Estuaries Vol. 21, No. 2, p. 318–327 June 1998

Postsettlement Patterns of Habitat Use by Sciaenid Fishes in Subtropical Seagrass Meadows

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ABSTRACT: Spatial and temporal patterns of distribution and abundance were examined for postsettlement sciaenids collected from seagrass meadows in the Aransas Estuary, Texas. Overall, 5443 sciaenid larvae and early juveniles were identified from biweekly epibenthic sled collections taken from August 1994 to August 1995. Eight species were present in seagrass meadows, with five accounting for over 99.9% of sciaenids collected: silver perch (*Bairdiella chrysoura*), spotted seatrout (*Cynoscion nebulosus*), spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and red drum (*Sciaenops ocellatus*). Settlement to seagrass meadows was partitioned temporally with little overlap among the five species. Postsettlers from inshore spawners (*B. chrysoura, C. nebulosus, S. ocellatus*) inhabited seagrass meadows during the spring and summer, while individuals from offshore spawners (*L. xanthurus, M. undulatus*) were present in the late fall and winter. Densities of *B. chrysoura, C. nebulosus, S. ocellatus* were highest for small individuals (4–8 mm SL) and these taxa remained in seagrass sites through the early juvenile stage. Conversely, *L. xanthurus* and *M. undulatus* maintained longer pelagic periods and generally entered seagrass meadows at larger sizes (10–14 mm SL). Moreover, these taxa were only temporary residents of selected seagrass meadows, apparently migrating to alternative habitats shortly after arrival. During peak settlement, mean and maximum densities among species ranged from 0.1 m^{-2} to 0.8 m^{-2} and 0.7 m^{-2} to 23.8 m^{-2}, respectively. Density and mean size of postsettlement sciaenids differed significantly between seagrass species (*Halodule wrightii, Thalassia testudinum*) and among sites within the estuary.

Introduction

Seagrass meadows provide critical nursery habitat for a diversity of fishes during their early life stages (Olney and Boehlert 1988; Bell and Pollard 1989). Increased abundance and diversity of fishes associated with seagrass meadows have been related to the physical complexity of the seagrass canopy. Increased complexity provides such benefits as refuge from predators (Heck and Orth 1980; Stoner 1982; Ryer 1988; Savino and Stein 1989) and increased food supply (Orth 1992). In addition, the physical nature of the seagrass canopy may affect the hydrodynamics of larval recruitment (Eckman 1983) and influence the chance of settlement by pelagic larvae (Bell et al. 1987).

Larvae of several estuarine fishes settle into seagrass meadows following a dispersive pelagic phase (Bell and Pollard 1989; Day et al. 1989; Leis 1991). Since postsettlement mortality is typically high and variable, recruitment success or failure can be linked to differential survival during this period (Jones 1991; Carr and Hixon 1995; Rooker 1997). As a result, studies focusing on the postsettlement phase are essential for understanding the dynamics of early life. However, detailed ecological assessments of habitat requirements during the postsettlement phase are incomplete for many estuarine species. This information is required for effective conservation and management of the estuarine fish-habitat complex and will provide the foundation for future studies addressing the causes and consequences of early life mortality.

Species from the family Sciaenidae (drums) are vital to the recreational fishery in the Gulf of Mexico, and several sciaenids exploit seagrass meadows during early life (e.g., Stoner 1983; Tolan et al. 1997). From limited data, it appears that certain sciaenids immigrate to seagrass meadows following a pelagic interval of approximately 15–30 d and remain in these habitats for weeks to months (Holt et al. 1983; Peters and McMichael 1987; McMichael and Peters 1989; Rooker and Holt 1997). To date, few studies have examined postsettlement patterns of habitat use in seagrass meadows and important life history data (e.g., duration and timing of set-

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tlement, size-at-settlement, and spatial distribution) are lacking for many species.

The purpose of the present study was to examine sciaenid utilization of seagrass meadows during the postsettlement phase. Specific objectives of this research were to describe quantitatively the sciaenids inhabiting seagrass meadows in the Aransas Estuary, Texas, determine the temporal patterns of settlement, including the timing and duration of events, and determine the consistency of habitat use over different spatial scales.

Methods

STUDY AREA

The study was conducted in the Aransas Estuary, an 86.4 km^2, bar-built estuary consisting of two major bays (Aransas Bay, Redfish Bay) oriented parallel to the coast. The estuary is located in the vicinity of the Aransas Pass tidal inlet (Fig. 1), which is approximately 400 m wide and connects Gulf of Mexico waters to inshore habitats. Seagrass meadows within the estuary are dominated by shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*). Both species occur primarily in shallow water (ca. <1 m), low-energy areas and are considered the major primary producers in these areas (Zieman and Wetzel 1980). Water temperature, salinity, and turbidity are variable within the estuary; however, our study sites were in close proximity to the tidal inlet (<10 km) and maintained conditions relatively similar to nearshore waters in the Gulf of Mexico.

POSTSETTLEMENT SURVEY

Densities were estimated by enumerating sciaenids in biweekly samples taken from August 1994 to August 1995 (postsettlers were defined as individuals ≤40 mm standard length collected in seagrass meadows). Collections were taken at six sites within the estuary (Fig. 1): Aransas Bay 1, 2, and 3 (AB1, AB2, AB3); Redfish Bay 1 and 2 (RB1, RB2); and Corpus Christi Bay (CB1). At each of the six locations, *H. wrightii* meadows were sampled. At one site within each bay (AB1, RB1, CB1), co-occurring, monotypic stands (>90% single species) of *H. wrightii* and *T. testudinum* were present (designated paired sites) and sampled separately. Seagrass meadows at paired sites were adjacent to one another and less than 50 m apart.

Postsettlement sciaenids were collected from seagrass meadows with an epibenthic sled. The sled opening measured 0.75 m (length) × 0.50 m (height) and was equipped with a 505-μm conical plankton net. The sled was towed by hand at a constant speed (~ 0.7 m s^{-1}) through seagrass meadows. Triplicate sled tows were made at each sampling site on each trip. Sled tows were 20 m in length and the area of seagrass sampled per tow was 15.0 m^2. Individuals were preserved in 95% ethanol immediately after capture. Standard lengths (SL) were measured in the laboratory to the nearest 1.0 mm.

Throughout the postsettlement survey, environmental conditions were recorded in the Aransas Pass at the University of Texas, Marine Science Institute Pier Laboratory. In addition, depth, salinity, and water temperature were measured from each site on all sampling trips. Estimates of seagrass complexity were also made from samples collected with a 7.5-cm diameter coring device. Shoot density, blade height, and number of blades per shoot were measured from three replicate cores taken from each site at 3–4 mo intervals. Estimates of blade height and blades per shoot for each core were mean values based on 10 blades and shoots, respectively.

STATISTICAL ANALYSIS

Three-way factorial analysis of variance (ANOVA) was applied to postsettlement density data (main effects: habitat, site, date). This analysis was performed separately on each taxon and based only on samples from paired sites (AB1, RB1, CB1). Two-way factorial ANOVA (main effects: site, date) was used to examine variation in density among the six *H. wrightii* sites (AB1, AB2, AB3, RB1, RB2, CB1). Prior to ANOVA testing, density data were $\log_e (x + 1)$ transformed to minimize heteroscedasticity. Since seasonal patterns of recruitment were pronounced, many samples contained zero values. As a result, the assumption of multivariate normality (normality of error terms) was not met in some cases. ANOVA is robust to most types and magnitudes of departure from normality and, therefore, non-normality is unlikely to compromise results (Underwood 1981). Tukey's HSD test was used to find a posteriori differences ($\alpha = 0.05$) among sample means. Mean sizes of sciaenids in *H. wrightii* and *T. testudinum* were compared using a one-way ANOVA. Due to heteroscedasticity and unequal sample sizes, means were weighted by the reciprocal of the sample variances of the group means (JMP 1989).

Results

ENVIRONMENTAL CONDITIONS AND SITE CHARACTERISTICS

Temporal variation in water temperature and salinity in the Aransas Pass were pronounced (Fig. 2); temperature and salinity ranged from 12.2°C to 31.1°C and 22.5‰ to 35.7‰, respectively. Measurements were also recorded each trip at the different sampling sites within the Aransas Estuary; however, it is difficult to compare temperature and

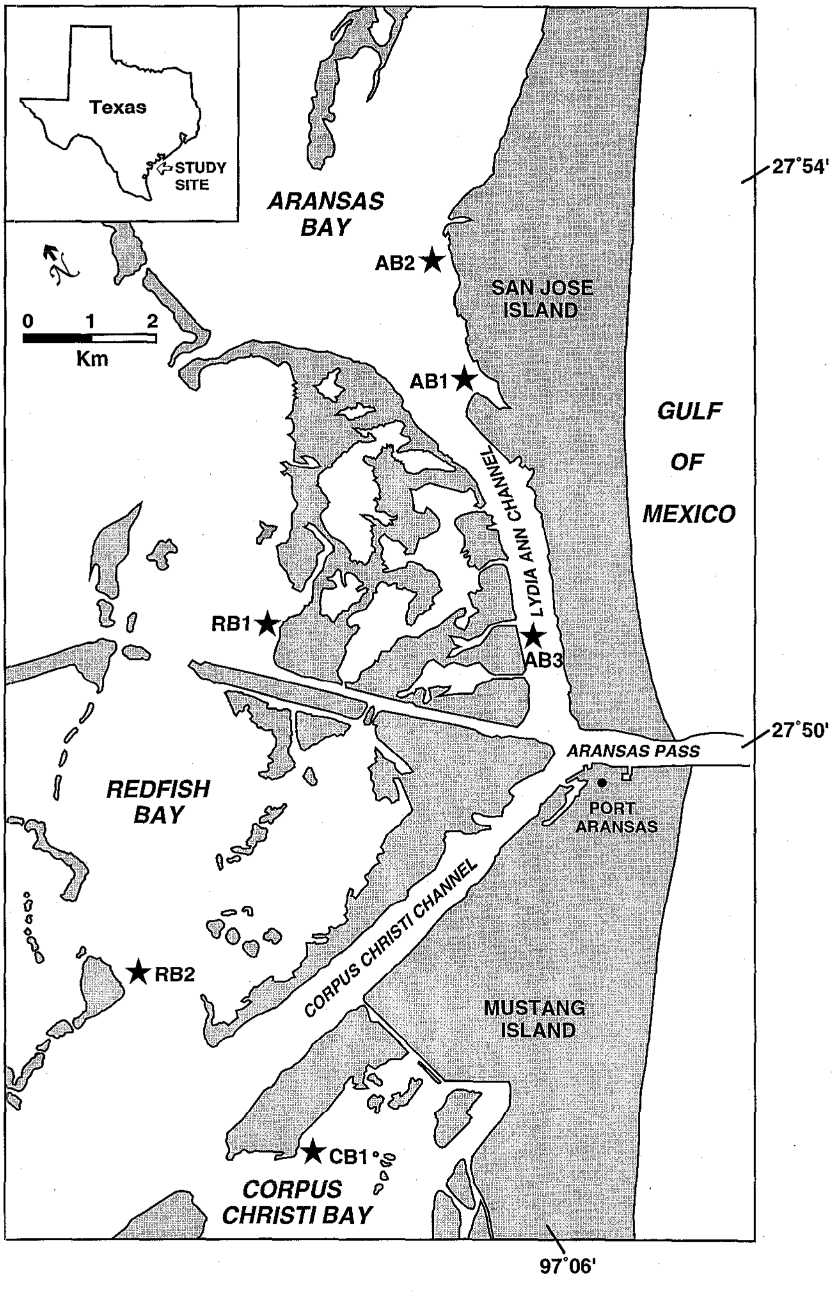

Fig. 1. Map of Aransas Estuary showing location of sampling sites in Aransas Bay (AB1, AB2, AB3), Redfish Bay (RB1, RB2), and Corpus Christi Bay (CB1).

salinity profiles among sites due to the time-of-day effect. In general, temperature changes in the Aransas Estuary closely matched recordings at the Aransas Pass, but larger fluctuations were apparent in the shallower waters of the estuary. Salinity measurements at the tidal pass were representative of conditions at study sites within the estuary.

Monotypic stands of *H. wrightii* and *T. testudinum* differed in physical structure and complexity. On average, *T. testudinum* was present at depths 10–20 cm > *H. wrightii* (0.58 m and 0.44 m, respectively). Shoot densities in *H. wrightii* were approximately 5–10 times higher than *T. testudinum* during the summer and fall, while blade heights were generally lower. Shoot densities and blade heights varied among sites and seasonal patterns were observed (Table 1). The most salient feature was the marked decline in the shoot density and blade height of

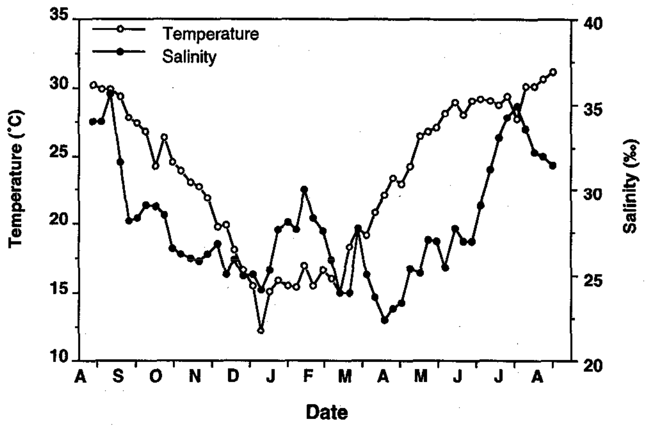

Fig. 2. Weekly water temperature and salinity records for the Aransas Pass from August 1994 to August 1995.

H. wrightii during the winter (Table 1). Number of blades per shoot was similar between *H. wrightii* (2.6 ± 0.7 SD) and *T. testudinum* (2.4 ± 0.7 SD).

ICHTHYOFAUNAL COMPOSITION OF SEAGRASS MEADOWS

The taxonomic composition of ichthyofauna from seagrass meadows in the Aransas Estuary was diverse, with 54 species from 26 families (Table 2). Individuals from four families composed over 85% of the total catch: Sparidae (27.4%), Gobiidae (22.8%), Sciaenidae (18.6%), and Syngnathidae (17.6%). Numerical dominants were pinfish (*Lagodon rhomboides*) (27.1%), darter goby (*Gobionellus boleosoma*) (16.6%), gulf pipefish (*Syngnathus scovelli*) (15.2%), and a suite of sciaenids.

Eight species from the family Sciaenidae were present in seagrass samples (Table 3). Of these, five species were abundant and accounted for over 99.9% of sciaenids collected: silver perch (*Bairdiella chrysoura*), spotted seatrout (*Cynoscion nebulosus*), spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and red drum (*Sciaenops ocellatus*). Sciaenids collected in seagrass meadows with the epibenthic sled were almost exclusively postsettlers; 98.4% of sciaenids collected were ≤40 mm. Further quantitative description will be limited to postsettlers of these five species.

TEMPORAL VARIATION IN SETTLEMENT

Settlement events (based on densities of postsettlement sciaenids) were species-specific and partitioned temporally (Fig. 3). Newly settled *C. nebulosus* were present in seagrass meadows from late spring through summer (April to October); densities were highest in August. *Sciaenops ocellatus* entered seagrass meadows in late August and highest densities were reached from late September through October. Shortly thereafter, *M. undulatus* dominated seagrass meadows and settlement was bimodal, with two primary periods: November and February. Similarly, the settlement of *L. xanthurus* was characterized by two peaks (December, March), each following *M. undulatus* peaks by 2–4 wk. The number of new settlers was highest for *M. undulatus* and *L. xanthurus* during the first (November) and second (March) settlement pulse, respectively. From April to June, *B. chrysoura* was the

TABLE 1. Mean shoot density (shoots m^{-2}) and blade height (cm) of seagrass meadows in the Aransas Estuary. Estimates of seagrass complexity are given by site, habitat, and date. Values in parentheses represent standard deviations.

		June 27, 1994		November 11, 1994		February 27, 1995	
Site	Habitat	Density	Height	Density	Height	Density	Height
AB1	*Halodule*	8,773 (4,402)	19.7 (2.9)	5,094 (0)	14.5 (1.6)	943 (865)	4.0 (0.0)
AB1	*Thalassia*	377 (163)	24.6 (4.5)	849 (283)	20.6 (8.5)	849 (490)	14.2 (3.3)
AB2	*Halodule*	7,169 (2,198)	12.9 (5.2)	4,528 (1,201)	14.7 (2.3)	472 (423)	6.3 (0.6)
AB3	*Halodule*	8,207 (849)	15.0 (3.3)	4,151 (1,559)	13.3 (4.5)	2,358 (2,614)	8.7 (5.4)
CB1	*Halodule*	11,131 (1,424)	12.9 (3.1)	8,301 (1,143)	14.6 (4.8)	283 (283)	5.0 (0.0)
CB1	*Thalassia*	1,320 (865)	16.5 (2.6)	991 (200)	17.4 (3.0)	1,792 (432)	13.9 (3.7)
RB1	*Halodule*	6,320 (1,276)	13.9 (3.0)	5,188 (432)	12.3 (5.1)	566 (980)	3.3 (1.2)
RB1	*Thalassia*	943 (712)	25.2 (4.8)	1,698 (283)	20.8 (2.4)	1,792 (432)	9.8 (3.6)
RB2	*Halodule*	7,075 (2,136)	22.0 (3.2)	5,754 (432)	18.6 (4.9)	4,905 (2,891)	7.5 (2.4)
All sites	*Halodule*	8,113	16.1	5,503	14.7	1,588	5.8
All sites	*Thalassia*	880	22.1	1,179	19.6	1,478	12.6

TABLE 2. Number and percent composition of fishes (by family) collected from seagrass meadows in the Aransas Estuary.

Family	Number	Percent
Sparidae	8,014	27.37
Gobiidae	6,686	22.83
Sciaenidae	5,443	18.59
Syngnathidae	5,149	17.59
Cyprinodontidae	1,046	3.57
Clupeidae	894	3.05
Haemulidae	693	2.37
Mugilidae	465	1.59
Gerriidae	390	1.33
Atherinidae	179	0.61
Engraulidae	116	0.40
Cynoglossidae	38	0.13
Bothidae	38	0.13
Lutjanidae	33	0.11
Blenniidae	32	0.11
Ophichthidae	15	0.05
Batrachoididae	12	0.04
Synodontidae	11	0.04
Other taxa	26	0.08
Total	29,280	100

TABLE 3. Number and percent composition of sciaenids collected from seagrass meadows in the Aransas Estuary.

Species	Common Name	Number	Percent[a]
Leiostomus xanthurus	spot	2,015	37.0
Bairdiella chrysoura	silver perch	1,271	23.4
Sciaenops ocellatus	red drum	1,170	21.5
Micropogonias undulatus	Atlantic croaker	723	13.3
Cynoscion nebulosus	spotted seatrout	258	4.7
Pogonias cromis	black drum	4	0.1
Cynoscion arenarius	sand seatrout	1	<0.1
Menticirrhus americanus	southern kingfish	1	<0.1

[a] Based on total number of sciaenids collected.

dominant sciaenid in seagrass meadows with peak densities occurring in May.

SIZE-AT-SETTLEMENT

Bairdiella chrysoura, C. nebulosus, and *S. ocellatus* were first detected at approximately 3–4 mm and peak numbers of settlers entered seagrass meadows at 4–8 mm (Fig. 4). Individuals from these species were present at collection sites throughout much of the early juvenile stage (≤40 mm). In contrast, newly settled *L. xanthurus* and *M. undulatus* were considerably larger. Although individuals <10 mm were collected in seagrass meadows, densities were highest for individuals 10–14 mm. Moreover, *L. xanthurus* and *M. undulatus* remained in these habitats for short periods of time before moving to other habitats; individuals >20 mm were caught infrequently.

SPATIAL DISTRIBUTION AND ABUNDANCE

Densities of postsettlers varied markedly between habitats and among sites at paired sites (AB1, RB1, CB1). A significant habitat effect was observed for three species: *B. chrysoura* ($F_{1,288}$ = 9.48, p = 0.001), *C. nebulosus* ($F_{1,288}$ = 4.07, p = 0.045), and *S. ocellatus* ($F_{1,288}$ = 18.11, p < 0.001). Densities of *C. nebulosus* and *S. ocellatus* were approximately 2–3 times higher in *H. wrightii* than *T. testudinum.* Mean densities of *S. ocellatus* during the primary settlement period (defined as trips with >50% of samples with target species) were 0.34–1.79 m^{-2} and 0.04–0.73 m^{-2} in *H. wrightii* and *T. testudinum,* respectively (Table 4). Although mean densities of *C. nebulosus* were lower, trends were similar: *H. wrightii* (0.04–0.21 m^{-2}) and *T. testudin-*

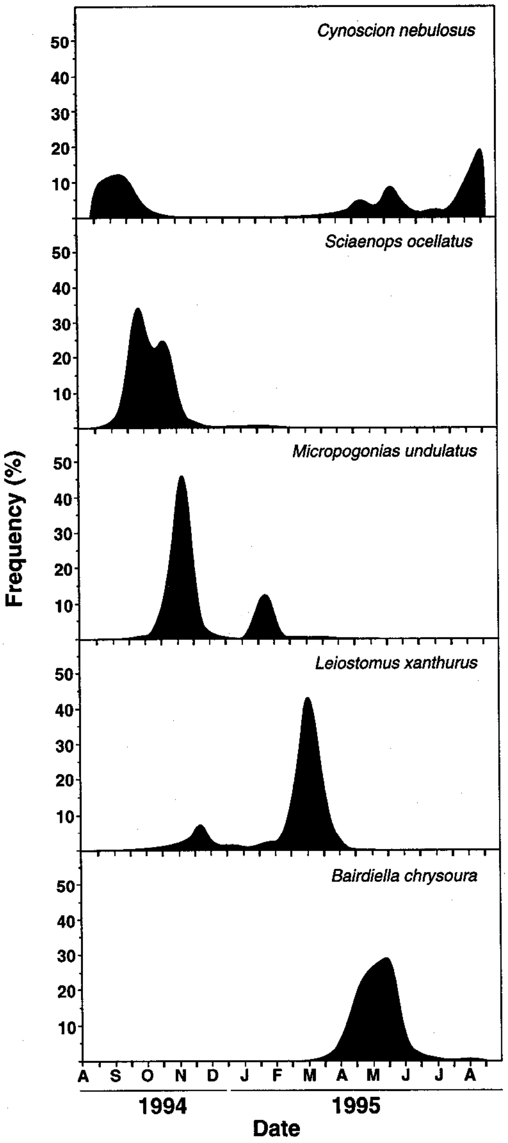

Fig. 3. Relative abundance of sciaenids (≤40 mm SL) collected from seagrass meadows during biweekly sampling trips in the Aransas Estuary. Percent frequency estimates based on the number of individuals per sampling date.

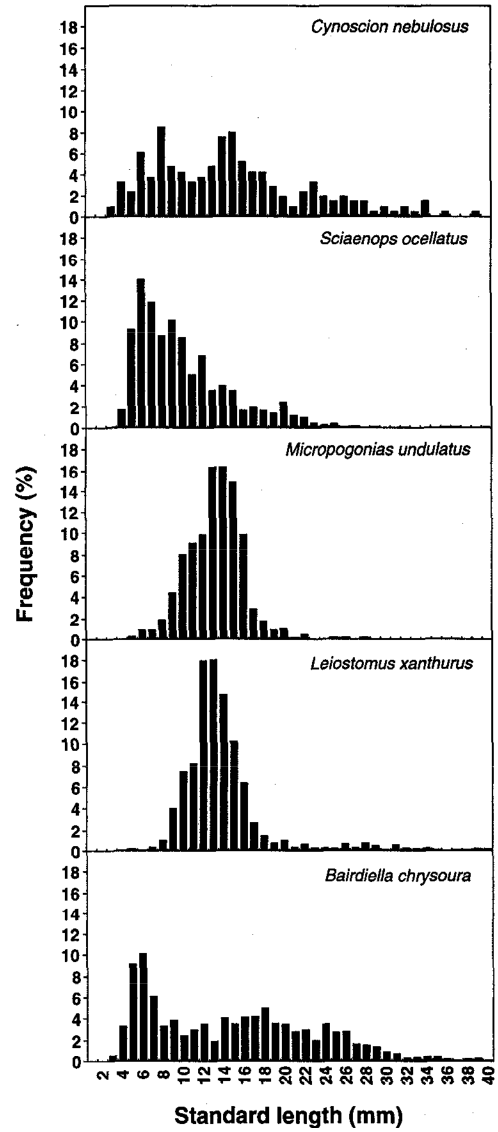

Fig. 4. Length distributions of sciaenids (≤ 40 mm SL) collected from seagrass meadows in the Aransas Estuary. Percent frequency estimates based on the number of individuals per 1-mm size class.

um (0.01–0.07 m^{-2}). Conversely, densities of *B. chrysoura* were significantly higher in *T. testudinum* with over 70% collected from this habitat. Mean densities ranged from 0.12 m^{-2} to 1.01 m^{-2} in *H. wrightii* and 0.04 m^{-2} to 2.61 m^{-2} in *T. testudinum*. Although mean densities of *L. xanthurus* and *M. undulatus* were markedly higher in *T. testudinum*, significant differences between habitat types were not detected ($F_{1,288} = 3.27$, $p = 0.072$ and $F_{1,288} = 1.27$, $p = 0.261$, respectively). Densities of *L. xanthurus* and *M. undulatus* during the primary settlement period ranged from 0.00 m^{-2} to 9.80 m^{-2} and 0.00 m^{-2} to 23.80 m^{-2}, respectively. Significant ($p < 0.05$) habitat × date interactions were observed for all five species, indicating that the magnitude of differences between habitats was not consistent over time.

Densities of all five species differed significantly among sites (Table 4). At paired sites, densities of *B. chrysoura* ($F_{2,288} = 98.90$, $p < 0.001$), *C. nebulosus* ($F_{2,288} = 42.49$, $p < 0.001$), *L. xanthurus* ($F_{2,288} = 35.09$, $p < 0.001$), *M. undulatus* ($F_{2,288} = 19.88$, $p < 0.001$), and *S. ocellatus* ($F_{2,288} = 45.16$, $p < 0.001$) were significantly different among the three bay sites: AB1, RB1, and CB1. Postsettlers of *S. ocellatus, B. chrysoura, L. xanthurus,* and *C. nebulosus* were significantly more abundant at AB1 than RB1 or CB1 (Tukey's HSD, $p < 0.05$). Densities of *M. undulatus* were significantly lower in CB1 than AB1 or RB1 (Tukey's HSD, $p < 0.05$). Again, significant first-order interactions with date (site × date) were present for each species, suggesting that the relative magnitude of postsettlement densities among sites was not uniform over sampling dates. Variation in settlement density among the six *H. wrightii* sites was also examined separately and, similar to results described above, significant ($p < 0.01$) site effects were observed for all five species. In general, densities were highest in Aransas Bay, particularly sites AB1 and AB2.

The mean size of postsettlement sciaenids found in *H. wrightii* and *T. testudinum* also varied. Mean lengths of two species, *M. undulatus* and *S. ocellatus,* differed significantly ($p < 0.001$) between habitats (Table 5). Postsettlement *M. undulatus* were markedly smaller in *H. wrightii* (12.6 mm) than *T. testudinum* (14.1 mm). A similar trend was observed for *S. ocellatus*; however, the size difference between habitats was larger. Mean lengths of *S. ocellatus* were 9.5 mm in *H. wrightii* and 16.1 mm in *T. testudinum.* No habitat-specific differences in size were observed for *B. chrysoura, C. nebulosus,* or *L. xanthurus* ($p > 0.05$).

Discussion

Ichthyofauna utilizing seagrass meadows in the Aransas Estuary were typical of assemblages reported in the northern Gulf of Mexico (Stoner 1983) and southeastern Florida (Brown-Peterson et al. 1993). Of the dominant taxa, syngnathids and gobiids can be considered permanent members of the assemblage since these taxa utilize seagrass meadows over protracted periods, often present from larval to adult stages. In contrast, sciaenids and other taxa (e.g., sparids, haemulids) were only seasonal residents and annual fluctuations in densities may result from recruitment, migration, and natural mortality. These taxa appear to inhabit shallow seagrass meadows for short periods of time (weeks to months), primarily as larvae and early

TABLE 4. Mean and maximum densities (individuals m^{-2}) of sciaenids ($\leq$40 mm SL) from different sampling sites in the Aransas Estuary during the primary recruitment episode (defined as trips with >50% of samples with target species). Percent frequency of occurrence estimates (based on presence or absence of individuals in sled tows) are shown. Values in parentheses are standard errors.

		Bairdiella chrysoura		*Cynoscion nebulosus*		*Leiostomus xanthurus*		*Micropogonias undulatus*		*Sciaenops ocellatus*	
Site	Seagrass	Mean	Max	Mean	Max	Mean	Max	Mean	Max	Mean	Max
AB 1	*Halodule*	1.01 (0.24)	3.46	0.21 (0.05)	0.47	1.31 (0.34)	5.33	0.38 (0.22)	2.07	1.79 (0.20)	2.53
AB 1	*Thalassia*	2.61 (0.55)	7.67	0.07 (0.03)	0.27	4.00 (1.63)	23.80	2.62 (1.27)	9.80	0.73 (0.20)	2.07
AB 2	*Halodule*	1.11 (0.36)	4.53	0.31 (0.08)	0.73	0.23 (0.09)	1.47	0.26 (0.08)	0.80	1.66 (0.23)	2.87
AB 3	*Halodule*	0.01 (0.01)	0.20	0.11 (0.04)	0.40	0.31 (0.12)	1.80	0.07 (0.04)	0.33	0.90 (0.35)	2.87
CB 1	*Halodule*	0.12 (0.02)	0.33	0.07 (0.03)	0.27	0.22 (0.09)	1.33	0.03 (0.01)	0.07	0.34 (0.07)	0.67
CB 1	*Thalassia*	0.04 (0.02)	0.20	0.01 (0.01)	0.01	0.29 (0.15)	2.40	0.00 (0.00)	0.00	0.04 (0.04)	0.33
RB 1	*Halodule*	0.06 (0.02)	0.33	0.04 (0.02)	0.20	0.20 (0.08)	1.33	0.33 (0.10)	0.80	1.11 (0.64)	4.73
RB 1	*Thalassia*	0.11 (0.03)	0.33	0.04 (0.02)	0.13	0.06 (0.02)	0.27	0.31 (0.15)	1.47	0.33 (0.09)	0.93
RB 2	*Halodule*	0.36 (0.18)	2.46	0.16 (0.04)	0.33	0.39 (0.14)	2.20	0.25 (0.09)	0.80	0.71 (0.12)	1.20
All sites		0.62 (0.11)		0.11 (0.04)		0.78 (0.21)		0.47 (0.16)		0.84 (0.09)	
% Frequency		64.3		59.3		67.3		66.7		82.7	
n[a]		135		81		135		81		81	

[a] Represents number of sled tows (27 per trip).

juveniles. In this study, sciaenids >40 mm were caught in limited numbers, suggesting that these individuals may migrate to different habitats. However, Rooker (1997) showed that larger sciaenids (>40 mm) are more capable of avoiding the epibenthic sled and thus low collection numbers may be attributed to both sampling bias and migration activity.

Temporal variation in settlement of sciaenids to seagrass meadows was pronounced and habitat use was staggered over time. Each of the five sciaenids inhabiting seagrass meadows showed distinct settlement periods with little temporal overlap among species. Similarly, Deegan and Thompson (1985) found that in Louisiana estuaries peak occurrences of sciaenids were segregated temporally with limited overlap. Moreover, Chao and Musick (1977) suggested that the coexistence of young sciaenids in a Virginia estuary was made possible in part because recruits entered nursery habitats at different times of the year. If resources within seagrass meadows are in limited supply (e.g., food, space), it is possible that newly settled sciaenids are exposed to reduced interspecific competition through differences in the timing of settlement.

Variability in size-at-settlement was observed among sciaenids and appears related to the location of adult spawning grounds (i.e., distance from estuary). *Bairdiella chrysoura* and *C. nebulosus* spawn primarily in estuarine habitats (e.g., bays, channels), often in close proximity to nursery areas (Johnson 1978; Overstreet 1983a; Brown-Peterson et al. 1988). Settlers from these taxa arrive in peak numbers at relatively small sizes (4–8 mm). Conversely, *M. undulatus* and *L. xanthurus* generally spawn offshore, several kilometers from tidal passes (Johnson 1978; Warlen and Chester 1985; Cowan and Shaw 1988). Individuals were markedly larger (10–14 mm) than settlers from inshore spawners, supporting the assumption that the source population was far removed from the tidal pass. The spawning strategy of *S. ocellatus* differs

TABLE 5. ANOVA comparisons of mean lengths of sciaenids ($\leq$40 mm SL) between different seagrass habitats in the Aransas Estuary. Estimates based on length estimations from the three sites containing monotypic stands of both *Halodule wrightii* and *Thalassia testudinum* (AB1, RB1, CB1).

Species	Habitat	n	Mean Length (mm)	F Ratio[a]	p
Bairdiella chrysoura	*Halodule*	279	15.3 (0.53)	1.543	0.215^{ns}
	Thalassia	537	14.5 (0.38)		
Cynoscion nebulosus	*Halodule*	71	17.7 (1.39)	0.028	0.866^{ns}
	Thalassia	43	18.1 (1.79)		
Leiostomus xanthurus	*Halodule*	528	15.3 (0.30)	0.304	0.581^{ns}
	Thalassia	525	15.1 (0.30)		
Micropogonias undulatus	*Halodule*	106	12.6 (0.23)	27.971	<0.001
	Thalassia	376	14.1 (0.13)		
Sciaenops ocellatus	*Halodule*	441	9.5 (0.34)	49.855	<0.001
	Thalassia	163	16.1 (0.56)		

[a] ANOVA based on means weighted by the reciprocal of the sample variances of the group means; ^{ns} nonsignificant comparisons ($p > 0.05$).

from both inshore and offshore spawners. *Sciaenops ocellatus* spawning locations range from coastal (i.e., near tidal passes) to offshore waters (Johnson 1978; Overstreet 1983b; Comyns et al. 1991). The pattern of size-at-settlement observed for *S. ocellatus* was similar to inshore spawners with peak settlement densities occurring at 6–8 mm. Recent work using hydrophones to monitor sound production associated with courtship and spawning of *S. ocellatus* has shown that activity is particularly high in the confines of the Aransas Pass (S. A. Holt unpublished data). Thus, it appears that some spawning sites for *S. ocellatus* are in coastal waters, probably in or near the Aransas Pass.

Although conspicuous differences in size-at-settlement were reported in this study, our estimates were based on size-at-capture data. As a result, the frequency of collections may have biased size-at-settlement estimates to some degree. For example, with biweekly collections there is a limit to the amount of postsettlement growth that could have occurred in seagrass meadows. Still, estimates of size-at-settlement are going to be overestimated to some degree depending on the amount of time individuals spend in the seagrass meadows prior to capture. Nevertheless, length-frequency profiles of each sciaenid examined in this study are based on a series of cohorts, which enter seagrass beds over a number of months. Since estimates of size-at-settlement are averaged across many cohorts for each taxon, bias associated with length-frequency profiles should be minimized.

Densities of newly settled sciaenids were influenced by seagrass species. Some sciaenids were significantly more abundant in one seagrass species or the other, suggesting that settlers may discriminate between habitats, either during or after the initial settlement event. These data support studies which have shown that patterns of distribution for larvae and early juveniles are seagrass-specific (Tolan et al. 1997; Stoner 1983; Middleton et al. 1984), but appear to challenge the "settle-and-stay" hypothesis (Bell and Westoby 1986; Bell et al. 1987). According to this hypothesis, larval recruits do not discriminate between meadows of different complexity when they settle, and redistribution only occurs within the original meadow since individuals that re-enter the plankton or migrate across unvegetated substrata will be more vulnerable to predators. It should be noted, however, that proponents of the "settle-and-stay" hypothesis recognize that it may not hold for species capable of safely migrating to different habitats. In this study, paired sites were composed of adjoining *H. wrightii* and *T. testudinum* meadows. As a result, postsettlement migration activity may have been more likely since individuals were not required to cross areas of bare substrate to reach different seagrass species.

Patterns in length-frequency data support the view that postsettlement migration occurs for certain taxa. Inshore-spawned *B. chrysoura* and *C. nebulosus* were common in seagrass meadows from larval through early juvenile stages, suggesting that these taxa settle and stay in seagrass meadows for extended periods. In contrast, individuals larger than 20 mm from offshore-spawned *M. undulatus* and *L. xanthurus* were rarely observed and apparently migrate to different habitats shortly after arrival. Since migratory behaviors were only conspicuous for species utilizing seagrass meadows in the late fall and winter, it is possible that activities are related to changes in environmental conditions (e.g., temperature, food supply).

Postsettlement densities of sciaenids varied between seagrass habitats in close proximity (<50 m) and patterns of this nature are often attributed to either food supply and/or predation pressure. Since recent studies have shown that growth and foraging conditions for certain sciaenids in the Aransas Estuary are similar between *H. wrightii* and *T. testudinum* (Rooker et al. 1997; Rooker and Holt 1997; Soto 1997), it seems plausible to assume that patterns of abundance were directly or indirectly related to predation. Predator efficiency is often correlated with macrophyte complexity (e.g., shoot or blade density, biomass; Coen et al. 1981; Stoner 1982; Stoner and Lewis 1985; Ryer 1988; Heck and Crowder 1991). As complexity increases, the visibility of prey (encounter rate) declines and predator movements are restricted (Stoner 1980; Savino and Stein 1989), resulting in lower predator efficiency. Although *H. wrightii* and *T. testudinum* differ in complexity (i.e., shoot density) and morphology (blade width and height), Rooker et al. (1998) demonstrated that the vulnerability of postsettlement red drum to predatory fish did not differ between the seagrass species. Consequently, other factors related to predation may be responsible for observed patterns. For example, habitat complexity (e.g., physical structure of seagrass canopy) and predator fields vary over spatial and temporal scales and may influence settlement patterns and postsettlement survival.

On larger scales, significant correlations between density of settlers and habitat complexity are rare (Stoner 1983; Bell and Westoby 1986; Sogard et al. 1987) and recruitment variability is often attributed to hydrodynamic processes (Miller et al. 1984; Boehlert and Mundy 1988; Shaw et al. 1988). Recent studies have elucidated the importance of hydrodynamic processes in estuarine systems (i.e., tidal flux) and suggested that such processes are responsible for spatial variability in larval supply and settlement (Boehlert and Mundy 1988; Pietrafesa and Janowitz 1988; Jenkins et al. 1996). Tidal flow rates in the three channels leading from the Aransas Pass (see Fig. 1) were measured in 1995 (R. Solis, Texas Water Development Board personal communication), and it appears that densities of sciaenids in the Aransas Estuary were positively associated with tidal flow rates. On average, flow rates in Lydia Ann Channel (Aransas Bay) were 4–6 times higher than Aransas Channel (Redfish Bay) and post-settlement density was 3 times higher in Aransas Bay. There was no correlation between density and flow rate in Corpus Christi Bay; however, our only sampling site was relatively far removed and indirectly connected to the water conduit from the Aransas Pass. Although variation in tidal flow rates is probably a key component in the estuarine-ocean exchange mechanism, a variety of nontidal factors, both biological (e.g., behavior of fish larvae) and physical (e.g., meteorological forcing mechanisms) are also important and likely to influence large-scale patterns of settlement within the Aransas Estuary.

Acknowledgments

We thank Kathy Binney, Patti Pickering, and Cameron Pratt for providing assistance in the laboratory and field. Lee Fuiman, Sharon Herzka, Chris Onuf, and two anonymous reviewers provided valuable comments on the manuscript. This study was funded in part by grants from the Texas Higher Education Coordinating Board Advanced Research Program (grant no. 003658-392), Texas A&M Sea Grant Program (grant no. NBR: RIF65), Sid W. Richardson Foundation, and fellowships to J. R. R. (E. J. Lund, Julian C. Barton). This is contribution no. 1026 of The University of Texas at Austin, Marine Science Institute.

Literature Cited

BELL, J. D. AND D. A. POLLARD. 1989. Ecology of fish assemblages and fisheries associated with seagrasses, p. 569–609. *In* A. W. D. Larkum, A. J. McComb, and S. A. Shepard (eds.), Biology of Seagrasses. Elsevier, New York.

BELL, J. D. AND M. WESTOBY. 1986. Variation in seagrass height and density over a wide spatial scale: Effects on common fish and decapods. *Journal of Experimental Marine Biology and Ecology* 104:275–295.

BELL, J. D., M. WESTOBY, AND A. S. STEFFE. 1987. Fish larvae settling into seagrass: Do they discriminate between beds of different leaf density? *Journal of Experimental Marine Biology and Ecology* 111:133–144.

BOEHLERT, G. W. AND B. C. MUNDY. 1988. Roles of behavior and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* 3:51–67.

BROWN-PETERSON, N. J., M. S. PETERSON, D. A. RYDENE, AND R. W. EAMES. 1993. Fish assemblages in natural versus well-established recolonized seagrass meadows. *Estuaries* 16:177–189.

BROWN-PETERSON, N., P. THOMAS, AND C. R. ARNOLD. 1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in south Texas. *Fishery Bulletin, United States* 86:373–388.

CARR, M. H. AND M. A. HIXON. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Marine Ecology Progress Series* 124:31–42.

CHAO, L. N. AND J. A. MUSICK. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the New York River Estuary, Virginia. *Fishery Bulletin, United States* 4:657–702.

COEN, L. D., K. L. HECK, JR., AND L. G. ABELE. 1981. Experiments on competition and predation among shrimps of seagrass meadows. *Ecology* 62:1484–1493.

COMYNS, B. H., J. LYCZKOWSKI-SHULTZ, D. L. NIELAND, AND C. A. WILSON. 1991. Reproduction of red drum, *Sciaenops ocellatus*, in the north central Gulf of Mexico: Seasonality and spawner biomass. National Oceanic and Atmospheric Administration Technical Report NMFS 95:17–26.

COWAN, J. H. AND R. F. SHAW. 1988. The distribution, abundance, and transport of larval sciaenids collected during the winter and early spring from the continental shelf waters off west Louisiana. *Fishery Bulletin, United States* 86:129–142.

DAY, J. W., JR., C. A. S. HALL, W. M. KEMP, AND A. YÁNEZ-ARANCIBIA. 1989. Estuarine Ecology. John Wiley and Sons, Inc. New York.

DEEGAN, L. A. AND B. A. THOMPSON. 1985. The ecology of fish communities in the Mississippi River Deltaic Plain, p. 35–56. *In* A. Yánez-Arancibia (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Toward an Ecosystem Integration. Editorial Universitaria, DR (R) UNAM Press, Mexico.

ECKMAN, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography* 28:241–257.

HECK, K. L., JR. AND L. V. CROWDER. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems, p. 281–289. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky (eds.), Habitat Complexity: The Physical Arrangement of Objects in Space. Chapman and Hall, New York.

HECK, K. L., JR. AND R. J. ORTH. 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages, p. 449–464. *In* V. S. Kennedy (ed.), Estuarine Perspectives. Academic Press, New York.

HOLT, S. A., C. L. KITTING, AND C. R. ARNOLD. 1983. Distribution of young red drums among different sea-grass meadows. *Transactions of the American Fisheries Society* 112:267–271.

JENKINS, G. P., M. J. WHEATLEY, AND A. G. B. POORE. 1996. Spatial variation in recruitment, growth, and feeding of postsettlement King George whiting, *Sillaginodes punctata*, associated with seagrass beds of Port Phillip Bay, Australia. *Canadian Journal of Fisheries and Aquatic Sciences* 53:350–359.

JONES, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: A multifactorial perspective, p. 294–328. *In* P. F. Sale (ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, California.

JOHNSON, G. D. 1978. Development of fishes of the mid-Atlantic Bight: An atlas of egg, larval and juvenile stages. Volume IV. Carangidae through Ephippidae. United States Department of the Interior, Biological Services Program.

JMP. 1989. JMP User's Guide. SAS Institute Inc., Cary, North Carolina.

LEIS, J. M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes, p. 183–230. *In* P. F. Sale (ed.), The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, California.

MCMICHAEL, R. H., JR. AND K. M. PETERS. 1989. Early life history of spotted seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries* 12:98–110.

MIDDLETON, M. J., J. D. BELL, J. J. BURCHMORE, D. A. POLLARD, AND B. C. PEASE. 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. *Aquatic Botany* 18: 89–109.

MILLER, J. M., J. P. REED, AND L. J. PIETRAFESA. 1984. Patterns, mechanisms and approaches to the study of migration of estuarine-dependent fish larvae and juveniles, p. 209–255. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (eds.), Mechanisms of Migration in Fishes. Plenum, New York.

OLNEY, J. E. AND G. W. BOEHLERT. 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Marine Ecology Progress Series* 45:33–43.

ORTH, R. J. 1992. A perspective on plant-animal interactions in seagrasses: Physical and biological determinants influencing plant and animal abundance, p. 147–164. *In* D. M. John, S. J. Hawkins, and J. H. Price (eds.), Plant-Animal Interactions in the Marine Benthos. Claredon Press, Oxford, England.

OVERSTREET, R. M. 1983a. Aspects of the biology of the spotted seatrout, *Cynoscion nebulosus,* in Mississippi. *Gulf Research Reports,* Supplement 1:1–43.

OVERSTREET, R. M. 1983b. Aspects of the biology of the red drum, *Sciaenops ocellatus,* in Mississippi. *Gulf Research Reports,* Supplement 1:45–68.

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.

PIETRAFESA, L. J. AND G. S. JANOWITZ. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *American Fisheries Society Symposium* 3:34–50.

ROOKER, J. R. 1997. Early life history of red drum (*Sciaenops ocellatus*) in subtropical seagrass meadows: Patterns of condition, growth, and mortality. Ph.D. Dissertation, The University of Texas at Austin, Austin, Texas.

ROOKER, J. R., G. J. HOLT, AND S. A. HOLT. 1997. Condition of larval and juvenile red drum (*Sciaenops ocellatus*) from estuarine nursery habitats. *Marine Biology* 127:387–394.

ROOKER, J. R., G. J. HOLT, AND S. A. HOLT. 1998. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: Is early life survival enhanced by seagrass meadows? *Marine Biology* 131:145–151.

ROOKER, J. R. AND S. A. HOLT. 1997. Utilization of subtropical seagrass meadows by newly settled red drum (*Sciaenops ocellatus*): Patterns of distribution and growth. *Marine Ecology Progress Series* 158:139–149.

RYER, C. H. 1988. Pipefish foraging: Effects of fish size, prey size and altered habitat complexity. *Marine Ecology Progress Series* 48: 37–45.

SAVINO, J. F. AND R. A. STEIN. 1989. Behavioral interactions between fish predators and their prey: Effects of plant density. *Animal Behavior* 37:311–321.

SHAW, R. F., B. D. ROGERS, J. H. COWAN, JR., AND W. H. HERKE. 1988. Ocean-estuarine coupling of ichthyoplankton and nekton in the northern Gulf of Mexico. *American Fisheries Society Symposium* 3:77–89.

SOGARD, S. M., G. V. N. POWELL, AND J. G. HOLMQUIST. 1987. Epibenthic fish communities on Florida Bay banks: Relations with physical parameters and seagrass cover. *Marine Ecology Progress Series* 40:25–39.

SOTO, M. A. 1997. Food habits and resource partitioning of larval and juvenile red drum (*Sciaenops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*). M.S. Thesis, Texas A&M University-Kingsville, Kingsville, Texas.

STONER, A. W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bulletin of Marine Science* 30:537–551.

STONER, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 58:271–284.

STONER, A. W. 1983. Distribution of fishes in seagrass meadows: Role of macrophyte biomass and species composition. *Fishery Bulletin, United States* 81:837–846.

STONER, A. W. AND F. G. LEWIS, III. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *Journal of Experimental Marine Biology and Ecology* 94:19–40.

TOLAN, J. M., S. A. HOLT, AND C. P. ONUF. 1997. Distribution and community structure of ichthyoplankton in Laguna Madre Seagrass Meadows: Potential impact of seagrass species succession. *Estuaries* 20:450–464.

UNDERWOOD, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology Annual Review* 19:513–605.

WARLEN, S. M. AND A. J. CHESTER. 1985. Age, growth, and distribution of larval spot, *Leiostomus xanthurus,* off North Carolina. *Fishery Bulletin, United States* 83:587–599.

ZIEMAN, J. C. AND R. G. WETZEL. 1980. Productivity of seagrasses: Methods and rates, p. 87–118. *In* D. C. Phillips and C. P. McRoy (eds.), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press. New York.

Received for consideration, March 17, 1997
Accepted for publication, October 14, 1997