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Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits

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Abstract

Several species of butterflyfishes (Chaetodontidae) possess extremely elongate jaws, and feed mostly by probing the benthos and biting off pieces of attached invertebrates. In contrast, *Forcipiger longirostris*, the longest-jawed chaetodontid, exhibits a novel pattern of prey use, feeding almost exclusively on small caridean shrimp, a mobile and highly elusive prey type that lives within the structure of coral reefs. We explored the functional basis of this novel pattern of prey use by comparing prey capture kinematics in this and four other butterflyfish species, including two other species that possess elongate jaws. High speed video recordings of feeding events on live adult brine shrimp were analyzed from individuals of five species: *Forcipiger longirostris*, *F. flavissimus*, *Chelmon rostratus*, *Heniochus acuminatus*, and *Chaetodon xanthurus*. We focused on a comparison among species of the relative contribution of ''suction'', measured as the amount of movement of the prey toward the predator's mouth, and ''ram'', measured as the distance moved by the predator toward the prey during the strike. All five species utilized a combination of suction and ram while feeding on brine shrimp. The contribution of suction did not differ significantly among species. However, *F. longirostris* exhibited a ram contribution to the strike that was more than twice that seen in any of the other species, permitting this species to initiate strikes from the greatest initial predator-prey distance. *F. longirostris* is known to possess a major structural novelty in the feeding mechanism that permits anterior movement of the entire jaw apparatus. The ability of this species to feed successfully on elusive prey appears to be related to exceptional jaw protrusion, resulting in greater use of ram during prey capture. This ability to protrude long, slender jaws toward the prey may allow it to move the jaws without detection within close enough proximity of the prey to then permit the effective use of suction. The use of extensive ram in this manner by small-mouthed fishes may be more widespread than previously thought. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Jaw protrusion; Specialist; Functional morphology; Prey capture; Suction feeding; Ram feeding

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1. Introduction

The spectacular diversity of fish feeding mechanisms presents a rich challenge for biologists interested in understanding the consequences of variation in form and function for patterns of prey use. The task of interpreting this diversity is made easier by the recognition that there are only three major mechanisms of prey capture that are used by fishes (Liem, 1980): (1) ‘‘suction feeding’’ in which they expand the oral cavity, thus generating a pressure gradient that draws water and prey into the mouth; (2) ‘‘ram feeding’’ in which the prey remains stationary and the predator overtakes and engulfs the prey in the oral cavity; and (3) ‘‘manipulation’’ in which the fish directly applies its jaws to the prey, removing it from the substratum with a scraping or biting action. As far as is known, all teleost fish prey capture events can be described by one, or more frequently, a combination of these three behaviors. Extensive theoretical and experimental research over the past three decades has produced a clearer understanding of the functional morphology and biomechanics of these prey capture methods, and the behavioral attributes that are expected to most affect their performance (Alexander, 1967; Lauder and Liem, 1981; Barel, 1983; Aerts et al., 1987; Muller, 1996).

Some general patterns of association between prey type, predator anatomy and prey capture mechanism have been noted. The muscles and skeletal linkage systems of manipulating species are often robust and otherwise modified to enhance the strength of the bite, while ram and suction feeders frequently show mechanical features reflecting their potential for more rapid motion (Barel, 1983; Wainwright and Richard, 1995; Westneat, 1994, 1995). Among non-biting predators of mobile prey, large-mouthed fishes feeding on relatively large, elusive prey often utilize a ram-dominated prey capture mode (Norton, 1991; Norton and Brainerd, 1993; Nemeth, 1997). In contrast, some small-mouthed predators of smaller, less elusive prey, have been found to employ a suction-dominated prey capture mode (Norton and Brainerd, 1993; Gibb, 1997). In addition, morphologies and behaviors that are presumed to facilitate the production of suction have been described in the recent literature. These include the labial cartilages of certain sharks that rotate anteriorly, like the premaxillae of several teleosts, to create a more tubular and elongate mouth opening (Ferry-Graham, 1998; Wilga and Motta, 1998), and the presence of extensive hyoid depression, jaw protrusion, and small gape in suction feeding teleost fishes (Lauder, 1979; Motta, 1984; Gillis and Lauder, 1995; Gibb, 1997).

In this paper we analyze the prey capture mechanism used by the enigmatic long-snouted butterflyfish, *Forcipiger longirostris*. This Indo-Pacific coral reef species possesses a strikingly elongate jaw complex (Fig. 1), a feature it shares with several closely related species. However, the feeding biology of *F. longirostris* differs markedly from the other long-snouted butterflyfishes. The long-snouted *F. flavissimus*, and species of *Chelmon* and *Chelmonops*, feed on a wide range of predominantly attached, benthic invertebrate prey, and some free-living, mobile prey (Harmelin-Vivien and Bouchon-Navarro, 1983; Hobson, 1974; Motta, 1988; Sano, 1989). It is thought that the ‘‘manipulation’’ method is used by butterflyfishes to grip and remove pieces from polychaetes, nemerteans, corals, ascidians, echinoids, hydroids and other attached prey. Suction feeding is thought to be used when preying upon mobile prey such as calanoid

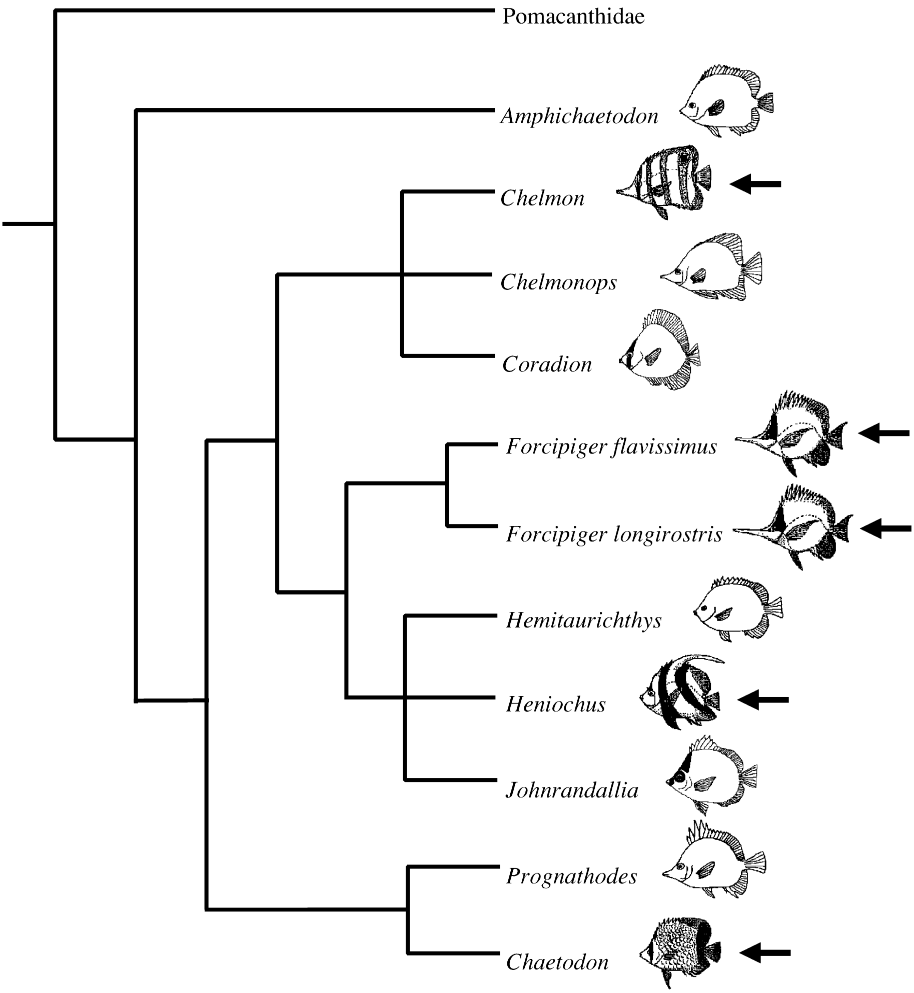

Fig. 1. Phylogeny of chaetodontid genera based on 34 morphological characters (after Blum, 1988 and Ferry-Graham et al., in press). Note the frequent occurrence of long jaws in the clade including *Forcipiger*, *Chelmon* and *Chelmonops*. Arrows indicate the species used in this analysis: *Forcipiger longirostris*; *F. flavissimus*; *Chelmon rostratus*; *Heniochus acuminatus*; *Chaetodon xanthurus*.

copepods, amphipods, and crab larvae which are ingested intact (Hobson, 1974; Harmelin-Vivien and Bouchon-Navarro, 1983; Motta, 1988). In contrast to other chaetodontids, detailed observations in Hawaii and Moorea suggest that *F. longirostris* is a specialized predator of mobile decapod shrimps, particularly the elusive caridians (Randall, 1961; Hobson, 1974; Harmelin-Vivien and Bouchon-Navarro, 1983). It is noteworthy that of the 18 butterflyfish species examined in Moorea, the congeners *F. flavissimus* and *F. longirostris* exhibited the broadest and narrowest diets respectively (Harmelin-Vivien and Bouchon-Navarro, 1983). *F. longirostris* stands apart from all other well studied butterflyfishes as the only species in which the diet is dominated by elusive prey.

Published dietary information and direct field observations of feeding behavior led Motta (1988, 1989) to infer that *F. longirostris* is a high-performance suction feeder. Our purpose in this paper is to explore the functional basis of the exceptional feeding habits of *F. longirostris*. We focus on the mechanism of prey capture, using data from high-speed video recordings to measure the relative contribution of suction and ram during prey capture. In order to place observations of the feeding kinematics of *F. longirostris* into a comparative context we also present data on four other butterflyfish species, including other long-snouted species, as well as more generalized taxa.

2. Materials and methods

We selected three individuals from each of five butterflyfish species for study that encompass a range of morphologies and natural feeding habits: *Forcipiger longirostris* (8.4, 8.7, and 8.8 cm OTL = anterior orbit margin to tail tip, a measure of fish length that excludes the contribution of the snout), *F. flavissimus* (9.8, 11.4, 11.6 cm OTL), *Chelmon rostratus* (8.1, 8.7, 9.9 cm OTL), *Heniochus acuminatus* (5.4, 6.6, 9.0 cm OTL) and *Chaetodon xanthurus* (6.0, 6.6, 6.6 cm OTL). The current phylogeny of butterflyfishes is equivocal on the issue of whether the long-jawed trait has evolved once or twice in the clade that includes *Forcipiger*, *Chelmon* and their relatives (Fig. 1). Nevertheless, it is apparent that jaw length has undergone considerable change within this family, with *F. longirostris* possessing the most elongate jaw morphology in the Chaetodontidae (Motta, 1988). *F. flavissimus* and *Chelmon rostratus* possess moderately elongate jaws, but both differ from *F. longirostris* in feeding largely on attached and/or benthic prey. *Heniochus acuminatus,* is a short-jawed member of this clade that feeds predominantly on zooplankton and some benthic invertebrates (Randall et al., 1997; Myers, 1999). Finally, we included a representative species of *Chaetodon*, *C. xanthurus.* This species presumably feeds on coral polyps, other small benthic invertebrates and algae, like its close relative *C. paucifasciatus* (Randall, 1983). The natural ranges of these five species overlap over a large area of the Indo-Pacific (Allen et al., 1998).

Our aim was to assess the relative contribution of ‘‘suction’’ and ‘‘ram’’ to the feeding mechanism used by these five species during encounters with a mid-water prey. We used live brine shrimp (*Artemia* sp.) in our feeding trials so that we obtained video sequences of each species feeding on a common prey. While a more evasive prey would have been more directly relevant to the unusual feeding habit of *F. longirostris,* brine shrimp were the most elusive prey that all of our study species would feed on in the laboratory. *F. longirostris* were collected on the Great Barrier Reef with the assistance of a commercial collector in Cairns, Australia and maintained at 23°C±2 in 100 l aquaria at James Cook University in Townsville, Australia. Feeding sequences of this species were recorded at 300 or 500 images s^{-1} with an Adaptive Optics Kineview digital video system. The other species were obtained from Hawaii (*F. flavissimus*), Indonesia (*Chel. rostratus* and *H. acuminatus*), and the Philippines (*C. xanthurus*) through commercial fish importers based the United States and housed at 27°C±2 in 100 l aquaria at the University of

California, Davis. Video sequences of these four species were obtained with a NAC Memrecam ci digital video system recording at 250 images s^{-1} (*F. flavissimus*) or 500 images s^{-1} (*Chel. rostratus*, *H. acuminatus*, and *C. xanthurus*). Video recording rates were selected so that a minimum of 20 images were contained within each prey capture sequence.

To minimize measurement error due to parallax we analyzed only sequences in which the fish appeared to be oriented in square lateral view of the camera. Fish were offered prey one or a few items at a time and recording sessions lasted until the fish was satiated. Recording generally occurred over a two to three day period for each individual. For subsequent analysis, feeding sequences were stored as a stack of digital images on a PC hard drive. Four feeding sequences were analyzed from each individual using NIH Image 1.6 for Macintosh (National Institutes of Health, Washington, DC) or Didge β6.0 for PC (A. Cullum, University of California Irvine). To quantify movement of cranial elements the X, Y coordinates were taken for four points in each video frame (Fig. 2), beginning with the onset of jaw depression or protrusion (= time zero or t_0), until the jaws had been retracted to their fully recovered position. The four points were: (1) the antero-dorsal tip of the premaxilla, or upper jaw; (2) the anterior tip of the nasal bone (representing a fixed reference point on the head); (3) the anterior tip of the dentary, or lower jaw; and (4) the posterior margin of the pectoral fin insertion (a reference point on the body). The species differed in the shape of the head, so that the relative positions of the points varied among species (Fig. 3).

To calculate the displacement of these points, the position of each point in X, Y

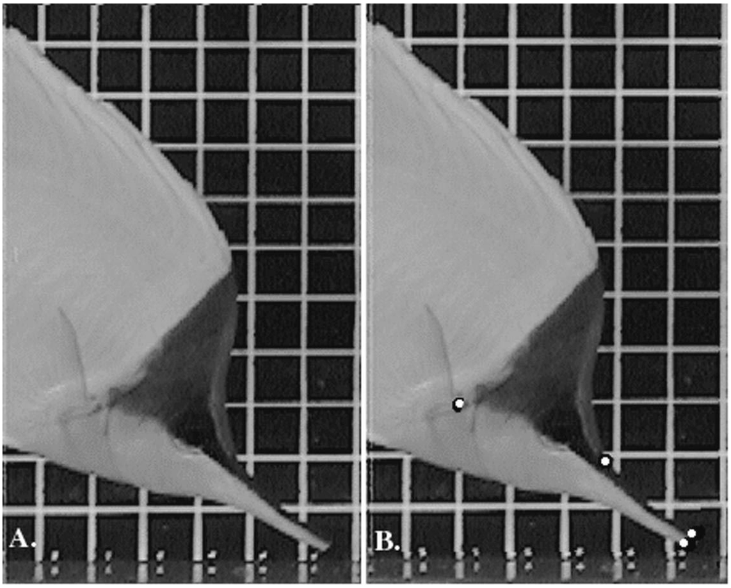

Fig. 2. Digitizing protocol for analysis of high-speed video footage: (A) a sample high-speed video image from the NACci camera; and (B) the four points digitized on each of the five species. Shown is *Forcipiger flavissimus*.

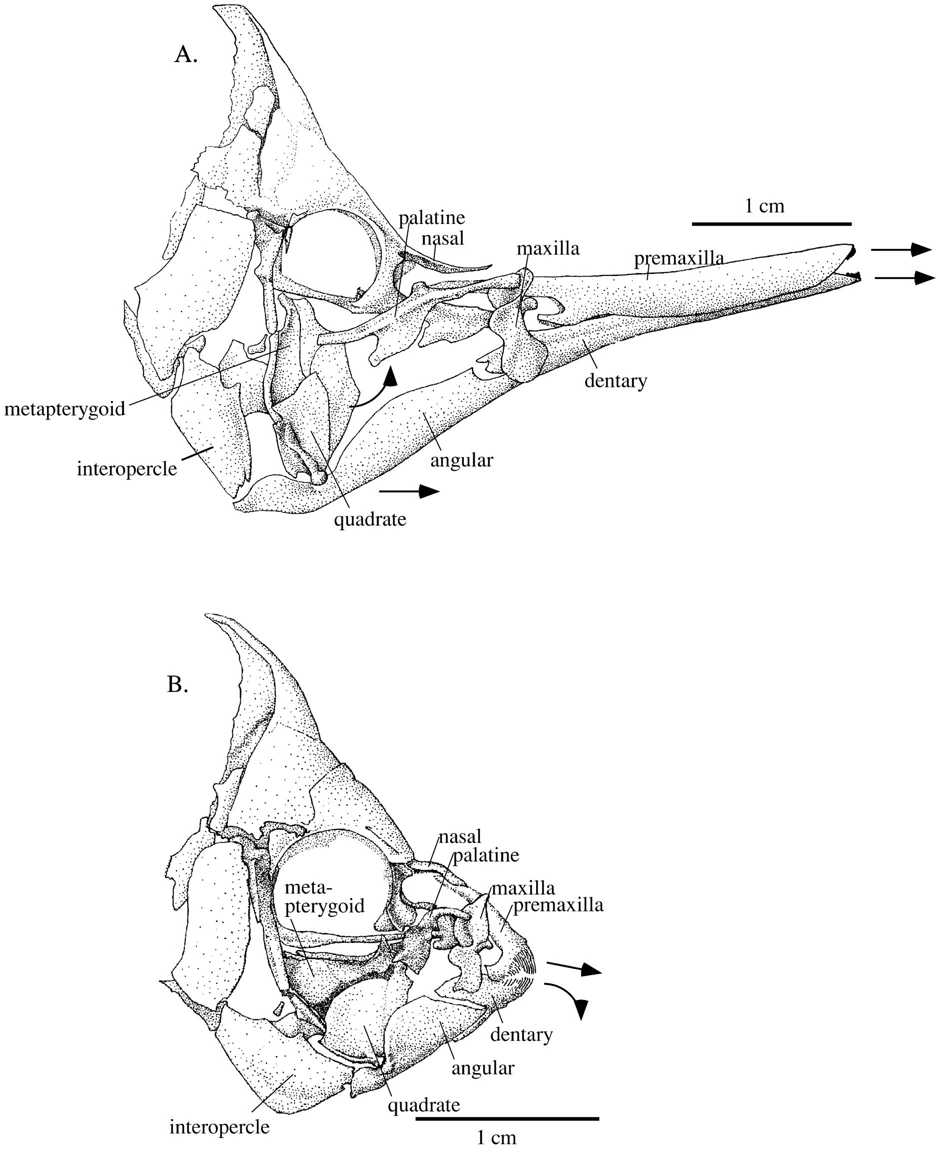

Fig. 3. Anatomy of two morphological extremes: (A) *Forcipiger longirostris* (8.8 mm OTL); and (B) *Chaetodon xanthurus* (6.6 mm OTL) shown in the relaxed positions. Diagrams are drawn from cleared and stained specimens. Scale bars are 1 cm. Arrows indicate the path of motion of movable elements. Note that the suspensorium (quadrate and attached elements) rotates in *Forcipiger longirostris* facilitating anteriorly directed upper and lower jaw protrusion. In *Chaetodon xanthurus* the upper jaw protrudes and the lower jaw is rotated and depressed ventrally. The elements of the lower jaw are labeled dentary and angular according to the convention set forth by Rojo (1991).

coordinate space at each time, t, was subtracted from a reference point at the same time to place the point in the fish frame of reference. The position at time t was then subtracted from the position at the onset of the strike to estimate displacement relative to t_0. The onset of the strike (t_0) is normally determined as the time at which the mouth begins to open. However, several of the species studied here routinely swam around the aquarium with their mouths held slightly agape. Additionally, in species with elongate jaws the lower jaw is not necessarily depressed during feeding. Thus, the onset of the strike was determined as the time at which the lower jaw began to protrude or depress.

In addition to the kinematic variables, several behavioral and performance variables were quantified for each species. For these metrics, a greater number of feeding sequences was used to collect data. At least eight sequences were analyzed for each individual so that there were 30–35 sequences for each of the five species. Each sequence was scored as a successful ‘‘suction-draw capture’’, a successful ‘‘suction-bite capture’’, or a ‘‘miss’’. ‘‘Suction-draw captures’’ were those in which the prey item was drawn completely into the mouth in a single action. Forward movement of the predator (i.e., ram feeding) contributed to these capture events; however, this level of categorization is meant only to distinguish events in which the prey item was drawn into the mouth in one movement from those in which a bite was used to capture the item. ‘‘Suction-bite captures’’ were those in which suction was generated but the prey was grasped in the anterior teeth prior to transport into the buccal cavity.

For each sequence, four variables were measured: (1) the distance between the lower jaw tip and margin of the prey item closest to the fish at t_0 (predator-prey distance; cm); (2) the time when the prey item entered the mouth fully, if capture was successful, relative to t_0 ($t_{\text{prey capture}}$; s); (3) how far the predator had advanced in a rostral direction, measured at the lower jaw tip, from t_0 to $t_{\text{prey capture}}$ (D_{predator}; cm) as well as how far the predator’s jaw alone had advanced when the locomotory contribution of the body is removed ($D_{\text{predator jaw}}$; cm); and (4) how far the prey item had moved towards the predator over that same time period (D_{prey}; cm). We used the variable D_{predator} as a direct estimate of the ‘‘ram’’ component of the strike, and D_{prey} as an estimate of the effective contribution of ‘‘suction’’ to each prey capture event (Norton and Brainerd, 1993).

To facilitate comparisons to some previously studied taxa, we calculated the Ram-Suction Index; a dimensionless index of the relative contribution of ram and suction to each strike (RSI; Norton and Brainerd, 1993). The RSI is calculated as $(D_{\text{predator}} - D_{\text{prey}})/(D_{\text{predator}} + D_{\text{prey}})$. It varies between -1 and 1 with positive values indicating a greater ram component to the strike and negative values indicating a greater suction component.

The kinematic variable maximum premaxilla protrusion was compared among species using one-factor ANOVA (Statview v4.5). Preliminary analyses indicated no apparent effect of body size on these data. The performance variables predator-prey distance, $t_{\text{prey capture}}$, D_{predator}, and D_{prey} were compared among species with a MANOVA (Statview v4.5). Since RSI is calculated from D_{predator} and D_{prey} it was omitted from the analysis. Given a significant MANOVA result, univariate ANOVAs were used as *post hoc* tests to determine which variables accounted for the significant species effect. A Fishers’ PLSD *post hoc* test was used given a significant ANOVA result to determine which species were different from one another. Mean values for variables that described missed capture events were compared with the same variables for successful captures within individuals and species using a paired-*t*-test. For all variables the assumptions of normality and equal variances were satisfactorily met following Underwood (1981).

3. Results

During feeding sessions individual fish swam about the aquarium searching for brine shrimp. Once a prey item was spotted, the fish approached it but usually slowed almost to a full stop, using the pectoral fins to brake, in preparation for the strike (Fig. 4). The body often continued to slowly move forward during the strike. Prey capture was initiated within a centimeter of the prey. At the onset of the strike the premaxilla, or upper jaw, was protruded towards the prey item while suction was employed to draw the prey into the oral cavity. The prey item was either trapped in the oral jaws in a bite or, more frequently, drawn fully into the buccal cavity. The suction-bite prey capture mode was used most by *Chaetodon xanthurus*, which employed this behavior in about half of the strikes (Table 1, Fig. 4A). Finally, the jaws were returned to their relaxed, pre-feeding position. Butterflyfish rarely missed the brine shrimp prey and only the two *Forcipiger* species and *Chelmon rostratus* were unsuccessful (Table 1). Unsuccessful strikes were generally followed immediately by another prey capture attempt on the same individual prey item.

Across species, the absolute amount of upper jaw protrusion differed ($F = 17.4$; df $= 4, 57$; $P < 0.0001$), with the two *Forcipiger* species and *Chel. rostratus* protruding

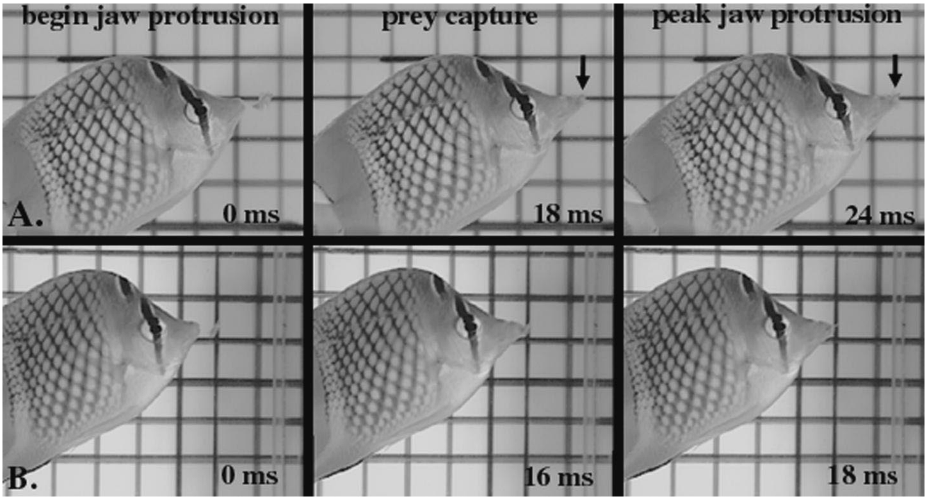

Fig. 4. High-speed video frames of different capture modes. Shown is *Chaetodon xanthurus* exhibiting a suction-bite (A), and a suction-draw (B). The kinematic event pictured is indicated above the frames. The time (ms) relative to t_0 is indicated on each frame and refers only to the individual sequence shown. Arrows in sequence A indicate the location of the prey item in the jaws of the fish. The bulge on the ventral surface of the fish is the exposed pectoral girdle.

Table 1
Performance data by species expressed as capture success and mode of capture used[a]

Species	n	OTL (cm)	Proportion of strikes utilizing each capture behavior		
			Suction-draw	Suction-bite	Miss
Forcipiger longirostris	3	8.6	0.83	0	0.17
		(9.8–11.6)	(0.085)	(0)	(0.084)
Forcipiger flavissimus	3	11.0	0.90	0.03	0.07
		(9.8–11.4)	(0.007)	(0.030)	(0.037)
Chelmon rostratus	3	8.3	0.92	0.04	0.05
		(8.0–8.7)	(0.043)	(0.037)	(0.048)
Heniochus acuminatus	3	7.0	0.87	0.13	0
		(6.2–9.8)	(0.019)	(0.019)	(0)
Chaetodon xanthurus	3	6.4	0.55	0.46	0
		(6.0–6.6)	(0.109)	(0.109)	(0)

[a] Values are means of individual means per species. An average of 11 strikes per individual was analyzed. The values in parentheses are standard errors, based on $n = 3$ individuals, except for fish OTL. For OTL the value in parentheses is the range of fish sizes used in the experiments. Note that strikes categorized in the two suction modes of prey capture also had a ram component not reflected here.

their premaxillae significantly farther than *Heniochus acuminatus* and *C. xanthurus* (Fisher's PLSD; all $P < 0.0001$). Mean peak premaxilla protrusion ranged from 0.63 to 0.25 cm (Fig. 5).

The primary difference between successful and missed strikes was in the distance at which the strike was initiated. For the three species that had misses, failed strikes were initiated at larger predator-prey distances than successful strikes (paired $t = -4.36$; $\mathrm{df} = 4$; $P = 0.012$; Fig. 6A).

For successful captures there were significant differences among species in the other performance measures (Table 2). *F. longirostris* initiated successful strikes from an average of about 0.6 cm from the prey, a predator-prey distance significantly farther from the prey than any other species (Table 2; Fig. 6A). *H. acuminatus* initiated strikes the closest to the prey, about 0.2 cm away. This distance was significantly shorter than found in both *Forcipiger* species (but not different from *Chel. rostratus* or *C. xanthurus*, Table 2; Fig. 6A). The mean time to prey capture of 0.022 s for *F. longirostris* was about twice as long as all other species (Fig. 5), and significantly different from all other species (Table 2). *F. longirostris* achieved an average $D_{\text{predator jaw}}$ of greater than 0.4 cm, which in turn was larger than all of the other species (Table 2; Fig. 6B). *Chel. rostratus* achieved an average $D_{\text{predator jaw}}$ of around 0.3 cm, which was also significantly larger than the contribution of $D_{\text{predator jaw}}$ for the remaining species (Table 2; Fig. 6B). The same analysis performed using D_{predator} rather than $D_{\text{predator jaw}}$ further indicated that *F. longirostris* had a much larger ram component to the strike. *F. longirostris* covered an average distance of nearly 0.6 cm with combined body and jaw movements, while the other species moved about 0.3 cm or less. *Chel. rostratus* was not significantly different from the other three species when this metric was used. The differences between *F. longirostris* and the other species in D_{predator} were not due to effects of body size. This is illustrated in Fig. 7A, note that there is no trend present. D_{prey} did not differ among

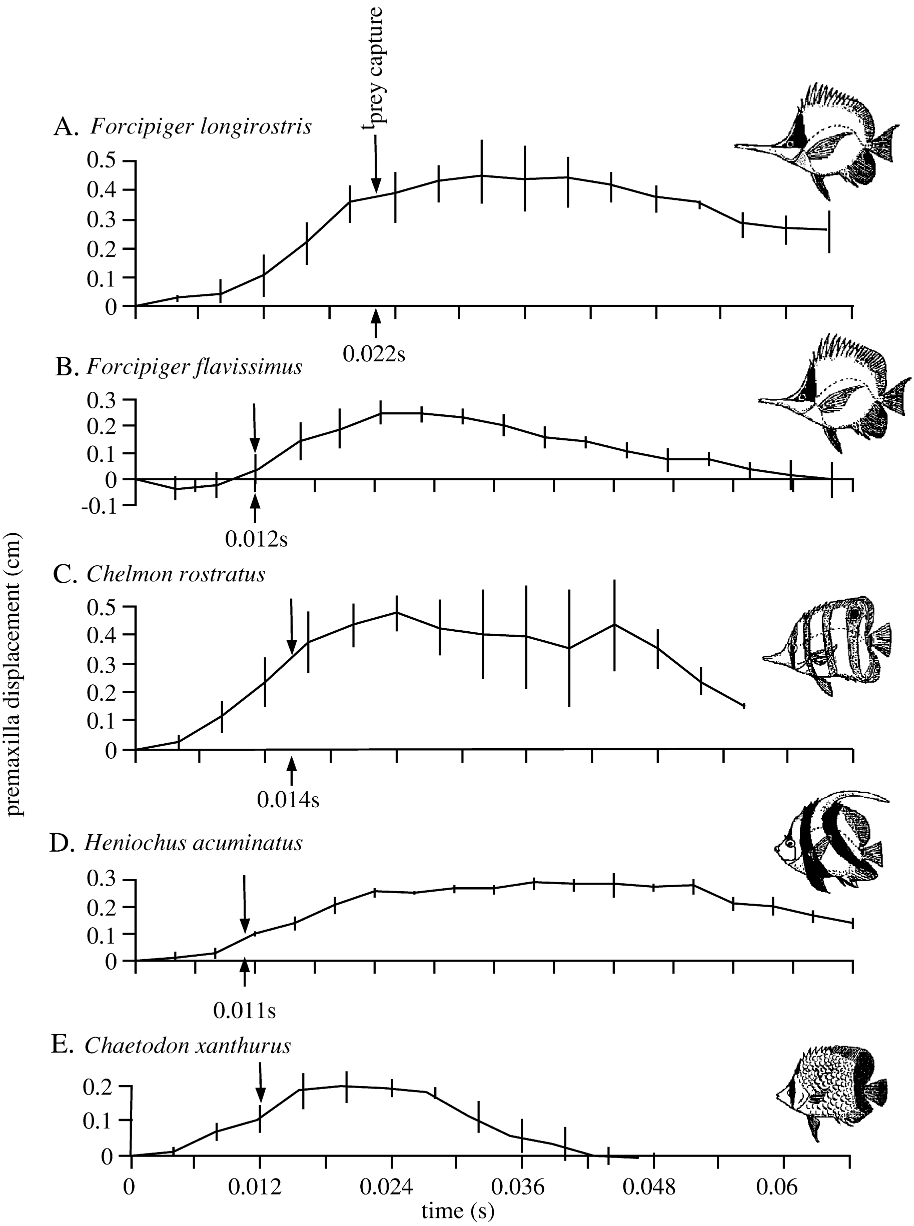

Fig. 5. Kinematic profiles of the relative displacement (i.e., protrusion or depression) of the premaxilla during prey capture for each species. Data shown are means of individual means ± S.E. per species. Means and S.E. are estimates from four prey capture events per individual from each of three individuals ($n = 3$), with the exception of *F. flavissimus*, for which five individuals were used ($n = 5$), and *Forcipiger longirostris*, for which only two individuals could be analyzed for this figure ($n = 2$). Displacements are measured as a change relative to zero at t_0. For ease of comparison, species filmed at 500 frames s^{-1} have been sub-sampled down to 250 frames s^{-1}. Indicated on each plot are the average times to prey capture (solid arrow) for each species.

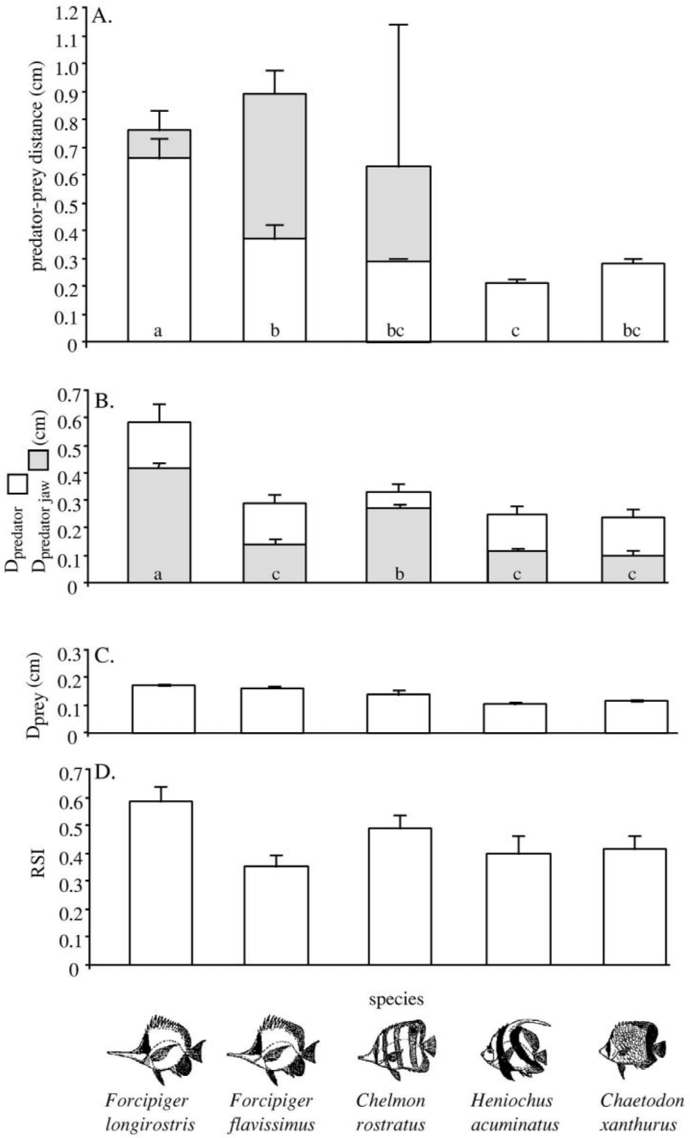

Fig. 6. (A) Predator-prey distance in successful strikes (suction-draw or suction-bite; clear bars) and missed strikes (filled light gray bars), (B) ''ram'' or the distance moved by the predator ($D_{predator}$; light gray bars) and by the lower jaw exclusively ($D_{predator\ jaw}$; clear bars) during successful strikes, (C) ''suction'' or the distance moved by the prey item (D_{prey}) during suction strikes only and, (D) RSI values for successful strikes. The bars for missed strikes in A begin at zero and are behind the successful strikes for the species in which they occurred for visual comparison. Plots are means of three individual means ± S.E. for each species ($n = 3$ for each species). Lower case letters in A and B indicate species effects that are not significant; for example, all ''a'' are not significantly different from each other, ''a'' and ''b'' are significantly different from one another. In A, only the successful strikes were compared to one another statistically. There were no species effects detected for plots C and D.

Table 2
Statistical results for the species effect given a significant MANOVA[a] result for performance variables from successful prey capture events for the five butterflyfish species[b]

Dependent variable	ANOVA $F_{4,10}$	P	Post hoc result	P
Predator-Prey distance	22.5	<0.0001	Fl > (Ff, Cr, Cx, Ha) (Fl, Ff) > Ha	0.013– < 0.0001
$t_{\text{prey capture}}$	11.1	0.001	Fl > (Ff, Cr, Cx, Ha)	0.0025–0.0002
$D_{\text{predator jaw}}$	28.09	<0.0001	Fl > Cr > (Ff, Cx, Ha)	0.018– < 0.0001
D_{prey}	0.79	0.56	na	na

[a] MANOVA Species effect: Wilks'; $F = 6.79$; df = 20, 21; $P < 0.0001$.

[b] For post hoc test the species in parentheses are not statistically different. A range of P values is given for all pairwise comparisons performed. Species are: Fl, *Forcipiger longirostris*; Ff, *Forcipiger flavissimus*; Cr, *Chelmon rostratus*; Ha, *Heniochus acuminatus*; Cx, *Chaetodon xanthurus.*

species (Table 2; Fig. 6C), ranging from 1.0 mm in *C. xanthurus* to 1.5 mm in *F. longirostris*. This suggests that there was no difference in the amount of suction that contributed to prey capture. The RSI, while not tested for statistical significance, generally mirrored the trends in D_{predator} (Fig. 6D). Differences in prey capture mode among the five species studies were only found in the amount of ram produced (Figs. 6B and 7B).

4. Discussion

All five butterflyfish species used a combination of both ram and suction, with or without a bite, to capture brine shrimp. The species that we examined did not differ significantly in the distance that shrimp were drawn toward the mouth (Fig. 6C). Thus, the contribution of effective suction to the strike was similar across species (Fig. 7). However, the ram component of the strike in *Forcipiger longirostris* was twice that of any other species (Figs. 6B and 7). When the ram and suction components of the strike are plotted against each other the differences among the five species in prey capture methods become particularly apparent (Fig. 7), as species and individuals vary most in the amount of ram used to close the distance between themselves and the prey.

The larger ram contribution by *F. longirostris* during the strike is attributable to jaw protrusion that was significantly greater than seen in the other butterflyfish species (Fig. 6B and Motta, 1988). *F. longirostris* possesses a novel joint in the suspensorium that facilitates exceptional jaw protrusion (Ferry-Graham et al., in press). This joint permits elements of the suspensorium to rotate anteriorly and dorsally, allowing for considerable anterior translation of the jaw joint (see Fig. 3). The resulting pattern of jaw motion during prey capture is characterized by anteriorly directed motion of the coupled upper and lower jaws. *F. flavissimus* does not possess the same degree of modification and cannot protrude the jaws as far (Ferry-Graham et al., in press). *Chelmon rostratus* protrudes the jaw both anteriorly and ventrally. *Heniochus acuminatus* and *Chaetodon xanthurus*, like generalized perciforms (Lauder and Clark, 1984), show only ventral

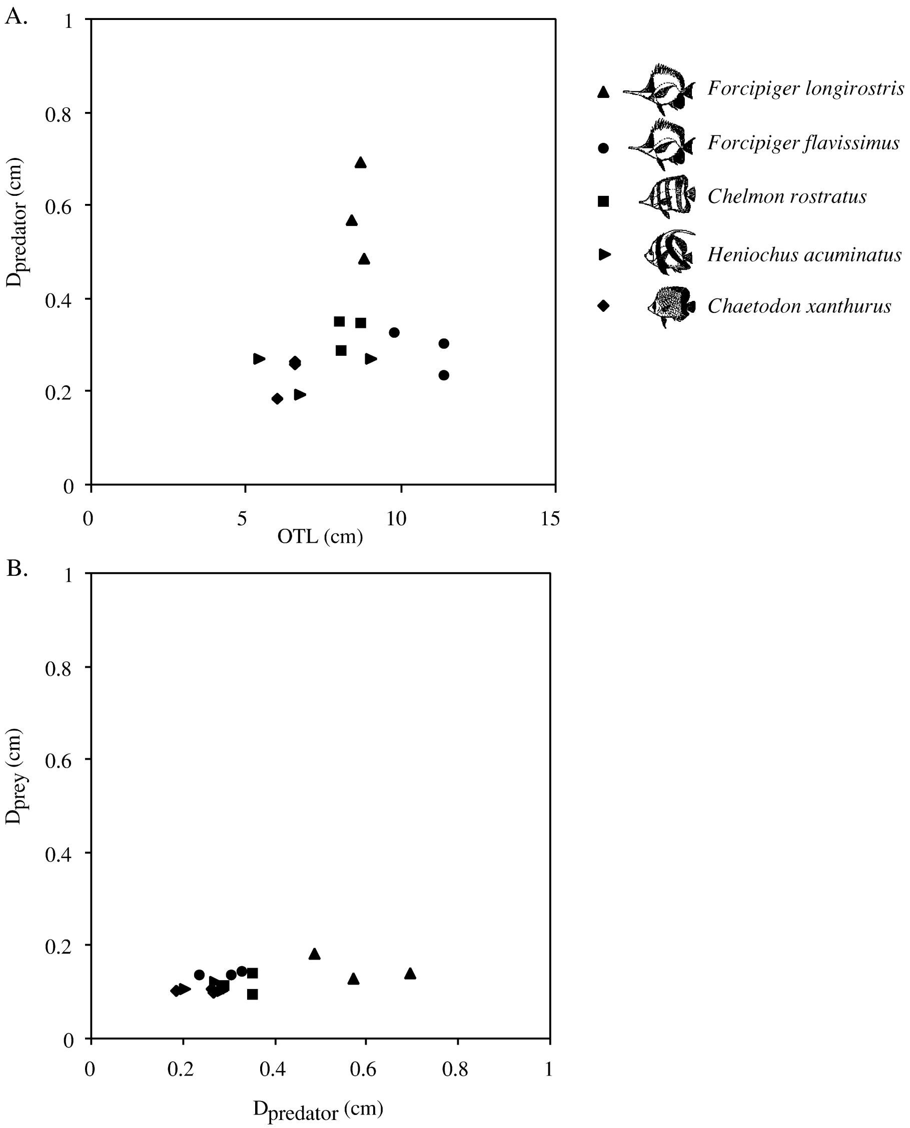

Fig. 7. “Ram” component of prey capture expressed as $D_{predator}$. Shown in A is the lack of a relationship between whole body ram and body size (OTL) in the five species studied. In B, the suction component, or D_{prey} is shown plotted against $D_{predator}$ = whole body ram (including contributions of forward locomotion and jaw protrusion). Note that differences among species are due to differences in the contribution of ram.

rotation of the jaw tip during the strike, compromising the directness of jaw movement toward the prey and limiting the extent of jaw protrusion (see Fig. 3).

Field studies in French Polynesia (Harmelin-Vivien and Bouchon-Navarro, 1983; Bouchon-Navarro, 1986), Hawaii (Hobson, 1974) and the central Indo-Pacific (Randall,

1961) have all found that *F. longirostris* stands out among chaetodontids in feeding almost exclusively on small caridean shrimp, a mobile and elusive prey. This specialized diet suggests that this species may possess an enhanced ability to capture mobile, highly elusive prey within the reef, although studies that directly compare prey capture success on elusive prey in this and other species have not been conducted. Motta (1988) interpreted the elongate snout and tendency to feed on mobile prey as evidence of strong suction feeding, and likened the long, thin jaws to a ‘‘pipette’’. However, in the present study, we found no difference between *F. longirostris* and the other four butterflyfish species in the degree of suction used when feeding on mobile prey. Our kinematic data provide a different perspective on the functional basis of this novel feeding habit. *F. longirostris* differed from a broad sample of other butterflyfish species in using significantly more ram during prey capture. The key to the association between an exceptional diet and the novel mechanism of extreme jaw protrusion in this species may be that the latter facilitates a substantial advance in the capacity for ram feeding relative to the condition seen in its congener, *F. flavissimus*, and other long snouted species (e.g., *Chel. rostratus*).

We do not mean to imply that suction was not produced by *F. longirostris*, or that the amount produced was an unimportant component of prey capture. Most aquatic feeding organisms are expected to produce some suction during feeding, if only to compensate for their own forward movement in a dense and viscous medium (Summers et al., 1998; Van Damme and Aerts, 1997). Even if *F. longirostris* produced a strong subambient pressure pulse in the oral cavity, the amount of effective suction, as indicated by D_{prey}, was not greater than that produced by any of the other butterflyfish species we examined. Although prey more elusive than brine shrimp may elicit greater suction, there is no evidence to suggest that strikes by *F. longirostris* in this study were reserved. Indeed, given the number of missed strikes, brine shrimp still appeared to present some degree of difficulty.

It should be noted that exceptional ram feeding does not necessarily preclude exceptional suction feeding. Despite the fact that the RSI implies that fish fall along a continuum ranging from high ram to high suction, ram and suction can vary independently. It is conceivable that some fish species are exceptional at performing both ram and suction feeding behaviors, having very high D_{predator} and D_{prey} values. However, the finding that D_{prey} was the same among species suggests that *F. longirostris* does not rely *more* strongly on suction to capture prey than the other four species of butterflyfishes. This may be because suction, as a mechanism of closing the distance between predator and prey, is only effective over a limited distance. The velocity imparted to water by the suction that is generated within the oral cavity declines rapidly as a function of distance from the oral aperture (Lauder and Clark, 1984; Weihs, 1980). Suction, therefore, may tend to vary over a smaller scale than ram.

An important element of the prey capture strategy in many fishes involves moving the mouth into close enough proximity to the prey such that suction can be used effectively to draw the prey into the buccal cavity. Numerous workers have noted the role of jaw protrusion in enhancing forward body motion, momentarily increasing the effective rate of approach of the fish toward the prey (Gosline, 1961; Alexander, 1967; Nyberg, 1971; Motta, 1984). *F. longirostris* stands out among the butterflyfish species studied here in the extent to which it used jaw protrusion during the strike. Motta (1988) observed that while feeding on Hawaiian coral reefs, *F. longirostris* ''. . . slowly swims while searching, and then momentarily either stops just before it rapidly protrudes the jaws . . . or it may lunge at the prey simultaneously''. Motta also noted that this species, like other long jawed species, feeds in crevices within the reef (pers. comm.). Extreme ram may confer an additional advantage in this environment, allowing the jaws to approach alert decapod prey, protected within crevices, where suction can then be used effectively.

The extent to which *F. longirostris* utilizes ram more than suction during prey capture is comparable, in terms of the RSI, to species that rank as the most extreme ram-feeding predatory teleosts. We calculated an average ram-suction index for *F. longirostris* of 0.59. The most ram-dominated species described by Norton and Brainerd (1993) in a survey of four species was the largemouth bass, *Micropterus salmoides*, with an RSI value of about 0.58. When feeding on the most elusive of five prey types, *Hexagrammus decagrammus*, exhibited an RSI of 0.58 (Nemeth, 1997). All of the species in our analysis showed RSI values that indicate heavier reliance on the ram component of the strike than on suction, as the lowest RSI values were all above 0.35 (Fig. 6).

The use of a large ram component in the strike is characteristic of predators on more mobile and elusive prey (Nyberg, 1971; Van Leeuwen and Muller, 1983; Norton, 1991; Norton and Brainerd, 1993). In this regard, the enhanced use of ram by *F. longirostris* fits a common theme seen in predatory fishes. Ram may be a particularly effective strategy for predators feeding on mobile prey because of the ability of such prey to detect approaching danger and respond by moving away quickly. An explosively rapid approach to the prey allows a predator to cover the last few millimeters or centimeters between it and the prey quickly, overtaking the prey and then finally entrapping it in the water that is accelerated into the oral cavity by the generation of buccal suction. There is evidence from other studies that ram feeding predators are frequently able to traverse that final few centimeters between predator and prey in considerably less time than closely related species that rely more heavily upon suction (Nyberg, 1971; Norton, 1991; Norton and Brainerd, 1993). *F. longirostris* did not fit this pattern, but instead exhibited a significantly longer time to prey capture than the other four butterflyfish species (see Fig. 5). Time to prey capture averaged 22 ms in this species and about 12 ms in the other four species. However, during this time *F. longirostris* moved the jaw and body about twice as far as any other species (Fig. 6B), suggesting that the rate at which these five species closed the distance between themselves and the prey was broadly comparable.

While the strike was not necessarily faster, it was initiated from farther away in *F. longirostris*. Successful strikes were initiated approximately twice as far from the prey as the other four species (Fig. 6A). If the likelihood of eliciting an escape response from the prey increases as the predator draws closer to the prey, it may be that the ability of *F. longirostris* to initiate its strike from further away enhances its success in attempting to capture elusive shrimp.

Ram feeding predators frequently possess a relatively large oral gape (Norton and Brainerd, 1993). In this respect, the small 2 mm gape of *F. longirostris* may appear to be unusual for a ram feeding fish. This paradox may have contributed to the expectation that *F. longirostris* relies mostly on suction, as a small gape is often interpreted as being associated with strong suction feeding abilities (Barel, 1983; Norton and Brainerd, 1993). Since a small mouth is a widespread trait in chaetodontids, it is unnecessary to advocate a novel scenario for its function in *F. longirostris*. However, strong ram feeding by small-mouthed fishes may be more widespread than generally recognized. As noted previously, all of the small-mouthed chaetodontids studied here utilized more ram than suction when capturing prey. The sling-jawed wrasse (*Epibulus insidiator*, Labridae) protrudes its upper and lower jaws, creating a long tubular extension with a relatively small mouth opening. In this species, most of the distance between predator and prey is covered by jaw protrusion (Westneat and Wainwright, 1989). Seahorses and pipefishes (Syngnathidae) are also small-mouthed predators of elusive prey. These taxa use rapid cranial elevation to rotate the mouth into close proximity of their prey (Bergert and Wainwright, 1997), a behavior that could be categorized as a ram behavior.

Given our findings here, experiments with *F. longirostris* feeding on more elusive prey are clearly warranted to add to our understanding of how small-mouthed fishes capture elusive prey. It is possible that prey more elusive than brine shrimp will elicit the quicker feeding response observed in other ram feeders. It may also be possible to test the hypothesis that initiating the strike from a greater distance enhances prey capture success in this species. If prey routinely detect and then escape from the predator, one can determine the relationship between strikes where the prey initiated an escape response and the distance at which the strike was initiated. A small mouth may provide an additional, more general advantage in capturing elusive prey. Long, slender jaws extended towards the prey may create smaller disturbances in the water, thus reducing the potential for detection of the predator by the prey.

5. Conclusions

Forcipiger longirostris possesses the longest jaws found in chaetodontid butterflyfishes. It also preys almost exclusively upon highly elusive caridean shrimps. Despite being small-mouthed, this predator utilizes a capture mode that is as ram-dominated, and is similar in RSI value to other ram-feeding predators reported in the literature. There was no difference between *F. longirostris* and the other species studied in the amount of effective suction produced, as indicated by D_{prey}. Ram feeding in *F. longirostris* is enhanced by extensive protrusion of the elongate jaws, a behavior that is made possible by a novel jaw joint in this species (Ferry-Graham et al., in press). Jaw protrusion distance was significantly greater and the strike was initiated from a greater distance than that measured in four other butterflyfish species. The use of elusive prey by *F. longirostris* may be facilitated by a feeding mechanism that allows this fish to initiate its strike further from wary prey, and overtake prey with extensive jaw protrusion.

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