BULLETIN OF MARINE SCIENCE, 63(3): 481–501, 1998

NEKTON USE OF SALT MARSH, SEAGRASS, AND NONVEGETATED HABITATS IN A SOUTH TEXAS (USA) ESTUARY

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ABSTRACT

We quantified nekton densities to estimate relative nursery values of *Spartina alterniflora* salt marsh, seagrass dominated by *Ruppia maritima* and *Halodule wrightii*, and shallow (<1 m deep) nonvegetated habitat in the Aransas National Wildlife Refuge in Texas. In each of two seasons of high nekton abundance, fall (September 1993) and spring (May 1994), we took 100 quantitative samples using a 1-m^2 drop sampler. We collected a total of 38 species of fishes and 19 species of decapod crustaceans. Vegetated habitats supported significantly higher densities of most numerically dominant species. Densities of total crustaceans, daggerblade grass shrimp *Palaemonetes pugio*, blue crabs *Callinectes sapidus*, and brackish grass shrimp *Palaemonetes intermedius* were significantly higher in salt marsh than seagrass. However, densities of total fishes, naked gobies *Gobiosoma bosc*, spotted seatrout *Cynoscion nebulosus*, pinfish *Lagodon rhomboides*, gulf pipefish *Syngnathus scovelli*, brown shrimp *Farfantepenaeus aztecus* (fall), white shrimp *Litopenaeus setiferus*, and pink shrimp *Farfantepenaeus duorarum* were not significantly different in salt marsh and seagrass. In spring, brown shrimp densities were higher in seagrass than salt marsh. In contrast to other abundant species, mean densities of bay anchovies *Anchoa mitchilli* were higher over nonvegetated bottom than in vegetated habitats in both seasons. Nekton size also differed among habitats, and organisms generally were smaller in seagrass beds than in marsh habitat. Our results provide further documentation that shallow vegetated habitats are important nurseries for many estuarine species. Furthermore, our study showed that where salt marsh and seagrass co-occur, most decapod crustaceans either selected for marsh habitat or showed no preference between these two vegetated habitats.

Shallow regions of estuaries contain some of the most productive fishery habitats, including tidal flats, salt marshes, seagrass beds, oyster reefs, and mangroves (Pihl and Rosenberg, 1982; Weinstein, 1982). The relative values of these habitats have been estimated in numerous studies by comparing nekton densities. An important tenet of these comparisons is that high animal densities (facilitated by either active selection or higher survival rates relative to other habitats) indicate high habitat quality and preferred habitat (Pearcy and Myers, 1974; Zimmerman and Minello, 1984; Sogard and Able, 1991; Baltz et al., 1993).

Most interhabitat comparisons published thus far have contrasted animal densities in seagrass and over nearby nonvegetated substrates (see reviews by Orth et al., 1984 and Pollard, 1984 and papers cited therein). Such studies have generally found significantly higher densities of animals in seagrass compared with nonvegetated areas (Hanekom and Baird, 1984; Heck and Thoman, 1984; Orth and van Montfrans, 1987; Heck et al., 1989; Lubbers et al., 1990; Williams et al., 1990; Ferrell and Bell, 1991; Sogard and Able, 1991; Sheridan, 1992; Connolly, 1994a; Heck et al., 1995; West and King, 1996), and have documented the role of seagrass as an important nursery for many fishery species (Hoese and Jones, 1963; Thayer et al., 1978; Bell and Pollard, 1989). Although fewer interhabitat studies have compared tidal marsh and nonvegetated sites (Zimmerman and Minello,

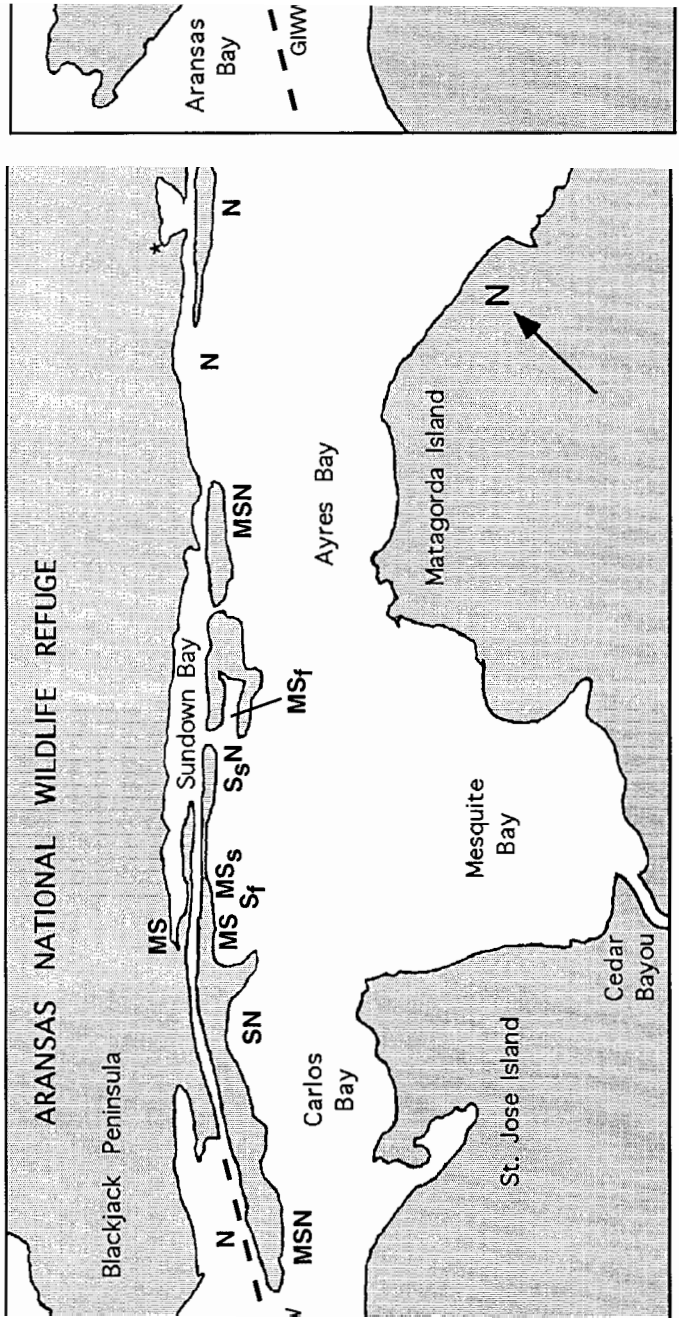

Figure 1. Map of the study area on the Texas coast. We sampled 20 locations containing salt marsh (M), seagrass (S), and nonvegetated (N) habitats between San Antonio Bay and Aransas Bay. Seagrass locations S_f and S_s were sampled only in the fall and spring, respectively. Location of False Live Oak tide gauge (*) is near latitude 28°14′N and longitude 96°48′W.

1984; Minello et al., 1991, 1994), estuarine marshes are also widely recognized as important nursery areas, vital to supporting valuable coastal fisheries (Boesch and Turner, 1984).

Published studies comparing the use of tidal marsh and seagrass are rare. Two such studies are limited to a comparison of blue crab *Callinectes sapidus* densities between habitats (Thomas et al., 1990; Heck et al., 1994). Therefore, little information exists about the relative habitat quality of salt marsh and seagrass, even though they are both considered primary nursery areas and often co-occur in temperate estuaries worldwide.

Specific objectives of our study were to quantify and compare nekton densities (as a measure of habitat quality) among salt marsh, seagrass, and shallow (<1m deep) nonvegetated areas on the Texas coast in the Aransas National Wildlife Refuge (ANWR). Although previous studies had quantified benthic infaunal populations in the area (Harper, 1976; Ray and Wilber, 1991), nekton assemblages of aquatic habitats in the refuge had not been quantitatively sampled before we initiated our research. We discuss our findings as they relate to current thinking about the nursery values of salt marshes and seagrass beds.

Materials and Methods

The study area is located in South Texas along the southeastern boundary of ANWR and encompasses shallow areas near the Gulf Intracoastal Waterway (GIWW) between Aransas Bay and San Antonio Bay (Fig. 1). Tides in the estuary are mixed, but primarily diurnal, and have a mean daily range of approximately 0.1 m (Rockport Gauge, National Ocean Service, NOAA). Salt marsh dominated by *Spartina alterniflora* Loisel. borders shallow embayments, ponds, and channels in the study area; other wetland plants (e.g., *Borrichia frutescens* (L.) DC., *Batis maritima* L., *Salicornia* spp. L.) occur higher in the intertidal zone behind these monotypic bands of *Spartina*. Low intertidal and subtidal areas within waterways are either nonvegetated or occupied by mixed stands of *Ruppia maritima* L. and *Halodule wrightii* Aschers.; these two species commonly coexist in grassbeds of southern Texas (Pulich, 1985).

We selected two sampling periods, one in fall (20–23 September 1993) and one in spring (9–12 May 1994), when high densities of fishery species are known to occur in the study area. Relative habitat use by animals was determined by sampling during the day over a short period of time (4 days) when all three habitats were completely inundated and by comparing densities of nekton (fishes and decapod crustaceans) among habitats.

During each sampling period, we collected a total of 100 nekton samples from salt marsh, seagrass, and shallow nonvegetated bottom at 20 habitat locations; these included six *Spartina alterniflora* marsh locations, seven seagrass locations, and seven shallow nonvegetated locations (Fig. 1). We sampled the same locations and habitats during both sampling periods with two exceptions. In spring, we sampled seagrass at two different locations because seagrass coverage was sparse at locations where we had sampled earlier in September (Fig. 1). At each habitat location, we sampled five replicate sites that we selected using a random number generator and a grid placed over all potential sample sites.

We collected macrofauna with a drop sampler, a 1.14-m diameter cylinder that we dropped from a boom mounted on a shallow-draft aluminum boat, using the procedure described by Zimmerman et al. (1984). We chose the drop sampler for quantifying nekton densities among habitats because the catch efficiency of this enclosure device does not appear to vary substantially with habitat characteristics typical of shallow estuarine areas, e.g., presence or absence of vegetation (Rozas and Minello, 1997). Two persons positioned the cylinder over a sample site by slowly pushing from the boat's stern. When released from the boom, the cylinder rapidly enclosed a 1.0-m^2 sample area. By using this procedure, we minimized disturbance to the sample site prior to releasing the cylin-

Table 1. Analysis of Variance (ANOVA) table for comparing habitats. Model includes the test for the main effect of Habitat and the contrasts that compare marsh vs seagrass and vegetated (marsh plus seagrass) vs nonvegetated habitats. The dependent variable used in the example presented here is total nekton (sum of total fishes and total crustaceans).

Source	df	Sum of squares	Mean square	F value	P value	Error term
September 1993						
Habitat	2	199.199	99.599	142.738	0.0001	Location (habitat)
Location (habitat)	17	11.862	0.698	1.174	0.3040	Site (location)
Site (location)	80	47.539	0.594			
Contrasts						
Marsh vs seagrass	1	41.553	41.553	59.550	0.0001	Location (habitat)
Vegetated vs nonvegetated	1	164.778	164.778	236.147	0.0001	Location (habitat)
May 1994						
Habitat	2	282.835	141.418	73.914	0.0001	Location (habitat)
Location (habitat)	17	32.526	1.913	4.691	0.0001	Site (location)
Site (location)	80	32.628	0.408			
Contrasts						
Marsh vs seagrass	1	62.698	62.698	32.770	0.0001	Location (habitat)
Vegetated vs nonvegetated	1	230.512	230.512	120.480	0.0001	Location (habitat)

der. Distances from the bow and stern of the boat to the center of the sample site were 4.0 and 8.8 m, respectively.

After the cylinder was dropped, we measured water temperature and dissolved oxygen in the sampler with a YSI Model 51B meter. We determined salinity with an American Optical temperature-compensated refractometer. We estimated water depth at the sample site by averaging the maximum and minimum depths measured within the sampler. Using this measure of sample water depth and concurrent water-level data from a tide gauge, we estimated the substrate elevation relative to the tide gauge and determined flooding duration (percentage of time a site was submerged) for each sample site.

We obtained hourly water-level data from two sources: the Conrad Blucher Institute for Surveying and Science, Texas A&M University-Corpus Christi for the False Live Oak gauge (NOS Station I.D. = 8774230) located 1 km north of False Live Oak Island, and NOAA's National Ocean Service for the Rockport gauge (NOS Station I.D. = 8774770) located 13 km west-southwest of our most westerly sampling location (Fig. 1). Water levels from the two gauges were highly correlated (r^2 = 80.5%) for the period of 26 January–20 May 1994, when data were available from both gauges. However, the False Live Oak data appeared to be influenced by vessel traffic in the GIWW. Because of the low signal to noise ratio of the False Live Oak data and the longer period of record provided by the Rockport gauge, we used data from the Rockport gauge to estimate habitat flooding durations.

At marsh sites, stems were clipped at ground level, counted (dead and alive combined), and removed from the cylinder. At seagrass sites, we determined vegetation biomass (above- and below-ground combined) from three 5-cm diameter cores collected at random locations inside the drop sampler; vegetation was identified, washed, dried to a constant weight, and weighed to the nearest 0.1 g.

We captured natant macrofauna trapped in the drop sampler using dip nets and by pumping the water out of the enclosure and through a 1-mm mesh net. When the sampler was completely drained, we removed any animals remaining on the bottom by hand. We preserved samples in formalin with Rose Bengal stain and returned them to the laboratory for processing. In the laboratory, we sorted the samples and identified macrofauna to species or lowest feasible taxon. We identified penaeid shrimps using characters described by Pearson (1939), Williams (1953, 1959), Ringo and Zamora

(1968), Zamora and Trent (1968), Perez Farfante (1969, 1970, 1978), and Perez Farfante and Kensley (1997). Shrimps in the genus *Farfantepenaeus* (brown shrimp *F. aztecus* and pink shrimp *F. duorarum*) up to 13 mm in total length (TL) were distinguished based on the shape of the antennal scale (Williams 1959); larger specimens were distinguished based on characters described by Perez Farfante (1970). Some specimens (45) of *Farfantepenaeus* between 13-18 mm TL could not be reliably identified, and along with some damaged specimens (14), these shrimps were assigned as *F. aztecus* or *F. duorarum* based on the proportion of identified specimens in each species and each habitat. These 59 specimens were not used in size analyses. Penaeid shrimps were measured to the nearest mm in total length; other crustaceans and fishes were measured (carapace width for crabs and total length for other taxa) and assigned to 5 mm size categories.

DATA ANALYSES.—Fall and Spring data were analyzed separately because many species of nekton were only abundant enough to include in the statistical analysis for one season. We used a nested Analysis of Variance (ANOVA) followed by a priori contrasts to examine differences in densities of abundant fishes and decapod crustaceans and environmental characteristics (mean dissolved oxygen, salinity, water temperature, and water depth) among habitats. In the ANOVA model, sites were nested within locations and the among location error term was used to test the main effect of Habitat (Table 1). We considered alpha levels of 0.05 to be significant in all results, but we also calculated adjusted alpha levels for the Habitat effect using the sequential Bonferroni method described by Rice (1989). These adjusted levels should be used if the reader would like to buffer against error introduced by making multiple comparisons (i.e., testing a hypothesis for several species). We used *a priori* contrasts to test for significant differences between nekton densities in marsh and seagrass habitats and between vegetated (marsh plus seagrass) and nonvegetated habitats (Table 1). Differences in sizes of numerically dominant species among habitats were tested similarly from mean lengths computed for each species and sample. We estimated the total length of each animal assigned to a 5-mm size category as one half the size range to which it was assigned. Densities of fishes and crustaceans were positively related to the standard deviation; therefore, we performed a log (x + 1) transformation of the original density values prior to analyses. Other variables were not transformed. All tabular and graphical data presented in this paper are untransformed means. We conducted all analyses with SuperANOVA software (Abacus Concepts, 1989).

RESULTS

We collected a total of 25 species of fishes and 13 species of crustaceans in fall and 29 species of fishes and 13 species of crustaceans in spring (Table 2). Numerically, crustaceans dominated the catch and accounted for 88% and 93% of the total fauna in fall and spring, respectively. Nekton densities (all taxa included) were higher in marsh than seagrass, and densities in vegetated habitat (marsh and seagrass combined) were greater than on nonvegetated bottom (Tables 1,2). Total fish densities were significantly higher in vegetated habitats than on nonvegetated bottom, but densities in marsh and seagrass were not significantly different (Tables 2,3). Total crustacean densities were also greater in vegetated than nonvegetated habitat, but densities in marsh were significantly higher than in seagrass (Tables 2,3).

In fall, naked gobies *Gobiosoma bosc* and rainwater killifish *Lucania parva* numerically dominated the fish assemblages and accounted for 65% of the fishes we collected (Table 2). Naked gobies were significantly more abundant in vegetated habitat than on nonvegetated bottom, but densities of this species in marsh and seagrass were not significantly different (Fig. 2A, Tables 2,3). Although densities of rainwater killifish were not statistically different among habitats, the highest mean density of this species occurred in marsh, and it was not collected on nonvegetated bottom (Fig. 2A, Table 2). Mean densities of spotted seatrout *Cynoscion nebulosus* were similar in vegetated habitats and rela-

Table 2. Mean densities, number per m^2 , (with standard errors, S.E.) of animals that were commonly collected are presented for each habitat sampled in September 1993 and May 1994. The mean number of species (with S.E.) taken in each sample within a habitat and the total number of species in all habitats combined (total spp) also are listed. Each mean is estimated from 30 drop samples in marsh and 35 samples each in seagrass and nonvegetated habitat. The total number of animals collected in all habitats combined (total catch) is given for each species and major category (fishes and crustaceans). The relative abundance (RA) of species within each major category also is given when it is at least 1% for all habitats combined. List does not include uncommon species (i.e., species with < 10 individuals). Results (P values) of ANOVA's comparing mean densities among the three habitats are given for each taxa included in the analyses. An * indicates that the probability value was significant after alpha was adjusted as described by Rice (1989).

	Spartina marsh		Seagrass beds		Nonvegetated bottom				
SPECIES	MEAN	S. E.	MEAN	S. E.	MEAN	S. E.	Total Catch	RA (%)	P
September 1993									
FISHES (Total spp=25)									
Number of Species	2.6	(0.20)	2.2	(0.20)	0.7	(0.17)			
TOTAL FISHES	8.7	(0.99)	10.1	(1.46)	1.9	(0.50)	680		0.0001*
Naked goby *Gobiosoma bosc*	4.3	(0.80)	6.4	(1.25)	0.4	(0.21)	367	54.0	0.0004*
Rainwater killifish *Lucania parva*	1.5	(0.55)	0.9	(0.44)	0.0	(0.00)	77	11.3	0.1932
Bay anchovy *Anchoa mitchilli*	0.3	(0.19)	0.5	(0.28)	0.8	(0.31)	55	8.1	
Spotted seatrout *Cynoscion nebulosus*	0.5	(0.13)	0.5	(0.12)	0.1	(0.05)	36	5.3	
Unidentified larval fish	0.3	(0.10)	0.2	(0.10)	0.2	(0.10)	23	3.4	
Sheepshead minnow *Cyprinodon variegatus*	0.3	(0.22)	0.2	(0.14)	0.0	(0.00)	16	2.4	
Gulf killifish *Fundulus grandis*	0.5	(0.16)	0.0	(0.00)	0.0	(0.00)	15	2.2	
Pinfish *Lagodon rhomboides*	0.2	(0.07)	0.3	(0.13)	0.0	(0.00)	15	2.2	
Unidentified fish	0.2	(0.20)	0.1	(0.06)	0.1	(0.05)	11	1.6	
Gulf pipefish *Syngnathus scovelli*	0.2	(0.10)	0.1	(0.05)	0.0	(0.00)	10	1.5	
Flagfin mojarra *Eucinostomus melanopterus*	0.0	(0.03)	0.3	(0.26)	0.0	(0.00)	10	1.5	
CRUSTACEANS (Total spp=13)									
Number of Species	5.2	(0.19)	4.1	(0.30)	0.9	(0.17)			
TOTAL CRUSTACEANS	130.5	(15.02)	23.4	(3.64)	1.8	(0.42)	4,798		0.0001*
Daggerblade grass shrimp *Palaemonetes pugio*	106.0	(14.48)	4.4	(1.37)	0.0	(0.00)	3,333	69.5	0.0001*
Blue crab *Callinectes sapidus*	11.1	(0.93)	7.5	(1.42)	0.4	(0.22)	610	12.7	0.0001*
Brown shrimp *Farfantepenaeus aztecus*	5.0	(0.82)	5.3	(1.05)	0.1	(0.05)	339	7.1	0.0001*
White shrimp *Litopenaeus setiferus*	4.2	(0.87)	1.9	(1.51)	0.0	(0.03)	194	4.0	0.0027*
Pink shrimp *Farfantepenaeus duorarum*	1.3	(0.27)	2.6	(0.68)	0.1	(0.07)	137	2.9	0.0003*
Brackish grass shrimp *Palaemonetes intermedius*	1.9	(1.06)	0.5	(0.28)	0.0	(0.00)	74	1.5	
Harris mud crab *Rhithropanopeus harrisii*	0.5	(0.20)	0.6	(0.28)	0.1	(0.05)	39		
Estuarine ghost shrimp *Callianassa jamaicensis*	0.0	(0.00)	0.1	(0.04)	0.8	(0.33)	29		

Table 2. Continued.

SPECIES	*Spartina* marsh MEAN	*Spartina* marsh S. E.	Seagrass beds MEAN	Seagrass beds S. E.	Nonvegetated bottom MEAN	Nonvegetated bottom S. E.	Total Catch	RA (%)	P
May 1994									
FISHES (Total spp=29)									
Number of Species	3.2	(0.31)	2.9	(0.24)	0.9	(0.13)			
TOTAL FISHES	11.2	(1.91)	9.0	(1.44)	2.1	(0.34)	723		0.0011*
Pinfish *Lagodon rhomboides*	4.6	(1.08)	2.1	(0.43)	0.0	(0.00)	214	29.6	0.0008*
Naked goby *Gobiosoma bosc*	2.1	(0.58)	3.8	(1.03)	0.3	(0.17)	208	28.8	0.0226*
Gulf pipefish *Syngnathus scovelli*	1.2	(0.36)	0.9	(0.20)	0.0	(0.00)	69	9.5	0.0280*
Bay anchovy *Anchoa mitchilli*	0.0	(0.00)	0.3	(0.14)	1.1	(0.25)	52	7.2	
Inland silverside *Menidia beryllina*	0.6	(0.30)	0.2	(0.17)	0.0	(0.03)	27	3.7	
Silver perch *Bairdiella chrysoura*	0.9	(0.90)	0.0	(0.00)	0.0	(0.00)	27	3.7	
Sheepshead *Archosargus probatocephalus*	0.3	(0.11)	0.2	(0.10)	0.0	(0.00)	17		
Sheepshead minnow *Cyprinodon variegatus*	0.2	(0.14)	0.3	(0.22)	0.0	(0.00)	16		
CRUSTACEANS (Total spp=13)									
Number of Species	4.5	(0.18)	4.3	(0.22)	0.9	(0.16)			
TOTAL CRUSTACEANS	270.8	(30.78)	47.7	(13.30)	1.3	(0.24)	9,840		0.0001*
Daggerbiade grass shrimp *Palaemonetes pugio*	233.3	(26.37)	28.7	(12.23)	0.0	(0.00)	8,003	81.3	0.0001*
Brackish grass shrimp *Palaemonetes intermedius*	21.2	(6.73)	2.3	(0.92)	0.0	(0.00)	717	7.3	0.0001*
Brown shrimp *Farfantepenaeus aztecus*	4.5	(0.88)	11.3	(1.25)	0.7	(0.16)	557	5.7	0.0001*
Blue crab *Callinectes sapidus*	10.3	(0.96)	2.5	(0.32)	0.1	(0.06)	401	4.1	0.0001*
Harris mud crab *Rhithropanopeus harrisii*	0.6	(0.18)	1.7	(0.29)	0.1	(0.07)	83		
Big claw snapping shrimp *Alpheus heterochaelis*	0.6	(0.28)	0.0	(0.00)	0.0	(0.00)	18		
Grass shrimp *Palaemonetes* spp.	0.0	(0.03)	0.4	(0.23)	0.1	(0.04)	16		
Thinstripe hermit *Clibanarius vittatus*	0.2	(0.14)	0.2	(0.08)	0.1	(0.05)	15		

Table 3. Summary of a priori contrasts (1, 17 df) testing for significant differences in mean densities between marsh and seagrass and between vegetated (marsh plus seagrass) and nonvegetated habitats. The habitat with the higher mean density is listed for each contrast in which a significant difference was found. P values are not given for species when their abundance was too low in a season to be analyzed.

	Contrasts							
	September 1993				May 1994			
Taxa	Marsh vs seagrass	p	Veg vs nonveg	p	Marsh vs seagrass	p	Veg vs nonveg	p
Total fishes		0.8949	veg	0.0001		0.5309	veg	0.0001
Naked goby		0.5393	veg	0.0001		0.4720	veg	0.0001
Pinfish						0.1655	veg	0.0003
Gulf pipefish						0.8603	veg	0.0084
Total crustaceans	marsh	0.0001	veg	0.0001	marsh	0.0001	veg	0.0001
Daggerblade grass shrimp	marsh	0.0001	veg	0.0001	marsh	0.0001	veg	0.0001
Brown shrimp		0.6935	veg	0.0001	seagrass	0.0061	veg	0.0001
Blue crab	marsh	0.0066	veg	0.0001	marsh	0.0001	veg	0.0001
White shrimp		0.0842	veg	0.0015				
Pink shrimp		0.2073	veg	0.0001				
Brackish grass shrimp					marsh	0.0001	veg	0.0001

tively low on nonvegetated bottom (Fig. 2A, Table 2). A comparison of densities in all three habitats using ANOVA was marginally significant (main effect of Habitat, P = 0.0324); the effect was not significant if alpha levels were adjusted using the sequential Bonferroni technique. Densities of spotted seatrout in vegetated habitats, however, were significantly higher than on nonvegetated bottom (ANOVA contrast, P = 0.0099).

In spring, naked gobies were again numerically dominant among fishes, as were pinfish *Lagodon rhomboides* and gulf pipefish *Syngnathus scovelli*; these three species accounted for 68% of the fishes collected (Table 2). Pinfish, naked gobies, and gulf pipefish were significantly more abundant in vegetated than nonvegetated habitat, but there was no significant difference in densities of these species between the two vegetated habitats (Fig. 2B, Tables 2,3). Nonvegetated habitat contained the highest mean density of bay anchovies *Anchoa mitchilli*, and this species was entirely absent from marsh habitat (Fig. 2B, Table 2).

Numerically dominant crustaceans in the fall included daggerblade grass shrimp *Palaemonetes pugio*, blue crabs, brown shrimp, white shrimp *Litopenaeus setiferus*, and pink shrimp; and these five species represented 96% of the crustaceans in our samples (Table 2). Abundances of all five dominant crustaceans were significantly greater in vegetated habitats (marsh and seagrass combined) than on nonvegetated bottom (Fig. 3A, Tables 2,3). Daggerblade grass shrimp and blue crabs were significantly more abundant in marsh than seagrass; however, densities of brown shrimp, white shrimp, and pink shrimp were not significantly different between the two vegetated habitats (Table 3).

In spring, daggerblade grass shrimp, blue crabs, brown shrimp, and brackish grass shrimp *Palaemonetes intermedius* were numerically dominant, accounting for 98% of the crustaceans we collected (Table 2). Densities of these four crustaceans were significantly greater in vegetated than nonvegetated habitat, but the greatest densities (except brown shrimp) occurred in marsh (Fig. 3B, Tables 2,3). Brown shrimp densities were highest in seagrass (Fig. 3B, Tables 2,3).

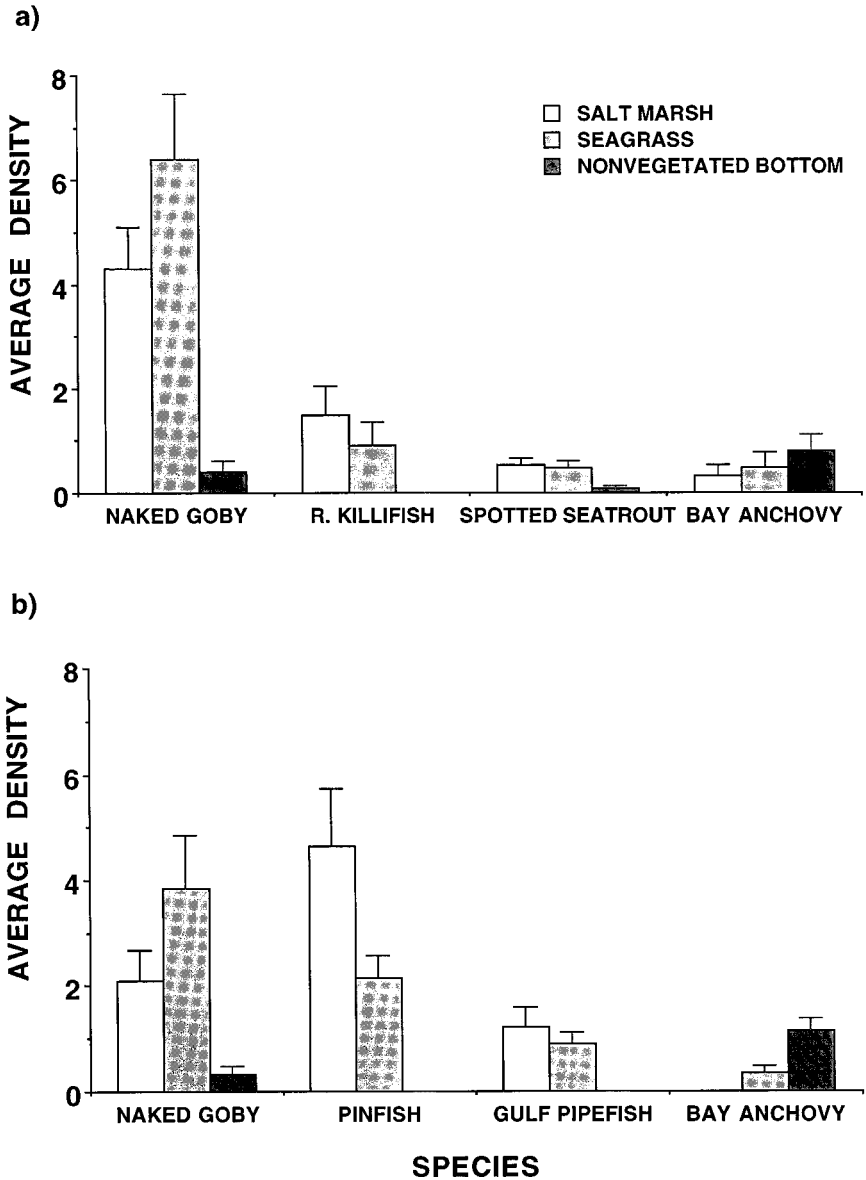

Figure 2. Average density (individuals m^{-2}) of abundant fishes collected in (a) September 1993 and (b) May 1994 from marsh, seagrass, and nonvegetated habitats. R. Killifish = Rainwater Killifish. Error bars = one standard error (SE). Means and SEs were calculated from 30 marsh, 35 seagrass, and 35 nonvegetated samples.

We also collected 18 species of molluscs, but our sampling technique was not designed to quantitatively sample benthic infauna. Most molluscs were collected on nonvegetated bottom and in seagrass and consisted mainly of Atlantic rangia *Rangia cuneata*, brown rangia *Rangia flexuosa*, and minor jackknife *Ensis minor*.

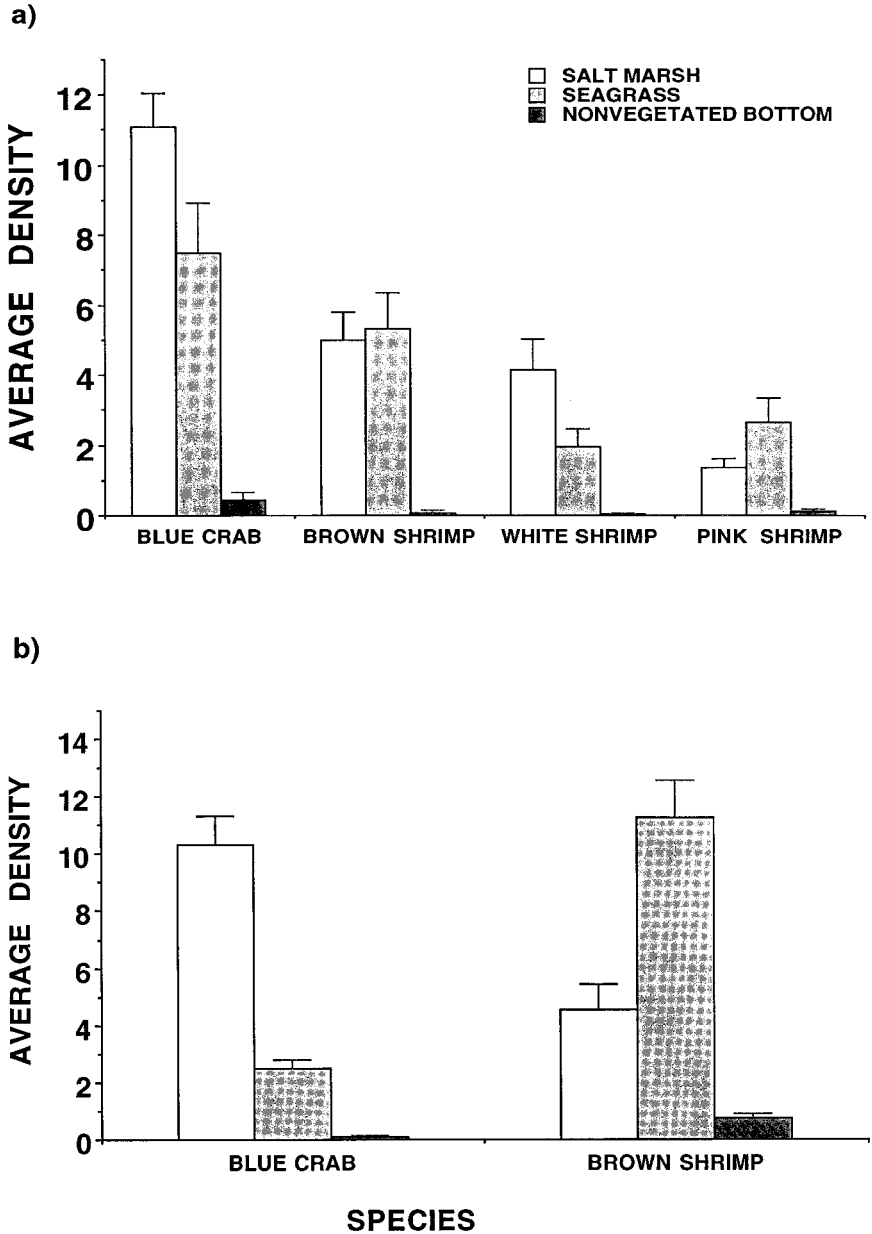

Figure 3. Average density (individuals m^{-2}) of abundant crustaceans other than grass shrimp collected in (a) September 1993 and (b) May 1994 from marsh, seagrass, and nonvegetated habitats. Error bars = one standard error (SE). Means and SEs were calculated from 30 marsh, 35 seagrass, and 35 nonvegetated samples.

The size of nekton also differed among habitats (Table 4). Although most species were taken too infrequently at nonvegetated sites to include this habitat in the analysis, brown shrimp in spring were significantly larger on nonvegetated bottom than within vegetation (ANOVA contrast P = 0.0005). Within vegetation, there were no significant differences in

Table 4. Mean sizes, mm, (with standard errors, S.E.) of numerically dominant animals collected in vegetated habitats in September 1993 and May 1994. Each mean (total length for fishes and shrimps or carapace width for crabs) for a habitat was estimated from the mean size of a species in n samples that contained that species. The P value listed is from an ANOVA comparing mean size in the two habitats. An * indicates that the probability value was significant after alpha was adjusted as described by Rice (1989).

	Spartina marsh			Seagrass beds			
SPECIES	MEAN	S. E.	n	MEAN	S. E.	n	P
September 1993							
Naked goby	17.8	(1.13)	23	15.1	(0.65)	26	0.4593
Spotted seatrout	53.5	(5.64)	12	27.0	(2.65)	13	0.0020*
Brown shrimp	38.2	(2.41)	26	29.5	(2.22)	25	0.1307
Daggerblade grass shrimp	21.9	(0.50)	30	17.3	(1.11)	19	0.0074*
Blue crab	13.6	(1.05)	30	8.9	(0.54)	27	0.0335
White shrimp	35.1	(2.46)	21	31.0	(3.78)	18	0.2722
Pink shrimp	33.1	(3.49)	17	27.0	(3.75)	20	0.2020
May 1994							
Naked goby	25.0	(2.25)	19	11.9	(0.82)	21	0.0200
Pinfish	38.1	(1.90)	24	37.2	(2.19)	20	0.5345
Gulf pipefish	64.6	(4.19)	13	55.0	(2.84)	16	0.7762
Brown shrimp	44.4	(2.39)	26	24.9	(0.97)	34	0.0002*
Blue crab	18.2	(0.57)	30	10.4	(0.81)	28	0.0006*
Brackish grass shrimp	23.2	(0.54)	29	20.2	(0.78)	14	0.0397
Daggerblade grass shrimp	25.8	(0.69)	30	19.8	(1.10)	26	0.0975

size between marsh and seagrass habitats for most of the abundant fishes we examined (Table 4). Spotted seatrout, however, were significantly larger in salt marsh habitat. The mean size of all crustaceans examined was larger in the marsh than in seagrass, and some differences were significant (Table 4). Size-frequency data within habitats confirmed these habitat-size relationships (Fig. 4).

Some environmental parameters differed significantly among habitats (Table 5). Mean dissolved oxygen concentrations were significantly greater at vegetated than nonvegetated sites, but values in all habitats were well above levels that would cause stress. Although mean salinities were similar among habitats within a season, overall salinities were higher in spring than fall (21.9–22.1 ‰ vs 14.5–14.8‰). Stem density in the *Spartina* marsh was higher in fall than in spring, and seagrass biomass was greater in spring than fall (Table 5). Mean water depths at sample sites were generally greater in fall than spring, but differences among habitats were similar (Table 5). Because samples within a season were taken at similar tide stages, these water-level differences are an indication of elevation differences among habitats. The elevation of nonvegetated bottom was 30–36 cm below that of seagrass habitat which was 11 cm below the marsh edge habitat.

Most nonvegetated sites were constantly submerged during the 12 mo encompassing our study periods, although three nonvegetated sites were exposed for a short time in January 1994. Even so, the average flooding duration for nonvegetated sites in January was >99.8%. Marsh and seagrass sites were submerged less in winter than at other times of the year (Fig. 5), but overall, monthly flooding durations of these habitats were high (marsh >72% and seagrass>86%). During the months we sampled, both habitats were nearly constantly inundated (marsh >97% and seagrass >99%), and therefore almost always accessible to nekton. Although these marsh flooding durations are high relative to the few available published values (e.g., Rozas and Reed, 1993), the values were con-

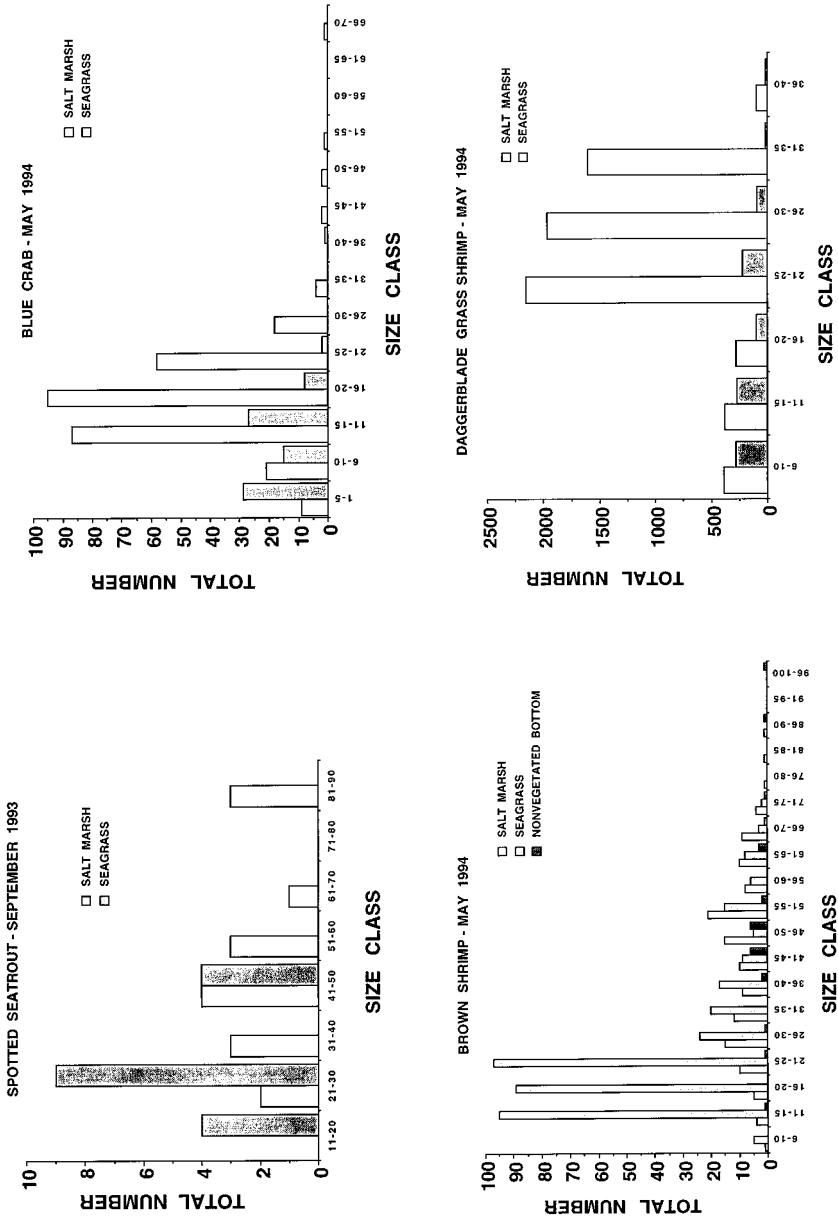

Figure 4. Distributions of size classes within habitats for four selected species: spotted seatrout in September 1993 and blue crab, brown shrimp and daggerblade grass shrimp in May 1994.

Table 5. Environmental characteristics of habitats. Mean and (S.E., one standard error) are given for five parameters measured in September 1993 and May 1994. Vegetation was characterized for *Spartina* marsh as stem density (stems/m^2) and for seagrass beds as biomass, dry weight (g/58.9 cm^2). Sample number: marsh=30, seagrass=35, and nonvegetated bottom=35 (except for three missing values for water depth in September and one missing value for dissolved oxygen concentration during May). Means for each parameter not connected by a line are significantly different among habitats (ANOVA, contrast procedure). P values for the ANOVA main effect of Habitat also are given. An * indicates that the probability value was significant after alpha was adjusted as described by Rice (1989).

	Spartina marsh		Seagrass beds		Nonvegetated bottom		
Parameter	MEAN	S. E.	MEAN	S. E.	MEAN	S. E.	P
September 1993							
Water depth (cm)	37	(1.4)	48	(1.7)	78	(1.1)	0.0001*
Oxygen (ppm)	7.0	(0.26)	8.1	(0.27)	5.8	(0.11)	0.0012*
Water temperature (ºC)	31.3	(0.24)	31.1	(0.26)	29.4	(0.16)	0.0336
Salinity (‰)	14.5	(0.33)	14.6	(0.34)	14.8	(0.32)	0.9657
Vegetation	117	(12)	0.33	(0.06)	0	(0)	
May 1994							
Water depth (cm)	19	(1.3)	30	(1.7)	66	(2.2)	0.0001*
Oxygen (ppm)	8.7	(0.41)	8.1	(0.14)	6.6	(0.16)	0.0272
Water temperature (ºC)	27.3	(0.22)	27.7	(0.28)	26.4	(0.13)	0.1960
Salinity (‰)	22.1	(0.05)	22.1	(0.04)	21.9	(0.14)	0.7300
Vegetation	83	(8)	0.48	(0.12)	0	(0)	

firmed by calculating flooding durations using the False Live Oak data for the 3 mo when we had data from both gauges. Flooding durations estimated with the False Live Oak data were equal to or higher than flooding durations derived from the Rockport data for February–April 1994.

Discussion

The salt marsh and seagrass habitats in our study area supported much higher densities of fishes and decapod crustaceans than nearby nonvegetated sites. Bay anchovy was the only abundant species that was collected in nonvegetated areas at mean densities that were similar to (fall) or greater than (spring) the vegetated habitats. These results are corroborated by studies conducted in other estuaries that also document greater direct use of salt marshes and submerged grass beds in comparison with nonvegetated habitat (Zimmerman and Minello, 1984; Heck et al., 1989; Lubbers et al., 1990; Thomas et al., 1990). Our data also show that several species such as blue crab, daggerblade grass shrimp, and brackish grass shrimp selected for salt marsh habitat over seagrass.

Few direct comparisons have been made of nekton use between seagrass and salt marsh habitats. Earlier studies comparing the habitat value of these estuarine systems sampled tidal channels rather than the marsh surface (Weinstein and Brooks, 1983; Orth and van Montfrans, 1987; Wilson et al., 1990; Sogard and Able, 1991), and the results of such studies are not comparable with our findings. To our knowledge, ours is the first published study of a direct seagrass-salt marsh comparison that is not limited to a single species. In a study of blue crab distributions in Christmas Bay, Texas (located approximately 115 km northeast of our study area), crab densities from the shoreline edge of a *Halodule* bed were significantly greater than within shoreline *Spartina alterniflora* dur-

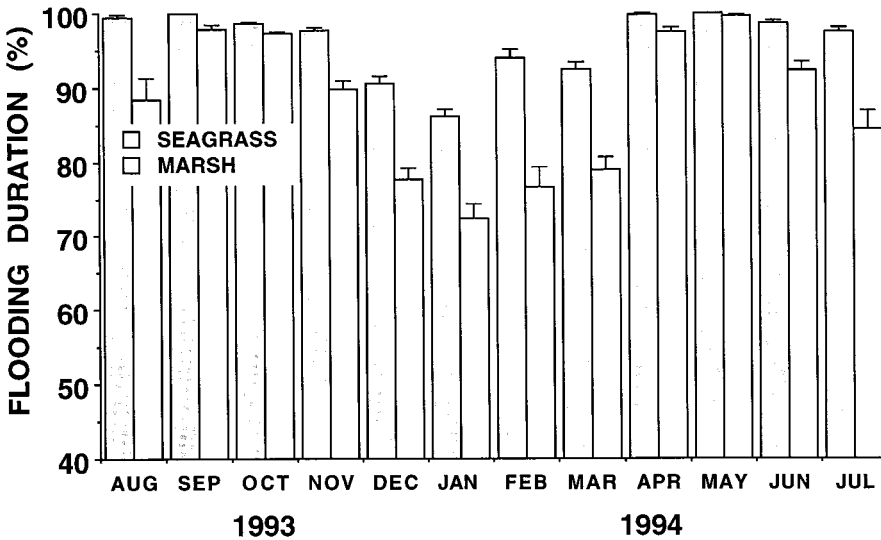

Figure 5. Estimated average monthly flooding durations [(hours habitat inundated) / (total hours in month) × 100] from August 1993 to July 1994 of seagrass and marsh sample sites. Error bars = one standard error (SE). Means and SEs were calculated for 59 marsh and 70 seagrass sites.

ing 7 of the 12 mo tested (Thomas et al., 1990). Interestingly, differences in crab densities between the two habitats in their study were relatively low during spring and fall, and densities were not significantly different between seagrass and *Spartina* during their 27 August, 24 September, and 18 April sampling periods. Flooding dynamics may be important in determining these habitat density patterns. As along most of the Texas coast, these spring and fall periods are times of seasonally high water when seagrass and salt marsh are usually extensively flooded (Zimmerman and Minello, 1984; Thomas et al., 1990). In ANWR, both seagrass and salt marsh were flooded almost constantly in spring and fall. In Christmas Bay, however, habitat elevation differences (from unpublished water depth data) would suggest that seagrass was flooded more than *Spartina* edge habitat during much of the year. Heck et al. (1994) also compared blue crab densities in shallow estuarine habitats; they sampled tidal marsh, submerged grassbeds, and nonvegetated substrates across a wide range of salinities in Mobile Bay and Mississippi Sound, Alabama. No single habitat type was consistently selected by juvenile blue crabs in their study, but average monthly crab densities were always greatest in mixed beds of *Ruppia* and *Halodule* or salt marsh dominated by *S. alterniflora* or *Juncus roemerianus* Scheele.

Differences in environmental factors among habitats at ANWR likely contributed to the observed nekton density patterns. Dissolved oxygen concentrations and water temperatures (in fall) were lower in nonvegetated than vegetated habitats, but these relatively small differences probably cannot explain the low densities of nekton on nonvegetated bottom. However, in addition to the presence of vegetative structure, vegetated and nonvegetated habitats differed substantially in water depth. The combined factors of vegetation and water depth may be most important in influencing nekton habitat use because the risk of predation in deep, nonvegetated areas is high (Baltz et al., 1993; Minello, 1993; Ruiz et al., 1993; Miltner et al., 1995), especially in Gulf coast estuaries (Heck and

Coen, 1995). Water depth, in itself, appears important in determining predation risk. For example, in a Chesapeake Bay subestuary, known predators of small fishes and decapods (e.g., large spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonias undulatus*, and blue crabs) are often most abundant in waters >70 cm deep, and the mortality rates of tethered daggerblade grass shrimp, killifish, and small blue crabs significantly increase with depth (Ruiz et al., 1993). Variation in water depth may also affect habitat use seasonally. In our study, a difference in average water depth between fall and spring coincided with a change in apparent habitat selection by brown shrimp. In the fall, brown shrimp were similarly distributed in salt marsh and seagrass when the water depth in the marsh averaged 37 cm. However, in the spring when the average flooding depth in marsh habitat was only 19 cm, brown shrimp densities were relatively low in the marsh.

Nekton distributions may also be affected by differences in the structural complexity of vegetation among and within habitats. This structural complexity may affect habitat use both at the scale of individual plants (e.g., leaf structure, surface area) and at larger scales (e.g., habitat interspersion, patch size). Nekton abundance in seagrass has been related to differences in leaf height and density (Bell and Westoby, 1986), plant biomass (Heck and Wetstone, 1977; Stoner, 1983), patch size (Holt et al., 1983), and current velocity (Murphey and Fonseca, 1995). One reason for the importance of structure is that structurally complex habitats such as marshes and seagrass beds provide animals protection from predators (Heck and Thoman, 1981; Minello and Zimmerman, 1983; Wilson et al., 1987; 1990; Rozas and Odum, 1988; Minello et al., 1989; Minello, 1993). In addition, habitat structural complexity may affect nekton distributions by influencing settlement patterns of new recruits to an area. For example, blue crab megalopae have been shown to preferentially settle within vegetation rather than on nonvegetated substrate, but it has not been shown whether or not megalopae can discriminate between seagrass and marsh vegetation (Morgan et al. 1996). In our study, seasonal differences in the structural complexity of the two vegetated habitats may have contributed to a change in habitat use by brown shrimp. In fall, when the density of *Spartina* stems was high (117 m^{-2}), brown shrimp were similarly abundant in seagrass and marsh habitats. However, in spring, when *Spartina* was less dense (83 stems m^{-2}) and seagrass biomass was higher than in fall, brown shrimp were most abundant in seagrass.

Densities of nekton on the marsh surface may also be affected by the presence of submerged aquatic vegetation in adjacent subtidal areas (Rozas and Odum, 1987). Submerged vegetation provides an alternative, structurally complex habitat at low tide when the marsh surface is not accessible to aquatic organisms. At low tide, grassbeds may provide food and shelter to organisms that reside on the marsh surface at high tide, and may therefore help maintain higher densities of nekton in marshes than would occur otherwise in the absence of adjacent grassbeds (Rozas and Odum, 1987). In addition, we have observed that vegetation fragments from nearby seagrass beds often collect around the base of *Spartina* stems at the marsh edge, adding to the structural complexity of marsh edge habitat and perhaps its attractiveness to some species.

Other factors that could affect nekton distributional patterns in shallow-water habitats are (1) food availability, (2) proximity of larval supply, (3) habitat submergence time, and (4) seasonal availability of habitats (see review by Orth and van Montfrans, 1990). We did not examine differences in food resources among habitats, but prey densities for nekton predators have been shown to be higher in structurally complex habitats (Rader, 1984; LaSalle and Rozas, 1991; Zimmerman et al., 1991; Connolly, 1994b). Location within an

estuary may influence habitat use if the rate of recruitment to the habitat decreases with distance to a larval source (Young and Wadley, 1979; Heck and Thoman, 1984; Bell et al., 1988). In our study, however, proximity to a larval supply should not have been a factor because we sampled different habitats adjacent to one another; the opportunity for new recruits to settle should have been similar among habitats. Tidal inundation patterns can be important in determining habitat use; certainly, habitats that are not flooded cannot be used by most nekton. In addition, however, flooding patterns may affect habitat use even at times when all habitats in an area are flooded and equally accessible to nekton (Rozas and Reed, 1993; Minello and Webb, 1997). In our study, flooding durations for marsh and seagrass sites differed very little, especially during spring and fall when we collected our samples. However, in situations where marsh habitat is flooded for much shorter periods than seagrass, nekton utilization of marsh may be much less than seagrass. A greater difference in submergence times between salt marsh and seagrass habitats may be more typical of southeast Atlantic coast estuaries, where submergence times of salt marshes are thought to be much less than on the northern Gulf coast (Zimmerman et al., 1991; Rozas, 1995). Differences in habitat submergence times may result in different habitat-use patterns between the Gulf and Atlantic coasts (Zimmerman and Minello, 1984; Orth and van Montfrans, 1990; Rozas, 1995). Unfortunately, direct comparisons of seagrass and salt marsh use do not exist for Atlantic coast estuaries. Seasonal changes in the phenology of dominant plants or in flooding regimes also may influence habitat use. On the northern Gulf coast, for example, salt marsh and some seagrass habitats are largely unavailable as nursery areas in winter months because of low water levels and leaf blade exfoliation, respectively (Thomas et al., 1990).

The habitat-related size pattern we observed of larger animals (mainly crustaceans) on the marsh surface than in seagrass beds, could result from either differential mortality or growth among habitats or from active habitat selection. A discussion of the mechanisms that could produce such a pattern is presented by Orth and van Montfrans (1987) from a study in which they reported significantly smaller blue crabs in seagrass beds than in a marsh creek of Chesapeake Bay. Thomas et al. (1990) also collected significantly smaller blue crabs in seagrass than *Spartina* marsh in Christmas Bay, and Sheridan (1992) took significantly smaller pink shrimp (in December) and blue crabs (in September) in seagrass beds than nonvegetated areas of Florida Bay. Also consistent with the size pattern we observed is a scenario in which young recruits initially settle in seagrass beds and later shift to marsh habitat after they grow to small juvenile size. Such a habitat shift could be a response to ontogenetic changes in food or refuge requirements (Conrow et al., 1990; Thomas et al., 1990). Because smaller nekton appear to use seagrass over marsh habitat, differences in overall densities between these habitats may also be related to the size distribution of animals within the population at the time of sampling. More study is needed of such ontogenetic changes in habitat requirements and linkages between shallow estuarine habitats (McIvor and Rozas, 1996).

Our marsh samples were confined to low marsh adjacent to shallow subtidal areas, and caution is advised in applying our results more generally. For example, our results may not be applicable to high marsh or areas remote from subtidal bottom, because marsh elevation and proximity to subtidal habitat may influence habitat selection within salt marshes (Rozas, 1993; Kneib and Wagner, 1994; Minello et al., 1994; Peterson and Turner, 1994). In a Louisiana marsh, gulf killifish *Fundulus grandis* and diamond killifish *Adinia xenica* were found to select high *Distichlis spicata* (L.) marsh over low *S. alterniflora*

marsh, whereas brown shrimp and white shrimp selected low *S. alterniflora* marsh (Rozas and Reed, 1993). Densities of daggerblade grass shrimp and brown shrimp were 1.2 to 4.3 times higher on low than high *S. alterniflora* marsh in Galveston Bay, Texas (Minello et al., 1994). In addition, the location of marsh relative to shallow subtidal areas may influence habitat selection. Salt marsh habitat at the marsh-water interface (marsh edge habitat) has been shown to contain greater densities of most nekton species, especially those of commercial value (Minello et al., 1994; Peterson and Turner, 1994). Because we sampled only marsh edge habitat in our study, the nekton densities in salt marsh that we report cannot be extrapolated to the entire marsh surface in our study area, and we would expect different results from a study comparing seagrass with inner marsh located far from the marsh-water interface. However, marsh edge habitat abounds along the Texas and Louisiana coasts where much of the salt marsh in the region is highly reticulated due to coastal submergence and marsh fragmentation.

In summary, salt marsh and seagrass habitats in ANWR supported significantly greater densities of most nekton than shallow nonvegetated sites. These vegetated areas also provide valuable nursery habitat, supporting the young of many fishery species (Zimmerman and Minello, 1984; Rozas, 1993). Where marsh and seagrass habitats co-occurred, most numerically dominant crustaceans selected salt marsh over seagrass. The specific causes of this distributional pattern and whether the pattern can be extended more broadly to other estuaries or to areas outside the Gulf coast await further research.

Acknowledgments

We gratefully acknowledge the logistical support and information about the Aransas National Wildlife Refuge provided by B. Geezentanner, T. Stehn, and other refuge personnel. T. Baumer, J. Boyd, R. Burditt, J. Doerr, Q. Forrest, B. Heinisch, M. Lehr, M. Pattillo, M. Pattillo, W. Smith, and S. Whaley helped collect and process the samples. J. Doerr identified the penaeid shrimps collected in the study. Suggestions by P. F. Sheridan, W. J. Richards, and two anonymous reviewers improved earlier drafts of the manuscript. We acquired water-level data from the Ocean and Lake Levels Division of NOAA's National Ocean Service and from the Texas Coastal Ocean Observation Network which is operated by the Conrad Blucher Institute for Surveying and Science at Texas A&M University, Corpus Christi. This research was funded by the Southeast Fisheries Science Center of the National Marine Fisheries Service and the Galveston District of the U.S. Army Corps of Engineers.

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DATE SUBMITTED: April 17, 1996. DATE ACCEPTED: December 10, 1996.

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