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Interpopulation variation in prey use and feeding biomechanics in Caribbean triggerfishes

Abstract The relationships between prey utilization and jaw biomechanics were explored in two Caribbean populations (La Parguera and Mona Island) of four trigger-fishes. The volumetric contribution of major prey types and six biomechanical features of the jaws that characterize biting strength were contrasted between populations. At Mona, *Xanthichthys ringens* ate 45% benthic organisms, whereas conspecifics at La Parguera fed exclusively on plankton. *Balistes vetula* at Mona consumed 63% soft and nonelusive invertebrates, in contrast to their La Parguera conspecifics, which consumed 62% hard prey. Differences in diet between populations were associated with differences in jaw biomechanics. *Xanthichthys* at Mona had jaw muscles, bones, and closing-lever ratios larger than those of fish at La Parguera, indicating a stronger bite. *Balistes* at Mona had 50% smaller jaw bones, muscles, and closing-lever ratios than their La Parguera conspecifics, indicating a weaker but swifter bite. *Melichthys niger* and *Cantherhines macrocerus* ate similar prey at the two locations and showed little difference in trophic anatomy. We hypothesize that the interpopulation differences in morphology are induced by the activities of feeding on different prey and enhance the feeding ability of fishes for locally dominant prey. Plasticity of the feeding mechanism may be a widespread attribute of fish feeding systems that promotes the ability of species to occupy multiple habitat types successfully.

Key words Diet · Ecomorphology · Functional morphology · Tetraodontiformes · Trophic morphology

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Introduction

Many species occupy broad geographic areas and occur in a variety of habitats. In different environments organisms may experience different resource assemblages and, in general, different challenges and selective regimes. The ability of species to respond to local conditions, through either developmental plasticity or local adaptation, may be a major factor in determining the species' distribution and overall success (Wright 1931; Via and Lande 1985; Stearns 1989). Recent interest in the adaptive role of phenotypic plasticity has highlighted the need for studies that document intraspecific variation in the relationship between resource use and morphology (Stearns 1989; Scheiner 1993; Travis 1994). Many studies have demonstrated intraspecific variation in either resource use or morphology, but fewer papers have related these two factors in attempts to understand how organisms respond to local conditions (e.g., Schlichting 1986; Williams and Moore 1989; Meyer 1990).

Among vertebrates, freshwater fishes have provided some of the clearest cases in which intraspecific variation in resource use, primarily food, is associated with morphological variation (see, e.g., Lindsey 1981; Lavin and McPhail 1986; Skulason et al. 1989; Ehlinger 1990; Meyer 1990; Mittelbach et al. 1992), but only a handful of studies have elucidated the specific role of morphological variation in enhancing fish feeding ability (Meyer 1989; Osenberg et al. 1992). Our ability to relate morphology to behavioral performance and to identify specific feedback mechanisms that may underlie plasticity or selection depends on (1) our understanding of the biomechanics and functional morphology of fish feeding mechanisms and (2) knowledge of mechanisms of phenotypic plasticity in musculoskeletal systems. Thus, understanding the mechanical or performance consequences of morphological differences is crucial to interpretations of intraspecific morphological variation.

In this study we explore patterns of food use and trophic morphology in four coral-reef fish species at two Caribbean locations. Our aim is to ask (1) whether dif-

ferent populations of each species eat different prey and (2) if so, whether feeding habits are associated with morphological variation that can be interpreted as contributing to the dietary differences. Rather than directly measuring feeding performance in this study, we focus on morphological variables that have clear functional significance in feeding, so that any differences we find between populations can be directly related to feeding performance.

Matrials and methods

Diet and morphology

Four Caribbean species of the Balistoidea (order Tetraodontiformes) were investigated: queen triggerfish (*Balistes vetula*), black durgon (*Melichthys niger*), sargassum triggerfish (*Xanthichthys ringens*), and white-spotted filefish (*Cantherhines macrocerus*). Comparisons were made between fish collected from two locations. Fishes at La Parguera, along the southwest coast of Puerto Rico, inhabited fringing coral reefs from 7 to 40 m depth. Fishes at Mona Island, between Puerto Rico and Hispanola, inhabited a narrow fringing reef from 2 to 10 m depth.

Fishes were collected by spear beginning 4 h after the onset of their diurnal feeding activities. The gastrointestinal tract was removed from each fish and, together with the fish, was fixed in 10% formalin and stored in 75% ethanol. For each species, ten specimens from each population that spanned approximately the same range of standard length were selected for analysis. The single exception was *Balistes*, which showed a strikingly different size distribution at the two sites, probably due to heavier fishing pressure at La Parguera. Gut contents were classified into broad prey categories based on the presumed functional demands prey impose upon their predators, and the volumetric contribution of each category was estimated (see Turingan 1994 for details of this method).

These balistoid fishes provide a particularly good system for studies of intraspecific variation in design of the feeding system because each species eats prey that are captured by either suction feeding or direct biting. Suction-feeding fishes employ a rapid strike with a premium on speed of mouth opening, buccal expansion, and subsequent mouth closing (Barel 1983; Norton 1991). In contrast, fishes that directly bite hard sessile prey rely on their ability to exert a strong bite, rather than a rapid one (Wainwright and Richard 1995). Many design features of the jaw apparatus that enhance one of these feeding modes will either decrease the ability to use the other mode or will not influence the other mode. In this study, we selected six morphological characteristics (1) that represent biomechanical properties of the feeding mechanism that underlie feeding ability and (2) that contrast the functional attributes associated with performance in suction feeding and biting. These variables are mass of the upper-jaw adductor muscle, mass of lower-jaw adductor muscle, mass of the upper jaw bone (fused premaxilla and maxilla), mass of the lower jaw bone, jaw-opening lever ratio, and jaw-closing lever ratio. The morphology of these measurements is indicated in Fig. 1, and their consequences for aspects of feeding performance are summarized in Fig. 2. Muscle and bone masses were measured to the nearest milligram after excess moisture was removed with paper towels. All measurements were made from the left side of the head of each fish.

The adductor mandibulae muscles of balistoids have various configurations and subdivisions (Winterbottom 1974). The upper-jaw adductor muscle consists of all subdivisions of the adductor mandibulae that insert on the upper jaw, and the lower-jaw adductor muscle consists of all subdivisions that insert on the lower jaw (Fig. 1; see also Turingan 1994). We measured muscle mass as an indicator of the relative force-producing capacity of the upper- and lower-jaw adductor muscles (Fig. 2A). Adductor mandibulae muscle mass can influence feeding performance (i.e. biting strength)
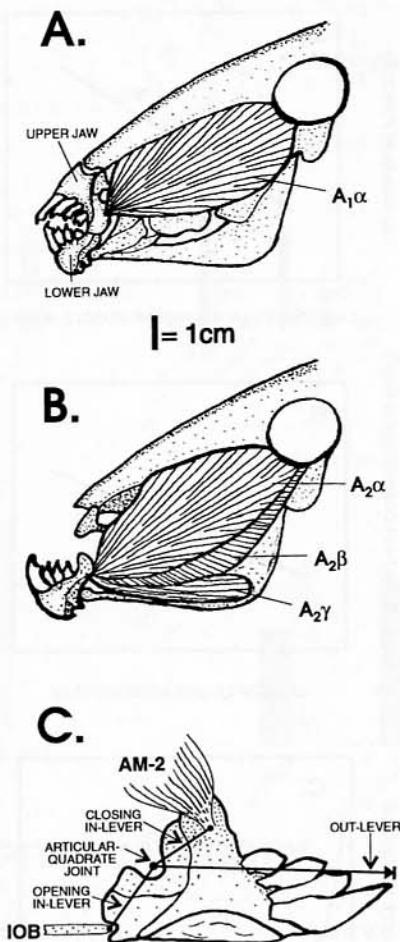

Fig. 1 Lateral-view diagrams of a representative triggerfish skull illustrating the superficial subdivisions of the **A** upper-jaw adductor muscles, **B** lower-jaw adductor muscles, and **C** the points of measurement for the jaw lever arms ($A1\alpha$ subdivision of the upper-jaw adductor muscle, $A2\alpha$, $A2\beta$ and $A2\gamma$ subdivisions of the lower-jaw adductor muscle, AM-2 lower-jaw adductor muscle, IOB = interopercle bone)

because the maximum force a muscle can generate increases with the 2/3 power of muscle mass (Calow and Alexander 1973; Powell et al. 1984). Thus, as long as internal organization of the muscle is the same in the two populations studied here, an individual with a larger adductor mandibulae muscle will have a stronger bite than one with a smaller muscle.

We measured bone mass as an indicator of the relative compressive strength of oral jaw bones [Fig. 2B; see Currey 1984 for other mechanical properties of bone (tensile, shearing, torsion, or bending)]. Bones must resist the forces exerted on them by contracting muscles, and a heavier bone, given a constant general design, can be expected to have greater strength (Herring 1993). It is difficult to generalize about the net gain in compressive strength per unit of increase in bone mass, but an overall positive relationship between bone strength and bone mass has been observed repeatedly in vertebrates (see citations in Currey 1984).

The mechanical lever ratios (i.e. in-lever length divided by out-lever length) for jaw opening and closing were measured for each fish (Fig. 1C). The distance from the mid-point of the articular-quadrate joint to the mid-point of the interopercle-angular joint was used as the in-lever for jaw opening. The jaw-closing in-lever was measured as the distance between the mid-point of the articular-quadrate joint and the insertion site of the lower-jaw adductor muscle. The out-lever for both jaw opening and jaw closing was
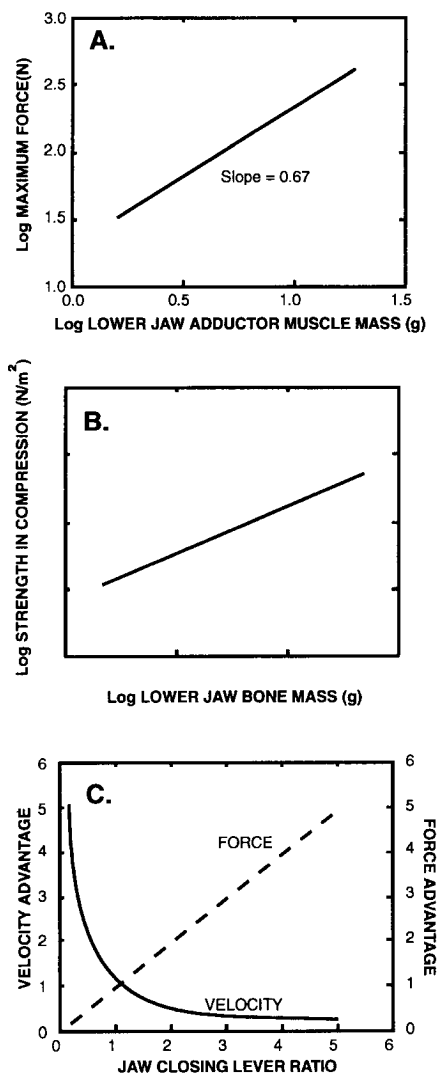
Fig. 2A–C Plots of the relationships between three of the morphological variables measured in this study and the mechanical quantities they represent. **A** Maximum contractile tension, given a constant internal design of the muscle, scales to the 2/3 power of muscle mass. Maximum contractile force of jaw-adductor muscle is the primary determinant of oral-jaw biting strength. **B** The compressive strength of bone generally increases with increasing bone mass, assuming a constant bone design. Increases in lower-jaw bone mass indicate greater strength of the jaw in resisting the forces generated during biting activities. **C** The lever ratio of the jaw-closing system has inverse affects on the velocity and force transmission of the jaw-closing musculature. The jaw-closing lever ratio produces a mechanical trade-off between the strength and speed of the oral-jaw bite. See Materials and methods for further details

measured as the distance between the mid-point of the articular-quadrate joint and the tip of the anterior most tooth.

The lower-jaw lever system involves a direct trade-off between the transmission of force from the adductor muscles to the jaws and the transmission of muscle-shortening speed to movements at the jaw tip (Barel 1983; Wainwright and Richard 1995; Westneat 1995). As the jaw-closing lever ratio increases (Figs. 1C and 2C), the force exerted by the jaw adductor muscles is amplified at the tooth row, resulting in a stronger bite. However, as biting force increases with an increasing jaw-closing lever ratio, the velocity of

jaw movement is decreased (Fig. 2C), so a jaw-lever system that maximizes biting force will minimize the speed of jaw movement (Fig. 2C). In contrast, a jaw-lever system that maximizes jaw-closing velocity will minimize biting force. A high jaw-closing lever ratio confers a strong bite, which is a performance feature of fishes that eat hard, benthic prey (Lauder 1983; Wainwright 1988; Turingan 1994). Low jaw-closing and opening lever ratios confer a relatively rapid strike and have been noted in fishes that use suction feeding to capture soft, mobile prey (Wainwright and Richard 1994; Westneat 1994).

Data analysis

We compared the arcsine-transformed volumetric contributions of major prey categories in the two populations of each species using overall MANOVAs followed by ANOVAs for the individual prey categories. We tested the prediction that diet influenced jaw biomechanics by comparing the values of the six biomechanical variables in the two populations of each balistoid species. The logarithms of muscle and bone masses were positively correlated with the logarithm of fish standard length, so, to control for the effect of fish size on these variables, we compared the adjusted means by ANCOVA, using standard length as the covariate. Lower-jaw opening and closing lever ratios did not vary with standard length, so the means were compared by ANOVA. We report the ratios of adjusted means (in the case of ANCOVAs) or means (in the case of ANOVAs) to indicate the magnitude of the differences between populations in each morphological variable.

Results

Food habits

Triggerfishes consume a variety of prey organisms (Fig. 3). *Xanthichthys* and *Balistes* showed significant interpopulation differences in the volumetric contributions of several prey (Table 1). *Melichthys* showed slight but significant diet differences between La Parguera and Mona, but the diet of *Cantherhines* did not exhibit significant interpopulation variation.

Xanthichthys at La Parguera was strictly planktivorous. About 86% of its diet consisted of plankton (mostly copepods and invertebrate larvae, Fig. 3). The fully digested animal remains (14% of the gut contents) that were not included in the analysis were probably also planktonic. Planktonic prey move freely in the water column, and our observations of feeding fishes revealed that *Xanthichthys* employs suction feeding to capture them. In contrast, about half of the prey consumed by *Xanthichthys* at Mona were attached, benthic organisms (3% sponge, 12% sand/hard coral, and 28% benthic and coraline algae), so *Xanthichthys* at Mona must employ biting to snip off pieces of their benthic prey in addition to suction feeding on plankton.

Balistes consumed more prey types than the other species included in this study (Fig. 3). Six of the eight prey categories differed (at $P = 0.05$) between populations (Table 1). More than half (63%) of the food consumed by the Mona population consisted of soft, infaunal holothuroids and polychaetes. In contrast, over half (62%) of the diet of the La Parguera population consisted of hard-shelled organisms (35% echinoids, 10% deca-

Fig. 3 Volumetric contribution of each prey category found in the gastrointestinal tracts of four balistoid species at La Parguera and Mona Island. Data represent average percentages. *Error bar* represents SEM. Sample size = 10 for each population
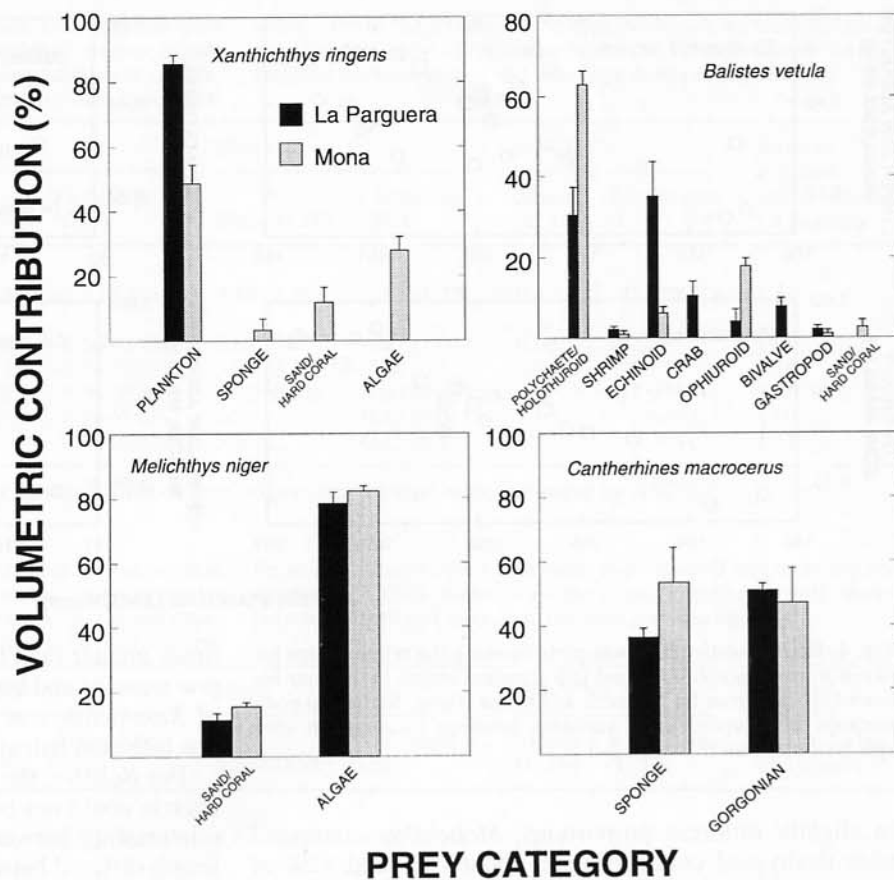

Table 1 Univariate and multivariate statistics comparing diet of La Parguera and Mona Island populations of four Caribbean balistoid fishes. Sample size was 10 individuals per population.

	ANOVA		MANOVA		
	$F(1,18)$	P	Wilks' λ	F (df)	P
Xanthichthys ringens			0.137	23.7 (4, 15)	0.000
Plankton	40.491	0.000			
Sponge	1.000	0.333			
Sand/hard coral	6.065	0.024			
Algae	41.638	0.000			
Balistes vetula			0.200	6.0 (8, 11)	0.006
Polychaete/holothuroid	16.098	0.001			
Shrimp	1.025	0.325			
Echinoid	6.520	0.020			
Crab	8.201	0.010			
Ophiuroid	14.151	0.001			
Bivalve	13.753	0.001			
Gastropod	0.822	0.376			
Sand/hard coral	2.157	0.159			
Melichthys niger			0.568	6.5 (2,17)	0.008
Sand/hard coral	2.846	0.109			
Algae	0.839	0.372			
Cantherhines macrocerus			0.7199	3.3 (2,17)	0.061
Sponge	2.874	0.107			
Gorgonian	0.093	0.764			

pods, 4% ophiuroids, 2% gastropods, 8% bivalves, and 3% sand/hard coral). We observed Balistes exposing buried prey by blowing on sandy substrates, suction-feeding on the exposed infaunal invertebrates, and directly biting sea urchins and molluscs.

The two populations of the remaining balistoid fishes fed on the same prey organisms (Fig. 3; Table 1). Although MANOVA revealed that the diets of *Melichthys* at the two study sites differed significantly, this species consumed the same prey types at the two locations, but
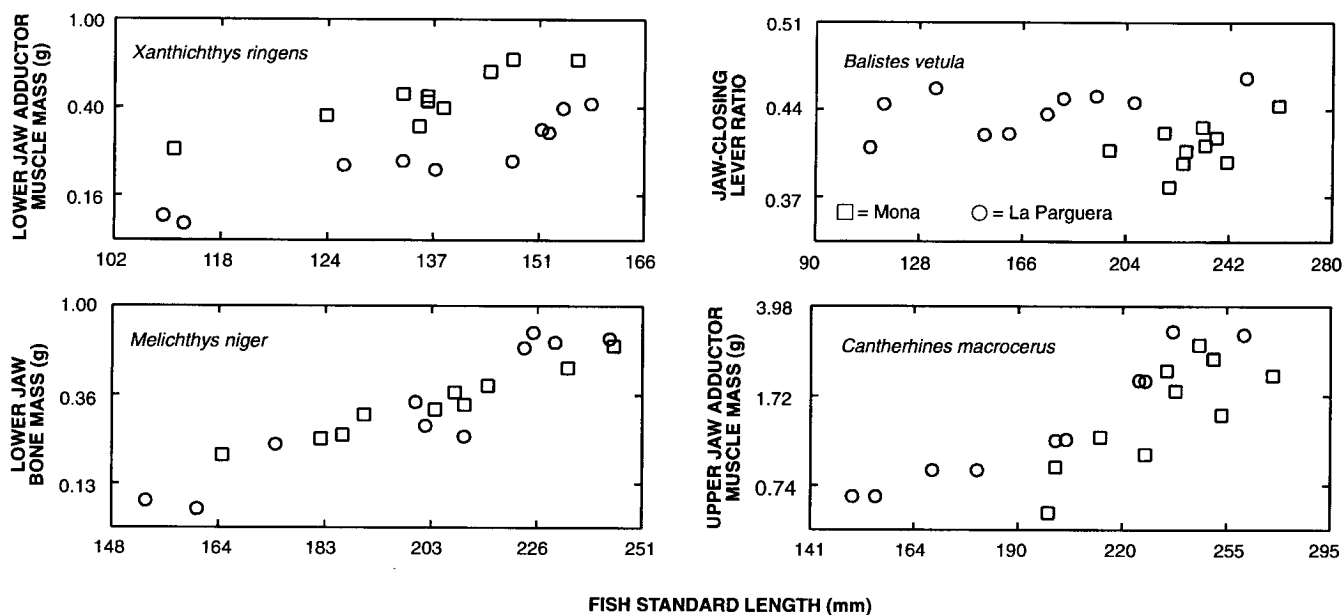
Fig. 4 Representative bivariate plots showing the relationships between trophic morphology and fish standard length in the four balistoid species from La Parguera and Mona Island. Statistical comparisons of morphological variables between locations in each species are shown in Tables 2–5

in slightly different proportions. *Melichthys* consumed both fleshy and coraline algae; about 78% and 82% of the diet at La Parguera and Mona, respectively. A considerable portion of the gut contents of this species (La Parguera, 11%; Mona, 15%) consisted of pieces of hard coral and sand. No direct observations of this fish feeding in the field or in captivity have been published, and we were unable to observe *Melichthys* feeding in this study, but the presence of bite-size benthic algae and pieces of dead hard corals in the guts of individuals we examined indicates that *Melichthys*, at least occasionally, directly bites or scrapes algae from the substratum. The diets of *Cantherhines* did not differ significantly between sites (Table 1, Fig. 3). Pieces of sponge (La Parguera, 37%; Mona, 53%) and gorgonians (La Parguera, 51%; Mona, 47%) were the major food of *Cantherhines*. We observed this filefish biting off pieces of its benthic prey.

Trophic morphology

The two species that showed considerable interpopulation differences in diet, *Xanthichthys* and *Balistes*, also exhibited major differences in trophic morphology (Fig. 4; Tables 2–5). The sizes of the jaw adductor muscles and jaw bones differed between populations of *Xanthichthys* (Table 2; Fig. 4). The ratios of adjusted means indicate that *Xanthichthys* at Mona had jaw muscles and bones that were 1.2–1.9 times more massive than fish at La Parguera. Of the two lever ratios, only the jaw-closing lever ratio differed between populations. The jaw-closing lever ratio of *Xanthichthys* at Mona was 1.11

times greater than that of fish at La Parguera. The larger jaw muscles and bones and higher jaw-closing lever ratio of *Xanthichthys* at Mona indicate that it has a stronger jaw bite than fish at La Parguera.

For *Balistes*, the mean mass of the upper jaw adductor muscle could not be compared because the slopes of the relationship between this variable and fish standard length differed between populations (Table 3). *Balistes* at Mona, which fed mostly on soft, nonelusive prey, had significantly smaller lower-jaw adductor muscle and smaller upper- and lower-jaw bones than fish at La Parguera, which fed mostly on hard prey (Table 3). The jaw-closing lever ratio for fish at Mona was also smaller than that for fish at La Parguera, but no difference was detected in the jaw-opening lever ratio. Thus, relative to fish at Mona, *Balistes* at La Parguera had larger jaw bones and muscles and higher jaw-closing lever ratio, features that enhance biting strength.

Melichthys and *Cantherhines* showed few interpopulation differences in trophic morphology. Of the six morphological variables compared, two for *Melichthys* and one for *Cantherhines* showed differences between Mona and La Parguera populations (Tables 4 and 5; Fig. 4). In both species, the upper-jaw adductor-muscle mass was about 30% smaller for fish at Mona. Because there is no large difference in diet between populations of these species, the observed variation in upper-jaw adductor-muscle mass may not be related to their feeding habits.

Discussion

Triggerfishes at La Parguera and Mona differed in patterns of prey use and associated trophic morphology. To our knowledge, this study is the first demonstration of a link between patterns of prey use and trophic morphology between populations of marine fishes. Populations of *Xanthichthys* and *Balistes* that capture and process hard,

Table 2 Regression and ANCOVA statistics for morphological features of the sargassum triggerfish, *Xanthichthys ringens*, in two populations, La Parguera and Mona; *n*=10 individuals per population. Regression and ANCOVA statistics for the four mass vari-ables refer to $\log_{10}$-transformed data, with fish standard length as the covariate. ANCOVA statistics are the F-ratios testing for differences between slopes and intercepts between populations

| | La Paguera | | Mona | | ANCOVA | | Ratio of adjusted, means, Mona/ La Paguera |
	Slope (±SE)	Y intercept (±SE)	Slope (±SE)	Y intercept (±SE)	Slopes (1, 16)	Y intercepts (1, 17)	
Adductor mandibulae muscle, section 1 mass (g)	2.52 (0.19)	−5.9 (0.40)	2.88 (0.59)	−6.39 (1.23)	0.4	73.3**	1.67
Adductor mandibulae muscle, section 2 mass (g)	2.83 (0.34)	−6.66 (0.73)	2.69 (0.49)	−6.07 (1.04)	0.06	102.5**	1.90
Upper-jaw mass (g)	3.05 (0.13)	−7.58 (0.27)	3.04 (0.24)	−7.50 (0.52)	0.01	38.1**	1.19
Lower-jaw mass (g)	2.36 (0.68)	−6.35 (1.45)	3.22 (0.32)	−7.94 (0.68)	1.0	37.9**	1.80
Jaw-opening lever ratio	NS	0.29 (0.01)	NS	0.32 (0.01)	−	1.64	1.07
Jaw-closing lever ratio	NS	0.32 (0.01)	NS	0.35 (0.1)	−	5.39*	1.11

* *P*<0.05; ** *P*<0.01 Jaw lever ratios did not change with body size, so population means were compared by ANOVA

Table 3 Regression and ANCOVA statistics for morphological features of the queen triggerfish, Balistes vetula, in two populations, La Parguera and Mona; *N*=10 individuals per population. Regression and ANCOVA statistics for the four mass variables re-fer to $\log_{10}$-transformed data, with fish standard length as the co-variate. ANCOVA statistics are the F-ratios testing for differences between slopes and intercepts between populations

| | La Paguera | | Mona | | ANCOVA | | Ratio of adjusted means, Mona/ La Paguera |
	Slope (±SE)	Y intercept (±SE)	Slope (±SE)	Y intercept (±SE)	Slopes (1, 16)	Y intercepts (1, 17)	
Adductor mandibulae muscle, section 1 mass (g)	2.74 (0.08)	−6.03 (0.18)	3.84 (0.42)	−8.69 (0.98)	8.51*	−	−
Adductor mandibulae muscle, section 2 mass (g)	2.45 (0.08)	−5.26 (0.40)	3.56 (0.46)	−7.97 (1.10)	3.61	10.2**	0.78
Upper-jaw mass (g)	3.28 (0.24)	−7.68 (0.52)	3.08 (0.26)	−7.40 (0.61)	0.09	27.2**	0.66
Lower-jaw mass (g)	2.78 (0.08)	−6.67 (0.17)	3.19 (0.32)	−7.77 (0.74)	1.75	60.1**	0.73
Jaw-opening lever ratio	NS	0.30 (0.01)	NS	0.29 (0.01)	−	0.60	0.98
Jaw-closing lever ratio	NS	0.44 (0.01)	NS	0.41 (0.01)	−	13.2**	0.94

* *P*<0.05; ** *P*<0.01 Jaw lever ratios did not change with body size, so population means were compared by ANOVA

Table 4 Regression and ANCOVA statistics for morphological features of the black durgon, Melichthys niger, in two populations, La Parguera and Mona; *N*=10 individuals per population. Regression and ANCOVA statistics for the four mass variables refer to $\log_{10}$-transformed data, with fish standard length as the covariate. ANCOVA statistics are the F-ratios testing for differences between slopes and intercepts between populations

| | La Paguera | | Mona | | ANCOVA | | Ratio of adjusted means, Mona/ La Paguera |
	Slope (±SE)	Y intercept (±SE)	Slope (±SE)	Y intercept (±SE)	Slopes (1, 16)	Y intercepts (1, 17)	
Adductor mandibulae muscle, section 1 mass (g)	3.32 (0.58)	−7.34 (1.33)	2.58 (0.30)	−5.80 (0.69)	1.02	15.0**	0.70
Adductor mandibulae muscle, section 2 mass (g)	3.18 (0.34)	−7.19 (0.79)	2.51 (0.43)	−5.67 (1.00)	1.46	1.1	0.93
Upper-jaw mass (g)	3.75 (0.38)	−8.97 (0.87)	2.95 (0.22)	−7.26 (0.50)	2.71	24.4**	0.73
Lower-jaw mass (g)	4.51 (0.59)	−10.86 (1.36)	3.18 (0.23)	−7.81 (0.53)	3.34	0.01	0.99
Jaw-opening lever ratio	NS	0.30 (0.003)	NS	0.30 (0.006)	−	0.07	1.00
Jaw-closing lever ratio	NS	0.52 (0.01)	NS	0.51 (0.01)	−	0.97	0.98

* *P*<0.05; ** *P*<0.01 Jaw lever ratios did not change with body size, so population means were compared by ANOVA

benthic prey by biting possessed more massive jaw-adductor muscles and bones and higher jaw-closing lever ratios than populations that suction feed on planktonic or soft prey. *Xanthichthys* ate harder prey at Mona, and *Balistes* consumed harder prey at La Parguera, so location did not have a consistent effect on diet, strengthening the interpretation of a functional link between feeding habits and morphology.

Melichthys and *Cantherhines* showed fewer interpopulation differences in diet and morphology. In both spe-

Table 5 Regression and ANCOVA statistics for morphological features of the white-spotted filefish, Cantherhines macrocerus, in two populations, La Parguera and Mona; $N=10$ individuals per population. Regression and ANCOVA statistics for the four mass variables refer to $\log_{10}$-transformed data, with fish standard length as the covariate. ANCOVA statistics are the F-ratios testing for differences between slopes and intercepts between populations

	La Paguera		Mona		ANCOVA		Ratio of adjusted means, Mona/ La Paguera
	Slope (±SE)	Y intercept (±SE)	Slope (±SE)	Y intercept (±SE)	Slopes (1, 16)	Y intercepts (1, 17)	
Adductor mandibulae muscle, section 1 mass (g)	3.01 (0.31)	−6.79 (0.71)	3.99 (1.01)	−9.27 (2.38)	1.11	10.2**	0.66
Adductor mandibulae muscle, section 2 mass (g)	3.14 (0.36)	−6.89 (0.82)	4.41 (0.46)	−9.92 (1.08)	3.95	0.9	0.91
Upper-jaw mass (g)	3.10 (0.53)	−7.42 (1.22)	3.03 (0.4)	−7.31 (0.85)	0.01	0.2	0.88
Lower-jaw mass (g)	3.15 (0.40)	−7.80 (0.91)	3.18 (0.23)	−7.81 (0.53)	0.05	1.8	1.01
Jaw-opening lever ratio	NS	0.27 (0.01)	NS	0.27 (0.01)	–	0.01	1.00
Jaw-closing lever ratio	NS	0.49 (0.01)	NS	0.50 (0.01)	–	0.23	1.01

* $P<0.05$; ** $P<0.01$ Jaw lever ratios did not change with body size, so population means were compared by ANOVA

cies, only features of the upper jaws differed between populations. Our diet analysis revealed minor but significant differences between populations of *Melichthys* and no differences for *Cantherhines*. *Melichthys* at Mona ate slightly greater proportions of algae than fish at La Parguera, but we would not expect this minor difference (82% vs. 78%) to be manifested in key morphological features. It appears that the upper-jaw characteristics we measured are not as important as the other features of the oral jaw system in constraining the hardness of prey that these fishes are capable of capturing and processing. Thus, we found no evidence that the observed morphological differences between populations of *Melichthys* and *Cantherhines* were related to patterns of prey use.

Several factors could underlie patterns of prey use in fishes, for example (1) prey availability, (2) prey-capture abilities, (3) predator-prey energetics, (4) inter- and intraspecific competition, and (5) the threat of predation. We consider it likely that the Mona and La Parguera sites represent different ecological conditions and induced two of the species, through some combination of the above mechanisms, to eat different prey at the two locations. Below, we discuss the possible causes of the inter-population differences in feeding biomechanics and diet.

Genetic differentiation or phenotypic plasticity?

Two processes that could potentially cause differences in trophic morphology between populations of Caribbean triggerfishes are (1) genetic divergence between populations due to local adaptation or genetic drift and (2) developmental plasticity induced by environmental differences. The most direct way to assess the relative roles of these two factors would be through a reciprocal transplant experiment in which young from parents at both locations were raised under dietary treatments that match the two locations. Variation in the resulting trophic morphology could then be partitioned between effects of diet and those of the genetic stock the individuals came from. We currently lack specific tests of these two factors and

therefore cannot say with certainty what role each factor played in shaping the morphological differences we observed, but available information leads us to suspect that environmental differences between populations and developmental plasticity are the major forces underlying the dietary and morphological differences.

The morphological differences we observed between populations of *Xanthichthys* and *Balistes* might have been induced by feeding on different prey types. Both bone (Wolff 1892; Currey 1984; Lanyon and Rubin 1985) and muscle (Goldspink and Howells 1974) are well known to remodel in response to patterns of dynamic loading during development. Responses to heavier loads include increased muscle and bone mass (Moore 1965; Bouvier and Hylander 1981; Smith 1981; Beecher et al. 1983; Goldspink 1983). Eating prey that require a more forceful bite during capture and processing imposes a loading regime on jaw adductor muscles and bones that could induce increases in the sizes of these structures. Eating hard prey like echinoids and chitons, in the case of La Parguera *Balistes*, and coraline algae and sponges, in the case of Mona *Xanthichthys*, probably increased the stress that jaw adductor muscles and bones experienced, inducing these structures to undergo hypertrophy. In some freshwater fishes, different food types have been demonstrated to induce changes in feeding-related morphological characters, although most of these changes have been in patterns of body shape (Greenwood 1965; Lavin and McPhail 1986; Meyer 1987, 1989; Wimberger 1991). Wainwright et al. (1991), Mittelbach et al. (1992), and Robinson et al. (1993) demonstrated a strong correlation between the amount of gastropods consumed and the mass of crushing muscles and jaw bones in pumpkinseed sunfish.

It is less clear how the differences in lever ratios might arise in direct response to prey-induced loading regime. We are unaware of studies that have demonstrated plasticity in the sites of insertion of muscles or the lengths of lever arms in response to different loading regimes, but previous comparative work has shown that jaw levers have changed during the evolution of fishes,

often matching changes in feeding habits (Wainwright and Richard 1995; Westneat 1995). Further work will be needed to evaluate the plasticity of jaw lever arms directly and to elucidate the physical feedback mechanism that induces any plasticity.

Consequences of morphological variation

The extent to which trophic morphological characters reflect feeding performance of fishes is a crucial issue in studies that examine relationships between anatomy and patterns of prey use (e.g., Gatz 1979; Ehlinger 1990; Winemiller 1991). We suggest that our ability to interpret the ecological consequences of morphological differences between populations and species is only as good as our ability to interpret the consequences of morphological variation for behavioral performance. Morphological variables with a clear functional interpretation are the most likely to be useful in attempts to understand the matching of organismal design to patterns of resource use (e.g., Karr and James 1975; Wheelwright 1985; Robinson et al. 1993; Ricklefs and Miles 1994). Here, we focused on morphological characteristics that are mechanically linked to key aspects of feeding performance (see Materials and methods): (1) muscle mass is directly related to force-producing capacity in the adductor mandibulae muscles, (2) bone mass is positively related to the compressive strength of the upper and lower jaws, and (3) jaw-lever ratios reflect the trade-off between strength of the bite and speed of jaw movement.

Regardless of what causes the interpopulation difference in morphology observed in this study, the expected consequences of the differences are clear. Within each species, populations with more massive jaw bones and adductor muscles and higher jaw-closing lever ratios will, all else being equal, have a stronger bite. A stronger bite increases the range of hard, benthic prey that can potentially be consumed. Biting strength in fishes that consume hard prey has been shown to play a central role in shaping feeding performance and patterns of prey use during ontogeny (Hoogerhoud 1986; Wainwright 1987; Osenberg and Mittelbach 1989) and between species (Wainwright 1988). Thus, the increased biting strength of Xanthichthys and Balistes populations that feed on hard, benthic prey probably gives those fishes a greater ability to handle tougher prey than fish in populations with more gracile jaws. In contrast, populations of the same species that have thinner jaw bones and muscles and lower jaw-closing lever ratios rely on a less forceful but swifter jaw-closing action, possibly advantageous for suction-feeding on mid-water plankton and other soft prey.

Interestingly, two components of the jaw apparatus did not reflect differences in diet: the jaw-opening lever ratio and upper-jaw adductor-muscle mass. The jaw-opening lever ratio did not differ between populations of any of the four species, suggesting that this variable was not influenced by the same factors that shaped interpopulation differences in the other variables. Upper-jaw adductor-muscle mass differed between populations in all four species, implying that the difference was not necessarily linked to the differences in feeding habits. Because both Melichthys and Cantherhines showed minimal or no differences between populations in diet, variation in this muscle mass may be related to some unmeasured aspects of the biology of these fishes. Even the two species whose diet differed between populations (Xanthichthys and Balistes) showed that the population effect on the upper-jaw adductor mass was not as great as that in the other variables. Thus, in the populations studied here, the jaw-opening lever ratio and the upper-jaw adductor-muscle mass are not tightly coupled to patterns of prey use. It is noteworthy that interspecific comparative analyses have also found that these two variables are not as strongly indicative of diet as the other four we measured (Turingan 1994; Wainwright and Richard 1995).

Variation among populations in feeding habits may be fairly widespread in fishes, but intraspecific variation in feeding habits and trophic morphology have received almost no attention in studies of coral-reef fishes. Thus, the extent to which the substantial interpopulation differences observed in this study are typical will have to await future research. Adaptive phenotypic plasticity is potentially a major factor in the evolution of trophic relationships in animals, and studies of the relationship between resource use and trophic morphology offer an initial, descriptive step toward understanding the role of plasticity in natural systems.

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