exerted on the prey can only be made on attached prey, and we could apply the hydrodynamic model only with an established correlation between feeding kinematics and external flows in bass and bluegill. Therefore, the aim of this study was not to determine the force requirements for planktivory and piscivory but to assess possible kinematic and mechanisms for interspecies variation in the force exerted on the prey, measured as a metric of suction performance.

The use of mechanistic models has the potential to mitigate one of the major challenges in testing animal performance, the need to maintain a constant motivation through replicated measurements or while measuring different individuals. Under many circumstances, behavioral issues (such as satiation and learning) can affect the observed performance as much as physiological and morphological parameters, possibly masking the relationships between function and structure. A common solution to this problem is to regard the highest observed value (or other cut-off percentile) for each individual subject as a representation of maximum performance (e.g. Carroll et al., 2004; Higham et al., 2006; Kargo et al., 2002; Smith, 1991). Along with the uncertainty in relating observed and maximal performance, dismissing potentially informative data (often gained with considerable effort) can lead to a significant loss of statistical and explanatory power. This study demonstrated how intraspecific and interspecific variations and differences in the magnitude of acceleration of fluid at the frame of reference of the mouth can be taken into account if the effects on performance can be assessed by a mechanistic model. Clearly, a key to this approach in our study was the validation of the model, indicated by the good fit between observed and calculated force. A similar approach was demonstrated in an earlier study (Holzman et al., 2007) where the force model was used to assess the effects of strike initiation distance on the force exerted on the prey.

In the present study, we measured the force exerted on attached prey by bluegill sunfish and largemouth bass as an indication of their suction feeding performance. Strike kinematics of bass were slower than that of bluegill, and estimated flow speeds, as well as force exerted on the prey, were lower for bass. This difference in force persisted after taking into account the faster suction flows and acceleration of bluegill, and was only accounted for by considering interspecific differences in gape size, mouth displacement speed, and the fish's ability to locate the prey at the optimal position. The contribution to interspecific differences in the force exerted on the prey was estimated as 42% for flow speed, 25% for positioning ability, 3% for gape size and 30% for mouth displacement speed. This study demonstrates that while the ability to produce fast flows and accelerations at the mouth aperture are a fundamental aspect of suction feeding performance, there is a set of mechanisms and behaviors that modify the flow in the frame of reference of the prey that can substantially alter the effectiveness of these flows.

APPENDIX

Use of strike kinematics to calculate the force exerted on aquatic prey

In this Appendix, we show the framework for deducing the force exerted on the prey from fish strike kinematics. The link between strike kinematics and flows external to the mouth is based on insights from PIV studies on live fish, including the observed relationship between speed of mouth opening (TTPG) and the magnitude of peak flow speed, and the relationship between gape size and the spatial patterns of decaying flow velocity in front of the mouth. Our methods are summarized in the following text and in Fig. S1 in supplementary materials.

First, the temporal pattern of flow at the mouth ($u_{m(t)}$) was described as a continuous function using the equation:

$$u_{m(t)} = u_{\max} \left[\left(\frac{t - t_{\text{nul}}}{t_{\text{max}}} \right) \cdot \exp \left(\frac{t - t_{\text{nul}}}{t_{\text{max}}} \right) \right]^\alpha \quad (\text{A1})$$

(modified from Muller et al., 1982). The time of flow initiation (t_{nul}) and time of peak flow speed (t_{max}) were set to equal the observed time of 20% and 95% of peak gape (Day et al. 2005) for each strike.

Initial flow speed was 0, and peak flow speed u_{\max} was estimated based on TTPG using the relationships found in Day et al. (Day et al., 2005) for bluegill and in Higham et al. (Higham et al., 2006) for bass. The form coefficient α for the flow speed profile was equated to the observed form coefficient of the gape for each strike. Acceleration at the mouth was calculated as the instantaneous change in flow speed at the mouth (Holzman et al., 2007). Flow speed at the location of the prey was then estimated at each time step as a function f of flow speed at the mouth (u_m ; Eqn A1) and the distance from the mouth aperture x' at time t :

$$u_x = f(u_m, x')_{(t)}. \quad (\text{A2})$$

Eqn A2 was parameterized based on the empirical relationships between gape and flow speed as in Day et al. (Day et al., 2005) for bluegill and in Higham et al. (Higham et al., 2006) for bass.

The speeds and derived accelerations at the location of the prey were used, in turn, to calculate the total and component forces exerted on the prey [drag, pressure gradient force and acceleration reaction (Batchelor, 1967; Wainwright and Day, 2007)] using observed strike kinematics and measured prey size. To account for the differences in flow speeds along the long axis of the prey, we integrated the forces over a series of 2 mm long bins along this axis (Holzman et al., 2007).

Pressure gradient force (F_{pg}) was calculated from the temporal and spatial gradients of velocity [local and convective accelerations, respectively (Batchelor, 1967)] and prey dimensions using the momentum equation (Batchelor, 1967; Wainwright and Day, 2007) so that:

$$F_{\text{pg}} = -\rho \cdot \left(\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} \right)_p \cdot L_x \cdot A_f, \quad (\text{A3})$$

where ρ is the density of the surrounding medium (kg m^{-3}), L_x is the effective dimension of the prey in the x -direction (m) and A_f is the frontal area of the prey (m^2).

Local acceleration $\partial u / \partial t$ is defined as the rate of change of flow velocity at a given point in space (the prey, p , in this case) with time t (Batchelor, 1967). Local acceleration was calculated at 0.0003 s increments, based on the temporal pattern of flow at the fish's mouth (Eqn A1), the rate of decreasing flow with distance from the mouth, and the distance between the mouth and the location of the prey (Eqn A2) so that:

$$\left(\frac{\partial u}{\partial t} \right)_p = \frac{f(u_m, x')_{(t_2)} - f(u_m, x')_{(t_1)}}{t_2 - t_1}, \quad (\text{A4})$$

with Eqn A2 used to parameterize $u_x = f(u_m, x')_{(t)}$ (see above).

Convective acceleration $u(\partial u / \partial x)$ is defined as the rate of spatial change in the flow speed at the prey u along the flow's main axis x (perpendicular to the gape; Batchelor, 1967) and was calculated at 0.1 mm increments (Δx) so that:

$$\left(\frac{\partial u}{\partial x} \right)_p = \frac{f[u_m, (x' - \Delta x)]_{(t_1)} - f[u_m, (x' + \Delta x)]_{(t_1)}}{2\Delta x} \quad (\text{A5})$$

with Eqn A2 used to parameterize $f(u_m, x')_{(t)}$.

Similarly, acceleration reaction force (F_{ar}) depends on the sum of local and convective acceleration at the prey, on the volume of the prey V (m^3), the density of the surrounding water ρ , and the coefficient of added mass C_{am} :

$$F_{\text{ar}} = C_{\text{am}} \cdot V \cdot \rho \cdot \left(\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} \right)_p. \quad (\text{A6})$$

Lastly, drag was calculated using the prey's drag coefficient (C_d), wetted area (A_w), the density of the surrounding medium and the flow speed (u_p) squared:

$$F_d = 0.5 \cdot C_d A_w \rho (u_x)^2. \quad (A7)$$

Prey volume, length, and diameter were obtained for each sequence from our video records, whereas drag and added mass coefficients were measured or estimated for our prey (Holzman et al., 2007).

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