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Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms

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Synopsis

We examined patterns of habitat selection in wild-caught and hatchery-reared early juvenile red drum, *Sciaenops ocellatus*, using mesocosm experiments. Experiments were performed in the presence and absence of a pinfish, *Lagodon rhomboides*. We hypothesized that newly recruited red drum would have distinct patterns of habitat selection, and these patterns could be influenced by the presence of a pinfish predator. Red drum were introduced to replicate mesocosms containing all possible pair-wise comparisons of four different habitat types: marsh *Spartina alterniflora*, non-vegetated bottom/sand, oyster reef *Crassostrea virginica*, and seagrass *Halodule wrightii*. Wild-caught and hatchery-reared red drum showed distinctively different patterns of habitat selection. In general, wild-caught red drum selected structured habitats, while hatchery-reared fish did not show strong selection for any habitat type. When a predator was present, wild-caught red drum either changed habitat selection or showed significant selection for other structured habitats. This predator effect was similar albeit weaker for hatchery-reared red drum, but as in the trials without a predator, overall habitat selection was reduced compared to wild-caught red drum. Our results suggest that in the absence of seagrass, other habitat types such as marshes and oyster reefs may be important recruitment habitat for red drum. Additionally, hatchery-dependent behaviors may need to be assessed in designing stock enhancement programs.

Introduction

Understanding the causes and consequences of variable recruitment of pelagic larvae to demersal habitats is critical for understanding the dynamics of fish populations (Cushing 1975, Bailey & Houde 1989). Recruitment of larvae may be affected by structural complexity of the habitat (Levin & Hay 1996, Tupper & Boutilier 1997), which can influence the foraging effectiveness of predators (Crowder & Cooper 1982, Stoner 1982, Minello & Zimmerman 1983, Werner & Gilliam 1984, Hixon & Beets 1993), the abundance of food resources (Rozas & Odum 1988, Levin 1994), and the ability of new recruits to procure food (Heck & Thoman 1981). Consequently, selection for high quality habitats can play an important role in determining the dynamics and structure of marine fish populations (Shulman 1984, Hixon & Beets 1989, 1993, Connell & Jones 1991, Eggleston 1995).

Fish are not typically distributed randomly, and the mechanisms underlying the non-random use of habitats can be complex. Patterns of habitat use may be caused by behavioral responses of fish to specific habitat types. For example, some fish selectively settle in seagrass (Bell & Westoby 1986), coral reef (Sale et al. 1994), and rocky reef (Levin 1996), and this selection affects subsequent patterns of abundance. Habitat associations may also result from differential mortality. Connell & Jones (1991), for example, showed that variability in abundance of blennioid fish resulted from lower predation rates in habitats of high structural complexity. Predators may also indirectly affect the abundance of their prey by influencing their behavior (Sih 1982, 1994). For example, the presence of brook charr, *Salvelinus fontinalis,* in streams increases the rate at which their prey emigrate from habitat patches thus reducing local prey densities (Forrester 1994).

The red drum, *Sciaenops ocellatus*, has been a highly exploited estuarine-dependent fish throughout the Gulf of Mexico and southeastern United States (Pattillo et al.[1]). Over-fishing resulted in the total closure of the commercial fishery in 1986 (Swingle et al.[2]), but currently, red drum remain an important part of the recreational fishery (Pattillo et al.[1]). Red drum spawn in early fall in offshore waters near passes and inlets, where the pelagic eggs, embryos, and larvae are carried by tides and currents into shallow bays and estuaries (Holt et al. 1983, Comyns et al. 1991). Following a short pelagic interval, larvae (ca. 6–8 mm) settle into estuarine habitats (primarily seagrass) and remain in these areas through early ($\leq$40 mm) and late-juvenile ($\sim$500 cm) stages (Pattillo et al. 1997, Holt et al. 1983, Rooker & Holt 1997, Rooker et al. 1998b).

Seagrass meadows are important to numerous commercially and recreationally exploited fishes and invertebrates (Orth et al. 1984), and red drum are known to settle in seagrass beds when they are available (Holt et al. 1983, Rooker & Holt 1997, Rooker et al. 1998b). Many estuarine areas have suffered extensive loss of seagrasses (Pulich & White 1991, Thayer 1992, Adair et al. 1994, Short & Wyllie-Echeverria 1996), and the Galveston Bay system of Texas has lost 80% of its submerged aquatic vegetation since the 1970's (Adair et al. 1994, Sheridan et al. 1998). Nevertheless, Galveston Bay, as well as many other estuaries devoid of seagrass, support a large stock of red drum (Fuls & Hensley[3]). In the absence of seagrass, it is unclear what habitats are used by newly recruited red drum.

In an attempt to artificially enhance natural red drum stocks, managers in Texas initiated a stock enhancement program in 1983 using hatchery-reared red drum (McEachron et al. 1995). Stock enhancement programs can be successful (Travis et al. 1998), but the viability of hatchery-reared fishes is of major concern (Grimes 1998). Normal survival behaviors may be compromised by the hatchery experience (Munro & Bell 1997), and evidence from hatchery-reared salmonids suggests that underdeveloped ability to recognize and avoid predators results in high mortality (Olla et al. 1998). Therefore, it is important to understand the processes of habitat selection and predator avoidance for both hatchery-reared and wild-caught red drum when designing an artificial enhancement program for red drum stocks.

In this study, our goal was to experimentally examine habitat selection of juvenile red drum using laboratory mesocosms. Specifically, we examined whether: (1) red drum select for habitat types such as salt marsh, nonvegetated bottom, oyster reef, and seagrass; (2) the presence of a predator influences their habitat selection; and (3) differences in habitat selection exist between wild-caught and hatchery-reared red drum.

Methods

Experimental organisms

We obtained hatchery-reared red drum from Texas Parks and Wildlife Seacenter Texas hatchery in Lake Jackson, Texas. These fish were reared from captive-induced spawns, where eggs were collected and embryos hatched in 380 l tanks. After 36 h, larvae were transferred to 0.4 ha polyethylene-lined ponds and fed wild zooplankton and commercial 'fry feed' (Rangen). Fish ranging from 15–25 mm SL (20–30 days in age) were collected from ponds using dip nets and used as experimental animals. Wild red drum used in the experiments were of similar size (15–25 mm SL) and were seined from saltmarsh and seagrass meadows in Galveston Bay, Texas. Red drum were held for less than 1 week before experimental trials, and new fish were used for each trial. Red drum were maintained in the laboratory in fiberglass flow-through tanks with filtered seawater (25–30‰; 24–28°C) pumped from the Gulf of Mexico and were fed with frozen or live mysid shrimp daily.

Pinfish, *Lagodon rhomboides* (ca. 80–100 mm SL), an abundant predator of young red drum

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[1] Pattillo, M.E., T.E. Czapla, D.M. Nelson & M.E. Monaco. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Volume II: species life history summaries. ELMR Rep. No. 11 NOAA/NOS Strategic Environmental Assessments Division, Silver Spring. 377 pp.

[2] Swingle, W., T. Leary, C. Davis, V. Blomo, W. Tatum, M. Murphy, R. Taylor, G. Adkins, T. Mcllwain & G. Matlock. 1984. Fishery profile of red drum. Gulf of Mexico Fish. Manag. Coun. Gulf States Mar. Fish. Comm., Ocean Springs. 74 pp.

[3] Fuls, B.E. & R.A. Hensley. 1998. Trends in relative abundance and size of selected finfishes and shellfishes along the Texas coast: November 1975–December 1996. Manag. Data Ser. 159, Texas Parks and Wildlife, Coastal Fisheries Division, Austin. 8 pp.

(Fuiman 1994, Rooker et al. 1998a), were selected as the experimental predator. Pinfish were seined from the same marsh and seagrass areas as the wild-caught red drum and were maintained in the same facility and conditions. Pinfish were held for less than 1 week and fed a diet of both live and frozen grass shrimp (*Palaemonetes* spp.).

Experimental mesocosms

Experimental mesocosms were constructed from 125 l circular plastic tanks (60 cm diameter × 44 cm deep). We placed 5 cm of washed beach sand on the bottom of each tank, followed by plastic mesh (5 mm) and an additional 5 cm of sand. Each tank was filled to a depth of 30 cm with filtered seawater. Water in the tanks was maintained at salinities of 25–30‰, temperatures of 24–28°C, and oxygen levels of 6–6.8 mg $O_2\,l^{-1}$ using airstones. Light was supplied by skylights and florescent bulbs with levels ranging from 10–12 $\mu E\ sec^{-1} m^{-2}$.

Four common natural habitat types were simulated in experimental mesocosms: (1) salt marsh, (2) non-vegetated sand bottom, (3) oyster reef, and (4) seagrass. Mesocosms were divided in half, and one habitat type was constructed in each half. Every possible pair-wise combination of habitats (6 total) was used in the experiment. Placement of the mesocosms and locations of the habitat types within each mesocosm were randomized.

To minimize the complication of food effects on habitat selection, we did not feed red drum in experimental mesocosms, and we attempted to simulate only the structure of each habitat type. The sand habitat consisted of washed beach sand. Seagrass habitat was represented by cores of *Halodule wrightii* collected from seagrass meadows in Galveston Bay. Cores were washed of sediment in the field and brought to the laboratory where plants were washed and dipped in freshwater. Leaves were wiped to remove epiphytic growth and were planted into the sand substratum of the mesocosm. Once planted, mean shoot densities were 8828 m^{-2} (SE = 421) and were similar to densities in natural seagrass beds in Galveston Bay as estimated from core samples taken during collection. Oyster shells (*Crassostrea virginica*) were obtained from a commercial processing plant, sun dried, and washed with fresh water. Shells (3.8 l) were placed in half of the mesocosm by first covering the bottom and then forming an elevated reef-like structure. Salt marsh was constructed by cutting *Spartina alterniflora* from Galveston Bay marshes and sun drying culms for 14 d. Fifty-two culms (184 m^{-2}) were planted into half of a mesocosm and held in place by pressing the culms through the plastic mesh under the substrate.

Habitat selection in the absence of predators

To test the hypothesis that red drum select among the experimental habitats, we set up the six mesocosms with one pair of habitats, ran a selection trial, and then repeated the trial with different fish (twelve replicates). The six mesocosms were then re-established with a different pair of habitats. For each trial, five red drum were placed into the center of each mesocosm, airstones were removed, and the fish were monitored for any abnormal behavior for 24 h. Red drum densities (17.7 m^{-2}) were higher in experimental mesocosms than reported for wild populations; however, densities of this magnitude have been reported for other sciaenid juveniles in estuarine habitats (Rooker et al. 1998b). After this 24 h acclimation period, the location of each red drum in the mesocosm was visually assessed every hour for 10 h. Preliminary observations indicated that the location of all fish could be detected by visual inspection, and this assessment did not disturb or alter fish behavior. For each replicate mesocosm (N = 12) we calculated the percent occurrence of red drum based on 50 observations (5 fish per mesocosm × 10 hourly observations). The data were arcsine transformed to normalize the distribution of percentage data (Zar 1996), and a paired student's t-test was used to determine if the difference between mean percentages of fish in each habitat type was significant.

Habitat selection in the presence of a predator

To examine the effects of a predator on habitat selection, the above experiment was repeated using a tethered pinfish in one of the habitat types. The pinfish was tethered to a large weight using small metal clip in the lower jaw attached to a 20 cm monofilament line. Predators were monitored for normal behavior prior to introduction of the red drum. New pinfish were used for each trial and subsequently released into the field. Each possible pair-wise habitat combination was performed with a predator present in each of the habitat types (6 habitat combinations;12 total trials). Data were collected and analyzed as in the above experiments.

Results

Habitat selection in the absence of predators

Wild-caught red drum showed strong selection for structured habitat types, significantly selecting oyster, seagrass, and marsh over nonvegetated sand bottom (Figure 1a). Additionally, wild-caught red drum selected seagrass over marsh, oyster reef over marsh, and oyster reef over seagrass. Patterns of habitat selection by hatchery-reared red drum were distinctly different from wild-caught fish (Figure 1b). In all trials comparing structured habitat (seagrass, marsh, or oyster reef) with nonvegetated bottom, hatchery-reared fish showed no significant selection (marsh vs. sand, p = 0.91; oyster vs. sand, p = 0.65; and seagrass vs. sand, p = 0.96). Comparisons between structured habitats revealed that hatchery-reared red drum selected seagrass over marsh (p = 0.018) or oyster reef (p < 0.001), but did not select for marsh over oyster reef (p = 0.62) when these two habitat types were compared.

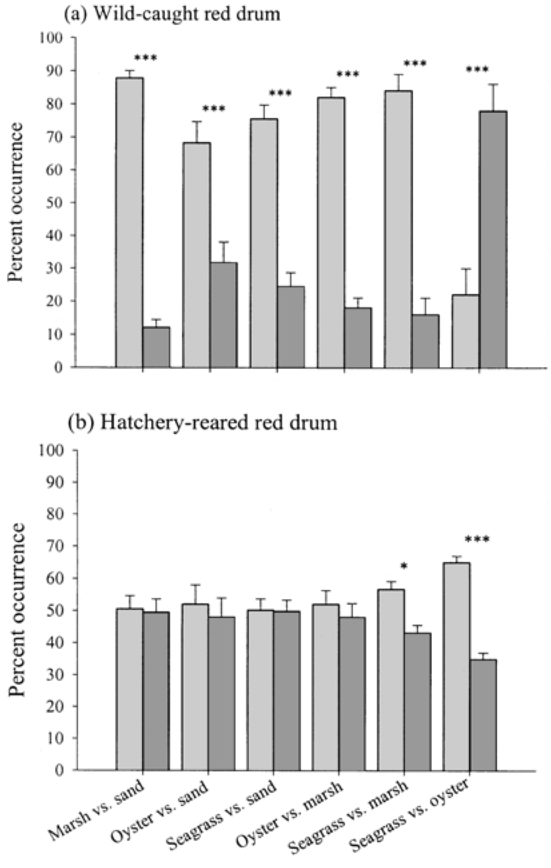

Figure 1. Mean percent occurrence (± SE) of (a) wild-caught and (b) hatchery-reared red drum in each habitat type for all possible habitat comparisons. Separate trials were run for wild-caught and hatchery-reared fish. Each comparison represents twelve replicate mesocosms. Significant results from paired Student's t-tests are indicated by * = p < 0.05, ** = p < 0.01, and *** = p < 0.001.

Habitat selection in the presence of predators

The presence of pinfish generally altered habitat selection for wild-caught red drum (Figure 2, Table 1a). Without predators, wild-caught red drum selected for all structured habitats over sand. When a predator was tethered in the structured habitat, selection for the structure was reduced; with oyster habitat, selection was reversed and the red drum selected sand over structure. Adding a predator to the sand habitat (previously selected against) had relatively little effect on the selection pattern. In comparisons between structured habitats, red drum selected for the structured habitat that did not have the predator. We defined a predator effect as an avoidance or non-selection of a habitat type that was otherwise selected for when a predator is present in that habitat type. The predator effect for wild-caught red drum was significant for 6 out of 12 trials.

Hatchery-reared red drum showed stronger habitat selection patterns in the presence of a predator (Figure 3, Table 1b); hatchery-reared fish only selected seagrass habitat over oyster and marsh when predators were absent. Adding a predator to the seagrass reduced use of this habitat. In comparisons between sand and structured habitat, hatchery-reared red drum did not select for structured habitat when predators were absent. However, when a predator was added to the sand habitat, red drum avoided the predator and selected structure. When a predator was added to marsh habitat, there was no effect on the selection pattern of hatchery-reared red drum. The predator effect for hatchery-reared red drum was significant for 6 out of 12 trials.

Other behavioral differences between wild-caught and hatchery-reared red drum were observed. When introduced to experimental mesocosms, wild-caught red drum immediately sought shelter near the substrate, and they did not move around extensively. Hatchery-reared fish usually remained in the water column, only a few centimeters below the water's surface. During experiments, hatchery fish generally schooled and slowly moved around the tank; and when predators

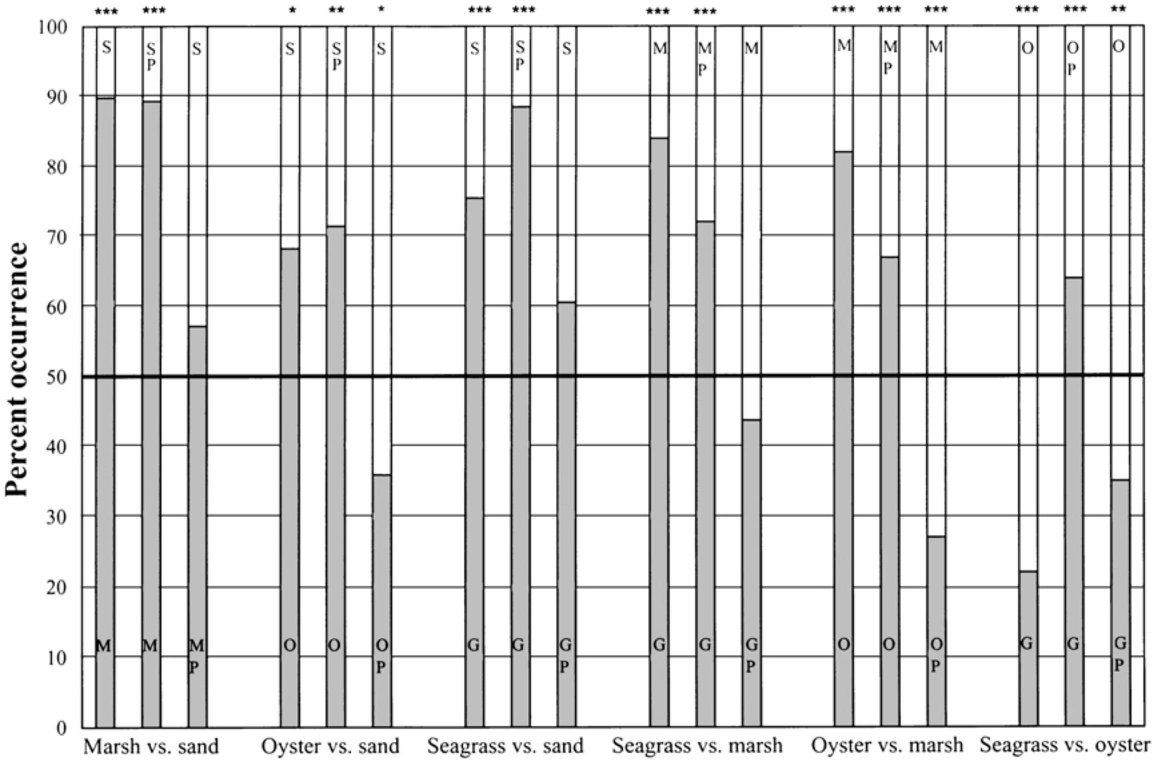

Figure 2. The effect of a pinfish predator on habitat selection of wild-caught red drum. The mean percent occurrence is indicated for each habitat comparison; habitat designations are M = marsh, O = oyster, S = nonvegetated sand bottom, and G = seagrass. The first bar in each triplet represents the selection pattern without predators; the presence of a predator in particular habitat is indicated by a ‘p’ on the bar. Each comparison represents twelve replicate mesocosms. Significant results from paired Student’s t-tests are indicated by * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

were present, hatchery-reared fish always exhibited this surface schooling behavior. Consequently, we observed less habitat selection and a lower rate of predator-induced habitat switching than was characteristic of wild-caught fish.

Discussion

Habitat selection influences the distribution and abundance of demersal marine fishes (Bell et al. 1987, Levin et al. 1997), and the vulnerability of newly recruited fishes to predation generally decreases as habitat complexity increases (Heck & Orth 1980). Our results are consistent with the hypothesis that newly recruited red drum would have distinct patterns of habitat selection; we observed significant selection in all six habitat comparisons. Wild-caught red drum strongly preferred complex structured habitat types, selecting oyster reef over seagrass, seagrass over marsh, and marsh over nonvegetated sand bottom. Selection for structured habitats in the form of marshes, oyster reefs, and seagrass meadows is common for many estuarine species, and may reduce the risk of predation (Heck & Thoman 1981, Sogard 1989, Minello & Zimmerman 1991, Wenner et al. 1996). If habitat complexity is critical to the survival of young red drum (Rooker et al. 1998a), then habitat selection will influence the abundance and survival of newly recruited fish.

Juvenile red drum appear to use seagrass meadows as their primary nursery habitat (Holt et al. 1983, Rooker & Holt 1997, Minello 1999). Given the extensive loss of seagrass in many estuaries, including Galveston Bay (Orth & Moore 1981, Pulich & White 1991, Adair et al. 1994, Sheridan et al. 1998) where the seagrass in now restricted to one small satellite bay, the presence and use of alternative structured habitats such as oyster reef and marsh may be important. When

Table 1. Habitat selection of (a) wild-caught and (b) hatchery-reared red drum in the presence of predators. Separate experiments were conducted for wild-caught and hatchery-reared fish. Twelve replicate trials (N = 12) were run for each comparison and examined for significant ($p < 0.05$) habitat selection using paired Student's t-tests. A predator effect (†) is defined as an avoidance or non-selection (ns) of a habitat type that was otherwise selected for, when a predator is present in that habitat.

Comparison	Habitat selection without predator	p	Habitat selection with predator	p
(*a*) *Wild-caught red drum*:				
Predator in marsh:				
Oyster vs. marsh	Oyster	<0.001	Oyster	<0.001
Sand vs. marsh	Marsh	<0.001	ns†	0.102
Seagrass vs. marsh	Seagrass	<0.001	Seagrass	0.001
Predator in oyster:				
Marsh vs. oyster	Oyster	<0.001	Marsh†	<0.001
Sand vs. oyster	Oyster	<0.001	Sand†	0.029
Seagrass vs. oyster	Oyster	<0.001	Seagrass†	0.007
Predator in sand:				
Marsh vs. sand	Marsh	<0.001	Marsh	<0.001
Oyster vs. sand	Oyster	<0.001	Oyster	0.002
Seagrass vs. sand	Seagrass	<0.001	Seagrass	<0.001
Predator in seagrass:				
Marsh vs. seagrass	Seagrass	<0.001	ns†	0.191
Oyster vs. seagrass	Oyster	<0.001	Oyster	0.001
Sand vs. seagrass	Seagrass	<0.001	ns†	0.120
(*b*) *Hatchery-reared red drum*:				
Predator in marsh:				
Oyster vs. marsh	ns	0.622	ns	0.652
Sand vs. marsh	ns	0.906	ns	0.425
Seagrass vs. marsh	Seagrass	0.018	Seagrass	0.017
Predator in Oyster:				
Marsh vs. oyster	ns	0.622	Marsh†	<0.001
Sand vs. oyster	ns	0.647	Sand†	0.020
Seagrass vs. oyster	Seagrass	<0.001	Seagrass	<0.001
Predator in sand:				
Marsh vs. sand	ns	0.906	Marsh†	<0.001
Oyster vs. sand	ns	0.647	ns	0.570
Seagrass vs. sand	ns	0.963	Seagrass†	0.003
Predator in seagrass:				
Marsh vs. seagrass	Seagrass	0.018	Marsh†	0.011
Oyster vs. seagrass	Seagrass	<0.001	ns†	0.120
Sand vs. seagrass	ns	0.963	ns	0.840

given a choice in mesocosm experiments, wild-caught fish selected oyster reef over seagrass. Few studies have assessed the use of oyster reefs by juvenile fishes (Zimmerman et al.[4], Coen et al. 1999, Minello 1999), although this habitat type is abundant in Texas and Louisiana. In the Galveston Bay system, oyster reefs are extensive (10 800 ha, covering 10.4% of the bay bottom; Powell[5]) and may be important nursery habitat for newly recruited red drum. Young red drum also selected for marsh over nonvegetated bottom in our experiments. Salt marshes support high densities of nekton in many estuaries (Baltz et al. 1993, Minello 1999); and in Galveston Bay, Texas, Stunz (1999) found relatively high densities of red drum near the marsh edge when seagrass was unavailable. Intertidal marshes occur along approximately 61% of the Galveston Bay shoreline (Paine & Morton 1991) and also could be important nursery areas for young red drum in this bay system. Using wild-caught red drum, our experiments showed that habitat selection for one structured habitat could be switched to another structured habitat by the presence of a predator. For example, strong selection for oyster reef observed in trials without predators was reversed, and red drum selected another structured habitat (i.e., marsh or seagrass) when pinfish were present in oyster reef. This predator-induced switching behavior was not observed when we compared a structured habitat with nonvegetated bottom. These results are consistent with our hypothesis that predator avoidance may be a factor in habitat selection. Experimental studies have shown higher red drum mortality on nonvegetated bottom compared to seagrass (Rooker et al. 1998a) and structured habitat types (Stunz 1999). Other research has shown that habitat structure provides a refuge from predation and can affect the efficiency and prey selectivity of predators (Heck & Thoman 1981, Stoner 1982, Crowder & Cooper 1982, Minello & Zimmerman 1991, Schmitt & Holbrook 1985).

The abundance of available food resources may affect selection among natural habitat types (Heck & Thoman 1981, Rozas & Odum 1988) and can interact with the effect of predators (e.g. Werner et al. 1983, Schmitt & Holbrook 1985). For example, rich food resources in sand may result in red drum spending more time in nonvegetated habitats than predicted by our experiments, despite higher rates of predation that may occur in such environments (Holt et al. 1983, Werner et al. 1983, Rooker et al. 1998a, Stunz 1999). In

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[4] Zimmerman, R.J., T.J. Minello, T.J. Baumer & M.C. Castiglione. 1989. Oyster reef as habitat for estuarine macrofauna. NOAA Technical Memorandum, NMFS-SEFC-249. 16 pp.

[5] Powell, E.N. 1993. Status and trends analysis of oyster reef habitat in Galveston Bay. pp. 207–209. *In*: R.W. Jensen (ed.) Proceeding, Second State of the Bay Symposium, Galveston.

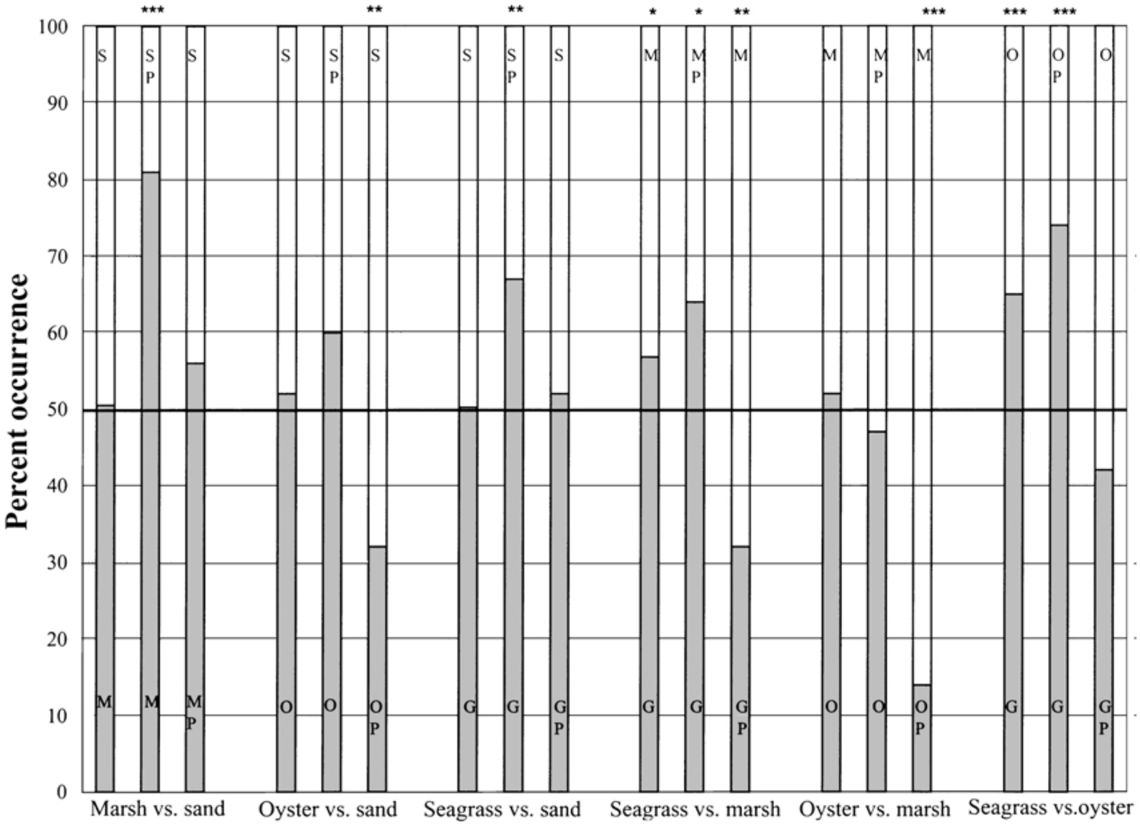

Figure 3. The effect of a pinfish predator on habitat selection of hatchery-reared red drum. The mean percent occurrence is indicated for each habitat comparison; habitat designations are M = marsh, O = oyster, S = nonvegetated sand bottom, and G = seagrass. The first bar in each triplet represents the selection pattern without predators; the presence of a predator in particular habitat is indicated by a ‘p’ on the bar. Each comparison represents twelve replicate (N = 12) mesocosms. Significant results from paired Student’s t-tests are indicated by * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

field enclosure experiments, Stunz (1999) found higher growth rates in vegetated habitats over oyster reef and nonvegetated bottom, suggesting that red drum may select these areas for their food resources.

In contrast to wild-caught red drum, hatchery-reared fish failed to exhibit strong patterns of habitat selection. In the absence of predators, hatchery fish only showed significant habitat selection in two of the six comparisons, selecting seagrass over marsh and oyster. This selection pattern was likely influenced by the surface schooling behavior of hatchery-reared fish. Behavioral and habitat selection differences between hatchery-reared and wild-caught fish may be related to methods of hatchery rearing. In the red drum hatchery, fish larvae settle into ponds that lack vegetation or other structure. This hatchery experience may compromise the normal basic survival behavior of these fish (Munro & Bell 1997). For hatchery-reared salmonids, predation is a major cause of mortality and may be due to underdeveloped ability to recognize and avoid predators (Olla et al. 1998). The schooling behavior of hatchery-reared red drum may be a mechanism for these fish to reduce the risk of predation in ponds without structure (Parrish & Edelstein-Keshet 1999).

Different patterns of habitat selection by wild-caught and hatchery-reared red drum clearly have potential implications for marine enhancement programs. Red drum have been a popular species for stocking programs (McEachron & Daniels 1995, Grimes 1998), yet the current juvenile recruitment success rate for hatchery red drum is unknown (Grimes 1998). Since the efficacy of stock enhancement programs for red drum depends, in large part, on the mortality rate of young fish, there is a clear need to document the fate of these fish (Grimes 1998). If hatchery-reared red drum suffer greater mortality than natural fish because of differences in habitat selection patterns, this information could be used to modify rearing techniques and enhance survival.

Development of coastal areas is affecting estuarine nursery habitats that are critical for a variety of fishes and invertebrates (Orth & Moore 1981, Pulich & White 1991, Adair et al. 1994). As these extensive habitat alterations in estuaries increase, our need to understand how estuarine ecosystems function becomes even more pressing (Thayer 1992, Short & Wyllie-Echeverria 1996). Although seagrass is generally recognized as the most important nursery habitat type for young red drum, our laboratory experiments suggest that these fish also may select other structured habitats, specifically salt marshes and oyster reefs. The near absence of seagrass in many estuaries along with the abundance of salt marshes and oyster reef suggests that these alternate habitat types may also function as important nursery areas for red drum.

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