

RESEARCH ARTICLE

Independently evolved upper jaw protrusion mechanisms show convergent hydrodynamic function in teleost fishes

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SUMMARY

A protrusible upper jaw has independently evolved multiple times within teleosts and has been implicated in the success of two groups in particular: Acanthomorpha and Cypriniformes. We use digital particle image velocimetry (DPIV) to compare suction feeding flow dynamics in a representative of each of these clades: goldfish and bluegill. Using DPIV, we contrast the spatial pattern of flow, the temporal relationship between flow and head kinematics, and the contribution of jaw protrusion to the forces exerted on prey. As expected, the spatial patterns of flow were similar in the two species. However, goldfish were slower to reach maximal kinematic excursions, and were more flexible in the relative timing of jaw protrusion, other jaw movements and suction flows. Goldfish were also able to sustain flow speeds for a prolonged period of time as compared with bluegill, in part because goldfish generate lower peak flow speeds. In both species, jaw protrusion increased the force exerted on the prey. However, slower jaw protrusion in goldfish resulted in less augmentation of suction forces. This difference in force exerted on prey corresponds with differences in trophic niches and feeding behavior of the two species. The bluegill uses powerful suction to capture insect larvae whereas the goldfish uses winnowing to sort through detritus and sediment. The kinethmoid of goldfish may permit jaw protrusion that is independent of lower jaw movement, which could explain the ability of goldfish to decouple suction flows (due to buccal expansion) from upper jaw protrusion. Nevertheless, our results show that jaw protrusion allows both species to augment the force exerted on prey, suggesting that this is a fundamental benefit of jaw protrusion to suction feeders.

Key words: fluid dynamics, Cypriniformes, DPIV, digital particle image velocimetry, premaxillary protrusion, suction feeding.

INTRODUCTION

Predator–prey interactions in an aquatic environment are subject to the physical constraints of life in a fluid. Given that water is 900 times denser and 80 times more viscous than air (Vogel, 1994), the forward motion of an aquatic predator can exert a hydrodynamic force on the prey in the same direction and push the prey away from the predator (Van Damme and Aerts, 1997). The majority of aquatic vertebrates exploit this physical reality by suction feeding (Lauder, 1980; Lauder, 1982; Lauder, 1985), during which they expand the volume of the buccal cavity, thus decreasing intra-oral pressure and creating a flow of water into the mouth (Muller et al., 1982; Day et al., 2005; Van Wassenbergh and Aerts, 2009). During prey acquisition strikes, many fishes move the mouth opening closer to the prey *via* a structural decoupling of the jaws from the neurocranium, known as premaxillary protrusion or jaw protrusion.

Although hypotheses to explain the advantages of premaxillary protrusion have been made for almost a century (e.g. Eaton, 1935; Alexander, 1967; Motta, 1984; Osse, 1985), only within the last few decades have technical advances in functional morphology allowed the rigorous testing of some hypotheses. For example, jaw protrusion has long been hypothesized to enhance suction generation (Lauder and Liem, 1981; Motta, 1984). However, using modern experimental methods, Waltzek and Wainwright (Waltzek and Wainwright, 2003) showed that cichlids exhibiting extreme jaw protrusion generate less suction than species with smaller protrusion

distances. Empirical evidence shows that a protrusible upper jaw is advantageous because it increases ram velocity of the predator (Waltzek and Wainwright, 2003; Westneat and Wainwright, 1989; Ferry-Graham et al., 2001). Recently, it has been shown that premaxillary protrusion in bluegill can increase total forces exerted on prey by up to 35% (Holzman et al., 2008c). This is because the rapid advancement of the mouth towards the prey increases the acceleration of the fluid around the prey, a major component of force when prey resist the flow by clinging to a holdfast or swimming away from the predator (Wainwright and Day, 2007; Holzman et al., 2007; Van Wassenbergh and Aerts, 2009).

Given force augmentation and other potential performance advantages associated with premaxillary protrusion, it is not surprising that this trait has independently evolved numerous times in teleosts (Westneat, 2004) (Fig. 1). Moreover, jaw protrusion has been suggested as a major factor in the trophic diversification seen in two major radiations that represent independent origins of jaw protrusion, the Cypriniformes and the Acanthomorpha (Schaeffer and Rosen, 1961; Rosen, 1982; Albertson et al., 2005).

Although members of both groups protrude their upper jaws toward their prey, they achieve jaw protrusion through different mechanisms (Fig. 1B,C). Briefly, acanthomorphs possess linkages between the upper and lower jaws so that when the lower jaw is depressed, the upper jaw is pulled anteriorly (Schaeffer and Rosen, 1961). Although cypriniforms also possess linkages between the

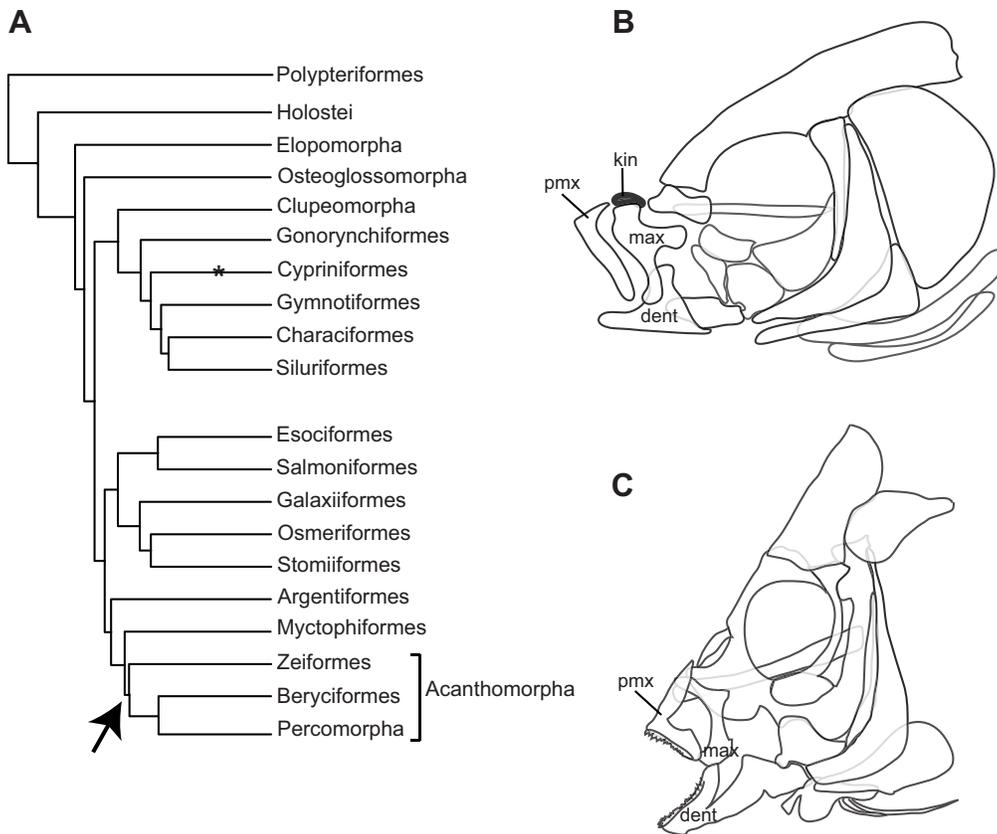


Fig. 1. (A) Two of the origins of jaw protrusion within teleosts, Cypriniformes (*) and Acanthomorpha (arrow). In each group, jaw protrusion is widespread, has been modified in numerous ways and is the prominent feature of the feeding mechanism. The tree is based on data from Santini et al. (Santini et al., 2009). (B) Goldfish, a representative cypriniform, protrudes its upper jaw using the kinethmoid, a midline sesamoid bone. The kinethmoid, a cypriniform synapomorphy, is ligamentously attached to the premaxillae, maxillae, palatines, and neurocranium. (C) Bluegill, a centrarchid perciform, protrudes its upper jaw via linkages to the lower jaw (see Introduction). Dent: dentary; kin: kinethmoid; max: maxilla; pmx: premaxilla.

upper and lower jaws, these fishes have an additional bone involved in the jaw protrusion mechanism. The kinethmoid, a synapomorphy uniting cypriniforms, is a novel median bone that is suspended by ligaments linking the upper jaws to the neurocranium (Hernandez et al., 2007; Staab and Hernandez, 2010). As the mouth opens, the kinethmoid rotates anteriorly, and the premaxillae are protruded by forces acting at the posterior end of the premaxilla ascending process. Although variation in jaw protrusion distance and speed has been noted across many taxa (Westneat and Wainwright, 1989; Waltzek and Wainwright, 2003; Westneat et al., 2005; Westneat, 2006; Gibb and Ferry-Graham, 2005), its effect on suction-feeding fluid speed and the hydrodynamic force exerted on the prey has been studied only in Centrarchidae, a group of acanthomorphs (Holzman et al., 2008b). It is not yet understood how cypriniform jaw protrusion affects fluid flow patterns during suction feeding.

The primary objective of this study was to test for convergence in the hydrodynamic effects of jaw protrusion in acanthomorphs and cypriniforms. Using goldfish as a representative cypriniform, we employed digital particle image velocimetry (DPIV) to characterize the flows produced during feeding events and compare these data with patterns observed in bluegill, a representative acanthomorph. We measured the timing and magnitude of peak fluid speeds and accelerations generated by goldfish during suction and used these measurements to calculate the forces exerted on the prey. The specific goals of this work were to: (1) quantify the spatial and temporal patterns of flow anterior to the goldfish's mouth during feeding events, (2) calculate the force exerted on the prey and evaluate the effect of jaw protrusion on force generation, and (3) test whether these flow patterns and the effect of jaw protrusion on force generation are convergent in goldfish and bluegill. We found that although goldfish produce similar spatial patterns of flow, they do so using longer times to maximal excursions. Jaw protrusion in

goldfish does augment the force exerted on prey items, but to a lesser degree than what has been shown in bluegill.

MATERIALS AND METHODS

We studied the goldfish (*Carassius auratus* Linnaeus 1758), a cyprinid, and compared it with the bluegill (*Lepomis macrochirus* Rafinesque 1819), a centrarchid. The goldfish data presented herein are original, but were collected using the same methods as those used for bluegill (Day et al., 2005; Holzman et al., 2007; Holzman et al., 2008b; Holzman et al., 2008c) to facilitate the comparison. Those methods will therefore be only briefly described here.

Goldfish were purchased through the aquarium trade and were housed in 200 l aquaria at 22°C. All fish maintenance and experimental procedures followed a protocol approved by the University of California, Davis, Animal Care and Use Committee (no. 12790). The experimental aquaria consisted of a holding area and a filming area separated by a trap door. Within the filming area, an Innova I-90 5W Argon-Ion continuous wave laser (Coherent Inc., Santa Clara, CA, USA) was reflected off of mirrors to create a vertical sheet that corresponds with the sagittal plane of the fish. Prey (Cichlid Staple, a commercially available pellet; Hikari, Hayward, CA, USA) were attached to small wires suspended within the laser sheet. Neutrally buoyant 12 µm silver-coated reflective beads were suspended within the water and were used to visualize flow. To obtain food, fish were trained to swim through a trap door that oriented the fish to swim directly into the plane of the laser sheet.

Flow speeds and kinematics of goldfish head movements were analyzed from high-speed video sequences for three individual fish, and 10 feeding events were analyzed per individual. Videos of prey capture were recorded at 1000 images s⁻¹ with a Hi-Spec video camera (Fastec Inc., San Diego, CA, USA). The camera was

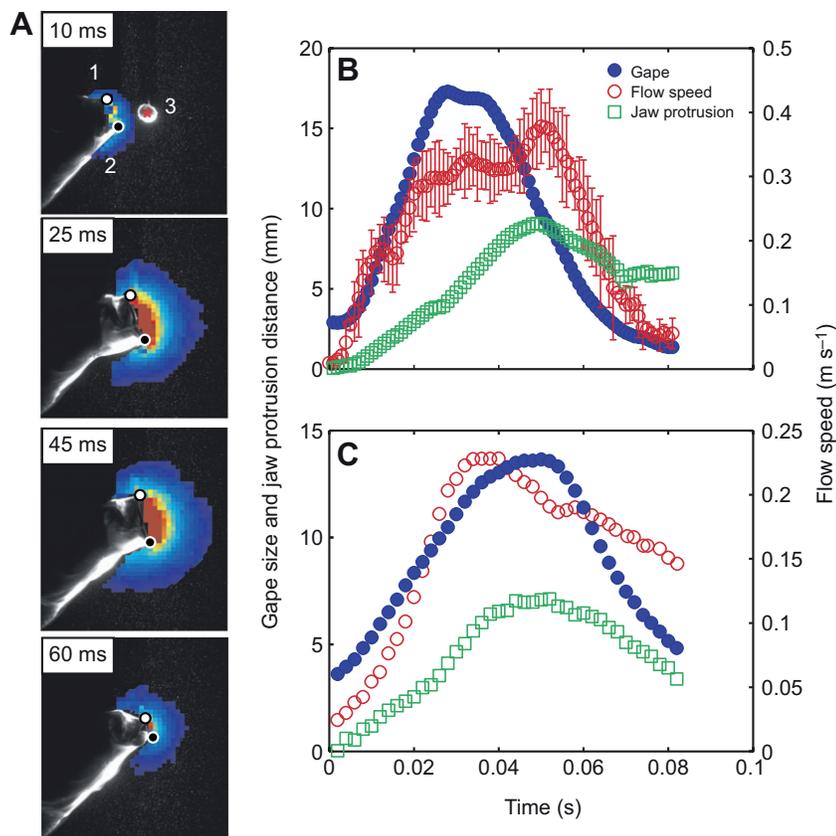


Fig. 2. The development of flow during feeding. (A) Four frames from a single feeding event showing the goldfish jaws and fluid flow. Warmer colors indicate faster fluid speeds. Digitized points are highlighted: (1) upper jaw (open circle), (2) lower jaw (filled circle) and (3) center of prey (red asterisk). (B) Representative kinematic plot of goldfish from the same feeding event shown in A. Error bars for flow speed indicate standard error of the 21 points along the radian at which flow speed was quantified (see Materials and methods) for more details). Note that peak flow speed occurs well after peak gape. (C) Representative kinematic plot of a bluegill feeding event (Holzman et al., 2008a). Peak flow speed occurs near the time of peak gape in bluegill.

positioned at a right angle to the light sheet, and captured lateral views of the fish. Distances in the videos were scaled by recording an image of a ruler placed in the field of view. Feeding sequences were saved as avi files and analyzed in MatPIV, a freely available toolbox for analyzing DPIV in MATLAB software (The MathWorks, Natick, MA, USA). MatPIV treats the avi files as a series of frames that are analyzed as image pairs, each pair consisting of two successive frames from the high-speed video sequence. MatPIV uses a cross-correlation algorithm to produce two components of velocity for each location on a regularly spaced grid for each image pair, estimating the speed and direction of each particle in 1 ms intervals. The algorithm also calculates a signal-to-noise ratio to validate the velocity measurements.

Simultaneously, a separate digital camcorder (Sony Inc., Tokyo, Japan) was used to capture anterior views of the fish at 30 Hz to verify that the plane of the laser sheet was positioned near the midline of the feeding fish's mouth during the strike. No measurements were taken from the anterior view; these sequences were used to eliminate high-speed footage not within the laser sheet and to exclude strikes in which the body axis of the fish was not parallel to the light sheet.

Spatial patterns

To examine the spatial distribution of flow velocities in front of the fish's mouth, flow speeds were calculated along five transects that extended anteriorly at different angles from the center of the mouth. The centerline transect (0 deg) extended forward along the long axis of the fish from the center of the gape in the sagittal plane. Four more sagittal transects extended at 30, -30, 60 and -60 deg from the center of the mouth. The length of each transect was fixed at twice the distance of maximum gape diameter for each feeding event and distances along each transect were scaled to the peak gape distance for that particular feeding sequence. Measured fluid speeds

were scaled (μ_{scaled}) by dividing by the speed located at a distance of $\frac{1}{2}$ gape in front of the fish. This scaling method accounts for strike-to-strike variation in the magnitude of fluid speeds (Day et al., 2005) and facilitates comparison with previous work on bluegill (Day et al., 2005; Holzman et al., 2008b). For each strike, the velocities along these transects were calculated at a random point in time when gape was >50% of peak gape.

Temporal patterns

We examined the temporal relationship between flow and head kinematics in the goldfish with a focus on the timing of flows relative to jaw protrusion and gape kinematics. Because the external flows are radially symmetrical with respect to the mouth (Day et al., 2005) (see Results), we calculated fluid speeds at 21 points along a radian that was a distance of $\frac{1}{2}$ peak gape from the front of the mouth. The 21 points were located at angular intervals of 5 deg from 50 to -50 deg with respect to the midline transect. The mean of these 21 measurements ($\mu_{1/2\text{PG}}$) was used for analysis of temporal patterns, and compared with feeding kinematics (Holzman et al., 2008a).

To track feeding kinematics, the anterior tip of the upper jaw, the anterior tip of the lower jaw, the center of the prey (along the anterior-posterior axis) and a landmark on the fish's body (when visible) were digitized from the lateral view camera using DLTdv3 (Hedrick, 2008). From these digitized points (Fig. 2A), we calculated the following distance and timing variables: peak gape distance, body ram, jaw protrusion distance (which is the movement of mouth center with respect to the body), mouth displacement (the sum of both body ram and jaw protrusion distance, which is equivalent to the movement of mouth center in the earth-bound frame of reference), time to peak gape (TTPG), time to maximum jaw displacement, time to prey capture, and maximum jaw displacement speed. To account for variation in timing of kinematic variables,

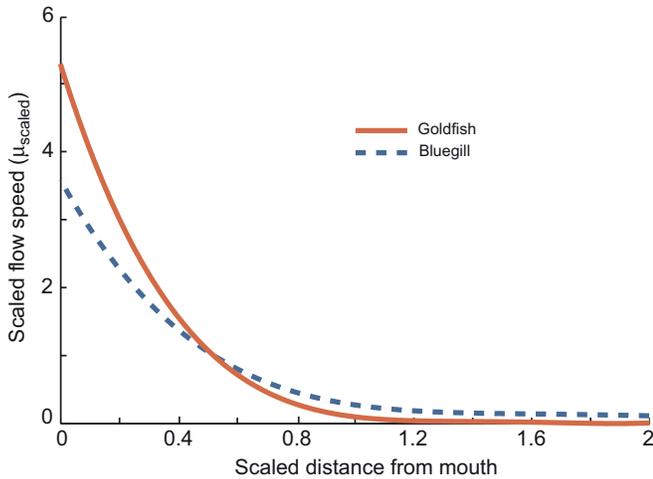


Fig. 3. Comparison of the spatial distribution of fluid velocities generated by goldfish and bluegill. Measurements were taken at the time of peak fluid speed. Both lines represent the data fit to the quadratic equation used by Day et al. (Day et al., 2005). The solid line represents the decay of flow in front of goldfish ($r^2=0.81$) and the dashed line represents data for bluegill [$r^2=0.986$ (Day et al., 2005)].

time 0 was set at the time of 20% peak gape and the time of peak gape was set when the mouth diameter was at 95% peak gape. Therefore, the time to peak gape (TTPG) is defined as the time interval between 20 and 95% peak gape (see Day et al., 2005). Ten strikes were analyzed for each of three fish.

Force calculations

We used the kinematics and flow field at the center of the mouth to evaluate forces exerted on prey with 0.3 ms resolution using the suction induced flow field (SIFF) model (Holzman et al., 2012).

The analysis simulated a situation of attached prey, which remained at a fixed position (in the earthbound frame of reference) through the strike. To measure the contribution of jaw protrusion to force production in each strike, we compared the forces exerted during the observed strikes (which included mouth displacement through jaw protrusion) with a hypothetical event in which there was no jaw protrusion. The specifics of these calculations are described elsewhere (Holzman et al., 2012), and SIFF is freely available at http://iui-eilat.ac.il/faculty/roi_SIFF/roi_SIFF.aspx. In brief, SIFF is based on the finding that fluid acceleration at the frame of reference of the prey is a major component of the forces exerted on prey, and that those accelerations are augmented by the rapid displacement of the mouth towards the prey (Holzman et al., 2008b; Holzman et al., 2008c; Holzman et al., 2012). SIFF uses mouth diameter (from the videos), flow speed at the center of the mouth (measured using the PIV), and the distance from predator to the prey to determine the gradient of flow speed across the simulated prey at each time point of the feeding event. For these calculations, ‘center of the mouth’ was defined by drawing an imaginary line from the tip of the premaxilla to the tip of the lower jaw and dividing by two for any time point. For these calculations, we used the observed strike initiation distance. In strikes where prey item was not present (when the fish struck after engulfing the prey), a predator–prey distance of ½ peak gape was used for the simulation.

Contrasting goldfish with bluegill

To compare performance variables between two independently derived mechanisms of upper jaw protrusion, we used our data collected from goldfish and contrasted them with previously measured data from bluegill (Day et al., 2005; Holzman et al., 2008b; Holzman et al., 2008c). Because each of the three goldfish was used more than once, there were two sources of variation in our data set: inter-individual and intra-individual. Moreover, our dependent variables (e.g. TTPG and peak flow speed) were correlated (see Results). To account for both of these sources of variance, we used

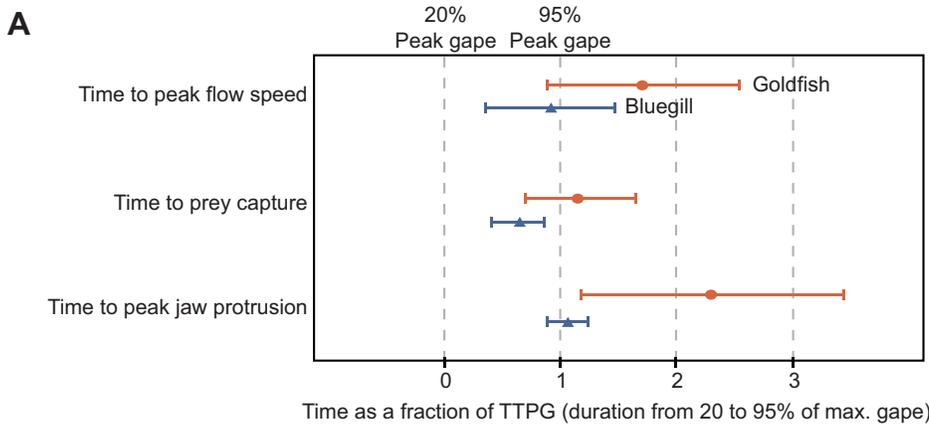
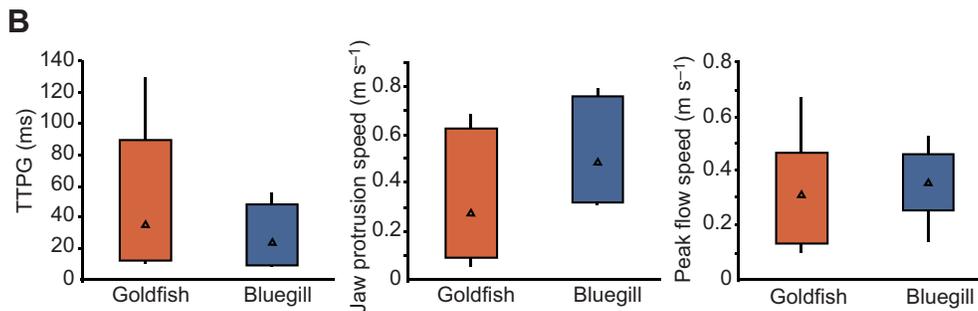


Fig. 4. Comparison of temporal patterns of flow and head kinematics in goldfish versus bluegill. (A) Timing to peak flow speed, prey capture and maximal protrusion as compared to peak gape (95% peak gape) in goldfish and bluegill. Differences between goldfish and bluegill are significant for each variable. Means with standard deviation are shown. All times are expressed as a proportion of time to peak gape (TTPG). (B) Boxplot showing comparisons of absolute magnitudes of TTPG, jaw protrusion speed and peak flow speed in goldfish and bluegill. Triangles show means for each species. Boxes enclose 95% confidence intervals. Error bars represent minimum and maximum measurements.



a repeated-measures multivariate ANOVA (MANOVA), which partitions the variance between and within individuals. We therefore used repeated-measures MANOVA to test for differences in the spatial and temporal patterns of flow between the bluegill and the goldfish. In that analysis, species was the categorical factor, strike order was the repeated-measures factor, and the following measurements were the multiple dependent variables: peak $\mu_{1/2PG}$, TTPG, time to peak $\mu_{1/2PG}$, time to peak mouth displacement, gape size, and mouth displacement speed.

To test the effect of jaw protrusion on force exerted on the prey, we used a mixed model approach (Pinheiro and Bates, 2000), which is a regression-like analysis that also partitions the variance between and within individuals. In this test, force on the prey was the independent variable and both jaw protrusion speed and acceleration of the flows were the dependent variables. Statistical analyses were performed using R (R Development Core Team, 2009).

RESULTS

Our primary objective was to contrast the hydrodynamics of suction feeding in two species that represent independent evolutionary origins of premaxillary protrusion. For bluegill, a detailed description of the hydrodynamics during suction feeding (Day et al., 2005) and the effect of premaxillary protrusion on the forces exerted on prey (Holzman et al., 2008c) has been presented elsewhere. Here we first present data on goldfish (Fig. 2) and then contrast these data with previously published data on bluegill (Day et al., 2005; Holzman et al., 2008b; Holzman et al., 2008c).

Spatial patterns

To quantify the distribution of flow velocities anterior to the goldfish mouth, we measured flow speed at each of 40 points along each of five transects extending at different angles from the mouth at the time of peak fluid speed. Flow velocities decreased rapidly as a function of distance from the mouth (Fig. 3). Spatial patterns of flow in the goldfish were best described by Muller's theoretical model [eqn 25 (Muller et al., 1982)]:

$$\mu_{\text{scaled}} = \frac{4.2 \times (0.5)^3}{\sqrt{(x^2 + 0.25)^3}}, \quad (1)$$

where μ_{scaled} is flow speed divided by flow speed at the center of the mouth, and x is the distance in units of gape size ($R^2=0.91$). There was no significant difference in slopes among angles (mixed effect model; $t=1.3$, $P<0.18$). The quadratic model used by Day et al. (Day et al., 2005) also provided a good fit for the scaled speeds, averaged along all five angles ($R^2=0.81$; Fig. 3). There was no significant difference in slope among the five angles (mixed effect model, $t=-0.66$, $P>0.5$). The decay of flow speed as a function of the scaled distance in front of the mouth can also be described using the quadratic model:

$$\mu_{\text{scaled}} = 0.97x^4 - 6x^3 + 13.8x^2 - 13.96x + 5.13. \quad (2)$$

Goldfish and bluegill produced a spatial pattern of flow that decays in a similar way, which can be described by quadratic functions. To statistically compare spatial patterns of flow between goldfish and bluegill, the observed fluid speeds in goldfish were regressed against what is expected in bluegill, based on the quadratic equation reported by Day et al. (Day et al., 2005). Observed speeds for goldfish were also regressed against the Muller equation [eqn 25 (Muller et al., 1982)], which had been parameterized for bluegill. Although the correlations were high for both the quadratic model and the Muller model ($R^2=0.915$ and 0.89 , respectively), spatial patterns of fluid speed in goldfish were significantly different than the patterns seen in bluegill

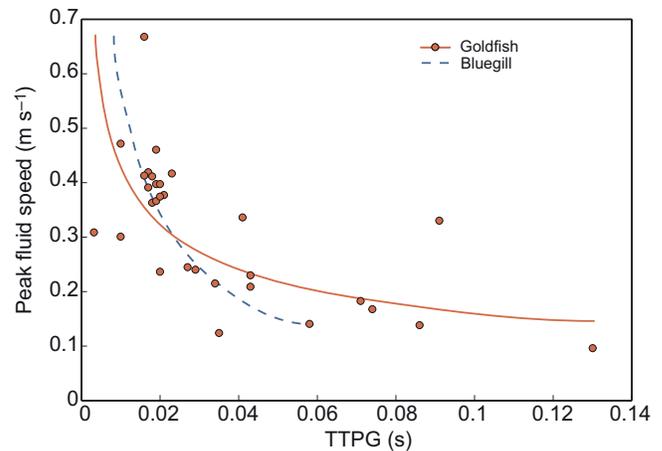


Fig. 5. The relationship of peak fluid speed with time to peak gape (TTPG) for each strike. Points represent individual goldfish strikes; solid line indicates goldfish power fit; dashed line shows bluegill power fit (Day et al., 2005). Maximum fluid speed anterior to the mouth is linked with TTPG, but this relationship is more obvious in the bluegill.

in both the quadratic comparison (slope= 0.61 ± 0.04 , $P<0.0001$) and the Muller comparison (slope= 0.7 ± 0.01 , $P<0.0001$). That is, both regressions of fluid speeds in goldfish against expected speeds in bluegill produced slopes that were significantly smaller than 1, indicating a steeper decline in goldfish.

Temporal patterns

In goldfish, the time of most key kinematic events occurred after the time of peak gape (Fig. 2B, Fig. 4A). The general sequence of events was: peak gape distance and peak jaw protrusion speed occurring almost simultaneously, followed by prey capture, peak $\mu_{1/2PG}$ and finally peak jaw protrusion distance. $\mu_{1/2PG}$ in the goldfish peaked much later than peak gape, taking almost twice as long to reach peak fluid speeds, and high fluid speeds were often sustained throughout the remainder of the strike. Higher fluid speeds were generated during faster strikes (Fig. 5, solid line). A large amount of variation in the relative timings of kinematic events suggests that goldfish exhibit a flexible kinematic pattern during feeding.

When compared with bluegill, the timings in goldfish were slower and more variable. In general, bluegill generated peak fluid speeds almost simultaneously with peak gape and peak jaw protrusion (Fig. 4A). We found a significant species effect for mean TTPG (repeated-measures MANOVA, $P=0.04$), with bluegill being much faster to reach maxima (24 ms) than the goldfish (34 ms; Fig. 4B), despite having similar gape sizes ($N=3$ each for goldfish and bluegill). Time to peak $\mu_{1/2PG}$ (in units of TTPG) was also significantly different between the two species, with bluegill achieving peak flows before TTPG and goldfish achieving peak flows much later (repeated-measures MANOVA, $P<0.001$; Fig. 2B,C, Fig. 4A). The bluegill was significantly faster than the goldfish in terms of time to peak mouth displacement (repeated-measures MANOVA, $P<0.001$) and mouth displacement speed (repeated-measures MANOVA, $P<0.001$). Faster strikes generally generated higher fluid speeds for both species (Fig. 5) and, accordingly, goldfish produced lower fluid speeds than bluegill (repeated-measures MANOVA, $P<0.007$).

Force exerted on prey

In goldfish, faster fluid acceleration at the mouth was associated with a higher force exerted on the prey (Fig. 6). Multiple regression

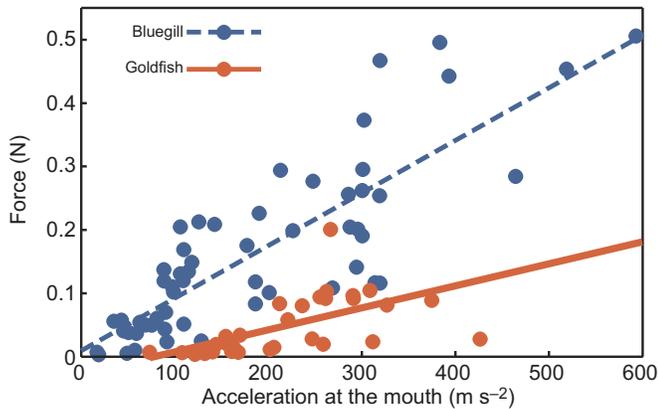


Fig. 6. Force exerted on prey as a function of acceleration of fluid at the mouth. Note that at any given fluid acceleration, bluegill exert more force on the prey compared with goldfish. Forces were measured during bluegill feeding events (Holzman et al., 2008b) and calculated for goldfish (see Materials and methods).

analysis showed that both jaw protrusion speed ($t=5.5$, $P<0.001$) and acceleration of flows ($t=3.7$, $P<0.001$) were significantly correlated with force exerted on the prey (whole-model $R^2=0.72$, $F_{2,27}=28.7$, $P<0.001$). However, for any given fluid acceleration, the bluegill exerted a greater force on the prey than goldfish (Fig. 6).

We also tested the effect of jaw protrusion on the acceleration-based forces exerted on prey using a simulation that compared observed jaw protrusion with a hypothetical condition of no protrusion. This allowed us to estimate the contribution of jaw protrusion to force production, that is, the amount that jaw protrusion augmented suction forces exerted on prey items. Jaw protrusion in goldfish augmented the total force exerted on prey by $\sim 10\%$ (Fig. 7). A plot of the residual force (after accounting for acceleration at the mouth) *versus* mouth displacement speed resulted in a positive correlation, which indicates a significant contribution of jaw protrusion to the force on the prey. Given that jaw protrusion in bluegill was found to augment forces exerted on prey (Holzman et al., 2008c) (Fig. 7), the finding that jaw protrusion also enhances suction forces in goldfish shows that there is convergence in this hydrodynamic effect of jaw protrusion.

DISCUSSION

We have shown that species representing two evolutionary origins of jaw protrusion use this ability to increase the hydrodynamic forces exerted on prey items. This shared function of jaw protrusion is in spite of considerable differences in the feeding biology of these two species, where bluegill are strong suction-feeding predators and goldfish sort through bottom debris for edible material. The potential for jaw protrusion to augment forces could be realized by most jaw-protruding suction feeders and the fundamental nature of force augmentation suggests that it may have been a factor in the origin of protrusion mechanisms and the subsequent trophic diversification of these two highly successful fish groups. Force enhancement should be added to the already extensive list of performance advantages of jaw protrusion for fish feeding mechanisms (Alexander, 1967; Motta, 1984).

Any process that allows the opening mouth to move rapidly toward the prey has the potential to increase the forces exerted on the prey by increasing the rate at which the suction velocity increases around the prey. Swimming toward the prey during the strike, often

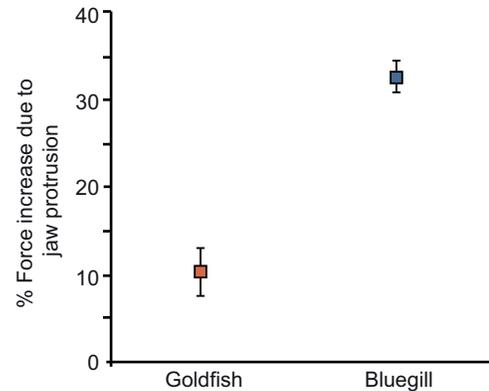


Fig. 7. Plot showing the percent force increase due to jaw protrusion for bluegill and goldfish. A percent force increase of zero indicates a hypothetical simulated scenario where the prey remains a fixed distance from the predator (no jaw protrusion). Note that force augmentation by protrusion in bluegill is approximately three times that in goldfish.

referred to as ‘ram’ can have this effect (Holzman et al., 2007), as can the rotation of the head toward the prey, as happens in seahorses and other syngnathiforms (Roos et al., 2009). In many fish, ram and jaw protrusion will jointly increase the rate of approach of the mouth opening and one advantage of jaw protrusion is that it permits the fish to decouple two mechanisms of increasing the rate of approach to the prey. Suction feeders that use little or no ram, such as bluegill and goldfish, can still benefit considerably from the enhancement of suction-feeding performance that is provided by jaw protrusion. Our observations of feeding goldfish indicate that they capitalize on this mechanism, but that their feeding behavior is highly variable, particularly in terms of the timing of jaw protrusion relative to suction flows. Their use of jaw protrusion to enhance suction forces is facultative.

Goldfish and bluegill produce similar spatial patterns of fluid velocity in front of the mouth as described by quadratic functions (Fig. 3), a similarity that is probably because the shape of the open mouth in both species is nearly circular or slightly elliptical (Higham et al., 2006). Fluid speeds are fastest close to the mouth and rapidly decrease as a function of distance from the mouth opening. For both species, the strongest spatial gradient of fluid speeds occurs at distances within one mouth diameter in front of the mouth, and similar patterns have also been found in largemouth bass (Higham et al., 2006). The statistical differences between the quadratic functions of the goldfish and bluegill may be due to slight differences in the shape of the mouth that may not have been accounted for in our two-dimensional calculations; however, our results suggest that the hydrodynamic pattern that characterizes suction feeding may be similar across a broad range of teleost species.

Similar patterns are also found in the relative timing of prey capture and peak fluid speed. During feeding events with both species, prey capture occurs at or slightly before the time of peak fluid speed (Fig. 4A). Interestingly, this has also been found in largemouth bass (Higham et al., 2006), a ram-suction predator with a mouth larger than that of the two species of this study. Peak forces are exerted on the prey at the time of peak acceleration, before peak flow velocity is reached. Prey therefore typically enter the mouth between the time of peak acceleration and peak flow velocity. One consequence of high flow velocity following the prey into the mouth is that this enhances the transport of prey farther into the buccal cavity, perhaps helping to ensure their capture.

Differences between goldfish and bluegill

Force augmentation by convergent means of suction-producing jaw protrusion is perhaps surprising given the considerable morphological and ecological differences between goldfish and bluegill jaws (Fig. 1). Although jaw protrusion in both species increases the amount of force exerted on prey, it does so to different degrees (Fig. 7). Differences between species are also found in the timing of jaw movements during feeding (Fig. 4). We emphasize that these differences represent measurements in two species and therefore may not reflect general patterns found in the diverse clades to which goldfish and bluegill belong. For example, the patterns found in goldfish should not be interpreted as the norm for all cypriniform species. Nevertheless, the significant differences in jaw morphology and kinematics between goldfish and bluegill are worth noting here.

Although both goldfish and bluegill have the ability to protrude the upper jaw toward the prey, they do so using completely different mechanisms (Fig. 1). Jaw protrusion in the bluegill is tightly linked to lower jaw depression because of ligaments uniting the lower and upper jaws. Stimulation of the hyoid musculature results in not only lower jaw depression but also premaxillary protrusion in bluegill (Lauder, 1980). Bluegill possess premaxillae with elongate ascending processes, which extend posteriorly and slide along the rostral end of the neurocranium. The ascending processes of the premaxillae are shorter in goldfish, but the incorporation of the kinethmoid in the upper jaw protrusile mechanism of all cypriniforms adds an aspect of complexity that is not seen in any other group.

Furthermore, the musculature and ligamentous attachments of the upper jaw differ in these species. Both basal and derived teleosts close the mouth *via* the adductor mandibula, a subdivided cheek muscle. In cypriniforms, the A1 division of the adductor mandibula inserts on the maxillae and plays a role in jaw protrusion, whereas in acanthomorphs this muscle appears to always function only to retract the maxillae and premaxillae (Motta, 1984). Although bluegill possess a single branch of the A1 division of the adductor mandibula (Lauder and Lanyon, 1980), goldfish have two branches of A1 that both insert on the maxillae (Staab et al., 2012). Previous work in carp, which has an A1 morphology similar to that of goldfish, has suggested that the additional branch of A1 plays a role in closed-mouth protrusion, allowing the fish to expand the buccal cavity during processing without risk of prey escaping (Ballintijn, 1972; Sibbing et al., 1986). The differences in the timing of premaxillary excursions in bluegill and goldfish may reflect this capacity for jaw protrusion by the adductor mandibula muscle.

Goldfish and bluegill differ in both the timing of jaw movements and the resulting fluid speeds during suction feeding. Goldfish take longer to reach peak gape during a strike (Fig. 4B) and the relationship between peak gape and peak flow velocity is different between goldfish and bluegill. The expanding cone model of suction feeding (Muller et al., 1982) predicts that peak fluid flow at the mouth will occur early in the gape cycle at approximately 30–50% of peak gape. This prediction is not supported by measurements of flow in bluegill, where peak velocity of fluid flow occurs at approximately the time of peak gape (Day et al., 2005). Subsequent modeling has revealed that an anterior to posterior wave of buccal expansion, which cannot be accomplished by a simple expanding cone, is required to allow peak flow to be delayed until peak mouth opening (Bishop et al., 2008). Goldfish show an even more extreme departure from the expectation of an early peak flow (Bishop et al., 2008), reaching peak fluid speeds at an average of 175% of the time of peak gape (Fig. 4A). It is not entirely clear how

goldfish achieve peak fluid flow speeds after peak gape, but this may be the result of a modified pattern of internal buccal or opercular expansion relative to what has been measured in bluegill (Day et al., 2005).

Timing of key events is more variable for goldfish than for bluegill and this is especially true with respect to timing of jaw movement and fluid velocity. For example, goldfish display a range of times to peak gape that is over twice the range in bluegill (Fig. 4B, Fig. 5). In goldfish, time to peak jaw protrusion relative to TTPG has a range of measurements almost an order of magnitude greater than that of the bluegill (Fig. 4A). Recent work examining the feeding kinematics of five cypriniform species has shown that strikes are more variable than what has been shown in acanthomorphs (Staab et al., 2012). This kinematic flexibility illustrates the goldfish's ability to modulate jaw movements during feeding. It is likely that the aforementioned morphological complexity of the goldfish jaw may allow for such kinematic flexibility during feeding.

Previous work has shown that hydrodynamic force exerted on the prey is primarily determined by fluid acceleration around the prey (Wainwright and Day, 2007; Holzman et al., 2008b). However, we have shown that for a given fluid acceleration at the mouth, the bluegill exerts a greater amount of force on prey items (Fig. 7). Two primary factors account for this difference. First, although jaw protrusion in bluegill increases the forces exerted on prey by up to 35%, the increase was only approximately 10% in goldfish, mostly because jaw protrusion is slower in goldfish. Second, bluegill time their approach to the prey in a way that allows them to expose the prey to the maximum fluid accelerations produced during the strike (Holzman et al., 2008b), whereas goldfish are less precise with their timing and likely achieve lower efficiency.

The feeding ecology of goldfish and bluegill differs considerably and this may be partially due to differences in fluid dynamics and kinematics. Bluegill are the most planktivorous of all centrarchid species (Collar et al., 2009), feeding on both midwater cladocerans and benthic insects. In contrast, goldfish have been called 'benthic grazers' (Sibbing and Witte, 2005), probing the substrate and taking up detritus, insect larvae and worms along with the substratum. Planktivory and benthivory likely require very different feeding strategies to manipulate the fluid during prey capture. Although efficient use of potential suction forces may be valuable when feeding on plankton and insect larvae that cling to holdfasts, sorting through the benthic detritus likely requires a different hydrodynamic approach, one in which flow is sustained for a longer period to more efficiently vacuum detritus. Our data suggest that goldfish have a very flexible feeding behavior (Fig. 4A) in addition to producing slower flow speeds (Fig. 4B) and lower force magnitudes (Fig. 5). This increased flexibility may be useful as the goldfish stirs detritus searching for prey items in the benthos. Further performance tests examining benthivory within goldfish are warranted.

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