Estuaries Vol. 29, No. 2, p. 286–296 April 2006

Nekton of New Seagrass Habitats Colonizing a Subsided Salt Marsh in Galveston Bay, Texas

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ABSTRACT: Subsidence and erosion of intertidal salt marsh at Galveston Island State Park, Texas, created new areas of subtidal habitat that were colonized by seagrasses beginning in 1999. We quantified and compared habitat characteristics and nekton densities in monospecific beds of stargrass *Halophila engelmanni* and shoalgrass *Halodule wrightii* as well as adjacent nonvegetated substrates. We collected 10 replicates per habitat type during April, July, October, and December 2001. Most habitat characteristics varied with season. Water temperature, salinity, and dissolved oxygen were similar among habitat types. Turbidity and depth were greatest in *H. engelmanni* beds and least in *H. wrightii* beds. *H. engelmanni* exhibited shorter leaves and higher shoot density and biomass core^{-1} than *H. wrightii*. Densities of almost all dominant species of nekton (fishes and decapods) were seasonally variable, all were higher in seagrass habitats than in nonvegetated habitats, and most were higher in one seagrass species than the other. Naked goby *Gobiosoma bosc*, code goby *Gobiosoma robustum*, bigclaw snapping shrimp *Alpheus heterochaelis*, and blue crab *Callinectes sapidus* were most abundant in *H. engelmanni*. Brown shrimp *Farfantepenaeus aztecus*, brackish grass shrimp *Palaemonetes intermedius*, and daggerblade grass shrimp *Palaemonetes pugio* were most abundant in *H. wrightii*. Pinfish *Lagodon rhomboides* and pink shrimp *Farfantepenaeus duorarum* were equally abundant in either seagrass. Most dominant nekton varied in size by month, but only two (*L. rhomboides* and *C. sapidus*) exhibited habitat-related differences in size. Nekton densities in these new seagrass habitats equaled or exceeded densities associated with historical and current intertidal smooth cordgrass *Spartina alterniflora* marsh. Continued seagrass expansion and persistence should ensure ecosystem productivity in spite of habitat change.

Introduction

Shallow vegetated habitats are critical to fisheries productivity, in as much as they support juveniles of many fishery species and their forage. Salt marshes and seagrasses are particularly important in maintaining productivity by supporting higher densities, faster growth, or better survival for fishes and decapods inhabiting them (Minello 1999; Heck et al. 2003; Minello et al. 2003). Unfortunately, vegetated subtidal and intertidal habitats are most at risk from human development, and much valuable acreage has already been converted to nonvegetated substrates or emergent habitats (Short and Wyllie-Echeverria 1996; Spalding et al. 1997; Burke et al. 2001). Loss of vegetated habitats is predicted to cause direct or indirect loss of fisheries production (Zimmerman et al. 1991).

Galveston Bay is the second largest coastal embayment in Texas, and it is now populated by well over 4 million people in the four surrounding counties (Whitledge and Ray 1989; U.S. Census Bureau 2000). Among the numerous human-induced stresses placed on this system is the extraction of subsurface oil, gas, and water resources that has caused land subsidence and subsequent loss of intertidal marshes (White et al. 1985, 1993). The undeveloped bay margin of Galveston Island is characterized by extensive stands of smooth cordgrass *Spartina alterniflora*. Most of the island has experienced a relatively low subsidence rate compared to other areas in the estuary (<0.6 m during 1906–1987 versus > 3.0 m in the most affected areas of Galveston Bay; White et al. 1993). Galveston Island State Park (GISP) is <15 km from a major subsidence zone (White et al. 1985, 1993; Coplin and Galloway 2001), which was most active prior to 1980 but continued through the 1990s (Buckley 2000; Center for Space Research 2001). The slow fragmentation and disappearance of salt marshes at GISP was linked to subsidence by Zimmerman et al. (1991) and to eustatic sea level rise and wind-induced erosion by White et al. (1993). Substantial conversion of intertidal salt marsh to subtidal nonvegetated bottom occurred at GISP from the 1970s through the 1990s (Glass personal communication).

The value of salt marsh habitat at GISP prior to major marsh loss was documented during 1982–1983 by Zimmerman and Minello (1984). Monthly high tide comparisons of flooded marsh versus adjacent nonvegetated substrates indicated that densities of abundant fishes, such as naked goby *Gobiosoma bosc* and pinfish *Lagodon rhomboides*, and

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Fig. 1. Time sequence of aerial photographs of Galveston Island State Park: June 1987 (infrared), showing extent of salt marsh, land/water margins, and lack of evidence for seagrass; March 2000, showing land loss, geotextile tubes (geo-tube), constructed terraces, and small seagrass patches; and December 2001, showing widespread seagrasses. Dana Cove is located at 29.20°N, 94.97°W. Terrace cells are 60 × 60 m.

decapod crustaceans, such as brown shrimp *Farfantepenaeus aztecus*, daggerblade grass shrimp *Palaemonetes pugio*, and blue crab *Callinectes sapidus*, were usually higher in vegetated than nonvegetated habitats.

A series of geotextile tubes was placed seaward of the GISP marsh remnants during 1999 to forestall further wave-induced erosion and marsh loss (Glass personal communication). Patches of subtidal stargrass *Halophila engelmanni* and shoalgrass *Halodule wrightii* were noted during placement of the tubes in Dana Cove on the eastern half of GISP, and their spread was monitored during 2000. We assessed the value of these new seagrass habitats by comparing densities of fishes and decapods (nekton) inhabiting monospecific seagrass meadows or nonvegetated flats and contrasting these densities to past densities associated with emergent marshes in the vicinity. To our knowledge, nekton densities in monospecific *H. engelmanni* beds have not been documented, whereas fauna in *H. wrightii* beds and mixed assemblages containing *H. engelmanni* are relatively well studied (Huh 1984; Lewis 1984; Tolan et al. 1997; Sheridan et al. 2003; Sheridan and Minello 2003).

Materials and Methods

GISP is located on West Bay, part of the Galveston Bay system in Texas. GISP encompasses Dana Cove on the east and Carancahua Cove on the west (Fig. 1). All samples from seagrass and nonvegetated substrates were collected from Dana Cove, centered approximately at 29.20°N, 94.97°W.

H. wrightii and wigeongrass *Ruppia maritima* (a salt-tolerant freshwater plant) historically were recorded along the bay side of Galveston Island (Pulich and White 1991; Scott 1998), although *H. wrightii* was last reported in GISP during 1969 (Gilmore and Trent 1974). *H. wrightii* was not recorded in quantitative faunal sampling of GISP bottom habitats during 1982–1999 (Zimmerman and Minello 1984; Minello personal communication). *H. engelmanni* has not been documented in the Galveston Bay system outside of Christmas Bay, 25 km southwest of GISP (Pulich and White 1991). We also searched Carancahua Cove in western GISP for seagrasses during 2000–2001 when marsh restoration projects were being constructed (terraces in March 2000 and December 2001 images, Fig. 1), but we found none.

Seagrasses present in Dana Cove during 1999 most likely originated from experiments conducted during 1995–1999 that were designed to stabilize subtidal sediments by introducing seagrass either as rooted transplants or as roots or seeds in power plant screen debris (Roach personal communication). Although there was no reported survival from those experiments, viable propagules may have escaped detection.

By December 2000, *H. engelmanni* and *H. wrightii* were widespread throughout the shallow waters of Dana Cove. Seagrasses typically formed monospe-

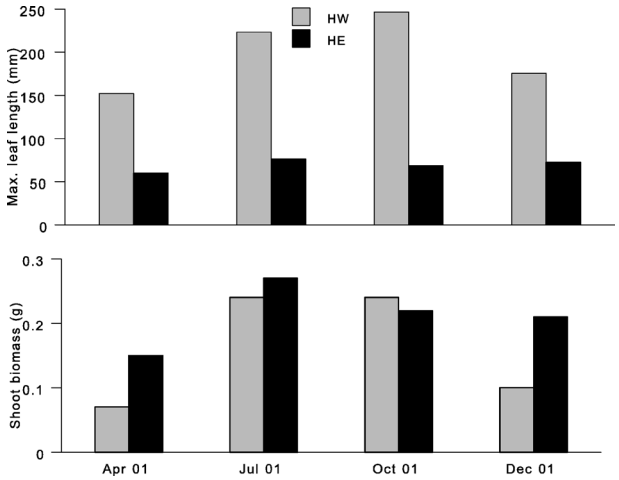

Fig. 2. Means of maximum leaf length (top) and shoot biomass (bottom) illustrating significant month × habitat interactions. HE = *Halophila engelmanni*, HW = *Halodule wrightii*.

cific beds, but both *H. engelmanni* and *H. wrightii* were interspersed with nonvegetated substrate around the cove margin in waters with and without geotextile tube protection.

Sampling Methods

Aerial photographs of GISP taken during December 2000 were overlaid with a grid dividing the subtidal area of Dana Cove into 10 × 10 m blocks from which we chose sampling locations. During each sampling period, 10 replicate blocks were assigned randomly to each of three habitat types (*H. engelmanni*, *H. wrightii*, or nonvegetated), and a sample set (see below) was collected within each block. Blocks could be seaward or shoreward of geotextile tubes. If a block did not contain the designated habitat type or was deeper than our sampling gear could access, an alternate block was selected randomly. Sample size (n = 10 per habitat type) was derived from a power analysis (Sokal and Rohlf 1981) of seagrass community measurements along the upper Texas coast (mixed *H. wrightii*-*H. engelmanni* bed, 25 throw trap samples, October 1993, log(x + 1) transformed data; Sheridan unpublished data). Ten samples per habitat type would permit detection of a 100% difference in means between any two habitat types with $\alpha = 0.10$ and $1 - \beta$ = power = 0.90 for densities of dominant nekton and seagrass shoots.

Sample sets were collected in April, July, October, and December 2001 during spring high tides to ensure faunal access to all habitat types. Densities of fishes and decapods (together referred to as nekton) were compared by deploying and clearing a quantitative 1 m^2 × 0.8 m deep throw trap constructed of solid aluminum sheets and bars

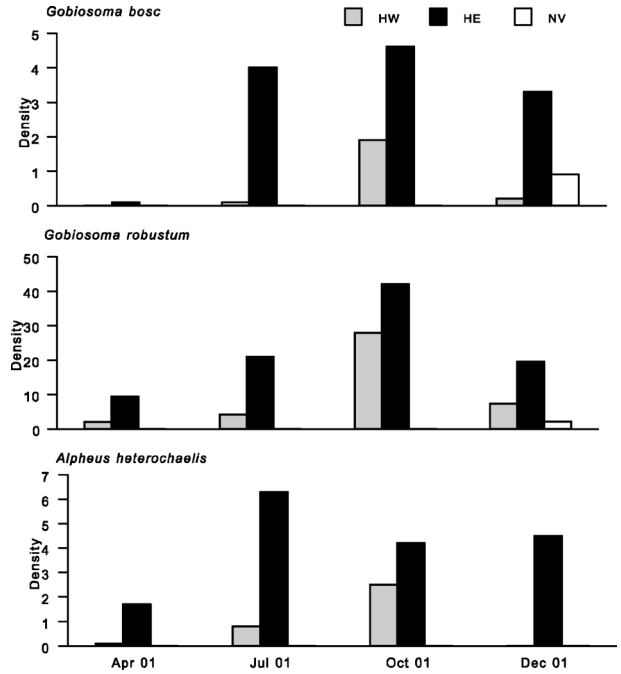

Fig. 3. Mean densities (individuals m^{-2}) of nekton with high densities in *Halophila engelmanni*, illustrating significant month × habitat interactions. HE = *Halophila engelmanni*, HW = *Halodule wrightii*, NV = non-vegetated.

(modified from Kushlan 1981). The throw trap was swept repeatedly with a rigid, form-fitting, 3-mm mesh seine until no organisms were recovered in three consecutive sweeps (6 sweeps minimum, 10 sweeps maximum). Fishes and decapods were preserved in 10% formalin-seawater, then identified to genus and species if possible, counted, blotted dry, and weighed (0.01 g) in the laboratory.

After deploying the throw trap but prior to clearing nekton, we measured water temperature (°C), salinity (psu), dissolved oxygen (mg l^{-1}), depth (cm), and turbidity (NTU) as outlined by Sheridan (2004). We also collected a core (10 cm diam × 10 cm deep; 78.6 cm^2) immediately adjacent to each throw trap to estimate seagrass shoot density, leaf length, and aboveground biomass. The core contents were rinsed of sediments and preserved as above for later analysis. In the laboratory, seagrasses were rinsed in freshwater and shoots were separated from rhizomes and roots. Shoots in each core were counted, the length of the longest undamaged shoot was measured (mm), then shoots were dried at 60°C for 48 h and weighed (0.1 mg). Epiphytes were not removed from shoots.

Data Analysis

Two-way analysis of variance (ANOVA) was used to assess effects of habitat and time on means of the

following characteristics: water depth, temperature, salinity, dissolved oxygen, and turbidity; seagrass shoot density, maximum leaf length, and shoot biomass; and number of individuals for dominant nekton species (herein defined as those with counts averaging at least 1 ind m^{-2} in any habitat type in a given sampling period). One-way ANOVA was used to assess effects of habitat or time on nekton biomass per individual since there were many missing cell values (none captured = no biomass measurement). Habitat and time were considered fixed factors, although time is arguably so (daytime spring high tides 2 or 3 mo apart were chosen). Examination of the distribution of error terms for abundant taxa of nekton and for water and seagrass characteristics indicated nonnormality. ANOVA is robust to nonnormality, particularly if sample sizes are large (Underwood 1997). Positive relationships between means and variances were detected for most seagrass and all nekton variables, indicating transformation was needed prior to ANOVA. $Log_{10}(x + 1)$ transformation was employed for those variables, but it was not always successful in achieving homogeneity of variances prior to ANOVA, so we conducted analyses using a lower probability level for significance ($p < 0.025$; Underwood 1997). We employed Scheffé's test in multiple comparisons of treatment means. Analyses were conducted using STATISTICA personal computer software (StatSoft, Inc., Tulsa, Oklahoma).

Results

Water Column

We found significant differences related to month but not habitat type for temperature, salinity, and dissolved oxygen (Table 1). Water temperatures followed a predictable sinusoidal pattern, being coldest in December, warmest in July, and intermediate in April and October. Waters were generally polyhaline throughout the sampling period, varying unpredictably from a low of 17 in April to a high of 24 in July. Dissolved oxygen also varied unpredictably with a low in October (5.4 mg l^{-1}) and a high in December (10.3 mg l^{-1}).

Depth and turbidity varied significantly with both month and habitat type, but interactions were not significant (Table 1). Seasonal differences in depth were expected, given that the highest high tides are predicted for April–May and September–October. Habitat-related differences in depth were due to finding *H. engelmanni* in significantly deeper waters than *H. wrightii*. Nonvegetated habitat patches were typically situated at intermediate depths, but there was broad overlap in depth ranges for each habitat type (*H. engelmanni* 30–75 cm, *H. wrightii* 21–65 cm, nonvegetated 18–72 cm). Turbidity was significantly lower in December than in other months, coinciding with depth minima, and was significantly different among all habitat types, mirroring the habitat-related differences in depth.

Seagrasses

Seagrasses in the northwestern Gulf of Mexico typically grow during spring and summer months, then shed a portion of the aboveground biomass as the photoperiod shortens during fall and winter (Dunton 1994). *H. wrightii* produces relatively long shoots with filamentous leaves, whereas *H. engelmanni* develops relatively short shoots with ovate leaves. It is not surprising that we found significant differences in seagrass bed characteristics due to these factors (Table 1). Seagrass shoot densities were significantly greater in *H. engelmanni* patches than in *H. wrightii* but were not related to month. Both leaf length and shoot biomass exhibited significant interactions between month and habitat type (Fig. 2). There was clear sinusoidal pattern in leaf length for *H. wrightii* with a minimum in April and a maximum in October, and *H. wrightii* leaf lengths were always greater than those of *H. engelmanni*. Maximum leaf lengths for *H. engelmanni* exhibited little temporal variation except for being shortest in April. Both seagrass species exhibited seasonal cycles in shoot biomass (Fig. 2), although *H. engelmanni* peaked in July while *H. wrightii* appeared to hold biomass longer through July and October, perhaps peaking in August or September when we had no samples. *H. wrightii* also had dramatically lower shoot biomasses in April and December than did *H. engelmanni*.

Nekton

We collected 2,635 individuals among 22 species of fishes and 3,022 individuals among 16 taxa of decapods (for complete listing contact corresponding author). Some individual decapods were assigned only to genera due to small size or damage and potential for misclassification as congeners (*Callinectes* spp., *Farfantepenaeus* spp., and *Palaemonetes* spp.). Only 9 taxa were considered numerical dominants. Three fish species comprised 94.2% of all fish captured, led by code goby *Gobiosoma robustum* (51.4%), *L. rhomboides* (37.1%), and *G. bosc* (5.7%). All other fishes individually comprised <1% of the total fish caught. Six dominant decapods combined to form 82.8% of all decapods captured, led by *C. sapidus* (39.3%), pink shrimp *Farfantepenaeus duorarum* (11.3%), *P. pugio* (10.4%), brackish grass shrimp *Palaemonetes intermedius* (8.4%), *F. aztecus* (6.8%), and bigclaw snapping shrimp *Alpheus heterochaelis* (6.7%). Densities of *A. heterochaelis* were likely underestimated because this

TABLE 1. Results of two-way ANOVA comparisons of water column and seagrass parameters in Galveston Island State Park during 2001. Seagrass shoot biomass includes epiphytes. HE = *Halophila engelmanni*, HW = *Halodule wrightii*, NV = nonvegetated.

Effect	df	MS	F	p	Scheffé Test of Main Effect Means
Temperature (°C)					
Month	3	1338.72	319.99	<0.001	Jul 30.9 > Apr 24.6 = Oct 24.4 > Dec 14.7
Habitat	2	1.10	0.26	0.769	
M × H	6	1.01	0.24	0.961	
Residual	108	4.18			
Salinity					
Month	3	288.51	572.78	<0.001	Jul 24 > Oct 22 > Dec 20 > Apr 17
Habitat	2	0.16	0.31	0.731	
M × H	6	0.60	1.20	0.314	
Residual	108	0.50			
Dissolved oxygen (mg l^{-1})					
Month	3	149.78	70.03	<0.001	Dec 10.4 > Jul 8.4 > Apr 6.5 > Oct 5.2
Habitat	2	0.84	0.39	0.677	
M × H	6	2.09	0.98	0.445	
Residual	108	2.14			
Depth (cm)					
Month	3	3399.76	35.89	<0.001	Oct 58 > Apr 43 > Jul 40 > Dec 32
Habitat	2	1819.01	19.20	<0.001	HE 51 > NV 43 > HW 37
M × H	6	46.60	0.49	0.813	
Residual	108	94.72			
Turbidity (NTU)					
Month	3	38.05	10.37	<0.001	Apr 5.3 = Oct 5.2 = Jul 4.7 > Dec 2.9
Habitat	2	21.50	5.86	0.004	HE 5.3 > NV 4.3 > HW 3.9
M × H	6	1.71	0.47	0.833	
Residual	108	3.67			
Seagrass shoot density (core^{-1})					
Month	3	0.09	2.84	0.044	
Habitat	1	0.91	30.23	<0.001	HE 107 > HW 66
M × H	3	0.02	0.73	0.540	
Residual	72	0.03			
Maximum leaf length (mm)					
Month	3	11167.9	5.90	0.001	Oct 157 = Jul 150 > Dec 124 = Apr 106
Habitat	1	340083.2	179.68	<0.001	HW 199 > HE 69
M × H	3	7935.43	4.19	0.009	
Residual	72	1892.71			
Seagrass shoot biomass (g core^{-1})					
Month	3	0.09	18.46	<0.001	Jul 0.85 = Oct 0.73 > Dec 0.45 = Apr 0.30
Habitat	1	0.06	11.18	0.001	HE 0.67 > HW 0.50
M × H	3	0.02	3.51	0.019	
Residual	72	0.01			

species constructs permanent burrows and could escape capture. An additional 15.6% of the decapod catch was classified as *Farfantepenaeus* spp., a mixture of *F. aztecus* and *F. duorarum* that probably changed seasonally. These specimens were either damaged or of a size (13–18 mm total length) that could not be identified reliably (Rozas and Minello 1998).

We found significant differences in densities due to month × habitat interactions for most of the dominant nekton species (Table 2), with two exceptions. Densities of *P. intermedius* were significantly related only to habitat type, with all specimens collected in seagrasses and with significantly higher densities in *H. wrightii* than in *H. engelmanni*. Densities of *C. sapidus* were significantly related to month (October and December > April and July) and to habitat (*H. engelmanni* > *H. wrightii* > nonvegetated), but there was no significant month × habitat interaction. Three species of dominant nekton were associated primarily with *H. engelmanni* and secondarily with *H. wrightii*, including *G. bosc*, *G. robustum*, and *A. heterochaelis* (Fig. 3 and Table 2). All three species exhibited abundance peaks during July or October, were found at relatively high densities during 3 or 4 mo, and were rarely captured in nonvegetated habitat. The four remain-

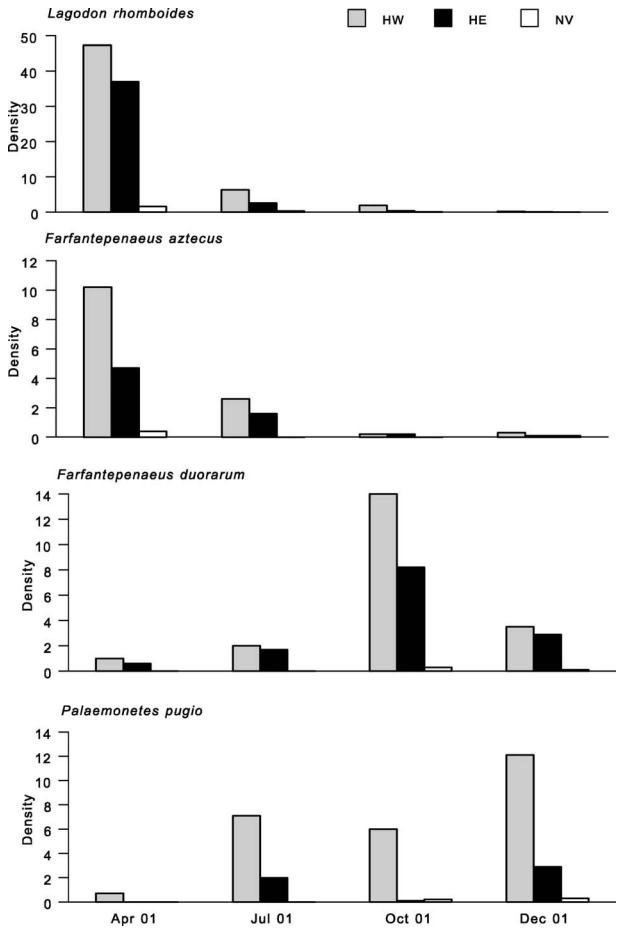

Fig. 4. Mean densities (individuals m^{-2}) of nekton with high densities in *Halodule wrightii* illustrating significant month × habitat interactions. HE = *Halophila engelmanni*, HW = *Halodule wrightii*, NV = non-vegetated.

ing species of dominant nekton were associated primarily with *H. wrightii* and secondarily with *H. engelmanni*, including *L. rhomboides*, *F. aztecus*, *F. duorarum*, and *P. pugio* (Fig. 4 and Table 2). The first three species exhibited a single monthly peak in density followed by rapid declines, whereas densities of the latter species were relatively high for 3 mo. Again, all four of these species were rarely captured in nonvegetated habitat.

Our category *Farfantepenaeus* spp. contained 472 individuals that could have been either *F. aztecus* or *F. duorarum*, since both species were collected each month. About half of these individuals (229) were collected during April and were most likely *F. aztecus*, since we actually identified 153 *F. aztecus* and only 16 *F. duorarum* at that time. Another 40% of the *Farfantepenaeus* spp. specimens (190) were collected during October and were most likely *F. duorarum*, since we actually identified 225 *F. duorarum* and only 4 *F. aztecus* at that time. Mean densities of *F. aztecus* and *F. duorarum* given in Table 2 and Fig. 4 should be considered conservative. The likely shifts in abundance of the two species that make up *Farfantepenaeus* spp. would not affect the trends of the two species described above.

The total nekton catch represented 1,003.3 g of fishes and 548.9 g of decapods (blotted wet weight). The three most numerous fishes represented 79.2% of the fish biomass, including *L. rhomboides* (57.0%), *G. robustum* (19.0%), and *G. bosc* (3.2%). Also ranking high in total fish biomass were spot *Leiostomus xanthurus* (6.1% of biomass; 22 individuals) and southern flounder *Paralichthys lethostigma* (7.9% of biomass; 1 individual). The 6 numerically dominant decapods also comprised 95.7% of the decapod biomass, formed by *C. sapidus* (52.3%), *F. duorarum* (15.9%), *A. heterochaelis* (12.7%), *F. aztecus* (6.2%), *P. pugio* (4.7%), and *P. intermedius* (3.9%). An additional 3.4% of the decapod biomass was classified as *Farfantepenaeus* spp.

Most differences in biomass per individual of dominant nekton (6 of 9 species) were significantly related to month (Table 3), except for *A. heterochaelis*, *C. sapidus*, and *P. intermedius*. Highest monthly biomasses were usually associated with lowest monthly densities (Table 2), although not for *P. pugio*. Biomass per individual was only significantly related to habitat for *L. rhomboides* and *C. sapidus*.

Discussion

The newly-formed *H. engelmanni* and *H. wrightii* beds at GISP were generally found to harbor greater densities of fishes and decapods during most seasons than did nonvegetated substrates. This follows the general trend noted for seagrass beds versus unstructured habitats elsewhere in Texas (Rozas and Minello 1998; Sheridan and Minello 2003; Sheridan et al. 2003; Sheridan 2004), the U.S. Gulf of Mexico (Lewis 1984; Sheridan 1992; Sheridan et al. 1997; Minello 1999), and the northern hemisphere (but not in the southern hemisphere; Heck et al. 2003).

Although these seagrass beds were less than 3 yr old when sampled, densities of fishes and decapods were similar to those found in older stands of seagrasses located on the Texas coast. Total nekton densities in the present study were 8.6–50.5 fish m^{-2} and 25.1–51.2 decapods m^{-2}, depending on the sampling period. Seagrass beds elsewhere in Texas seasonally support densities of up to 28.2 fish m^{-2} and 80.0 decapods m^{-2} (Rozas and Minello 1998; Sheridan and Minello 2003; Sheridan et al. 2003; Sheridan 2004). While there are latitudinal and seasonal differences in species densities among these studies, our results are in agreement with

TABLE 2. Results of two-way ANOVA comparison of nekton densities (ind m^{-2}) in Galveston Island State Park during 2001. HE = *Halophila engelmanni*, HW = *Halodule wrightii*, NV = nonvegetated.

Effect	df	MS	F	p	Scheffé Test of Main Effect Means
Gobiosoma bosc					
Month	3	0.62	16.42	<0.001	Oct 2.2 = Dec 1.5 = Jul 1.4 > Apr 0.0
Habitat	2	2.40	63.72	<0.001	HE 3.0 > HW 0.6 = NV 0.2
M × H	6	0.31	8.16	<0.001	
Residual	108	0.04			
Gobiosoma robustum					
Month	3	1.89	33.17	<0.001	Oct 23.3 > Dec 9.7 = Jul 8.4 > Apr 3.8
Habitat	2	14.64	256.55	<0.001	HE 23.0 > HW 10.3 > NV 0.5
M × H	6	0.61	10.77	<0.001	
Residual	108	0.06			
Lagodon rhomboides					
Month	3	5.25	63.08	<0.001	Apr 28.6 > Jul 3.1 > Oct 0.8 = Dec 0.1
Habitat	2	3.13	37.64	<0.001	HW 13.9 = HE 10.0 > NV 0.5
M × H	6	0.79	9.54	<0.001	
Residual	108	0.08			
Alpheus heterochaelis					
Month	3	0.29	4.26	0.007	Jul 2.4 = Oct 2.2 = Dec 1.5 > Apr 0.6
Habitat	2	2.83	41.12	<0.001	HE 4.2 > HW 0.9 = NV 0.0
M × H	6	0.18	2.69	0.018	
Residual	108	0.07			
Callinectes sapidus					
Month	3	0.72	15.47	<0.001	Dec 13.9 = Oct 12.1 > Apr 7.8 = Jul 5.8
Habitat	2	11.48	248.30	<0.001	HE 17.8 > HW 10.7 > NV 1.2
M × H	6	0.06	1.23	0.294	
Residual	108	0.05			
Farfantepenaeus aztecus					
Month	3	1.84	45.62	<0.001	Apr 5.1 > Jul 1.4 > Oct 0.2 = Dec 0.1
Habitat	2	1.29	31.99	<0.001	HW 3.3 > HE 1.7 > NV 0.1
M × H	6	0.41	10.18	<0.001	
Residual	108	0.04			
Farfantepenaeus duorarum					
Month	3	1.89	32.06	<0.001	Oct 7.5 > Dec 2.2 = Jul 1.2 > Apr 0.5
Habitat	2	3.32	56.39	<0.001	HW 5.1 = HE 3.4 > NV 0.1
M × H	6	0.35	6.00	<0.001	
Residual	108	0.06			
Palaemonetes intermedius					
Month	3	0.26	2.56	0.059	
Habitat	2	3.09	29.97	<0.001	HW 4.6 > HE 1.8 > NV 0.0
M × H	6	0.08	0.79	0.579	
Residual	108	0.10			
Palaemonetes pugio					
Month	3	1.26	19.30	<0.001	Dec 5.1 > Jul 3.0 = Oct 2.1 > Apr 0.2
Habitat	2	4.26	63.36	<0.001	HW 6.5 > HE 1.3 > NV 0.1
M × H	6	0.39	6.02	<0.001	
Residual	108	0.07			

prior observations that maximum densities of fishery species, such as *F. aztecus*, *F. duorarum*, and *C. sapidus*, are higher in northern Texas than in southern Texas (Sheridan and Minello 2003). Those authors speculated that reduced densities of juvenile fishery species in southern Texas seagrasses were due to increased predator abundance.

The seasonal fluctuations in densities found for most dominant species were expected, since few of the numerical dominants are true residents (Minello 1999). We did find some dominant taxa with significantly higher densities in one seagrass species over the other. Densities of *G. bosc*, *G. robustum*, *A. heterochaelis*, and *C. sapidus* were higher in *H. engelmanni*, whereas those of *F. aztecus*, *P. intermedius*, and *P. pugio* were higher in *H. wrightii*. The seagrass habitats themselves have differing morphological and water quality characteristics, with *H. engelmanni*

TABLE 3. Results of one-way ANOVA comparison of nekton biomass (wet g ind^{-1}) in Galveston Island State Park during 2001. MSr = residual mean square. * = not found in nonvegetated habitat. HE = *Halophila engelmanni*, HW = *Halodule wrightii*, NV = nonvegetated.

Factor	df	MS	MSr	F	p	Scheffé Test of Main Effect Means
Gobiosoma bosc						
Month	3, 30	0.32	0.02	13.91	<0.001	Apr 1.14 > Dec 0.31 = Jul 0.21 = Oct 0.14
Habitat	2, 30	0.06	0.02	2.39	0.109	
Gobiosoma robustum						
Month	3, 71	0.10	0.02	6.53	0.001	Jul 0.25 = Apr 0.24 > Dec 0.14 = Oct 0.10
Habitat	2, 71	0.03	0.02	1.73	0.184	
Lagodon rhomboides						
Month	3, 49	337.60	10.85	31.15	<0.001	Oct 14.6 > Dec 4.39 = Jul 3.13 = Apr 0.47
Habitat	2, 49	148.72	10.85	13.71	<0.001	NV 10.59 > HE 5.41 > HW 2.53
*Alpheus heterochaelis**						
Month	3, 38	0.24	0.21	1.19	0.326	
Habitat	1, 43	0.07	0.21	0.34	0.562	
Callinectes sapidus						
Month	3, 84	0.19	0.09	2.23	0.090	
Habitat	2, 84	0.69	0.09	7.98	0.001	HW 0.46 > HE 0.23 = NV 0.13
Farfantepenaeus aztecus						
Month	3, 35	0.61	0.04	14.44	<0.001	Oct 0.67 = Jul 0.52 > Dec 0.31 = Apr 0.10
Habitat	2, 35	0.03	0.04	0.71	0.501	
Farfantepenaeus duorarum						
Month	3, 51	1.46	0.31	4.73	0.005	Jul 0.91 > Apr 0.40 = Dec 0.39 = Oct 0.14
Habitat	2, 51	0.03	0.31	0.11	0.897	
Palaemonetes intermedius						
Month	3, 37	<0.01	<0.01	0.31	0.821	
Habitat	2, 37	<0.01	<0.01	0.40	0.671	
Palaemonetes pugio						
Month	3, 38	<0.01	<0.01	3.66	0.021	Dec 0.09 = Apr 0.08 = Oct 0.07 > Jul 0.04
Habitat	2, 38	<0.01	<0.01	0.72	0.496	

being short and dense and found in deeper, more turbid waters relative to *H. wrightii*. Correlative studies such as ours indicate items for future experimental verification since apparent habitat preference may be due to synergisms or unmeasured factors (Underwood et al. 2004). Depth and turbidity are confounded with seagrass type in our study. Prior attempts to describe the relationships among habitat variables and organism densities using correlative techniques, such as multiple regression, often fail to make significant connections or make connections with relatively low predictive capacity (e.g., $R^2 < 0.7$; examples in Zimmerman and Minello 1984; Szedlmayer and Able 1996; Baltz et al. 1998; Hovel et al. 2002; Sheridan and Minello 2003). We also note that there is little consistency in these apparent habitat preferences across study sites, as reviewed by Sheridan and Minello (2003). Manipulative experiments could verify whether apparent habitat preferences are related to water quality, seagrass architecture, competition for food or space, interactions with predators, or a combination of factors (Underwood et al. 2004).

Perhaps of greater importance is whether faunal densities in present seagrass habitats equal or exceed those in intertidal salt marsh prior to losing marsh to subsidence. Flooded *S. alterniflora* marsh edge habitats in Texas and Louisiana generally support greater mean densities of total nekton than do adjacent seagrass and nonvegetated habitats (91.2, 64.2, and 15.5 ind m^{-2}, respectively; Minello 1999), although this trend primarily reflects decapod densities and it may not be true on a global basis (Minello et al. 2003). GISP salt marsh supported higher densities of 3 of 4 dominant decapod species and 6 of the top 10 fish species than did nonvegetated habitat during 1982–1983 (Zimmerman and Minello 1984), long before intertidal *S. alterniflora* was replaced first by subtidal nonvegetated substrates then by seagrasses. We compared their data with our data collected nearly 20 yr later (Table 4). Zimmerman and Minello (1984) found higher densities of decapods and lower densities of fishes in *S. alterniflora* than we found in either seagrass habitat. They recorded higher densities of *Palaemonetes* spp. and white

TABLE 4. Minimum and maximum mean densities (ind m^{-2}) of nekton by season in Galveston Island State Park *Spartina alterniflora* marsh during 1982–1983 (2–4 collection dates per season; Zimmerman and Minello 1984) and between seagrass species examined during 2001 (one collection date per season; this study). March–May = spring.

Taxon	March–May		June–August		September–November		December–February	
	Marsh	Seagrass	Marsh	Seagrass	Marsh	Seagrass	Marsh	Seagrass
Total fishes	5.5–29.9	47.3–50.5	7.2–9.5	14.5–28.5	26.7–32.2	34.9–48.5	3.7–7.6	8.6–23.7
Lagodon rhomboides	2.7–16.0	37.0–47.3	0.5–1.8	2.6–6.3	0.0–0.0	0.4–1.9	0.0–0.0	0.1–0.2
Gobiosoma spp.	0.4–1.5	2.0–9.5	1.0–3.0	4.3–25.0	21.8–24.8	29.7–46.6	0.0–3.6	7.5–22.9
Total decapods	34.4–53.2	30.8–41.1	64.0–80.2	25.1–27.9	45.7–69.3	43.5–51.2	34.9–53.2	36.9–38.3
Palaemonetes spp.	15.9–35.8	0.0–5.4	13.3–69.9	4.8–12.4	14.0–23.1	1.0–9.6	29.7–39.4	6.2–16.7
Litopenaeus setiferus	0.0–0.2	0.0–0.0	0.6–36.3	0.0–0.0	6.8–14.3	0.0–0.0	0.0–3.3	0.0–0.1
Farfantepenaeus spp.	10.6–21.2	13.1–25.6	6.8–15.0	3.9–6.8	9.6–9.9	16.0–25.5	0.1–2.3	3.6–5.6
Callinectes sapidus	2.6–4.1	7.7–15.2	2.8–3.9	7.0–10.0	15.0–22.3	13.3–22.3	5.1–8.2	14.6–23.8

shrimp *Litopenaeus setiferus* than we did, but we found equal or higher densities of *C. sapidus* and *Farfantepenaeus* spp. in seagrasses. With respect to fishes, maximum densities of *L. rhomboides* and *Gobiosoma* spp. were lower in *S. alterniflora* during 1982–1983 than in seagrass during 2001 (Table 4). Differences could be related to monthly sampling in 1982–1983 versus our quarterly sampling, to any number of local physical or biological factors, or even to broader scale factors such as changes in recruitment success following decadal changes in oceanographic patterns.

Marine organisms have shown a variety of responses to habitat change that prevent accurate prediction of the results of those changes. A slow conversion from marsh to open water then to seagrass could result in a change from structurally-oriented nekton taxa to water column taxa and back (Zimmerman et al. 1991; Matheson et al. 1999). Fish community composition or size composition differs between salt marsh and seagrass habitats (Rozas and Minello 1998), among seagrass habitats with differing architecture (Zupo and Nelson 1999; Hyndes et al. 2003; for exceptions see Sheridan and Minello 2003), or depending on whether or not seagrass adjoins salt marsh (Irlandi and Crawford 1997; Rozas and Minello 1998; Stunz et al. 2002a). These trends may be connected with the observations that the nekton forage base is also influenced by a variety of complex factors extending beyond the basic morphology and structural complexity of vegetation (Knowles and Bell 1998; Attrill et al. 2000). As well, habitat use may change with organism growth (Pardieck et al. 1999) or not (this study), and vegetation type or density may or may not influence growth rates (Baltz et al. 1998; Spitzer et al. 2000; Stunz et al. 2002b) and survival rates (Minello et al. 2003). The net effects of the slow conversion of GISP salt marsh habitat to seagrass habitat are unpredictable and may not even be detectable at the scale of present faunal monitoring efforts (Hensley and Fuls 1997).

Overall, standing crops of small fishes and decapods seem to be relatively unchanged between measurements made 20 yr apart (although we have no intervening data), and the current nekton assemblages appear to be as dense or denser than assemblages recently found inhabiting seagrass beds elsewhere in Texas. We expect there would have been some disruption in secondary production during the period after marsh loss and before seagrass expansion, since nekton densities are consistently lower over nonvegetated than vegetated habitats. One way to check whether production has been altered would be to examine the time series of relative densities of fishery and forage organisms monitored monthly by Texas Parks and Wildlife Department (Hensley and Fuls 1997). The smallest area reported by such monitoring efforts is by bay system, not by localities within bays. One would need access to the raw data, and this was beyond the scope of our research. Another method would be to obtain estimates of intertidal *S. alterniflora* acreage lost and subtidal nonvegetated and seagrass acreage gained over time (e.g., through aerial photography), then to model effects of gains or losses on nekton standing crops and secondary production (see for example Clark et al. 2004; Haas et al. 2004).

While Pulich and White (1991) did not think subsidence was a factor in the loss of seagrasses along western Galveston Island, the slow fragmentation and disappearance of salt marshes at GISP first noted by Zimmerman et al. (1991) is likely linked to subsidence. In spite of the changes in acreage of vegetated habitat types and in nekton densities, we would be hard pressed to say that loss of *S. alterniflora* and its replacement by *H. wrightii* and *H. engelmanni* has resulted in a net change of secondary production (for better or worse) in GISP. The new seagrass beds seem to be functioning as well as *S. alterniflora* habitat and should continue, unless persistent subsidence and erosion remove the substrate to levels below those within the light regime required for seagrass maintenance and growth.

Acknowledgments

Funding for this project was provided by the National Marine Fisheries Service (NMFS) Galveston Laboratory. Harley Clinton, David Evans, Mike Lowe, Guy Myers, and Suraida Nanez-James assisted in the field, Phil Caldwell provided geographical information systems support, and Jim Ditty provided larval fish identifications (all NMFS Galveston Laboratory). Andy Tirpak (Texas Parks and Wildlife Department) provided aerial photographs. David Riskind (Texas Parks and Wildlife Department) provided Texas State Park Scientific Study Permit No. 04-01. Our thanks to Park Superintendent Angela Denton (Texas Parks and Wildlife Department) for allowing access to the seagrasses. Constructive comments were provided by Andy David and two anonymous reviewers.

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Received, March 29, 2005
Revised, October 6, 2005
Accepted, December 7, 2006