Submerged Beds of *Vallisneria americana* Michx. (wild celery) as Essential Fish Habitat in Estuaries

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By:
Lawrence P. Rozas and Thomas J. Minello
NOAA/National Marine Fisheries Service/SEFSC
[1]Estuarine Habitats and Coastal Fisheries Center
646 Cajundome Boulevard, Lafayette, LA 70506

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Lawrence P. Rozas[1] and Thomas J. Minello[2]
NOAA/National Marine Fisheries Service/SEFSC
[1]Estuarine Habitats and Coastal Fisheries Center
646 Cajundome Boulevard
Lafayette, LA 70506
337-291-2110
lawrence.rozas@noaa.gov

and

[2]Galveston Laboratory
4700 Avenue U
Galveston, TX 77551

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Abstract

We quantified and compared nekton densities and biomasses among submerged aquatic vegetation (SAV, *Vallisneria americana*), marsh edge, and subtidal nonvegetated bottom (SNB) using a $1m^2$ drop sampler. In two seasons (fall=September 2003, spring=May 2004) of high nekton abundance, we collected 120 samples in six habitat types (marsh edge, SAV inside edge, SAV interior, SAV outside edge, SNB near, SNB far). We also compared species richness and the size of selected species among habitat types. Mean densities of most abundant species were significantly different among habitat types, and densities were generally much higher in vegetated habitat types than over SNB. Species richness also was greater at vegetated than nonvegetated sites. Most species, including 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 in the *Vallisneria* bed than over SNB. The *Vallisneria* bed supported densities of most species that were similar to those in marsh vegetation. However, 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 interior, 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. Our results show that *Vallisneria* beds provide an important nursery habitat for young blue crab and white shrimp that use oligohaline estuarine areas. *Vallisneria* beds can provide an important alternative structural habitat to emergent vegetation during periods

of low water, because this habitat type occurs in the subtidal and generally persists throughout the year on the Gulf coast. Species whose young thrive in low salinity and also depend on structure would benefit most from *Vallisneria* habitat.

Introduction

Numerous studies have examined the role of seagrasses in providing habitat for aquatic organisms, 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). Few habitat assessments, however, have included species of submerged aquatic vegetation (SAV) that occur in low-salinity estuarine waters.

As in other regions, nekton use of SAV beds in oligohaline regions of estuaries seldom has been examined in the northern Gulf of Mexico, and comparisons with emergent marsh vegetation are rare. Duffy and Baltz (1998) used throw traps to compare fish densities among different SAV habitat types (including *Vallisneria americana*) and nonvegetated bottom in Lake Pontchartrain, Louisiana. An assessment of SAV and marsh habitat types in the Mobile Bay estuary also included low-salinity areas, but this study was limited to a single species, blue crab (Heck et al. 2001). Weaver and Holloway (1974) described the fishes and decapod crustaceans associated with SAV in brackish ponds at Marsh Island, Louisiana. However, their study ponds were located in an area under structural marsh management, which likely influenced the abundance and composition of the species they collected (Rogers et al. 1994, Rozas and Minello 1999). The sampling method employed by Weaver and Holloway (1974) also may have biased their results. Samples were collected using surface and bottom trawls, which are notoriously ineffective in dense submerged vegetation (Rozas and Minello 1997). Even with these limitations, two fishery species (blue crab *Callinectes sapidus* and brown shrimp *Farfantepenaeus aztecus*) were found to be important components of the SAV community.

Vallisneria americana Michx. (wild celery) is a common species of SAV that is widespread in low-salinity estuarine areas (Adair et al. 1994). Although the total areal coverage of *Vallisneria* in estuaries along the northern Gulf coast is unknown, this species can occupy large areas at some locations (e.g., Doering et al. 2001, Estevez et al. 2002). Estuaries in Louisiana, particularly those receiving freshwater from the Mississippi River, contain sizable shallow, low-salinity areas where *Vallisneria* can exist. For example, extensive areas of *Vallisneria* beds exist within shallow lakes and ponds of the upper Barataria estuary, and approximately 80 ha of *Vallisneria* beds occur along the northern shore of Lake Pontchartrain (Poirrier, personal communication).

Research examining the habitat value of *Vallisneria* beds for fishery species is needed because this habitat type is often located near developed areas where grass beds are vulnerable to expanding human populations (Peterson et al. 2000). Documentation of habitat value may be useful in protecting *Vallisneria* beds. In addition, habitat restoration efforts in Louisiana can provide opportunities to increase areas of *Vallisneria* habitat. Large river diversions planned to combat coastal landloss may significantly increase the size of the area in which *Vallisneria* can exist by freshening coastal waters previously too saline to support this vegetation. An assessment of the nursery value of *Vallisneria* habitat is required to determine its role in supporting coastal fisheries and necessary to develop sound management plans for estuaries and estuarine-dependent fishery species.

Our research objective was to evaluate the role of *Vallisneria* beds in providing nursery habitat for fishery species. Densities of fishery species and other species of nekton were measured and compared among *Vallisneria* beds, natural marsh, and shallow nonvegetated bottom. We also examined the spatial distribution of animals within these SAV beds and the effect of *Vallisneria* or marsh proximity on the nekton community of adjacent habitat types. The data from this research can be used to predict the habitat value of *Vallisneria* beds at other locations in Louisiana and other estuaries along the Gulf coast.

Materials and Methods

Our study area was located on the northwest shore of Little Lake within the Barataria Bay system (Figure 1). During years of average rainfall, mean salinities are $\leq$5 psu in this region of the Barataria Bay system (Orlando et al. 1993). Tides are predominantly diurnal and have a mean daily range of <0.3m (Byrne et al. 1976, Baumann 1987).

The focus of our study was an extensive (~ 860 m by 130 m) SAV bed located in shallow water along a marsh peninsula north of Bay L'Ours (Figure 1). The vegetation of this SAV bed was predominantly *Vallisneria americana*. Myriophyllum *spicata* L. also was present, but much less abundant. Submerged aquatic plants were absent in deeper water offshore and in a narrow band of very 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 from randomly selected sites in the study area; sites were selected using random numbers and a grid placed over an aerial photograph. We collected 10 samples in each of four vegetated habitat types, including the marsh edge and three locations within the *Vallisneria* bed (Table 1). In addition, we collected a total of 20 samples over subtidal nonvegetated bottom (SNB); half of these were near the SAV bed and half were 10 m or more from the SAV bed (Table 1). All samples were collected in the day at high tide during periods of tropical tides September 3-4, 2003 and May 4-5, 2004.

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-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 *F. aztecus*. Grass shrimp (144) 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 species of *Callinectes* was assumed to be a blue crab *C. sapidus*. Animals that could not be readily identified were not used in size analysis. Total length of fishes and shrimps and carapace width of crabs were measured to the nearest mm. Individuals of a species in each sample were pooled to determine biomass (wet weight) to the nearest 0.1g.

Data Analyses

We used 1-way Analysis of Variance (ANOVA) followed by *a priori* contrasts to examine differences in densities, biomass, species richness, size of selected animals, and environmental variables (mean dissolved oxygen, salinity, water temperature, turbidity, water depth, and distance to edge) among habitat types (Table 2). We made the following comparisons with *a priori* contrasts: (1) SAV vs Marsh Edge, (2) SAV vs SNB, (3) SAV Inside Edge vs SAV Outside Edge, (4) SAV Edge vs SAV Interior, and (5) SNB Near vs 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. With contrast 4, we tested for an edge effect within the SAV bed. We used contrast 5 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; therefore, we did a ln (x+1) transformation of the original values prior to analyses. Other variables were not transformed. All tabular and graphical data presented in this paper are untransformed means. We conducted statistical analyses using SuperANOVA (Version 5 Ed., Abacus Concepts, Inc., Berkeley, California, 1989).

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, composing 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 decapod crustaceans represented 81% of the total biomass in spring (Table 4). The most abundant decapod species in fall (Harris mud crab *Rhithropanopeus harrisii*, Ohio shrimp *Macrobrachium ohione*, blue crab, daggerblade grass shrimp, marsh grass shrimp, and white shrimp *Litopenaeus setiferus*) composed 74% of the total. In spring the numerically dominant species (79% of total crustaceans) included daggerblade grass shrimp, blue crab, and Harris mud crab. An unidentified xanthid crab accounted for an additional 25.7% and 10.7% of the total crustaceans that we collected in fall and spring, respectively. 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, rainwater killifish *Lucania parva*, naked goby *Gobiosoma bosc*, bay anchovy *Anchoa mitchilli*, striped mullet *Mugil cephalus*, and code goby *Gobiosoma robustum* composed 79% of the total. 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. An unidentified killifish composed an additional 6.7% of this total. Most of the biomass in our samples was composed of 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).

Species assemblages differed among habitat types (Figure 2). In fall, Harris mud crab, Ohio shrimp, and blue crab numerically dominated the SAV habitat types. Within *Vallisneria*, rainwater killifish was abundant only at SAV Inside Edge sites (Figure 2a). Blue crab ranked third in abundance within SAV and only seventh at marsh sites. In contrast, 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 (Figure 2b). Bay anchovy and gulf menhaden numerically dominated nonvegetated sites in fall and spring, respectively.

Mean densities of most species and species richness (number of species) varied significantly among habitat types (Table 3, Figure 3). Two important fishery species, white shrimp (fall) and blue crab, were much more abundant in the *Vallisneria* bed than over nearby nonvegetated sites (Table 3, Figures 2 and 4). Densities of other abundant species, including Harris mud crab, Ohio shrimp, daggerblade grass shrimp, rainwater killifish, naked goby, code goby (fall), speckled worm eel (fall), and gulf pipefish (spring) also were significantly higher, and more species were taken, in SAV than over SNB (Table 3, Figure 2). Among abundant species, bay anchovy was an exception; this species was more abundant at nonvegetated 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, speckled worm eel was more abundant in marsh than SAV (Table 3, Figure 2). Our statistical analysis also showed that during fall, Harris mud crab and rainwater killifish were more abundant in marsh than SAV; mean densities of these species at SAV Inside Edge sites (i.e., near the marsh), however, were comparable to those at marsh sites.

Nekton densities were not evenly distributed throughout the SAV bed (Table 3, Figure 2). 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. Other species, including striped mullet (fall), code goby (fall), Ohio shrimp (spring), and brackish grass shrimp (spring), were generally more abundant within the interior of the SAV bed than along the edges of the bed, but our analysis did not show that this pattern was statistically significant for these species (Table 3, Figure 2).

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 (Table 3, Figure 2). Species richness and total crustacean densities over nonvegetated bottom, however, were higher in the fall over sample sites located within 5m (SNB Near) than 10m 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). For species that accounted for most of the biomass in our samples, most had much more biomass at SAV than SNB sites. Blue crab and white shrimp (fall) mean biomass was significantly greater in the two vegetated habitat types (SAV and Marsh Edge) than over SNB (Figure 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 (Table 4, Figure 4b). In addition, all of the biomass for saltmarsh topminnow came from marsh sites. In contrast, 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, originated from 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 ppm 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. In general, we collected the largest blue crabs from emergent marsh, intermediate size crabs from SAV sites, and the smallest crabs from nonvegetated sites (Figure 5). 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 similar among habitat types (ANOVA Habitat Effect: p=0.2727, Figure 5). 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 in TL.

Discussion

Our results show that *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 *Cynoscion nebulosus* in our study area, these fishery species were taken exclusively from *Vallisneria* sites. *Vallisneria* beds located within shoals of the St. Johns River also were reported to be an important habitat for juvenile (<40mm CW) blue crabs in Florida (Tagatz 1968), and *Vallisneria* beds and oligohaline marshes in the upper Mobile Bay system, Alabama were thought have a significant nursery function for blue crab juveniles >8mm 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 *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 *Myriophyllum 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* were shown to be nursery areas for several fishery species in southeast Australia (West and King 1996). Castellanos and Rozas (2001) reported that within a tidal freshwater system, blue crab densities 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, Reed et al. 2004).

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; and 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 were the most abundant resident fishes of *Vallisneria* beds in Lake Pontchartrain (Duffy and Baltz 1998). Jordan (2002) reported that the rainwater killifish was abundant in *Vallisneria*, yet nearly absent from adjacent sand flats, within the St. Johns River estuary, Florida. 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. Similarly, 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, although rainwater killifish and Harris mud crab were as abundant at near-marsh SAV sites as in marsh, these species were more abundant in marsh than at the other SAV sites. The speckled worm eel was more abundant in marsh than SAV, and we collected the saltmarsh topminnow exclusively in marsh vegetation. The saltmarsh topminnow has a limited distribution, with populations endemic to the northern Gulf of Mexico, and this species has been listed as vulnerable (i.e., at risk of being designated as endangered or threatened in the near future, Musick et al. 2000). Oligohaline marshes in our study area may provide an important habitat for this species.

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 therefore benefited from the continuous availability of vegetation structure at this location (Raposa and Oviatt 2000). 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 1987, Irlandi and Crawford 1997, Raposa and Oviatt 2000). Pinfish held in experimental cages that contained both emergent vegetation and seagrass gained approximately 90% more biomass than individuals held in enclosures with either emergent vegetation alone or that lacked 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 Stone 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 contained 64% more calories in the form of associated prey for fishes than nonvegetated areas, and growth rates of bluegill held in experimental enclosures that contained *Vallisneria* were significantly higher than those for fish held in enclosures that lacked SAV (Richardson et al. 1998). Further, prey populations were higher in the *Vallisneria* enclosures than the nonvegetated ones, even though fish within these *Vallisneria* enclosures had consumed more prey than fish in the nonvegetated cages, presumably because of the refuge provided by the plants (Richardson et la. 1998). Recently, Minello et al. (2003) reviewed the available literature on studies that compared nekton growth and survival between salt marsh and other estuarine habitats, and they also concluded that growth rates (based on five available studies) were generally higher in SAV than marsh vegetation or SNB. 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). In their review, Minello et al. (2003) reported 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 recent review of papers on the nursery role of seagrass beds, Heck et al. (2003) concluded that structure rather than the type of structure appeared to be a critical 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. In addition, this habitat 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). Additionally, 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). Therefore, *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 (Inside Edge) than at SAV sites located farther away (Interior and Outside Edge). 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 10m away from SAV. In a previous study, Irlandi and Crawford (1997) observed that pinfish were more than twice as abundant within seagrass beds near marsh than in seagrass beds adjacent to SNB. Similarly, Raposa and Oviatt (2000) showed that both the abundance and species of fishes within seagrass beds were related to marsh proximity. In their study, densities of species generally associated with marsh vegetation (e.g., rainwater killifish, other killifishes, and daggerblade grass shrimp) decreased within seagrass beds with distance from the marsh shoreline (Raposa and Oviatt 2000).

We observed some evidence for a negative edge effect within *Vallisneria* beds. Ohio shrimp (in fall) were more abundant within the interior of the bed than near the edges. Bologna and Heck (1999) documented that bay scallop living near seagrass edges grew more rapidly, but also experienced higher rates of predation, than scallops within the interior of seagrass beds. Perhaps the higher densities of Ohio shrimp we observed in the interior of the *Vallisneria* bed was related to a higher risk of predation near SAV edges.

Shallow SNB was apparently more important than the vegetated habitat types for some species. Bay anchovy, gulf menhaden, and striped mullet were 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.

As discussed above, the environmental variables, vegetation presence, water depth, distance to marsh, and distance to SAV edge seemed to affect animal distributions in our study area most. The small differences in water temperature and dissolved oxygen concentration that we observed among habitat types were unlikely to be biologically significant. We measured these variables only during the day, however, and some environmental conditions may change substantially over a diel cycle. For example, dissolved oxygen concentrations in SAV may fluctuate dramatically over a 24-hr 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). A 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.

At least one species showed a clear pattern of size distribution among habitat types. The mean size of blue crabs increased from open water to SAV to marsh sites. A similar pattern of larger crabs in marsh than in SAV and SNB has been documented for other locations on the northern Gulf coast (Thomas et al. 1990, Rozas and Minello 1998, Castellanos and Rozas 2001, Rozas et al. submitted). Glancy et al. (2003) observed that blue crabs were larger in SNB at the marsh edge than in seagrass beds. Perhaps, we collected the smallest blue crabs over SNB before they had a chance to reach the *Vallisneria* bed. New recruits to vegetated habitats may settle first in SAV and then later, as larger juveniles, move into emergent vegetation. The white shrimp we collected in our study area were mostly large juveniles. In a previous study within the same estuary (Barataria), we observed that the sizes of both white shrimp and blue crab increased with distance up the estuary (Reed et al. 2004). A similar pattern was observed for juvenile blue crab in the Mobile River estuary (Heck et al. 2001). This pattern is consistent with post-settlement up-estuary migrations. Perhaps the larger animals in the upper estuary are older individuals that have slowly migrated up the estuary from populations in the lower estuary composed mostly of newly settled recruits. Blackmon and Eggleston (2001) have shown that, after they initially settle in the lower estuary as megalopae, blue crab use planktonic, post-settlement dispersal to reach nursery areas in the upper estuary. It is not known if white shrimp also use this dispersal mechanism to migrate to the upper estuary.

In summary, *Vallisneria americana* provided an important nursery habitat for the young blue crab and white shrimp that were present in our oligohaline study area. 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. 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. Finally, the distribution of some animals within the *Vallisneria* bed appeared to be influenced by marsh proximity, as has been documented for other systems in previous studies (Rozas and Odum 1987b, Irlandi and Crawford 1997, Raposa and Oviatt 2000).

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FIGURE LEGENDS

Figure 1. Map showing the northwest portion of Little Lake and its location within the coastal zone of Louisiana. Our study area was located within the box that is drawn north of the marsh peninsula and Bay L'Ours.

Figure 2. Distributions among habitat types of abundant fishes and crustaceans collected in (a) September 2003 and (b) May 2004. Error bars = 1 standard error (SE). Means (individuals m^{-2}) and SEs were calculated from 10 samples per habitat type. D. grass shrimp=daggerblade grass shrimp, M. grass shrimp=marsh grass shrimp, B. grass shrimp=brackish grass shrimp.

Figure 3. Comparisons of species richness among habitat types in September 2003 and May 2004. Each mean (number of species m^{-2}) and SE was calculated from 10 samples per habitat type.

Figure 4. 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 (a) September 2003 and (b) May 2004. Each mean (density=individuals m^{-2} or biomass=g m^{-2}) and SE was calculated from 30 SAV, 10 marsh edge, and 20 SNB samples.

Figure 5. 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.