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Nekton Use of *Vallisneria americana* Michx. (Wild Celery) Beds and Adjacent Habitats in Coastal Louisiana

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ABSTRACT: We compared nekton use of *Vallisneria americana* Michx. (submerged aquatic vegetation, SAV) with marsh shoreline vegetation and subtidal nonvegetated bottom (SNB) using a 1-m² drop sampler in the oligohaline area of Barataria Bay, Louisiana. Mean densities of most abundant species were significantly different among six habitat types. Harris mud crab *Rhithropanopeus harrisii*, Ohio shrimp *Macrobrachium ohione*, blue crab *Callinectes sapidus*, daggerblade grass shrimp *Palaemonetes pugio*, white shrimp *Litopenaeus setiferus* (fall), rainwater killifish *Lucania parva*, naked goby *Gobiosoma bosc*, code goby *Gobiosoma robustum* (fall), speckled worm eel *Myrophis punctatus* (fall), and gulf pipefish *Syngnathus scovelli* (spring), were much more abundant, and species richness also was greater, in *Vallisneria* than over SNB. *Vallisneria* supported densities of most species that were similar to those in marsh vegetation, although naked goby and gulf pipefish were more abundant in *Vallisneria*, and speckled worm eel and saltmarsh topminnow *Fundulus jenkinsi* were more abundant in marsh. Within the *Vallisneria* bed, densities of Harris mud crab, rainwater killifish, and speckled worm eel were higher at sites near the marsh (SAV Inside Edge) than at sites more distant from the marsh (SAV Outside Edge), and Ohio shrimp (fall) densities were higher in the interior of the bed than along the edges. The mean size of blue crab was larger in marsh than *Vallisneria* and larger in *Vallisneria* than SNB. White shrimp did not differ in size among habitat types. *Vallisneria* beds may provide an important nursery habitat for young blue crab and white shrimp that use oligohaline estuarine areas. These SAV beds can provide an alternative structural habitat to emergent vegetation during periods of low water, because *Vallisneria* occurs in the subtidal and generally persists throughout the year on the Gulf coast. Species whose young thrive in low-salinity waters and also depend on structure would benefit most from *Vallisneria* habitat in estuaries.

Introduction

The role of seagrasses in providing habitat for aquatic organisms has been studied extensively, and seagrass beds are widely recognized as important nursery areas for fishery species (Orth et al. 1984; Bell and Pollard 1989; Heck et al. 2003). *Vallisneria americana* Michx. provides similar habitat structure in low-salinity estuarine waters, but the use and habitat value of *Vallisneria* beds rarely have been examined for fishery species.

Quantitative comparisons of habitat use in the oligohaline region of estuaries are uncommon. In the northern Gulf of Mexico, Duffy and Baltz (1998) used a drop sampler to compare fish densities among different submerged aquatic vegetation (SAV) habitat types (including *V. americana*) and nonvegetated bottom in Lake Pontchartrain, Louisiana. At Marsh Island, Louisiana, Weaver and Holloway (1974) reported blue crab *Callinectes sapidus* and brown shrimp *Farfantepenaeus aztecus* to be important components of SAV communities in brackish ponds under structural marsh management. In low-salinity areas of Mobile Bay, Alabama, Heck et al. (2001) recorded juvenile blue crab in *Vallisneria* beds.

V. americana is common in low-salinity estuarine areas along the Gulf coast (Adair et al. 1994; Doering et al. 2001; Estevez et al. 2002), and extensive beds occur along the northern shore of Lake Pontchartrain (Cho and Poirrier 2005) and in the upper Barataria estuary. Salt-water intrusion threatens the existence of these beds, but river diversions planned to combat coastal land loss in Louisiana may significantly increase the area of *Vallisneria* beds by freshening coastal waters previously too saline to support this vegetation.

An assessment of the nursery value of *Vallisneria* habitat is necessary to determine its role in supporting coastal fisheries and to develop sound management plans for estuaries and estuarine-dependent fishery species. Comparisons of nekton densities among habitat types is the first step in identifying nurseries (Beck et al. 2001) and is valuable in identifying Essential Fish Habitat (Minello 1999).

Our main objective was to evaluate the role of *Vallisneria* beds in providing nursery habitat for fishery species. Densities of juvenile fishery species

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TABLE 1. Habitat types examined in this study. SAV = submerged aquatic vegetation, SNB = subtidal nonvegetated bottom. Ten samples were collected each season in each of the six habitat types.

Habitat Category	Description of Habitat Types
Marsh	Marsh edge = emergent vegetation < 2 m from the shoreline
SAV	SAV inside edge = SAV ≤ 5 m from the inside (near marsh) edge of the SAV bed
SAV	SAV outside edge = SAV ≤ 5 m from the outside (north) edge of the SAV bed
SAV	SAV interior = SAV ≥ 10 m from either edge of the SAV bed
SNB	SNB far = SNB ≥ 10 m from the outside edge of the SAV bed
SNB	SNB near = 5 samples ≤ 5 m from the outside edge of the SAV bed and 5 samples within nonvegetated patches located inside the SAV bed

and other nekton were measured and compared among a *Vallisneria* bed, shoreline marsh, and shallow nonvegetated bottom. We also examined the spatial distribution of animals within this SAV bed and the effect of *Vallisneria* or marsh proximity on the nekton community of adjacent habitat types.

Materials and Methods

Our study area was located on the northwest shore of Little Lake within the Barataria Bay system. During years of average rainfall, mean salinities are <5‰ in this region of the Barataria Bay system (Orlando et al. 1993). Tides are predominantly diurnal and have a mean daily range of <0.3 m (Byrne et al. 1976; Baumann 1987).

The focus of our study was an extensive (860 × 130 m) SAV bed located in shallow water along a marsh peninsula north of Bay L'Ours (29°32′N, 90°12′W). The entire study area, which also included the marsh shoreline and subtidal nonvegetated bottom (SNB) adjacent to this SAV bed, was approximately 15 ha. The vegetation of this SAV bed was predominantly *V. americana*; *Myriophyllum spicatum* L. also was present, but much less abundant. Submerged aquatic plants were absent in deeper water offshore and in a narrow band of shallow water located between the SAV bed and the adjacent marsh peninsula. The marsh would be classified as an oligohaline mix (Visser et al. 1998); the vegetation consisted mostly of bulltongue *Sagittaria lancifolia* L. but also contained smooth cordgrass *Spartina alterniflora* Loisel., giant cutgrass *Zizaniopsis miliacea* (Michx.) Doell & Aschers., and leafy three-square *Schoenoplectus maritimus* L.

In each of two seasons (spring and fall), we collected a total of 60 nekton samples. We collected 10 samples in each of four vegetated habitat types, including the marsh edge and three locations within the *Vallisneria* bed (Table 1). We also collected a total of 20 samples over SNB; half of these were <5 m from SAV (SNB Near) and half were 10 m or more from the SAV bed (SNB Far, Table 1). Because SNB Near sites were located both within nonvegetated patches inside the *Vallisneria* bed and on the outside of the SAV bed, and our goal was to accurately represent the entire population of SNB Near sites, we took samples for this habitat type from both locations. During each sampling event (September 3–4, 2003 and May 4–5, 2004), samples were collected throughout the day during periods of high tropical tides. Sample sites within habitat types were randomly selected using random numbers and a grid placed over an aerial photograph. Two boats and crews of three persons each were used simultaneously to collect these samples, and we arranged the order in which samples were taken to avoid disturbing sites before they were sampled.

Fishes and decapod crustaceans were quantitatively sampled using a 1-m^2 drop sampler and the method described by Zimmerman et al. (1984). Immediately after the drop sampler was deployed to enclose a sample area, we measured water temperature, dissolved oxygen, salinity, and turbidity using the methods described by Minello and Zimmerman (1992). We determined water depth at each sample site by averaging five depth measurements taken within the sampler. We also measured the distance from the center of the sampler to the nearest marsh edge and to the nearest edge of the SAV bed. At marsh sites, stems of emergent vegetation were clipped at the ground level, counted, and removed from the sampler. At SAV sites, we estimated coverage within the sampler (0–100%) and identified the species of plants present. Aboveground shoots of SAV also were clipped and removed from the sampler. This vegetation was vigorously shaken before removing to dislodge any animals that may have been attached to the plants or contained within the vegetation.

After measuring environmental variables, we removed the animals by using dip nets and filtering the water pumped out of the sampler through a 1-mm mesh net. When the sampler was completely drained, we removed by hand any animals remaining on the bottom. Samples were preserved in formalin and returned to the laboratory for processing.

In the laboratory, animals were separated from detritus and plant parts and identified to the lowest feasible taxon. We used the nomenclature of Perez-

TABLE 2. Analysis of variance table for comparing six habitat types including Marsh Edge, three types of submerged aquatic vegetation (SAV Inside Edge, SAV Interior, SAV Outside Edge), and two types of subtidal nonvegetated bottom (SNB Near and SNB Far) in September 2003 and May 2004. The model tests for the main effect of habitat type, and a priori contrasts compare specific habitat types. The dependent variable used in this example is the ln(x + 1) transformation of total macrofauna density (sum of total fishes and crustaceans).

Source	df	Mean Square	F Value	p Value
September 2003				
Habitat type	5	18.156	24.516	0.0001
Contrasts				
(SAV Inside Edge + SAV Interior + SAV Outside Edge) versus Marsh Edge	1	4.089	5.521	0.0225
(SAV Inside Edge + SAV Interior + SAV Outside Edge) versus (SNB Near + SNB Far)	1	63.128	85.243	0.0001
SAV Inside Edge versus SAV Outside Edge	1	2.549	3.443	0.0690
(SAV Inside Edge + SAV Outside Edge) versus SAV Interior	1	0.019	0.025	0.8742
SNB Near versus SNB Far	1	2.234	3.017	0.0881
Residual error	54	0.741		
May 2004				
Habitat type	5	13.539	21.468	0.0001
Contrasts				
(SAV Inside Edge + SAV Interior + SAV Outside Edge) versus Marsh Edge	1	0.960	1.523	0.2226
(SAV Inside Edge + SAV Interior + SAV Outside Edge) versus (SNB Near + SNB Far)	1	54.561	86.515	0.0001
SAV Inside Edge versus SAV Outside Edge	1	0.000	0.000	0.9962
(SAV Inside Edge + SAV Outside Edge) versus SAV Interior	1	0.014	0.022	0.8818
SNB Near versus SNB Far	1	0.902	1.431	0.2368
Residual error	54	0.631		

Farfante and Kensley (1997) for penaeid shrimps and identified species using the protocol described in Rozas and Minello (1998). Five specimens of *Farfantepenaeus* could not be reliably identified either because of their size (total length 13–18 mm) or because they were damaged; these shrimps were assumed to be brown shrimp. Grass shrimp (144 specimens) that could not be identified to species were assigned to one of four species (daggerblade grass shrimp *Palaemonetes pugio*, brackish grass shrimp *P. intermedius*, marsh grass shrimp *P. vulgaris*, or riverine grass shrimp *P. paludosus*) based on the proportion of identified species in each sample. One unidentified specimen of *Callinectes* was assumed to be a blue crab. Animals that could not be readily identified were not used in size analysis. Total length of fishes and shrimps and carapace width (CW) of crabs were measured to the nearest millimeter. Individuals of a species in each sample were pooled to determine biomass (wet weight) to the nearest 0.1 g.

Our analysis of nekton density patterns was focused on juvenile fishery species and dominant resident nekton. We used a one-way analysis of variance (ANOVA) to compare nekton densities of individual species among the habitat types followed by a priori contrasts (SuperANOVA, Version 5 Ed., Abacus Concepts, Inc., Berkeley, California, 1989). Comparable analyses also were conducted for nekton biomass, species richness, and environmental variables (Table 2). Contrasts were designed to make the following comparisons: SAV versus Marsh Edge, SAV versus SNB, SAV Inside Edge versus SAV Outside Edge, SAV Edge versus SAV Interior, and SNB Near versus SNB Far. The first two contrasts combine all three types of SAV and were used to compare SAV with marsh and SNB (both types combined) included in our study. We used the contrast comparing the two SAV Edge habitat types to examine the potential effect of marsh proximity on SAV use by nekton. We tested for an edge effect within the SAV bed with the contrast SAV Edge versus SAV Interior. We used the contrast SNB Near versus SNB Far to look for an effect of SAV proximity on SNB use by nekton.

In the ANOVA procedure, we analyzed the data collected each season separately because several species were only abundant enough to include in the statistical analysis in one season. We considered alpha levels of 0.05 to be statistically significant in all results, but we also assessed significance after adjusting alpha levels for the Habitat Type effect using the sequential Bonferroni method described by Rice (1989), which buffers against error introduced by making multiple comparisons with the same sample set (i.e., testing a hypothesis for several species or variables). Mean densities, biomasses, and animal sizes were positively related to the standard deviation, and Cochran's test indicated that variances were heterogeneous ($p < 0.05$), so we used a ln(x + 1) transformation on the original values prior to analyses to obtain homogeneity of variances and improve normality (Underwood 1997). Other variables were not transformed. We also examined differences in nekton assemblages among habitat types using a rank-order analysis and Kendall's

coefficient of concordance (Sokal and Rohlf 1995). All tabular and graphical data presented in this paper are untransformed means.

Species richness in each habitat type was measured as the mean number of species collected in a sample, but we also examined cumulative species richness as the number of samples or area in a habitat increased. This pattern of increase in the number of species collected in relation to the area sampled provides additional information on habitat heterogeneity and on overall species diversity in habitats. A randomization procedure was used to calculate these cumulative curves. The ten samples from each habitat type were randomly arranged into a different sequence 1,000 times to calculate the mean number of species present in different combinations of samples.

Results

We collected a total of 3,956 organisms (26 fish and 8 decapod crustacean species) and a biomass of 2.22 kg wet weight in September 2003 and 1,180 animals (16 fish and 7 decapod crustacean species) and a biomass of 0.77 kg in May 2004 (Tables 3 and 4). Decapod crustaceans outnumbered fishes in both seasons and represented 79% and 59% of the total animals we collected in fall and spring, respectively. Fishes accounted for most (67%) of the total biomass in fall, but 81% of the total biomass in spring was from decapod crustaceans (Table 4). Five abundant decapod species (Harris mud crab *Rhithropanopeus harrisii*, Ohio shrimp *Macrobrachium ohione*, blue crab, daggerblade grass shrimp, marsh grass shrimp, and white shrimp *Litopenaeus setiferus*) represented 74% of the total crustaceans in fall. In spring, the numerically dominant species (79% of total crustaceans) included daggerblade grass shrimp, blue crab, and Harris mud crab. An unidentified xanthid crab (individuals < 1 mm in CW that lacked characteristics used to identify larger juveniles and adults) accounted for an additional 25.7% and 10.7% of the total crustaceans that we collected in fall and spring, respectively. Other decapod species taken in our samples included brown shrimp, brackish grass shrimp, and riverine grass shrimp. Crustacean species that accounted for most of the biomass in our samples were blue crab, white shrimp (fall only), Harris mud crab, daggerblade grass shrimp, Ohio shrimp (fall only), brown shrimp (fall only), and brackish grass shrimp (spring only; Table 4).

Killifishes and gobies accounted for most of the fishes in our samples (Table 3). In fall, 79% of the total consisted of rainwater killifish *Lucania parva*, naked goby *Gobiosoma bosc*, bay anchovy *Anchoa mitchilli*, striped mullet *Mugil cephalus*, and code goby *Gobiosoma robustum*. Rainwater killifish, gulf menhaden *Brevoortia patronus*, naked goby, gulf pipefish *Syngnathus scovelli*, and saltmarsh topminnow *Fundulus jenkinsi* accounted for 74% of all the fishes we collected in spring. We infrequently collected (10 individuals or less) clown goby *Microgobius gulosus*, sheepshead minnow *Cyprinodon variegatus*, chain pipefish *Syngnathus louisianae*, bayou killifish *Fundulus pulvereus*, sailfin molly *Poecilia latipinna*, spotted seatrout *Cynoscion nebulosus*, inland silverside *Menidia beryllina*, black cheek tonguefish *Symphurus plagiusa*, bluegill *Lepomis macrochirus*, Atlantic croaker *Micropogonias undulatus*, pinfish *Lagodon rhomboides*, skilletfish *Gobiesox strumosus*, freshwater goby *Gobionellus shufeldti*, lined sole *Achirus lineatus*, redear sunfish *Lepomis microlophus*, bay whiff *Citharichthys spilopterus*, leatherjack *Oligoplites saurus*, gulf killifish *Fundulus grandis*, largemouth bass *Micropterus salmoides*, and silver perch *Bairdiella chrysoura*. Most of the biomass in our samples originated from striped mullet, bluegill (4 specimens), largemouth bass (1 specimen), rainwater killifish, and naked goby in fall and pinfish (4 specimens), rainwater killifish, saltmarsh topminnow, gulf menhaden, naked goby, and gulf pipefish in spring (Table 4).

Rankings of the abundant species differed among habitat types (Kendall's coefficient of concordance: fall = 0.49, $p < 0.001$; spring = 0.36, $p < 0.025$). In fall, Harris mud crab, Ohio shrimp, and blue crab numerically dominated all three SAV habitat types, but rainwater killifish was abundant only at SAV Inside Edge sites. Blue crab ranked third in abundance within SAV and only seventh at marsh sites. Daggerblade grass shrimp was more important in the marsh (ranking third) than at SAV sites. In spring, the species assemblages appeared more similar between SAV Inside Edge and Marsh Edge sites than among the three SAV habitat types, although saltmarsh topminnow was collected only in marsh vegetation, and naked goby was abundant only in SAV. Bay anchovy and gulf menhaden numerically dominated SNB sites in fall and spring, respectively.

Species richness, measured as the mean number of species in a sample, was significantly different among habitat types (Fig. 1 and Table 3). *Vallisneria* sites contained more species than SNB sites, but there was no significant difference in species richness between *Vallisneria* and marsh sites. More species also were taken at SNB Near than SNB Far sites in fall. The relationship between sample size and the cumulative number of species indicated that rare species were still being collected in each habitat type by the 10th sample and that more than 10 samples are needed to completely characterize the faunas of these habitats. The slopes of the ascending curves appeared shallower in SNB habi-

TABLE 3. Mean densities as number m^{-2} (SE) of abundant decapod crustaceans and fishes collected among six habitat types including Marsh Edge, three types of Submerged Aquatic Vegetation (SAV Inside Edge, SAV Interior, SAV Outside Edge), and two types of Subtidal Nonvegetated Bottom (SNB Near and SNB Far) in September 2003 and May 2004. The mean number of species (fishes and crustaceans) collected per sample in each habitat type is presented as species richness. Means were estimated from 10 samples in each habitat type. Results (p values) are given from ANOVAs used to compare all habitat types (Habitat Effect) and five *a priori* contrasts testing different habitat combinations. An * indicates that the ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). Contrast p values were not adjusted.

			Submerged Aquatic Vegetation						Subtidal Nonvegetated Bottom							Contrast p values				
	Marsh Edge		Inside Edge		Interior		Outside Edge		Near		Far									
Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Total Number Collected	Habitat Effect p value		(1) SAV vs Marsh	(2) SAV vs SNB	(3) SAV Inside Edge vs SAV Outside Edge	(4) SAV Edge vs SAV Interior	(5) SNB Near vs SNB Far
September 2003																				
Crustaceans	116.6	(21.27)	81.1	(20.27)	61.4	(10.67)	48.0	(17.75)	3.5	(0.82)	0.7	(0.30)	3113	0.0001	*	0.0152	0.0001	0.1914	0.5496	0.0108
Harris mud crab	43.4	(14.17)	42.4	(13.81)	20.6	(9.06)	10.9	(3.25)	1.9	(0.67)	0.4	(0.22)	1196	0.0001	*	0.0209	0.0001	0.0183	0.2568	0.2369
Unidentified Xanthidae	42.1	(17.94)	19.9	(11.72)	11.3	(3.82)	7.1	(3.94)	0.2	(0.13)	0.0	(0.00)	806	0.0008	*	0.0594	0.0006	0.5386	0.3085	0.8222
Ohio shrimp	12.6	(6.49)	4.9	(2.37)	16.5	(4.42)	13.3	(9.99)	0.1	(0.10)	0.0	(0.00)	474	0.0001	*	0.8861	0.0001	0.3073	0.0049	0.8728
Blue crab	3.6	(0.67)	9.1	(3.25)	7.5	(1.55)	6.5	(1.58)	1.2	(0.39)	0.3	(0.15)	282	0.0001	*	0.1113	0.0001	0.8246	0.6835	0.1954
Daggerblade grass shrimp	9.5	(4.22)	3.5	(1.82)	3.1	(1.02)	6.1	(2.15)	0.0	(0.00)	0.0	(0.00)	222	0.0002	*	0.2517	0.0001	0.2889	0.8997	
Marsh grass shrimp	4.7	(4.48)	0.0	(0.00)	0.7	(0.52)	1.6	(1.12)	0.0	(0.00)	0.0	(0.00)	70	0.2737						
White shrimp	0.7	(0.42)	1.1	(0.43)	1.5	(0.50)	2.0	(0.65)	0.1	(0.10)	0.0	(0.00)	54	0.0033	*	0.0654	0.0001	0.2548	0.8326	0.7778
Fishes	25.0	(4.70)	23.6	(5.78)	9.0	(1.87)	9.3	(1.77)	6.3	(2.21)	11.1	(7.09)	843	0.0002	*	0.0500	0.0007	0.0711	0.2609	0.3411
Rainwater killifish	7.7	(2.63)	13.8	(6.14)	0.2	(0.20)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	217	0.0001	*	0.0030	0.0377	0.0003	0.0624	
Naked goby	5.9	(2.07)	4.7	(2.57)	1.8	(0.74)	5.0	(1.71)	1.5	(0.90)	0.1	(0.10)	190	0.0072	*	0.3652	0.0031	0.4939	0.1266	0.2342
Bay anchovy	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	0.5	(0.50)	2.6	(1.66)	10.7	(7.06)	140	0.0133	*	0.7481	0.0016	0.6260	0.9492	0.1155
Striped mullet	1.5	(1.39)	0.6	(0.40)	3.2	(2.21)	0.2	(0.20)	0.4	(0.31)	0.0	(0.00)	59	0.4300						
Code goby	1.2	(0.92)	0.5	(0.40)	2.7	(0.96)	1.5	(0.56)	0.0	(0.00)	0.0	(0.00)	59	0.0110	*	0.3175	0.0019	0.1314	0.0656	
Speckled worm eel	2.5	(0.81)	1.1	(0.35)	0.2	(0.13)	0.2	(0.13)	0.0	(0.00)	0.0	(0.00)	40	0.0001	*	0.0001	0.0234	0.0202	0.1729	
Species Richness	8.3	(0.63)	7.9	(0.92)	7.3	(0.54)	7.2	(0.65)	3.5	(0.72)	1.5	(0.48)		0.0001	*	0.2875	0.0001	0.4644	0.7624	0.0399
May 2004																				
Crustaceans	23.2	(6.55)	15.9	(5.25)	16.7	(5.75)	13.0	(1.78)	0.9	(0.28)	0.2	(0.13)	699	0.0001	*	0.1948	0.0001	0.8354	0.9297	0.1930
Daggerblade grass shrimp	9.5	(3.08)	6.8	(4.64)	7.8	(3.13)	5.7	(1.54)	0.0	(0.00)	0.0	(0.00)	298	0.0001	*	0.3092	0.0001	0.3952	0.6312	
Blue crab	2.8	(0.57)	3.5	(0.97)	3.2	(0.71)	4.6	(0.88)	0.7	(0.26)	0.2	(0.13)	150	0.0001	*	0.3753	0.0001	0.1670	0.6050	0.2059
Harris mud crab	4.3	(1.71)	3.5	(1.27)	0.7	(0.21)	1.6	(0.45)	0.2	(0.13)	0.0	(0.00)	103	0.0003	*	0.0901	0.0005	0.4040	0.0599	0.6432
Unidentified Xanthidae	6.4	(4.14)	0.9	(0.55)	0.0	(0.00)	0.2	(0.20)	0.0	(0.00)	0.0	(0.00)	75	0.0030	*	0.0005	0.3641	0.3271	0.3107	
Fishes	10.5	(2.93)	18.0	(10.94)	6.4	(1.04)	7.5	(1.86)	4.7	(3.93)	1.0	(0.39)	481	0.0001	*	0.4690	0.0001	0.9317	0.7834	0.5190
Rainwater killifish	5.2	(2.70)	11.6	(7.97)	1.3	(0.45)	0.4	(0.31)	0.0	(0.00)	0.1	(0.10)	186	0.0258		0.1730	0.0284	0.0511	0.9084	0.8664
Gulf menhaden	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1.0	(0.67)	4.0	(4.00)	0.3	(0.30)	53	0.4907						
Naked goby	0.4	(0.40)	1.3	(0.80)	1.2	(0.33)	1.9	(0.62)	0.3	(0.15)	0.1	(0.10)	52	0.0102		0.0120	0.0012	0.1478	0.9947	0.5694
Gulf pipefish	0.2	(0.13)	0.6	(0.31)	1.8	(0.65)	1.4	(0.60)	0.0	(0.00)	0.0	(0.00)	40	0.0009	*	0.0121	0.0001	0.1592	0.1417	
Saltmarsh topminnow	2.3	(0.82)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	23							
Species Richness	5.1	(0.55)	4.5	(0.70)	6.4	(0.87)	6.2	(0.63)	1.5	(0.40)	0.8	(0.25)		0.0001	*	0.3916	0.0001	0.0508	0.1600	0.4143

TABLE 4. Comparison of biomasses, mean m^{-2} and (SE), in grams of dominant (contributing most biomass) decapod crustaceans and fishes collected among six habitat types including Marsh Edge, three types of Submerged Aquatic Vegetation (SAV Inside Edge, SAV Interior, SAV Outside Edge), and two types of Subtidal Nonvegetated Bottom (SNB Near, SNB Far) in September 2003 and May 2004. Each mean is estimated from 10 samples. Results (p values) are given for ANOVA analyses used to compare all habitat types (Habitat Effect) and five *a priori* contrasts testing different habitat combinations. An * indicates that the ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). Contrast p values were not adjusted.

													ANOVA			Contrast p values				
			Submerged Aquatic Vegetation						Subtidal Nonvegetated Bottom											
	Marsh Edge		Inside Edge		Interior		Outside Edge		Near		Far		Total Biomass Collected	Habitat Effect p value		(1) SAV vs Marsh	(2) SAV vs SNB	(3) SAV Inside Edge vs SAV Outside Edge	(4) SAV Edge vs SAV Interior	(5) SNB Near vs SNB Far
Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE								
September 2003																				
Crustaceans	20.4	(7.92)	21.4	(13.48)	12.6	(3.94)	18.2	(5.59)	0.8	(0.73)	0.0	(0.02)	734.69	0.0001	*	0.7543	0.0001	0.7712	0.6443	0.5838
Blue crab	14.8	(7.57)	16.4	(13.56)	7.6	(4.02)	10.3	(5.43)	0.1	(0.04)	0.0	(0.01)	492.03	0.0121		0.4520	0.0009	0.9597	0.9873	0.9341
White shrimp	2.0	(1.34)	2.7	(1.28)	2.7	(1.34)	5.1	(2.44)	0.7	(0.74)	0.0	(0.00)	132.78	0.0770						
Harris mud crab	1.6	(0.54)	1.4	(0.28)	0.4	(0.14)	0.3	(0.06)	0.0	(0.01)	0.0	(0.01)	36.57	0.0001	*	0.0035	0.0001	0.0001	0.0552	0.9669
Daggerblade grass shrimp	1.1	(0.60)	0.7	(0.47)	0.8	(0.29)	1.0	(0.39)	0.0	(0.00)	0.0	(0.00)	36.04	0.0230		0.7624	0.0016	0.2843	0.8925	
Ohio shrimp	0.4	(0.22)	0.2	(0.06)	0.6	(0.14)	0.6	(0.40)	0.0	(0.00)	0.0	(0.00)	17.07	0.0070	*	0.9270	0.0012	0.1894	0.0726	0.9876
Fishes	36.0	(21.83)	31.3	(21.63)	41.0	(26.97)	19.2	(18.30)	19.4	(14.08)	1.2	(0.80)	1480.56	0.1965						
Striped mullet	25.1	(19.70)	25.1	(21.52)	39.7	(27.14)	18.3	(18.33)	19.0	(14.11)	0.0	(0.00)	1272.29	0.7817						
Bluegill	7.1	(7.08)	0.1	(0.07)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	71.50							
Largemouth bass	0.0	(0.00)	3.2	(3.24)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	32.41							
Rainwater killifish	0.6	(0.23)	1.2	(0.59)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	17.21	0.0010	*	0.1107	0.0804	0.0011	0.0541	
Naked goby	1.1	(0.41)	0.2	(0.12)	0.1	(0.03)	0.1	(0.03)	0.0	(0.00)	0.0	(0.00)	14.03	0.0001	*	0.0001	0.2326	0.6906	0.4997	0.9665
May 2004																				
Crustaceans	29.2	(5.60)	10.1	(3.10)	15.5	(6.72)	7.1	(1.88)	0.3	(0.15)	0.0	(0.01)	622.19	0.0001	*	0.0001	0.0001	0.6302	0.2961	0.5952
Blue crab	23.7	(5.34)	5.3	(2.26)	11.3	(6.69)	4.1	(1.31)	0.3	(0.15)	0.0	(0.01)	446.27	0.0001	*	0.0001	0.0001	0.8891	0.1470	0.6534
Daggerblade grass shrimp	4.6	(1.62)	3.1	(2.25)	3.1	(1.13)	2.4	(0.68)	0.0	(0.00)	0.0	(0.00)	131.41	0.0004	*	0.1806	0.0001	0.4596	0.4836	
Harris mud crab	0.8	(0.36)	1.4	(0.69)	0.1	(0.07)	0.5	(0.22)	0.0	(0.01)	0.0	(0.00)	28.73	0.0078	*	0.4941	0.0066	0.2061	0.0256	0.9299
Fishes	4.4	(0.94)	1.4	(0.31)	5.1	(3.27)	2.0	(0.43)	1.3	(1.10)	0.5	(0.18)	146.29	0.0001	*	0.0153	0.0005	0.3305	0.1379	0.8560
Pinfish	0.0	(0.00)	0.0	(0.00)	3.3	(3.21)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	32.92							
Rainwater killifish	0.8	(0.35)	0.5	(0.28)	0.6	(0.25)	0.2	(0.19)	0.0	(0.00)	0.0	(0.03)	21.81	0.0236	*	0.1645	0.0159	0.4414	0.1585	0.8796
Saltmarsh topminnow	1.8	(0.70)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	18.47							
Gulf menhaden	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.6	(0.47)	1.1	(1.12)	0.1	(0.10)	17.86	0.4968						
Naked goby	0.1	(0.07)	0.3	(0.21)	0.3	(0.12)	0.4	(0.14)	0.1	(0.06)	0.0	(0.01)	12.34	0.0425		0.0232	0.0044	0.3587	0.9494	0.4569
Gulf pipefish	0.0	(0.03)	0.2	(0.10)	0.4	(0.14)	0.3	(0.13)	0.0	(0.00)	0.0	(0.00)	8.52	0.0051	*	0.0164	0.0006	0.3194	0.1093	

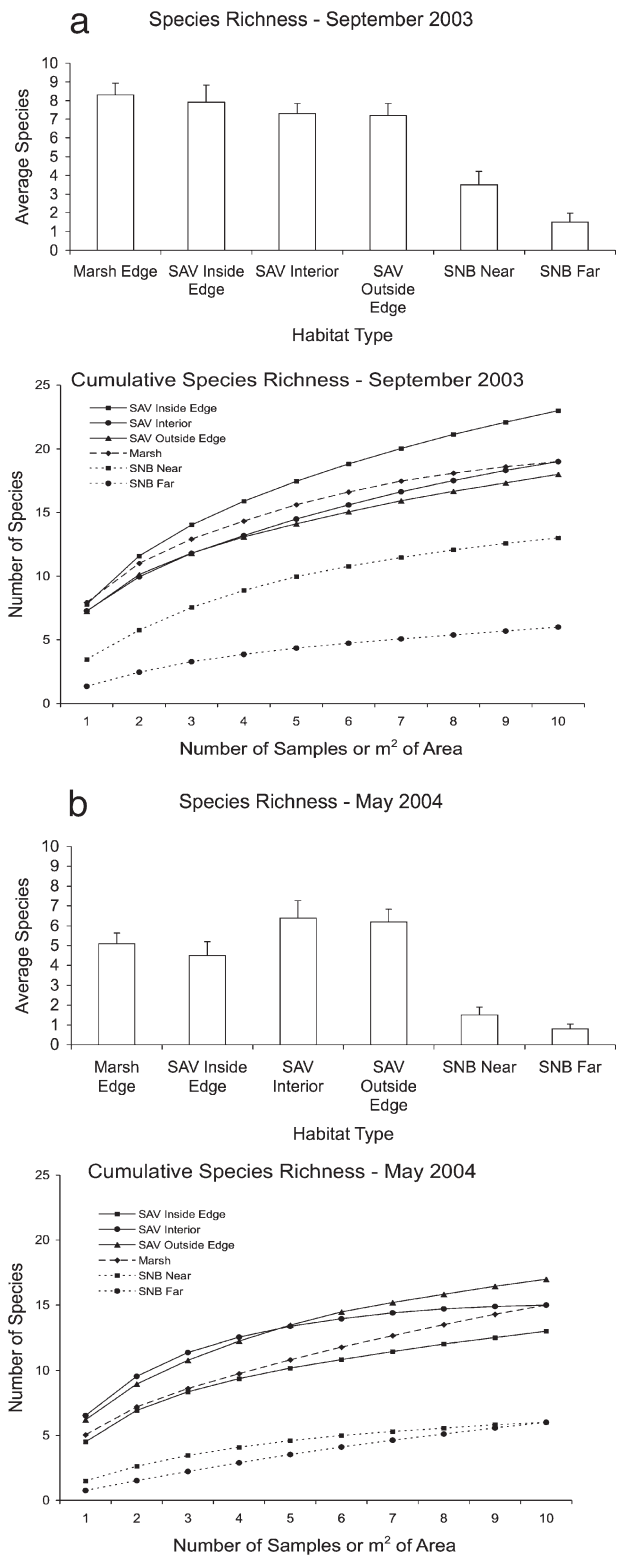

Fig. 1. Comparisons of species richness, measured as the mean number of species in a sample (above), and the cumulative number of species collected versus sample size or sample area (below) among habitat types in September 2003 and May 2004.

tats, suggesting that most species present on nonvegetated bottom were represented in 10 m^2 of area sampled. In fall, the pattern for the inside edge of SAV suggested that diversity in this habitat type might be greater than in other parts of the *Vallisneria* bed or in the marsh.

Mean densities of most species also varied significantly among habitat types (Table 3). Two important fishery species, white shrimp (fall) and blue crab, were much more abundant in the Vallisneria bed than over nearby SNB sites (Fig. 2 and Table 3). Densities of other abundant species, including Harris mud crab, Ohio shrimp, daggerblade grass shrimp, rainwater killifish, naked goby, code goby (fall), speckled worm eel *Myrophis punctatus* (fall), and gulf pipefish (spring) also were significantly higher, and more species were taken, in SAV than over SNB (Table 3). Among abundant species, bay anchovy was an exception; in fall, this species was more abundant at SNB sites than in SAV.

Our analysis detected few statistically significant differences in mean animal densities between marsh and SAV. In spring, mean densities of naked goby and gulf pipefish were higher in SAV than marsh, whereas in fall, Harris mud crab, speckled worm eel, and rainwater killifish were more abundant in marsh than SAV (Table 3).

Nekton densities were not evenly distributed throughout the SAV bed (Table 3). In fall, Harris mud crab, rainwater killifish, and speckled worm eel were all more abundant at the SAV edge near the marsh than at SAV sites along the outside edge of the bed, and mean densities of Ohio shrimp were higher in the interior than along the edges of the bed.

Densities of most species were relatively low over nonvegetated bottom (SNB), and we detected no statistical difference in densities between the two nonvegetated habitat types for any species. Total crustacean densities over nonvegetated bottom were higher in the fall over sample sites located within 5 m (SNB Near) than 10 m or more (SNB Far) away from the *Vallisneria* bed (Table 3).

The distribution of animal biomass among habitat types generally mirrored the patterns for densities, although fewer of these patterns for biomass were statistically significant (Table 4). The mean biomass of blue crab, Harris mud crab, daggerblade grass shrimp, Ohio shrimp, rainwater killifish (spring), naked goby (spring), and gulf pipefish (spring) was significantly greater in the *Vallisneria* bed than over SNB (Fig. 2 and Table 4).

The mean biomass for some species also differed between marsh and SAV (Table 4). Harris mud crab and naked goby in fall and blue crab in spring had more biomass at marsh than SAV sites (Fig. 2 and

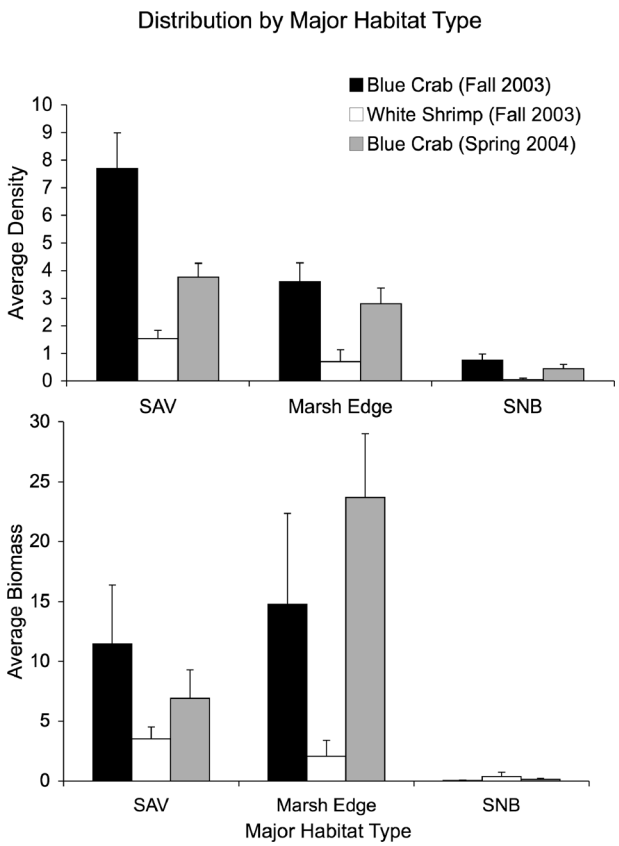

Fig. 2. Comparisons of density and biomass for two fishery species, blue crab and white shrimp, among three major habitat types (SAV = submerged aquatic vegetation dominated by *Vallisneria americana*, marsh edge, SNB = subtidal nonvegetated bottom) in September (fall) 2003 and May (spring) 2004. Each mean (density = ind m^{-2} or biomass = g m^{-2}) and SE was calculated from 30 SAV, 10 marsh edge, and 20 SNB samples.

Table 4). All of the biomass for saltmarsh topminnow came from marsh sites. Mean biomass for gulf pipefish and naked goby in spring was higher for SAV than marsh sites.

The distribution of biomass within the SAV bed differed significantly for two species (Table 4). In fall, Harris mud crab and rainwater killifish had more biomass at SAV Inside Edge than SAV Outside Edge sites, and in spring, more Harris mud crab biomass came from SAV Edge sites than SAV Interior sites.

Little of the total biomass collected in our study, other than that from striped mullet in fall and gulf menhaden in spring, was present at nonvegetated sites. We detected no significant differences in mean animal biomass between the SNB habitat types (Table 4).

Habitat types differed in environmental characteristics by water depth, dissolved oxygen concentration, distance to marsh edge, distance to SAV edge, and (in spring only) water temperature (Table 5). Water depth generally increased with distance away from the marsh. Marsh sites were shallower than SAV sites, and SAV sites were shallower than the SNB sites >10 m from the SAV bed. The mean depth of SNB sites near the SAV bed was within the range of depths for the SAV bed overall. Mean dissolved oxygen concentrations were >5 mg l^{-1} at all sites, but higher at SAV sites than marsh sites in fall and higher at SAV than SNB sites in spring. SAV Interior sites in spring had higher water temperatures than SAV Edge sites. SAV cover also differed within the SAV bed in spring; percent cover was >90% at Interior and Outside Edge sites, but <70% along the inside edge of the bed. In fall, SAV cover averaged >90% and was similar throughout the *Vallisneria* bed.

We examined the pattern of size distribution among habitat types for blue crab and white shrimp. We collected the largest blue crabs from emergent marsh, intermediate size crabs from SAV sites, and the smallest crabs from nonvegetated sites (Fig. 3). The mean carapace width of blue crabs was significantly larger in marsh than SAV (ANOVA Contrasts, fall: $p = 0.0158$; spring: $p = 0.0001$) and larger at SAV than SNB sites (ANOVA Contrasts, fall: $p = 0.0238$; spring: $p = 0.0232$). We did not observe this pattern for white shrimp. The mean total length (TL) of white shrimp was not detectably different among habitat types (ANOVA Habitat Effect: $p = 0.2727$; Fig. 3). The size range of white shrimp in our samples was 12–109 mm TL, but most individuals were large juveniles. Only 20% of the white shrimp in our samples were <50 mm TL.

Discussion

Vallisneria beds may be an important habitat type for at least two fishery species (blue crab and white shrimp) whose range of estuarine use extends into low salinity areas. In our study area, blue crabs were 8 and 10 times more abundant at *Vallisneria* than SNB (nonvegetated) sites in spring and fall, respectively. Densities of white shrimp were 30 times higher at *Vallisneria* than SNB sites in fall. Although we collected few brown shrimp and spotted seatrout in our study area, these fishery species were taken exclusively from *Vallisneria* sites. *Vallisneria* beds located within shoals of the St. Johns River also are reported to be an important habitat for juvenile (<40 mm CW) blue crabs in Florida (Tagatz 1968), and *Vallisneria* beds and oligohaline marshes in the upper Mobile Bay system, Alabama, are thought to have a significant nursery function for blue crab juveniles >8 mm CW (Heck et al. 2001). Duffy and Baltz (1998) sampled fishes in SAV beds (including *Vallisneria*-dominated sites) and SNB along the northern shore of Lake Pontchartrain. As in our study, they collected juvenile spotted seatrout in

TABLE 5. Comparison of environmental characteristics among habitat types. Mean and (SE) are given for variables measured in each habitat type that we sampled in September 2003 and May 2004. Each mean was estimated from 10 samples [exceptions: In September—Distance to SAV Edge: Marsh Edge (n = 9), SAV Interior (n = 2), SAV Outside Edge (n = 9), SNB near (n = 8), SNB far (n = 9); SAV Cover: SAV Interior (n = 9). In May—Distance to Marsh Edge: SAV Inside Edge (n = 9); Distance to SAV Edge: SNB near (n = 5); SAV Cover: SAV Outside Edge (n = 9)]. Results (p values) are given for ANOVA analyses used to compare all habitat types (Habitat Effect) and five *a priori* contrasts testing different habitat combinations. An * indicates that the ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). Contrast p values were not adjusted.

			Submerged Aquatic Vegetation						Subtidal Nonvegetated Bottom						Contrast p values				
	Marsh Edge		Inside Edge		Interior		Outside Edge		Near		Far								
Environmental Variable	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Habitat Effect p value		(1) SAV vs Marsh	(2) SAV vs SNB	(3) SAV Inside Edge vs SAV Outside Edge	(4) SAV Edge vs SAV Interior	(5) SNB Near vs SNB Far
September 2003																			
Water Temperature (°C)	31.4	(0.57)	31.8	(0.60)	31.8	(0.21)	30.9	(0.30)	31.9	(0.28)	31.3	(0.34)	0.5258						
Salinity (‰)	4.4	(0.22)	4.6	(0.22)	4.0	(0.37)	4.4	(0.27)	4.2	(0.33)	4.4	(0.37)	0.7982						
Water Depth (cm)	38.7	(2.72)	56.5	(2.19)	76.9	(1.51)	87.7	(1.84)	73.0	(5.00)	94.9	(2.76)	0.0001	*	0.0001	0.0003	0.0001	0.1821	0.0001
Dissolved Oxygen (mg l^{-1})	5.1	(0.47)	6.3	(0.64)	8.7	(0.55)	6.5	(0.65)	8.6	(0.63)	7.4	(0.57)	0.0002	*	0.0031	0.1328	0.8199	0.0025	0.1321
Turbidity (FTU)	13.2	(5.80)	8.5	(2.06)	10.8	(2.13)	10.2	(1.54)	15.3	(5.42)	10.2	(1.12)	0.7925						
Distance to Marsh Edge (m)	0.7	(0.11)	4.3	(0.62)	36.0	(8.22)	51.8	(8.76)	47.3	(10.24)	85.4	(9.52)	0.0001	*	0.0011	0.0001	0.0001	0.3912	0.0007
Distance to SAV Edge (m)	4.1	(0.61)	1.1	(0.33)	45.0	(23.00)	2.2	(0.58)	3.2	(0.42)	24.3	(3.80)	0.0001	*	0.0005	0.3921	0.7381	0.0001	0.0001
SAV Cover (%)			91.6	(6.70)	93.3	(2.60)	95.0	(5.00)					0.8840						
Stem Density (stems m^{-2})	186.0	(31.19)																	
May 2004																			
Water Temperature (°C)	24.3	(0.70)	24.5	(0.72)	26.0	(0.33)	23.7	(0.49)	24.2	(0.43)	24.0	(0.36)	0.0478		0.4751	0.2230	0.2636	0.0039	0.7787
Salinity (‰)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.2	(0.13)	0.1	(0.10)	0.2015						
Water Depth (cm)	19.7	(2.24)	34.5	(2.33)	57.3	(4.25)	72.0	(1.84)	54.5	(6.12)	76.3	(2.45)	0.0001	*	0.0001	0.0015	0.0001	0.3550	0.0001
Dissolved Oxygen (mg l^{-1})	9.7	(0.66)	10.3	(0.53)	11.2	(0.36)	8.7	(0.21)	9.3	(0.18)	8.9	(0.26)	0.0005	*	0.4151	0.0144	0.0083	0.0010	0.3992
Turbidity (FTU)	31.7	(4.97)	28.5	(3.42)	24.1	(1.81)	28.9	(3.13)	28.2	(2.00)	26.7	(2.38)	0.6680						
Distance to Marsh Edge (m)	0.6	(0.06)	6.8	(1.18)	53.3	(7.53)	79.1	(19.82)	53.4	(9.46)	106.5	(18.72)	0.0001	*	0.0022	0.0045	0.0002	0.4986	0.0035
Distance to SAV Edge (m)	2.6	(0.38)	3.5	(0.58)	28.7	(5.15)	2.3	(0.57)	3.2	(0.66)	28.5	(4.12)	0.0001	*	0.0096	0.1497	0.7656	0.0001	0.0001
SAV Cover (%)			68.4	(10.70)	98.2	(1.10)	94.4	(5.60)					0.0110	*			0.0159	0.0617	
Stem Density (stems m^{-2})	148.7	(25.11)																	

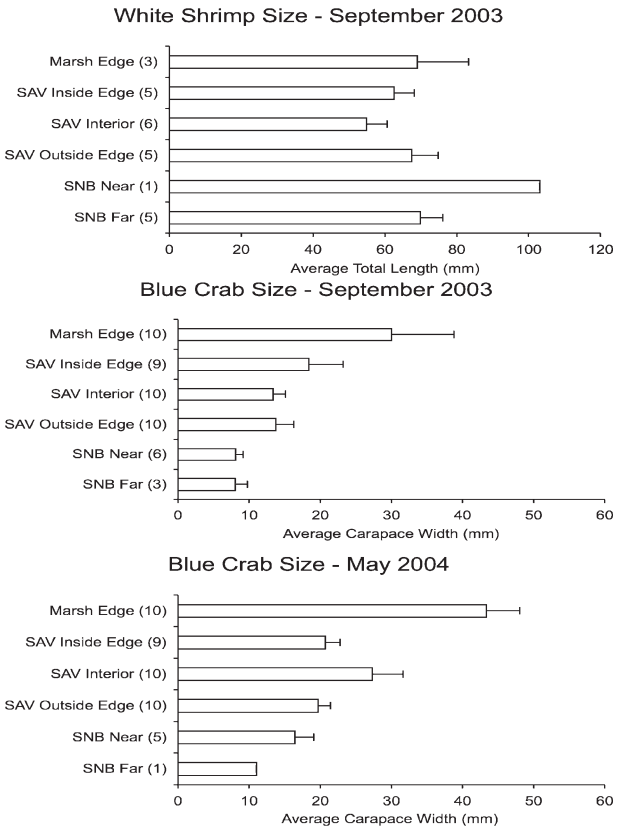

Fig. 3. Comparison of sizes (mean + 1 standard error) in mm for selected fishery species that were abundant in our study area in September 2003 and May 2004. Each mean (total length of white shrimp or carapace width of blue crab) was estimated from the mean sizes of n samples (shown in parentheses following each habitat type) that contained that species.

Vallisneria beds, but not over nearby nonvegetated lake bottom (Duffy and Baltz 1998). In their study, the diversity of fishes also was higher in *Vallisneria* than in *Ruppia maritima* L. or *M. spicatum*, although the total abundance of fishes and the density of some species were greater in these other SAV species than in *Vallisneria* (Duffy and Baltz 1998). Species richness of the nekton community in the *Vallisneria* bed we studied was similar to that in the marsh edge community and much richer than in the adjacent SNB. A few additional investigations have assessed the habitat value of SAV dominated by species other than *V. americana* in low-salinity estuarine areas. Shallow areas in the Clarence River estuary vegetated by *Vallisneria gigantea* are nursery areas for several fishery species in southeast Australia (West and King 1996). Castellanos and Rozas (2001) reported that within a tidal freshwater system in Louisiana, blue crab densities during fall in SAV (up to 17 m^{-2}) and emergent marsh (up to 14 m^{-2}) were comparable to those documented for similar habitat types within saline regions of estuaries located in the northern Gulf of Mexico; penaeid shrimps were not collected in their study. Other studies also show that within oligohaline environments, juvenile penaeid shrimps and blue crab are closely associated with SAV (Rozas and Minello 1999; Heck et al. 2001).

Organisms, other than fishery species, that were associated with *Vallisneria* in our study area included Harris mud crab, Ohio shrimp, daggerblade grass shrimp, rainwater killifish, naked goby, and gulf pipefish; densities of most of these species were at least as high in SAV as in emergent vegetation. Rainwater killifish, naked goby, and gulf pipefish also are the most abundant resident fishes of *Vallisneria* beds in Lake Pontchartrain (Duffy and Baltz 1998). Within the St. Johns River estuary, Florida, rainwater killifish are abundant in *Vallisneria*, yet nearly absent from adjacent sand flats (Jordan 2002). Castellanos and Rozas (2001) also observed few differences in nekton densities between SAV and marsh, but in their study, the blue crab was more abundant in *Potamogeton nodosus* (SAV) than marsh in fall. Gulf pipefish and naked goby (spring) were more abundant in *Vallisneria* than marsh in our study.

A few species were more abundant in marsh than *Vallisneria*. In fall, rainwater killifish and Harris mud crab were more abundant at marsh sites than at interior or outside edge SAV sites. The speckled worm eel also was more abundant in marsh than SAV. The oligohaline marshes in our study area provide an important habitat for the saltmarsh topminnow (Peterson et al. 2003), and we collected this species exclusively in marsh vegetation. The saltmarsh topminnow has a limited distribution, with populations endemic to the northern Gulf of Mexico, and is considered rare or threatened throughout its range (Thompson 1980; Musick et al. 2000; Peterson et al. 2003).

The young of blue crab, white shrimp, spotted seatrout, and other species are strongly attracted to vegetation structure during their stay in estuarine nursery areas (Minello et al. 2003; Heck et al. 2003). Emergent vegetation in marshes provides a structural environment for these species, but this habitat type is not available during low water events. The animals in our study area that were abundant in marsh vegetation at high tide likely moved to the adjacent *Vallisneria* bed at low tide and benefited from the continuous availability of vegetation structure at this location. Estuarine locations that have both SAV and emergent vegetation may support larger populations and higher individual growth rates than locations that lack one or both habitat types (Rozas and Odum 1987b; Irlandi and Crawford 1997; Raposa and Oviatt 2000). Pinfish gain approximately 90% more biomass when held

in experimental cages containing both emergent vegetation and seagrass than individuals held in enclosures with either emergent vegetation alone or that lack vegetation entirely (Irlandi and Crawford 1997).

Vallisneria beds likely function as habitat by providing aquatic organisms with a rich prey resource and with a refuge from predators. Compared to areas that lack vegetation, submerged aquatics, including *Vallisneria*, harbor dense populations of infaunal and epibenthic organisms that are potential prey for nekton predators (Menzie 1980; Lewis and Stoner 1983; Rozas and Odum 1987a; Lubbers et al. 1990; Corona et al. 2000). Potential prey associated with estuarine *Vallisneria* beds include small fishes, gammarid amphipods, hydrobiid snails, ephemeropterans, and chironomid larvae (VanderKooy et al. 2000; Jordan 2002). *Vallisneria* growing in freshwater ponds contains 64% more calories in the form of associated prey for fishes than nonvegetated areas, and growth rates of bluegill held in experimental enclosures that contain *Vallisneria* are significantly higher than those for fish held in enclosures that lack SAV (Richardson et al. 1998). Remaining prey populations are higher in these *Vallisneria* enclosures than nonvegetated ones, even though fish within the *Vallisneria* enclosures consume more prey than fish in the nonvegetated cages (Richardson et al. 1998). The structure of these vegetated habitats also provides young fish and decapod crustaceans with protection from predators and increases their chance of survival (Jordan 2002). Minello et al. (2003) reviewed the available literature on studies that compared nekton growth and survival between salt marsh and other estuarine habitats and concluded that growth rates (based on five available studies) were generally higher in SAV than marsh vegetation or SNB and that survival rates (based on 11 studies) in SAV and marsh vegetation were higher than in SNB, although less than for oyster reefs. In a review of studies on the nursery role of seagrass beds, Heck et al. (2003) concluded that structure itself rather than the type of structure was an important determinant of nursery value. They found few differences in abundance, growth, or survival when seagrass beds were compared to other structured habitat types.

The presence of *Vallisneria* and other species of SAV extends the area of structural habitat available to nekton both in space and time relative to areas without SAV. Where SAV is present within the estuary, the total area of vegetation structure is expanded beyond what would be provided by emergent vegetation alone. This habitat also is extended in time because SAV, unlike emergent vegetation, is available during low water periods that occur during the tidal cycle or in response to meteorological events (Rozas 1995). Unlike many species of SAV, southern populations of *Vallisneria* do not completely die back in winter unless the plants become exposed and subjected to freezing temperatures and drying (Dawes and Lawrence 1989; Doering et al. 2001; Jordan 2002; Poirrier personal communication). *Vallisneria* beds along much of the Gulf coast may provide structural habitat all year except when these SAV beds are subjected to a combination of very low water and freezing temperatures during severe winters or when droughts or other prolonged high-salinity events cause exfoliation and high mortality (Doering et al. 2001; Lores and Sprecht 2001; Estevez et al. 2002).

For estuarine habitats, position within the landscape mosaic is an important determinant of the nekton community, because the abundance and distribution of species at a location are partially determined by the faunal assemblages associated with adjacent habitats (Robblee and Zieman 1984; Rozas and Odum 1987b). In our study, Harris mud crab, rainwater killifish, and speckled worm eel were much more abundant at *Vallisneria* sites near the marsh than at SAV sites located farther away. We also observed some, albeit weaker, evidence for an effect of SAV proximity on the use of SNB by nekton. In fall, we collected more species and higher densities of total crustaceans at SNB sites adjacent to the *Vallisneria* bed than at SNB sites located at least 10 m away from SAV. In a previous study, Irlandi and Crawford (1997) observed that pinfish are more than twice as abundant within seagrass beds near marsh than in seagrass beds adjacent to SNB. Raposa and Oviatt (2000) showed that both the abundance and species of fishes within seagrass beds are related to marsh proximity. Densities of species generally associated with marsh vegetation (e.g., rainwater killifish, other killifishes, and daggerblade grass shrimp) decrease within seagrass beds with distance from the marsh shoreline (Raposa and Oviatt 2000).

The degree of influence that an adjacent marsh has on the nekton assemblage may vary over time and depend on the spatial extent of an SAV bed. When distances across the SAV bed are short and tidal inundation periods are of long duration, any patterns caused by proximity to marsh are likely to become dissipated. In situations with regular daily tides, patterns of abundance are more likely to reflect the influence of adjacent habitats. We also would expect different distributions during the tidal cycle; spatial distributions would likely be different immediately after low tide than at slack high water. A large SAV bed may exhibit this pattern longer than a narrow bed across which nekton could quickly disperse.

Shallow SNB was apparently more important than the vegetated habitat types for some species. Bay anchovy was abundant over SNB even at high tide when SAV and marsh were available as alternative habitats. These shallow nonvegetated areas also would be used by species usually associated with vegetation when extreme low water events rendered marsh and SAV inaccessible.

Species richness appeared greatest in *Vallisneria* and marsh habitat types, but such comparisons are sensitive to the area of habitat sampled. During fall, there was no significant difference in the mean number of species collected in a sample among the SAV habitat types, but the inside edge of the SAV appeared to support more species than the other SAV habitat types when all ten samples were analyzed. In all habitat types, the number of species collected continued to increase with the area sampled, indicating that 10 m^2 of area is insufficient to characterize species richness. These data emphasize that sample size and the total sample area are important considerations when measuring species richness and comparing this variable among habitat types.

The most important environmental variables affecting nekton distributions in our study appeared to be the presence of vegetation, water depth, and the distance to marsh or the SAV edge. The small differences observed among habitat types in water temperature and dissolved oxygen concentration were unlikely to be biologically significant. We measured these variables only during the day, but some environmental conditions may change substantially over a diel cycle. Dissolved oxygen concentrations in SAV may fluctuate dramatically over a 24-h period, and low oxygen during the night could affect animal movement among habitat types (Wannamaker and Rice 2000). Although most estuarine organisms are unaffected by short periods of low dissolved oxygen, prolonged periods of sublethal hypoxia may significantly reduce growth rates in some species (McNatt and Rice 2004). The general lack of information about diel changes in the environment of shallow estuarine habitats and the response of the nekton community to these changes warrant further study.

Relationships between habitat type and nekton size can reflect differential recruitment or ontogenetic changes in habitat value. The mean size of blue crabs increased from open water to SAV to marsh sites. In conjunction with abundance patterns, this size distribution of blue crab was consistent with an initial settlement in *Vallisneria* as small juveniles and later movement to emergent vegetation as larger juveniles. A similar pattern of larger crabs in marsh than in SAV and SNB is documented for other locations on the northern Gulf coast (Thomas et al. 1990; Rozas and Minello 1998; Castellanos and Rozas 2001; Rozas et al. 2005). Glancy et al. (2003) observed that blue crabs were larger in SNB at the marsh edge than in seagrass beds. Blackmon and Eggleston (2001) have shown that, after they initially settle in the lower estuary as megalopae, blue crabs use planktonic, postsettlement dispersal to reach nursery areas in the upper estuary.

V. americana beds that occur in estuaries may provide an important nursery habitat for the young of blue crab and white shrimp. Our study comparing densities of these species in *Vallisneria* and adjacent habitat types represents an important first step, but additional studies are required to determine conclusively whether *Vallisneria* beds in estuaries should be designated as Essential Fish Habitat for these species (Minello 1999; Beck et al. 2001). Because this SAV species occurs in the subtidal and persists throughout most years, *Vallisneria* beds can provide an important alternative structural habitat to emergent vegetation during periods of low water. The size distribution of blue crab among habitat types in our study area was consistent with initial settlement in *Vallisneria* as small juveniles and later to emergent vegetation as larger juveniles. Species whose young thrive in a low salinity environment and also depend on vegetation structure would benefit most from *Vallisneria* beds within estuaries.

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