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MORPHOLOGY AND ECOLOGY: FUNCTIONAL BASIS OF FEEDING CONSTRAINTS IN CARIBBEAN LABRID FISHES¹

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Abstract. This study examines the role of functional morphology of the feeding apparatus in constraining the food habits of Caribbean wrasses (Labridae) in the genus *Halichoeres*. Like other wrasses, these fishes crush prey with powerful pharyngeal jaws. Estimates of pharyngeal jaw crushing strength were made, based on muscle size and architecture, for an ontogenetic series of fish from each of six species. The resultant scaling relationships indicated that, at any given body length, the six species differed in crushing strength. The ability to crush prey items was, therefore, predicted to vary among species.

The relative importance of crushing strength and pharyngeal jaw gape in constraining predation was examined in laboratory feeding trials using three species that differed in estimated crushing strength: *H. garnoti*, *H. bivittatus*, and *H. maculipinna*. The feeding trials determined the largest individuals of three prey species that fishes could eat. Two hard-bodied prey species (a gastropod and a crab) and a softer bodied crab species were offered to wrasses. Feeding ability on the two hard-shelled prey was predicted best by crushing strength; fishes of equivalent crushing potential were able to eat the same maximum size prey, in spite of considerable interspecific variation in pharyngeal jaw gape and body length at any given crushing strength.

The consequences of ontogenetic and interspecific differences in crushing ability for feeding habits were explored by analyzing the intestinal contents of fishes collected from the Belizean barrier reef. Crushing strength appeared to play a central role in constraining diets of these fishes. Ontogenetic diet analysis of three species revealed that fishes switched from soft-bodied to hard-shelled prey at ≈ 3 –5 N crushing strength, even though this crushing strength occurred at a different body size and pharyngeal jaw gape in each species. This switch was followed by a reduction in dietary breadth as fishes specialized on hard-bodied prey. Few other Caribbean coral reef fishes are capable of crushing molluscs effectively. Wrasses thus utilize a relatively unexploited trophic niche on the prey-hardness resource dimension.

Key words: Caribbean fishes; coral reefs; feeding constraints; feeding ontogeny; functional morphology; gape limitation; Halichoeres; Labridae; mollusc crushing; predation.

INTRODUCTION

A fundamental aim in trophic ecology is to identify the factors that determine patterns of prey use. Predators invariably consume only a subset of the prey present in their environment, and considerable effort has centered around elucidating the forces that shape these restricted diets (Hutchinson 1959, Paloheimo and Dickie 1966, Hyatt 1979, Zaret 1980, Schoener 1986). One factor that can restrict prey use is the ability of the predator to capture and consume different prey types; feeding ability constrains the range of prey an animal can utilize. Feeding ability is, in turn, determined largely by functional morphology of the trophic apparatus, and revealing the nature of this relationship is a key to understanding the role of morphology in limiting prey use.

Several components of feeding ability may be affected by a predator's morphology. The abilities to

detect, pursue, capture, and successfully handle prey, all may have an underlying functional basis related to morphology. Among fishes, most work has examined the influence of prey size on feeding performance (Lawrence 1957, Werner 1974, 1977, Kislalioglu and Gibson 1976, Hairston et al. 1982, Wright et al. 1983, Bentzen and McPhail 1984, Mummert and Drenner 1986). The most frequent finding of these studies is that mouth size limits the maximum size prey that many fish taxa can eat (e.g., Lawrence 1957, Werner 1974, 1977). Other significant findings are that in some planktivorous fish species, gill raker spacing determines the minimum size prey retained by the branchial apparatus (Mummert and Drenner 1986), and eye size can constrain visual acuity, thus limiting the ability of some fish to detect small prey (Hairston et al. 1982).

Morphologically based feeding limitations have been invoked to explain ontogenetic and interspecific differences in fish diets (Bentzen and McPhail 1984, Mittlebach 1984, Mummert and Drenner 1986) and can have considerable predictive power (e.g., Werner 1977).

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Yet, in spite of this potential value, the actual role of predator morphology in shaping food habits in fishes is poorly known (Werner 1977, Liem 1984). In this study I link morphology to patterns of prey use in six Caribbean wrasses (Labridae) of the genus *Halichoeres* by (1) exploring the morphological basis of feeding ability and (2) examining the dietary correlates of interspecific and ontogenetic differences in feeding ability.

Because wrasses, unlike most other reef-dwelling fishes, eat large amounts of hard-bodied prey (molluscs, echinoderms, armored decapod crustaceans [Randall 1967, Yamaoka 1978]), which they crush in their powerful pharyngeal jaws (Liem and Sanderson 1986, Wainwright 1987), I focused on crushing ability as a relevant functional attribute and contrasted its importance, in limiting predation, with pharyngeal jaw gape (oral jaw gape is much larger than pharyngeal jaw gape in these fishes, making the latter more restrictive). Using a functional description of prey crushing, I estimated pharyngeal jaw crushing strength for a size range of individuals from each species. These estimates indicated considerable variation among species in expected crushing strength; at any given body length some species should have stronger jaws than others. Laboratory feeding experiments with one gastropod and two crab prey species were then used to test the relative importance of crushing strength and pharyngeal jaw gape in limiting prey-handling ability in three wrasse species that varied in predicted crushing strength.

The second purpose of this study was to determine the influence of interspecific and ontogenetic differences in feeding ability on the dietary habits of fishes in natural populations. Does pharyngeal jaw crushing strength limit the hardness of prey fish can eat? If so, does this constraint play an important role in shaping patterns of prey use? These questions were addressed by examining the feeding habits of the six *Halichoeres* species on the Belizean barrier reef, describing in detail the diet ontogeny in three of them. In particular, I tested two predictions. First, by analogy with gape-limited predators (Wilson 1975, Zaret 1980), ontogenetic and interspecific increases in crushing strength broaden the range of potential prey a fish can eat. Thus, the dietary breadth of fishes was predicted to increase with pharyngeal jaw strength. Second, if crushing strength is an important limitation on prey use by wild fish, stronger fish should eat harder bodied prey. Both the ontogeny of diet and interspecific feeding differences were explored in the light of these predictions.

MATERIALS AND METHODS

Fieldwork was conducted during April and December 1986 and January 1987 at the Smithsonian Institution's field station on Carrie Bow Cay, located on the Caribbean barrier reef off of Belize, Central America (16°48' N, 88°05' W). This portion of the Belizean reef

experiences minimal human fishing pressure, and, thus, offers a relatively undisturbed coral reef community.

The species of *Halichoeres* studied were *Halichoeres garnoti*, *H. bivittatus*, *H. maculipinna*, *H. radiatus*, *H. poeyi*, and *H. pictus*. Species of *Halichoeres* are typically <200 mm standard length and, like other wrasses, feed during the day on a variety of benthic invertebrates (Hiatt and Strasburg 1960, Randall 1967, Yamaoka 1978).

Functional morphology of feeding

Preliminary observations of individuals maintained in laboratory aquaria indicated that hard-shelled prey were manipulated and crushed between the pharyngeal jaws before being swallowed. Prey that were not successfully crushed were rejected. Subsequent stomach content analysis revealed that hard, or shell-bearing, prey were always crushed before being swallowed.

Pharyngeal jaw anatomy of several fresh and formalin-preserved specimens of each of the six species was studied by dissection under a stereo microscope. For more detailed examination of skeletal anatomy additional whole specimens of each species were cleared and double stained for bone and cartilage (Dingerkus and Uhler 1977).

Scaling relationships of crushing strength with fish standard length were obtained by estimating force capability of the pharyngeal crushing musculature for a size series of individuals from each species (as done previously; see Wainwright 1987). For each fish the left-side crushing musculature was dissected from the head, and its force-generating capability (P') was estimated following Calow and Alexander (1973):

$$P' = (V/w)\sigma \sin 2\alpha,$$

where V is muscle volume, w is muscle width, σ is force production per unit cross-sectional area of the muscle tissue, and α is the angle of pinnation made by the muscle fibers attaching to the central tendon. A σ value of 200 kN/m² was taken from the literature on teleost white muscle (Altringham and Johnston 1982, Johnston and Salamonski 1984), but all other parameters were measured directly. Although the actual value of σ may have differed from 200 kN/m², the critical assumption was that this value is about the same for the six species and does not change during ontogeny. Muscle volume was obtained by dividing muscle mass (in grams) by fish muscle density (1.05 g/cm³; Lowndes 1955). Angle of pinnation and muscle width were measured in at least 10 locations per muscle, and the averages of each were used in calculations of P' . Accounting for left and right sides of pharyngeal jaw musculature the overall force potential of an individual was taken as $2P'$. The crushing apparatus of wrasses involves no lever arms or joints (see Results: Feeding Mechanism) so $2P'$ was taken to estimate prey-crushing strength.

Scaling relationships of pharyngeal jaw gape with fish

standard length were estimated for *H. garnoti*, *H. bivittatus*, and *H. maculipinna*. Maximum gape was measured on a size range of freshly killed specimens from each species by determining the largest diameter plastic dowel that would fit snugly between the upper and lower pharyngeal jaws.

Reduced major axis regressions were fitted to \log_{10} transformed data to estimate the scaling relationships of pharyngeal jaw gape and predicted crushing force with standard length. Reduced major axes were used because considerable measurement error existed in both variables, making the least squares assumption of no variance associated with the independent variable problematic (Ricker 1973, Sokal and Rohlf 1981).

Feeding performance

The purpose of the laboratory feeding performance experiments was twofold: first, to test the morphologically based predictions of relative crushing ability among species and among size classes within species, and second, to contrast the importance of crushing strength with pharyngeal jaw gape in limiting prey-handling ability. Experiments were conducted with seven *H. garnoti*, eight *H. bivittatus*, and six *H. maculipinna*. Feeding performance was assayed for each fish on three prey types: the gastropod mollusc *Cerithium litteratum*, the majid crab *Mithrax sculptus*, and a portunid crab, *Portunus* sp. The objective in these experiments was to determine, for each prey type, the largest individual that each fish could consume.

The force required to crush the gastropod *Cerithium litteratum* increases with increasing shell size (Wainwright 1987), so it was expected that this prey would provide a good measure of prey-crushing ability of fishes. *Mithrax sculptus* is a heavily armored crab with a strong shell; *Portunus* offered a contrast to it in having a softer shell and being a better swimming, more elusive prey. All three prey were eaten commonly by the three fish species, particularly *Cerithium* and *Mithrax*.

Fishes were captured on reefs near Carrie Bow Cay and were maintained separately in 70-L, running-seawater aquaria ($\approx 27^\circ\text{C}$), with a large rock that served as a prey refuge. In feeding trials fishes were offered single prey items, and, after 10 min, a record was made of the success of the feeding attempt. Over several days, 20 individuals of each prey type were offered to each fish including the maximum size that the fish could eat. Care was taken to avoid experimenting with satiated fish. *Cerithium* size was measured as the diameter of the largest whorl perpendicular to the long axis of the shell, and the size of the two crab prey types was taken as the anterior-posterior diameter of the carapace. Since the probability of feeding success decreased gradually, rather than abruptly, with increasing prey size, maximum prey size was estimated as the size at which the probability of a fish eating the items offered was 50% (Wainwright 1987).

Scaling relationships of maximum prey size eaten to

estimated crushing force and pharyngeal jaw gape were estimated with least squares regression (all variables were \log_{10} transformed for analysis). In using least squares regression for these analyses it was assumed that error in the independent variables was negligible, relative to error in the dependent variables. These scaling relationships, both y intercepts and slopes, were compared among species with analysis of covariance (ANCOVA). Significantly different slopes or elevations falsified the hypothesis that the morphological variable is a common functional constraint that predicts feeding performance in the three species. Nonsignificant comparisons indicated similar scaling relationships and were taken as support of the hypothesis that the independent variable (crushing strength or jaw gape) is a common causative factor in limiting predation on that prey type.

Fish diets

Scuba divers and skin divers using handspears collected specimens of all six *Halichoeres* species from four major reef zones around Carrie Bow Cay. Prey availability may vary with reef zone, and, coupled with ontogenetic or interspecific differences in habitat distribution, could lead to variation in observed dietary patterns of fishes. To minimize this possible effect approximately equal numbers and size distributions of each species were collected from each zone, except when a species did not occur in a particular habitat. All species were collected in at least three habitats, except *H. pictus* and *H. poeyi*, which each occurred in a single reef zone. Because wrasses feed only by day all collections were made after 1000, at least 4 h after the onset of feeding. Within 2 h of capture each fish was weighed (in grams), its standard length recorded (in millimetres), and its entire intestinal tract preserved in 10% buffered formalin.

Individual intestinal contents were later sorted under a stereo microscope and identified to the lowest taxonomic level possible (usually family or genus). Length, width, and depth of each item were measured with an ocular micrometer and used to estimate the volumetric contribution of the prey. Dietary breadths were calculated with the diet data from size classes of fish within each species using the Shannon-Wiener diversity index (Shannon 1949):

$$H' = - \sum_{i=1}^n p_i \ln p_i,$$

where p_i is the proportion by volume of a particular prey category, for n prey categories. The percent volumes used to calculate diet breadth were means averaged across all individuals in the size class. Volumetric contribution to the diet was chosen as the best representation of resource utilization because prey volume varied by five orders of magnitude depending on type. The contribution to the diet by small prey items could not be equated with large items. Gut contents of

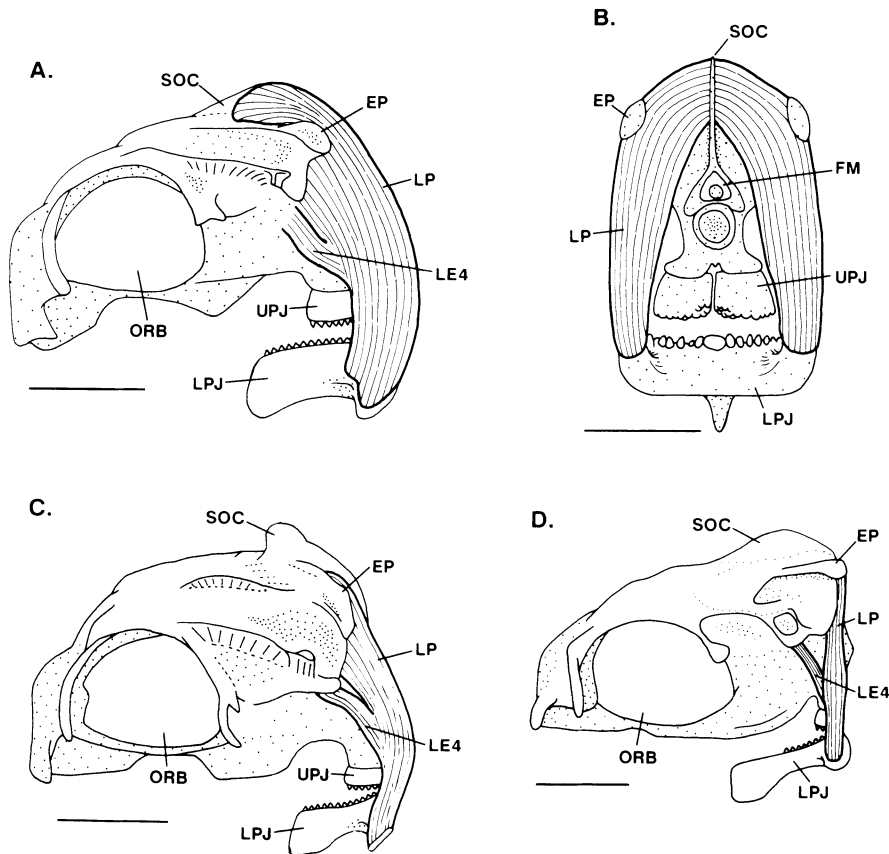


FIG. 1. Diagram of the pharyngeal jaw apparatus in three species of *Halichoeres*: (A) *H. bivittatus* in lateral view, (B) *H. bivittatus* in posterior view, (C) *H. maculipinna* in lateral view, (D) *H. pictus* in lateral view. Structures of the oral jaws, the suspensorium, the opercle series, and most of the branchial apparatus have been removed to show only the most prominent features of the pharyngeal jaw crushing apparatus. Abbreviations: EP, epiotic process; FM, foramen magnum; LE4, fourth levator externus muscle; LP, levator posterior muscle; LPJ, lower pharyngeal jaw; ORB, orbit; SOC, supraoccipital crest; UPJ, upper pharyngeal jaw. Scale bar is 5 mm.

a total of 499 specimens of the six *Halichoeres* species were analyzed.

RESULTS

Feeding mechanism

Wrasses display a derived condition in the arrangement of the pharyngeal jaw apparatus (Kaufman and Liem 1982, Liem 1986), in which two muscles, the levator posterior and fourth levator externus, originate from the neurocranium and insert on the lower pharyngeal jaw (Fig. 1). This facilitates the forceful occlusion of these jaws and the crushing of hard prey (Yamaoka 1978, Liem and Sanderson 1986, Wainwright 1987). Prey are crushed between the knobbly toothed surfaces of paired upper-jaw elements and a singular lower pharyngeal jaw that is suspended by muscles from the neurocranium (Fig. 1). No joints or lever arms are involved in crushing movements.

The levator posterior is a bipinnately structured muscle that originates from several bones on the back of the neurocranium and inserts on a tendon to the

lower jaw (Fig. 1). Originating anterior to the levator posterior, the fourth levator externus has a parallel fiber arrangement and inserts independently onto the tendon to the lower pharyngeal jaw. This muscle is much smaller than the levator posterior, and its fibers are intimately interconnected with those of the latter. For these reasons it was not possible reliably to disconnect it from the levator posterior and to estimate its specific contribution to overall crushing strength. Consequently, the two muscles were weighed together, and the fiber architecture of the levator posterior was analyzed and used in estimating crushing force potential. Because of the relatively small size of the fourth levator externus this procedure was not expected to bias the force calculations significantly.

Scaling of predicted crushing strength as a function of body length differed among the six species (Fig. 2, Appendix 1) because of interspecific differences in both the fiber orientation and relative size (volume) of the crushing musculature. Two patterns of levator posterior fiber arrangement were found; *H. pictus* possessed an average pinnation angle of 20°, the other five species

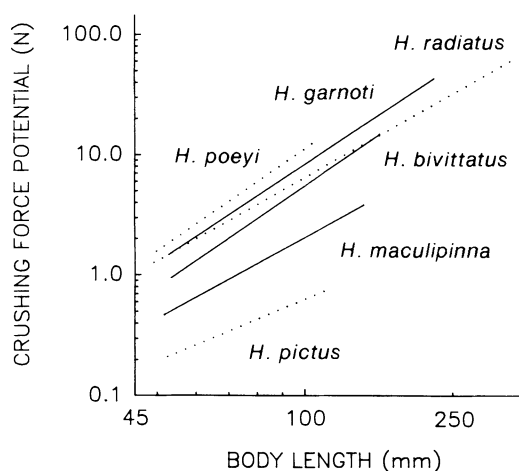


FIG. 2. \log_{10} - \log_{10} plots of estimated pharyngeal jaw crushing force potential and fish standard length, showing the scaling relationships between these variables in six *Halichoeres* species. The size ranges indicated are bounded by the smallest and largest fish examined from each species. Further studies were performed with the three species indicated with solid lines: *H. garnoti*, *H. bivittatus*, and *H. maculipinna*. See Appendix 1 for scaling equation parameters.

had average pinnation angles that ranged from 34.4° to 37.2°. A fiber angle of 45° would maximize the force-producing capability of this muscle; assuming constant muscle mass, smaller angles indicate lower relative crushing force potential. Fiber angle did not vary significantly among individuals within species.

Four patterns were observed in the scaling of muscle mass to body length. *H. garnoti*, *H. bivittatus*, and *H. poeyi* possessed large crushing muscles that exhibited the highest rate of growth relative to fish standard length (Appendix 1). *H. radiatus* also had relatively large muscles, but they did not grow with body length to the degree shown by the other three species (Appendix 1). An intermediate condition was observed in *H. maculipinna*, and *H. pictus* had the slowest growing, smallest muscles. Thus, while *H. maculipinna* has the same fiber orientation as *H. garnoti*, *H. bivittatus*, *H. radiatus*, and *H. poeyi*, at any given body length it is not expected to be as strong as the latter group because its muscle mass is smaller. *H. pictus* exhibited the lowest estimated crushing strength among the six species because of both a low muscle fiber angle and small muscle mass.

Pharyngeal jaw gape scaled isometrically with standard length (gape remains a constant proportion of standard length) in *H. garnoti*, *H. bivittatus*, and *H. maculipinna* (results of *t* tests comparing slopes with the isometric value of 1.0 were nonsignificant for all species). In addition, the *y* intercepts for all species were not significantly different from each other (ANCOVA, $P > .05$). Thus, pharyngeal jaw gape is the same constant proportion of standard length in all three species. As a consequence, any other body size-related feature (e.g., crushing strength) will have the same scaling relationship with both gape and standard length.

This result permits the interchangeable use of the latter two variables in the following discussions of the effect of body size on feeding abilities and diet of these three species.

Feeding performance

The gastropod feeding experiments provided strong confirmation of the anatomically based predictions of relative crushing abilities of *H. garnoti*, *H. bivittatus*, and *H. maculipinna*. The largest gastropods crushed by *H. maculipinna* were significantly smaller than those eaten by *H. garnoti* and *H. bivittatus* of the same body size or pharyngeal gape (see triangles in Fig. 3B). The three smallest *H. maculipinna* were unable to crush even the smallest snails offered, so the sample size for this species is quite small. Among all species, fishes of equivalent crushing strength crushed snails of equal size (Fig. 3A). Thus, as shown by crushing force potential-body size relationships (Fig. 2), *H. garnoti* and *H. bivittatus* are stronger than similar-sized *H. maculipinna* and can crush larger, harder gastropods.

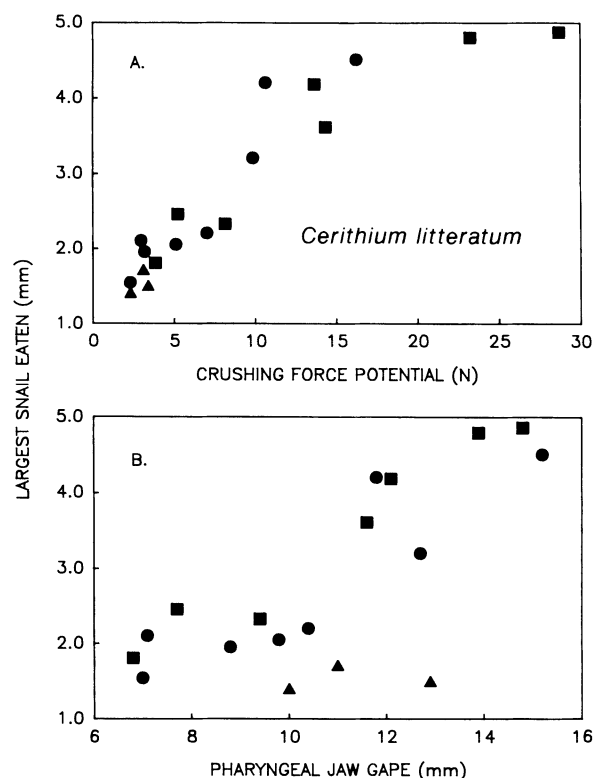


FIG. 3. The maximum size snail (*Cerithium litteratum*) successfully eaten by individuals of three *Halichoeres* species, in laboratory feeding trials, plotted against: (A) predicted pharyngeal jaw crushing force potential (ANCOVA comparison of species slopes: $P = .91$; ANCOVA for species effect: [comparison of intercepts]: $P = .21$) and (B) pharyngeal jaw gape of fishes (ANCOVA comparison of species slopes: $P = .78$; ANCOVA for species effect [comparison of intercepts]: $P < .001$). However, note small sample size for *H. maculipinna*. ■ = *H. garnoti*, ● = *H. bivittatus*, and ▲ = *H. maculipinna*.

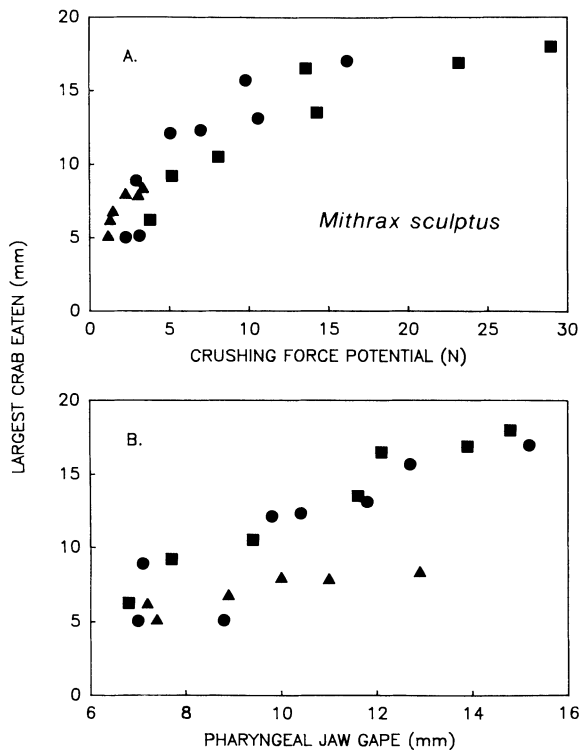


FIG. 4. The largest hard-shelled crab, *Mithrax sculptus*, (anterior–posterior carapace diameter) eaten by individuals of three *Halichoeres* species in laboratory feeding trials, plotted against (A) estimated pharyngeal jaw crushing force potential (ANCOVA comparison of species slopes: $P = .46$; ANCOVA for species effect [comparison of intercepts]: $P = .56$) and (B) pharyngeal jaw gape of fishes (ANCOVA comparison of species slopes: $P = .21$; ANCOVA for species effect [comparison of intercepts]: $P = .003$). ■ = *H. garnoti*, ● = *H. bivittatus*, and ▲ = *H. maculipinna*.

Different factors appeared to constrain predation on the two crab species. Feeding performance on the heavily armored *Mithrax* showed a pattern similar to snail predation (compare Figs. 3 and 4). Except for the smallest individuals, *H. maculipinna* ate consistently smaller *Mithrax* than did *H. garnoti* or *H. bivittatus* (see triangles in Fig. 4B), while fish of similar crushing force potential were able to successfully handle *Mithrax* of equal size (Fig. 4A). In contrast, crushing strength did not explain interspecific differences in ability to handle *Portunus* (Fig. 5A). Instead, fishes with the same pharyngeal jaw gape ate the same maximum size crabs (Fig. 5B).

Wrasses handled the two crabs differently. The hard-shelled *Mithrax sculptus* was generally eaten piecemeal. Only small individuals were engulfed and crushed whole. Larger *Mithrax* were grasped by a leg or chela and smashed against a rock until the structure broke away from the rest of the crab. The leg or chela was then crushed in the pharyngeal jaws before being swallowed. After the wrasse dismembered and ate the limb it repeatedly attacked the underside of the carapace in

a similar fashion until only the dorsal carapace remained. Two findings indicated that this was normal feeding behavior. This prey-handling technique was observed in all three species on several occasions in the field, and stomach contents often contained only a chela or leg from *Mithrax*.

Portunus was a more elusive prey. It was usually grasped by the carapace and engulfed whole. If the crab was too big to fit into the mouth it was smashed against a rock to remove limbs or break up the carapace. Occasionally, a chela was grasped, broken off, and eaten separately, but this usually resulted in the crab's escape.

The differences constraining predation on the two crabs appeared to relate to the softer bodied, elusive nature of *Portunus*. Unlike *Mithrax*, the largest *Portunus* that wrasses were able to engulf was never too hard to crush. Because it was more elusive, *Portunus* was rarely grasped by a limb, as was *Mithrax*, and often escaped while being manipulated. By contrast, *Mithrax* usually escaped only after a fish had unsuccessfully attempted to crush a disarticulated limb and subsequently lost interest in it.

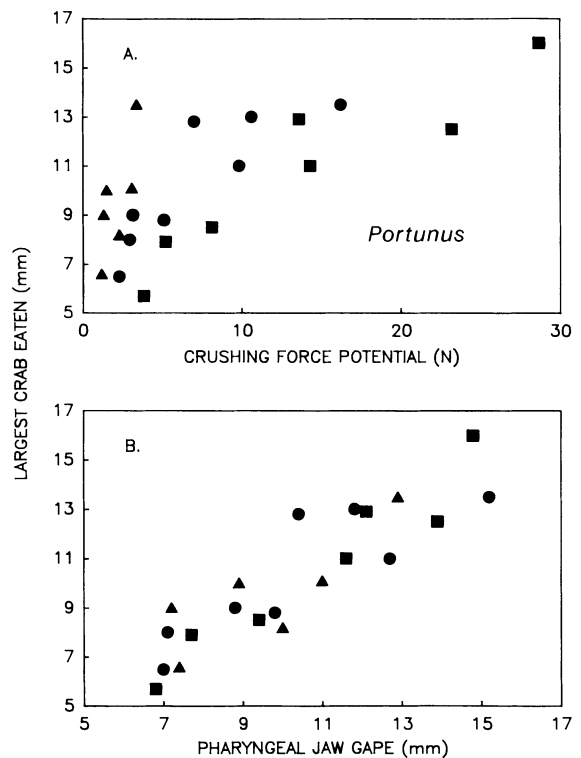


FIG. 5. The largest soft-bodied crabs, *Portunus* sp., (anterior–posterior carapace diameter) successfully consumed by individuals of three species of *Halichoeres* in laboratory feeding trials plotted against (A) estimated pharyngeal jaw crushing force potential (ANCOVA comparison of species slopes: $P = .63$; ANCOVA for species effect [comparison of intercepts]: $P < .001$) and (B) pharyngeal jaw gape (ANCOVA comparison of species slopes: $P = .43$; ANCOVA for species effect [comparison of intercepts]: $P = .86$). ■ = *H. garnoti*, ● = *H. bivittatus*, and ▲ = *H. maculipinna*.

TABLE 1. Dietary composition, from gut contents, of species of Caribbean *Halichoeres*. Table entries are percent of total pooled volume contributed by each prey category to each species' diet.

Fish species Size range (mm) N	<i>H. radiatus</i> 69–415 23	<i>H. poeyi</i> 61–121 27	<i>H. garnoti</i> 50–178 176	<i>H. bivittatus</i> 38–139 131	<i>H. maculipinna</i> 49–131 128	<i>H. pictus</i> 67–116 14
Prey category						
Gastropods (includes scaphopods and chitons)	22.8	19.3	15.0	23.8	4.4	0.0
Pelecypods	43.0	4.3	12.4	6.0	1.1	0.0
Ophiuroids	4.6	8.6	14.4	8.2	13.9	0.0
Echinoids	5.8	13.1	15.1	0.8	3.7	0.0
Crabs	13.0	38.2	25.6	20.4	10.3	0.0
Polychaetes	10.3	6.9	8.1	24.0	38.4	0.0
Copepods	0.0	0.0	3.1	3.0	0.9	44.7
Isopods	0.5	0.3	3.5	7.6	7.4	0.0
Amphipods	0.0	0.0	0.6	2.7	3.4	0.0
Ostracods	0.0	0.0	0.1	0.9	1.3	2.1
"Shrimp"	0.0	7.3	0.0	0.0	9.9	0.0
Other**	0.0	2.3	2.1	2.6	5.3	53.2***

* "Shrimp" includes decapod shrimp, mysids, and stomatopods.

** "Other" includes sipunculans, foraminiferans, fish remains, and unidentified animal material.

*** For *H. pictus* "other" includes 15.3% pteropods, 23.7% siphonophores, 12% phytoplankton, and 1.1% radiolarians.

Fish diets

In general, species' diets were composed of a broad range of invertebrate taxa (Table 1). The species with the lowest estimated pharyngeal jaw crushing strength, *H. pictus*, is strictly a planktivore, consuming small zooplankters and substantial amounts of phytoplankton. The four species with the greatest estimated crushing strength, *H. garnoti*, *H. bivittatus*, *H. radiatus*, and *H. poeyi*, ate considerable amounts of hard prey, crabs, and polychaetes ("hard" prey, as used here and henceforth, includes gastropods, pelecypods, ophiuroids, and echinoids). *H. maculipinna* was intermediate in crushing musculature, and polychaetes dominated its diet with hard prey contributing relatively less.

H. garnoti, *H. bivittatus*, and *H. maculipinna* exhibited considerable ontogenetic changes in diet (Appendix 2). Crabs were a major dietary component of most size classes of the three species (except the four smallest size classes of *H. maculipinna*). In addition to crabs, the smallest individuals of these species ate mostly polychaetes and small crustaceans, but all species ate more hard-bodied prey as they grew. This was particularly evident in the species with higher estimated crushing strength, *H. garnoti* and *H. bivittatus*. In the species with the lowest estimated crushing strength, *H. maculipinna*, hard prey became important only in the two largest size classes. Among the three species, the proportion of hard prey in the diet was significantly more closely related to estimated crushing force potential (Fig. 6A) than to body length (Fig. 6B). At 3–5 N crushing strength there was an abrupt increase in the proportion of hard prey eaten by all three species, in spite of the fact that this crushing strength occurred at very different body sizes (and thus pharyngeal jaw gapes) in each species (Fig. 6).

Diet breadth, as a function of estimated crushing

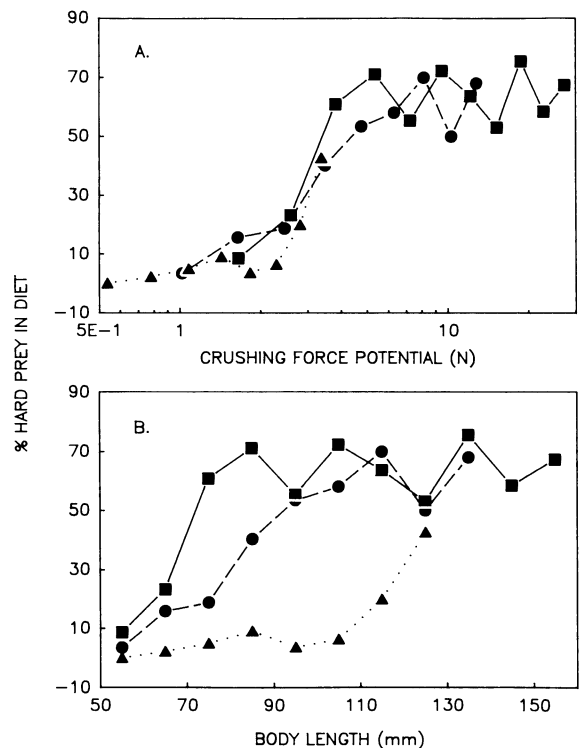


FIG. 6. Average volume percent of "hard" prey (gastropods, pelecypods, ophiuroids, and echinoids) found in the intestinal contents of 10-mm size classes of three species of *Halichoeres*, plotted against (A) estimated pharyngeal jaw crushing force potential (ANCOVA comparison for species slopes: $P = .31$; ANCOVA for species effect [comparison of intercepts]: $P = .31$) and (B) standard length of fishes (ANCOVA comparison of species slopes: $P = .19$; ANCOVA for species effect [comparison of intercepts]: $P < .001$). See Appendix 2 for sample sizes. ■ = *H. garnoti*, ● = *H. bivittatus*, and ▲ = *H. maculipinna*.

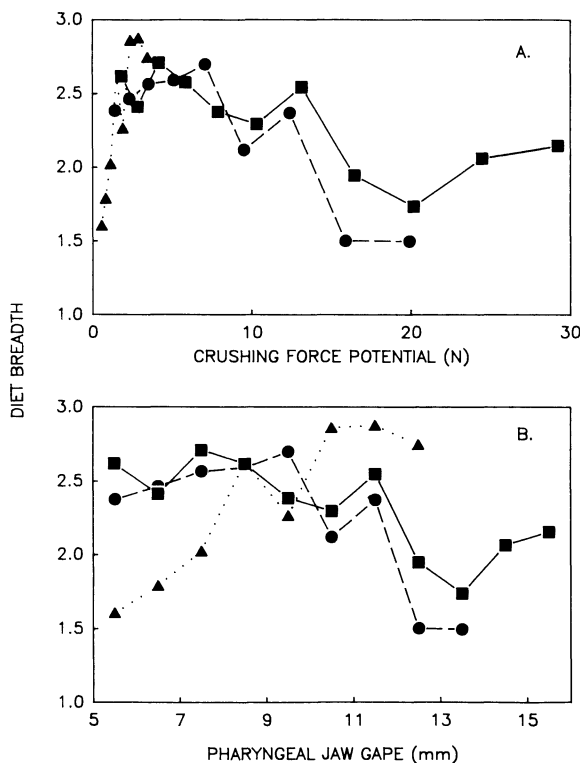


FIG. 7. Mean diet breadth of three *Halichoeres* species, plotted against (A) estimated pharyngeal jaw crushing force potential (linear regressions of force potential on diet breadth: *H. garnoti*, $P = .01$; *H. bivittatus*, $P = .005$; *H. maculipinna*, $P = .005$) and (B) pharyngeal jaw gape (linear regressions of pharyngeal jaw gape on diet breadth: *H. garnoti*, $P = .008$; *H. bivittatus*, $P = .023$; *H. maculipinna*, $P = .002$). See Appendix 2 for sample sizes and details of diet ontogeny. ■ = *H. garnoti*, ● = *H. bivittatus*, and ▲ = *H. maculipinna*.

strength, showed a similar pattern for *H. garnoti* and *H. bivittatus* (Fig. 7A). Diet breadth increased up to a crushing force potential of 3–5 N, but above 5 N the diet became increasingly narrow as wrasses specialized on hard-prey types and crabs. This trend toward greater specialization in *H. garnoti* and *H. bivittatus* involved both a reduction in the number of prey categories in the diet and the tendency for the diet to be dominated by only a few, hard-prey types (Appendix 2). The upward trend in diet breadth for the two largest size classes of *H. garnoti* (Fig. 7) was caused by a more even distribution of the hard-prey types eaten, rather than the addition of softer prey to the diet (Appendix 2). For *H. maculipinna*, which never reached an estimated crushing strength of 5 N, diet breadth generally increased over the range of size classes (Fig. 7A). Considered as a function of pharyngeal jaw gape, diet breadth did not show a consistent pattern in the three species (Fig. 7B).

DISCUSSION

The main conclusion of this study is that pharyngeal jaw crushing strength plays a central role in constrain-

ing, and thus determining, the diets of Caribbean *Halichoeres*. The ontogeny of diet within the three species studied in detail was characterized by a transition from mostly soft-bodied prey to a diet dominated by hard prey in fishes with an estimated pharyngeal jaw crushing strength > 5 N. The conclusion that crushing strength underlies this transition is supported by two observations: (1) crushing strength limited the hardness of prey that fish ate in laboratory trials (Figs. 3 and 4), and (2) fishes of equivalent pharyngeal jaw strength consumed similar amounts of hard-bodied prey, in spite of the fact that a given jaw strength occurred at very different body sizes (and thus pharyngeal jaw gapes) in the different species (Figs. 2 and 6). Thus, *H. garnoti*, a relatively strong crushing species, achieved the feeding ability and diet of the weaker jawed *H. maculipinna* at a smaller body size (Fig. 6).

Diet comparisons among the six *Halichoeres* species also indicated that prey choice is constrained by crushing ability (Table 1). For example, based on estimates of pharyngeal jaw strength (Fig. 2), it would not be possible for *H. pictus* to eat the harder prey that characterize the diets of the other species. This expectation was confirmed for *H. maculipinna*, which showed crushing-strength-dependent feeding on hard prey in laboratory trials (Figs. 3 and 4). These results have important implications for the potential diets of fishes, as weaker jawed species are limited by their inability to utilize harder bodied prey types. No other mechanism (e.g., competition or optimal foraging considerations) need be invoked to explain why *H. pictus* does not eat the hard-bodied prey consumed by *H. garnoti* and *H. bivittatus*. It is simply not capable.

Although crushing strength appears to be a major factor in limiting diets of these fishes, other morphological factors also restrict prey use. Pharyngeal jaw gape potentially constrains predation on any prey that is not too hard to crush. This appeared to be the case with *Portunus* predation (Fig. 5). Depending on the physical properties of the prey, either gape or crushing strength may constrain handling ability. Gape limits the maximum diameter of prey that fishes can eat, while the hardness of prey that can be consumed is constrained by crushing strength.

While gape and crushing strength may set limits on pharyngeal jaw handling ability other mechanisms permit fish to partially circumvent these constraints. The complex manipulative behavior reported here for wrasses feeding on crabs allows them to overcome some gape limitations by breaking apart prey before it is passed to the pharyngeal apparatus. In this way, fishes were able to eat much larger *Mithrax sculptus* than those that could fit, whole, between their pharyngeal jaws.

Species with stronger pharyngeal jaws have the potential to eat a greater range of shelled prey types than weaker jawed congeners, and it may be tempting to conclude that weaker species are therefore at a com-

petitive disadvantage. However, species whose diets are characterized by softer prey (*H. pictus* and *H. maculipinna*) may possess adaptations that allow them to feed on softer prey types more effectively than stronger species. For example, *H. pictus*, a zooplanktivore, may have greater visual acuity than other *Halichoeres*, permitting it to detect small midwater zooplankters more effectively. No attempt was made to assess the abilities of wrasses to feed on soft prey such as zooplankton or small polychaete worms.

The mollusc-crushing niche

Gape-limited predators are expected to show a positive correlation between mouth width and both maximum prey size and the diversity of prey eaten (Wilson 1975, Zaret 1980). These correlations hold good in diverse taxa: snakes (Mushinsky et al. 1982), fruit-eating birds (Wheelwright 1985), microcarnivorous fishes (Schmitt and Holbrook 1984), and anurans (Toft 1980) are some examples. By analogy, crushing strength can be expected to influence the potential diets of prey-crushing predators in a similar fashion. More powerful individuals can crush harder prey, and thus a greater range of prey types. In the laboratory the freshwater mollusc-eating sunfish *Lepomis microlophus* has been shown to select among mollusc prey species based on a cost/benefit construct (Stein et al. 1984). This suggests that stronger fish can profitably consume harder prey than weaker fish. Stronger wrasses in this study did include harder prey in their diet (Table 1, Fig. 6, Appendix 2), but observed dietary breadths contrasted sharply with expectations (Fig. 7). Above an estimated crushing strength of 5 N dietary breadth declined as fishes specialized on hard-prey types. Thus, ontogenetic increases in the range of prey that a predator is capable of eating need not always be accompanied by increases in actual diet breadth. Indeed, improvements in feeding ability may lead to trophic specialization.

If the structural defenses of molluscs and echinoderms can be overcome they represent an available food resource that is utilized by few other sympatric predators. In a study of the feeding habits of 212 species of Caribbean reef fishes (Randall 1967), only 12 were found to crush and eat large amounts of molluscs (>20% of the diet, by volume). Six of these were labrids, one a large eagle ray (*Aetobatis narinari*), one a sparid (*Calamus bajonado*), one a carangid (*Trachinotus falcatus*), and three were diodontid spiny puffers. All possess specific morphological adaptations for crushing prey in the pharyngeal (*Trachinotus* and labrids) or oral jaws (Randall 1967, Palmer 1979, Wainwright 1987). The diets of these 12 species were almost exclusively (70–100%) hard-bodied prey (gastropods, pelecypods, ophiuroids, echinoids), showing a similar level of specialization as that reported here for larger individuals of the stronger *Halichoeres* species.

Those fishes that can crush hard prey are able to occupy a relatively unexploited, rich trophic niche on

the prey-hardness resource dimension. On Caribbean coral reefs, species that attain that level of functional competence appear to specialize their feeding habits on hard-prey taxa, rather than continuing to include less demanding food in their diets. At least two possible explanations underlie this phenomenon. Species that exhibit the morphological specializations for effective prey crushing may sacrifice the ability to feed proficiently on many softer bodied prey. Alternatively, hard-bodied prey may represent such a rich food resource on coral reefs that species capable of taking advantage of it may find other prey so much less profitable as to be not worth including in their diets.

Work with North American freshwater sunfishes, *Lepomis* (Centrarchidae), indicates that the morphologically specialized molluscivore *L. gibbosus* gains, through eating snails, a competitive refuge from the zooplanktivorous *L. macrochirus* (Mittlebach 1984). Manipulations of artificial pond populations have shown that, at least young, *L. gibbosus* switch to a diet of zooplankton in the absence of the congeneric competitor (Werner and Hall 1976). The much greater diversity of hard-bodied prey on coral reefs may indicate a more profitable trophic niche than is found in this freshwater system, but the need for functional competence, in order to take advantage of it, is stressed here. The ability of wrasses to exploit this food resource is limited by crushing strength, a capacity that has a clear morphological basis and accounts for differences within and among species in the degree to which they utilize hard-bodied prey.

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APPENDIX 1

Scaling relationships of pharyngeal jaw crushing muscle mass and estimated crushing force potential to fish standard length in six species of Caribbean *Halichoeres*. Statistics are reduced major axis regressions fit to the allometric equation: $\log_{10} Y = b(\log_{10} X) + \log_{10} a$. Muscle mass and estimated crushing force potential are the dependent variables and fish standard length is the independent variable in each case. Crushing force potential relationships are plotted in Fig. 2.

Species	Muscle mass (g)				Crushing force potential (N)			
	<i>b</i>	$\log_{10} a$	r^2	<i>N</i>	<i>b</i>	$\log_{10} a$	r^2	<i>N</i>
<i>H. radiatus</i>	3.46	-8.06	0.98	10	2.32	-3.57	0.86	10
<i>H. poeyi</i>	3.71	-8.56	0.94	12	2.84	-4.36	0.80	10
<i>H. garnoti</i>	3.77	-8.86	0.97	20	2.71	-4.47	0.82	18
<i>H. bivittatus</i>	3.84	-9.80	0.97	23	2.88	-5.09	0.87	20
<i>H. maculipinna</i>	3.10	-8.07	0.97	23	2.24	-4.17	0.87	20
<i>H. pictus</i>	2.49	-7.39	0.82	15	1.73	-3.36	0.72	10

APPENDIX 2

Ontogeny of dietary composition, from gut contents, in three *Halichoeres* species. Entries are mean percent of total food volume contributed by each prey category for *N* individuals.

Fish species	Fish size class (mm)	<i>N</i>	Prey category										
			Gastro-pods	Pelecypods	Ophiuroids	Echinoids	Crabs	Polychaetes	Copepods	Isopods	Amphipods	Ostracods	Other
<i>H. garnoti</i>	50–60	15	1.4	3.4	0.4	3.4	20.0	24.7	18.6	22.5	4.6	0.9	0.0
	61–70	17	12.0	0.1	0.1	11.1	36.0	20.9	11.8	7.8	0.0	0.1	0.1
	71–80	18	25.8	8.3	23.0	3.7	12.5	18.5	3.6	3.5	0.9	0.2	0.0
	81–90	16	17.2	24.2	14.1	16.2	11.2	16.5	0.0	0.0	0.4	0.1	0.4
	91–100	10	7.6	16.7	16.2	14.9	37.1	7.4	0.0	0.2	0.0	0.0	0.0
	101–110	16	20.2	6.7	39.1	6.4	19.4	7.7	0.0	0.0	0.0	0.0	0.5
	111–120	15	26.4	14.4	12.2	10.6	28.3	3.1	0.0	4.5	0.3	0.0	0.4
	121–130	13	7.2	7.0	25.5	13.4	47.0	0.0	0.0	0.0	0.0	0.0	0.0
	131–140	14	21.8	4.6	0.0	49.2	23.6	0.8	0.0	0.0	0.0	0.0	0.0
	141–150	18	12.5	24.4	5.9	15.7	41.5	0.0	0.0	0.0	0.0	0.0	0.0
	151–160	18	13.2	39.0	2.1	13.1	27.6	5.0	0.0	0.1	0.0	0.0	0.0
<i>H. bivittatus</i>	50–60	19	3.5	0.0	0.0	0.0	11.1	35.3	16.6	24.1	0.0	6.3	3.1
	61–70	19	5.8	0.9	9.2	0.0	16.4	42.4	6.1	13.5	5.2	0.5	0.0
	71–80	10	17.7	1.1	0.0	0.0	19.3	30.7	0.0	16.7	7.1	1.3	6.1
	81–90	10	21.0	4.4	14.9	0.0	20.1	24.6	0.0	7.1	0.1	0.3	7.5
	91–100	13	26.2	7.7	16.5	3.1	27.5	7.9	0.0	3.0	5.2	0.0	2.8
	101–110	13	45.7	2.6	7.5	2.4	29.3	8.4	0.0	2.4	0.0	0.0	1.7
	111–120	11	35.9	25.0	9.1	0.0	8.8	12.2	0.0	8.7	0.2	0.0	0.2
	121–130	12	25.0	0.0	25.0	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
	131–140	13	49.4	18.6	0.0	0.0	31.9	0.1	0.0	0.0	0.0	0.0	0.0
<i>H. maculipinna</i>	50–60	13	0.0	0.0	0.0	0.0	0.0	24.1	55.2	1.1	1.0	0.8	17.8
	61–70	18	0.8	1.5	0.0	0.0	0.0	61.3	12.2	12.5	2.5	0.2	8.9
	71–80	18	4.6	0.4	0.0	0.0	8.8	59.8	5.6	10.0	4.1	0.3	6.3
	81–90	17	2.3	1.8	2.1	2.9	2.4	40.2	5.3	24.4	9.8	5.4	3.3
	91–100	13	1.5	2.1	0.0	0.0	36.6	37.5	0.5	8.5	6.4	1.1	11.7
	101–110	16	5.4	0.0	0.0	1.1	27.1	19.0	0.2	9.4	6.6	8.1	23.0
	111–120	19	8.7	2.6	3.4	5.5	13.2	34.0	0.2	10.7	8.1	0.4	13.2
	121–130	14	14.6	10.3	17.9	0.0	16.7	24.2	0.0	11.2	3.6	0.9	0.6

* "Other" includes sipunculans, decapod shrimp, mysids, stomatopods, and foraminiferans.