

**Biomechanical limits to ecological performance: mollusc-crushing
by the Caribbean hogfish, *Lachnolaimus maximus*
(Labridae)**

PETER C. WAINWRIGHT

*Department of Developmental & Cell Biology, University of California, Irvine, CA 92717,
USA*

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(With 6 figures in the text)

Functional limitations on feeding ability were investigated in the mollusc-crushing Caribbean hogfish, *Lachnolaimus maximus* (Labridae). Two constraints were proposed to limit the maximum size prey *L. maximus* can eat: pharyngeal jaw gape and crushing force. These factors yield different quantitative expectations for the relationship between fish size and maximum prey size. Their relative importance for predation on a frequently consumed gastropod (*Cerithium litteratum*) was investigated in laboratory performance tests designed to determine the largest snails fish could eat. *Cerithium* predation was found to be force limited rather than gape limited. The importance of this functional constraint in determining the largest *Cerithium* consumed by wild fish was examined by comparing hogfish feeding capability, as determined by the performance tests, to the maximum size snails found in the stomach contents of field-collected fish. Crushing ability appears to limit *Cerithium* predation in natural fish populations. The utility of performance testing for determining the functional and ecological importance of morphology is discussed.

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Introduction

A fundamental aim in ecology is to identify the factors that determine patterns of resource use by organisms. One such factor is the capability of an organism to exploit its environment. In principle, defining the limits of these capabilities sets the borders within which other factors may exert their influence (i.e. competition, predation, active choice, various stochastic processes, and the relative abundance of resources). Resource use abilities are in turn related to functional morphology, which both permits and constrains exploitation of the environment. Thus, understanding the functional basis of these constraints is a key step toward elucidating the role of morphology in determining patterns of resource use.

Morphology is generally believed to be a major determinant of feeding habits in fishes (Alexander, 1967; Randall, 1967; Gatz, 1970; Zaret, 1980). Dietary differences among species (Keast & Webb, 1966; George & Hadley, 1979; Barel, 1983) and among individuals within species (Randall, 1965; Stark & Schroeder, 1971; Stoner, 1980) are often claimed to be due to differential prey capture abilities inferred from morphological variation. Mouth size, mouth position, jaw length, dentition, gill raker spacing, eye size, skull shape, and body form are some factors frequently assumed to be indicative of fish feeding abilities (e.g. Magnuson & Heitz, 1971; Galis & Barel, 1980; Felley, 1984; Witte, 1984). However, only rarely are the inferences relating morphological differences to functional abilities supported with direct empirical data. Mouth width has been shown to limit maximum prey size in several fish taxa (Lawrence, 1957; Okada & Taniguchi, 1971; Werner, 1974, 1977), and gill raker spacing can set a lower limit on prey size (Ebeling & Calliet, 1974; Mummert & Drenner, 1986). In young and small fish, eye size can limit visual acuity because larger eyes can detect smaller prey (Blaxter & Jones, 1967; Hairston, Li & Ester, 1982). In spite of these and other efforts, the feeding constraints imposed by morphology are poorly known for most fish taxa (Werner, 1977; Liem, 1984).

One general protocol for exploring the role of morphology in trophic ecology involves dividing the task into two steps (Emerson, 1978; Arnold, 1983; Radinsky, 1985). First, the approach of functional morphology is used to develop quantitative predictions relating variation in morphology to feeding abilities along some descriptive prey axis (e.g. prey size). These predictions can then be tested in the laboratory with behavioural experiments designed to measure feeding performance of individual fish along the prey axis of interest. Performance tests (Arnold, 1983) establish the limits of feeding abilities and thus reveal what can be viewed as the fish's *potential* trophic niche. In the second step, field observations are used to determine whether these limitations are, in fact, actively constraining the dietary habits of fish in natural populations or whether the actual diets contain only a subset of the prey which can be consumed. That is, does the realized niche mirror the potential niche? Some constraints, although theoretically justified, may not turn out to have ecological relevance.

In this paper, I utilize this approach to study functional constraints in the feeding biology of the mollusc-crushing Caribbean hogfish, *Lachnolaimus maximus* (Labridae). Based on a biomechanical analysis of the feeding mechanism, two functional constraints are proposed that yield conflicting predictions concerning the maximum feeding capability (maximum prey size) of hogfish as a function of their body size. Predation by hogfish is potentially limited by pharyngeal jaw gape or crushing strength. Predictions of each model were tested in the laboratory by feeding performance experiments designed to determine the largest individuals of a common gastropod prey that could be crushed by feeding fish. These tests establish the actual limits of hogfish feeding abilities and thus identify one boundary in the potential niche of this species. The ecological

significance of this constraint was then assessed by comparing maximum prey sizes from stomach contents of wild-caught fish to the limits of the potential niche. The goals of this study are thus two-fold: first, to elucidate the morphological basis of hogfish feeding constraints, and second, to test the role of these limitations in determining patterns of prey consumption in a natural population of fish.

Materials and methods

Field work was carried out during August and October 1985 and April 1986 at the Smithsonian Institution's research facility on Carrie Bow Cay, located on the Belizean barrier reef off the Caribbean coast of Central America (16° 48' N: 88° 05' W). This is a relatively undisturbed portion of the Belizean reef, receiving minimal human fishing pressure.

Feeding anatomy

The descriptive anatomy is based on dissections of 5 fresh specimens, 3 formalin preserved specimens and 2 fish that were cleared with trypsin and double stained for bone and cartilage (Dingerkus & Uhler, 1977). Muscle names follow Winterbottom (1974) and skeletal terminology is from Stiassny (1981).

Lachnolaimus maximus crush molluscs in their pharyngeal jaws and do not swallow prey that cannot be crushed. Two mechanisms can limit the maximum size prey a hogfish could successfully handle. The prey may be too large to fit into the pharyngeal apparatus (gape limited) or the prey may be too hard for the fish to crush (force limited). Measurements of maximum pharyngeal gape and maximum potential crushing force were made on a size series of fish and used to construct quantitative predictions of the limits of hogfish feeding abilities as a function of body size.

Maximum gape was estimated by inserting plastic dowels of increasing diameter (1 mm increments) into the pharyngeal jaws of 20 freshly killed specimens. The width of the largest dowel that fitted snugly between the jaws of each fish was taken as maximum gape.

Maximum potential crushing force of 13 fish was estimated from measures of physiological cross-sectional area of the primary biting musculature. For each fish, this muscle mass was removed from the left side and the method of Calow & Alexander (1973) used to calculate its potential force capability (P'):

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

Here V is muscle volume, w is the muscle width, δ is stress (force production per unit area of muscle) and α is the pinnation angle of the muscle fibres against the central tendon. A stress value of 200 kN/m², typical for fish white muscle, was taken from the literature (Altringham & Johnston, 1982; Johnston & Salamonski, 1984), but all other parameters were measured directly. For each muscle sampled, pinnation angle and muscle width were measured in 10 locations and the average for each muscle used in calculating P' . Accounting for both left and right crushing musculature, the potential crushing force of the pharyngeal jaw apparatus was taken as $2P'$.

Feeding performance

Performance experiments were used to test the 2 models of maximum feeding ability with respect to a primary prey species, *Cerithium litteratum*, a gastropod mollusc. To facilitate this comparison it was necessary to relate snail size (gape limited model) to the force required to crush the shell (force limited model). This was accomplished by crushing 61 live *C. litteratum* in compression grips with a Monsanto XL100 tensometer outfitted with a 300, 600 or 1200 Newton force beam, depending on snail size. The maximum force borne by each shell was read directly off a Hewlett-Packard X-Y plotter. Analysis of feeding anatomy and behaviour indicates that this is an accurate replication of the actual crushing kinematics (see **Results: Feeding**

mechanism). The upper and lower pharyngeal jaw bones from a 1150 g hogfish were mounted in fibreglass epoxy and used as the crushing surfaces. These knobble-toothed biting surfaces may reduce the force required to crush the shell by concentrating stresses. To test this possibility, 50 *C. litteratum* were crushed between hard flat surfaces in the tensometer and the regressions of maximum load on snail size were compared for the 2 loading surfaces.

For the performance experiments, 9 *L. maximus* (170–300 mm) were captured in fish traps and maintained separately in 70 l aquaria with flow through sea water at ambient temperature (about 27 °C). These tests determined the largest *C. litteratum* that each fish could eat. A series of 30 feeding trials was performed with each fish over several days. In each trial, the fish was presented with 5 snails randomly chosen from 8 size categories. The 8 size classes (0.5 mm shell diameter increments) spanned the maximum size the fish could crush. During the trials, a record was made of all feeding attempts. After 20 min the uneaten snails were retrieved and their sizes noted. Care was taken to avoid experimenting with satiated fish.

Feeding habits

SCUBA and skin divers collected 67 *L. maximus* with spearguns from coral reefs and reef-seagrass bed interfaces around Carrie Bow Cay. Mass (g) and standard length (mm) were measured on each fish and the entire intestinal tract was preserved in a solution of 10% buffered formalin in sea water. Contents of the intestinal tract were later sorted and identified. The percentage volumetric contribution and frequency of occurrence were calculated for the major prey categories.

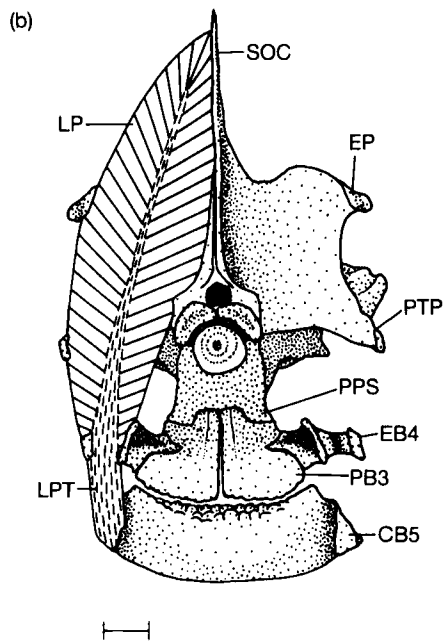
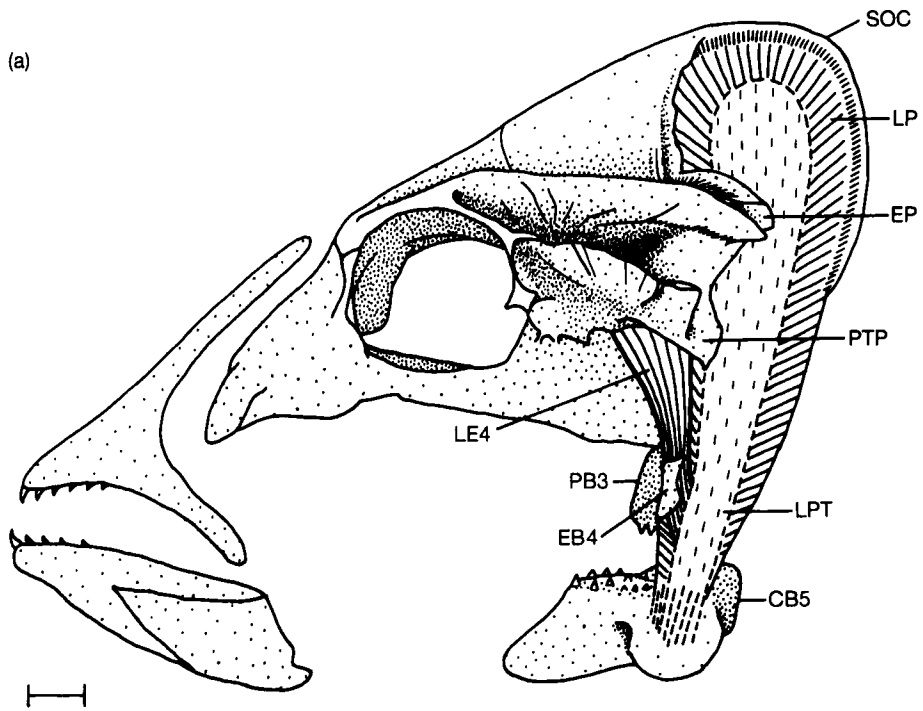
All gastropod opercula were identified and their maximum diameter measured with an ocular micrometer under a dissecting microscope. Operculum diameter was used as a snail size metric. The relation between operculum diameter and the minimum shell diameter (found to be the axis perpendicular to the shell's opening) was determined independently with the series of 61 *C. litteratum* for which crushing force was measured. Opercula not only reflect snail size accurately but are also the only hard part of the gastropod that *L. maximus* consistently swallow. During the laboratory feedings, the operculum was always swallowed with the snail flesh, while most of the crushed shell was expelled.

The feeding performance tests revealed the actual limits of hogfish predation on *C. litteratum*. The relevance of this constraint to the trophic ecology of wild *L. maximus* was investigated by comparing the size of the largest *C. litteratum* in the intestines of the 67 fish to that predicted by the performance experiments.

Statistical analysis

Statistical analyses were performed on \log_{10} transformed data. In all regression situations, reduced major axes (RMA) were used to estimate relationships rather than least squares. Ricker (1973) and Sokal & Rohlf (1981) discuss the advantages of RMA when natural and measurement variation exists in both variables. Regression lines were of the standard allometric form: $\log y = \log a + b \log x$. The two models of feeding limitations were treated as theoretical predictions and the results of the performance experiments were compared to them in one sample *t*-tests for differences in slope and *y*-intercept (Ricker, 1973). Other comparisons of regression coefficients were made with one and two-sample *t*-tests.

FIG. 1. (a) Diagram of pharyngeal jaw apparatus of *Lachnolaimus maximus* with suspensorium, opercular series and most of the branchial bones removed to reveal the upper and lower pharyngeal jaws. Only two muscles are illustrated and the LP is shown in sagittal section. (b) Posterior view of pharyngeal jaw topography. Right side musculature has been removed. Abbreviations: CB5, fused fifth ceratobranchials; EB4, fourth epibranchial; EP, epiotic process; LE4, fourth levator externus muscle; LP, levator posterior muscle; LPT, tendon of levator posterior; PB3, third pharyngobranchial; PPS, pharyngeal process of the parasphenoid forming diarthrosis with the third pharyngobranchial; PTP, pterotic process; SOC, supraoccipital crest. Scale bar is 10 mm.



Results

Feeding mechanism

The pharyngeal jaw apparatus of *L. maximus* exhibits the typical labrid condition, illustrated in detail elsewhere (Kaufman & Liem, 1982; Liem & Sanderson, 1986). Only those structures central to a discussion of the crushing mechanism are described here.

The upper pharyngeal jaw (UPJ) is composed of right and left enlarged third pharyngobranchials armed on their ventral surface with many low, rounded molariform teeth (Figs 1 and 2). The dorsal surfaces of these elements articulate through a true diarthrosis with the underside of the neurocranium (Kaufman & Liem, 1982). The fourth epibranchials articulate with the expanded lateral edge of the third pharyngobranchials and form half cylinders that cup the tendon of the levator posterior muscle (Figs 1 and 2).

The lower pharyngeal jaw (LPJ) is a stout structure composed of fused fifth ceratobranchials (Figs 1 and 2). It too is heavily toothed along its dorsal crushing surface. Laterally it forms expanded muscular processes that receive the tendon of the levator posterior muscle and articulate posteriorly and ventrally in a sliding joint with the cleithrum.

In *L. maximus*, the levator posterior (LP) is the dominant muscle in the crushing apparatus. This tremendously hypertrophied bipinnate muscle occupies a space bordered medially by an expanded supraoccipital crest and anteriorly by a ridge extending between the pterotic and epiotic processes (Fig. 1). The muscle fibres originate from neurocranial bone or a tendinous sheath that encases the regions of the muscle not arising from bone and converge inward to insert on a broad, flattened central tendon. This tendon tapers into a thick, rounded structure and inserts on the muscular process of the LPJ.

Two smaller muscles also insert on this tendon and contribute to crushing actions. The fourth levator externus (LE4) arises from the neurocranium anterior to LP and converges into the latter at the fourth epibranchial bone (Fig. 1). The short lateral head of the obliquus posterior (OPL) originates on the muscular process of the LPJ and joins the tendon at the level of the fourth epibranchial, forming the ventral-most portion of the crushing musculature. The weight of these two muscles was included in the force calculations but their independent effects could not be estimated accurately because of the high degree of fusion between them and the LP. Average pinnation angle of muscle fibres in the LP was 45.9° (S.D. = 4.3) in the sample of 13 fish examined and did not change with body size ($r = 0.23$, $P > 0.2$). Pharyngeal crushing muscle mass showed a slight positive allometry with body mass ($\log \text{muscle mass} = 1.13$, $\log \text{body mass} - 2.6$, $r^2 = 0.86$).

It is inferred from the morphology of these structures and functional work on other labrids (Liem & Sanderson, 1986) that the major crushing behaviour of *L. maximus* involves dorsal movements of the lower pharyngeal jaw against the upper. The orientation and size of the paired LP muscles indicate that they are the primary force producing mediators of this action (Fig. 1). This simple system has no lever arms so the maximum crushing force can be estimated by the combined potential of the paired LP, LE4 and OPL muscles.

The regressions of peak pharyngeal jaw gape and estimated crushing force ability on fish body mass are given in Table I. These relations can be used to predict the maximum diameter and hardness of prey that *L. maximus* can handle. Predictions of maximum force were transformed into expected shell diameters (Table I; Force limited model B) using the relation determined by the tensometer crushing data (see below).

Considerable variation was found in the force required to crush shells of all sizes (Fig. 3; RMA: slope = 1.67, S.E. = 0.114, y -intercept = 1.02, S.E. = 0.086). Crushing shells between flat surfaces

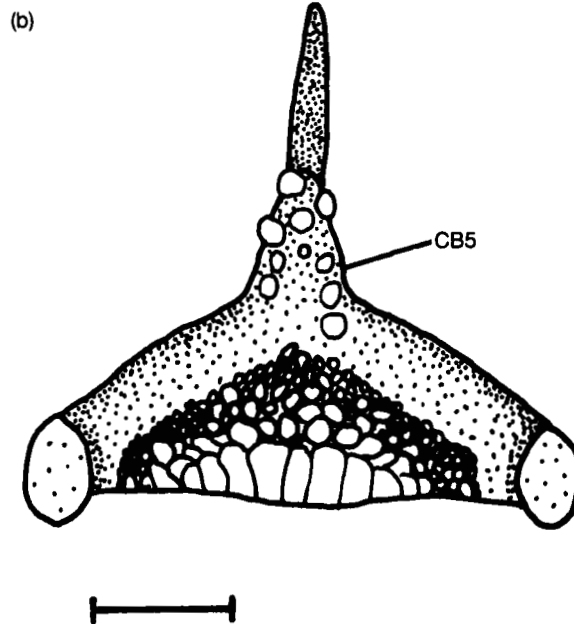
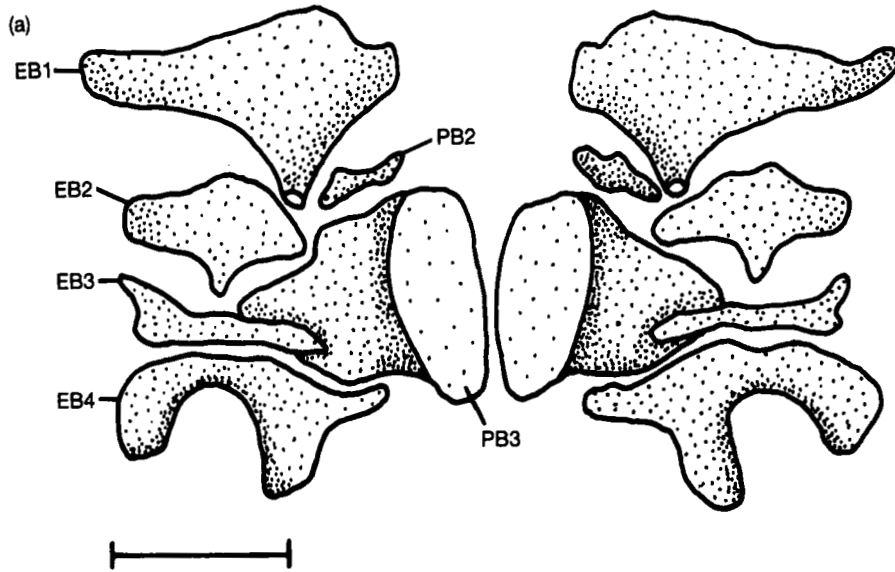


FIG. 2. (a) Diagram of dorsal branchial bones of *L. maximus* in dorsal view. (b) Lower pharyngeal jaw in dorsal view. Abbreviations: CB5, fused fifth ceratobranchials; EB 1-4, first through fourth epibranchials; PB2, 3, second and third pharyngeal branchials. Scale bar is 10 mm.

TABLE I

Two models of maximum feeding capability of *L. maximus*. Statistics are reduced major axes of measurements made on a size series of fish fit to the allometric equation: $\text{Log}_{10} Y = b (\text{Log}_{10} \text{fish mass}) + \text{Log}_{10} a$

Model	Y	b	S.E.	Log a	S.E.	r ²	n
Gape limited	shell diameter (mm)	0.29	0.023	0.15	0.11	0.91	25
Force limited (A)	force (N)	0.71	0.058	-0.34	0.15	0.85	13
Force limited (B)*	shell diameter (mm)	0.43	0.051	-0.42	0.14	0.85	13

* Force limited model B is derived from A by transforming values of force into estimated *Cerithium litteratum* shell sizes using the relation shown in Fig. 3.

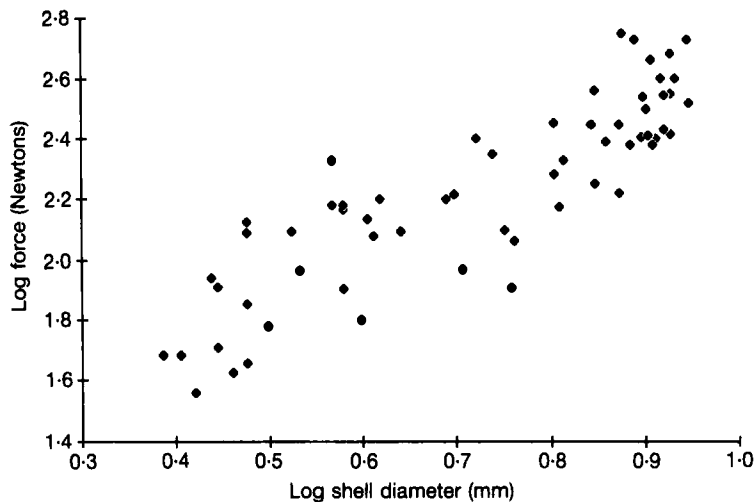


FIG. 3. Log-log plot of shell size of 61 *Cerithium litteratum* vs. the force required to crush each shell.

had no significant effect on maximum load borne (RMA: slope = 1.53, S.E. = 0.131, y-intercept = 1.17, S.E. = 1.08; comparison of slopes: $t = 0.82$, $d.f. = 109$, $P > 0.4$; comparison of y-intercepts: $t = 0.27$, $d.f. = 109$, $P > 0.5$). Thus, at least with this species, the uneven biting surfaces do not appear to concentrate stress effectively, and do not reduce forces needed to crush shells.

Feeding performance

In the laboratory feeding trials, hogfish picked up individual *C. litteratum* and, after briefly manipulating them, crushed the shell with mouth slightly open. Shell fragments were expelled after winnowing them from the snail flesh. Actual crushing lasted from 1–10 seconds and unsuccessful bouts were often followed by reorientation and further crushing attempts. Under favourable conditions it was possible to observe the snail, inside the mouth, being crushed between the pharyngeal jaws.

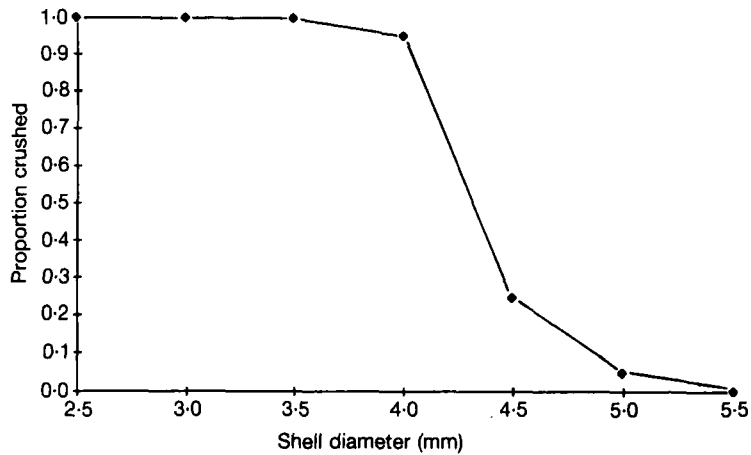


FIG. 4. Results of a laboratory feeding performance experiment designed to determine the maximum size snail (*Cerithium litteratum*) a 175 mm, 265 g *Lachnolaimus maximus* could eat. Points represent the proportion of 20 snails in each size category that were successfully crushed and eaten by the fish.

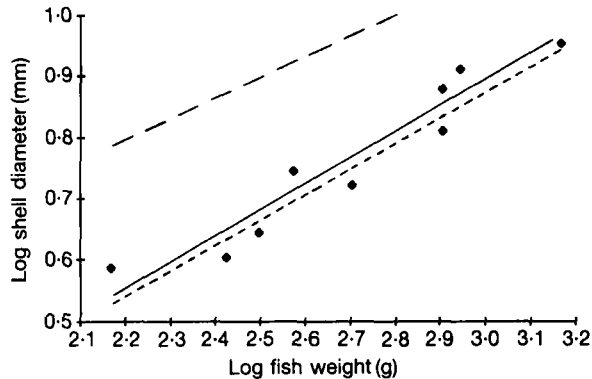


FIG. 5. Comparison of two models of maximum feeding ability with results of feeding performance experiments on nine *Lachnolaimus maximus*. Points represent the maximum size snail (*Cerithium litteratum*) each fish could eat. The solid line (—) is the RMA regression line for the nine fish. The long dashed line (---) is the prediction of maximum prey size as a function of fish size from the pharyngeal gape limited model. The short dashed line (- - -) is the prediction of maximum *Cerithium* size based on the pharyngeal crushing strength limited model. The models define the largest and hardest snail a given sized fish can eat, the zone above the lines representing snails which fish are unable to eat. Note that the actual performance data are inconsistent with the gape limited model but are coincident with the crushing strength model. See text for statistical comparisons.

Typical feeding performance results for individual fish did not show a distinct largest edible prey size (Fig. 4). Therefore, maximum snail size for each fish was taken as the shell diameter at which 50% were successfully crushed. This metric of performance has the same scaling relation with fish mass as does absolute largest snail size eaten (two-sample comparisons of RMA slopes; $t = 1.12$, $d.f. = 16$, $P > 0.2$). Thus, these measures provide equivalent tests of the two models.

TABLE II

Primary prey taxa identified from intestinal tract contents of 67 Lachnolaimus maximus collected in Belize, Central America. Percentage of total sample volume contributed by the major taxa and the percentage of individual fish which had eaten primary prey types are presented

Prey type	Volume (%)	Frequency (%)
Pelecypoda*	34	100
Gastropoda**	47	100
<i>Cerithium litteratum</i>		64
<i>Astraea</i> spp.		35
<i>Tegula fasciata</i>		30
Crustacea	15	62
Anomura (hermit crabs)		43
Brachyura (crabs)		30
Amphipoda		5

* 17 pelecypod taxa were identified

** 43 gastropod taxa were identified

The performance data for the nine *L. maximus* (Fig. 5; RMA of maximum shell size on body size: slope = 0.44, S.E. = 0.048, y -intercept = -0.42, S.E. = 0.132) are clearly inconsistent with the gape limited model for *Cerithium* predation (comparison of gape limited model to performance RMA slope; $t = 3.13$, $d.f. = 7$, $P < 0.05$). However, the force limited model accurately predicts maximum feeding performance (comparison of force limited model to performance RMA slope: $t = 0.20$, $d.f. = 7$, $P > 0.5$; comparison of y -intercepts: $t = 0.14$, $d.f. = 7$, $P > 0.4$). The hypothesis that force production by the pharyngeal jaws limits predation on *Cerithium* cannot be rejected.

The use of the shell size at which 50% of snails are crushed is a particularly appropriate performance metric for the force limited model. At any shell size, about half of all snails will not fail under the expected crushing load for that size class (Fig. 3). For this reason a hogfish will only be able to crush half of the shells of a size that corresponds to its expected maximum force capability. This natural variation in shell strength (Fig. 3) may account for the lack of a distinct maximum edible snail size in the performance experiments (Fig. 4).

Feeding habits

Gastropod (47% of the total sample volume) and pelecypod (34%) molluscs were the dominant prey found in the sample of 67 *L. maximus* intestines (Table II). The gastropod taxa eaten by the most fish were *Cerithium litteratum* (present in 65% of the intestines examined), *Astraea* spp. (in 35%) and *Tegula fasciatus* (in 30%).

Among the 43 fish that had *C. litteratum* in their intestines, the average number of opercula per fish was 9.2 (S.D. = 7.6). Within this subsample, fish mass explained over 75% of the variation in operculum size ($r^2 = 0.76$). Operculum diameter was highly correlated with shell diameter (RMA of operculum diameter on shell diameter: slope = 1.11, S.E. = 0.029, y -intercept = -0.89, S.E. = 0.051, $n = 61$, $r^2 = 0.96$), permitting an accurate transformation. The largest *C. litteratum* operculum found in each individual was transformed into an expected shell diameter and is plotted against fish size in Fig. 6 (RMA of maximum shell size on fish body mass: slope = 0.39, S.E. = 0.031, y -intercept = -0.34, S.E. = 0.091). Regression slopes of the force limited model, the

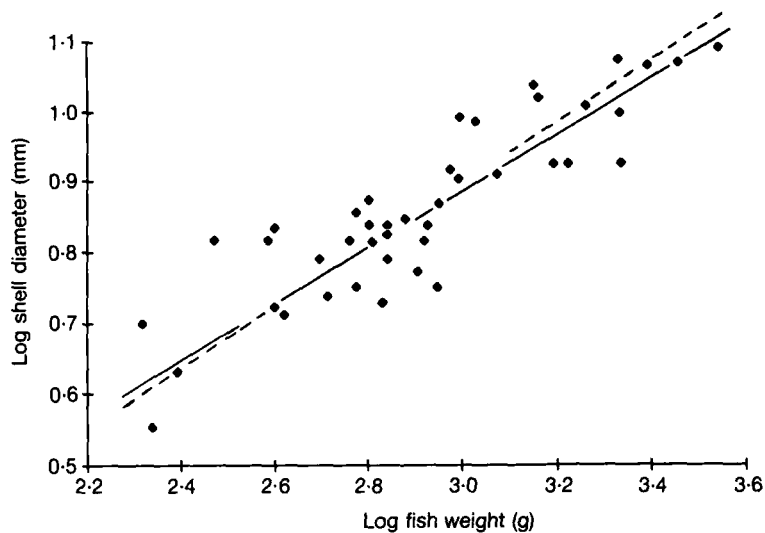


FIG. 6. Comparison of the maximum feeding ability of *Lachnolaimus maximus*, determined using performance experiments, with the largest *Cerithium litteratum* from the intestinal tracts of wild-caught fish. Points (●) represent the largest snails eaten by 43 fish and the straight line (—) is the RMA regression of these data. The dashed line (---) is the RMA representing the maximum feeding ability from the performance experiments (Fig. 5). Note that the two lines are coincident, indicating that feeding ability actively limits *Cerithium* predation by wild fish. See text for statistical comparisons.

performance data and the dietary data are not significantly different in any pairwise comparisons (Fig. 6; performance data vs. diet: two-sample *t*-test: $t=0.33$, $d.f.=50$, $P>0.5$; force model vs. diet: one sample *t*-test: $t=1.29$, $d.f.=41$, $P>0.2$).

Discussion

Hogfish feeding constraints

Three primary conclusions concerning the trophic biology of *Lachnolaimus maximus* can be drawn from this study. First, hogfish feeding is potentially limited by pharyngeal gape or crushing strength. Secondly, handling of *Cerithium litteratum* is constrained by crushing strength, not pharyngeal gape. Thirdly, this functional limitation in feeding ability appears to be the primary determinant of the maximum size *C. litteratum* eaten by Belizean hogfish in the wild.

The performance tests established the upper limits of *L. maximus* predation on *Cerithium*. Hogfish cannot eat snails that they cannot crush, but this constraint might not be the limiting factor on the size of *Cerithium* consumed by fish in nature. Many factors, such as optimal foraging considerations, competition with other molluscivores, or even the ability of fish to locate and capture different size prey, may further restrict the actual pattern of resource use. Fish may actively select small snails, for example, indicating an insignificant role of the biomechanical constraints. However, the tendency for the largest *Cerithium* eaten by Belizean hogfish to approximate the maximum size shell they can crush (Fig. 5) indicates that this functional limitation is, in fact, an important determinant of feeding habits.

Although this investigation focused on a single prey species, hogfish diets include many pelecypod and gastropod molluscs (Table II; Randall & Warmke, 1967). Whether pharyngeal gape or crushing strength limits predation on other prey types will depend on the relation between shell diameter and shell strength for each species. Consumption of those that can be crushed with relatively small forces may be restricted by gape limitation rather than force production. Both gape and crushing strength are viable feeding constraints, their relative importance depending on the physical properties of prey items.

High variation in maximum force borne (Fig. 3) is typical of fracture failure and occurs in other mollusc shells loaded in compression (see data in Currey, 1976). Because of this uncertainty in the force required to crush any given shell, snails of a size corresponding to up to twice the expected maximum force capability of hogfish were occasionally crushed (Figs 4 and 6). This variability in shell strength has implications for *L. maximus* foraging strategy. Fish can be expected to sample a broad range of prey sizes. It was noted in laboratory feeding trials that hogfish attempted to eat virtually all prey items they were offered.

Labrid trophic biology

The Labridae are a group of about 470 species (Liem & Sanderson, 1986) of predominantly warm water marine teleost fishes that exhibit remarkable trophic diversity (Randall, 1967; Yamaoka, 1978). This diversity has been linked to modifications of the pharyngeal jaw apparatus present only in labrids and other fishes of the perciform suborder Labroidei (Kaufman & Liem, 1982; Liem & Sanderson, 1986). One such modification is the presence of direct muscular attachments between the neurocranium and the lower pharyngeal jaw that facilitate direct occlusion of the lower against the upper jaw. Thus equipped with a potentially powerful pharyngeal bite, labrid diets generally differ from other tropical marine fishes in containing large amounts of hard-bodied prey which have been crushed in these jaws (Randall, 1967; Hobson, 1974; Yamaoka, 1978; Liem & Sanderson, 1986).

Yamaoka (1978) has shown that, among Pacific labrids, relative size of this pharyngeal crushing musculature is correlated with prey type. He found that larger muscles occurred in species with a greater proportion of hard-bodied prey in the diet (molluscs, echinoderms, some crustaceans). The results of the present work indicate that size of this musculature is indeed indicative of pharyngeal jaw crushing strength. Thus, it appears that this strength is a measure of feeding ability that has a clear morphological basis and plays a central role in determining dietary differences among species of one of the most successful modern groups of marine fishes.

Morphology, performance and ecology

That morphology underlies feeding proficiency and thus influences dietary habits is a central concept in vertebrate trophic biology (Rosenzweig & Sterner, 1970; Hespenheide, 1973; Grant, Grant, Smith, Abbott & Abbott, 1976; Kiltie, 1982; Barel, 1983). Certainly, functional morphology can be used to predict some theoretical limits of animal diets and many studies have examined the usefulness of this approach for testing the importance of functional constraints in determining vertebrate feeding habits (e.g. Mittelbach, 1984; Wheelwright, 1985). By 'functional constraint' I refer to properties of the organism that restrict the range of prey it can exploit. They are one proximate cause of patterns of resource (prey) use and can play central roles in studies that seek explanations for such patterns, whether the focus be intraspecific or interspecific.

Understanding the functional significance of morphology is a crucial step in identifying trophic constraints and this key link between anatomy and dietary habits can be made with performance testing (Werner, 1977; Emerson, 1978; Arnold, 1983; Radinsky, 1985). Hypotheses about the functional implications of particular structures can be tested by examining the effect of morphological variation on performance (Arnold, 1983). Only when this effect is known can the morphological feature be used as an index of feeding ability (e.g. Werner, 1974; Hairston *et al.*, 1982; Kiltie, 1982). In this way, it was possible to show that hogfish crushing potential can be estimated by the mass of the levator posterior muscle (Table I and Fig. 5).

Performance tests can also help distinguish among two or more potentially important factors that may influence feeding proficiency. When competing models have quantitatively different expectations, their relative effects on performance can be resolved. Such cases highlight the advantages of testable *a priori* predictions based on biomechanical analyses (e.g. Emerson & Diehl, 1980). A common problem occurs in trophic studies where many models of feeding limitation predict an increase in prey size with greater body size (Grant *et al.*, 1976; Zaret, 1980). This arises because most anatomical structures tend to be highly correlated with overall body size and their effects on feeding proficiency are often similarly correlated. Identifying which features actually govern the limits of feeding abilities is dependent on quantitative interpretations of their function that lead to testable predictions.

The limits of feeding abilities, or functional constraints, define boundaries of the animal's potential niche. The biological role (Radinsky, 1985) of these constraints can be tested by comparing the potential niche to the actual dietary habits. Only when the two are coincident can it be concluded that the constraint plays an important ecological role in limiting the range of prey eaten. Understanding the role of trophic structures in determining animal diets therefore requires knowledge of how morphology influences feeding abilities.

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