

Effect of predator exposure on the performance and survival of red drum (*Sciaenops ocellatus*)

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Abstract The influence of predator exposure on the survival of hatchery red drum, *Sciaenops ocellatus* was investigated under laboratory conditions. Several prey-capture (attack distance, mean attack velocity, capture time, and gape cycle duration) and anti-predator (reaction distance, response distance, mean velocity, and maximum velocity) performance variables were quantified using high-speed video for juvenile red drum (25–30 mm standard length, L_S) reared with and without predators (pinfish, *Lagodon rhomboides*). Univariate contrasts of prey-capture events demonstrated that attack distance (mean \pm s.e.) was significantly greater in red drum reared with (1.20 \pm 0.16 mm) versus without (0.65 \pm 0.09 mm) pinfish predators. During anti-predator events, red drum reared with predators had approximately 300% greater reaction distance and 20%–30% greater response distance, mean velocity and maximum velocity versus fish reared without predators; however, these differences were not statistically significant. Following video assessments, a series of mortality

experiments were conducted using free-ranging pinfish predators. Mortality rates (Z) ranged from 0.047 to 0.060 (Z /hr/predator) and did not differ significantly among treatments.

Keywords Anti-predator · Hatchery · Prey-capture · Survival skills

Introduction

During early life marine teleosts typically experience high levels of predation-related mortality, often resulting in significant losses to a cohort (Houde 1987). Predation is a strong selective force, and its pervasiveness over the course of an individual's lifetime has led to the development of various anti-predator defenses. Many of these defenses are behavioral in nature, including the ability to 'freeze' (Järvi and Uglem 1993; Brown and Smith 1998; Lehtiniemi 2005), bury (Howell and Baynes 1993; Kellison et al. 2000), school (Seghers 1974; Pitcher and Parrish 1993) or use habitat refugia (Sogard and Olla 1993; Kats and Dill 1998) when a predatory threat arises. Fish react to predatory threat based upon visual (Helfman 1989; Engström-Öst and Lehtiniemi 2004), chemical (Magurran 1989; Chivers and Smith 1994a; Kristensen and Closs 2004), and/or mechano-sensory cues (Blaxter and Fuiman 1990; Fuiman 1994). While such behaviors are often considered to be genetically based (Patten 1977; Giles 1984),

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increasing evidence suggests that anti-predator responses are often learned or modified with experience (Magurran 1990; Magurran and Seghers 1990; Kelley and Magurran 2003).

The ability of fish to 'learn' to respond to predatory threat is of particular interest to hatchery managers since fish produced for supplemental stocking are often deficient in their ability to detect and avoid predators (Olla et al. 1998). It has been argued that these deficits arise as a result of the lack of predatory stimuli in the rearing environment (Olla et al. 1998), resulting in the production of naïve progeny that experience high rates of mortality following release (Kristiansen et al. 2000; Brown and Laland 2001). Previous studies have demonstrated that exposure to predatory stimuli, whether visual (Olla and Davis 1989; Suboski and Templeton 1989; Järvi and Uglem 1993) or chemical (Brown and Smith 1998; Vilhunen 2006), may significantly enhance anti-predator behaviors and overall survival in captive-reared species. Nevertheless, few fisheries managers have applied such techniques to hatchery-release programs and many questions remain regarding the proper methods and circumstances under which they should be implemented (Brown and Laland 2001).

The purpose of this study was to determine whether exposure to predators impacts the survival of hatchery red drum, *Sciaenops ocellatus*. Red drum is an important recreational species in the U.S. and is currently the focus of several large-scale stock enhancement programs in the Gulf of Mexico and parts of the eastern seaboard (Smith et al. 2001). In Texas alone, over 460 million red drum fingerlings have been stocked into local bays and estuaries by the Texas Parks and Wildlife Department (TPWD) since the early 1980's (Robert Vega, TPWD, pers. comm.); however, there is little evidence that these fish enhance natural populations (Scharf 2000). In both laboratory (Rooker et al. 1998; Stunz and Minello 2001) and field studies (Serafy et al. 1999), hatchery red drum have been shown to experience high rates of predation. These individuals have also demonstrated deficiencies in behaviors associated with predator detection and avoidance (Smith and Fuiman 2004), and this may be linked to the absence of predators in the rearing environment. This study tested the hypothesis that exposure to predators will impact survival in hatchery red drum. Prey-capture and anti-predator performance (i.e. survival skills) of hatchery

red drum reared with and without exposure to pinfish (*Lagodon rhomboides*) predators were examined using high-speed video. Additionally, mortality experiments using free-ranging pinfish predators were conducted in order to quantify the rate of instantaneous hourly mortality (Z) experienced by individuals with and without predator exposure.

Materials and methods

Predators and prey

In May 2006, red drum were obtained from the TPWD SeaCenter (SCT) hatchery in Lake Jackson, Texas. These fish were spawned from SCT broodstock (2–3 females and 2–3 males per tank, 8 tanks) under artificial temperature and photoperiod regimes. Fertilized eggs were collected and reared in 12 000 l tanks until three days post hatch (dph), when they were transferred to a 2 acre polyethylene lined pond at SCT. Fish used in this study were collected during harvesting and randomly sampled from transport trailers. Individuals were 25–30 mm standard length (L_S), encompassing current TPWD release sizes for this species. Fish were immediately transported to a wet-lab in Galveston, Texas, where they were stocked into 37.5 l fiberglass tanks (1.5 m diameter, 0.75 m deep) containing sand-filtered water (26.5 to 29.2°C, 30 to 32 salinity) pumped from the Gulf of Mexico. Fish were fed a mixture of commercial pellet diets (Rangen and Otohime feeds), mysid shrimp (*Americamysis bahia*, <4 mm total length) and 2 and 3 day post-hatch brine shrimp (*Artemia franciscana*) enriched with Algamac 2000 (www.algamac.com) once daily.

Pinfish (*L. rhomboides*, 80–100 mm L_S) were used as predators in this study since evidence has shown that they are natural predators of red drum larvae and juveniles (Fuiman 1994; Rooker et al. 1998). Pinfish were collected from Galveston Bay, Texas, using a 50 ft bag seine and transferred to separate tanks (37.5 l) at the wet-lab in Galveston. Pinfish were fed a mixture of live and dead shrimp once daily to satiation, with food being withheld for 24 h prior to the start of all trials to encourage active feeding during exposure periods. Predators were held for less than 1 wk before use in experiments to minimize the impact of captivity on behavior.

Predator exposure trials

Twenty-four hours after collection, red drum were stocked into nine separate tanks at a density of 100 fish per tank (~ 88 fish/m³). Tanks represented three treatments: with predator, without predator, and control (sweep) (3 treatments \times 3 replicates = 9 tanks). A seine net (1.5 m \times 1.5 m) was used three to four times in each ‘control’ (sweep) treatment in order to mimic the disturbance caused by capturing pinfish, while those treatments designated as ‘without predator’ were left undisturbed. Pre-trial experiments indicated that pinfish exhibited normal feeding behaviors only when placed with another conspecific, and pinfish dramatically reduced feeding levels on red drum after 1 h. As a result, two free-ranging predators were introduced into ‘with predator’ treatments for a 1 h period over the course of five days. New predators were used for each trial to reduce any variability which could be attributed to learning effects. To keep densities consistent across all treatments as well as to reduce any ‘culling’ effects on behavioral performance (Patten 1977; Olla et al. 1992), several red drum were randomly removed from without predator and control tanks following each exposure period.

After exposure trials had been completed, three red drum were randomly selected from each tank and placed into separate chambers (18 cm \times 10 cm) containing 3 cm of seawater. Following a 4–6 h acclimation period, prey-capture and anti-predator performance behaviors were quantified using a high-speed (250 frames per second) videocamera (Redlake MotionScope PCI 1000S). A 1 cm \times 1 cm grid was used to provide scale during all filming events.

Prey-capture performance was evaluated by filming individual red drum feeding on live mysid shrimp, a major prey item for red drum larvae and juveniles (Soto et al. 1998). Several mysid shrimp were released into the chamber at a time and only those feeding events during which red drum fed at a lateral angle to the camera and remained in focus throughout the entire event were used in the final analysis. Four prey-capture variables were quantified: 1) attack distance, distance from the tip of the premaxilla to the closest point on the prey at the beginning of prey capture, mm, 2) mean attack velocity, average red drum velocity from time zero to when prey completely entered the mouth, mm/sec, 3) capture time, time to when prey completely entered the mouth, ms, and 4)

gape cycle duration, time elapsed from time zero to when mouth closes, ms.

Anti-predator performance of each red drum was recorded while responding to a visual stimulus. The stimulus consisted of a 4.5 cm diameter bulls-eye target on a swinging pendulum arm that was modeled after Batty (1989). This stimulus has previously been shown to effectively produce escape responses in red drum larvae and juveniles (Fuiman and Cowan 2003; Smith and Fuiman 2004). Each chamber was placed within a separate control box and red drum were allowed to acclimate to the chamber for 20 min before the stimulus was introduced. Anti-predator events were filmed from above and began when the red drum was near the front of the container and facing less than 90° toward the direction of the stimulus. When the red drum was in this position, the observer released the stimulus, sending it towards the fish but blocking it prior to making contact with the chamber. In many cases, red drum either made contact with the sides of the container or swam outside the field of view during the course of an escape event; therefore, only the first 100 ms of each event was analyzed. At least 15 min were allowed between anti-predator responses for each individual to prevent habituation to the stimulus. Four anti-predator variables were quantified: 1) reaction distance, distance between red drum and center of target at time zero, mm, 2) response distance, distance traveled during the first 100 ms of response, mm, 3) mean velocity, averaged velocity over the duration of response, mm/sec, and 4) maximum velocity, maximum velocity reached during response, mm/sec.

After the completion of filming trials, red drum were immediately anesthetized with tricaine methanesulfonate (MS-222) and L_5 of each fish was measured to the nearest 0.01 mm. An average of three prey-capture and three anti-predator events were recorded for each red drum (27 red drum total). These events were saved to a PC hard drive and analyzed at 2–4 \times magnification using Redlake MotionScope 2.30.0 and Peak Motus 8.0 software. Prey-capture events were referenced to time zero, corresponding to the frame prior to mouth opening during feeding, and the frame immediately preceding the first movement away from the stimulus during anti-predator events. Velocity measures were calculated by tracking a digitized point on the center of the eye during prey-capture events, and the center of mass during anti-

predator events (~30% from tip of snout, verified from preserved specimens). A generalized cross-validatory (GCV) quintic spline algorithm was applied to the displacement data using QuickSAND (Walker 1997) for accurate velocity measurements as this algorithm has been shown to accurately estimate velocity at the frame rate (250 fps) and magnification (2–4×) used in this study (Walker 1998; Bergmann and Irschick 2006).

Mortality experiments (Z)

Mortality experiments were conducted according to the protocol outlined in Rooker et al. (1998). Twenty red drum were randomly selected from each tank and placed into separate tanks (3 treatments × 3 replicates = 9 tanks) at 16:00 h and allowed to acclimate for 15 h before mortality experiments began. At 07:00 h the next day, two pinfish predators were released into each tank. After a 6 h period, pinfish were removed using a seine net and the number of surviving red drum was recorded. The remaining red drum were then captured and anesthetized with tricaine methanesulfonate for measurement purposes. Each tank was drained and refilled with water to remove any chemical alarm cues before beginning the next set of trials. Three mortality experiments were conducted for a total of 9 replicates per treatment and recovery trials were conducted after the final mortality experiment in order to determine the recovery rate of red drum in the absence of pinfish predators (Rooker et al. 1998). The protocol for the recovery trials was the same as the predation experiments with the exception that no pinfish were used. Due to limited numbers of remaining red drum, only one set of recovery trials was conducted (3 treatments × 3 replicates × 1 trial).

Data analysis

All data were tested for normality and equality of variance using Kolmogorov-Smirnov and Levene's tests, respectively. Data was regressed against L_S of each red drum in order to account for any differences in size. Repeated-measures analysis of variance (ANOVA) was conducted on the size-removed residuals for each variable since red drum within the same tank were not truly independent measures. Analysis of variance for each variable on tank means, i.e. average response of three individuals per tank, gave similar

results to repeated-measures ANOVA; therefore, results are restricted to repeated-measures ANOVA.

The following equation was used during mortality experiments to estimate instantaneous hourly mortality (Z /hr/predator):

$$Z = [\ln(N_i/N_f) - \ln(N_i/N_c)]/T*P \quad (1)$$

where N_i indicates the initial number of prey stocked within each tank, N_f is the final number of prey recovered, N_c is the mean number of prey recovered from tanks with no predators (N_c was 20 red drum or 100% for all recovery trials), T is the duration of the experiment in hours, and P is the number of predators added to each tank. This equation was the same used by Rooker et al. (1998). One-way ANOVA was used to test for differences in the instantaneous hourly mortality (Z) among treatment groups (with predator, without predator, control).

In the event that a significant treatment effect was detected for either predator exposure trials or mortality experiments, Tukey's HSD post hoc test was used to determine which factor levels differed from one another. Additionally, the amount of inter-individual variability for red drum within each tank ($n=3$) was measured for each prey-capture and anti-predator variable. Variability was quantified using the coefficient of variation, expressed as a percentage ($CV = S.D./\text{mean} * 100$). All statistics were conducted with SYSTAT (version 12.0) and SPSS (version 13.0) statistical software and $\alpha=0.05$.

Results

Predator exposure trials

Pinfish began actively pursuing red drum prey within 5–10 min after release. Red drum reared with predators responded to predatory attacks by schooling at the surface and becoming mottled in coloration, indicating that fish were in distress. Such behaviors were not observed for individuals from tanks without predators. On average, two to five red drum were consumed by pinfish during the 1 h exposure periods. Final red drum L_S (mean ± s.e.) were 30.33 ± 0.29 mm (with predator), 29.06 ± 0.58 mm (without predator), and 29.83 ± 1.04 mm (control) and no significant differences in L_S were found among treatments

(ANOVA, d.f.=2 and 6, $P=0.482$). The amount of inter-individual variability (CV) was high, ranging from 3.8% to 98.9% and 3.3% to 88.8% for prey-capture and anti-predator performance variables, respectively (Table 1).

Red drum prey-capture attempts were successful $\geq 95\%$ of the time, regardless of treatment. Attack distance (ANOVA, d.f.=2 and 6, $P=0.025$) and gape cycle duration (ANOVA, d.f.=2 and 6, $P=0.037$) differed significantly among treatment groups. Tukey’s HSD test found that red drum reared with predators had approximately 2× greater attack distance than those reared without predators (Tukey, d.f.=2 and 6, $P=0.022$), while individuals from control treatments exhibited longer gape cycle duration (5 ms) than those reared without predators (Tukey, d.f.=2 and 6, $P=0.031$) (Fig. 1a, d). Mean attack velocity (ANOVA, d.f.=2 and 6, $P=0.158$, power=0.331) and capture time (ANOVA, d.f.=2 and 6, $P=0.249$, power=0.242) did not differ significantly among treatments; however, both variables were greatest for red drum reared with predators (Fig. 1).

No significant differences among treatment groups were found for reaction distance (ANOVA, d.f.=2 and 6, $P=0.387$, power=0.167), response distance (ANOVA, d.f.=2 and 6, $P=0.188$, power=0.295), mean velocity (ANOVA, d.f.=2 and 6, $P=0.197$, power=0.286), or maximum velocity (ANOVA, d.f.=2 and 6, $P=0.212$, power=0.272). Nevertheless, mean values for all four variables were noticeably greater for red drum reared with predators (Fig. 2). In particular, reaction distance

of red drum reared with predators was almost 3× greater than that of red drum reared without predators (Fig. 2a). Response distance, mean velocity, and maximum velocity of red drum from predator treatments were also 20%–30% greater for individuals reared with predators (Fig. 2b, c, d).

Mortality experiments (Z)

Instantaneous hourly mortality (Z) rates of hatchery red drum did not differ significantly among treatments (ANOVA, d.f.=2 and 6, $P=0.840$, power=0.067). Overall, mean Z (\pm s.e.) for the three predation experiments were 0.056 ± 0.009 , 0.047 ± 0.015 , and 0.060 ± 0.020 , for with predator, without predator, and control treatments, respectively. Daily Z rates were highly variable among replicates as well as days (Fig. 3). For example, red drum reared without predators experienced greater mortality rates compared to red drum reared with predators on day 1, yet this trend was reversed on day 2 and day 3 (Fig. 3).

Discussion

During prey capture, several variables were found to differ significantly among treatments (with predator, without predator, control). Red drum reared with predators attacked mysid shrimp from a further distance compared to individuals reared without predators. Greater attack distance may lower the

Table 1 Variability in prey-capture and anti-predator performance variables for hatchery red drum within each tank ($n=3$) as measured by the coefficient of variation (CV = SD/mean * 100)

Variable	w/ Predator			w/o Predator			Control		
	Tank 1	Tank 2	Tank 3	Tank 1	Tank 2	Tank 3	Tank 1	Tank 2	Tank 3
Prey-capture performance:									
Attack distance (mm)	33.2	57.2	98.9	33.5	31.5	27.7	91.8	8.4	28.7
Mean attack velocity (mm/sec)	14.0	43.9	28.8	35.9	64.9	34.7	47.5	28.6	52.7
Capture time (ms)	17.3	11.9	35.3	13.9	10.2	20.0	28.6	19.9	17.6
Gape cycle duration (ms)	3.8	8.3	21.8	4.5	17.3	22.9	15.4	12.0	4.6
Anti-predator performance:									
Reaction distance (mm)	27.4	88.8	59.5	11.5	35.8	45.4	7.1	38.8	8.3
Response distance (mm)	42.4	57.6	28.1	29.9	36.5	28.3	15.7	43.1	8.6
Mean velocity (mm/sec)	41.7	58.9	26.2	29.1	37.0	30.5	16.3	43.1	10.2
Maximum velocity (mm/sec)	38.9	65.5	25.9	3.3	9.7	17.1	8.0	26.4	12.8

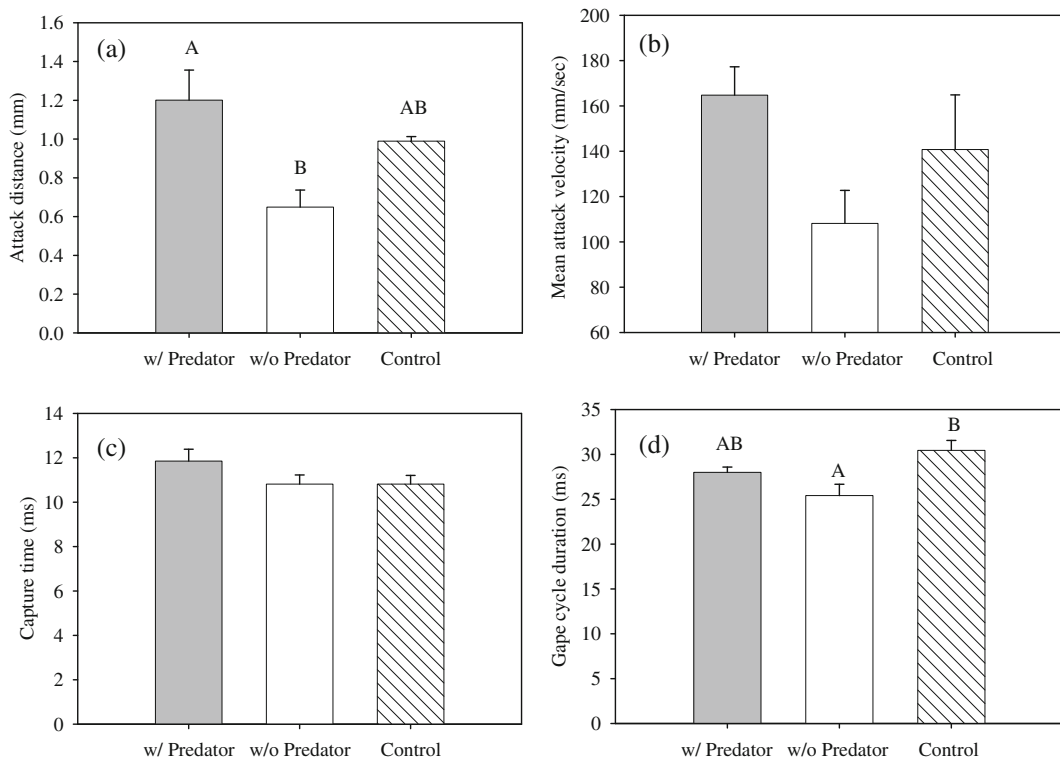


Fig. 1 Mean \pm s.e. for prey-capture performance variables in red drum: **a** attack distance, **b** mean attack velocity, **c** capture time, and **d** gape cycle duration. Upper case letters represent

significant differences based on Tukey's HSD post hoc tests ($P < 0.05$). Treatments = ■, With predator; □, Without predator; ▨, Control

probability that prey may detect an approaching predator (Hunter 1972; Heath 1993; MacKenzie and Kjørboe 2000), possibly enhancing capture success. The ability to attack from a further distance would be especially beneficial when feeding on more elusive prey items such as copepods as these zooplankters possess a large number of mechanoreceptors (Kerfoot et al. 1980). While the mechanism for this difference is not clear, these results indicate that exposure to predatory stimuli may impact feeding performance in this species. Gape cycle duration was also found to be significantly greater for red drum from control tanks versus those reared without predators. It has been suggested that a longer gape cycle may negatively impact feeding performance by increasing the prey's chances of escape (Wintzer and Motta 2005); however, this did not appear to influence prey-capture ability in red drum as feeding attempts were $\geq 95\%$ across all treatments. Although not significant, overall trends indicated that mean attack velocity, capture time, and gape cycle duration were all greater in red drum reared with versus without predators. This suggested

that red drum reared with predators approached prey more quickly, yet took longer to acquire prey during feeding attempts.

Numerous studies have demonstrated that exposure to live predators improves anti-predator behaviors in naïve fish (Järvi and Uglem 1993; Malavasi et al. 2004). For example, Nødtvedt et al. (1999) reported that 'predator-trained' cod (*Gadus morhua* L.) maintained longer distances to a predator than 'predator-naïve' individuals, while Dill (1974) documented that escape velocity of the zebra danio (*Danio rerio* Hamilton) increased significantly in naïve fish following exposure to predatory stimuli. In this study, hatchery red drum exposed to predators demonstrated a 300% increase in reaction distance and 20%–30% increase in response distance, mean velocity, and maximum velocity relative to individuals receiving no predator exposure; however these differences were not significant. Greater distances and velocities during anti-predator responses have been shown to increase the chances of surviving a predation strike in the guppy, *Poecilia reticulata* (Peters) (Walker et al.

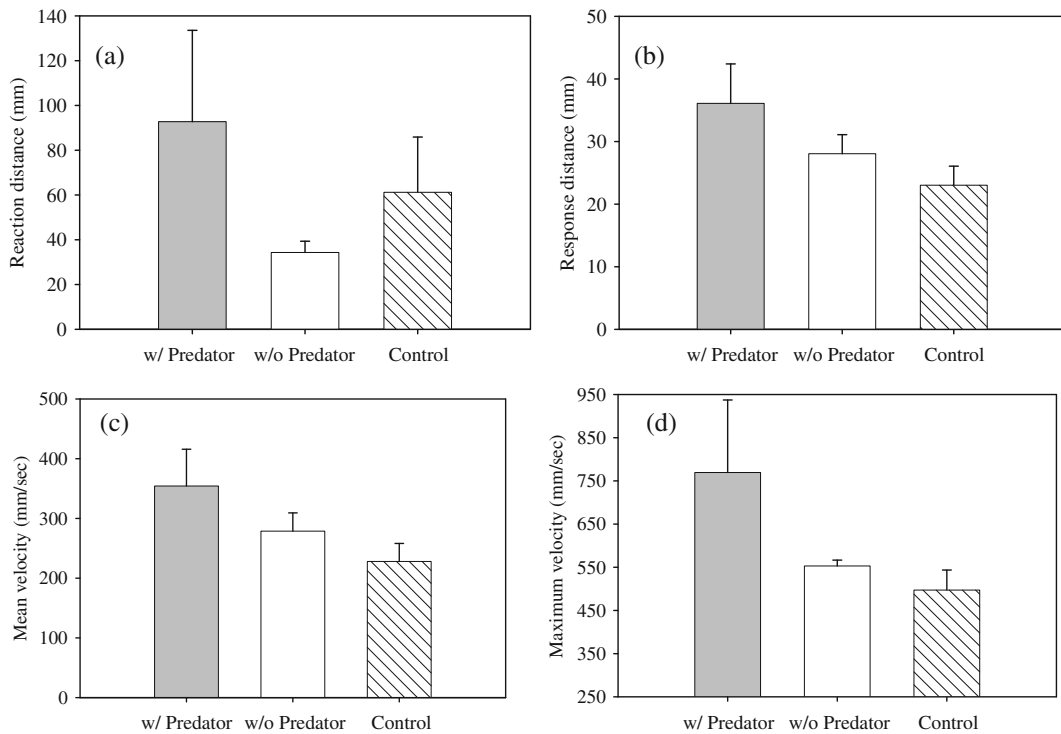


Fig. 2 Mean \pm s.e for anti-predator performance variables in red drum: **a** reaction distance, **b** response distance, **c** mean velocity, and **d** maximum velocity. Treatments = ■, With predator; □, Without predator; ▨, Control

2005). Fuiman et al. (2006) also demonstrated that greater reactive distance and swimming speeds are linked to escape potential in red drum.

Behavioral studies are often confounded by high amounts of variability among individuals (Gregory

and Wood 1998; Kolok et al. 1998) as well as populations (Nicoletto and Kodric-Brown 1999; Pon et al. 2007). Here, the level of inter-individual variability (CV) for red drum within each tank (3.8%–98.9% and 3.3%–88.8% for prey-capture and anti-predator variables, respectively) were much higher than that reported for other species such as coho salmon, *Oncorhynchus kisutch* (Walbaum) (9.5%–16.6%, Taylor and McPhail 1985), yellow perch, *Perca flavescens* (Mitchill) (9.7%–15.6%, Nelson 1989), and Atlantic cod, *Gadus morhua* L. (9.9%–35.4%, Reidy et al. 2000). Intra-cohort variability in performance has been documented for larval red drum (Fuiman et al. 2005), and increased variability may be related to the fact that red drum were spawned from multiple breeding pairs in the hatchery. These elevated CV values may have also contributed to the low power ($\beta < 0.300$) associated with statistical tests, thus the lack of significant findings in the present study may be linked to high variability (low power).

Average mortality rates (Z/hr/predator) for juvenile hatchery red drum were approximately 3–4×

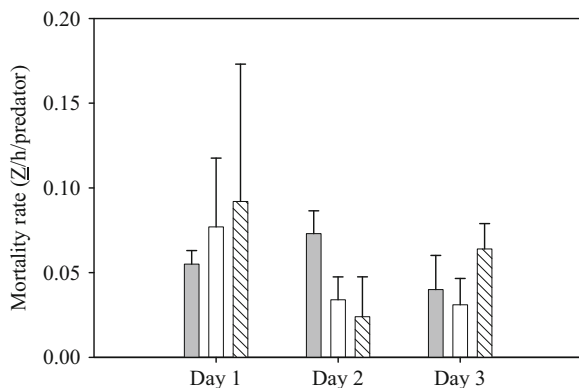


Fig. 3 Comparison of instantaneous hourly mortality (Z) of hatchery-reared red drum exposed to pinfish (*Lagodon rhomboides*) predators across days. Bars represent mean \pm s.e for red drum from with predator (■), without predator (□), and control (▨) treatments

lower than previously reported values for red drum larvae ($Z=0.192$, 3.6–6.9 mm L_S , Fuiman 1994) and early juveniles ($Z=0.193$, 10.7–20.9 mm L_S , Rooker et al. 1998). Evidence suggests that responsiveness to predatory stimuli increases with ontogeny in red drum (Fuiman 1994) and other species such as herring, *Clupea harengus* L. (Blaxter and Fuiman 1990). Moreover, the vulnerability of red drum to piscivores has been shown to decrease substantially when individuals exceed 20 mm in total length (Fuiman 1994). Thus, the larger sizes of red drum in this study (25–30 mm L_S) may have influenced the amount of predation within each tank, resulting in lower Z rates compared to previous predation trials for this species. Physical differences between this study and others (container volume, De Lafontaine and Leggett 1988; Cowan and Houde 1993; temperature, Elliott and Leggett 1996, 1997) may have impacted the degree of mortality experienced by red drum, and therefore cannot be ruled out as possible sources of variability. Interestingly, a high level of variability in Z was detected among tank replicates as well as among days. Rooker et al. (1998) and Fuiman (1994) also documented variability for red drum mortality rates among replicates when using pinfish predators, suggesting that predator motivation may vary substantially within this species.

This study indicated that predator exposure impacts survival skills linked to prey-capture and anti-predator performance in hatchery red drum. Experimental evidence has shown that even a single exposure to predatory stimuli enhanced survival behaviors in naïve fathead minnows, *Pimephales promelas* (Rafinesque) (Gazdewich and Chivers 2002), while repeated exposure events were needed to produce similar responses in Arctic charr, *Salvelinus alpinus* L. (Vilhunen 2006). Thus the timing and duration of exposure needed for naïve individuals to learn to avoid predators may vary among species. In some cases, the use of chemical cues, either alone (Brown and Smith 1998; Mirza and Chivers 2001) or in combination with visual stimuli (Chivers and Smith 1994a, b; Wisenden et al. 2004), are necessary to train naïve fish to respond to predators similar to that of their wild counterparts. Here, the use of live predators allowed red drum to be subjected to a variety of cues (e.g. visual, chemical, and mechano-sensory) during exposure periods, all of which have been shown to be important in the development of predator detection and avoidance behaviors.

Although there are ethical concerns with using live predators (Huntingford 1984), such methods may provide the necessary stimuli in order to properly train naïve individuals for subsequent predator-prey encounters. Currently, no exposure protocol exists for red drum; however, findings of this study suggest that even short exposure durations (1 h/day for 5 days) can influence survival behaviors, i.e. greater distances and velocities, of naïve hatchery individuals. While these results are encouraging, future studies should investigate whether longer exposure periods, exposure at different ontogenetic stages and/or the use of alternate predators or cues may lead to significant differences in the survival behaviors of hatchery red drum.

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