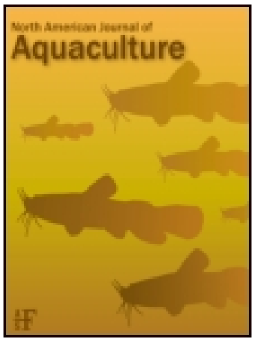

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[Article]

The Effect of Habitat Exposure and Ontogeny on the Survival Skills of Hatchery Red Drum

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Abstract.—We examined the influence of prerelease exposure to natural vegetation on the survival skills of a marine finfish, the red drum *Sciaenops ocellatus*. Red drum larvae at 18 d posthatch (10–12 mm standard length [SL]) were collected from a Texas Parks and Wildlife Department hatchery and reared with and without smooth cordgrass *Spartina alterniflora*, for either 10 or 20 d. High-speed video was then used to quantify a suite of prey capture and antipredator performance variables at days 28 (~23 mm SL) and 38 (~32 mm SL). Repeated-measures analysis of variance indicated that the timing and distance of key variables (e.g., maximum gape, time to maximum gape, gape cycle duration) increased significantly in older fish, while reaction distance and time to maximum velocity decreased with age. The time to reach maximum velocity was less for individuals reared in vegetation, yet these fish also had a shorter reaction distance to predatory stimuli and took longer to capture prey. Additionally, interindividual variability (as measured by the coefficient of variation) ranged from 0.0% to 101.3% and from 3.4% to 110.1% for the prey capture and antipredator variables, respectively, indicating that performance varied substantially among individuals. Our results indicate that while prerelease exposure to smooth cordgrass habitat does not afford any obvious survival benefits to red drum, ontogeny appears to have a direct effect on the development of key survival skills in this species.

Over the past century, increasing demands on recreationally and commercially important fish stocks have led to severe population declines worldwide. This growing trend has prompted fisheries managers to focus on stock enhancement initiatives to help remedy the current situation. One common form of stock enhancement involves large-scale releases of hatchery-reared individuals to supplement natural populations (Olla et al. 1998; Welcomme and Bartley 1998; Brown and Laland 2001). While stocking efforts have been reported in over 90 countries (Welcomme and Bartley 1998), the fate of hatchery-reared progeny in natural environments is largely unknown as estimates of survival rates are rarely documented empirically (Blankenship and Leber 1995).

Hatchery fish should demonstrate behaviors similar to those of their wild counterparts (Brown and Laland 2001); however, research has indicated that hatchery-reared individuals exhibit behavioral deficiencies in prey capture (Suboski and Templeton 1989; Ellis et al. 2002; Wintzer and Motta 2005), antipredator performance (Suboski and Templeton 1989; Álvarez and Nicieza 2003; Smith and Fuiman 2004), and the ability to use complex habitats (Stunz and Minello 2001; Stunz et al. 2001). These behaviors have been linked to the sensory-deprived hatchery environment, which is typically void of many natural elements (Olla et al. 1998).

Whereas basic survival behaviors may be compromised by the hatchery experience (Munro and Bell 1997), these deficits can be reduced via prerelease exposure to natural stimuli (Jarvi and Uglem 1993; Brown and Laland 2001). Specifically, exposing naïve hatchery fish to predators, mobile prey, or complex habitats while in captivity may stimulate the development of certain behavioral traits that improve survival (Jarvi and Uglem 1993; Brown et al. 2003; Wintzer and Motta 2005; Vilhunen 2006). For example, manipulation of the rearing environment through the addition of complex habitat or structure, also known as environmental enrichment, is thought to promote behavioral flexibility in captive animals (Hunter et al. 2002; Kempermann et al. 2002; Braithwaite and Salvanes 2005). Recent experiments with hatchery Atlantic cod *Gadus morhua* have demonstrated that even simple exposure to complex habitats (e.g., cobble and plastic kelp) aids in the development of feeding and antipredator behaviors conducive to postrelease survival in reared individuals (Brown et al. 2003; Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005). Such findings suggest that the addition of habitat to rearing vessels may affect a range of behaviors in hatchery progeny not specifically linked to the use of habitat.

In this study, we examined whether prerelease exposure to complex habitat affects the development

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of survival skills in a recreationally important marine species, the red drum *Sciaenops ocellatus*. Red drum historically supported a thriving commercial fishery in the Gulf of Mexico, and supplemental stocking programs for red drum currently exist in several U.S. states (Florida, Texas, South Carolina, and Georgia; Woodward 2000; Smith et al. 2001). Experimental evidence to date has shown that hatchery-reared red drum lack certain survival skills and experience higher mortality than their wild counterparts (Stunz and Minello 2001; Stunz et al. 2001; Smith and Fuiman 2004), and there is concern that this may reduce the effectiveness of supplemental stocking programs. We tested the hypothesis that habitat exposure will enhance survival skills in naïve hatchery red drum since rearing environments often lack structural complexity and there is evidence that the addition of habitat to these areas enhances survival behaviors in other stocked species (Berejikian et al. 2000, 2001; Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005). Moreover, hatchery managers in Texas have begun to incorporate structure into rearing ponds for red drum (R. R. Vega, Texas Parks and Wildlife Department, personal communication) since this species has been shown to use complex habitat during the early life stages (Rooker et al. 1998). To assess the effect of habitat exposure on red drum survival, a suite of prey capture and antipredator performance variables (defined here collectively as "survival skills") were quantified for fish reared with and without natural vegetation using high-speed video after predetermined exposure periods. Survival skills were quantified at two different intervals (e.g., 10 and 20 d of exposure) to assess the effect of ontogeny (i.e., age) on prey capture and antipredator performance.

Methods

Exposure trials.—The red drum larvae used for experimental trials were obtained from the Texas Parks and Wildlife Department SeaCenter hatchery in Lake Jackson. Red drum at 18 d posthatch (10–12 mm standard length [SL]) were collected from a single pond using a dip net and transported to a wet-laboratory facility in Galveston, Texas. This size was chosen since it parallels the age when wild red drum are fully recruited to estuarine nursery habitats (Rooker et al. 1999). The effect of habitat exposure on performance was evaluated by stocking red drum (35 fish per tank) into fiberglass mesocosms (1.5 m diameter, 0.75 m deep) with and without vegetation (four replicates per treatment, total = 8). Smooth cordgrass *Spartina alterniflora* at a shoot density of approximately 100 stems/m^2 was used for the vegetated treatment, which was a rough approximation of natural densities found in nearby salt marsh communities. Marsh-edge environments containing smooth cordgrass are commonly used by newly settled red drum in the northern Gulf of Mexico (Baltz et al. 1993; Stunz et al. 2002a), and, thus, represented suitable vegetation for our habitat exposure trials. Each mesocosm contained sand approximately 10 cm deep and was filled with sand-filtered seawater pumped from the Gulf. Red drum were fed a mixture of natural prey (mysid shrimp) and enriched 2-d-old brine shrimp *Artemia franciscana* once daily throughout the course of the trials. Fish were reared for either 10 or 20 d, after which SL was measured to the nearest 0.01 mm. Lighting was provided by fluorescent bulbs placed on a 12 h light : 12 h dark cycle to simulate natural light conditions.

High-speed video analysis.—At day 10 and day 20 of the rearing trials, three individual red drum were sampled at random from each tank and placed into individual chambers (18 cm × 10 cm) for high-speed video analysis. Chambers were void of vegetation as this facilitated accuracy when digitizing specific landmarks (e.g., tip of the premaxilla, center of mass). Six prey capture performance variables were quantified at both exposure periods: attack distance, mean attack velocity, capture time, maximum gape, time to maximum gape, and gape cycle duration (Table 1). Prey capture performance was evaluated by recording a series of feeding strikes on mysid shrimp, a natural prey item of red drum at this stage (Soto et al. 1998). The size of mysid shrimp prey used in this experiment was similar across all experimental trials.

Immediately following the prey capture trials, we recorded the antipredator performance of these same individuals using a visual stimulus. The stimulus consisted of a 4.5-cm-diameter bull's-eye target on a swinging pendulum arm that was modeled after Batty (1989). This apparatus has been shown to effectively produce an escape response in red drum larvae and juveniles (Fuiman and Cowan 2003; Smith and Fuiman 2004). All antipredator trials were conducted in a separate control box to minimize the effect of observer influence, and fish were allowed to acclimate for 20 min before the stimulus was introduced. The pendulum was released by the observer when the fish was near the front of the chamber and pointing towards the direction of the stimulus. Preliminary trials indicated that the velocity of the stimulus as it approached the container was approximately 120 cm/s. Six variables were recorded for red drum at day 10 and day 20, including: reaction distance, response distance (distance traveled in 100 ms), maximum velocity, time to maximum velocity, mean velocity, and maximum acceleration (Table 1). Filming began immediately

TABLE 1.—Variables associated with prey capture and antipredator performance in red drum. All variables are referenced to time zero.

Variable	Units	Description
Prey capture performance		
Attack distance	mm	Distance from the tip of the premaxilla to the closest point on the prey at the beginning of prey capture
Mean attack velocity	mm/s	Average red drum velocity from time zero to the time the prey enters the mouth
Capture time	ms	Time to the point when the prey enters the mouth
Maximum gape	mm	Greatest distance from the tip of the premaxilla to the tip of the dentary bone
Time to maximum gape	ms	Time to the point when maximum gape is reached
Gape cycle duration	ms	Time elapsed from mouth opening to closing
Antipredator performance		
Reaction distance	mm	Distance between the red drum and the center of the target at time zero
Response distance	mm	Distance traveled during the first 100 ms of a response
Maximum velocity	mm/s	Maximum velocity reached during a response
Time to maximum velocity	ms	Time to the point when maximum velocity is reached
Mean velocity	mm/s	Average velocity during a response
Maximum acceleration	mm/s^2	Maximum acceleration reached during a response

after the stimulus was released, and the pendulum was blocked before making contact with the container. During a typical antipredator event, fish bent sharply to the right or left away from the approaching stimulus (C-start) and swam rapidly towards the opposite end of the container. In many cases, we were unable to analyze an entire antipredator event since fish either made contact with the sides of the container or swam outside the field of view during the course of an escape event. Therefore, we analyzed only the first 100 ms of each event.

The prey capture and antipredator performance of each red drum was filmed at 250 frames per second (fps) using a Redlake MotionScope PCI-1000s high-speed video camera. Prey capture events were filmed laterally to the camera and antipredator events were filmed from above. A 1-cm × 1-cm grid placed behind the fish was used to provide scale during footage analysis. An average of three successful prey capture and antipredator events were recorded for each fish (three trials × three fish × two habitat treatments × two exposure periods). Each fish was given 15–20 min between successive events to allow for recovery time and prevent habituation to the stimulus. Prey capture and antipredator footages were saved to a computer hard drive and analyzed using Redlake MotionScope 2.30.0 and Peak Motus 8.0 software at 2–4× magnification. Each variable was referenced to time zero, corresponding to the frame just before mouth opening during feeding, and the frame immediately preceding the first movement during an escape response. Velocity and acceleration data were calculated by tracking a digitized point on the center of the eye during prey capture events and the center of mass during antipredator events (~30% from tip of snout, as verified from preserved specimens). Resulting displacement data were uploaded to QuickSAND (Quick Smoothing and Numerical Differentiation) software and were smoothed using a generalized cross-validatory (GCV) quintic spline (Walker 1997). The GCV algorithm has been shown to accurately estimate velocity and acceleration at the frame rate (250 fps) and magnification (2–4×) specified in this study (Walker 1998; Bergmann and Irschick 2006). A second quintic spline with a previously determined mean squared error (MSE) produced similar results to the GCV quintic spline and therefore is not reported.

Data analysis.—Data were tested for normality and equality of variance using Kolgomorov–Smirnov and Levene's tests, respectively. Significant values for three variables (reaction distance, response distance, maximum acceleration) were $\log_e$ transformed to minimize heteroscedasticity. Repeated-measures analysis of variance (ANOVA) was used to test for differences in survival skills between rearing habitats (nonvegetated versus vegetated) or days (10 versus 20 d), since fish from the same tank were not truly independent measures. Repeated measures were based upon the responses of each of three fish sampled per tank ($n = 3$) and separate repeated-measures ANOVAs were generated for each prey capture and antipredator variable. Initially, analysis was conducted on the size-removed residuals to account for any differences in size. This approach yielded similar results in regards to habitat effects, indicating that sizes were comparable across rearing treatments; however, it did not allow us to properly examine the effects of the day or the interaction term (habitat × day). Therefore, analysis of the main effects and interactions were based upon the original data rather than residuals. All statistics were conducted with SPSS statistical software (version 13.0) and at $\alpha = 0.05$, which was not adjusted as this would have compromised power estimates (Perneger 1998). Additionally, the amount of interindividual variability for red drum within each tank ($n = 3$) was measured for each prey capture and antipredator variable. Variability was quantified using the coefficient of variation, expressed as a percentage (CV = [SD/mean] × 100).

Results

Prey Capture Performance

Red drum feeding attempts were successful 87% and 90% of the time for fish reared with and without vegetation, respectively. Prey capture performance in red drum was highly stereotypical and began with an individual focusing on a particular prey and lunging toward it while rapidly opening the mouth. Once the prey entered the mouth, fish would initiate mouth closure, signifying the end of the feeding event. The duration of each feeding event ranged from 25 to 30 ms, regardless of treatment.

Repeated-measures ANOVA indicated that capture time was the only variable that was significantly different between habitats; fish reared without vegetation captured prey at a faster rate (~1 ms) than fish reared with vegetation ($F = 5.030$; df = 1, 12; $P = 0.045$; Figure 1). While the differences were not statistically significant, red drum reared with vegetation exhibited a greater attack distance, mean attack velocity, and time to maximum gape than those reared without vegetation (Figure 1). The mean ± SE standard length of red drum did not differ between nonvegetated ($n = 4$) and vegetated tanks ($n = 4$) at day 10 (23.04 ± 1.14 versus 24.25 ± 1.05 mm; $F = 0.606$; df = 1, 6; $P = 0.466$) or day 20 (32.42 ± 1.62 versus 33.29 ± 0.94 mm; $F = 0.217$; df = 1, 6; $P = 0.657$), suggesting that growth was not affected by exposure to the different habitats.

Several performance variables increased in magnitude from day 10 to day 20 in red drum (Figure 1); however, only maximum gape, time to maximum gape, and gape cycle duration were found to be significantly greater in red drum after 20 d of exposure (Figure 1D–F). This finding corresponded to a significant increase in overall SL with ontogeny (i.e., day 10 to day 20), from 23.04 ± 1.14 to 32.42 ± 1.62 mm for fish reared without vegetation ($F = 22.296$; df = 1, 6; $n = 12$; $P = 0.003$) and from 24.25 ± 1.05 to 33.29 ± 0.94 mm for fish reared with vegetation ($F = 41.161$; df = 1, 6; $n = 12$; $P = 0.001$). A significant interaction effect (habitat × day) was detected for maximum gape ($F = 12.236$; df = 1, 12; $P = 0.004$). Fish reared in vegetation had a greater maximum gape after 10 d of exposure, while the same was true for fish from nonvegetated habitats after 20 d (Figure 1D). Additionally, the CV ranged from 0.0% to 101.3% for the prey capture variables, indicating a high level of variability among individuals (Table 2). Maximum gape, time to maximum gape, and gape cycle duration exhibited the lowest CVs (≤20%), while those for attack distance, mean attack velocity, and capture time were typically higher (≥20%).

Antipredator Performance

Red drum exhibited a typical C-start escape maneuver in response to the approaching predator stimulus. When the stimulus was recognized, fish bent sharply about their center of mass away from the stimulus and accelerated forward with a single propulsive tail stroke, followed by continuous burst swimming activity.

Repeated-measures ANOVA indicated that reaction distance and time to maximum velocity were significantly greater for fish reared without vegetation (Figure 2). Reaction distance for fish from nonvegetated habitats was nearly twice the distance of that reported for individuals reared in vegetation ($F = 8.555$; df = 1, 12; $P = 0.013$). Additionally, time to maximum velocity was as much as 40% longer for fish reared in nonvegetated habitats ($F = 8.140$; df = 1, 12; $P = 0.015$). No effect of habitat was detected for the remaining antipredator performance variables (response distance, maximum velocity, mean velocity, and maximum acceleration; Figure 2).

Mean reaction distance decreased by as much as 50% from day 10 to day 20 for fish reared with ($n = 12$) and without vegetation ($n = 12$) ($F = 10.990$; df = 1, 12; $P = 0.006$; Figure 2A). Likewise, time to maximum velocity decreased approximately 40% from day 10 to day 20, although this trend only occurred for fish in the nonvegetated habitat ($F = 6.478$; df = 1, 12; $P = 0.026$; Figure 2D). The remaining four variables were not significantly different; however, interaction effects of day and habitat were detected for time to maximum velocity ($F = 7.532$; df = 1, 12; $P = 0.018$). Time to reach maximum velocity was approximately 40% longer after 10 d versus 20 d of exposure for fish reared in nonvegetated habitats but remained consistent between these exposure periods for fish reared in vegetation (Figure 2D). The CV ranged from 3.4% to 110.1% for antipredator variables (Table 2). Overall, CVs were at least 20% for the majority of variables tested; however, CVs were highest for reaction distance and maximum acceleration.

Discussion

Prey Capture Performance

Analysis of red drum feeding events indicated that prey capture performance was not significantly improved by exposure to marsh vegetation. Red drum exhibited similar feeding behaviors when capturing mysid shrimp prey, with the exception of capture time, which occurred an average of a millisecond slower for

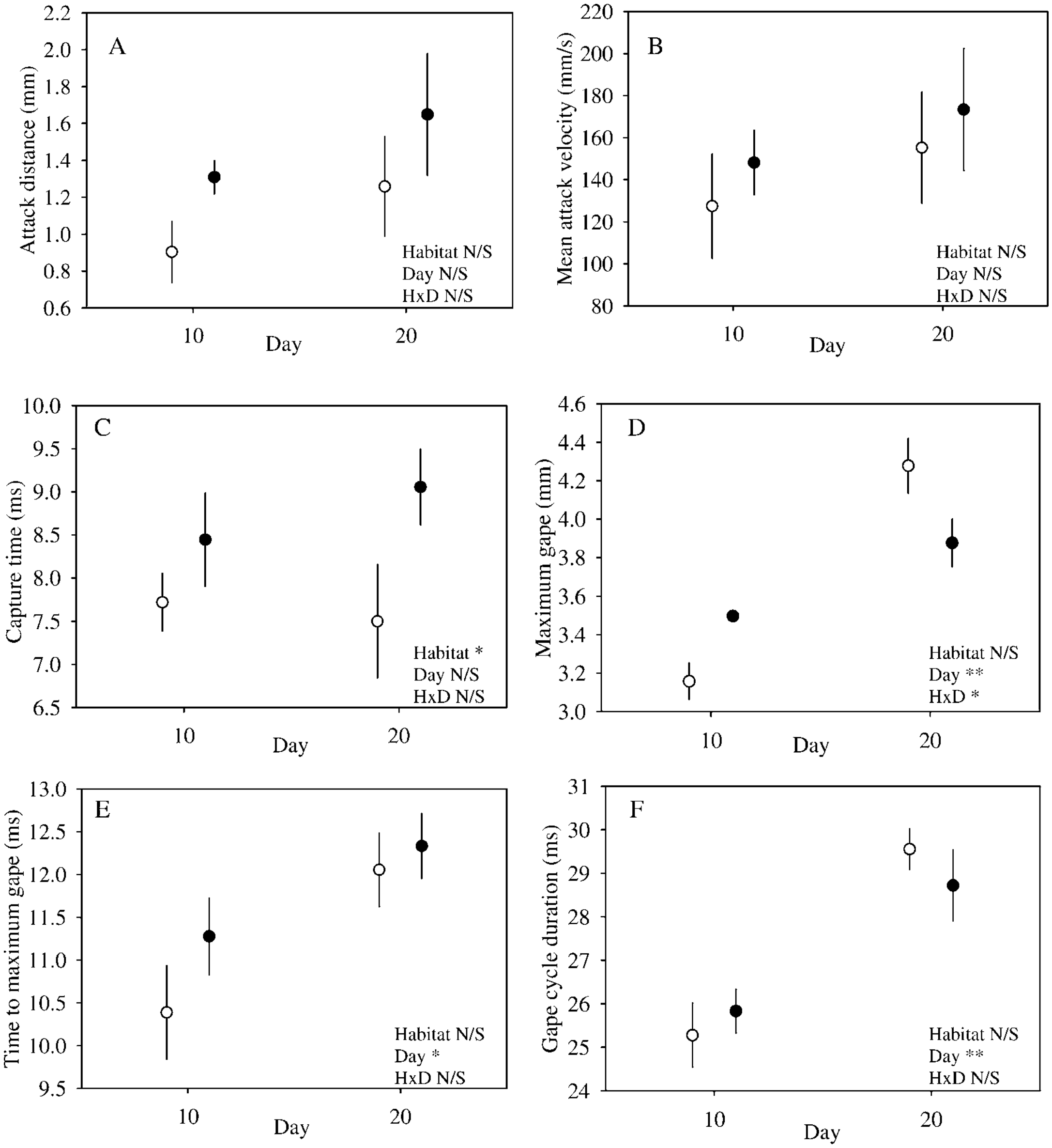

FIGURE 1.—Mean ± SE values of the variables associated with prey capture performance in red drum: (**A**) attack distance, (**B**) mean attack velocity, (**C**) capture time, (**D**) maximum gape, (**E**) time to maximum gape, and (**F**) gape cycle duration. Open circles designate nonvegetated habitats, closed circles vegetated habitats. Asterisks represent significant differences between habitats, days, and the interaction between them (H×D; *$P < 0.05$, **$P < 0.01$, N/S = not significant).

fish reared in vegetation. Although longer capture times may negatively affect feeding performance by increasing the possibility of prey escape, this did not appear to affect feeding ability in red drum, as the percentage of successful prey capture attempts was approximately 90% regardless of treatment.

Previous studies have demonstrated a negative relationship between feeding performance in fish and increasing habitat complexity. For example, mummichog *Fundulus heteroclitus* (Heck and Thoman 1981), largemouth bass *Micropterus salmoides* (Savino and Stein 1982), pinfish *Lagodon rhomboides* (Minello and Zimmerman 1983), razor fish *Pelecus cultratus* (also known as zlege; Tátrai and Herzig 1995), and stone moroko *Pseudorasbora parva* (Manatunge et al. 2000) have all shown reduced foraging efficiency (e.g.,

TABLE 2.—Variability in prey capture and antipredator performance variables among red drum reared with and without vegetation in four tanks for 10 or 20 d, as measured by the coefficient of variation ([SD/mean] × 100); T = tank.

	With vegetation								Without vegetation							
	Day 10				Day 20				Day 10				Day 20			
Variable	T1	T2	T3	T4	T1	T2	T3	T4	T1	T2	T3	T4	T1	T2	T3	T4
Prey capture performance																
Attack distance (mm)	48.3	37.4	66.4	97.9	71.7	24.2	101.3	18.2	38.9	79.9	57.5	33.0	68.9	44.9	61.4	99.5
Mean attack velocity (mm/s)	21.9	39.9	52.0	39.1	52.3	55.5	83.4	33.3	47.5	69.3	64.9	37.6	56.0	43.3	56.9	63.4
Maximum gape (mm)	2.9	10.9	17.9	14.7	16.3	11.8	9.4	9.5	15.6	13.0	2.4	5.8	15.31	14.8	18.0	17.7
Time to maximum gape (ms)	10.2	16.3	6.7	0.0	20.0	6.7	6.2	0.0	14.5	20.0	0.0	20.0	18.6	10.0	14.2	6.7
Capture time (ms)	32.7	21.7	28.6	44.1	28.6	30.1	20.8	24.7	9.1	25.0	10.2	14.8	31.2	16.7	15.8	53.3
Gape cycle duration (ms)	4.3	7.9	3.2	11.9	11.6	8.9	7.5	4.0	3.2	0.0	8.8	9.1	7.9	2.6	3.8	2.7
Antipredator performance																
Reaction distance (mm)	107.8	37.3	90.5	76.1	21.4	73.7	82.3	31.8	33.7	19.3	110.1	47.1	23.8	77.0	47.4	11.9
Response distance (mm)	3.7	24.6	22.9	17.6	57.2	37.8	28.4	23.7	56.2	45.5	31.2	6.8	78.5	4.4	23.5	12.1
Maximum velocity (mm/s)	11.5	40.3	41.3	26.5	57.1	32.4	20.8	31.1	31.8	39.5	22.5	24.6	63.5	27.7	6.3	32.6
Time to maximum velocity (ms)	10.8	52.3	57.6	78.7	7.3	18.4	56.9	41.8	14.9	18.9	44.7	41.9	35.9	34.3	25.2	35.7
Mean velocity (mm/s)	3.7	25.8	22.7	11.1	57.6	37.5	28.2	34.6	54.4	44.8	30.9	3.4	78.6	4.6	23.5	12.0
Maximum acceleration (mm/s^2)	47.2	56.7	70.9	50.5	75.6	42.6	37.4	11.3	43.7	58.2	26.5	51.7	61.3	74.7	73.4	69.0

number of prey captured) in more structurally complex environments. In some cases, the number of prey consumed decreased by as much as 50% in areas of high cover (Heck and Thoman 1981), although the overall effect of structure on feeding success varied among species (Minello and Zimmerman 1983; Winfield 1986). It should be noted that our study examined red drum prey capture performance in nonvegetated areas, but previous evidence suggests that the presence or absence of vegetation has little effect on red drum predation rates (Minello and Zimmerman 1983). As a result, it is likely that red drum feeding behaviors will remain consistent, regardless of the presence of habitat.

Ontogeny had a pronounced effect on prey capture performance in red drum. The maximum gape was larger in older red drum (20 d of exposure), corresponding to a significant increase in overall size (Richard and Wainwright 1995; Cook 1996; Hernández 2000; Huskey 2003). Larger gape would allow these individuals to exploit a wider range of prey items (Krebs and Turingan 2003), and possibly lead to a competitive advantage over younger, smaller red drum as well as other fishes. Conversely, time to reach maximum gape and gape cycle duration were longer for older red drum, probably resulting from a reduction in muscle contraction velocity with age (Richard and Wainwright 1995). As mentioned previously, slower feeding events may negatively affect prey capture performance, yet there was no indication of this during filming trials as the majority of feeding strikes (~90%) resulted in successful prey acquisition. It is noteworthy that red drum reared in vegetation had a larger gape than fish from nonvegetated tanks after 10 d of exposure, while this trend was reversed after 20 d. While the reason for this is not clear, slight size differences among fish from vegetated and nonvegetated tanks may have resulted in a significant interaction term (habitat × day) for this variable. In addition to overall differences among habitat and day treatments, a high level of variability in prey capture performance was witnessed for red drum within each tank. This was most apparent for attack distance, mean attack velocity, and capture time, for which the CVs were typically 20% or more regardless of tank. By contrast, CVs were lower ($\leq$20%) for maximum gape, time to maximum gape, and gape cycle duration. Since timing and distance of cranial elements are closely linked to size (Richard and Wainwright 1995), low CVs for these variables may reflect the restricted size range of individuals within each treatment.

Antipredator Performance

Antipredator behaviors in red drum were consistent with the typical Mauthner-initiated response described for fish (Eaton et al. 1991). In general, escape reactions of red drum reared with and without vegetation appeared to be similar for the majority of variables measured. Still, individuals reared in vegetation consistently demonstrated a shorter reaction distance to our visual stimulus. Reaction distance determines the amount of time that prey would have to fully execute escape maneuvers and reach safety (Dill 1974). For example, reacting too late (short reaction distance) may reduce the chances of prey escape, while reacting too soon (long reaction distance) could also provide the opportunity for predators to correct their path of attack, thereby influencing capture probability. Previously, Grant and Noakes (1987) demonstrated that the

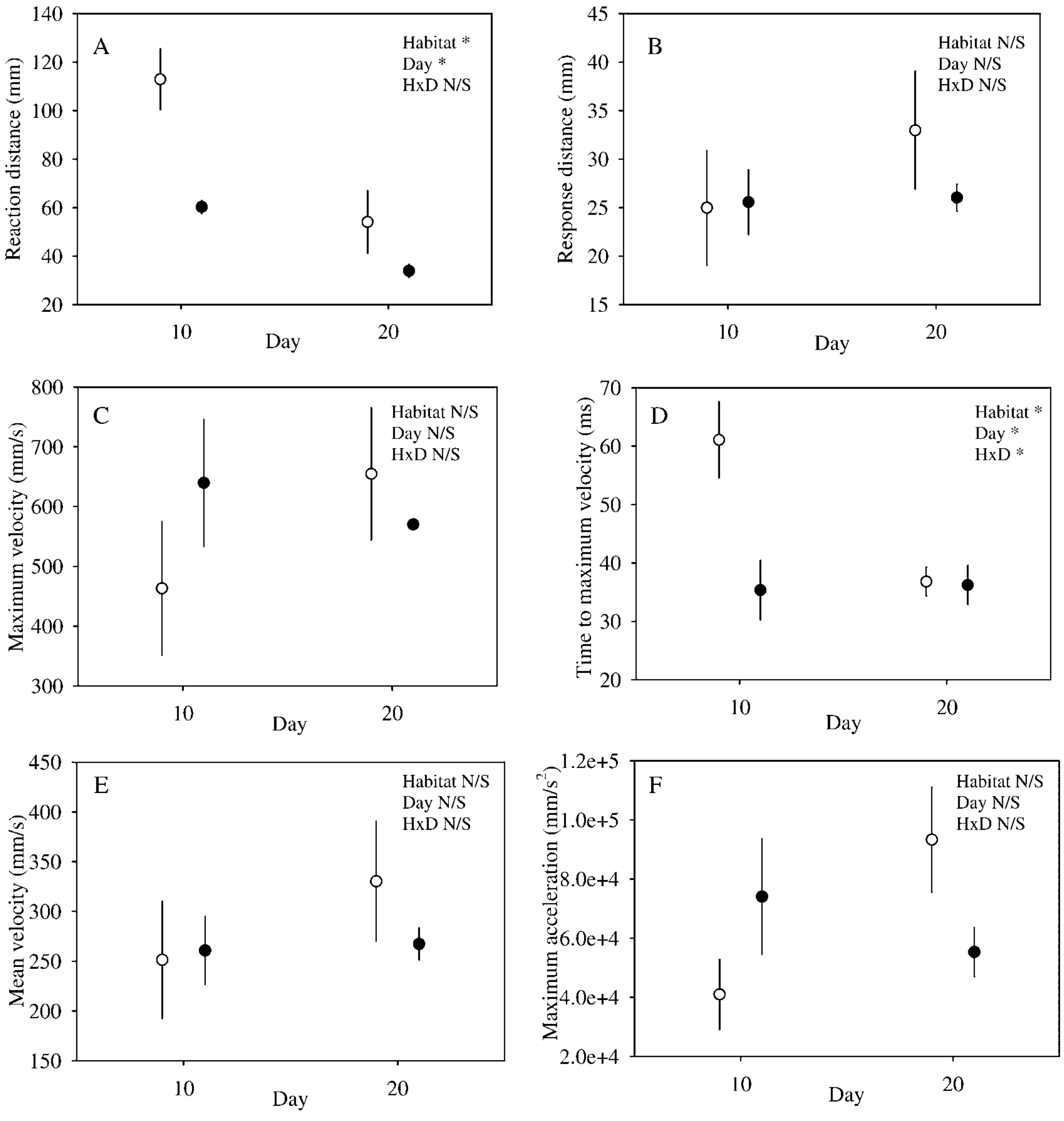

FIGURE 2.—Mean ± SE values of the variables associated with antipredator performance in red drum: **(A)** reaction distance, **(B)** response distance, **(C)** maximum velocity, **(D)** time to maximum velocity, **(E)** mean velocity, and **(F)** maximum acceleration. See Figure 1 for additional details. (Note: 2.0e + 4 = 2,000)

reactive distance of age-0 brook trout *Salvelinus fontinalis* was shorter for fish that were located in close proximity to vegetation. Grant and Noakes (1987) hypothesized that these fish adjusted their reactive distance based on the risk of predation, as approaching predators were seen as less threatening when cover was nearby. It is possible that red drum reared in vegetation also increased their reaction distance as a result of exposure to vegetation. Alternatively, exposure to vegetation may have simply resulted in red drum's being less perceptive to their surroundings and thus less responsive to the approaching stimuli, particularly since red drum from the vegetated tanks typically dispersed among vegetative clusters—in contrast to the red drum in the nonvegetated tanks, which often schooled in larger groups and displayed increased swimming activity. Interestingly, while reaction distance was shorter for red drum reared in vegetation, time to maximum velocity was generally less for these individuals, suggesting that they attempt to compensate for their latency in response by reaching their maximum swimming speed at a faster rate. This was most apparent after 10 d of exposure, with red drum reared in vegetation reaching maximum velocity approximately 40% faster than fish from nonvegetated tanks. After 20 d of exposure, this difference was almost negligible (<1%), as red drum from both vegetated and nonvegetated tanks typically attained maximum velocity at 36 ms into the response.

Ontogeny also appeared to be a significant factor in determining the extent of antipredator performance exhibited by red drum. Since visual acuity improves during ontogeny (Breck and Gitter 1983; Poling and Fuiman 1999), older fish should have larger reaction distances compared with younger individuals. Nevertheless, we observed a decrease in red drum reaction distance by almost half from day 10 to day 20 of exposure. Age may have affected motivation and physiology in red drum, as suggested by Braithwaite and Salvanes (2005) who found that Atlantic cod reared in heterogeneous environments for 20 weeks took longer to recover their opercular beat rate following a simulated predator attack compared with individuals reared for 14 weeks. Still, there is the possibility that the extended rearing time (20 d) compromised antipredator behaviors in some way that was not measured during the filming trials (e.g., declining health caused by conditioning to an artificial environment). Time to maximum velocity also decreased in older red drum; however, this difference was only witnessed for red drum reared in nonvegetated tanks. Swimming performance in fish generally improves with age, concurrent with development of the fins and increased muscle capacity (Webb and Weihs 1986; Goolish 1989; Osse and van den Boogaart 1999; Ojanguren and Braña 2003). The ability of older red drum to achieve maximum velocity at a faster rate reflects this trend and may help reduce predator efficiency on these individuals by allowing fish to move more of their body outside of the predator's gape path during an attack sequence (Paglianti and Domenici 2006). As was the case with prey capture, there was a high degree of variability in anti predator performance among the red drum within each tank. In general, the CVs were 20% or more for each of the six variables tested, although these values were highest for both reaction distance and maximum acceleration. High levels of interindividual variability may reflect the genetic diversity of the population since individuals were spawned from multiple adults (2–3 females and 2–3 males per tank, eight tanks) at the SeaCenter hatchery. Alternatively, differences in condition (e.g., gut fullness and RNA : DNA ratio) among individuals may have also influenced the CVs, but this was not directly examined. The amount of variability in this study was relatively large compared with the interindividual variability in critical swimming velocity reported for wild Atlantic salmon *Salmo salar* (9.9–35.4%; Reidy et al. 2000). Abundant food reserves and lack of predators in the hatchery environment may allow the persistence of more poorly performing individuals; therefore, the range of CVs reported here is probably not consistent with that found in wild red drum populations.

In conclusion, this study led to two major findings in regard to the prerelease exposure of red drum: (1) habitat exposure does not substantially improve survival skills and (2) prey capture and antipredator performance vary with ontogeny. Exposure to smooth cordgrass vegetation had little influence on prey capture in red drum, yet several antipredator variables decreased in magnitude as a result of this exposure. This trend was most apparent for reaction distance, suggesting that fish reared in vegetation are less responsive to an approaching stimulus, perhaps because they would be able to find shelter quickly when threatened. Consequently, we suggest that hatchery releases of red drum be conducted in close proximity to vegetated areas regardless of the condition of hatchery tanks. Exposure to other types of vegetation (e.g., sea grass) should also be investigated as these areas are important nursery grounds for red drum (Stunz et al. 2002b).

Ontogenetic effects on red drum survival skills were substantial, and several prey capture variables were found to increase with size. Conversely, several antipredator variables, including reaction distance and time to maximum velocity, decreased from day 10 to day 20, indicating that older fish may not be as responsive to an approaching stimulus as are younger individuals. Further experiments should be conducted to determine whether these differences occurred because of increasing size, age, or rearing period. Another important aspect to this study was that high levels of variability in performance were witnessed among individuals from the same tank. Although this may be linked to genetic diversity or condition, it also suggests that some individuals possess poorly developed survival skills. Such individuals may be problematic for stocking efforts, as they could fall victim to starvation and predation pressures shortly after release.

Overall, red drum reared in vegetation after 10 d appeared to perform better than fish from all other treatments in terms of prey capture and antipredator behaviors. For example, red drum reared in vegetation achieved similar behavioral levels earlier (day 10) than did fish from nonvegetated tanks. Additionally, the response of red drum reared in vegetation appeared to diminish over time. Based on this evidence, we suggest that red drum be reared in vegetated tanks and released at a younger age to solidify any survival benefits gained by habitat exposure. Finally, we suggest that future prerelease exposure trials incorporate other natural elements (e.g., predators and prey types) in addition to complex habitat to determine whether a combination of stimuli will further enhance survival behaviors in hatchery red drum.

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References

Álvarez, D., and A. Nicieza. 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. Journal of Fish Biology 63:1565–1577.

Baltz, D. M., D. Rakocinski, and J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36:109–126.

Batty, R. S. 1989. Escape responses of herring larvae to visual stimuli. Journal of the Marine Biological Association of the United Kingdom 69:647–654.

Berejikian, B. A., E. P. Tezak, T. A. Flagg, A. L. LaRae, E. Kummerow, and C. V. W. Mahnken. 2000. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. Canadian Journal of Fisheries and Aquatic Sciences 57:628–636.

Berejikian, B. A., E. P. Tezak, S. C. Riley, and A. L. LaRae. 2001. Competitive ability and social behaviour of juvenile steelhead reared in enriched and conventional hatchery tanks and a stream environment. Journal of Fish Biology 59:1600–1613.

Bergmann, P., and D. J. Irschick. 2006. Effects of temperature on maximum acceleration, deceleration, and power output during vertical running in geckos. Journal of Experimental Biology 209:1404–1412.

Blankenship, H. L., and K. M. Leber. 1995. A responsible approach to marine stock enhancement. Pages 167–175 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Braithwaite, V. A., and A. G. V. Salvanes. 2005. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. Proceedings of the Royal Society of London B 272:1107–1113.

Breck, J. E., and M. J. Gitter. 1983. Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. Canadian Journal of Fisheries and Aquatic Sciences 40:162–167.

Brown, C., T. Davidson, and K. Laland. 2003. Environmental enrichment and prior experience of live prey improve foraging behaviors in hatchery-reared Atlantic salmon. Journal of Fish Biology 63(Supplement A):187–196.

Brown, C., and K. Laland. 2001. Social learning and life skills training for hatchery-reared fish. Journal of Fish Biology 59:471–493.

Cook, A. 1996. Ontogeny of feeding morphology and kinematics in juvenile fishes: a case study of the cottid fish *Clinocottus analis*. Journal of Experimental Biology 199:1961–1971.

Dill, L. M. 1974. The escape response of the zebra danio (*Brachydanio rerio*), I. The stimulus for escape. Animal Behaviour 22:710–721.

Eaton, R. C., J. Nissanov, and R. DiDomenico. 1991. The role of the Mauthner cell in sensorimotor integration by the brainstem escape network. Brain Behavior and Evolution 37:272–285.

Ellis, T., R. N. Hughes, and B. R. Howell. 2002. Artificial dietary regime may impair subsequent foraging behaviour of hatchery-reared turbot released into the natural environment. Journal of Fish Biology 61:252–264.

Fuiman, L. A., and J. H. Cowan. 2003. Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. Ecology 84:53–67.

Goolish, E. M. 1989. The scaling of aerobic and anaerobic muscle power in the rainbow trout (*Salmo gairdneri*). Journal of Experimental Biology 147:493–505.

Grant, J. W. A., and D. L. G. Noakes. 1987. Escape behavior and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 44:1390–1396.

Heck, K. L., and T. A. Thoman. 1981. Experiments on predator–prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology 53:125–134.

Hernández, L. P. 2000. Intraspecific scaling of feeding mechanics in an ontogenetic series of zebrafish, *Danio rerio*. Journal of Experimental Biology 203:3033–3043.

Hunter, S. A., M. S. Bay, M. L. Martin, and J. S. Hatfield. 2002. Behavioral effects of environmental enrichment on harbor seals (*Phoca vitulina concolor*) and gray seals (*Halichoerus grypus*). Zoo Biology 21:375–387.

Huskey, S. H. 2003. Functional and morphological bases of intraspecific variation in the feeding ecomorphology of largemouth bass, *Micropterus salmoides*. Doctoral dissertation. Florida Institute of Technology, Melbourne.

Jarvi, T., and I. Uglem. 1993. Predator training improves the antipredator behaviour of hatchery-reared Atlantic salmon (*Salmo salar*) smolts. Nordic Journal of Freshwater Research 68:63–71.

Kempermann, G., D. Gast, and F. H. Gage. 2002. Neuroplasticity in old age: sustained fivefold induction of hippocampal neurogenesis by long-term environmental enrichment. Annals of Neurology 52:135–143.

Krebs, J. M., and R. G. Turingan. 2003. Intraspecific variation in gape–prey size relationships and feeding success during early ontogeny in red drum, *Sciaenops ocellatus*. Environmental Biology of Fishes 66:75–84.

Manatunge, J., T. Asaeda, and T. Priyadarshana. 2000. The influence of structural complexity on fish–zooplankton interactions: a study using artificial submerged macrophytes. Environmental Biology of Fishes 58:425–438.

Minello, T. J., and R. J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. Journal of Experimental Marine Biology and Ecology 72:211–231.

Munro, J. L., and J. D. Bell. 1997. Enhancement of marine fisheries resources. Reviews in Fisheries Science 5:185–222.

Ojanguren, A. F., and F. Braña. 2003. Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish 12:241–246.

Olla, B. L., M. W. Davis, and C. H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. Bulletin of Marine Science 62:531–550.

Osse, J. W. M., and J. G. M. van den Boogaart. 1999. Dynamic morphology of fish larvae, structural implications of friction forces in swimming, feeding, and ventilation. Journal of Fish Biology 55(Supplement A):156–174.

Paglianti, A., and P. Domenici. 2006. The effect of size on the timing of visually mediated escape behavior in staghorn sculpin *Leptocottus armatus*. Journal of Fish Biology 68:1177–1191.

Perneger, T. V. 1998. What's wrong with Bonferroni adjustments? British Medical Journal 316(7139):1236–1238.

Poling, K. R., and L. A. Fuiman. 1999. Behavioral specialization in developing sciaenids and its relationship to morphology and habitat. Environmental Biology of Fishes 54:119–133.

Reidy, S. P., S. R. Kerr, and J. A. Nelson. 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. Journal of Experimental Biology 203:347–357.

Richard, B. A., and P. C. Wainwright. 1995. Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. Journal of Experimental Biology 198:419–433.

Rooker, J. R., S. A. Holt, G. J. Holt, and L. A. Fuiman. 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. U.S. National Marine Fisheries Service Fishery Bulletin 97:581–590.

Rooker, J. R., S. A. Holt, M. A. Soto, and G. J. Holt. 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. Estuaries 21:315–324.

Salvanes, A. G. V., and V. A. Braithwaite. 2005. Exposure to variable spatial information in the early rearing environment generates asymmetries in social interactions in cod (*Gadus morhua*). Behavioral Ecology and Sociobiology 59:250–257.

Savino, J. F., and R. A. Stein. 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111:255–266.

Smith, M. E., and L. A. Fuiman. 2004. Behavioral performance of wild-caught and laboratory-reared red drum *Sciaenops ocellatus* (Linnaeus) larvae. Journal of Experimental Marine Biology and Ecology 302:17–33.

Smith, T. I. J., W. E. Jenkins, M. R. Denson, and M. R. Collins. 2001. Stock enhancement research with anadromous and marine fishes in South Carolina. Pages 175–189 *in* Proceedings of the thirtieth U.S.–Japan Meeting on Aquaculture. Mote Marine Laboratory, Sarasota, Florida.

Soto, M. A., G. J. Holt, and J. R. Rooker. 1998. Food habits and dietary overlap of newly settled red drum (*Sciaenops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*) from Texas seagrass meadows. Gulf Research Reports 10:41–55.

Stunz, G. W., P. S. Levin, and T. J. Minello. 2001. Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms. Environmental Biology of Fishes 61:305–313.

Stunz, G. W., and T. J. Minello. 2001. Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). Journal of Experimental Marine Biology and Ecology 260:13–25.

Stunz, G. W., T. J. Minello, and P. S. Levin. 2002a. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. Estuaries 25:76–85.

Stunz, G. W., T. J. Minello, and P. S. Levin. 2002b. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. Marine Ecology Progress Series 238:227–236.

Suboski, M. D., and J. J. Templeton. 1989. Life skills training for hatchery fish: social learning and survival. Fisheries Research 7:343–352.

Tátrai, I., and A. Herzig. 1995. Effect of habitat structure on the feeding efficiency of young stages of razor fish (*Pelecus cultratus* [L.]): an experimental approach. Hydrobiologia 299:75–81.

Vilhunen, S. 2006. Repeated antipredator conditioning: a pathway to habituation or to better avoidance? Journal of Fish Biology 68:25–43.

Walker, J. A. 1997. QuickSAND: quick smoothing and numerical differentiation for the power MacIntosh. Available: jaw.fmnh.org. (March 2007).

Walker, J. A. 1998. Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. Journal of Experimental Biology 201:981–995.

Webb, P. W., and D. Weihs. 1986. Functional locomotor morphology of early life stages of fishes. Transactions of the American Fisheries Society 115:115–127.

Welcomme, R. L., and D. M. Bartley. 1998. Current approaches to the enhancement of fisheries. Fisheries Management and Ecology 5:351–382.

Winfield, I. J. 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. Journal of Fish Biology 29(Supplement A):37–48.

Wintzer, A. P., and P. J. Motta. 2005. A comparison of prey capture kinematics in hatchery and wild *Micropterus salmoides floridanus*: effects of ontogeny and experience. Journal of Fish Biology 67:409–427.

Woodward, A. G. 2000. Red drum stock enhancement in Georgia: a responsible approach. Georgia Department of Natural Resources, Brunswick.