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## Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early-life survival enhanced by seagrass meadows?

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**Abstract** We conducted predation experiments to evaluate the vulnerability of red drum *Sciaenops ocellatus* (Linnaeus) larvae and early juveniles to pinfish *Lagodon rhomboides* (Linnaeus) predators. Experiments were designed to analyze the effects of habitat complexity, prey size, and rearing condition on prey vulnerability. Three structurally different habitats [unvegetated (substrate only), shoal grass *Halodule wrightii* (Aschers) and turtle grass *Thalassia testudinum* (Bank ex König)] were simulated in experimental mesocosms. Instantaneous hourly mortality rates ( $Z \text{ h}^{-1} \text{ predator}^{-1}$ ) for hatchery-reared red drum were significantly higher in the unvegetated habitat (0.189) than in either shoal grass (0.069) or turtle grass (0.046). A similar trend in predation mortality was observed for wild-caught red drum; instantaneous hourly mortality rates were 0.166, 0.047, and 0.021 in unvegetated, shoal grass, and turtle grass habitats, respectively. Mortality rates (adjusted means) for hatchery red drum were higher than for wild individuals in all three habitats; however, the differences were not significant. Predation mortality decreased with increasing prey size (3 to 9% decrease in  $Z$  per mm increase in length), suggesting that small red drum (i.e. new settlers) were most vulnerable to predators. We conclude that habitat complexity is critical to the survival of newly settled red drum, and changes in the complexity or areal coverage of natural seagrass meadows may affect early-life survival and possibly recruitment levels.

### Introduction

Predation-mediated mortality is typically high during the early life-stages of fishes (Houde 1987), and is thought to be of major importance in determining recruitment and year-class strength (Leggett and DeBlois 1994; Paradis et al. 1996). Vulnerability of larvae and juveniles to predators is essentially the product of a series of probabilities (i.e. encounter, attack, and capture), and each component is regulated by a variety of biotic and abiotic factors (Fuiman and Magurran 1994). Consequently, early-life predation mortality is often variable and unpredictable (Bailey and Houde 1989), and it is difficult to identify and partition the controlling factors, particularly under natural conditions.

Empirical data from laboratory and enclosure studies on predation have provided important insight into the causal mechanisms of early-life mortality. Experiments in mesocosms have been used to investigate a variety of factors that influence the vulnerability of fish larvae and juveniles to predators, including prey size and age (Fuiman 1989; Litvak and Leggett 1992; Pepin et al. 1992; Fuiman 1994; Juanes and Conover 1994), predator and prey density (Fuiman and Gamble 1989; Cowan et al. 1992; Purcell et al. 1994), condition of prey (Gamble and Fuiman 1987; Rice et al. 1987), and physical conditions (e.g. temperature: Elliot and Leggett 1996). Experimental work has significantly enhanced the understanding of predation-mediated processes, particularly for pre-settlement larvae. However, assessments of prey vulnerability during the settlement period are less common (Van der Veer and Bergman 1987; Hixon 1991; Carr and Hixon 1995), and environmental factors such as habitat complexity and rearing condition warrant further consideration.

Red drum *Sciaenops ocellatus* (Linnaeus) is a common inhabitant of estuaries and coastal waters in the Gulf of Mexico, and an important part of the recreational fishery (Swingle 1990; NOAA 1991). Spawning commonly occurs from September to November, and

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spawning grounds range from nearshore (i.e. tidal passes) to offshore locales in the Gulf (Peters and McMichael 1987; Comyns et al. 1991). In south Texas, tidal currents move eggs and larvae into estuarine nursery grounds and settlement occurs in demersal habitats when larvae reach 6 to 8 mm (Holt et al. 1983; Rooker et al. 1997). Although settlement in unvegetated habitats (e.g. sand and mud bottom) occurs, the majority of red drum settle in seagrass meadows (Holt et al. 1983; Rooker and Holt 1997), suggesting that the structural complexity of the seagrass canopy affords some benefit to settlers.

In the present study, we report the use of experimental mesocosms to assess the effect of habitat complexity on predation mortality of newly settled red drum. The effect of complexity was examined by measuring predation mortality in three structurally different nursery habitats: unvegetated (substrate only), shoal grass *Halodule wrightii* (Aschers), and turtle grass *Thalassia testudinum* (Bank ex König). Since prey size is an important factor of predation (Bailey and Houde 1989; Pepin et al. 1992; Paradis et al. 1996), we examined the effect of size-selective vulnerability to predators by running trials on different sizes of red drum, but holding predator size constant. In addition, trials were conducted on both hatchery-reared and wild-caught red drum to assess the importance of rearing condition on predation mortality.

## Materials and methods

### Predators and prey

Larvae and early juveniles of hatchery and wild red drum, *Sciaenops ocellatus* (Linnaeus) were used as prey in this study. Hatchery red drum larvae came from induced spawns at the Texas Parks and Wildlife GCCA-CPL Marine Research Center located in Flour Bluff, Texas. Eggs from hatchery spawns were initially placed in 150-liter cone-bottom, vertical tanks maintained at 26 °C, and hatched within 24 h. At 3 d post-hatch, larvae were transferred to 0.4 or 0.8-hectare ponds. Larvae were reared on wild zooplankton and remained in ponds at the Flour Bluff facility for at least 15 d before being collected by dip net for predation experiments. Wild red drum were seined from seagrass meadows in the Aransas Estuary, Texas (27°52'N; 97°02'W). Actively swimming larvae were removed from the seine with a 5 cm diam cup, size-sorted (a limited size range was targeted on each sampling trip), and placed into a cooler filled with seawater. Hatchery and wild red drum were transferred to The University of Texas Marine Science Institute—Fisheries and Mariculture Laboratory (FAML) and placed into 0.75 m<sup>3</sup> circular tanks filled with filtered seawater. Both hatchery and wild larvae were fed brine shrimp nauplii (*Artemia* sp.) and commercial fry feed (BioKyowa, Rangen). Wild red drum were held at FAML no longer than 2 d to minimize changes in behavior and nutritional condition arising from captivity.

The pinfish *Lagodon rhomboides* (Linnaeus) was chosen as the predator because this species is the dominant taxon inhabiting seagrass meadows in the Aransas Estuary (Rooker et al. 1998). Moreover, Fuiman (1994) showed that pinfish are voracious predators of red drum larvae in controlled laboratory and mesocosm experiments. Pinfish were seined from seagrass meadows in the Aransas Estuary and transported to FAML, where they were placed in 0.75 m<sup>3</sup> tanks filled with filtered seawater. Pinfish were fed commercial feed (Rangen) in holding tanks, and food was

withheld for 24 h prior to the initiation of a predation trial. Changes in foraging behavior were minimized by using predators only once or twice and restricting their time in captivity to less than 1 wk. The standard length of predators used in all trials was restricted (68 to 82 mm) to minimize predator-prey scaling effects on vulnerability (Fuiman 1994). Temperature and salinity in predator and prey holding tanks were maintained at 26 °C ( $\pm 1$  °C) and 33‰ ( $\pm 2$ ‰).

### Predation experiments

Predation experiments were conducted in 0.48 m<sup>3</sup> circular fiberglass tanks (1.0 m diam  $\times$  0.6 m height) located outdoors at FAML. To moderate daily temperature fluctuations, tanks were placed inside a 28.0 m<sup>3</sup> circular tank (6.0 m diam) filled with 0.5 m seawater. A fiberglass shade cloth (60% decrease of incident light) was also positioned 2.5 m above the tanks. Consistent water quality was maintained by replacing the water in the tanks with ozone-treated seawater every 1 to 2 d, using a flow-through system.

Three structurally different habitats were simulated to assess the effect of complexity. Two different seagrass species, shoal grass *Halodule wrightii* (Aschers) and turtle grass *Thalassia testudinum* (Bank ex König), were transplanted into experimental tanks. Whole-plant seagrass cores (15 cm diam) of both species were taken from one site in the Aransas Estuary, Texas. Approximately 48 cores were transplanted into each tank. Resulting shoot densities (mean  $\pm$  SE) were 8110 m<sup>-2</sup>  $\pm$  575.9 and 1018 m<sup>-2</sup>  $\pm$  130.5 for shoal and turtle grass, respectively. Shoot densities in the tanks were representative of values observed in the Aransas Estuary during the fall (Dunton 1994; Lee and Dunton 1996). In addition to shoal and turtle grass, an unvegetated treatment was included in the experimental design. Similar to seagrass habitats, the substratum in unvegetated tanks (silt-sand sized particles) was 10 to 12 cm deep. Four replicates were simulated for each of the three habitats, resulting in 12 mesocosms.

Effects of prey size and rearing condition (hatchery vs wild) were examined by conducting several separate trials on red drum. A series of seven trials employing all 12 mesocosms was conducted using hatchery red drum ( $N = 28$  replicates per habitat). The size of hatchery red drum (mean  $\pm$  1 SE) used in each trial differed: 10.7  $\pm$  0.2, 12.2  $\pm$  0.3, 13.6  $\pm$  0.2, 15.3  $\pm$  0.3, 16.6  $\pm$  0.5, 17.9  $\pm$  0.4, 20.9  $\pm$  0.3. Different size classes of wild red drum were also examined in experimental mesocosms: the mean size of wild red drum used in each of four trials was 11.8  $\pm$  0.1, 14.7  $\pm$  0.2, 15.1  $\pm$  0.3, 19.5  $\pm$  0.3. Due to limited numbers of fish collected, trials using wild red drum were based on 2, 3 or 4 sets of the three treatments (6 to 12 mesocosms per trial, respectively;  $N = 12$  replicates per habitat).

Predation trials were conducted from September to November 1996 at water temperatures and salinities ranging from 22.0 to 26.5 °C and 30.0 to 36.0‰. Each trial required 2 d to complete, and our sampling protocol was similar to the design used by Fuiman (1994). A few hours before sunset on the first day of each trial, red drum were removed from holding tanks, counted, and placed in 1-liter beakers filled with seawater (20 per beaker). In addition, a sample of 20 individuals was immediately returned to the laboratory, anesthetized with tricaine methanesulfonate (MS-222), and measured (standard length) to the nearest 0.1 mm to estimate the initial mean prey length of the trial. After  $\approx$ 30 min, the prey in the beakers were examined, and individuals showing signs of injury were replaced. At 17:00 hrs, prey were transported to mesocosms and stocked at a rate of 20 individuals per tank (25.5 m<sup>-2</sup>). Stocking density in mesocosms was higher than natural densities observed for wild populations of red drum; however, densities of this magnitude have been reported for other sciaenid larvae and juveniles in seagrass meadows (Rooker et al. 1998). Prey were allowed to acclimate to mesocosms for 15 h before predators were introduced at 08:00 hrs the following day. Two pinfish were placed in each mesocosm and prey were exposed to predators for 6 h. Following the exposure period, predators and the remaining prey were removed by bubbling CO<sub>2</sub> into the mesocosms to anesthetize

the fishes. Predators generally responded before prey, and thus predation on red drum during the delivery of CO<sub>2</sub> was not a concern. Induction times averaged 2 to 10 min, after which predators and prey surfaced due to a loss of equilibrium. Individuals at the surface were collected with dip nets and counted. Recovery operations lasted 1 to 2 h, depending on the number of mesocosms used. Thus, exposure periods sometimes lasted beyond 6 h. Nevertheless, no adjustments were made to exposure times because the presence of collectors in and around mesocosms during recovery operations appeared to terminate predator activity. The collection sequence was randomly stratified among treatments to minimize collection bias. Sodium bicarbonate (NaHCO<sub>3</sub>) was added to mesocosms following recovery operations to adjust for changes in pH caused by the addition of CO<sub>2</sub>.

Control trials were conducted to determine recovery rates in the absence of predators. The protocol was identical to predation trials; however, no pinfish were added. Control trials were performed throughout the study, generally before or after each predation trial. Recovery rates were estimated from a series of control trials using partial and full complements of mesocosms. Overall, mean recovery rates were estimated in 51 mesocosms (17 replicates per treatment).

#### Data analysis

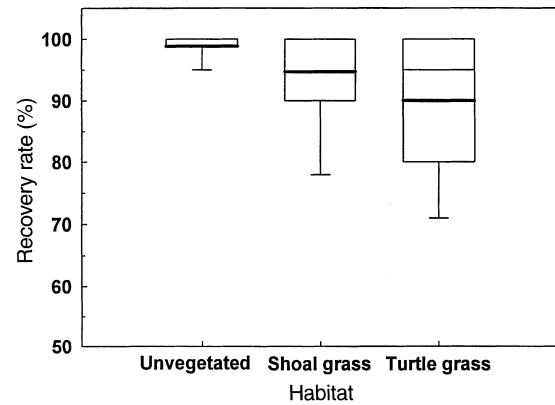
Instantaneous hourly mortality rates per predator ( $Z \text{ h}^{-1} \text{ predator}^{-1}$ ) were calculated using the equation (modified from Fuiman 1994):  $Z = [\ln(N_i/N_f) - \ln(N_i/N_c)]/T \cdot P$ , where  $N_i$  = initial number of prey stocked in each mesocosm,  $N_f$  = final number of prey recovered,  $N_c$  = mean number of prey recovered in control trial (no predators),  $T$  = duration of predation trial in hours, and  $P$  = number of predators added to each mesocosm.

Relationships between instantaneous hourly mortality rates ( $Z$ ) and the effects of habitat complexity and prey size were evaluated using an interaction-regression model (Wilkinson et al. 1996). This type of regression is similar to an analysis of covariance (ANCOVA) model, with one continuous variable (covariate) and one categorical variable (factor). However, the model also includes an interaction term (covariate  $\times$  factor). Differences in recovery rates among control treatments were also determined using interaction regression. In both control and predation trials, length and habitat represented the continuous and categorical factors, respectively. Alternatively, differences in mortality rates between hatchery and wild red drum were examined using an ANCOVA model, since length adjustments between treatments were necessary. The assumption of homogeneity of slopes was satisfied ( $p > 0.05$ ) prior to ANCOVA-testing. Models detecting a significant treatment effect (i.e. habitat complexity) were further examined with Tukey's HSD multiple-comparisons to test for differences ( $\alpha = 0.05$ ) among treatment means (Zar 1996).

## Results

### Control trials

Recovery of *Sciaenops ocellatus* from mesocosms without pinfish (*Lagodon rhomboides*) predators was generally high (~95%), but differed among habitats ( $p = 0.004$ ,  $df = 2$ , 48,  $F = 6.274$ ; Fig. 1). The mean recovery rate in the unvegetated habitat (98.8%) was greater than estimates in shoal grass (*Holodule wrightii*) and turtle grass (*Thalassia testudinum*) (94.7 and 90.0%, respectively). Tukey's HSD comparisons revealed that recovery rates in turtle grass were significantly lower than in shoal or unvegetated habitats. As a result, separate mean recovery rates were used in the calculation of instantaneous mortality rates for each habitat. No



**Fig. 1** *Sciaenops ocellatus*. Recovery rates of red drum in control trials (no predators). Interquartile range (25th and 75th percentile) is shown by extent of boxes, with normal and boldface horizontal lines within boxes representing median (50th percentile) and mean, respectively (Error bars range of 10th and 90th percentiles)

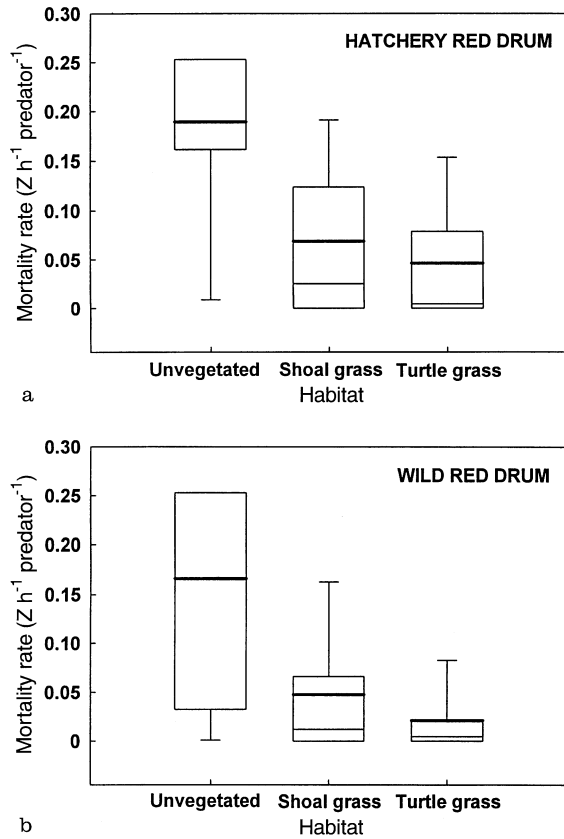
significant differences in recovery rates were detected among trials using different sized prey ( $p = 0.060$ ,  $df = 1$ , 48,  $F = 3.704$ ).

### Predation trials

Predation mortality of hatchery red drum was significantly different among habitats ( $p = 0.004$ ,  $df = 2$ , 78,  $F = 6.007$ ; Fig. 2a). Tukey's HSD test indicated that instantaneous hourly mortality rates (mean  $Z \text{ h}^{-1} \text{ predator}^{-1} \pm 1 \text{ SE}$ ) were significantly higher in the unvegetated habitat ( $Z = 0.189 \pm 0.018$ ) than in either shoal or turtle grass. Mortality rates in shoal grass ( $Z = 0.069 \pm 0.016$ ) and turtle grass ( $Z = 0.046 \pm 0.013$ ) were  $\approx 30$  to 50% of those in the unvegetated habitat. No significant difference was observed between shoal and turtle grass.

A similar trend in predation mortality among habitats was observed for wild red drum (Fig. 2b). Again, predation mortality was significantly different among habitats ( $p = 0.017$ ,  $df = 2$ , 22,  $F = 4.932$ ) and mortality rates were highest in the unvegetated habitat ( $Z = 0.166 \pm 0.038$ ). Moreover, analogous to trials on hatchery red drum, mortality rates in seagrass habitats were markedly lower than in the unvegetated habitat:  $Z = 0.047 \pm 0.021$  and  $0.021 \pm 0.011$  for shoal and turtle grass, respectively. Mean mortality rates in turtle grass were slightly lower than in shoal grass; however, no significant difference was detected.

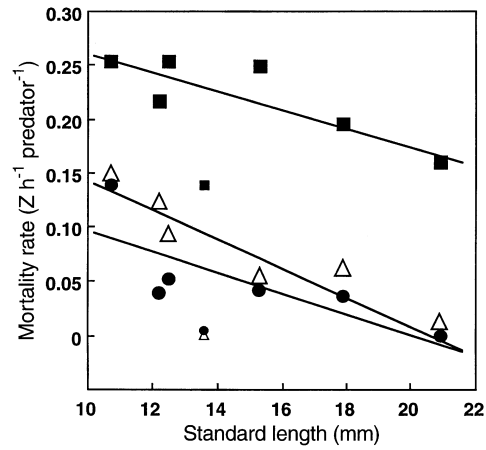
Differences in size-adjusted mean mortality rates (ANCOVA) were observed for hatchery and wild red drum, suggesting that predation mortality was influenced by rearing condition (Table 1). In all three habitats, size-adjusted mortality rates for hatchery red drum were higher than for wild individuals (unvegetated 31%, shoal grass 49%, turtle grass 123% higher). Despite the conspicuous trend in mortality rates between the two rearing conditions, no significant differences were



**Fig. 2** *Sciaenops ocellatus*. Comparison of instantaneous hourly mortality ( $Z$ ) of hatchery-reared (a) and wild (b) red drum exposed to pinfish (*Lagodon rhomboides*) predators in three habitats (Unvegetated = substrate only; Shoal grass = *Halodule wrightii*; Turtle grass = *Thalassia testudinum*; boxes, lines, error bars as in Fig. 1)

detected for any of the habitats (unvegetated  $p = 0.452$ ; shoal grass  $p = 0.647$ ; turtle grass  $p = 0.343$ ).

A significant effect of prey size on mortality rate was detected in predation experiments conducted with both hatchery ( $p = 0.004$ ,  $df = 1$ , 78,  $F = 28.437$ ) and wild ( $p = 0.007$ ,  $df = 1$ , 22,  $F = 8.705$ ) red drum. Although highly variable, mortality rates were negatively associated with prey size. Best-fit regressions between mean mortality rate (per trial) and prey size were developed for hatchery red drum from each habitat (Fig. 3). Regression models were significant ( $p < 0.05$ ) and explained 59 to 90% of the observed variability in mean mortality rates. Mortality rates decreased by 3 to 9% per mm increase in length. No significant first-order inter-



**Fig. 3** *Sciaenops ocellatus*. Relationships between mean instantaneous hourly mortality rate per trial and prey size for hatchery-reared red drum from unvegetated (■), shoal grass (△), and turtle grass (●) habitats. Standard errors of means (each based on 4 replicates) were variable (range: unvegetated  $\pm 0.000$  to 0.046; shoal grass  $\pm 0.002$  to 0.062; turtle grass  $\pm 0.005$  to 0.044). Best-fit regressions: unvegetated  $Z = 0.345 - 0.008SL$ ,  $r^2 = 0.70$ ; shoal grass  $Z = 0.270 - 0.013SL$ ,  $r^2 = 0.90$ ; turtle grass  $Z = 0.189 - 0.009SL$ ,  $r^2 = 0.59$  (where  $SL =$  standard length). Mean mortality rates from one trial ( $SL$  13.6) are not included in regression plots (= rejected outliers: small symbols represent estimates from this trial)

actions (habitat  $\times$  length) were observed (hatchery  $p = 0.214$ ,  $df = 2$ , 78;  $F = 1.571$ ; wild  $p = 0.083$ ,  $df = 2$ , 22,  $F = 2.787$ ).

**Discussion**

Empirical evidence from this study suggests that the structural complexity of a habitat is an important determinant of survival for newly settled *Sciaenops ocellatus*. Mortality rates of red drum in unvegetated habitats were  $\approx 3$  to 4 times higher than in seagrass habitats, and this finding is consistent with the view that the vulnerability of prey to predators decreases as habitat complexity increases (Heck and Orth 1980; Orth et al. 1984; Stoner and Lewis 1985; Heck and Crowder 1991; Orth 1992). In complex habitats (seagrass meadows), the physical structure and opaqueness of the substrate can serve as physical and/or visual barriers between predators and prey (Main 1987). These barriers enhance an individual's probability of survival by reducing prey visibility (encounter rate with predators)

**Table 1** *Sciaenops ocellatus*. Size-adjusted instantaneous hourly mortality rates ( $Z$  h<sup>-1</sup> predator<sup>-1</sup>) and standard errors ( $\pm 1$  SE) for hatchery-reared and wild-caught red drum. Adjusted  $Z$  and

probability values are from ANCOVA (covariate = length) comparing mortality rates between rearing conditions

| Habitat                                      | Adjusted Z            |                       | p     |
|--|-----------------------|-----------------------|-------|
|  | Hatchery              | Wild                  |       |
| Unvegetated (substrate only)                 | 0.193 ( $\pm 0.015$ ) | 0.147 ( $\pm 0.029$ ) | 0.452 |
| Shoal grass ( <i>Halodule wrightii</i> )     | 0.070 ( $\pm 0.014$ ) | 0.047 ( $\pm 0.024$ ) | 0.647 |
| Turtle grass ( <i>Thalassia testudinum</i> ) | 0.047 ( $\pm 0.011$ ) | 0.021 ( $\pm 0.018$ ) | 0.343 |

and limiting a predator's ability to pursue and capture mobile prey (Ryer 1988; Savino and Stein 1989). Therefore, it is likely that the differential mortality rates observed for red drum in unvegetated and vegetated habitats were the result of changes in the ability of the pinfish *Lagodon rhomboides* to detect and capture prey.

Predator-prey interactions often influence distribution patterns, and prey species frequently enter complex habitats in the presence of predators (Savino and Stein 1989; Sogard and Olla 1993). Since prey often modify their distribution to avoid predators (Gilliam and Fraser 1987), positive relationships between ichthyofaunal density and habitat complexity in natural environments would lend support to the view that complexity reduces predator efficiency. Positive correlations between areal complexity and the density of resident fauna have been observed for a variety of seagrass-associated species (e.g. Sogard et al. 1987; Orth 1992; Fonseca et al. 1996), including red drum larvae and juveniles in the Aransas Estuary (e.g. Holt et al. 1983; Holt unpublished data). In general, recruitment densities of these taxa are markedly higher in seagrass meadows than in unvegetated habitats. Whether spatial variation in recruitment density is the result of habitat selection by new recruits or differential predation rates by piscivores, it appears selectively advantageous for individuals to settle in seagrass meadows since these habitats afford added protection from predators.

Although mortality rates of red drum in unvegetated and vegetated habitats differed greatly, no salient trend in predation mortality was detected between the two seagrass habitats. Areal shoot density of shoal grass (*Halodule wrightii*) in experimental mesocosms was approximately eight times greater than that of turtle grass (*Thalassia testudinum*). Thus, it seems plausible to assume that the structural complexity of the shoal grass habitat was greater than that of the turtle grass. However, other morphological features of the seagrass canopy must also be considered (e.g. blade width, blades per shoot, blade height) to accurately assess complexity. For example, blade widths in turtle grass meadows (6 to 8 mm) are greater than in shoal grass (1 to 2 mm), and this feature may enhance an individual's ability to avoid detection. Ryer (1988) showed that blade width is an important component of habitat complexity in seagrass habitats and that width variation influences the foraging efficiency of predatory pipefish. Since no aggregate measure of seagrass complexity was developed for experimental treatments, it is difficult to evaluate the importance of the different vegetational characteristics on predation mortality in this study.

Trends in mortality rates verify that vulnerability of newly settled red drum to predation is a function of size. For both hatchery and wild red drum, mortality rates decreased with increasing prey size, with two or three-fold differences between the smallest (10 to 12 mm) and largest (18 to 20 mm) red drum. These results support the general tenet that susceptibility of larvae to predators is size-dependent, and appear in accordance with

conceptual models relating larval mortality (susceptibility) to prey size (Bailey and Houde 1989; Fuiman and Magurran 1994). Paradis et al. (1996) demonstrated that prey vulnerability is maximal (apex of dome-shaped function) when fish larvae are  $\approx 10\%$  of the predator's length. In this study, red drum were always greater than 10% of the predator's length (range:  $\sim 14$  to 28%). As a result, prey:predator size ratios were in a region of the dome-shaped function where mortality rates are expected to decrease with increasing prey size.

Predators in each of the trials were presented with different-sized red drum (range in size per trial ca.  $\pm 1$  to 2 mm) and size-dependent predation mortality was determined by comparing results from separate trials. To generate the desired size range, red drum of different ages were used. Therefore, our experimental design actually combined the effects of age and size. Recent studies have attempted to separate the effects of age and size (independent of age) (Litvak and Leggett 1992; Bertram 1995), because size within a given cohort can often show considerable variation (Chambers et al. 1989). Due to the wide variety of predators in natural habitats and the interacting probabilities of encounter, attack, and capture, being smaller at a given age may actually enhance an individual's probability of survival under certain conditions (Litvak and Leggett 1992). Hence, the relationship between prey size and vulnerability to predators observed in this study might change were different-sized red drum from a single cohort used as prey.

The effects of habitat complexity and prey size played a significant role in the predation of hatchery-reared and wild-caught red drum. While general trends were similar in both rearing conditions, hatchery red drum appeared more susceptible to pinfish predators. Recent studies have confirmed that an individual's anti-predator skills (e.g. flight response, stimulus recognition) are closely linked to early-life experiences (Huntingford and Wright 1993; Fuiman and Magurran 1994). Findings from experimental studies on salmonid fry and smolts have shown that hatchery fishes are more vulnerable to predators than conspecifics from natural habitats (Patten 1977; Suboski and Templeton 1989). Furthermore, studies in natural environments have demonstrated a relationship between social learning and survival. Huntingford et al. (1994) showed that sticklebacks from sites with high predator densities were more capable of avoiding predators than conspecifics from low-risk sites. Similar relationships have been observed for a variety of other taxa (Goodey and Liley 1986; Magurran and Pitcher 1987). Results from the present study appear to support the hypothesis that the lack of appropriate early-life stimuli may reduce an individual's probability of survival. Mortality rates were lower for wild red drum in all three habitats examined; however, no statistical differences were detected between rearing conditions, and thus further interpretation of these data is not warranted.

Predation experiments in mesocosms, like other empirically based studies in ecology, often rely on a significant amount of subjective input from the investigator.

By altering control variables in the experimental protocol, an investigator can influence the outcome of a predation trial and, as a result, direct comparisons of instantaneous mortality rates with other studies are not recommendable. Apart from predator and prey effects (age, density, size, and type), a number of control variables have been shown to significantly affect predation rates in experimental mesocosms. For example, the duration of an experiment appears critical, since lower predation rates are generally associated with longer predation trials (Fuiman and Gamble 1989; Paradis et al. 1996). In addition, De Lafontaine and Leggett (1988) demonstrated that mortality rates are dependent on container volume. The effect of container volume is probably due to changes in both encounter rate (higher in smaller containers) and behavioral characteristics (e.g. swimming speed) (Tang and Boisclair 1993; Paradis et al. 1996). Furthermore, physical conditions (e.g. temperature) have been shown to influence predation rates in mesocosms (Elliott and Leggett 1996). Since the aforementioned variables were controlled in our mesocosm experiments, data derived in this study on the effects of habitat complexity, prey size, and rearing condition were not compromised; however, caution should be exercised when comparing our results to other empirical estimates of predation mortality.

This study demonstrates that habitat complexity is critical to the survival of newly settled red drum. Experimental evidence indicates that individuals inhabiting vegetated habitats will have a higher potential for survival than conspecifics in unvegetated areas. Therefore, it is postulated that seagrass meadows represent a critical nursery habitat for red drum, and changes in the complexity or coverage in natural environments may influence early-life survival and possibly recruitment levels. Thus, the decline in the areal coverage and biomass of seagrass meadows along the Texas coast, due primarily to anthropogenic inputs and modifications (Pulich and White 1991; Onuf 1996), is cause for concern. Future losses of seagrass meadows may be detrimental to red drum populations as well as other estuarine-dependent fauna utilizing these nursery habitats.

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