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Mechanisms of benthic prey capture in wrasses (Labridae)

Abstract Teleost fishes capture prey using ram, suction, and biting behaviors. The relative use of these behaviors in feeding on midwater prey is well studied, but few attempts have been made to determine how benthic prey are captured. This issue was addressed in the wrasses (Labridae), a trophically diverse lineage of marine reef fishes that feed extensively on prey that take refuge in the benthos. Most species possess strong jaws with stout conical teeth that appear well-suited to gripping prey. Mechanisms of prey capture were evaluated in five species encompassing a diversity of feeding ecologies: *Choerodon anchorago* (Bloch, 1791), *Coris gaimard* (Quoy and Gaimard, 1824), *Hologymnosus doliatus* (Lacepède, 1801), *Novaculichthys taeniourus* (Lacepède, 1801) and *Oxycheilinus digrammus* (Lacepède, 1801). Prey capture sequences were filmed with high-speed video at the Lizard Island Field Station (14°40′S, 145°28′E) during April and May 1998. Recordings were made of feeding on pieces of prawn suspended in the midwater and similar pieces of prawn held in a clip that was fixed to the substratum. Variation was quantified among species and between prey types for kinematic variables describing the magnitude and timing of jaw, hyoid, and head motion. Species differed in prey capture kinematics with mean values of most variables ranging between two and four-fold among species and angular velocity of the opening jaw differing seven-fold. The kinematics of attached prey feeding could be differentiated from that of midwater captures on the basis of faster angular velocities of the jaws and smaller movements of cranial structures which were of shorter duration. All five species used ram and suction in combination during the capture of midwater prey. Surprisingly, ram and suction also dominated feedings on attached prey, with only one species making greater use of biting than suction to remove attached prey. These data suggest an important role for suction in the capture of benthic prey by wrasses. Trade-offs in skull design associated with suction and biting may be particularly relevant to understanding the evolution of feeding mechanisms in this group.

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Introduction

The Labridae (including wrasses, odacids and parrotfishes; Kaufman and Liem 1982) is a group of about 580 species of marine fishes found on coral and rocky reefs around the world. As conspicuous members of reef communities, they show an exceptional range of trophic habits, including herbivory, planktivory, piscivory, durophagy (hard prey including molluscs and corals), ectoparasite feeding, and species that feed on a broad range of the invertebrates found in reef environments (Randall 1967; Hobson 1974; Westneat 1995). Because of this ecological diversity and their significance as a major teleost radiation, labrid feeding mechanics have received considerable attention. To date, prey capture mechanisms have been studied in herbivorous parrotfishes (Bellwood and Choat 1990; Alfaro and Westneat 1999) and predatory wrasses (Westneat and Wainwright 1989; Westneat 1990, 1991; Sanderson 1990). It is known that parrotfishes move their oral jaws in a biting action

to scrape or excavate rocky substrata or crop algae, and odacids may perform similar behaviors with their parrotfish-like teeth (Nelson 1994). In contrast, studies indicate that wrasses use inertial suction feeding as their primary mechanism of capturing animal prey (Westneat and Wainwright 1989; Westneat 1990, 1991; Sanderson 1990).

However, there is some reason to question whether inertial suction is the dominant feeding mechanism in wrasses. Previous studies focused on the capture of midwater prey, but most wrasse species include in their diet a large number of prey that hide in confined spaces within the rocky reef matrix which may require considerable effort in order to extricate them from their holdfasts. The cryptic nature of such prey suggests that wrasses may also frequently employ biting and gripping behaviors during prey capture, rather than rely solely on inertial suction.

Additional evidence of an important role for biting behavior is found in the morphology of the wrasse oral jaws (Fig. 1). Most species have robust jaw bones with several stout, conical teeth positioned anteriorly on the lower and upper jaws. The adductor mandibulae muscle is usually well developed and has a high mechanical advantage where it inserts on the mandible (Westneat 1994; Wainwright and Richard 1995). The wrasse jaw has been interpreted on a number of occasions as being specialized for biting (Gregory 1933; Rognes 1973; Tedman 1980).

In the light of these observations on the diversity of suction and biting strategies in wrasses, we sought to determine specifically how attached benthic prey are captured by these fishes. A previous analysis of prey capture kinematics in the cheiline wrasse *Oxycheilinus digrammus* (Ferry-Graham et al. 2001) indicated that this species used inertial suction to remove attached prey from its holdfast. Although this result is inconsistent with the expectation of prey capture by biting, *O. digrammus* is unusual among wrasses in being a specialized predator of fishes and free-moving, elusive invertebrates such as penaeid shrimp and mysids (Westneat 1995) so it may not represent a general model for wrasse prey capture. We therefore broadened our analysis by incorporating four additional wrasse species that feed predominantly on benthic invertebrates including those that potentially grip the substratum (i.e., gastropods, echinoderms and decapod crabs). Using data derived from high-speed video recordings we contrasted the kinematics of prey capture during feeding on midwater prey to patterns of movement when feeding on an attached benthic prey.

Materials and methods

We studied feeding in five wrasse species (Fig. 1): *Choerodon anchorago* (Bloch, 1791), *Coris gaimard* (Quoy and Gaimard, 1824), *Hologymnosus doliatus* (Lacepède, 1801), *Novaculichthys taeniourus* (Lacepède, 1801) and *Oxycheilinus digrammus* (Lacepède, 1801). *Choerodon anchorago* is robust-jawed, has large blunt canine teeth,
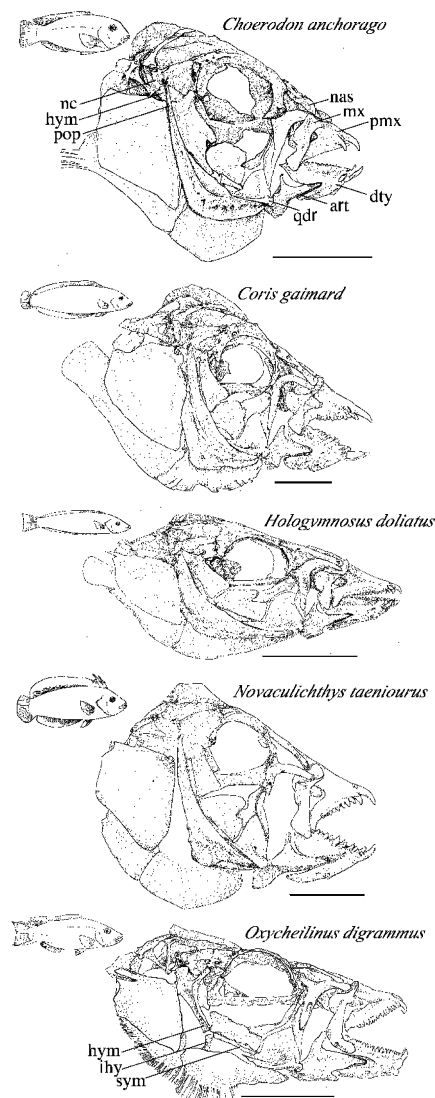

Fig. 1 Drawings of the cephalic osteology of the five study species: *Choerodon anchorago*, *Coris gaimard*, *Hologymnosus doliatus*, *Novaculichthys taeniourus*, and *Oxycheilinus digrammus*. All scale bars are 1 cm. Abbreviations are as follows: *nas* nasal; *mx* maxilla; *pmx* premaxilla, *dty* dentary; *art* articular (dentary + articular = lower jaw); *qdr* quadrate; *pop* preopercle; *hym* hyomandibula; *nc* neurocranium; *ihy* interhyal; *sym* symplectic. *O. digrammus* was drawn with the preopercle removed to more clearly reveal the position of the hyoid apparatus. Note the differences in head and tooth size and shape among species. Thumbnail sketches of the intact fish are provided to further show relative differences in body shape, head shape, and mouth size

and a dorso-ventrally deep skull (Fig. 1). This species feeds largely on hard invertebrate prey such as molluscs and crabs (Tedman 1980). In contrast, both *Coris gaimard* and *H. doliatus* have smaller mouths, more finely structured jaws, and smaller teeth (Fig. 1). *Coris gaimard* feeds primarily on small infaunal bivalves and gastropods (Hiatt and Strasburg 1960). *H. doliatus* captures more elusive small invertebrates and fishes. *N. taeniourus* has a slightly larger mouth (Fig. 1), and is known for its behavior of turning over rocks and preying upon the exposed crabs and other invertebrates (Randall et al. 1990). *O. digrammus* has the largest mouth size of the five species studied (Fig. 1) and is unusual among wrasses in that it feeds primarily on fish and highly mobile invertebrate prey (Westneat 1995).

Specimens were collected with barrier nets from the reefs around Lizard Island (14°40′S, 145°28′E), on the mid-shelf of Australia's Great Barrier Reef. The standard lengths (cm) of the individuals were as follows: *Choerodon anchorago*: 16.2, 16.4, 24.5; *Coris gaimard*: 15.9, 21.5, 22.1; *H. doliatus*: 17.7, 21.8; *N. taeniourus*: 12.2, 14.8, 19.3; and *O. digrammus*: 17.0, 18.4, 18.5. They were maintained at 23 ± 2°C in 100 l flow-through aquaria at the Lizard Island Research Station during April and May 1998. Fish were held for several days prior to experimentation while they acclimated to captivity and became accustomed to feeding on pieces of prawn.

Two experimental prey treatments were used to study prey capture kinematics: attached prey and prey suspended in the water column. We used the same prey in each treatment to control for other prey item effects, such as size or type. The prey used was a commercially available prawn (*Penaeus* sp.); the cephalothorax and abdominal segments without the exoskeleton were cut into pieces approximately 2 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 to create the midwater treatment.

Feeding sequences were recorded at 400–1,000 images s^{-1} with an Adaptive Optics Kineview digital video system. Frame rates were selected so that at least 20 frames per feeding sequence were obtained (defined below). During filming, the tanks were illuminated with two 600 W floodlights. For scale, a rule was placed in the field of view and recorded for several frames. 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 aquaria where the fish were maintained and generally occurred over a 3- to 5-day period for each individual. Sequences were stored digitally for analysis.

We analyzed only sequences in which the camera was not moving, a lateral view of the fish could clearly be seen in the image, and the fish body axis was perpendicular to the camera to minimize measurement error. Time zero (t_0), the onset of the strike, was taken as the first image showing movement of the jaws. Sequences began at t_0 and ended at the conclusion of the strike as indicated by the return of the mandible to the relaxed, pre-feeding position. Five feeding sequences were analyzed from each prey item for each of the three individuals (except *Hologymnosus doliatus* for which only two individuals were analyzed).

To quantify movement of skeletal elements on the predator, as well as whole movements of the prey and predator, eight points were digitized in each video frame of each sequence using NIH Image 1.6 for Macintosh (Fig. 2). From the digitized points we calculated several kinematic variables. Displacement 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 (points 8 and 1; Fig. 2). 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 thusly express the movement relative to the body of the fish. Angular kinematic variables were the angle of the neurocranium relative to the body (cranial elevation, degrees; an angle created by connecting points 2, 3, and 5; Fig. 2) and the angle of the lower jaw relative to the neurocranium (lower jaw rotation, degrees; points 4, 7, 8; Fig. 2). Angles were expressed as a change in angle relative to the angle at t_0, thus the starting position at t_0 was subtracted from each subsequent measure and all angular excursions begin at 0°. The maximum achieved for each displacement and angular kinematic variable from each feeding sequence was used in the statistical analyses.

We also determined several timing and velocity variables for each feeding sequence. Timing variables were defined as the time at which the maxima were achieved for each angular and displacement variable relative to t_0. Time to jaw closure (in seconds) was estimated from the time of maximum gape to the time that the jaws
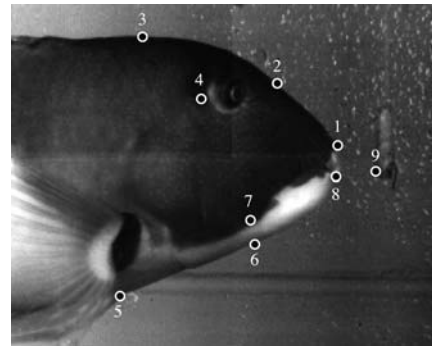

Fig. 2 *Choerodon anchorago*. Sample image from the Kineview high-speed video system of fish approaching the midwater prey treatment with the nine digitized points for determining kinematic variables: *1* the anterior tip of the premaxilla (upper jaw); *2* the posterior margin of the nasal bone; *3* the dorsal-most point on the neurocranium as approximated by external morphology; *4* the approximate point of articulation of the hyomandibula with the neurocranium; *5* the dorsal margin of the insertion of the pelvic fin on the body (a reference point); *6* antero-ventral protrusion of the hyoid; *7* the approximate articulation of the lower jaw with the quadrate (the jaw joint); *8* the anterior tip of the dentary (lower jaw); and *9* the margin of the prey item closest to the predator

came together at the end of the sequence. This variable can be confounded by whether or not the jaws closed on a prey item in a bite, or whether the jaws closed fully after engulfing the prey. Lower jaw angular velocity (0 s^{-1}) was also calculated for each digitized frame by dividing the change in the lower jaw angle by the time between frames. These incremental velocities were then averaged over two periods, time to maximum lower jaw angle (time to jaw opening), and the time from maximum lower jaw angle to the time to jaw closure (time to jaw closing). Therefore, the angular velocity variables were the average angular velocity achieved during jaw opening, and the average angular velocity achieved during jaw closing.

We quantified three variables that summarized the amount of ram and suction used to draw prey into the mouth. The first of these was predator–prey distance (cm), a measure of the distance between the lower jaw tip of the predator and the point digitized on the prey item at onset of the strike (points 8 and 9; Fig. 2). Suction distance (cm) was taken as the distance moved by the prey item towards the predator from t_0 to the time when the prey item was captured using the points defined above (Wainwright et al. 2001). Capture is defined here as the time when the prey was engulfed within the mouth, or was trapped by the teeth if a bite occurred. Ram distance (cm), the distance moved by the predator towards the prey, was measured over the same time interval. The tip of the lower jaw was used as the digitized marker for estimating this distance. This measure is largely a reflection of body ram, however, the contribution of jaw ram to prey capture can be estimated from the kinematic variable premaxilla protrusion described above. Kinematic and ram–suction variables were measured on a total of 140 prey capture sequences.

Finally, we were able to review a larger number of feeding sequences on both the midwater (88 sequences total) and attached prey (80 sequences total) and categorize the strikes as being suction, suction-bite, or aggressive-bite strikes. The suction category was applied when the prey was drawn into the mouth and buccal cavity using only ram and suction, and the jaws did not make contact with the prey item during closing. A suction-bite strike occurred when the prey item was mostly drawn into the mouth with suction but the jaws closed on the prey. In these strikes, the bite was not used to pull the prey off its holdfast. Aggressive-bite strikes incorporated suction to partly draw the prey into the mouth, but the primary action used to remove the prey was a vigorous bite, often accompanied by turning or shaking of the head and body.

Statistical analyses

We used discriminant function analysis (DFA) to determine if kinematic and ram–suction variables could be used to distinguish strikes among species and between prey types, and to identify the characteristics of strikes on each kind of prey item that contributed to the distinction (Systat 9.0 and JMP). The DFA uses the data from all prey types and all individuals for the 16 dependent vari-ables identified above (see also Tables 1, 2, 3). However, DFA permits the use of only one independent or discriminating variable. Thus, to analyze species and prey type effects simultaneously sep-arate categories were created for each species capturing each prey type resulting in ten categories or ten levels of possible discrimi-nation (i.e., *Oxycheilinus digrammus* on midwater prey, *O. di-grammus* on attached prey, etc.). The classifications for each strike predicted by the DFA were compared with the actual classifications

Table 1 Maximum displace-ments for measured kinematic variables for the five species studied separated by prey type, midwater and attached. Values are means ($\pm$SE) of individual means ($n=3$ except for *Holo-gymnosus doliatus* where $n=2$). Species are as follows: *Ca, Choerodon anchorago; Cg, Cor-is gaimard; Hd, Hologymnosus doliatus; Nt, Novaculichthys taeniourus; Od, Oxycheilinus digrammus*

Midwater prey						
Species	SL (cm)	Gape (cm)	Lower jaw angle (°)	Premaxilla protrusion (cm)	Cranial elevation (°)	Hyoid depression (cm)
Ca	19.0	1.51 (0.17)	26.17 (0.66)	0.25 (0.06)	4.12 (0.42)	0.36 (0.06)
Cg	19.8	0.86 (0.07)	24.13 (2.96)	0.22 (0.05)	4.08 (1.02)	0.19 (0.01)
Hd	19.8	0.68 (0.01)	16.21 (0.68)	0.16 (0.05)	9.91 (2.61)	0.30 (0.02)
Nt	15.4	1.27 (0.05)	41.99 (2.47)	0.22 (0.03)	4.90 (0.53)	0.26 (0.04)
Od	18.0	1.26 (0.10)	25.09 (2.38)	0.34 (0.02)	5.47 (1.07)	0.53 (0.02)
Attached prey						
Ca	19.0	1.24 (0.16)	20.13 (0.22)	0.30 (0.06)	3.66 (1.37)	0.42 (0.11)
Cg	19.8	0.82 (0.07)	22.44 (1.44)	0.16 (0.02)	2.32 (0.16)	0.35 (0.09)
Hd	19.8	0.60 (0.01)	17.11 (0.31)	0.13 (0.01)	3.14 (0.52)	0.16 (0.01)
Nt	15.4	1.02 (0.08)	30.89 (1.53)	0.31 (0.04)	8.90 (2.65)	0.30 (0.03)
Od	18.0	1.10 (0.09)	22.47 (2.37)	0.37 (0.02)	6.76 (0.96)	0.54 (0.04)

Table 2 Timing and velocity variables for the five species studied separated by prey type, midwater and attached. Values are means ($\pm$SE) of individual means ($n=3$ except for *Holo-gymnosus doliatus* where $n=2$). Species are as follows: *Ca, Choerodon anchorago; Cg, Coris gaimard; Hd, Hologym-nosus doliatus; Nt, Novaculich-thys taeniourus; Od, Oxycheilinus digrammus*

Midwater prey							
Species	Time to maximum (ms)				Time to (ms)	Average angular velocity (° s^{-1})	
	Lower jaw angle[a] (°)	Premaxilla protrusion (cm)	Cranial elevation (°)	Hyoid depression (cm)	Jaw closure	Jaw opening	Jaw closing
Ca	100.67 (13.27)	123.08 (16.89)	123.33 (22.50)	91.50 (6.21)	73.00 (14.01)	222.08 (20.36)	370.74 (54.52)
Cg	54.62 (3.01)	51.95 (5.10)	58.61 (4.10)	55.71 (1.76)	35.34 (4.87)	357.27 (46.47)	384.71 (69.59)
Hd	38.25 (7.72)	32.64 (9.03)	56.67 (11.79)	68.49 (6.66)	29.40 (0.42)	292.17 (19.30)	447.42 (83.42)
Nt	38.67 (1.66)	44.30 (7.05)	42.88 (1.94)	50.80 (3.43)	33.97 (1.81)	1063.45 (44.74)	673.62 (18.72)
Od	46.00 (4.10)	55.67 (2.04)	37.36 (7.86)	63.17 (5.69)	44.33 (3.34)	423.97 (37.09)	463.11 (21.28)
Attached prey							
Ca	102.33 (8.19)	80.92 (13.74)	112.67 (23.36)	109.00 (11.89)	60.33 (7.93)	194.84 (27.16)	360.91 (22.76)
Cg	27.67 (2.27)	15.28 (1.72)	48.08 (6.84)	28.09 (3.51)	48.79 (5.39)	863.42 (16.83)	430.15 (46.57)
Hd	18.50 (1.41)	15.88 (2.18)	38.25 (3.18)	41.50 (2.36)	34.50 (2.83)	825.59 (4.08)	325.71 (65.73)
Nt	25.72 (3.49)	34.79 (2.00)	39.95 (4.94)	41.48 (0.59)	30.38 (2.09)	1387.23 (95.77)	496.77 (6.84)
Od	25.38 (1.52)	29.08 (2.10)	28.21 (1.53)	37.83 (2.80)	20.79 (0.41)	612.27 (88.65)	654.57 (90.38)

[a] The times to maximum gape and lower jaw angle were determined independently but are identical

Table 3 Positional variables for the five species studied separated by prey type, midwater and attached. Values are means (±SE) of individual means ($n = 3$ except for *Hologymnosus doliatus* where $n = 2$). Species are as follows: Ca, *Choerodon anchorago*; Cg, *Coris gaimard*; Hd, *Hologymnosus doliatus*; Nt, *Novaculichthys taeniourus*; Od, *Oxycheilinus digrammus*

Midwater prey				
Species	SL (cm)	Suction distance[a] (cm)	Ram distance (cm)	Predator–prey distance (cm)[b]
Ca	19.0	0.70 (0.07)	1.78 (0.32)	1.30 (0.22)
Cg	19.8	0.79 (0.06)	1.09 (0.12)	0.94 (0.06)
Hd	19.8	0.65 (0.01)	1.22 (0.29)	1.10 (0.25)
Nt	15.4	0.71 (0.02)	1.28 (0.08)	1.06 (0.09)
Od	18.0	0.93 (0.08)	1.51 (0.09)	1.61 (0.04)
Attached prey				
Ca	19.0	0.29 (0.08)	1.83 (0.29)	1.26 (0.07)
Cg	19.8	0.17 (0.01)	0.93 (0.04)	0.38 (0.04)
Hd	19.8	0.37 (0.04)	1.02 (0.04)	0.48 (0.01)
Nt	15.4	0.37 (0.08)	0.97 (0.03)	0.55 (0.07)
Od	18.0	0.53 (0.11)	1.16 (0.12)	0.63 (0.08)

[a] Suction distance measures on attached prey are confounded by the nature of the attachment but they illustrate that fish were often still able to exert some influence on the prey
[b] Note that ram distance can exceed predator–prey distance for several reasons, most notably if the prey is pushed or moved by the attacking fish prior to taking it into the mouth fully, and because, in the absence of biting, ram and suction distance are calculated from t_0 until the time that the prey is engulfed fully to incorporate the effects of suction late in the strike

in a 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: a random distribution of the strikes among the ten cells. The mean scores from the canonical factors with eigenvalues greater than one were plotted against one another to visualize the position of strikes in canonical space. The canonical loadings were used to determine which of the original dependent variables were most 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 0.50. This is well above the value of *r* that is significant at $P = 0.05$ for the sample size used in the DFA (Zar 1984).

Because DFA is meant only to determine group identity, we also performed a series of ANCOVA models to explicitly test the hypothesis that strikes from different species and on each type of prey were different from one another. We included a covariate in this model in order to further determine if there was a detectable effect of fish size since sizes did vary among individuals. In the absence of a significant covariate we dropped this level of the analysis and performed multiple ANOVAs. To increase the power and limit the total number of tests performed we tested only those kinematic variables that proved to be informative in the DFA, or those that loaded strongly on the significant canonical factors from the DFA. The model used was a two-way model with prey type and species as fixed factors. Significance of *P*-values for all kinematic variables was determined using a table-wide sequential Bonferroni correction for multiple tests (Rice 1989). Given a significant ANOVA result for a main effect on a kinematic variable, Fisher's protected least significant difference (PLSD) tests were performed post hoc to determine which species differed. The assumptions of equal variances and normality were satisfactorily met.

We used the ANOVA results to estimate the variance components (ω^2) attributable to each of the factors, species and prey treatment, as well as the interaction term following the methods prescribed in Graham and Edwards (2001). Variance components indicate which of the factors account for more of the total variance in the dataset, which can then be used to infer which of the factors has a larger effect on prey capture kinematics. Variance components describe the statistical fit of the ANOVA model; the fit is a measure of the magnitude of the effect of any factor on the response variables (Graham and Edwards 2001), and is analogous to the coefficient of determination (r^2) in regression analyses. For our two-fixed-factor ANOVA model, variance components for the species effect were determined using the formula: $(MS_{species} - MS_{error})(J-1)/nJK$, where *n* is the sample size at the lowest level (individuals, $= 3$), *J* is the number of levels of species ($= 5$), and *K* is the number of levels of prey ($= 2$). Variance components for the prey effect were determined from the equation $(MS_{prey} - MS_{error})(K-1)/nJK$, and for the interaction term $(MS_{species \times prey} - MS_{error})(J-1)(K-1)/nJK$. The variance component for the error term of the ANOVA is the MS_{error}. These four values are summed and the fraction of the total variance attributed to each term is calculated.

Results

In all feeding trials, after the prey was placed into the tank, fish rapidly responded and approached the prey item. During some encounters fish came to a distinct halt before conspicuously orienting towards the prey, but the same species also frequently charged forward to attack the prey without the initial orientation. In all cases, the attack was initiated by jaw depression. This was usually, but not always accompanied by elevation of the cranium (Table 1). The most extensive cranial elevation, 9–10°, was observed in *Hologymnosus doliatus* feeding on

midwater prey. *Novaculichthys taeniourus* feeding on attached prey also achieved angles of nearly 9° (Table 1). Average cranial elevation was about 5° or less in the other species, although this measure varied considerably among strikes. Premaxilla protrusion and hyoid depression were modest, 0.5 cm or less, regardless of the prey type or the predator species (Table 1). *N. taeniourus* consistently achieved the largest lower jaw rotation, greater than 30° for both prey types, although *Choerodon anchorago* achieved the largest absolute gape distance (Table 1). The longest strike duration was found in *Choerodon anchorago* which required 0.10 s to achieve peak gape and lower jaw angle plus 0.06–0.07 s to close the jaws. Other species took 0.05 s or less to achieve peak gape and lower jaw angle, and tended to close the jaws in about the same amount of time (except *Coris gaimard* which took about twice as long to close the jaws as open them when feeding on attached prey, Table 2). *Choerodon anchorago* also consistently demonstrated the largest ram distances of nearly 2 cm, with *Oxycheilinus digrammus* being the next closest at about 1.2–1.5 cm for the two prey types (Table 3).

The DFA correctly categorized at least 85% of the prey capture events for eight of the ten categories of species by prey type that we created (Table 4). The analysis was less successful at identifying strikes on midwater prey by *Choerodon anchorago* (62% correct) and strikes on attached prey by *N. taeniourus* (71% correct). The chi-square likelihood ratio statistic indicated that the predicted classifications were significantly different from a random distribution ($\chi^2 = 417.96$; $P < 0.0001$). Three canonical factors were extracted from the analysis that had eigenvalues of 0.972 or greater. These three factors together explained 75.9% of the total variance in the dataset. The first factor was highly correlated with time to maximum gape, time to maximum lower jaw angle, and ram distance (Fig. 3). Strikes on midwater prey tended to have lower scores on this axis than attached prey strikes from the same species, indicating longer times to maximum gape and lower jaw angle, and longer ram distance. The second factor was correlated with maximum gape and maximum lower jaw angle, and midwater strikes tended to have the higher scores on this axis relative to attached prey strikes from the same species (Fig. 3). This suggests that larger maximum gapes and lower jaw angles were achieved during midwater strikes when compared with strikes on attached prey for the same species. The third factor was correlated with lower jaw opening velocity as well as predator–prey distance, and midwater strikes typically scored lower on this axis than attached prey strikes for the same species (Fig. 3). Attached prey strikes were initiated at closer range, and the prey were usually captured with faster jaw-opening angular velocities.

No size effects were detected by the ANCOVA models, thus ANOVA was used for further hypothesis testing. The ANOVAs revealed that significant differences existed among species in prey capture kinematics (Table 5). *Choerodon anchorago*, the species that was frequently an exception to the prey-type effects noted above, had the largest maximum gape and took the longest to achieve this gape, but did not use the largest lower jaw angle to achieve this (Fig. 4). The maximum lower jaw angle of *Choerodon anchorago* was not different from *O. digrammus* or *Coris gaimard* (Table 5). *N. taeniourus* achieved the largest maximum lower jaw angle, and a large gape (Fig. 4); however it did not take longer than any other species to achieve these angles or displacements (Table 5). This species had the highest jaw-opening velocity (Fig. 4, Table 5). *Choerodon anchorago* tended to show the largest average ram and predator–prey distances, although *O. digrammus* had a larger predator–prey distance when striking midwater prey (Fig. 4). Species with larger ram distances and larger predator–prey distances consistently exhibited reduced jaw-opening angular velocities (Fig. 4).

High jaw rotational velocities can be achieved by reducing the time taken for the excursion of the jaw or by increasing the angle that is traversed. Both effects were seen on our study (Fig. 5). As noted above, *N. taeniourus* consistently achieved the highest maximum jaw angle and in a relatively short period of time (Table 2). At the

Table 4 DFA results indicating the ability of the analysis to categorize strikes by predatory species and prey type. Species are as follows: *Ca, Choerodon anchorago; Cg, Coris gaimard; Hd, Hologymnosus doliatus; Nt, Novaculichthys taeniourus; Od, Oxycheilinus digrammus*

| Species	No. correctly classified		Misclassified as:
	Midwater prey	Attached prey	
Ca	62%	89%	1 *Ca* midwater strike classified as a *Ca* attached strike, 3 *Ca* midwater strikes classified as *Cg* midwater strikes, 1 *Ca* midwater strike classified as an *Od* attached strike
Cg	92%	100%	1 *Cg* midwater strike classified as a *Hd* midwater strike
Hd	86%	100%	1 *Hd* midwater strike classified as an *Od* midwater strike
Nt	86%	71%	1 *Nt* midwater strike classified as a *Hd* attached strike, 1 *Nt* midwater strike classified as an *Od* attached strike 1 *Nt* attached strike classified as a *Cg* midwater strike, 1 *Nt* attached strike classified as a *Cg* attached strike, 1 *Nt* attached strike classified as a *Nt* midwater strike, 1 *Nt* attached strike classified as an *Od* attached strike
Od	92%	82%	1 *Od* midwater strike classified as a *Cg* attached strike, 1 *Od* attached strike classified as a *Nt* attached strike, 1 *Od* attached strike classified as a *Nt* midwater strike
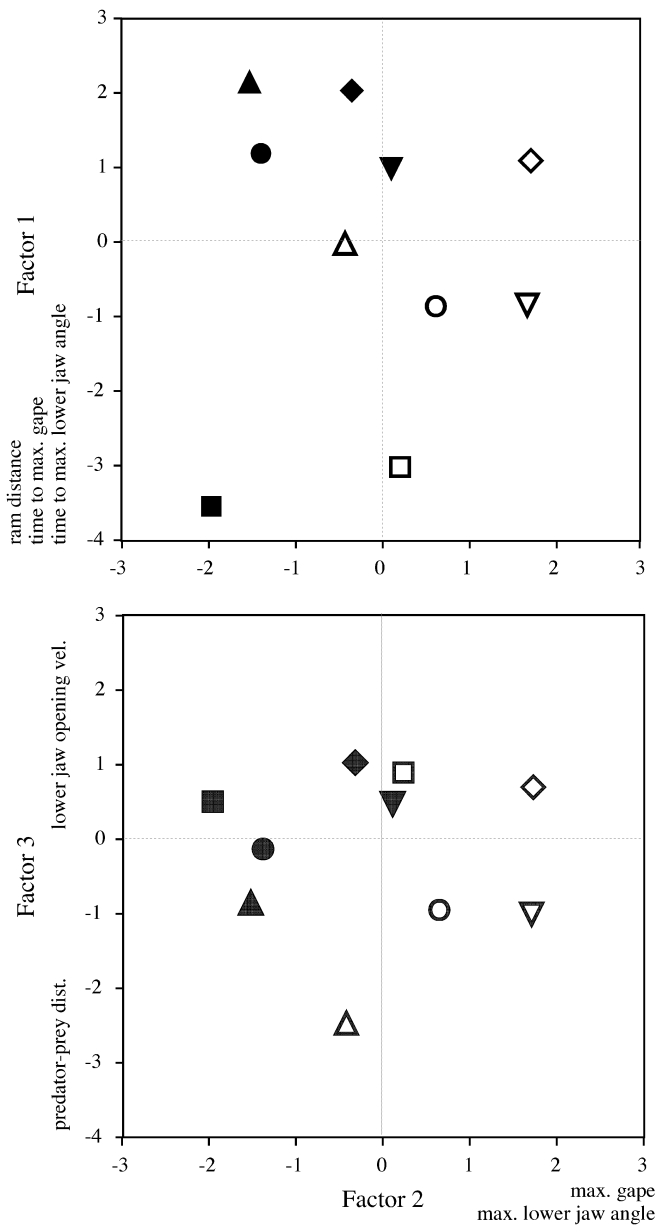
Fig. 3 Mean canonical scores for each species by prey type for the first three canonical factors generated by the DFA analysis. The kinematic variables that loaded on each canonical factor are labeled on the appropriate axis. Variables placed in the positive region of each axis load positively on that axis (towards the top on the *Y-axes* and to the right on the *X-axis*), indicating a positive correlation with that axis. Variables in the negative region of each axis loaded negatively on that axis. In each plot the symbols are coded as midwater prey (*open*) and attached prey (*filled*). Species are: *Choerodon anchorago* (*squares*), *Coris gaimard* (*circles*), *Hologymnosus doliatus* (*triangles*), *Novaculichthys taeniourus* (*diamonds*), and *Oxycheilinus digrammus* (*inverted triangles*)

often much smaller maxima were achieved. The overall effect is seen in the steeper slope of increasing jaw angle on attached prey relative to midwater prey (Fig. 5), and in faster jaw-opening velocities for all species but *Choerodon anchorago* (Figs. 4, 5).

All species combined some ram with some suction to capture both prey types (Table 3). Values of ram distance differed among species (Table 5), and suction distance was shorter when feeding on attached prey for all species (Table 3). Differences between prey type in suction distance may partly reflect modulation of feeding effort, but this is confounded by the difference in resistance to water flow presented by the two treatments (note that a significant species effect was not detected for this variable; ANOVA $F = 1.54$, $P = 0.19$, power $= 48\%$). Attached prey were rarely pulled free using suction alone (Fig. 6). However, in all feeding events, including those on attached prey, some suction was detected. A major distinction between attacks on midwater and attached prey was that midwater attacks rarely involved the fish gripping the prey in a biting action, while attached prey were usually captured using a combination of suction and biting (Fig. 6). Only in *O. digrammus* did we observe capture of the attached prey using only suction and no biting, which occurred in 4 out of 15 strikes. The most common pattern with attached prey was for fish to employ suction to draw the prey into the mouth, and to complete the strike by closing the jaws on the portion of the prey not drawn into the mouth by suction ('suction-bite' in Fig. 6). In 20–35% of attached prey feedings *N. taeniourus*, *Coris gaimard* and *H. doliatus* used an aggressive bite, often coupled with a lateral jerk of the head or whole body, to remove the prey. However, even in these feedings it was always possible to see the prey being drawn into the mouth by suction prior to the biting action. *O. digrammus* never used this aggressive bite strategy, but *Choerodon anchorago* used it in 11 of 16 strikes on attached prey.

The variance components from each of the ANOVAs revealed that the species factor tended to explain more of the variance in the dataset than the prey type factor (Table 6). Variability within displacement and timing variables, such as maximum gape and time to maximum gape, was explained mostly by species-level effects. This trend generally held true even for the non-informative displacement and timing variables not included in Table 6. Variation in the positional variable, ram distance, was also explained mostly by species-level effects. Predator–prey distance was the only variable where prey-type effects explained more of the total variance than species effects. Variability in lower jaw-opening velocity was divided nearly equally between the two factors.

Discussion

Wrasses display flexibility within species and diversity among species in how they capture prey. A combination

other extreme *Choerodon anchorago* had among the lowest maxima and the longest average times to maxima (Tables 1, 2). The effect of prey type also becomes clearer when the components of jaw-opening velocity are considered. The attached prey treatment usually elicited slighty shorter times to maximum lower jaw angle, and

Table 5 Results of univariate ANOVAs on indicator variables selected from the DFA. Abbreviations are as follows: Ca, *Choerodon anchorago*; Cg, *Coris gaimard*; Hd, *Hologymnosus doliatus*; Nt, *Novaculichthys taeniourus*; Od, *Oxycheilinus digrammus*; m midwater prey; a attached prey

	Effect							
	Species			Prey			Interaction	
Variable	$F_{4,122}$	P	PLSD	$F_{1,122}$	P	PLSD	$F_{4,122}$	P
Max. gape	16.97	< 0.0001	Ca > (Od, Nt) > Cg > Hd*	6.09	0.015	m > a*	0.74	0.569
Max. lower jaw angle	19.63	< 0.0001	Nt > (Ca, Od,Cg) > Hd*	7.03	0.009	m > a*	2.24	0.069
Time to max. lower jaw angle	61.88	< 0.0001	Ca > (Od,Nt, Cg,Hd)*	16.37	< 0.0001	m > a*	2.37	0.056
Av. jaw opening angular velocity	35.27	< 0.0001	Nt > (Od, Cg,Hd) > Ca*	27.02	< 0.0001	m < a*	2.94	0.023
Ram distance	8.45	< 0.0001	Ca > (Od, Nt,Cg,Hd)*	3.66	0.058	m > a*	0.56	0.692
Predator–prey distance	10.81	< 0.0001	(Ca,Od) > (Nt,Cg,Hd)*	58.25	< 0.0001	m > a*	3.82	0.006

*Significance at $P = 0.05$ after correction for multiple tests

Fig. 4 Plots of the species by prey type effect from the ANOVAs performed on indicator variables. Species are arranged along the *X-axis* in each plot and the symbols are also coded as in previous plots. Species are as follows: Ca, *Choerodon anchorago*; Cg, *Coris gaimard*; Hd, *Hologymnosus doliatus*; Nt, *Novaculichthys taeniourus*; Od, *Oxycheilinus digrammus*. The prey types are midwater (*open*) and attached (*filled*). Each point is a mean (±SE) of individual means for each species
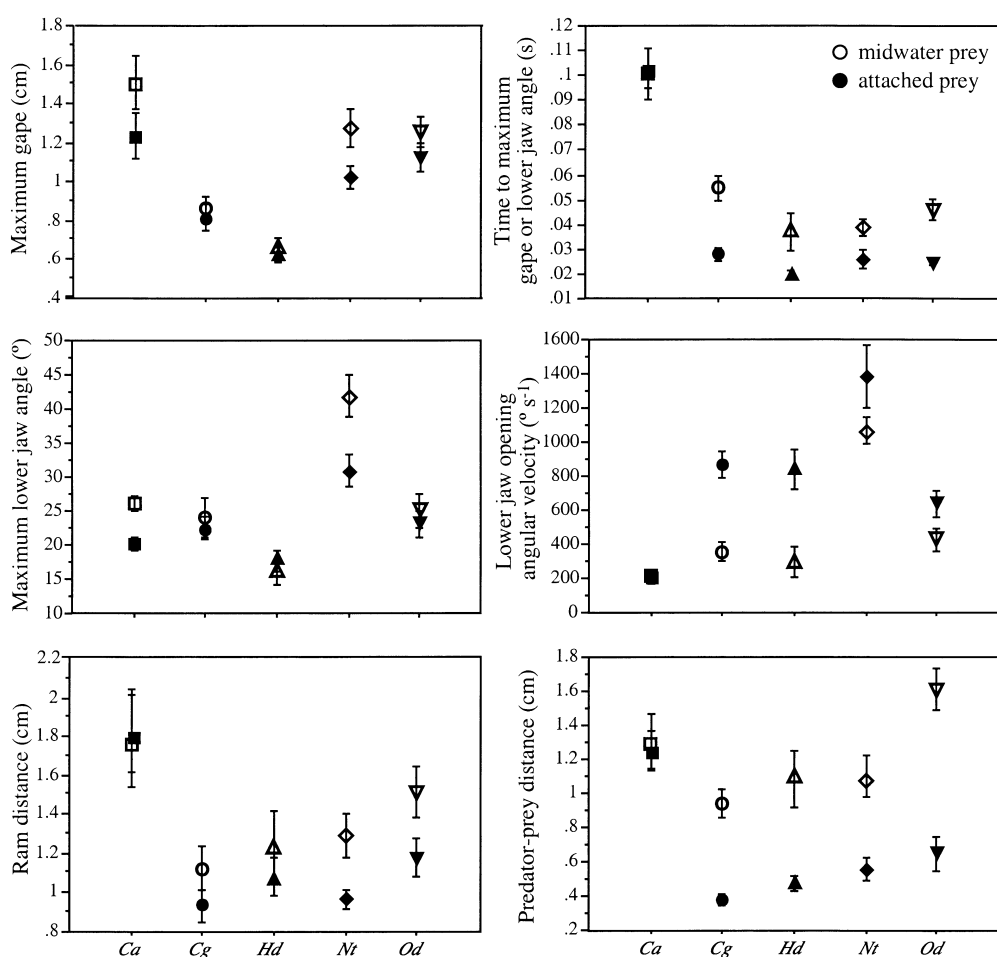
of forward body motion and suction was employed by all five species to capture prey suspended in midwater, although numerous differences were found among species in the details of cranial kinematics. The capture of attached prey involved modifications of feeding kinematics and usually included the use of biting, but this was always combined with ram and some suction. Indeed, in most sequences with attached prey, suction was clearly a dominant force used to dislodge prey and parts of the prey not removed by suction were usually left

Fig. 5 Profile of lower jaw angle during prey capture. Top image shows strikes on midwater prey (*open symbols*), the bottom graph shows strikes on attached prey (*filled symbols*). Each point is a mean of individual means from each species, *error bars* have been omitted for clarity. Species are: *Choerodon anchorago* (squares), *Coris gaimard* (circles), *Hologymnosus doliatus* (triangles), *Novaculichthys taeniourus* (diamonds), and *Oxycheilinus digrammus* (inverted triangles). Note that different strikes ended at different times, thus average jaw angle does not go all the way to zero at the time shown (in particular the *error bars* for *Choerodon anchorago* suggest variation in strike duration). Also, strikes may end with the prey held in the teeth, thus preventing jaw angle from returning to zero. Because these represent averages by time points, the maxima seen in these plots are not directly comparable to the maxima recorded in the tables
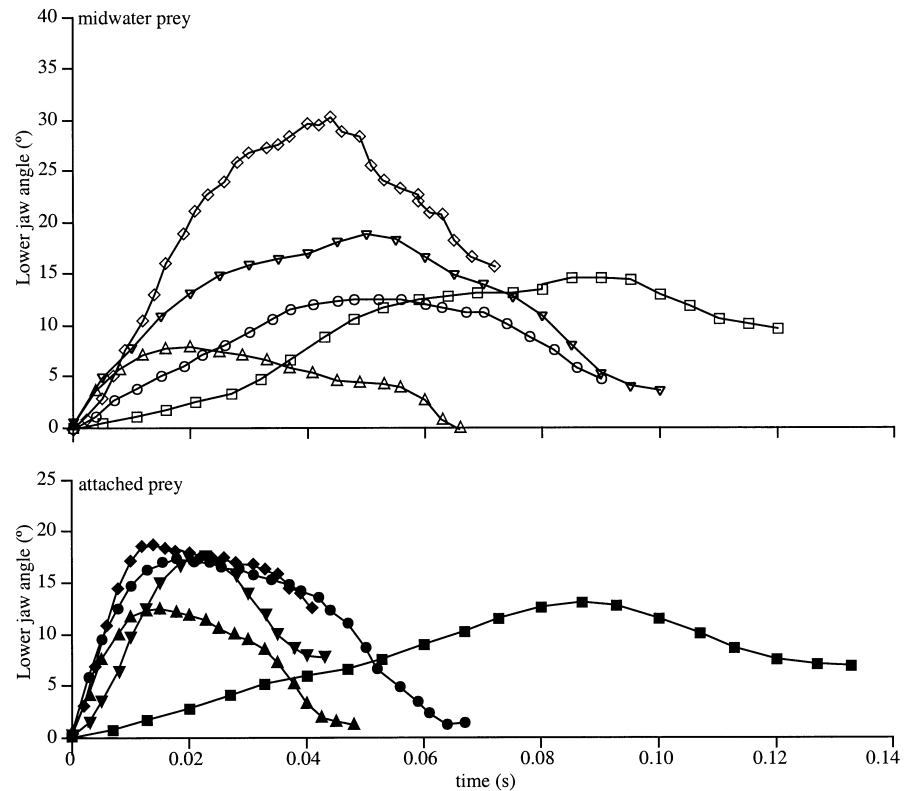
behind. Only one of the five species, *Choerodon anchorago*, relied more heavily on biting than on suction to dislodge the attached prey. Below we discuss the nature and implications of the influence of prey type on prey capture kinematics and the nature of among species variation.

Prey type effects

Of all the variables, only predator–prey distance was influenced more strongly by prey type than species effects, always being shorter in the attached treatment. It is possible that the predators perceived the midwater prey treatment as "free-swimming", and thus avoided a closer approach to avoid eliciting an escape response. It is also possible that hydrodynamic principles were dictating predator–prey distance. Because the speed of water flow that is generated during suction feeding drops off exponentially with distance away from the predator (Muller et al. 1982; Wainwright et al. 2001), the shorter initial predator–prey distance implies that suction forces acting on the prey may have been greater during the strikes on attached prey. As attached prey can be expected to be more difficult than midwater prey to accelerate into the mouth with suction, the possibility must be considered that wrasses initiate strikes closer to attached prey to capitalize on the enhanced flow speeds closer to their mouth opening. The two hypotheses are not mutually exclusive and aspects of both may be acting in wrasses.

The effect of prey type on prey capture kinematics was generally consistent among species. Attached prey tended to elicit shorter times to maximum gape (or lower jaw angle), and faster jaw-opening velocities. This pattern could be interpreted as evidence that the attached prey were captured using more suction. Faster mouth opening has been shown to correspond with increased suction (Liem 1990; Grubich and Wainwright 1997). Additional displacement variables provide some indirect evidence for the use of suction in this context. The prey pieces in the two treatments were the same size, yet the attached prey elicited smaller maximum gapes and lower jaw angles. If other aspects of the strike remain the same (i.e., rate and volume of buccal expansion), a smaller mouth opening should facilitate increased flow rate due to suction (Norton and Brainerd 1993; Norton 1995; Cook 1996).

It is often expected that attached prey should be removed by biting, although suction as a mechanism for removing clinging or grasping prey has been observed in a number of fishes (Liem 1990; Norton 1991; Nemeth 1997). Our results indicate that in wrasses suction can play a prominent role in dislodging and capturing attached prey. Although our observations suggest that the role of biting increases with the tenacity of the prey, it appears that the forces exerted by suction feeders may be sufficient to dislodge many potential food items. It is difficult to assess the limitations on suction forces because surprisingly little is known about the flow rates generated during suction feeding (Ferry-Graham and Lauder 2001), and no attempts have yet been made to
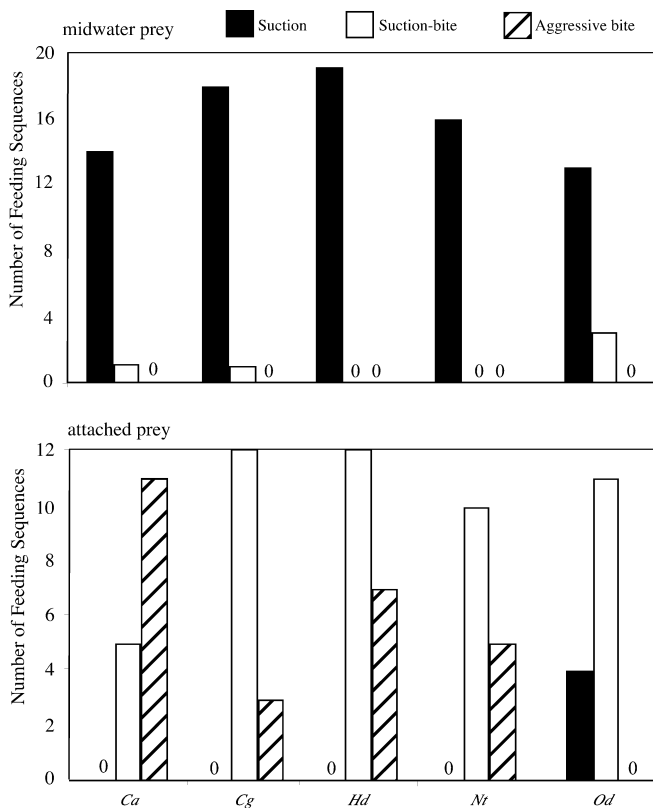
Fig. 6 Bar diagram showing relative use of three strategies during feeding on pieces of prawn suspended in the midwater (*above*) and attached to the substratum (*below*). Species are as follows: *Ca, Choerodon anchorago; Cg, Coris gaimard; Hd, Hologymnosus doliatus; Nt, Novaculichthys taeniourus; Od, Oxycheilinus digrammus* . 'Suction' strikes involved the exclusive use of ram and suction to move the prey into the mouth and dislodge it. 'Suction-bite' strikes involved the use of ram and suction to draw the prey into the mouth, but these actions did not fully dislodge the prey and at the conclusion of the strike the jaws closed on the part of the prey left attached. 'Aggressive bite' strikes involved ram and suction in conjunction with an aggressive biting action, often accompanied by a vigorous turn of the head. In these strikes biting was clearly used as a method to dislodge the prey item

Table 6 Variance components (ω^2) for factors in ANOVAs. Values expressed as a percent of the total variance for that factor. The fraction of the total variance explained by random error is not included in the table. Indicated in bold are those components that suggest a trend towards a single dominant factor

Variable	Effect		
	Species	Prey	Interaction
Max. gape	**37.6**	18.7	0
Max. lower jaw angle	**37.3**	18.9	6.2
Time to max. lower jaw angle	**55.1**	25.5	3.2
Av. jaw-opening angular velocity	34.8	41.3	4.9
Ram distance	**24.8**	13.8	0
Predator–prey distance	7.8	**71.5**	5.6

presentation of prey treatments during experiments, suggests that the wrasses in this study were performing natural and innate behaviors.

Our finding that wrasses combined suction and biting behaviors when capturing attached prey raises questions about how diversification of the feeding mechanism may proceed during evolution. Enhanced suction or enhanced biting are usually regarded as conflicting mechanical features of the feeding apparatus. The design of linkage systems in the skull of suction feeders is expected to favor displacement and speed of motion, while biting is expected to be associated with a large adductor mandibulae muscle with high mechanical advantage in its attachment on the mandible (Westneat 1994; Wainwright and Richard 1995). Mechanical advantage and motion transfer in linkage systems cannot be maximized simultaneously. Thus, if natural selection were acting to favor both suction performance and biting ability, compromises in musculoskeletal design may be expected. It is not known how wrasse suction feeding performance compares in general to other taxa but analyses within the Labridae have established that trade-offs between motion transfer and mechanical advantage represent a major axis of diversification (Westneat 1995; Wainwright et al. 2001; Wainwright and Bellwood 2002).

estimate the magnitude of the acceleration reaction induced by the highly unsteady flows created by the explosive suction feeding actions.

As the wrasses were acclimated on prawn pieces, an alternative hypothesis is that they learned prior to beginning experiments that prawn pieces are easily captured by suction. During the experiments, therefore, the fishes may have opted to use suction despite the presence of the clip, and may not have normally used suction on attached prey in the wild. However, if this hypotheses is valid, then they should have learned that a bite was needed to remove attached prey as quickly as they learned that lose prey could be captured via suction, and we should have seen evidence of this learning given the time course of the study. There were no trends in the data with time to suggest that the wrasses were learning about the attached prey, or, similarly, that the midwater prey could not escape. Further, the detection of a directional prey type effect, regardless of the order of

Species effects

Both the magnitude and timing of prey capture kinematics varied considerably among species. All timing variables varied by 2- to 4-fold among taxa, suggesting differences in jaw linkage mechanics and properties of cranial muscles. The rotational velocity of jaw opening was over seven times faster in *Novaculichtys taeniourus* than in *Choerodon anchorago*. Overall, the interspecific variability in prey capture kinematics was much greater than has been shown in previous comparative studies among fairly closely related taxa (Liem 1979; Wainwright and Lauder 1986; Wainwright and Shaw 1999). An important goal of future research will be to determine the extent to which this interspecific kinematic variation can be accounted for by considering differ-

ences in the mechanics of the musculo-skeletal system operating the jaws.

The magnitude of effect estimates for the displacement and angular variables suggest that variation among species is greater than variation between prey types in the dataset as a whole. These species-level differences may reflect ecomorphological variation in feeding performance and ecology. For example, *N. taeniourus*, which routinely turns over rocks to find prey (Randall et al. 1990), consistently had the largest gape angle. *Oxycheilinus digrammus* feeds on fishes and elusive crustaceans (Westneat 1995). We found that *O. digrammus* had the largest amounts of buccal expansion as indicated by hyoid depression and premaxillary protrusion, showed slightly larger suction distances on midwater prey, and relied more heavily on suction than any of the other species. Among the species studied, *Choerodon anchorago* is the most specialized on hard invertebrate prey such as molluscs and crabs, and consistently showed the largest absolute gape distances, had the largest ram distances, and the slowest jaw opening.

In closing we emphasize the two most significant findings of this study. First, suction feeding played a prominent role in the capture of attached prey. This suggests that to understand feeding performance and diversity in wrasses and other labrid fishes the integration of biting and suction modes of benthic prey capture must be appreciated. Second, wrasses showed marked interspecific variation in prey capture kinematics and in the extent to which suction dominated biting in capturing attached prey. This underscores the potential functional consequences of the extensive morphological and mechanical variation in labrid feeding systems that has recently come to light (Westneat 1995; Wainwright et al. 2000; Wainwright and Bellwood 2002).

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