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A Comparison of Early Juvenile Red Drum Densities Among Various Habitat Types in Galveston Bay, Texas

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ABSTRACT: Seagrass meadows are often cited as important nursery areas for newly settled red drum even though many estuaries, such as Galveston Bay, Texas, support large numbers of red drum and have limited seagrass cover, suggesting the use of alternate nursery areas. We examined patterns of habitat use for newly settled red drum at six sampling areas in Galveston Bay; two areas had seagrass beds and four areas had no seagrass. We measured densities in different habitat types using epibenthic sleds and enclosure samplers. Peak recruitment of young red drum to the estuary occurred during September through December. Highest densities of new settlers were found in seagrass meadows (primarily Halodule wrightii), but when seagrass was absent, the highest densities of red drum occurred along the Spartina alterniflora marsh edge interface. Densities were relatively low on nonvegetated bottom away from the marsh edge. We also examined density patterns in other habitat types at selected sampling areas and found no red drum within marsh vegetation away from the marsh edge interface (5 and 10 m into the marsh interior). Oyster reef Crassostrea virginica was sampled using lift nets, and we found no red drum using this habitat, although adjacent seagrass and marsh interface habitats were used. Even though red drum densities in marsh edge were low relative to seagrass, the large areal extent of marshes in the bay complex probably makes marsh edge the most important nursery habitat for red drum in Galveston Bay.

Introduction

Many economically and ecologically important fish species use shallow estuarine areas as nursery grounds (Weinstein 1979; Heck and Thoman 1981; Boesch and Turner 1984; Day et al. 1989; Minello 1999), and their young rely on particular habitat types within estuaries for survival and growth (Weinstein 1979; Kneib 1984; Day et al. 1989; Baltz et al. 1993). Young fishes may enhance their relative fitness by selecting estuarine habitats where they can optimize net energy gain, avoid predation, and minimize competitive interactions (Sogard 1992; Kneib 1993; Baltz et al. 1998).

Densities of fish often vary among habitat types, and density patterns can provide useful information on relative habitat value (Baltz et al. 1993; Minello 1999). Some of the most common habitat types in estuaries include oyster reefs, salt marshes, seagrass beds, and both tidal and subtidal mud flats (Day et al. 1989). Although all of these habitats are widely recognized as potentially important to fish, most studies examining estuarine habitat use have contrasted nonvegetated bottom with vegetated areas such as subtidal seagrass meadows (reviews by Orth et al. 1984; Pollard 1984) or salt marshes (Zimmerman et al. 1984; Baltz et al. 1993; Rozas

and Zimmerman 2000). Fish use of oyster reefs is rarely examined (Zimmerman et al. 1989; Wenner et al. 1996; Coen et al. 1999), and few comparisons have been made between subtidal (e.g., seagrass) and intertidal (e.g., salt marsh) vegetation (Rozas and Minello 1998; Minello 1999). Given the decline of both salt marshes (Penland and Ramsey 1990; White and Tremblay 1995) and seagrass meadows (Thayer et al. 1992; Adair et al. 1994; Short and Wyllie-Echeverria 1996; Sheridan et al. 1998) in many estuaries, a comparative evaluation of all habitat types is needed.

The red drum *Sciaenops ocellatus* is an estuarine-dependent fish (Sciaenidae) common to the Gulf of Mexico and southeastern U.S. This species supports an important recreational fishery (Pattillo et al. 1997). Red drum spawn during early fall near passes and inlets in nearshore waters. Currents carry eggs and planktonic larvae into bays and estuaries (Peters and McMichael 1987; Comyns et al. 1991) where they settle (ca. 6–8 mm) into seagrass meadows when available (Holt et al. 1983; Rooker and Holt 1997).

In contrast to many other Texas estuaries, the Galveston Bay system has little remaining seagrass. This estuarine system continues to support large populations of red drum (Fuls and Hensley 1998), suggesting use of alternate nursery habitat types or immigration of older individuals from other bay

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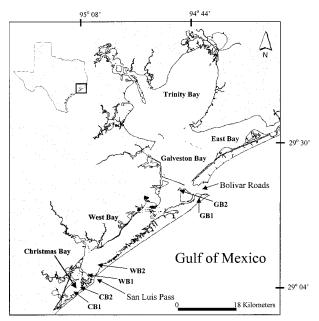


Fig. 1. Map of Galveston Bay system on the Texas coast showing sampling areas in Christmas Bay (CB1, CB2), Galveston Bay (GB1, GB2), and West Bay (WB1, WB2).

systems. Galveston Bay has many potential nursery areas that could be used by young red drum as alternatives to seagrass including marsh, oyster reefs, and nonvegetated bottom. We examine patterns of habitat use for newly settled red drum in Galveston Bay by comparing densities among different habitat types.

Materials and Methods

STUDY LOCATION

We conducted this study in the Galveston Bay system located on the upper Texas Gulf Coast (Fig. 1). This barrier-built estuary covers approximately 1,420 km² and consists of four major bays and numerous secondary bays. Two major inlets (Bolivar Roads and San Luis Pass) connect the estuary to the Gulf of Mexico. The tides are mixed and primarily diurnal with a mean daily range of 0.3 m (Galveston Pier 21, National Ocean Service, National Oceanic and Atmospheric Administration). Spartina alterniflora is the dominant intertidal emergent shoreline vegetation. Tidal inundation of the marsh is most extensive during the spring and fall, but marsh edge vegetation is available for use by nekton throughout the year, remaining flooded approximately 78% of the time in the lower bay (Minello and Webb 1997). Seagrasses, dominated by Halodule wrightii, historically ranged throughout a large portion of the complex, but declines of about 80% over the past three decades have left seagrass meadows restricted to one small

satellite bay, Christmas Bay, located in the southwestern portion of the estuary (Adair et al. 1994; Sheridan et al. 1998). In addition to large areas of shallow nonvegetated bottom, oyster reefs are also abundant in the bay, covering approximately 10% of the bay bottom (Powell 1993).

LARGE-SCALE PATTERNS OF HABITAT USE

We assessed overall patterns of habitat use by newly settled (≤ 40 mm SL) red drum at six sampling areas (Fig. 1), two each within three bays of the complex: Galveston Bay (GB1, GB2), West Bay (WB1, WB2), and Christmas Bay (CB1, CB2). All sampling areas were within 5 km of a major pass because Holt et al. (1983) indicated these areas support high densities of newly settled red drum. Within the 6 sampling areas we made triplicate sled tows at each of four locations: tidal creeks (TC), marsh edge interface just outside of S. alterniflora vegetation (ME), and 15 and 30 m from the marsh edge interface towards open water. The marsh edge interface is the ecotonal zone between open water and the emergent vegetation, S. alterniflora (Zimmerman et al. 1984; Baltz et al. 1993). The tidal creeks were narrow (< 2 m width), and the sled was pulled along the marsh edge interface as we sampled from 10 m inside the mouth up to 50 m along the creek into the interior marsh. In Christmas Bay, the bottom substrate at the 15 and 30 m locations was seagrass, and seagrass was interspersed along the marsh edge interface. The tidal creeks did not contain seagrass. In Galveston and West Bays (GB1, GB2, WB1, WB2), the bottom substrate was nonvegetated at all sampling locations.

In 1997 we took biweekly samples during the August to January settlement season using epibenthic sleds adapted from Holt et al. (1983). This sled included a metal frame opening of 0.6 m (length) \times 0.75 m (height) equipped with a 1-mm mesh conical plankton net. We placed the sled on the bottom and walked a semicircular route around the sampling location to minimize disturbance. For each tow, we pulled the sled by hand for 16.7 m covering 10 m² of bottom. We placed red drum in 70% ethanol immediately after capture, and measured fish to the nearest 0.1 mm SL upon return to the laboratory. We did not adjust measurements for possible shrinking during preservation.

Marsh Use

We further characterized patterns of red drum habitat use by comparing densities within a *S. alterniflora* marsh to other adjacent habitat types at the GB2 sampling area. These samples were collected during November 13, 1997 at high tide and peak recruitment. Because epibenthic sleds cannot

be towed in the dense vegetation of salt marsh, we employed drop samplers (Zimmerman et al. 1984) to estimate densities of juvenile red drum at three locations within the marsh vegetation (1, 5, and 10 m from the marsh edge interface) and at the nonvegetated marsh edge interface. Drop samplers efficiently sample shallow marsh habitat and have been used previously to sample nekton on the marsh surface (Rozas and Minello 1997). The 2.6m² cylindrical sampler was suspended from a boom mounted on a shallow draft boat. We pushed the boat from the stern to minimize disturbance and dropped the cylinder rapidly to enclose the sampling area. The enclosed area was swept with dip nets and drained by pumping water out through a 1-mm mesh net. Any remaining animals were removed by hand. We collected five replicate drop samples at each of the four marsh habitat types. Samples were stored in formalin for identification and enumeration in the laboratory. In addition to drop samples, we made 10 sled tows at the nonvegetated marsh edge interface to compare catch efficiency of the two gear types. We also made 10 sled tows at 15 and 30 m from the marsh edge interface towards open water for comparison with drop sampler data.

OYSTER REEF USE

Oyster reefs are difficult to sample, and the hard structure of reefs can make both towed nets and drop samplers ineffective. We employed lift nets as described by Rozas (1992) and Wenner et al. (1996) to quantify red drum abundance on intertidal oyster reefs. These nets allowed us to enclose a 6-m² area of reef at high tide and sample fishes as the tide dropped and exposed the reef. We collected these samples on November 19–24, 1998 at Christmas Bay during peak red drum recruitment and maximum monthly tidal ranges. We used 6 lift nets and repeated the sampling effort twice for a total of 12 samples in this habitat type.

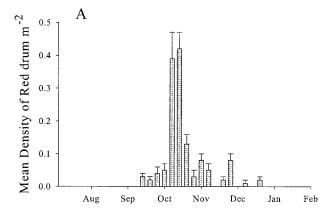
At the same time lift nets were deployed, we used drop samples and sled tows to examine relative abundance of red drum in other nearby habitat types. Although seagrass occurred over most of the bottom in the Christmas Bay sampling area, we identified patches of nonvegetated sand bottom adjacent to the beds for this comparative study. We sampled this nonvegetated sand bottom and seagrass using both 2.6-m² drop samplers (10 samples per habitat type) and epibenthic sleds (10 tows per habitat type). We also used drop samplers to estimate densities within salt marsh vegetation (~1 m from the edge). The marsh edge interface (interspersed with seagrass) was sampled using epibenthic sleds. Using both drop sampler and epibenthic

sleds in seagrass and on nonvegetated bottom allowed us to examine gear catch efficiency.

Lift nets were 2×6 m wide $\times 1$ m deep and constructed from 5-mm delta nylon mesh netting. We used a heavy galvanized chain sewn into a sleeve on the bottom perimeter of the net to ensure a good seal with the reef substrate. Nylon rope was sewn around the top perimeter of the net, and small loops (~15 cm diameter) of rope were sewn at each corner. Before sampling, we buried the nets and chain in a 20-cm deep trench at low tide and covered the trench with oyster rubble. We placed a collecting bucket (30-cm diameter × 30 cm deep) flush with the reef surface in the area of lowest elevation. We connected a 10-m nylon rope to the loop at each corner of the net and secured the other end to a metal stake with a ~10-cm diameter eye on each end. A stake was anchored into the sediment 1 m from each corner of the enclosure. At high tide, one person at each corner slowly approached the lift net, grabbed the rope from the stake on each corner of the enclosure, and simultaneously lifted the top perimeter of the net above the water's surface by rapidly pulling the ropes through the eye in the stakes. The chain sleeve remained buried in the sediment sealing the bottom of the net and trapping the fish. We secured the top net perimeter above the water with PVC stakes. Following reef exposure at low tide, the collecting buckets were removed, and the enclosed area was visually inspected for any additional animals. We reburied the nets, and after 48 h the procedure was repeated. During spring of 1998, we assessed the recovery rates of fishes from the oyster reef lift nets. We marked (anal fin clipped) and added 10 fish (Lagodon rhomboides and Cyprinodon variegatus) to each net after it was lifted at high tide and counted the number recovered.

STATISTICAL ANALYSES

We analyzed spatial patterns of red drum densities with analysis of variance (ANOVA) during the recruitment period from mid-September to mid-November when mean density of red drum from all areas was > 0.04 m⁻² (Fig. 2a). We used a twofactor ANOVA with blocks to examine the main effects of Sampling Area (CB1, CB2, GB1, GB2, WB1, and WB2) and location (ME, TC, 15M, and 30M). A priori contrasts within the sampling area × location interaction were used to test for differences ($\alpha = 0.01$) among locations within bay systems with and without seagrass. All observations were converted to number of fish m-2 (density) before analysis, and a $\log (x + 1)$ transformation was used to reduce heteroscedasticity. We used sampling date as a blocking variable to remove effects of sampling time. To provide information on



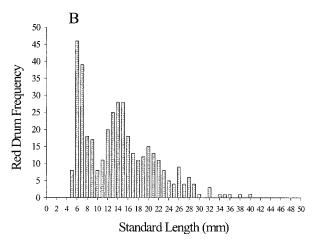


Fig. 2. A) Mean density (\pm SE) and B) length-frequency distribution of newly settled red drum collected with epibenthic sleds from Galveston Bay during the fall 1997 recruitment season

relative gear efficiencies, student's *t*-tests were used to compare densities collected with different gear within the same habitat type.

Results

PATTERNS WITHIN AND AMONG SAMPLING AREAS

Newly settled red drum first appeared in epibenthic sled samples during September 1997 and were collected through December 1997, with peak recruitment occurring during October and November (Fig. 2a). Young red drum first appeared at 5 mm SL with peak numbers settling at 6–8 mm SL, although early juveniles up to 40 mm SL were present in our samples (Fig. 2b). Modal frequencies occurred for individuals from 6–8 and 12–16 mm SL.

The presence of seagrass at sampling areas and locations was generally associated with high densi-

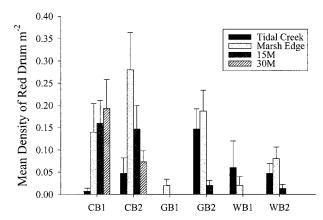


Fig. 3. Mean density (\pm SE) of newly settled red drum at four locations (tidal creeks, marsh edge interface, and 15 and 30 m toward open water from the marsh edge interface) in each of six sampling areas during the period of peak recruitment to Galveston Bay (mid-September to mid-November) in 1997. Each mean represents 15 epibenthic sled tows. See Table 1 for AN-OVA results.

ties of young red drum. Highest densities occurred in sampling areas of Christmas Bay (CB1 and CB2) where seagrass was present (Fig. 3; Table 1). In these areas, densities along the marsh edge interface (with interspersed seagrass) and at 15 and 30 m from the marsh edge (seagrass meadows) were not different and significantly higher than densities in nonvegetated tidal creeks (Fig. 4a; Table 1). Red drum densities were relatively low at sampling areas without seagrass, and few specimens were collected at area GB1. In bays without seagrass, significantly higher densities of fish occurred in tidal creeks and at the marsh edge interface (nonvegetated sand/mud bottom) than in subtidal habitats at 15 and 30 m distances (nonvegetated sand bottom) from marsh edge toward open water (Fig. 4b; Table 1).

The shallow intertidal creeks that we sampled were narrow (generally < 2 m in width) and nonvegetated. In areas without seagrass, these tidal creeks were physically and functionally similar to the nonvegetated marsh edge (Fig. 4b). In Christmas Bay, the tidal creeks represented the only nonvegetated marsh edge, because seagrass occurred in other marsh edge samples. We summarized habitat selection for the entire bay system sampled by combining data from tidal creeks in all sampling areas with marsh edge in Galveston Bay and West Bay into a nonvegetated marsh edge habitat type. In this comparison, mean red drum densities were highest in seagrass (which included marsh edge samples from Christmas Bay), intermediate in the nonvegetated marsh edge habitat type, and lowest on nonvegetated bottom away from the marsh edge (Fig. 5a). Mean lengths also varied across

TABLE 1. Analysis of variance table for red drum density patterns in Galveston Bay. The main effects in this analysis are sampling area (6 levels) and location (4 levels). There are two sampling areas within each of three bays: Christmas Bay, Galveston Bay, and West Bay. The locations examined were Marsh Edge Interface (ME), Tidal Creeks (TC), 15 m (15M), and 30 m (30M) toward open water from the marsh edge interface. A priori contrasts within the sampling area × location interaction were designed to compare locations from sampling areas that had seagrass (Christmas Bay, CB1, and CB2) and sampling areas without seagrass (Galveston and West Bays; GB1, GB2, WB1, and WB2).

Source	df	SS	F	P
Sampling area	5	0.122	11.783	< 0.001
Location	3	0.043	6.939	< 0.001
Sampling area × Location	15	0.117	3.748	< 0.001
Christmas Bay: $TC = ME + 15M + 30M$	1	0.055	26.576	< 0.001
Christmas Bay: $TC = ME$	1	0.059	28.493	< 0.001
Christmas Bay: ME = 15M	1	0.004	1.904	0.168
Christmas Bay: ME = 30M	1	0.008	4.024	0.046
Christmas Bay: $15M = 30M$	1	0.001	0.392	0.532
Galveston and West Bays: $TC = ME+15M+30M$	1	0.007	3.231	0.073
Galveston and West Bays: TC = ME	1	0.001	0.545	0.461
Galveston and West Bays: ME = 15M	1	0.020	9.622	0.002
Galveston and West Bays: ME = 30M	1	0.026	12.365	< 0.001
Galveston and West Bays: 15M = 30M	1	0.003	0.172	0.679
Date (block)	4	0.060	7.254	< 0.001
Residual	332	0.690		

these habitat types (Fig. 5b) with largest red drum (18.5 mm SL; SE = 0.80) in seagrass, an intermediate mean size (15.1 mm SL; SE = 0.49) at the marsh edge interface, and the smallest mean size (9.7 mm SL; SE = 0.44) over nonvegetated bottom.

SMALL-SCALE PATTERNS WITHIN SAMPLING AREAS

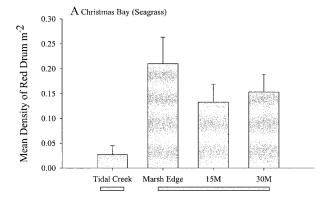
We examined smaller-scale distributions of red drum at the GB2 sampling area using epibenthic sleds and drop samplers. Densities varied dramatically from open water locations (15 and 30 m from marsh edge interface) to 10 m within the salt marsh interior (Fig. 6a). The highest mean densities occurred at the marsh edge interface (nonvegetated bottom) and within the marsh vegetation at 1 m from the edge. No red drum were collected from 5 and 10 m within the marsh or at 30 m from the marsh edge in open water (nonvegetated bottom).

In Christmas Bay, we used three types of sampling gear to examine small-scale density patterns. Lift nets used in oyster reef were effective at capturing many estuarine fishes and decapod crustaceans, and the mean recovery rate of marked fish was 87%. We did not collect any red drum from the oyster reefs, and no red drum were collected over nonvegetated bottom (Fig. 6b). Red drum were found only in vegetated samples including seagrass and *S. alterniflora* near the marsh edge.

We compared gear efficiency between the epibenthic sled and the drop sampler by collecting samples with both techniques in seagrass and on nonvegetated bottom at Christmas Bay and at the marsh edge interface at GB2. No fish were collected on nonvegetated bottom with either gear, but the efficiency of the sampling gear appeared similar in the other habitat types. Density estimates from the drop sampler and epibenthic sled were not significantly different for the marsh edge interface (t=1.411, df=20, p=0.174) or seagrass meadows (t=0.253, df=20, p=0.803). Based on the mean densities, the overall catch efficiency of the sled in relation to the drop sampler was 83% (81% over nonvegetated bottom and 85% in seagrass).

Discussion

Densities of newly settled red drum varied among the habitat types we examined in the Galveston Bay system. Seagrass meadows and marsh edge interface supported much higher densities than nearby nonvegetated bottom. We collected few red drum on oyster reefs or within salt marsh vegetation away from the marsh edge. Although seagrass meadows are considered important nursery areas for this species (Holt et al. 1983; Peters and McMichael 1987; Rooker and Holt 1997; Rooker et al. 1998a), geography influences the availability of these nurseries. Few studies have compared the use of alternate habitat types (reviewed in Minello 1999), especially when seagrass is limited or unavailable. Our data suggest that the marsh edge interface may function as a nursery area for newly settled red drum when seagrass coverage is sparse. Rakocinski et al. (1992) and Baltz et al. (1993) also found relatively high densities of red drum along the marsh edge ecotone in Louisiana estuaries where seagrass is limited. Such density patterns may reflect a combination of both habitat selection (Stunz et al. 2001) and differen-



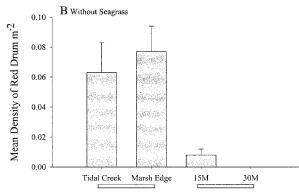
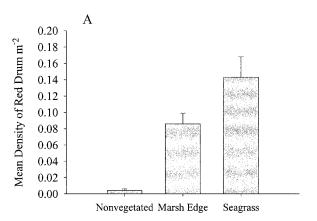


Fig. 4. Mean density (\pm SE) of newly settled red drum at four locations (marsh edge interface, tidal creeks, and 15 and 30 m toward open water from the marsh edge interface) at sampling areas with seagrass (A) and sampling areas without seagrass (B) during the period of peak recruitment to Galveston Bay (mid-September to mid-November) in 1997. No seagrass occurred at any of the tidal creek locations. Each mean represents 30 epibenthic sled tows in areas with seagrass and 60 tows in areas without seagrass. Horizontal lines below the bars illustrate contrasts among locations (Table 1), and bars sharing horizontal lines are not significantly different ($\alpha=0.01$).

tial mortality (Stunz and Minello 2001) associated with these habitat types.

Newly settled red drum were first captured in mid-September, and new recruits appeared through mid-December. This recruitment pattern corresponds to the reported fall spawning of red drum in Gulf of Mexico waters (Peters and Mc-Michael 1987; Murphy and Taylor 1990; Comyns et al. 1991). Peak settlement densities of fish 6-8 mm SL occurred in October and November. Similar temporal patterns of size-at-settlement have been observed in Florida (Peters and McMichael 1987) and in South Texas estuaries (Holt et al. 1983; Rooker et al. 1998a). Few red drum > 30 mm SL were captured, suggesting alternate habitat use or possible gear avoidance by larger individuals. Rooker and Holt (1997) also found few sciaenids > 40 mm in epibenthic sled tows in South Texas



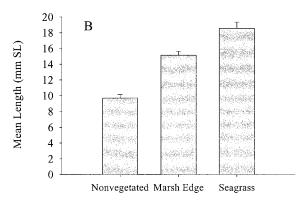
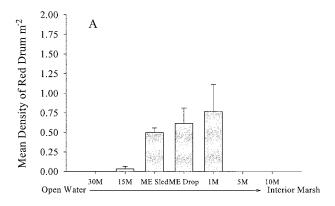


Fig. 5. A) Mean density (\pm SE) and B) mean length (mm SL \pm SE) of newly settled red drum collected with epibenthic sleds from marsh edge interface (including fish captured from tidal creeks), nonvegetated bottom, and seagrass habitat types from all samples collected in Galveston Bay during the period of peak recruitment to Galveston Bay (mid-September to mid-November) in 1997.

estuaries. In Florida, Peters and McMichael (1987) found few fish > 50 mm in seine collections, and they suggested red drum may migrate to deeper waters to avoid cold temperatures of winter.

Differences in the density of juvenile red drum were apparent at different spatial scales in the Galveston Bay system. Large-scale patterns were exhibited as differences among bays and sampling areas, with highest densities in Christmas Bay and at one sampling area (GB2) in Galveston Bay. Smallerscale patterns were exhibited as differences among habitat types within sampling areas, with highest densities in seagrass followed by marsh edge. To some extent, the large scale patterns can be explained by small scale density patterns and habitat availability; for example, Christmas Bay has most of the seagrass in the bay system. Differences in red drum densities between sampling areas within Galveston Bay (GB1 versus GB2) suggest that other factors such as larval supply and habitat-specific



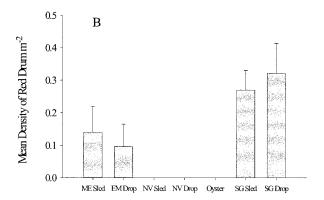


Fig. 6. A) Mean density (± SE) of newly settled red drum collected at varying distances from the marsh edge during the fall 1997 recruitment season (November 13) at a Galveston Bay sampling area (GB2). The 30M, 15M, and ME Sled (marsh edge interface) are densities on nonvegetated bottom from epibenthic sled tows (n = 10). The ME drop, 1M, 5M, and 10M are densities from drop samplers (n = 5) at the nonvegetated marsh edge interface and within marsh vegetation at 1, 5, and 10 m from the marsh edge. The ME drop and ME sled represent the same habitat type. B) Mean density (± SE) of newly settled red drum collected in Christmas Bay (November 19-24, 1998). The ME Sled, NV sled, and SG sled are densities from epibenthic sled tows in marsh edge interface (interspersed with seagrass), nonvegetated bottom, and seagrass, respectively. The EM Drop is from 1 m into marsh interior within the S. alterniflora. The NV Drop and SG Drop are densities from drop samplers in nonvegetated bottom and seagrass. Oyster densities are from lift nets in intertidal zone (n = 12). There were 12 drop samples and 10 sled tows per habitat type.

variability in growth and survival are important as well (Petrik et al. 1999).

Newly settled red drum were not uniformly distributed within the salt marsh. Based on data from drop samplers at GB2 where no seagrass was present, densities were highest along the marsh edge interface, both in open water just outside of the vegetation and 1 m inside *S. alterniflora* marsh. No red drum were taken 5 or 10 m into the marsh, and few were captured from open water locations

15 and 30 m from the marsh edge. Other studies examining marsh use also have found that transient fishes occur along the marsh edge to a greater extent than within interior marsh vegetation (Baltz et al. 1993; Minello et al. 1994; Peterson and Turner 1994; Rozas and Zimmerman 2000).

Although oyster reefs are common in many estuaries, few studies have assessed the use of this habitat type by juveniles of fishery species (but see Zimmerman et al. 1989; Wenner et al. 1996; Coen et al. 1999; Minello 1999). In the Galveston Bay system, extensive oyster reefs (10,800 ha covering 10.4% of the bay bottom; Powell 1993) may provide nursery habitat for newly settled red drum. We found no red drum in our lift net samples from intertidal oyster reef and oyster rubble in Christmas Bay. We simultaneously sampled adjacent marsh edge interface, nonvegetated sand bottom, and seagrass and found relatively high red drum densities at the marsh edge interface and in seagrass. Lift nets appear to be effective for capturing estuarine fishes (Rozas 1992; Wenner et al. 1996), and we collected a variety of other fishes and decapod crustaceans in the oyster reef samples. Minimal use of oyster reef by early juvenile red drum in Galveston Bay is corroborated by studies in other areas examining nekton use of oyster reefs (Wenner et al. 1996; Coen et al. 1999). The design of the lift nets we used limited us to sampling intertidal oyster reefs which may not be functionally equivalent to subtidal reefs that contain less oyster rubble and more live oysters. Oyster reefs in Christmas Bay are located near seagrass and salt marshes, and may function differently than isolated reefs located within expanses of nonvegetated bottom common to Galveston Bay. Zimmerman et al. (1989) sampled oyster reefs in the middle of West Bay (see Fig. 1) and did not collect red drum; but their samples were taken in mid-December, and they may have missed the period of peak recruitment for this species. These results suggest minimal use of oyster reef by newly settled red drum. Considering the large areal extent of oyster reefs in many estuarine systems, nekton use of this habitat type needs to be examined in more detail.

Predation can be a major factor contributing to variability in survival of newly settled marine organisms (Cushing 1975; Houde 1987). Predation rates on young fish can be reduced by the structural complexity of available habitat, affecting density patterns and eventual recruitment to fisheries (Leggett and Deblois 1994). In laboratory experiments, Rooker et al. (1998b) reported lower mortality rates for red drum in seagrass compared with nonvegetated bottom, and Stunz and Minello (2001) showed reduced mortality associated with seagrass, salt marsh, and oyster reef structure in

similar laboratory experiments. In our samples, the highest densities and largest mean sizes of red drum occurred in seagrass and at the marsh edge interface. These density patterns are consistent with increased survival associated with vegetative structure. The absence of red drum in oyster reefs suggests that factors other than predation affects red drum density patterns because the structure of oyster reefs appears to offer young red drum protection from predators (Stunz and Minello 2001).

Movement among habitats and differential growth may also be responsible for observed patterns of density and size. Variation in growth rates of newly settled fishes can be important for individual survival, and growth can influence successful recruitment to adult populations (Houde 1987; Connell and Jones 1991; Leggett and Deblois 1994). Growth rates in vegetated habitats may be related to differences in the quantity or quality of available food resources (Summerson and Peterson 1984; Sogard 1992; Levin et al. 1997) or perhaps to other physiochemical conditions associated with vegetation (Neill et al. 1994; Kamermans et al. 1995; Baltz et al. 1998). The differences we observed in mean red drum length among seagrass, the marsh edge interface, and nonvegetated bottom suggest that new settlers may grow faster in vegetated habitat types or that larger individuals may migrate to these areas. Although evidence for increased growth in vegetation is equivocal (Heck et al. 1997; Baltz et al. 1998), some studies have reported increased growth of fishes and crustaceans associated with vegetated estuarine habitats (Currin et al. 1984; Zimmerman and Minello 1984; Sogard 1992; Perkins-Visser et al. 1996; Phelan et al. 2000). In field-enclosure growth experiments conducted in Christmas Bay, Stunz (1999) found significantly higher growth rates of young red drum in seagrass and salt marsh vegetation compared with oyster reef and nonvegetated bottom.

Tidal flooding dynamics can influence habitat use and may complicate density estimations of newly settled red drum among the various estuarine habitat types we examined, particularly within intertidal marshes (Rozas and Minello 1997). We sampled during high tides when all habitat types were equally available. During periods of low tide when the salt marsh surface is exposed, submerged aquatic vegetation and shallow nonvegetated bottom may become more important as individuals seek low tide refuges. Flooding durations at the marsh edge are high in Galveston Bay (approximately 78% of the time throughout the year), and the marsh edge interface is almost constantly flooded during the fall red drum recruitment season (Minello and Webb 1997).

A more complete understanding of nursery

functions in estuarine systems also requires information on habitat linkages. Synergistic connections between adjacent habitats can have important effects on the contribution of habitat types to the productivity of a species (Irlandi and Crawford 1997; Micheli and Peterson 1999). Such linkages may be important for red drum in systems such as Galveston Bay (and especially Christmas Bay) where many habitat types occur in close proximity.

Seagrass and marsh edge interface support the greatest densities of newly settled red drum in Galveston Bay. These density patterns are likely caused by increased settlement, survival, and growth in these habitat types, but the relative contribution of these factors is difficult to assess. Even though densities at the marsh edge interface were lower than in seagrass, the extensive marsh systems in the bay complex provide a large amount of marsh edge, and this habitat type may be functioning as a significant nursery for red drum in Galveston Bay. To fully understand the nursery potential of these habitat types and their contribution to red drum production, we need to consider not only density patterns, but the areal extent of habitat types, differential survival and growth, and movement of fish among habitat types and to the fishery.

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LITERATURE CITED

Adair, S. E., J. L. Moore, and C. P. Onuf. 1994. Distribution and status of submerged vegetation in estuaries of the upper Texas coast. *Wetlands* 14:110–121.

Baltz, D. M., J. W. Fleeger, C. F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: Factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environmental Biology of Fishes* 53:89–103.

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.

BOESCH, D. F. AND R. E. TURNER. 1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7:460–468.

COEN, L. D., M. W. LUCKENBACH, AND D. L. BREITBURG. 1999. The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives, p. 438–454. *In* L. R. Benaka (ed.), Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.

Comyns, B. H., J. Lyczkowski-Shultz, D. L. Nieland, and C. A. Wilson. 1991. Reproduction of red drum, *Sciaenops ocellatus*,

- in the northcentral Gulf of Mexico: Seasonality and spawner biomass. U.S. Department Commerce, National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service 95:17–26. Silver Spring, Maryland.
- CONNELL, S. D. AND G. P. JONES. 1991. The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecol*ogy 151:271–294.
- CURRIN, B. M., J. P. REED, AND J. M. MILLER. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: A comparison of tidal and nontidal nursery areas. *Estuaries* 7:451–459.
- Cushing, D. H. 1975. Marine Ecology of Fisheries. Cambridge University Press, Cambridge, England.
- DAY, JR., J. W., C. A. S. HALL, W. M. KEMP, AND A. YANEZ-ARAN-CIBIA. 1989. Estuarine Ecology. John Wiley and Sons, New York.
- FULS, B. E. AND R. A. HENSLEY. 1998. Trends in relative abundance and size of selected finfishes and shell fishes along the Texas coast: November 1975–December 1996. Management Data Series 159. Texas Parks and Wildlife, Coastal Fisheries Division. Austin, Texas.
- Heck, Jr., K. L., D. A. Nadeau, and R. Thomas. 1997. The nursery role of seagrass beds. *Gulf of Mexico Science* 15:50–54.
- HECK, JR., K. L. AND T. A. THOMAN. 1981. Experiments on predator-prey interaction in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* 53:125–135.
- HOLT, S. A., C. L. KITTING, AND C. R. ARNOLD. 1983. Distribution of young red drums among different seagrass meadows. *Transactions of the American Fisheries Society* 112:267–271.
- HOUDE, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2:17–29. Miami, Florida.
- IRLANDI, E. A. AND M. K. CRAWFORD. 1997. Habitat linkages: The effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110:222–230.
- KAMERMANS, P., K. Y. GUINDON, AND J. M. MILLER. 1995. Importance of food availability for growth of juvenile southern flounder (*Paralichthys lethostigma*) in the Pamlico River estuary, North Carolina, USA. *Netherlands Journal of Sea Research* 34:101–109.
- KNEIB, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: Causes and questions. *Estuaries* 7:392–412.
- KNEIB, R. T. 1993. Growth and mortality in successive cohorts of fish larvae within an estuarine nursery. Marine Ecology Progress Series 94:115–127.
- Leggett, W. C. and E. Deblois. 1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* 32:119–134
- LEVIN, P. S., R. PETRIK, AND J. MALONE. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* 112:55–63.
- MICHELI, F. AND C. H. PETERSON. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology* 13:869–881.
- MINELLO, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat, p. 438–454. *In* L. R. Benaka (ed.), Fish Habitat: Essential Fish Habitat and Rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.
- MINELLO, T. J. AND J. W. WEBB, JR. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas USA. *Marine Ecology Progress Series* 151:165–179.
- MINELLO, T. J., R. J. ZIMMERMAN, AND R. MEDINA. 1994. The im-

- portance of edge for natant macrofauna in a created salt marsh. *Wetlands* 14:184–198.
- MURPHY, M. D. AND R. G. TAYLOR. 1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. *Fishery Bulletin* 88:531–542.
- NEILL, W. H., J. M. MILLER, H. W. VAN DER VEER, AND K. O. WINEMILLER. 1994. Ecophysiology of marine fish recruitment: A conceptual framework for understanding interannual variability. Netherlands Journal of Sea Research 32:135–152.
- Orth, R. J., K. L. Heck, Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7:339–350.
- Pattillo, M. E., T. E. Czapla, D. M. Nelson, and M. E. Monaco. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Volume II: Species life history summaries. Estuarine Living Marine Resources Program Report No. 11. National Oceanic and Atmospheric Administration/National Ocean Service Strategic Environmental Assessments Division, Silver Spring, Maryland.
- Perkins-Visser, E., T. G. Wolcott, and D. L. Wolcott. 1996. Nursery role of seagrass beds: Enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology* 198:155–173.
- PETERS, K. M. AND R. H. MCMICHAEL, JR. 1987. Early life history of the red drum *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Estuaries* 10:92–107.
- Peterson, G. W. and R. E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17:235–262.
- Petrik, R., P. S. Levin, G. W. Stunz, and J. Malone. 1999. Recruitment of Atlantic croaker, *Micropongias undulatus*. Do postsettlement processes disrupt or reinforce initial patterns of settlement? *Fishery Bulletin* 97:954–961.
- PENLAND, S. AND K. E. RAMSEY. 1990. Relative sea-level rise in Louisiana and the Gulf of Mexico: 1908–1988. *Journal of Coast-al Research* 6:323–342.
- Phelan, B. A., R. Goldberg, A. J. Bejda, J. Pereira, S. Hagan, P. Clark, A. L. Studholme, A. Calabrese, and K. W. Able. 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries. *Journal of Experimental Marine Biology and Ecology* 147:1–28.
- POLLARD, D. A. 1984. A review of ecological studies on seagrassfish communities, with particular reference to recent studies in Australia. *Aquatic Botany* 18:3–42.
- POWELL, E. N. 1993. Status and trends analysis of oyster reef habitat in Galveston Bay, p. 207–209. In R. W. Jensen (ed.), Proceeding, Second State of the Bay Symposium, Galveston, Texas. The Galveston Bay National Estuary Program, Galveston, Texas.
- RAKOCINSKI, C. F., D. M. BALTZ, AND J. F. FLEEGER. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. Marine Ecology Progress Series 80:135–148.
- ROOKER, J. R. AND S. A. HOLT. 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocella*tus: Patterns of distribution and growth. *Marine Ecology Progress* Series 158:139–149.
- ROOKER, J. R., G. J. HOLT, AND S. A. HOLT. 1998b. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: Is early-life survival enhanced by seagrass meadows? *Ma-rine Biology* 131:145–151.
- ROOKER, J. R., S. A. HOLT, M. A. SOTO, AND G. J. HOLT. 1998a. Post-settlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21:315–324.
- ROZAS, L. P. 1992. Bottomless lift net for quantitatively sampling

- nekton on intertidal marshes. Marine Ecology Progress Series 89: 287–292.
- ROZAS, L. P. AND T. J. MINELLO. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20:199–213.
- ROZAS, L. P. AND T. J. MINELLO. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bulletin of Marine Science* 63:481–501.
- ROZAS, L. P. AND R. J. ZIMMERMAN. 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay estuary, Texas (USA). *Marine Ecology Progress Series* 193:217–239.
- SHERIDAN, P., G. McMahan, K. Hammerstrom, and W. Pulich, Jr. 1998. Factors affecting restoration of *Halodule wrightii* to Galveston Bay, Texas. *Restoration Ecology* 6:144–158.
- SHORT, F. T. AND S. WYLLIE-ECHEVERRIA. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23:17–27.
- SOGARD, S. M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* 85: 35–53
- SOGARD, S. M. AND K. W. ABLE. 1992. Growth variation of newly settled winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries as determined by otolith microstructure. *Netherlands Journal of Sea Research* 29:163–172.
- STUNZ, G. W. 1999. Causes and consequences of recruitment patterns in newly settled red drum (*Sciaenops ocellatus*). Ph.D. dissertation, Texas A&M University, College Station, Texas.
- 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 *Sciaen*-

- ops ocellatus (Linnaeus). Journal of Experimental Marine Biology and Ecology 260:13–25.
- SUMMERSON, H. C. AND C. H. PETERSON. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Marine Ecology Progress Series* 15:63–77.
- THAYER, G. W., P. L. MURPHEY, AND M. W. LA CROIX. 1992. Responses of plant communities in western Florida Bay to dieoff of seagrasses. *Bulletin of Marine Science* 54:718–726.
- WEINSTEIN, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fishery Bulletin 77:339–357.
- Wenner, E., H. R. Beatty, and L. Coen. 1996. A method for quantitatively sampling nekton on intertidal oyster reefs. *Jour*nal Shellfish Research 15:769–775.
- WHITE, W. A. AND T. A. TREMBLAY. 1995. Submergence of wetlands as a result of human-induced subsidence and faulting along the upper Texas Gulf Coast. *Journal of Coastal Research* 11:788–807.
- ZIMMERMAN, R. J. AND T. J. MINELLO. 1984. Fishery habitat requirements: Utilization of nursery habitats by juvenile penaeid shrimp in a Gulf of Mexico salt marsh, p. 371–383. In B. J. Copeland, K. Hart, N. Davis, and S. Friday (eds.), Research for Managing the Nation's Estuaries. UNC-SG-84-08, University of North Carolina Sea Grant Publication. Raleigh, North Carolina.
- ZIMMERMAN, R. J., T. J. MINELLO, T. J. BAUMER, AND M. C. CAS-TIGLIONE. 1989. Oyster reef as habitat for estuarine macrofauna. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service, Southeast Fisheries Science Center, Galveston, Texas.
- ZIMMERMAN, R. J., T. J. MINELLO, AND G. ZAMORA. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. *Fishery Bulletin* 82:325–336.

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