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A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*)

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Abstract Ram feeding is the process by which a predatory fish uses a high-velocity lunge or chase to overtake its prey. This study compares the strike and prey capture behaviors and kinematics of three species of ram-feeding fishes: Florida gar *Lepisosteus platyrhincus*, redfin needlefish *Strongylura notata*, and great barracuda *Sphyraena barracuda*. These ram-feeding piscivores are morphologically similar with fusiform bodies, posteriorly placed dorsal and anal fins, and large, conical teeth. Strike and prey capture kinematics for five individuals of each species were recorded with high-speed video. Pre-strike behavior in *L. platyrhincus* consists of a slow stalk, resulting in the close, lateral positioning of the predator's head relative to the prey. *Lepisosteus* employ a sideways lunge of the head during the strike, which lasts only 25–40 ms and is the most rapid strike among these three species. *Strongylura notata* and *Sphyraena barracuda* exhibit longitudinal orientation to the prey before the strike, followed by a high velocity, head-on lunge, initiated by an s-start in *Sphyraena barracuda*. Prey capture in adult *L. platyrhincus* and *Strongylura notata* is characterized by the jaws closing on the prey, with the prey held orthogonal to the jaws. This is followed by manipulation using the inertia of the prey to reposition the prey head first, and then suction transport into the buccal cavity. Prey capture in juvenile *Sphyraena* is accomplished by closing the jaws after the prey has entered the buccal cavity, resulting in possible ram trans-

port of the prey with no oral manipulation under these experimental conditions. Although these three species all employ ram feeding for prey capture of elusive prey, each species has a unique repertoire that appears to minimize hydrodynamic constraints and prey response, utilize locomotory capabilities, and may be suited to each species' specific habitat.

Introduction

The functional and ecological morphology of feeding is one of the most studied areas of morphology because it represents the interface between an animal, its environment, and the acquisition of energy. Aquatic vertebrates capture their prey using inertial suction feeding, ram feeding, and biting (Liem 1980). In the aquatic environment, the fluid properties of water, specifically the density and viscosity, make prey capture by inertial suction feeding possible. Inertial suction feeding involves a rapid expansion of the mouth and buccal cavity, causing a rapid decrease in pressure in the buccal cavity. This sub-ambient pressure results in a high-velocity flow of water which carries the prey into the mouth. Inertial suction feeding has been thoroughly studied in many taxa of fishes and is reputed to be the most common mode of feeding in teleosts (Lauder 1980).

On the other end of the prey capture continuum is ram feeding, during which the predator lunges toward its prey at a high velocity with its large mouth open, overcoming the prey and engulfing it. This is most often used by stalking or lie-in-wait piscivorous fishes such as esocids, some sharks, and aquatic tetrapods such as turtles (Lauder and Prendergast 1992; Sanderson et al. 1994; Summers et al. 1998; Motta 2004). A predator may use each of these feeding modes exclusively, or more commonly, a component of each (Norton and Brainerd 1993; Sass and Motta 2002).

Ram feeding is particularly effective in the capture of elusive prey (Norton 1991). Typically, it is characterized

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as a high-velocity body lunge towards the prey initiated by an s-start (i.e., predator assumes an s-shaped posture prior to acceleration), exemplified by the pikes and pickerels (Esocidae) (Rand and Lauder 1980; Webb and Skadsen 1980; Harper and Blake 1991). Optimal tactics for a striking piscivore are to strike the prey as rapidly as possible, from the side, towards the prey's center of mass (Webb and Skadsen 1980) or a cryptic, stalking attack, so that the prey is captured before it can initiate an escape response.

Variations on the ram feeding strategy do exist. Bonnethead sharks *Sphyrna tiburo* swim over their prey, catching the prey in their jaws before utilizing suction for prey transport (Wilga 1997; Wilga and Motta 2000). Paddlefish *Polyodon spathula* ram feed plankton from the water column with their extremely wide mouths open, filtering organisms with their gill rakers (Sanderson et al. 1994). *Luciocephalus* uses high velocity protrusion of its jaws to capture prey. The jaws can protrude at a velocity of approximately 150 cm/s to overtake the prey without movement of the body rather than relying on suction to pull the prey into its mouth (Lauder and Liem 1981). The long-jawed butterflyfish *Forcipiger longirostris* possesses a novel feeding mechanism that allows for the anterior movement of the entire jaw apparatus, resulting in the ability of this fish to use ram feeding to capture elusive prey such as small shrimp (Ferry-Graham et al. 2001a, 2001b). It has also been suggested that the rapid cranial elevation exhibited by seahorses could be categorized as a ram behavior (Bergert and Wainwright 1997; Ferry-Graham et al. 2001a).

Behavior can be defined as the control of morphological systems by motor output, and can be quantified by measuring the kinematics or movement of the morphological system (Reilly and Lauder 1992). It is the intermediary between the form/function complex and the environment. Morphology can be, but is not always, a good predictor of behavior. For example, some morphologically similar species such as centrarchid and cichlid fishes have shown similar feeding kinematics. The large-mouthed piscivores, *Micropterus salmoides* and *Cichla ocellaris*, exhibited strikes with a large ram component. In contrast, the small-mouthed benthic invertebrate pickers, *Lepomis* spp. and *Cichlasoma severum* exhibited strikes with a greater similarity in buccal and opercular pressures with each other than with their large-mouthed confamilials (Norton and Brainerd 1993).

Morphologically similar taxa have also been found to exhibit dissimilar kinematics (Norton 1991). A small-mouthed species of sculpin, *Rhamphocottus richardsonii*, was predicted to be as unsuccessful at capturing elusive prey as its other small-mouthed, suction-feeding confamilials. However, this species utilized ram feeding via a lateral lunge of its jaws that was highly successful for capturing elusive prey. On the other hand, morphologically dissimilar taxa may exhibit very similar kinematics (Reilly and Lauder 1992). Species of salamanders that

did not share morphological space on a principal components analysis were found to share kinematic or behavioral space. Thus, the relationship between morphology and behavior is frequently variable.

The goal of this study is to examine similarities in feeding kinematics among three species of ram-feeding fishes: Florida gar *Lepisosteus platyrhincus*, redbfin needlefish *Strongylura notata*, and great barracuda *Sphyrna barracuda*. These fishes share similar morphologies: elongate, fusiform bodies; tapered heads with terminal mouths; large jaws with conical teeth; non-protrusible premaxillae; slender caudal peduncles; and dorsal and anal fins placed posteriorly on the body. Lepisosteids are neopterygian fishes that exhibit plesiomorphic characters including numerous dermal bones in the skull and a heavy exoskeleton of ganoid scales. In contrast, *Strongylura notata* (Belonidae) and *Sphyrna barracuda* (Sphyrnaeidae) are derived acanthopterygian fishes. These two species are more closely related to each other than to *Lepisosteus*. Liem (1978) speculated that success in piscivory is the result of exhibiting a highly specialized or extreme morphology or behavior, rather than an intermediate or generalized form or behavior. *Lepisosteus*, *Strongylura*, and *Sphyrna*, with their elongate jaws and bodies, fixed upper jaws, and numerous conical teeth, represent a morphological extreme.

This investigation will attempt to answer the following questions: Do all three species exhibit similar feeding kinematics when presented with the same prey item? If not, what differences in feeding kinematics exist among these species and how does it relate to prey capture and piscivory?

Materials and methods

Lepisosteus platyrhincus were collected in freshwater canals east of Big Cypress Basin in Dade County, Fla. (25°52'N, 80°57'W). Lepisosteids are found in rivers, lakes, and occasionally estuaries. *Lepisosteus platyrhincus* is found in peninsular Florida and throughout the Suwannee River drainage system as far north as Georgia. They are stalking, water-column predators that wait for the approach of an unaware fish, slowly moving closer to the prey until the prey is close enough to strike at (Lauder and Norton 1979; Seidensticker 1987). *Lepisosteus* feeds mainly on water-column-dwelling fishes such as minnows (Cyprinidae) and shad (*Dorsoma* spp.) but has also been known to feed on bottom-dwelling fishes and invertebrates as well as scavenge benthic food (Crumpton 1970; Seidensticker 1987).

Strongylura notata were collected in the Gulf of Mexico at the south beach of Fort de Soto State Park, St. Petersburg, Fla. (27°38'N, 82°44'W) and in Sarasota Bay, Fla. (27°21'N, 82°34'W) at Mote Marine Laboratory. Belonids are found in estuaries, seagrass beds, reefs, and waters fringing sandy beaches. They are generally surface cruisers that capture prey in the water

column (Randall 1967). *Strongylura notata* inhabits warm coastal waters of the Atlantic from Bermuda to Central America, including the Caribbean. Large *Strongylura* prey upon small fishes in seagrass beds, such as silversides (Atherinidae) and anchovies (*Anchoa* spp.), while smaller individuals rely more on crustaceans and insects to supplement their piscivory (Springer and Woodburn 1960; Carr and Adams 1973).

Juvenile *Sphyræna barracuda* were collected in the seagrass beds of Biscayne Bay and Key Largo, Fla. (25°41'N, 80°13'W). *Sphyræna barracuda* is a lie-in-wait predator, that forages on the edges of reefs or above seagrass beds before striking at prey using a high velocity lunge (Hiatt and Strasburg 1960; de Sylva 1963). *Sphyræna barracuda* can be found in the Atlantic from Massachusetts to Brazil, and has a highly diverse diet of mid-water-dwelling fish and cephalopod species. Juvenile individuals, similar to those investigated here, have been observed to include atherinids, herrings and sardines (Clupeidae), mojarras (Gerreidae), small parrotfishes (Scaridae), small mullets (Mugilidae), jacks (Carangidae), and cephalopods in their diet (de Sylva 1963).

Five individuals each of *L. platyrhincus*, *Strongylura notata*, and *Sphyræna barracuda* were used for analysis. All individuals were housed and filmed in 265-l aquaria, and were maintained on live, commercially available fathead minnows *Pimephales promelas*. *Lepisosteus platyrhincus* individuals were housed in freshwater. *Sphyræna barracuda* and *Strongylura notata* were housed in seawater maintained at 33‰. All individuals were kept at 25°C and experienced a light cycle of approximately 12 h light and 12 h dark.

Fifteen strikes by five individuals of each of the three species (*L. platyrhincus*, *Strongylura notata*, *Sphyræna barracuda*) were recorded with a NAC HSV200 two-camera video system at 200 fields·s⁻¹. This gave a total of 225 strike trials that were analyzed across all three species. A camera positioned close to the tank recorded the prey capture event from a lateral view. A mirror positioned at 45° above the tank provided a dorsal view of the strike, which was recorded by a second camera. The two cameras were automatically synchronized by the NAC system.

Predators were fed one prey individual per trial, dropped through a feeding tube (3 cm diameter) positioned in the same place at the top of the tank during each feeding. It has been demonstrated that feeding kinematics become slower as a predator becomes satiated (Sass and Motta 2002). Therefore no more than five strike trials per individual were recorded during the same feeding, with 24–48 h between feedings. Strike sequences used in this analysis were not necessarily from the same hunger state because all prey were offered sequentially during a feeding with a 3- to 5-min interval between prey introductions. However, the data are comparable as the strike trials analyzed are representative of the range of hunger states for each individual.

Total length of prey used was standardized to 10–20% of the total length of the predator. Total length of the predator was used rather than gape width or area because of the extreme differences in gape size of the three predators, and the large difference between the gape at the tip of the jaws and the oral gape of the *L. platyrhincus* and *Strongylura notata*. Mean standard lengths for *L. platyrhincus*, *Strongylura notata*, and *Sphyræna barracuda* were 28.62 cm, 32.0 cm, and 19.62 cm, respectively. There was a significant difference in the mean standard lengths among species ($P=0.003$, one-way ANOVA) with juvenile *Sphyræna barracuda* individuals being significantly smaller than the other two species.

Variables measuring strike and prey capture kinematics were analyzed with Sigma Scan Pro (Jandel Scientific) using a Panasonic AG-1970 video player and monitor after downloading the video with ATI multimedia video capture software.

Strike variables

Four strike variables were measured on all 225 strike sequences. Strike sequences where the predator was laterally positioned to the camera and all kinematic variables were visible were chosen for analysis. All variables measuring time that occurred after the initiation of the strike were measured relative to strike initiation (time zero). Strike initiation was considered to be the field (5 ms) prior to the rapid lunge of the predator towards the prey, not including any slow stalking of the prey prior to the strike. Strike distance was measured as the distance from the tip of the predator's upper jaw to the approximate center of mass of the prey, roughly at one-third of the body length posterior to the head and in the center of the body, at strike initiation. Strike duration was the total time from strike initiation to the time of prey contact with the jaws. Mean velocity (cm·s⁻¹) of the strike was calculated as the strike distance divided by the strike duration. Lateral excursion of the tip of the jaw was used in the case of the lateral strike of *L. platyrhincus*. Mean velocity was then converted to body lengths·s⁻¹ using standard length. Lateral body curvature was measured as the radius created by the circle of best fit applied to the outside curve of the predator's body at the time of prey capture. Strike distance and lateral body curvature radius were converted to percent body lengths using standard length.

Prey capture variables

Nine prey capture variables were measured for each of the 225 strike sequences. Time to mouth opening was measured from the onset of the strike until the time the jaws began to open. Duration of mouth opening was measured from the time the jaws began to open until maximum gape was reached. Maximum gape was mea-

sured as the maximum distance between the anterior tip of the predator's upper jaw and the anterior tip of the dentary during prey capture, and was converted to percent head length using the distance from the anterior point of the jaws to the posterior edge of the operculum. In *L. platyrhincus* and *Strongylura notata* maximum gape may also be referred to as the distal oral gape, and is distinct from the proximal oral gape, the actual entrance to the oral cavity at the posterior margin of the elongate jaws. Duration of maximum gape was measured as the length of time the jaws were held at their maximum gape, from the time maximum gape was reached until the jaws began to close. Duration of mouth closing was measured as the time from the end of maximum gape until the jaws were closed on the prey or fully occluded. The time to hyoid depression was measured from the onset of the strike until the time the hyoid began to depress. Duration of hyoid depression was measured as the time from the onset of hyoid depression until maximum hyoid depression was reached. Duration of maximum hyoid depression was measured as the length of time the hyoid was held at maximum depression, from the time the hyoid had reached its maximum excursion until the onset of elevation. Duration of hyoid retraction was measured as the time from the onset of hyoid elevation until full recovery of the hyoid to its initial resting state. Hyoid variables were often difficult to see on film so the sample sizes for hyoid measurements are unbalanced. Total prey capture duration, therefore, was from the onset of jaw opening until the retraction of the hyoid apparatus.

Data analysis

All tests were performed using SigmaStat 2.0 (Jandel Scientific) SPSS 10.0 (SPSS Software). An *F*-max test was used to determine homogeneity of variances of the data. A Kolmogorov-Smirnoff test was used to test normality of the data. Variables were log-10 transformed to achieve normality and equal variances.

Differences among individuals of the same species were tested to explore the degree of individual variability, to ensure that the variation among individuals within a species would not be greater than that among species, and to determine which kinematic variables were potentially size-dependent. To test the null hypotheses that there were no differences in kinematic variables among individuals, one-way repeated measures ANOVAs were performed for each species separately with strike as the repeated measure. Bonferroni corrections were not used as it has been recently argued that this correction is not a solution to the problem of type-I errors in exploratory data analysis and needlessly increases type-II error rates, as well as reduces the ability to find anything significant in the data (Cabin and Mitchell 2000; Moran 2003). Tukey multiple comparisons tests were performed post hoc to examine all pair-wise differences. If differences among individuals were

found and a relationship between the kinematic variable and predator size was indicated by the multiple comparisons test, linear regressions were performed for that species to test relationships between predator standard length and the kinematic variable. The resulting residuals were then used in a one-way repeated measures ANOVA. A non-significant result from the ANOVA indicates size was the main factor in contributing to the individual variability for that species.

To compare kinematics among species, a principle components analysis was performed to reduce the data into a few non-correlated factors or groups of variables. The resulting PCA loadings for each species were then analyzed using a two-way mixed model ANOVA with type III sums of squares. Species was designated as the fixed factor and individual as the random factor nested within species. If significant differences were found, Tukey multiple comparison tests were performed post hoc to examine all pair-wise differences among the three species.

Results

Feeding kinematics of *Lepisosteus platyrhincus*

The feeding patterns of *L. platyrhincus* individuals followed a consistent pattern of events (Fig. 1). When the prey was detected, the predator slowly approached the prey. This stalking behavior could take several minutes, and resulted in the predator aligning its jaws lateral to the prey (Fig. 2a).

When the predator was oriented in this position to the prey, the strike was initiated by a lateral bending of the body towards the prey, resulting in a sideways strike of the jaws at the prey as they opened. Strike distances were small, with a mean of 11.7% of the predator's body length. Strike durations ranged from 25 to 45 ms with a mean of 32 ms. Mean strike velocity was 3.60 body lengths·s⁻¹ (Table 1).

During prey capture, kinematic events occurred in a posteriorly directed sequence. Movements started with the opening of the most anterior structure, the mouth, and ended with the elevation of the most posterior structure, the hyoid. Mouth opening began almost concurrently (3 ms) with strike initiation (Fig. 1, Fig. 2b). Hyoid depression followed mouth opening. Maximum gape averaged 3.6 cm or 43.38% of the length of the head (Table 1, Fig. 2c). Mouth closing (7 ms) occurred after maximum gape and resulted in the closing of the jaws on the prey. This was followed by hyoid elevation. Maximum body curvature was reached at the moment the jaws closed on the prey (Fig. 2e) at a mean radius of 17.6 cm or 52.82% of the body length (Table 1). Using rapid lateral movements of the head and very brief forward lunges, the predator manipulated the prey between the jaws by inertial manipulation before transporting it via suction.

Individual effects were important for a few of the kinematic variables. There were significant differences

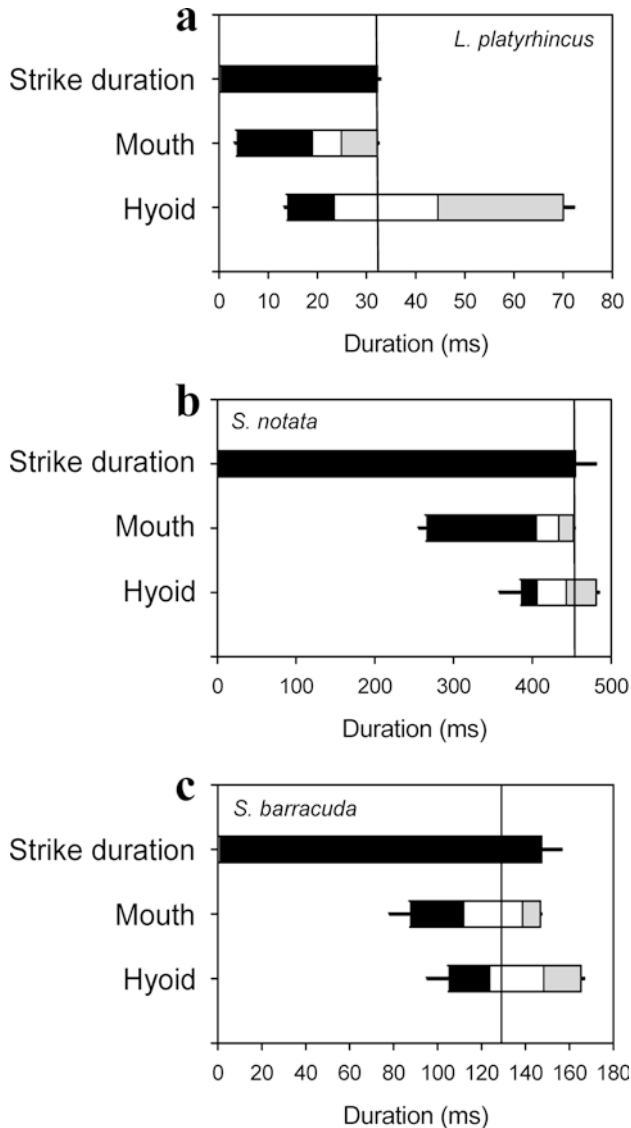


Fig. 1 Strike and prey capture profiles for **a** *Lepisosteus platyrhincus*, **b** *Strongylura notata*, and **c** *Sphyraena barracuda*. Black bars represent the duration of kinematic onset, white bars represent the duration of kinematic maximum, and gray bars represent the duration of kinematic recovery. Small black bars represent the standard error. The vertical solid line indicates the time jaws close on the prey or the prey is engulfed

among individuals for strike duration and time to mouth opening. Difference in predator size could not explain the difference in time to mouth opening ($P=0.178$, $R^2=0.024$), however it could explain the difference in strike duration ($P=0.033$, $R^2=0.060$) and the subsequent ANOVA using the size-corrected regression residuals showed no significant differences among individuals ($P=0.124$).

Feeding kinematics for *Strongylura notata*

The feeding patterns of *Strongylura notata* individuals followed a consistent pattern of events (Fig. 1). When

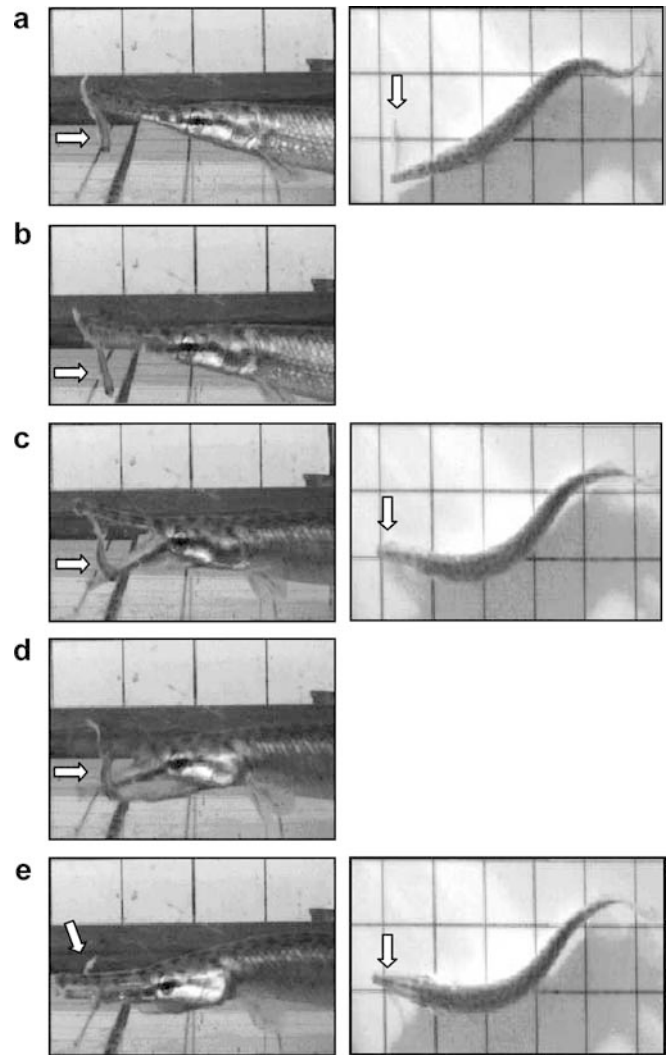


Fig. 2a–e Feeding sequence of *L. platyrhincus* from strike initiation until the jaws close on the prey. White arrows indicate prey position. **a** Strike initiation, 0 ms; **b** onset of mouth opening, 3.4 ms; **c** maximum gape, 19 ms; **d** maximum hyoid depression, 23.6 ms; **e** jaws close on prey, 32.2 ms. The time is the average time to the event from strike initiation in milliseconds ($n=5$)

the prey was detected, the predator lined up its longitudinal axis with the approximate midpoint of the prey. When the predator was oriented to the prey, it used lateral undulatory swimming at a moderate velocity, averaging 1.7 body lengths $\cdot s^{-1}$, to overtake the prey. Mean strike distance was 68.9% of the predator's body length. Mean strike duration was relatively long (455 ms), ranging from 160 ms to 1,040 ms (Table 1).

During prey capture, kinematic events occurred in a posteriorly directed sequence (Fig. 1). Mouth opening began 264 ms after strike initiation, or approximately halfway through the strike (Fig. 3b). Hyoid depression, when visible, was short in duration and began just before maximum gape was reached (Fig. 1, Table 1). Maximum gape averaged 4.2 cm (Table 1). Maximum hyoid depression coincided with maximum gape

Table 1 Comparison of strike variables among all three species ($n = 5$)

Variable	<i>Lepisosteus platyrhinchus</i>	<i>Strongylura notata</i>	<i>Sphyraena barracuda</i>
Strike distance (% body length)	11.7 ± 0.69	68.9 ± 4.54*	102.4 ± 5.09*
Strike duration (ms)	32 ± 0.7*	455 ± 26.6	147 ± 9.3
Mean velocity (body lengths·s ⁻¹)	3.6 ± 0.69	1.7 ± 0.11*	7.5 ± 0.31*
Lateral body curvature (cm)	17.1 ± 1.63	NA ^a	NA ^a
Time to mouth opening (ms)	3 ± 0.3 [†]	264 ± 24.5	87 ± 9.2*
Duration of mouth opening (ms)	16 ± 0.5	141 ± 9.1*	25 ± 0.67*
Maximum gape (cm)	3.6 ± 0.10	4.2 ± 0.11*	3.0 ± 0.06*
Duration of maximum gape (ms)	6 ± 0.2	28 ± 2.3	27 ± 1.2*
Duration of mouth closing (ms)	7 ± 0.3	19 ± 1.9	8 ± 0.6
Time to hyoid depression (ms)	14 ± 0.7	385 ± 27.1	105 ± 9.7
Duration of hyoid depression (ms)	10 ± 0.2	22 ± 1.8	19 ± 0.5
Duration of maximum hyoid depression (ms)	21 ± 2.2	37 ± 4.1	25 ± 1.2
Duration of hyoid retraction (ms)	26 ± 2.1	38 ± 3.9	17 ± 1.6*

* Significant differences among individuals (one-way RM ANOVA) at $P < 0.05$

^a Lateral body curvature not present during feeding in *Strongylura notata* and *Sphyraena barracuda*

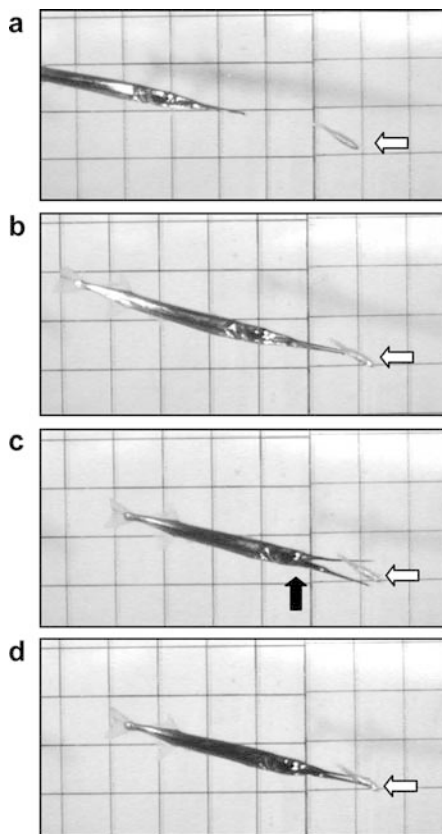


Fig. 3a–d Feeding sequence of *S. notata* from strike initiation until the jaws close on the prey. *White arrows* indicate prey position. Note appreciable lack of hyoid depression (*black arrow*). **a** Strike initiation, 0 ms; **b** onset of mouth opening, 264.2 ms; **c** maximum gape, 405.6 ms; **d** jaws close on prey, 454.6 ms. The time is the average time to the event from strike initiation in milliseconds ($n = 5$)

(Fig. 3c). Mouth closing followed maximum gape and resulted in the capture of the prey between the anterior margin of the jaws in most cases (Fig. 3d). Hyoid kinematics were often not evident (Fig. 3c). Prey were manipulated between the jaws using inertial manipulation towards the proximal gape before being transported into the oral cavity via suction. During manipulation,

the predator would swim backwards briefly to give the prey momentum directed towards the posterior of the predator. The predator then released the prey by opening the mouth and executed a rapid forward lunge. The jaws then closed rapidly again on the prey. This sequence was repeated until the prey was close enough to the proximal gape for suction transport.

Individual effects were important for four of the kinematic variables. There were significant differences among individuals for strike distance and mean velocity. Predator size did not appear to be a factor affecting strike distance ($P = 0.051$, $R^2 = 0.051$), mean velocity ($P = 0.059$, $R^2 = 0.048$). Significant differences among individuals were also found in the duration of mouth opening and maximum gape. Duration of mouth opening increased with predator size ($P = 0.014$, $R^2 = 0.080$) as did maximum gape ($P < 0.001$, $R^2 = 0.202$). The subsequent one-way repeated measures ANOVA performed on the regression residuals showed a significant difference in duration of mouth opening ($P = 0.050$) and in maximum gape ($P = 0.029$), therefore although size explains some of the differences, it is not the only factor effecting the variation among individuals.

Feeding kinematics of *Sphyraena barracuda*

The feeding kinematics of *Sphyraena barracuda* individuals also followed a consistent pattern of events (Fig. 1). When the prey was detected, the predator aligned its longitudinal axis with the approximate midpoint of the prey (Fig. 4a). The predator used high acceleration s-starts (Webb 1984c) to capture the prey (Fig. 4b). Prey were captured by head-on strikes at velocities averaging 7.5 body lengths·s⁻¹. Strike distances were also relatively large averaging 102% of the predator's body length (Table 1).

During prey capture, kinematic events occurred in a posteriorly directed sequence (Table 1). Prey capture began 87 ms after the start of the strike, or approximately halfway through the strike. The onset of hyoid depression was initiated at 105 ms, just prior to maxi-

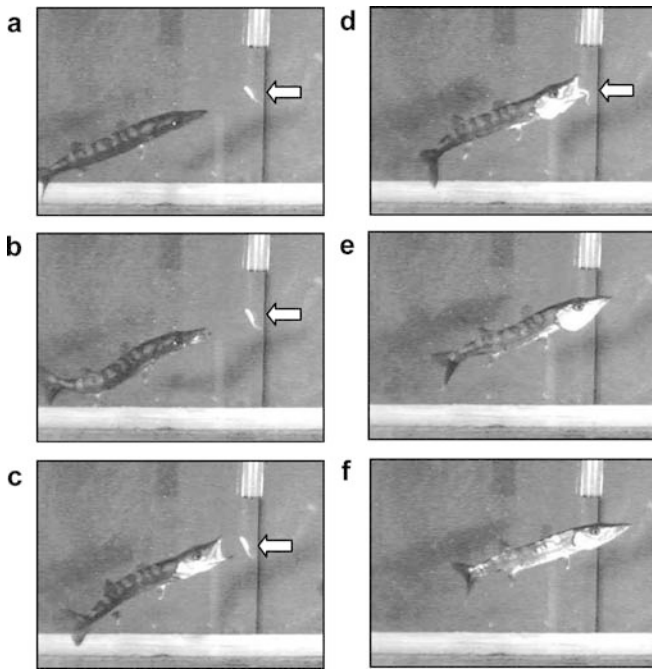


Fig. 4a–f Feeding sequence for *S. barracuda* from strike initiation to hyoid retraction. *White arrow* indicates prey position. **a** Strike initiation, 0 ms; **b** s-start, 5 ms; **c** maximum gape, 115 ms; **d** prey enters buccal cavity, 135 ms; **e** mouth closed, 151 ms; **f** hyoid retraction, 165 ms. The time is the average time to the event from strike initiation in milliseconds ($n = 5$)

imum gape. Maximum gape averaged 3 cm or 45.89% of the head length and occurred some distance from the prey (Fig. 4c, Table 1). Maximum hyoid depression was reached during maximum gape, prior to the predator reaching the prey. The prey was engulfed by the predator's gape during maximum gape (Fig. 4d), and the mouth closed rapidly (8 ms) after the prey passed the oral gape (Fig. 1). Hyoid elevation began after mouth closing (Fig. 4e, f) and signaled the recovery of all structures to their original positions. There was no visible manipulation, and the predator appeared to ram transport the prey directly through the buccal cavity.

Significant individual effects were found for two of the kinematic strike variables, strike distance and mean velocity (Table 1). Strike distance was found to be inversely related to predator size: larger individuals struck from a shorter distance than smaller individuals. A regression of strike distance against predator standard length was significant ($P < 0.001$, $R^2 = 0.230$), and a subsequent one-way repeated measures ANOVA performed on the regression residuals resulted in no significant differences among individuals ($P = 0.190$). However, size did not account for all of the differences among individuals for mean velocity. A regression revealed a significant relationship between mean velocity and predator standard length ($P < 0.001$, $R^2 = 0.336$). Larger individuals exhibited a faster strike. After the effect of size was removed, there were still significant

differences among individuals ($P = 0.004$), indicating that size was not the only factor causing differences in mean velocity.

All variables associated with the jaws during prey capture, with the exception of the duration of mouth closing, were found to be significantly different among individuals. Of these variables, only maximum gape could be significantly correlated with predator size ($P = 0.007$, $R^2 = 0.094$). The one-way ANOVA performed on the residuals was significant ($P < 0.001$), therefore size was not the only factor contributing to differences in maximum gape. Of the variables associated with the hyoid during prey capture, only the duration of hyoid elevation was found to be significantly different among individuals (Table 1). Predator size was positively related to the duration of hyoid elevation: larger individuals exhibited faster elevation of the hyoid ($P = 0.029$, $R^2 = 0.100$).

Comparison of feeding kinematics among species

The strike was shortest in duration and distance for *L. platyrhincus* and longest in duration and strike distance for *Strongylura notata*. *Sphyræna barracuda* exhibited the fastest mean velocity of the three species (Table 1). *Lepisosteus platyrhincus* was the only species to exhibit a lateral strike. *Sphyræna barracuda* and *Strongylura notata* both struck the prey head-on.

During prey capture, the kinematic events observed in all three species occurred in a posteriorly directed sequence, beginning with mouth opening and ending with hyoid elevation. In general, the kinematic variables for *L. platyrhincus* were the shortest in duration and had the earliest onset, while the kinematics of *Strongylura notata* were the longest in duration and had the latest onset.

Principle components analysis revealed a distinct difference in kinematics among species (Fig. 5). Kinematic variables were grouped into three factors, which explained 75.6% of the variance in the data (Table 2). The first principle component, PC1 (41.6% of the total variance), comprised variables relating to "prey approach": strike distance, strike duration, time to mouth opening, duration of mouth opening, duration of maximum gape, time to hyoid depression, and duration of hyoid depression. The second principle component, PC2 (23.4% of the total variance), described those variables relating to "prey contact": mean velocity, maximum gape, and duration of mouth closing. Predator size also loaded highly on this axis, possibly indicating that these variables also correlated highly with size. The third principle component, PC3 (10.6% of the total variance), grouped those variables related to "recovery": duration of maximum hyoid and duration of hyoid elevation.

Two-way ANOVAs performed on the principle component scores for each strike showed significant differences in the variables making up PC1 and PC2

Fig. 5 Principle components plot of kinematic variables for all three species. *L. platyrhincus* (●), *S. notata* (■), and *S. barracuda* (▲)

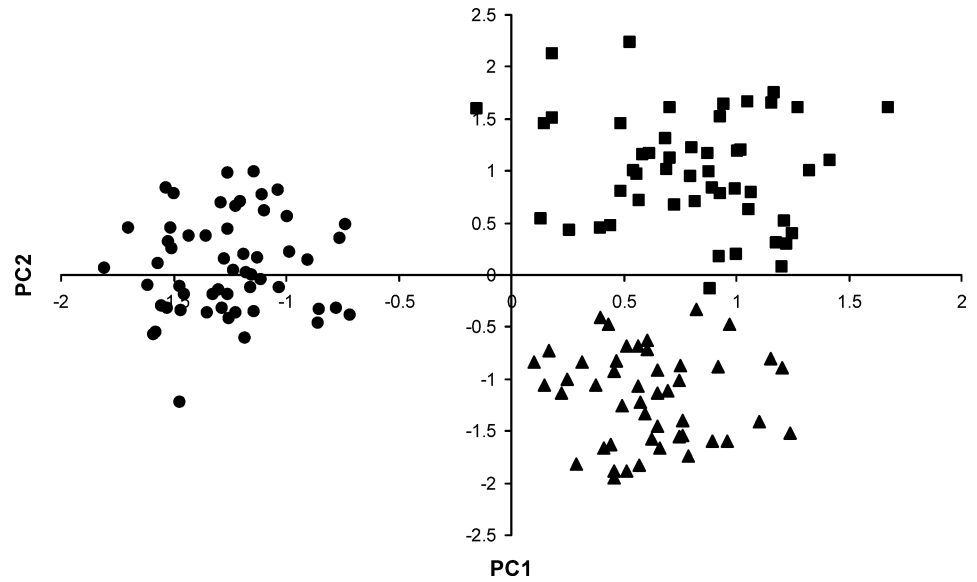


Table 2 Principle component loadings for all kinematic variables

Variable	PC1 (41.6%)	PC2 (23.4%)	PC3 (10.6%)
Predator size	-0.159	0.889	0.010
Strike distance	0.914	-0.284	0.006
Strike duration	0.917	0.324	0.114
Mean velocity	-0.001	-0.900	-0.010
Time to mouth opening	0.907	0.105	0.006
Duration of mouth opening	0.693	0.597	0.010
Maximum gape	0.146	0.642	0.006
Duration of maximum gape	0.869	-0.121	0.152
Duration of mouth closing	0.336	0.435	0.187
Time to hyoid depression	0.914	0.311	0.113
Duration of hyoid depression	0.781	0.005	0.112
Duration of maximum hyoid depression	0.268	-0.001	0.847
Duration of hyoid elevation	0.003	0.415	0.722

Table 3 Results of PCA scores comparing species from two-way ANOVAs

Principle component	Species		Individual	
	F	P	F	P
PC1 “Prey approach”	289.221	< 0.001	2.756	0.002
Strike distance				
Strike duration				
Time to mouth opening				
Duration of mouth opening				
Time to hyoid depression				
Duration of hyoid depression				
Duration of maximum gape				
PC2 “Prey contact”	40.723	< 0.001	12.047	< 0.001
Mean velocity				
Maximum gape				
Duration of mouth closing				
Predator size				
PC3 “Recovery”	0.206	0.816	2.815	0.002
Duration of maximum hyoid depression				
Duration of hyoid elevation				

among species, but no significant differences were found among species for PC3 (Table 3). Significant individual effects were found for all three principle components, as

would be expected given the results from the one-way ANOVAs performed for each species. A Tukey multiple comparisons test showed that all three species were

significantly different from each other ($P < 0.002$) for both PC1 and PC2.

Discussion and conclusions

The original premise of this study that similarities in body and jaw morphology lead to similarities in behavior appears to be not true for these morphologically similar species. Although all three species in this study use ram feeding and share similar broad kinematic patterns, in this instance morphology was not a good predictor of strike behavior and feeding kinematics. While there are some similarities in individual behaviors, each species exhibits a distinct behavioral repertoire during feeding that differs in prey approach, kinematic timings, and prey processing.

Ram feeding and the consequences of elongate jaws

All three species, *Lepisosteus platyrhincus*, *Strongylura notata*, and *Sphyraena barracuda* use ram feeding to capture elusive piscine prey. Ram feeding has been observed in other species to be particularly effective for capturing mobile and elusive prey (Norton 1991; Ferry-Graham et al. 2001a, 2001b). During the strike, all predators used a high velocity lunge of either the whole body or the jaws to overtake the prey. Although a ram-suction index (Norton and Brainerd 1993) was not used to measure the specific ram and suction components of the strike, prey movement towards the predator was minimal and predator movement towards the prey appeared to dominate.

Other long-jawed aquatic vertebrates are known to utilize ram feeding for the capture of elusive prey. The long-jawed butterflyfish, *Forcipiger longirostris*, which feed on more elusive prey than its confamilials, also exhibits a greater ram-feeding component than its confamilials (Ferry-Graham et al. 2001a). The American alligator *Alligator mississippiensis*, when feeding on live prey in the water, uses a series of lateral lunges to capture prey (Busbey 1989), similar to the prey capture observed in *L. platyrhincus*. *Esox*, or pike, another ram-feeding piscivorous fish, uses rapid lunges with wide open jaws to engulf its prey, behaviors that are extremely similar to the behaviors that characterize the feeding of *Sphyraena barracuda* (Rand and Lauder 1980; Harper and Blake 1991).

In all three species, the elongation of the jaws has been accomplished by a forward inclination to the suspensorium and a secondary lengthening of the upper and lower jaws (Gregory 1933). Long jaws have a mechanical disadvantage at their most anterior points in terms of force production when compared to short jaws, but are well suited for closing the tips of the jaws at high angular velocities. As is suitable for their elongate jaws, these three species rely on high velocity jaw closure for capturing prey.

Pre-strike behaviors

Lepisosteus platyrhincus, *Strongylura notata*, and *Sphyraena barracuda* oriented to the prey before actually striking. The predators seemed to orient most quickly to the prey when the prey was moving, indicating possible visual stimulation. This orientation is a common behavior among stalking predators, who tend to approach their prey head-on to minimize visible movement (Curio 1976). Other fishes, both ram and suction feeders such as pikes (Esocidae) (Webb and Skadsen 1980) and trumpetfish (Aulostomidae) that feed on fish (Hobson 1974), sculpins (Cottidae) (Norton 1991) and reef fishes such as butterflyfish (Chaetodontidae) (Ferry-Graham et al. 2001a, 2001b) that feed on zooplankton, crustaceans, and other highly mobile prey, orient to their prey before feeding.

Strike kinematics

Lepisosteus platyrhincus, *Strongylura notata*, and *Sphyraena barracuda* utilize different strike tactics and modes of locomotion when striking prey. After orientation to the prey, *L. platyrhincus* utilizes minimal undulations of the caudal, dorsal, and anal fins to slowly approach the prey, with very little axial undulation and a slow forward velocity. In contrast, *Strongylura notata* exhibits a head-on, high velocity (51.77 cm/s) strike using undulations of the body. *Strongylura* species have been found to increase their lateral swimming amplitudes until, at the highest velocities, are exhibiting anguilliform locomotion (Liao 2001). This is most efficient for extremely long-bodied fishes, as more body length is recruited for thrust as the velocity increases.

Sphyraena barracuda lunges head-on at prey at the highest velocity and relatively furthest distance of the three species (144.5 cm/s) in spite of the individuals being the smallest of the three species studied, accelerating rapidly using an s-start. The s-start, during which the predator assumes an s-shaped posture prior to acceleration, is ideal for achieving a high velocity in a short distance (Webb 1984c). The strike of *Sphyraena barracuda* is very similar to that of the morphologically similar esocid fishes such as pike and muskellunge (Webb 1978, 1984b, 1984c; Rand and Lauder 1980; Webb and Skadsen 1980; Harper and Blake 1991). Esocids and sphyraenids share those characteristics that define acceleration specialists: torpedo-shaped, streamlined bodies, fins placed posteriorly on the body to maximize thrust, and a low proportion of non-muscle mass (Webb 1984a).

Prey response times to predators can be defined in terms of the "looming effect" (Dill 1974). Prey fishes are visually sensitive to an oncoming predator's size and velocity. A prey fish's reactive distance (the distance between the predator and the prey at which the escape response is triggered) decreases with decreasing velocity and size of predator. A predator approaching at very

low speeds increases the prey's response threshold to the point where the prey may not react at all. The slow approach of *L. platyrhincus* may function to eliminate predator recognition by the prey in this manner and may be utilized while stalking prey in a weedy riverine environment. Prey fish are also sensitive to the cross-sectional shape of predators, such that an elliptical cross-section elicits an escape response sooner than a circular cross-section of the same size and velocity (Webb 1982, 1984a, 1984c). Consequently, slender, torpedo-shaped predators such as *Sphyraena barracuda* and *Strongylura notata* have a better chance of successfully approaching prey than more fusiform predators like largemouth bass (*Micropterus salmoides*) during a ram-strike, reducing the strike distance and therefore the amount of time a prey fish is allowed for escape.

Strongylura notata and *Sphyraena barracuda* both capture prey head-on. Both species rely on a large gape that overtakes the prey before the jaws close. This head-on approach, combined with having the deepest part of the body located posteriorly, also serves to reduce the looming effect and decreases the prey's reactive distance. The farther back on the body the deepest body depth occurs, as well as focus points such as the predator's eyes, the better chance the predator has of approaching the prey (Dill 1974). From a head-on perspective, elongate jaws appear to disappear; they are not visible against the greater circumference of the body, perhaps giving the illusion that the predator is farther away than it really is.

Lepisosteus platyrhincus may also be limited in its locomotory performance compared to *Strongylura notata* and *Sphyraena barracuda*. The heavily armored integument of lepisosteids has been found to decrease swimming performance in these fishes due to a trade-off between skin mass and muscles mass and the passive stiffening of the skin by ganoid scales. This decrease in swimming performance has been hypothesized to decrease performance during piscivory (Webb et al. 1992; Long et al. 1996). Similar-sized euteleost fishes have a greater amount of muscle and less skin mass compared to that of a lepisosteid, giving rise to more propulsive power and less non-muscle mass to accelerate. It is also thought that the opisthocoelous vertebrae of lepisosteids play a role in restricting the lateral flexibility of the body (Long et al. 1996). These things in concert may restrict *L. platyrhincus* in its mode of prey capture: unable to form the s-shaped posture necessary for a high-speed lunge and requiring more energy to do so, it instead relies on stealth and a lateral strike for capturing prey. There is, however, no evidence as of yet whether or not this difference in strike behaviors gives rise to a difference in actual feeding performance.

When striking at prey, *L. platyrhincus* exhibits a rapid lateral lunge of its head and jaws. Lateral strikes are common in broad-jawed, aquatic-feeding vertebrates. Crocodylians (Busbey 1989; Cleuren and de Vree 1992), roseate spoonbills *Platalea leucordia* (Weihs and Katzir 1994), and water snakes *Nerodia* (Cundall and Gans

1979) all use this behavior for capturing prey under water. These species have flattened, elongate mandibles in common. The spatulate bill of *P. leucordia* is associated with a hydrodynamic function in feeding. The lateral sweep of the bill creates vortices that lift prey items off the substrate to be captured during the subsequent, opposite sweep of the bill. Other hydrodynamic consequences of having broader, elongate jaws relate to drag: a broad plate perpendicular to flow has a higher drag coefficient than a streamlined body (Vogel 1994). The open gape of *L. platyrhincus* may somewhat resemble a flat plate hydrodynamically, preventing a head-on lunge from being an effective method of prey capture for these fishes.

Lepisosteus platyrhincus is found in abundance in southern Florida canals and rivers. Florida freshwater canals and rivers can have low visibility due to turbidity and complex structures such as fallen logs and heavy vegetation (Hunt 1953). *Lepisosteus platyrhincus* tends to be olive green in color with distinct spots over most of its body and fins, allowing it to be well camouflaged in the riverine environment. The lateral strike with its short strike distance and reliance on stealth may be highly successful for capturing elusive prey in a complex habitat, where prey may not be visible at a distance and there is little room for maneuvering.

Strongylura notata and *Sphyraena barracuda* are found in seagrass beds, along sandy beaches, and around coral reefs, in midwater or near the surface where there is little cover and generally good visibility (Hiatt and Strasburg 1960; de Sylva 1963; Randall 1967). In this type of habitat, a long-distance strike with as much reduction of prey response as possible may be the most successful strategy for catching elusive, mobile prey.

Strongylura notata appears more similar in strike behavior to *Sphyraena barracuda* than to *L. platyrhincus* despite the fact that *Strongylura notata* and *L. platyrhincus* share the characteristic of extremely long jaws. The slender, more conical jaws and lack of extensive body armor of *S. notata* might result in less hydrodynamic constraints as compared to *L. platyrhincus*. The same head-on lunging behavior exhibited by *S. notata* has been reported in other species of belonids such as the freshwater Asian needlefish *Xenentodon cancila* (Foster 1973), and *Strongylura* and *Tylosaurus* spp. of the Caribbean (Randall 1967). However, lateral strikes have been described in some belonids such as *Strongylura gigantean* of the Pacific (Hiatt and Strasburg 1960) and Amazonian *Potamorhaphis* spp. (Goulding and Carvalho 1984).

Prey capture kinematics

All three species follow the characteristic kinematic sequence of expansive, compressive, and recovery phases observed in other aquatic-feeding vertebrates (Liem 1978). A preparatory phase was not obvious but might

have been present. These ram-feeding predators rely on a large gape to overcome the prey followed by rapid closing of the jaws. The elongate jaws of these species contribute to the ability of these species to achieve gapes ranging from 30 to 45% of the total length of the head. A large gape is important in ram feeding, allowing the predator to engulf the prey or seize the prey between the jaws (Norton 1995). Jaw protrusion, when possible, can contribute to the ram component of a strike and effectively increase attack velocity (Motta 1984; Wainwright et al. 2001). Lacking the ability to protrude the jaws, these three ram feeding fishes rely instead on stealth and high attack velocity, either by lateral swiping or forward lunging. Interestingly, maximum attack velocity of *Strongylura notata* and *L. platyrhincus* is within the range measured for seven species of cichlid fishes attacking guppy prey (approximately 20–100 cm/s), whereas *Sphyraena barracuda* was considerably faster (144 cm/s).

Suction feeders rely on a rapid opening of the mouth and rapid expansion of the buccal cavity to create the pressure differential responsible for pulling water and prey into the mouth (Liem 1980). While these three fishes may have generated some suction merely by the opening of their mouths, the small amount of suction had a negligible and unobservable effect on the prey, such that there was little to no movement of the prey towards the predator's mouth. The closer the prey is to the mouth aperture of a fish, the greater the influence of the generated suction, and that suction dissipates rapidly with distance from the mouth aperture (Van Leeuwen and Muller 1984; Wainwright et al. 2001).

Since little effective suction is generated during prey capture in these three species, rapidly closing jaws become important in order to successfully capture elusive prey before it can escape. Both *L. platyrhincus* and *Strongylura notata* closed their jaws directly on the prey, puncturing and holding the prey with numerous conical teeth. *Sphyraena barracuda* closed their mouths after the prey passed the anterior margin of the jaws, fully enclosing the prey with the oral cavity. Many ram feeders hold their prey between the teeth. Some sharks use this to crush and cut their prey prior to transport. After capturing the prey between the jaws, many shark species shake their heads, effectively cutting the prey to pieces with their teeth (Motta et al. 1997; Wilga and Motta 1998; Motta and Wilga 2001). While this was not observed in *S. barracuda* during the course of this study, large adult *S. barracuda* have been observed to first grasp relatively larger prey between the jaws, bite it in two, and then swallow the pieces separately (personal observation).

Relative differences in feeding kinematics among species were variable, with *L. platyrhincus* being up to six times as fast as *Strongylura notata* (total gape duration). However, some variables can be attributed a greater biological significance than others. Variables most important in defining differences in feeding behavior were, for example, strike distance and duration, mean

velocity, lateral body curvature (only present during feeding in *L. platyrhincus*), time to mouth opening, and duration of maximum gape. There were large absolute differences in these variables resulting in the differences in feeding patterns among species. Perhaps less biologically significant among species were differences in duration of mouth closing and the variables associated with the hyoid during prey capture. Rapid closing of the jaws is common in ram feeders, and movements of the hyoid are less important during ram feeding. These kinematics are not as important in defining the differences in the feeding patterns among these species.

While suction-feeding aquatic vertebrates have been well studied, ram-feeding aquatic vertebrates seem to have been largely ignored, apart from the documentation of the locomotory aspects of their feeding. Perhaps it has been thought that there was very little deviation from a general behavioral pattern. These data show that there are in fact distinct feeding repertoires exhibited by different ram-feeding fishes. Although these three species all employ ram feeding for prey capture of elusive prey, each species has a unique repertoire that appears to minimize hydrodynamic constraints and prey response, utilize locomotory capabilities, and may be suited to each species' specific habitat.

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