

MODULATION OF BUCCAL PRESSURE DURING PREY CAPTURE IN *HEXAGRAMMOS DECAGRAMMUS* (TELEOSTEI: HEXAGRAMMIDAE)

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Summary

Changes in intraoral pressure during prey capture were recorded for a trophic generalist, *Hexagrammos decagrammus*, feeding on different prey species. Prey were grouped into elusive (shrimps), grasping (isopods and crabs) and non-elusive (pieces of shrimp) categories. Elusive and grasping prey elicited strikes with a larger and faster reduction in buccal pressure than did non-elusive prey. The suction force generated by the predator differed for strikes among the shrimp genera in the elusive prey category. The most sedentary shrimps (*Crangon alaskensis* and *C. nigricauda*) elicited the fastest and greatest reduction in pressure relative to the most evasive shrimps (*Pandalus danae* and *Heptacarpus stylus*). A preparatory phase, during which the buccal cavity is compressed prior to the strike, occurred significantly more frequently in strikes at grasping prey than in strikes at elusive and non-elusive prey, and more frequently for elusive than for non-elusive prey. Prey size did not influence the suction force

generated by the predator. No differences in buccal pressure patterns were detected between strikes that resulted in a capture or a miss, suggesting that misses were due to the escape behavior of the prey and were not the result of an inappropriate suction force. These data support the current view that fish can modify their feeding mode in response to prey behavior, and they emphasize that the behavioral responses of the individual prey must be considered when defining the appropriate strategy for prey capture. The use of a flexible, modifiable feeding behavior is associated with a broad diet in *H. decagrammus* and may increase capture success on diverse prey relative to that of other species showing stereotypical feeding responses.

Key words: suction feeding, modulation, pressure recordings, elusive prey, kelp greenling, *Hexagrammos decagrammus*, prey capture.

Introduction

Suction feeding is the primary mode of prey capture in fishes (Liem, 1979; Lauder, 1980*a,b*, 1986; Muller *et al.* 1985) and is common among other aquatic vertebrates (Lauder and Shaffer, 1985, 1993; Lauder and Reilly, 1988; Lauder and Prendergast, 1992). This feeding mode involves rapid expansion of the mouth cavity, resulting in a decrease in pressure inside the mouth relative to the ambient water pressure (Lauder, 1985). The subambient pressure generated within the oral cavity creates a flow of water into the mouth; prey are dragged into the buccal cavity by this high-velocity flow.

Critical to the success of this feeding method is the ability of the predator to develop enough drag force to carry the prey into the buccal cavity. This drag force is influenced by passive characteristics of the prey (surface area, volume, size, shape, orientation) and the fluid medium as well as by predator behavior and morphology (Denny *et al.* 1985; Norton and Brainerd, 1993). As drag is proportional to the square of the velocity of water passing by the prey, a small increase in flow

velocity will lead to a large increase in the drag experienced by the prey (Denny *et al.* 1985; Norton and Brainerd, 1993). The predator is able to increase drag on the prey by increasing the flow velocity and acceleration of the fluid moving past the prey, presenting the flow as close to the prey as possible and centering the prey in the flow. The velocity of water entering the mouth of the predator can be increased by reducing the area of the gape, maximizing the change in buccal volume or increasing the rate of buccal expansion (Lauder, 1980*b*; Lauder and Clark, 1984; Van Leeuwen and Muller, 1984; Norton, 1991; Liem, 1993; Norton and Brainerd, 1993). Thus, modulation of feeding behavior by the predator should influence its success during a suction-feeding attempt.

Suction feeding is not likely to be an effective strategy in all feeding situations. Suction feeding depends on the predator being able to approach its prey closely enough that the prey is caught up in the jet of water being sucked into the predator's mouth. Thus, suction is predicted to be most effective on

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stationary prey or grasping prey that are not capable of moving rapidly away from the predator (Norton, 1991, 1995). For prey that do not allow a close approach by the predator (e.g. elusive shrimp and fish), suction feeders may need to adjust their feeding strategy. Predators may respond to evasive prey either by increasing their suction effort to overcome a potential escape response or by switching to a different feeding mode.

The ability of fishes to modulate their feeding behavior in response to prey type is well documented. One way that predators can respond to evasive prey is by switching from a suction-feeding strategy to a ram-feeding strategy, in which the predator overtakes the prey at a relatively high velocity in an attempt to surprise the prey before it can initiate an escape (Liem, 1978; Lauder, 1980b; Vinyard, 1982; Sanderson, 1988, 1990, 1991; Coughlin and Strickler, 1990; Norton, 1991; Norton and Brainerd, 1993). However, modulation of the suction force or buccal pressure waveform generated by the predator have only been superficially examined for a few species feeding on a limited number of prey items. Lauder (1980b) noted differences in the buccal pressure waveform of sunfishes (*Lepomis* spp.) striking at worms and goldfish; Liem (1978) observed more rapid pressure changes for cichlids striking at 'agile' chubs (*Fundulus*) compared with strikes at 'sluggish' goldfish (*Carassius*), but neither study quantified these differences. Norton and Brainerd (1993) found that *Cichlasoma severum* used greater subambient buccal pressures during strikes at elusive versus non-elusive prey, but that *Micropterus salmoides* did not modify its strike. The studies reviewed above, using two prey types to represent extreme differences in prey behavior, have shown clearly that fishes have the ability to recognize prey and to modify their feeding mode. However, the prey species used in previous functional studies have not always represented the natural prey species of the predator. To explore completely the extent and importance of modulation in the predator's natural feeding situation, a broad spectrum of potential prey may be required.

The goal of the present paper is to determine whether the kelp greenling (*Hexagrammos decagrammus*), a trophic generalist with a diverse diet, modulates buccal pressure patterns during prey capture in response to different prey which vary in their escape behaviors. To test for differences in the suction force generated by the predator, I examined the following variables: (1) the peak subambient pressure developed in the mouth cavity, (2) the time course of that pressure change, and (3) the presence and size of a preparatory phase preceding the strike. I also examined the effect of intraspecific variation in prey size on the buccal pressure variables listed above. Finally, I compared strikes at prey that resulted in captures or misses to determine whether predator failure is a function of the inappropriate choice of feeding modes by the predator or results from evasive behavior by the prey.

Materials and methods

Study species

Hexagrammos decagrammus (Pallas, 1810) is a common benthic carnivore in the North Pacific Ocean found on

nearshore rocky reefs, kelp beds and cobble substrata. *H. decagrammus* consumes an extremely broad spectrum of prey including amphipods, crabs, shrimps, sea cucumbers, isopods, small fishes, bivalves, gastropods, polychaete worms and tunicates (Miller *et al.* 1977; Moulton, 1977; Simenstad *et al.* 1979). Its diet is broad relative to that of most other nearshore fishes in North Puget Sound as well as to that of other hexagrammid fishes (Miller *et al.* 1977; Moulton, 1977; Simenstad *et al.* 1979). Five kelp greenling (*Hexagrammos decagrammus*, 21–25 cm standard length) were collected with a beach seine off San Juan Island, Washington. Prey species were also collected from around San Juan Island.

Prey species used in the laboratory experiments were selected on the basis of their diversity of predator avoidance/escape responses, their importance in the natural diet of *H. decagrammus* and their availability for collection. I designated three categories of prey response: elusive prey, non-elusive prey and grasping prey. 'Elusive prey' included three shrimp genera: *Pandalus danae* (common dock shrimp), *Heptacarpus stylus* (stiletto shrimp) and *Crangon* spp. (*C. alaskensis* and *C. nigricauda*, sand shrimp). Laboratory experiments were conducted to test for differences in escape behavior by these shrimp species (Nemeth, 1997). *Pandalus* and *Heptacarpus* are the most evasive because of their tendency to use the tail-flip escape more frequently than *Crangon*. *Pandalus* and *Heptacarpus* do not let the predator approach as closely as does *Crangon* before initiating an escape response. *Crangon* allows the predator to approach within 15 mm on average before escaping, *Heptacarpus* no closer than 22 mm, and *Pandalus*, 40 mm (Nemeth, 1997). One reason why *Crangon* tends to remain very still when approached is that it is typically found buried in soft mud or sand and may rely on crypsis rather than escape ability to avoid predation. 'Non-elusive prey' were created by cutting large *Pandalus* shrimps into 10 mm long sections.

The 'grasping prey' category included two crab species and one isopod species. *Cancer magister* (Dungeness crab) typically occurs on sand or mud bottoms; *Pugettia gracilis* (kelp crab) lives on kelp and other algae. The isopod *Idotea wosnesenskii* is typically found on algae and rocks. Although differences in clinging ability were not quantified, *Idotea*, with its six pairs of legs, seemed to hold onto the mesh substrata used during the experiment better than the two crabs (four pairs of grasping legs). *Pugettia*, which is commonly found clinging to algae or harder substrata, appeared to have a better grasping ability than the soft-substratum-oriented *Cancer magister*.

A fairly broad size range of the live prey species was used in the experiments, which could have influenced the prey capture method used by the predator. The drag force required to carry a prey item into the predator's mouth depends in part on the prey's volume, mass and surface area (Denny, 1988, as cited in Norton and Brainerd, 1993). Thus, predators might react to larger prey by increasing their suction force. To control for potential effects of varying prey size, I tested for a relationship between prey size and the magnitude and timing of buccal pressure change for each prey species. Prey size was

Table 1. Prey sizes offered to *Hexagrammus decagrammus*

	<i>N</i>	Mean (mm)	s.d.	Range (mm)
<i>Crangon</i> spp.	50	32.86	6.325	20–47
<i>Pandalus danae</i>	50	26.30	3.754	10–32
<i>Heptacarpus stylus</i>	47	23.75	5.479	16–42
<i>Idotea wosnesenskii</i>	49	18.04	2.784	13–26
<i>Pugettia gracilis</i>	24	6.50	2.377	4–14
<i>Cancer magister</i>	27	5.04	0.940	3–8
Piece of shrimp	50	10.0	0	10

N, number of prey individuals; s.d., one standard deviation.
See text for the dimension of the prey that was measured.

measured as the distance from the eye to the end of the telson in the three shrimps and the isopod, and as the broadest carapace dimension for the two crabs (Table 1). Shrimp body length was a maximum of 60–80% of predator head length (approximately 1.5–2.0 times gape width). This was the largest prey that *H. decagrammus* could ingest without extensive manipulation (which would have complicated the interpretation of buccal pressures).

Experimental procedure

Fish were anesthetized in tricaine methanesulfonate (MS-222), and a small hole was drilled through the ethmo-frontal region of the skull. An 80 cm length of polyethylene tubing (Intramedic, outer diameter 1.9 mm, inner diameter 1.4 mm) was flanged at one end by heating and flattening it. The tubing was then inserted through the mouth and pulled out through the drilled hole until the flanged end rested flush against the roof of the buccal cavity. The narrow hole held the tubing snugly in place, and the skin healed around the cannula tubing on the top of the head. Cannulae remained in place for up to 4 weeks with no ill effects on the fish's behavior or health.

Before each feeding trial, a Millar Mikro-Tip pressure transducer (Houston, TX, USA) was threaded down the cannula until it rested within 5–10 mm of the buccal cavity. The Millar Mikro-Tip transducer has a strain gauge bonded to the membrane at its distal tip; its proximity to the buccal cavity minimized potential damping due to the cannula. The high-frequency response (10 kHz) of the Millar transducer makes it ideal for recording the rapidly changing pressures that occur during suction feeding (Van Leeuwen and Muller, 1983). The cannula was filled with sea water to remove air bubbles and sealed with modelling clay at the trailing end. A square wave generated by a transducer control unit (Millar model TCB-500) was used to calibrate the voltage change on the oscilloscope. The pressure change in the buccal cavity was recorded on a Nicolet oscilloscope for the first strike only at each prey item (regardless of outcome).

Prey were introduced into the tank in random order. Grasping prey were allowed to cling to a piece of fine nylon mesh window screen glued to a vertical surface before the fish were given access to them. Other prey were introduced to the bare tank bottom when

the fish was at the opposite side of the aquarium. Capture success was recorded for the first strike at each prey item. Ten attacks on each prey species were recorded per predator with the exception of grasping prey. Owing to the difficulties of collecting small crabs and isopods, only 4–7 strikes per predator were recorded for these prey species. To avoid satiation, fish received no more than ten pieces of prey per day.

Data analysis

All buccal pressures recorded are relative to the ambient pressure at the depth of the predator during the attack. The following variables were measured from the pressure waveform of each feeding event: the peak subambient buccal pressure, the duration of the expansive phase (time to peak subambient pressure), the duration of the compressive phase and the peak superambient pressure of the preparatory phase (when present). To minimize variation due to fluctuations around the pressure baseline, time 0 was defined as the time at which the buccal pressure reached 10% of the peak subambient pressure. The duration of the compressive phase was measured from the time of peak subambient pressure to the time when the buccal pressure had returned to 10% of the peak subambient pressure (Liem, 1978). The preparatory phase, when present, was quantified as the peak superambient pressure in the buccal cavity just prior to the rapid decrease in pressure during the strike.

Statistical analyses were performed using SuperAnova v. 1.11 (Abacus Concepts). Data were square-root-transformed when necessary to meet the analysis of variance (ANOVA) assumption of homoscedasticity (Winer *et al.* 1991). Homogeneity of variances was tested before and after transformation using Cochran's test (Winer *et al.* 1991). A significance level of $P < 0.05$ was set for statistical comparisons.

Parameters of the pressure waveform (listed above) were compared among prey categories using a two-factor mixed-model ANOVA, with prey category (fixed) and predator individual (random) as the independent factors. Prey were grouped *a priori* into categories on the basis of their anti-predator strategy, with 'elusive prey' including the three shrimp genera, 'grasping prey' including the two crab species and the isopod, and pieces of shrimp as 'non-elusive prey'. Separate two-factor mixed-model ANOVAs were also used to compare pressure variables among the three prey species within the elusive and grasping prey categories, with prey species (fixed) and predator individual (random) as the independent factors.

When the effect of prey category or prey species was significant, *post-hoc* comparisons were evaluated using the Tukey–Kramer test (Day and Quinn, 1989). In the one case where transformation did not homogenize the variances (one-way ANOVA for elusive prey species; dependent variable, duration of expansive phase), the Games–Howell test was used because of its robustness with respect to heterogeneous variances and unequal sample sizes (Day and Quinn, 1989).

The presence of a preparatory phase, created by compression of the buccal cavity just prior to buccal expansion, allows for a greater overall change in buccal volume during the strike. The

frequency with which a preparatory phase occurred during strikes at different prey was evaluated using a χ^2 -test. Three separate χ^2 -tests were conducted on the basis of *a priori* groupings of prey: among prey categories (elusive, grasping and non-elusive), among elusive prey species and among grasping prey species. If the results of these tests were significant, categories or species were compared using a Tukey-type multiple-comparison test for proportions discussed in Zar (1984).

Pressure profiles for strikes that resulted in misses were compared with those for captures for each of the elusive shrimp species using single-factor ANOVAs for which strike outcome (capture or miss) was the fixed independent variable and the characteristics of the pressure profile (magnitude and timing) were the dependent variables. Predator individuals were pooled for this analysis because captures and misses were not equally distributed among all the individuals. Sample sizes were usually unequal between captures and misses for a given prey type, since a fixed number of strikes was recorded irrespective of strike outcome. Homogeneity of variances was tested between captures and misses for each prey species using the variance ratio test (Zar, 1984); variances were equal for all comparisons.

Prey size was compared between captures and misses for each of the shrimp species and the isopod, with a separate single-factor ANOVA per prey species (strike outcome as the fixed independent factor, prey size as the dependent variable). As pieces of shrimp were all 10 mm and as too few misses were recorded for the two crabs, prey size effects were not examined for these prey species. The relationships between prey size and the peak subambient buccal pressure, the duration of the expansive phase, the duration of the compressive phase and the magnitude of the preparatory phase were also evaluated using least-squares regression for all prey species.

Results

The general pattern of change in pressure in the buccal cavity during strikes by *H. decagrammus* was similar to that

reported for other teleost fishes (Alexander, 1970; Lauder, 1980a, 1983; Van Leeuwen and Muller, 1983; Norton and Brainerd, 1993). A preparatory phase characterized by a small superambient pressure peak (0.2–6.8 kPa) was often present before the rapid decrease in pressure associated with buccal expansion. During a strike, pressure in the buccal cavity reached its minimum after 11–50 ms and returned to ambient in 4–172 ms. The development of peak subambient pressure occurred rapidly. Maximum velocity of pressure change was 5.0 kPa ms^{-1} and peak subambient pressure attained was -70.5 kPa for strikes at *Crangon*.

H. decagrammus altered the magnitude and timing of buccal pressure change in response to the different prey categories (Table 2). Strikes at elusive prey and grasping prey had significantly greater peak subambient buccal pressures than did strikes at non-elusive prey (Fig. 1). The duration of the expansion phase was also significantly different among the prey categories (Table 2). Peak subambient pressure was achieved more rapidly for elusive prey and grasping prey relative to non-elusive prey (Fig. 2). Thus, strikes at live prey should result in higher velocities of water being sucked into the mouth. Elusive prey and grasping prey categories did not differ significantly from one another in peak subambient buccal pressure or in the duration of the expansive phase (Figs 1, 2).

H. decagrammus distinguished among the elusive prey species, but not among the grasping prey species, in the magnitude and timing of buccal pressure change (Table 3). Within the elusive prey category, *Crangon* (the most sedentary shrimp) elicited significantly greater subambient buccal pressures than did both *Pandalus* and *Heptacarpus* (Fig. 1). Strikes at *Crangon* and *Heptacarpus* reached peak subambient pressure more quickly than did strikes at *Pandalus* (Fig. 2).

In contrast to the magnitude and duration of the expansive phase of the strike, the duration of the compressive phase did not vary among prey categories or among species within a category (Tables 2, 3). The duration of the compressive phase

Table 2. ANOVA results comparing strikes among the three prey categories for the three buccal pressure variables

Dependent variable	Independent variable	d.f.	MS	F
Peak subambient pressure	Prey	2	1000.53	91.93**
	Individual	4	18.01	1.87
	Prey \times Individual	8	10.88	1.13
	Error	282	9.67	
Duration of expansive phase	Prey	2	4.87	9.09*
	Individual	4	0.84	3.15*
	Prey \times Individual	8	0.54	2.01
	Error	277	0.27	
Duration of compressive phase	Prey	2	1066.92	2.00
	Individual	4	4682.22	9.39**
	Prey \times Individual	8	532.84	1.07
	Error	264	498.83	

Prey, prey category; Individual, predator individual; d.f., degrees of freedom; MS, mean square error.

Significant at * $P < 0.05$, ** $P < 0.01$ using the sequential Bonferroni method (correction applied at both α levels, $k=9$ tests) described by Rice (1989).

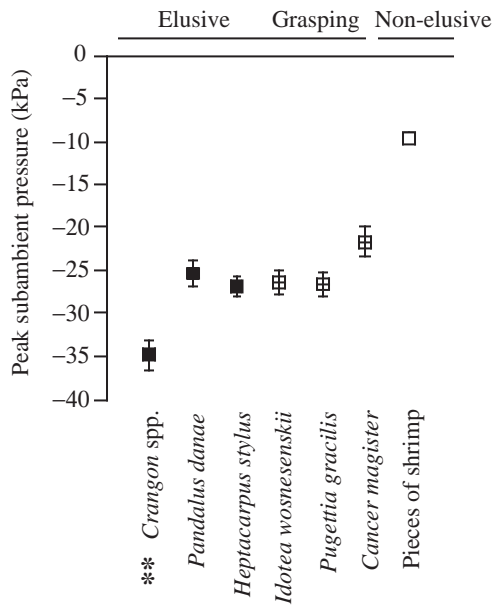


Fig. 1. Peak subambient buccal pressure (mean \pm 1 S.E.M.) recorded for strikes by *Hexagrammos decagrammus* at different prey. See Table 1 for sample sizes. Lines above the graph connect categories that are not significantly different from one another at $P < 0.01$. See Tables 2 and 3 for ANOVA summary statistics. ***Crangon* spp. is significantly different ($P < 0.01$) from the other two shrimp species in the elusive prey category.

was highly variable, ranging from 4 to 172 ms. Interindividual differences in timing of the pressure profile were detected in the duration of the compressive phase as well as the expansive phase (Table 2).

Although a preparatory phase preceded buccal expansion in 54–96% of strikes depending on prey type, it did not contribute much to the overall change in pressure in the buccal cavity (Table 4). The magnitude of the preparatory phase, averaging less than 1 kPa (Table 4), contributed on average only 2–3% of the total pressure change in the buccal cavity [preparatory phase magnitude/(preparatory phase magnitude + peak subambient pressure)]. The frequency of occurrence of a preparatory phase before the strike varied among prey

categories (d.f.=2, $\chi^2=37.16$, $P < 0.0001$). Grasping prey elicited a preparatory phase significantly more frequently than did the other prey categories ($P < 0.001$); elusive prey elicited a preparatory phase significantly more frequently than non-elusive prey ($P < 0.001$). Among grasping prey, there were no differences in the frequency with which a preparatory phase was used (d.f.=2, $\chi^2=0.02$, $P=0.99$), but there were differences among elusive prey (d.f.=2, $\chi^2=16.13$, $P < 0.001$). Strikes at *Pandalus* were significantly less likely to involve a preparatory phase than were strikes at either *Crangon* or *Heptacarpus* ($P < 0.001$). The magnitude of the preparatory phase, when present, did not differ among prey categories or among elusive or grasping prey species (Table 4).

Predator failure was always associated with avoidance behavior by the prey, but not with differences in the predator's buccal pressure profile. Misses at elusive prey were always associated with a tail-flip by the shrimp; misses at grasping prey always left the prey clinging to the mesh substratum. A comparison of strikes that resulted in captures versus misses revealed no differences in the peak subambient buccal pressure, the time to peak subambient pressure or the duration of the compressive phase for *Crangon*, *Heptacarpus*, *Pandalus* or *Idotea* (Table 5). Captures and misses were not contrasted for the other prey species because only one miss was recorded for *Pugettia* and no misses were recorded for *Cancer* or pieces of shrimp.

Prey size is another factor which could affect the outcome of a feeding event, given the two- to threefold range of prey lengths within a prey species (Table 1). Captures and misses were contrasted in mean prey size for four of the seven prey species (Table 5). Prey size was not significantly different between captures and misses for *Crangon*, *Heptacarpus* or *Idotea*; captures were actually associated with slightly larger prey for *Pandalus* (Table 5).

Although prey size varied among the prey species, there was no clear relationship between the size of prey (Table 1) used in the experiment and their elusiveness. The smallest prey species (crabs) were not the least elusive, and the lowest suction force used by the predator was associated with non-elusive prey, not with the smallest prey. However, the largest

Fig. 2. The duration of the expansive phase (mean \pm 1 S.E.M.) recorded for strikes by *Hexagrammos decagrammus* at different prey. See Table 1 for sample sizes. Lines to the left of the graph connect categories that are not significantly different from one another ($P < 0.01$). See Tables 2 and 3 for ANOVA summary statistics. ***Pandalus danae* is significantly different ($P < 0.01$) from the other two shrimp species in the elusive prey category.

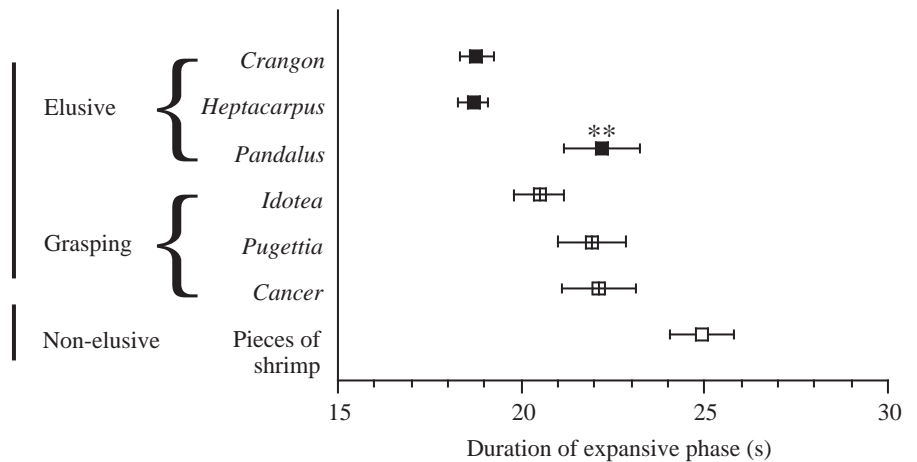


Table 3. ANOVA results comparing strikes at prey species within elusive and grasping prey categories for three buccal pressure variables

Dependent variable	Independent variable	d.f.	MS	F
Peak subambient pressure	Elusive			
	Prey	2	134235.38	14.35*
	Individual	4	13898.88	1.23
	Prey × Individual	8	9355.27	0.83
	Error	132	11294.24	
	Grasping			
	Prey	2	29321.22	4.14
	Individual	4	14563.08	1.81
	Prey × Individual	8	7076.91	0.88
	Error	85	8040.25	
Duration of expansive phase	Elusive			
	Prey	2	178.65	11.84*
	Individual	4	33.80	1.41
	Prey × Individual	8	15.09	0.63
	Error	127	23.98	
	Grasping			
	Prey	2	32.63	2.19
	Individual	4	93.61	4.79*
	Prey × Individual	8	14.90	0.76
	Error	85	19.54	
Duration of compressive phase	Elusive			
	Prey	2	713.42	2.83
	Individual	4	2603.79	6.16**
	Prey × Individual	8	252.19	0.60
	Error	122	423.10	
	Grasping			
	Prey	2	665.34	1.47
	Individual	4	2308.77	3.92*
	Prey × Individual	8	451.84	0.77
	Error	84	588.45	

Prey, prey species; Individual, predator individual; d.f., degrees of freedom; MS, mean square error.

Significant at * $P < 0.05$, ** $P < 0.01$ using the sequential Bonferroni method (correction applied at both α levels, $k=9$ tests) described by Rice (1989).

Table 4. Frequency of occurrence and magnitude of the preparatory phase for strikes among and within prey categories

	Among prey categories				Within prey categories		
	N	% Occurrence	Magnitude (kPa)		n	% Occurrence	Magnitude (kPa)
Elusive	138	73.9	0.704±0.083	<i>Crangon</i> spp.	41	85.4	0.631±0.097
				<i>Heptacarpus stylus</i>	47	85.1	0.724±0.115
				<i>Pandalus danae</i>	50	54.0	0.768±0.236
Grasping	100	96.0	0.612±0.044	<i>Idotea wosnesenskii</i>	48	95.8	0.674±0.071
				<i>Pugettia gracilis</i>	28	96.4	0.526±0.076
				<i>Cancer magister</i>	24	95.8	0.577±0.074
Non-elusive	50	54.0	0.466±0.052	Piece of shrimp	50	54.0	0.466±0.052

Magnitude is presented as mean ± S.E.M.

N, number of strikes in each prey category; n, number of strikes at each prey species.

Table 5. Mean values of three buccal pressure variables and prey size, for successful and unsuccessful strikes at four prey species

Prey	Strike outcome	N	Peak subambient pressure (kPa)	Duration of expansive phase (ms)	Duration of compressive phase (ms)	Prey size (mm)
<i>Crangon</i> spp.	Capture	44	35.91±1.59	18.50±0.49	32.60±3.11	32.32±0.97
	Miss	6	26.68±7.35	21.00±0.78	43.20±7.05	36.83±1.68
<i>Pandalus danae</i>	Capture	23	26.49±2.31	22.11±1.68	47.09±8.31	27.80±0.47*
	Miss	27	24.25±2.20	22.25±1.29	32.17±2.60	25.94±0.72
<i>Heptacarpus stylus</i>	Capture	38	26.97±1.20	18.40±0.46	31.76±2.77	23.84±0.88
	Miss	9	25.81±2.84	20.00±0.94	30.56±3.68	23.33±2.03
<i>Idotea wosnesenskii</i>	Capture	42	27.28±1.54	20.60±0.78	39.46±4.20	18.19±0.44
	Miss	7	20.54±2.38	19.86±1.10	30.86±6.50	17.14±0.94

Values are presented as means ± S.E.M.

N, number of strikes.

* $P < 0.05$, results of intraspecific ANOVA with respect to strike outcome, for the four dependent variables related to buccal pressure and prey size investigating whether captures and misses differ within a prey species.

Too few misses were recorded from strikes at *Pugettia gracilis*, *Cancer magister* and pieces of shrimp to test for differences.

prey species (*Crangon*) was associated with the greatest suction force. To determine whether differences in size among the prey species could have as great an effect on feeding strategy as differences in elusiveness, the relationship between pressure variables and prey size was examined. Since the size ranges of the prey species overlap, if there is no clear effect of prey size, then the conclusions should not be biased by species-specific differences in prey size.

Since prey size could affect the suction force necessary to capture a particular prey, regression analysis of pressure variables on prey size was used to determine whether *H. decagrammus* increased the magnitude of the subambient buccal pressure change or shortened the expansive phase of the strike for larger prey. Prey size was not correlated with peak subambient buccal pressure within any prey type; a regression of peak subambient pressure on prey size was not significant (slope not different from 0) in any prey species ($P > 0.07$ for all species). Prey size only poorly explained variation in peak subambient buccal pressure within a prey species, with r^2 values ranging from 0.01 in *Heptacarpus* to 0.07 in *Pandalus*. The duration of the expansive phase increased slightly with increasing prey size for the two prey with the greatest size range, *Crangon* (Fig. 3A; $P < 0.002$) and *Heptacarpus* (Fig. 3B; $P < 0.03$), but not for *Pandalus* (Fig. 3C), *Idotea*, *Pugettia* or *Cancer* ($P > 0.63$ for the latter four prey). The duration of the compressive phase increased significantly with prey size in *Pugettia* ($y = 4.838x + 17.300$, $r^2 = 0.217$, $P < 0.002$), but did not vary significantly with prey size in *Crangon*, *Pandalus*, *Heptacarpus*, *Idotea* or *Cancer* ($r^2 < 0.093$, $P > 0.30$ for the latter five). During the preparatory phase, superambient pressure increased only slightly with prey size for *Idotea* ($y = 0.577x - 3.811$; $r^2 = 0.100$, $P < 0.027$), but not for any other prey species ($P > 0.605$ in all other species).

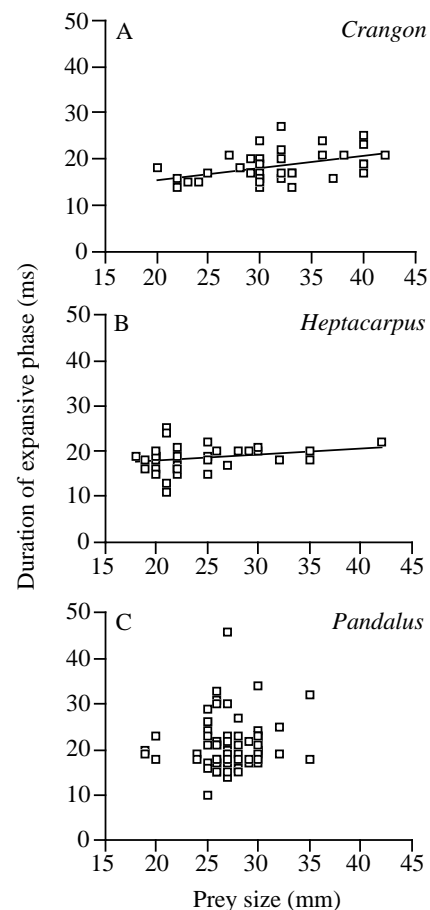


Fig. 3. The duration of the expansive phase (y) as a function of prey size (x) for strikes at (A) *Crangon* spp. ($y = 0.257x + 10.598$, $r^2 = 0.203$, $P < 0.002$), (B) *Heptacarpus stylus* ($y = 0.170x + 14.654$, $r^2 = 0.107$, $P < 0.03$) and (C) *Pandalus danae* ($y = 0.132x + 18.672$, $r^2 = 0.003$, $P > 0.63$, not significant).

Discussion

Modulation of buccal pressure patterns and the categorization of prey species

Hexagrammos decagrammus modulates its buccal pressure profile in response to prey that differ in predator avoidance behavior. Elusive and grasping prey elicited strikes with a faster and greater change in buccal pressure relative to strikes at non-elusive prey. Strikes at the seven prey items fell along a continuum in terms of the magnitude and timing of buccal pressure change (Fig. 4), indicating the possibility of fine control over the suction forces generated. Intensifying the drag force exerted on the prey could improve the predator's feeding performance on all evasive prey, but will have the greatest effect in situations where the prey allows the predator to approach closely. Increasing the magnitude of and time to peak subambient buccal pressure is an appropriate response for *Crangon*, which relies on crypsis as its primary antipredator behavior but may require a high suction force to overcome a last-minute escape attempt or to pull it up out of the sand (in the natural environment). *Pandalus* and *Heptacarpus*, when trying to avoid being eaten, start their tail-flip escape response before the predator is within suction-feeding range: for these shrimps, *H. decagrammus* switches to a ram-feeding attack rather than increasing its suction effort (Nemeth, 1997).

The predator's use of different buccal pressure profiles for the prey in this study highlights the difficulties in categorizing prey by either their taxonomic position or their superficial functional characteristics. Taxonomically similar prey (i.e. a group of shrimp species, or crabs) may show subtle differences in their behavior that radically change their susceptibility to predators (Main, 1985, 1987; Norton, 1991). For example, the shrimp species used in this study are vulnerable to different capture strategies (see also Nemeth, 1997). This is in contrast to what would be predicted simply by the fact that they make use of a tail-flip escape response. By grouping the shrimps into one category, differences in prey behavior that have more predictive information were obscured. Similarly, fish are generally grouped with shrimp as evasive, but differences among fish species in their escape behavior have profound

effects on their susceptibility to capture and on the appropriate feeding mode used by the predator (Liem, 1978). The differences in grasping ability that I assumed for *Cancer*, *Pugettia* and *Idotea* had no effect on the magnitude or timing of the change in buccal pressure. Either there were no differences from the perspective of the predator or the predator was using some alternative feeding behavior that I could not detect in this study. Even non-behavioral differences among prey, such as snail shell hardness, can have a profound effect on their susceptibility to different predators. The predictive nature of ecomorphological studies depends on an accurate assessment of the functional demands of different prey and a consideration of their repertoire of antipredator behaviors (see Main, 1987; Norton, 1991; Nemeth, 1997). Using natural prey species in ecomorphology studies is thus essential.

Prey size can also influence the suction force needed to capture prey. In addition to increasing the drag force necessary to move a prey item towards the predator, larger prey might be expected to have better clinging or swimming ability because of larger muscles involved in locomotion (see Norton, 1991). If prey size were to influence buccal pressure modulation or capture success, it would be apparent for the largest prey used in this study, which reached the size limit that could be handled by the predator using suction. As in Lauder's (1981) experiments with characoid fishes, prey of equivalent size elicited prey-type-specific responses.

The slight increase in the duration of the expansive phase with prey size for *Crangon* and *Heptacarpus* is puzzling. Since peak subambient pressure did not increase with prey size, this longer time to reach peak subambient pressure would probably reduce the suction force by slowing the rate of pressure change. Alternatively, if longer prey physically take more time to enter the mouth, perhaps this is reflected in an extension of the expansive phase. Buccal compression might be delayed slightly until the prey is transported fully into the mouth cavity.

Modulation of feeding behavior and implications for diet

Modulation of prey capture behavior for different feeding situations broadens the prey spectrum that can be consumed by

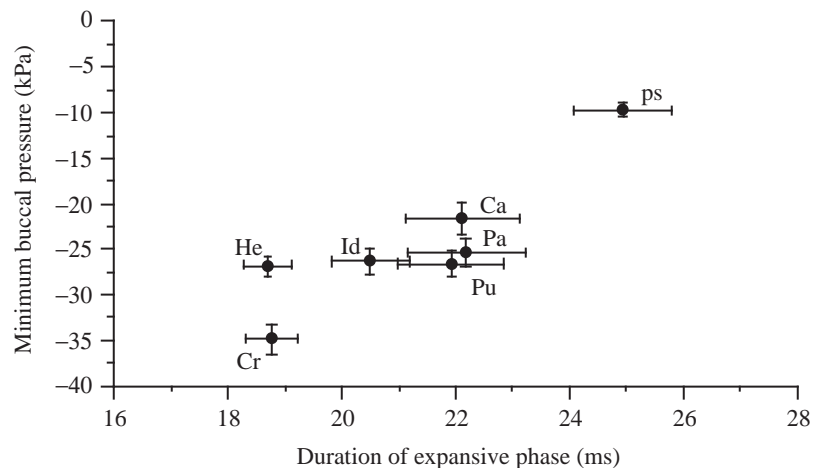


Fig. 4. Peak subambient buccal pressure plotted against the mean time to reach that subambient pressure (lines indicate ± 1 S.E.M.) for *Hexagrammos decagrammus* feeding on the following prey: Cr, *Crangon* spp.; Pa, *Pandalus danae*; He, *Heptacarpus stylus*; Id, *Idotea wosnesenskii*; Pu, *Pugettia gracilis*; Ca, *Cancer magister*; ps, pieces of shrimp. Strikes that achieve a lower buccal pressure in a shorter period generate a higher velocity of water flowing into the mouth of the predator.

an organism. The use of high suction forces for *Crangon* spp. means that *H. decagrammus* gains access to a prey species it might not be able to capture with the lower suction forces used for *Pandalus* and *Heptacarpus*. Behavioral flexibility can also be used to mitigate potential morphological constraints that might hinder feeding performance on certain prey. For example, Norton (1991) found that small-mouthed sculpins tended to have high capture success in suction-feeding situations, but low capture success on elusive prey. One small-mouthed cottid, however, increased its capture success on elusive prey by using ram-feeding behaviors characteristic of larger-mouthed cottids. The broad diet of the kelp greenling is associated with behavioral flexibility in suction feeding and other prey capture strategies (Nemeth, 1996, 1997). It would be interesting to compare the behavioral flexibility of *H. decagrammus* with that of other members of the family Hexagrammidae having more specialized diets and morphology (e.g. *Ophiodon elongatus* is a large-mouthed piscivore; *Oxylebius pictus* has a smaller mouth and a narrower diet). Are these species capable of modulating their buccal pressure profiles when faced with different prey? How does feeding performance on elusive prey compare between *H. decagrammus* and *Ophiodon elongatus*, a specialist on such prey types? Even other species in the genus *Hexagrammos* have narrower diets than the kelp greenling. Is this narrower diet associated with a narrower behavioral repertoire? By asking these types of questions, modulation of behavior can be incorporated into ecomorphological studies.

The importance of modulation, and its effect on performance, can be assessed by comparing successful and unsuccessful feeding events. I found no significant differences in the pressure profile between captures and misses, a result shared by several other studies (Lauder and Liem, 1981; Norton, 1991; Norton and Brainerd, 1993). Misses were attributed to prey escape behavior, not to the failure of the predator to select an appropriate suction profile. The predator's use of a particular suction profile often allowed it to capture a shrimp that was trying to escape, leading me to conclude that the suction profiles generated by *H. decagrammus* were typically appropriate, but that the predator could not anticipate all the possible escape tactics of the prey. The existence of prey-specific differences in buccal pressure changes in this study supports the hypothesis that modulation enhances feeding performance: the greatest capture success on mobile prey is associated with the prey species (*Crangon*) that elicited the greatest adjustment in suction force (relative performance data are presented in Table 5; see Nemeth, 1997, for a statistical analysis of performance data).

The modification of suction force for different prey types by *H. decagrammus* suggests that a suction profile is selected on the basis of pre-strike information. This is in contrast to Aerts' (1990) hypothesis that pressure is modulated at the moment the prey enters the mouth. Aerts (1990) observed that, for unsuccessful strikes, the expansive phase (defined on the basis of head expansion, not time to peak subambient pressure) was extended, as if the predator were waiting for the hydrodynamic signal that the prey had entered the mouth. *H. decagrammus*

did not show this extended expansive phase during unsuccessful strikes.

Ecomorphological studies try to match the morphological features of a predator (e.g. mouth size) to its ecology (e.g. diet) and to provide a functional explanation for that correlation (Wainwright, 1988, 1994; Motta and Kotrschal, 1992). The strength of this ecomorphological hypothesis depends on (1) a functional explanation for the mechanism by which morphology affects feeding performance on different prey, (2) an understanding of the effect of the predator's behavioral flexibility on performance, and (3) accurate information on prey behavior and the susceptibility of the prey to different types of predator attack. A close match between morphology and diet is expected to have predictive value in other ecological communities or in other clades of organisms (Karr and James, 1975; Grossman, 1986).

Ecomorphological studies that try to match morphological design with feeding performance and diet are likely to find the strongest correlations when the species of interest are trophic specialists. By examining the modulation of suction feeding in a single species, it is clear that behavior plays a more important role in determining the dietary breadth of a trophic generalist. This study also emphasizes that the antipredator behavior of the prey, which also may not be apparent from prey morphology, will influence the type of prey capture behaviors the predator should use. When prey organisms present a diversity of challenges to a predator, the behavioral repertoires of both must be considered in describing the factors that link morphology, performance and diet.

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References

- AERTS, P. (1990). Variability of the fast suction feeding process in *Astatotilapia elegans* (Teleostei: Cichlidae): a hypothesis of peripheral feedback control. *J. Zool., Lond.* **220**, 653–678.
- ALEXANDER, R. MCN. (1970). Mechanics of the feeding action of various teleost fishes. *J. Zool., Lond.* **162**, 145–156.
- COUGHLIN, D. J. AND STRICKLER, J. R. (1990). Zooplankton capture by a coral reef fish: an adaptive response to evasive prey. *Env. Biol. Fish.* **29**, 35–42.
- DAY, R. W. AND QUINN, G. P. (1989). Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* **59**, 433–463.
- DENNY, M. W. (1988). *Biology and the Mechanics of the Wave-swept Environment*. Princeton: Princeton University Press.

- DENNY, M. W., DANIEL, T. L. AND KOEHL, M. A. R. (1985). Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**, 69–102.
- GROSSMAN, G. D. (1986). Food resource partitioning in a rocky intertidal fish assemblage. *J. Zool., Lond.* **B 1**, 317–355.
- KARR, J. R. AND JAMES, F. C. (1975). Ecomorphological configurations and convergent evolution in species and communities. In *Ecology and Evolution of Communities* (ed. M. L. Cody and J. M. Diamond), pp. 258–291. Cambridge: Belknap Press.
- LAUDER, G. V. (1980a). Hydrodynamics of prey capture by teleost fishes. In *Biofluid Mechanics*, vol. 2 (ed. D. Schneck), pp. 161–181. New York: Plenum Press.
- LAUDER, G. V. (1980b). The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. exp. Biol.* **88**, 49–72.
- LAUDER, G. V. (1981). Intraspecific functional repertoires in the feeding mechanism of the characoid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia* **1991**, 154–168.
- LAUDER, G. V. (1983). Prey capture hydrodynamics in fishes: experimental test of two models. *J. exp. Biol.* **104**, 1–13.
- LAUDER, G. V. (1985). Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. Bramble, K. F. Liem and D. B. Wake), pp. 210–229. Cambridge: Harvard University Press.
- LAUDER, G. V. (1986). Aquatic prey capture in fishes: experimental and theoretical approaches. *J. exp. Biol.* **125**, 411–416.
- LAUDER, G. V. AND CLARK, B. D. (1984). Water flow patterns during prey capture by teleost fishes. *J. exp. Biol.* **113**, 143–150.
- LAUDER, G. V. AND LIEM, K. F. (1981). Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fishes. *Env. Biol. Fish.* **6**, 257–268.
- LAUDER, G. V. AND PRENDERGAST, T. (1992). Kinematics of aquatic prey capture in the snapping turtle, *Chelydra serpentina*. *J. exp. Biol.* **164**, 55–78.
- LAUDER, G. V. AND REILLY, S. M. (1988). Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic changes in function. *J. exp. Biol.* **134**, 219–233.
- LAUDER, G. V. AND SHAFFER, H. B. (1985). Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *J. Morph.* **185**, 297–326.
- LAUDER, G. V. AND SHAFFER, H. B. (1993). Design of feeding systems in aquatic vertebrates: major patterns and their evolutionary interpretations. In *The Skull*, vol. 3, *Functional and Evolutionary Mechanisms* (ed. J. Hanken and B. K. Hall), pp. 113–149. Chicago: University of Chicago Press.
- LIEM, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morph.* **158**, 323–360.
- LIEM, K. F. (1979). Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool., Lond.* **189**, 93–125.
- LIEM, K. F. (1993). Ecomorphology of the teleostean skull. In *The Skull*, vol. 3, *Functional and Evolutionary Mechanisms* (ed. J. Hanken and B. K. Hall), pp. 422–452. Chicago: University of Chicago Press.
- MAIN, K. L. (1985). The influence of prey identity and size on selection of prey by two marine fishes. *J. exp. mar. Biol. Ecol.* **88**, 145–152.
- MAIN, K. L. (1987). Predator avoidance in seagrass meadows: prey behavior, microhabitat selection and cryptic coloration. *Ecology* **68**, 170–180.
- MILLER, B. S., SIMENSTAD, C. A., MOULTON, L. L., FRESH, K. L., FUNK, F. C., KARP, W. A. AND BORTON, S. F. (1977). *Puget Sound Baseline Program Nearshore Fish Survey. Final Report July 1974–1977, FRI-UW-7710*. Washington State Department of Ecology, Lacey, WA.
- MOTTA, P. J. AND KOTRSCHAL, K. M. (1992). Correlative, experimental and comparative evolutionary approaches in ecomorphology. *Neth. J. Zool.* **42**, 400–415.
- MOULTON, L. L. (1977). An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. PhD dissertation, University of Washington. 181pp.
- MULLER, M., VAN LEEUWEN, J. L., OSSE, J. W. M. AND DROST, M. R. (1985). Prey capture hydrodynamics in fishes: two approaches. *J. exp. Biol.* **119**, 389–394.
- NEMETH, D. (1996). Functional morphology and modulation of prey capture behavior in hexagrammid fishes (Scorpaeniformes). PhD dissertation, Harvard University. 174pp.
- NEMETH, D. H. (1997). Modulation of attack behaviour and its effects on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J. exp. Biol.* **200**, 2155–2164.
- NORTON, S. F. (1991). Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology* **72**, 1807–1819.
- NORTON, S. F. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Env. Biol. Fish.* **44**, 37–60.
- NORTON, S. F. AND BRAINERD, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. exp. Biol.* **176**, 11–29.
- RICE, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- SANDERSON, S. L. (1988). Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). *Brain Behav. Evol.* **32**, 257–268.
- SANDERSON, S. L. (1990). Versatility and specialization in labrid fishes: ecomorphological implications. *Oecologia* **84**, 272–279.
- SANDERSON, S. L. (1991). Functional stereotypy and feeding performance correlated in a trophic specialist. *Funct. Ecol.* **5**, 795–803.
- SIMENSTAD, C. A., MILLER, B. S., NYBLADE, C. F., THORNBURGH, K. AND BLEDSOE, L. J. (1979). *Food Web Relationships of Northern Puget Sound and the Strait of Juan de Fuca*. Fisheries Research Institute, University of Washington. Prepared for the MESA (Marine Ecosystems Analysis) Puget Sound Project.
- VAN LEEUWEN, J. L. AND MULLER, M. (1983). The recording and interpretation of pressures in prey-sucking fish. *Neth. J. Zool.* **33**, 425–475.
- VAN LEEUWEN, J. L. AND MULLER, M. (1984). Optimum sucking techniques for predatory fish. *Trans. zool. Soc. Lond.* **37**, 137–169.
- VINYARD, G. L. (1982). Variable kinematics of Sacramento Perch (*Archoplites interruptus*) capturing evasive and nonevasive prey. *Can. J. Fish. aquat. Sci.* **39**, 208–211.
- WAINWRIGHT, P. C. (1988). Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* **69**, 635–645.
- WAINWRIGHT, P. C. (1994). Functional morphology as a tool in ecological research. In *Ecological Morphology* (ed. P. C. Wainwright and S. M. Reilly), pp. 42–59. Chicago: University of Chicago Press.
- WINER, B. J., BROWN, D. R. AND MICHELS, K. M. (1991). *Statistical Principles in Experimental Design*. New York: McGraw-Hill.
- ZAR, J. H. (1984). *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall, Inc.