

MODULATION OF ATTACK BEHAVIOR AND ITS EFFECT ON FEEDING PERFORMANCE IN A TROPHIC GENERALIST FISH, *HEXAGRAMMOS DECAGRAMMUS*

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Summary

This study examines the ability of a temperate marine fish, *Hexagrammos decagrammus*, to modulate its prey capture behavior in response to differences in prey type. This species has an extremely broad diet, feeding on prey which demonstrate very different anti-capture behaviors. Video-taped attacks on three shrimp species, one crab and pieces of shrimp were analyzed to determine the relative contributions of suction-feeding and ram-feeding behaviors to prey capture. The prey capture behaviors used by the predator were related to differences in escape behavior among the three shrimp species. *H. decagrammus* used behaviors characteristic of other ram-feeding predators when feeding on the two most elusive shrimp species: high attack velocity, attack initiated at a greater distance from the prey, and greater movement of the predator relative to the prey. Strikes at crabs and pieces of shrimp elicited strikes more typical of other suction-

feeding predators, with lower attack velocities, shorter initial predator–prey distances and greater relative movement of the prey towards the predator. Attacks on the least elusive shrimp species showed elements of both ram and suction feeding. Modulation of attack velocity increased capture success on elusive prey, supporting the hypothesis that diet diversity is associated with the presence of a repertoire of feeding behaviors. These data suggest that functional differences in prey anti-capture behavior, as well as the functional versatility of the predator, must be addressed in ecomorphological studies that try to correlate predator morphology with diet.

Key words: modulation, prey capture, performance, ram feeding, suction feeding, ram-suction index, *Hexagrammos decagrammus*, kelp greenling, behavior.

Introduction

The morphological design of a predator has a strong influence on its feeding ecology. Morphology can be a potential constraining force on diet through its effect on feeding performance (Kiltie, 1982; Lauder, 1983a; Wainwright, 1987, 1988). For example, mouth size can limit the maximum size of prey that can be consumed by a predator (Lawrence, 1957; Werner, 1974, 1977); mouth size and shape can also affect suction feeding efficiency, through their effect on the velocity of the water entering the mouth (Lauder, 1983b; Lauder and Clark, 1984; Liem, 1990). Although morphology may be used to predict the functional limitations or capabilities of an organism (its potential niche), it is not always a good predictor of the realized trophic niche (McKaye and Marsh, 1983; Schluter and Grant, 1984; Smith and Redford, 1990). The correlation between morphology and the observed diet may be weakened by intrinsic factors, such as behavioral flexibility or physiological specialization, which may provide for a greater or lesser range of function than would be predicted

on the basis of morphology alone (Baker, 1979; Liem, 1980b, 1984; Grossman, 1986). In order to understand the role of a particular morphological structure in determining diet, it is essential to examine how that structure is used during prey capture, the behavioral flexibility in the use of that structure, and how morphology and behavior interact to affect feeding performance (Mittelbach, 1984; Norton, 1988, 1991; Emerson and Koehl, 1990).

Despite a surge of recent interest in behavioral repertoires and modulation of prey capture in fishes and other aquatic vertebrates (Liem, 1978, 1979, 1980b; Lauder, 1981; Vinyard, 1982; Shaffer and Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988, 1990; Chu, 1989; Coughlin and Strickler, 1990; Lauder and Prendergast, 1992), very few studies have addressed the performance consequences of modulation (Wainwright, 1986; Norton, 1991; Sanderson, 1991; Norton and Brainerd, 1993; see also Wainwright and Richard, 1995). Modulation of the jaw apparatus, a term first

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used by Liem (1978), refers to the ability of some species to change the kinematic, electromyographic and pressure profiles of jaw function in direct response to varying feeding conditions (Liem, 1978; Lauder, 1981; Wainwright and Lauder, 1986). Variation in organismal performance is likely to have a large influence on fitness. To assess the adaptive role of behavioral modulation, it is necessary to show a causal relationship between behavioral flexibility and feeding performance (Bock, 1980; Arnold, 1983; Emerson and Arnold, 1989). Because modulation has implications for the trophic ecology of a species, many researchers have tried to correlate the presence of a behavioral repertoire with dietary diversity (Liem, 1978, 1980b; Sanderson, 1988, 1990, 1991; Chu, 1989). However, the benefits of (or necessity for) flexible feeding behavior in the natural environment of the predator have been difficult to evaluate in most functional morphological analyses, as the majority of these studies have substituted commercially available prey for natural prey species in their experiments (but see Coughlin and Strickler, 1990; Norton, 1991).

The three major prey capture methods used by fishes are suction feeding, ram feeding and biting (Liem, 1980a). Prey anti-capture behaviors will influence their susceptibility to these different capture methods (Endler, 1986; Norton, 1995). Prey which have no major morphological defenses, or avoid predation by adhering to or grasping the substratum, are most vulnerable to suction-feeding predators because the predator can approach the prey closely enough for suction to work effectively. Prey that use their locomotory ability to escape from a predator are most vulnerable to high-velocity ram attacks, which allow the predator to overtake the prey before it can begin its escape response. Prey that are too large, or too firmly attached to the substratum, to be captured by suction are most vulnerable to predators with sharp cutting teeth and a strong bite. The three prey capture methods, as well as the categorization of prey by the functional challenge they present to the predator, represent extremes in a range of possible behaviors. The ability of a predator to use a combination of different feeding methods effectively will increase the range of functionally diverse prey it can efficiently handle.

My goal in the present paper is to determine whether *Hexagrammos decagrammus*, the kelp greenling, modulates its feeding behavior in response to a variety of natural prey species. *H. decagrammus* consumes a greater diversity of prey species than most other fishes in the nearshore rocky reef habitat of the northeast Pacific (Miller *et al.* 1977; Moulton, 1977). Is this diet breadth a function of the use of multiple feeding modes (Liem, 1980b; Sanderson, 1991)? Differences in prey capture methods will be related to prey escape behaviors to test the generality of the predictions outlined above. The effect of modulation on capture success is also addressed to determine the significance of modulation for improving predator feeding performance.

Materials and methods

Five *H. decagrammus* (Pallas 1810) (25.5–28.0 cm standard

length) were collected near Friday Harbor, Washington, USA. Individuals were maintained separately in circular acrylic outdoor aquaria (103 cm diameter) that contained a single shelter. The covered aquaria received a constant flow of sea water at ambient water temperature (approximately 11–12 °C). Five natural prey types were selected to represent a range of anti-predator behaviors and were collected in areas where *H. decagrammus* also occur. Prey included three species of shrimp (*Pandalus danae*, *Heptacarpus stylus* and *Crangon alaskensis*) and one crab species (*Pugettia gracilis*); pieces of shrimp (*Pandalus danae*, 10 mm long) were used to represent a prey with a total lack of response to the predator. The range of prey sizes used is listed below as (carapace length/total length) for the shrimps and as carapace length for *Pugettia gracilis*: *Pandalus danae* (5–19 mm/26–61 mm), *Heptacarpus stylus* (7–10 mm/28–44 mm), *Crangon alaskensis* (7–18 mm/29–60 mm) and *Pugettia gracilis* (8–20 mm). Prey length ranged from 3 to 8% of the standard length of the predator.

Capture success

Prey were introduced to the aquarium individually, *via* an opaque plastic tube (8.5 cm diameter) and were allowed to settle on the bottom before the tube was removed to allow predator access. Crabs were introduced to the aquarium over a small weighted platform covered in nylon mesh window screen, giving them a substratum they could grasp firmly. Shrimps were introduced onto a bare plastic grid. Prey species were introduced in random order, and the predators consumed 1–8 prey items per feeding trial. At least 24 h passed between feeding trials.

Capture success was recorded as the outcome of the first strike at an individual prey item. Prey were removed from the aquarium following an unsuccessful feeding attempt. Total length of prey (to the nearest millimeter) was measured along the anteroposterior body axis to control for the possible effect of differences in prey size on capture success.

Predator and prey movements

Feeding events were video-taped at 200 fields s⁻¹ using an NAC high-speed video system. A plastic 1 cm×1 cm grid was placed on the bottom of each tank. The camera was positioned to record a dorsal view of the feeding event; lateral views were obtained using a mirror inclined at 45° next to the grid. The mirror was placed inside the aquarium at the start of each feeding trial, with a second plastic grid placed opposite the mirror and perpendicular to the bottom grid (providing a stationary reference for lateral images). The total feeding area delimited by the mirror and vertical grid measured 27 cm×35 cm, and the fish was free to enter and exit the area from either side.

The relative movements of predator and prey and the characteristics of prey escape behavior were determined from field-by-field analysis of video-taped feeding events. Thirty-two video fields (over a 250 ms time period) were analyzed for each feeding event. The video field in which the prey began to

enter the mouth was designated as time zero, and all other fields included in the analysis are labeled relative to this reference point: -200, -150 to -50 (in 10 ms increments), -45 to +50 (in 5 ms increments). The following points were digitized in the dorsal view of each of the 32 video fields: the distal tip of the premaxilla, the distal tip of the neurocranium (ethmoid), the point on the prey nearest the predator, the point on the prey farthest from the predator, and a stationary reference point for both the predator and prey in their line of travel. *H. decagrammus* lacks a swim bladder, spending most of its time resting on its fins on the bottom; thus, its attacks generally occurred in a two-dimensional plane. When a lateral view (in the mirror) was clear, the frame just prior to mouth opening was noted. Predator body velocity_{body} (v_{body}) was calculated as the distance the predator traveled between two video fields, using the tip of the ethmoid as a landmark, divided by the time elapsed between those fields. Predator $v_{\text{body+pmx}}$ uses the distal tip of the premaxilla as a landmark to account for the added velocity due to premaxillary protrusion. It is this measure of velocity, body velocity plus protrusion velocity, that has the most direct influence on the prey. All velocity measurements reported are the maximum values recorded.

To determine whether the predator used different attack behaviors for different prey species, each strike was characterized by its position along the ram feeding/suction feeding continuum (Norton and Brainerd, 1993). The ram-suction index (RSI), developed by Norton and Brainerd (1993), is calculated as:

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

where D_{predator} is the net distance moved by the predator and D_{prey} is the net distance moved by the prey. The index ranges in value from +1, a pure ram strike in which only the predator moves, to -1, a pure suction strike in which only the prey moves. The net distance moved is determined for the time frame starting with the video field just prior to mouth opening and ending with the last field before the prey disappears into the predator's mouth. Only strikes in which the prey did not attempt to escape were included in the calculation of this index (Norton and Brainerd, 1993). To investigate the contribution of premaxillary protrusion to the forward motion of the predator, the position of the predator was recorded relative to the distal tip of the ethmoid (RSI_{body}) and to the tip of the premaxilla (RSI_{pmx}) for each strike. Because jaw protrusion involves anterior extension of the premaxilla, the value of RSI_{pmx} will never reach -1 (a 'pure' suction strike) because protrusion always incorporates forward motion of the predator (Summers, 1993).

The maximum velocity of prey entering the mouth was also used to compare the relative contribution of suction feeding to prey capture for each strike. The distance moved by the prey (relative to a stationary point on the background) between two video fields was divided by the time elapsed between those two fields.

$v_{\text{body+pmx}}$, v_{body} and predator-prey distance at the time of mouth opening were compared between strikes that resulted in

captures and misses to determine whether unsuccessful strikes were related to predator error. Captures and misses were contrasted for the three shrimp species only; too few misses were video-taped for *Pugettia* and for pieces of shrimp. Prey size was also compared between strikes that resulted in captures and misses to determine whether it was correlated with capture success.

Prey behavior

Three variables were used to characterize shrimp escape behavior: the proportion of predator attacks in which a tail-flip occurred, the maximum escape velocity and the reaction distance. The tendency of the shrimp species to attempt to escape was quantified as the number of predator attacks that elicited a tail-flip divided by the total number of video-taped attacks on that prey species. Prey escape velocity was calculated as the distance traveled between two video fields divided by the time elapsed between those fields for all events in which the shrimp attempted to escape. Reaction distance is the minimum distance between the predator and prey in the frame just prior to the initiation of a tail-flip escape.

Statistical analyses

Inter-individual variation in capture success was assessed using a heterogeneity χ^2 to test the null hypothesis that all five individuals could have come from the same population (Zar, 1984). The heterogeneity χ^2 was not significant (d.f.=11, $\chi^2=9.355$, $0.50 < P < 0.75$), so data from the five individuals were pooled for a more powerful χ^2 -test (Zar, 1984). Differences in capture success among the five prey species were evaluated using a χ^2 -test. When the null hypothesis of no difference in capture success among prey species was rejected, a Tukey-type multiple-comparison test for proportions (Zar, 1984) was used to determine which prey species were significantly different from one another.

Differences in predator attack behavior were assessed using a two-way, mixed-model analysis of variance (ANOVA) with prey species as the fixed effect and predator individual as the random effect. The fixed effect was tested over the interaction (prey species \times individual) mean square, while the random effect and interaction term were tested over the error mean square (Zar, 1984). The statistical variables tested using an ANOVA included (1) v_{body} , (2) $v_{\text{body+pmx}}$, (3) predator-prey distance at the start of mouth opening, (4) RSI_{body} , (5) RSI_{pmx} and (6) the velocity of the prey entering the mouth. The sequential Bonferroni technique was used to calculate adjusted significance levels for the above six tests, to control for the group-wide Type I error rate (Rice, 1989). Significance was tested at table-wide values of $\alpha=0.05$ and $\alpha=0.01$, for $k=6$ tests. Because the RSI is a proportion, its values may deviate from normality when the proportions are very large or very small (Sokal and Rohlf, 1981). However, the proportions calculated for strikes in the present study were not extreme and thus were not arcsine-transformed for statistical analysis. In those cases where a significant prey species effect was found, the Tukey-Kramer test was used to determine which of the prey species were associated with

differences in predator behaviors. One-way ANOVAs were used to test for differences in predator behavior and prey size between captures and misses for each prey type.

Differences in shrimp escape velocity and reaction distance were assessed using a one-way ANOVA (model I) and the Tukey–Kramer *post-hoc* test to determine which species differed from one another when the main effect was statistically significant. Differences in the proportion of attacks resulting in a tail-flip were evaluated using a χ^2 -test. When the null hypothesis of no difference in tendency to tail-flip among shrimp species was rejected, a Tukey-type multiple-comparison test for proportions (Zar, 1984) was used to determine which species were significantly different from one another.

Results

Capture success

Hexagrammos decagrammus had differential success in capturing the five prey species (Fig. 1). Strikes at pieces of shrimp were 100 % successful; capture success was poorest for strikes at two of the live shrimp species. Unsuccessful strikes at all shrimps were always associated with evasive behavior (tail-flip) of the prey. Unsuccessful strikes at crabs always left the crab clinging tightly to the mesh substratum. As reported below, predator attack behavior was also partially responsible for failed feeding attempts.

Shrimp behavior

Differences in shrimp escape behavior were correlated with differences in the capture success of the predator for these prey species. *Pandalus* and *Heptacarpus*, which were the most difficult prey for *H. decagrammus* to capture (Fig. 1), reacted to the predator in a way that tended to make them more elusive relative to *Crangon*. Table 1 shows the ANOVA results for the

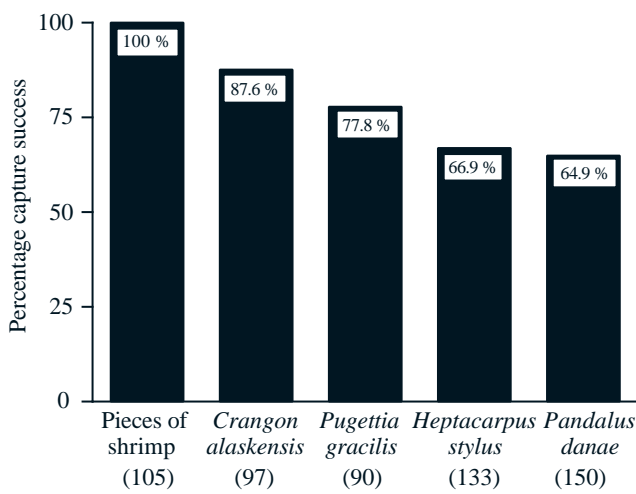


Fig. 1. Percentage capture success for strikes by *Hexagrammos decagrammus* at five types of prey. Sample size is indicated in parentheses. Horizontal lines connect species whose capture success was not significantly different ($P < 0.01$) in a *posteriori* comparisons of proportions.

Table 1. Results of one-way ANOVAs comparing the escape behavior of the three shrimp species

| Variable | d.f. | F | P |
|-------------------|-------|-------|--------|
| Reaction distance | 2, 34 | 5.745 | 0.0071 |
| Escape velocity | 2, 37 | 0.969 | 0.3890 |

maximum escape velocity and reaction distance of the shrimps. The reaction distance of *Pandalus* was significantly greater than that of the other two shrimp species in terms of absolute distance (Table 2) as well as in terms of the distance relative to shrimp body length. *Pandalus* (mean body length of individuals in analysis of escapes, 44.5 mm) initiated an escape response when the predator was still nearly a full shrimp body-length away; *Crangon* (50.0 mm) and *Heptacarpus* (36.5 mm) waited until the predator approached to within 0.3–0.6 shrimp body-lengths. The maximum escape velocity attained did not differ significantly among the three shrimp species (Tables 1, 2). The frequencies with which the shrimp species used a tail-flip escape response are summarized in Table 3. *Pandalus* and *Heptacarpus* attempted to escape in a significantly greater proportion of predator attacks compared with *Crangon*.

Predator attack kinematics

H. decagrammus demonstrated modulation in attack behavior in response to different prey. Table 4 summarizes the

Table 2. Mean maximum escape velocity and reaction distance of the three shrimp species

| Species | Reaction distance (mm) | Escape velocity (mm s ⁻¹) |
|---------------------------|------------------------|---------------------------------------|
| <i>Crangon alaskensis</i> | 14.6±5.4 (6) | 1464.7±238.2 (6) |
| <i>Heptacarpus stylus</i> | 22.2±3.6 (16) | 1395.9±68.3 (16) |
| <i>Pandalus danae</i> | 39.9±5.8* (15) | 1676.9±185.9 (18) |

Values are means ± S.E.M. (N).

* $P < 0.05$, Tukey–Kramer *post-hoc* test.

Table 3. Results of χ^2 -tests for the proportion of predator attacks resulting in a tail-flip response by three shrimp species

| Species | N | % Occurrence of tail-flip response | χ^2 | P |
|---------------------------|----|------------------------------------|----------|--------|
| <i>Crangon alaskensis</i> | 39 | 15.4* | 43.35 | 0.0001 |
| <i>Heptacarpus stylus</i> | 60 | 63.3 | | |
| <i>Pandalus danae</i> | 69 | 79.7 | | |

*Significantly different from other species at $P < 0.05$, using a Tukey-type multiple-comparison *post-hoc* test.

Table 4. Mean values for six statistical variables measured during attacks by *Hexagrammos decagrammus* on five prey types

| Variable | <i>Crangon alaskensis</i> | <i>Heptacarpus stylus</i> | <i>Pandalus danae</i> | <i>Pugettia gracilis</i> | Pieces of shrimp |
|---|---------------------------|---------------------------|-----------------------|--------------------------|----------------------|
| v_{body} (mm s ⁻¹) | 1134.1±122.5 (21) | 1198.8±120.3 (19) | 1430.2±131.7 (16) | 842.5±60.3 (22) | 956.2±75.5 (22) |
| $v_{body+pmx}$ (mm s ⁻¹) | 1477.0±129.2 (23) | 1566.2±118.2 (19) | 1685.9±132.0 (16) | 1058.1±90.5 (24) | 1129.3±109.2 (22) |
| Predator-prey distance (mm) | 13.5±1.6 (19) | 14.1±1.5 (17) | 16.9±1.7 (14) | 7.2±0.7 (21) | 10.2±1.0 (21) |
| RSI _{body} | -0.10±0.15 (14) | 0.25±0.26 (15) | 0.43±0.13 (12) | -0.39±0.12 (16) | -0.03±0.09 (16) |
| RSI _{pmx} | 0.13±0.11 (16) | 0.40±0.11 (15) | 0.58±0.08 (12) | 0.11±0.07 (17) | 0.17±0.08 (16) |
| Velocity of prey entering mouth (mm s ⁻¹) | 2015.9±218.7 (23) | 1444.4±160.0 (18) | 998.3±132.1 (16) | 1050.8±138.1 (24) | 1185.8±129.3 (23) |

Values are means ± S.E.M. (N).

RSI, ram-suction index; pmx, premaxilla; v_{body} , attack velocity calculated from the tip of the ethmoid; $v_{body+pmx}$, attack velocity calculated from the tip of the premaxilla.

data for the kinematic variables associated with strikes at the five prey species; statistical results are reported in Table 5 for the main effects.

Strikes at shrimp were of higher attack velocities than strikes at crab or pieces of shrimp when either body velocity (v_{body}) or body velocity plus the added velocity of premaxilla protrusion ($v_{body+pmx}$) was considered (Table 4; Fig. 2). Attacks on *Crangon* were intermediate in velocity between the those on elusive shrimps and those on the other two prey species. The predator-prey distance at the start of the strike was also significantly greater for attacks on shrimp, relative to crabs and pieces of shrimp, with strikes at *Crangon* again being intermediate to those for the other four prey species (Table 4; Fig. 3).

The ram-suction index was also useful in detecting differences among strikes at the five prey species (Tables 4, 5). Strikes at the most evasive shrimps, *Pandalus* and *Heptacarpus*, were more characteristic of ram attacks than strikes at *Crangon* or the other two prey (Fig. 4). Strikes at

Pandalus had significantly greater RSI values than strikes on all other prey species except *Heptacarpus*; strikes at *Crangon* were more similar to strikes at *Pugettia* crabs and pieces of shrimp than to strikes at the other two shrimp species (Fig. 4). When premaxilla protrusion was incorporated into the distance moved by the predator (RSI_{pmx}), strikes at all prey species showed a greater contribution of predator movement relative to prey movement (RSI>0; Fig. 4). The ranking of prey species by their RSI value remained the same using both RSI_{body} and RSI_{pmx}; however, there were fewer significant differences detected among prey species using RSI_{pmx}.

The maximum velocity of prey entering the mouth provided an indirect measure of the suction force generated for different prey. *Crangon* was carried into the mouth of the predator at a higher velocity than all other prey except *Heptacarpus* (Table 4; Tukey-Kramer *post-hoc* test for ANOVA reported in Table 5, $P<0.05$). This observation agrees with direct measurements of buccal pressure changes during strikes at different prey by *H. decagrammus* (Nemeth, 1997).

Table 5. Results of the two-way mixed-model ANOVAs for predator attack variables compared among five prey species

| Variable | Error d.f. | Prey d.f.=4 | Individual d.f.=4 | Prey × Individual d.f.=12 |
|---------------------------------|------------|-------------------|-------------------|---------------------------|
| v_{body} | 78 | 3.517 (0.0403)* | 5.874 (0.0003) | 0.873 (0.5768) |
| $v_{body+pmx}$ | 83 | 7.118 (0.0035)* | 6.572 (0.0001) | 0.692 (0.7549) |
| Predator-prey distance | 71 | 7.015 (0.0038)* | 0.760 (0.5547) | 0.403 (0.9581) |
| RSI _{body} | 54 | 11.111 (0.0011)** | 2.549 (0.0496) | 0.457 (0.9098) |
| RSI _{pmx} | 54 | 8.006 (0.0037)* | 3.020 (0.0255) | 0.621 (0.7891) |
| Velocity of prey entering mouth | 83 | 4.288 (0.0220)* | 1.506 (0.2081) | 0.698 (0.7487) |

Table entries are *F* values (*P*); * $P<0.05$, ** $P<0.01$, using sequential Bonferroni correction for prey effect (Rice, 1989).

RSI, ram-suction index; pmx, premaxilla; v_{body} , attack velocity calculated from the tip of the ethmoid; $v_{body+pmx}$, attack velocity calculated from the tip of the premaxilla.

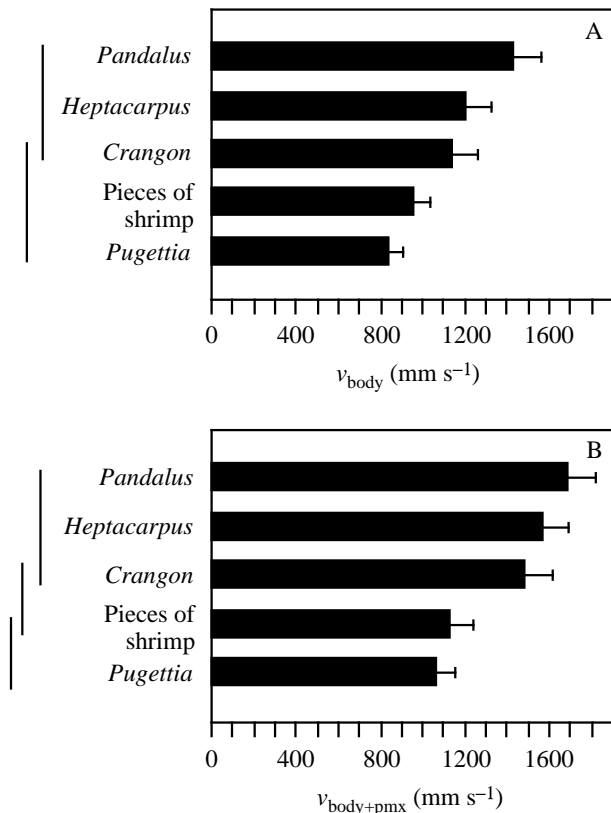


Fig. 2. Maximum attack velocity (mean + 1 S.E.M.) of *Hexagrammos decagrammus* during strikes at five types of prey calculated from (A) the tip of the ethmoid (v_{body}) and (B) the tip of the premaxilla ($v_{\text{body+pmx}}$) as the reference point on the predator. Vertical lines connect species whose means were not significantly different ($P < 0.05$) in a posteriori comparisons of means (Tukey-Kramer test). See Table 4 for values of N .

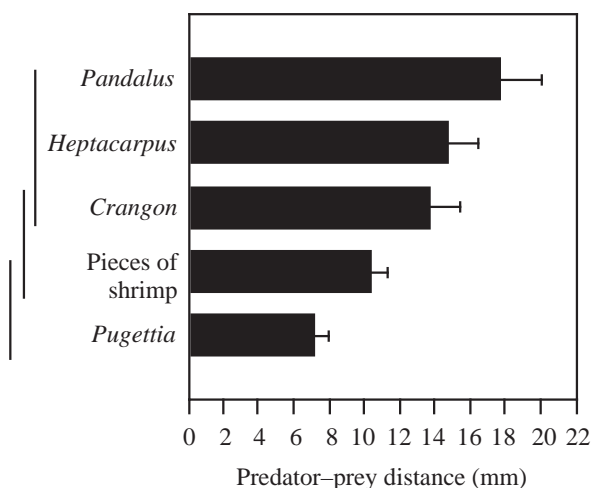


Fig. 3. Predator-prey distance at the start of an attack (mean + 1 S.E.M.) for *Hexagrammos decagrammus* during strikes at five types of prey. Vertical lines connect species whose means were not significantly different ($P < 0.01$) in a posteriori comparisons of means (Tukey-Kramer test). See Table 4 for values of N .

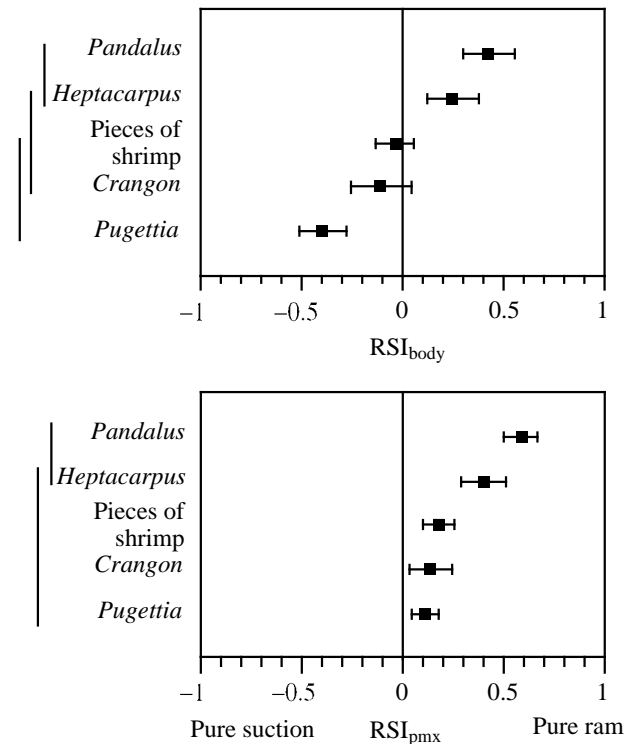


Fig. 4. Ram-suction indices (mean \pm 1 S.E.M.) for strikes by *Hexagrammos decagrammus* at five types of prey, using the tip of the ethmoid (RSI_{body}) or the tip of the premaxilla (RSI_{pmx}) as the reference point on the predator. Vertical lines connect species whose means were not significantly different ($P < 0.05$) in a posteriori comparisons of means (Tukey-Kramer test). See Table 4 for values of N .

Captures versus misses

Prey size had no effect on capture success over the narrow range of prey lengths used in this study (Table 6). Although misses were generally associated with evasive behavior by the prey (see above), there were also some differences in predator attack behavior correlated with predator failure.

Predator $v_{\text{body+pmx}}$ had a significant effect on capture success for the shrimp species. Successful strikes at *Crangon*, *Heptacarpus* and *Pandalus* were associated with significantly higher attack velocities (body plus jaw protrusion) than unsuccessful strikes (Fig. 5). However, v_{body} did not differ significantly between captures and misses (Fig. 5). In nearly all unsuccessful strikes at *Pandalus* and *Heptacarpus*, the predator began the strike after the prey had initiated a tail-flip. The predator-prey distance at that time was confounded by escape movements of the shrimp away from the predator. Thus, it was difficult to assess this aspect of predator behavior in terms of its effect on capture success, since the higher predator-prey distances for misses seemed to be a consequence of the prey's escape rather than the result of poor judgement of distance by the predator.

Discussion

The main conclusion of this study is that modulation of attack behavior by *H. decagrammus* improves its feeding

Table 6. Mean prey size for strikes resulting in captures and misses, with results of one-way ANOVA for each prey species

| Prey | Captures | Misses | <i>F</i> | <i>P</i> |
|---------------------------|------------------|------------------|----------|----------|
| <i>Crangon alaskensis</i> | 11.1±0.2 (85) | 11.3±0.3 (12) | 0.03 | 0.86 |
| <i>Heptacarpus stylus</i> | 8.5±0.1 (88) | 8.7±0.1 (44) | 2.24 | 0.14 |
| <i>Pandalus danae</i> | 13.0±0.2 (97) | 13.3±0.3 (53) | 0.66 | 0.42 |
| <i>Pugettia gracilis</i> | 13.2±0.3 (70) | 13.8±0.7 (20) | 0.81 | 0.37 |

Values are means ± S.E.M. (*N*), and prey size is given in millimeters.

performance on a diversity of prey species. This predator is able to recognize subtle differences in prey behavior and adjusts its attack kinematics to increase the likelihood of prey capture.

The modulation of attack kinematics and the use of different feeding behaviors were correlated with the evasive behavior of the prey, as observed in a number of previous studies (Elshoud-Oldenhave and Osse, 1976; Liem, 1978, 1980*b*; Lauder and Liem, 1980; Lauder, 1981; Vinyard, 1982; Sanderson, 1988, 1990; Coughlin and Strickler, 1990; Norton, 1991). For grasping crabs or stationary pieces of shrimp, *H. decagrammus* uses kinematics typical of a suction-feeding attack: the predator approaches the prey at low velocity, gets very close to the prey before starting the strike, and uses a combination of suction and jaw protrusion to shorten the distance between the predator and prey. For the most elusive prey, *Pandalus* and *Heptacarpus*, *H. decagrammus* uses a ram-feeding attack: the attack is initiated at a greater distance from the prey, is of higher velocity and involves a greater contribution of predator movement (body plus premaxilla protrusion) to shorten the predator-prey distance. Jaw protrusion appears to play an important role in ram-feeding events by *H. decagrammus*. When the velocity of jaw protrusion is added to the forward velocity of the predator's body, a greater separation in attack velocities is detected among the five prey types (Fig. 2). Attack $v_{\text{body+pmx}}$ also had a greater effect than attack v_{body} on feeding performance (Fig. 5).

H. decagrammus was apparently able to distinguish among the shrimp species on the basis of differences in their responsiveness to predator attack. Strikes at *Crangon* were often more similar to strikes at the stationary prey than to strikes at the other two shrimps (Fig. 4). Prior to analyzing the video-tapes of shrimp behavior, I (and many others) would have categorized *Crangon* as an elusive prey species on the basis that it uses a high-velocity tail-flip to escape, often in unpredictable directions (Neil and Ansell, 1995). Although *Crangon* is capable of such an escape response, its first defense appears to be reliance on its cryptic speckled-brown coloration to escape detection. This species is common on sand or mud

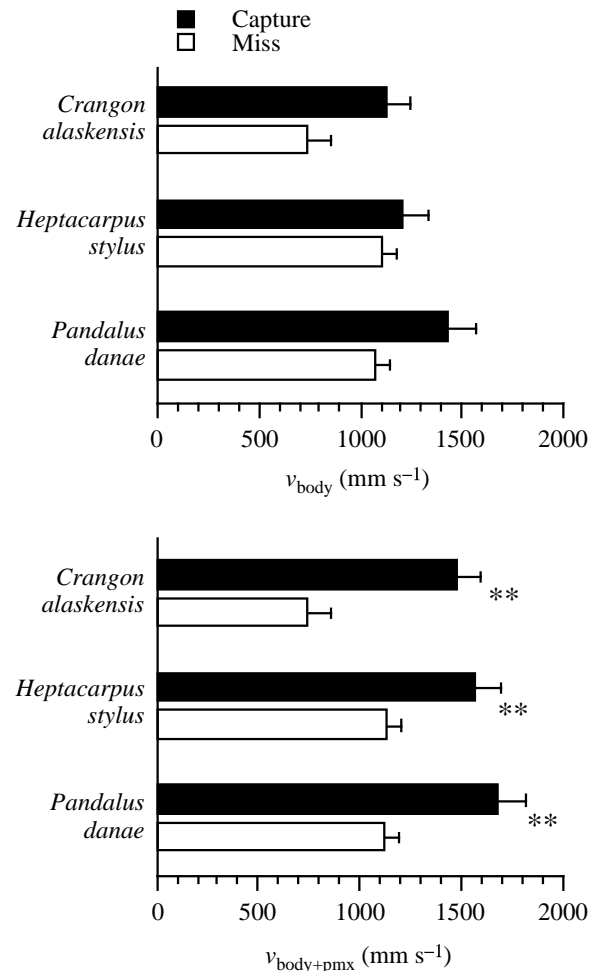


Fig. 5. Captures and misses contrasted for strikes at the three shrimp species, for v_{body} and $v_{\text{body+pmx}}$ (see Fig. 2 for an explanation of abbreviations). Values are means + 1 S.E.M. **Significant difference between captures and misses ($P < 0.01$) detected using one-way ANOVA for that prey species. See Table 6 for values of *N*.

and generally buries itself partially in the soft sediment (Butler, 1980). *Crangon* allowed the fish in this study to approach it very closely and only rarely used a tail-flip escape response. This combination of behaviors allows *H. decagrammus* to use suction effectively for capturing this prey, because the predator can get close enough to the prey to trap it in a high-velocity jet of water being sucked into the mouth. In contrast, *H. decagrammus* cannot get close enough to the other two shrimp species to use suction and must use a ram-feeding approach to surprise, and overtake, the prey. These differences in prey behavior have important implications for the type of capture method that is effective and would have not been detected without a detailed examination of predator-prey interactions. The data reported here show that, while functional classifications of prey are useful in making predictions regarding the trophic biology of a predator (diet, foraging and capture method), it is not always easy to categorize prey

without studying their interactions with the predator of interest (Main, 1985, 1987; Luczkovich *et al.* 1995; Norton, 1995).

The ram-suction index (RSI) was developed in order to quantify the relative contributions of ram and suction elements to individual strikes (Norton and Brainerd, 1993). This index thus provides a quantitative evaluation of 'the hydrodynamic consequences of intraspecific, interspecific, and interprey variation in strike mechanics' (Norton and Brainerd, 1993). In the present study, the RSI was very useful for distinguishing among strikes at prey differing in their escape behavior. There was a clear gradient of RSI values, ranging from positive values for the most elusive prey to negative values (RSI_{body}) for non-elusive prey. This is in contrast to the results of Norton and Brainerd (1993), which showed no differences in the RSI among strikes at elusive *versus* non-elusive prey by three fish species (*Micropterus salmoides*, *Lepomis macrochirus* and *Cichlasoma severum*). This is interesting because these authors did detect a prey-type effect in measurements of buccal pressure change in *C. severum*, with strikes at elusive prey being of greater subambient pressures than strikes at non-elusive prey. *H. decagrammus* also modulates the timing and magnitude of buccal pressure change for different prey, generating the greatest suction force for elusive prey relative to non-elusive prey and using the largest and fastest reduction in buccal pressure (relative to all other prey) during strikes at the most stationary of the shrimps, *Crangon* spp. (Nemeth, 1997).

The lack of separation between strikes at elusive and non-elusive prey on the RSI scale in the study of Norton and Brainerd (1993) may reflect the morphological specialization of the species they considered. The four species in their study were selected for their convergence in large *versus* small mouth sizes. These fishes used feeding behaviors that maximized the effectiveness of their morphologies (e.g. the use of suction feeding by small-mouthed predators), rather than switching to the prey capture behavior that would be most appropriate for a particular prey (e.g. ram feeding for elusive prey). Perhaps species possessing an intermediate mouth size are less likely to employ one particular feeding method, because they are less constrained by their morphology when selecting between ram and suction modes. The gape diameter and the buccal volume relative to the gape area of *H. decagrammus* are intermediate between those of the two centrarchid fishes used in several studies of the effect of mouth size on feeding mode (Norton and Brainerd, 1993; Wainwright and Richard, 1995; D. H. Nemeth, unpublished data). Although morphological specialization in terms of mouth size does not preclude the ability of a species to modulate along the ram/suction continuum, a species using a feeding method not 'matched' to its morphology will probably have lower capture success relative to predators whose morphology is better suited to using that capture method (Norton, 1991, 1995). Small-mouthed cottids typically have low capture success on elusive prey; however, one small-mouthed species that uses a ram-type feeding method for elusive prey has a higher capture success on such prey relative to other small-mouthed cottids (but does

not reach the level of success seen in large-mouthed cottids) (Norton, 1991).

To understand the potential adaptive advantage of modulation, the causal relationship between behavioral variation and predator performance must be assessed (Bock, 1980; Arnold, 1983; Emerson and Arnold, 1989; Emerson and Koehl, 1990; Wainwright, 1994). For *H. decagrammus*, capture success for elusive prey is highly dependent on achieving a high attack velocity. Although misses at shrimps were always associated with evasive behavior by the prey, increasing the velocity of the attack often permitted the predator to overtake an escaping shrimp. This pattern is similar to that seen in some cottid fishes, in which unsuccessful strikes are sometimes associated with inadequate attack velocities, but misses more often result from evasive behavior by the prey (Norton, 1991). The ability of *H. decagrammus* to shift its attack behavior towards the ram-feeding end of this behavioral continuum enables it to capture elusive prey that it would not be able to capture as effectively using suction feeding. Successful strikes at *Crangon*, while associated with high velocities of premaxilla protrusion, also depend on the generation of a strong suction force (Nemeth, 1997). *H. decagrammus* relies on characteristics of both ram and suction feeding to ensure success in capturing a diversity of shrimps found in its natural diet.

There were very few differences in attack behavior between strikes at *Pandalus* and *Heptacarpus*, and capture success on these two prey did not differ for *H. decagrammus*. In contrast, cottid fishes showed a marked difference in capture success between these two prey species, with nearly twice the success rate for *Heptacarpus* (Norton, 1991). Norton suggests that this difference is consistent with biomechanical predictions of shrimp escape velocity based on differences in shrimp adductor muscle size (Daniel and Meyhöfer, 1989). However, the present study also found no differences in maximum escape velocity by the two shrimps, even though the *Pandalus* individuals used in the present study were slightly larger than the individuals of *Heptacarpus* (Table 6). There may be other differences in shrimp escape behavior, such as the direction or unpredictability of escape, the timing of maximum acceleration or the total distance traveled, that have a greater effect on predator-prey interactions in cottids than in *H. decagrammus* (Daniel and Meyhöfer, 1989; Neil and Ansell, 1995).

The differences in capture success among the prey types in this study reflect their evasiveness and suggest that the predator is challenged more by some prey species than others. Functional challenges presented by prey can result in selection for morphological changes that increase feeding performance; alternatively, selection may act to increase behavioral variation and neural control over such variation. For trophic generalists, broadening the repertoire of prey capture behavior can lead to increased capture success on a diversity of prey, ultimately increasing diet breadth. The ability to switch among a variety of prey species may give some predators a competitive advantage in areas where food resources fluctuate in abundance or may reduce the negative effects of competitive exclusion.

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