

## RELATIONSHIP BETWEEN DUROPHAGY AND FEEDING BIOMECHANICS IN GRAY TRIGGERFISH, *BALISTES CAPRISCUS*: INTRASPECIFIC VARIATION IN ECOLOGICAL MORPHOLOGY

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**ABSTRACT:** *The relationship between oral jaw biomechanics and consumption of hard prey was compared between Gulf of Mexico (Gulf) and Atlantic Ocean (Atlantic) populations of gray triggerfish (Balistes capriscus) to examine intraspecific ecomorphological variation between these fish. Gut content analysis revealed that Atlantic fish fed more on hard-shelled invertebrates, such as crabs and sea urchins, than Gulf conspecifics. Difference in the relative magnitude of durophagy between Gulf and Atlantic triggerfish was associated with intraspecific differences in key biomechanical properties of the prey-capture and processing mechanism. The more durophagous Atlantic B. capriscus had more massive jaw bones and muscles than Gulf fish. The mechanical advantage of the lower jaw appeared to be less reflective of the dietary differences between fish from both locations. We hypothesize that B. capriscus has the ability to alter the development of its feeding mechanism to match the requirements for capturing and processing locally available prey-resources at post-recruitment habitats in the Atlantic and Gulf coasts of Florida.*

THE central theme of ecomorphological studies is understanding the functional-ecological relationship between an organism and its environment. In fishes, previous studies have shown that the constructional design of feeding mechanisms constrain the diversity of prey that can be consumed because the functional morphology of the feeding mechanism underlies the ability of fishes to capture and process prey (Liem, 1991; Turingan and Wainwright, 1993). Key features of the feeding apparatus, such as oral-jaw gape (Hoyle and Keast, 1988), pharyngeal-jaw gape (Wainwright, 1988), pharyngeal-jaw crushing strength (Wainwright, 1987, 1988), and oral-jaw crushing strength (Turingan, 1994; Hernandez and Motta, 1997) have been shown to reflect the size, hardness and elusiveness of prey consumed by fishes. However, most studies that attempted to relate functional morphology to ecology were conducted at the interspecific level of analysis. We know very little about the extent to which within-species variation in ecomorphology exists.

Many species of marine-coastal fishes inhabit a variety of post-recruit-

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ment habitats. Although conspecific fish collected from different locations have been shown to exhibit different food habits, the association between intraspecific differences in prey consumption and intraspecific differences in feeding biomechanics has not been thoroughly investigated. Previous experimental studies on lacustrine fishes (e.g., cichlids [Meyer, 1990] and centrarchids [Mittelbach et al., 1999]) have demonstrated that phenotypic-developmental plasticity underlies diet-induced changes in feeding morphology. A recently concluded study on the effects of two contrasting diets on the development of feeding biomechanics in sheepshead (*Archosargus probatocephalus*) from Florida is the first known experimental study on a marine-coastal fish species that demonstrated a similar diet-induced phenotypic plasticity (M. Fougerolle, unpublished MS thesis). In this study, we examined two populations of gray triggerfish (*Balistes capriscus*) located in the Atlantic Ocean and the Gulf of Mexico. In general, *B. capriscus* has a durophagous feeding habit, consuming hard-shelled invertebrates such as barnacles and sea urchins (Vose, 1990; Vose and Nelson, 1994). It has also been shown that *B. capriscus* is an opportunistic feeder, having the ability to switch between soft prey (e.g., polychaetes) and hard prey (e.g., crabs and barnacles) depending on the relative abundance of these prey organisms in different locations (Frazer et al., 1991; Vose and Nelson, 1994). This study addresses two specific questions: (1) Is there a difference in the relative consumption of hard prey (durophagy) between Atlantic and Gulf populations of *B. capriscus*? (2) If so, is intraspecific variation in durophagy associated with intraspecific difference in feeding biomechanics?

**MATERIALS AND METHODS**—Representative Atlantic Ocean *B. capriscus* were collected off the coast of Cape Canaveral, Florida (28°32'45" N, 81°30'0" W). Collection sites were dominated by hard bottom structures such as artificial and natural reefs; predominant invertebrate prey included hard-shelled mollusks, crabs and sea urchins (Vose, 1990; Vose and Nelson, 1994). Gulf of Mexico *B. capriscus* were caught in Tampa Bay (27°32'0" N, 82°47'0" W) and off Turkey Point (29°53'0" N, 84°28'0" W), Florida. Collection sites in the Gulf were characterized by soft-bottom communities that included polychaetes, soft corals, sand dollars and bivalve mollusks (Frazer et al., 1991; Posey et al., 1998).

The gastro-intestinal tract of each triggerfish was dissected and examined. To minimize sampling bias associated with hook and line, the main method of fish collection, only fish that had at least 75% full stomach (based on visual inspection of stomach fullness under a dissecting microscope) were included in the dietary analysis. Furthermore, pieces of squid and fish used as bait were carefully eliminated before quantifying the relative contribution of natural prey in the diet of *B. capriscus*. Gut contents of 20 Atlantic and 33 Gulf fish were classified into 12 prey categories (Echinoidea, Asteroidea, Bivalvia, Gastropoda, Cirripedia, Polychaeta, crab, shrimp, Ophiuroidea, Porifera, Anthozoa and algae). The volumetric contribution of each prey category was calculated by water displacement, as outlined in Turingan (1994). Difference in magnitude of durophagy between Atlantic and Gulf *B. capriscus* was determined by comparing the average consumption of hard prey (i.e., pooled volumetric contribution of Echinoidea, Bivalvia, Gastropoda, Cirripedia, crab, Ophiuroidea).

The same fish (including 10 more Gulf caught *B. capriscus*) used in the dietary analysis were measured for standard length (SL) and biomechanical features of the oral-jaw apparatus. Oral-jaw bones (upper and lower jaws) and muscles (adductor mandibulae 1 and 2) were

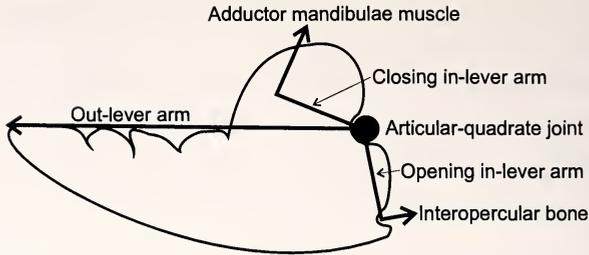


FIG. 1. Schematic diagram of *B. capricus* lower jaw, showing the distances (out-lever, closing in-lever, and opening in-lever) measured to quantify mechanical advantage.

dissected from the left side of the head, patted dry with a paper towel and weighed to the nearest 0.01 gram using a Sartorius® analytical balance. The mechanical advantage (i.e., lever ratio) of the lower jaws was estimated from three linear measurements on the jaw bone (Wainwright and Richard, 1995; Turingan et al., 1995): (1) opening and closing out-lever was the distance between the articular-quadrate joint and the most anterior tip of the biting teeth; (2) opening in-lever was the distance between the articular-quadrate joint and the insertion point of the inter-opercular bone on the mandible; (3) closing in-lever was the distance between the articular-quadrate joint and the insertion point of the adductor mandibulae on the lower jaw (see Turingan et al., 1995 for details of this procedure; Fig. 1).

To remove the confounding effects of body size in intraspecific comparisons of feeding biomechanics,  $\log_{10}$ -transformed bone and muscle mass were compared between Atlantic and Gulf fish using Analysis of Covariance (ANCOVA), with  $\log_{10}$ -transformed SL as covariate. Interpopulation differences in arcsine-transformed jaw-opening and closing lever ratios were compared using Analysis of Variance. Graphical and statistical analyses were conducted using Sigmaplot® and Systat®, respectively (SPSS, Inc.).

**RESULTS**—Atlantic *B. capricus* fed almost exclusively on hard-shelled invertebrates; on average, about 85% of prey consumed included echinoids, crabs, bivalves, gastropods, and Cirripedia (Table 1). In contrast, only about 55% of prey consumed by Gulf *B. capricus* were considered hard prey, primarily infaunal bivalves. Exclusive of bivalves, errant polychaetes dominated the diet of Gulf *B. capricus*. On average, Atlantic *B. capricus* consumed relatively more hard prey than Gulf conspecifics (t-test to compare mean percentage volumetric contribution of hard prey:  $t = 2.901$ ;  $df = 49,2$ ;  $P = 0.004$ ).

Mass of oral-jaw bones and muscles of individual *B. capricus* at both locations increased with body size (Fig. 2; Table 2). Analyses of Covariance revealed that Atlantic *B. capricus* had significantly higher upper and lower jaw mass, as well as adductor mandibulae 1 and 2 mass than Gulf conspecifics (Table 3). Of the two measures of mechanical advantage of the lower jaw, only the opening lever ratio was significantly different between the two *B. capricus* populations.

**DISCUSSION**—Gray triggerfish, *B. capricus* is an important component of the fish fauna along the Atlantic Ocean and Gulf of Mexico coasts of Florida. This ubiquitous species appear to successfully settle on different

TABLE 1. Mean percentage volumetric contribution ( $\pm$  SE) of prey consumed by *B. capricus* in the Atlantic Ocean and Gulf of Mexico.

|             | Atlantic Ocean    | Gulf of Mexico    |
|-------------|-------------------|-------------------|
| Hard Prey   |                   |                   |
| Bivalvia    | 16.56 $\pm$ 6.37  | 38.26 $\pm$ 6.80  |
| Cirripedia  | 10.27 $\pm$ 4.86  | 1.76 $\pm$ 0.68   |
| Crab        | 25.70 $\pm$ 7.45  | 7.36 $\pm$ 3.16   |
| Echinoidea  | 27.14 $\pm$ 8.53  | 6.10 $\pm$ 3.35   |
| Gastropoda  | 2.72 $\pm$ 1.44   | 1.55 $\pm$ 0.51   |
| Ophiuroidea | 5.07 $\pm$ 4.46   | 0.00 $\pm$ 0.00   |
| Soft Prey   |                   |                   |
| Algae       | 0.00 $\pm$ 0.00   | 0.12 $\pm$ 0.07   |
| Asteroidea  | 5.00 $\pm$ 5.00   | 0.866 $\pm$ 0.866 |
| Soft Coral  | 0.00 $\pm$ 0.00   | 2.18 $\pm$ 2.16   |
| Polychaeta  | 4.98 $\pm$ 2.78   | 21.89 $\pm$ 4.32  |
| Shrimp      | 0.00 $\pm$ 0.00   | 0.01 $\pm$ 0.01   |
| Sponge      | 2.44 $\pm$ 1.76   | 0.00 $\pm$ 0.00   |
| Unknown     | 0.114 $\pm$ 0.114 | 16.43 $\pm$ 3.22  |

habitats within its natural range of distribution (Vose, 1990; Frazer et al., 1991; Vose and Nelson, 1994). The ecomorphological analysis conducted in this study revealed three important characteristics of this species. First, *B. capricus* in the Atlantic Ocean fed primarily on hard-shelled invertebrates that appear to dominate the prey-resource available on natural and artificial reefs characteristic of this habitat. Second, *B. capricus* in the Gulf of Mex-

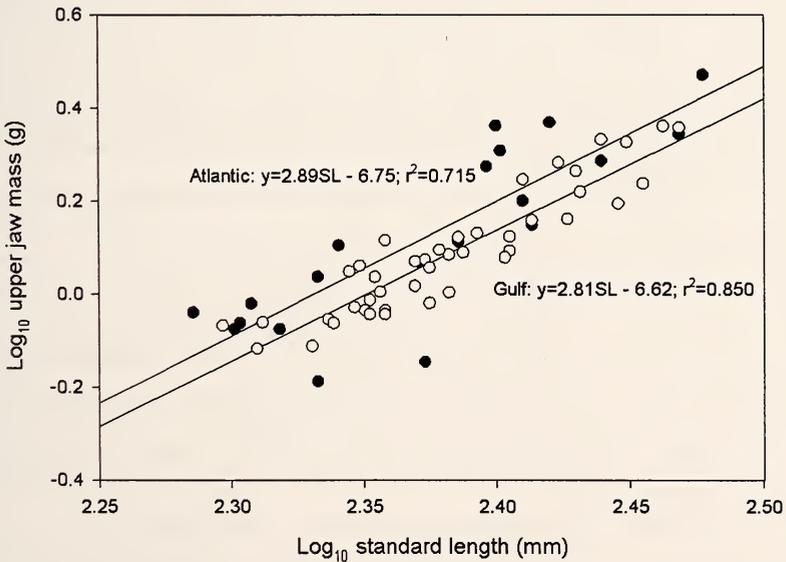


FIG. 2. Representative covariate regression plot showing the relationship between jaw bones and muscles in *B. capricus*.

TABLE 2. Summary of regression analyses of the  $\log_{10}$  transformed biomechanical variables on  $\log_{10}$  transformed Standard Length of *B. capriscus* caught in the Atlantic Ocean and Gulf of Mexico.

| Biomechanical variable | Location | Y intercept | Slope | R <sup>2</sup> | P      |
|------------------------|----------|-------------|-------|----------------|--------|
| Upper Jaw Mass         | Atlantic | -6.75       | 2.89  | 0.715          | ≤0.001 |
|                        | Gulf     | -6.61       | 2.81  | 0.850          | ≤0.001 |
| Lower Jaw Mass         | Atlantic | -6.73       | 2.85  | 0.752          | ≤0.001 |
|                        | Gulf     | -6.86       | 2.88  | 0.854          | ≤0.001 |
| Add. Mandibulae 1 Mass | Atlantic | -7.02       | 3.19  | 0.909          | ≤0.001 |
|                        | Gulf     | -6.48       | 2.93  | 0.754          | ≤0.001 |
| Add. Mandibulae 2 Mass | Atlantic | -5.88       | 2.74  | 0.858          | ≤0.001 |
|                        | Gulf     | -7.02       | 3.21  | 0.875          | ≤0.001 |

ico included more soft prey invertebrates, such as errant polychaetes and soft corals in their diet. Third, difference in magnitude of durophagy between Atlantic and Gulf *B. capriscus* was reflected in differences in key biomechanical features of the oral-jaw apparatus, such as jaw muscle and bone mass.

Several studies have concluded that at both intra- and interspecific levels of analysis, there is a strong positive association between key features of feeding mechanism and food habits in fishes (Motta, 1988; Turingan et al., 1995; Wainwright and Richard, 1995). It has been argued that the validity of conclusions drawn from ecomorphological analyses become apparent only if the choice of functional morphological variables is based on knowledge of their biological and ecological roles (Turingan, 1994; Norton et al., 1995). Here we categorized prey consumed based on predator's method of prey

TABLE 3. Results of Analysis of Covariance comparing the mass of oral-jaw bones and muscles as well as Analysis of Variance comparing opening and closing lever ratios between Atlantic and Gulf *B. capriscus*. Sample mean values for the jaw-bones and muscles are adjusted for a 239.9 ( $\pm 1.0$  SE) mm fish.

|                          | Mean $\pm$ (SE)   |                 | Statistical comparison                    |
|--------------------------|-------------------|-----------------|---|
| Jaw Bone and Muscle Mass | Atlantic (n = 20) | Gulf (n = 43)   |   |
| Upper Jaw (g)            | 1.39 $\pm$ 1.04   | 1.20 $\pm$ 1.03 | ANCOVA: F = 11.10; d.f. = 1,60; P = 0.001 |
| Lower Jaw (g)            | 1.13 $\pm$ 1.04   | 0.99 $\pm$ 1.02 | ANCOVA: F = 9.56; d.f. = 1,60; P = 0.003  |
| Add. Mand. 1 (g)         | 3.64 $\pm$ 1.04   | 3.14 $\pm$ 1.02 | ANCOVA: F = 11.62; d.f. = 1,60; P = 0.001 |
| Add. Mand. 2 (g)         | 4.47 $\pm$ 1.03   | 4.01 $\pm$ 1.02 | ANCOVA: F = 9.22; d.f. = 1,60; P = 0.004  |
| Mechanical Advantage     |                   |                 |   |
| Opening Lever Ratio      | 0.18 $\pm$ 0.00   | 0.15 $\pm$ 0.00 | ANOVA: F = 13.92; d.f. = 1,61; P = <0.001 |
| Closing Lever Ratio      | 0.27 $\pm$ 0.00   | 0.25 $\pm$ 0.00 | ANOVA: F = 2.93; d.f. = 1,61; P = 0.092   |

capture and processing (e.g., the predator would bite and crush hard prey such as crabs and bivalves, whereas it would suction feed on soft, elusive prey such as errant polychaetes [Turingan and Wainwright, 1993]). In addition, we chose biomechanical properties of the oral jaws that are directly linked to feeding performance. For example, mass of the oral-jaw adductor muscle reflects force-producing capability, oral-jaw bone mass is indicative of compressive strength, and lever ratios represent a compromise between speed of jaw movement and biting strength (Barel, 1983; Wainwright, 1987, 1988; Turingan, 1994; Wainwright and Richard, 1995; Turingan et al., 1995; Hernandez and Motta, 1997).

Although the quantification of substratum type and invertebrate communities in the Atlantic and Gulf sites was beyond the scope of this study, it is hypothesized that differential consumption of hard prey between populations of *B. capriscus* reflected difference in the relative abundance of prey organisms in these two locations. As opportunistic predators, most fishes likely feed on the most abundant prey available in their foraging habitats. Results of our dietary analysis were consistent with previous reports on the food habits of *B. capriscus* in the Atlantic Ocean and Gulf of Mexico. Vose (1990) and Vose and Nelson (1994) also found that the main dietary items of *B. capriscus* located in the Atlantic Ocean were bivalves and barnacles (Cirripedia). In contrast, Frazer and co-workers (1991) found that *B. capriscus* inhabiting the Gulf of Mexico fed primarily on sand dollars.

Is variation in magnitude of durophagy between Atlantic and Gulf *B. capriscus* associated with between-location difference in the biomechanical features of the prey-capture and processing mechanism? It is likely that difference in prey-resource base and food habits between the two *B. capriscus* populations influenced the development of different feeding biomechanical designs between conspecifics. The relatively more massive oral-jaw bones and muscles of Atlantic *B. capriscus* appear to give them the ability to capture and process the hard-prey invertebrates that dominate their diet. Several studies have shown that feeding on different prey types induced changes in the development of feeding mechanisms: sticklebacks (Lavin and McPhail, 1986), cichlids (Greenwood, 1965; Meyer, 1987, 1989; Wimberger, 1991; Smits, 1996) and *A. probatocephalus* (M. Fougerolle, unpublished MS thesis). Muscle and bone physiology responds to changes in dynamic loading (Goldspink and Howells, 1974; Goldspink and Ward, 1979; Currey, 1984; Lanyon and Rubin, 1985). Vertebrate striated muscle hypertrophies in response to increased loads, resulting in increased mass and physiological cross-sectional area (Goldspink, 1983). Vertebrate bone tissue also has the ability to remodel and gain mass and size when subjected to increased stress (Wolff, 1892; Moore, 1965; Smith, 1981; Bouvier and Hylander, 1981; Beecher et al., 1983). Feeding on benthic, hard-shelled prey requires a forceful bite to capture prey and repeated chewing to crush prey before being swallowed (Turingan and Wainwright, 1993; Wainwright and Turingan, 1993; Turingan, 1994; Turingan et al., 1995; Cutwa, 1997; Hernandez and Motta,

1997). During prey capture and processing, jaw muscles and bones experience a loading regime that could induce them to increase mass and size (Turingan et al., 1995).

In addition to hypertrophy of jaw bones and muscles, increased durophagy would be expected to correlate with increased mechanical advantage of the lower jaw (i.e., lever ratio indicates the trade-off between speed of jaw movement and transmission of force from the adductor mandibulae muscle to the biting surface of the jaw). Although this trend has been demonstrated in interspecific comparisons (Westneat, 1990, 1994; Turingan, 1994; Wainwright and Richard, 1995), we found that intraspecific difference in jaw closing lever ratios were not consistent with the pattern seen in oral-jaw bones and muscles. However, there was a significant difference in opening lever ratios between Gulf and Atlantic fish. This could be attributed to the difference in opening in-lever arm between the two triggerfish populations (ANCOVA to compare average opening in-lever arm:  $F = 18.966$ ;  $df = 1,60$ ;  $P = <0.001$ ). We hypothesize that subtle differences in the hardness of prey consumed by conspecifics in the wild induced hypertrophy of bones and muscles, but had inconsistent effect on the lever systems of the lower jaw. Perhaps during development, mechanical advantage of the lower jaws is less responsive to difference in magnitude of durophagy in *B. capriscus*.

The ability of *B. capriscus* to alter its feeding habits is coupled with its ability to alter the development of its feeding mechanism to match the demands for prey capture and processing of locally available prey. Intraspecific variation in ecomorphological patterns may be as widespread in fishes as the existence of interspecific variation. This has important implications for our understanding of the mechanisms that underlie the ability of a fish species to successfully occupy heterogeneous habitats such as those found within the range of distribution of *B. capriscus* in Florida.

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