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Seasonal and Spatial Variations in Fish and Macroinvertebrate Communities of Oyster and Adjacent Habitats in a Mississippi Estuary

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Abstract In Grand Bay National Estuarine Research Reserve (Grand Bay NERR), Mississippi, we used quantitative drop sampling in three common shallow estuarine habitats—low profile oyster reef (oyster), vegetated marsh edge (VME), and nonvegetated bottom (NVB)—to address the dearth in research comparing nekton utilization of oyster relative to adjacent habitats. The three habitats were sampled at two distinct marsh complexes within Grand Bay NERR. We collected a total of 633 individual fishes representing 41 taxa in 22 families. The most diverse fish family was Gobiidae (seven species) followed by Blennidae and Poeciliidae (three species each). We collected a total of 2,734 invertebrates representing 24 taxa in 11 families. The most diverse invertebrate family was Xanthidae (six species) followed by Palaemonidae (five species). We used ordination techniques to examine variation in species relative abundance among habitats, seasons, and sampling areas, and to identify environmental gradients correlated with species relative abundances. Our resulted indicated that oyster provided a similarly complex and important function as the adjacent VME. We documented three basic trends related to the importance of oyster and VME habitats: 1) Oyster and VME provide habitat for significantly more species relative to NVB, 2) Oyster and VME provide habitat for rare species, and 3) Several species collected across multiple habitats occurred at higher abundances in oyster or VME habitat. We also found that salinity, temperature, and depth were associated with seasonal and spatial shifts in nekton communities. Lastly, we found that the relative location of the two marsh complexes we studied within the context of the whole estuary may also explain some of the temporal and spatial differences in communities. We conclude that oyster habitat supported a temporally diverse and spatially distinct nekton community and deserves further attention in research and estuarine conservation efforts.

Keywords Estuarine · Communities · Habitat · Oyster reef · Vegetated marsh edge

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Introduction

Estuaries along the Gulf of Mexico are characterized by a patchwork of shallow water estuarine habitats. Estuarine residents, such as grass shrimp (Palaemonidae), mud crabs (Xanthidae), gobies (Gobiidae), and toadfish (*Opsanus* spp.), depend on these shallow habitats for food resources, refuge from predation, and sites for reproduction (Breitburg et al. 2000; Kneib 1997; Shervette et al. 2004). Estuarine-dependent marine residents, including several of economic importance, such as blue crabs *Callinectes sapidus*, white shrimp *Litopenaeus setiferus*, brown shrimp *Farfantopeneaus aztecus*, and spot *Leiostomus xanthurus*, also utilize these habitats for food and refuge (Boesch and Turner 1984; Baltz et al. 1993; Howe and Wallace 2000; Harding and Mann 2001).

Common estuarine habitats such as vegetated marsh, oyster reef, and nonvegetated bottom are considered

essential for a multitude of fishes and invertebrates. Many studies have documented the importance of structurally complex vegetated marsh habitats to fishes and invertebrates (see review in Minello et al. 2003). Juveniles of several species are dependent on vegetated marsh habitats as evidenced by studies reporting higher growth rates in *Spartina* marsh edge habitat when compared to adjacent habitats (Minello et al. 1989; Stunz et al. 2002). Other studies have demonstrated high survival rates of juveniles in salt marsh habitats (Minello and Zimmerman, 1983, 1985; Minello et al. 1989). Not as much literature substantiates the importance of oyster habitat (see review: Peterson et al. 2003) relative to adjacent habitats. Glancy et al. (2003) found that oyster reefs support distinct assemblages of decapod crustaceans and represent an important ecological component of estuarine habitats. Glancy et al. (2003) speculated that the mechanisms underlying the importance of oyster habitat may include increased survival or greater forage availability for decapods. Nonvegetated bottom habitats, often adjacent to vegetated marsh edge, sea grass, oyster, and other habitats, also support many estuarine species (Zimmerman et al. 1990; Minello et al. 1994; Rozas and Minello 1998; Castellanos and Rozas 2001). In fact, some species, such as Atlantic croaker *Micropagonias undulatus* and spot *L. xanthurus*, may select for open water habitat (including nonvegetated bottom areas) over vegetated marsh (Minello et al. 2003).

Several studies have characterized the inhabitants of oyster reef habitats along the coastal Gulf of Mexico and the Atlantic through various sampling strategies (Zimmerman et al. 1989; Larsen et al. 2001; Perry et al. 2001; Grabowski 2002; Glancy et al. 2003). However, few published studies have compared fish and macroinvertebrate communities, species abundances, and species richness between oyster and adjacent vegetated and unvegetated habitats (Zimmerman et al. 1989; Glancy et al. 2003; Hosack et al. 2006). In fact, no previously published research has compared the fish and invertebrate communities of oyster, marsh, and nonvegetated bottom habitats. Such comparisons are essential in determining relative habitat value and targeting conservation efforts within estuaries (Beck et al. 2001).

The goal of our study was to evaluate the relationship between habitat and nekton community structure. In addition, we investigated relationships among physicochemical variables, habitats, and spatiotemporal variation in nekton community structure in a Mississippi estuary. We specifically characterized species composition, relative abundance, and richness of fishes and invertebrates occupying oyster reefs and oyster shell (oyster), vegetated marsh edge (VME), and nonvegetated bottom (NVB) habitats in Grand Bay National Estuarine Research Reserve (Grand Bay NERR). To address the current lack of quantitative studies comparing oyster and adjacent habitats, we designed our study to determine if oyster, vegetated marsh edge, and nonvegetated bottom support distinct nekton communities and if observed patterns vary seasonally and spatially within Grand Bay NERR.

Materials and Methods

Study Areas

Grand Bay NERR is located on the Mississippi coast in the north central Gulf of Mexico (Fig. 1). It is a productive and diverse estuary occupying a total area of 74.5 km^2 and is bordered on the west by the heavily industrialized Pascagoula estuary and on the east by another heavily industrialized estuary, Mobile Bay. The Grand Bay estuary is microtidal with a typical tidal range of 30–60 cm. For this study, we focused sampling in two main marsh complexes within Grand Bay NERR: Bayou Heron and Crooked Bayou (Figs. 1 and 2). Bayou Heron is located in the upper zone of the estuary and is characterized by oligohaline salinities. Common shallow habitats included vegetated *Spartina alterniflora* marsh edge and inner marsh, low profile *Crassostrea virginica* oyster shell from oyster midden deposits (with no live oyster), and shallow nonvegetated bottom. In addition, Bayou Heron had small amounts of subtidal *Ruppia maritima* that occurred in small, sparse, patchy beds. Crooked Bayou, located closer to the outer zone of the estuary, is approximately 6 km southwest of Bayou Heron. Crooked Bayou is characterized by polyhaline salinities and is connected directly with Mississippi Sound. Common shallow habitats in the Crooked Bayou marsh complex included vegetated *Spartina alterniflora* marsh edge and inner marsh, low profile *C. virginica* oyster reefs and oyster midden deposits, and shallow nonvegetated bottom. No subtidal seagrasses were observed in Crooked Bayou.

Quantitative Nekton Sampling

To determine nekton community composition of vegetated marsh edge (VME), oyster, and nonvegetated bottom (NVB) habitats of Grand Bay NERR, we sampled in Crooked Bayou and Bayou Heron, two marsh complexes that had all three of these habitats (Figs. 1 and 2). For both marsh complexes, sampling occurred in Fall 2003 (4–10 October), Spring 2004 (13–20 May), and Summer 2004 (16–28 July) within 2 hours of high tide when all target habitats were completely inundated. To determine where to sample within each habitat, we created a rough map of each sampling area on a numbered grid. We used a random numbers table with the map to determine where in each

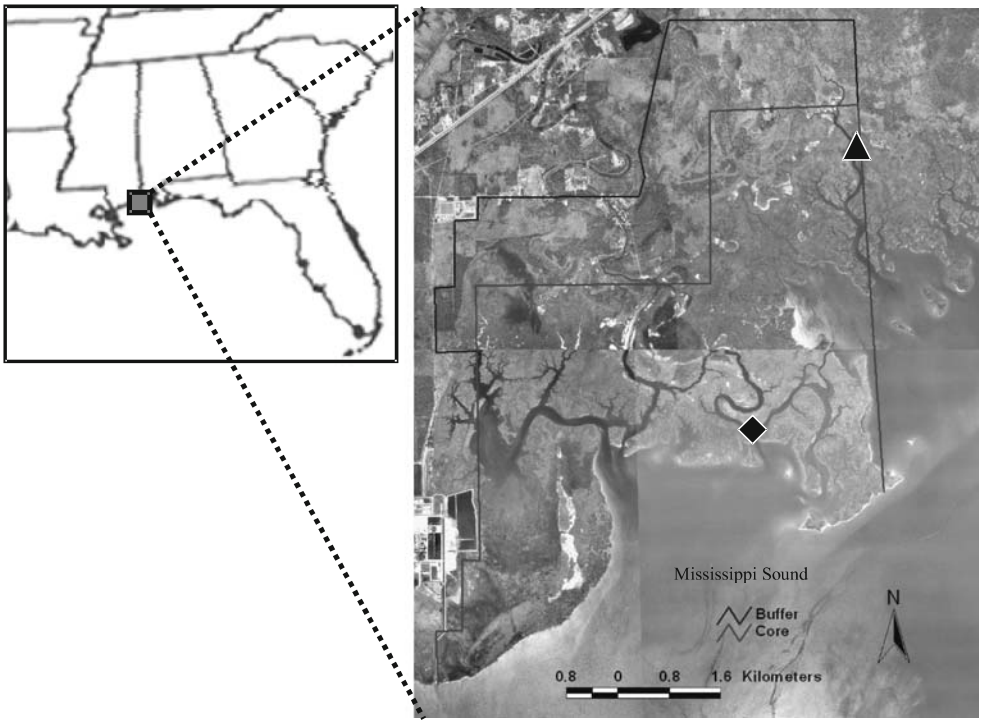

Fig. 1 Map of Grand Bay National Estuarine Research Reserve, MS, where density and growth experiments were conducted. Triangle represents Bayou Heron sampling area and diamond represents Crooked Bayou site. Note the proximity of the Crooked Bayou sampling area to the Mississippi Sound

habitat to sample each replicate. We repeated this procedure each season for both sampling areas.

We chose drop sampling for assessing nekton communities of the three habitats because the catch efficiency does not appear to vary significantly with habitat characteristics (Rozas and Minello 1997). We randomly collected four replicates in each of the three habitats present at the two sampling areas with a 1.17-m^2 drop sampler according to the procedures of Zimmerman et al. (1984). A total of 72 drop samples (two sampling areas × three habitats × four replicates × three seasons) were collected by dropping a 1.4-m diameter × 1.5-m-tall cylinder from a boom mounted on the bow of a 5.1-m boat with the boom extending an additional 2.4 m. Two people positioned the cylinder over the randomly selected site by slowly pushing the skiff by the stern. Once the cylinder was in place it was released from the boom and rapidly enclosed a 1.17-m^2 area.

In each drop sample, we measured temperature (°C), salinity (Practical Salinity Units: PSU), and dissolved oxygen (DO: mg/L) using a YSI 85 meter and water depth (cm) using measuring tape. After collecting these data, we used a pump and hose with plastic mesh (1 mm) fixed to the intake nozzle to pump out water from within the sampler. In the VME habitat, we removed marsh vegetation from the sampler and

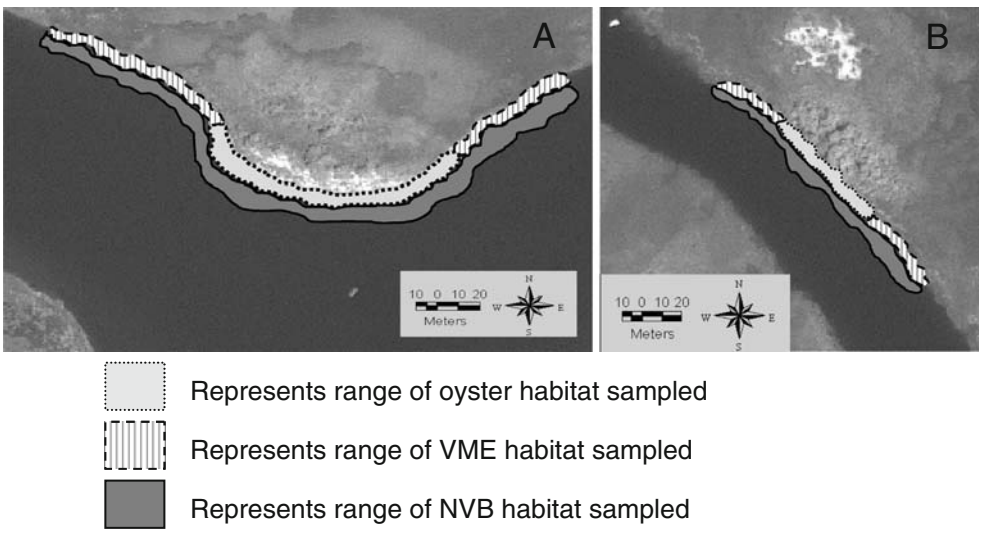

Fig. 2 This imagery represents the range of habitats sampled at (A) Bayou Heron and (B) Crooked Bayou. The background image is a panchromatic IKONOS scene taken at high tide

recorded the number of stems present. Stems were pulled apart over a 3-mm sieve and rinsed thoroughly so any organisms hiding within the roots were collected. In oyster habitat, percent oyster cover was recorded after water was removed. All oysters were removed from the sampler and washed over 3-mm plastic mesh sieve, and the organisms recovered were collected. Oyster clusters were always broken apart and rinsed thoroughly so organisms hiding in the interstitial spaces were collected. If any oyster was found in VME or NVB samples, percent oyster was recorded and oyster was processed as described previously. Percent oyster was always assessed by V. Shervette for consistency. While the water was being pumped out of the drop sampler, we collected nekton from the drop sampler with dipnets (3.2-mm mesh) until each of the two dipnetters had five consecutive no-catches once the water was completely removed. In addition, we inspected the bottom of the sampled area for organisms missed by nets after water was pumped out. All organisms collected were euthanized with MS-222, preserved in 10% buffered formalin for at least 4 days then stored in 70% ethanol. Fish and invertebrates were identified to species and measured with digital calipers: fish were measured to 0.1 mm standard length (SL), crabs to 0.1 mm carapace length (CL), and shrimp to 0.1 mm total length (TL).

Statistical Analyses

Seasonal data were analyzed separately, unless otherwise indicated, because many species occurred during one season only. We calculated species diversity using Shannon's Index of Diversity (H^1),

$$H^1 = -\sum p_i * \ln(p_i),$$

where p_i is the proportion of the density comprised by the ith taxa. We also assessed species richness (number of species collected) for each habitat, season, and the two sampling areas.

We used randomized block analysis of variance (ANOVA) to test for significant differences in total density (fish and macroinvertebrates combined) among habitats. Assumptions for the ANOVA test included normality and homogeneity of variance. Density data were $\log(x+1)$ transformed to meet the assumptions. Density was the dependent factor, habitat was the independent factor, and sampling area was the blocking factor. We conducted additional separate randomized block ANOVA to determine significant differences among habitats and between sampling areas for the following dependent variables: salinity, temperature, DO, depth, and species richness. If needed, data were $\log(x+1)$ or square-root transformed to meet assumptions of tests.

Correspondence analysis (CA) of the species-by-replicate matrix was used to examine variation in species relative abundance among habitats, seasons, and between sampling areas. Density data were $\log(x+1)$ transformed. Multi-response permutation procedures (MRPP) were performed to test the null hypothesis of no difference in species relative abundance among the three seasons within and among the two sampling areas and three habitats. MRPP is a nonparametric technique used to test the significance of a priori sample groupings when the data violate the assumptions of parametric procedures such as multivariate analysis of variance. When significant sample groupings were detected, comparisons were made using Bonferroni corrected p values.

Canonical correspondence analysis (CCA) was used to identify environmental gradients correlated with species relative abundance. CCA is a weighted averaging method, which directly relates community data to environmental variables by constraining species ordination patterns that correlate maximally with the environmental variables. Inter-set correlations between environmental variables (salinity, temperature, depth, stem density, and percent oyster) were used to determine each variable's contribution. Monte Carlo permutation analysis simulation was used to test the significance ($p=0.05$) of the contribution of each variable to the CCA axes. Only significant, non-redundant variables were retained for interpretation. Both CA and CCA (including the Monte Carlo permutation analysis) were performed using CANOCO (Version 4, Microcomputer Power) and MRPP was performed using PC-ORD version 4 (McCune and Mefford 1999).

Results

Environmental Data

Salinity did not vary significantly across habitat types during any of the sampling periods (randomized block ANOVA: $p>0.05$; Table 1) but was consistently higher at Crooked Bayou compared to Bayou Heron (for all three seasons randomized block ANOVA: $p<0.001$). Mean temperature varied seasonally (Table 1). Consistent for the three sampling periods, temperature did not vary significantly among habitats or between sampling areas (randomized block ANOVA: $p>0.05$). Depth was significantly less in intertidal VME habitat relative to the other two habitats during the three sampling periods at both sampling areas (Table 1).

Species Richness and Abundance

A total of 633 individual fishes representing 41 taxa in 22 families were collected with the drop sampler (Table 2). Twenty-eight species were collected in VME, 13 exclu-

Table 1 Environmental variables collected each season

	Bayou Heron			Crooked Bayou		
	Marsh	NVB	Oyster	Marsh	NVB	Oyster
October 2003						
Salinity (PSU)	19.4 (0.09)	19.4 (0.13)	19.5 (0.16)	23.1 (0.06)	22.8 (0.19)	22.6 (0.10)
DO (mg/L)	6.85 (0.119)	6.83 (0.209)	6.56 (0.095)	7.04 (0.347)	6.43 (0.415)	6.34 (0.146)
Temperature (°C)	26.2 (0.51)	25.1 (0.75)	26.3 (0.46)	27.3 (0.72)	25.8 (0.48)	25.4 (0.35)
Depth (cm)	37 (4.7)	72 (9.9)	39 (5.6)	47 (4.3)	52 (9.6)	52 (5.4)
Stem density m^{-2}	92 (14.0)	–	2 (1.5)	143 (26.6)	–	–
Percent oyster	–	3 (2.5)	75 (5.0)	44 (10.7)	14 (8.0)	93 (2.5)
May 2004						
Salinity (PSU)	11.7 (0.96)	12.0 (1.41)	14.1 (0.72)	20.7 (0.19)	21.3 (0.41)	21.4 (0.09)
DO (mg/L)	5.63 (0.405)	5.55 (0.367)	5.88 (0.157)	6.42 (0.495)	6.04 (0.274)	6.30 (0.203)
Temperature (°C)	28.3 (0.43)	28.0 (0.34)	26.8 (0.35)	28.8 (0.82)	29.8 (0.70)	28.8 (0.91)
Depth (cm)	47 (7.2)	50 (10.7)	57 (3.9)	43 (4.9)	61 (8.1)	51 (4.7)
Stem density m^{-2}	190 (21.9)	1 (1.0)	–	175 (46.1)	–	–
Percent oyster	9 (1.3)	–	50 (12.4)	16 (5.9)	3 (1.4)	61 (13.0)
July 2004						
Salinity (PSU)	10.6 (0.53)	9.9 (1.03)	9.3 (1.08)	19.1 (0.44)	20.8 (0.03)	19.4 (0.74)
DO (mg/L)	4.72 (0.266)	5.01 (0.313)	4.82 (0.435)	5.62 (0.198)	6.32 (0.038)	5.19 (0.301)
Temperature (°C)	33.1 (0.15)	31.7 (0.49)	32.2 (0.73)	32.3 (0.13)	32.8 (0.09)	31.5 (0.46)
Depth (cm)	16 (1.4)	40 (18.5)	51 (18.4)	28 (5.3)	45 (1.7)	32 (6.4)
Stem density m^{-2}	137 (15.5)	–	–	93 (34.1)	–	–
Percent oyster	–	3 (2.5)	49 (9.2)	38 (16.1)	5 (5.0)	76 (13.8)

Values listed are means (standard error) for samples from each habitat at both sampling areas

sively; 13 species were collected from NVB, none exclusively; and 27 species were collected in oyster, nine exclusively. In Fall 2003, Spring 2004, and Summer 2004, we collected 27, 17, and 25 fish species, respectively. Ten species were collected exclusively in Fall 2003, four species were collected exclusively in Spring 2004, and five species were collected exclusively in Summer 2004.

A total of 2,734 individual invertebrates representing 24 taxa in 11 families were collected with the drop sampler. Twenty-two species were collected in VME habitat with three species exclusively; 10 species were collected in NVB habitat with none exclusively; 20 species were collected in oyster, two species exclusively. Fall 2003 samples had 17 species of invertebrates with one species collected exclusively during that season. Spring 2004 samples had 16 species of invertebrates with two species exclusively. Summer 2004 samples had 19 species of invertebrates with four exclusively (Table 2).

Nonvegetated bottom habitat had the highest overall diversity compared to the other two habitats, but only 24 species were collected in NVB (Table 3). Oyster habitat had the second highest diversity and a total of 49 species. VME habitat had the highest number of species overall (52), but the lowest diversity. Among seasons, Spring 2004 had the lowest overall species richness (34 species collected), but the highest diversity. Fall 2003 had the second highest diversity. Both Fall 2003 and Summer 2004 had a species richness of 46. Summer 2004 had the lowest diversity. Bayou Heron had lower diversity and richness than Crooked Bayou (Table 3).

For each of the three sampling periods, mean total richness among habitats was significantly different (Fig. 3a). Within each season, mean total richness was significantly greater in VME and oyster habitat relative to nonvegetated habitat (Bonferroni post hoc comparisons $p<0.005$; Fig. 3a).

In Fall 2003, mean total density was significantly different among habitats (randomized block ANOVA: $F_{4,\ 2}=20.8$, $p<0.001$) and not significantly different between sampling areas ($F_{0.2,\ 1}=0.9$, $p=0.4$). Bonferroni post hoc tests indicated the following relationship for mean total density among the habitats (when significant $p<0.001$): VME = oyster > NVB (Fig. 3b). In Spring 2004 sampling, mean total density was significantly different among habitats ($F_{1.7,\ 2}=48.3$, $p<0.001$) and between sampling areas ($F_{11,\ 1}=6.1$, $p=0.02$), with Crooked Bayou having the higher mean density. Post hoc tests indicated the following relationships among habitats for mean density: VME > oyster > NVB ($p<0.03$). Mean densities in Summer 2004 sampling differed significantly among habitats ($F_{4.1,\ 2}=25.3$, $p<0.001$) and did not differ significantly between sampling areas ($F_{0.3,\ 1}=1.8$, $p=0.2$). Post hoc tests indicated

Table 2 Fishes and macroinvertebrates relative abundances (total number collected) from drop sampling

Species	Code	Habitat			Season		
		Marsh	NVB	Oyster	Fall	Spring	Summer
Fishes							
Ophichthidae							
Myrophis punctatus	Myr pun	3.6 (8)	3.0 (2)	0.6 (2)	1.5 (5)	3.4 (4)	1.6 (3)
Ophichthus gomesi	Oph gom	0.5 (1)	–	–	0.3 (1)	–	–
Engraulidae							
Anchoa mitchtchelli	Anc mit	–	4.6 (3)	1.5 (5)	0.9 (3)	4.3 (5)	–
Anchoa sp.	Anc sp	–	1.5 (1)	0.3 (1)	–	–	1.1 (2)
Synodontidae							
Synodus foetens	Sun foe	–	1.5 (1)	0.3 (1)	–	1.7 (2)	–
Batrachoididae							
Opsanus beta	Ops bet	1.4 (3)	–	–	0.6 (2)	0.9 (1)	–
Gobiesocidae							
Gobiesox stromosus	Gob str	2.7 (6)	–	3.8 (13)	1.2 (4)	8.6 (10)	2.6 (5)
Atherinidae							
Menidia berrylina	Men ber	6.8 (15)	–	2.9 (10)	2.2 (7)	8.6 (10)	4.2 (8)
Fundulidae							
Fundulus grandis	Fun gra	9.0 (20)	3.0 (2)	1.7 (6)	0.6 (2)	–	13.7 (26)
Fundulus jenkinsi	Fun jen	6.3 (14)	–	–	–	–	7.4 (14)
Poeciliidae							
Adenia xenica	Ade xen	0.5 (1)	–	–	–	–	0.5 (1)
Gambusia affinis	Gam aff	–	–	0.3 (1)	0.3 (1)	–	–
Heterandria formosa	Het for	0.5 (1)	–	–	–	0.9 (1)	–
Cyprinodontidae							
Cyprinodon variegatus	Cyp var	3.6 (8)	–	2.6 (9)	–	5.1 (6)	5.8 (11)
Syngnathidae							
Syngnathus floridae	Syn flo	0.9 (2)	–	–	0.3 (1)		0.5 (1)
Syngnathus louisianae	Syn lou	0.5 (1)	–	–	–	–	0.5 (1)
Triglidae							
Prionotus longispinosus	Pri lon	–	–	0.3 (1)	0.3 (1)	–	–
Lutjanidae							
Lutjanus griseus	Lut gri	0.5 (1)	–	–	–	–	0.5 (1)
Gerreidae							
Eucinostomus argenteus	Euc arg	0.9 (2)	–	–	0.6 (2)	–	–
Eucinostomus melanopterus	Euc mel	3.6 (8)	–	2.6 (9)	5.2 (17)	–	–
Haemulidae							
Orthopristis chrysoptera	Ort chr	2.3 (5)	.	0.6 (2)	2.2 (7)	–	–
Sparidae							
Archosargus probatocephalus	Arc pro	0.9 (2)	–	–	0.3 (1)	–	0.5 (1)
Lagodon rhomboides	Lag rho	2.7 (6)	1.5 (1)	1.2 (4)	0.6 (2)	6.0 (7)	1.1 (2)
Sciaenidae							
Cynoscion nebulosus	Cyn neb	0.5 (1)	–	–	0.3 (1)	–	–
Leiostomus xanthurus	Lei xan	1.8 (4)	18.2 (12)	9.3 (32)	–	38.5 (45)	1.6 (3)
Mugilidae							
Mugil cephalus	Mug cep	–	–	0.3 (1)	–	–	0.5 (1)
Blennidae							
Chasmodes bosquianus	Cha bos	0.5 (1)	–	0.6 (2)	0.3 (1)	–	1.1 (2)
Hypsoblennius hentzi	Hyp hen	–	–	0.6 (2)	–	–	1.1 (2)
Hypsoblennius ionthas	Hyp ion	–	–	1.5 (5)	0.3 (1)	–	2.1 (4)
Gobiidae							
Ctenogobius boleosoma	Cte bol	14.4 (32)	25.8 (17)	6.1 (21)	11.7 (38)	7.7 (9)	12.1 (23)
Ctenogobius shufeldti	Cte shu	–	–	0.9 (3)	0.9 (3)	–	–
Evorthodus lyricus	Evo lyr	1.8 (4)	–	–	1.2 (4)	–	–
Gobionellus hastatus	Gob has	–	–	0.3 (1)	–	–	0.5 (1)
Gobiosoma bosc	Gob bos	30.6 (68)	25.8 (17)	56.2 (194)	62.6 (204)	4.3 (5)	36.8 (70)

Table 2 (continued)

Species	Code	Habitat			Season		
		Marsh	NVB	Oyster	Fall	Spring	Summer
Gobiosoma robustum	Gob rob	1.4 (3)	–	–	0.9 (3)	–	–
Microgobius gulosus	Mic gul	0.5 (1)	1.5 (1)	–	–	1.7 (2)	–
Paralichthyidae							
Citharichthys spilopterus	Cit spi	0.5 (1)	4.6 (3)	0.6 (2)	0.9 (3)	1.7 (2)	0.5 (1)
Paralichthys lethostigma	Par let	–	–	0.3 (1)	–	0.9 (1)	–
Cynoglossidae							
Symphurus diomedianus	Sym dio	–	1.5 (1)	0.6 (2)	0.3 (1)	0.9 (1)	0.5 (1)
Symphurus plagiusa	Sym pla	1.4 (3)	7.6 (5)	3.2 (11)	3.1 (10)	5.1 (6)	1.6 (3)
Tetrodontidae							
Sphoeroides parvus	Sph par	–	–	1.2 (4)	0.3 (1)	–	1.6 (3)
Invertebrates—Shrimp							
Penaidae							
Farfantopenaeus aztecus	Far azt	5.4 (53)	34.6 (9)	9.0 (47)	1.2 (8)	51.8 (100)	0.2 (1)
Farfantopenaeus duroram	Far dur	0.1 (1)	3.8 (1)	–	0.3 (2)	–	–
Litopenaeus setiferus	Lit set	19.8 (193)	61.5 (16)	70.6 (368)	56.2 (371)	3.1 (6)	29.9 (200)
Palaemonidae							
Macrobrachium ohione	Mac ohi	–	–	0.2 (1)	–	0.5 (1)	–
Palaemonetes intermedius	Pal int	0.4 (4)	–	–	–	–	0.6 (4)
Palaemonetes pugio	Pal pug	68.2 (664)	–	13.4 (70)	30.9 (204)	44.6 (66)	66.5 (444)
Palaemonetes vulgaris	Pal vul	1.4 (14)	–	0.2 (1)	0.5 (3)	–	1.8 (12)
Palaemonetes sp.	Pal sp	2.2 (24)	–	–	3.2 (21)	–	–
Alpheidae							
Alpheus sp.	Alp sp	2.5 (24)	–	6.5 (34)	7.7 (51)	–	1.0 (7)
Invertebrates—Crabs							
Paguridae							
Clibanarius vittatus	Cli vit	14.5 (59)	5.0 (3)	2.5 (16)	12.6 (58)	5.9 (11)	1.9 (9)
Portunidae							
Callinectes sapidus	Cal sap	20.2 (82)	23.3 (14)	9.1 (59)	13.6 (63)	20.4 (38)	11.7 (54)
Callinectes similis	Cal sim	0.5 (2)	1.7 (1)	0.2 (1)	0.2 (1)	1.6 (3)	–
Xanthidae							
Eurypanopeus depressus	Eur dep	41.1 (167)	16.7 (10)	45.4 (293)	52.0 (240)	27.4 (51)	38.7 (179)
Eurytium limosum	Eur lim	0.5 (2)	–	0.9 (6)	–	4.3 (8)	–
Menippe adina	Men adi	1.0 (4)	–	0.3 (2)	–	–	1.3 (6)
Panopeus obesus	Pan obe	0.7 (3)	–	6.8 (44)	–	5.4 (10)	8.0 (37)
Panopeus simpsoni	Pan sim	10.1 (41)	10.0 (6)	14.7 (95)	16.0 (74)	11.3 (21	26.4 (122)
Rithropanopeus harrisii	Rit har	8.9 (36)	33.3 (20)	18.5 (119)	5.4 (25)	15.1 (28)	26.4 (122)
Unidentified xanthid	Xan sp	2.0 (8)	10.0 (6)	1.4 (9)	0.2 (1)	8.6 (16)	1.3 (6)
Grapsidae							
Sesarma reticulatum	Ses ret	0.5 (2)	–	–	–	–	0.4 (2)
Porcelanidae (unidentified)	Por sp	–	–	0.2 (1)	–	–	0.2 (1)
Invertebrates—Gastropods							
Littorinidae							
Littorina irrorata	Lit irr	33.8 (22)	–	5.7 (2)	2.9 (1)	43.1 (22)	7.1 (1)
Muricidae							
Stramonita (Thais) haemastoma	Tha hae	21.5 (14)	–	37.1 (13)	34.3 (12)	7.8 (4)	78.6 (11)
Neritidae							
Neritina usnea	Ner usn	44.6 (29)	–	57.1 (20)	62.9 (22)	49.0 (25)	14.3 (2)

Relative abundances were calculated for the following subgroups: Fishes, shrimp, crab, gastropod. Species codes are listed for referencing. Habitat-specific relative abundances are given by habitat with data for sampling areas and seasons combined. Seasonal relative abundances are given with data for sampling areas and habitats combined.

Table 3 Overall values for diversity and richness for each habitat (with season and sampling area data aggregated), each season (with habitat and sampling area data aggregated), each sampling area (with season and habitat data aggregated)

	Habitat			Season			Sampling Area	
	Marsh	NVB	Oyster	Oct	May	Jul	Heron	Crooked
Diversity	2.42	2.71	2.57	2.43	2.80	2.33	2.42	2.61
Richness	52	24	49	46	34	46	45	48

the following relationship among habitats for mean density: VME = oyster > NVB ($p<0.001$).

Multivariate Community Analyses

Community structure differed significantly among the three seasons and between the two sampling areas (Fig. 4; Table 4). The CA produced two axes that explained 84% of the variation in species relative abundances. Samples collected in Spring 2004 generally had higher scores on Axis 1 associated with more *Callinectes similis*, *L. xanthurus*, and *F. aztecus*. Fall and Summer samples generally had lower scores on Axis 1 associated with more *Alpheus sp*., *Eucinostomus melanopterus*, and *Orthopristis chrysoura*. Spring VME and most of summer VME samples had higher scores on Axis 2 associated with more *Fundulus grandis*, *Cyprinodon variegates*, and *Menidia berrylina*.

Within Fall 2003 sampling season, community structure differed significantly between sampling areas and among the site-habitat combinations (Fig. 5a; Table 4). The CA produced two axes that explained 61% of the variation in species relative abundances. Bayou Heron samples generally had positive values on Axis 1 associated with the presence of *Palaemonetes pugio*, *M. berrylina*, and *Evorthodus minutus*. Crooked Bayou samples generally had negative values on Axis 1 associated with the presence of two of the gastropod species *Clibanarius vittatus* and *Stramonita haemastoma*. Community structure during Spring 2004 sampling differed significantly between sampling areas, among habitats, among habitats within Crooked Bayou, and among site–habitat combinations (Fig. 5b; Table 4). The CA produced two axes that explained 89% of the variation in species assemblages. Crooked Bayou samples generally had more positive values on Axis 1 and were characterized by higher abundances of *Ctenogobius bolesoma*, *Panopeus obesus*, and *S. haemastoma*. Bayou Heron samples were characterized by higher abundances of *Gobiosoma bosc*, *Litopanaeus setiferus*, and *Neritina usnea*. During this season, major habitat differences were characterized by higher abundances of *Littorina irrorata*

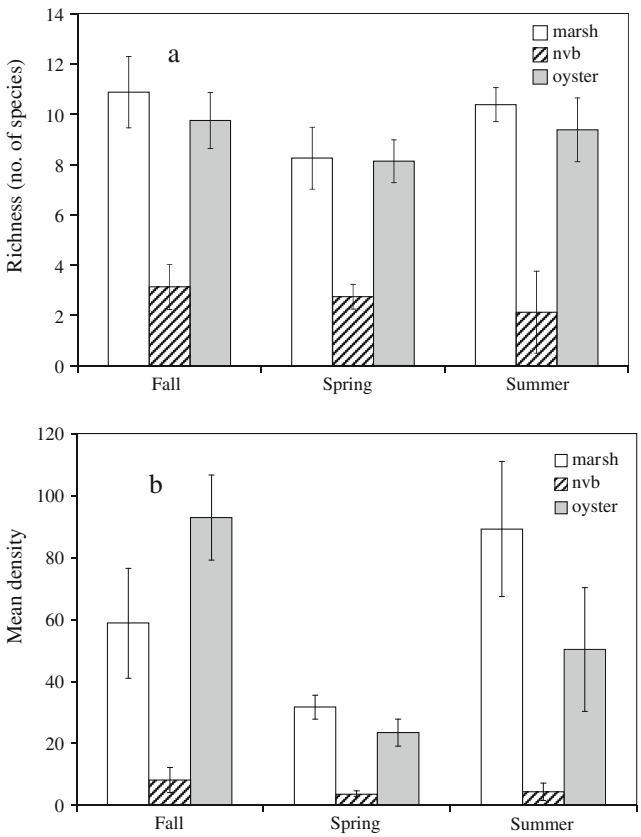

Fig. 3 Mean species richness (a) and organism abundance (b) for each habitat during the three seasons of collection: Fall (Oct03), Spring (May04), and Summer (July04). Standard error is represented by the vertical bars

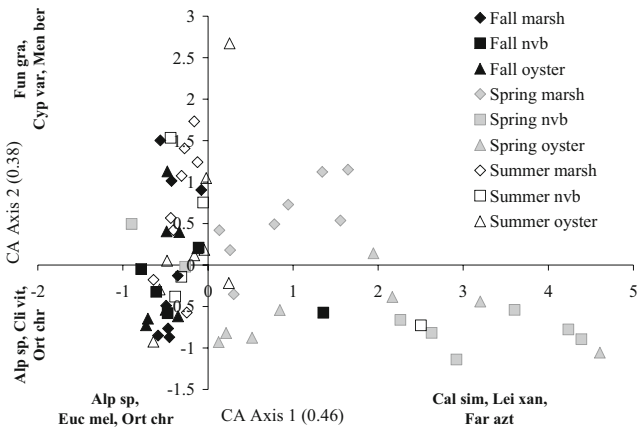

Fig. 4 First two axes of CA for Grand Bay NERR samples from each habitat by season (data combined over sampling areas). Eigenvalues are given in parentheses. Species with highest loading scores on the ends of each axis are listed

Table 4 Effect size (A) and probability values for comparisons of sampling groupings

Comparison	*A*	*p*
Season		
All	0.171	<0.0001*
Site	0.063	0.0001*
Habitat	0.033	0.0154
October 2003		
Site	0.193	<0.0001*
Habitat	−0.019	0.6746
Heron habitat	−0.023	0.6183
Crooked habitat	0.225	0.0332
Site-habitat combinations	0.213	0.0017*
May 2004		
Site	0.110	0.0007*
Habitat	0.099	0.0058*
Heron habitat	0.0762	0.132
Crooked habitat	0.400	0.0001*
Site-habitat combinations	0.300	<0.0001*
July 2004		
Site	0.154	0.0001*
Habitat	0.148	0.0013*
Heron habitat	0.206	0.0016*
Crooked habitat	0.070	0.1086
Site-habitat combinations	0.317	<0.0001*

For Season, we tested for significant differences among the three seasons (with all data within each season combined in three groups representing data for season), significant differences between sampling areas (with all season and habitat data from each sampling area combined representing data for sampling areas), and significant differences among habitats (with all data from each season and sampling area combined representing data for habitats). For each individual season, we tested for significant differences between sampling areas (habitat data combined), among habitats (sampling area data combined), just habitats for each sampling area individual, and among all six site/habitat combinations. Asterisk indicates significance after Bonferroni correction.

and *L. setiferus* in VME and *L. xanthurus* and *Symphurus plagiusa* in NVB (Fig. 5b). Community structure during Summer 2004 differed significantly between sampling areas, among habitats, among habitats within Bayou Heron, and among site-habitat combinations (Fig. 5c; Table 4). The CA produced two axes that explained 67% of the variation in species assemblages. Along Axis 1, Bayou Heron samples were characterized by higher abundances of *C. variegates* and *F. grandis*, whereas Crooked Bayou samples were characterized by higher abundances of *Alpheus* sp. and *Eurypanopeus depressus*. Along Axis 2, oyster habitat was characterized by higher abundances of *Gobiesox stromosus* and *C. variegates*.

Canonical Correspondence Analysis (CCA) resulted in a total model inertia of 3.35. Eigenvalues for the first four multivariate axes were 0.306 for CCA axis 1, 0.143 for CCA axis 2, 0.105 for CCA axis 3, and 0.078 for CCA axis 4. Cumulative percent variance of species-environmental relationship for all four CCA axes was 91.5%. Correlations between five of the six environmental variable and the first four axes were statistically significant ($p<0.03$ for percent oyster, salinity, depth, marsh stem density, and temperature). All environmental variables were retained except for DO (Fig. 6). Salinity, percent oyster, and depth were strongly correlated with Axis 1 (Fig. 6). Axis 1 explained 44.2% of the species environmental relationship. Depth, marsh stem density, and temperature were strongly correlated with Axis 2, which explained 20.7% of the species–environment relationship. Axis 1 models a salinity-oyster gradient that distinguishes species associated with the

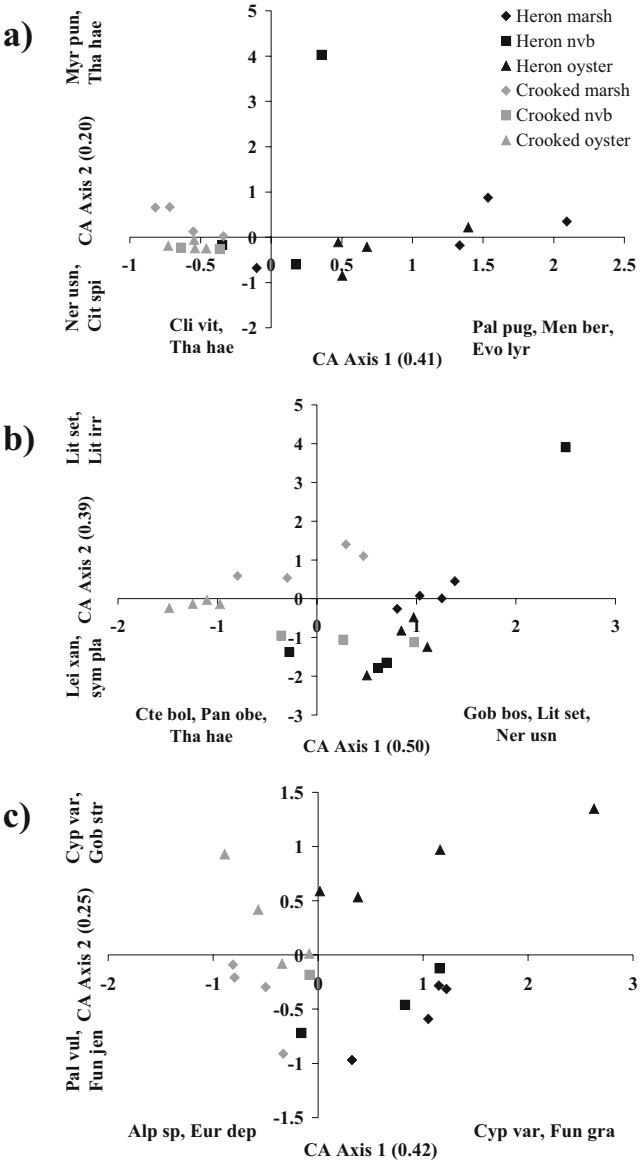

Fig. 5 First two axes for CA analyses plotted for **a**) Oct03, **b**) May04, and **c**) July04. Eigenvalues are given in parentheses. Species with highest loading scores on the ends of each axis are listed

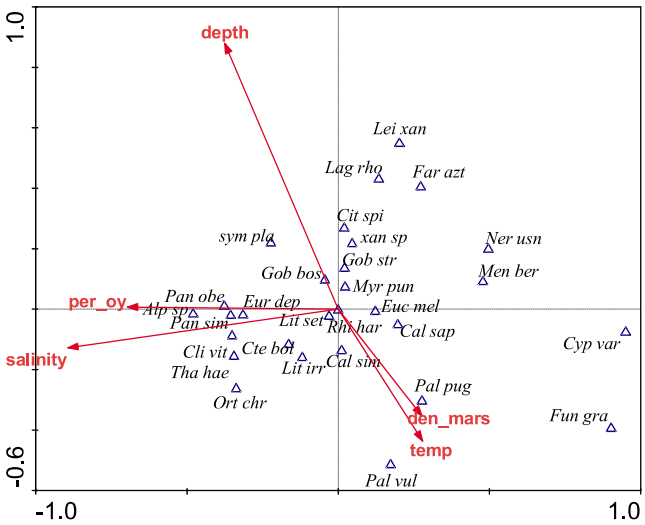

Fig. 6 Plot of species scores on the first two axes from CCA with environmental data. Triangles plot the scores for species and vectors represent stem density (den_mars), temperature (temp), salinity, percent oyster (per_oy), and depth

higher salinities of Crooked Bayou and some of the oyster-associated species. Axis 2 represents a more seasonal gradient with species collected mainly in Spring 2004 (high scores) separated from species collected through the study (scores close to the origin) and species collected in seasons other than Spring 2004 (low scores).

Some of the more notable species environmental relationships include: 1) *Alpheus* sp., *P. simpsoni*, *Panopeus obesus*, and *E. depressus* were strongly associated with samples in which oyster was present, 2) *C. vittatus* and *S. haemostoma* were associated with higher salinities, and 3) *P. pugio* was correlated with stem density (Fig. 6).

Discussion

Habitat-specific Trends in Nekton Abundances and Communities

When we examined nekton abundances, oyster, both spatially and temporally, supported similarly high densities of nekton as VME. Also, oyster consistently equated VME in species richness. Both oyster and VME supported significantly higher densities and species richness compared with adjacent NVB. Several studies have documented higher organism abundances and densities in structured habitats, such as marsh or oyster, relative to unstructured habitat (Glancy et al. 2003; Heck et al. 2003; Lehnert and Allen 2002; Zimmerman et al. 1989). In addition, some research has demonstrated higher species richness in structured habitats (Heck et al. 2003; Lehnert and Allen 2002). Our study supports the idea that oyster habitat, when compared with adjacent VME and NVB, is occupied by a distinct community of fishes and invertebrates and supports high densities of these residents and estuarine-dependent species.

Direct comparisons of fish and invertebrate communities between adjacent VME and oyster habitats are lacking in current literature. To our knowledge, ours is the first peer-reviewed study to directly compare communities of adjacent oyster, VME, and NVB habitats. One study, Glancy et al. (2003), examined the invertebrate communities of adjacent sea grass, nonvegetated marsh edge, and oyster habitats and documented habitat-specific communities. Many studies have examined fish and invertebrate use of oyster habitat in general (Glancy et al. 2003; Harding and Mann 2001, 1999 Coen et al. 1999; Wenner et al. 1996) and these studies have contributed greatly to the current understanding of oyster habitat. However, few studies that utilized enclosure sampling included oyster in habitat comparisons (Minello et al. 2003; but see Glancy et al. 2003; Zimmerman et al. 1989). This deficit has resulted in the low value ranking of oyster habitat compared to other salt marsh estuarine habitats (Minello et al. 2003). Our study and Glancy et al. (2003) do not support such findings. Both studies clearly demonstrate that oyster supports high nekton abundances relative to other shallow estuarine habitats.

The occurrence and prevalence of several species in our study appeared to be related to the presence of live oyster clusters and oyster shell within the three habitats. A similar relationship was documented in a Texas estuary (Zeug et al. 2007). In our study, sampling was conducted in a random design within a turbid environment, and on several occasions small clusters of oyster were discovered in and collected from VME and NVB habitats (Table 1). Mud crabs (*P. obesus*, *P. simpsoni*, *E. depressus*) and snapping shrimp (*Alpheus* sp.) were highly correlated with percent oyster present in samples according to CCA results (Fig. 4). These species were collected in the non-oyster habitats, but only when oyster was also collected in the samples. *Eurypanopeus depressus* and *Panopeus* spp. are common oyster reef residents (Glancy et al. 2003; Shervette et al. 2004) and *Alpheus* spp. have also been collected in habitats where oyster was present (Zimmerman et al. 1989; Lehnert and Allen 2002; Glancy et al. 2003; Shervette et al. 2004; Zeug et al. 2007). Differences in habitat-specific communities were not always strong because many species occurred in multiple habitats. If we had sampled exclusive NVB and VME habitats, we may have documented stronger differences in communities among habitats (Rozas and Minello 1997). In addition, the two sampling areas, Bayou Heron and Crooked Bayou, had a distinct difference between their oyster habitats. The Bayou Heron oyster habitat was comprised of shell hash with no live oyster (their settlement and growth inhibited by the lower

salinities), whereas the Crooked Bayou oyster habitat was comprised of a combination of shell hash and live oyster. The differences in the oyster habitat between the two areas may have contributed to the overall variability within the community of organisms utilizing oyster.

Oyster and VME may provide habitats for relatively rare species. Nine fish species and two invertebrate species were collected exclusively in oyster habitat. Similarly for VME habitat, 13 fish species and three invertebrate species were collected exclusively in VME. Our results indicate that at least some of the species we collected exclusively in one habitat may prefer that habitat over the others. In addition, these species can be considered relatively rare because they occur naturally in relatively low abundances, especially outside of their peak recruitment periods. The two blenny species collected exclusively in oyster habitat (*Hypsoblennius hentzi* and *H. ionthas*) are commonly associated with oyster reefs (Coen et al. 1999). *Fundulus jenkinsi* was collected exclusively in summer VME and is considered an uncommon species that occurs in Grand Bay NERR (M. Woodrey, research coordinator, Grand Bay NERR, personal communication). The two *Sygnathus* spp. were collected exclusively in VME in the current study and in a similar unpublished study (Zimmerman et al. 1989). The lyre goby *Evorthodus lyricus* also appears to prefer VME habitat and occurs at lower abundance than other estuarine gobies (V. Shervette, unpublished data). In addition, toadfish *Opsanus beta*, an oyster-associated fish (Shervette et al. 2004), was collected exclusively in marsh habitat, but only in samples with oyster. So, oyster and VME may provide important habitat for some of the less abundant fish species.

Many fish and invertebrate species found in two or more habitats occurred at higher densities in one specific habitat, either oyster or VME. For example, *F. grandis* was collected in all three habitats, but occurred at higher abundances in marsh samples. The goby *Gobiosoma bosc* was also collected in all three habitats, but more were collected in marsh samples. For the invertebrates, white shrimp *Litopenaeus setiferus*, the mud crabs *Panopeus simpsoni*, *P. obesus*, *E. depressus*, and *Rhithropanopeus harrisoni*, were collected in multiple habitats, but consistently occurred at higher abundances in oyster. The grass shrimp *P. pugio* occurred in VME and oyster habitats, but more *P. pugio* were consistently collected in VME. Other studies have found similar relationships with one or more of these species. During fall sampling, Minello and Webb (1997) collected a higher mean density of *Ctenogobius bolesoma* in natural VME (3.3 individuals per 2.6 m^2) relative to NVB (0.9 individuals per 2.6 m^2). That study also documented a higher mean density of *P. pugio* in VME (234.5 individuals per 2.6 m^2) relative to NVB (0.6 individuals per 2.6 m^2) for the same season. Rozas and Reed (1993) found that *F. grandis* used structured habitat (intact vegetated marsh) over non-structured habitat (deteriorated hummocky *Spartina* marsh).

Temporal and Spatial Trends in Nekton Abundances and Communities

Differences in fish and invertebrate abundances and community structure may be related to observed differences in environmental variables. Many studies have observed a relationship between temporal and spatial shifts in community structure and changes in environmental factors such as temperature, salinity, and DO (Rakocinski et al. 1996; Gelwick et al. 2001; Akin et al. 2003). In the current study we found that salinity, temperature, and depth were associated with seasonal and spatial shifts in nekton communities. The CA and MRPP results demonstrated that with each season and over the course of the whole study the fish and invertebrate community of Crooked Bayou differed from that of Bayou Heron (Table 4). We also found that salinity varied temporally and was consistently higher in Crooked Bayou. Temperature also increased temporally, but did not vary between the areas. Salinity is often cited as important in the organization of estuarine communities (Rakocinski et al. 1992; Baltz et al. 1998; Gelwick et al. 2001; Kupschus and Tremain 2001; Akin et al. 2003). In fact, salinity zones are commonly identified within an estuary and utilized in long-term monitoring of community dynamics as a measure of ecosystem health (Bulger et al. 1993). In our study common polyhaline species, such as the hermit crab *Clibanarius vittatus* and the oyster drill, *S. haemasroma*, occurred only in samples from Crooked Bayou, where salinity was within the polyhaline range. Results from the CCA confirmed the strong relationship between the abundances of many of the species we collected and salinity.

The relative location of the two marsh complexes within the context of the whole estuary may also explain some of the temporal and spatial differences in communities. Location also explains the differences in salinities between the two areas. Bayou Heron is situated in the upper zone of Grand Bay NERR within 1 km of an underground freshwater source. Crooked Bayou, although receiving some freshwater from rain events, is located in a lower zone of the estuary and is directly connected to Mississippi Sound (Fig. 1). These different locations may vary in their proximity to marine larval and freshwater larval supplies. Proximity to larval sources has been documented as an important factor in determining community composition and organismal abundances (Heck and Thoman 1984). Timing of larval recruitment also plays a role in temporal fish and invertebrate community composition and abundance patterns (Akin et al. 2003) and our study demonstrated through the seasonal occurrence of several species

how temporal recruitment affects nektonic communities. For example, in our study we collected the majority of brown shrimp in Spring 2004, which coincided with the timing of their recruitment period into Mississippi estuaries.

Conclusions

The goal of our study was to determine the relationship between three common shallow estuarine habitats (oyster, VME, and NVB) and nekton community structure to address the lack of research comparing oyster with adjacent habitats. In obtaining that goal, we documented three basic trends related to the importance of oyster and VME habitats: 1) Oyster and VME provide habitat for significantly more species relative to NVB; 2) Oyster and VME provide habitat for uncommon and rare species; and 3) Several species collected across multiple habitats occurred at higher abundances in oyster or VME habitat. We also found that contrary to the current low-value ranking of oyster habitat relative to other estuarine habitats (Minello et al. 2003), oyster provides high-quality habitat for many species. As a structured habitat, oyster, similar to VME and submerged aquatic vegetation, may provide higher growth rates for some species and refuge from predation for others. As documented in studies concerning other habitats, high abundances of certain species in oyster may be indicative of higher growth rates in oyster, greater refuge from predation in oyster, or both. Further research comparing habitat-specific growth and survival is essential in verifying the overall importance of oyster habitat for resident and nursery species. Oyster appears to support a temporally diverse and spatially distinct nekton community and deserves further attention in research and conservation. Our study also documented that differences in fish and invertebrate abundances and community structure were related to differences in environmental variables and site location within the estuary. Lastly, we found that the relative location of the marsh complexes within the context of the whole estuary may explain some of the temporal and spatial differences in communities.

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