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Ecomorphology: Experimental Functional Anatomy for Ecological Problems¹

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SYNOPSIS. It is generally believed that the functional design of an organism relates to its ecology, yet this ecomorphological paradigm has historically suffered from the lack of a rigorous framework for its implementation. I present a methodology for experimentally exploring the ecological consequences of variation in morphology. The central idea is that morphology influences ecology by limiting the ability of the individual to perform key tasks in its daily life. In this scheme the effect of morphological variation on behavioral performance is first tested in laboratory experiments. As the behavioral capability of an individual defines the range of ecological resources that it can potential niche of an individual to actual patterns of resource use (the realized niche). This permits a quantitative assessment of the significance of an organism's maximal capabilities in determining actual patterns of resource use.

An example is presented from work on the feeding biology of fishes in the family Labridae (wrasses and parrotfishes). Most labrids feed by crushing shelled prey in their powerful pharyngeal jaws. This example explores the dietary consequences of variation in crushing strength among and within species. Crushing strength was estimated from biomechanical analyses of the crushing apparatus in several species, and these predictions of relative strength were tested in laboratory feeding experiments with hard-shelled prey. Morphology accurately predicted relative crushing ability, and the final section of the study explored the effect of variation in crushing ability on diet. Within each of three species crushing strength appears to underlie a majo: ontogentic dietary switch from soft-bodied prey to a diet dominated by hard-shelled prey. In each species this switch occurred at about the same crushing strength, around 5 Newtons (N), in spite of the fact that this crushing strength is achieved by the three species at different body sizes. Diet breadth increases during ontogeny in each species, until a crushing strength of 5 N is achieved, when diet breadth begins to decline. The strongest fishes specialized almost entirely on molluscs and sea urchins. Thus, these labrids take advantage of ontogenetic and interspecific differences in crushing strength by including harder and harder prey in their diet, and ultimately specializing on hard prey types. The specialized organization of the labrid pharyngeal jaws can be viewed as a key innovation that has permitted this lineage of fishes to invade the mollusc eating niche, a relatively empty trophic niche within the highly speciose and diverse communities of coral reef fishes.

INTRODUCTION

Ecomorphology is the study of the relationship between the functional design of organisms and the environment. It shares a conceptual framework with several other disciplines within organismal biology, such as physiological ecology, biophysical ecology, and ecomechanics, and no distinction is implied here other than an emphasis on functional morphology. Within ecomorphology two primary axes of research have emerged that concentrate on either the effect of the environment on functional design or

its converse, the influence of functional morphology on the ecology of an organism. In the former, the environment is recognized as a central force in shaping functional systems during their ontogeny and evolution. Most evolutionary mechanisms emphasize the environment as a major cause of organismal design (see for example James, 1991), and the majority of ecomorphological research has focused on adaptive explanations for observed design patterns (Hespenheide, 1973; Leisler, 1980; Barel, 1983; Alexander, 1988). Recent advances have brought to the forefront the role of phylogenetic history as an alternate explanation for design (Lauder, 1981, 1990; Ridley, 1983; Huey, 1987) and integrative approaches that assess the relative contribution of phylogeny and adaptation are emerging (Cheverud et al., 1985; Huey and

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Bennett, 1987; Motta, 1988; Liem, 1989; Losos, 1990).

The relationship between functional design and the environment can also work the other way, however, because the way that an organism is constructed influences its ability to interact with the environment. Thus, the second major branch of ecomorphology looks at the role of functional morphology in shaping the ecological attributes of organisms. A tremendous literature exists documenting correlations between morphological and ecological patterns (James, 1970, 1982; Karr and James, 1973; Gatz, 1979; Findley and Black, 1983; Felley, 1984; Miles et al., 1987; Crome and Richards, 1988; Kotrschal, 1988), and an increasing amount of work has centered on the consequences of morphological variation for fitness (Boag and Grant, 1981; Price et al., 1984; Schluter, 1988; Jayne and Bennett, 1990). However, few studies have critically examined the causal role of functional morphology in determining aspects of an organism's general ecology (Werner, 1977; Kiltie, 1982; Lavin and McPhail, 1985). Clearly, functional morphology has some influence on the ability of an organism to obtain resources from the environment, but how does one go about rigorously quantifying the role of functional morphology in determining patterns of ecological resource use? In this paper I advocate an experimental approach for investigating this general problem. The method that is described takes advantage of the link between morphology and ecology provided by performance (Huey and Stevenson, 1979; Arnold, 1983; Emerson and Arnold, 1989), and emphasizes the role of experimental functional morphology in establishing causation in morphologyecology correlations. One contribution of this technique is that it supplies the answers to several questions that, taken together, quantitatively describe the "fit" of an organism to its environment. The process is illustrated with a discussion of the feeding biology of labrid fishes (Wainwright, 1987, 1988).

Morphology, performance and ecology

In a now classic paper, Arnold (1983) described a method for studying the effect

of morphology on fitness. I would like to extend the point that was made in that paper and suggest that the same general framework is appropriate for studying the link between morphology and other aspects of an individual's ecology. The central idea in this scheme is that morphology influences patterns of resource use by limiting the ability of the individual to perform key tasks that are relevant to obtaining resources from the environment. The limits of behavioral capabilities constrain the range of resources that an individual can obtain. Thus, the process of relating morphology to ecology can be separated into two stages. The first step is to determine the effect of morphological variation on performance, or the ability of the organism to perform some relevant task. This is accomplished with behavioral experiments conducted in the laboratory. Biomechanical analyses of functional systems lead to specific predictions regarding the effect that variation in the components of the system have on performance. The strength of the functional approach lies in the ability to assign causation to otherwise correlative relationships between specific design features and observed performance, based on independent functional analyses (Lauder, 1991).

The second step is to determine the effect of performance on actual patterns of resource use. It is on this problem that remarkably little work has been done. The basic idea is to compare potential resource use, determined from the performance experiments (i.e., the potential niche), with actual patterns of resource use, determined from field studies of natural populations (i.e., the realized niche). How important are the maximal capabilities of an individual in shaping resource use? What is the relative importance of different capabilities? Within the range of an individual's capabilities where does it most frequently operate on a dayto-day basis? These questions have only rarely been addressed, yet their answers provide a quantitative understanding of the nature of an organism's "fit" into its environment.

It is important to emphasize that a fundamental problem in ecology is to identify the factors that determine patterns of



Fig. 1. A three-dimensional visualization of the scaling of pharyngeal jaw gape and crushing strength in the Caribbean hogfish, *Lachnolaimus maximus*. The range of prey sizes and prey hardness that fish are able to handle are shown for individuals of 20, 350, and 2,000 g. All axes are log_{10} scales. During ontogeny crushing strength and gape increase, causing an increase in the range of prey on which hogfish are able to feed. Data are from Wainwright (1987).

resource use by organisms (Schoener, 1986). Much ecological research is devoted to assessing the relative significance of various factors in shaping resource use patterns, whether the resource be food (Osenberg and Mittelbach, 1989), space (Sale, 1980), time (Munz and McFarland, 1973), or reproductive opportunities (Hoffman *et al.*, 1985). In the discussion that follows I focus on the food resource for convenience, though the statements apply generally to any ecological resource.

Among the many factors that influence patterns of prey use, two may be viewed as fundamental: (1) prey availability, and (2) the *ability* of the predator to utilize each prey type. Thus, the types of prey and their relative abundance define the food resource for a predator, and the predator's ability to locate, capture, and handle the various prey types constrains the range of prey that can potentially make up the diet of the predator. Other factors that can shape patterns of prey use, such as competition, energetic considerations, and the threat of predation, may further restrict the actual range of prey that are used, but these factors must exert their effect within the fundamental range of prey determined by the feeding capabilities of the predator (*e.g.*, Holling, 1959; Grant, 1986; Osenberg and Mittelbach, 1989).

To illustrate some of these ideas an example is presented in Figure 1 based on previous work with the Caribbean hogfish, *Lachnolaimus maximus*, a coral reef predator that feeds almost entirely on molluscs which it crushes in its powerful pharyngeal jaws (Wainwright, 1987). Two factors determine the upper size limit of mollusc prey that hogfish can eat. The prey first must be small enough to fit between the jaws of the fish, and once positioned between the crush-



Log BODY MASS (g)

FIG. 2. Log₁₀-log₁₀ plot of hogfish (Lachnolaimus maximus) body mass against the shell diameter of the gastropod prey, Cerithium litteratum. The points on the graph indicate the shell size of all C. litteratum found in the stomach contents of 59 hogfish collected in Belize. The dashed line indicates the relationship between maximum pharyngeal jaw gape and hogfish body mass. The solid line indicates the maximum size C. litteratum shell that hogfish are strong enough to crush. This relationship is derived from morphologically based estimates of hogfish crushing strength and a determination of the force required to crush shells of different sizes. The relationship between shell size and force at failure was then used to transform estimates of maximal crushing strength of fish into expected shell sizes. No snails are eaten that lie near the limits of pharyngeal jaw gape, indicating that crushing strength actively constrains C. litteratum predation by hogfish in this natural population.

ing jaws, the fish must be able to exert enough crushing force to crack the mollusc shell. Jaw gape and crushing strength increase during ontogeny; Figure 1 illustrates the range of prey sizes and shell strengths that can be eaten by fish 20, 350, and 2,000 g. As gape and crushing strength increase the range of prey that hogfish can potentially eat also increases.

But how important are these two limitations in actually shaping the diets of hogfish in natural populations? An analysis of stomach contents of 59 hogfish collected along the Belizean barrier reef in Central America shows that crushing strength play a central role in determining patterns of predation on at least one prey species (Fig. 2). Plotted are the shell sizes of 331 individuals of the most commonly eaten gastropod,

Cerithium litteratum, found in the intestines of fish ranging in mass from 190 g to 3,600 g (since Cerithium shells are present in hogfish intestines only as fragments, snail size was determined from the diameter of opercula, which are generally left intact). This distribution is compared with the scaling of maximum gape (Fig. 2, dashed line) and maximum crushing strength (solid line) as they relate to Cerithium. The plot demonstrates that stronger fish eat larger Cerithium, in addition to smaller snails, and that crushing strength appears to be the factor actively constraining Cerithium predation by fish of all sizes. Hogfish frequently feed on snails at or near their maximal crushing capabilities. Further, the hardness of Cerithium shells is such that hogfish never appear to encounter their gape limitation when feeding on this prey species (Fig. 2). These conclusions were further supported in laboratory performance experiments designed to determined the size of the largest Cerithium that hogfish were able to crush (Wainwright, 1987). The maximum size Cerithium that fish were able to crush was accurately predicted by estimated crushing strength.

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By providing a formal description of the influence of functional morphology on patterns of resource use the technique suggested here permits a rigorous perspective on some major concepts in ecomorphology. One such concept is the key innovation, an evolutionary transformation in organismal design that causes qualitative changes in the performance gradient of a lineage, and ultimately in the range of environmental resources that can be used. Key innovations may underlie the ability of a lineage to invade new environments or occupy previously empty niches in crowded ecosystems (Mayr, 1960; Liem, 1974; Larson et al., 1981). Hypothesized key innovations can be tested first by functional analyses which elucidate the theoretical effect of the structural innovation on whole-animal performance, followed by laboratory performance experiments which test these predictions, and finally by showing the ecological consequences of variation in performance. The historical correlation between the morphological innovation and ecological consequence must also show precise congru-



FIG. 3. Pharyngeal jaw structures of three species of Caribbean Halichoeres. Most of the superficial bones and muscles of the head are not shown to permit an unobstructed view of the pharyngeal jaws. A and B are lateral and posterior views of *H. bivittatus*, respectively. C and D show lateral views of *H. maculipinna* and *H. pictus*, respectively. Abbreviations: EP, epiotic process; FM, foramen magnum; LE4, fourth levator externus muscle; LP, levator posterior muscle; LPJ, lower pharyngeal jaw composed of fused fifth ceratobranchials; ORB, orbit; SOC, supraoccipital crest; UPJ upper pharyngeal jaw composed of left and right third pharyngobranchials. Scale bar is 5 mm. From Wainwright (1988).

ence within the context of a phylogenetic hypothesis (Lauder and Liem, 1989), but the argument for causation ultimately rests on our ability to link morphology with ecology through performance. The concept of key innovation has played a major role in discussions of the evolution of the trophic biology of labrid fishes (Liem, 1974; Stiassny and Jensen, 1987), the subject of the case study discussed below.

Case Study: Feeding Biology of Caribbean Labrid Fishes

Coral reefs are well known as ecosystems that support a tremendous diversity of life. One of the most speciose and diverse group of fishes on coral reefs is the Labridae (wrasses and parrotfishes), a circumtropical family of some 590 known species. Members of the monophyletic Labroidei (which includes the Pomacentridae, Embiotocidae, Cichlidae, and Labridae), labrids possess a novel organizations of the pharyngeal jaw apparatus that both characterizes this group and has often been cited as a key innovation that may underlie the group's remarkable ecological success (Liem, 1974; Liem and Greenwood, 1981; Kaufman and Liem, 1982). The crucial functional feature of the labriod pharyngeal jaw is a direct muscular attachment between the neurocranium and lower pharyngeal jaw (Fig. 3). This is the basis of a strong pharyngeal bite, and underlies the potential for eating hard prey (Kaufman and Liem, 1982; Wainwright, 1987). The generalized perciform condition from which the labroids are thought to have evolved consists of no direct muscular connection between the neurocranium and lower pharyngeal jaw. In these taxa prey crushing involves complex lever arrangements and shearing actions of the jaws (Wainwright, 1989). As a group, labrids are trophically distinct from most other coral reef fishes in exhibiting diets typically dominated by hard prey, such as molluscs, echinoderms and coral rock, which are crushed in the powerful pharyngeal jaws.

In this study I explored the functional basis of prey crushing performance in several species of Caribbean wrasses in the genus *Halichoeres*, with the purpose of understanding the ecological consequences of variation among and within species in pharyngeal jaw crushing strength. Like other wrasses, these fish crush shelled prey in their pharyngeal jaws. Species of *Halichoeres* feed diurnally on a wide variety of primarily benthic invertebrates, including gastropod and pelecypod molluscs, ophiuroids, urchins, polychaetes, sipunculans, decapod shrimps, crabs, isopods, amphipods, and copepods.

The study fell into three parts. First, the crushing strength of six species was estimated based on a biomechanical analysis of the pharyngeal jaws. Second, these predictions of relative crushing strength were tested in laboratory performance experiments with three species that differ in expected crushing performance. Third, the effect of variation in crushing strength on patterns of prey use is explored in these three species.

Morphology

The pharyngeal jaw apparatus of labrids has been extensively described (Yamaoka, 1978; Liem and Sanderson, 1986; Wainwright, 1987, 1988; Gobalet, 1989) and only those aspects central to a discussion of prey crushing are dealt with here. Diagrams of the pharyngeal jaws in three species of Caribbean *Halichoeres* are presented in Figure 3. Most superficial bones and muscles are not illustrated to permit an unobstructed view of the pharyngeal region. The pharyngeal jaws are formed from modified gill arch elements. The massive lower pharyngeal jaw is composed of fused fifth ceratobranchials and their associated tooth plates. The upper jaw is composed of left and right third pharyngobranchials, each fused with an enlarged ventral tooth plate. The upper jaw bones articulate with the ventral surface of the neurocranium through a well developed diarthrosis. The key to crushing function is the organization of the paired levator posterior muscles, which originate on several bones of the posterior region of the neurocranium and insert on the lateral horns of the lower jaw (Fig. 3B). The fourth levator externus muscle also originates on the neurocranium and fuses with the tendon of the levator posterior. In most species the fourth levator externus muscle is relatively small. but in others it may approach the size of the levator posterior (e.g., Fig. 3D). Thus, the lower jaw is suspended from the neurocranium in a muscular sling. When prey are crushed they are held between the upper and lower pharyngeal jaws, and the primary crushing forces are generated by the two levator posterior muscles pulling the lower jaw against the upper jaws (Liem and Sanderson, 1986; Wainwright, 1987, 1988). There are no lever arms in this system so the maximum crushing strength is expected to be equal to the combined maximum tetanic tension of the left and right levator posterior muscles.

Maximum tetanic tension can be estimated by measuring the physiological cross sectional area of a muscle and assuming a typical value of the force producing capability of the muscle tissue per unit of cross sectional area (Powell et al., 1984). Physiological cross sectional area is not the same as the morphological cross sectional area of the muscle as it takes into account the orientation of muscle fibers as well as the thickness of the muscle. Morphologically based estimates of physiological cross sectional area were used to estimate maximal tetanic tension for the levator posterior and fourth levator externus muscles in an ontogenetic series of six species of Halichoeres (Fig. 4). A value of 20 N/cm² for the force producing capability of fish muscle tissue per unit of cross sectional area was taken from the literature (Altringham and Johnston, 1982; Akster et al., 1985). Two factors



FIG. 4. Relationship between estimated pharyngeal jaw crushing strength and body length for six species of Caribbean labrids. Both axes are \log_{10} scales. Size ranges are bounded by the smallest and largest individual examined from each species. Crushing strength estimates are based on morphological analyses. Further laboratory and field investigations were made into the feeding performance and diet of the three species indicated with solid lines. Only dietary data were obtained for the three species indicated with dashed lines. From Wainwright (1988).

contributed to extensive interspecific differences in estimated crushing strength (Fig. 4). First, species varied in the mass of the levator posterior muscle (Fig. 3). Second, in all species the levator posterior muscle had a bipinnate structure and the angle of pinnation formed by muscle fibers inserting on the central tendon varied from 20° in H. pictus to 37.2° in H. poeyi. By increasing the angle of pinnation of fibers in the levator posterior muscle (up to a fiber angle of 45°) relative crushing strength is increased (Calow and Alexander, 1973). However, a trade-off occurs in the extensibility of the muscle which decreases as the angle of pinnation increases (Alexander, 1971). The extensibility of the levator posterior muscle determines maximum pharyngeal jaw gape resulting in an inverse relationship between angle of pinnation of the levator posterior and pharyngeal jaw gape among Caribbean labrids (Fig. 5).

Performance

To test these morphologically based predictions of relative crushing strength, sev-



FIG. 5. Relationship between the mean angle of pinnation of muscle fibers of the levator posterior muscle inserting on that muscle's central tendon and pharyngeal jaw gape in seven species of Caribbean labrids. Each point represents data collected from between 8 and 20 individuals per species. Pinnation angles were measured on at least 10 muscle fibers per muscle. In no species was body size found to be correlated with angle of pinnation. Angles of pinnation up to 45° increase relative force producing capability of this primary crushing muscle, but as the angle of pinnation increases above zero the extensibility of the muscle is restricted. The extensibility of this muscle directly determines maximal pharyngeal jaw gape. See Wainwright (1988) for further details of angle measurements. Species indicated from left to right, Lachnolaimus maximus, Halichoeres poeyi, H. garnoti, H. radiatus, H. bivittatus, H. maculipinna, and H. pictus.

eral individuals from three species (H. garnoti, H. bivittatus, and H. maculipinna) were brought into the laboratory where performance experiments were conducted with several commonly eaten prey species, including a gastropod and two decapod crabs (Wainwright, 1988). In these experiments the largest individual of each prey species that could be consistently crushed and consumed was determined for individual fish. The basic expectation was that, when eating hard-shelled prey, fish with the same estimated crushing strength should be able to crush the same maximum size prey, in spite of the fact that these three Halichoeres species achieve the same crushing strength at very different body sizes (Fig. 4).

These experiments produced strong confirmation of the morphologically based predictions of relative crushing strength. Results from experiments conducted with the gastropod *Cerithium litteratum* are presented



FIG. 6. Results of laboratory feeding experiments with three species of *Halichoeres* designed to determine the largest size gastropod, *Cerithium litteratum*, that each fish could successfully crush and consume. Maximum shell size is plotted against (A) estimated crushing strength of fish (ANCOVA comparisons of species slopes: P = 0.91; ANCOVA for species effect: P = 0.21) and (B) pharyngeal jaw gape of fishes (ANCOVA for species slopes: P = 0.78; ANCOVA for species effect: P < 0.001). $\blacktriangle = H.$ maculipinna, $\blacksquare = H.$ garnoti, and $\blacklozenge = H.$ bivittatus. From Wainwright (1988).

in Figure 6. The largest snails eaten by H. maculipinna were not as large as those eaten by the same size fish in the other two species (see triangles in Fig. 6). However, among all species, fish of the same crushing strength crushed snails of the same size. As predicted, H. garnoti and H. bivittatus are stronger than similar sized H. maculipinna and are able to eat larger, harder gastropods. Similar results were found for a heavily armored species of crab prey. However, pharyngeal jaw gape limited maximum prey size in experiments with a soft bodied portunid crab, showing that the functional limitation on maximum prey size depends on the physical characteristics of the prey (Wainwright, 1988). Soft-bodied prey become too large to fit between the pharyngeal jaws of wrasses before the limits of crushing strength are reached.

Ecology

What are the dietary consequences of variation among and within species in pharyngeal jaw crushing strength? It is clear from the performance experiments that, for hardshelled prey, crushing strength limits the maximum size prey that the three *Halichoeres* species can feed on. But variation among species in crushing strength need not lead to differences in patterns of prey use. There is no reason *a priori* to expect that stronger fish will necessarily take advantage of their greater performance capabilities. Indeed, it is generally not well known how close to their maximal capabilities predators tend to feed.

To explore the relationship between crushing strength, gape, and patterns of prev use stomach contents were analyzed for an ontogenetic series of each of the three species used in the performance experiments. Each species was broken down into 10 mm size classes and the stomach contents of a total of 499 specimens of the three species were sorted into 11 taxonomic prey categories. These categories were primarily ordinal or lower levels (e.g., gastropods, pelecypods, isopods, polychaetes, echinoids, ophiuroids) so that the conclusions that were drawn concerning prey use patterns reflect the use of relatively broad phylogenetic groups of prey taxa. This level of analysis was chosen so that prev with similar defense characteristics tended to be grouped together (*i.e.*, gastropods are mostly hard-shelled, isopods were usually small and soft-bodied). All specimens were collected along the barrier reef off the Caribbean coast of Belize in Central America.

Two specific questions were addressed concerning the role of crushing strength in shaping patterns of prey use. First, do stronger fish eat harder-bodied prey? Second, given that the range of prey that these fish are able to crush and consume varies among species and increases continuously during ontogeny, (hence, the potential niche is broader for stronger fish) do stronger fish actually have broader diets?

To answer the first question the volume



FIG. 7. Mean volume percent of hard prey types (molluscs, echinoids, and ophiuroids) found in the stomach contents of three species of Caribbean *Halichoeres*. Each species is broken down into 10 mm size classes. Percent hard prey plotted against (A) estimated crushing strength of fishes (ANCOVA comparisons of species slopes: P = 0.31; ANCOVA for species effect: P = 0.31 and (B) body length of fish (ANCOVA for species slopes: P = 0.19; ANCOVA for species effect: P = 0.01). $\triangle = H$. maculipinna, $\blacksquare = H$. garnoti, and $\blacklozenge = H$. bivittatus. from Wainwright (1988).

percent of hard-bodied prev types found in the diet was calculated for all size classes of the three species. In each species there was a switch during ontogeny from small fish that eat very little hard prey, to larger fish whose diets are dominated by hard-shelled prey types (Fig. 7). The switch, however, occurred at different body sizes in each species. Thus, H. maculipinna, the weakest of the three species, switches to hard prey at around 120 mm SL, while the switch occurs between 70 and 80 mm in the two stronger species (Fig. 7B). In contrast, this diet switch occurs at about the same crushing strength in each of the three species. At around 3-5 Newtons crushing strength all three species switch over to a diet dominated by hard prey (Fig. 7A).

To test the prediction that stronger fish



FIG. 8. Diet breadth (Shannon-Wiener index) for size classes of species of *Halichoeres* plotted against (A) estimated crushing strength of fish, and (B) pharyngeal jaw gape. Below 5 N crushing strength diet increases as a function of crushing strength, above 5 N diet breadth declines. The strongest fishes specialized on hard prey like molluscs and echinoderms. $\triangle = H$. maculipinna, $\blacksquare = H$. garnoti, and $\bigcirc H$. bivittatus. From Wainwright (1988).

have broader diets the Shannon-Wiener diversity index (Shannon, 1949) was calculated as a measure of diet breadth. The two stronger species, H. garnoti and H. bivittatus, showed similar patterns of diet breadth scaling with crushing strength and body size (Fig. 8). During early ontogeny diet breadth increases with crushing strength, until around 5 N crushing strength when diet breadth begins to decline. The largest, strongest members of these two species exhibited the narrowest diets, specializing almost entirely on gastropod and pelecypod molluscs. Individuals of H. maculipinna never achieved crushing strengths above 5 N, and diet breadth in species increased continuously this throughout ontogeny (Fig. 8). Thus, while the range of prey that these Caribbean Halichoeres are able to consume increases continuously during ontogeny, diet breadth increases only up to a crushing strength of about 5 N. Fish stronger than 5 N become increasingly specialized on hard-shell prey types.

DISCUSSION

The major conclusion that is drawn from this study is that pharyngeal jaw crushing strength plays a central role in shaping the diets of Caribbean Halichoeres. Crushing ability is a performance characteristic that has a clear morphological basis in the size and architecture of the crushing musculature. From the ecological standpoint, a large component of the variation in patterns of prey use that occur among and within species can be explained by the correlated differences in feeding ability, specifically crushing strength. Within the three species studied the ontogeny of prey use was characterized by a transition from a diet of softbodied prey to a diet dominated by hard prey in fishes with an estimated crushing strength above about 5 N. The evidence supporting the causal nature of this relationship is two-fold: (1) crushing strength, as estimated from morphological analyses, limited the hardness of prey that fish were able to successfully crush in laboratory performance experiments (Fig. 6), and (2) fishes with the same estimated crushing strength consumed similar amounts of hard-bodied prey, in spite of the fact that the same crushing ability occurred at very different body sizes in the three species (Figs. 4, 7). Hence, H. garnoti, a relatively powerful species, achieved the feeding ability and diet of the weaker jawed H. maculipinna at a smaller body size (Fig. 7).

Cross-species comparisons of dietary habits among the three *Halichoeres* revealed patterns similar to those observed ontogenetically. Based on estimates of pharyngeal jaw crushing strength, individuals of *H. maculipinna* at 100 mm body length will have the same constraints on crushing ability that occur in *H. garnoti* at only 45 mm body length (Fig. 4). These predictions were supported in the feeding experiments (Fig. 6), but do these differences between species in feeding ability result in significant differences in dietary habits? How important are these differences in potential niche for structuring the realized niches? When viewed from the standpoint of crushing ability a common pattern of prey use emerges across species (Figs. 7, 8). Not only do fish of the same crushing ability eat about the same amount of hard prey, but crushing strength also appears to underlie the narrowing of diet breadth in fish stronger than 5 N (Fig. 8). Thus, no other mechanism need be invoked (e.g., competition or foraging strategies) to explain the major differences between the current diets of these two species. At any given body size H. maculipinna simply cannot successfully handle much of the prev eaten by *H. garnoti*. It is possible, however that past interactions between these species influenced the evolution of pharyngeal muscle design, contributing to the differences seen today.

If crushing strength plays such an important role in constraining the feeding biology of labrid fishes, then why is crushing strength not maximized in all species? One possible reason for the interspecific variability that is observed would be historical constraints. Perhaps the weaker jawed taxa (i.e., H. maculipinna and H. pictus) share an ancestry of weaker jawed predecessors. Unfortunately, this possibility cannot be critically examined because little is presently known of the phylogenetic relationships among Halichoeres species. Alternatively, two or more strategies may be represented here. There are known trade-offs in the design of the primary crushing muscle, the levator posterior (Fig. 3), that result in a sacrifice in pharyngeal jaw gape associated with the increase force production that is gained from larger angles of pinnation within the muscle. The two extremes of this trade-off are found in the previously discussed hogfish, Lachnolaimus maximus, and Halichoeres pictus. The hogfish's diet is made up almost entirely of molluscs, and this species has the highest pinnation angle known among Caribbean labrids, 45°. However, due to the trade-off between angle of pinnation and the extensibility of the levator posterior muscle of gape of a 25 g hogfish is only 3.5 mm, compared to a gape of 8.3 mm for a H. pictus of the same size. H. pictus feeds almost entirely on midwater zooplankton and phytoplankton, including large, soft-bodied

siphonophores that make up 24% of the diet (Wainwright, 1988). Unfortunately, no comparisons were made in this study of species feeding on softer prey, such as polychaetes, which may require very different skills than the crushing strength used in destroying mollusc shells.

Labrid success and the mollusc crushing niche

The novel organization of the labroid pharyngeal jaw apparatus has been hypothesized to be causally linked to the remarkable ecological and evolutionary success of this group (Liem, 1974). It was suggested that the presence of a direct muscular attachment between the neurocranium and the lower pharyngeal jaw provides a strong bite and results in tremendous plasticity in feeding function and, therefore, underlies much of the ecological diversity seen within the group. This proposal has been extensively discussed in the literature as a model case study in key innovations (Lauder, 1981; Kaufman and Liem, 1982: Stiassny and Jensen, 1987). Attempts to test the hypothetical key innovation have centered on historical arguments that look for similar diversity in other lineages possessing labroid characteristics of the pharyngeal jaws (see Stiassny and Jensen, 1987, for an excellent review). These tests have met with limited success, largely due to the difficulties in finding replicated instances of such a major innovation in the feeding apparatus.

But what are the ecological consequences of a strong pharyngeal bites? Are increases in crushing ability associated with breadth in feeding habits? Though more comparative data are needed before generalizations can be made, the present study speaks directly to these issues. Scaling of diet breadth with crushing ability in the three species studied in detail showed that above 5 N crushing strength, these species did not continue to include a broader and broader range of prey in their diet, as was the case for fish below 5 N (Fig. 8). Instead, diets became increasingly specialized until the strongest fish fed almost entirely on molluscs and sea urchins, all prey with hard, protective shells. One interpretation of this pattern is that hard-shelled prey represent a very rich and under utilized food resource on coral reefs, and fish that possess the ability to take advantage of this resource can feed free of competition from those species that are not able to eat molluscs and echinoderms. Support for this notion is found in the patterns of prey use seen in coral reef fishes around the world. In a study of the feeding habits of 212 species of Caribbean reef fishes (Randall, 1967), only 12 species were found to consume large amounts of molluscs (>20% of the diet by volume). Of the 12 species, six were labrids, one was an eagle ray (Aetobatis narinari) that averaged over one meter in diameter, one a sparid (Calamus bajonado), one a carangid (Trachinotus falcatus), and three were diodontid spiny puffers. Each of these species exhibits morphological specializations in the pharyngeal jaws or the oral jaws (Randall, 1967; Palmer, 1979; Wainwright, 1987, 1988). Similar patterns are seen in the Hawaiian reef fish community (Hobson, 1974) and in the central Indo Pacific (Hiatt and Strasburg, 1960), where reef fish diversity reaches its highest level. Thus, only about 5% of fish species on reefs have the ability to overcome the defenses of heavily armored molluscs, and among those in the Caribbean that do, all feed almost exclusively on hard prey (Randall, 1967).

No causal connection between feeding ability and diversity of labrids per se can be drawn from the present study, but if the results obtained here prove to be general, crushing ability clearly has major consequences for the trophic biology of labrids. Perhaps the labrid pharyngeal jaw condition is best viewed as a key innovation in the sense that it underlies the capability to effectively crush hard prey, and thus has permitted labrids to exist in a relatively unoccupied trophic niche. This reduces the opportunities for interspecific competitive interactions over prey, thus fulfilling one requirement of a key innovation in that a relatively unoccupied environment is opened up for those taxa possessing the specialized pharyngeal jaws. The causal connection between crushing strength and molluscivory was demonstrated here through combined biomechanical analyses, behavioral performance experiments, and ecological investigations. Whether this arrangement of the pharyngeal jaws is also causally related to the diversity of labrids and other labrids groups is a historical question that has been notoriously difficult to test (Stiassny and Jensen, 1987). In contrast, the methodology proposed and illustrated here provides a direct means of experimentally exploring the ecological consequences of morphological innovation. Hypotheses of causal connections between morphology and ecology can be tested by demonstrating the effect of morphology on performance capabilities, and the latter on patterns of ecological resource use.

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