Modulation of Prey Capture Kinematics in the Cheeklined Wrasse *Oxycheilinus digrammus* (Teleostei: Labridae)

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ABSTRACT The ability to modulate prey capture behaviors is of interest to organismal biologists as it suggests that predators can perceive features of the prey and select suitable behaviors from an available repertoire to successfully capture the item. Thus, behavior may be as important a trait as morphology in determining an organism's diet. Using high-speed video, we measured prey capture kinematics in three cheeklined wrasse, *Oxycheilinus digrammus*. We studied the effects of three experimental prey treatments: live fish, dead prawn suspended in the water column, and dead prawn pieces anchored to the substrate in a clip. Live prey elicited significantly more rapid strikes than dead prey suspended in the water column, and the head of the predator was expanded to significantly larger maxima. These changes in prey capture kinematics suggest the generation of more inertial suction. With greater expansion of the head, more water can be accelerated into the buccal cavity. The attached prey treatment elicited strikes as rapid as those on live prey. We suggest that the kinematics of rapid strikes on attached prey are indicative of attempts to use suction to detach the prey item. More rapid expansion of the buccal or mouth cavity should lead to higher velocities of water entering the mouth and therefore to enhanced suction. Further modulation in response to the attached prey item, such as clipping or wrenching behaviors, was not observed. *J. Exp. Zool. 290:88–100, 2001.* © 2001 Wiley-Liss, Inc.

The term "modulatory multiplicity" was first introduced by Liem ('78, '79) to characterize the observation that cichlid fishes could produce distinctly different sets of prey capture behaviors in response to two different prey. These behaviors were described using electromyographic (EMG) measurements of muscle activity or motor patterns, determining pressures generated inside the head or buccal cavity of the feeding fish (pressure transduction), and quantification of movements of cephalic elements (kinematics). These studies together comprised an important result as they suggested that cichlid fishes could respond to a prey item on the basis of a stimulus presented by the prey and could modify their feeding behavior rather than responding with a fixed or stereotyped behavior. These observations had implications not only for neurological and behavioral research but also for trophic ecology, as the range of behaviors a predator is able to perform may be as important as the morphology of the predator in influencing what items ultimately compose the diet (Wainwright and Lauder, '86).

Since the initial observation by Liem ('78, '79) that different prey items can elicit different responses from the predator attempting to capture them, several researchers have gone on to document that such modulation is prevalent within aquatic feeding organisms. In bony fishes and elasmobranchs, behaviors have been documented that suggest that more elusive prey elicit increased suction production by the predator. In two shark species it has been shown that changing

the size of the prey can lead to changes in the amount of head expansion (Ferry-Graham, '98) or in the timing of the strike (Wilga, '97). In teleost fish elusive prey are known to induce faster prey captures (Norton, '91; Wainwright and Turingan, '93, for EMG variables; Nemeth, '97a, for kinematic variables) and increased suction production as indicated by measurement of pressure within the mouth cavity (Nemeth, '97b). Thus, there are specific predictions regarding how prey elusivity should affect the prey capture behaviors performed by a predator.

Prey that are attached to the substrate or other surfaces may pose different challenges to the predator relative to the capture of midwater prey. Liem ('80) described three categories of feeding behaviors that aquatic feeders might utilize: inertial suction, as discussed above; ram feeding, where the predator overtakes the prey using forward locomotion; and manipulation, a broad range of prey capture behaviors that utilize the teeth, including biting, clipping, gripping, or scraping. One or all of these behaviors might be used by a predator in response to an attached prey, but it is unknown which behaviors might be used in response to which kinds of attached prey. Further, we lack a clear idea of how manipulative prey capture behaviors differ from behaviors leading to the production of inertial suction. Is the sequence of kinematic events seen during manipulative prey capture events different from those seen during suction prey capture events? We lack a kinematically based distinction between manipulation and suction feeding.

To add to the growing body of information regarding the ability and causes of modulation of prey capture behaviors in fishes, we studied the cheeklined Maori wrasse *Oxycheilinus digrammus* (formerly *Cheilinus digrammus* or *Cheilinus diagrammus*, Family Labridae). Members of the genus *Oxycheilinus* are somewhat unusual among wrasses in that they feed on elusive crustaceans and fishes as well as less evasive prey that are more firmly attached to structures within the reef (Westneat, '90, '95). The broad diet of *O. digrammus* permitted us to conduct prey capture experiments with several experimental levels. We used this species to test the hypothesis that two prey treatments: (1) attached versus unattached; and (2) elusive versus nonelusive would have significant effects on prey capture kinematics. Further, using kinematic data we tested the hypothesis that increasing elusivity should lead to behaviors that increase the production of inertial suction.

MATERIALS AND METHODS

We studied three similarly sized individuals of *O. digrammus* (17.0, 18.4, and 18.5 cm standard length, SL). Specimens were collected from the reefs around Lizard Island, Great Barrier Reef, Australia, and maintained at 23 ± 2°C in 100-l flow-through aquaria at the Lizard Island Field Station. Fish were held for several days prior to experimentation, allowed to acclimate to captivity, and fed a maintenance ration of thawed prawns.

To investigate the effects of prey type on prey capture kinematics, three experimental treatments were used: attached prey, dead prey in the water column (unattached, but no escape attempt possible), and live prey in the water column. The attached prey species used were prawn (*Penaeus* sp.), obtained frozen from commercial fishermen. These were cut into pieces approximately 3 cm long. To create the attached prey treatment, a metal clip was firmly mounted to the tank bottom and the prawn piece placed within the jaws of the clip. Prawn pieces were suspended with a thin thread in the midwater treatment, permitting us to evaluate the effect of having the prey attached versus unattached. The prey item could swing freely at the end of the thread and movement of the prey was only constrained in the ventral direction. Thus, these treatments were meant to create situations where manipulation and suction behaviors would be induced respectively. To explore responses specifically related to piscivory, we used a live fish prey; 3–4 cm SL *Cirrhilabrus punctatus* (Labridae) collected from the same reef sites as the *O. digrammus*. Live prey were tethered on the same thin thread as the prawn pieces allowing us to compare captures on live versus dead prey. Despite being tethered in this manner, in nearly half of the prey capture events recorded on live fish prey, the prey item still exhibited mobility and/or attempted a "C-start" escape response during the capture event (see below).

Feeding sequences were recorded at 400–1,000 images sec^{-1} with an Adaptive Optics Kineview digital video system. Frame rates were selected so that at least 20 frames per feeding sequence were obtained. During filming, the tanks were illuminated with two 600-W floodlights. A rule was placed in the field of view and also recorded for several frames so that the images could be scaled precisely. Fish were offered prey one item at a time in a haphazard order and allowed to feed until satiated. Filming took place in the same 100-l aquaria

where the fish were maintained and generally occurred over a three- to five-day period for each individual. Sequences were stored digitally for analysis.

We analyzed only sequences in which a lateral view of the fish could clearly be seen in the image and the fish body axis was perpendicular to the camera to prevent measurement error. Time zero (t_0) for feeding trials was taken as the onset of the strike, or first image that movement of the jaws was detected. Analysis of sequences began two frames prior to t_0 to ensure that the onset of mouth opening was captured in the analysis. Sequence analysis ended at the conclusion of the strike as indicated by the return of the jaw to the relaxed, pre-feeding position. Six feeding sequences were analyzed from each prey type for each of the three individuals. These were further divided based on what appeared to be two cases of potentially alternative behaviors performed by multiple individuals on the same prey types.

The first prey type for which potentially different behaviors were noted was the live prey. As noted above, some fish prey performed a C-start escape response or other locomotor behaviors, while other prey remained motionless, presumably employing a freeze response, or simply were stunned by the manipulation. Although differences in predator behavior were not readily apparent, differences in the behavior of the prey could elicit differences in a predator's response at a level not detectable by us when simply viewing the video footage. Thus, we considered these two levels (escape vs. nonescape) separately in our categorization of individual feeding events on the live fish prey treatment. All three individuals had these two categories within the live fish prey treatment.

The second difference was in the predator's response to the attached prey treatment. We observed two potentially different behavioral approaches to this prey item: (1) the fish approached the attached prey and removed it, usually applying suction and removing the prey in one continuous action rather than biting the prey and using subsequent transport events to ingest the prey; or (2) the fish placed its jaws on the prey item, weakly biting it, and usually not removing any part of the prey. Two of the three individuals exhibited both types of biting behaviors in response to the attached prey treatment. Six replicate feeding events per individual per prey item allowed us to sample each of these alternative behaviors equally within individuals that exhibited them, leaving us with a balanced statistical design over-

all; three replicates were performed at each level of the analysis.

To quantify movement of skeletal elements on the predator and whole movements of the prey relative to the predator (and vice versa), the following points were digitized in each video frame of each sequence using NIH Image 1.6 for Macintosh (Fig. 1): (1) the anterior tip of the premaxilla (upper jaw); (2) the posterior margin of the nasal bone; (3) the dorsal-most tip of the neurocranium as approximated by external morphology; (4) the dorsal margin of the insertion of the pelvic fin on the body (a reference point); (5) anteroventral protrusion of the hyoid; (6) the articulation of the lower jaw at the quadrate (the jaw joint), (7) the anterior tip of the dentary (lower jaw); and (8) a distinguishing landmark on the prey item farthest from the predator (i.e., a fin, a carapace edge, or a margin).

From the digitized points we calculated several kinematic variables. Angular kinematic variables were the angle of the neurocranium relative to the body (cranial elevation) and the angle of the lower jaw relative to the neurocranium (lower jaw rotation, degrees; Fig. 1b). Angles were expressed as a change in angle relative to t_0, thus the starting position at t_0 was subtracted from each subsequent measure and all angular excursions begin at 0°. Displacement kinematic variables included gape distance, premaxilla protrusion, and hyoid depression (cm). Gape distance was estimated as the straight-line distance between the upper and lower jaw tips. Premaxilla protrusion was calculated from the straight-line distance between the position of the premaxilla at t_0 and its position at any time t. Hyoid depression was calculated in the same manner. For both premaxilla protrusion and hyoid depression, the X,Y positions at t_0 and time t were subtracted from the reference point on the fin prior to calculating the straight-line distance in order to compensate for forward locomotion of the fish and to express the movement relative to the body of the fish. The maxima, and the time of the maxima, achieved for each angular and displacement variable for each sequence was recorded and used for further statistical analysis. Maximum angular velocity (deg sec^{-1}) was also calculated for each feeding sequence for the angular variables using two methods: (1) we determined the change in angle over each time interval digitized for each sequence and from those determined the single maximum change per interval during mouth opening (or cranial elevation); and (2) we calculated an average angular change
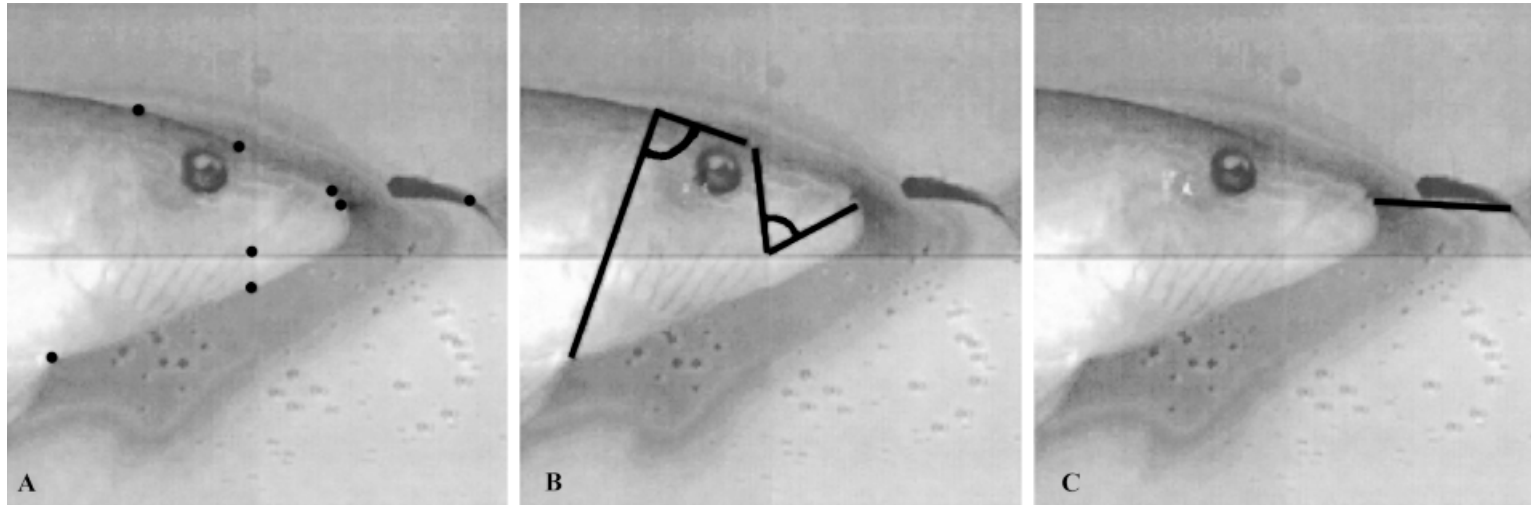
Fig. 1. (**a**) Digitized points used to calculate angular and displacement variables, (**b**) angles used to estimate cranial elevation and lower jaw rotation, and (**c**) predator–prey distance.

over the four frames of mouth opening (or cranial elevation) where the rate was at or near maximum. A shortcoming of the first method is that digitizing error has the potential to overestimate actual peak velocities. The second method should underestimate the true peak velocity because it integrates over a time that is longer than the period of maximal velocity and across several points of measurement. The combination of the two methods was used to set upper and lower bounds on the actual values of peak angular velocity.

We quantified three positional variables relating the predator and the prey to one another. The first of these was predator–prey distance (D), the measure of the distance between the lower jaw tip of the predator and the point digitized on the trailing edge of the prey item at t_0 (Fig. 1c). We also measured D_{prey}, the distance moved by the prey item toward the predator from t_0 to the time at which the prey item was engulfed fully. D_{prey} is used in this study as an indication of the degree to which suction is effective for drawing the prey into the mouth. $D_{predator}$, the distance moved by the predator toward the prey, was measured over the same time course. $D_{predator}$ includes movement toward the prey resulting from forward locomotion and from premaxilla protrusion. We measured D_{prey} and $D_{predator}$ directly and only analyzed feeding sequences in which the camera was motionless. In this species, maximum premaxilla

protrusion, measured above, can also be expressed as $D_{predator\ jaw}$, as $D_{predator\ jaw}$ is the movement toward the prey item by just the jaw of the predator as the jaw is protruded largely anteriorly.

We used discriminant function analysis (DFA) to determine if the kinematics of prey capture could be used to distinguish strikes on the three prey types, and to identify the characteristics of strikes on each kind of prey item that contributed to the distinction (Systat 9.0). The DFA uses a MANOVA model formed from the identity data matrix for all prey types and all individuals for the dependent variables identified above (see list, Table 1). Prey type was used as the discriminating independent variable in the model. The dependent variables used were maximum and time of maximum for the kinematic variables gape distance, lower jaw angle, premaxilla protrusion, and hyoid depression, and the positional variables D_{prey}, $D_{predator}$, and predator–prey D. (Note: to prevent redundancy in the analysis, angular velocities were not used.) The classifications for each strike predicted by the DFA were compared with the actual classifications in a 3×3 contingency table. A Chi-square statistic was used to determine if the number of strikes classified in each cell of the table was significantly different from the null model: an equal distribution of the strikes among the nine cells. The first and second canonical factor scores were plotted against one another

TABLE 1. Kinematic data by prey type[1]

Variables:	Prey type[2]		
	Attached	Midwater	Live
Predator–prey D (cm)	0.63 (±0.14)	1.64 (±0.06)	3.29 (±0.41)
D_{prey} (cm)[3]	0.56 (±0.19)	0.93 (±0.13)	2.26 (±0.21)
$D_{predator}$ (cm)[4]	1.13 (±0.19)	1.51 (±0.15)	3.01 (±0.55)
Max. gape distance (cm)	1.09 (±0.15)	1.24 (±0.17)	2.05 (±0.18)
Max. lower jaw rotation (deg)	22.27 (±4.0)	25.99 (±3.70)	42.56 (±3.60)
Max. premaxilla protrusion (cm)	0.39 (±0.04)	0.36 (±0.03)	0.67 (±0.03)
Max. cranial elevation (deg)	6.71 (±1.66)	5.24 (±1.68)	18.08 (±4.34)
Max. hyoid depression (cm)	0.53 (±0.05)	0.53 (±0.04)	0.95 (±0.03)
t max. gape distance (sec)[5]	0.026 (±0.003)①	0.044 (±0.005)②	0.024 (±0.001)②
t max. premaxilla protrusion (sec)	0.028 (±0.004)②	0.055 (±0.003)③	0.022 (±0.002)①
t max. cranial elevation angle (sec)	0.029 (±0.003)③	0.039 (±0.011)①	0.029 (±0.001)③
t max. hyoid depression (sec)	0.037 (±0.005)④	0.063 (±0.008)④	0.029 (±0.003)④
Max. lower jaw rotation vel. (deg sec^{-1})	2,811.2–1180.2	1,645–633.3	5,685.7–2,285.9
Max. cranial elevation vel. (deg sec^{-1})	1,651.6–238.2	882.9–130.1	4,572.7–970.1

[1]Values are the means of a mean for each individual (n = 3). SE is in parentheses except for velocities. Results from the two methods of calculating angular velocity are presented as mean upper and mean lower boundaries of the estimate.
[2]Small circled numbers indicate the sequence of events of timing variables.
[3]D_{prey} is given for attached prey pieces as the fish were able to exert some movement onto the prey item, lifting it away from the clip and occasionally effectively removing it. However, the presence of the clip certainly constrains this variable, and D_{prey} is not an accurate indicator of suction generated by the feeding fish on this prey item.
[4]D predator can exceed Predator-prey D because it is estimated from t_0 until the time that the prey is engulfed fully.
[5]t max. lower jaw rotation is the same value as t max. gape distance and therefore is not included with the timing data.

and 95% confidence ellipses drawn around clusters of data by prey type to visually illustrate the position of strikes in the canonical space. The canonical loadings were used to determine which of the original dependent variables were responsible for the separations among the clusters and to ascribe a functional description to each of the canonical axes. Variables that loaded strongly on either of the axes were identified using an arbitrary cutoff of 0.294. This is the minimum value of r that is significant at $P = 0.05$ for the sample size used in the DFA (Zar, '84).

Because DFA is meant to determine group identity of data, and not to test hypotheses of difference among or within data, we also performed a series of univariate ANOVAs to explicitly test the hypothesis that strikes on each type of prey were different from one another. However, we did not test all of the dependent variables. Rather, to increase the power of the univariate tests and limit the total number of tests performed, we tested only the variables that loaded strongly on the first or second canonical factors from the DFA. The univariate tests were performed with the added independent factor of "individual" to correctly account for the variance attributable to this source. The ANOVA model was a two-factor, mixed-model ANOVA with prey type the fixed factor and individual the random factor. F ratios were estimated for the prey type effect using the interaction term in the denominator (Zar, '84). Significance of P values for all kinematic variables was determined using a tablewide sequential Bonferroni correction for multiple tests (Rice, '89). Given a significant ANOVA result for the main effect of prey type on a kinematic variable, Fisher's protected least significant difference (PLSD) tests were performed post hoc to determine which prey types differed. The assumptions of equal variances and normality were satisfactorily met.

RESULTS

In all prey capture sequences, individual *O. digrammus* approached the prey item, opened the mouth and elevated the head while the premaxilla was protruded and the hyoid was depressed (Fig. 2). Prey were captured either by completely engulfing the item, presumably employing suction to draw the item into the mouth fully, or by placing the jaws on the item in a suction–bite combination. In captures where a bite occurred, an additional transport event was used to take the item into the mouth fully, or, in the case of attached prey, the item was left on the clip and the

capture attempt was unsuccessful (Fig. 2). The prey item was completely removed from the clip in six of the 18 feeding trials for the attached prey treatment. Individual *O. digrammus* initiated strikes on attached prey at a smaller distance than unattached, and initiated the strike from the greatest distance when feeding on live prey (Table 1). Live prey also elicited the greatest expansion of the head during feeding, as indicated by larger gape distances, greater lower jaw rotations, higher cranial elevation, more hyoid depression, and the largest D_{prey} (Table 1, Fig. 3. Higher angular velocities were generated in achieving these maxima (Table 1), as the large maxima were reached at approximately the same absolute time as the smaller maxima for midwater prey (Fig. 3). Midwater prey elicited similar displacement and angular maxima as attached prey; however, the maxima for attached prey took longer to achieve (Fig. 3), and were achieved in different order (Table 1). For example, in captures of midwater prey, maximum cranial elevation was achieved first, possibly because it was so small, followed by maximum gape. In other strikes, maximum gape was achieved before maximum cranial elevation angle. For all prey types, maximum hyoid depression was last in the sequence of events, but was much later in captures on midwater prey than on the other prey types (Table 1).

The DFA successfully determined the identity of the prey item from the kinematic data of most strike sequences. The DFA MANOVA model was significant (Wilks' λ $F_{24,64} = 12.32$, $P < 0.0001$). The classification matrix was 96% correct, having misclassified one strike at attached prey as a strike at midwater prey and vice versa (Fig. 4). The Chi-square statistic indicated that the predicted classifications were significantly different from a random classification ($\chi^2 = 86.20$; $P < 0.001$). We considered the additional effect of the alternative behaviors observed within strikes on prey types; however, whether or not the live prey attempted to escape had no apparent effect on this classification (Fig. 4). Further, for attached prey, successfully detaching the prey and engulfing it whole rather than biting the prey in the clip had no detectable effect on the analysis (Fig. 4).

The clusters that correspond to strikes on live prey and strikes on dead prey were separated along the first canonical axis (Fig. 4). The variables that loaded strongly on this axis were maximum gape distance, maximum lower jaw rotation, maximum hyoid depression, D_{prey}, and predator–prey D. These variables tend to increase away
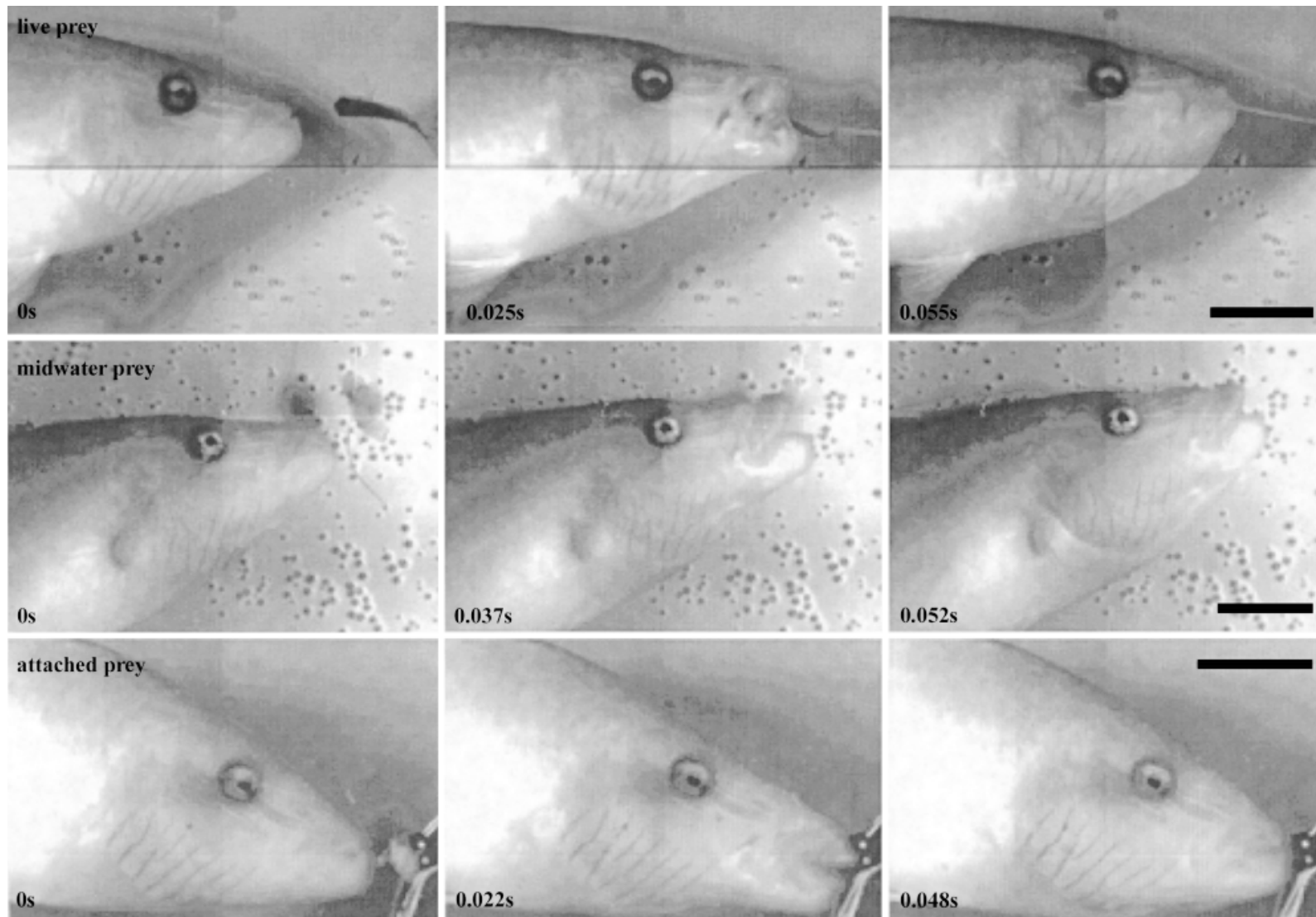
Fig. 2. Composite image of prey capture events from a single individual on the three prey types as labeled in the figure. Each sequence progresses from left to right as indicated by the standardized times at the corner of each frame. For each capture event, the sequence begins at t_0, the time of mouth opening. The next image is maximum gape distance. The last frame in each sequence is jaw closure, or the closest that the individual came to closing the jaws fully. Jaw closure signifies the completion of the gape cycle. The scale bar shown in the last image of each sequence is 2 cm in length.
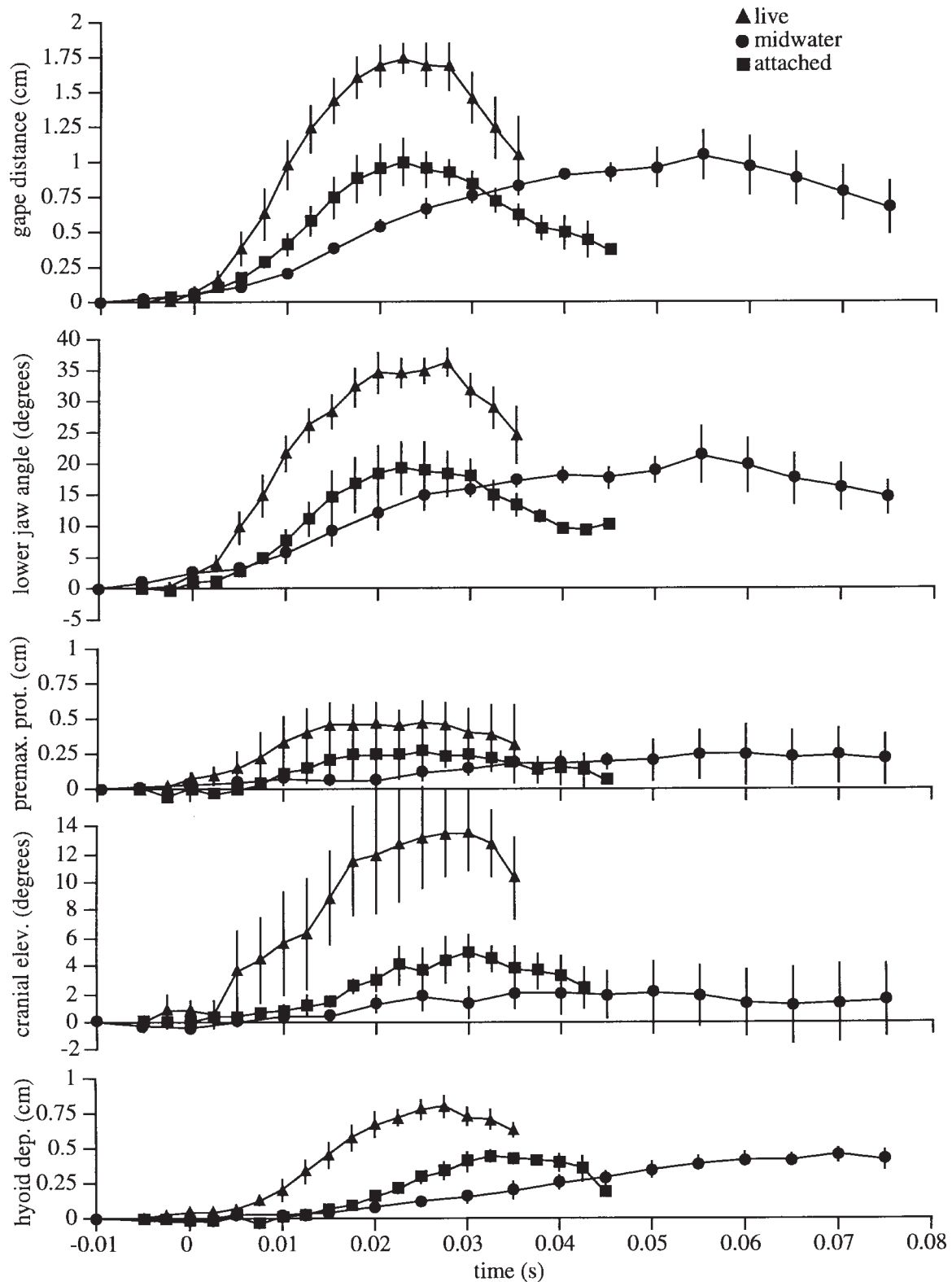
Fig. 3. Mean kinematic plots from the three individuals capturing the three prey types. Values are means of individual means ($n = 3$). Error bars are ±SE. Note that the profiles begin prior to t_0, as the frames digitized prior to the onset of the strike have been included. Due to the varying length of capture events, most profiles do not return to 0, as the means near the end of the event include some sequences that have ended and some that have not. The live fish and prawn in a clip captures were recorded at higher frame rates (400–1,000 images sec^{-1}) to ensure that approximately 20 frames were recorded for each capture event. Sequences recorded at rates >400 images sec^{-1} have been subsampled to facilitate the estimation of means among individuals for these prey types. Midwater prey captures were recorded at 200 images sec^{-1}.
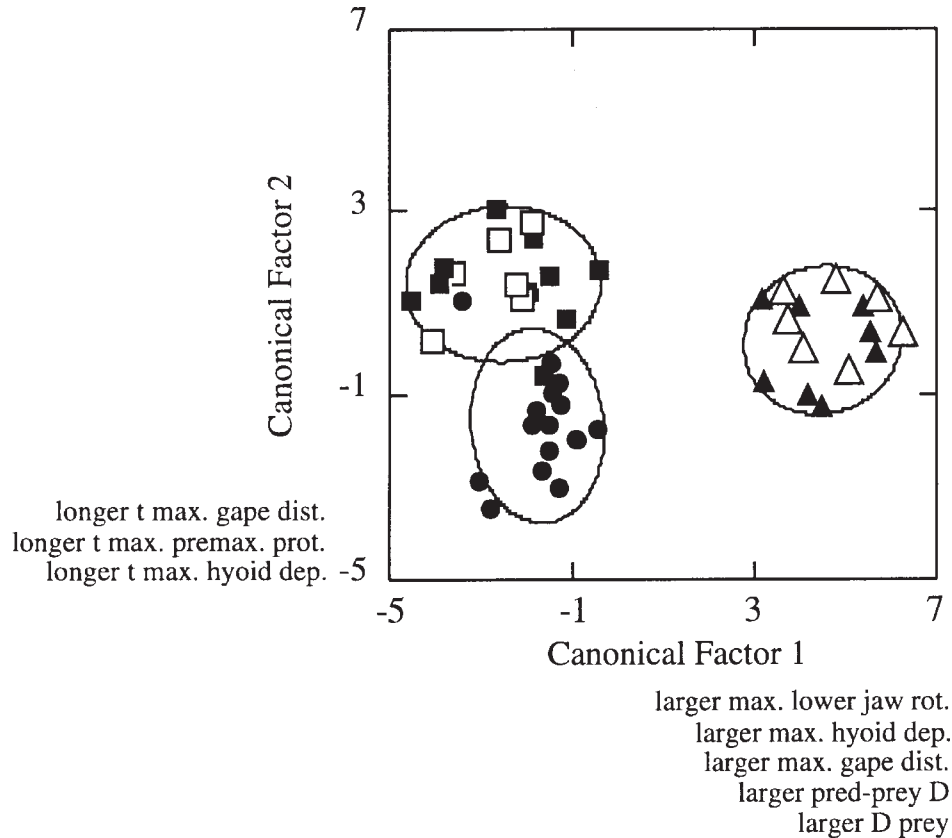
Fig. 4. Plot of the canonical scores for the first two canonical factors generated by the DFA analysis. Data are coded as indicated in the legend (open symbols of the same shape as the filled symbols represent strikes containing alternative behaviors for that prey type). Ellipses around the clusters are 95% confidence ellipses for each prey type. On each axis are the kinematic variables that load heavily on that canonical factor. The direction of change on each axis is indicated by the labels. ▲ live (△ attacks where the prey item attempted escape); ● midwater; ■ attached (□ attacks where the prey item was successfully detached from the clip).

from the origin; thus, increasingly positive scores indicate generally larger kinematic maxima. Attached and unattached prey were somewhat separated on the second canonical axis. The variables that loaded strongly on this axis were the time to maximum gape distance, the time to maximum premaxilla protrusion, and the time to maximum hyoid depression. These all loaded with the opposite sign; thus, the time to maximum for these kinematic events decreases away from the origin indicating a more rapid strike at attached prey than at midwater prey (Fig. 4).

The five kinematic variables that loaded significantly on the first canonical factor were further analyzed with univariate ANOVAs and all except maximum lower jaw rotation indicated a significant effect of prey type (Table 2). Fisher's PLSD post-hoc tests consistently indicated that for these variables, the means for strikes on live fish were significantly greater than the means for strikes

on either prawn prey (all $P < 0.0001$), which were not significantly different from one another (see also Table 1). The test of effects on maximum gape distance and maximum lower jaw rotation also indicated a significant interaction term, which can confound interpretation of main effects. However, the values for strikes on live prey are still consistently larger than values for strikes on the other prey types for all individuals (Fig. 5). The single timing variable of time to maximum gape distance was selected from those loading strongly on the second canonical axis, as the timing variables behave in a sequential manner and the response in one variable is carried over into a response in subsequent variables (Table 1). There was a significant prey type effect on time to maximum gape distance (Table 2). A Fisher's PLSD post-hoc test indicated that strikes on prawns on a string took significantly longer than strikes on either attached prey or on live prey, which were not significantly

TABLE 2. Results of univariate ANOVAs on indicator variables selected from the discriminant function analysis (DFA)[1]

	Effect						
	Prey item			Individual		Interaction term	
Kinematic variable:	$F_{2,4}$	P	Fisher's PLSD[2]	$F_{2,37}$	P	$F_{4,37}$	P
D_{prey}	36.42	0.004**	l > (a = m)***	0.43	0.23	1.32	0.28
Predator–prey D	21.32	0.015**	l > (a = m)***	1.08	0.35	1.60	0.19
Max. gape distance	16.42	0.03*	l > (a = m)***	14.54	< 0.0001**	4.45	0.005**
Max. lower jaw rotation	8.11	0.08	NA	4.10	0.02*	3.88	0.01**
Max. hyoid depression	57.40	0.003**	l > (a = m)***	2.07	0.14	0.40	0.81
t max. gape distance	19.88	0.02*	m > (a = l)***	3.85	0.03*	1.32	0.28

[1]Data exploration revealed that the only kinematic variable that had a significant prey item effect in the univariate ANOVA that did not load heavily in the DFA was max. premaxilla protrusion.
[2]l = live prey (fish); m = midwater prey (prawn on a string); a = attached prey (prawn in a clip).
*Significant at $P = 0.05$.
**Significant at $P = 0.01$.
***$P < 0.001$.

different (Table 2). Additional ANOVAs indicated no effect of the potential alternative behaviors within prey type.
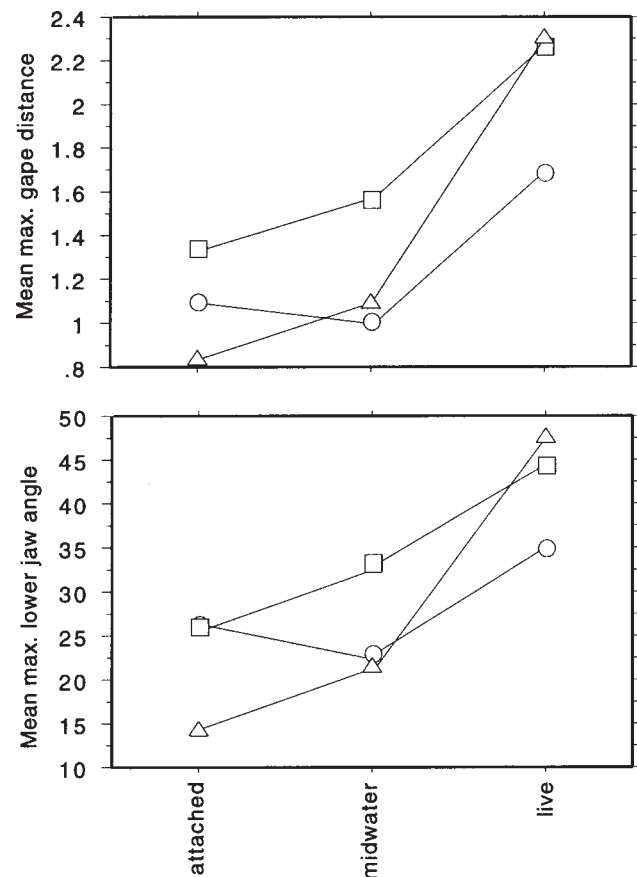

Fig. 5.   Plots of the interaction between the prey type effect and the individual effect for the two kinematic variables that had significant interaction terms in the ANOVAs (see Table 2). Prey types are labeled on the x axis. The symbols on the graph refer to the different individuals in the analysis.

DISCUSSION

Our analyses suggested that there were three kinematically distinct categories of predator response in this study that corresponded with the three kinds of prey treatments offered to the predator, *O. digrammus*. We discuss those categories below.

Kinematics of strikes on immobile, unattached prey

Strikes at the midwater prey represent what we believe to be the least challenging prey type of those that we offered, thus we use this prey type to establish a baseline for comparison with other prey types. Not surprisingly, strikes at midwater prey are of the same approximate magnitude and duration as strikes on shrimp pieces held in forceps analyzed in a previous study of slightly smaller *O. digrammus* (11.8–13.7 cm SL; Westneat, '90). Maximum gape distance, premaxilla protrusion, and hyoid depression were similar in the two studies, with average values reported in the Westneat ('90) study of approximately 1.3 cm, 0.5 cm, and 0.4 cm, respectively. This compares with 1.2 cm, 0.4 cm, and 0.5 cm, respectively, in our study. Cranial elevation was 5–7° in both studies. The only difference was the value reported for lower jaw rotation, which was approximately 35° in the Westneat ('90) study and only around 20° for captures of prey suspended from a string in our study. We measured angular changes of 35° in lower jaw rotation only for the live prey item. In the Westneat ('90) study, maximum gape distance, maximum lower jaw rotation, maximum cranial elevation, and maximum premaxilla protrusion all occurred at 0.035–0.04 sec into the strike. Hyoid depression occurred slightly

later at approximately 0.045 sec. These are similar to the times measured in our study; maximum gape distance, maximum lower jaw rotation, and maximum cranial elevation all occurred at about 0.04 sec. However, maximum premaxilla protrusion occurred slightly later at about 0.05 sec, and maximum hyoid depression occurred nearer to 0.06 sec in our study. These data can be viewed as a generalized response to simple, nonelusive, undefended prey items.

Live prey effects

The greatest values of D_{prey} were measured from strikes on live prey suggesting that the greatest suction pressure was produced by *O. digrammus* in response to that prey item (Table 1). D_{prey} is a measure of the prey item's response to suction production and is not a direct measure of suction pressure or induced water velocity. The live fish prey were more streamlined than the shrimp pieces; however, we assume that the drag properties of live fish and shrimp pieces are similar enough that differences in D_{prey} reflect real differences in inertial suction produced by the predator. Even if the drag and inertial properties of the two prey were slightly different, we would expect that the larger fish prey exerted a larger resistive drag force, especially if the prey were performing a C-start escape response. Therefore, if the same amount of suction were produced by *O. digrammus* in response to the two prey types, we should have seen smaller D_{prey} values for the live fish prey, not larger values.

D_{prey} may also be affected by the initial distance between the predator and prey at the onset of the strike, predator–prey D. Larger measures of D_{prey} may be a reflection of strikes that were initiated on live prey from a significantly greater distance. If strikes at midwater prey are initiated sufficiently close to the prey item, there may be no physical way for *O. digrammus* to achieve D_{prey} values comparable to those measured from strikes at live prey, even if the same absolute suction velocity was generated in strikes on both prey types. In fact, *O. digrammus* initiates strikes at midwater prey from an average distance of 1.64 cm, a distance that is smaller than the 2.26 cm covered by the prey alone, D_{prey}, in strikes at live prey (see Table 1). The average D_{prey} measured for live prey strikes is 69% of the average predator–prey D for that prey item, while the average D_{prey} measured for midwater prey strikes is 57% of the average predator–prey D for midwater strikes. For *O. digrammus* to generate the same suction ve-

locity over that fractional distance, it would need to capture the midwater prey slightly faster than live prey, in 0.020 sec versus 0.024 sec for strikes on live prey. The difference between 0.020 and 0.024 sec may be trivial; but strikes on midwater prey actually average 0.044 sec, indicating that the same suction velocities were not generated. A rough approximation of velocity can be obtained from the D_{prey} and time to maximum gape data in Table 1. These values suggest that suction velocities of about 21 cm sec^{-1} are generated for midwater prey and of around 94 cm sec^{-1} for live prey. D_{prey} appears to be a good proxy in this study for suction production, and more suction is used by *O. digrammus* to capture live prey.

Differences in D_{prey} are likely the result of modulation of the displacement variables. When feeding on live fish cranial elevation was the largest and hyoid depression reached its most depressed position. These variables reflect greater expansion of the head, which facilitates the acceleration of a larger volume of water. Note that for successful prey capture to occur in an aquatic medium, the prey item must be entrained in this volume of accelerating water and drawn into the mouth cavity. Flow visualization studies are needed to determine how much water is being accelerated by suction-feeding *O. digrammus*, and quantitatively how that volume is affected by greater expansion of the head.

Attached prey effects

Interestingly, like the live prey, the attached prey treatment elicited faster strikes. If modulation of prey capture behaviors is to increase prey capture success, then it would seem that strikes should be more rapid on prey types that have the potential to escape, as is the case with live prey. But it is less intuitive why strikes on attached prey would be faster. Because faster expansion of the head presumably leads to greater suction generation (Liem, '90), one interpretation is that *O. digrammus* is also using enhanced suction to dislodge attached prey. Nemeth ('97b) also found that the responses to elusive and clinging prey were similar. Both were faster and associated with greater suction production than nonelusive prey. There is evidence that some teleosts suck limpets—small gastropods with a muscular foot that adheres strongly to the substrate—off of rocks (Liem, '90). It seems likely that suction was attempted by *O. digrammus* as the primary mode of prey capture. This might explain why we did not detect a difference in kinematics between

strikes in which the prawn piece was successfully removed from the clip and strikes in which the piece remained behind. We suggest that the same type of suction prey capture was attempted by *O. digrammus* in all strikes on attached prey, but the prey was not always dislodged by the suction. If the attached prey was not removed, the jaws were subsequently closed on the item, rather than behind the item as they would be if suction effectively drew the prey into the mouth fully. Unsuccessful strikes were potentially just incomplete suction strikes.

This suction–biting differs from the manipulative biting prey capture described by Liem ('80) for cichlids. Liem ('79) described novel behaviors in which the muscles of the jaw were continuously modulated and were even activated asynchronously, presumably to produce forces necessary to shear or clip the attached prey item. Although we do not have electromyographic data in our study, the gross behavior of *O. digrammus* in response to the attached prey treatment would suggest that such modulation was not occurring. Once *O. digrammus* failed to suck the prey off the clip, it did not attempt additional strikes at the prey or different behaviors to get the prey off the clip. While vigorous lateral swings of the head to wrench attached prey free have been observed in other wrasse species, and in *O. digrammus* on occasion, this behavior was not documented in this study in response to the attached prey.

This finding illustrates the trade-off between biting and suction expressed in both behavior and morphology. The cichlids studied by Liem ('79) had a number of unique morphological features to enhance biting and other manipulations as a mode of prey capture, but the species studied were apparently still able to suction feed, and suction was utilized frequently (see also Robinson and Wilson, '98, and references therein). However, this does not necessarily mean that the species studied had high performance when suction feeding. Other studies suggest that there is a trade-off in performance when taxa are modified to enhance either suction or biting (De Visser and Barel, '96; Bouton et al., '98, '99). Biting and other manipulative modes of prey capture are often seen in predators possessing hypertrophied jaw bones and musculature, which have been shown to enhance force production (Wainwright et al., '91; Turingan and Wainwright, '93; Turingan et al., '95; De Visser and Barel, '96). Further, it has been proposed that these anatomical changes act to decrease the amount of suction that can be produced by ex-

pansion of the head because of modifications to the hyoid in biting species (De Visser and Barel, '96; Bouton et al., '99).

There is a basic trade-off in mechanical linkage systems between force and speed; systems capable of high force production sacrifice high-speed movements with the same architecture (Barel, '83; Westneat, '94; Wainwright, '96). This trade-off is evident in both the simple third-order lever system of the lower jaw and the more complex four-bar linkage of the anterior jaws of cheiline wrasses, a group containing both high-performance biters and suction feeders (Westneat, '94). Species modified for biting likely compromise their capacity for highly effective suction feeding, and species that are good inertial suction feeders are expected to perform poorly at high-force biting behaviors. However, it should be noted that for suction feeding, the mechanics of jaw opening determine speed, whereas for biting, jaw-closing mechanics determine force. Because different muscles drive the same morphology for suction and biting, the relative muscle masses, insertion angles, and motor patterns of jaw openers and closers represent key levels of design and function. Future work could combine studies of lever and linkage design with measurements of forces and contraction patterns in jaw opening and closing muscles to attain a more complete understanding of the force–velocity trade-off in fish jaws.

In this study we observed that three types of prey: live, midwater, and attached, elicited repeatable differences in the kinematic variables measured from *O. digrammus*. *O. digrammus* perceived differences in the prey treatments and responded with modified kinematic behaviors. However, *O. digrammus* did not always successfully capture the attached prey. Thus, modulation does not necessarily generate high performance. It may merely represent the maximum degree of behavioral change possible in attempting to capture novel prey. In response to the attached prey treatment, we observed what appeared to be attempts at removal via inertial suction. In our study, if this attempt failed, no subsequent prey capture behaviors were observed. The manipulative types of behaviors described by Liem ('80) were not observed; thus, either they are uncommon in the repertoire of *O. digrammus* or we did not present the right stimulus to induce them. We conclude that *O. digrammus*, typically feeding on evasive, moving prey such as fishes and decapods (Westneat, '95), exhibited low performance on attached prey due to constraints on the ability to

perform manipulative biting behavior. Such manipulative strategies may be more common in other cheiline wrasses, as they routinely eat hard prey items on the reef, and a biting and crushing mode of prey capture may be the basal behavior for the group (Westneat, '95).

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