Body ram, not suction, is the primary axis of suction feeding diversity in Spiny-Rayed Fishes

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SUMMARY

Acanthomorph fishes exhibit a large diversity of suction feeding behaviors, which is driven by variation in the contribution of body ram. Suction distances are constrained even at broad evolutionary scales.

ABSTRACT

Suction feeding fishes exhibit diverse prey capture strategies that vary in their relative use of suction and predator approach (ram), which is often referred to as the ram-suction continuum. Previous research has found that ram varies more than suction distances among species, such that ram accounts for most differences in prey capture behaviors. To determine whether these findings hold at broad evolutionary scales, we collected high-speed videos of 40 species of spiny-rayed fishes (Acanthomorpha) feeding on live prey. For each strike, we calculated the contributions of suction, body ram (swimming), and jaw ram (mouth movement relative to the body) to closing the distance between predator and prey. We confirm that the contribution of suction distance is limited even in this phylogenetically and ecologically broad sample of species, with the extreme suction area of prey capture space conspicuously unoccupied. Instead of a continuum from suction to ram, we find that variation in body ram is the major factor underlying the diversity of prey-capture strategies among suction-feeding fishes. Independent measurement of the contribution of jaw ram revealed that it is an important component of diversity among spiny-rayed fishes, with a number of ecomorphologies relying heavily on jaw ram, including pivot feeding in syngnathiforms, extreme jaw protruders, and benthic sit-and-wait ambush predators. A combination of morphological and behavioral innovations have allowed fish to invade the extreme jaw ram area of prey capture space. We caution that while two-species comparisons may support a ram-suction trade-off, these patterns do not speak to broader patterns across spiny-rayed fishes.

INTRODUCTION

The ability to produce suction is an important adaptation for capturing prey in aquatic environments. Suction-feeding organisms take up food by generating a flow of water into the mouth through rapid expansion of the oral cavity. Such mechanisms have evolved multiple times in aquatic groups of vertebrates and are found today in sharks and rays, fishes, turtles, amphibians, birds and mammals (Wainwright et al., 2015). By using suction to draw prey (and water) towards their mouth, predators use the viscosity of water to their advantage, as these flows and the forces they exert on prey are difficult to overcome during prey escape attempts (Van Leeuwen and Muller, 1984; Holzman and Wainwright, 2009). However, suction flows are only significant roughly a single mouth diameter in front of the predator's mouth, (Muller et al., 1982; Muller and Osse, 1984; Van Leeuwen, 1984; Ferry-Graham et al., 2003; Day et al., 2005) making the approach and positioning of the mouth near prey key to a successful prey capture strategy (de Jong et al., 1987; Holzman et al., 2012).

Suction feeding predators use a variety of mechanisms to quickly move their mouth in close proximity of the prey, including overtaking them with a burst of swimming, ambushing them from a concealed location in close quarters, or protruding their jaws toward the prey while the body remains motionless. A central challenge in understanding the diversity of feeding behaviors in aquatic feeding vertebrates has been to place this behavioral diversity into a mechanistic framework that captures the major axes of diversity. Movements of an aquatic predator towards prey are often summarized as the ram components of a feeding strike (Liem, 1980a), which are then split into two sources of movement: body ram, or movements of the predator's body towards the prey by swimming or coasting, and jaw ram, or movements of the predator's mouth towards the prey relative to the rest of the predator's body (Liem, 1980b; Norton and Brainerd, 1993; Nyberg, 1971; Osse, 1985). Body ram and jaw ram can be used in combination with suction to decrease the distance between predator and prey. The amount of body ram also influences initial predator-prey distance, strike speed, and strike duration, as well as the shape and volume of ingested water during the strike (Weihs, 1980; Harper et al., 1991; Higham et al., 2005; Tran et al., 2010; Oufiero et al., 2012). Jaw protrusion is the most common mechanism of jaw ram and has been shown to decrease the hydrodynamic disturbance detectable by prey while significantly increasing the suction forces on prey (Holzman et al., 2008; Holzman and Wainwright, 2009; Staab et al., 2012).

In this study, we explore the diversity of suction feeding behaviors shown by spiny-rayed fishes (Acanthomorpha). To characterize this diversity we separate the contributions of suction, body ram, and jaw ram to closing the distance between predator and prey. There is a long tradition of quantifying the relative contributions of ram and suction to prey capture (Norton, 1991; Norton and Brainerd, 1993; Norton, 1995; Cook, 1996; Gibb, 1997; Nemeth, 1997; Ferry-Graham et al., 2001a; Kerfoot and Turingan, 2011; Wainwright et al., 2001; Wintzer and Motta, 2005; Wilga et al., 2007; Tran et al., 2010; Ferry et al., 2012; Staab et al., 2012). It is well recognized that fishes vary in the relative amount of ram and suction employed during feeding, and hence, the “ram-suction continuum” is a pervasive framework used to characterize diversity (Norton and Brainerd, 1993). This framework has helped clarify ecomorphological traits that are often associated with the extremes of this continuum. For instance, two members of Centrarchidae, bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) have often been held up as examples of species that feed with suction or ram-dominated strikes respectively (Norton and Brainerd, 1993; Higham et al., 2006a; Higham et al., 2006b; Higham, 2007; Wainwright et al., 2007).

Recent studies have shown that the continuum between ram and suction may be more complex than was originally thought. The limited reach of suction has been found to lead to very little diversity in suction distance (Wainwright et al., 2001), while there is much more variation possible in ram distance (Ferry et al., 2001b; Wainwright et al., 2001; Tran et al., 2010). Instead of a straightforward continuum between ram speed and suction capacity, the *diversity* of suction capacity was dependent on attack speed among 30 serranid species (Oufiero et al., 2012). Others have recently focused on the duration of suction and predatory movements during feeding strikes in ray-fined fishes and found that the majority of variation among strikes is driven by the duration of ram movement (Ferry et al., 2015). Collectively, these studies suggest that due to the hydrodynamic constraints of suction, variation in prey capture diversity is driven almost entirely by the amount of ram employed.

Although jaw ram is part of the suction-feeding paradigm in acanthomorph fishes (Motta, 1984), most comparative analyses focus on jaw ram’s relationship to suction or how jaw ram contributes to overall ram (Norton and Brainerd, 1993; Wainwright et al., 2001; Oufiero et al., 2012). However, the kinematics of jaw ram are morphologically independent from body ram (fish can protrude their jaw without swimming), and therefore jaw ram provides an independent axis on which fish can diversify their prey capture strategies. Multiple independent origins of jaw protrusion among actinopterygian fishes (Wainwright et al., 2015) and novel morphological adaptations for extreme jaw protrusion in acanthomorphs (Ferry-Graham et al., 2001a; Waltzek and Wainwright, 2003; Westneat and Wainwright, 1989), attest to the adaptive significance of jaw ram in prey capture. On the other hand, reliance on jaw ram alone or in large proportion may be constrained in a similar fashion to suction; there should be inherent structural limits to how far and fast a fish can protrude or rotate the mouth or head relative to the rest of the body (Westneat, 1991). Adding a jaw ram axis to our analyses will allow us to look for patterns of variation in jaw ram that may not be otherwise apparent if jaw ram is simply lumped into total ram.

In this study, we ask if recent comparative findings hold for acanthomorphs in general and if the isolation of jaw ram contributes to clarifying the diversity of attack strategies used by suction feeding fishes. Across this group, do we see specialists that make almost exclusive use of suction, body ram, or jaw ram during prey capture? Is diversity governed by a continuum from suction to ram, or is it more accurately defined by the relative amount of ram? How constraining is the spatial limitation of suction feeding on prey capture behaviors? Evolution has a knack of finding ways around biomechanical constraints thought to be insurmountable (e.g., elastic-recoil mechanisms circumvent the limitations of the force-velocity trade-off of muscles (Roberts and Azizi, 2011)). Indeed, new evidence suggests that simple trade-offs do not limit the evolutionary diversification of complex mechanisms as expected (Holzman et al., 2011; Oufiero et al., 2012). Therefore, we might expect to find some acanthomorphs that have evolved morphological or behavior traits that allow them to be suction-specialists.

MATERIALS AND METHODS

Collection and husbandry

The majority of specimens included in this study were commercially obtained from the aquarium industry. *Lepomis macrochirus* and *Micropterus salmoides* were collected locally in Yolo County, CA. With the exception of *Macroramphosus scolopax*, fish were housed in the laboratory between 22-23°C. *M. scolopax* required colder temperatures and was housed at 17°C. Fish were kept in 18-110 liter aquaria, depending on the size of the fish. We filmed 40 species in 33 families of acanthomorph fishes (Table 1) covering a wide range of ecologies. More than one representative was included for some families to capture some diversity at this scale, including cichlids (Liem, 1973), haemulids (Tavera et al., 2012), and serranids (Oufiero et al., 2012). Among the prey capture strategies we targeted were sit-and-wait ambush predators (*Antennarius hispidus*, *Inimicus didactylus*), pivot-feeding syngnathiforms (*Aulostomus maculatus*, *Aeoliscus strigatus*), high-ram suction feeders (*Ephinephelus ongus, Caranx sexfasciatus*), ram-biters (*Sphyraena barracuda*), benthic invertebrate pickers or foragers from both freshwater and a saltwater environments (*Lepomis macrochirus*, *Dactylopus dactylopus*), water-column zooplanktivores (*Macroramphosus scolopax*, *Emmelichthyops atlanticus*), and some species with morphological adaptations for extreme jaw protrusion (*Epibulus insidiator*, *Caquetaia kraussi*). All fish were filmed feeding on live prey. Due to their extremely small gapes, pipefish (*Doryrhamphus exicus*) and shrimpfish (*Aeoliscus strigatus)* were fed freshly-hatched brine shrimp (*Artemia*). All other species were fed live cyprinid or poeciliid fish (mostly *Danio rerio* or *Gambusia affinis*).

The feeding kinematics of many species in this dataset have not been previously published on and deserve detailed attention, but that is beyond the scope of this study. Because the purpose of this dataset was to sketch the diversity of acanthomorph feeding in prey capture space and determine the axes of variation underlying their distribution, a single sequence representing a typical feeding event was chosen for each species. In practice, typical strikes approximated species means calculated from multiple individuals. We made one exception and included a somewhat atypical strike by *S. latus* to visually demonstrate the highest suction proportion we found, although including this strike or a typical one did not change the patterns we describe for acanthomorphs. We also investigated the sensitivity of our approach to variation in the choice of a typical strike using a resampling method (see Data visualization and statistical analysis).

Isolated comparisons focused on the prey capture strategy of three pairs of species previously identified as exemplars of closely related species at extremes of the ram-suction continuum. *Lepomis macrochirus* and *Micropterus salmoides* (Centrarchidae) were filmed feeding on tethered ghost shrimp (Higham et al., 2006a; Higham et al., 2006b; Norton and Brainerd, 1993; Wainwright et al., 2007). The cichlids *Heros severus* (previously *Cichlasoma severum*) and *Cichla ocellaris* were filmed feeding on live *Daphnia* (Norton and Brainerd, 1993; Wainwright et al., 2001). *Serranocirhittus latus and Ephinephelus ongus* were recently identified as occupying opposing ends of the ram-suction continuum and sequences from that study were included of these species feeding on live zebra fish (*Danio rerio*) (Oufiero et al., 2012). For each species in a pair, we analyzed multiple individuals (2-3 per species) and multiple strikes per individual (7-11 feeding strikes), totaling 169 videos. For each individual, the five fastest strikes (shortest time between strike onset and prey capture) were kept for downstream analyses. Because principal component analyses can be skewed by unequal representation between groups, equal numbers of sequences where retained for each species in a pair (e.g., five videos each from two *C. ocellaris* and five videos each from two *H. severus*); in cases where there were extra individuals in one pair, the individual with the slowest mean strike was discarded until representation was equal. Seventy videos were included in final analyses for ram-suction pairs. Means and standard deviations were first calculated for each individual, which were then used to calculate species-means and standard deviations.

High-speed video

All fish were filmed using either a NAC Memrecam ci digital system (Tokyo, Japan) high-speed camera at 500 frames s^{-1} or a Fastec HiSpec 1 system (San Diego, CA, USA) at 1000-2000 frames s^{-1}. Two 120 W halogen lights were used to light the field of view during filming. Fish were not fed for at least 24 hours prior to filming and were filmed in their housing tank. Videos were selected for analysis based on these criteria: predator’s entire head and a portion of the body were in view, the predator appeared to be oriented nearly perpendicular to the plane of the camera and was in-focus, and prey movement due to swimming or escape maneuvers was minimal. The last criterion is important since these movements can result in apparent negative suction distances in downstream analyses.

Kinematic analysis

For each video, the *x,y* coordinates of five landmarks were digitized on two frames corresponding to the onset of the strike (T0) and the time at prey capture (Tpc) (Fig. 1). T0 was defined as one frame before the start of craniofacial movement, relative to the body. In most strikes, the first craniofacial movement was the onset of lower jaw depression, but in some fishes the first craniofacial movement was jaw protrusion or hyoid rotation. Tpc was defined as the first frame in which the center of mass of the prey passed into the mouth. The difference in Tpc and T0 was used to determine the time to prey capture in seconds. Points were digitized using the DLTdv3 package in Matlab

(Hedrick, 2008), and all downstream analyses on their coordinates were carried out in the R statistical computing platform. Point 1 represented the anterior tip of the upper jaw, point 2 the anterior tip of the lower jaw, point 3 a stationary point on the body such as a scale or spot, point 4 the approximate center of mass of the prey, and point 5 was a stationary background point and used to control for camera movement during the course of the video sequence.

Using the coordinates from these five landmarks at T0 and Tpc, we calculated the contributions of suction, body ram, and jaw ram to prey capture. The contribution of suction to prey capture is the decrease in distance between the predator's mouth and the prey between time T0 and Tpc. We first calculated the distance between point 4 and the midpoint of points 1 and 2 at T0, then found the distance between point 4 at Tpc and the midpoint of points 1 and 2 at T0. The difference between these two distances is the suction contribution to prey capture. Performing the calculation this way focuses on movements of the prey that decrease predator-prey distance in the earthbound frame of reference at T0, and ensures that escape movements of the prey away from the predator result in negative calculations, which would indicate that the video sequence was not suitable for analysis. We calculated the body ram contribution to prey capture, or how much closer the predator's body moved towards the prey due to swimming and coasting between T0 and Tpc. This calculation used the stationary point on the body (point 3) at T0 and Tpc. To control for movement of the prey due to suction, point 4 was only used from time T0 in this calculation. We calculated the contribution of jaw ram to prey capture *independent* of body ram and suction. Because any change in the location of the mouth at Tpc can be due to body ram and jaw ram, the movement of the body (point 3) was first subtracted from points 1 and 2 at Tpc. Then we calculated the change in the distance between the midpoint of the mouth and prey at T0 from the distance between the translated gape midpoint at Tpc and the original location of the prey at T0. Finally, the suction, body ram, and jaw ram components were totaled, and we calculated their contributions as proportions of the total prey capture distance. Note that since all contributions were calculated as proportions, our analyses are scale independent, which is a useful characteristic for large comparative studies.

Data visualization and statistical analysis

We used ternary plots to visualize the contribution of suction, body ram, and jaw ram to prey capture. Ternary plots are a convenient two-dimensional representation when three variables add to a constant value. In our case, three prey capture contributions are represented as proportions and therefore all add to one. A ternary plot has three axes oriented at 120 degrees with respect to one another. Here, the axes are the suction, body ram, and jaw ram independent proportional contributions to prey capture. All ternary plots where created in a custom modified version of the R package 'robCompositions' (Templ et al., 2011) and will be shown in the same orientation: the suction axis runs from the midpoint of the bottom edge of the triangle to the top vertex, the body ram axis runs from the midpoint of the left edge of the triangle to the lower right vertex, and the jaw ram axis runs from the midpoint of right edge of the triangle to the lower left vertex.

Robust principal component analysis (PCA) for compositional data were calculated using a centered log-ratio transformation as implemented in the pcaCoDa function in the 'robCompositions' R package (Filmoser et al., 2009; Templ et al., 2011). Note that since body ram, jaw ram, and suction contributions to prey capture all add to a constant value, our dataset is two-dimensional and so only two principal component axes were obtained. Principal components plotted into the ternary diagrams appear as curves due to the log-ratio transformation used in their computation. For the large acanthomorph dataset, we calculated Pearson's correlation coefficients using the cor.test function in R, with a two-tailed *P* set to 0.05 to see how strike duration (natural logarithm of time to prey capture) was associated with prey capture strategy variables. For the ram-suction species-pairs dataset, we were primarily interested in determining how different components of prey capture strategy varied between the species in each pair. We used a nested mixed model ANOVA with species as the fixed independent effect and individual as the random independent factor, as has been done in previous studies (Norton and Brainerd, 1993). Nested mixed models were carried out using the lmer function in the lme4 package in R, and numerator degrees of freedom, denominator degrees of freedom, F-statistics and p-values were calculated with the anova function in the lmerTest package. We were unable to incorporate phylogenetic information in this analysis due to the lack of published trees including all the species in our dataset. However, we do not find reason to believe that evolutionary history has strongly biased our analysis since closely related species are not necessarily near one another in the ternary plots.

We investigated the sensitivity of our principal component analyses on representative strikes to variation in the choice of a typical strike using a resampling method and the species-pairs dataset for which we had multiple strikes per species (10-15 sequences per species, 70 sequences total). A single video was randomly selected from each of the six species to simulate choosing a representative strike for a species. This was repeated 10,000 times and we performed PC analysis as described above to determine the loadings of the jaw ram, body ram, and suction proportions on PC1 for each replicate. The resulting distributions of loadings were then compared to PC1 loadings based on species means to judge if our results are rigorous to variation in representative strike choice

RESULTS

The kinematics of feeding events from 40 species of spiny-rayed fishes are summarized in Table 1. Time to prey capture, or the time between the onset of craniofacial movement and prey capture, varied from 0.002-0.094 s. Body ram proportion ranged from 0.021 to 0.883 (mean 0.316, s.d. 0.24) jaw ram from 0.047-0.938 (mean 0.471, s.d. 0.22), and suction ranged from 0.003-0.507 (mean 0.213, s.d. 0.11). Thus, when considered as a proportion of the total strike distance, body ram and jaw ram had similar, large ranges (0.862 and 0.891, respectively), while the range of suction proportion was smaller (0.503), and the maximum contribution of suction was markedly lower than that for either of the ram components. The 40 species measured fill a large proportion of prey capture space, as visualized using a ternary plot (Fig. 2), and reached very near the extremes of high jaw ram (lower left vertex) and high body ram (lower right vertex); however, there were no points at or near the extreme suction area of prey capture space (top vertex). Strikes in which more than half of the strike distance was covered by suction were very rare.

For suction-feeding spiny-rayed fishes, principal component 1 (PC1) explained 86.2% of the variation in the data (Fig. 2), with body ram loading positively and heavily on this axis (0.82), and jaw ram and suction loading negatively with equal magnitude (-0.405 and -0.411, respectively). PC1 therefore largely reflects the amount of body ram compared to the other strike components. Principal component two (PC2) represents the remaining 13.8% of variation in the data. On this axis jaw ram and suction have strong but opposite loadings of -0.709 and 0.705, respectively, while body ram is negligible (-0.003).

In the acanthomorph data, the natural logarithm of time to prey capture was significantly correlated with PC1 (r=0.369, p=0.020; Fig. 3) and with body ram proportion (r=0.351, p= 0.0), and negatively correlated with jaw ram proportion (r=-0.313, p= 0.049). There was no relationship between strike duration and PC2 (r=0.115, p= 0.479) or with suction proportion (r=-0.120, p= 0.461).

The proportions of body ram, jaw ram, and suction contributions to prey capture were calculated for six species belonging to three ram-suction species pairs (Table 2). There was variation within an individuals, between individuals, and between species. Individuals within pairs seemed to cluster as expected, such that “high-ram” species (*Micropterus salmoides*, *Cichla ocellaris*, *Ephinephelus ongus;* squares in Fig. 4) had higher body ram, lower jaw ram, and lower suction proportions than their “high-suction” counterparts (*Lepomis macrochirus*, *Heros severus*, *Serranocirhittus latus*; circles in Fig. 4).

Nested mixed models for the centrarchid pair found that only body ram proportion was significantly different between *L. macrochirus* and *M. salmoides* (body ram $F_{1,4}$=15.4, p=0.017). Jaw ram proportion and suction proportion did not differ between species (jaw ram $F_{1,4}$=6.04, p=0.070, suction $F_{1,4}$= 3.78, p=0.124), which reflects the large amount of overlap along these axes in strikes from both species (Fig. 4A). PC1 for the centrarchid data explained 86.3% of the variation among strikes; with body ram and suction both loading heavily on PC1, this axis appears to represent a body ram-suction trade-off (body ram 0.717; suction -0.696; jaw ram -0.021). Nest mixed models showed that there was a significant difference between *L. macrochirus* and *M. salmoides* on PC1 ($F_{1,28}$=10.75, p=0.003).

The cichlids (Fig. 4B) were the only ram-suction pair for which all three proportions were significantly different between species (body ram $F_{1,18}$= 23.4, p=

0.0001; jaw ram $F_{1,18}$= 28.7, p= 4.3e-05; suction $F_{1,18}$= 6.1, p= 0.024). PC1 explained 90.8% of the variation in the data and, body ram and suction loaded heavily and oppositely on PC1 (body ram 0.712, suction -0.702, jaw ram - 0.010). *C. ocellaris* and *H. severus* were significantly different on PC1 ($F_{1,18}$=11.7, p=0.003), reflecting a body ram-suction trade-off underlying the majority of variation in this species pair.

In the serranid pair, only body ram proportion was significantly different between the “high-ram” (*E. ongus*) and “high-suction” (*S. latus*) species (body ram $F_{1,2}$=25.8, p= 0.037; jaw ram $F_{1,2}$=4.6, p=0.169; suction $F_{1,2}$=8.4, p=0.101). PC1 explained the majority of variation in the data (97.8%), and body ram and suction proportions loaded heavily and oppositely (body ram 0.766; suction -0.627). Though to a small degree, jaw ram also loaded on PC1 in the same direction as suction (jaw ram -0.139). Scores along PC1 were only marginally different between *S. latus* and *E. ongus* ($F_{1,2}$= 13.9, p= 0.065), despite the separation of these species in prey capture space (Fig. 4C).

A PCA on the means for the six species represented in the ram-suction pairs revealed a major axis of variation for the six species that closely mirrored the results for the 40 species dataset (Fig. 4D). PC1 explained almost all variation in the dataset (99.6%) with body ram loading heavily in one direction and jaw ram and suction loading in the opposite direction (body ram 0.813, jaw ram - 0.341, suction -0.472). We compared these loadings based on species means to the distribution of loadings on PC1 from 10,000 resampled datasets consisting of a single representative strike for each of the six-species. Although the resulting distributions (see supplementary figure) are skewed and therefore not amenable to parametric significance testing, the density curves show that the majority of replicates are quantitatively similar to the loadings calculated from species means. PC1 explained the vast majority of variation in replicates (mean 94.6%, median 97.4%) and the mean loadings were: body ram 0.743 (median 0.786), jaw ram -0.251 (median -0.252), and suction -0.491 (median -0.548). PC loadings are subject to qualitative interpretation, and the distributions indicate that most analyses would support a trade-off between body ram versus the combination of jaw ram and suction. For instance, jaw ram and suction only load in opposite directions in 1,790 out of 10,000 replicates (17.9%). There is some tendency for the representative datasets to underestimate the importance of jaw ram; the jaw ram peak is displaced towards zero relative to the species-mean loading

(Supplementary figure, green line), and there is a relatively high frequency with loadings near zero. Accordingly, the loading of suction on PC1 tends to be overestimated in the resampled data compared to the value obtained using species means (Supplementary figure, pink line). If these tendencies are true of our method in general, we would expect to be biased towards finding a strict body ram-suction trade-off when using representative strikes instead of species means. However, this is not what we found for our acanthomorph dataset. It should be noted that the variation in the distributions for jaw ram and suction is based on six species, but we would expect variation to be less if the same analysis was performed on the 40 species in our acanthomorph dataset, since a larger sample size will decrease the ability of one arbitrarily chosen strike to significantly influence the PC loadings. Not knowing of any bias in our selection of typical strikes and based on the findings of our resampling method, we conclude that our results regarding the major axis of diversity in acanthomorphs are robust to variations in representative strike choice.

DISCUSSION

The contribution of suction distance to prey capture is greatly limited compared to ram in acanthomorph fishes. The high-suction area of prey capture space is unoccupied, and the highest contribution of suction to prey capture distance exhibited by any fish in our dataset was only about half (Fig. 2). In contrast, there were strikes occupying the full range of jaw and body ram proportions. This is the largest published kinematic study to date for suction-feeding fishes in terms of family representation and number of species, and we purposefully included fishes from a range of trophic niches (e.g., benthic invertebrates, zooplankton, fish) and prey capture behaviors (e.g., water-column zooplanktivores, benthic sit-and-wait predators, pelagic ram-biters). Amongst this diversity, we see scant evidence that evolutionary innovation has surmounted the hydrodynamic constraints imposed on suction distance to bring any species into the extreme suction area of prey capture space.

Does the absence of suction-dominated strikes in our analysis reflect a constraint on suction feeding or did this feeding mode elude our investigation because it is relatively rare? We suggest that a combination of these factors is responsible. Suction feeders generate flows that are spatially limited, with flow velocity dropping by 95% at a distance of one mouth diameter from the predator (Day et al., 2005). Because suction distances are limited in this way, any forward movement of the mouth aperture during the strike by swimming or rotation of cranial linkages, is likely to make a significant contribution to prey capture distance. Suction dominated strikes require that the body and mouth do not advance toward the prey during the strike. One might expect to see this feeding mode in sit-and-wait predators that strike from a position resting on the substratum. However, the representatives of this feeding mode that we studied all used considerable jaw protrusion to close in on their prey (see below).

Since our study was limited to acanthomorphs feeding on mobile prey, it is possible that there are other taxa or prey types that could exhibit feeding strikes with high suction proportions. Jaw protrusion, while a synapomorphy of spiny-rayed fishes, is not a universal trait of suction feeders (Wainwright et al., 2015). Perhaps there are non-acanthomorph fishes or other aquatic vertebrates lacking jaw protrusion that have evolved strategies to feed on evasive prey using high-proportions of suction. However, even these taxa may generate ram by sucking themselves toward the prey (Summers et al., 1998). Furthermore, some of these lineages have independently evolved jaw protrusion (Wilga et al., 2007; Wainwright et al., 2015) and many use large amounts of body ram to lunge forward at the last moment, even if their prey capture strategies appear to be sit-and-wait. We also note that our study focused on strikes at mobile prey. When approaching prey that cannot escape, fishes can move to within less than a mouth diameter before initiating the strike, because there is no risk of disturbing the prey into an escape response. Such a strike could potentially reach the suction-dominated region of the continuum.

Our findings challenge the traditional view that a fundamental trade-off between ram and suction underlies the diversity of prey capture behaviors in suction-feeding fishes. Across spiny-rayed fishes, PC1 represented a strong trade-off between body ram and the combined contribution of suction *and* jaw ram; suction and jaw ram load in the same direction and with near equal magnitudes, such that the major axis of variation is not simply a ram-suction continuum. Instead, variation is better described by the relative amount of body ram involved in the strike, or a continuum between low and high body ram, as confirmed by the strong correlation between PC1 and body ram proportion. Combined with the apparent lack of suction-specialized strikes, our results corroborate previous studies that questioned the role of suction in generating diversity in prey capture distance (Wainwright et al., 2001; Ferry et al., 2015).

Simultaneously comparing the contributions of jaw ram, body ram, and suction clarifies the importance of jaw ram in the diversification of prey capture strategies among acanthomorph fishes. Body ram and jaw ram are often combined into a measurement of total ram, which implies that they function similarly and trade-off with suction in a comparable manner. However, PC1 reveals that jaw ram and suction combined trade-off with the relative amount of body ram in a strike. This sets jaw ram apart from body ram and illustrates that jaw ram provides a separate axis along which to generate variation in prey capture. The interaction between suction and jaw ram appears to be particularly important in strikes with low contributions of body ram: close-range strikes where both jaw ram and suction have the opportunity to have large proportional contributions to prey capture. We expect the synergistic effect of jaw protrusion on suction forces (Holzman et al., 2012) to be most important in close-range strikes where a predator has less distance to accelerate its mouth opening, but must still approach the prey fast enough to capture it despite attempts at escape. Indeed, many high jaw ram strikes in our dataset are from zooplanktivores and sit-and-wait predators that are known to only strike at close range. The close relationship between PC1 and time to prey capture also suggests that strikes dominated by short-range suction and jaw ram components are quicker than strikes relying more on body ram (Fig. 3).

We find that some species with reputations as suction specialists due to their rapid and powerful strikes are actually relying on jaw ram more than suction (or body ram) to decrease the distance between their mouth and prey. Pivot feeding seahorses and pipefish were identified as high jaw ram feeders previously (Flammang et al., 2009), but we show that syngnathiforms as a whole are specialized jaw ram feeders and include the most extreme jaw ram strikes in this study (Fig. 2, blue). In fact, trumpetfish (*Aulostomus maculatus*) and shrimpfish (*Aeoliscus strigatus*) exhibited higher proportions of jaw ram than the slingjaw wrasse (*Epibulus insidiator)*, which holds the record for highest jaw protrusion relative to head length among fishes (Westneat and Wainwright, 1989).

Frogfish (*Antennarius hispidus*) are another group of fish with very rapid feeding (Grobecker and Pietsch, 1979) that we find have greater jaw ram than suction distances during prey capture. In fact, all the benthic sit-and-wait predators included in our study grouped closely together in prey capture space (Fig. 2, orange). Although these fish are generally cryptic and may have large upturned mouths, they are morphologically and taxonomically diverse, in our dataset representing five families (Antennariidae, Batrachoididae, Centrogenyidae, Scorpaenidae, Synanceiidae) that have converged in kinematics. Predators like frogfish and pipefish may seem like evolutionary oddballs, but this study suggests that these are the type of fish that we should be studying to learn more about the interaction between jaw ram and the ability to produce fast, powerful suction (Van Wassenbergh et al., 2013).

In contrast to suction, a combination of morphological and behavioral adaptations have allowed fish to invade the extreme jaw ram area of morphospace. These include the slingjaw wrasse, *E. insidiator* (Fig. 2, #15), which has evolved a novel linkage allowing unusually high jaw protrusion (Westneat and Wainwright, 1989; Westneat, 1991; Ferry-Graham et al., 2001a; Ferry-Graham et al., 2001b; Waltzek and Wainwright, 2003). Syngnathiforms (Fig 2., blue) use a novel jaw ram mechanism referred to as pivot feeding, which relies on rapid rotation of their head and long snout (Bergert and Wainwright, 1997; de Lussanet and Muller, 2007; Van Wassenbergh et al., 2008; Flammang et al., 2009; Roos et al., 2009). At least some syngnathiforms power-amplify this pivoting motion using tendon elastic recoil (Van Wassenbergh et al., 2008; Van Wassenbergh et al., 2009), which is the only known elastic recoil feeding mechanism in fishes.

However, novelty in one trait does not guarantee that a species will have extreme strikes since morphology and behavior interact to produce kinematics. This is demonstrated by the cichlid, *Caquetaia kraussi*, which is from a lineage known to have a modified suspensorial linkage allowing high jaw protrusion relative to other cichlids (Waltzek and Wainwright, 2003). *C. kraussi* (Fig. 2, #7) may be extreme when compared to cichlids, but this individual's strike was not particularly unusual when compared across acanthomorphs and had a jaw ram proportion similar to or less than 12 other species. Therefore, adaptations for high jaw protrusion alone do not make a strike extreme. On the other hand, some benthic sit-and-wait predators and water-column zooplanktivores, such as *Inimicus didactylus,* and *Emmelichthyops atlanticus* (Fig. 2, #20 and #14) had relatively extreme kinematics and high values of jaw protrusion (as much as 48% of head length in *E. atlanticus*) without any obvious morphological innovations. Therefore, while a combination of behavior and unusual morphology are necessary for acanthomorphs to become *extreme* jaw ram specialists, many acanthomorph clades have achieved relatively high jaw ram prey capture behaviors despite potential biomechanical and kinematic constraints on jaw function and strike distance.

Specific pairs of closely related species have been used to illustrate a trade-off in ram and suction contributions to prey capture. Even with jaw ram as a separate source of variation, we found strong evidence that species within the centrarchid and cichlid pairs fell out along a ram-suction continuum. This is at odds with our findings from the larger sample of acanthomorph diversity where we did not recover a simple continuum between body ram and suction. We caution that focusing only on ram-suction pairs gives a skewed interpretation of the diversity of prey capture strategies in acanthomorph fishes. By looking at a larger taxonomic and ecomorphological sample of acanthomorph suction feeders and incorporating another source of variation in prey capture behavior, we show that the apparent ram-suction trade off in closely related pairs of fishes does not govern feeding diversity at broader evolutionary scales. In agreement with this conclusion, PC1 for the six species averages converges on the same axis found in the large-scale acanthomorph study (Fig. 4D). This suggests that as you add diversity, a strict body-ram versus suction continuum breaks down, and jaw ram and suction contributions combined trade-off with changes in body ram.

Our findings highlight the importance of considering ram, especially body ram, when studying how suction feeding fishes diversify across feeding niches on evolutionary time scales. It is worth pointing out that laboratory studies that record feeding events may greatly underestimate the maximum body ram that some species can exhibit, because laboratory feeding arenas are quite cramped compared to most natural settings. Also, methods that select for highly motivated strikes based on time to prey capture may also underestimate ram, because strikes with greater ram distances tend to increase prey capture times despite high ram speeds (Fig. 3; Tran et al., 2010). Further studies on locomotion during predator-prey interactions, and how different ram strategies affect feeding accuracy and suction performance, will be important in developing a better understanding of the diversity of prey capture strategies (Kane and Higham, 2014; Kane and Higham, 2015; Rice et al., 2008). Additionally, predator-prey interactions generally involve unsteady swimming modes, such as fast starts and quick turns (Harper et al., 1991; Domenici, 2001), which may not be best characterized by body ram speed as reported in most fish feeding studies. A better understanding of locomotor performance of predators in the context of prey capture will be important in understanding what behavioral options are available to suction feeding fishes and how locomotion is modified during evolution to enhance prey capture performance.

While relative measures of suction, body ram, and jaw ram, reveal new insights into how acanthomorph fish diversify their prey capture strategy at broad evolutionary scales, the use of proportions can be misleading and provides an incomplete view of attack strategies. For instance, *Monocirrhus polyacanthus* (Fig. 2, #25) is a freshwater fish that blends in among leaves and branches in the water column before striking with rapid forward jaw protrusion and is located in prey capture space almost on top of *Dactylopus dactylopus* (Fig. 2, #11), a forager that hovers along the benthos before striking with rapid ventral jaw protrusion. Our study finds that both fish rely largely on jaw ram (approx. 60%), but obscures other differences in prey capture strategy and kinematics that would become apparent with other metrics. Using proportions also tends to downplay strikes that employ a combination of approaches and can lead to the inference that two strikes are similar even though the absolute distances covered may be very different. Depending on the question being asked, absolute instead of relative measures may better characterize the difference in strikes between species (Wainwright et al., 2001).

The distance from which fishes draw prey into their mouth during feeding is significant to predator-prey encounters, but should not be interpreted as a measure of suction performance (Wainwright et al., 2007). The high accelerations reached by suction flows may be spatially restricted and temporally ephemeral, but suction forces over these small distances are crucial to successfully capture evasive aquatic prey (Holzman and Wainwright, 2009; Yen et al., 2015). Suction also serves an important role in prey transport within the oral cavity that was not captured by this study. For instance, we found that trumpetfish (Fig. 2, #3) are extreme jaw ram feeders that use head rotation to place their jaws very close to prey. However, once prey pass into the mouth, suction continues to transport the prey down what is essentially a long sealed tube. In the sequence included in this study, the distance that prey traveled down the snout after prey capture was more than 52 times greater than the distance suction moved prey outside the mouth. Intraoral transport can also be important in high-ram and ram-biting fish which often show large excursions of the hyoid and prolonged hyoid depression and can use suction to position prey during swallowing after capture (Liem, 1990; Porter and Motta, 2004; Gibb and Ferry-Graham, 2005; Tran et al., 2010). Suction distances outside the mouth may be constrained, so the diversity of suction among suction feeders may lie along axes that are rarely explored, including the ability to generate strong suction pressure gradients, high fluid accelerations, and the volume of water ingested during the strike (Nemeth, 1997; Higham et al. 2006a, 2006b; Van Wassenbergh et al., 2006; Wainwright et al. 2007; Motta et al., 2008; Kane and Higham, 2015).

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Tables

Table 1: Values for mean (± s.d.) time to prey capture and relative contributions of suction, body ram, and jaw ram to prey capture**.**

Genus	**Family**	**Time to prey capture (s)**	**Body Ram Proportion**	**Jaw Ram Proportion**	**Suction Proportion**
Ctenopoma kingsleyae	Anabantidae	0.041	0.527	0.138	0.335
Antennarius hispidus	Antennariidae	0.011	0.122	0.635	0.243
Aulostomus maculatus	Aulostomidae	0.013	0.021	0.938	0.041
Opsanus beta	Batrachoididae	0.017	0.104	0.545	0.351
Pterocaesio pisang	Caesionidae	0.014	0.334	0.502	0.164
Dactylopus dactylopus	Callionymidae	0.022	0.175	0.611	0.214
Caranx sexfasciatus	Carangidae	0.013	0.810	0.157	0.033
Lepomis macrochirus	Centrarchidae	0.018	0.355	0.442	0.204
Aeoliscus strigatus	Centriscidae	0.007	0.082	0.907	0.011
Macroramphosus scolopax	Centriscidae	0.010	0.269	0.677	0.054
Centrogenys vaigiensis	Centrogenyidae	0.008	0.065	0.657	0.278
Lates niloticus	Centropomidae	0.018	0.275	0.502	0.223
Boulengerochromis microlepis	Cichlidae	0.009	0.484	0.240	0.276
Caquetaia kraussi	Cichlidae	0.106	0.241	0.602	0.157
Pterophyllum scalare	Cichlidae	0.015	0.083	0.532	0.385
Oxycirrhites typus	Cirrhitidae	0.010	0.275	0.452	0.273
Datnioides microlepis	Datnioididae	0.038	0.178	0.548	0.273
Butis butis	Eleotridae	0.022	0.731	0.099	0.169
Stigmatogobius pleurostigma	Gobiidae	0.027	0.619	0.193	0.187
Emmelichthyops atlanticus	Haemulidae	0.008	0.181	0.677	0.141
Haemulon aurolineatum	Haemulidae	0.009	0.377	0.267	0.356
Haemulon vittatum	Haemulidae	0.008	0.161	0.545	0.294
Pristilepis oligolepis	Holocentridae	0.015	0.367	0.460	0.173
Epibulus insidiator	Labridae	0.030	0.129	0.760	0.111
Ocyurus chrysurus	Lutjanidae	0.025	0.341	0.268	0.391
Malacanthus purpureus	Malacanthidae	0.010	0.376	0.432	0.192
Ptereleotris heteroptera	Microdesmidae	0.016	0.411	0.444	0.145
Nandus nandus	Nandidae	0.094	0.409	0.407	0.184
Oplegnathus fasciatus	Oplegnathidae	0.040	0.798	0.199	0.003
Betta pugnax	Osphronemidae	0.016	0.182	0.393	0.425
Plesiops caerolineatus	Plesiopidae	0.021	0.242	0.532	0.226
Monocirrhus polyacanthus	Polycentridae	0.034	0.182	0.596	0.222
Inimicus didactylus	Scorpaenidae	0.019	0.059	0.683	0.258
Serranocirrhitus latus	Serranidae	0.005	0.101	0.392	0.507
Hypoplectrus puella	Serranidae	0.040	0.529	0.274	0.197
Epinephelus ongus	Serranidae	0.018	0.733	0.148	0.119
Sphyraena barracuda	Sphyraenidae	0.034	0.883	0.047	0.070
Synanceia sp.	Synanceiidae	0.024	0.084	0.615	0.301
Doryrhamphus excisus	Syngnathidae	0.002	0.044	0.784	0.172
Paracentropogon rubripinnis	Tetrarogidae	0.012	0.300	0.527	0.173

Table 2: Means (± sd) for time to prey capture and prey capture contributions for individuals and species within three ram-suction pairs. The centrarchid pair was filmed feeding on tethered ghost shrimp, the cichlids on live *Daphnia*, and the serranids on live fish prey.

ID	Time to prey capture (ms)	Body Ram Proportion	Jaw Ram Proportion	Suction Proportion	ID	Time to prey capture (ms)	Body Ram Proportion	Jaw Ram Proportion	Suction Proportion
CENTRARCHIDAE									
Lepomis macrochirus					*Micropterus salmoides*				
1	19.6±3.3	0.23 ± 0.161	0.583±0.091	0.192±0.090	1	62.8±6.1	0.546±0.078	0.247±0.048	0.207 ±0.071
2	12.8±2.3	0.122±0.034	0.563±0.074	0.315±0.107	2	30.4±3.8	0.389±0.074	0.422±0.032	0.189 ±0.062
3	16.4±3.0	0.284±0.069	0.425±0.040	0.291±0.089	3	48.8±3.6	0.556±0.125	0.372±0.082	0.072 ±0.052
sp	16.3±3.4	0.214±0.083	0.524±0.086	0.266±0.065	sp	47.2±16.1	0.497±0.094	0.347±0.090	0.156 ±0.073
CICHLIDAE									
Heros severus					*Cichla ocellaris*				
1	27.0±6.0	0.358±0.125	0.424±0.103	0.217±0.131	1	015.2±2.5	0.608±0.135	0.247±0.060	0.145±0.092
2	25.6±11.7	0.290±0.213	0.476±0.121	0.234±0.102	2	18.6±6.7	0.652±0.081	0.252±0.032	0.095±0.056
sp	26.3 ± 1.0	0.324 ± 0.063	0.450 ± 0.013	0.226 ± 0.020	sp	16.9 ± 2.4	0.630 ± 0.038	0.249 ± 0.020	0.120 ± 0.025
SERRANIDAE									
Serranocirrhitus latus					*Epinephelus ongus*				
1	5.6 ± 0.5	0.167 ± 0.141	0.416 ± 0.052	0.417 ± 0.104	1	12.6 ± 1.5	0.568 ± 0.147	0.311 ± 0.092	0.121 ± 0.065
2	5.4 ± 0.5	0.090 ± 0.061	0.652 ± 0.083	0.258 ± 0.079	2	14.0 ± 2.0	0.766 ± 0.110	0.184 ± 0.059	0.051 ± 0.052
sp	5.5 ± 0.1	0.129 ± 0.054	0.534 ± 0.167	0.337 ± 0.112	sp	13.3 ± 1.0	0.667 ± 0.140	0.248 ± 0.090	0.086 ± 0.050

Figures

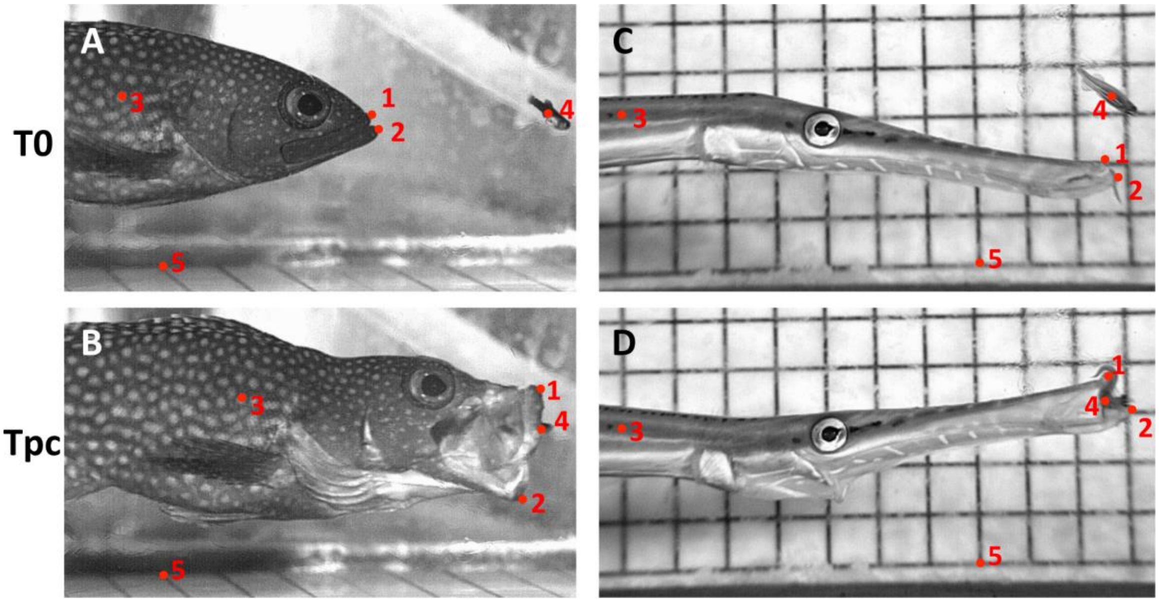

Figure 1: **Five landmarks were digitized at two time points in each feeding sequences, as demonstrated by a ram-ambush predator, *Epinephelus ongus* (A,B), and a pivot-feeder, *Aulostomus maculatus* (C,D).** T0 (A,C) was one frame before the first observed craniofacial movement and Tpc, (C,D), or time at prey capture, was at the first frame in which the prey passed into the mouth. See text for details regarding point placement.

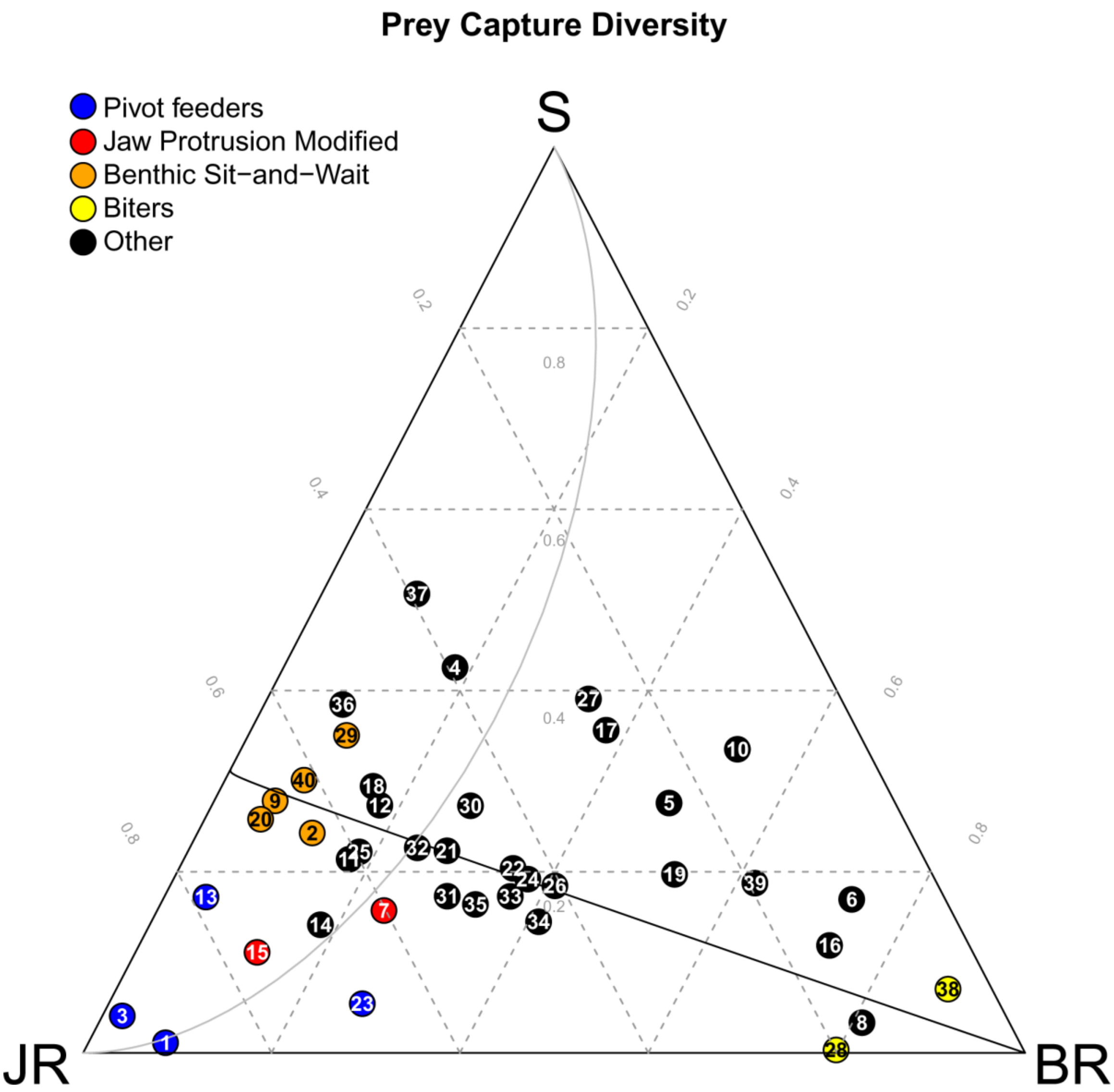

Figure 2: Ternary plot showing the diversity of strike behaviors as determined by the suction proportion (S), jaw ram proportion (JR) and body ram proportion (BR) that contributed to prey capture. Suction distances are constrained across acanthomorphs, and prey capture diversity does not follow a strict ram-suction trade-off. The first principal component (black) represents a strong trade-off between body ram and the combined contributions of jaw ram and suction and is shown by the black curve. The second principal component is largely a trade-off in jaw ram and suction and is shown by the gray curve. The distribution of acanthomorphs yields new insights into how behavioral and morphological convergence shapes prey capture diversity, and we have

highlighted some of the examples mentioned in the text (colored circles). Species are numbered as follows: 1 *Aeoliscus strigatus;* 2 *Antennarius hispidus;* 3 *Aulostomus maculatus;* 4 *Betta pugnax*; 5 *Boulengerochromis microlepis;* 6 *Butis butis*; 7 *Caquetaia kraussi*; 8 *Caranx sexfasciatus;* 9 *Centrogenys vaigiensis;* 10 *Ctenopoma kingsleyae;* 11 *Dactylopus dactylopus;* 12 *Datnioides microlepis.; 13 Doryrhamphus excisus;* 14 *Emmelichthyops atlanticus;* 15 *Epibulus insidiator*; 16 *Epinephelus ongus;* 17 *Haemulon aurolineatum;* 18 *Haemulon vittatum*; 19 *Hypoplectrus puella;* 20 *Inimicus didactylus;* 21 *Lates niloticus;* 22 *Lepomis macrochirus*; 23 *Macroramphosus scolopax;* 24 *Malacanthus purpureus;* 25 *Monocirrhus polyacanthus;* 26 *Nandus nandus*; 27 *Ocyurus chrysurus*; 28 *Opleglegnathus fasciatus;* 29 *Opsanus beta; 30 Oxycirrhites typus;* 31 *Paracentropogon rubripinnis;* 32 *Plesiops caerolineatus;* 33 *Pristilepis oligolepis;* 34 *Ptereleotris heteroptera;* 35 *Pterocaesio pisang;* 36 *Pterophyllum scalare;* 37 *Serranocirrhitus latus;* 38 *Sphyraena barracuda;* 39 *Stigmatogobius pleurostigma;* 40 *Synanceia sp*

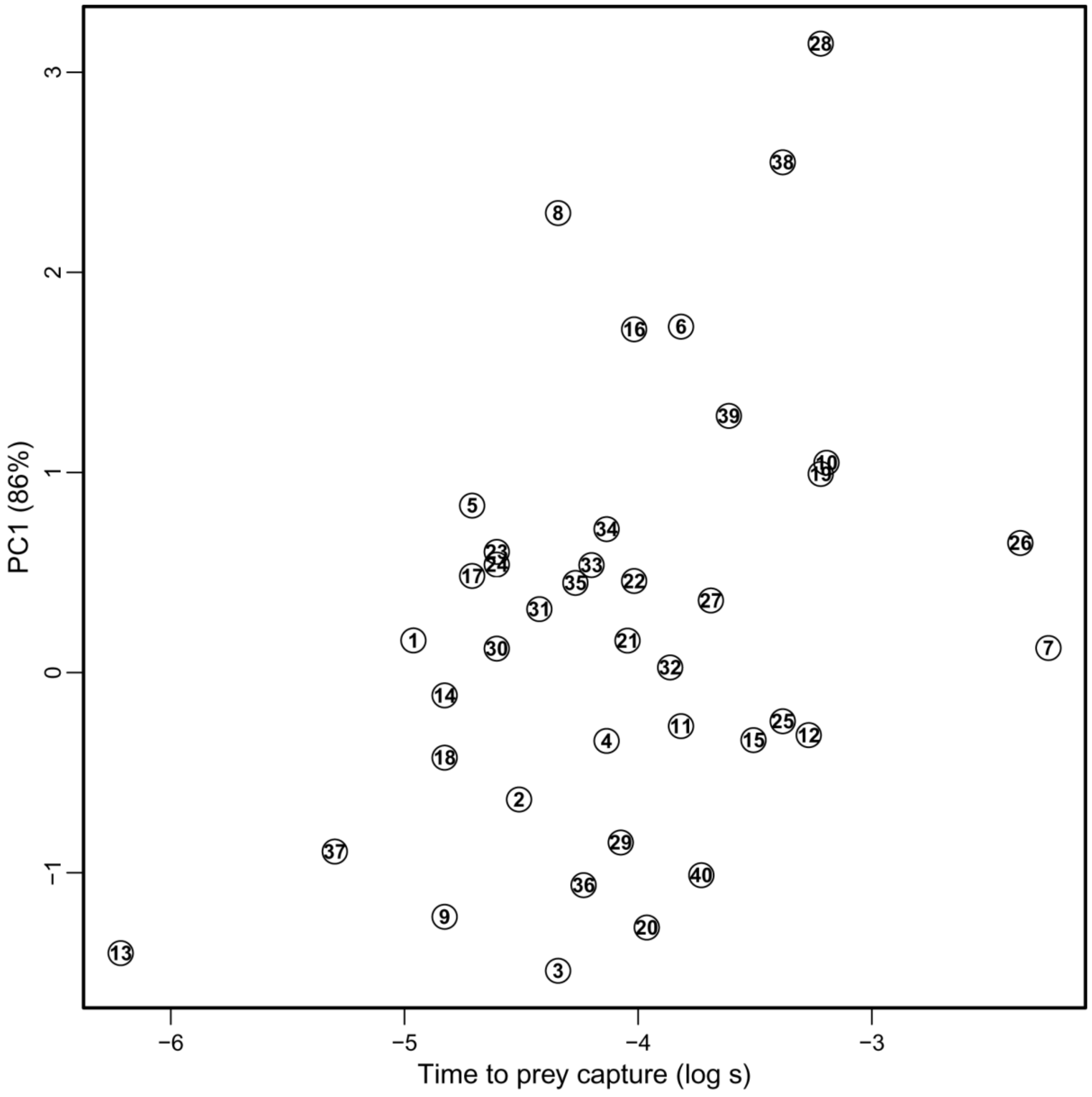

Figure 3: Strike duration is correlated with PC1 (r=0.392, P=0.011). Species with smaller values on PC1 (lower body ram proportions and higher combined suction and jaw ram proportions) tend to have quicker strikes overall. Species are numbered as in Fig. 2.

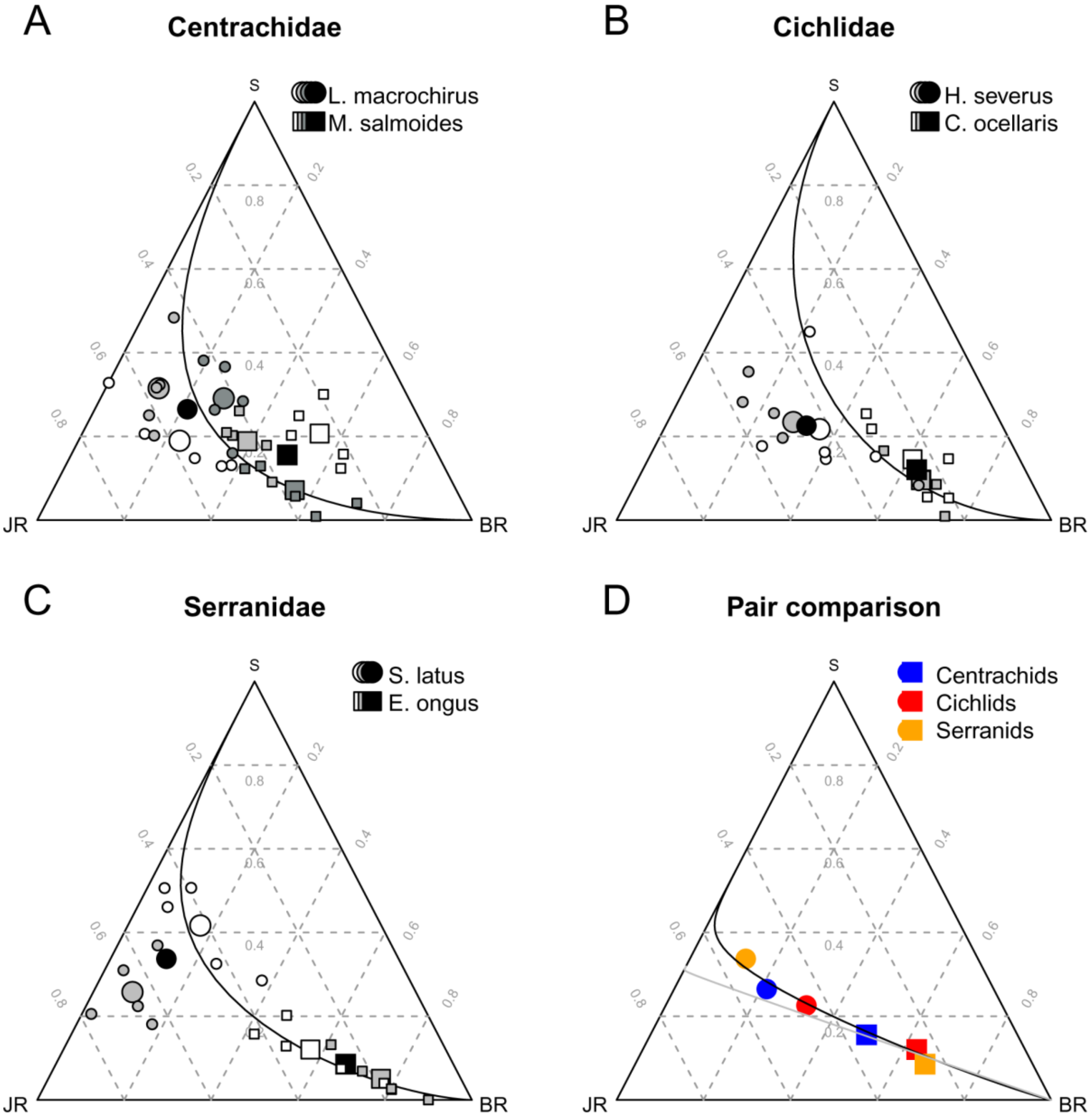

Figure 4: Comparison of prey capture from species-pairs used as exemplars of extremes of the ram-suction continuum in previous studies: the centrachids, *L. macrochirus* and *M. salmoides* (A), cichlids, *H. severus* and *C. ocellaris* (B), and serranids *S. latus* and *E. ongus* (C). Within each pair, circles represent the suction-dominated species and squares represent the ram-dominated species. Strikes from different individuals are represented by small circles/squares of different shades of white and grey, and individual means are plotted as larger circles/squares of the same shade.

Black coloration designates species means. Black curves represent the first principal component for each dataset. Mean prey capture proportions for each species are plotted for comparison (D). Note that PC1 (black curve, D) for the species means is similar to PC1 from the acanthomorph dataset (gray curve, D).