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Feeding Morphology, Diet, and Ecomorphological Relationships among Five Caribbean Labrids (Teleostei, Labridae)

KARI B. CLIFTON AND PHILIP J. MOTTA

The ecomorphological relationship between oral and pharyngeal jaw morphology and diet was investigated for five labrids: *Lachnolaimus maximus*, *Halichoeres garnoti*, *H. bivittatus*, *H. maculipinna*, and *Thalassoma bifasciatum*. The goals were to examine the following: (1) the relationship between diet and oral and pharyngeal jaw morphology; and (2) the influence of feeding behavior on diet. Twelve morphological measurements reflecting aspects of feeding ability were made. Interspecific differences in dentition were described. Principal components analysis (PCA) explained 96% of the variance among morphological variables with the first two PCs. Principal component 1 accounted for 92.2% of the variance, separating species by body size, whereas PC2 (3.8% of variance) separated species by oral jaw shape and degree of protrusibility. Twenty-six prey categories were identified. Canonical correspondence analysis (CCA) revealed that only 4.7% of the variation in diet was attributable to morphological variables, indicating a low correlation between oral and pharyngeal jaw characters and diet. However, variables that measured some aspect of performance were good predictors of diet. The proportion of hard prey consumed was correlated to the estimates of biting force for each species. Species with stronger pharyngeal jaw musculature consumed larger amounts of hard prey than those with lesser force generating ability. Feeding behaviors, classified as suction feeding, winnowing, or biting, corresponded to oral jaw morphology. Species with less protrusible jaws were found to bite their prey, and species with more protrusible jaws picked items out of the water column or winnowed on the substrate.

A major premise of ecological morphology is that an organism's ecology is influenced by its morphology. Ecomorphology aims to integrate anatomical, functional, ecological, behavioral, and evolutionary studies to gain not only an idea of how a structure functions but also how that structure is used by the organism in its environment (Bock and von Wahlert, 1965; Bock, 1980; Wainwright and Reilly, 1994). An approach commonly used to address ecomorphological hypotheses is to identify patterns in ecology and correlate them to patterns in morphology (Motta and Kotrschal, 1992; Reilly and Wainwright, 1994; Motta et al., 1995a). It is generally assumed that, if form and function vary together in a predictable way, we should be able to predict an organism's ecology from its morphology and vice versa (Wiens and Rotenberry, 1980; Ricklefs and Miles, 1994). For example, morphological adaptations of feeding structures limit an organism's ability to utilize food resources. Therefore, organisms with similar feeding morphologies may have similar diets (Karr and James, 1975; Wiens and Rotenberry, 1980; Grossman, 1986).

Some studies have found a correlation between morphology and ecology (Moyle and Senanayake, 1984; Norberg, 1994; Turingan, 1994). Other studies, however, have found little

correlation between morphology and ecology (Grossman, 1986; Kotrschal, 1989; Motta et al., 1995a). This apparent lack of correlation between ecological and morphological character sets can be due to complex interplay of factors (e.g., behavioral, ecological, physiological, historical, and morphological constraints) that influence the relationship (Motta et al., 1995b).

Although the majority of the former ecomorphological studies on fish feeding have focused on morphological characters associated with body form, the oral jaw apparatus (OJA), and gillrakers, the pharyngeal jaw apparatus (PJA) is an important food processing center situated between the OJA and the digestive tract. Wainwright (1987, 1988) found that the PJA plays a central role in constraining diets of Caribbean wrasses (Labridae) by limits in crushing strength and pharyngeal jaw gape. Specializations in the labroid PJA unite the labroid fishes (Labridae, Cichlidae, Embiotocidae, Odacidae, Scaridae, and possibly the Pomacentridae) and are correlated with morphological and ecological diversification (Kaufman and Liem, 1982; Stiassny and Jensen, 1987; but see Streebman and Karl, 1997).

This study investigates the relationship between oral and pharyngeal jaw morphology, diet, and feeding behavior in five labrid species.

Furthermore, this study employs direct gradient analysis, the statistical comparison of suites of morphological and ecological characters, to test the relationships between these character sets. The goals were to determine the relationship between diet and oral and pharyngeal jaw morphology among five labrid species and the influence of feeding behavior on diet.

MATERIALS AND METHODS

Five Caribbean labrid species were included in this study: *Halichoeres garnoti* (yellowhead wrasse, 105–129 mm SL), *H. bivittatus* (slippery dick, 102–126 mm SL), *H. maculipinna* (clown wrasse, 98–117 mm SL), *Thalassoma bifasciatum* (bluehead, 78–97 mm SL), and *Lachnolaimus maximus* (hogfish, 170–238 mm SL). Only supermales, or terminal color phase males, were used to avoid confounding of the data due to possible ontogenetic dietary and morphological changes. For *L. maximus*, both reproductively active males and females were utilized, due to its lack of obvious sexual dimorphism or dichromatism.

Fishes were collected by spear with the aid of SCUBA at Tennessee Reef in the middle Florida Keys and off Loggerhead Key in the Dry Tortugas. Collections at Tennessee Reef (24°45'N, 80°47'W) were made in January, May, and July 1990 at depths of 10–12 m. Additional specimens of *H. bivittatus* and *T. bifasciatum* were collected in the Dry Tortugas in November 1990. Collections were made at Loggerhead Key (24°38'N, 82°54'W), at a depth of 3–4 m. Fish guts were removed within 3 h after collection and preserved in 10% buffered formalin with rose bengal. The fishes were frozen for later morphological measurements. Feeding behaviors were observed at Conch Reef (24°57'N 80°27'W) in the Florida Keys in November 1991, at depths of 10–31 m.

Morphological analyses.—Based on studies by Motta et al. (1995a), Kotrschal (1989), and Gatz (1979), standard length and 12 morphological measurements found to be associated with feeding were made on each specimen. Variables were defined after Hubbs and Lagler (1967), Gatz (1979), and Motta et al. (1995a). Variables not defined in above sources are defined as follows: standard length (SL), head length (HL), head length protruded (HLP), mouth width protruded (MWP), mouth height protruded (MHP), total dentary length (TDL); length from symphysis to posteriormost margin of dentary, dentigerous dentary length (DDL); length from symphysis to posteriormost tooth on den-

tary, dentigerous dentary width (DW); width of lower jaw between posteriormost teeth on right and left dentaries, premaxilla ascending process length (APL), dentigerous premaxilla length (DPL); length from symphysis to posteriormost tooth on premaxilla, dentigerous premaxilla width (PW); width of upper jaw between posteriormost teeth on right and left premaxilla, dentigerous surface area of upper pharyngeal jaw (UPJ); area of ventral surface of upper pharyngeal jaw, dentigerous surface area of lower pharyngeal jaw (LPJ); area of dorsal surface of lower pharyngeal jaw. Standard length was measured with a ruler to the nearest 1 mm. All other linear measurements were made with vernier calipers to the nearest 0.1 mm. Surface area of the upper pharyngeal jaw was calculated using the geometric formula for the area of a triangle and for the lower jaw an isosceles triangle and a rectangle. Surface areas were calculated to the nearest 1 mm². Measurements were taken with an ocular micrometer fitted for a dissecting microscope. A sample size of 20 individuals per species was utilized as determined by the method of Bros and Cowell (1987). Principal components analysis (PCA) was conducted on 12 variables to detect patterns of morphological variation among species. Analysis was carried out on a correlation matrix of log₁₀-transformed variables (Ricklefs and Miles, 1994) performed with Statistical Analysis Systems using Proc Princomp (Cary, NC, 1985, unpubl.).

Relationships among morphological variables indicated by PCA were examined. To remove the effect of body size, each morphological variable was pooled among species and regressed against standard length (Humphries et al., 1981). ANOVAs were performed on residuals to detect significant differences among species. Tukey's studentized range test was used to identify significant differences among species. Tests were performed with Statistical Analysis Systems using Proc GLM (Cary, NC, 1985, unpubl.).

To assess the degree of oral jaw protrusibility (OJP) in these fishes, the difference between HL and HLP was expressed as a percent of HL. ANOVA was used to test for differences in OJP among species. Tukey's studentized range test was used to identify significant differences among species. Analysis was performed with Statistical Analysis Systems using Proc GLM (Cary, NC, 1985, unpubl.).

Scanning electron micrographs were taken of representative upper and lower oral and pharyngeal jaws of each species. Jaws were cleaned of all tissues using a weak bleach solution in a sonicator, allowed to air dry, then coated with gold-palladium in a Spelco model 3 sputter

coater. Micrographs were taken with an Hitachi HHS-2R scanning electron microscope at a magnification of 20× or 35× and a voltage of 15 kV.

Dietary analyses.—The sample size required for dietary analyses was determined by plotting the number of prey taxa against the number of fish sampled for each species. The maximum number of fish at which the addition of gut samples no longer added to the number of prey taxa (or where the rate of change was sharply reduced) was 15. A smaller sample size ($n = 10$) was used for *T. bifasciatum* because of difficulty in obtaining an adequate number of fish. To reduce bias due to differential digestibility of soft-bodied and hard-shelled prey, only prey items in the anterior half of each gut were used. When possible, prey items were identified to class or subclass with the aid of a dissecting microscope. Identical prey taxa were pooled within species, and wet weight was obtained to the nearest 0.001 g using a Mettler balance. Prey were divided into "hard-shelled" and "softer-bodied" categories to determine the percent contribution of each type to the diet of each species. Prey taxa possessing hard outer coverings or exoskeletons (e.g., molluscs, echinoderms), which required crushing by the pharyngeal jaws, were classified as hard-shelled. Prey taxa without hard shells or exoskeletons (e.g., polychaetes, sipunculins) were classified as softer-bodied. The majority of the arthropod taxa (e.g., copepods, shrimps) that possess hard exoskeletons but did not require crushing by the pharyngeal jaws were also classified as softer-bodied prey. Total percentages of hard and soft prey in the diet (by wet weight) were calculated by species.

The Shannon-Wiener diversity index (H') was used to assess dietary diversity for each species (Cailliet et al., 1986; Kotschal and Thomson, 1986; Ludwig and Reynolds, 1988). Wet weight was used as a proxy for volume. To further define dietary diversity, Hill's diversity numbers were calculated as follows:

$$N_1 = e^{H'}$$

where H' = Shannon-Wiener diversity index, and

$$N_2 = 1/\lambda,$$

where λ = Simpson's index. N_1 is the number of abundant prey taxa in the diet, and N_2 is the number of very abundant prey taxa. Both indices are expressed as numbers of taxa and are measures of the number of prey taxa in the sample where each taxon is weighted by its abundance (Ludwig and Reynolds, 1988).

Modified Hill's ratio (E_5) was used as an index of prey evenness:

$$E_5 = \frac{(1/\lambda) - 1}{e^{H'} - 1},$$

where λ = Simpson's index and H' = Shannon-Wiener index (Ludwig and Reynolds, 1988). Values range from 1, when all taxa are equally abundant, to 0 as one item dominates the diet. This index is not sensitive to the occurrence of rare items; therefore it is independent of sample size. In addition, it is effected very little by richness. The H' , N_1 , N_2 , and E_5 indices were computed using the SPDIVERS program of Ludwig and Reynolds (1988).

Horn's index was used to calculate dietary overlap between all species pairs. This index is affected very little by sample size and can be used when data are expressed as proportions (Horn, 1966; Krebs, 1989). Horn's index was calculated with the NICHE program of Krebs (1989).

Relationship of morphology to diet.—Canonical correspondence analysis (CCA) was performed to relate variation in morphological characters to dietary composition. CCA is a multivariate, direct-gradient analysis technique in which a set of species may be related directly to a set of environmental variables. This technique selects the linear combination of environmental variables (here, diet) that maximizes the dispersion of species (morphology) scores. It chooses the best weights for the environmental variables to construct the first axis. Subsequent axes also select linear combinations of environmental variables that maximize the dispersion of species scores but are subject to the constraint of being orthogonal to previous axes (Jongman et al., 1987; ter Braak, 1986, 1987). Analysis was performed on \log_{10} -transformed morphological variables and dietary data (percent wet weight) with the CANOCO program, version 3.12 (ter Braak, 1988).

Feeding behavior.—Individual fish ($n = 10$ –13 per species) were observed with focal animal sampling by pairs of divers for 10-min periods. Feeding events were recorded and classified as suctioning, biting, or winnowing. Suction feeding occurs when rapid expansion of the buccal cavity draws water and prey items into the oral cavity (Liem, 1980; Norton and Brainerd, 1993; Norton, 1995). Biting occurs when the oral jaws are used to tear the prey from the substrate or to bite a piece from a larger prey item (Liem, 1980; Norton, 1995). In winnowing, the food items are separated from nonfood items in the

oropharyngeal cavity. Food items are ingested while the debris is ejected from the mouth (Laur and Ebeling, 1983; Drucker and Jensen, 1991) or from the opercular slits (Sibbing et al., 1986). Substrate types upon which or over which fishes fed were classified as sand, rubble, hard coral, sponge, algae, or water column. The distance fishes fed from the substrate was recorded as 0–0.1 m, 0.1 m–0.5 m, 0.5–1.0 m, or > 1 m. Benthic feeding occurred in the 0–0.1 m category, whereas feeding in the water column occurred 0.1 m to > 1 m from the substrate.

Estimation of pharyngeal crushing force.—The force generating capability of the pharyngeal crushing musculature was estimated for 5–11 individuals of each species. The levator posterior (LP) is the dominant crushing muscle in the labroid pharyngeal jaw apparatus (Yamaoka, 1978; Liem and Greenwood, 1981; Wainwright, 1987). Because the fibers of the LP and the fourth levator externus (LE₄) are interconnected and difficult to separate from one another, both muscles were used to estimate crushing force. The LE₄ is considerably smaller than the LP and therefore not expected to bias force calculations significantly (Wainwright, 1988).

The method of Powell et al. (1984) was used to estimate maximum tetanic tension (P₀) generated by the pharyngeal crushing musculature. The estimated maximum tetanic tension (P_{Oest}) of each muscle was calculated using the equation:

$$P_{Oest} = (CSA)(\text{specific tension}).$$

A specific tension of 20 N/cm² for teleost white muscle was taken from Altringham and Johnston (1982). Cross-sectional area (CSA) was calculated using the equation:

$$CSA = (\text{muscle mass})(\cos \theta) / (\text{FL})(\text{muscle density})$$

where wet weight of the muscle (g) was used for muscle mass, θ = average angle of insertion of 10 haphazardly chosen fibers on the central tendon, FL = length of 10 haphazardly chosen fibers (cm), and muscle density = 1.05 g/cm³ (Lowndes, 1955). The total force generated by the pharyngeal crushing musculature of each fish was estimated as 2P_{Oest}. To detect significant differences in force-generating capability among species, Mann-Whitney *U*-tests were performed on all possible pairwise species combinations. To maintain an experimentwise error rate of 0.05, the Bonferonni method was used to calculate the level of significance used for 10 pairwise comparisons. Comparisons were con-

TABLE 1. PRINCIPAL COMPONENTS ANALYSIS OF 12 MORPHOLOGICAL VARIABLES RELATED TO FEEDING IN FIVE LABRID SPECIES.

	Principal component	
	1	2
Eigenvalue	11.061	0.451
% of total variance	92.200	3.800
Cumulative % of variance	92.200	96.000
Eigenvectors		
Head length	0.292	-0.081
Head length protruded	0.295	0.031
Mouth width protruded	0.296	0.149
Mouth height protruded	0.283	0.017
Dentary width	0.294	-0.180
Dentigerous dentary length	0.293	0.111
Total dentary length	0.297	0.148
Premaxillary width	0.291	-0.202
Dentigerous premaxilla length	0.279	-0.506
Ascending premaxilla length	0.259	0.746
LPJ surface area	0.297	0.039
UPJ surface area	0.285	-0.219

sidered significant if $P < 0.005$ (Gatz, 1979; L. Wilkinson, SYSTAT, vers. 5.1, Evanston, IL, 1991, unpubl.). Estimates of force generating capability were correlated to percent hard prey in the diet and to body size (SL) with Statistical Analysis Systems using Proc Corr (Cary, NC, 1985, unpubl.).

RESULTS

Morphological analyses.—Principal components 1 and 2 explained 96% of the variation among 12 morphological variables (Table 1). The first principal component (PC1) accounted for 92.2% of the total variance. All variables loaded positively and were similar in magnitude. Components for which all coefficients have the same sign and magnitude may be interpreted as general size components (Pimentel, 1979; Jolliffe, 1986). *Thalassoma bifasciatum* scored lowest on PC1 (Fig. 1), followed by *H. maculipinna*. *Hali-choeres garnoti* and *H. bivittatus* had similar size ranges and similar scores, and *L. maximus* had the highest score on PC1 (Figs. 1–2).

Principal component 2 accounted for 3.8% of the variability among morphological variables. Because coefficients had both positive and negative signs, PC2 could be interpreted as a change in oral and pharyngeal jaw shape (Table 1; Pimentel, 1979; Strauss, 1985; Jolliffe, 1986). Along PC2, the ascending process of the premaxilla became longer, and the dentigerous length on the premaxilla decreased as did the

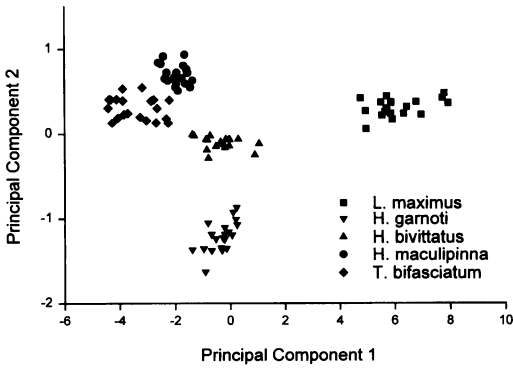


Fig. 1. Plot of principal components 1 versus 2 for 12 morphological variables associated with feeding in five labrids. Species separate on PC1 primarily by body size and on PC2 by length of the ascending process of the premaxilla and dentigerous area of the oral and pharyngeal jaws.

UPJ surface area. The remaining principal components accounted for 4% of the total variance. Species did not separate in any meaningful pattern on these axes; therefore they were not considered in this analysis.

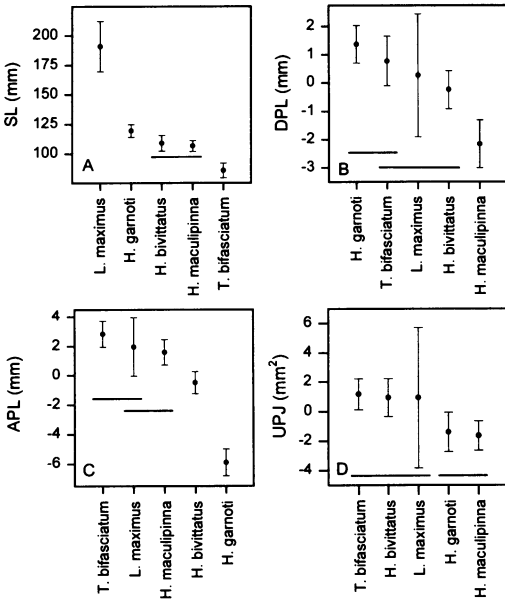


Fig. 2. Multiple comparisons of morphological variables for five labrids. Pooled residuals were compared by ANOVA. Means that were not significantly different are underlined. Only standard length and variables that loaded most heavily in the PCA are given. (A) SL = standard length; (B) DPL = dentigerous premaxilla length; (C) APL = premaxilla ascending process length; (D) UPJ = surface area of upper pharyngeal jaw.

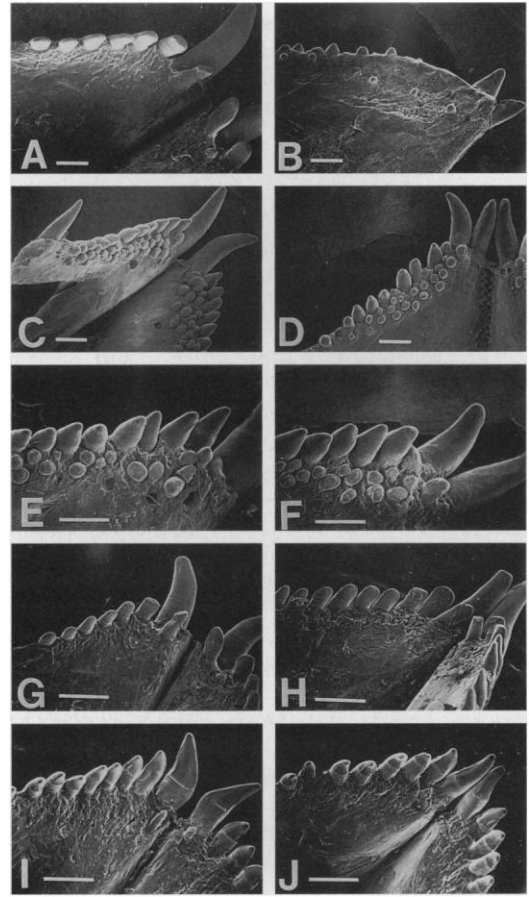


Fig. 3. Scanning electron micrographs of upper and lower oral jaws of five labrids. *Lachnolaimus maximus* (20×) (A) upper (B) lower left; *Halichoeres garnoti* (20×) (C) upper (D) lower; *H. bivittatus* (35×) (E) upper (F) lower; *H. maculipinna* (35×) (G) upper (H) lower; *Thalassoma bifasciatum* (35×) (I) upper (J) lower. Bar = 1 mm.

Significant differences between at least two species were found for all morphological variables. Standard length and variables that loaded heavily in the PCA are indicated in Figure 2. *Lachnolaimus maximus* was significantly larger than the other four species. When adjusted for body size, *H. garnoti* had a premaxilla with a significantly shorter ascending process but a long descending process. The remaining species had relatively long ascending processes with the exception of *H. bivittatus*, which was intermediate in length.

The oral jaw dentition patterns of *L. maximus* are markedly different than those of the other four species (Fig. 3A–B). The upper jaw has a single tooth row comprised of a few conical teeth, and two anterior, recurved, protruding,

caninelike teeth. The lower jaw is characterized by four anterior, canine teeth, smaller than those on the upper jaw. The remaining teeth are conical, small, and widely spaced on the dorsal margin of the jaw. There are a few small teeth scattered on the medial surface of the dentary near the dorsal margin.

Oral jaw dentition patterns of *H. garnoti* are most similar to *H. bivittatus* (Fig. 3C–F). Both species are characterized by two anterior, protruding, recurved, caninelike teeth on the upper jaw and four on the lower jaw. The lateral teeth are conical, closely spaced, and robust. Medial to this are multiple rows of irregularly spaced molariform teeth. Both species have a single caninelike tooth at the posterior margin of the descending process of the upper jaw.

Oral jaw dentition patterns of *H. maculipinna* and *T. bifasciatum* are similar (Fig. 3G–J). Both species possess two caninelike teeth on the upper and lower jaws and a single row of conical teeth on the margin of both jaws. The teeth are less closely spaced than those of *H. garnoti* and *H. bivittatus* and are less robust. *Halichoeres maculipinna* has a single caninelike tooth at the posterior margin of the descending process of the upper jaw, whereas *T. bifasciatum* has none.

Few interspecific differences in pharyngeal jaw dentition, other than relative surface area or size of the teeth, were documented among these species (Fig. 4). Relative to body size, *T. bifasciatum*, *L. maximus*, and *H. bivittatus* had the greatest surface area occupied by the pharyngeal teeth on both the upper (Fig. 2) and lower jaws. *Halichoeres maculipinna* and *H. garnoti* had the smallest relative PJA surface area. The pharyngeal jaws of *L. maximus* have abraded molariform teeth (Fig. 4A–B). The remaining four species are similar to one another in dentition patterns. In all four species, the UPJ has conical teeth. The medial teeth are worn to the point of being molariform in appearance. The LPJ possesses a narrow, anterior process bearing conical teeth. The two posterior processes bear large, molariform teeth medially, and smaller molariform teeth laterally. Generally, *H. garnoti* and *H. bivittatus* have more teeth on the anterior process and fewer, more robust teeth on the posterior processes than *H. maculipinna* and *T. bifasciatum* (Fig. 4D,F,H,J; KBC, unpubl. data). Unlike the *Halichoeres* congeners, *T. bifasciatum* lacks the large, medial, molariform tooth on the LPJ (Fig. 4J).

Oral jaw protrusibility (OJP) differed significantly among species (ANOVA, $P < 0.001$). *Halichoeres garnoti* had the lowest oral jaw protrusibility, 2.5% of the head length, and a corresponding low score on PC2 (Fig. 1). The re-

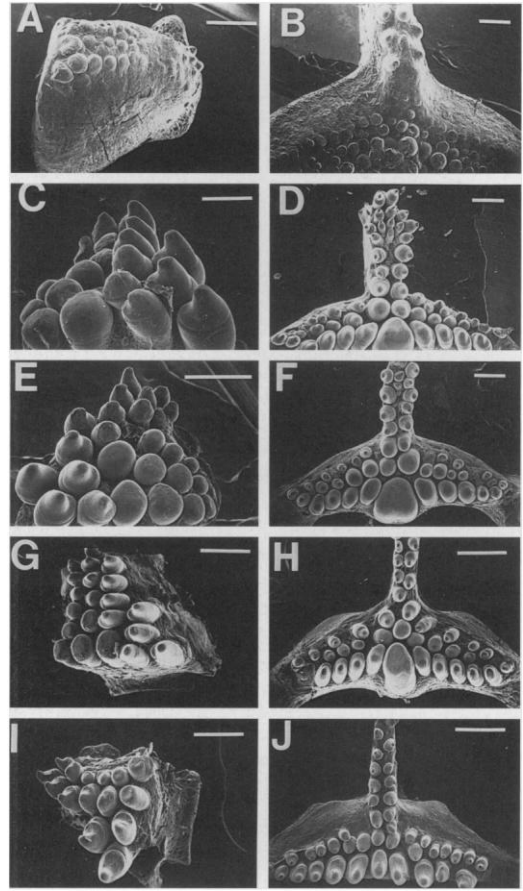


Fig. 4. Scanning electron micrographs of upper and lower pharyngeal jaws of five labrids. *Lachnolaimus maximus* (A) upper (35 \times) (B) lower (20 \times); *Halichoeres garnoti* (C) upper (35 \times) (D) lower (20 \times); *H. bivittatus* (E) upper (30 \times) (F) lower (20 \times); *H. maculipinna* (35 \times) (G) upper (H) lower; *Thalassoma bifasciatum* (35 \times) (I) upper (J) lower. Bar = 1 mm.

maining four species had significantly higher oral jaw protrusibilities, corresponding to higher scores on PC2. *Halichoeres bivittatus*, *H. maculipinna*, and *T. bifasciatum* were not significantly different from one another (OJP = 9.9%, 11.3%, and 10.5%, respectively). *Lachnolaimus maximus* (OJP = 14.1%) was significantly higher than both *H. bivittatus* and *T. bifasciatum* but not *H. maculipinna*.

Dietary analyses and feeding behavior.—A total of 26 prey categories were identified for all five species (Table 2). *Lachnolaimus maximus* consumed the largest proportion of hard prey (95.51% of diet by wet weight), followed by *H. bivittatus* (89.17%), *H. garnoti* (88.48%), *H. maculipinna* (55.36%), and *T. bifasciatum* (41.02%). A total of 17 prey taxa were consumed by *L.*

TABLE 2. PERCENT WET WEIGHT FOR 26 PREY CATEGORIES FOR FIVE LABRID SPECIES. Number indicates the percent contribution of each prey category of a sample size $n = 15$ ($n = 10$ for *Thalassoma bifasciatum*). -h after category indicates hard-shelled prey type, -s indicates soft-bodied prey type. — indicates no items in this category. * indicates items weighing <0.001 g and are not included in the richness, evenness, and diversity indices.

Prey category	Species				
	<i>L. maximus</i>	<i>H. garnoti</i>	<i>H. maculipinna</i>	<i>H. bivittatus</i>	<i>T. bifasciatum</i>
Foraminifera -s	0.70	*	0.12	*	*
Nematodes -s	*	0.08	—	*	*
Polychaetes -s	—	0.64	11.58	1.52	1.35
Total molluscs	51.55	23.45	34.24	41.51	1.48
Chitons -h	1.30	3.89	11.95	1.99	0.81
Gastropods -h	15.34	5.82	6.93	15.81	—
Limpets -h	—	—	—	0.41	—
Caecums -h	*	—	2.85	—	—
Scaphapods -h	1.74	*	0.50	*	—
Bivalves -h	9.18	11.78	12.01	23.36	0.67
Scallops -h	21.36	1.96	—	—	—
Oysters -h	2.63	—	—	—	—
Total arthropods	45.80	34.37	34.49	50.12	85.96
Pycnogonids -s	—	—	—	—	9.72
Cladocerans -s	—	—	1.30	—	—
Cypris larvae -s	—	—	0.74	—	—
Ostracods -s	0.61	—	4.89	—	—
Copepods -s	—	—	—	—	16.46
Portunid crabs -h	34.19	—	—	—	—
Unidentified crabs -h	6.83	29.00	13.38	44.20	28.74
Pagurid crabs -h	1.16	—	—	—	—
Decapod shrimps -s	1.84	0.76	5.33	2.52	—
Stomatopods -s	0.04	2.53	0.74	2.58	20.24
Tanaids -s	0.01	—	*	—	—
Cumaceans -s	0.01	—	—	—	—
Amphipods -s	—	0.04	0.06	0.70	—
Isopods -s	0.01	—	0.80	—	—
Unidentified crustaceans -s	0.65	2.04	7.25	0.12	10.80
Sipunculins -s	0.45	5.51	11.83	0.06	0.41
Total echinoderms	1.78	35.95	7.74	3.40	10.80
Ophiuroids -h	0.46	26.28	7.74	3.40	10.80
Echinoids -h	1.32	9.67	—	—	—
Larval fish -s	—	—	—	3.34	—
Seagrass -s	0.17	—	—	—	—

maximus, of which four taxa were abundant ($N_1 = 4.2$), and three of those four taxa were very abundant ($N_2 = 3.2$). Three very abundant taxa—gastropods, bivalves, and crabs—accounted for 86.76% (wet weight) of the prey items consumed. Uneven prey utilization by *L. maximus* resulted in the lowest dietary diversity ($H' = 1.44$) and a dietary evenness of 0.71.

Winnowing was the most frequently observed behavior (83.2% of 667 events) for *L. maximus* (Table 3). Another 14.1% of events were recorded as bites, and the remaining 2.7% were suction feeding. *Lachnolaimus maximus* fed al-

most exclusively on the bottom; 666 of 667 (99.9%) feeding events were observed in sand or coral rubble substrate. A single event was observed 0.1–0.5 m over the substrate.

Halichoeres bivittatus had a lower dietary richness than *L. maximus*, with 12 prey taxa. The diet was dominated by three very abundant hard-shelled prey items: crabs, gastropods, and bivalves, which accounted for 83.37% of the diet by wet weight. With three of 12 prey taxa dominating the diet, this species had the lowest dietary evenness ($E_5 = 0.67$) and a low dietary diversity ($H' = 1.60$).

TABLE 3. FEEDING BEHAVIORS OF FIVE LABRID SPECIES. Feeding events observed in 10-min periods were scored as suction (S), biting (B), or winnowing (W). Number of feeding events that occurred 0–0.1 m above six different substrates is given. — indicates behavior not observed in substrate. () indicates number of feeding events that occurred 0.1–0.5 m over substrate. Total indicates the total number of times feeding behavior occurred over all substrate types for that species.

Species (sample size)	Feeding behavior	Total	Substrate					
			Sand	Coral rubble	Hard coral	Algae	Sponge	Water column
<i>Lachnolaimus maximus</i> (n = 10)	S	18	17	1	—	—	—	—
	B	93 (1)	31	62 (1)	—	—	—	—
	W	555	342	195	1	17	—	—
<i>Halichoeres garnoti</i> (n = 12)	S	—	—	—	—	—	—	—
	B	225 (4)	17	85	5	134 (4)	13	1
	W	2	—	—	—	2	—	—
<i>Halichoeres maculipinna</i> (n = 13)	S	—	—	—	—	—	—	—
	B	40 (5)	2 (1)	10 (3)	—	27 (11)	1	—
	W	251 (3)	115 (3)	100	—	34	2	—
<i>Halichoeres bivittatus</i> (n = 11)	S	—	—	—	—	—	—	—
	B	57 (5)	15	15 (5)	—	23	4	—
	W	211	151	55	—	5	—	—
<i>Thalassoma bifasciatum</i> (n = 12)	S	— (29)	— (7)	— (22)	—	—	—	—
	B	27 (53)	—	16	1 (2)	8	—	2 (51)
	W	—	—	—	—	—	—	—

Winnowing was the most frequently observed behavior (77.3%) for *H. bivittatus*. The remaining 22.7% of events were bites. This species fed almost exclusively on the bottom, as 94.2% of the 273 feeding events scored were in sand or rubble. The remaining 5.8% of feeding events were bites that occurred in the water column.

Halichoeres garnoti, with prey representing 13 taxa, consumed slightly less hard-shelled prey (88.48%) than *H. bivittatus*. Of the six taxa that dominated the diet, five were hard-shelled (crabs, gastropods, bivalves, ophiuroids, and echinoids that comprised 82.55% of the diet); one was soft-bodied (sipunculins, 5.51%). This species was intermediate in both dietary evenness ($E_5 = 0.78$) and diversity ($H' = 1.90$).

A total of 261 feeding events were observed for *H. garnoti*. It was found to bite its prey 99.2% of the time, more than any other species. The remaining 0.8% of feeding events were winnowing. The majority of all feeding events (98.5%) occurred on the bottom, and the remaining 0.5% of feeding events were bites that occurred in the water column.

Halichoeres maculipinna consumed hard-shelled prey items (55.36% of diet) and softer-bodied items (44.64% of diet) in roughly equal proportions. Of the 17 prey types taken by this species, 11 were considered very abundant. Six of the 11 items were hard-shelled (crabs, bivalves, gastropods, ophiuroids, and chitons accounted for 52.01% of the diet), and five were

softer-bodied (sipunculins, polychaetes, decapod shrimps, ostracods, and unidentified crustaceans accounted for 40.88% of the diet). Consequently, this species had the highest dietary diversity ($H' = 2.41$) and evenness ($E_5 = 0.99$).

For *H. maculipinna*, 82.2% of the 309 feeding events were recorded as winnowing. The remaining 17.8% were bites. The majority of events (94.2%) occurred in sand or rubble, whereas 5.8% occurred in the water column.

Thalassoma bifasciatum had the lowest dietary richness, comprised of 10 prey taxa, and consumed the least hard-shelled prey (41.02% of all five species). Two of six very abundant taxa, crabs and ophiuroids, accounted for 39.54% of the diet. The four remaining very abundant taxa were softer-bodied, including stomatopods, unidentified crustaceans, copepods, and pycnogonids, which accounted for 57.22% of the diet. Although dietary richness was low, evenness was high, resulting in intermediate dietary diversity ($H' = 1.84$).

Thalassoma bifasciatum bit its prey 73.4% of the time. The remaining 26.6% of feeding events were suction feeding. In contrast to the other species, the majority of the 109 feeding events (75.2%) occurred in the water column. Of these, 35 events (32.1%) occurred 0.1–0.5 m from the substrate, 29 (26.6%) occurred 0.5–1.0 m from the substrate, and 18 events (16.5%) were observed > 1 m from the substrate. All 29

suction feeding events occurred 0.1–0.5 m from the substrate.

Horn's index of overlap indicated that *L. maximus* and *H. bivittatus* had the highest inter-specific dietary overlap (0.919) based on wet weight. Gastropods, bivalves, and crabs were consumed in nearly identical proportions by both species. When bivalves and crabs were identified beyond class, the diet of *L. maximus* was distinguished from that of *H. bivittatus* and the other species by the occurrence of such taxa as scallops, oysters, and portunid and pagurid crabs.

The *Halichoeres* species had moderate levels of overlap with one another (0.781–0.694), and *H. maculipinna* and *H. garnoti* (0.694) were most similar in diet. Crabs, bivalves, and gastropods were very abundant and were consumed in similar proportions by both species, although in smaller quantities than by *L. maximus* and *H. bivittatus*. In addition, ophiuroids and sipunculins were very abundant for both species, although they were consumed in different proportions. Both *H. garnoti* and *H. maculipinna* overlapped moderately with *L. maximus* (0.743 and 0.661, respectively), but overlap was generally lower than among congeners.

The diet of *T. bifasciatum* least resembled the other species (0.417–0.603). Although eight of its 10 prey taxa were also consumed by the *Halichoeres* species, they were taken by *T. bifasciatum* in much lower proportions. This species consumed the most soft-bodied prey, including copepods and pycnogonids, which were not taken by any other species.

Relationship of morphology to diet.—Principal components analysis indicated that *L. maximus* was morphologically distinct from the other four species, but it was similar to the *Halichoeres* congeners in diet, particularly *H. bivittatus*. In contrast, *T. bifasciatum* formed close morphological relationships with the *Halichoeres* congeners, particularly *H. maculipinna* but showed little resemblance to them in diet (Fig. 1).

Canonical correspondence analysis (CCA) indicated a low correlation between morphology and diet. The sum of the eigenvalues for all axes defined by CCA was 0.047. This is a measure of how much variation in the environmental variables (here, percent dietary composition) was explained by the species data (morphological variables). Only 4.7% of the differences in dietary composition was explained by variation in morphological variables.

Estimation of pharyngeal crushing force.—The numbers of fishes available were insufficient to

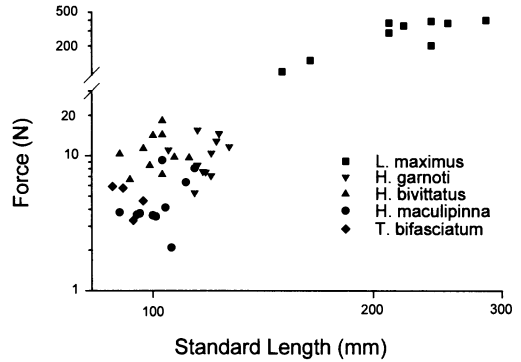


Fig. 5. $\text{Log}_{10}\text{-Log}_{10}$ plot of standard length versus estimated force generated by the pharyngeal crushing musculature for five labrids.

generate predictive regressions for estimates of force generated by pharyngeal crushing musculature, but it was possible to make generalizations about the relative force generating capabilities of each species based on the assumption that values obtained here are representative of the species. *Lachnolaimus maximus* was capable of generating significantly greater crushing forces ($\bar{x} = 290.3$ N, $\text{SD} = 116.7$, $n = 9$) than the other four species (Fig. 5). While species pairs *H. garnoti* ($\bar{x} = 10.2$ N, $\text{SD} = 3.3$, $n = 11$)–*H. bivittatus* ($\bar{x} = 11.0$ N, $\text{SD} = 3.6$, $n = 10$) and *H. maculipinna* ($\bar{x} = 4.8$ N, $\text{SD} = 2.3$, $n = 10$)–*T. bifasciatum* ($\bar{x} = 4.5$ N, $\text{SD} = 1.4$, $n = 5$) were not significantly different from each other, *H. garnoti* and *H. bivittatus* produced significantly greater crushing forces than *H. maculipinna* and *T. bifasciatum*.

Correlation of estimated crushing forces to percent hard prey in the diet produced a Pearson correlation coefficient of $r = 0.52$ ($P = 0.37$). This value was not significant because of the much higher estimated pharyngeal crushing forces generated by *L. maximus*. Excluding *L. maximus*, the correlation coefficient of $r = 0.98$ ($P = 0.03$) was significant. Correlation of estimated crushing forces to body size (SL) produced a Pearson correlation coefficient of $r = 0.96$ ($P = 0.01$). The ability to crush hard prey is directly related to body size.

DISCUSSION

A few of the morphological characters related to aspects of feeding were very good predictors of diet in the labrids examined here, whereas most were not. Variables that measured some aspect of performance, pharyngeal crushing force potential and feeding behavior, were good predictors of ecology. There was a significant

positive association between estimated pharyngeal crushing force potential and percentage of hard prey in the diet. In contrast to Wainwright (1988), we estimated pharyngeal crushing forces up to 9.3 N in individuals of *H. maculipinna*. On average, however, *H. maculipinna* and *T. bifasciatum* produced significantly lower crushing forces than *H. garnoti* and *H. bivittatus*, and this was reflected in lower percentages of hard prey in their diets. Robustness of the pharyngeal jaws and teeth were also directly related to pharyngeal crushing force potential and percentage of hard prey in the diet.

The inclusion of *L. maximus* in the correlation analysis resulted in a misleading low correlation coefficient because, although the percent hard prey in its diet is somewhat greater than two other species, the force-generating capability of its pharyngeal jaw musculature was significantly higher than all other species. This analysis did not take into account the size of the prey and the forces required to crush them. Many of the hard-shelled items taken by *L. maximus* were much larger than those taken by the other species. Correlating the force required to crush the prey to the force generating ability of all five species would likely have resulted in a significant positive association.

Similar to Wainwright (1988), we found decreased prey diversity in species with greater ability to process hard prey. *Lachnolaimus maximus*, with its large, robust pharyngeal jaws and strong crushing musculature, had the most hard prey in the diet and the lowest dietary diversity. In contrast, *H. maculipinna* and *T. bifasciatum* had the least robust pharyngeal jaws, the weakest pharyngeal jaw musculature, the least hard prey in the diet, and the highest dietary diversity. Performance tests by Wainwright (1988) indicated that *H. garnoti* and *H. bivittatus* produced greater pharyngeal crushing forces than did *H. maculipinna*. Above a pharyngeal crushing force of 3–5 N, dietary breadth of *H. garnoti* and *H. bivittatus* decreased, whereas *H. maculipinna* never reached a crushing force of 5 N, and dietary breadth increased with size. Oral jaw crushing force in the sheepshead *Archosargus probatocephalus* was found to be an important determinant of diet, and increased force production was correlated with increased durophagy (Hernandez and Motta, 1997).

In contrast to Wainwright (1988), we found a highly significant correlation between pharyngeal crushing force and body size. However, this was because all but two species were significantly different in body size (Fig. 2A), with the larger species generating greater crushing forces. Wainwright (1988) found that the *Halichoeres*

congenerics attained similar crushing strengths at different body sizes, and at any given size, *H. maculipinna* generated smaller crushing forces than either *H. garnoti* or *H. bivittatus*. Our data support this, because *H. bivittatus* and *H. maculipinna* were similar in size, but *H. bivittatus* generated significantly greater crushing forces. Body size alone largely accounts for differences in pharyngeal crushing ability and consequently, percent hard prey consumed.

Canonical correspondence analysis indicated a low correlation between the suite of oral and pharyngeal jaw characters and diet. Eigenvalues of 0.30 and higher are common in ecological studies, and ter Braak (1988) recommends that axes with low eigenvalues (≤ 0.02) be discounted. Although the eigenvalue of 0.047 obtained here is above the suggested critical value, it is substantially lower than values typically considered meaningful. Species associations indicated by PCA did not correspond to species associations based on dietary overlap. Similarly, Motta et al. (1995a) found poor correspondence between 15 morphological variables and diet in a group of seagrass fishes, with only 3% of dietary variation accounted for by morphology.

Several factors may have contributed to the low correlation between oral and pharyngeal jaw characters and diet. Identifying appropriate ecological and morphological variables remains one of the major problems in ecological morphology (Bock, 1980). Many investigators who attempted to detect ecomorphological associations between an a priori selected group of morphological variables and diet have found poor correspondence (Motta and Kotrschal, 1992). Westneat (1994), Wainwright (1988), and Hernandez and Motta (1997) emphasize that choosing biomechanically relevant characters is critical for demonstrating a link between morphology and diet. We selected variables because they were found to be appropriate for determining the influence of feeding morphology on diet by other investigators (Gatz, 1979; Kotrschal, 1989; Witte et al., 1990). For example, head length, mouth size, and tooth size and shape have been correlated to prey size. Variables quantifying dentigerous portions of the oral and pharyngeal jaws were chosen based on previous correlations between the presence and shape of jaw teeth and feeding behaviors. Although some variables in this study were correlated to feeding behavior, there was little direct correlation of oral and pharyngeal jaw variables to diet. Thus, many of the jaw morphometrics appear inappropriate for this analysis. The low correspondence may also be due to the level to which prey items were identified. If items had been pooled

into larger taxonomic groupings, overlap would likely have been higher. Likewise, if prey items had been identified to species, dietary overlap may have been substantially lower. In addition, it would have been more meaningful to organize prey in functional categories reflecting the fishes' ability to consume them. If prey had been categorized by absolute size rather than by taxonomy, mouth size variables would likely have played a significant role in PCA. Choice of fishes included in the analysis also influenced the congruence of morphology and ecology. Inclusion of more labrid species, or other labroids, might have led to different species groupings. Finally, inherent variability in morphological variables and factors such as seasonal fluctuations in diet, or the influence of behavior or phylogeny, may further confound the results.

Feeding behaviors were consistent with oral jaw morphology. Typical of many biters, *H. garnoti* had a short premaxilla ascending process, low average oral jaw protrusibility, and robust oral and pharyngeal jaws. The largest portion of hard prey consumed by this species was ophiuroids and echinoids, large prey that must be captured by biting off pieces. This species primarily used biting to procure benthic prey. *Thalassoma bifasciatum* has protrusible oral jaws, the smallest mouth, a reduced oral dentition, and small pharyngeal jaws. It captured plankton and suction fed off the benthos. *Lachnolaimus maximus*, *H. bivittatus*, and *H. maculipinna* had similar oral jaw protrusibilities, and all three were most often observed winnowing in sand and coral rubble on the bottom.

Numerous investigators have found a correlation between length of the premaxillary ascending process, feeding behavior, and diet. Length of the ascending arm of the premaxilla was related to the manner of feeding (i.e., suction feeding or biting) in *Haplochromis squamipinnis* (Witte, 1984; Witte et al., 1990), butterflyfishes (Motta, 1988), and the labrid *Epibulus insidiator* (Westneat and Wainwright, 1989). Feeding morphology and feeding behavior were related to diet in juvenile sciaenids (Chao and Musick, 1977) and in *Geophagus steindachneri* (Wimberger, 1991). Protrusion of the premaxilla has been a key element in the evolution of winnowing behavior in some surfperches (Drucker and Jensen, 1991) and carp (Sibbing et al., 1986).

Greater jaw protrusion enhances suction feeding and reduces the ability to generate powerful biting forces (Barel, 1983). Jaw protrusion has been hypothesized to increase attack velocity, thereby improving capture success (Motta, 1984; Westneat and Wainwright, 1989; Norton,

1991). Suction feeders often have a small mouth and reduced dentition (Suyehiro, 1942; Davis and Birdsong, 1973; Muller and Osse, 1984). In general, powerful biters have restricted jaw mobility (Norton, 1995), reducing their ability to generate strong suction forces. If the ability to protrude the jaws influences the types of prey these fishes are able to capture, species with similar jaw protruding abilities may be expected to have similar diets or feeding behaviors. However, there was no correlation between degree of oral jaw protrusibility and the amount of hard prey in the diet for these five species. Oral jaw protrusibility appears to be related more to where or how they feed than to the robustness of the prey. Motta et al. (1995a) also found that separation of seagrass fishes along morphological axes related more to microhabitat utilization than to dietary composition.

It has been argued that the phylogenetic relationships of species must be considered in ecomorphological studies, because species relatedness may influence the congruence of morphology and ecology among species (Felsenstein, 1985; Douglas and Matthews, 1992; Westneat, 1995). Douglas and Matthews (1992) argue that the influence of phylogeny is so great that ecological patterns should be tested against phylogenetic relationships. Species from the same phylogeny are inherently nonindependent, and this relationship will dictate a large portion of ecological similarity among species. When phylogeny is not accounted for in statistical tests that assume independence, the relationship between morphology and ecology may be overstated (Felsenstein, 1985). However, criticism has been made of studies that include distantly related species (e.g., Wiens and Rotenberry, 1980). As the species become less related, the adaptations or selection forces become too numerous and are therefore less meaningful. Patterns in morphology may be most detectable in congenics or confamilials (Findley and Black, 1983; Felley, 1984; Motta and Kotschal, 1992).

In this study, morphology, but not diet, reflected phylogenetic relatedness among species. The influence of nonindependence of species was not accounted for in statistical procedures due in part to the lack of a resolved phylogeny for these species. However, results can still be interpreted in terms of species relatedness. *Halichoeres garnoti* and *H. bivittatus* are closely related phylogenetically, are most similar in oral and pharyngeal jaw morphology, yet are divergent in feeding behavior and diet. *Thalassoma bifasciatum* is proposed to belong to the tribe Julidini along with *Halichoeres* (M. W. Westneat, pers.

comm.). It is most similar morphologically to *H. maculipinna*, yet it is most similar in diet and feeding behavior to *H. garnoti*. *Lachnolaimus maximus* is distantly related to the other four species and is morphologically distinct, yet its diet more closely resembles those of the *Hali-choeres* congeners than does *T. bifasciatum*. Feeding behavior and diet were nearly identical for *L. maximus* and *H. bivittatus*. These findings indicate interesting possibilities both about ecological divergence among closely related species and ecological convergence among distantly related species. Although it is outside the scope of this study to address these questions, the ecomorphological relationships revealed here may be attributed in part to phylogenetic relatedness.

In summary, pharyngeal jaw crushing ability and feeding behavior, both measures of some aspect of feeding performance, were good predictors of diet in this group of fishes. There was poor correspondence between oral and pharyngeal jaw variables to diet, possibly because selected variables may not be relevant to feeding in these fishes. Finally, phylogenetic relatedness among species may account, only in part, for the ecomorphological relationships identified here.

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