Are Kissing Gourami Specialized for Substrate-Feeding? Prey Capture Kinematics of *Helostoma temminckii* and Other Anabantoid Fishes

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ABSTRACT *Helostoma temminckii* are known for a "kissing" behavior, which is often used in intraspecific interactions, and an unusual cranial morphology that is characterized by an intramandibular joint (IMJ). The IMJ is located within the lower jaw and aids in generating the eponymous kissing movement. In other teleost linages the IMJ is associated with the adoption of a substrate-grazing foraging habit. However, because of anatomical modifications of the gill-rakers, *Helostoma* has been considered a midwater filter-feeding species. We offered midwater, benthic, and attached food to *Helostoma*, *Betta*, and two "true" osphronemid gouramis, to ask: (1) how do food capture kinematics differ in different foraging contexts; and (2) are *Helostoma* feeding kinematics distinct when compared with closely related anabantoids that lack an IMJ? For all anabantoid species except *Helostoma*, benthic prey were captured using a greater contribution of effective suction relative to midwater prey, though *Helostoma* was rarely willing to feed in the midwater. *Helostoma* individuals produced relatively less suction than other species regardless of the food type. *Helostoma* produced a much larger gape and more premaxillary protrusion than other species, but also took longer to do so. We suggest that the jaw morphology of *Helostoma* facilitates an extremely large mouth-gape to enhance substrate-scraping. The large amplitude mouth-opening that characterizes substrate-feeding may represent a functional trade-off, whereby the enhanced ability to procure food from the substrate is accompanied by a concomitant reduction in the ability to produce suction. *J. Exp. Zool. 9999A:1–9, 2012.* © 2012 Wiley Periodicals, Inc.

The Kissing gourami, *Helostoma temminckii*, has an unusual jaw morphology, which is used in a peculiar way: two individuals will "flare" the upper and lower jaws, in both the mediolateral and dorsoventral planes, and press the tips of their jaws against one another. This eponymous "kissing" behavior is an intraspecific, agonistic behavior. In fact, the distinctive oral jaw morphology of *Helostoma* was interpreted by the late Professor Karel Liem as an adaptation for this kissing behavior (Liem, '67).

A key feature of the distinctive oral jaw morphology of *Helostoma* is an additional joint within the mandible—between the dentary and articular—known as the intramandibular joint
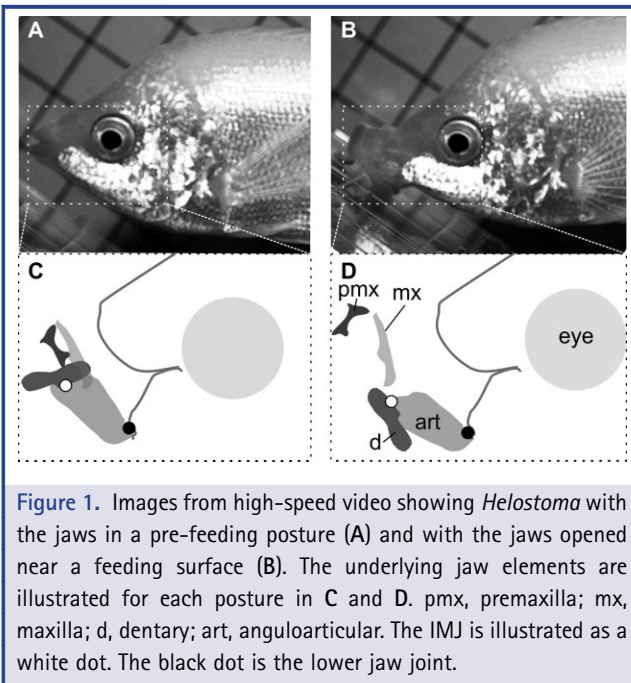
Figure 1. Images from high-speed video showing *Helostoma* with the jaws in a pre-feeding posture (**A**) and with the jaws opened near a feeding surface (**B**). The underlying jaw elements are illustrated for each posture in **C** and **D**. pmx, premaxilla; mx, maxilla; d, dentary; art, anguloarticular. The IMJ is illustrated as a white dot. The black dot is the lower jaw joint.

(IMJ; Fig. 1). The IMJ is present in taxa from many other teleost clades, including the marine Scaridae, Pomacanthidae, Acanthuridae, Girellidae, and the freshwater Poeciliidae and Characiformes (Vari, '83; Gosline, '85; Gibb et al., 2008; Konow et al., 2008). Most of these taxa feed on prey items that are attached to the substratum (Konow et al., 2008). By increasing the jaw opening angle, the IMJ facilitates increased contact between the lower jaw and the substrate (Konow and Bellwood, 2005; Gibb et al., 2008; Ferry-Graham and Konow, 2010; Konow and Bellwood, 2011). Other anabantoids (i.e., gouramis and *Betta*) also engage in jaw-to-jaw combat (Southwick and Ward, '68; personal observation), but they do *not* possess IMJs, nor do they display jaw flaring; to our knowledge, the only anabantoid bearing this structural innovation is *Helostoma*. Thus, this IMJ has evolved independently of other IMJ-bearing groups, and may be relevant to food acquisition as well as for behavioral displays.

Helostoma possesses elongate gill rakers (Liem, '67), and small invertebrates have been reported in the diet (Rainboth, '96). Consequently, it has been assumed that *Helostoma's* dominant food-capture mode is filter feeding in the water column (Gosline, '85) and/or ram-based capture of individual prey items (Liem, '67). Studies examining the oral morphology of *Helostoma* have interpreted it within the context of these presumptive prey capture modes (*sensu* Liem, '67; Gosline, '85). More recently, it has become apparent that algae comprise a significant portion of the diet in wild *Helostoma* (Amarasinghe and Wickramaratne, 2001; Hill and Yanong, 2002; Asyari, 2007). We have observed that, in the laboratory setting, *Helostoma* individuals constantly forage on

the substrate and other flat surfaces, in an apparent effort to dislodge attached food items. In addition, when unattached prey, such as brine shrimp adults/nauplii and commercial diets, are presented in the water column, they are consistently ignored (personal observation). Based on these observations, we hypothesized that an equally important function of the unusual jaw morphology of *Helostoma* is to facilitate substrate scraping—an under-appreciated mode of food acquisition for this species.

To identify any unusual features of *Helostoma* feeding mechanics, we compared the feeding behavior and kinematics of this species with three other anabantoid species offered midwater, benthic, and attached food sources. Specifically, we addressed the following questions: (1) How do the prey capture kinematics of these four anabantoid species differ when used in different foraging contexts? and (2) Are *Helostoma* feeding kinematics distinct when compared with closely related anabantoids that lack an IMJ?

METHODS

Four anabantoid species (*n* = 4 individuals of each species) were examined: kissing gourami *Helostoma temminckii* (Helostomidae; size range 8.1–8.2 cm total length, or TL), gold gourami *Trichogaster trichopterus* (Osphronemidae; size range 5.3–7.2 cm TL), dwarf gourami *Colisa lalia* (Osphronemidae; 3.6–4.8 cm TL), and common *Betta splendens* (Osphronemidae; 3.1–3.9 cm TL). *Helostoma* were selected for their highly specialized morphology. The other three species were selected to represent (1) relatively unspecialized anabantoid morphology and (2) taxonomic variation within the true gourami lineage (the Osphronemidae; Helostomidae is a single-species family), according to the most recent phylogeny (Ruber et al., 2006; Fig. 2).

During the feeding trials, members of all four species were placed individually into small glass aquaria (10–38 L) with a ruler or a calibrated grid included in the field-of-view of the high-speed camera view to determine scale. Representatives of all four species were offered food items placed in three locations to generate three experimental treatments: midwater, benthic, and attached, the latter to elicit scraping (hereafter referred to simply as scraping).
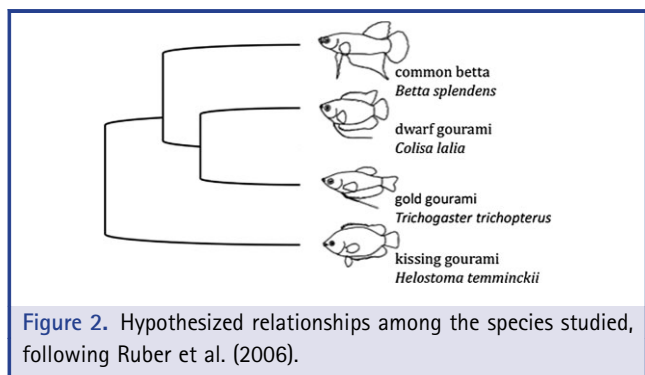
Figure 2. Hypothesized relationships among the species studied, following Ruber et al. (2006).

Fish were offered either thawed adult *Artemia*, thawed larval Chironomidae, or small commercial food pellets for the benthic and midwater treatments, and algal film attached to a PVC surface as the scraping treatment. Feeding sequences were imaged from the lateral aspect (camera body perpendicular to the front surface of the aquarium) using a Vision Research Phantom V5.2 high-resolution digital-imaging system recording at 250 fps; during feeding trials, the arena was illuminated by two 500 W tungsten photo-lamps.

Feeding events were initiated by introducing food into the arena with a pipette. Multiple feeding events were captured during a given feeding trial, but data recording was terminated before the individual was satiated (i.e., before the fish showed no interest in eating additional food items when presented). Following satiation, an individual would be maintained in the feeding arena over a period of days until the necessary prey capture sequences were collected. We attempted to collect three capture events for four individuals of each species in each location; however, *Helostoma* were extremely reluctant to feed in the water column. Thus, although numerous *Helostoma* individuals were repeatedly offered a variety of midwater food types, we were only able to obtain three midwater feeding events from two individuals. In addition, *Helostoma* was the only species that was willing to scrape attached food. Thus, data for this treatment were obtained from this species only.

Feeding sequences were analyzed using the custom image-analysis program Didge (Alistair Cullum, Creighton University). Seven maximum displacement and timing variables were extracted from the images (Fig. 3): lower jaw rotation (depression), cranial rotation, premaxillary protrusion, and gape distance, as well as gape cycle (the duration from first detectable mouth opening to complete mouth closure). Hyoid depression is traditionally measured in such studies, however hyoid movement was visible (and therefore quantified) only in *Betta*, and it was not included the comparative analysis. Cranial rotation, as we measured it (Fig. 3), could include rotation of the pectoral girdle, however we were not able to ascertain any additional movement in this region and thus used this approach as it was easily the most precise. All variables were determined relative to time zero, defined as the onset of rapid lower jaw depression leading to mouth opening.

The distance moved by the predator ($D_{predator}$) and the food item (D_{prey}) from time zero until the food entered the mouth were also measured. These data were used to calculate the Ram–Suction Index (RSI) for each species, following Norton and Brainerd ('93). RSI values greater than 0 indicate a feeding event that is ram-dominated, or that movement by the predator towards the prey contributes relatively more to the capture event than movement of the prey towards the predator (due to suction). RSI values less than 0 indicate a feeding event that is suction-dominated, or that movement by the prey towards the predator is proportionally larger than movement by the predator towards
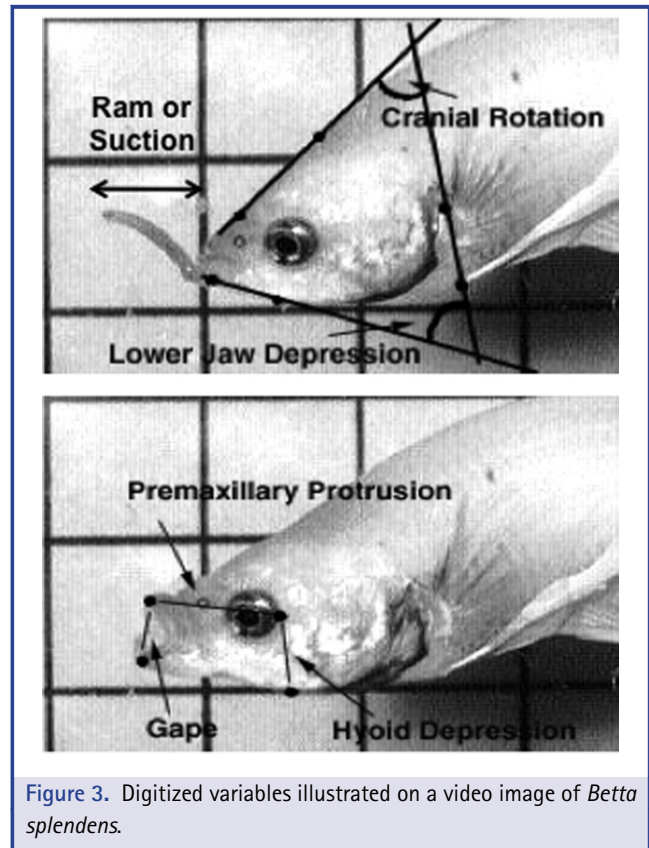

Figure 3. Digitized variables illustrated on a video image of *Betta splendens*.

the prey. We examined absolute D_{prey} directly as an indicator of suction production. In addition, we divided D_{prey} by maximum gape distance creating a ratio to account for mouth size, therefore providing a relative measure of effective suction generation.

To reduce the dimensionality of the dataset and to determine the degree of correlation among the kinematic variables, we performed a principal components analysis (PCA) using the underlying correlation matrix (PASW Statistics v18.0, IBM Corporation, New York). RSI was excluded from this analysis as D_{prey} cannot be obtained for scraping-based feeding events. We note that we did not use phylogenetically independent contrasts because of the small number of contrasts, and that the species used in the analysis have differing degrees of relatedness. We considered the resultant PCs with eigenvalues greater than one as dependent variables in a MANOVA conducted using species and food-treatment as the main effects. If the interaction term was not significant, this was subsequently dropped from the MANOVA model. If the main effects were significant, this was followed by ANOVA on the significant effect, then pairwise Fisher LSD post hoc tests to determine which species and food treatments differed from one another.

RESULTS

True gouramis and *Betta* rapidly approached prey items, stopped, and then initiated mouth opening when they were in close proximity to the prey item (Fig. 4). *Helostoma*, in contrast, tended to open the mouth farther away from the prey (Fig. 4), though the absolute distance moved by the prey during the feeding event was similar among species, ranging from 0.2 to 0.4 cm, meaning that *Helostoma* typically had a larger locomotory or ram contribution to the strike (Table 1). *Helostoma* also took absolutely longer than the other species to reach maximum gape and maximum upper jaw (premaxillary) protrusion, especially during midwater feeding events (Table 1). The resultant jaw opening velocities, coarsely estimated as gape distance divided by time to maximum gape, were slower for *Helostoma* midwater feeding events than for the other species. In *Helostoma*, midwater feedings were approximately six times longer in duration than those of the other species studied. In fact, midwater feedings lasted approximately two times

longer than benthic feedings in *Helostoma* (Table 1), making benthic feedings faster than midwater feeding events. Interestingly, because of the large distances traversed by the jaw elements during feeding in *Helostoma*, this resulted relatively fast velocities estimated for benthic feeding events. For the other three species, midwater feedings were typically shorter in duration than benthic feedings (Table 1). Only *Helostoma* individuals were willing to scrape material from the substrate (Fig. 5); scraping-based feeding events were, on average, kinematically similar to midwater feeding events.

The PCA revealed two major axes of variation in the kinematic data. Maximum gape distance and premaxilla protrusion as well as the timing (duration) variables (Fig. 6) loaded on the first PC, which explained 47.4% of the variance in the dataset (Table 2). Maximum cranial rotation and lower jaw depression loaded on the second PC, which explained an additional 19.3% of the variance. MANOVA detected significant species and food treatment effects
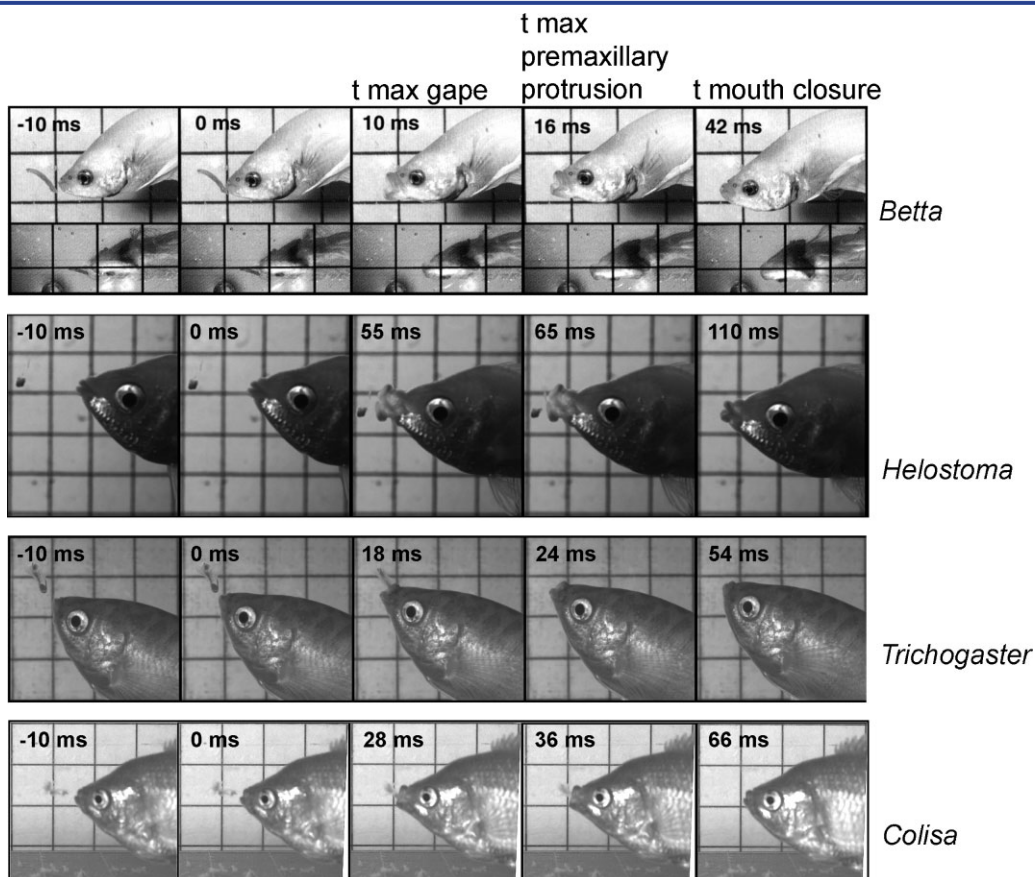
Figure 4. Composite image of each species capturing midwater food items. The relative moment in time of each panel is noted. For each species, mouth opening is initiated at time zero. Maximum gape, premaxillary protrusion, and time to mouth closure (gape cycle) follow as the next three frames in each sequence. Note that the times at which these occur vary by species. For *Betta*, lateral and ventral views are shown simply for reference.

Table 1. Mean kinematic maxima and timing of those maxima (±SE) for each of the four species on each food treatment for which data could be collected.

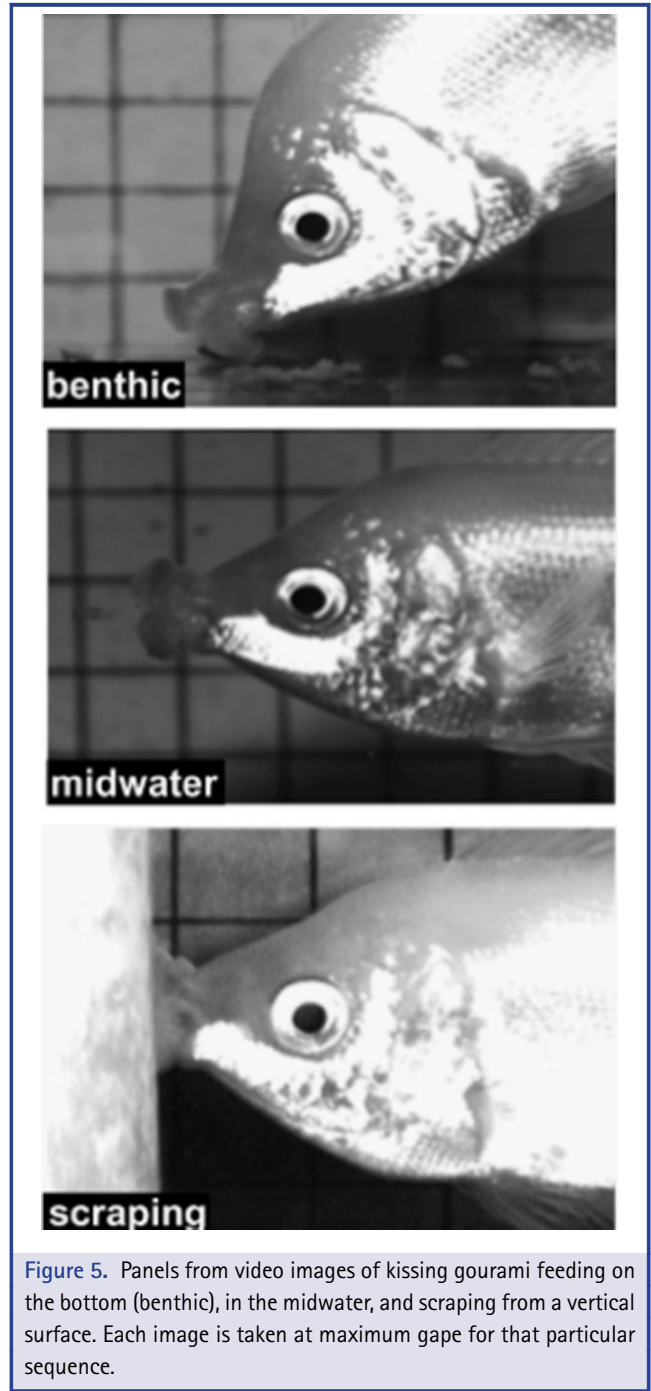|	Betta		Dwarf gourami		Gold gourami		Helostoma		
	Benthic	Midwater	Benthic	Midwater	Benthic	Midwater	Benthic	Midwater	Scrape
Max. cranial rotation angle (°)	18.19 (1.56)	17.81 (1.41)	9.78 (0.54)	9.20 (0.71)	9.17 (0.98)	12.54 (3.49)	10.58 (0.84)	12.87 (2.26)	9.0 (0.80)
Max. lower jaw depression angle (°)	46.25 (4.98)	45.15 (2.80)	49.90 (1.84)	35.57 (2.08)	45.67 (1.55)	43.65 (4.69)	32.15 (1.94)	43.03 (1.05)	38.42 (2.16)
Max. premaxillary protrusion (cm)	0.19 (0.01)	0.32 (0.02)	0.32 (0.02)	0.75 (0.07)	0.39 (0.02)	0.96 (0.24)	1.11 (0.20)	1.45 (0.54)	0.8 (0.10)
Max. gape distance (cm)	0.22 (0.02)	0.30 (0.02)	0.43 (0.03)	0.46 (0.02)	0.32 (0.03)	0.40 (0.05)	1.19 (0.05)	1.05 (0.13)	1.12 (0.03)
t_{max} lower jaw angle (ms)	16.83 (2.63)	9.91 (0.83)	12.91 (3.16)	10.53 (2.57)	12.0 (1.94)	5.83 (1.07)	25.0 (4.82)	64.41 (18.46)	52.33 (9.25)
t_{max} premaxilla protrusion (ms)	21.25 (1.56)	15.65 (1.12)	12.0 (2.01)	17.0 (3.23)	11.45 (1.57)	8.50 (1.79)	28.08 (6.94)	77.19 (10.61)	81.25 (14.11)
t_{max} gape distance (ms)	14.5 (2.31)	11.2 (1.73)	12.58 (2.40)	14.25 (2.93)	12.45 (1.61)	7.0 (1.31)	15.5 (2.57)	65.0 (7.61)	76.0 (13.19)
Ram–Suction Index	−0.10 (0.07)	0.15 (0.06)	−0.36 (0.18)	0.10 (0.05)	0.13 (0.09)	0.21 (0.05)	0.43 (0.10)	0.28 (0.03)	
D_{prey}/Gape distance	0.97 (0.04)	0.63 (0.06)	0.84 (0.14)	0.33 (0.05)	0.89 (0.30)	0.29 (0.08)	0.20 (0.02)	0.30 (0.03)	

Figure 5. Panels from video images of kissing gourami feeding on the bottom (benthic), in the midwater, and scraping from a vertical surface. Each image is taken at maximum gape for that particular sequence.

within the PCs. Post hoc tests revealed that kissing gourami and *Betta* were significantly different both from one another, and from *Trichogaster* and *Colisa* (the "true" gouramis) along PC1 (all LSD $P < 0.0001$ for significant comparisons), but that *Trichogaster* and *Colisa* were not different from one another. Thus, *Helostoma* took significantly longer to procure food than *Betta*, who again
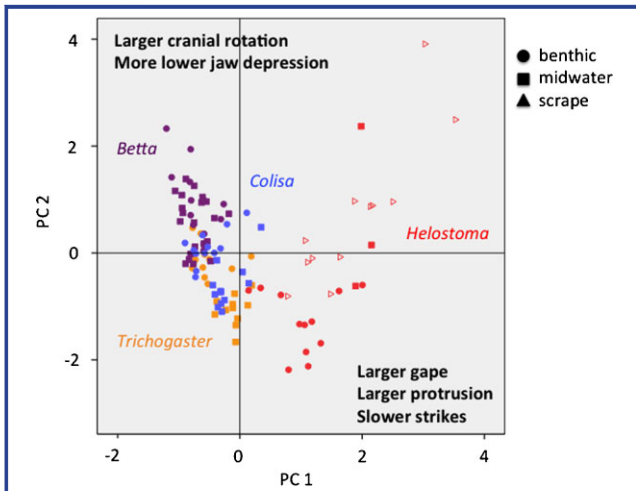
Figure 6. Plot of principle components 1 and 2 for all species and food types. Species are color-coded and prey type is separated by symbol type. Benthic feedings are indicated by circles, midwater feedings by squares, and scraping (kissing gourami only) as triangles. The kinematic variables that loaded strongly on each of the PCs are noted along the axes with the direction of change indicated (e.g., "larger" or "slower").

took longer than the two gouramis. *Helostoma* showed the largest gape of all species studied on PC1 (Fig. 6), consistently producing a gape distance that was double that of the other species, with a gape angle that often exceeded 100°. Premaxillary protrusion was also larger in *Helostoma*, though this variable did not load as strongly on PC1 (see also Table 1). Along PC2, *Betta* individuals were significantly different from all other species (all $P < 0.0001$), which were not different from one another; *Betta* had the greatest cranial elevation and lower jaw rotation. *Betta* produced nearly twice as much cranial elevation as the other taxa. However, cranial rotation for *Betta* was still only ~20° (see Table 1).

**Table 2.** Component loading scores from the PCA performed on the kinematic dataset.

	PC 1	PC 2
Variance explained (%)	47.34	19.37
Max. cranial rotation angle	−0.392	**0.611**
Max. lower jaw angle	−0.216	**0.595**
Max. premaxilla protrusion	**0.778**	−0.338
Max. gape distance	**0.868**	−0.197
Time of max. lower jaw angle	**0.595**	0.216
Time of max. premaxilla protrusion	**0.627**	0.296
Time of max. gape distance	**0.609**	0.264
Significant loadings (>0.5) are indicated in bold face text.		

Post hoc tests revealed that, for PC1 and PC2, scraping events differed significantly from benthic strikes ($P < 0.0001$). However, this finding applied only to *Helostoma* because no other species were willing to scrape algae during the feeding trials. In addition, only premaxillary protrusion varied in a consistent manner among food types (Fig. 7), and this appears to be why food treatments were difficult to distinguish from one another. Midwater food items elicited more protrusion relative to benthic food for all species, and kissing gourami consistently produced the greatest upper jaw protrusion (~1.5 cm). Scraping appeared to elicit less protrusion (when compared with benthic and midwater feedings), but, because the other species were unwilling to procure food by scraping, this result was observed only for kissing gourami. Although the sample size is small, midwater feeding appears similar to scraping in *Helostoma*.

The RSI varied among food types, with benthic strikes tending to be characterized by a stronger relative contribution of suction to the strike in *Betta* and true gouramis, but not in *Helostoma* (Table 1). The distance moved by the prey, relative to predator mouth size, also suggested that more was suction generated during benthic strikes, relative to midwater strikes, in true gouramis and *Betta* (Table 1). Absolute D_{prey} was actually similar among species, as noted earlier. For all species except *Helostoma*, the prey moved a distance approximately equal to the diameter of the mouth opening when fish were feeding from the benthos (Fig. 8). However, this effect was reduced by up to two-thirds when the same fish fed from the water column. Only *Helostoma* showed the opposite patterns when feeding on the benthos. However,
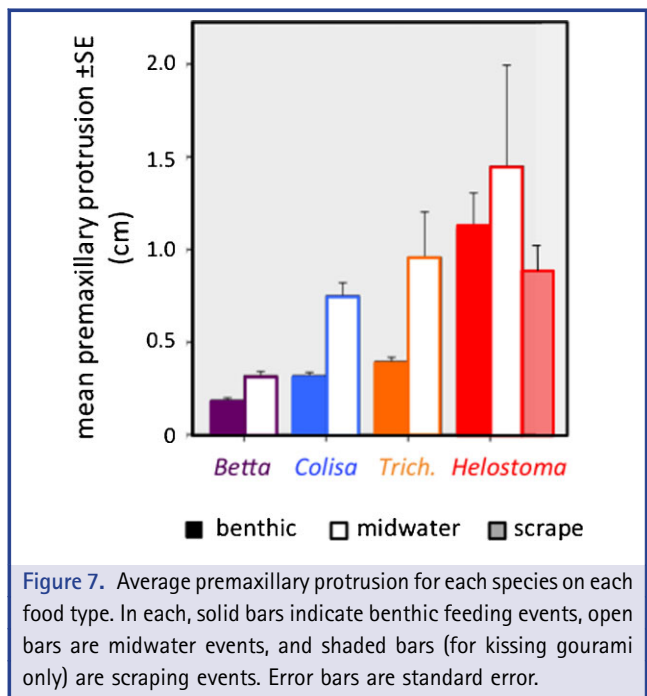
Figure 7. Average premaxillary protrusion for each species on each food type. In each, solid bars indicate benthic feeding events, open bars are midwater events, and shaded bars (for kissing gourami only) are scraping events. Error bars are standard error.
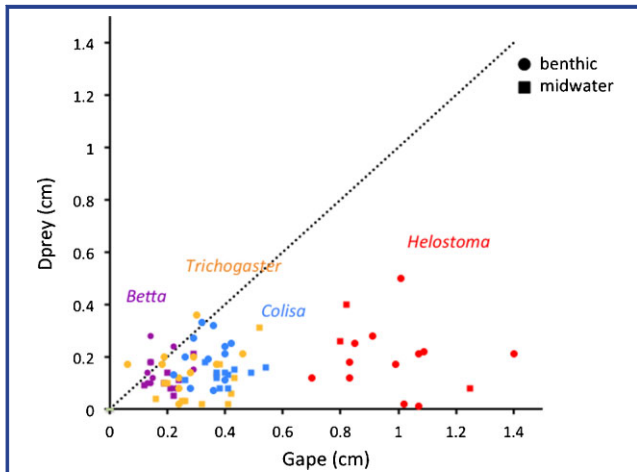
Figure 8. Distance moved by the prey from the onset of mouth opening (D_{prey}) versus gape distance. Species are color-coded and prey type is separated by symbol type. Benthic feedings are indicated by circles, midwater feedings by squares. All data for all individuals are shown (means can be found in Table 1). Shown is the 1:1 line, where D_{prey}, an indicator of suction production, would equal gape distance, which is the height of the maximally opened mouth during feeding. Note that for benthic feedings, the values approach the 1:1 line for all species except *Helostoma*. *Helostoma* demonstrate a disproportionately large gape as well as a disproportionately small amount of suction for their body size.

consistently low values for *Helostoma* when feeding in all locations suggest a relatively smaller contribution of suction to prey capture compared with the other three species.

DISCUSSION

The most striking aspect of prey capture in *Helostoma* is the extremely large gape produced—2–5 times greater than the other anabantoids considered here. The IMJ in *Helostoma*, as in other IMJ-bearing taxa, divides the mandible into two independent elements, which increases the functional degrees of freedom and the number of potential mechanical solutions for food capture (Vermeij, '73). Interestingly, even some terrestrial snakes demonstrate flexion at an IMJ, which is thought to increase mouth-gape (Kley, 2006). Among teleosts, this structural innovation also increases mouth-gape and has consistently been identified in taxa that use their oral jaws to remove attached prey items from the substrate. For example, deep-bodied squamipinnid reef fishes have independently evolved IMJs at least five times, either for grazing (acanthurids, girrelids), coral feeding (chaetodontids, scarids), or grab-and-tearing of robust food from the substratum (pomacanthids; Konow et al., 2008; Konow and Bellwood, 2011). Although *Helostoma* has been previously categorized as a

midwater filter-feeding species, we suggest that the unusual jaw morphology that produces jaw flaring during "kissing" also maximizes mouth opening diameter and contact with the substrate to facilitate removal of attached plant material.

While the use of the IMJ to consume a plant-based diet is consistent with recent diet studies of *Helostoma*, it is in striking contrast with classic ecomorphological studies of this species (Liem, '67; Gosline, '85), which hypothesized that *Helostoma* was a midwater suction feeder that consumes free-swimming, invertebrate prey. We emphasize that *Helostoma* individuals are extremely reluctant to feed from the water column, but readily take food from the bottom and scrape plant material from the substrate. We suggest that the modified gill-rakers of this species, which previously contributed to their misidentification as midwater filter feeders, could serve to entrap micro-invertebrates that are dislodged from the substrate during scraping. Thus, a scraping-based mode of feeding would explain both the "filter-feeder" gill morphology and the presence of invertebrate-prey items in the stomachs of wild-caught individuals.

When *Helostoma* did manage to procure midwater prey, they approached it with the mouth open in a very large gape and captured it using cranial movements that occurred over a relatively long time period. The Ram–Suction Index (RSI), while a coarse indicator at best (Wainwright et al., 2001), suggests that the true gouramis and *Betta* rely more heavily on a suction-based component of prey capture, relative to *Helostoma*. This conclusion is also supported by direct examination of the movement of the prey during the event. Absolute D_{prey} values were very similar among species, despite differences in body size. Relative to mouth size, the prey tended to move farther in the three species, suggesting that they generated more effective suction during the feeding event. All species except *Helostoma* demonstrated relative increases in suction generation during benthic feeding events, suggesting that the substrate was required to enhance the effect of any flows being generated into the open mouth (Wilga and Sanford, 2008). The data for *Helostoma*, in contrast, suggested relatively less suction was potentially being generated during benthic feeding events. It has been shown in other fishes (i.e., centrarchids) that a larger gape size results in reduced suction production (Carroll, 2004; Holzman et al., 2008). The IMJ, in *Helostoma*, appears to increase gape distance, which in turn seems to result in reduced suction production.

If this interpretation is correct, then *Helostoma* may represent an unusual and previously unrecognized example of an ecological trade-off: enhanced scraping performance is achieved at the expense of suction-production ability. Here, we document a possible loss of effective suction-feeding, suggesting that *Helostoma* does not, or perhaps cannot, alter feeding mechanics to switch between divergent feeding modes. Although not as well studied in this context, the IMJ-bearing girellid fishes also show a reduced potential for modulating suction-generation in response to differing food presentations (Moran, 2011), as do

the IMJ-bearing poecillids (personal observation). *Helostoma* appears to be highly modified to produce the jaw movements associated with "kissing" and substrate-scraping, and we posit that the IMJ plays a key role in this modification. It is noteworthy here that lineages containing multiple IMJ-bearing taxa contain species that secondarily revert to the more basal suction-feeding mode. In these species, there is reduced flexion at the joint (Konow et al., 2008; Konow and Bellwood, 2011), implying that the joint must become more rigid to permit efficient suction generation. This could be because IMJ flexion impairs the creation and maintenance of a small and tubular mouth aperture, which enhances suction generation (Carroll, 2004; Holzman et al., 2008).

Trade-offs between removing food from the substrate and feeding from the water column are not observed in taxa without IMJs: for example, the clariid catfishes (van Wassenbergh et al., 2007) are able to employ both suction-feeding and biting mechanisms effectively to procure food. Thus, *Helostoma* provides an instance where the feeding behavior falsifies the hypothesis that the IMJ, a morphological novelty, *increases* behavioral ecological versatility (Vial and Ojeda, '90). Instead, it appears that the IMJ may *decrease* feeding versatility, in that suction was not apparently produced in an effective way when feeding in the midwater. While suction may not be absolutely necessary for successful feeding in the midwater, the extreme reluctance of *Helostoma* to feed on food items in the midwater suggests to us a reliance on other feeding locations. The potential loss of an ability to utilize the midwater feeding niche would represent decreased feeding versatility. While we must emphasize that these results are tentative, given the small amount of midwater data that we were able to collect and analyze, the findings are provocative.

Truly understanding versatility and trade-off within a mechanical system relies upon a solid knowledge of the musculoskeletal mechanism that generates flexion of the IMJ. A single, clear explanation for how the IMJ works remains remarkably elusive. Based on other IMJ systems, candidate mechanisms for generating IMJ flexion range from direct actuation of the joint by contraction of the hyoid protractor muscles (Konow and Bellwood, 2005) to dedicated biomechanical linkages that simultaneously drive jaw depression, IMJ rotation, gape expansion, and jaw protrusion (Ferry-Graham and Konow, 2010) to simple passive responses to contact with a firm substrate (Moran, 2011). It is possible that highly divergent mechanisms within the disparate IMJ lineages have resulted in convergent feeding behaviors. However, irrespective of the underlying mechanism, the convergent evolution of the IMJ joint in *Helostoma*, and its repeated association with substratum feeding, underscore the critical role that the IMJ plays in altering the functional properties of the gnathostome mandible to increase gape and allow animals to exploit novel and unusual food items within their habitats. The consequences of such novelty have yet to be determined.

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