



Effects of ram speed on prey capture kinematics of juvenile Indo-Pacific tarpon, *Megalops cyprinoides*

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ARTICLE INFO

Article history:

Received 16 April 2009

Received in revised form

13 July 2009

Accepted 15 August 2009

Keywords:

Megalops cyprinoides

Tarpon

Ram speed

Feeding kinematics

Ram-suction feeding

ABSTRACT

We examined the effects of variation in swimming speed, or 'ram speed', on the feeding kinematics of juvenile Indo-Pacific tarpon, *Megalops cyprinoides*. Tarpon were filmed feeding on non-elusive prey at 500 images s⁻¹. Prey items were offered at one end of the filming tank, the opposite end where tarpon grouped, to encourage them to use a ram strategy to capture their prey. We describe tarpon as ram-suction feeders. Ram speed varied among strikes from 0.19 to 1.38 m/s and each individual produced speeds that spanned at least 0.9 m/s across trials. Although suction distances were much less variable, prey movement towards the predator was present in all feeding trials. There was a strong positive relationship between initial predator – prey distance and ram speed ($r^2=0.72$, $P<0.001$). When tarpon initiated their strike from further away, they achieved higher ram speeds, but also took longer to capture their prey. All other timing variables were unaffected by ram speed whereas at higher ram speeds tarpon exhibited greater expansion of the mouth and buccal cavity. Greater buccal expansion accomplished in the same period of time implies that both the total volume of water captured and the water flow rate entering the mouth was greater in strikes at higher ram speeds. Our results demonstrate how feeding kinematics may vary as a function of ram speed, and how fish predators that lack jaw protrusion and have a large gape capacity can maximize their feeding success by altering their swimming speed.

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Introduction

Vertebrates use a wide array of tactics to overcome their prey, ranging from cryptic ambush strategies to chase. These broad categories can be broken down further as each species copes with its distinct environmental conditions and characteristics of its prey. In the aquatic environment the density and viscosity of water have affected the design and therefore prey capture strategies of predators (Liem, 1990; Lowry et al., 2005). Inertial suction feeding is the most common method of prey capture in teleost fishes and has now been well documented in diverse fish taxa (Lauder, 1980, 1981; Norton, 1991; Hernandez, 2000; Gibb and Ferry-Graham, 2005; Van Wassenbergh et al., 2005). To generate suction, a fish rapidly expands its buccal cavity, generating a flow of water in front of its mouth (Lauder, 1982, 1985). Suction feeding is often coupled with some component of forward movement of the body and/or jaws, frequently termed 'ram' (Alexander, 1969; Nyberg, 1971; Norton, 1991; Norton and Brainerd, 1993).

Predators exhibit differences in the way they employ ram during prey capture. Many piscivorous fishes rely heavily on a high-velocity lunge at the start of the strike or maintain high swimming speeds to chase down their prey (centrarchids: Nyberg, 1971; Higham et al., 2005, 2006b; lepisosteids, belonids, and sphyraenids: Porter and Motta, 2004; sphyraenids: Walters, 1966; Grubich et al., 2008; cichlids: Wainwright et al., 2001; esocids: Rand and Lauder, 1981; Harper and Blake, 1991). Ram feeding has not only been viewed as a means by which the predator can shorten the distance between itself and a prey item, but several studies have pointed out the influence of ram on feeding kinematics and behavior in sharks (Tricas and McCosker, 1984; Wilga and Motta, 2001; Motta et al., 2002; Matott et al., 2005) as well as bony fishes (Rand and Lauder, 1981; Harper and Blake, 1991; Sanderson et al., 1994; Wainwright et al., 2001; Porter and Motta, 2004; Higham et al., 2005, 2006a,b; Lowry et al., 2005; Holzman et al., 2008a,b). Therefore, ram speed is one of many variables that a predator may vary to enhance prey capture success.

Variation in ram speed likely depends on a multitude of factors that are assessed before a predator strikes at its prey, such as the initial distance of the prey item from the predator, the motivation of the predator to capture the prey item, the degree of challenge the prey item presents, and the presence of competitors.

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Changes in ram speed may also coincide with changes in the magnitudes and timing of peak kinematic events, thereby affecting prey capture success of the predator. The goal of this manuscript is to examine the effects of ram speed on the magnitudes and timing of cranial kinematics during prey capture in juvenile Indo-Pacific tarpon, *Megalops cyprinoides* (Brousset).

Indo-Pacific tarpon are predatory fish that feed mainly on other fish and crustaceans. Adults can grow up to 1.5 m in length (Coates, 1987). Tarpon were chosen for this study because they are able to generate a wide range of observable speeds under controlled laboratory conditions and they lack jaw protrusion so the only contribution to ram feeding during the strike is the movement due to swimming. Tarpon capture their prey by forward movement of the body (Guigand and Turingan, 2002) which is combined with suction (Grubich, 2001; Westneat, 2006). Therefore, in addition to measuring the effects of ram speed on prey capture kinematics, we assess the effects of ram speed on suction distance and discuss how ram speed may influence the predator's ability to simultaneously use suction to draw prey into the mouth.

Materials and methods

Three juvenile Indo-Pacific tarpon, *Megalops cyprinoides*, standard lengths 13.5, 13.8, and 14.2 cm, were obtained from a commercial dealer. The three tarpon were housed together in a single 100 l aquarium at 30 °C and were fed thawed pieces of frozen krill (*Euphasia* sp.) and pieces of shrimp (*Palaeomonetes* sp.) approximately three times a week. Tank salinity was maintained at 28–32 ppt. Once acclimated, the fish were trained to feed in front of two 600 W lights. We encouraged them to vary their swimming speed when approaching food by dropping prey into the water column at varying distances from one end of the aquarium where they commonly grouped. Video sequences of prey capture were recorded at 500 images s⁻¹ with a NAC Memrecam Ci camera (NAC Image Technology, Simi Valley, CA, USA). Distances in the images were scaled by recording an image of a ruler placed in the field of view.

All maintenance and experimental procedures used in this study were approved by the University of California, Davis Animal Care and Use Committee (Protocol # 12790).

At the conclusion of the experiments, tarpon were euthanized with MS-222 and the suction index (SI) for each individual fish was measured. SI is a metric of the potential to produce negative

pressure in the buccal cavity and is proportional to the maximum suction capacity (Carroll et al., 2004). We measured the following morphological variables: cross-sectional area of the epaxialis muscles (CSA_{Epax}), the epaxialis muscle moment arm (L_{in}) which is used to rotate the neurocranium (measured from the center of the epaxialis to the supracleithrum/posttemporal bone joint), the moment arm of the buccal cavity (L_{out}) (measured from the supracleithrum/posttemporal bone joint to the center of the buccal cavity), buccal length (measured from the anteriormost tip of the dentary to the anteriormost tip of the lower pharyngeal tooth plate), and gape width. SI was calculated by taking the product of CSA_{Epax} and the mechanical advantage of the epaxialis muscles, which is the ratio of L_{in} to L_{out} , and dividing it by the product of buccal length and gape width:

$$SI = CSA_{\text{Epax}}(L_{\text{in}}/L_{\text{out}})/\text{gape width} \cdot \text{buccal length}.$$

To quantify the effects of ram speed on feeding kinematics, we first digitized the x, y coordinates of 8 landmarks on the fish in several video frames: (i) anterior tip of the premaxilla

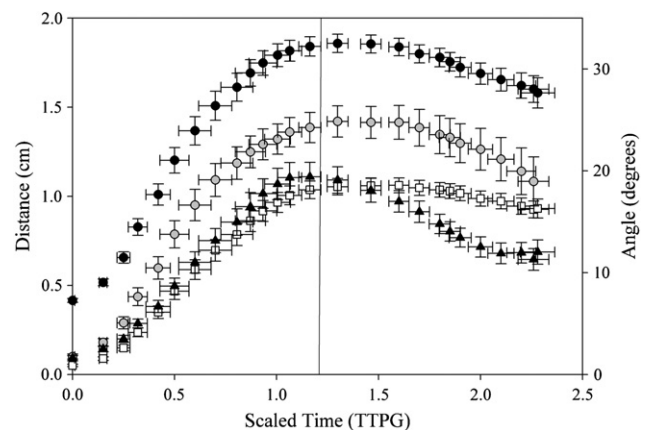


Fig. 2. Kinematic profile of cranial movements observed during prey capture in the Indo-Pacific tarpon. Data points represent averages of three individuals. Time is scaled to time to peak gape (TTPG) to account for the variation in time of prey capture. Scaled time $T_{(0)}$ represents the point when 20% of peak gape is reached at the beginning of every trial. Vertical error bars represent the SE of each measured variable while horizontal error bars represent the SE of the scaled time. The single black vertical line represents the average time to prey capture from all trials. The following symbols correspond to the different kinematic events: (●) gape, (●) lower jaw rotation, (▲) cranial elevation, (□) hyoid depression.

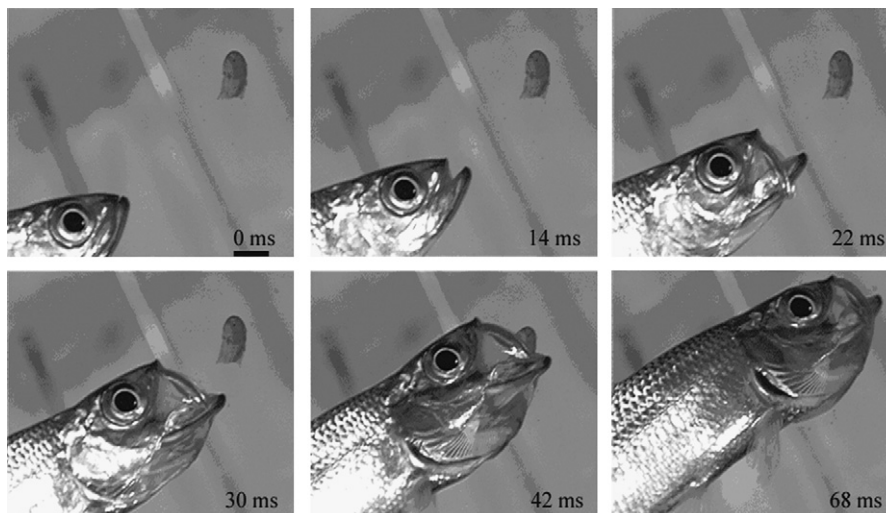


Fig. 1. Kinematic sequence of prey capture behavior for the Indo-Pacific tarpon, *Megalops cyprinoides*. Scale bar=1 cm.

(upper jaw), (ii) quadrate–articular joint, (iii) anterior tip of the dentary (lower jaw), (iv) landmark on the fish dorsum, (v) neurocranium–vertebral joint, (vi) center of the orbit (reference point on the neurocranium), (vii) ventralmost extension of the floor of the mouth (perpendicular distance between a line at the center point of the orbit), and (viii) center of the prey.

These landmarks were measured at seven points in time: (i) time of strike initiation, defined as the time from when the mouth opened starting at 20% of peak gape, (ii) time of peak lower jaw rotation, (iii) time of peak cranial elevation, (iv) peak gape, (v) time of peak hyoid displacement, (vi) time the prey began to move towards the predator's mouth, and (vii) time of prey capture, defined as the frame in which the prey completely disappeared into the predator's mouth. Time to peak gape (TPPG) was measured as the time required for gape to increase from 20% to 95% of peak gape and was measured this way in order to eliminate the high variability of mouth opening

and the difficulty in identifying exactly when peak gape is reached in an asymptotic relationship (Sanford and Wainwright, 2002; Day et al., 2005; Higham et al., 2005). The time when the mouth opened to 20% of peak gape was used as the reference time, or time zero, and we calculated “time to” variables in ms for each of the events listed above.

The coordinates of these points were used to calculate the following kinematic variables: (i) peak gape distance (mm), (ii) maximal angular rotation of the lower jaw and head (degrees), (iii) peak hyoid depression (mm), and (iv) strike initiation distance (mm). Strike initiation distance was defined as the distance from the prey to the midpoint of the line made between the tips of the upper and lower jaw (the line used to measure gape) when gape reached 20% of maximum. Lastly, we measured suction distance, the distance the prey moved towards the plane of the open mouth during the strike (Norton and Brainerd, 1993; Wainwright et al., 2001;

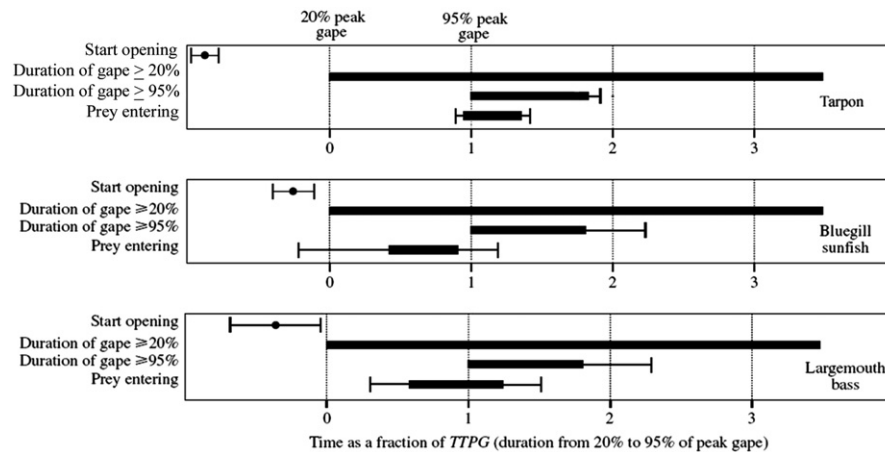


Fig. 3. Relative timing of kinematic events (mouth opening and prey entering the mouth) for tarpon, *Megalops cyprinoides*, in comparison to bluegill, *Lepomis macrochirus*, and largemouth bass, *Micropterus salmoides* (taken from Higham et al., 2006a). To account for variation in time of prey capture, all times are normalized to time to peak gape. 20% and 95% of peak gape are located at 0 and 1, respectively. All symbols and error bars represent the mean $\pm$ SE for all feeding trials analyzed. Events that have some duration are shown with filled bars. Note that tarpon begin opening their mouth much earlier than bluegill and bass and capture their prey later.

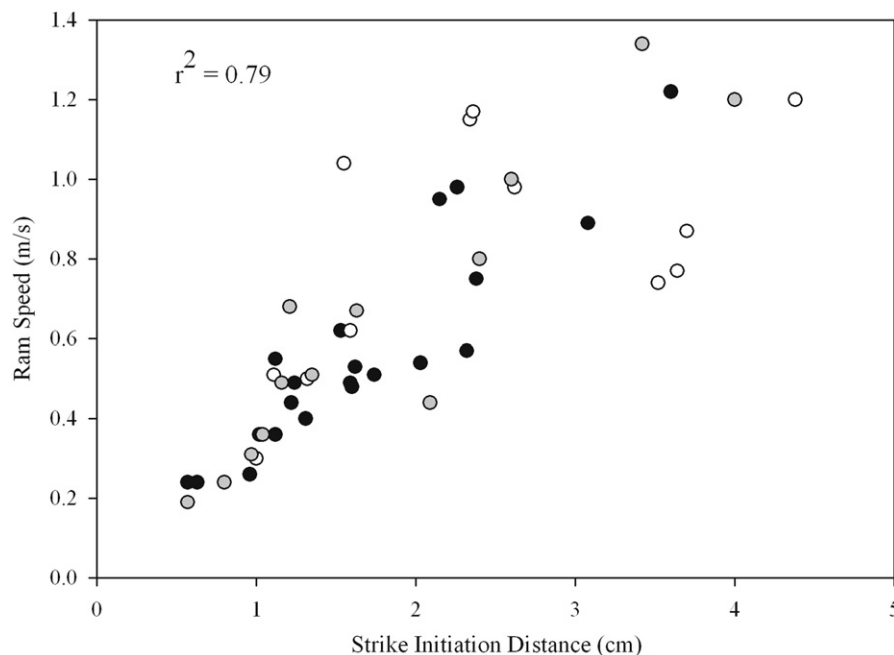


Fig. 4. The relationship between strike initiation distance and ram speed (m/s). Strike initiation distance is measured as the distance from the fish's mouth to the prey at the beginning of the strike (when 20% PG is reached). Each data point represents a feeding trial and individuals are shown in different gray scales. Note how individuals exhibit variation in their range of ram speed and how more variable strike initiation distances are observed at higher ram speeds.

Svanback et al., 2002). Ram speed was calculated as the change in prey distance over time from the beginning of the strike until just before the prey disappeared into the tarpon's mouth.

The relative use of ram and suction can be viewed as a spectrum ranging from purely ram to purely suction feeding with most fishes occupying a position somewhere in between. We used the ram-suction-index (RSI) to quantify the contribution of each to prey capture (Norton and Brainerd, 1993). The RSI attempts to quantify this continuum by using the distance the predator swims during the strike (D_{predator}) and the distance the prey moves towards the predator during the strike (D_{prey}):

$$\text{RSI} = (D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}}).$$

We only analyzed sequences where a lateral view of the fish could be clearly observed throughout the video. Video sequences were analyzed using DLTdataviewer2 (<http://www.unc.edu/~7Ethedrick/software1.html>), a free toolbox for automated kinematic analysis in Matlab.

All data were $\log_{10}$ transformed and inspected to assure normalization of variances. A generalized linear mixed model (GLMM) was used to examine the effect of ram speed on kinematic variables of interest while accounting for individual variation. A sequential Bonferroni correction was used to account for multiple comparisons. We also used a principal components analysis to analyze the relationship between kinematic variation and ram speed. SPSS (Version 13.0, SPSS Inc., Chicago, IL, USA) was used to conduct all statistical analyses.

Results

A total of 42 prey capture sequences were analyzed with sample sizes ranging from 12 to 21 for each individual. Tarpon approached their prey at variable swimming speeds and initiated their strike as far away as 4.7 cm from the prey (Fig. 1). On average, strikes were initiated 1.9 ± 0.15 cm from the prey and

Table 1

The effect of ram speed, individual and their interaction on feeding kinematic variables measured for the Indo-Pacific tarpon, *Megalops cyprinoides*.

Dependent variables	Mean $\pm$ S.E.	F-Ratio ^a		
		Ram speed	Individual	Individual/ram speed interaction
Initial predator – prey distance (cm)	2.15 $\pm$ 0.15	89.46**	0.78	0.46
Strike initiation distance (cm)	1.9 $\pm$ 0.15	108.23**	0.15	0.19
TTP gape (ms)	21.72 $\pm$ 1.10	0.196	0.65	0.46
TTP cranial elevation (ms)	27.30 $\pm$ 1.03	0.91	0.904	0.19
TTP jaw rotation (ms)	27.54 $\pm$ 0.99	0.93	0.83	0.52
TTP hyoid displacement (ms)	30.74 $\pm$ 1.25	0.05	0.46	0.31
Time to prey capture (ms)	28.67 $\pm$ 1.69	9.69**	1.13	0.01**
Peak Cranial Elevation	21.71 $\pm$ 0.95	34.42**	0.63	3.79*
Peak jaw rotation	28.24 $\pm$ 1.49	44.48**	1.68	0.07**
Peak hyoid displacement	1.14 $\pm$ 0.04	42.72**	2.29	5.89**
Peak gape distance (cm)	1.98 $\pm$ 0.04	42.63**	3.08	5.93**
Suction distance (cm)	0.27 $\pm$ 0.12	0.04	0.77	3.04

TTP=time to peak.

^a Represents Bonferroni corrected level of significance at * $P=0.05$, ** $P=0.001$.

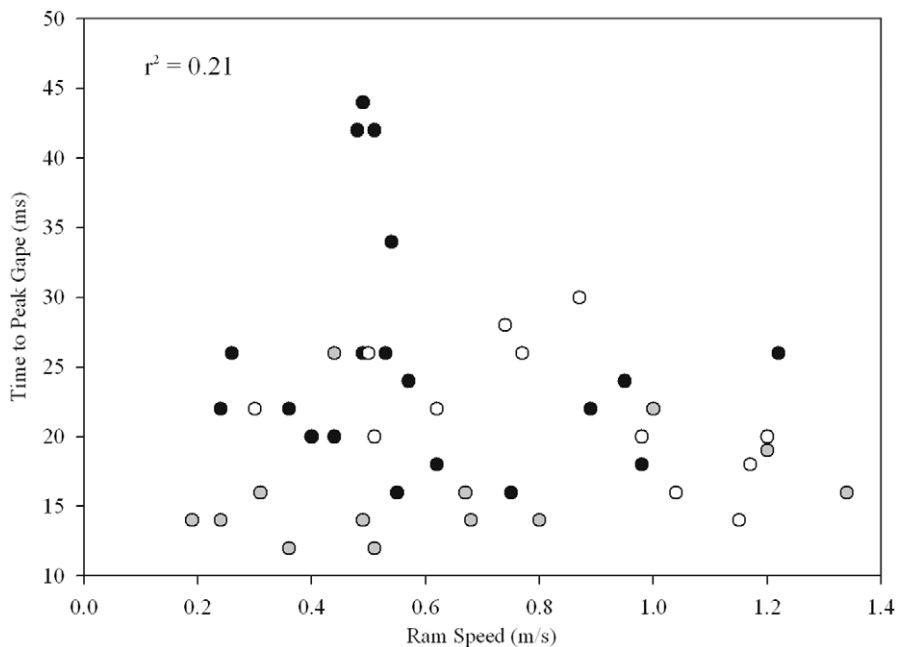


Fig. 5. Time to peak gape (TTPG) as a function of ram speed. Each data point represents a feeding trial and individuals are shown in different gray scales. Note the large amount of variability in TTPG at nearly all ram speeds.

prey were captured in 25.35 ± 1.47 ms. The kinematic sequence started with peak lower jaw rotation, closely followed by peak cranial elevation and peak hyoid displacement (Fig. 2). Hyoid displacement, however, maintained peak values longer than the other kinematic variables. Juvenile tarpon begin opening their mouths early on in the gape cycle (Fig. 3). Despite a tendency of early mouth opening, prey entered the mouth at 95% of peak gape.

Ram speed varied across trials ranging from 0.19 to 1.38 m/s with an average speed of 0.65 m/s. Each fish varied ram speed producing speeds that spanned at least 0.9 m/s across trials. Overall, the farther away tarpon initiated their strike, the faster they swam towards the prey (Fig. 4). Ram speed was strongly and positively correlated with initial predator – prey distance ($r^2=0.72$, $F_{1,45}=89.46$, $P<0.001$) and strike initiation distance ($r^2=0.79$, $F_{1,45}=108.27$, $P<0.001$). Initial predator – prey distance and strike initiation distance did not differ

among individuals ($P=0.46$, $P=0.86$; Table 1). Ram speed had variable effects on skull kinematics of the strike (Table 1). Most timing variables, notably time to peak gape, were unaffected by changes in ram speed ($r^2=0.21$, $F_{2,45}=0.19$; $P=0.66$; Fig. 5). The only timing variable that was significantly affected by ram speed was prey capture time ($r^2=0.32$, $F_{2,45}=9.69$; $P=0.003$; Fig. 6A). When tarpon initiated their strike from further away, they achieved higher ram speeds and they took significantly longer to capture their prey ($r^2=0.53$, $F_{2,45}=12.32$; $P<0.001$; Fig. 6B).

Ram speed affected the magnitude of all cranial variables (Table 1). Although the magnitude of cranial elevation, hyoid depression, jaw rotation, and gape were greater at faster ram speeds, ram speed explained more of the variation in peak hyoid displacement and peak jaw rotation than in peak gape distance and peak cranial elevation (Fig. 7).

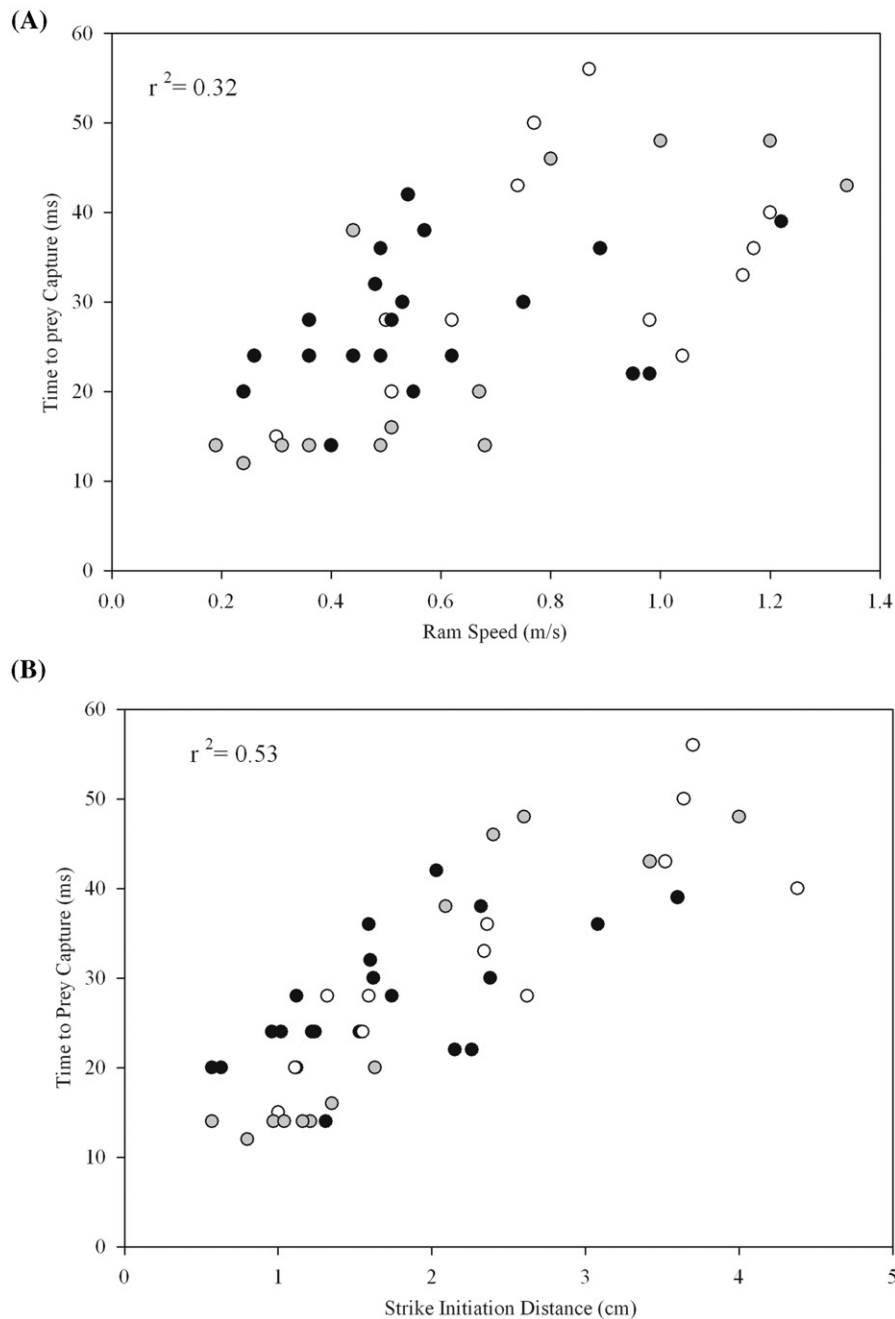


Fig. 6. Time to prey capture (TPPC) as a function of (A) ram speed and (B) strike initiation distance. TPPC is defined as the time from the start of the strike to when the prey crosses the center of the fish's mouth. Each data point represents a feeding trial and individuals are shown in different gray scales.

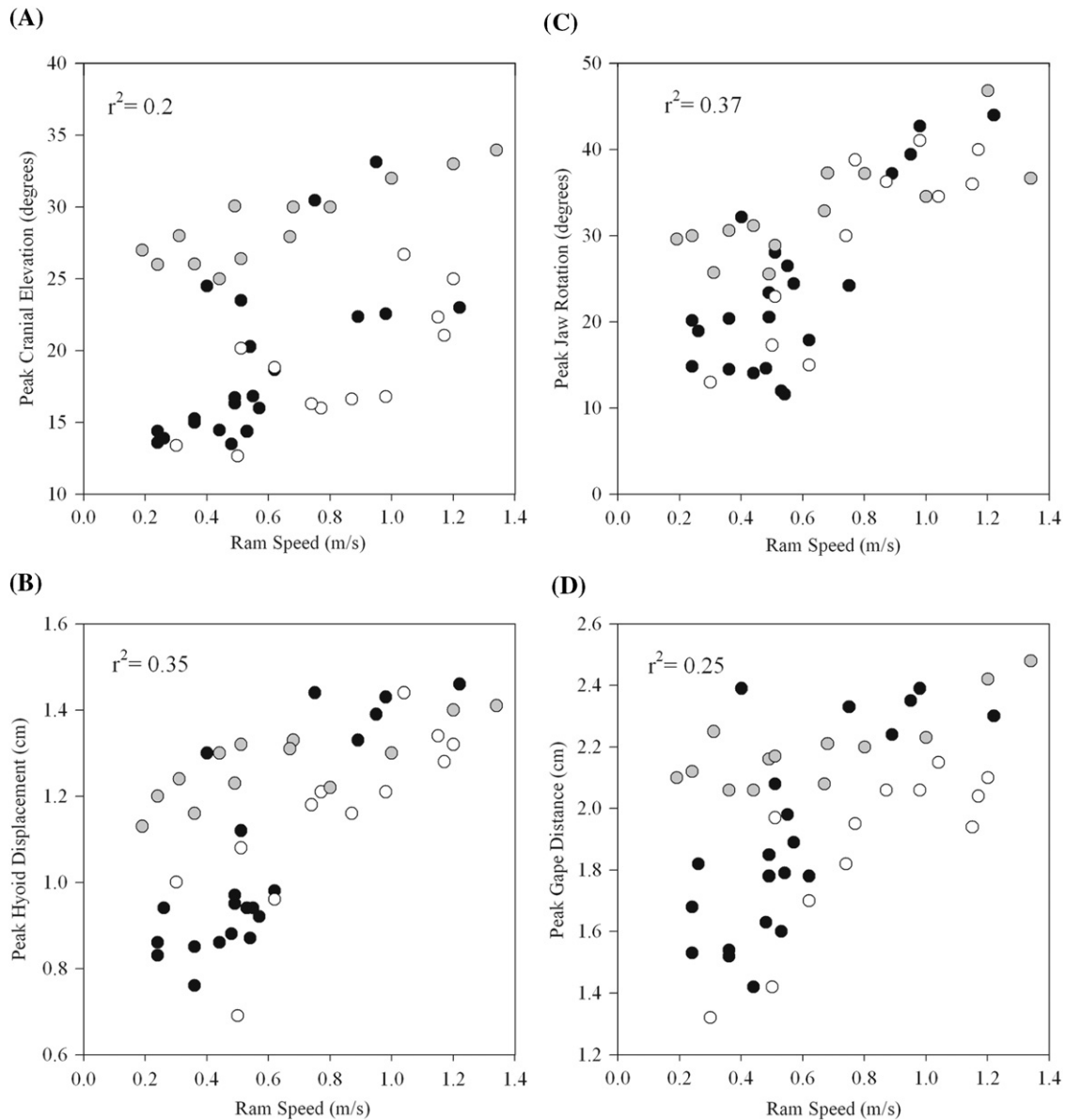


Fig. 7. Plots depicting the relationship between ram speed and the following kinematic events: (A) peak cranial elevation; (B) peak hyoid displacement; (C) peak jaw rotation and (D) peak gape distance. Individuals are shown in different gray scales.

RSI values for tarpon were positive, indicating that tarpon rely more on ram than suction to capture their prey. Although the majority of RSI values fell close to 1, movement of the prey towards the predator could always be quantified. An RSI value of 1 represents a pure ram strike in which the prey item enters the buccal cavity by movement of the predator only (Norton and Brainerd, 1993). Our high RSI values support the SI values recorded for tarpon which ranged from 0.02 to 0.03. Low SI values such as these suggest that tarpon are unable to generate strong suction pressures in their buccal cavity and may rely on fast swimming to overtake their prey. When we examined the contribution of ram and suction distances separately, we observed greater variation in ram distances compared to suction distances. Ram distances ranged from 0.57 to 4.38 cm while all suction distances measured less than 0.5 cm (Fig. 8). Suction distance was unaffected by increases in ram speed ($r^2=0.24$, $F_{2,45}=0.04$; $P=0.85$).

A principal components analysis, in which we included nine kinematic variables and suction distance, resulted in three axes

explaining 85.4% of the kinematic variation in the tarpon strike. Principal components 1 and 2 explained the majority of this variation (74.6%; Table 2). Principal component 2 (PC2) was the only axis that revealed a strong positive relationship with ram speed ($r^2=0.46$, $F_{2,45}=40.27$, $P<0.001$; Fig. 9). The kinematic variables that loaded heavily on PC2 were prey capture time, peak gape, peak hyoid displacement, and peak jaw rotation.

Discussion

The main purpose of our study was to determine the effects of ram speed on the prey capture kinematics of juvenile Indo-Pacific tarpon. Here, we briefly discuss prey capture terminology in fishes in order to categorize tarpon feeding behavior. We define ram as the forward movement of the body and/or jaws towards the prey item (Alexander, 1969; Nyberg, 1971; Norton, 1991; Norton and Brainerd, 1993). Ram, which is often paired with suction or biting during prey capture, is considered a prey capture strategy in and

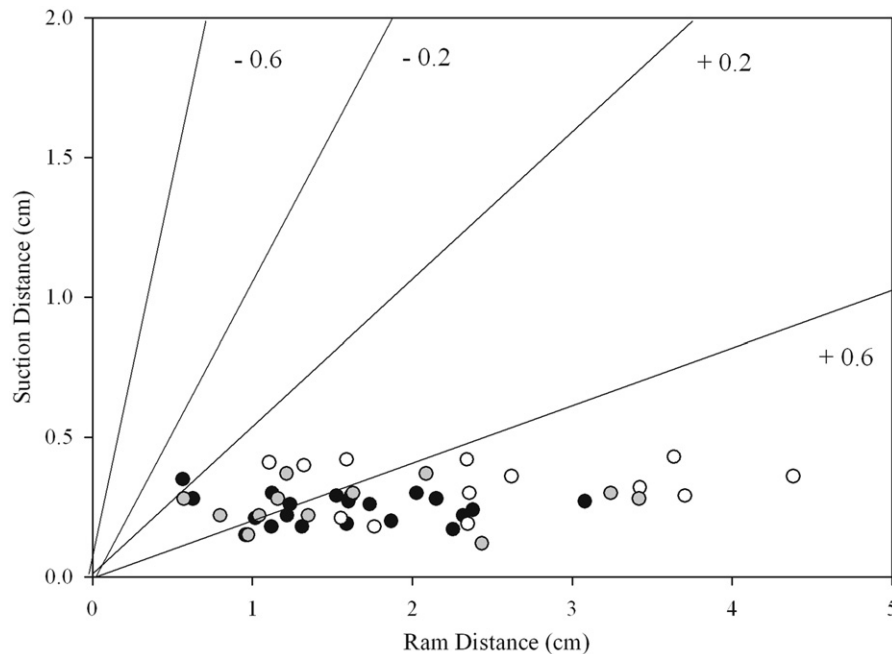


Fig. 8. Relationship between ram distance and suction distance. Isoclines represent possible values of the ram-suction index (RSI). Higher values of RSI indicate larger values of ram distance relative to suction distance. Note the large amount of variability in ram distances compared to suction distances. Individuals are shown in different gray scales.

Table 2

Loadings of nine kinematic variables and suction distance on the first three principal components axes which comprise 85.4% of the kinematic variation of the tarpon strike.

TTP prey	Principal components		
	PC1 (52.53%)	PC2 (22.14%)	PC3 (10.69%)
Peak gape	−0.78	0.53	−0.18
TTP gape	0.86	0.36	−0.17
Peak hyoid	−0.81	0.51	0.01
TTP hyoid	0.83	0.43	0.03
Peak cranial	−0.82	0.33	−0.21
TTP cranial	0.84	0.20	−0.25
Peak jaw	−0.67	0.63	0.01
TTP jaw	0.71	0.47	0.10
Suction	−0.04	0.21	0.94

TTP=time to peak.

of itself. Previous prey capture studies on ram-feeding predators have defined ram feeders as those predators that exhibit significant movement towards the prey whereas the prey movement towards the predator is minimal (Porter and Motta, 2004). In this study we use the usual definition of ram feeding: a feeding event in which the predator overtakes and engulfs its prey by rapid acceleration of the whole body (Rand and Lauder, 1981; Wilga et al., 2007). In other words, a pure ram strike is one in which the predator moves and the prey does not (*sensu stricto* Norton and Brainerd, 1993). On the other hand, ram-suction feeding is when there is forward movement of the predator towards the prey as well as movement of the prey towards the predator (Wilga et al., 2007). A ram-biting prey capture strategy is one where the predator uses a high-velocity lunge or rapid acceleration to overtake the prey and the strike ends in a powerful bite (Grubich et al., 2008) or high-velocity jaw closure on the prey. Our analyses of prey capture behavior indicate that juvenile Indo-Pacific tarpon are ram-suction feeders. Although tarpon mostly relied on forward movement of the body to approach the prey, buccal expansion resulted in prey drawn into the mouth.

Individual juvenile tarpon exhibited as much as a sevenfold difference in ram speed across feeding trials. Although we would anticipate adult tarpon to be much faster, juvenile speeds were comparable to those of other predators that utilize ram during prey capture such as cichlids (Wainwright et al., 2001), and redbfin needlefish and gar (Porter and Motta, 2004). On average, juvenile tarpon velocity in mid-water strikes was 6 body lengths per second which was faster than that reported for largemouth bass (Nyberg, 1971) and silver arawanas attacking in the water (Lowry et al., 2005). The fastest ram speeds analyzed in this data set were around 140 cm/s, which were almost as fast as those reported for juvenile barracuda (Porter and Motta, 2004) but much slower than the maximum velocities reported for chain pickerel (Rand and Lauder, 1981) and northern pike (Harper and Blake, 1991).

Ram speed did affect the feeding kinematics of Indo-Pacific tarpon, but in unexpected ways. When tarpon initiated their strike from further away, they achieved higher ram speeds but longer overall strike times revealing that juvenile tarpon were unable to fully compensate for the increase in distance by swimming faster. The magnitudes for excursion of the lower jaw, cranial elevation, hyoid displacement, and gape distance all increased with ram speed, suggesting that tarpon engulfed a larger volume of water into their buccal cavity at greater swimming speeds. Although the magnitude of mouth and buccal expansion increased with greater approach speed, the time required to reach peak skull movements, such as time to peak gape, was not affected by ram speed. Nyberg (1971) also found that time to peak gape in largemouth bass was not affected by their swimming velocity.

Gape distance, hyoid displacement, cranial elevation, and lower jaw rotation were all observed increasing nearly simultaneously and reached their peak values within a few milliseconds of each other. This pattern is similar to other fishes that use varying degrees of suction during prey capture (Lauder, 1981, 1985; Westneat, 1990, 1994; Gillis and Lauder, 1995; Gibb and Ferry-Graham, 2005). The tendency of tarpon to maintain peak hyoid depression beyond the retraction phase of other structures

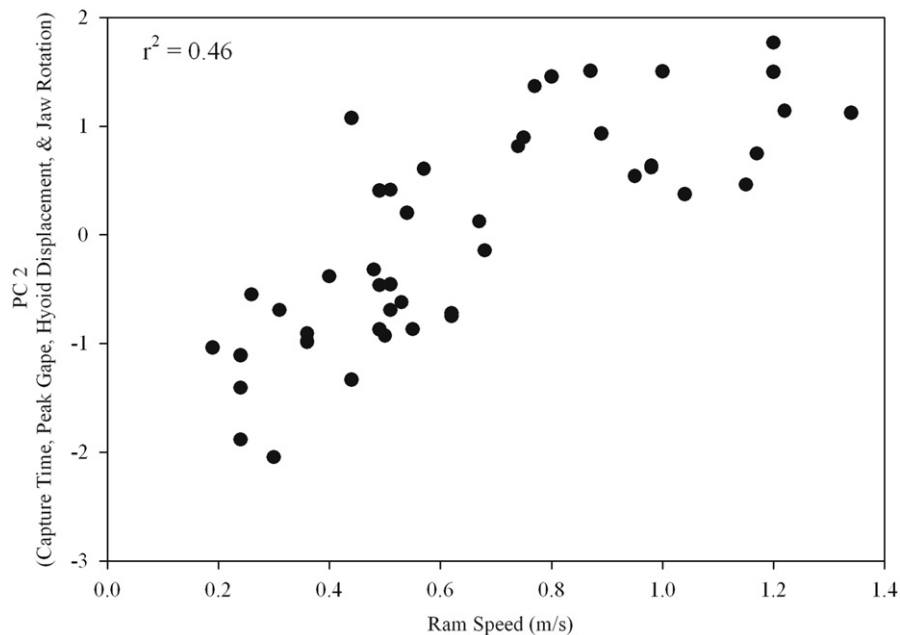


Fig. 9. The relationship between ram speed and principal component 2 (PC2). The variables that loaded strongly on PC2 were prey capture time, peak gape, hyoid displacement, and jaw rotation.

has also been observed in other suction feeders (Lauder and Liem, 1981; Cook, 1996), predators that mostly rely on ram (Porter and Motta, 2004), but most notably in primitive suction feeders such as *Amia calva* and *Polypterus senegalus* (Lauder, 1980). As tarpon are members of the Elopomorpha, a relatively basal group of ray-finned fishes (Lauder and Liem, 1983), their cranial morphology shares similarities with *A. calva*, rather than with derived suction feeders. Similar to *Amia*, tarpon lack premaxillary protrusion. Tarpon are able to form a relatively rounded gape by swinging their maxilla forward during mandibular depression. This maxillary movement brings the buccal chamber forward towards the prey, thereby increasing flow velocity (Lauder, 1979) and minimizing sideways flow of water (Nyberg, 1971).

Although juvenile Indo-Pacific tarpon approached prey from head-on rather than underneath like the Atlantic tarpon (Guigand and Turingan, 2002), the cranial kinematics for both *Megalops* species followed a similar series of kinematic events during the expansive phase of mouth opening. Guigand and Turingan (2002) noted that the overall kinematic profile for juvenile Atlantic tarpon did not follow a symmetrical bell-shaped curve suggesting that buccal expansion occurred at a faster rate than mouth closing. In this study, we were unable to digitize frames for the latter half of the compressive phase because tarpon either swam out of the field of view or turned away from the camera so the complete mouth-closing cycle could not be observed. However, we digitized enough frames during the beginning of the compressive phase to determine that buccal expansion in juvenile *M. cyprinoides* also occurred at a faster rate compared to mouth-closing as observed in *M. atlanticus* (Fig. 2). As noted in Guigand and Turingan (2002), the actual shape of the kinematic curve may provide additional insight into feeding strategies and may help us identify different prey capture methods. Although many studies have shown that kinematic displacement profiles typically follow a symmetrical bell shape curve (Gibb, 1995; Richard and Wainwright, 1995; Westneat and Wainwright, 1989; Gibb and Ferry-Graham, 2005), during inertial suction feeding or ram-suction feeding the rate of buccal expansion is presumably more important than the rate of buccal compression. In a ram-biter, however, we might expect the rate of mouth closing to be faster

and more important than the rate of mouth opening (Lauder and Norton, 1980; Porter and Motta, 2004; Grubich et al., 2008). In a pure ram feeder, peak values may be maintained longer at the end of the expansive phase and similar to some inertial suction feeders and ram-suction feeders, we might expect the compressive phase to be slower than the expansive phase (Fig. 10). Predators that utilize a pure ram strategy or a combination of ram and suction may have a longer compressive phase due to continual forward movement of the body with the mouth open to initiate prey transport (Guigand and Turingan, 2002; Porter and Motta, 2004).

The relative timing of kinematic events such as the start of mouth opening and the duration of the gape cycle were similar to published values for bluegill and largemouth bass, two centrarchid species whose feeding kinematics have been well studied (Higham et al., 2006a; Fig. 3). Despite a tendency of early mouth opening, prey entered the mouth at about 95% of peak gape, as observed in bluegill and bass (Higham et al., 2006a). Tarpon often reached 95% of peak gape well before nearing the prey, especially at higher ram speeds. In bluegill sunfish and largemouth bass 95% of peak gape is the moment when maximal suction forces are exerted on the prey (Holzman et al., 2007, 2008a, b). Strikes where peak gapes were achieved well before reaching the prey still resulted in the prey being sucked into the mouth, indicating that suction flows persisted well after peak gape. Grubich (2001) noted the strong activity of muscles that laterally expanded the operculum during the tarpon's strike and postulated the importance and influence of lateral expansion during suction feeding. Although we did not measure opercular abduction in this study, prey capture sequences reveal that the opercles are open throughout the gape cycle and remain open as the mouth begins to close. In seventeen sequences, where the timing of peak opercular abduction could be estimated, we found that peak opercular abduction followed peak gape and that prey capture time usually preceded peak opercular abduction. These findings are similar to those reported for largemouth bass (Nyberg, 1971). Contrary to our results, Grubich (2001) found that peak opercular abduction coincided with peak gape in *Megalops atlanticus*.

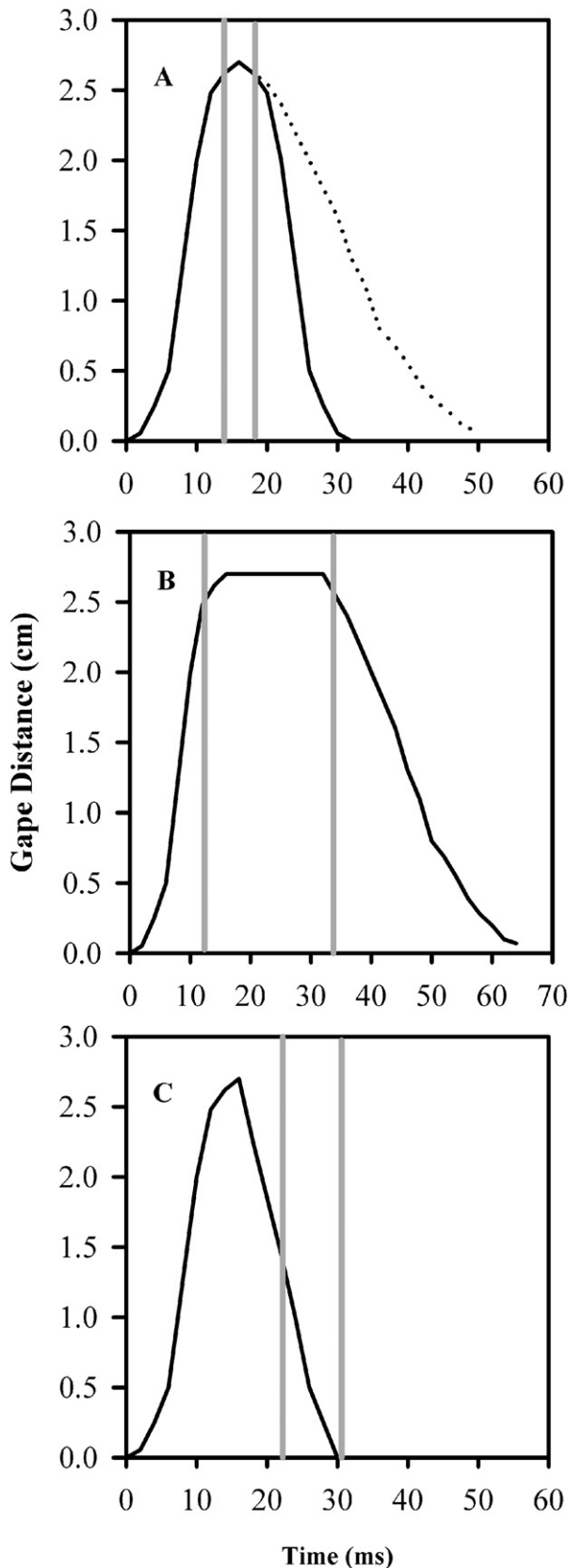


Fig. 10. Graphs depicting hypothetical kinematic displacement profiles for gape distance for three prey capture strategies: (A) inertial suction feeding; (B) ram-suction feeding or ram feeding and (C) ram-biting. Gray lines indicate where the start and end of prey capture are expected to take place. The dotted line in (A) represents a predator that has slower mouth closing than mouth opening.

The hydrodynamic relationship between the buccal and opercular cavity during the strike is also important to our understanding of prey capture strategies. Isolation of the two chambers by the gill bars has been found in one suction feeder but not in a species that mostly relies on ram (Lauder, 1983). Forward movement of the body is important when the buccal and opercular chambers are hydrodynamically connected to prevent backflow of water into the opercular cavity. Future studies on the muscles responsible for laterally expanding the buccal cavity in Indo-Pacific tarpon are necessary in order to understand the relationship between the buccal and opercular chambers as well as the evolution of cranial kinematics in ram-suction feeding elopomorphs.

It is well known that suction feeding is enhanced in fishes with small mouths, large mouth opening muscles, and protrusible jaws (Liem, 1980; Lauder, 1985; Carroll et al., 2004; Higham et al., 2005, 2006a,b; Westneat, 2006). Predators with a large mouth such as the Atlantic tarpon, *M. atlanticus*, or largemouth bass, *Micropterus salmoides*, combine suction with ram due to the trade-off that exists between gape size, flow volume, and flow speed (Carroll et al., 2004; Higham et al., 2005, 2006a,b; Westneat, 2006). We found that tarpon SI values ranged from 0.02 to 0.03. These values are lower than in any species of Centrarchidae, including *Micropterus* species (Collar and Wainwright, 2006), to which tarpon are most often compared, suggesting that tarpon generate weak suction pressures. The lack of an effect of ram speed on the timing of buccal expansion kinematics indicates that the approach speed did not influence suction strategies of tarpon beyond the probable increase in flow speed in the fish's frame of reference with higher ram speed. Increases in ram speed also result in a more narrow volume of water taken in at higher fluid speeds than by suction alone (Higham et al., 2005). This enables the predator to close more quickly on the prey while still using suction, facilitating capture of elusive prey (Wainwright et al., 2001; Svanback et al., 2002; Ferry-Graham et al., 2001; Carroll et al., 2004; Day et al., 2005; Higham et al., 2006a,b; Wainwright and Day, 2007). Since flow velocity decreases precipitously with increasing distance from the mouth, suction is only effective within approximately one mouth width in front of the mouth (Muller et al., 1982; Day et al., 2005). In the case of the juvenile tarpon used in this study, this translates into 14 mm from the mouth. We observed average prey movement to be 12 mm from the tarpon's fully opened mouth.

RSI values for tarpon were always positive, indicating large ram distances compared to suction distances (Fig. 8). RSI values were influenced more by the greater variation in ram distances observed than by the suction distances, which were smaller and relatively constant. These results are similar to those of a previous study that examined RSI in seven species of cichlid fishes (Wainwright et al., 2001). Despite the diversity of fishes examined in that study, suction distance varied little. The lack of variation in suction distance is explained by the fact that fluid speeds around the mouth decrease rapidly with increasing distance from the mouth (Day et al., 2005). Therefore, suction distance can be expected to be much more limited than ram distance. Wainwright et al. (2001) stressed that the primary role of ram is to position the mouth aperture close enough to the prey to permit successful use of suction. On the other hand, Wilga et al. (2007) mention how drawing prey in a short distance enables elasmobranchs to not have to get as close to the prey as a ram-biting shark which must chase down its prey and get close enough to grab the prey in its jaws. We agree with these ideas and feel that tarpon species are good examples of predators that utilize ram to maximize their suction feeding capacity. By varying their ram speed and increasing their gape magnitude, tarpon can manipulate a larger volume of water in front of their mouths and increase fluid speed in the fish's frame of reference.

Acknowledgements

We wish to thank Tom Waltzek for helping us obtain healthy tarpon specimens. We are grateful to Sandy Kawano for providing assistance with fish maintenance and filming. We also thank Chris Martin for offering valuable comments on earlier versions of this manuscript. Lastly, we thank two anonymous reviewers for their suggestions that greatly improved our manuscript. This work was supported by NSF grants IOB-0444554 and IOS-0819009.

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