ELSEVIER

Journal of Experimental Marine Biology and Ecology 349 (2007) 284 – 294

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Trophic plasticity and foraging performance in red drum, *Sciaenops ocellatus* (Linnaeus)

Clifton B. Ruehl *, Thomas J. DeWitt *

Department of Wildlife and Fisheries Sciences and Sustainable Coastal Margins Program, Texas A&M University, 2258 TAMU, College Station, TX 77843-2258, USA

Received 20 October 2006; received in revised form 20 May 2007; accepted 24 May 2007

Abstract

Matching behavior, morphology, or physiology to current environments based on experience or cues can be an adaptive solution to environmental change. We examined morphological and behavioral plasticity induced by durophagy (consumption of hard foods) in red drum (*Sciaenops ocellatus*), an ecologically and recreationally important fish species undergoing stock enhancement. At the conclusion of the experiment, we conducted feeding performance trials to address the potential adaptive significance of diet-induced traits. Relative to soft foods, hard food induced a deeper head in the area of the pharyngeal mill, anterio-dorsally shifted eyes, and 8% heavier feeding muscles in juvenile *S. ocellatus*. These fish initially consumed hard food 2.6 times faster than fish raised on soft food. However, in subsequent feeding trials, handling time rapidly converged until both groups appeared equally efficient. This result indicates that learning may compensate for small magnitude morphological differences within a species. We discuss the importance of performance trials for testing the adaptive significance of induced plasticity and the value of separating behavioral and morphological development in studies of phenotypic plasticity. We conclude with a discussion on the implications of our results for successful supplementation of wild populations.

Keywords: Estuaries; Feeding behavior; Fish hatcheries; Geometric morphometrics; Phenotypic plasticity; Resource polymorphism; Stock enhancement

1. Introduction

Natural environments are variable over time and space (Hutchinson, 1961; Levins, 1968; Grime, 1977; Menge and Sutherland, 1987). To persist, organisms must cope with these environmental fluctuations. When environments favor different trait values (divergent natural selection), several evolutionary responses are possible depending on population structure, patterns of gene flow, and the tempo and mode of environmental variation. In general, population differentiation evolves in response to environmental variation between spatially isolated populations (MacArthur and Wilson, 1967; Levins, 1968; Schluter, 2000). In contrast, ecological generalization or tolerance may evolve when environments vary rapidly or inscrutably (Levins, 1968; Gabriel and Lynch, 1992; Wilson and Yoshimura, 1994; DeWitt and Scheiner, 2004). Phenotypic plasticity often evolves

* Corresponding authors. C. Ruehl is to be contacted at Department of Biological Sciences, Florida International University, Miami, Florida 33199, USA. Tel.: +1 305 348 6253. T. DeWitt, Texas A&M University, Department of Wildlife & Fisheries Sciences, 2258 TAMU, College Station, TX 77843-2258, USA. Tel.: +1 979 845 7522; fax: +1 979 845 4096.

E-mail addresses: clifton.ruehl@fiu.edu (C.B. Ruehl), tdewitt@tamu.edu (T.J. DeWitt).

0022-0981/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2007.05.017

in response to temporal variation occurring within or between generations (Bradshaw, 1965; Moran, 1992; DeWitt and Langerhans, 2004). Plasticity is adaptive when environmentally dependent trait expression increases phenotype-environment matching, resulting in higher fitness (DeWitt and Scheiner, 2004).

The adaptive significance of induced phenotypes is often argued from biomechanical principles or from general functional paradigms defined by pre-existing work. This practice is often reasonable for certain traits and taxa. For example, in fishes strong paradigms exist for interpreting the functional significance of morphological variation (Keast and Webb, 1966; Winemiller et al., 1995). However, it is always best to offer direct tests for the functional consequences of induced traits (DeWitt and Scheiner, 2004). Several studies in fishes have conducted performance tests of induced phenotypes to determine their adaptive value (Brönmark and Miner, 1992; Day and McPhail, 1996; Andersson, 2003; Andersson et al., 2005; Carter and Wilson, 2006; Parsons and Robinson, 2007). Among these studies, Day and McPhail (1996) separated the adaptive significance of morphological and behavioral plasticity in a single study. They concluded that behavioral plasticity (intraspecific differences after experience) affects searching time, while morphological plasticity influences resource-handling time in sticklebacks (*Gasterosteus* sp.). Resource variation is an interesting gradient for studying the evolution of phenotypic plasticity because resource quantity and type often vary across space and time.

Resource polymorphism, generated through genetic variation or phenotypic plasticity, is well documented in fishes (Smith and Skulason, 1996; Robinson and Parsons, 2002). Accommodations for prey processing often manifest through changes in body depth (Schluter, 1993; Svanback and Eklov, 2003), mouth position (Meyer, 1987; Ruehl and DeWitt, 2005), gill-raker length and number (Schluter, 1993), as well as pharyngeal jaw dentition and musculature (Wainwright et al., 1991). Developmental flexibility in these and similar traits should be especially important to species living in highly variable environments like estuaries.

Estuaries are particularly heterogeneous environments that connect freshwater and marine systems. These environments exhibit substantial variation in biotic (e.g. predators, competitors) and abiotic parameters (e.g. salinities, temperature) that likely influence resource availability (Gray et al., 1996). In particular, as resources vary within and between estuaries, feeding modes necessary to acquire different prey may also vary, presenting challenges to fishes. Therefore, estuarine fishes in particular, may have evolved plasticity to increase matching of phenotypes to locally abundant resources. However, no studies have explicitly examined trophic plasticity in estuarine species, despite strong suggestive evidence it exists (Cutwa and Turingan, 2000).

Sciaenops ocellatus is an estuarine fish species of ecological, recreational, and commercial fishery importance. They are generalist foragers consuming fish, penaeid shrimp, crabs, and other crustaceans after reaching 30 mm (Boothby and Avault, 1971; Bass and Avault, 1975; Overstreet and Heard, 1978; Scharf and Schlicht, 2000). Over-harvest of *S. ocellatus* for several decades culminated in the implementation of catch limits and hatchery supplementation to revive the fishery (Swingle, 1990; McEachron et al., 1998). Catch limits are known to aid recovery of fishery stocks, however there has been little documentation that supplementation of any species significantly contributes to wild populations (Blaxter, 2000). Aside from research on Artic charr (*Salvelinus alpinus*) (see Alexander and Adams, 2004), few studies have considered resource-based plasticity in commercial fisheries, despite research suggesting the important role of trophic plasticity in morphological divergence (Meyer, 1987; Robinson and Wilson, 1994; Skulason and Smith, 1995).

In this study, we examine the extent of diet-induced morphological and musculature variation in red drum (*S. ocellatus*). We also test the performance value of induced traits and examine the extent of behavioral plasticity using feeding trials. Specifically, we test the hypothesis that *S. ocellatus* fed diets supplemented with crush-resistant foods will develop larger heads, larger crushing muscles, thicker pharyngeal jaws, and consume crush-resistant foods more efficiently, than those fed soft foods. Additionally, we focus on a species undergoing stock supplementation, which provides the potential to use knowledge of phenotypic plasticity to improve stock enhancement practices.

2. Methods

2.1. Rearing experiment

We obtained juvenile *S. ocellatus* (~28 mm) from the Sea Center marine fish hatchery in Lake Jackson, Texas and transported them to our laboratory. Fish were acclimated for 2 weeks in a re-circulating tank with physical and biological filtration. During acclimation to the laboratory environment *S. ocellatus* were treated with a 0.15 ppt copper solution (Cutrine) to guard against parasites (Gaylord and Gatlin, 1996). After acclimation, we moved fish into a 2350-l re-circulating system composed of twenty-four 75-l aquaria, a 100-l settling

tank, a 300-l biological filtration chamber and a sand filter. A 1-hp pump circulated brackish water (5 ppt) through the system. Mesh panels divided each 75-l tank in half, yielding 48, 37.5-l sectors. We used a 12:12 h light:dark cycle and maintained water temperature at 27 °C.

We assigned treatments to sectors systematically within blocks to provide adequate interspersion of treatments often not achieved with strict randomization (Hurlbert, 1984). We divided the 48 sectors into 6 blocks of 8 and assigned treatments in an alternating pattern within each block; the pattern was reversed for each adjacent block so the same treatment never appeared side-by-side. Three fish were randomly assigned to each sector yielding 72 fish per treatment (144 total).

Diets consisted of crayfish (*Procambarus clarkii*) limb segments for hard-food treatments or an equivalent mass of crayfish meat without exoskeleton for soft-food treatments. We increased the crayfish limb-segment size and amount during the experiment to match *S. ocellatus* growth. Crayfish have been identified in the diets of *S. ocellatus* by Bass and Avault (1975) and they readily ate small pieces of crayfish in the lab (CBR personal observation). Additionally, crayfish was a good surrogate for the crush-resistant blue crab (*Callinectes sapidus*) that are common in *S. ocellatus* diets (Boothby and Avault, 1971; Bass and Avault, 1975). Fish received treatment food in the mornings and a commercially prepared food (Rangen Corp. starter diet #2) in the evenings.

Aggressive behavioral interactions (e.g. fin nipping, chasing, food hoarding) caused the mortality of 49 individuals during the first 30 days of the experiment (1.6 fish day^{-1}). However, mortality was not biased by treatment (21 hard food and 28 soft food; Fisher's exact test, $P=0.39$). To alleviate the negative effects of aggression, we reduced the number of fish in each sector to one by removing them at random on the 30th day of the experiment. Fish removed from the experiment after 30 days were preserved for morphometric analysis. Those remaining in the tanks (24 hard food and 24 soft food) were fed for another 30 days (60 experimental rearing days total), during which time three fish died (2 hard food and 1 soft food). Thus, the experiment started with 144 individuals, was reduced to 48 individuals at the halfway point, and ended with 45 individuals (22 hard food and 23 soft food).

The sixty-day time course was selected based on growth rates reported in the literature. Rooker et al. (1999) and Stunz et al. (2002) report growth rates of 0.83 mm day^{-1} and 0.69 mm day^{-1} respectively, for newly settled *S. ocellatus*, while Johnson et al. (2002) report growth rates of 0.80 mm day^{-1} over 10 days in a laboratory experiment. These data suggest that our fish would more than double in size over 60 days. We anticipated that this would be sufficient growth and development for fish to exhibit plasticity even if it were moderate in magnitude. Our fish were not measured prior to the experiment because small fishes are vulnerable to handling, but mean growth rates of *S. ocellatus* were 0.96 mm day^{-1} (47% increase) over the second 30 days of the experiment, which are similar to those reported in natural and laboratory environments.

At the conclusion of the experiment, fish underwent performance trials and were preserved for morphometric analysis. The random removal of almost half the fish at the mid point of the experiment facilitated examination of induced external morphology at two points during ontogeny, after 30 days and 60 days of development. Internal morphology of fish that were reared for 30 days was not quantified because their smaller size made accurate dissections impractical.

2.2. Morphometrics

2.2.1. External morphology

External morphology was measured using geometric morphometrics. This method retains the geometry of shape (spatial covariation among landmarks) throughout the analysis and facilitates visualization of shape differences between groups. This is a considerable improvement over traditional morphometric methods employing linear distances that typically produce incomplete shape information (Rohlf and Marcus, 1993). Lateral and dorsal images of each fish were captured using a video imaging system with a telecentric lens. TpsDig software (v. 2.05; Rohlf, 2006) was used to digitize twelve landmarks on lateral images and seven landmarks on dorsal images (Fig. 1A, B). External landmarks were digitized at a resolution of 0.22 mm pixel^{-1} for all images.

On lateral images, a semilandmark was added by projecting to the body outline at 90° from the midline of a chord between the snout and anterior dorsal fin landmarks. To facilitate calculation of gape width an additional point was digitized at the distal tip of the lower jaw. Gape width served as a covariate to characterize and statistically control for non-shape postural artifacts created when fish happened to be preserved with their mouths open (Fig. 1A). Raw gape size was divided by the centroid size of the fish to scale it relative to fish size. No bias in scaled gape occurred across food treatment groups (experiment-day 30 $t=0.03$, $df=45$, $P=0.98$; experiment-day 60 $t=1.02$, $df=43$, $P=0.43$). Lateral landmarks were superimposed (adjusted for location, rotational position and size) using tpsRelw (v. 1.42; Rohlf, 2005a) with default settings. During

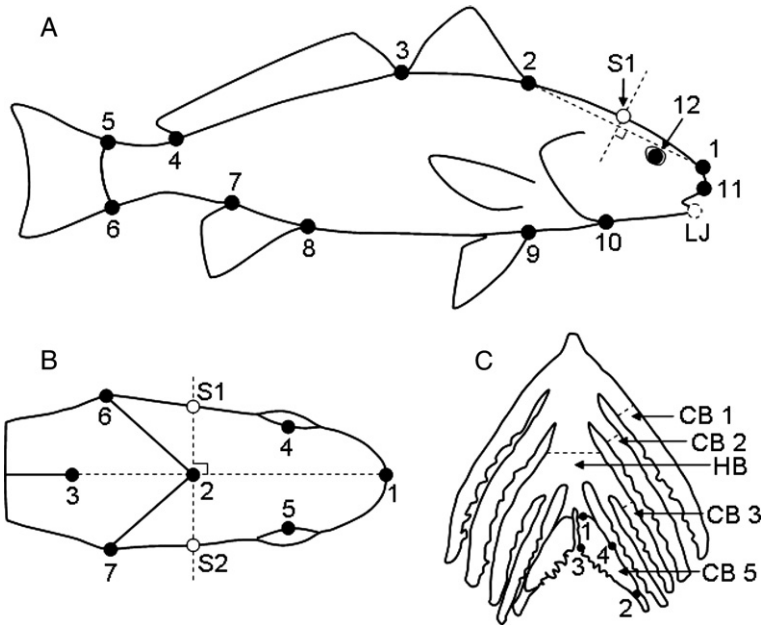

Fig. 1. Landmarks used in geometric morphometric analysis. (A) Lateral view. Landmark S1 (unfilled) was used to help define head shape and was treated as a semilandmark for analysis. Point LJ was used to calculate gape and was not used to calculate shape variables. (B) Dorsal view. Dorsal configurations (landmarks 1–7 and semilandmarks S1 and S2) were rotated to the major axis of landmarks 1–3 and all coordinates were reflected and averaged for analysis. (C) Lower jaw. Measurements were made at the dashed lines of ceratobranchial 1–3 (CB 1–3) and the hyobranchial (HB). The four landmarks digitized on ceratobranchial 5 (CB 5) were treated as an ellipse to calculate area for analysis.

superimposition, tpsRelw slides the semilandmark between the two reference landmarks that define it until it reaches a position of minimum bending energy relative to the consensus (average) conformation (Bookstein, 1991). Sliding semilandmarks are necessary when a landmark coded in two dimensions (*X* and *Y* coordinates) contains only one dimension of information. By minimizing bending energy exerted by semilandmarks we reduce their information content to compensate for the dimensional deficiency.

On dorsal images, we added semilandmarks to the body perimeter on both sides of the fish, perpendicular to landmark 2 (Fig. 1B). We removed theoretically redundant information in our midline and lateral points by assuming bilateral symmetry. We first centered and rotated dorsal configurations to the major axis of their midline points (points 1, 2, 3; Fig. 1B). The resulting bilateral coordinates were reflected about the midline points, averaged, and then centered and scaled to unit size for analysis.

For all shape analyses, we calculated partial warps of superimposed coordinate values using tpsRelw with default settings. Partial warps served as shape variables for analysis.

2.2.2. Pharyngeal jaw morphology

After external images were captured, we removed pharyngeal jaws of experiment-day 60 *S. ocellatus*. Jaws were cleared and stained for cartilage and bone using alcian blue and alizarin red, according to Taylor and Van Dyke (1985). Images of the lower pharyngeal jaws were captured using a digital camera (Olympus Camedia C-5050). The width of ceratobranchial (CB) 1–3, the hyobranchial (HB), and the area of the lower crushing plate (CB 5) were measured from these images (Fig. 1C). TpsDig (v. 2.05; Rohlf, 2006) software was used to measure the width of ceratobranchials and digitize the two most distal points in the *X* and *Y* directions (Fig. 1C). We calculated the area of CB 5 by approximating the shape to an ellipse. CB 5 is involved in prey processing and is representative of all tooth structures (Grubich, 2000). Likewise, ceratobranchials are indicative of prey processing and are known to be plastic in fishes (Schluter, 1993; Robinson and Wilson, 1994). Measurements of lower jaws were made at a resolution of 0.035 mm pixel^{-1} for all images.

2.3. Muscle mass

In addition to pharyngeal jaws, we dissected the levator posterior (LP) muscle and the levator externus 3 and 4 muscle complex (LE) from experiment-day 60 fish. Both of these muscles are involved in operation of the pharyngeal jaws during feeding (Sasaki, 1989; Grubich, 2000). After dissection, we preserved muscles in 95%

ethanol. For weighing, we removed each muscle from ethanol, blotted dry, weighed, and returned the muscle to ethanol three separate times. All three weights, for both muscles, were recorded on the same day. The LE complex was weighed collectively following Grubich (2003).

2.4. Performance

At the conclusion of the experiment, *S. ocellatus* underwent feeding trials with hard food to assess performance differences resulting from learning and morphological plasticity. We hypothesized *S. ocellatus* from the hard-food treatment would manipulate and consume hard food more quickly than fish reared on soft foods. To assess the effects of learning and morphological plasticity on performance, we examined handling time after each trial. Behavior, and thus learning is usually expected to respond on a faster time scale than morphology (Day and McPhail, 1996). Therefore, evidence of a short-term performance plateau (i.e. consistent handling times between trials) would indicate behavioral accommodation for consuming hard foods. This plateau represents the combination of behavioral and morphological effects on performance, while performance differences in later trials represent only morphological plasticity.

Four performance trials were conducted in 2 days; two trials on the first day and two on the second day. There was approximately 6 h between the start of the first trial and the start of the second trial on the same day. During the trials, fish were fed one crayfish limb segment per trial (72 $mm^3 \pm 2$ mm^3, 115 mm^3, 181) (mean ± S.E., range, *N*). Trials were considered successful if the food item was picked up and manipulated at least once. The trial was terminated if 7 min passed without any response. One researcher observed the fish while another recorded time intervals. We measured performance through 1) time-to-first-contact with food, 2) handling time and 3) total time. Time was recorded from the presentation of the food until the fish either consumed, or rejected the item. If the fish rejected the food item, and did not pick it up again for 2 min, the trial was terminated. To calculate handling time, we subtracted the length of time a fish manipulated the food item in its mouth from the time-to-consumption or rejection, thus removing the time the food item was not manipulated.

2.5. Analysis

We tested for differences in final size using *t*-tests. External morphology was analyzed using multivariate analysis of covariance (MANCOVA) where partial warps of superimposed landmarks served as dependent variables. We tested for effects of treatment (hard versus soft food), using centroid size and gape as covariates. Centroid size was used (as a covariate) to estimate and statistically adjust for multivariate allometry (i.e. the change in shape with growth). We tested for non-linear allometry in all analyses of shape variation. Centroid size was highly correlated with standard length ($r = 0.99$, $P < 0.001$ in all cases). Gape was used as an additional covariate, which in this case adjusts for distortion in landmark locations resulting from effects of preservation posture. We tested for heterogeneity of slopes for covariates and removed non-significant interactions from our statistical models. TpsRegr software (v. 1.31; Rohlf, 2005b) was used to visualize the linear shape gradient defined by the MANCOVA. We used MANCOVA to test for treatment effects on jaw morphology where the widths of the three ceratobranchials, the hyobranchial, and the area of ceratobranchial 5 served as dependent variables using centroid size as a covariate. Muscle masses were analyzed with ANCOVA. Feeding performance and behavior were analyzed with ANCOVA and Cochran's *Q*-test respectively. Centroid size was used as a covariate in all three analyses. Log-transformed data were used in statistical analyses of muscle mass and performance to meet assumptions of normality, while back-transformed means were used in calculations of percent-difference for muscle mass and performance trials. All statistical procedures were conducted with JMP software (Version 5.0.1.2, SAS Institute Inc., Cary, NC).

3. Results

3.1. External and internal morphology

Size did not differ between treatments for either the experiment-day 30 ($t = 1.11$; $df = 45$; $P = 0.27$) or day 60 fish ($t = 0.216$; $df = 43$; $P = 0.83$). Allometry was noted in both groups for lateral and dorsal perspectives (Table 1). However, in all cases allometry was consistent across treatments (no heterogeneity of slopes; $P > 0.15$ in all cases). There was no evidence of non-linear allometry ($P > 0.06$ for external morphology). Lateral shape also varied with the gape covariate (Table 1) but this relationship was also homogeneous across treatments (no heterogeneity of slopes; $P > 0.20$ in all cases).

Fish raised for 30 days on alternative diets showed no diet-induced external morphological variation in either lateral or dorsal perspectives (Table 1). However, after 60 days, *S. ocellatus* differed in lateral body morphology (Table 1; Fig. 2). Fish experiencing hard food developed deeper heads, a more anteriorly and

Table 1
MANCOVA results for external morphological variation due to hard vs. soft foods for 30 or 60 days of experimental rearing in *S. ocellatus*

Exp. day	Perspective	Effect	*F*	*df*	*P*
30	Lateral	Food type	1.66	22, 22	0.12
		C. size	2.87	22, 22	0.008
		Gape	19.11	22, 22	<0.001
	Dorsal	Food type	0.91	8, 37	0.52
		C. size	4.41	8, 37	0.001
60	Lateral	Food type	2.44	22, 20	0.02
		C. size	3.43	22, 20	0.004
		Gape	7.71	22, 20	<0.001
	Dorsal	Food type	0.95	8, 35	0.50
		C. size	1.83	8, 35	0.10

Dorsal and lateral aspects of shape were analyzed separately.

dorsally set eye position, and a more upwardly arched (i.e. concave, viewed from above) posture (Table 2; Fig. 2).

There was no diet-induced morphological variation noted in pharyngeal jaw morphology ($F_{5,\ 35}=0.65$; $P=0.66$). There was little evidence for linear allometry ($F_{5,\ 35}=2.34$; $P=0.06$), but there was evidence for non-linear allometry ($F_{5,\ 35}=2.80$; $P=0.03$) in pharyngeal jaw morphology. However, the higher order allometric relationships were homogeneous across treatments (no heterogeneity of slopes; $F_{5,\ 34}=0.76$; $P=0.59$).

3.2. Muscle mass

S. ocellatus fed hard food for 60 days developed 8% more massive LE muscles than those fed soft food ($F_{1,\ 41}=4.25$, $P=0.046$, $R^2=0.30$, Fig. 3). There was evidence of allometry ($F_{1,\ 41}=16.28$; $P<0.001$) but it was consistent across treatments (no heterogeneity of slopes; $F_{1,\ 40}=0.60$; $P=0.44$). There was no difference between food types in the LP muscle ($F_{1,\ 40}=1.31$; $P=0.26$).

3.3. Performance

Forty-four *S. ocellatus* were subjected to performance trials. The number of fish across diet types responding per-trial increased from 34% in the first trial to 66% in the final trial, nearly a two-fold increase. Cochran's *Q*-test, designed to determine how the same individuals respond to a treatment over time (Sokal and Rohlf, 1981), indicated that more fish attempted to consume the hard food, as the trials progressed ($Q_3=14.17$, $P<0.005$). Within treatments, 14% of *S. ocellatus* reared on soft food responded in the first trial compared to 39% in the fourth trial. A similar trend was noted for the number of responders reared on hard

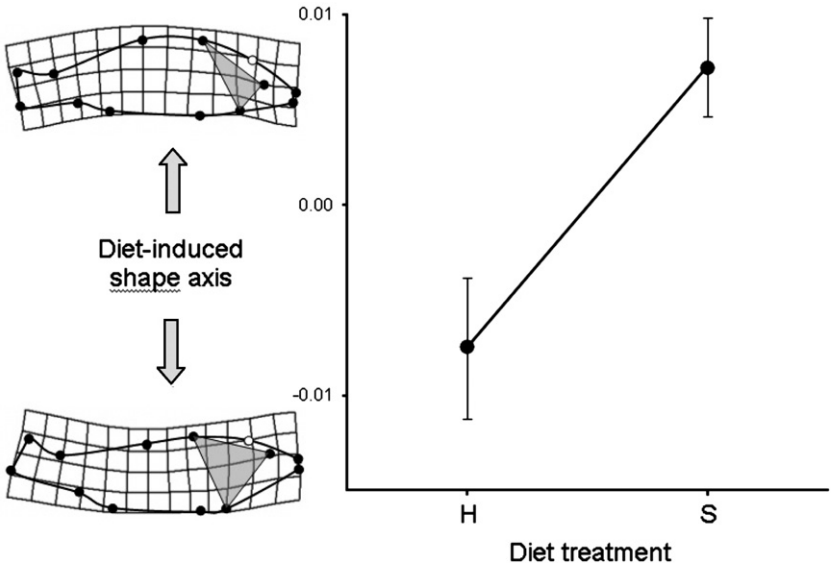

Fig. 2. Reaction norm for durophagy in *S. ocellatus*. Transformation grids illustrate the effect of diet hardness on lateral body shape measured after 60 days of experimental rearing. Grids are magnified 10× to better illustrate the effect given the relatively low sample size involved in generating the shape gradient. Major shape effects are highlighted with a shaded triangle and include deepening of the head around the pharyngeal mill and anterior-dorsal eye displacement.

Table 2
Pearson correlations between superimposed lateral landmark coordinates and the diet type (hard vs. soft food) effect score in *S. ocellatus*

Landmark	*r*
1*X*	−0.29
1*Y*	**0.87**
2*X*	0.06
2*Y*	**−0.82**
3*X*	0.27
3*Y*	**−0.79**
4*X*	**0.47**
4*Y*	**0.48**
5*X*	0.23
5*Y*	**0.86**
6*X*	−0.12
6*Y*	**0.73**
7*X*	−0.16
7*Y*	**−0.49**
8*X*	−0.13
8*Y*	**−0.75**
9*X*	**−0.38**
9*Y*	**−0.79**
10*X*	−0.25
10*Y*	**−0.76**
11*X*	**0.56**
11*Y*	**0.89**
12*X*	0.13
12*Y*	**0.64**
s1*X*	**−0.52**
s1*Y*	−0.25

Correlations ≥|0.35| are in bold to highlight landmarks that vary the most among fish fed alternative diets. Positive signs indicate increases in *X* or *Y* coordinates associated with the hard-food treatment; negative signs indicate the opposite relationship. Landmarks are as in Fig. 1.

food, but the magnitude of change across trials was much less (1st trial = 21%, 4th trial = 27%). A *Q*-test for each treatment, across all four trials indicated that fish reared on soft food were largely responsible for the increase in response during later trials (soft food: $Q_3 = 14.64$, $P < 0.005$; hard food: $Q_3 = 2.18$, $P > 0.05$). However, within each trial, *S. ocellatus* from the different treatments had similar propensities to respond ($P > 0.2$ for all trials, two-tailed Fisher's exact test).

Only 16% of the fish from both treatments responded in every trial, although 77% of them responded in at least one or more trials. The low number of fish responding in every trial, especially the first two trials, prevents the use of repeated measures analysis of variance on handling time, but also indicates each trial was relatively independent. Thus, each trial was analyzed separately. Handling time was 160% longer for fish in the soft food treatments during the first trial ($F_{1,\,12} = 8.93$, $P = 0.011$; Fig. 4). There was no performance difference between treatments for the remaining three trials ($P > 0.15$ in all cases; Fig. 4). Log mean handling times and standard errors for the two treatments were very similar by the fourth trial (Fig. 4).

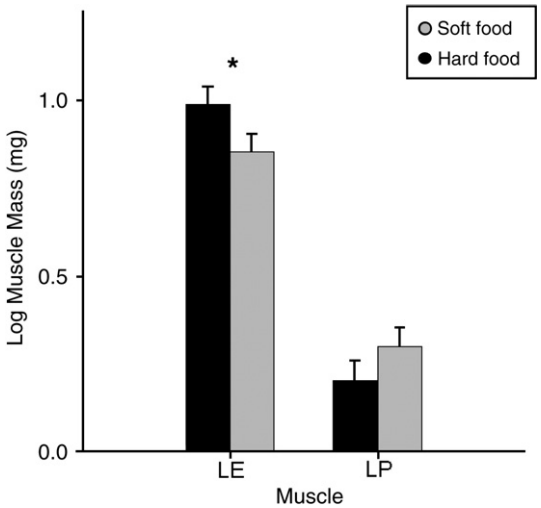

Fig. 3. Levator externus 3 and 4 (LE) and levator posterior (LP) muscle masses in *S. ocellatus* after 60 days of receiving either hard foods (black) or soft foods (gray). The single asterisk (*) indicates a significant difference between diet groups at $P \leq 0.05$. Error bars represent standard error.

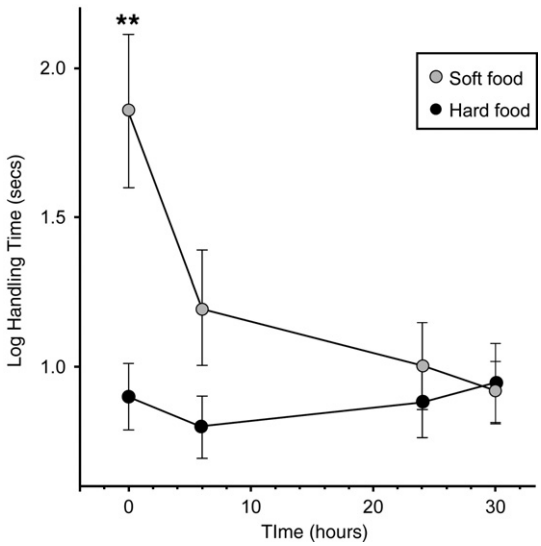

Fig. 4. Mean log handling time and standard errors of hard food for *S. ocellatus* reared on hard (black) versus soft (gray) foods. Four separate trials were conducted in 2 days. Univariate tests indicated fish reared on soft food took longer to consume hard food in the first trial (** indicates $P \leq 0.01$). Feeding times did not differ by diet group for subsequent trials.

4. Discussion

There was no evidence of external morphological plasticity in *S. ocellatus* after receiving crush-resistant food for 30 days. However, developmental plasticity in *S. ocellatus* was present after 60 days of receiving diets differing in crush resistance. These fish developed deeper heads in the region of the pharyngeal mill and anterior-dorsally displaced eyes (Fig. 2). Additionally, the levator externus muscle complex (LE), an integral component of prey processing in *S. ocellatus*, was more massive in fish from the treatment with crush-resistant food (Fig. 3). Performance differences in hard food consumption appeared to be mediated through learning, and not strictly limited by morphological and musculoskeletal plasticity.

Large pharyngeal muscles and deep heads in the pharyngeal mill area are often found in fish species that consume crush-resistant prey (Keast and Webb, 1966; Winemiller et al., 1995; Grubich, 2003). Such morphologies are necessary for generating the biting or crushing forces needed to consume hard-bodied prey. Black drum (*Pogonias cromis*), also a member of the Sciaenid family and a durophagous specialist, has a characteristically deep head with large pharyngeal muscles that aid in consuming hard-shelled molluscs and crabs (Pearson, 1929; Grubich, 2000). In a comparative analysis on the evolution of durophagy, Grubich (2003) found *P. cromis* to have larger pharyngeal muscles and heavier pharyngeal crushing plates than *S. ocellatus*, independent of size. *S. ocellatus* from our hard-food treatment resemble *P. cromis* in the relevant aspect of head depth and in the direction of muscle mass change. Although the morphological shift observed in *S. ocellatus* is small compared to morphological variation between species, the parallelism of the trend suggests that the induced morphology may be adaptive. Presumably, the larger muscle mass induced in *S. ocellatus* fed hard food should result in greater crushing ability. Increased crushing strength should reduce handling time of hard-bodied prey, and in turn, expand the range of crush-resistant food profitably incorporated into the diet.

Disparity in muscle mass between hard- and soft-food treatments likely resulted from the elevated pharyngeal muscle activity required to manipulate and consume hard-food items. These results are similar to those in pumpkinseed sunfish (*Lepomis gibbosus*), a freshwater molluscivore that exhibits substantial phenotypic plasticity in muscle mass and jaw morphology between populations with high and low densities of snails (Mittelbach et al., 1999). Unlike *L. gibbosus*, *S. ocellatus* did not display evidence of diet-induced morphological variation in pharyngeal jaws. Variation in skeletal morphology may have existed in unmeasured structures, or manifested if the experiment were longer in duration. Similarly, food items of even greater crush-resistance might have induced morphological variation in skeletal structures. At present, it appears that differences in muscle mass between treatments are responsible for observed external morphological variation (Fig. 3).

For inducible morphology to be profitable over fixed development, trade-offs must exist between alternative morphologies depending on the environment experienced (Hjelm et al., 2001; Robinson and Parsons, 2002; Svanback and Eklov, 2003; DeWitt and Scheiner, 2004). For example, the shifted eye position induced by consuming hard foods in *S. ocellatus* may be a secondary effect of conformational changes in trophic structures, but have costs if the shift affects their ability to see predators or prey. The idea of cross domain trade-offs remains an interesting and vital topic within the sphere of phenotypic plasticity and phenotypic integration studies (DeWitt and Langerhans, 2003; DeWitt and Scheiner, 2004). We do not know whether such trade-offs exist for *S. ocellatus*, but they seem likely as the cichlid *Astatachromis alluaudi* exhibits trade-offs between induced feeding structures for durophagy and gill structures needed to cope with hypoxia (Smits et al., 1996; Chapman et al., in press).

Resource polymorphism in *S. ocellatus* populations might occur if crush-resistant foods like blue crab varied in abundance across space or time. For example, in locations or times of high blue crab abundance, *S. ocellatus* might develop deeper heads and larger crushing muscles to account for the increased crush resistance of prey. The morphological accommodations would likely be absent when blue crab abundance was low. Resource polymorphism might also manifest between hatchery and wild *S. ocellatus* if hatchery induced morphologies, regardless of their origin, persist after release into natural environments. In the present study, we show evidence of diet-induced plasticity so there is potential for resource polymorphism in *S. ocellatus*, however field collections have not been made to test for these possibilities.

In addition to documenting morphological plasticity in *S. ocellatus*, we also wanted to consider the performance value of induced structures. Only a handful of studies have tested for performance consequences of induced morphology in fishes (Andersson, 2003; Schaack and Chapman, 2003; Andersson et al., 2005; Carter and Wilson, 2006; Parsons and Robinson, 2006). Day and McPhail (1996) took the additional step of separating behavioral and morphological plasticity. They examined plasticity in the threespine stickleback (*Gasterosteus* sp.) and found evidence of diet-induced morphology in head depth after 72 days. Day and McPhail (1996) assessed behavioral plasticity after sticklebacks experienced novel

prey for 10 days to remove the effects of learning, although we feel learning should be considered a form of behavioral plasticity. Foraging efficiency on benthic prey increased continuously with experience throughout the experiment. They concluded that morphology affected handling time and behavior affected prey searching, after accounting for learning, (Day and McPhail, 1996).

We conducted multiple performance trials to determine the benefits of diet-induced traits on feeding efficiency and attempted to distinguish between acquired morphology and acquired behavior (learning). Through either mechanism, we expected *S. ocellatus* reared on hard food to have greater performance on hard food. Fish were not placed on common diets before performance trials because we were interested in quantifying the learned (short-term), as well as the morphological (long-term) effects of durophagy. To consider both, we examined handling time after each performance trial. Performance differences between treatments would signify diet-induced behavioral learning, morphological plasticity, or both affected feeding efficiency. Behavior is usually expected to respond on a faster time scale than morphology. Therefore, rapid convergence of inexperienced fish toward greater performance would suggest that behavioral learning was a large component of initial performance differences. Remaining performance differences after accounting for behavior would be attributed to morphology, indicating evidence of adaptive morphological plasticity.

S. ocellatus were able to behaviorally compensate (sensu DeWitt and Langerhans, 2003) for morphological and musculature differences between treatments with learned proficiency. Fish reared on soft food developed a higher propensity to respond to the presence of hard food in later trials signifying they learned to recognize hard food as a resource (Fig. 4). Their handling times decreased over the four trials and converged by the fourth trial indicating they learned how to manipulate and consume hard food just as efficiently as those with experience consuming hard food. Therefore, diet-induced plasticity in external morphology and muscle mass did not improve performance on hard food. The rate of behavioral accommodation in *S. ocellatus* is remarkable given that other fish species require 10 days to become efficient consumers of novel resources (Dill, 1983; Werner et al., 1983; Ehlinger, 1989; Day and McPhail, 1996). We would have overlooked the importance of learning in the feeding ecology of *S. ocellatus* if we had conditioned fish prior to feeding trials. Without replicating individual foraging trials over time, we would have likely concluded the results from the first trial to be long lasting with strong impacts on foraging success.

We also wanted to consider the consequences of diet-induced plasticity for the success of fish supplementation. An important factor determining the success of hatchery supplementation of wild fish populations involves their pre-release experiences in hatcheries. There is mounting evidence hatchery reared *S. ocellatus* do not perform as well as their wild counterparts in habitat choice (Stunz and Minello, 2001), predator avoidance (Stunz and Minello, 2001), routine swimming speed, or startle response (Smith and Fuiman, 2004). The present study contributes to this body of literature indirectly by reporting diet-induced plasticity and behavior in *S. ocellatus*. Our results yield insight into the developmental mechanisms allowing *S. ocellatus* to transition from hatcheries to natural environments. Although, performance trials indicate rapid learning that likely improves the success of released fish, we may not have captured the vital consequences of induced morphology and musculature. For example, induced musculature might allow fish to include a wider array of food items in their diet, but this was untested given our method of presenting only single prey items during performance trials. Future studies should combine resource consumption and other aspects of *S. ocellatus* ecology like threats of predation (e.g. Rooker et al., 1998; Stunz and Minello, 2001), to determine how multiple factors combine to affect the success of released hatchery fish. The present study examined the extent of phenotypic flexibility in morphology (developmental plasticity) and behavior (learning) of *S. ocellatus*, a recreationally important species of the Gulf and Atlantic coasts of the United States. The nature of body shape and muscle mass variation we observed appeared to be adaptive based on biomechanical principles, functional ecological paradigms for fish feeding, and a comparative look across fish taxa specialized for durophagy. Despite the compelling disparity in shape and musculature of *S. ocellatus* from alternative diet groups, there was little evidence for performance enhancements through morphological plasticity. However, behavioral plasticity appears to be of considerable importance to the ecology of *S. ocellatus*. Multiple performance trials revealed that they quickly learn to make behavioral adjustments to the novel (hard) food items. The behavioral flexibility of *S. ocellatus* emphasizes the importance of repeated performance trials in phenotypic plasticity studies. These results suggest that resource-based plasticity might be important to the success of other estuarine fish species. Hatcheries should consider the implications of morphological and behavioral plasticity for the survival of released organisms although behavioral plasticity appears to be of greater importance in *S. ocellatus*.

Acknowledgements

We thank Kirk Winemiller, Jay Pinckney, Brian Langerhans, Joel Trexler's lab group, and two anonymous reviewers for commenting on the manuscript. We would like to acknowledge Robert Vega at the Marine Development Center and staff at the Lake Jackson Fish Hatchery (Texas Parks and Wildlife) for providing *S. ocellatus*. Delbert Gatlin III and Jonathan Goff assisted in fish transport, David Hoeinghaus helped conduct performance trials, and Peter Wainwright provided guidance on dissection.

Financial support was received from the Texas Higher Education Coordinating Board (ATP 010298-0020 to TJD), the National Science Foundation (DEB 0344488 to TJD) and Texas A&M University's Sustainable Coastal Margins Program and Coastal Conservation Association Fellowships to CBR. **[RH]**

References

Alexander, G.D., Adams, C.E., 2004. Exposure to a common environment erodes inherited between-population trophic morphology differences in Artic charr. J. Fish Biol. 64, 253–257.

Andersson, J., 2003. Effects of diet-induced resource polymorphism on performance in arctic charr (*Salvelinus alpinus*). Evol. Ecol. Res. 5, 213–228.

Andersson, J., Bystrom, P., Persson, L., De Roos, A.M., 2005. Plastic resource polymorphism: effects of resource availability on Arctic char (*Salvelinus alpinus*) morphology. Biol. J. Linn. Soc. 85, 341–351.

Bass, R.J., Avault, J.W., 1975. Food-habits, length–weight relationship, condition factor, and growth of juvenile red drum, *Sciaenops ocellatus*, in Louisiana. T. Am. Fish. Soc. 104, 35–45.

Blaxter, J.H.S., 2000. The enhancement of marine fish stocks. Adv. Mar. Biol. Vol. 38 (38), 1–54.

Bookstein, F.L., 1991. Morphometric Tools for Landmark Data. Cambridge University Press, Cambridge.

Boothby, R.N., Avault, J.W., 1971. Food habits, length–weight relationship, and condition factor of red drum (*Sciaenops ocellatus*) in Southeastern Louisiana. T. Am. Fish. Soc. 100, 290–295.

Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13, 115–155.

Brönmark, C., Miner, J.G., 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science 258, 1348–1350.

Carter, A.J., Wilson, R.S., 2006. Improving sneaky-sex in a low oxygen environment: reproductive and physiological responses of male mosquito fish to chronic hypoxia. J. Exp. Biol. 209, 4878–4884.

Chapman, L.J., DeWitt, T.J., Paterson J., Tzaneval V., in press. Interdemic variation in the gill morphology of a eurytopic African cichlid. Proceedings of the 9th international symposium on fish physiology, toxicology, and water quality EPA publication 600R07010.

Cutwa, M.M., Turingan, R.G., 2000. Intralocality variation in feeding biomechanics and prey use in *Archosargus probatocephalus* (Teleostei, Sparidae), with implications for the ecomorphology of fishes. Environ. Biol. Fishes 59, 191–198.

Day, T., McPhail, J.D., 1996. The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp). Oecologia 108, 380–388.

DeWitt, T.J., Langerhans, R.B., 2003. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. J. Sea Res. 49, 143–155.

DeWitt, T.J., Langerhans, R.B., 2004. Integrated solutions to environmental heterogeneity: theory of multimoment reaction norms. In: DeWitt, T.J., Scheiner, S.M. (Eds.), Phenotypic Plasticity Functional and Conceptual Approaches. Oxford University Press, New York, pp. 98–111.

DeWitt, T.J., Scheiner, S.M., 2004. Phenotypic variation from single genotypes: a primer. In: DeWitt, T.J., Scheiner, S.M. (Eds.), Phenotypic Plasticity Functional and Conceptual Approaches. Oxford University Press, New York, pp. 1–9.

Dill, L., 1983. Adaptive flexibility in the foraging behaviour of fishes. Can. J. Fish Aquat. Sci. 40, 398.

Ehlinger, T.J., 1989. Learning and individual variation in bluegill foraging: habitat-specific techniques. Anim. Behav. 38, 643–658.

Gabriel, W., Lynch, M., 1992. The selective advantage of reaction norms for environmental tolerance. J. Evol. Biol. 5, 41–59.

Gaylord, T.G., Gatlin, D.M., 1996. Determination of digestibility coefficients of various feedstuffs for red drum (*Sciaenops ocellatus*). Aquaculture 139, 303–314.

Gray, C.A., McElligott, D.J., Chick, R.C., 1996. Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Mar. Freshw. Res. 47, 723–735.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

Grubich, J.R., 2000. Crushing motor patterns in drum (Teleostei: Sciaenidae): functional novelties associated with molluscivory. J. Exp. Biol. 203, 3161–3176.

Grubich, J.R., 2003. Morphological convergence of pharyngeal jaw structure in durophagous perciform fish. Biol. J. Linn. Soc. 80, 147–165.

Hjelm, J., Svanback, R., Bystrom, P., Persson, L., Wahlstrom, E., 2001. Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. Oikos 95, 311–323.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145.

Johnson, M.W., Rooker, J.R., Gatlin, D.M., Holt, G.J., 2002. Effects of variable ration levels on direct and indirect measures of growth in juvenile red drum (*Sciaenops ocellatus*). J. Exp. Mar. Biol. Ecol. 274, 141–157.

Keast, A., Webb, D., 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23, 1966.

Levins, R., 1968. Evolution in Changing Environments. Princeton University Press, Princeton, NJ.

MacArthur, Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

McEachron, L.W., Colura, R.L., Bumguardner, B.W., Ward, R., 1998. Survival of stocked red drum in Texas. Bull. Mar. Sci. 62, 359–368.

Menge, B.A., Sutherland, J.P., 1987. Community regulation — variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. Am. Nat. 130, 730–757.

Meyer, A., 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution 41, 1357–1369.

Mittelbach, G.G., Osenberg, C.W., Wainwright, P.C., 1999. Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? Evol. Ecol. Res. 1, 111–128.

Moran, N.A., 1992. The evolutionary maintenance of alternative phenotypes. Am. Nat. 139, 971–989.

Overstreet, R.M., Heard, R.W., 1978. Food of the red drum, *Sciaenops ocellatus*, from Mississippi sound. Gulf Res. Rep. 6, 131–135.

Parsons, K.J., Robinson, B.W., 2006. Replicated evolution of integrated plastic responses during early adaptive divergence. Evolution 60, 801–813.

Parsons, K.J., Robinson, B.W., 2007. Foraging performance of diet-induced morphotypes in pumpkinseed sunfish (*Lepomis gibbosus*) favors resource polymorphism. J. Evol. Biol. 20, 673–684.

Pearson, J.C., 1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. Bur. Fishs. 44, 129–214.

Robinson, B.W., Wilson, D.S., 1994. Character release and displacement in fishes. A neglected literature. Am Nat 144, 596–627.

Robinson, B.W., Parsons, K.J., 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. Can. J. Fish Aquat. Sci. 59, 1819–1833.

Rohlf, F.J., 2005a. tpsRelw. Deparment Ecology and Evolution, State Univ., Stony Brook, NY.

Rohlf, F.J., 2005b. tpsRegr, Stony Brook, NY.

Rohlf, F.J., 2006. tpsDig. Deparment Ecology and Evolution, State Univ., Stony Brook, NY.

Rohlf, F.J., Marcus, L.F., 1993. A revolution in morphometrics. Trends Ecol. Evol. 8, 129–132.

Rooker, J.R., Holt, S.A., Soto, M.A., Holt, G.J., 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. Estuaries 21, 318–327.

Rooker, J.R., Holt, S.A., Holt, G.J., Fuiman, L.A., 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. Fish B-Noaa 97, 581–590.

Ruehl, C.B., DeWitt, T.J., 2005. Trophic plasticity and fine-grained resource variation in populations of western mosquitofish, *Gambusia affinis*. Evol. Ecol. Res. 7, 801–819.

Sasaki, K., 1989. Phylogeny of the Family Sciaenidae, with Notes on its Zoogeography (Teleostei, Perciformes), Memoirs of Faculty of Fisheries, Hokkaido University. Hokkaido University Press, Hokkaido, Japan, p. 133.

Schaack, S., Chapman, L.J., 2003. Interdemic variation in the African cyprinid *Barbus neumayeri*: correlations among hypoxia, morphology, and feeding performance. Can. J. Zool.-Revue Canadienne De Zoologie 81, 430–440.

Scharf, F.S., Schlicht, K.K., 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator-prey size relationships. Estuaries 23, 128–139.

Schluter, D., 1993. Adaptive radiation in sticklebacks — size, shape, and habitat use efficiency. Ecology 74, 699–709.

Schluter, D., 2000. Ecological character displacement in adaptive radiation. Am. Nat. 156, S4–S16.

Skulason, S., Smith, T.B., 1995. Resource polymorphisms in vertebrates. Trends Ecol. Evol. 10, 366–370.

Smith, M.E., Fuiman, L.A., 2004. Behavioral performance of wild-caught and laboratory-reared red drum *Sciaenops ocellatus* (Linnaeus) larvae. J. Exp. Mar. Biol. Ecol. 302, 17–33.

Smith, T.B., Skulason, S., 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annu. Rev. Ecol. Syst. 27, 111–133.

Smits, J.D., Witte, F., Van Veen, F.G., 1996. Functional changes in the anatomy of the pharyngeal jaw apparatus of *Astatoreochromis alluaudi* (Pisces, Cichlidae), and their effect on adjacent structures. Biol. J. Linn. Soc. 59, 389–409.

Sokal, R.R., Rohlf, F.J., 1981. Biometry. W.H. Freeman and Company, New York.

Stunz, G.W., Minello, T.J., 2001. Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). J. Exp. Mar. Biol. Ecol. 260, 13–25.

Stunz, G.W., Minello, T.J., Levin, P.S., 2002. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. Mar. Ecol. Prog. Ser. 238, 227–236.

Svanback, R., Eklov, P., 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? Oikos 102, 273–284.

Swingle, W.E., 1990. Status of the commercial and recreational fishery. In: Chamberlain, G.W., M.R.J., M.G., Haby (Eds.), Red Drum Aquaculture. Texas A&M Sea Grant Program (TAMU-SG-90-603), College Station, TX, pp. 22–24.

Taylor, W.R., Van Dyke, G.C., 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9, 107.

Wainwright, P.C., Osenberg, C.W., Mittelbach, G.G., 1991. Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus). Effects of environment on ontogeny. Funct. Ecol. 5, 40–55.

Werner, E.E., Gilliam, J.F., Hall, D.J., Mittelbach, G.G., 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64, 1540–1548.

Wilson, D.S., Yoshimura, J., 1994. On the coexistence of specialists and generalists. Am. Nat. 144, 692–707.

Winemiller, K.O., Kelso-Winemiller, L.C., Brenkert, A.L., 1995. Ecomorphological diversification and convergence in fluvial cichlid fishes. Environ. Biol. Fish 44, 235–261.