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SYMPOSIUM

Suction, Ram, and Biting: Deviations and Limitations to the Capture of Aquatic Prey

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Synopsis When feeding, most aquatic organisms generate suction that draws prey into the mouth. The papers in this volume are a demonstration of this fact. However, under what circumstances is suction ineffective as a feeding mechanism? Here we consider the interplay between suction, ram, and biting, and analyze the contribution of each to the capture of prey by a wide variety of species of fish. We find, not surprisingly, that ram is the dominant contributor to feeding because suction, and biting, are only effective when very close to the prey. As species utilize more strongly ram-dominated modes of feeding, they may be released from the morphological and behavioral constraints associated with the need to direct a current of water into the head. Morphological and behavioral changes that facilitate larger gapes and stronger jaws are explored here, including predators that lack a protrusile upper jaw, predators with elongate jaws, predators that rely on suspension feeding, and predators that bite. Interestingly, while the mobility of the jaws and the shape of the opening of the mouth are modified in species that have departed from a primary reliance on suction feeding, the anterior-to-posterior wave of expansion persists. This wave may be greatly slowed in ram and biting species, but its retention suggests a fundamental importance to aquatic feeding.

Background

Wainwright (2015, this volume) postulated that there are three major innovations of suction feeding: (1) a protrusile upper jaw, (2) a planar mouth-opening, and (3) an anterior to posteriorly directed wave of expansion produced in coordination with opening of the mouth. Indeed, each of these evolutionary innovations appears critical to the generation of a current of water into the mouth. Generation of this suction is effective for drawing prey into the mouth if the current is strong enough and/or if the prey can be mobilized by it (i.e., drag forces can be overcome such that the prey can be pulled into the mouth). However, what about the instances where it is not effective? Here we address the following inter-related questions: Under what circumstances do fish abandon these innovations in suction feeding? What morphological and behavioral changes are present in species that have abandoned these innovations? For what types of prey or feeding situations is suction feeding no longer possible or effective?

Suction, ram, and biting

Traditionally, suction feeding was considered as the antithesis of ram feeding. For example, the ram–suction index (RSI) was developed decades ago to quantify the relative contribution both of movement of the predator (movement of the body and/or jaws) and movement of the prey (via a current of water generated by suction) to the strike (Norton and Brainerd 1993). However, because suction dissipates as an inverse function of distance (e.g., Nauwelaerts et al. 2008), suction only works if the fish can get its mouth close enough to the prey. So, for most species, the body, oral jaws, or both, move toward the prey to place the mouth in sufficient proximity to the prey that the current of water that is produced can entrap the prey and move it into the buccal cavity. More recent work has recognized the interpretive limitations of placing ram and suction in a relative context rather than in an absolute context (Wainwright et al. 2001). Yet, the utility of the RSI as an informative tool and as a complement to other measures remains.

One axis of behavioral variation that is present in many species of fish, but which is not captured by the RSI, is biting. Although there is a rich literature on biting as a mode of capturing prey, including behavioral, mechanical, ecological, and evolutionary perspectives (e.g., Alfaro et al. 2001; Mehta and Wainwright 2007), a false dichotomy often has been created between suction feeding and biting. That is, species often are thought to use either biting *or* suction. In reality, there are many species of fish that procure food using ram, suction, biting, combinations of two of these, and combinations of all three.

A primary aim of this article is to place feeding into a quantitative framework that incorporates all three of these behaviors. Work in the past has focused on physical displacement of the predator and prey. The RSI, for example, uses ''suction-distance'' and ''ram-distance'' as variables. Suction-distance typically is the distance moved by the prey toward the predator from the time that the mouth begins to open until the prey crosses the plane of the open mouth. Similarly, ram-distance is the distance moved by the predator toward the prey in the same time-frame. However, if we want to quantify biting, a measure of distance is less helpful because the action of biting is simply to close the jaws on the prey.

To incorporate ram, suction, and biting into one index, duration can be used, instead of distance, because duration enables the simultaneous measurement of the contribution of suction, ram, and biting to prey capture. This requires defining a number of variables, some of which have not been previously defined in this context:

> Ram-duration: The length of time that the predator is moving toward the prey during the strike or event (see definition of event-duration). The fish may be moving toward the prey for the entire event, or for only a subset of the event. Ram-duration is only that portion of the event when the fish is moving toward the prey. While this distinction was not made in the present symposium, ram-duration could be further subdivided into jaw-ram-duration (the movement only of the jaws toward the prey) and body-ram-duration (the movement only of the body toward the prey).
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> Suction-duration: The length of time that the prey is moving toward the predator during the event. As with ram-duration, suction-duration may last for only a portion of the event, and can start at the time of mouth opening, or later into the event. Suction-duration necessarily ends once the prey enters the open mouth and is effectively captured (*sensu* ''suction distance'' as defined by Norton and Brainerd 1993).
>
> Bite-duration: The length of time between the instant when the jaws begin to close and when they cease to move toward one another. If the jaws contact the prey in a bite, and the feeding event ends with the prey item held in the teeth, bite duration ends when movement of the jaw ends. If the bite continues such that a piece of food is removed, and the jaws physically close on one another, bite duration would include additional time.
>
> Event-duration: The length of time between the onset of opening the mouth and closure of the mouth, or to the end of bite-duration. This duration is also known as strike-duration, however the term ''strike'' makes less sense when the prey is non-elusive.

These definitions may require further refining as the comparative approach is put into practice. Yet, they provide a robust starting point for making new observations about the contribution of ram and biting to suction feeding.

The opaleye, *Girella nigricans,* is useful in this context as it is a species that uses all three feeding behaviors in one feeding event. When the durations of the ram, suction, and bite components are quantified, the feeding event is clearly ram-dominated (Fig. 1A). By converting absolute durations to relative durations, it is possible to compare all three simultaneously, and plot them in a format that allows for easy comparison among species. This is achieved simply by dividing ram-duration, suction-duration, or bite-duration by event-duration so that one can estimate the relative contribution of each to the event as a whole (Fig. 1A). Note, however, that this necessitates loss of such information as the absolute overlap in beginning and ending times of ram-duration, suction-duration, and bite-duration. All three relative durations are plotted on a triangular plot where the axes are ram-duration, suction-duration, or bite-duration (Fig. 1B). These are labeled at the apices, such that the closer you are to any one apex, the stronger the contribution of that feeding mode to the event. A purely ram event would be located right at the ram apex. A ram–biting event would be located along the axis between the ram apex and the biting apex. An event with all three feeding modes would be somewhere in the body of the triangle.

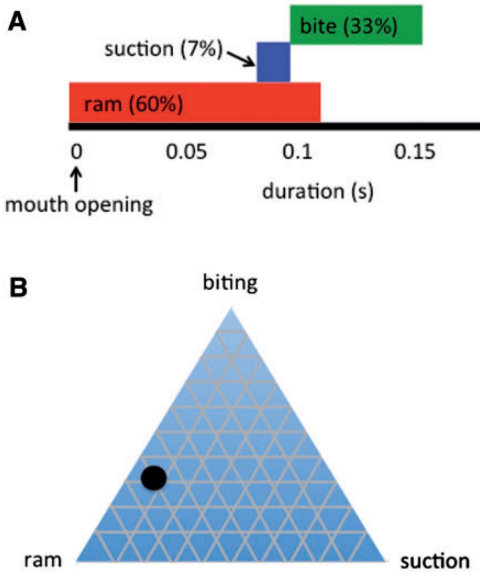

Fig. 1 Two ways to look at ram-duration, suction-duration, and bite-duration. Data are from a single feeding event from the opaleye, *G. nigricans*, feeding on a leafy alga (note that in this species the kinematics will change based on the type of prey). The event was recorded using high-speed video at 250 frames per second and the images analyzed using NIH Image J. In **A**, the absolute durations are plotted as bars. Onset and offset times are the beginnings and ends of bars, and the length of the bar represents duration. The onset and offset times are relative to the time of mouth-opening, which is defined as time zero. Note that there are times when the fish is still moving forward, and the prey is simultaneously being drawn toward the predator or being captured by the bite. This is indicated by overlap in the three bars indicating duration. In an absolute sense, this is permissible as they are independent events contributing to the overall capture, and can reasonably co-occur. In parentheses is the relative contribution of each of the durations to the event, calculated by dividing each of the three absolute durations (the lengths of the bars) by the total duration of the strike. In **B**, the relative contributions of ram, suction, and biting are plotted. Note that the data-point for this feeding event is closest to the apex of ram, which is an indication of the relatively larger contribution of ram to the event. The score at each apex would be 100% contribution of that feeding mode. Lines on the graph correspond to 10% intervals and the range is from 0% to 100%. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

Data from 16 different species were chosen nonrandomly in an attempt to fill every possible space within the ram–suction–biting domain (Fig. 2). In two cases we used the same species feeding on different food items (attached versus unattached) to specifically generate data-points hypothesized to represent extremes. The results of this initial large-scale comparison suggest three key findings:

(1) None of the species considered here spent more than 50% of the duration of the feeding event producing suction. Most of these species spend relatively more time producing ram as opposed to suction. Only three species (Fig. 2: the cod *Gadus macrocephalus*, the convict cichlid *Amatitlania nigrofasciata*, and the turbot *Pleuronichthys verticalis*) occupy a position on the graph where there is 50:50 time commitment to produce ram versus suction. Note that these same three species might be considered suction-dominated if examined using the RSI, which takes into account suction distance, but not duration. This new index considers simple proportions of ram and suction, and not the more complex calculation that is used in RSI. It is also noteworthy that this new index based on all three feeding behaviors supports the findings of recent hydrodynamic work: suction simply cannot be effective unless the fish is in close proximity to the food item. Even in the most patient of ambush predators, such as the frogfishes of the Lophiiformes, who wait for the prey to approach the jaws with a stillness one could mistake for death, there is a final and rapid lunge that closes the distance between

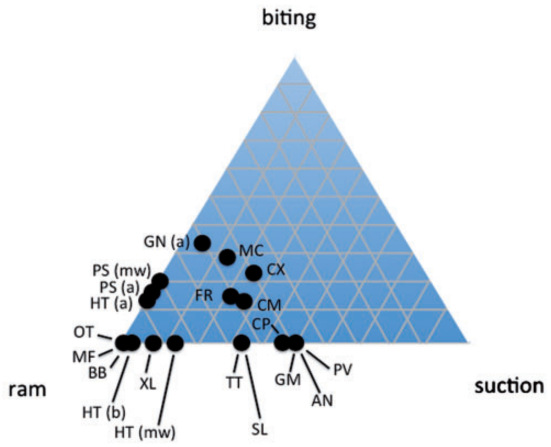

Fig. 2 Ram–suction–biting in 16 species of fish, including elasmobranchs. Each data-point is a single feeding event. Data were collected from high-speed video. The data shown are from GN, *Girella nigricans* (opaleye); PS, *Poecilia sphenops* (molly—mw, mid-water food; a, attached food); HT, *Helostoma temmincki* (kissing gourami—a, attached food; b, benthic food; mw, mid-water food); OT, *Onchorynchus tshawytscha* (salmon); MF, *Meda fulgida* (spikedace); BB, *Belonesox belizianus* (pike killifish); XL, *Xystreurys liolepis* (sole); TT, *Trichopodus trichopterus* (gold gourami); SL, *Syngnathus leptorhynchus* (pipefish); GM, *Gadus macrocephalus* (cod); AN, *Amatitlania nigrofasciata* (convict cichlid); PV, *Pleuronectes verticalis* (turbot); CP, *Chiloscyllium plagiosum* (bamboo shark); CM, *Cyprinodon macularius* (pupfish); FR, *Fundulus rubifrons* (killifish); CX, *Chaetodon xanthurus* (butterflyfish); MC, *Mustelus canis* (smoothhound shark). Lines on the graph correspond to 10% intervals and the range is from 0% to 100%, with 100% occurring at each apex. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

predator and prey just prior to actual capture of the prey (L. A. Ferry, personal observation). While the need to get close to the prey has been recognized, it has been, perhaps, underappreciated in terms of its contribution to capture. Hence, the innovation of protrusion of the jaws, not only serves to enhance the production of suction, but also likely serves to extend the moth toward the prey in a stealthy manner, or perhaps with less output of energy (Motta 1984).

(2) None of the species considered here spent more than 50% of the duration of the feeding event engaged in biting; all biters spent a large portion of the event moving toward the prey (ram). In addition, biters open their mouths when they are physically quite far away from the food. Fish that rely heavily on biting are not constrained by the hydrodynamics of suction feeding. Suction feeders open their mouths when they are in close proximity to the food because suction only operates over a short distance in front of the open mouth (e.g., Nauwelaerts et al. 2008). If a fish that relies on suction as a major component open too early, relative to the placement of the food, the water pulled in by the wave of expansion won't contain the desired food. However, biters are typically feeding on larger food, components of large food items, or attached food items, which are typically non-elusive. Biters do not have to worry about when they open their mouths relative to when they come near the prey, or about how widely they open their mouths, as their intended prey is unlikely to be affected in any consequential way by the physics of their approach. Biters are relieved of the constraint of a planar mouth-opening and possibly even of the need to create and anterior-to-posterior wave of expansion. In fact, it might be best for a fish with a very large gape to open the mouth very early and very far away so that the jaws won't incidentally encounter the prey item during the opening process.

(3) There are species that spend most, or all, of the feeding event engaged in ram behavior, in contrast with points 1 and 2. These species may generate some suction as the head expands, but prey are not actively moved into the mouth cavity by this movement. Compensatory suction has been invoked to explain the suction that is generated simply in compensation for the forward locomotion of the predator. When a predator swims forward in the water, water is pushed along in a sort of bow wave. If the prey is in front of the predator, the prey is likely to be pushed away by the predator. It has been argued that there are inertial suction feeders (those that use suction to capture prey), and compensatory suction feeders (those that generate only enough suction to compensate for their own locomotory effects on the surrounding watery medium). Species at the ram apex (Fig. 2) may not be able to generate even compensatory suction. Although many factors may contribute to this (see below), one key driver of this phenomenon may be that these species are not constrained to produce a planar opening of the mouth opening during the capture of prey.

What are the ramifications of these findings? Because fishes and many other aquatic vertebrates feed in a dense and viscous aquatic medium, suction is often the most common solution to the physical challenges posed by the environment. Fish that reduce the suction component of the strike must contend with a slightly different, but still demanding, set of physical requirements. Hydrodynamic constraints may reduce the ability of fish to occupy some areas of the possible ram–bite–suction behavioral space. Perhaps because fish must place themselves in close proximity for either suction or biting to function properly, there are no suction-biters, there are no 100% suction feeders and there are no 100% biters. Ram will always contribute strongly to the feeding event and, although most fish rely on suction as a key component of the capture of prey, it can be argued that most fishes rely even more heavily on ram, at least that is the case for the species used here. In addition, fish that spend a large amount of time in ram behavior during the capture of prey may have a different suite of physical challenges to overcome relative to fish that proportionally spend more time producing suction. Following is a series of cases that serve as exemplars of variations in feeding behavior in fish that spend a large proportion of their feeding events engaged in ram movements.

Case 1: large-gaped predators

Large-mouthed fishes encounter a physical problem when feeding: the more a fish open its mouth, the larger the cross-sectional area it presents as it moves through the water. Correspondingly, a large bow wave should be produced as the fish moves forward and the fish would have to produce even more suction to overcome this. Yet, having a large mouth is contraindicated when it comes to suction feeding (sensu Motta 1984), because a large wave of expansion immediately posterior to a small mouth yields a higher velocity of flow (into the mouth) than does a similar wave of expansion that occurs immediately posterior to a large mouth. Higher velocities of water should have higher probabilities of entraining prey, or at least of creating flows from which it is harder for prey to escape. Because of this, small mouths are often correlated with improved performance in suction feeding (Norton and Brainerd 1993; Wainwright et al. 2001).

In addition, the action of the mouth opening, or the lower jaw depressing, tends to pull on the upper jaw (maxilla and/or premaxilla) and protrude/depress it due to linkages in most fishes between the upper and lower jaws (Westneat 2004). When the upper jaw protrudes, the descending arm of the premaxilla and the maxilla typically rotate forward and occlude the sides of the open mouth (Gibb 1996). Indeed, this helps create the round or planar opening of the mouth thought to be a key component of effective suction feeding (Wainwright, this volume). However, if the sides of the open mouth are occluded in large-mouthed predators, this potentially creates an even larger effective cross-sectional area, and an even larger negative effect on the intended prey.

van Wassenbergh et al. (2010) examined this phenomenon and noted that for large-mouthed predators a deep V-shaped opening of the mouth is essential because the V functions to channel water away from the front of the mouth and toward its corners. This funneling reduces and relocates the bow wave more posteriorly, so that it does not push the prey away from the open mouth as the fish approaches. Given this hydrodynamic observation, there may be an inverse relationship in large-mouthed predators between occlusion of the gape and the gape-distance (the distance between the tips of the upper and lower jaws). That is, the larger the gape-distance, the greater is the hydrodynamic ‘‘cost’’ of opening the mouth. Therefore, evolution should favor large-gaped fish that have reduced lateral occlusion of the gape, either via the premaxilla or maxilla.

Kinematic data from several species of large-mouthed fishes (gape >50% of the length of the head) were used to ascertain if this tradeoff exists (Fig. 3). From these data it appears that the more these predators open their jaws to produce a large gape, the less they occlude the gape, and this relationship holds true even in species with highly mobile upper jaws and that hypothetically are capable of considerable protrusion and/or occlusion. This is a broad evolutionary pattern, as it holds true across various taxa, e.g., salmoniform (OT), an atherinomorph (MES), and a cypriniform (MF) (see Fig. 3).

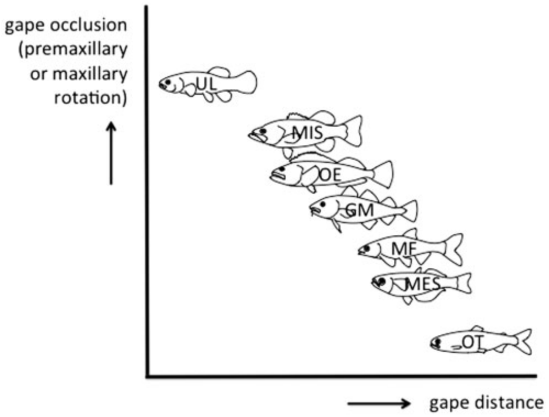

Fig. 3 Trade off between gape-distance (the distance between the tips of the upper and lower jaws) and gape-occlusion (swing of the premaxilla or maxilla) in large-mouthed predators. Each data-point is an average of at least nine feeding events. Data were collected from high-speed video. The data shown are from UL, *Umbra limi* (mudminnow); MIS, *Micropterus salmoides* (large-mouth bass); OE, *Ophiodon elongatus* (lingcod); GM, *Gadus macrocephalus* (cod); MF, *Meda fulgida* (spikedace); MES, *Melanotaenia splendida* (rainbowfish); OT, *Onchorynchus tshawytscha* (salmon).

Noteworthy here is the mudminnow. *Umbra limi*, which is a member of the Esociformes. Mudminnows, on average, demonstrated a small gape—with the sides of the mouth largely occluded (see Fig. 3). However, the individuals studied also showed a spectrum of behaviors, including strikes in which a given mudminnow produced very large gapes, and did not occlude the sides of the open mouth at all (Fig. 4), and there were also strikes in which the same individual produced smaller gapes that were occluded. This spectrum of behaviors was produced across a range of body sizes, and prey types (the original study was meant to investigate modulation in response to type of prey) (Lines et al. 2015), yet neither of these elicited consistent changes in gape-distance or premaxillary-protrusion. For example, both kinds of strikes, larger gape with little occlusion versus smaller gape with more occlusion, were produced in response to bloodworm (chironomid larvae) as prey. The cause of this variability in behavior is not clear.

However, it is clear that, even within a single species, depression of the lower jaw does not always drive motion of the premaxilla. This potential decoupling might represent a release from a constraint imposed by suction feeding. These species are, by

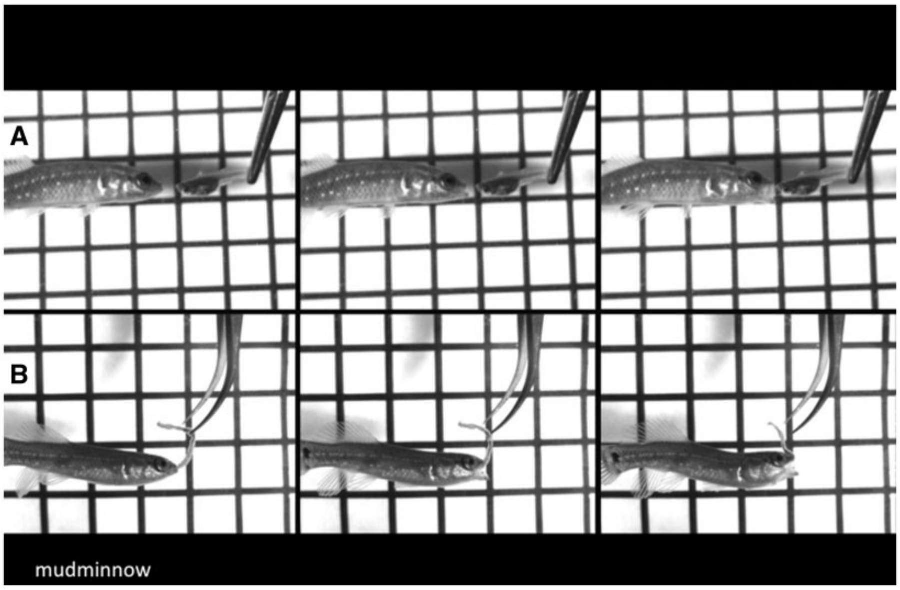

Fig. 4 Mudminnow capturing prey both with and without occlusion of the gape. In **A**, the mudminnow shows behaviors more like a large mouth bass (with occlusion); in **B**, the mudminnow shows behaviors more like a salmon (without occlusion). Notice the differences in cranial elevation between the strikes. There are differences in the prey items in A and B (guppy versus blood worm), but the type of prey item did not consistently elicit these differences across individuals, and these same differences were observed even within prey-capture events only on blood worms. Figure after Lines et al. (2015).

and large, pure ram feeders, very near or at the ram apex in Fig. 2. When one move away from a reliance on suction, a coupling between depression of the lower jaw and protrusion of the upper jaw becomes less important.

Case 2: long-jawed predators

Some species that spend a large proportion of the total strike engaged in ram behavior have elongate anterior jaws, e.g., the pike killifish, *Belonesox belizianus,* at the ram apex of ram in Fig. 2. For fishes, we define ‘‘elongate jaws’’ as an increase in the lengths of the premaxilla and/or maxilla on the upper jaw, and the dentary and/or the angularticular on the lower jaw (mandible), relative to closely related, plesiomorphic species. Why do some species of fish possess elongate jaws?

> Hypothesis 1: The elongated upper and lower jaws are advantageous because they can increase gape-distance during the strike. If the jaws are elongated relative to shorter-jawed plesiomorphic taxa, the same degree of rotation of the lower jaw will result in a larger gape (sensu Ferry-Graham et al. 2010). Therefore, elongate jaws generate more output-motion for the same input. Hence, if the angle of gape is conserved across taxa, gape-distance will increase with increasing length of the jaw.
>
> Hypothesis 2: Elongated upper and lower jaws function to increase the speed with which the jaws open and close (sensu Burnette and Gibb 2013). If the jaws are longer, relative to plesiomorphic taxa, the same gape-distance can be achieved with less angular rotation at the joint (quadratomandibular) of the lower jaw. Therefore, the jaws can be closed faster because there is a shorter linear distance to be traversed. Stated in another way, the jaw is a lever, and its length has increased. So, with the same input of motion, a faster output can be produced. If gape-distance is conserved, the increase in lever-length will yield a faster output of motion.

Given that these two hypotheses are mutually exclusive, there again appears to be an intrinsic trade-off. Species could either have a large gape or a fast mouth-closing speed, but not both. This prediction can be tested using kinematic data from six species with elongate jaws (Fig. 5). These six species, can, in theory, fall into one of four quadrants: small gape with fast closing of the jaws; small gape with slow closing of the jaws; large gape with slow closing of the jaws; and large gape with fast closing of the jaws. A trade-off-based hypothesis suggests, however, that our long-jawed species should fall in either the ‘‘small gape, fast closing’’ quadrant, or the ‘‘large gape, slow closing’’ quadrant.

Interestingly, no species appear to fall squarely into the ‘‘large gape, slow closing’’ quadrant, at the lower right-hand corner of the graph. There were two species with exceptionally large gapes; the pike,

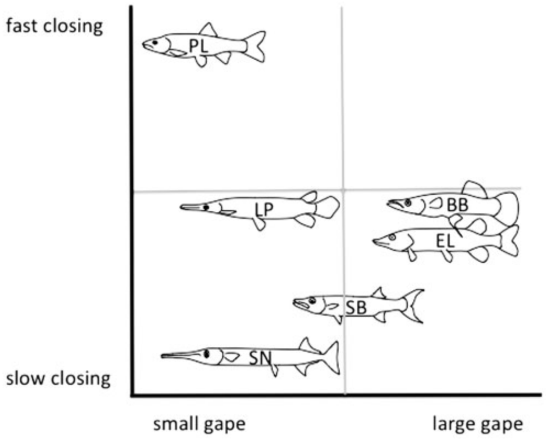

Fig. 5 Trade off between the speed of closing the mouth and the gape-distance (distance between the tips of the upper and lower jaws) routinely achieved during prey capture in long-jawed predators. Each data-point is an average of at least seven feeding events. Data were collected from high-speed video footage. The data shown are from PL, *Ptychocheilus lucius* (pike minnow); LP, *Lepisosteus platyrhincus* (gar); BB, *Belonesox belizianus* (pike killifish); EL, *Esox lucius* (pike); SB, *Sphyraena barracuda* (barracuda); SN, *Strongylura notata* (needlefish).

Esox lucius, and the pike killifish, *B. belizianus.* These had somewhat intermediate closing speeds, not the very slow closing speeds predicted by our trade-off hypothesis. These species are known to eat large prey, sometimes as large as their own heads; because of the shape of the mouth (see Case Study 1), they likely will not push the prey away from the gape as they approach rapidly. Larger prey are subject to drag forces, and the prey can neither be pulled in by suction, nor displaced anteriorly by a bow wave (van Wassenbergh et al. 2010). These fish literally ram into the prey as they attack it (L. A. Ferry and A. C. Gibb, personal observation).

There were several species in this analysis that produce small gapes and had lower speeds of mouth-closing. Pike minnow, *Ptychocheilus lucius,* appear to represent a tidy tradeoff between the two factors: small gape, fast closing speed. Pike minnows' "anatomical gape" (the degree to which the mouth can be forcibly opened in a fresh specimen) is similar to barracuda or even to pike. However, the "functional gape" (i.e., the gape produced during capture of prey) is approximately 30% of anatomical gape (Burnette and Gibb 2013). This appears to be the only published study of a long-jawed species for which functional gape was measured directly, but the result may be more generally true. Many long-jawed species, such as gar, *Lepisosteus platyrhincus,* and barracuda, *Sphyraena barracuda,* in this study (Fig. 5), may be capable of producing very large gapes, similar to that of the pike, but they may not produce these maximal gapes in a functional sense (i.e., when feeding). This may explain the rather odd location of the gar in Fig. 5.

These data suggest that at least some long-jawed species do not swim forward, jaws maximally agape. These species instead take advantage of speedily closing the jaws, and of the reduced rotation needed about the quadratomandibular joint, necessary to close the jaws. Thus, long jaws in fishes might best be considered a morphology that facilitates: (1) stealth, because the shape streamlines the profile of the fish as it moves through the water and (2) the velocity at which the jaws open and close. In addition, as described above, the V-shape of the mouth diverts flow to the corners of the mouth, thereby reducing the bow wave (van Wassenbergh et al. 2010).

Perhaps the most unusual species included in this analysis is the needlefish, *Strongylura notata*, which (surprisingly) has a proportionally small gape and slow movements of the jaws (Fig. 5). Thus, needlefish do not appear to maximize either size of the gape or the speed at which the jaws are closed. Curiously, when mechanical advantage (MA) for the needlefish's jaw is calculated using muscle insertions and in-lever/out-lever ratios, the MA suggests that jaws of needlefish are "velocity amplified". The MA for needlefish during jaw-closing was 0.042 ± 0.002 ($n = 12$, mean SL 27.3 cm). This is in contrast to barracuda, for which MA is nearly an order of magnitude greater at 0.401 ± 0.003 ($n = 19$; mean SL 16.3 cm), and gar, which have an MA of 0.154 ± 0.005 ($n = 10$, mean SL 23.7 cm).

If needlefish utilize a small gape and relatively slow movements of the jaws, why do they possess such an extreme morphology? There are several possible, non-exclusive reasons why they may have this extreme morphology, but a non-extreme behavior. (1) All studies of needlefish to date are laboratory-based studies; perhaps needlefish in the wild produce more rapid movements or of higher magnitude. (2) It is possible that this extreme morphology serves as a form of crypsis, wherein potential prey items cannot see the needlefish even when it is very close by because its frontal profile is so small. (3) It is possible that the extremely elongate shape of the needlefish provides it with some as-yet-to-be-described hydrodynamic advantage during feeding.

Case 3: large bodies, large gapes, and very tiny prey

Suspension feeding is often completely overlooked when considering the myriad of ways in which aquatic predators capture prey. Such predators face similar challenges as other fishes in terms of getting the food into the mouth or onto the structures used to extract particles from the surrounding water. However, the sheer size of the predator versus their tiny prey make this challenge even more complicated.

These predators are sometimes assumed to employ a strategy of swimming like a giant open tube through the water. True, the wide-open mouth reduces the bow wave in front of the predator and prevents the prey from being pushed away, and the sides of the open mouth are not occluded in the same manner as in the other suction feeders previously discussed. However, at the level of the structures used in suspension feeding (i.e., gill rakers, mucus, filter pads), in which the prey actually comes into contact with the predator, the same sorts of issues arise in terms of foraging in a dense and viscous medium. These large-scale suspension-feeding predators need to compensate for the aquatic medium if food is to be ingested.

Like other aquatic predators mentioned thus far, suspension feeding may be accomplished with the additional assistance of ram, or suction, or both. Generating suction as the mouth is opened will solve the problem of the bow wave generated by the very large predator. This suction-suspension feeding is a tactic utilized by the whale shark, *Rhincodon typus*, although not exclusively (Motta et al. 2010). Even with a large gape and an elliptical mouth opening, a massive wave of expansion posterior to the mouth facilitates generation of suction. For ram feeders, the challenge is different. A minimized bow wave and a wide mouth allow particles to easily enter the buccal cavity; however, extraction of these particles from the water requires contact with a filter. Ram-suspension feeding is exemplified by the mobulids such as *Manta birostris* and *Mobula japonica* (Paig-Tran et al. 2013).

Whether a suspension feeder uses ram or suction may depend upon the density of the prey in the water column. We predict that prey that are more evenly dispersed throughout the column, rather than existing as a concentrated bolus, will lend themselves to capture via ram, as opposed to suction. While quantitative data are difficult to obtain for many suspension feeders, we can make predictions about which species might rely more on suction versus ram (Fig. 6). Megamouth, *Megachasma pelagios*, presumably feeds on tightly packed balls of plankton (Paig-Tran et al. 2013). Manta rays, *M. birostris*, and basking sharks, *Cetorhinus maximus*, feed mostly on dispersed food, the former mostly on zoeas and sergestid shrimp (E. M. Paig-Tran, personal observations), while the latter feed primarily on calanoid copepods (Sims 2008). Thus, manta rays and basking sharks should exclusively use ram to capture prey.

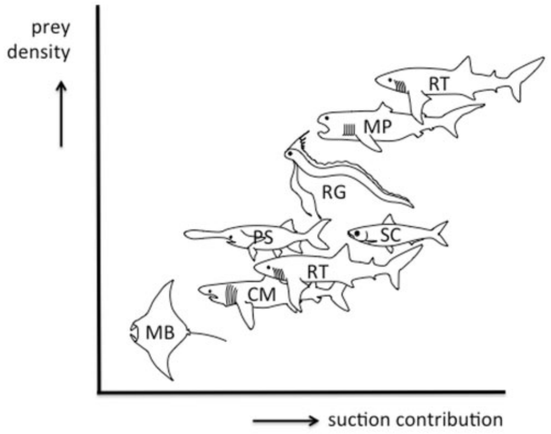

Fig. 6 The predicted relationship between dispersion of prey and the relative use of suction. When the prey are packed into a tighter bolus, more suction should be used. The species shown are MB, *Manta birostris* (manta ray); CM, *Cetorhinus maximus* (basking shark); MP*, *Megachasma pelagios* (megamouth shark); RT, *Rhincodon typus* (whale shark); PS*, *Polyodon spathula* (paddlefish); RG*, *Regalecus glesne* (oarfish); SC*, *Sardinops caeruleus* (sardine). The whale shark appears in two locations on the graph in accordance with their different modes of feeding on densely packed versus more highly dispersed prey. The placement of species with asterisks is inferred from observations of feeding, but lacks quantitative data.

Indeed, this appears to fit with qualitative observations of their feeding (Fig. 6). Megamouth is hypothesized to utilize a suction-style engulfment (Nakaya et al. 2008), although the density of prey in the region where the individuals feed is unknown. Densities of plankton in patches where basking sharks feed are reported to be 1050–1480 m^{-3} (Sims 2008). Those in the vicinity of ram-feeding whale sharks were $1841 \pm 616\,\text{m}^{-3}$, which was more than twice the density of plankton in non-feeding sites (Motta et al. 2010). Plankton densities near ram-feeding mantas in the Yucatán are similar to those found for ram-feeding whale sharks as both species often are found feeding in the same plankton blooms (E. M. Paig-Tran, personal observation). Motta et al. (2010) reported that density of prey was three to four times higher in areas where whale sharks were ram feeding than in areas where whale sharks were suction feeding; however, the prey are very patchy where suction feeding occurs. In the patches, the density of prey is extremely high, but when averaged across an area, which includes the low-density spaces between patches, the overall density of prey in areas where suction feeding occurs appears lower. Thus, whale sharks use ram when feeding in areas where the prey is more evenly dispersed and not occurring in dense clumps, consistent with our predictions (Fig. 6).

This same pattern may hold true in suspension-feeding teleosts as well as large elasmobranchs. Oarfish, *Regalecus glesne/Regalecus russelii*, appear to suction feed on small blooms of plankton while remaining suspended in the water column. Paddlefish, *Polyodon spathula,* feed on dispersed plankton as do sardines, *Sardinops caeruleus.* Thus, we should see a stronger component of suction feeding in the oarfish than in paddlefish or sardines. Again, observations both of paddlefish and of sardines suggest that this is the case, and both of these species are ram-suspension feeders (Burggren and Bemis 1992), although the data supporting their placement on Fig. 6 is less quantitative than for the elasmobranchs shown.

As an aside, it is worth noting the differences in functional gape among the large elasmobranch suspension feeders. Megamouth has a remarkable height of its gape, approximately 18% of its total length (Nakaya et al. 2008). Manta has a width to its gape of 30% of the width of the disk, although the height of the gape is about half of that (E. M. Paig-Tran, personal observation). Basking sharks have a height of gape of 10–12% of their total body length (Sims 2008). Whale sharks have the smallest height of gape, closer to 5–7% of their total length (Motta et al. 2010). Thus, in cartilaginous fishes as well as in bony fishes, ram-feeding predators tend to have larger and more wide-open gapes when they approach the prey.

Case 4: biters

For species of fish that spend a large portion of the strike producing a bite, a bow wave produced during open-mouthed swimming will not matter because large, non-elusive food will not move in an attempt to evade capture. Thus, the predator does not need to place the mouth close to the prey and then create a rapid expansion of the buccal cavity. Consequently, biters can open their mouths at some distance from the prey and swim toward the prey with the mouth open and there is likely no constraint on the magnitude of the opening of the mouth.

This leads to the prediction that strike-distance will be positively correlated with gape-distance. That is, the closer to the prey the mouth is opened, the smaller the mouth opening will be, and vice versa. We tested this prediction using kinematic data from 10 species of ‘‘biters’’, defined as species that use some amount of biting behavior during the capture of prey, or taxa closely related to a biting species (outgroup species; Fig. 7). This analysis considered two major clades, atherinomorphs (cyprinodontiforms with an atheriniform outgroup) and anabantoids (gouramis with betta for comparison).

As predicted, biting species that opened the mouth to a greater extent were farther from the 0.0 origin. While a relaxed reliance on suction permits this finding, the strength of the result was impressive. It was not simply that species who open their mouths more had a greater amount of variability in strike-distance, as might be expected if suction simply was unimportant. Species with larger gapes absolutely opened the mouth father from the prey, which could be taken to mean a stronger reliance on biting relative to other biters. Kissing gourami, *Helostoma temmincki,* consistently opened their mouths about twice as far from the food than did either gold gourami, *Trichopodus trichopterus,* or dwarf gourami, *Trichogaster lalius* (Fig. 7). Molly, *Poecilia sphenops,* and pupfish, *Cyprinodon macularius,* also consistently opened their mouths farther from the food than did other cyprinodontiforms such as the killifish, *Fundulus rubifrons,* and mosquitofish, *Gambusia affinis* (Fig. 7). This perhaps indicates that species are cognizant of the distance between themselves and their food/substrate, and are opening the mouth at a greater distance to avoid a collision with said surfaces during opening of the mouth. Interestingly, species like the pike killifish, *B. belizianus*, described above, routinely collide with their prey, mouth agape.

Are cranial movements modified in ways that enhance feeding behaviors beyond suction feeding?

Previous work from our laboratories attempted to identify the fundamental movements (kinematics) that characterize suction feeders with a multiple-species comparison that considered a wide phylogenetic range of fish (see Gibb and Ferry-Graham 2005). These species are known, or thought, to move prey into the mouth by suction. In the present paper, the analysis has been expanded to include a total of 24 species with representative biters, scrapers, nippers, and ram-feeders. These would be species close to the biting and ram apices, respectively, in Fig. 2. However, the data that are included in the analysis have been selected to represent the feeding of fish on unrestrained, non-elusive, midwater prey. Under these circumstances, suction should be used to capture the prey item if the predator is capable of

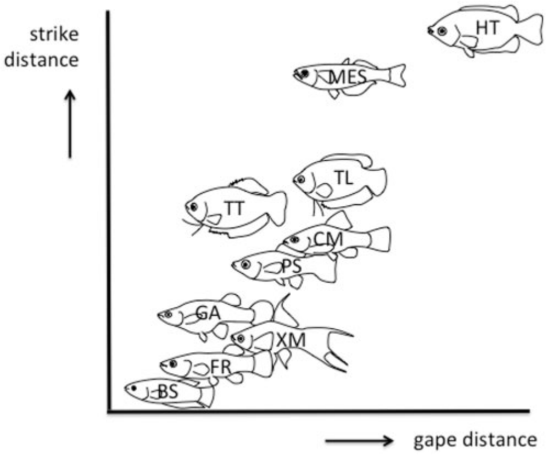

Fig. 7 Positive relationship between strike-distance (distance from the prey at which the mouth is opened) and gape-distance. Each data-point is an average of at least nine feeding events. Data were collected from high-speed video footage. The data shown are from the gourami HT, *Helostoma temmincki* (kissing gourami); TT, *Trichopodus trichopterus* (gold gourami); TL, *Trichogaster lalius* (dwarf gourami). The outgroup for these three is BS, *Betta splendens* (fighting fish). Data are also shown for the cyprinodontiforms PS, *Poecilia sphenops* (molly); CM, *Cyprinodon macularius* (pupfish); FR, *Fundulus rubifrons* (killifish); GA, *Gambusia affinis* (mosquitofish), XM, *Xiphophorus maculatus* (swordtail). The atheriniform outgroup for these five species is MES, *Melanotaenia splendida* (rainbowfish).

producing it, as opposed to, for example, biting. Species were selected for analysis for which datasets were available that contained 10 critical kinematic variables (see legend to Fig. 8). The PCA produced four axes that each explained more than 10% of the total variation, and cumulatively explained 83.7% of the total variation in the dataset (Fig. 8).

Remarkably, a broad range of taxa produce virtually identical feeding kinematics according to the PCA. On all four axes of variation, many species thought to use a strong component of suction during the capture of prey possess factor scores that are close to zero, which creates a clustering of these species at the 0.0 region of the kinematic space (Fig. 8).

However, some species are more ‘‘extreme’’. Bay pipefish, *Syngnathus leptorhynchus*, use a large amount of cranial rotation to produce an unusual type of jaw-ram that places the mouth of the fish in close proximity to the prey. Several biting species, the molly, *P. sphenops,* and the wrasse, *Choerodon anchorago*, and two large-gaped predators, salmon, *Onchorynchus tshawytscha*, and lingcod, *Ophiodon elongatus*, were unusually slow movers; this suggests that the rapid wave of expansion of the head is no longer a key feature of prey-capture for these four taxa. The finding that two ram-dominated species are similar to two species that normally rely on biting as a primary mode of capturing prey is surprising and enlightening. Pike killifish, *B. belizianus*, is the only species included in the analysis that exhibits an exceptionally large gape; in this species a large gape is produced by extreme depression of the lower jaw. Finally, of those included in the analysis, the only fish that appear to produce kinematics that maximize suction are the two flatfish species: the sole, *Xystreurys liolepis*, and the turbot, *Pleuronectes verticalis*. Both of these fish have extended protrusion of the premaxilla, depression of the hyoid, and a small gape.

Note that while the magnitude of kinematic events changed in these extremists, the relative timing of the events did not. As with previous multi-species analyses (Gibb and Ferry-Graham 2005), all of the timing variables consistently loaded on the first PC, and very strongly so. This suggests that the anterior-to-posterior wave of expansion is retained, even among these 24 very different species. The wave might be slowed down, such as in wrasse (*C. anchorago)*, salmon (*O. tshawytscha*), and lingcod (*Ophiodon elongates*) but the coordination among kinematic events is omnipresent.

Conclusions

From the new analyses and hypotheses considered here, five patterns emerge:

(1) Ram, biting, and suction often co-occur within the same strike from the same individual and the relative contributions of each of these can be quantified using the duration of these activities. When these are considered simultaneously, it is clear that purely suction is unlikely to occur in mobile, aquatic-feeding vertebrates. This is likely because suction cannot be employed to move prey over great distances, and this limits duration of the suction component of feeding behavior relative to the ram component.

(2) Suction may constrain key aspects of behavior (i.e., kinematics) and morphology in taxa that rely heavily on this mechanism of capturing prey, possibly because of the physical requirements of moving a bolus of water into the buccal cavity. Indeed, key morphological and behavioral features are retained across diverse lineages of fishes, such as the protrusile upper jaw, a small, planar mouth-opening, and a rapid and coordinated anterior-to-posterior wave of expansion (Wainwright 2015, this volume). These behavioral and morphological

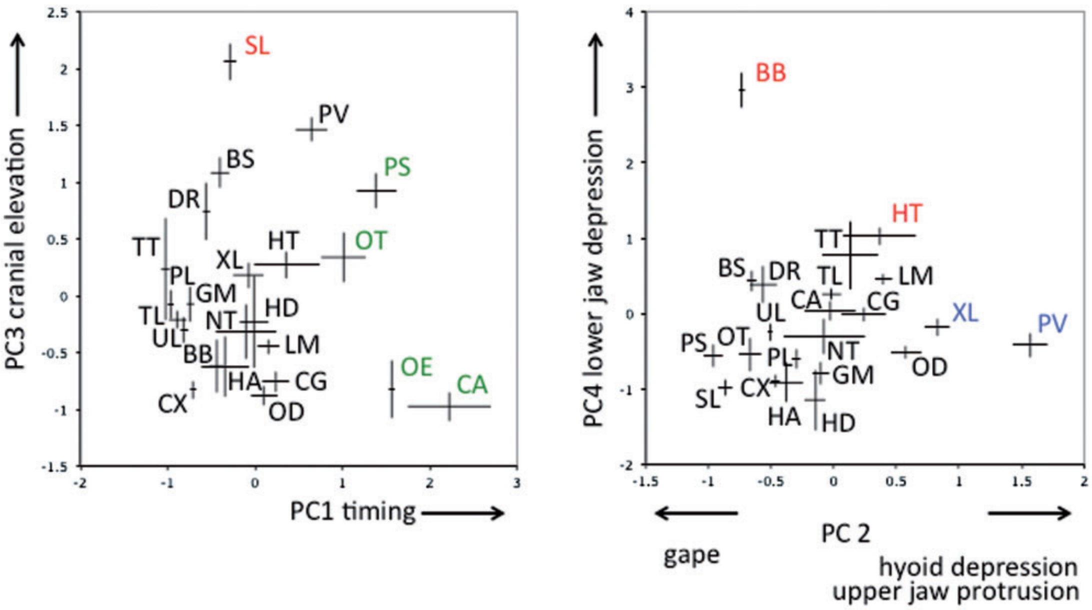

Fig. 8 PCA from 24 species of fish all capturing unrestrained and non-elusive prey. The species included in this analysis are OT, *Onchorynchus tshawytscha* (salmon); GM, *Gadus macrocephalus* (cod); DR, *Danio rerio* (zebrafish); PL, *Ptychocheilus lucius* (pike minnow); UL, *Umbra limi* (mudminnow); HT, *Helostoma temmincki* (kissing gourami); TT, *Trichopodus trichopterus* (gold gourami); TL, *Trichogaster lalius* (dwarf gourami); BS, *Betta splendens* (fighting fish); XL, *Xystreurys liolepis* (sole); PV, *Pleuronectes verticalis* (turbot); LM, *Lepomis macrochirus* (bluegill); PS, *Poecilia sphenops* (molly); BB, *Belonesox belizianus* (pike killifish); OE, *Ophiodon elongatus* (lingcod); OD, *Oxycheilinus digrammus* (cheek-lined wrasse); NT, *Novaculichthys taeniourus* (rockmover wrasse); CA, *Choerodon anchorago* (orange-dotted tuskfish or wrasse); CG, *Coris gaimard* (yellowtail wrasse); HD, *Hologymnosus doliatus* (ring wrasse); HA, *Heniochus acuminatus* (longfin bannerfish or butterflyfish); CX, *Chaetodon xanthurus* (pearlscale butterflyfish); SL, *Syngnathus leptorhynchus* (bay pipefish). Note that for some of the taxonomic groupings, several species were included in an effort to assess variation within a closely related group of species relative to variation across distantly related species. Most heavily sampled in this context were the wrasses (labrids). The 10 variables entered into the analysis were maximum gape-distance (distance between the upper and lower tips of the jaw), maximum premaxillary-protrusion (distance that the premaxilla moves anteriorly or ventrally away from the neurocranium), maximum cranial-rotation (degree of rotation of the neurocranium dorsally or ventrally), maximum rotation of the lower jaw (degree of rotation of the entire mandible ventrally), maximum hyoid depression (distance the hyoid apparatus protrudes ventrally), and the times of each of these five maxima relative to the start of the feeding event at time zero (time the mouth opens). The PCA was generated using the correlation matrix and un-rotated scores are reported here. Labeled on each axis are the kinematic variables whose variation contributed most to that axis. Arrows indicate the direction of increasing movement for that particular variable. The first axis is a "timing" axis and contains all of the variables of timing (all loadings >0.80), the second is gape (loading negatively at −0.51), depression of the hyoid and protrusion of the upper jaw (loading at 0.67 and 0.77); the third is cranial elevation (loading at 0.86), and the fourth is depression of the lower jaw (loading at 0.81). Note that the loadings and variance explained is extremely similar to our previous analysis of 14 species (Gibb and Ferry-Graham 2005). (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

hallmarks of suction feeders work remarkably well for generating a current of water into the open mouth, and there are few other solutions imaginable for this task (Ferry-Graham and Lauder 2001). However, as our data reveal, generation of suction accounts for half, or less, of the duration of the feeding event.

(3) Ram feeding thus may be one of the evolutionary forces responsible for the morphological diversity seen in extant fishes. In terms of time dedicated to producing prey-capture behaviors, ram always accounts for more than half of the time spent in the feeding event. Suction and biting are only effective when the jaws are in proximity to the prey, and ram is needed to bring the jaws into a suitable position. The only feeding behavior that occurs alone, not in conjunction with contributions from biting or suction, is ram feeding. Thus, ram-based behaviors may be a key force in shaping the kinematics and morphologies of capturing prey. In other words, while suction may explain the conservation of traits, it is ram that may well be responsible for their diversification.

(4) Many biting, nipping, scraping, and ram-dominated feeders (i.e., those approaching the apices in Fig. 2) can still produce a stereotypical capture of prey by suction. Relatively

modest changes to the features of the head and jaws, or their movements, may not lead to a concomitant reduction in the production of suction, and is consistent with the findings of many others who have worked in this field (e.g., Liem 1990). However, those species of fish that have evolved distinct feeding-morphologies are also associated with highly unusual kinematics; for example, (1) greater cranial rotation that produces jaw-ram (pipefishes); (2) greater depression of the lower jaw that produces a very large gape (pike killifish); and (3) very slow movements that produce a large gape, used either for biting or for some forms of ram-dominated feeding. The protrusile upper jaw and small, planar opening of the mouth are features lost in many ram and ram-biting feeders. The timing of mouth-opening, similarly, is less important. These deviations allow for a release from the constraints posed by the production of suction, and those traits are now available, in a sense, for evolutionary modification.

(5) Even in the most radically modified species (at least among those considered here), there is little, or no, evidence for the loss of the anterior-to-posterior wave of expansion. The elements of the cranium and jaws continue to expand in close coordination with one another; this wave of expansion is simply slowed down in species that have increased reliance on biting and ram during prey-capture. Interestingly, Hernandez (2015, this volume) found that "slow suction" works effectively when feeding on particulate prey, at least in benthic-feeding Cypriniformes. Further, it seems likely that suction remains a key component of prey-transport in the majority of aquatic feeders (Gillis and Lauder 1995); thus, a wave of expansion remains a required element of a successful feeding event, even in a species with a large component of ram or biting in capture-behavior. This may, in turn, prevent fishes and other aquatic vertebrates from decoupling the relative timing of the movement of the anatomical features of the head.

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