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

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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).

Acknowledgments

This research was conducted through the NOAA Fisheries Service, Southeast Fisheries Science Center by personnel from the Fishery Ecology Branch (FEB) located at the Galveston Laboratory and the Estuarine Habitats and Coastal Fisheries Center in Lafayette, Louisiana. The assistance of everyone in the FEB was essential for the successful completion of this project. In particular, we thank Harley Clinton, Molly Dillender, Jim Ditty, Jennifer Doerr, Shawn Hillen, Joni Kernan, Kirk Kilfoyle, Genni Miller, Freddie Nix, Matt Prine, Juan Salas, Katie Turner, Katrinyda Williams, and Elizabeth Wilson for helping to collect and process samples and Philip Caldwell for producing Figure 1. We also thank Dean Blanchard with the Barataria-Terrebonne National Estuary Program for logistical support and assistance with fieldwork and Stephanie Cogburn for processing samples as a laboratory volunteer. We acknowledge the U.S. Environmental Protection Agency, Barataria-Terrebonne National Estuary Program, and NOAA

Fisheries Service for funding this research project. The findings and conclusions in this report are those of the authors and do not necessarily represent the views of the NOAA Fisheries Service.

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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 $\pm$ 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.

Appendix I

Quality Assurance Project Plan
for
Study of Habitat Importance of *Vallisneria* Beds

Prepared by:

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Funded by a Clean Water Act Section 320 (g) grant from the U.S. Environmental Protection Agency

Conducted under LUMCON/BTNEP Joint Agreement Number BTNEP02-6

QUALITY ASSURANCE PROJECT PLAN

FOR

STUDY OF HABITAT IMPORTANCE OF *VALLISNERIA* BEDS

Implementing Organizations:
- Barataria-Terrebonne National Estuary Program
- National Marine Fisheries Service

Approved by:

Lawrence P. Rozas — Date: 6-19-02
Dr. Lawrence P. Rozas, Principal Investigator
National Marine Fisheries Service

Jim Ditty — Date: 6-19-02
Mr. James Ditty, Quality Assurance Manager
National Marine Fisheries Service

Kerry M. St. Pé. — Date: 6-24/02
Mr. Kerry St. Pé, Director and Quality Assurance Manager
Barataria-Terrebonne National Estuary Program

Kenneth E. Landrum — Date: 6/20/02
Dr. Kenneth E. Landrum, Quality Assurance Officer
Barataria-Terrebonne National Estuary Program

Dean Blanchard Date: 4/5/2002

Mr. Dean Blanchard, Project Coordinator
Barataria-Terrebonne National Estuary Program

_____ Date:_____

Ms. Joan E. Brown, Chief of Assistance Programs Branch
U.S. Environmental Protection Agency

_____ Date:_____

Ms. Betty Ashley, Project Officer
U.S. Environmental Protection Agency

In lieu of signatures, NMFS contractors (End to End Technical Services and Jardon & Howard Technologies, Inc.) will receive "return receipt" letters and copies of the approved QAPP. Recipients will sign the letters stating adherence to the provisions of the QAPP and will return the letters to the Project Coordinator.

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DISTRIBUTION LIST

A final copy of this Quality Assurance Project Plan will be sent by the Project Coordinator to the following individuals:

Dr. Lawrence P. Rozas, NMFS Principal Investigator
Dr. Thomas J. Minello, NMFS Co-Principal Investigator
Mr. James Ditty, NMFS Fishery Ecology Branch Quality Assurance Manager

Mr. Kerry St. Pé, BTNEP Director and Quality Assurance Manager
Dr. Kenneth E. Landrum, BTNEP Quality Assurance Officer
Mr. Dean Blanchard, BTNEP Project Coordinator

Ms. Betty Ashley, USEPA Project Officer

Mr. Fred Neely, End to End Technical Services, Program Management Director
Mr. Don Fox, Jardon & Howard Technologies, Inc., Vice President of CASU Operations

A4
PROJECT/TASK ORGANIZATION

The National Marine Fisheries Service (NMFS) Galveston Laboratory has entered into a joint agreement with the Barataria-Terrebonne National Estuary Program (BTNEP) to perform work necessary to achieve the objectives of the project. NMFS staff, contractors, and BTNEP personnel will be involved in the project. An organizational chart (Figure 1) indicates relevant personnel involved in data and information exchange.

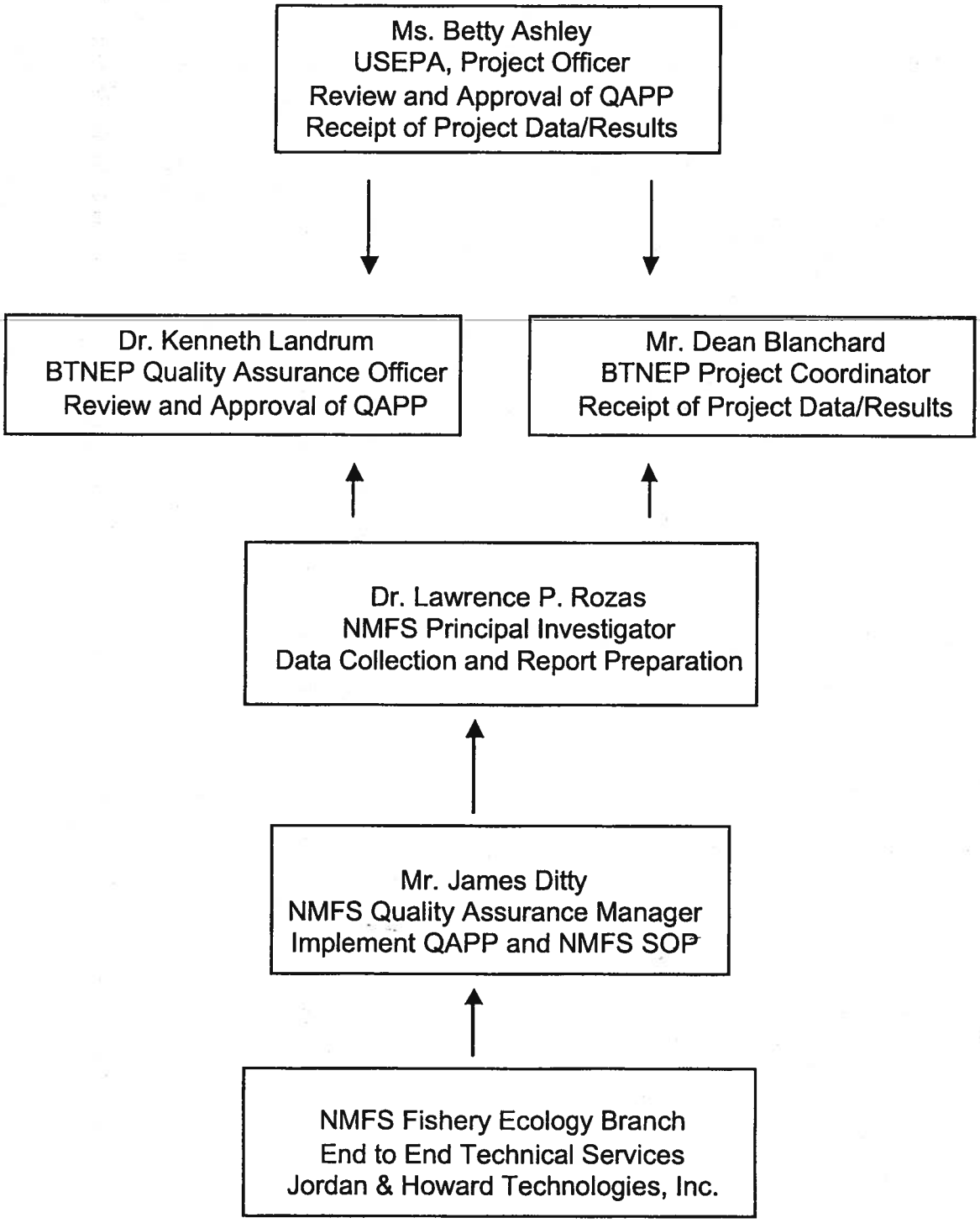
Dr. Lawrence P. Rozas is Principal Investigator (PI) and Dr. Thomas J. Minello is Co-principal investigator for NMFS. Dr. Rozas is responsible for obtaining background information and required permits, site selection, general oversight of field activities, conducting data analyses, writing reports, and responding to information requests from outside agencies. Mr. James Ditty, the NMFS Fishery Ecology Branch Laboratory Manager, has direct oversight of the majority of field and laboratory activities of NMFS branch staff and contractors and serves as the Branch Quality Assurance Manager (QAM) for staff and contractor services. The QAM is responsible for implementation and adherence to the quality assurance and quality control program outlined in the QAPP and specified in the NMFS Field and Lab Standard Operating Procedures (see Appendix 1). NMFS and BTNEP staff members will assist the PI in site surveys and collecting field samples. End to End Technical Services and Jardon & Howard Technologies, Inc. provide technical staff biologists to NMFS who will assist the PI in collecting and processing field samples.

The BTNEP is the sponsor of this project. Mr. Dean Blanchard is the BTNEP Project Coordinator who will monitor progress of NMFS in achieving the objectives of this project. This is accomplished through interaction with the PI and through review of the required progress reports.

Dr. Kenneth Landrum, BTNEP Quality Assurance Officer, and Mr. Kerry St. Pé, BTNEP Director and Quality Assurance Manager, will review the QAPP to insure that it meets all necessary quality assurance and quality control requirements and will approve the QAPP when those requirements have been met.

Ms. Betty Ashley, USEPA Project Officer, also reviews the QAPP and approves the QAPP when all applicable requirements have been met.

Figure 1
Project Organization Chart



A5
PROBLEM DEFINITION/BACKGROUND

Although the habitat function of seagrasses is well established (Orth et al. 1984, Bell and Pollard 1989), relatively few habitat assessments have included species of submerged aquatic vegetation (SAV) that occur in low-salinity estuarine waters, and SAV communities in oligohaline regions of estuaries along the northern Gulf of Mexico have almost been completely overlooked. Weaver and Holloway (1974) described the fishes and decapod crustaceans (nekton) associated with SAV in brackish ponds at Marsh Island, Louisiana. However, their study ponds were located behind weirs, 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 an important component of the SAV community. Duffy and Baltz (1998) compared nekton densities among different SAV habitats in Lake Pontchartrain, Louisiana; however, their study was limited to fishes. In their study, spotted seatrout *Cynoscion nebulosus* was taken in all three SAV habitats they sampled, but this species was not collected over nearby nonvegetated lake bottom (Duffy and Baltz 1998).

Vallisneria americana 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 may occupy large areas at some locations. 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 occur in the Barataria estuary within embayments and tidal channels located along the shores of Little Lake and Bay L'Ours. Approximately 80 ha of *Vallisneria* beds occur along the northern shore of Lake Pontchartrain (Poirrier, personal communication).

Research documenting the habitat value of *Vallisneria* beds for fishery species is urgently needed. This habitat is often located near developed areas where grass beds are vulnerable to expanding human populations. In contrast, restoration efforts in Louisiana could have a positive effect on *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.

Decision-makers for this project include NMFS, BTNEP, and EPA. Users of the results include government agencies like NMFS, EPA, Army Corps of Engineers, Louisiana

Department of Environmental Quality, Louisiana Department of Natural Resources, Louisiana Department of Wildlife and Fisheries, and local planning and resource management agencies, and non-governmental organizations involved in habitat protection, restoration, and management.

A6
PROJECT/TASK DESCRIPTION

The primary goal of this project is to document the relative value of *Vallisneria* beds as habitat for estuarine-dependent fishery species. We propose to sample nekton at Little Lake and Bay L'Ours in the Barataria Estuary to assess the nursery value of *Vallisneria* habitat (Figure 2). We also will sample other nearby shallow-water habitat types to compare nekton use patterns. We will quantify and compare densities of nekton in *Vallisneria* beds, emergent marsh vegetation, and shallow nonvegetated bottom at the study area to evaluate the relative value of these habitats for juvenile fishery species and small resident nekton. 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 northern Gulf of Mexico coast.

Following QAPP approval, we will reconnoiter the study area and select sample sites. We will collect 60 samples each in spring and fall. Samples will be processed, data will be analyzed, and a final report of the results will be prepared. The final report summarizing the data and synthesizing the results of the study will be written and submitted to the project manager within one year of collecting the first set of samples.

A successful project will require us to complete eight tasks. The PI will complete **Task 1** by writing a QAPP for the project, submitting this document, and obtaining approval for the plan from both BTNEP and EPA.

After the QAPP is approved, we will accomplish **Task 2** during a field trip to the study area by the PI and the BTNEP Project Coordinator. We will survey the study area by boat to identify the present extend of *Vallisneria* occurrence in Little Lake and Bay L'ours. From this survey, we will select potential sample locations from areas containing *Vallisneria* beds, in adjacent areas of nonvegetated bottom, and in emergent vegetation (marsh) along nearby shorelines.

We will accomplish **Task 3** by collecting the spring set of nekton samples. We will collect all nekton samples using a 1-m^2 drop sampler. Procedures for collecting nekton samples are given in Zimmerman et al. (1984, p. 328) and Rozas and Zimmerman (2000, p. 218). Appendix 2 contains copies of these publications. Briefly, nekton abundance will be compared among habitat types using randomly deployed samplers. Drop samplers are deployed from the bow of a boat which is maneuvered to the sample site. Once a sampler is deployed and seated into the bottom, the enclosed water column is swept with 1 mm-mesh dip nets, the water inside the sampler is removed and filtered through a 1 mm-mesh plankton net, and the substrate of the sample area is inspected for animals. All organisms taken in dip nets or by inspecting the sample area are placed in the plankton net. The contents of the plankton net are then rinsed and the cod-end containing the sample is removed and preserved in 10% formalin for later sorting, identification, and enumeration of organisms. Samples will be collected in each

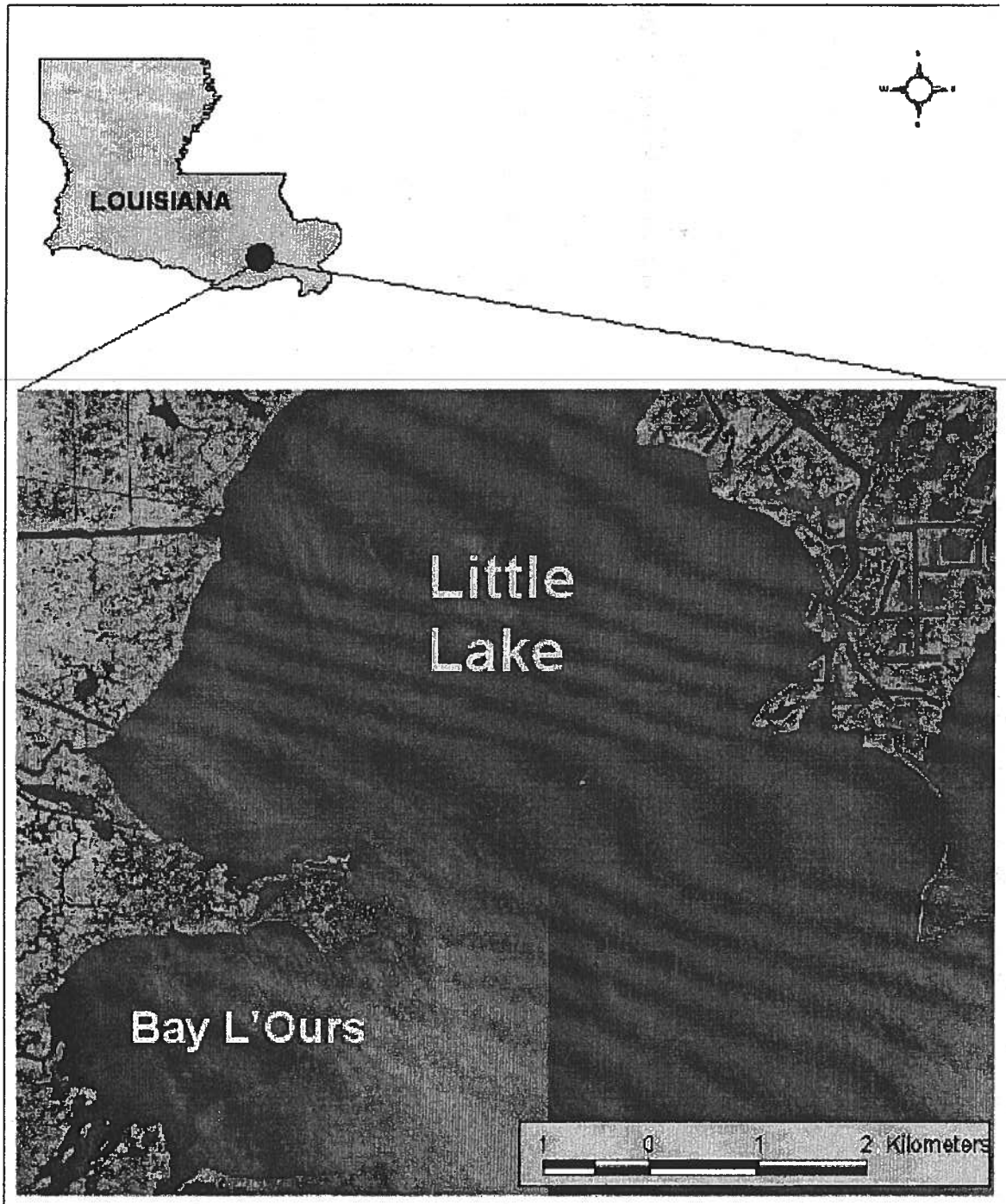


Figure 2. Map of Study Area at Little Lake in Barataria Estuary.

of the following habitats: 30 samples in *Vallisneria* beds, 10 samples in marsh located along lake shoreline or tidal channels, and 20 samples in shallow open-water habitat. Each sample will be taken at a different randomly-selected site within the habitat locations identified during the initial field survey (see Task 2).

Task 4 will be completed in the laboratory by processing the spring set of nekton samples. Sample processing requires three steps (sorting, identification, and enumeration). Samples will first be sorted by separating the animals from any extraneous material (e.g., detritus, plant parts, shell hash) in the samples. Animals will then be identified to species or lowest feasible taxon and counted. Data from samples will be recorded and then transferred to an electronic data base.

We will accomplish **Task 5** by collecting the fall set of nekton samples. We will collect these samples in the same habitat types and following the same methods as outlined for Task 3.

Task 6 will be accomplished by processing the fall set of nekton samples. We will complete this task using the same procedure described above for Task 4.

We will accomplish **Task 7** by analyzing the spring and fall nekton data, synthesizing the results of the study, preparing a draft final report of the study results, and submitting this report to BTNEP and EPA for review. Any consensus-based comments arising from this review will be incorporated into the final report. **Task 8** will be considered accomplished when the final report is approved by BTNEP and EPA.

NMFS Fishery Ecology Branch staff and contract personnel have all received undergraduate training in marine and environmental sciences. All personnel will receive training in use of sampling gear and laboratory methods prior to their use. The NMFS Standard Operating Procedures explain general operations of sampling gear and laboratory methodology (attached as Appendix 1). All training in the use of sampling gear and laboratory methods are accomplished under the supervision of the PI or the NMFS Laboratory Manager and are described in Appendix 1.

The project work schedule shown in Table 1 is based on BTNEP approval and the requirement that data not be collected until the QAPP is approved. QAPP approval is expected by March 2002, and inspection of the study area and selection of sample sites is expected to begin at that time. However, sampling dates are flexible. Provision of quarterly reports to the BTNEP Project Coordinator will begin in June 2002. The Project Coordinator will forward these reports to EPA for review. Quarterly reports will document progress toward accomplishing each task, preliminary tabulation of data as spring and fall data sets are completed, and summaries of laboratory QA/QC monitoring as appropriate. Draft final and final reports will be provided in March and April, 2003,

respectively. Draft final and final reports will include general results, tabulated data, statistical analyses, and conclusions.

Table 1. Projected Work Schedule for Accomplishing Project.

		PROJECTED COMPLETION DATE													
		2002										2003			
	TASK	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
1	Submit and have the Quality Assurance Project Plan (QAPP) approved.	X															
2	Inspect the study area and select sample sites.		X														
3	Collect 60 samples in spring.			X													
4	Process Spring 2002 samples.								X								
5	Collect 60 samples in fall.									X							
6	Process Fall 2002 samples.													X			
7	Analyze data collected and prepare a draft final report of the results for review by the action plan team. Any consensus-based comments will be incorporated in the final report.														X		
8	Prepare a final report summarizing the data. Synthesizing the results of the study, and incorporating any consensus-based comments.															X	
***	NMFS will submit quarterly progress reports with invoices during the implementation of the project. In addition, NMFS shall submit a monitoring report, requisition for payment, and other standard contract forms.					X			X			X					

A7
QUALITY OBJECTIVES AND CRITERIA FOR MEASUREMENT DATA

Project Scope

This project will produce conclusions applicable to the Barataria and Terrebonne estuaries and other coastal areas in the northern Gulf of Mexico where *Vallisneria* occurs. Results will apply to sites where *Vallisneria* habitat currently exists and to areas where this habitat type could be restored.

Project Constraints

The main constraint on this project is time. Nekton samples must be collected in April or May and September or November to coincide with peak abundance of important fishery species that occur annually during spring and fall in estuaries of the northern Gulf of Mexico. Therefore, site selection and identification of study sites must be completed before May (at the latest) if this research project is to be initiated in Spring 2002.

Project Objectives

To determine whether statistically significant ($p<0.05$) differences in mean densities of nekton (fishes, shrimps, and crabs), and more specifically for fishery species, can be demonstrated among *Vallisneria* beds and other co-occurring major estuarine habitat types.

The objective will be achieved by taking nekton samples from three major habitat types (*Vallisneria* beds, emergent marsh, and nonvegetated bottom) in spring and fall. Mean densities of common species are being compared among habitat types using analysis of variance with $\alpha = 0.05$. There are no standards for nekton densities in various estuarine habitats.

The data collected in this project will be representative of the conditions found in the Barataria-Terrebonne Basin if all procedures are followed in accordance with this QAPP. Data comparability is assured because the procedures used in this study have been used previously by NMFS in quantitative studies of nekton in Barataria Bay and elsewhere in the northern Gulf of Mexico.

Data Required to Fulfill Project Objectives

Density (individuals per m^2) data and specific identification of fishes, shrimps, and crabs are required to fulfill the project objectives. These data will be used to determine the relative value of major habitat types by comparing densities of abundant taxa among three estuarine habitat types (*Vallisneria*, marsh, and shallow nonvegetated bottom).

Data Sensitivity, Precision, Accuracy, and Completeness

The biological sampling employed in this project does not lend itself well to normal sensitivity analysis as does chemical sampling or mechanical measuring. However, analyses are still possible. The drop sampler is well suited for quantifying nekton densities in shallow estuarine habitats because the catch efficiency of this gear is high, relatively constant, and measurable (Rozas and Minello 1997). Sensitivities for the nekton variables (density and species composition) = one fish, shrimp, or crab, since less than one is not possible. The accuracy of sorting samples and identifying and enumerating organisms will be measured using the procedures outlined in the NMFS Field and Lab Standard Operating Procedures (see Appendix 1). Accuracy will be estimated by repeating a minimum of 10% of the measurements by the most experienced person (initially, the PI or the NMFS Fishery Ecology Branch Laboratory Manager) such that there is no significant difference among measurements at the 95% confidence level (Appendix 1, p. 13). Precision will be estimated by repeating a minimum of 10% of the measurements several times to achieve an acceptable standard deviation at the 95% confidence level.

Intended Uses of the Data

The project will demonstrate to state and federal agencies the habitat value of *Vallisneria* beds relative to emergent marsh and shallow nonvegetated bottom habitat types. The results of this study will be used to develop sound management plans for estuaries and estuarine-dependent fishery species.

A8
SPECIAL TRAINING/CERTIFICATION

NMFS laboratory personnel (including contractors) have all received undergraduate training in marine or environmental sciences, and some personnel have received Master's and Ph.D. level training. BTNEP personnel will receive on-site training in use of sampling gear prior to their use. Laboratory personnel will receive training in use of sampling gear and laboratory methods as part of their continuing education process.

A9
DOCUMENTS AND RECORDS

The following information and records will be included in quarterly reports to the BTNEP Project Coordinator:

1) statement describing progress toward completing tasks

2) raw data on nekton density and species composition

3) tabulated summaries of raw data

4) results of quality control procedures

Quarterly reports will provide measures of task completion. For Task 1, these measures include approval of the QAPP by BTNEP and EPA. For Task 2, these measures include dates of the preliminary inspection of study area and a map showing sample locations. For Task 3, these measures will indicate how many spring nekton samples have been collected. The measure for Task 4 will be the number of spring nekton samples processed along with preliminary estimates of nekton taxonomic composition and abundances. For Task 5, these measures will indicate how many fall nekton samples have been collected. The measure for Task 6 will be the number of fall nekton samples processed along with preliminary estimates of nekton taxonomic composition and abundances. The measures for Tasks 7 and 8 will be completion of draft and final reports, respectively. Draft final and final reports will contain full documentation of nekton taxonomic composition and densities among habitat types, a synthesis of the study results, and a discussion of major findings in the context of the scientific literature. These reports will be provided as hard copies and, if required, on diskette in standard word processing format (Microsoft Word) and data base format (Microsoft Excel). Hard and electronic copies of all reports and records for this project will be kept by the PI and by the NMFS Fishery Ecology Branch Laboratory Manager (LM) for one year after project completion.

In addition, all field data sheets, sample inventory and progress reports, individual and master sorting logs, invertebrate and fish identification sheets, quality control sorting logs, and identification correction records (see Appendix 1) will be archived by the NMFS LM as above. Permit documentation will be archived by the PI as above. A copy of the approved QAPP and any revisions will be provided to NMFS laboratory personnel by the LM.

B1
SAMPLING PROCESS DESIGN (EXPERIMENTAL DESIGN)

Densities of mobile fishes, shrimps, and crabs will be measured and compared among three different habitat types (*Vallisneria* beds, emergent marsh, and shallow nonvegetated bottom) in the study area. A drop sampler, a standard quantitative sampling gear, will be used to collect nekton samples in each habitat type (Zimmerman et al. 1984). Nekton samples will be preserved in formalin until processed. Sampling and processing methods are described in detail in sections A6 and B2.

Sample Requirements

A total of 60 nekton samples each will be taken in spring and fall for a total of 120 samples. The PI and the NMFS Lab Manager will be responsible for retrieving substitute samples should the original sampling or measurement systems fail during use of gear or analytical procedures.

Sampling Guidelines

The sampling locations will be chosen within the southwest portion of Little Lake and Bay L'Ours where we identify established *Vallisneria* beds during our preliminary inspection of the study area in March 2002. Extensive *Vallisneria* beds in the area have been documented in the past. Nekton samples will be collected at random locations in each habitat type within the study area.

Sample Classification

Sample measurements of nekton density in each habitat type are classified as critical. Measurements of density for common fishery species in the three major habitat types are required to achieve project objectives.

B2
SAMPLING METHODS

The drop sampler is a fiberglass enclosure with a galvanized metal skirt along the bottom. The device samples 1-m^2 of bottom habitat when released from a boom mounted on the bow of a shallow-draft boat (Zimmerman et al. 1984). To collect a sample, the engine is turned off as the boat approaches the sampling site to minimize site disturbance prior to sampling. The boat is allowed to drift or is slowly guided to the sampling site by pushing from the stern. When the boat reaches a sample site, a person in the boat releases the drop sampler. Immediately after deployment of the drop sampler, field personnel will push the sampler approximately 15-cm into the sediment to obtain a proper seal along the bottom, thereby preventing the escape of organisms or a blow-out.

At marsh sample sites, vascular marsh plants enclosed in the sampler will be clipped at ground level to assist in retrieving animals. At sample sites containing submerged aquatic vegetation (SAV), we will use a quadrat sectioned into 25 equal-size squares and placed on the substrate inside the sampler to estimate percent vegetative coverage. If SAV is present inside a given square, the entire square is considered vegetated. Percent coverage will be determined by dividing the number of vegetated squares by the total number of squares (25) and multiplying by 100.

After pushing the drop sampler into the substrate, we will use dip nets to sweep the bottom of the sampler and remove nekton. We will then pump the enclosed water from the sampler and filter it through a 1-mm mesh plankton net. As the water level drops, the sampler will be continually swept with dip nets because efficiency of animal capture increases with reduced water depth. Once the sample area is drained, we will visually and manually inspect the area inside the sampler for animals remaining on or burrowed into the sediment. Animals taken in dip nets or found during substrate inspection will be placed into the plankton net. Animals and other material (vegetation, macro-algae, shell hash, and detritus) pumped into the plankton net will be rinsed and the cod-end containing the sample will be detached from the net. The sample will then be labeled, preserved, and returned to the laboratory for processing as described below.

Labeled, waterproof shipping tags are placed inside and attached to the outside of each bag containing animal samples. Sample bags are immediately placed on ice in coolers. Samples are completely covered with ice at all times to prevent degradation prior to fixing with formalin. At the end of the day, samples are stored in 3- or 5-gallon buckets containing 10% formalin. Ten percent formalin is made by mixing one part full-strength formalin (37% formaldehyde) with nine parts water. If animals are too large to fit in a sample bag, the specimen is identified, measured, recorded on the field sheet, and released.

B3
SAMPLE HANDLING AND CUSTODY

Field data will be recorded on waterproof paper and will include: 1) project name, 2) sampling gear, 3) date, 4) location/site, 5) sample number, 6) time, and 7) habitat type. See Appendix 1, Appendix Table 3 for sample data sheet.

Nekton samples will be collected and processed using the Standard Operating Procedures of the NMFS Galveston Laboratory Fishery Ecology Branch (see Appendix 1). All nekton samples will be placed in mesh bags, labeled with unique site/date codes on waterproof paper tags inserted in the container, initially fixed in buffered 10% formalin, identified, then stored in 70% isopropanol. Formalin-preserved samples are stored in plastic buckets with snap-on lids. Waterproof paper identification tags will have the following components: 1) project name, 2) sample number, 3) date, and 4) sampling gear (see Appendix 1, p. 3). All field samples are returned to the laboratory by boat and van. Standard references will be used for identification of fishes and invertebrates in the laboratory. Taxa will be identified, counted and recorded on habitat-specific data sheets for later computer entry. As samples are processed in the laboratory, they will be checked against the field data sheets. Nekton samples collected in a given month will be completely analyzed within five months. Nekton samples will be retained for one year after the last sampling period, then discarded unless otherwise requested.

B4
ANALYTICAL METHODS

Field measurements of *Vallisneria* areal coverage and laboratory identification and measurement of fishes and decapods require no special equipment beyond quadrats and drop samplers, neither of which have moving parts or need calibration. Replacements for these sampling gear are available in case of malfunction.

B5
QUALITY CONTROL

For laboratory processing of nekton samples, personnel will be using the Standard Operating Procedures of the NMFS Galveston Laboratory Fishery Ecology Branch (Appendix 1). The Laboratory Manager will randomly examine 10% of the faunal samples immediately after they are completed by fishery biologists in the laboratory, comparing both sorting (separating animals from extraneous material in sample), taxonomic identification, and counts. If the accuracy of any particular biologist falls below 90% for sorting or 95% for counts and identification, all portions of each sample processed by that individual will be re-processed under the supervision of the Laboratory Manager.

B6
INSTRUMENT/EQUIPMENT TESTING, INSPECTION, AND MAINTENANCE

Field samples of nekton and *Vallisneria* cover and laboratory identification and measurement of fishes and decapods require no special equipment beyond quadrats and drop samplers, which have no moving parts and need no calibration. Replacements for these sampling gear are available in case of malfunction.

B7
INSTRUMENT/EQUIPMENT CALIBRATION AND FREQUENCY

Field samples of nekton and *Vallisneria* cover and laboratory identification and measurement of fishes and decapods require no special equipment beyond quadrats and drop samplers, which have no moving parts and need no calibration. Replacements for these sampling gear are available in case of malfunction.

B8
INSPECTION/ACCEPTANCE OF SUPPLIES AND CONSUMABLES

Manufacturer's specifications or laboratory standard operating procedures define the criteria necessary for purchasing supplies and consumables. These criteria are used to purchase materials from reputable scientific supply houses. Labels on incoming materials are compared to those specified in manufacturer of laboratory standards by the NMFS Laboratory Manager. Only correctly labeled and sealed supplies and consumables are accepted.

B9
NON-DIRECT MEASUREMENTS

There are no data acquisition components to this project.

B10
DATA MANAGEMENT

After returning from the field, samples are recorded in the log book in sequential order. The log book serves as a sample inventory and is used to verify sample arrival and condition. Field data are entered into an electronic file in sequential sample order using Microsoft Excel or another data base manager. Data entered include project name, sampling date and time, PI, gear type, area sampled, sample number, environmental measurements, GPS coordinates of sample site, and any sampling comments. Entered data are checked and verified against field sheets. Date and last name of the person entering the data are entered, and a printout is given to the NMFS Laboratory Manager and the PI for review.

Laboratory data also are entered into the computer using Microsoft Excel or another data base management program. A text file is created that describes the data. The data are printed out and checked against ID sheets to ensure all information is correct. Corrections to data are made at this time. The person verifying and correcting the data initials and records the current date on the printout after making corrections. A hard copy of the file is stored in the project folder along with original field and laboratory data sheets.

When finalized, electronic data files are given to the NMFS Laboratory Manager for review before turning them over to the PI. The data are saved as both an Excel file with the extension 'xls' and with a 'csv' extension. Data with a 'csv' extension are much smaller, less likely to be corrupted, and easily transferred across platforms [PC and Macintosh]. Final computer files are saved in four locations: (1) 3.5" floppy disk given to PI; (2) 3.5" floppy disk kept in the NMFS Taxonomy and Ecology Laboratory; (3) back-up zip cartridge or CD kept in NMFS Taxonomy and Ecology Lab; and (4) back-up file transferred through NMFS LAN for storage. After computer files are saved to these four locations, the name and location of each file and disk are recorded in the computer file log-book located in the NMFS Taxonomy and Ecology Laboratory computer room and also on the inside cover of the project folder.

C1
ASSESSMENTS AND RESPONSE ACTIONS

Surveillance:

The PI is responsible for ensuring that all data collection personnel have adhered to all data collection procedures. This will include checks of field and laboratory procedures and analysis of field and laboratory data collection forms. Estimates of *Vallisneria* cover should agree within 10% between the PI and field personnel while in the field. Laboratory measurements will be monitored by the NMFS Laboratory Manager for compliance with NMFS SOPs. If necessary, corrective measures will be implemented immediately by either the PI or the NMFS Laboratory Manager. Response actions and corrective measures will be documented in writing by the PI and the Project Coordinator.

Data Reviews:

The Project Coordinator will review data generated by the project on a quarterly basis. Results of the review will be provided to the PI who will initiate immediate corrective action, if necessary. Corrective actions will be documented in writing by the PI and the Project Coordinator. All reports submitted by the PI to the Project Coordinator for review by the U. S. EPA Region VI will be reviewed first by the Project Coordinator to ensure that all issues are addressed.

U. S. EPA Region VI Review:

Quarterly reports will be submitted to the EPA Region VI Project Officer. The Project Officer will assess quarterly technical reports, project QA/QC compliance with the QAPP, and will approve and accept the final products and deliverables. EPA comments on QA/QC inadequacies will be directed to the Project Coordinator. Corrective actions will be documented in writing from the Project Coordinator to the EPA Project Officer.

C2
REPORTS TO MANAGEMENT

Quarterly reports will be prepared and issued by the Principal Investigator to the BTNEP Project Coordinator, who will forward them to all personnel on the QAPP distribution list. The quarterly reports will contain the following information:

- Status of project, in terms of completion of tasks, objectives, and deliverables
- Results of quality assessments
- Significant quality assurance problems and recommended solutions
- Raw data and tabular summaries of raw data, as appropriate

D1
DATA REVIEW, VERIFICATION, AND VALIDATION

Data generated during the course of this project that have adhered to all sampling procedures and protocols will be accepted as valid. Critical data must conform to reasonable standards given below:

- nekton density < 200 individuals m^{-2} *
- nekton species composition - only species known to inhabit the Gulf of Mexico

where asterisk (*) indicates maximum observed in previous studies in the same geographical area (Rozas and Minello 1999, Rozas and Minello, unpublished data)

Habitat-related nekton density differences during each sampling period will be examined by analysis of variance (ANOVA) with $\alpha = 0.05$. Tests will be conducted for differences in percent *Vallisneria* coverage and density of dominant and total fishes and decapods (dominance defined as species averaging ≥ 1 individual m^{-2}). One-way ANOVA will be used to compare nekton densities among habitat types. Data will be transformed (if necessary) prior to ANOVA as follows: arcsine for percentages; log (x+1) for counts.

D2
VERIFICATION AND VALIDATION METHODS

Data verification, validation, chain-of-custody, and transfer are all conducted according to NMFS Standard Operating Procedures (see Appendix 1, which includes samples of forms used). Basically, all data are initialed by the recorder at each step, then reviewed by a peer or supervisor before final acceptance.

D3
RECONCILIATION WITH USER REQUIREMENTS

For this research project, there is no right or wrong answer. Densities of fishes and decapods will be compared among the three habitat types using statistical tests. Results of these tests will be useful in documenting the relative habitat value of *Vallisneria* beds for fishery species.

However, results obtained from this project will be evaluated and measured against the data quality objectives given in Section A7. The results will be reconciled as follows. Assuming that *Vallisneria* beds in the study area function similar to other types of SAV habitat types, it is hypothesized that we will document a greater abundance of fishes and decapods in these *Vallisneria* beds than over shallow nonvegetated bottom and similar abundances of these animals in *Vallisneria* and emergent marsh. This will be verified by finding statistically significantly higher mean faunal densities in *Vallisneria* beds than in shallow nonvegetated areas and higher or similar mean densities of animals in *Vallisneria* than in emergent marsh at the 95% level. If this criterion is met, it will be concluded that the presence of *Vallisneria* beds does enhance local productivity of fishery and forage organisms and the recommendation will be to protect these areas and restore areas that previously contained this habitat type. If the hypothesis is rejected, then relatively high habitat value for *Vallisneria* will not have been demonstrated, and the need for new protective measures or restoration of this habitat type will have to be re-considered.

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Appendix 2

National Marine Fisheries Service Galveston Laboratory

Field and Lab Standard Operating Procedures

March 14, 2001

Field and Lab Standard Operating Procedures

for

Quantitatively Sampling Nekton and Associated Organisms in Shallow Estuarine Habitats

National Marine Fisheries Service
Galveston Laboratory
Fishery Ecology Branch
4700 Avenue U
Galveston, TX 77551

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Field Trip Preparation

Vehicles and boats need to be reserved, equipment repaired, necessary supplies purchased, and everything packed in advance. One fishery biologist/technician is assigned as trip organizer to oversee preparation prior to each collecting trip. The Principal Investigator (PI) arranges hotel accommodations for overnight trips, requests travel orders for each participant, obtains all required collecting permits, and provides the trip organizer with an itinerary and **checklist of required equipment and supplies** [Appendix Table 1]. The trip organizer ensures that all supplies and equipment are available, including purchase and replacement of any items not currently on hand.

About one week before trip departure, vehicles, pumps, trailers, boats, and boat motors are tested to ensure proper function. Boat trailers are checked for working brake lights, turn signals, and proper tire inflation (check spare tire also); and "buddy bearings" are filled with grease. Vehicle, pump, and boat gas tanks are filled the day before departure. Pumps are filled with motor oil and all moving parts are lubricated. Any pivot points on the pumps (e.g., for governor mechanisms, choke, or throttle) are lightly oiled. Boats are loaded with the required safety equipment, including a Type I, II, III, or V PFD for every occupant and at least one throwable device (e.g., seat cushion) per boat. Drop boats are checked to insure that booms are in lowered position for highway travel. If possible, vehicles are loaded with all required supplies and equipment and hitched to boat trailers the day before departure.

Standardized waterproof data sheets and sample labels* are prepared in advance by filling in as much information as possible (using pencil or waterproof and alcohol-resistant ink), thereby minimizing label preparation time in the field. Standardized labels should contain project name, sample number, date, and gear. Three- or five-gallon buckets are filled approximately 1/3 full with 10% pH-adjusted formalin (Carson's solution) for fixing samples in the field. A sample label is taped to the lid or side of each bucket sent into the field to record bucket contents. Carson's solution is prepared in the lab using seawater (see instructions, **Appendix Table 2**).

Field Sampling Procedures

Description of Sampling Gear:

Two types of throw traps and a cylindrical drop trap are used to sample small nekton such as fish and crustaceans in vegetated and non-vegetated areas depending on

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* **Labels should contain a code that is unique to each project and sample. Each code selected by the PI will be composed of a project acronym, date (year), and sample number (numbered sequentially beginning with the number "1"). For example, JB2000-1 and HSC2001-23 would be written on labels for the first sample of the "Jamaica Beach" project collected in the Year 2000 and the twenty-third sample of the "Houston Ship Channel" project taken in the Year 2001, respectively.**

habitat type. Mesh throw traps are used to sample muddy or soft bottom areas. Mesh throw traps are either 1-m or 1.5-m high and constructed of 1.6-mm nylon mesh netting attached to square top and bottom frames (1 m on a side). The top frame is a foam-filled PVC pipe that floats. The bottom frame is constructed of steel (0.64-cm diameter) which causes the net to rapidly sink preventing organism escape. Solid wall, aluminum throw traps are used to sample over sand-bottom or hard-bottom substrates. Solid throw traps are square as well, and either 50-cm or 76-cm high. These throw traps are used in areas where the added weight of the aluminum allows the trap to sink or be pushed into the sand, thus preventing organism escape by ensuring a good seal along the bottom. Both types of throw traps enclose 1-m^2 of bottom and sample shallow waters. Cylindrical drop traps or drop samplers are used in water up to 1.5-m deep and allow sampling of intertidal marsh habitat where the rigid structure of the vegetation often precludes the use of throw traps. The drop trap is a fiberglass enclosure with a galvanized metal skirt along the bottom. Drop traps enclose either 1-m^2 or 2.6-m^2 of bottom depending on trap size. Throw traps are tossed from the bow of the boat or while wading in shallow water, whereas drop traps are released from a bow-mounted boom [Figure 1].

Measuring Environmental Variables:

Environmental data are collected immediately after deployment of drop or throw traps and before animals are collected. Data collected in the field are recorded on standardized waterproof field sheets [Appendix Table 3]. A *GPS reading* is taken for each sampling site. When there is a marsh in the general vicinity of the sampling site, *distance of sample site (measured from center of sampler) to the marsh edge* (in meters) is determined and recorded along with whether the marsh is flooded. *Water temperature* and *salinity* are measured and a water sample taken for *turbidity*. Salinity also is checked by refractometer upon return to the lab. Water temperature and salinity are measured either inside the sampler or in a nearby undisturbed area of the same habitat type. Water depth is taken with a meter stick at the center and in each of four quadrants inside the sampler and recorded to the nearest cm. Additional variables may also be required for specific projects. Field sheets are checked to ensure all required and optional environmental data are correctly recorded. The data recorder then prints his/her first initial, last name, and the date at the bottom of the field sheet.

Sampling of Nekton and Associated Plants:

The engine is turned off once the boat approaches the sampling site to minimize site disturbance prior to sampling. The boat drifts or is slowly guided to the sampling site by pushing from the stern. One person in the boat either tosses the throw trap from the bow or releases the drop trap. Immediately after deployment of the drop trap, field personnel push the sampler approximately 15-cm into the sediment to obtain a proper seal along the bottom, thereby preventing the escape of organisms or a blow-out. Environmental data are collected next (see above). If the sample is taken in a marsh, vascular marsh plants enclosed in the sampler may be clipped at ground level to assist in animal retrieval. If required, these marsh plants are placed in labeled plastic bags, stored on ice, and returned to the lab to determine stem density and standing biomass. If a sample includes seagrass or submerged aquatic vegetation (SAV), an appropriate size quadrat sectioned into at least 25 squares is placed on the substrate inside the

sampler to determine percent vegetative coverage. If SAV is present inside a given square, the entire square is considered vegetated. Percent coverage is determined by dividing the number of vegetated squares by the total number of squares and multiplying by 100. Plant species are identified and recorded in the field if possible; unidentifiable plants are placed into labeled plastic bags, put on ice, and returned to the lab for identification (ID). If information on SAV biomass or leaf density is required, bottom samples are collected with plastic cores (core size/diameter and depth must be recorded), rinsed through a 0.5-mm sieve to remove sediments, and returned to the lab in plastic bags on ice or preserved. When a clearing net is used with a mesh throw trap (see below), vegetation from inside the sampler is removed first in order to facilitate animal removal.

Removal of Animals from Samplers:

Mesh throw traps:

Clearing nets are used to remove animals from mesh throw traps. A clearing net is constructed of 1.6-mm nylon mesh stretched across a 1.3-m^2 frame made from 0.64-cm diameter steel bar. Two people clear the throw trap. First, the leading edge of the clearing net is placed against one side of the trap. The clearing net is pushed through the top layer of sediment and under the trap. Once the clearing net is completely under the trap, the net and trap are lifted out of the water together. The throw trap is lifted from atop the clearing net and the contents rinsed to remove sediment. Rinsed samples are placed in a 1-mm mesh bag, labeled, preserved, and returned to the lab for processing as described below.

Solid-wall aluminum throw traps:

Organisms are removed from solid-walled throw traps by sweeping the inside of the sampler with an aluminum bar seine. The bar seine resembles a square dip net with either 3.0-mm or 1.6-mm mesh netting (depending on study objectives) and is designed to sweep a 1-m^2 area of the sampler water. The bar seine is swept from alternating sides of the trap until three consecutive passes yield no organisms or for a minimum of ten passes. Organisms are removed from the bar seine, placed in a 1-mm mesh bag, labeled, preserved, and returned to the lab for processing as described below.

Drop traps:

After the drop trap is pushed into the substrate, dip nets are used to sweep the bottom of the trap and remove nekton. Enclosed water is then pumped from the trap and filtered through a 1-mm mesh plankton net. As the water level drops, the sampler is continually swept with dip nets because efficiency of animal capture increases with reduced water depth. Once drained, the sediment is visually and manually inspected for animals remaining on or burrowed into the sediment. Animals taken in dip nets or found during substrate inspection are added to drop trap catch. Animals and other material (vegetation, macro-algae, shell hash, and detritus) pumped into the net cod-end are rinsed and the bag is detached. Samples are labeled, preserved, and returned to the laboratory for processing as described below.

Gear Catch Efficiency:

Catch efficiency has two components: gear capture efficiency and recovery efficiency (Kjelson and Colby 1977). Gear capture efficiency is the proportion of target animals within the sample unit area that is enclosed or captured by the gear. Capture efficiency is reduced by gear avoidance. Recovery efficiency is the proportion of target animals enclosed by or taken into the gear that is recovered from the sampling device and enumerated. Recovery efficiency is diminished, for example, if some animals within a sampler cannot be recovered or if small organisms escape from a sampling device through large-mesh netting.

Enclosure samplers such as throw traps and drop traps generally have high catch efficiencies; although efficiencies depend on gear type, method used to remove animals from the enclosed sample area, target species, and environmental conditions (especially water clarity). Kushlan (1981) estimated a catch efficiency of 70-76% for a 1-m^2 throw trap by sampling an enclosed area in which the total population was later estimated following an application of rotenone. A catch efficiency of 96% for a 2.6-m^2 drop sampler was estimated by sampling a small pond into which a known density of penaeid shrimp had been added (Zimmerman et al. 1986). Jordan et al. (1997) estimated the mean catch efficiency of a 1-m^2 throw trap at 63% (range=43-84%) using a method similar to that of Kuslan (1981).

Recovery efficiencies for throw traps and drop traps are easy to measure and values for these gear reported in the literature are relatively high. The efficiency of recovering animals from the enclosed sample area of these devices can be measured either by using marked animals (Rozas and Odum 1987, Jordan et al. 1997) or using depletion estimates (i.e., fitting the data from repeated recoveries within the sampler to an exponential decay function) (Kneib 1991, Connolly 1994). Recovery efficiencies have been reported as follows: 91-98% (Zimmerman et al. 1986) and 82% (Sheridan 1992) for 2.6-m^2 drop sampler; 93-100% for 1-m^2 (Rozas and Odum 1987), 44-66% for 1.5-m^2 (Wenner and Beatty 1993), and 85-100% for 2-m^2 (Rozas and Reed 1994) throw traps. No sampling device is completely unbiased, and an evaluation of gear limitations should be done routinely prior to selecting sampling gear for studies to estimate population densities (Rozas and Minello 1997).

Care of Nekton Samples in the Field:

Labeled, waterproof shipping tags are placed inside and attached to the outside of each bag containing animal samples. Sample bags are immediately placed on ice in coolers. Samples should be completely covered with ice at all times to prevent degradation prior to fixing with formalin. At the end of the day, samples are stored in 3- or 5-gallon buckets containing 10% formalin. Ten percent formalin is made by mixing one part full-strength formalin (37% formaldehyde) with nine parts water. If animals are too large to fit in a sample bag, the specimen is identified, measured, recorded on the field sheet, and released. Specimens of red drum, spotted seatrout, mullet, or southern flounder are occasionally required for diet and feeding studies. If so, stomachs of large specimens are removed and preserved in a labeled jar.

Sampling of Benthic Infauna and Sediment:

A 50x50-cm square quadrat constructed of PVC pipe and divided into at least 25

squares (10-cm^2 each) is placed on the sediment surface either inside or adjacent to the nekton sampling device. Benthos cores (5-cm diameter and 5-cm deep) are extracted from three randomly selected squares inside the quadrat. These three core samples are pooled to represent a 60.8-cm^2 area. Samples are sieved through a 0.5-mm mesh net and placed in a bag along with a waterproof shipping tag containing project name, date, sample number, and other information. The core sample is preserved in 10% formalin solution with Rose Bengal added. Rose Bengal assists in sorting by staining organisms pink or red, although some organisms resist stain. If requested, a sediment core may be randomly extracted from inside the quadrat to determine organic content and grain size. Sediment cores are placed in labeled plastic bags, stored on ice, and refrigerated or frozen back in the lab.

Procedures Following a Field Trip:

On returning to the laboratory after a field trip, vehicles, boats, pumps, and all other equipment that were exposed to salt water are thoroughly washed with freshwater. All electronic equipment is wiped clean, dried, and properly stored. Pumps and the cooling system of outboard motors are flushed with freshwater. Care should be used when washing pumps. Do not flush interior exhaust or blast water into air intake. After washing pumps, allow to air dry or wipe entire unit with dry cloth. Access plate to pump impeller is removed and interior of plate and threads of bolts and nuts are coated with Vaseline or anti-seize grease. Pump air filter is checked and threads to fastening bolts are coated with Vaseline. Pump hose fittings are coated with Vaseline. Grease reservoir on pump engine is filled. Pump engine oil is checked and filled if needed (Oil is changed immediately, if water is observed in the oil). All pivot points on pump engines (e.g., for governor mechanism, choke, or throttle) are lightly oiled.

Laboratory Procedures

Initial Processing of Field Data and Samples:

After returning from the field, samples are recorded in the log book in sequential order. The log book serves as a sample inventory and is used to verify sample arrival and condition. Sample buckets are unloaded and placed in the designated yellow environmental spill-containment trays until sorted. Sediment samples are organized by number and refrigerated or frozen until processed. Turbidity samples are analyzed immediately after returning to the lab, and the information is transferred to the field data sheets. Field data are entered into an electronic file in sequential sample order using MS Excel or a data base manager. Data entered includes project name, sampling date and time, PI, gear type, area sampled, sample number, environmental measurements, GPS coordinates of sample site, and any sampling comments. Copies of the original field data sheets are provided to the PI. Entered data are checked and verified against field sheets. Date and last name of the person entering the data are printed on the **Sample Inventory and Progress Report** sheet [Appendix Table 4], and a printout is given to the Lab Supervisor and PI for review.

Laboratory Processing of Nekton Samples:

Master and Individual Sorting Log:

Fishery biologists/technicians are assigned to a particular project team as necessary. Each project team processes one sample at a time to reduce the possibility of sample mix-up. Each person sorting a portion of the sample has an **Individual Sorting Log** [Appendix Table 5] and records the daily number of organisms found in his/her portion of the sample and amount of sorting time required. This information assists in the quality control of individual sorters. In addition, every person on the project team that sorts a portion of any sample should initial the **Master Sorting Log** [Appendix Table 6].

Caution: Gloves, protective clothing, and eye protection should be worn when working with hazardous chemicals (including formalin).

Sample Sorting:

1. The next, consecutive, unsorted sample is selected from the Master Sorting Log.

2. Sample jar is retrieved and a second tag is prepared containing all information from the original sample tag, and the word "sorted". After information on the new tag is double-checked, the new tag is taped to the outside of another sample jar that contains the sorted portion of the sample. Each sorter has a labeled jar with his/her initials in which to store the portion of the sample he/she sorted (anything other than fish, shrimp, and crabs).

3. The sample is strained through a sieve. The formalin solution is saved in a container labeled 'Used Formalin' and is re-used to preserve plant material. The contents of the sample are rinsed with tap water under a fume hood to remove excess formalin. A portion of the rinsed sample is then placed in a white porcelain sorting tray (40-cm x 24-cm x 6-cm) partially filled with water. The tray is rough sorted for large organisms and the vegetation is examined for clinging invertebrates. The tray is turned 90° and re-examined to ensure that no organisms are missed. Each sorter keeps an individual tally of the number of fish, shrimp, and crabs in his/her portion of the sample. Every time the sorter leaves the sorting area for an extended period, tally counts are written down to prevent loss of data if another sorter borrows the counter. When each sorter finishes for the day, they record the number of organisms in each category on the **Individual Sorting Log** [Appendix Table 5]. Organisms from all individual sorters are combined into one jar and the total number of organisms in each category are recorded on the **Master Sorting Log** [Appendix Table 6].

4) After the sample is sorted, *the sample and specimen jars are filled with 2-3% formalin (i.e., mixture of 0.25 part full-strength formalin and 9.75 parts water). Jars should never be more than about 1/3 full of organisms.* The original tag is transferred from the original sample to the specimen jar containing organisms from all sorters. The specimen jar and sorted gallon sample jars are then placed in the designated area separate from the unsorted samples.

***Species Identification, Measurement, and Sub-sampling Procedures*:** [Appendix Tables 7 - 9]

1) A specimen jar is selected for identifications. Samples are processed in numerical order unless otherwise directed. Since accurate species identifications are a vital part of any survey, new biologists must demonstrate an adequate knowledge of taxonomy by keying out reference specimens under the direction of the lab supervisor before they begin to process samples. This confirms the classifier's familiarity with taxonomic characters and keys.

2) A separate sample tag is prepared for each target species (e.g., pink shrimp and brown shrimp) contained in the sample. After double-checking information on each new tag, place tag in each vial/jar or plastic bag that will contain the target species. Specimens are initially rough sorted and fish and crabs are transferred into one jar and shrimp into a separate jar. Each species of shrimp is placed into a separate vial. Specimen ID is begun and the species name is recorded on the appropriate **Identification sheet** [Appendix Tables 7 - 9].

3) The largest and smallest individuals of each species (i.e., min-max lengths) are located and measured. All specimens are measured if there are <22 total specimens of a given species (20 + largest + smallest). If there are >22 specimens of a species, a sub-sample of 20 specimens is randomly measured [see sub-sampling procedures below]. A total count of each species is recorded even though only 22 specimens of a given species are measured.

4) Organisms are measured to the nearest millimeter to determine total length (TL), standard length (SL), or total carapace width (CW). Two measurements are taken on fish. Each specimen should be measured after it has been placed flat on its side and its mouth closed. **TL** is the distance from the snout to the tip of the longest caudal fin ray. **SL** is the distance from the snout to the base of the caudal fin. Two measurements are taken on penaeid shrimp if the rostrum is intact. TL is measured from the tip of the rostrum to the tip of telson [Figure 2]. If the rostrum is broken, "broken rostrum" is recorded on the data sheet for that specimen and its TL is not measured. Postorbital carapace length (**POL**) is measured on all shrimp. POL is measured from the postorbital margin to the posterior edge of the carapace along the dorsal midline (Perez-Farfante 1988). A single measurement is taken on crabs. Carapace width (**CW**) of crabs is measured across the widest part of the carapace (from tip to tip of the lateral spines if present) [Figure 3]. If lateral spines are broken, "broken lateral spine" is recorded on the data sheet for that individual and its CW is not measured. Hermit crabs are not measured.

5) After measuring and identifying specimens, fish are placed in one jar and decapods (crabs and shrimp) into another. Pink shrimp and brown shrimp are placed in separate vials or bags by species and placed into the decapod sample jar.

6) Identification and sample data are written in pencil on a waterproof tag and taped to the lid of each specimen jar. Sample jars are boxed for storage and labels are placed on the side and top of each box containing project name, date, and sample numbers enclosed inside the box.

Identification of Organisms Missing Appendages:

If an organism is missing a character necessary for proper identification, the organism is identified to the lowest possible taxon and recorded as 'unidentified (taxon name)'. Each incomplete organism and the missing part(s) are recorded on the data sheet under 'Comments'. For penaeids, count only heads or only tails but not both. Other fragments are counted only when they clearly represent a single organism.

Sub-Sampling Procedure for Measuring Size in Large Samples:

If greater than 22 individuals of a given taxon are present in the sample, then sub-sample that taxon to select individuals for measuring size. First, remove the largest and smallest specimens from the sample and measure them. Place the remaining specimens in a 15-cm plastic petri dish that is sub-divided into 9 squares. Distribute specimens evenly throughout the dish. Use random numbers to select the squares (1-9) to sub-sample. If >50% of the body of an organism is inside a given square, consider that this animal is entirely within the square. Continue randomly selecting animals in this manner until 20 specimens have been selected for measurement. Count all specimens remaining in the dish and add 22 to arrive at the total number of individuals for that taxon.

Preservation and Storage of Fish and Invertebrates:

After sorting and identification, organisms are preserved in 70% ETOH (i.e., mixture of 7.4 parts 95% ETOH and 2.6 parts water) for long-term storage. Sample jars are always filled with preservative and lids should be taped to prevent loosening and fluid evaporation. Samples are boxed by project and stored in the dark at the appropriate location to minimize color loss; jars are periodically checked to monitor their condition. See **Chemical Preparation** [Appendix Table 2]. A detailed description of where the processed samples are stored is included in the project's file folder located in the Taxonomy and Ecology Lab to assist in easy retrieval of samples.

Laboratory Processing of Benthic Core Samples:

After a benthic core is selected for sorting, the following procedure is used to track the sample:

1. The sample tag is located and the sample number is recorded in the log book along with the word 'benthos', sorter's first initial and last name, and current date.

2. Three new sample tags are prepared which contain all information on the original tag. After double-checking information on the new tags, 'annelids' are written on the back of the first tag and 'other inverts' on the back of the second tag. Each tag is placed in a vial. The third tag and both smaller vials are placed into a larger jar after the sample is sorted.

3. The sample is poured under the fume hood through a 0.5-mm mesh sieve. A gallon jar is placed under the sieve to collect the formalin. The gallon jar is removed and the sample rinsed with tap water to remove excess formalin. A sieve with a smaller mesh size is placed under the running water so that any organisms rinsed from the sample are retained on the sieve. Vegetation is untangled using forceps and each piece is rinsed. Intact seagrass (those plants complete with stems and roots) are rinsed, placed in a small tray, and set aside.

4. The original sample tag is placed in a plastic bag with the seagrass. The seagrass is preserved with the 2-3% waste formalin and placed in the designated seagrass bucket. After intact seagrass is removed, material remaining on the sieve (primarily detritus and shell fragments) is transferred to a sorting tray. The sieve is examined for remaining animals and these are transferred to the appropriate sample vial.

5. Small amounts of material are transferred from the tray of mainly detritus and shell hash into a petri dish partially filled with water. A petri dish with numbered quadrats assists in keeping your place in the dish. Contents are examined under a dissecting microscope and animals are removed. Two full revolutions are made through the material and organisms are transferred to ETOH for long-term storage.

Annelids, **crustaceans**, and **mollusks** are the dominant groups found in benthic cores. Other types of animals such as sea cucumbers and brittle stars are also found in samples. All annelids are placed in a vial marked 'annelids' and all non-annelids in a second vial marked 'other'.

All **gastropod shells** are examined for occupants by looking for either an operculum (which is usually stained dark purple) or the body of a mollusk in the aperture of the shell. If the sorter is unsure whether the shell is occupied after examination, the entire shell is placed in the sample vial. Do not damage the shell since it is important for the proper identification of mollusks.

Measuring Biomass of Plants and Animals:

Emergent marsh plants: If requested, emergent marsh plants are sorted and stored in mesh bags to air dry.

1) Sample tag is located. Sample number is recorded in the sorting log book along with the words 'marsh plants' or the species name, sorter's initial and last name, and current date.

2) Plants are separated by species (if necessary) and number of stems counted.

3) If dry weight is requested, plants are placed in a drying oven at 60° C to a constant weight.

Seagrass and freshwater SAV: If collected, seagrass and SAV samples are stored in the refrigerator or in 10% formalin.

1) Sample tag is located. Sample number is recorded in the sorting log book along with the words 'seagrass' or 'SAV', or the species name. Sorter's initial, last name, and current date are also recorded.

2) Sample is rinsed through a sieve under the fume hood.

3) Seagrasses are placed in a pan partially filled with water and separated by species (if necessary). Shoots are separated from roots/rhizomes, number of shoots is counted, and longest, undamaged leaf length (mm) is measured and recorded.

4) A set of numbered and pre-weighed foil drying pans are then prepared.

   a) If wet weight is required, plant is blotted dry, placed in a pre-weighed drying pan, and weighed to the nearest 0.0001 gram.

   b) If dry weight is required, the plant is put in a pre-weighed pan and placed in the drying oven at 60° C for 24 hrs. Sample is re-weighed again after 24 hrs and every 12 hrs thereafter until a constant weight is obtained. The tray is removed from the drying oven and placed in the dessicator to cool and prevent re-absorption of ambient moisture before final weighing. Foil pan + plants are weighed. Plant dry weight is obtained by subtraction.

Wet or dry weights are taken for animals by following these same procedures.

Organism Data Entry and Validation

Laboratory and field data are entered into the computer using a spreadsheet (e.g., Microsoft Excel) or data base manager. A text file is created that describes the data set and any abbreviated variables. The data are printed out and checked against ID sheets to ensure all information is correct. Corrections to data are made at this time. The person verifying and correcting the data initials and records the current date on the printout after making corrections. Hard copies of the file are given to the PI and stored in the project folder along with the original field and laboratory data sheets.

The electronic data file is then transformed in preparation for statistical analyses. A code is assigned to each species using the Fishery Ecology Branch revised species code list. Species not found on the code list are assigned a new code number which is added to the master code file. When finalized, data files are given to the Lab Supervisor for review before turning them over to the PI. The data should be saved as both an Excel file with the extension '.xls' and with a 'csv' extension. Data with a '.csv' extension are much smaller, less likely to be corrupted, and easily transferred across platforms [PC & MAC].

Final computer file is saved as follows:

(1) 3.5" floppy disk given to PI;
(2) 3.5" floppy disk kept in Taxonomy and Ecology Lab;
(3) Back-up zip cartridge or CD kept in Taxonomy and Ecology Lab;
(4) Back-up file transferred through LAN to Frank Patella for storage.

After computer files are saved to these four places, the name and location of each file and disk are recorded in the computer file log-book located in the Taxonomy and Ecology Lab computer room and also on the inside cover of the project folder.

Quality Control/Quality Assurance

Sorting Accuracy:

As samples are sorted, each sorter puts his/her individual portion of the sample in a jar clearly labeled with sample information and sorter name. This method allows determination of individual sorter accuracy and the cumulative accuracy for the entire sample. Initially, 10% of the total number of samples collected for a project are randomly selected for QC. If the accuracy of a particular sorter falls below 90%, all portions of that sorter's most recent five samples are re-examined. This procedure reduces the time necessary for QC by restricting re-sort time to smaller portions of the sample. In addition, individual sorters can be retrained. Furthermore, this procedure allows subsequent determination of the need to resort the sample if the mean total accuracy of all sorters is above 90%. If sorting accuracy of the total sample remains consistently high, the number of QC'd samples can be reduced to 5% [Appendix Table 10].

Identification and Measurement Accuracy for Nekton Samples:

Each fishery biologist/technician involved with sample ID uses a specimen sheet to record characters they used for identification [Appendix Table 8]. After organisms are identified, measured, and weighed using **S**tandard **O**perating **P**rocedures **(SOP's)**, 10% of the completed samples are randomly selected for QC. Sample QC determines the accuracy of specimen identification and measurement. All organisms are counted, identified, and measured, with corrections entered on the **Identification Correction Record** [Appendix Table 11].

Target accuracy and precision:

	Accuracy:	**Precision:**
Sorting	90 %	NA
Taxonomic identification	95 %	NA
Organism counts	95 %	NA
Size	± 2 mm	2 mm
Biomass	± 0.1 g	0.1 g

Accuracy Calculations:

Sorting (%) = $\frac{\text{Original \# animals found x 100}}{\text{Original \# found + QC \# found}}$

Taxonomic identification (%) = $\frac{\text{\# animals correctly identified x 100}}{\text{Total \# animals in sample}}$

Organism counts (%) = $\frac{\text{\# animals counted x 100}}{\text{Total \# animals}}$

Accuracy of organism measurements is determined by comparing the mean, maximum, and minimum lengths recorded by the identifier with that found by the QC coordinator. Data are entered from QC/QA procedures into an electronic spreadsheet and monitored for each project. Once QC procedures are complete, QC data sheets and other pertinent information are stored in the project's file folder located in the file cabinet in the Taxonomy and Ecology Lab.

Identification Aides

The following are examples of dichotomous keys and papers used to identify fish, shrimp, crabs, other invertebrates, and seagrasses:

Fish:

Douglas, N. 1974. Freshwater fishes of Louisiana. Claitor's Publishing Division, Baton Rouge, LA, 443 p.

Eddy, S. and J. C. Underhill. 1978. How to know the freshwater fishes. Wm. C. Brown Co. Publ., Dubuque, IA, 215 p.

Gallaway, B. J., J. A. Parker, and D. Moore. 1972. Key to the estuarine and marine fishes of Texas. Texas A&M Univ. Sea Grant College Prog., TAMU-SG-72-402, 177 p.

Hoese, H. D. and R. H. Moore. 1998. Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters. 2nd ed., Texas A&M Univ. Press, College Station, 422 p.

McEachran, J. D. and J. D. Fechhelm. 1998. Fishes of the Gulf of Mexico. Volume 1: Myxiniformes to Gasterosteiformes. Univ. Texas Press, Austin, 1112 p.

Murdy, E. O. 1983. Saltwater fishes of Texas. A dichotomous key. Texas A&M University, College Station, TAMU-SG-83-607, 220 p.

Crabs, Shrimp, and Other Invertebrates:

Abele, L. and W. Kim. 1986. An illustrated guide to the marine decapod crustaceans of Florida. Part 1. Florida State Univ., Tallahassee, 706 p.

Chaney, A. H. 1983. Keys to selected marine invertebrates of Texas. Caesar Kleberg Wildlife Res. Inst., Tech. Bull. No. 4, 86 p.

Felder, D. L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. Louisiana State Univ., Center for Wetland Resources, Sea Grant Publ., LSU-SG-73-02, 103 p.

Heard, R. W. 1982. Guide to common tidal marsh invertebrates of the northeastern Gulf of Mexico. Mississippi-Alabama Sea Grant Consortium, MASGP-79-004, 82 p.

Perez-Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*. Fish. Bull., U. S. 67: 461-591.

Perez-Farfante, I. 1970. Diagnostic characters of juveniles of the shrimps *Penaeus aztecus aztecus*, *P. duorarum*, and *P. brasiliensis* (Crustacea, Decapoda, Penaeidae). U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fish., No. 599, 26 p.

Powers, L. W. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. Contrib. Mar. Sci., Univ. Texas, Supplement to Vol. 20, 190 p.

Ringo, R. D. and G. Zamora, Jr. 1968. A penaeid postlarval character of taxonomic value. Bull. Mar. Sci. 18(2): 471-476.

Stuck, K. C., H. M. Perry, and R. W. Heard. 1979. An annotated key to the Mysidacea of the north central Gulf of Mexico. Gulf Res. Rep. 6(3): 225-238.

Williams, A. B. 1959. Spotted and brown shrimp postlarvae (*Penaeus*) in North Carolina. Bull. Mar. Sci. 9(3): 281-290.

Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Inst. Press, Washington, D. C., 550 p.

Wood, C. E. 1974. Key to the Natantia (Crustacea, Decapoda) of the coastal waters of the Texas coast. Contrib. Mar. Sci., Univ. Texas, 18: 35-56.

Zamora, G. and L. Trent. 1968. Use of dorsal carinal spines to differentiate between brown shrimp from white shrimp. Contrib. Mar. Sci., Univ. Texas, 13:17-19.

Seagrasses:

Edwards, P. 1976. Illustrated guide to the seaweeds and sea grasses in the vicinity of Port Aransas, Texas. Univ. Texas Press, 130 p.

Lazarine, P. Undated. Common wetland plants of southeast Texas. U. S. Army Corp of Engineers, Galveston District. Manual.

Sorensen, L. O. 1979. A guide to the seaweeds of South Padre Island, Texas. Manual, 123 p. Copyrighted by L. O. Sorensen.

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Connolly, R. M. 1994. Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. Marine Ecology Progress Series 109:305-309.

Jordan, F., S. Coyne, and J. C. Trexler. 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m2 throw trap. Transactions of the American Fisheries Society 126:1012-1020.

Kjelson, M. A. and D. R. Colby. 1977. The evaluation and use of gear efficiencies in the estimation of estuarine fish abundance, p. 416-424. *In:* M. Wiley (ed.) Estuarine Processes, Vol. II, Circulation, Sediments, and Transfer of Material in the Estuary. Academic Press, Inc., New York.

Kneib, R. T. 1991. Flume weir for quantitative collection of nekton from vegetated intertidal habitats. Marine Ecology Progress Series 75:29-38.

Kushlan, J. A. 1981. Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110:557-562.

Perez-Farfante, I. 1988. Illustrated key to the penaeoid shrimps of commerce in the Americas. NOAA Technical Report, National Marine Fisheries Service, 64: I-IV, 1-32.

Rozas, L. P. and D. J. Reed. 1994. Comparing nekton assemblages of subtidal habitats in pipeline canals traversing brackish and saline marshes in coastal Louisiana. Wetlands 14:262-275.

Rozas, L. P. and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. Estuaries 20:199-213.

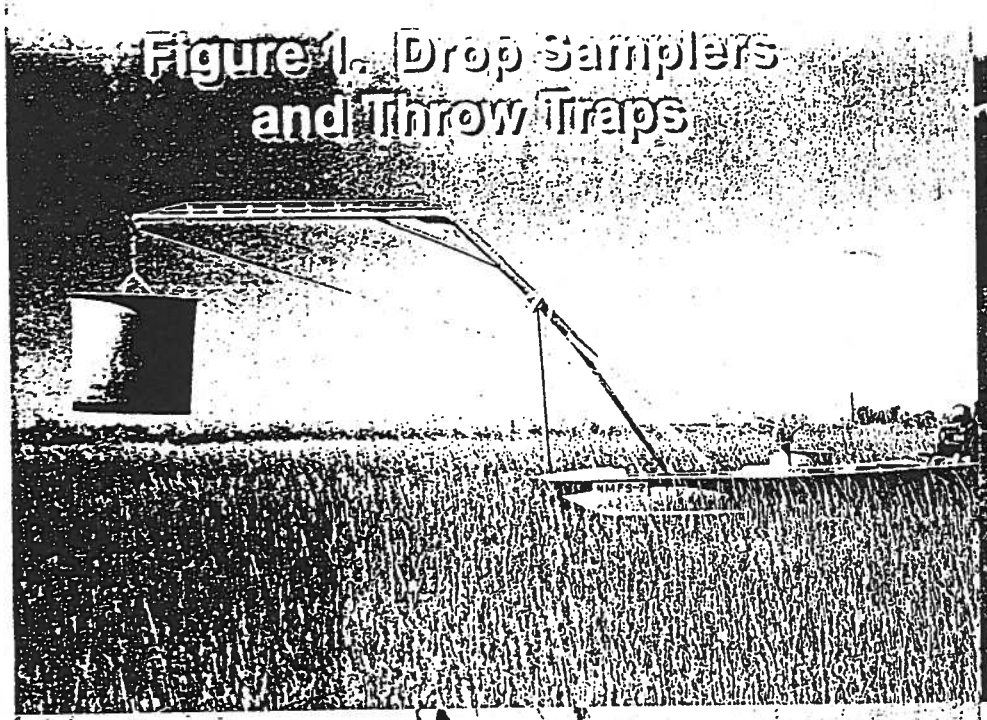
Rozas, L. P. and W. E. Odum. 1987. Fish and macrocrustacean use of submerged plant beds in tidal freshwater marsh creeks. Marine Ecology Progress Series 38:101-108.

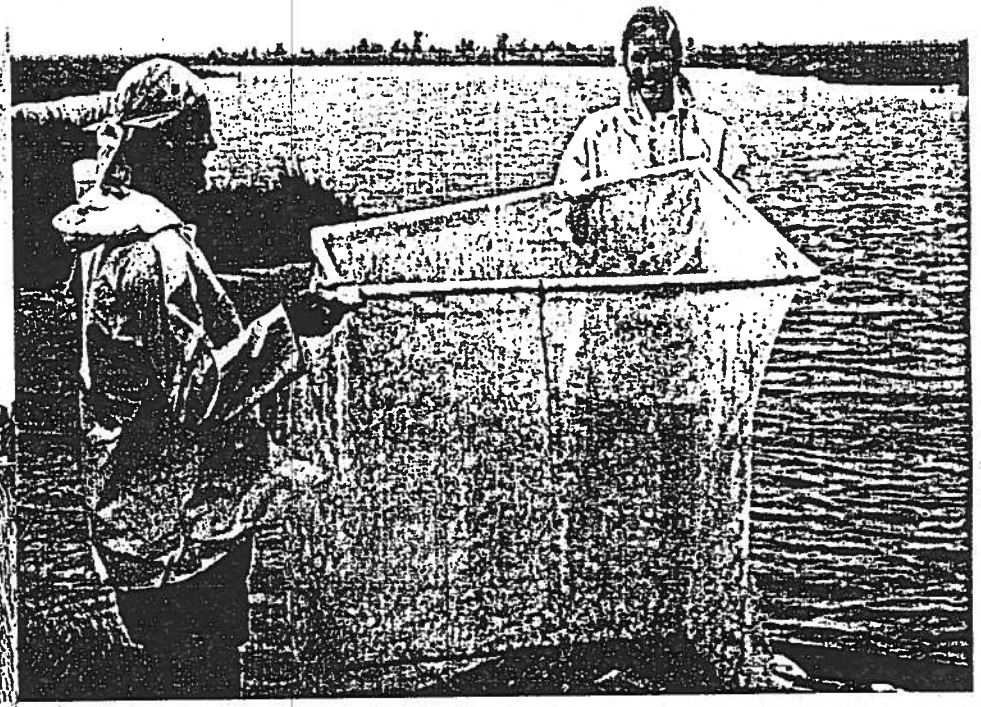
Sheridan, P. F. 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. Bulletin of Marine Science 50:21-39.

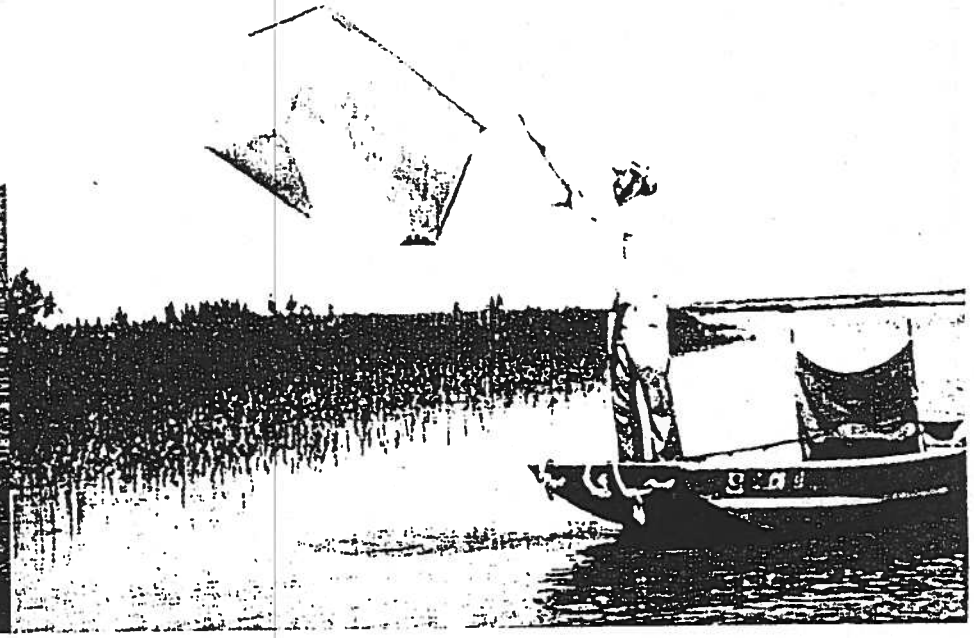
Wenner, E. L. and H. R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, USA, by postlarval and juvenile stages of *Penaeus* spp (Decapoda, Penaeidae). Journal of Crustacean Biology 13:280-295.

Zimmerman, R. J., T. J. Minello, G. Zamora, Jr., and E. Martinez. 1986. Measurements of estuarine shrimp densities applied to catch predictions, p. 37-55. *In*: A. M. Landry and E. F. Klima (eds.) Proceedings of the Shrimp Yield Prediction Workshop. Texas A & M University Sea Grant College Program, Galveston, TX.

Figure 1. Drop Samplers and Throw Traps







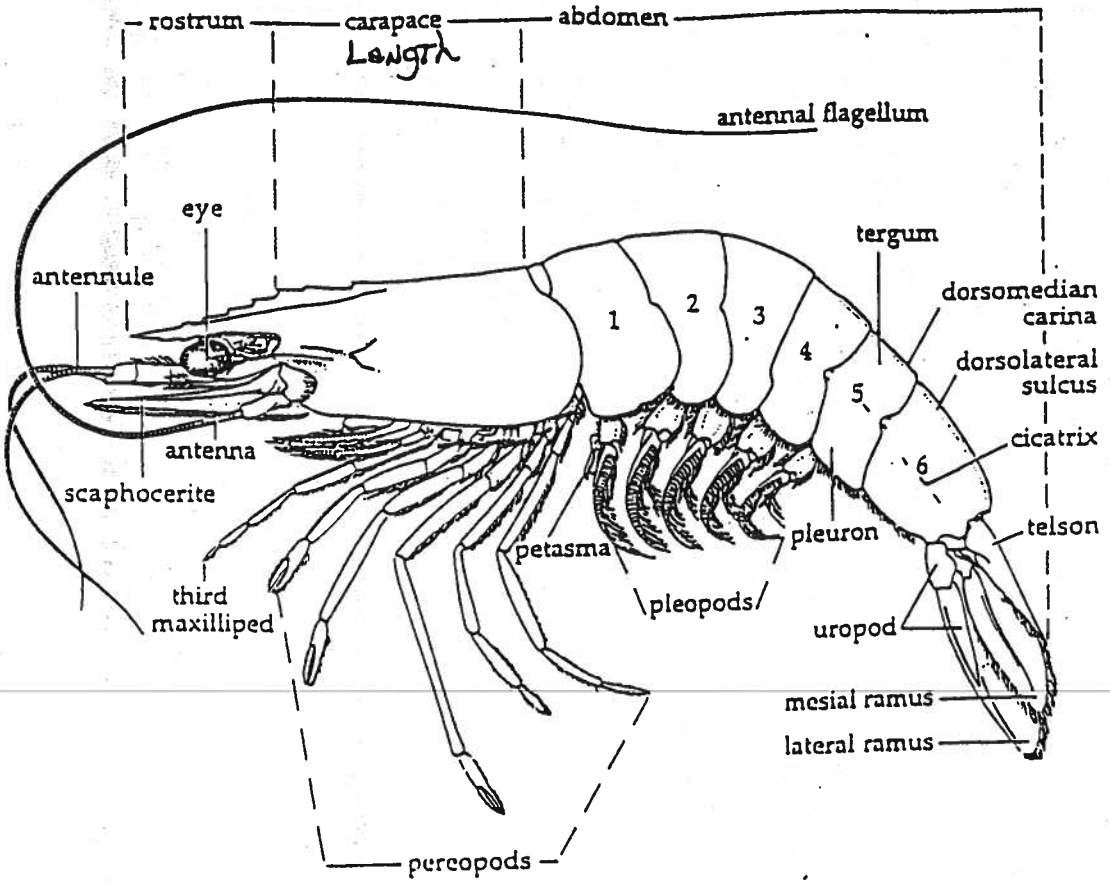


Fig. 2. — Schematic drawing of a penaeidean shrimp in lateral view.

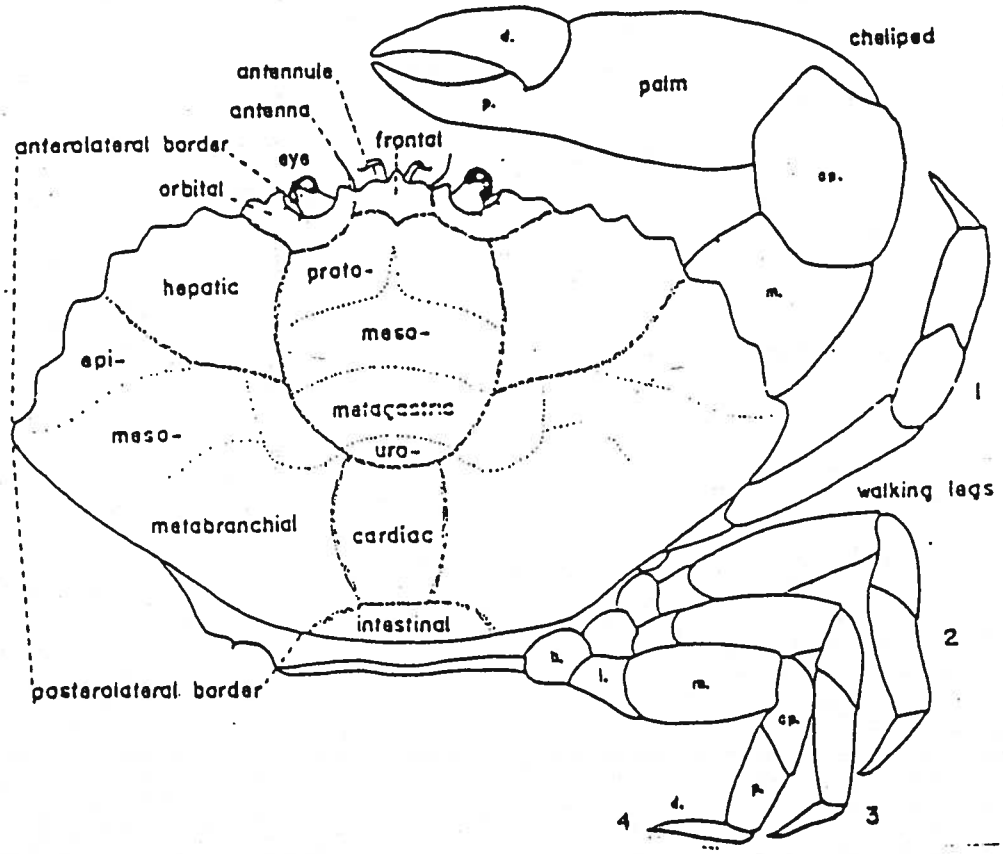


Figure 3.—Schematic drawing of brachyuran crab in dorsal view; areas of carapace indicated; legs of right side only shown; b., basis; cp., carpus; d., dactyl; i., ischium; m., merus; p., propodus.

Appendix Table 1. Example Field Trip Checklist. Date: _____ Project: _____

	Need	Have	Packed	Repair/Buy		Need	Have	Packed	Repair/Buy
Boat					**Pump**				
oars					hoses				
cushions					gas can				
gas tanks					oil				
jerry cans									
anchor					**Gear**				
outboard oil					samplers				
life vests					dipnets				
battery					buckets				
ear muffs					lids				
hose					ziplocks				
plugs					meter stick				
fire extinguisher					thermometer				
air horn					refractometer				
charger					labels				
					clipboard				
Tools					markers, pencils				
clamps					water-proof data sheets				
shackles					PVC poles				
cable ties					corer				
WD40					sieves				
knife					ice chests				
duct tape					water jug				
pliers					first aid kit				
wrenches					rope				
sockets					locks				
nut driver					flashlight				
spark plugs					Q-beam				
plug wrench					camp light				
hammer					trawl gaer				
grease gun					baitsaver				
grease					large cooler				
					sg quadrats				
Round Trip					rain gear				
VHF radio					reflectors				
permits									
camera					**Expendables**				
film					formalin				
cod ends					rose bengal				
snorkel gear					sun block				
personal gear					bug spray				
Other Misc.:					**Other Misc.:**				

Path: NMFS\Sheets\LabSheetsMisc.xls\Field Trip Checklist 03/09/2000

Appendix Table 2: Chemical Preparation

10% Neutral Buffered Formaldehyde Solution (Carson's Solution)

To prepare, put the stirrer and large beaker under the fume hood with the fan running. Add 75.6 grams of dibasic sodium phosphate and 122.8 grams of monobasic sodium phosphate to the beaker and place the beaker on top of the magnetic stirrer. Fill beaker 3/4th full of water and begin stirring until grains of sodium phosphate have dissolved. Pour buffer solution into 5-gal (~20 l) carboy, add 1.9 l of full strength formaldehyde, and fill with seawater. To make one gallon (~3.8 l) of full strength formaldehyde, add 151.4 grams of dibasic sodium phosphate and 246.0 grams of monobasic sodium phosphate to the formaldehyde.

70% Ethanol

To prepare 70% ethanol, use the 95% ethanol stored in the yellow safety cabinet. Mix with water at a 70/30 ratio.

Rose Bengal Stain

To prepare, add several grains of Rose Bengal to ethanol until the alcohol is dark red. Be careful with both the dry grains and prepared dye because both are potent stains. Add this mixture to the formaldehyde solution a little at a time until the proper color is attained. Formaldehyde used for preserving benthic cores should be prepared a shade darker than the formaldehyde solution used for drop samples.

PI: ____________

Sampling Gear: ____________

Appendix Table 3. Environmental Data Field Sheet.

Date	Location /Site	Sample No.	Time	Habitat Type	Marsh Edge Distance (m)	GPS Lat.	GPS Long.	°C	Sal. (ppt)	Water Depth (cm)	Turb.	Bot. D.O.	Wind Dir	Wind Speed	Cloud Cover (%)	Comments
																Recorder:

Path: NMFS\Sheets\LabSheetsMisc.xls\Enviro Field Sheet 03/14/2000

Appendix Table 4

Sample Inventory and Progress Report

(to be kept in project folder)

Project: _____

Sampling Dates: _____ Sampling Gear: _____

Principle Investigator: _____

Type of samples:	No. of containers:	Location stored:
_____	_____	_____
_____	_____	_____
_____	_____	_____

		Checked by:	Date:
Samples preserved correctly	☐	_____	_____
Turbidity and salinity samples processed	☐	_____	_____
Environmental data from field sheets entered into electronic files	☐	_____	_____
Environmental data files verified and corrected	☐	_____	_____
Envir. data files saved on disk and stored in file cabinet	☐	_____	_____
All samples sorted	☐	_____	_____
All samples identified, measured and weighed	☐	_____	_____
Quality control - SORTING completed	☐	_____	_____
Quality control - IDENTIFICATION completed	☐	_____	_____
Sample data entered into electronic file	☐	_____	_____
Data file verified and corrected	☐	_____	_____
Species codes added to file (any new species should be listed below)	☐	_____	_____
Sample data entered into electronic file	☐	_____	_____
Hard copy of date file in project folder (lab file cabinet)	☐	_____	_____
Sample data entered into electronic file	☐	_____	_____
Text file created with project info. attached to data files	☐	_____	_____
Data & text files checked by quality control manager	☐	_____	_____
Electronic files saved on 3.5" Disk given to Principle Investigator	☐	_____	_____

New species to be added to Master Species Code List: _____

Electronic data files and project information text files stored:

	File name(s)
(1) 3.5" Disk kept in Fishery Ecology Branch Lab	_____
(2) Hard Drive on FEB Lab computer	_____
(3) Back-up cartridge stored in fire-proof cabinet	_____

Appendix Table 5. Taxonomy and Ecology Individual Sorting Logs.

PI: _____

	A	B	C	D	E	F	G	H	I	J	K	L	M
1	QC	Sorter	Collectio	Sample	Station/	Gear/	Today's	Daily	Daily	Daily	Daily	Other	Comments
2		Initials	Date	Number	Site	Method	Date	Sort	Fish	Crabs	Shrimp	Misc.	
3								Time					
4													
5													
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Path: NMFS\Sheets\LabSheetsMisc.xls\Individual Sorting Logs 03/09/2000

Appendix Table 6. Taxonomy and Ecology Lab Master Sorting Log (Example).

PI: _____

	A	B	C	D	E	F	G	H	I	J	K	L	M
1	QC'd	Collection	Sample	Station/	Gear/	Sample	Sample	Total	Total	Total	Total	Other	Comments
2		Date	Number	Site	Method	Start	End	Sort	Fish	Crabs	Shrimp	Misc.	
3						Date	Date	Time					
4		10/19/98	1	BNUT									
5		10/19/98	2	BNUT									
6		10/19/98	3	BNUT									
7		10/19/98	4	BNUT									
8		10/19/98	5	BNUT									
9		10/19/98	6	NEST									
10		10/19/98	7	NEST									
11		10/19/98	8	NEST									
12		10/19/98	9	NEST									
13		10/19/98	10	NEST									
14		10/20/98	11	DEER									
15		10/20/98	12	DEER									
16		10/20/98	13	DEER									
17		10/20/98	14	DEER									
18		10/20/98	15	DEER									
19		10/20/98	16	EAGL									
20		10/20/98	17	EAGL									
21		10/20/98	18	EAGL									
22		10/20/98	19	EAGL									
23		10/20/98	20	EAGL									
24		10/20/98	21	BBET									
25		10/20/98	22	BBET									
26		10/20/98	23	BBET									
27		10/20/98	24	BBET									
28		10/20/98	25	BBET									

Path: NMFS\Sheets\LabSheetsMisc.xls\Master Sorting Log 03/09/2000

Descriptive terms: Mangled; Smashed; Fins broken; Poorly preserved; Head/tail only

Appendix Table 7. Taxonomy and Ecology Lab: Fish ID.

Taxa	No.	Mas	Min.	Max.	TL1	TL2	TL3	TL4	TL5	TL6	TL7	TL8	TL9	TL1	TL1	TL1	TL1	TL14	TL15	TL16	TL17	TL18	TL19	TL20	Counts		Specimen
		(g)	Length		SL1	SL2	SL3	SL4	SL5	SL6	SL7	SL8	SL9	SL1	SL11	SL12	SL13	SL14	SL15	SL16	SL17	SL18	SL19	SL20	Dorsa	Anal	condition/ Comments

Appendix Table 8. Taxonomy and Ecology Lab Penaeid Shrimp ID Sheet.

Descriptive terms : Mangled; Smashed; Head/tail only; Poorly preserved

	A	B	C	D	E	F	G	H	I	J
1	Taxa	Sex	No.	Mass	POL	Antennal scale	Carinal spines		Missing	Comments
2				(g)	(mm)	(% to scale tip)	Rostrum	6th Abdom.	Parts	
3						[if <3 mm POL]				
4										
5										
6										
7										
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Appendix Table 9. Other Invertebrates ID Sheet.

	A	B	C	D	E	F	G	H	I	J
1	Taxa	Taxa	Number	Min.	Max.	Carapace (mm)	TL (mm)	Mass	Missing	Comments
2		Code		Length	Length	Up to 20 #s	Up to 20 #s	(g)	Parts	
3										
4										
5										
6										
7										
8										
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Path: NMFS\Sheets\LabSheetsMisc.xls\Invertebrate ID 03/09/2000

Appendix Table 10. ID Correction record.

Project: _____

Investigator: _____

Station/ Site	Date	Sample Number	Original ID	Corrected ID	Length (mm)	Original Identifier	Corrected By	Comments

Path: NMFS\Sheets\LabSheetsMisc.xls\ID Correction Record 03/09/2000

Appendix Table 10. Taxonomy and Ecology Lab: QC Sorting Log.

QC'd by: _____
Date QC'd: _____

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
1	Sorter	Project	Collection	Station	Sample #	Gear	Total Organisms			QC Organisms			Percent	Total
2			Date				Fish	Shrimp	Crabs	Fish	Shrimp	Crabs	Missed	QC Time
3														
4														
5														
6														
7														
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31														
32														

Path: NMFS\Sheets\LabSheetsMisc.xls\QC Sort Log 03/09/2000

Project: ______________
Investigator: ____________

Appendix Table 11. Taxonomy ID Correction Record.

Station/ Site	Date	Sample Number	Original ID	Corrected ID	Length (mm)	Original Identifier	Corrected By	Comments

SELECTION OF VEGETATED HABITAT BY BROWN SHRIMP, *PENAEUS AZTECUS*, IN A GALVESTON BAY SALT MARSH

ROGER J. ZIMMERMAN,[1] THOMAS J. MINELLO,[2] AND GILBERT ZAMORA, JR.[3]

ABSTRACT

Densities of the brown shrimp, *Penaeus aztecus*, in vegetated and nonvegetated habitats of a Galveston West Bay salt marsh were compared. Each of 81 sample pairs taken between 29 March and 23 July 1982 consisted of one sample from *Spartina alterniflora* habitat and another from nonvegetated habitat. Overall a mean density for shrimp of 11.7/m² in vegetation was significantly greater than the mean density of 1.4/m² in nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). In addition, shrimp densities varied according to a pattern of lower numbers and less apparent attraction to vegetation in the outer bayside part of the marsh to that of highest numbers and greatest attraction in the innermost marsh. Accordingly, respective means for the outer, middle, and inner marsh zones in vegetated/nonvegetated sample pairs were 7.5/2.3, 11.0/1.0, and 16.6/0.6. Simple presence or absence of *S. alterniflora*, area covered by vegetation, and location within the marsh were the primary observed correlates to shrimp density patterns. Mean high water in vegetation was 22.1 cm compared with 41.8 cm for adjacent nonvegetated habitat, making vegetated habitat less accessible during periods of low water. Mechanisms that may have enhanced utilization of vegetated habitat for *P. aztecus* were reticulation in salt marsh macrostructure, relatively low tidal range, and seasonal periods of high water. The nursery function of the salt marsh was confirmed by dominance of small shrimp, with 95% of all individuals being smaller than 50 mm in rostrum through telson length. During April, the maximum mean density of postlarvae under 30 mm was 16.4/m². Recruitment of postlarvae continued throughout the summer.

A 2.8m² drop sampler, used to obtain the data, was found to be 2 to 5 times more effective for estimating densities of *P. aztecus* than trawls or seines. Consequently, our study improved the accuracy of estimates on estuarine shrimp densities, while also providing reliable evidence that *P. aztecus* may select for vegetated marsh habitat.

Estuaries have long been cited in their role as nurseries for penaeid shrimp (Anderson et al. 1949; Kutkuhn 1966; Thayer et al. 1978; Weinstein 1979). Growth and production of penaeids in estuaries have been associated with temperature (St. Amant et al. 1966; Zein-Eldin and Griffith 1966; Aldrich et al. 1968; Pullen and Trent 1969), salinity (Hildebrand and Gunter 1952; Gunter 1961; Barrett and Gillespie 1973; Browder and Moore 1981), and vegetation (Turner 1977; Faller 1979).

In salt marshes, vegetation may function variably to provide food, substrate, and protection for young penaeids. It is well known that *Spartina alterniflora* contributes to a detritus-based food web (Teal 1962; de la Cruz 1965) which at least potentially includes shrimp (Jones 1973). Microalgae and epibenthic biota associated with marshes may also serve in the food web (Haines 1977) and be used as food by foraging shrimp (Trent et al. 1969; Jones 1973). Since dense aquatic vegetation impedes certain predators (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981), marsh grasses could also furnish protective cover for postlarval and juvenile penaeids. Unfortunately, our understanding of shrimp relationships to vegetation has been impaired by the inherent difficulty of sampling in marine vegetation.

Our aim was to overcome the sampling problem and to obtain accurate data on shrimp densities that could reliably depict differences between estuarine habitats. In the present study, *Penaeus aztecus* densities were compared between adjacent vegetated and nonvegetated habitats within a Galveston West Bay salt marsh. Since our experimental design incorporated paired sampling of habitats and samples with actual as opposed to relative numbers of shrimp, both the resolution

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and reliability of our analyses were improved over previous studies.

METHODS

Study Site

A salt marsh on the West Bay side of Galveston Island was selected as the study site (Fig. 1). The marsh extended into the island for about 2.5 km, allowing tidal circulation throughout numerous coves and bayous. The intertidal marsh was dominated by vegetation, *S. alterniflora*, and the subtidal was not vegetated. Water depth was generally <1 m, but subtidal bottom was always 10 to 20 cm deeper than adjacent intertidal vegetation. Vegetation occurred in irregular patches, creating a reticulated effect on marsh macrostructure, and occupied about 25% of the area (Fig. 2).

Experimental Design

A paired sampling design was employed to compare shrimp densities between marsh habitats. Each sample pair consisted of one sample taken in vegetated habitat and another in adjacent nonvegetated habitat as close as practically possible.

Sampling was scheduled to coincide with the

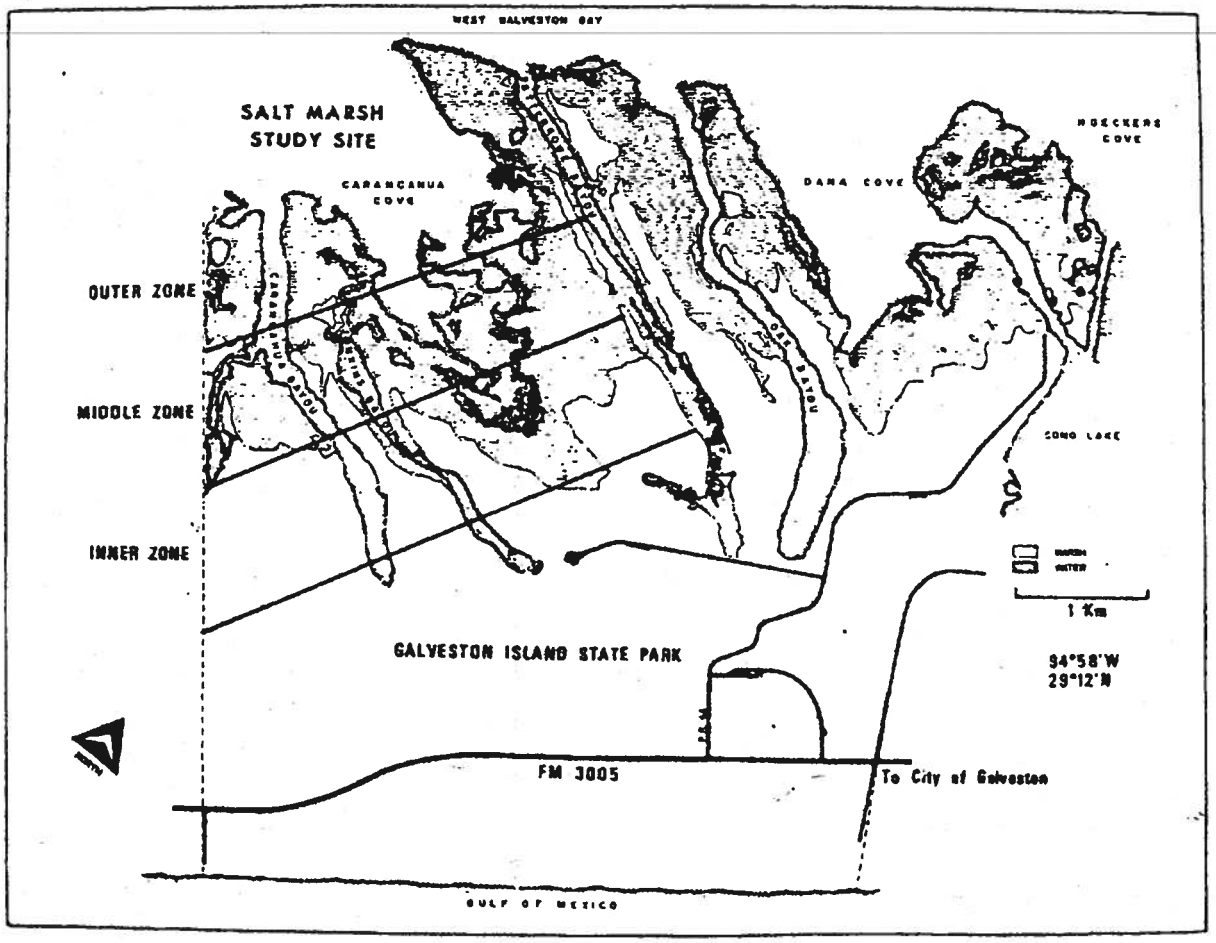
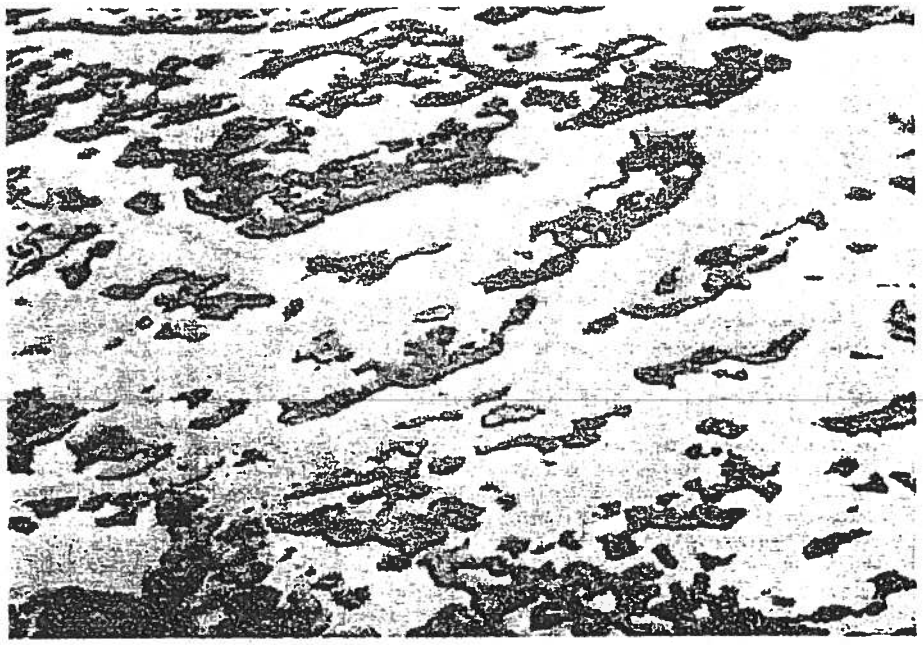
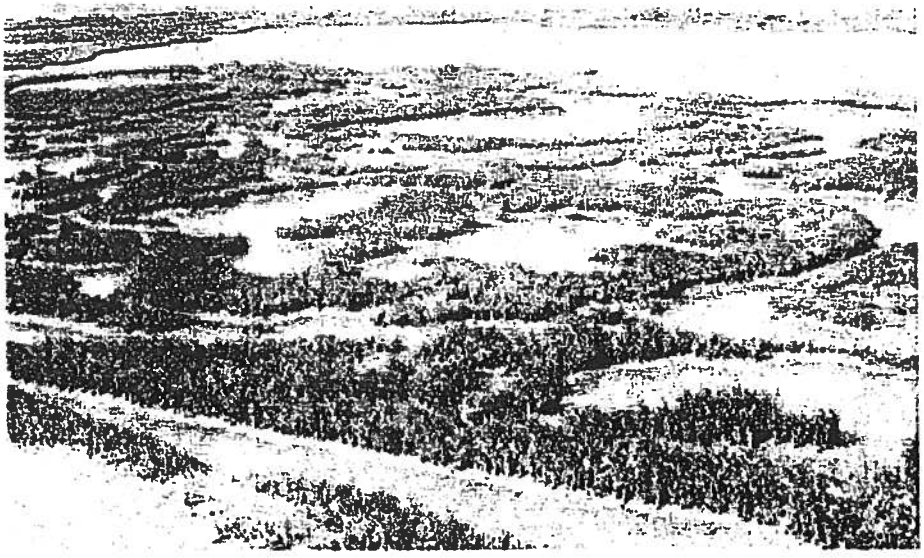


FIGURE 1.—Galveston Island State Park showing the salt marsh study site in Carancahua Cove fronting Galveston West Bay. (Redrawn from Texas Parks and Wildlife Leaflet 4000-42.)

FIGURE 2.—Upper: Reticulation between vegetated and nonvegetated habitats in a salt marsh on Galveston Island. Areal view at about 500 ft altitude. Lower: Stands of intertidal *Spartina alterniflora* and adjacent subtidal nonvegetated bottom in a salt marsh at Galveston Island State Park.





period of maximum seasonal immigration for *P. aztecus* as described by Baxter and Renfro (1967). Accordingly, seven sets of samples were taken between 29 March and 23 July 1982. Each set was obtained over a period of 3 d, and sets were taken biweekly (29 March through 28 May) and monthly (28 May through 23 July). Ordinarily, a set contained 12 sample pairs that were subdivided to sample the inner, middle, and outer marsh zones equally, i.e., during each of three sampling days four vegetated-nonvegetated sample pairs were taken from a single zone. Sample sites within zones were chosen randomly each month from subunits in a grid superimposed on a map of the area. The map and aerial photographs were used to estimate percent coverage of vegetated and nonvegetated habitats within different zones.

A *t*-test of paired observations (Steel and Torrie 1960) provided the primary means for evaluating differences in shrimp density between habitats. Other analyses were performed using Pearson product-moment correlations and ANOVAs across sample sets, and Kendall's nonparametric concordance tests (Tate and Clelland 1957) within sample sets. Analyses across sets incorporated an element of temporal variability that was specifically eliminated in analyses within sets. Data were log transformed for ANOVAs to assure homogeneity of variances.

Procedures

A drop sampler (Fig. 3) was designed to operate in the marsh from the bow of a skiff. The device was an open-ended fiber glass cylinder, reinforced on one end with galvanized metal, that enclosed 2.8 m^2 of marsh bottom. The sampler was deployed endwise and pushed at least 15 cm into the substrate to insure a good seal against leakage. After marsh grass was removed, water was pumped from the sampler and the enclosed bottom was swept with dip nets to capture the entrapped organisms. The water and the contents of the dip nets were placed into a 1 mm square mesh plankton net with a removable cod end bag. When all sample contents were washed, the cod end bag was detached, labelled, and stored in a container with Formalin[4] and Rose Bengal stain.

Two identical sampling cylinders were used to obtain sample pairs. Typically, the first sampler was hoisted above the bow of the skiff and quietly maneuvered into position over either vegetated or barren substrate. The device was released and allowed to free fall to the bottom. After disconnecting the first sampler, the second sampler was hoisted and the operation repeated in the opposing habitat. The sequence of habitats was reversed from pair to pair so that one would not continually precede the other. Sample pairs were always within two sample diameters of each other (3.6 m) and care was taken to not disturb the site until the second sampler was deployed.

Within all samples, the water temperature,

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

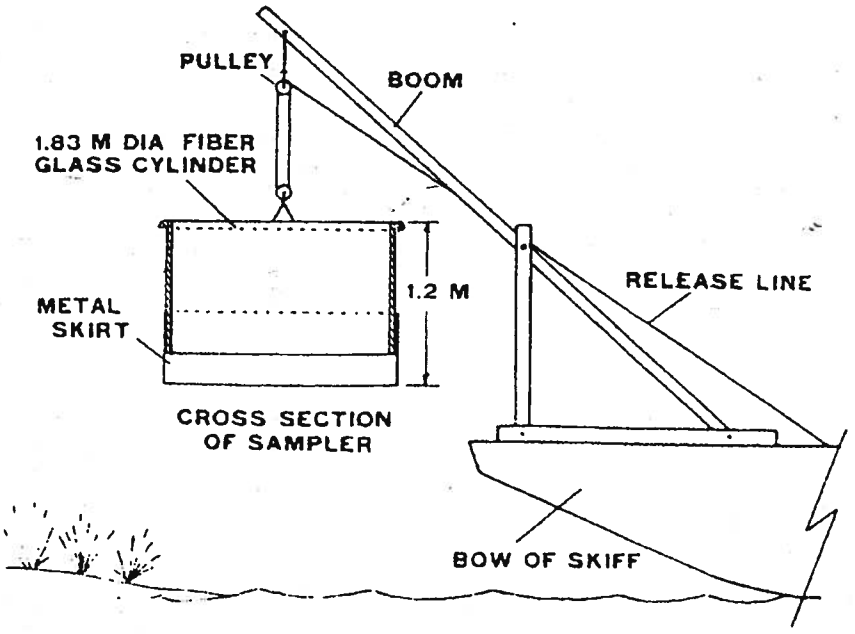


FIGURE 3.—A hand-operated drop sampler used to estimate *Penaeus aztecus* densities in a Galveston West Bay salt marsh.

oxygen (YSI oxygen meter, Model 51 B) and maximum and minimum depth were recorded. Water samples (500 ml) were also procured in order to measure turbidity (HF Instruments, Model DRT-15). In vegetated samples, emergent plant material was cut and removed to measure plant biomass and to facilitate capturing the macrofauna. Tide level was recorded from a permanent station at the beginning and end of each sampling operation. All field work was done during daylight within about 2 h before and after high tide.

In the laboratory, shrimp were identified, sorted, and measured to the nearest millimeter from rostrum tip to end of telson. Shrimp numbers for each millimeter size interval were recorded for each sample. Associated macrofauna from each sample, including fish, crabs, and other shrimp, were identified, measured, and counted. Gut contents of the fish were examined for penaeid shrimp as well as other identifiable material. Plant biomass from each sample was dried in sunlight until weight change was negligible. Sediments and epiphytes were allowed to fall away as the material dried. The resulting dry weight was taken using a Mettler K-7 toploading balance and reported as grams above-ground dry plant biomass. Stem density was calculated by weighing a subsample (about 20% of the total) and counting the number of culms.

Sampler Effectiveness

Since the experimental design assumed no sampling bias, the method was tested for recovery efficiency both in vegetated and nonvegetated habitats. Fifty shrimp, in the size range of 23 to 91 mm, were marked by clipping a uropod and placed into deployed samplers. After a 30-min adjustment period, the usual sampling procedure was followed and recovery was recorded.

Since our density data were compared with other surveys, it was useful to test the effectiveness of the drop sampler in relation to other collecting devices. These included a 1 m beam trawl, a 5.5 m bag seine, and a 3.7 m otter trawl. During the initial test, eight replicate vegetated-nonvegetated sample pairs were taken using the 1 m beam trawl (3.0 m^2) and the drop sampler (2.8 m^2). Later, 10 nonvegetated sample replicates were obtained for each of the following: the drop sampler, a 5.5 m bag seine (110 m^2), and a 3.7 m otter trawl (75 m^2). The data were reported as mean and standard deviation of shrimp density (per m^2) for each sampler. The efficiency for each device was calculated relative to the drop sampler.

RESULTS

A total of 3,277 penaeid shrimp (97% *P. aztecus*) were collected in 81 paired samples taken between 29 March and 23 July 1982. Shrimp densities in the marsh were significantly higher in *S. alterniflora* habitat than adjacent nonvegetated habitat ($P < 0.001$, *t*-test, 81 paired observations). The magnitude and integrity of the relationship between shrimp density and habitat type held consistently throughout all sampling dates (Table 1, Fig. 4) and zones within the marsh, except for the outer zone during March and April (Table 2). Comparison of marsh zones (Table 2) revealed highest *P. aztecus* densities and greater selection for vegetated habitat in the innermost marsh diminishing toward the outer zone. Shrimp densities in nonvegetated habitat were highest in the outer zone and diminished significantly toward the inner zone (ANOVA, $P < 0.001$).

TABLE 1.—Percent of *Penaeus aztecus* in vegetated (*Spartina alterniflora*) and nonvegetated habitats of a Galveston West Bay salt marsh, 29 March through 23 July 1982.

Sampling period	Shrimp number (*n*)	Habitat	
		Vegetated (% *n*)	Nonvegetated (% *n*)
3/29-4/1	355	94.4	5.6
4/13-15	519	81.7	18.3
4/26-28	802	88.3	11.7
5/11-14	309	90.3	9.7
5/26-28	388	91.8	8.2
6/22-24	237	97.0	3.0
7/21-23	559	90.2	9.8

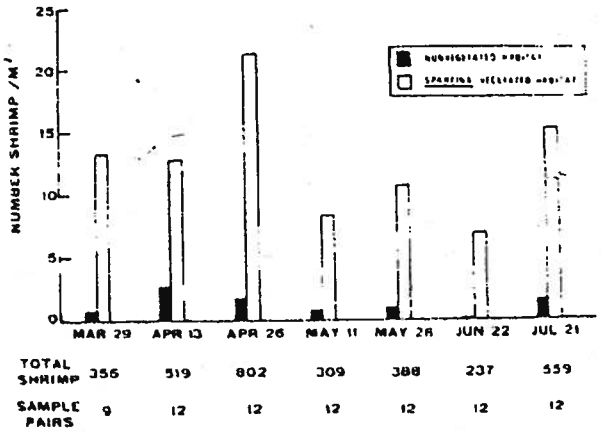


FIGURE 4.—Mean densities of *Penaeus aztecus* compared between vegetated *Spartina alterniflora* habitat and adjacent nonvegetated habitat.

TABLE 2.—Mean number of *Penaeus aztecus* per m² by zone in vegetated and nonvegetated salt marsh habitats from Galveston West Bay 29 March through 23 July 1982.

Sampling period	Marsh zone and habitat: Outer Veg/Non[1]	Middle Veg/Non	Inner Veg/Non	Overall Veg/Non
3/29-4/1	[2] 2.7/1.9	12.3/2.0	16.7/1.1	12.6/2.8
	[2] 8.8/5.5			
4/26-28	12.3/6.8	28.5/1.3	22.4/0.4	21.1/2.8
5/11-14	7.2/1.2	9.6/1.3	8.0/0.3	8.3/0.9
5/26-28	12.0/1.5	10.6/0.9	9.2/0.4	10.6/1.0
6/22-24	3.8/0.2	9.7/0.3	7.0/0.2	6.8/0.2
7/21-23	10.9/1.8	13.8/1.9	20.3/1.3	15.0/1.6
Overall	7.5/2.3	11.0/1.0	16.6/0.6	11.7/1.4

[1]Veg = *Spartina alterniflora* habitat; Non = Nonvegetated habitat.
[2]Difference within brackets not significant between vegetated and nonvegetated pairs; for all others, the difference was highly significant ($P < 0.001$, t-test, paired observations).

Penaeus aztecus densities for each 20 mm size interval were more abundant in *Spartina* habitat than adjacent nonvegetated bottom (Fig. 5). Vegetated habitat contained 89 to 96% of all shrimp in size classes under 50 mm and 75 to 78% of larger size classes (Table 3). Those under 30 mm in length comprised 77,% of all shrimp and those under 60 mm made up 98% of the total (Table 3). Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$; Fig. 5), but the very small sample size from nonvegetated habitat decreased the strength of this observation.

The highest *P. aztecus* densities in vegetation and the lowest on nonvegetated bottom were characteristic of the innermost zone (Table 1). The degree of vegetated-nonvegetated differences suggested an apparent selection for vegetated habitat and greater selection in the inner zone compared with the outer zone. The increase in vegetated to nonvegetated shrimp densities coincided with an increase in *S. alterniflora* coverage between the outer and inner marsh (Fig. 6). Areal coverage of vegetation, determined from aerial photographs (Fig. 2), differed by a factor of 3 between the outer and inner marsh, and selection, as measured by the ratio of shrimp density in vegetated habitat to density in nonvegetated habitat, differed by a factor of 9 from outer to inner zones (Fig. 6). In addition, the ratio differed between the middle and inner zone, but shrimp densities within vegetation between those zones (Table 2) did not change significantly (ANOVA, Duncan's multiple range test, 0.05 level). Due to the intertidal nature of vegetated habitat, shrimp were forced into subtidal areas at low tide and redis-

TABLE 3.—Percent abundance among size classes for *Penaeus aztecus* in a Galveston West Bay salt marsh, 29 March through 23 July 1982. n = number of shrimp per size interval; N = total number of shrimp collected.

Size class (mm)	Shrimp abundance: Overall n	Overall % N	Overall Cum. %	Spartina (% n)	Nonvegetated (% n)
<20	1,117	47.7	47.7	89.4	10.6
21-30	683	29.2	76.9	95.6	4.4
31-40	234	10.0	86.9	94.9	5.1
41-50	184	7.8	94.7	88.6	11.4
51-60	86	3.7	98.4	77.9	22.1
61-70	25	1.1	99.5	76.0	24.0
71-80	8	0.3	99.8	75.0	25.0
81-90	4	0.2	100	75.0	25.0
Total (N) = 2,341					

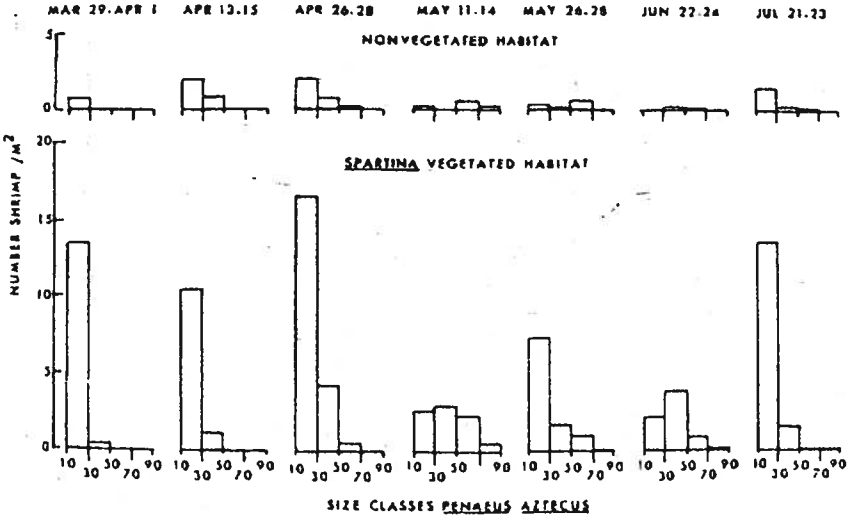


FIGURE 5.—Densities of *Penaeus aztecus* by size class in adjacent vegetated and nonvegetated habituts from Galveston West Bay during 1982. Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$).

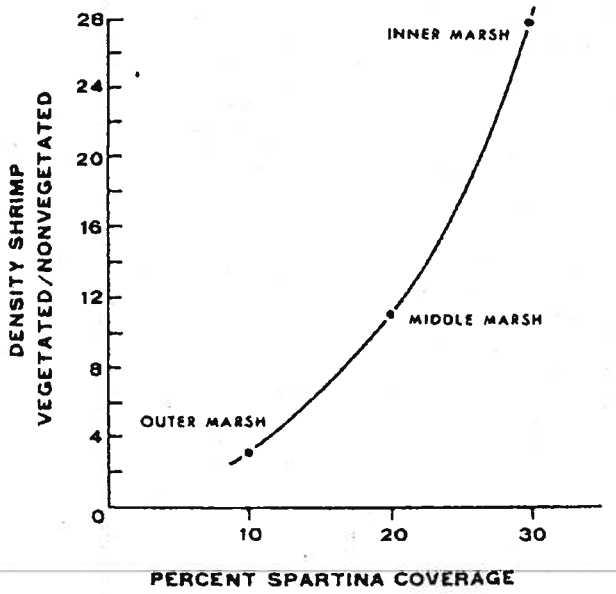


FIGURE 6.—Selection by *Penaeus aztecus* for vegetated habitat compared against percent coverage of *Spartina alterniflora*.

tributed anew on each subsequent flood tide.

Differential predation by fish did not account for shrimp differences between habitats. Of four species preying on shrimp, 328 were in vegetation versus 48 on nonvegetated bottom. Among these, 18 from vegetated (5%) and 3 from nonvegetated (6%) contained shrimp in gut contents. The predators, in order of vegetated/nonvegetated abundance, were *Lagodon rhomboides* (pinfish 246/36), *Fundulus grandis* (gulf killifish 45/0), *Cynoscion nebulosus* (spotted seatrout 22/2), and *Paralichthys lethostigma* (southern flounder 15/10). Only southern flounder contained shrimp in gut contents (3 of 10) from nonvegetated habitat. In vegetated habitat, 8 of 15 southern flounder, 10 of 22 spotted seatrout, 1 of 45 gulf killifish, and 3 of 246 pinfish contained shrimp.

Mean density of *P. aztecus* in vegetation was 11.7/m² overall with a range of 0.7 to 43.2/m² (Table 4). Densities were highest in the innermost marsh ($\bar{x}$ = 16.6/m²; range = 1.8 to 43.2/m²) and lowest in the outer marsh ($\bar{x}$ = 7.5/m²; range = 0.7 to 28.2/m²). The overall variance was less than the overall mean. Among marsh zones, shrimp patchiness in vegetation decreased slightly from the outer to inner marsh (Table 4).

Density of *P. aztecus* in nonvegetated habitat was 1.4/m² with a range of 0 to 18.2/m² (Table 4). Densities on nonvegetated bottom were highest in the outer marsh ($\bar{x}$ = 2.3/m²; range = 0 to 18.2/m²) and lowest in the inner marsh ($\bar{x}$ = 0.6/m²; range = 0 to 2.1/m²). Overall distribution on nonvegetated bottom, as reflected by the variance to mean ratio (coefficient of variation, Table 4), was patchier (more clumped) than on vegetated bottom. Shrimp distributions also were patchier in nonvegetated outer and middle zones, than in the nonvegetated inner zone.

TABLE 4.—Within habitat densities of *Penaeus aztecus* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. n = number of samples.

Marsh habitat and zone	n	Individuals/m² $\bar{x}$	Median	1 SD	Coeff. var. (%)	Range
With vegetation						
Outer	27	7.5	6.4	6.8	90	0.7-28.2
Middle	26	11.0	11.4	8.9	81	0.4-39.6
Inner	28	16.6	13.8	12.5	75	1.8-43.2
Overall	81	11.7	10.5	9.4	80	0.7-43.2
Without vegetation						
Outer	27	2.3	1.4	3.6	157	0-18.2
Middle	26	1.0	0.7	1.2	120	0- 4.6
Inner	28	0.6	1.0	1.5	56	0- 2.1
Overall	81	1.4	1.1	1.9	136	0-18.2

Stem density and above-ground biomass of *S. alterniflora* were positively correlated (Table 5). The overall range of values was 41 to 784 g/m² for biomass and 33 to 629 stems/m² with respective means of 298 g/m² (1 SD = 175, n = 81) and 234 stems/m² (1 SD = 72, n = 81). Between zones, plant biomass from the outer to inner zone increased from 258 to 348 g/m². The weight per stem increased (larger diameters) from outer to inner marsh. Although the trend suggested a negative relationship between shrimp density and vegetational density and biomass, correlation was not significant over the range examined.

Abiotic Relationships

Water depth between vegetated and nonvegetated sample pairs was significantly different ($P < 0.01$, t-test of 81 paired observations). The mean water depth was 22.1 cm (1 SD = 10.0, n = 81) in

TABLE 5.—Density and biomass of *Spartina alterniflora* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. n = number of samples.

Biomass and density	n	$\bar{x}$	1 SD	Coeff. var. (%)	Range
Biomass (g/m²)					
Outer zone	27	258	164	64	41-634
Middle zone	26	289	187	65	41-784
Inner zone	28	348	174	50	69-731
Overall	81	298	175	59	41-784
Density (stems/m²)					
Outer zone	28	234	88	38	37-576
Middle zone	26	231	65	28	33-629
Inner zone	28	236	64	27	47-496
Overall	81	234	72	31	33-629

vegetated samples compared with 41.8 cm (1 SD = 11.8, $n = 81$) in nonvegetated samples. Changes in tide level were not large (about 30 cm) but were important relative to sample depths. Since sampling was executed at high tide, tide station measurements were comparable between sampling periods and useful for establishing variability in high-water level. Mean high water during the summer was 12 cm lower than in the spring reflecting seasonally variable tidal inundation (Hicks et al. 1983) and greater accessibility to vegetation (Provost 1976) in the spring.

A weak negative relationship between shrimp density and temperature within a range of 17.0° to 34.0°C was apparent ($r = -0.34$ in vegetation, $P < 0.01$, $n = 57$). Since temperature and oxygen levels were inversely related, the trend, attributed to temperature, also extended to an observed relationship between oxygen concentration and shrimp density. However, oxygen levels were always near saturation (vegetated $\bar{x} = 8.2$ ppm, 1 SD = 1.4, $n = 81$; nonvegetated $\bar{x} = 8.1$ ppm, 1 SD = 1.4, $n = 81$) and unlikely to have influenced shrimp distribution. Shrimp densities did not correlate well with salinities (range of 19 to 35 ppt), turbidities (range of 3.0 to 55 nephelometer turbidity units), or water depths (overall range of 5.5 to 76 cm). In addition, temperature, salinity, oxygen, and turbidity did not differ between habitats (t-test of 81 paired observations for each).

Sampler Performance

Test results suggested that shrimp recovery from the drop sampler was more variable and somewhat less effective in vegetation ($\bar{x} = 91\%$ recovery, 1 SD = 6.6%, $n = 4$) than in habitat without vegetation ($\bar{x} = 97.5\%$ recovery, 1 SD = 2.5%, $n = 4$). However, a t-test between means by habitat revealed no significant difference ($P > 0.1$) and justified combining means (94%, 1 SD = 5.8%, $n = 8$).

Mean shrimp densities on nonvegetated bottom, comparing our 1.8 m diameter drop sampler, a 5.5 m wide bag seine, and a 3.7 m wide otter trawl, were 0.285/m², 0.104/m², and 0.054/m², respectively. Assuming 97.5% recovery and no avoidance with the drop sampler, conservative estimates of efficiency were 33% for the bag seine and 17% for the otter trawl. Clearly, the data from the drop sampler were more accurate (Table 6).

DISCUSSION

Habitat Selection

Significant differences in habitat-related shrimp densities from a Galveston salt marsh (Table 2, Fig. 4) demonstrate that *P. aztecus* may select for *S. alterniflora* habitat. In support, laboratory data of Giles and Zamora (1973) suggest that *P. aztecus* and *P. setiferus* each prefer *S. alterniflora* as opposed to barren substrate. In addition, marsh grass transplanted on a dredge spoil in Galveston Bay increased shrimp numbers (Trent et al. 1969) and elimination of marsh habitat to create waterfront housing diminished shrimp abundance (Mock 1966; Gilmore and Trent 1974; Trent et al. 1976). In other instances, *P. aztecus* has been associated with vegetation including *Ruppia* and *Vallisneria* in Mobile Bay (Loesch 1965), seagrasses in the Laguna Madre (Stokes 1974), and *Juncus*, *Spartina*, and seagrasses in Mississippi Sound (Christmas et al. 1976). The latter reported movement of postlarvae into marsh vegetation during tidal inundation.

The determinants of selection may have less to do with *S. alterniflora* per se than with other characteristics of vegetated habitat. For example, in our case, shrimp numbers were not related to the density or biomass of marsh grass (Table 5) but simply to its presence or absence. Also, attraction to vegetation differed between outer and inner marsh (Table 2). Other studies have shown that

TABLE 6.—Comparative gear efficiencies for sampling *Penaeus aztecus* in a Galveston West Bay salt marsh. Area sampled and number of replicates for each device are as follows: Drop sampler 2.8 m² ($n = 22$); beam trawl 3.0 m² ($n = 12$); bag seine 109 m² ($n = 10$); otter trawl 72 m² ($n = 10$).

	$\bar{x}$ Efficiency			
Habitat type	Drop sampler	Beam trawl	Bag seine	Otter trawl
Spartina vegetation				
(Shrimp count, $\bar{x}$/m² ±SD)	94% (8.9 ±3.7)	23% (2.2 ±2.2)	not operable	not operable
Nonvegetated				
(Shrimp count, $\bar{x}$/m² ±SD)	98% (0.30 ±0.3)	82% (0.25 ±0.46)	33% (0.10 ±0.06)	17% (0.05 ±0.04)

the presence of estuarine macrophytes can be associated with an increase in epifaunal abundance (Heck and Wetstone 1977; Heck and Orth 1980) as well as providing protective cover (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981). For shrimp selecting vegetated marsh, this may translate into a greater variety and abundance of food and some degree of protection from predation.

Zonal and Areal Relationships

Penaeus aztecus demonstrated a greater degree of attraction to vegetated habitat in the inner than the outer marsh. Accordingly, shrimp densities were higher among vegetation and lower on nonvegetated bottom in the innermost zone compared with the outer zone. This relationship is adequately reflected by comparing ratios of vegetated with nonvegetated shrimp density. Using the ratios, the change in selection from the outer, middle, to inner zone was 3.3:1, 11.0:1, and 27.7:1, respectively. The percent area covered by *S. alterniflora* (Fig. 2) also increased (by a factor of three) from outer to inner marsh, but as vegetational coverage increased arithmetically selection by *P. aztecus* increased geometrically (Fig. 6). This implies that salt marshes with more vegetational coverage have disproportionately greater attractive value to *P. aztecus* than do those with less coverage. On a larger scale, Turner (1977) revealed a positive correlation between extensiveness of estuarine vegetation and offshore shrimp yield. However, the relationship may not be simple; it is likely to depend upon characteristics such as the configuration, accessibility, and quality of vegetational patches within a marsh. For instance, an edge effect has been identified which associates large numbers of shrimp with the nonvegetated zone adjacent to vegetation (Mock 1966; Christmas et al. 1976). Since our *Spartina* habitat was intertidal, and often not inundated during low tides, the nonvegetated subtidal habitat provided a refuge against stranding. We have assumed that it did and that shrimp redistributed accordingly each tidal cycle. It is evident that an increase in the amount of ecotone edge (between habitats) would facilitate movement for the shrimp population. It is also evident that the amount of edge is proportionally related to the degree of reticulation in the marsh (Fig. 2). Thus, reticulation may be an important mechanism for increasing the accessibility of intertidal vegetation to *P. aztecus*.

Shrimp Densities

Density estimates for penaeid shrimp in *S. alterniflora* vegetation have not been reported previously. We found a density range for *P. aztecus* in *Spartina* habitat of 0.7 to 43.2/m² with an overall mean, from March through July, of 11.7/m² (1 SD = 9.4, $n = 81$). Comparable densities from adjacent nonvegetated habitat ranged between 0 and 18.2/m². All densities were taken when *P. aztecus* numerically dominated the shrimp population. By August, when *P. setiferus* first began to dominate, the combined mean for both species in vegetation increased to 50.8/m² (1 SD = 31.6, $n = 12$) and a single sample attained a density of 118.6 shrimp/m². These data may indicate a potential for higher *P. aztecus* densities earlier in the season and suggest that *P. aztecus* were not restricted by lack of space.

To our knowledge, we have provided the first accurate estimates of shrimp density in marsh vegetation, and our densities are among the few available for any estuarine system. Due to method limitations, most researchers have only reported relative abundances of restricted sizes, usually over nonvegetated bottom. The single exception was data by Allen and Hudson (1970), using a suction sampler in seagrasses in Florida Bay. From 43 trials, they reported a mean of 6.2/m² ± 3.4 SD for *P. duorarum*.

Estimates of *P. aztecus* densities from nonvegetated bottom in three other Galveston Bay salt marshes were available from the Texas Parks and Wildlife Department (TPWD) from 1976 through 1981 (Benefield 1982, footnote 5.). The data were taken using a marsh net (Renfro 1963) which was relatively effective for capturing shrimp on nonvegetated bottom (Table 6 compares a beam trawl, similar to the marsh net, with other sampling devices). Mean TPWD densities for *P. aztecus* during the latter half of March were 10.4/m² for 1976, 5.2/m² for 1977, 0.3/m² for 1978, 1.3/m² for 1979, 8.7/m² for 1980, and 5.1/m² for 1981 with an overall mean of 5.2/m². In our study, on nonvegetated bottom, the March mean for *P. aztecus* was 0.9/m² and overall (March through July) the mean was 1.4/m². It is evident that our nonvegetated densities for *P. aztecus* were within the range, but low compared with the mean calculated from TPWD data.

These densities of *P. aztecus* may not be strictly

[5]R. L. Benefield, Bay Shrimp Project Leader, Texas Parks and Wildlife Department, Coastal Fisheries Branch, P.O. Box 8, Seabrook, TX 77586, pers. commun. September 1982.

comparable, since sampling was executed during unknown variable tidal stages and the degree of flooding in intertidal vegetation appears to greatly influence shrimp densities on nearby nonvegetated subtidal bottom. Perhaps the only meaningful density estimates are those taken during low tide in nonvegetated habitat or those taken in vegetated habitat at flood tide. In any case, tide stage must be uniform for data to be comparable.

Sampling Integrity

The sampling approach in our investigation provided more realistic density estimates than traditional methods for sampling shrimp in estuaries (Table 6). We agree with Loesch et al. (1976) in concluding that techniques such as the area-swept method using an otter trawl are among the poorest for quantifying *P. aztecus*. Past recognition of this problem stimulated development of the push net (Allen and Inglis 1958), small beam trawl (Renfro 1963; Loesch 1965), and marsh net (Pullen et al. 1968). These samplers improved accuracy on nonvegetated bottom, but were ineffective when vegetation was present and did not solve avoidance problems. Further improvement came for sampling in seagrasses, but not salt marshes, with the invention of a sled-mounted suction sampler (Allen and Hudson 1970) and modification of a drop net technique (Hoese and Jones 1963; Gilmore et al. 1976). Our methodology has been designed to minimize escape, improve recovery from the area sampled (including burrowed shrimp), and to operate in salt marsh habitats. The drop-sampler method proved to be nearly as effective among vegetation as on nonvegetated bottom.

CONCLUSION

We contend that differences in *P. aztecus* densities between vegetated and nonvegetated marsh bottom were due to habitat selection. In support, we refer to Loesch (1965), Trent et al. (1969), and Stokes (1974) who have associated brown shrimp distributions with estuarine vegetation, and a laboratory experiment by Giles and Zamora (1973) demonstrating *P. aztecus* prefer *S. alterniflora* instead of barren substrate. Finally, our fish gut examinations indicate that immediate effects of predation did not account for the density differential.

Since *S. alterniflora* is characteristically intertidal, and not continuously available to shrimp, the adjacent subtidal zone provided an important alternate habitat during low tide. We propose that the amount of edge between habitats facilitated shrimp movement, and the reticulated nature of the salt marsh was an important feature for increasing the amount of edge. In addition, intertidal vegetation was more accessible and its potential for utilization greater during spring and fall high tides. This interaction may in part account for seasonal peaks in *P. aztecus* populations. In our investigation, recruitment began abruptly with equinox tides. The shrimp population during the spring and early summer was dominated entirely by *P. aztecus*.

Our shrimp densities from vegetated habitat were higher than any previously reported including those from seagrass and mangrove systems. The high densities in vegetation were possibly governed by the amount of total marsh, ratio of vegetated to nonvegetated habitat, and size of recruitment. The densities on nonvegetated marsh bottom were probably controlled by the relative accessibility of nearby vegetated habitat. In any case, the observed density differential strongly implies that marsh vegetation provides a vital function for juvenile brown shrimp.

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Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA)

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ABSTRACT: We quantified and compared nekton and infaunal densities among vegetated (edge *Spartina alterniflora*, inner *Spartina alterniflora*, *Scirpus maritimus*, *Juncus roemerianus*, and *Spartina patens* marsh) and shallow nonvegetated (marsh pond, marsh channel, cove, and shallow bay) areas of upper Galveston Bay and East Bay, Texas. In 2 seasons (spring and fall) of high nekton abundance, and over 2 yr, we collected 267 quantitative samples (upper Galveston Bay, 1993 = 127 and East Bay, 1994 = 140) using a 1 m^2 drop sampler. The vegetated marsh surface consistently contained more species (i.e. higher species richness) and total numbers of decapod crustaceans than nonvegetated areas. In contrast, fish species richness and densities of total fishes on the marsh and in nonvegetated areas were not significantly different in most comparisons. Most numerically dominant species of nekton seemed to exhibit at least some degree of habitat selection. Within vegetation, 2 factors, elevation and proximity to open water, were most important in influencing the distribution of nekton. Low marsh edge dominated by *Spartina alterniflora* or *Scirpus maritimus* was apparently selected by most species that used the marsh surface including brown shrimp *Farfantepenaeus aztecus*, blue crab *Callinectes sapidus*, and daggerblade grass shrimp *Palaemonetes pugio*. White shrimp *Litopenaeus setiferus* and striped mullet *Mugil cephalus* also were concentrated in low edge marsh; although in one comparison, densities of these 2 species in edge and inner *S. alterniflora* were not significantly different. In contrast, gulf killifish *Fundulus grandis* and sheepshead minnow *Cyprinodon variegatus* were most abundant on inner *S. alterniflora* or *S. patens* marsh. Other fishes (gulf menhaden *Brevoortia patronus*, spot *Leiostomus xanthurus*, bay anchovy *Anchoa mitchilli*, blackcheek tonguefish *Symphurus plagiusa*, and Atlantic croaker *Micropogonias undulatus*) had higher densities over nonvegetated bottoms than on the marsh surface. Specific habitat types that these pelagic species seemed to favor were marsh channels (gulf menhaden, bay anchovy), marsh ponds (spot), and coves (Atlantic croaker, blackcheek tonguefish). Overall, marsh-surface and adjacent nonvegetated habitat types contained much higher densities of most nekton than the shallow bay. Infaunal densities were estimated from sediment cores, and taxa (mainly annelids, crustaceans, molluscs, and insects) were most abundant in nonvegetated areas contiguous with marsh in the spring. Factors that influenced infaunal abundance are complex and may include predation, flooding patterns, elevation, and distance to edge. Our study has important implications for designing marsh-creation projects. Based on our results, we recommend creating a variety of marsh and contiguous shallow-water areas to enhance nekton biodiversity. To maximize fishery habitat, priority should be given to constructing low marsh edge by creating large areas of low marsh interspersed with a dense network of shallow channels and interconnected ponds.

KEY WORDS: Fishery species · Gulf of Mexico · Habitat comparisons · Habitat selection · Nursery areas · Penaeid shrimps · Tidal marsh · Restoration

INTRODUCTION

Shallow areas along estuarine shorelines often contain large nekton populations, reflecting the high productivity of estuaries (Pihl & Rosenberg 1982, Kneib 1997). Here, aquatic organisms use a complex habitat mosaic composed of tidal marshes and adjacent intertidal and subtidal waters (Kneib 1997). The different habitat types that compose this mosaic are not only connected by proximity, but also by tidal flow. Many natant organisms, for example, move freely between the vegetated marsh surface and contiguous open water as water level changes with tide stage (Zimmerman & Minello 1984, McIvor & Odum 1988, Hettler

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1989, Rozas & Reed 1993, Kneib & Wagner 1994, Kneib & Knowlton 1995, Irlandi & Crawford 1997, Cicchetti 1998).

Tidal marshes are widely recognized as important nursery areas that support valuable coastal fisheries (Boesch & Turner 1984, Minello 1999, Zimmerman et al. 2000). The young of many fishery species and all life stages of numerous estuarine resident species use the flooded marsh surface much more intensively than adjacent nonvegetated bottom (Zimmerman & Minello 1984, Thomas et al. 1990, Rakocinski et al. 1991, Baltz et al. 1993, Wenner & Beatty 1993, Minello et al. 1994, Castellanos 1997, Rozas & Minello 1998, Howe et al. 1999, Minello 1999). Tidal marsh channels connect the marsh surface with open estuarine waters. These channels appear to be used as nursery areas by some organisms, and subtidal channels serve as low-tide refugia and staging areas for animals using adjacent intertidal areas (Cain & Dean 1976, Hackney et al. 1976, Rozas & Hackney 1984, Rozas & Odum 1987, Rozas et al. 1988, Rountree & Able 1992, Cattrijsse et al. 1994). Whether marsh ponds function similarly to tidal channels may depend on their hydrology. Marsh ponds that are constantly flooded and hydrologically connected to tidal channels support relatively high nekton populations (Rogers et al. 1992). In contrast, isolated ponds apparently support fewer organisms because limited tidal exchange with adjacent waterways restricts recruitment, and animals confined within these ponds must withstand rigorous environmental conditions (Rowe & Dunson 1995) and competition for food (Layman 1999).

The literature comparing the use of major habitat types in the shallow region of estuaries is limited. Most studies comparing nekton populations in estuarine marshes were conducted in salt marsh dominated by a single species, *Spartina alterniflora* Loisel. Little information exists about how nekton use marsh vegetation dominated by species other than *S. alterniflora*. In addition, comparisons of different habitat types employing quantitative methods are limited, and few studies have examined major habitat types concurrently. Assessment of the relative habitat value of tidal marsh and adjacent areas is best accomplished through comparisons of nekton densities using quantitative gear and by sampling all sites at the same time (Rozas & Minello 1997).

The overall objective of our study was to examine nekton use of marsh and contiguous open-water areas within a shallow region of Galveston Bay, Texas, USA, by comparing the small-scale distribution of organisms among major habitat types. Our study was part of a larger project to build a database from which design parameters could be developed for constructing ecologically functional marshes using dredged material (Rozas & Zimmerman 1994, Rozas et al. 1995). Specific goals of our study were to: (1) compare densities of dominant species of fishes and decapod crustaceans (as a measure of habitat quality) among major marsh and shallow nonvegetated areas of Galveston Bay, (2) describe the composition, relative abundance, and seasonal abundance of fishes, decapod crustaceans, and infauna using these areas, and (3) identify the habitat attributes that could account for the distributional patterns we observed.

MATERIALS AND METHODS

Study area. Our study area included 2 locations on the north Texas coast in the Galveston Bay estuary, upper Galveston Bay and East Bay (Fig. 1). The Galveston Bay system is microtidal. Tides within the study area are predominantly diurnal, and the mean tidal range is approximately 0.3 m (Orlando et al. 1991).

The upper Galveston Bay location encompassed the marsh complex and adjacent open water of Atkinson Island and Hog Island. Salt marsh occupies the intertidal zone, and the dominant plant species within the marsh vary with elevation (Wermund et al. 1992). *Spartina alterniflora* is present in the low intertidal zone, and the most robust form of this species occurs in narrow bands at the marsh edge adjacent to subtidal and low, nonvegetated intertidal areas. *Scirpus maritimus* L. is found at slightly higher elevations, but it too occurs low enough in the intertidal zone to experience frequent flooding events. *Spartina patens* (Aiton) Muhl. grows in the highest part of the intertidal zone and floods only infrequently. Nonvegetated shallow-water areas within and contiguous with the marsh vegetation in the study area include channels, ponds, and coves. Coves are large semi-enclosed embayments that are subjected to less wave energy than bay waters because they are partially surrounded by marsh.

The East Bay location was centered on a large salt marsh system at Elmgrove Point on the bay side of the Bolivar Peninsula (Fig. 1). As in upper Galveston Bay, *Spartina alterniflora* is the dominant vegetation of the low intertidal marsh at East Bay. However, *S. patens* and *Scirpus maritimus* are not major marsh types at the East Bay location; rather, *Juncus roemerianus* Scheele replaces *S. alterniflora* at the higher intertidal elevations; *Juncus* marsh is most extensive at the northeast portion of the Elmgrove Point marsh.

Nekton/infauna sampling. Nekton (fishes and decapod crustaceans) were quantitatively sampled with a drop sampler using the procedure described by Zimmerman et al. (1984). We chose a drop sampler for this study because the catch efficiency of this enclosure device does not appear to vary substantially with habi-

tat characteristics typical of shallow estuarine areas, and unlike many other gear, it is effective in dense emergent vegetation (Rozas & Minello 1997). We employed a 1.14 m diameter cylinder that was dropped from a boom attached to a shallow-draft boat. Two persons positioned the cylinder over a sample site by slowly pushing from the boat's stern. When released from the boom, the cylinder rapidly entrapped organisms within a 1.0 m^2 sample area. Disturbance to the sample area prior to releasing the cylinder was minimized using this procedure, as distances from the bow and stern of the boat to the edge of the sample area were 3.5 and 8.3 m, respectively.

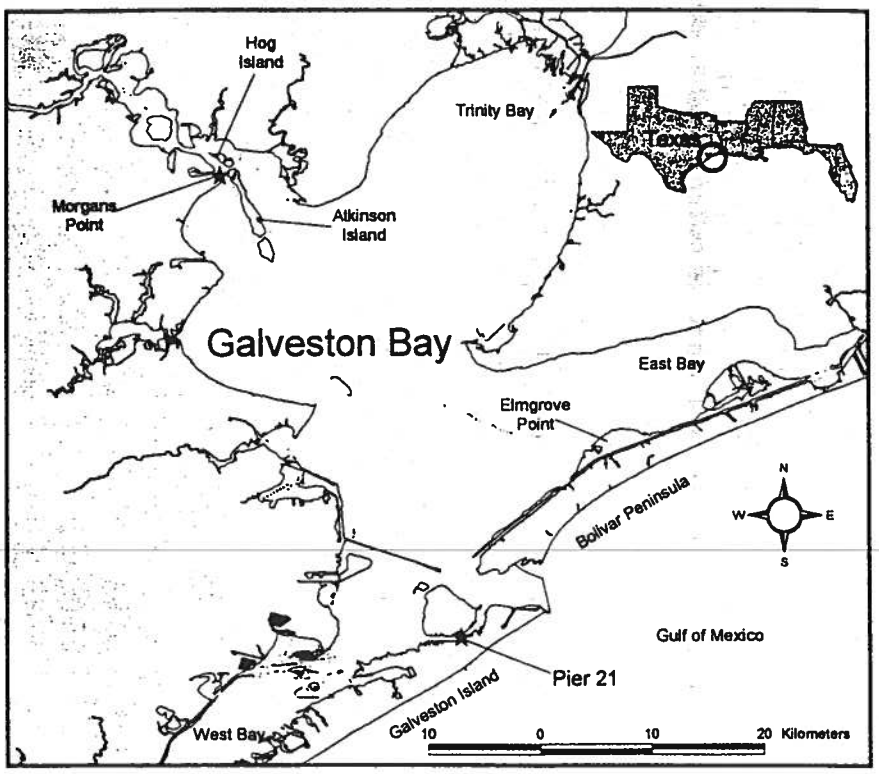

Fig. 1. Map showing the 2 locations (upper Galveston Bay and East Bay) in the study area and the position of the Galveston Bay estuary on the upper Texas coast. We collected samples at Hog Island and Atkinson Island in upper Galveston Bay and near Elmgrove Point in East Bay. Locations of NOAA tide gauges are at Morgans Point (upper Galveston Bay) and Pier 21 (bayside of Galveston Island)

We sampled 8 distinct areas within the marsh complex and adjacent shallow water in upper Galveston Bay that included 4 vegetated areas (edge *Spartina alterniflora*, inner *S. alterniflora*, *S. patens*, and *Scirpus* marsh) and 4 shallow nonvegetated areas (marsh pond, marsh channel, marsh cove, and shallow bay waters). Ponds were not isolated hydrologically but connected to tidal marsh creeks. Sample sites in inner *S. alterniflora* marsh were 5 to 6 m from the marsh edge (vegetation-water interface), whereas samples of other vegetated areas were taken within 1 to 2 m of the marsh edge. Although all vegetated areas except inner *S. alterniflora* marsh can be classified as marsh edge, for brevity, 'edge' will be used as a modifier only with *S. alterniflora* to distinguish this habitat type from inner *S. alterniflora* marsh. We collected a total of 127 nekton samples during 2 seasons in 1993: spring (May 5–7, 21) and fall (October 12, 18–20). Most habitat types were sampled 8 times each season. However, we collected only 7 shallow bay samples in the fall. We based the number of samples collected at each island (Atkinson Island or Hog Island) in a particular habitat type on the ratio of the area of a habitat type at an island to the total area of the habitat type (both islands combined).

In 1994, we sampled 7 areas in East Bay that included all habitat types sampled in upper Galveston Bay (except *Spartina patens* and *Scirpus*) as well as *Juncus* marsh. We took 10 replicate samples in each habitat type in spring (April 25–28) and fall (September 12–15), for a total of 140 nekton samples.

At each location, we randomly selected replicate sample sites using random numbers and a grid placed over an aerial photograph of the potential sample area. Shallow bay sample sites were selected from areas of Galveston Bay along the shoreline of each marsh system (Atkinson Island, Hog Island, East Bay marsh). We collected all samples during the day at high tide when all habitat types were inundated and available to aquatic organisms; sample sites were all <1 m deep.

After the cylinder was dropped, we measured water temperature, dissolved oxygen, salinity, turbidity, and water depth using the methods described by Minello & Zimmerman (1992). We also measured the distance from the sample area to the nearest marsh-water interface. At vegetated sites, we clipped plant stems at ground level, counted them (dead and alive combined), and removed them from the cylinder. We also determined the standing biomass of vegetation each season by oven drying 3 air-dried subsamples of each species at 75°C to a constant weight and calculating a conversion factor (oven-dried weight/air-dried weight) using these data. By multiplying the total air-dried weight of each species in each sample by the appropri-

ate conversion factor and totaling the weights within each sample, we converted all values to oven-dried biomass.

In each major habitat type each season, we collected 5 (upper Galveston Bay) or 6 (East Bay) samples for benthic infauna. Each replicate sample consisted of 3 pooled 5 cm-deep cores taken from randomly selected locations within the cylinder with a 5 cm diameter plastic core (total area = 60.8 cm^2). Samples were washed on a 0.5 mm mesh sieve, and the material retained was fixed with 10% formalin stained with Rose Bengal. In the laboratory, organisms were separated from detritus and plant parts and identified to the lowest feasible taxon.

After we measured environmental parameters and collected benthic cores, we captured nekton trapped in the drop sampler using dip nets and by filtering the water pumped out of the enclosure through a 1 mm mesh net. When the sampler was completely drained, any animals remaining on the bottom were removed by hand. Samples were preserved in formalin with Rose Bengal stain and returned to the laboratory for processing. In the laboratory, the samples were sorted, and animals were identified to lowest feasible taxon.

Flooding duration. The Conrad Blucher Institute for Surveying and Science, Texas A&M University-Corpus Christi supplied us with water-level data. We used continuously collected water-level data for 1993 and 1994 from Morgans Point (NOS Station I.D. = 87700613) and Pier 21 (NOS Station I.D. = 8771450) to estimate flooding durations at each location. Using water depth measured at each sample site in upper Galveston Bay and concurrent water-level data from Morgans Point (located approximately 1 km west of Atkinson Island, Fig. 1), we estimated substrate elevation relative to this tide gauge and determined flooding duration (percentage of time a site was submerged) for each sample site.

We used an equation from Minello & Webb (1997) to compute water levels in East Bay from Pier 21 (located approximately 20 km south-southwest of Elmgrove Point, Fig. 1) data because our East Bay location lacked a nearby tide gauge. This equation incorporates a 2 h lag in tides between Elmgrove Point and Pier 21 (i.e. tides reached the East Bay location 2 h after Pier 21), and there is good agreement between tide levels at Pier 21 and water levels in East Bay (Minello & Webb 1997). We estimated elevations and flooding durations of East Bay sample sites by relating the water depth measured at each site to concurrent East Bay tide data computed from this equation.

We also estimated a mean surface elevation (relative to Mean Tide Level, MTL) for each habitat type at a location. This elevation was estimated at each location by subtracting the MTL of the nearest tide gauge from the average substrate elevation that was determined as described above. The MTL used for habitat types at the East Bay location was calculated from the MTL of the Pier 21 gauge using the equation from Minello & Webb (1997).

Data analyses. We used 1-way analysis of variance (ANOVA) followed by *a priori* contrasts to examine differences in densities of abundant organisms, species richness (number of fish and decapod crustacean taxa), and environmental characteristics (mean dissolved oxygen, salinity, water temperature, turbidity, water depth, distance to edge, and vegetation stem density and biomass) among habitat types (Table 1). In this procedure, we analyzed the data collected at each location (upper Galveston Bay and East Bay) and during each season separately, because many species were only abundant enough to include in the statistical analysis–at 1 location or in 1 season. We considered alpha levels of 0.05 to be significant in all results, but we also calculated adjusted alpha levels for the Habitat effect using the sequential Bonferroni method described by Rice (1989). These adjusted levels should be used if the reader would like to buffer against error introduced by making multiple comparisons (i.e. testing a hypothesis for several species or parameters). We compared the following habitat types with *a priori* contrasts (Table 1). Upper Galveston Bay: all vegetated areas versus all nonvegetated areas, edge *Spartina alterniflora* versus *Scirpus*, edge *S. alterniflora* versus *S. patens*, edge *S. alterniflora* versus inner *S. alterniflora*, inner *S. alterniflora* versus *Scirpus*, inner *S. alterniflora* versus *S. patens*, and *S. patens* versus *Scirpus*; East Bay: all vegetated areas versus all nonvegetated areas, edge *S. alterniflora* versus *Juncus*, edge *S. alterniflora* versus inner *S. alterniflora*, and inner *S. alterniflora* versus *Juncus*.

We used 8 predictor variables (salinity, water temperature, dissolved oxygen, turbidity, distance to edge, water depth, stem density, and elevation) in 2 discriminant function analyses to distinguish among habitat types. From the first analysis, we constructed a discriminant model that used these environmental variables to separate the 9 habitat types we sampled. We used the Wilks' lambda multivariate test statistic to determine whether habitat types could be separated, and we examined the canonical variates in the model to identify the most important predictor variables in determining this separation. In a second discriminant analysis, we used this same procedure to distinguish among the 5 marsh types we sampled. We used 2 canonical analyses to examine potential relationships between densities of fishes and decapod crustaceans and environmental characteristics of habitats. In the first canonical analysis, we included data from all habitats. We used only data collected at marsh sites in the

Table 1. Analysis of Variance (ANOVA) table for comparing habitat types. Model includes the test for the main effect of Habitat and the *a priori* contrasts that compare specific habitat types. The example presented here uses data from upper Galveston Bay and the dependent variable total macrofauna (sum of total fishes and total crustaceans)

Source	df	Sum of squares	Mean square	*F* value	p value
May 1993					
Habitat	7	27.896	3.985	4.293	0.0007
Contrasts					
Vegetated vs nonvegetated habitat types	1	14.184	14.184	15.281	0.0003
Edge *Spartina alterniflora* vs *Scirpus maritimus*	1	4.062	4.062	4.376	0.0410
Edge *Spartina alterniflora* vs *Spartina patens*	1	6.152	6.152	6.628	0.0127
Edge *Spartina alterniflora* vs inner *Spartina alterniflora*	1	3.853	3.853	4.151	0.0463
Inner *Spartina alterniflora* vs *Scirpus maritimus*	1	0.003	0.003	0.003	0.9567
Inner *Spartina alterniflora* vs *Spartina patens*	1	0.268	0.268	0.288	0.5934
Spartina patens vs *Scirpus maritimus*	1	0.216	0.216	0.233	0.6313
Residual error	56	51.982	0.928		
October 1993					
Habitat	7	35.362	5.052	5.721	0.0001
Contrasts					
Vegetated vs nonvegetated habitat types	1	19.391	19.391	21.961	0.0001
Edge *Spartina alterniflora* vs *Scirpus maritimus*	1	0.696	0.696	0.788	0.3786
Edge *Spartina alterniflora* vs *Spartina patens*	1	11.361	11.361	12.866	0.0007
Edge *Spartina alterniflora* vs inner *Spartina alterniflora*	1	5.828	5.828	6.600	0.0129
Inner *Spartina alterniflora* vs *Scirpus maritimus*	1	2.496	2.496	2.827	0.0984
Inner *Spartina alterniflora* vs *Spartina patens*	1	0.915	0.915	1.036	0.3132
Spartina patens vs *Scirpus maritimus*	1	6.434	6.434	7.286	0.0092
Residual error	55	48.564	0.883		

second canonical analysis. We combined the data collected at each location and during each season in both multivariate procedures (discriminant function and canonical analyses) described above.

Densities of animals were positively related to the standard deviation; therefore, we performed a $\ln(x + 1)$ transformation of the original density values prior to analyses. Other variables were not transformed. All tabular and graphical data presented in this paper are untransformed means. We used SuperANOVA (Version 5 edn, Abacus Concepts, Inc., Berkeley, California, 1989) to do 1-way ANOVA and SAS (Version 6, SAS Institute, Cary, NC, 1989) to run the canonical and discriminant function analyses.

RESULTS

Decapod crustaceans and fishes

At upper Galveston Bay, we collected a total of 21 species of fishes and 10 species of crustaceans in spring; and 17 species of fishes and 8 species of crustaceans in fall (Table 2). We recorded slightly more species from East Bay: 22 species of fishes and 15 species of crustaceans in spring; 25 species of fishes and 16 species of crustaceans in fall (Table 3). Marsh sites consistently yielded significantly more species (i.e. higher species richness; ANOVA Contrasts, all p values = 0.0001) and total numbers of crustaceans than nonvegetated areas (both locations and seasons, Tables 2 & 3). In contrast, fish species richness and densities of total fishes in marsh and nonvegetated areas were not significantly different in most comparisons (ANOVA Contrasts, Upper Galveston Bay, p = 0.0869 [spring], p = 0.7591 [fall]; East Bay, p = 0.9243 [fall]); although at East Bay in spring, we took significantly more fish species (ANOVA Contrast, p = 0.0001, means = 2.5 vs 1.2), and total fishes (means = 43.9 vs 6.1, see Table 5) in nonvegetated areas than at marsh sites.

Upper Galveston Bay

Decapod crustaceans (49%) and fishes (51%) were similarly abundant in spring, but decapods accounted for 90% of all animals taken in fall at upper Galveston Bay sample sites (Table 2). Daggerblade grass shrimp *Palaemonetes pugio*, brown shrimp *Farfantepenaeus aztecus* (formerly *Penaeus aztecus*, Perez-Farfante & Kensely 1997), white shrimp *Litopenaeus setiferus* (formerly *Penaeus setiferus*, Perez-Farfante & Kensely 1997), blue crab *Callinectes sapidus*, gulf marsh fiddler crab *Uca longisignalis*, heavy marsh crab *Sesarma reticulatum*, and marsh grass shrimp *Palaemonetes vulgaris* accounted for >95% of total decapod crustaceans

Table 2. Mean densities as number m^{-2} and (SE, 1 standard error) of animals commonly collected (i.e. at least 20 ind. mo^{-1}) in each habitat type of upper Galveston Bay sampled in May and October 1993. The mean number of fish and crustacean species taken in each habitat type as well as the (total fish and total crustacean species) collected in all habitat types combined also are given. Each mean is estimated from 8 drop samples in each habitat (except only 7 samples for shallow bay habitat in October). Results (p values) are given for ANOVA analyses we used to compare mean densities and species richness (number of species) among the 8 habitat types and *a priori* contrasts testing for significant differences between: 1= vegetated and nonvegetated habitat types; 2 = edge *Spartina alterniflora* and *Scirpus maritimus*; 3 = edge *S. alterniflora* and *Spartina patens*; 4 = edge *S. alterniflora* and inner *S. alterniflora*; 5 = inner *S. alterniflora* and *S. maritimus*; 6 = inner *S. alterniflora* and *S. patens*; and 7 = *S. patens* and *S. maritimus*. See Table 1 for an example of the ANOVA model. *Probability value was significant after alpha was adjusted as described by Rice (1989)

Species	*Spartina patens* Mean	SE	*Scirpus maritimus* Mean	SE	Inner *S. alterniflora* Mean	SE	Edge *S. alterniflora* Mean	SE	Pond Mean	SE	Channel Mean	SE	Cove Mean	SE	Shallow bay Mean	SE	ANOVA p value	Contrast p values 1	2	3	4	5	6	7
May 1993																								
Fish species (21)	1.1	(0.30)	0.9	(0.23)	2.1	(0.40)	1.5	(0.33)	1.4	(0.32)	3.3	(0.70)	1.9	(0.44)	1.1	(0.35)	0.0032*							
Total fishes	2.0	(0.85)	6.9	(5.10)	4.6	(1.35)	46.3	(34.02)	7.8	(5.40)	23.8	(13.66)	7.3	(3.19)	9.3	(8.11)	0.1669							
Gulf menhaden	0.0	(0.00)	6.4	(5.18)	0.3	(0.16)	44.5	(34.12)	6.0	(4.52)	20.5	(13.30)	6.0	(3.18)	8.6	(8.06)	0.1075							
Striped mullet	0.4	(0.38)	0.1	(0.13)	1.6	(0.68)	1.1	(0.48)	0.0	(0.00)	0.3	(0.16)	0.1	(0.13)	0.0	(0.00)	0.0021*	0.0018	0.0147	0.0410	0.5021	0.0023	0.0076	0.6715
Spot	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.13)	1.5	(0.80)	0.8	(0.37)	0.1	(0.13)	0.0	(0.00)	0.0001*	0.0007	0.5854	0.5854	0.5854	1.0000	1.0000	1.0000
Gulf killifish	0.6	(0.38)	0.0	(0.00)	1.4	(0.71)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0001*	0.0018	1.0000	0.0250	0.0001	0.0001	0.0559	0.0250
Crustacean species (10)	3.8	(0.53)	3.9	(0.35)	2.4	(0.32)	2.9	(0.30)	1.4	(0.38)	1.6	(0.18)	1.1	(0.23)	1.0	(0.27)	0.0001*							
Total crustaceans	13.5	(2.71)	13.8	(1.56)	19.4	(5.37)	38.4	(7.21)	7.8	(2.67)	5.8	(2.95)	3.0	(0.85)	2.1	(0.61)	0.0001*	0.0001	0.0306	0.0195	0.0477	0.8461	0.7041	0.8525
Daggerblade grass shrimp	5.8	(1.44)	3.4	(0.68)	9.5	(3.92)	25.6	(5.23)	0.8	(0.41)	1.4	(1.10)	0.0	(0.00)	0.0	(0.00)	0.0001*	0.0001	0.0001	0.0021	0.0017	0.4369	0.9409	0.3948
Brown shrimp	3.3	(1.82)	5.4	(1.94)	0.5	(0.33)	8.8	(3.59)	6.5	(2.26)	4.1	(1.93)	2.6	(0.82)	1.5	(0.57)	0.0327	0.0734	0.7732	0.0711	0.0024	0.0055	0.1871	0.1267
Gulf marsh fiddler crab	1.8	(0.25)	3.8	(1.24)	8.8	(2.36)	1.8	(1.11)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0001*	0.0001	0.0035	0.1243	0.0001	0.0071	0.0001	0.1429
Blue crab	0.5	(0.19)	0.5	(0.27)	0.6	(0.32)	2.0	(1.45)	0.5	(0.33)	0.1	(0.13)	0.4	(0.26)	0.1	(0.13)	0.0270	0.0084	0.0079	0.0304	0.0354	0.5512	0.9490	0.5946
Heavy marsh crab	1.5	(0.60)	0.5	(0.27)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0001*	0.0006	0.0332	0.0001	1.0000	0.0332	0.0001	0.0054
October 1993																								
Fish species (17)	0.8	(0.25)	2.0	(0.42)	1.5	(0.19)	1.1	(0.40)	0.6	(0.18)	1.6	(0.38)	2.1	(0.35)	1.3	(0.36)	0.0150							
Total fishes	1.0	(0.38)	3.9	(1.06)	4.6	(1.77)	1.1	(0.40)	0.9	(0.30)	4.4	(1.71)	4.4	(0.65)	2.4	(0.84)	0.0047*	0.4849	0.0299	0.8809	0.0199	0.8657	0.0136	0.0208
Blackcheek tonguefish	0.0	(0.00)	0.5	(0.27)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2.0	(0.96)	2.8	(0.56)	0.6	(0.30)	0.0001*	0.0001	0.1403	1.0000	1.0000	0.1403	1.0000	0.1403
Gulf killifish	0.8	(0.31)	0.8	(0.41)	2.4	(0.75)	0.5	(0.19)	0.0	(0.00)	0.0	(0.00)	0.4	(0.26)	0.0	(0.00)	0.0002*	0.0001	0.8140	0.6383	0.0032	0.0063	0.0117	0.8140
Sheepshead minnow	0.0	(0.00)	1.0	(0.76)	2.0	(1.16)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0080*	0.0141	0.0732	1.0000	0.0018	0.1496	0.0018	0.0732
Bay anchovy	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.1	(0.13)	1.1	(0.99)	0.1	(0.13)	1.4	(0.69)	0.0306	0.0057	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Crustacean species (8)	2.8	(0.37)	3.6	(0.57)	2.4	(0.38)	3.8	(0.56)	1.8	(0.37)	2.0	(0.33)	2.1	(0.30)	1.3	(0.29)	0.0001*							
Total crustaceans	10.6	(3.51)	51.9	(14.84)	17.8	(9.67)	101.1	(34.97)	7.5	(2.20)	5.3	(0.94)	5.6	(0.80)	2.4	(0.57)	0.0001*	0.0001	0.5267	0.0029	0.0041	0.0219	0.9040	0.0163
Daggerblade grass shrimp	5.0	(2.15)	34.4	(12.43)	9.4	(6.65)	70.9	(28.24)	0.3	(0.16)	0.3	(0.16)	0.3	(0.16)	0.0	(0.00)	0.0001*	0.0001	0.3360	0.0006	0.0003	0.0060	0.8510	0.0099
White shrimp	0.0	(0.00)	9.3	(5.01)	2.9	(2.47)	13.5	(5.05)	6.0	(2.20)	3.1	(0.88)	3.4	(0.89)	1.3	(0.52)	0.0013*	0.4498	0.2290	0.0001	0.0021	0.0499	0.2431	0.0024
Blue crab	1.0	(0.33)	3.8	(1.41)	0.8	(0.31)	7.3	(2.47)	1.3	(0.45)	1.3	(0.45)	1.1	(0.55)	0.6	(0.20)	0.0030*	0.0171	0.0822	0.0013	0.0003	0.0413	0.6427	0.1103
Gulf marsh fiddler crab	3.8	(1.59)	3.0	(1.07)	4.4	(1.16)	2.8	(1.46)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0001*	0.0001	0.3615	0.4186	0.0607	0.3242	0.2762	0.9166
Brown shrimp	0.0	(0.00)	0.6	(0.32)	0.4	(0.26)	2.3	(1.42)	0.0	(0.00)	0.6	(0.42)	0.8	(0.37)	0.3	(0.18)	0.0754							
Marsh grass shrimp	0.0	(0.00)	0.1	(0.13)	0.0	(0.00)	4.5	(2.96)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0139	0.0677	0.0037	0.0013	0.0013	0.7173	1.0000	0.7173

Table 3. Mean densities as number m^{-2} and (SE, 1 standard error) of animals commonly collected (i.e. at least 20 ind. mo^{-1}) in each habitat type of East Bay sampled in April and September 1994. The mean number of fish and crustacean species collected in each habitat type as well as the (total fish and total crustacean species) taken in all habitat types combined also are given. Each mean is estimated from 10 drop samples in each habitat type. Results (p values) are given for ANOVAs we used to compare mean densities and species richness (number of species) among the 7 habitat types and *a priori* contrasts testing for significant differences between: 1 = vegetated and nonvegetated habitat types; 2 = edge *Spartina alterniflora* and *Juncus roemerianus*; 3 = edge *S. alterniflora* and inner *S. alterniflora*; and 4 = *J. roemerianus* and inner *S. alterniflora*. See Table 1 for an example of the ANOVA model. *Probability value was significant after alpha was adjusted as described by Rice (1989)

Species	*Juncus roemerianus* Mean SE	Inner *S. alterniflora* Mean SE	Edge *S. alterniflora* Mean SE	Pond Mean SE	Channel Mean SE	Cove Mean SE	Shallow bay Mean SE	ANOVA p value	Contrast p values 1	2	3	4
April 1994												
Fish species (22)	0.8 (0.25)	0.9 (0.38)	1.9 (0.43)	1.5 (0.31)	3.6 (0.45)	2.8 (0.44)	2.2 (0.39)	0.0001*				
Total fishes	0.8 (0.25)	1.1 (0.53)	16.5 (13.44)	4.2 (1.69)	133.6 (76.22)	8.0 (3.35)	29.9 (26.68)	0.0001*	0.0001	0.0592	0.0668	0.9555
Gulf menhaden	0.0 (0.00)	0.0 (0.00)	11.8 (11.69)	2.8 (1.79)	129.7 (75.56)	3.4 (2.80)	26.9 (26.90)	0.0001*	0.0007	0.3560	0.3560	1.0000
Atlantic croaker	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.3 (0.21)	0.9 (0.23)	1.3 (0.34)	0.7 (0.21)	0.0001*	0.0001	1.0000	1.0000	1.0000
Striped mullet	0.0 (0.00)	0.1 (0.10)	2.6 (1.78)	0.0 (0.00)	0.2 (0.13)	0.0 (0.00)	0.0 (0.00)	0.0335*	0.0843	0.0036	0.0099	0.7182
Blackcheek tonguefish	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1 (0.10)	0.2 (0.13)	1.8 (0.76)	0.6 (0.34)	0.0001*	0.0004	1.0000	1.0000	1.0000
Crustacean species (15)	5.9 (0.41)	4.9 (0.48)	6.2 (0.33)	1.5 (0.22)	1.6 (0.45)	2.0 (0.39)	2.9 (0.35)	0.0001*				
Total crustaceans	49.4 (6.69)	50.6 (11.10)	117.6 (14.54)	5.5 (1.30)	3.8 (1.87)	6.9 (2.59)	10.3 (2.58)	0.0001*	0.0001	0.0074	0.0046	0.8655
Daggerblade grass shrimp	10.9 (1.67)	9.8 (3.30)	43.6 (8.76)	0.4 (0.27)	0.3 (0.30)	0.0 (0.00)	1.3 (0.72)	0.0001*	0.0001	0.0001	0.0001	0.0931
Gulf marsh fiddler crab	8.1 (1.74)	29.4 (7.45)	26.3 (11.27)	0.0 (0.00)	0.4 (0.27)	0.0 (0.00)	0.0 (0.00)	0.0001*	0.0001	0.4225	0.0067	0.0006
Brown shrimp	3.5 (0.79)	3.4 (0.76)	24.7 (2.68)	4.4 (1.44)	1.3 (0.50)	5.2 (2.32)	4.9 (2.27)	0.0001*	0.0001	0.0001	0.0001	0.9278
Heavy marsh crab	18.7 (4.38)	3.8 (1.50)	14.3 (6.42)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0001*	0.0001	0.0019	0.2501	0.0001
Blue crab	0.8 (0.25)	0.7 (0.26)	2.8 (0.70)	0.4 (0.22)	0.4 (0.16)	0.5 (0.22)	1.0 (0.39)	0.0009*	0.0030	0.0023	0.0009	0.7497
Squareback marsh crab	0.9 (0.41)	0.1 (0.10)	3.9 (1.60)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0001*	0.0001	0.0016	0.0001	0.0446
September 1994												
Fish species (25)	2.4 (0.37)	2.4 (0.31)	2.9 (0.53)	2.3 (0.62)	2.9 (0.28)	2.9 (0.53)	2.3 (0.47)	0.8621				
Total fishes	2.8 (1.45)	11.1 (3.64)	6.4 (1.77)	1.4 (0.60)	4.9 (2.26)	4.5 (2.02)	6.5 (2.28)	0.0374	0.3351	0.3787	0.1495	0.5689
Bay anchovy	0.0 (0.00)	0.0 (0.00)	0.2 (0.20)	1.0 (0.60)	15.0 (11.44)	2.2 (1.31)	3.8 (1.80)	0.0026*	0.0003	0.7785	0.7785	1.0000
Naked goby	1.9 (0.50)	0.0 (0.00)	3.0 (1.05)	1.0 (0.63)	6.9 (4.03)	2.6 (1.22)	3.9 (1.53)	0.0236	0.2131	0.6218	0.0068	0.0244
Darter goby	2.6 (0.56)	0.7 (0.34)	2.6 (0.60)	1.0 (0.47)	1.3 (0.40)	1.0 (0.47)	0.4 (0.31)	0.0030*	0.0049	0.8789	0.0081	0.0053
Blackcheek tonguefish	0.0 (0.00)	0.0 (0.00)	0.2 (0.20)	0.6 (0.50)	1.0 (0.68)	1.1 (0.31)	0.7 (0.30)	0.0183	0.0007	0.5895	0.5895	1.0000
Crustacean species (16)	6.3 (0.45)	5.6 (0.27)	6.4 (0.52)	2.0 (0.39)	1.9 (0.41)	1.9 (0.41)	2.5 (0.40)	0.0001*				
Total crustaceans	73.9 (7.46)	63.7 (17.93)	107.8 (13.54)	8.4 (2.45)	5.8 (2.47)	3.9 (1.11)	5.2 (1.32)	0.0001*	0.0001	0.2857	0.0409	0.3162
Daggerblade grass shrimp	13.8 (4.19)	26.0 (14.06)	47.6 (7.94)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1 (0.10)	0.0001*	0.0001	0.0001	0.0002	0.0919
White shrimp	12.5 (2.91)	9.9 (3.01)	20.0 (4.80)	5.6 (2.17)	3.8 (2.11)	1.0 (0.45)	0.0 (0.00)	0.0001*	0.0001	0.3359	0.0718	0.3921
Gulf marsh fiddler crab	12.7 (1.58)	17.5 (3.80)	14.8 (5.57)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0001*	0.0001	0.1026	0.0457	0.7038
Heavy marsh crab	25.4 (2.60)	3.9 (1.18)	5.5 (1.99)	0.0 (0.00)	0.0 (0.00)	0.1 (0.10)	0.0 (0.00)	0.0001*	0.0001	0.0001	0.5986	0.0001
Blue crab	1.2 (0.63)	1.6 (0.58)	7.9 (3.40)	0.6 (0.16)	0.8 (0.25)	0.8 (0.42)	1.0 (0.45)	0.0048*	0.0058	0.0013	0.0088	0.5024
Brown shrimp	0.9 (0.38)	0.6 (0.22)	3.3 (1.75)	1.3 (0.65)	0.5 (0.34)	0.6 (0.40)	1.9 (0.71)	0.2069				
Marsh grass shrimp	2.3 (1.11)	0.1 (0.10)	3.9 (3.11)	0.8 (0.70)	0.0 (0.00)	0.2 (0.20)	0.0 (0.00)	0.0937				
Harris mud crab	0.0 (0.00)	0.0 (0.00)	3.2 (2.98)	0.1 (0.10)	0.5 (0.31)	0.8 (0.42)	1.1 (0.55)					
Brackish grass shrimp	4.4 (2.04)	0.3 (0.21)	0.9 (0.43)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)					

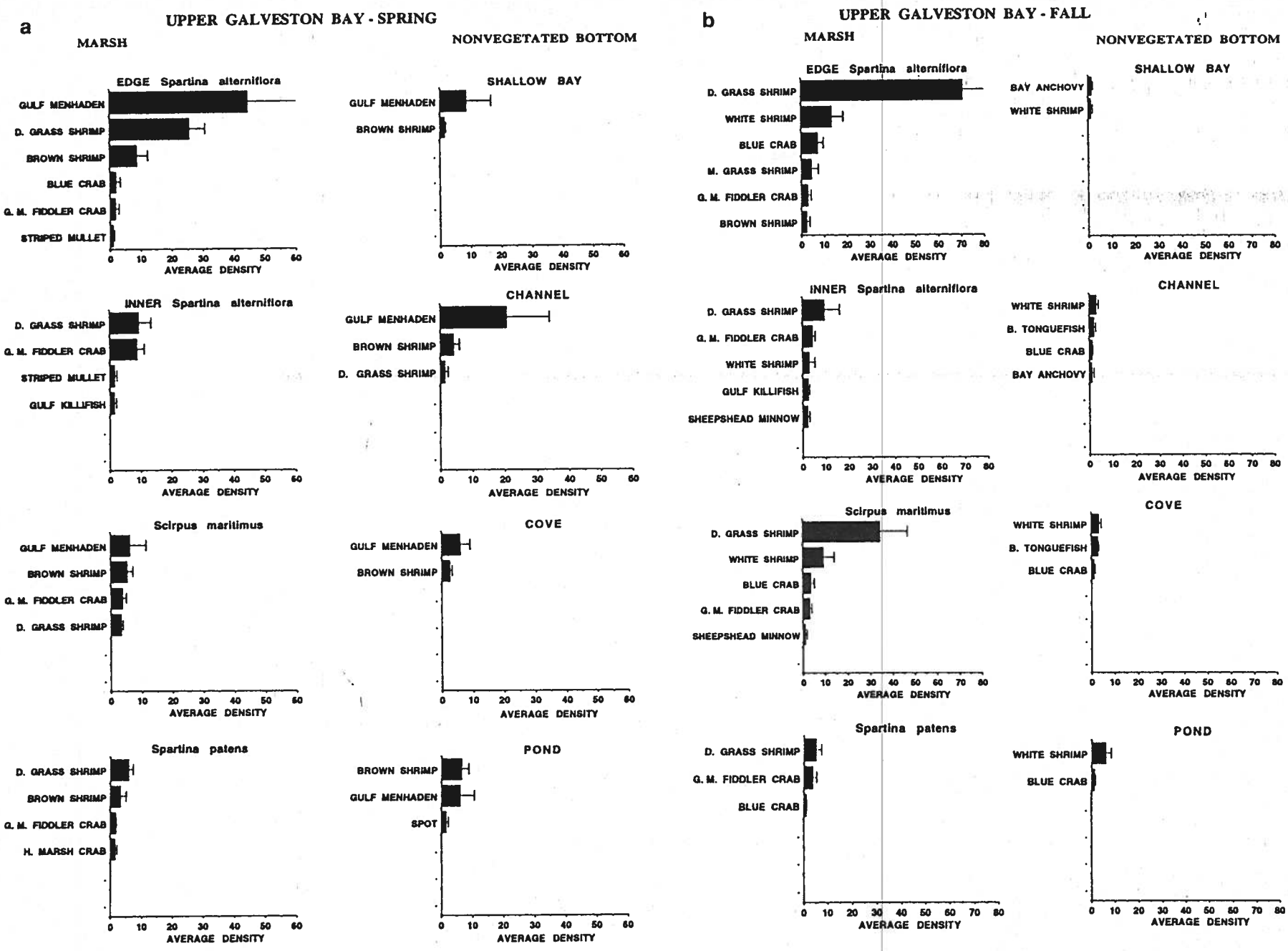

Fig. 2. Distributions among habitat types of abundant fishes and decapod crustaceans taken during (a) spring and (b) fall in upper Galveston Bay. Error bars = 1 standard error (SE). Means (ind. m^{-2}) and SEs were calculated from 8 samples per habitat type (except in October: shallow bay = 7). D. grass shrimp: daggerblade grass shrimp; g.m. fiddler crab: gulf marsh fiddler crab; h. marsh crab: heavy marsh crab; m. grass shrimp: marsh grass shrimp; b. tonguefish: blackcheek tonguefish

taken in our drop samples. Nine species numerically dominated the fish assemblage in upper Galveston Bay, and accounted for >95 and >75% of fishes collected in spring and fall, respectively. Gulf menhaden *Brevoortia patronus*, striped mullet *Mugil cephalus*, spot *Leiostomus xanthurus*, and gulf killifish *Fundulus grandis* dominated the fish assemblage in spring (Table 2). In fall, gulf killifish, bay anchovy *Anchoa mitchilli*, blackcheek tonguefish *Symphurus plagiusa*, and sheepshead minnow *Cyprinodon variegatus* were most abundant (Table 2).

Species assemblages differed among habitat types (Table 2, Fig. 2). The assemblage of edge *Spartina alterniflora* marsh was numerically dominated by gulf menhaden, daggerblade grass shrimp, and brown shrimp in spring, and daggerblade grass shrimp, white shrimp, and blue crab in fall. Of the 3 other marsh types we sampled in upper Galveston Bay, *Scirpus* marsh had an assemblage most like that of edge *S. alterniflora* marsh. Gulf menhaden and brown shrimp in spring and daggerblade grass shrimp and white shrimp in fall dominated *Scirpus* marsh. Inner *S. alterniflora* marsh was dominated by gulf marsh fiddler crab and daggerblade grass shrimp. The assemblage of *S. patens* marsh was dominated by daggerblade grass shrimp, brown shrimp (spring), and gulf marsh fiddler crab (fall). Nonvegetated areas were dominated by gulf menhaden and brown shrimp in spring and white shrimp in fall.

The vegetated marsh surface contained high densities of decapod crustaceans and some fishes (Table 2, Fig. 2). Most decapod crustaceans were taken either exclusively at marsh sites (gulf marsh fiddler crab, heavy marsh crab, marsh grass shrimp) or were significantly more abundant in marsh than at nonvegetated sample sites (daggerblade grass shrimp, blue crab), although there were exceptions. In spring, mean densities of brown shrimp were relatively high in marsh channels and ponds, and similar to densities at marsh sites; therefore, brown shrimp densities did not differ significantly between marsh and nonvegetated sites (Table 2). In fall, white shrimp densities in marsh and nonvegetated areas were not significantly different due largely to an abundance of white shrimp in marsh ponds and their absence in *Spartina patens* marsh (Table 2). Three fishes also were strongly associated with the vegetated marsh surface. Striped mullet, gulf killifish, and sheepshead minnow all had higher densities in marsh than in nonvegetated areas (Table 2).

Apparent habitat selection also occurred among marsh types. We collected marsh grass shrimp (in fall) almost exclusively in edge *Spartina alterniflora* marsh, whereas 3 other species with an affinity for the marsh surface (gulf killifish, sheepshead minnow, and heavy marsh crab) were rarely or never collected in edge *S. alterniflora* marsh (Table 2). *Scirpus* marsh was similar to edge *S. alterniflora* marsh in that mean densities of brown shrimp (spring), blue crab (fall), and white shrimp (fall) in the 2 marsh types were not significantly different, and the densities of these species in *Scirpus* marsh were greater than in inner *S. alterniflora* marsh. Densities of gulf marsh fiddler crab and heavy marsh crab were greater in *Scirpus* marsh than in edge *S. alterniflora* marsh, whereas striped mullet, daggerblade grass shrimp, and blue crab in spring and marsh grass shrimp in fall were significantly less abundant in this habitat type than in edge *S. alterniflora* marsh (Table 2).

Although floristically similar, edge and inner *Spartina alterniflora* marshes differed substantially in animal densities (Table 2). Inner *S. alterniflora* marsh contained significantly fewer daggerblade grass shrimp, blue crab, brown shrimp in spring, and white shrimp and marsh grass shrimp in fall than edge *S. alterniflora* marsh. Compared with edge *S. alterniflora* marsh, inner *S. alterniflora* marsh had significantly higher densities of gulf killifish, gulf marsh fiddler crab (spring), and sheepshead minnow (fall). Densities of gulf killifish were higher in inner *S. alterniflora* marsh than in all other marsh types except *S. patens* in spring and higher than all other marsh types in fall (Table 2).

Of the other marsh types, *Spartina patens* marsh differed most in species and animal densities from edge *S. alterniflora* marsh (Table 2). Densities of daggerblade grass shrimp, blue crab, and striped mullet (spring) were relatively low in *S. patens* marsh when compared with their densities in edge *S. alterniflora* marsh. Other species were absent (e.g. white shrimp), or infrequently collected, from this marsh type. In contrast, densities of heavy marsh crab (spring) were higher in *S. patens* marsh than any other marsh type.

Several fishes exhibited an apparent affinity for open water. Spot, bay anchovy, and blackcheek tonguefish were all more abundant in nonvegetated areas than on the vegetated marsh surface (Table 2, Fig. 2). We collected bay anchovy exclusively in nonvegetated habitat types, and bay anchovy densities in fall were highest in the shallow bay. Blackcheek tonguefish was abundant in marsh channels and coves in fall. We collected most spot from marsh ponds and channels; none were taken in shallow bay waters (Table 2).

We also collected 10 species of molluscs, although our sampling technique was not designed to quantitatively sample benthic infauna. Most molluscs were taken from emergent marsh habitats and consisted mainly of marsh periwinkle *Littoraria irrorata* and eastern melampus *Melampus bidentatus*. Marsh periwinkle was most abundant in *Scirpus maritimus* and inner *Spartina alterniflora* marsh. Eastern melampus densities were highest in *S. patens* and inner *S. alterniflora* marsh.

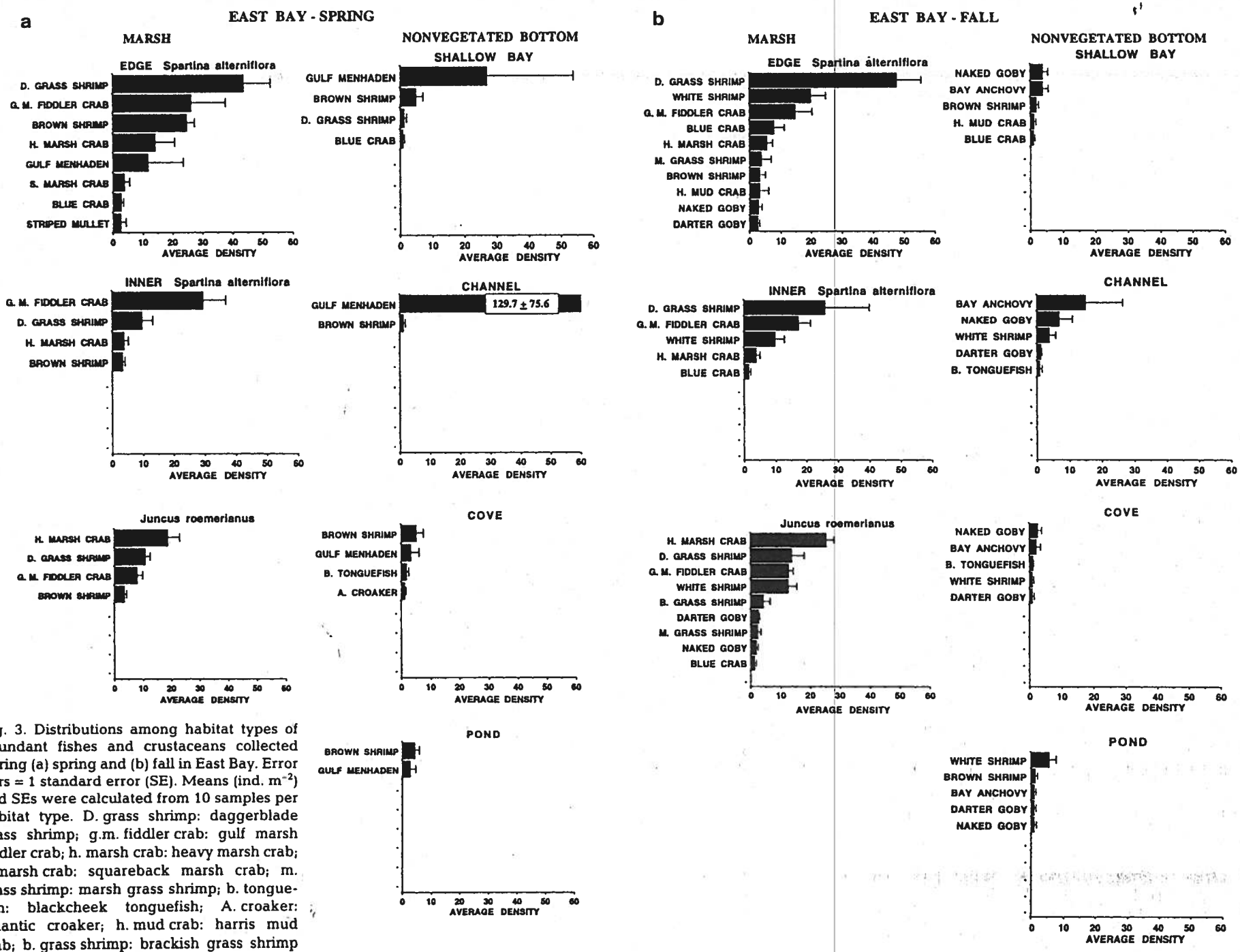

Fig. 3. Distributions among habitat types of abundant fishes and crustaceans collected during (a) spring and (b) fall in East Bay. Error bars = 1 standard error (SE). Means (ind. m^{-2}) and SEs were calculated from 10 samples per habitat type. D. grass shrimp: daggerblade grass shrimp; g.m. fiddler crab: gulf marsh fiddler crab; h. marsh crab: heavy marsh crab; s. marsh crab: squareback marsh crab; m. grass shrimp: marsh grass shrimp; b. tonguefish: blackcheek tonguefish; A. croaker: Atlantic croaker; h. mud crab: harris mud crab; b. grass shrimp: brackish grass shrimp

East Bay

Crustaceans were more numerous than fishes at East Bay both in spring (56 vs 44%) and in fall (81 vs 19%). Ten species dominated the decapod crustacean assemblage at East Bay. Daggerblade grass shrimp, gulf marsh fiddler crab, heavy marsh crab, brown shrimp, white shrimp, blue crab, squareback marsh crab *Sesarma cinereum*, Harris mud crab *Rhithropanopeus harrisii*, marsh grass shrimp, and brackish grass shrimp *Palaemonetes intermedius* accounted for >95 and >97% of total decapods taken in East Bay samples during spring and fall, respectively. Densities of most decapod crustaceans collected at East Bay were significantly greater in marsh than in nonvegetated areas (Table 3).

Seven species numerically dominated the fish assemblage at East Bay, and accounted for >96 and >90% of fishes collected in spring and fall, respectively. Gulf menhaden, Atlantic croaker *Micropogonias undulatus*, striped mullet, and blackcheek tonguefish dominated the fish assemblage in spring, whereas bay anchovy, naked goby *Gobiosoma bosc*, darter goby *Gobionellus boleosoma*, and blackcheek tonguefish were most abundant in fall (Table 3). Although striped mullet, darter goby, and naked goby were associated with emergent vegetation, other numerically dominant fishes showed an apparent preference for nonvegetated sites. Gulf menhaden, Atlantic croaker, blackcheek tonguefish, and bay anchovy were all more abundant in nonvegetated areas than in marsh vegetation (Table 3).

The assemblage of edge *Spartina alterniflora* marsh species was dominated by daggerblade grass shrimp and gulf marsh fiddler crab in addition to brown shrimp in the spring and white shrimp in the fall (Fig. 3). Several other species (squareback marsh crab, striped mullet, gulf menhaden, Harris mud crab) were commonly taken from edge *S. alterniflora* marsh, but were rare or absent in collections from inner *S. alterniflora* or *Juncus* marshes.

Inner *Spartina alterniflora* marsh was numerically dominated by daggerblade grass shrimp, gulf marsh fiddler crab, and white shrimp (fall) (Fig. 3). Densities of gulf marsh fiddler crab were higher in inner *S. alterniflora* marsh than either edge *S. alterniflora* or *Juncus* marsh (Table 3). In contrast, significantly fewer daggerblade grass shrimp, brown shrimp, blue crab, naked goby, and darter goby were taken in inner than edge *S. alterniflora* marsh (Table 3).

Species most abundant in *Juncus* marsh included heavy marsh crab, daggerblade grass shrimp, gulf marsh fiddler crab, and white shrimp (fall) (Fig. 3). Heavy marsh crab was more abundant in *Juncus* marsh than in edge *Spartina alterniflora* marsh, whereas fewer striped mullet, daggerblade grass shrimp, brown shrimp, and blue crab occurred in *Juncus* than edge *S. alterniflora* marsh (Table 3).

Nonvegetated areas were dominated by gulf menhaden and brown shrimp in spring and bay anchovy and naked goby in fall (Table 3, Fig. 3). Within nonvegetated areas, we found highest mean densities of gulf menhaden, bay anchovy, and naked goby in marsh channels (Table 3). Of all the nonvegetated areas, coves contained the highest mean density of brown shrimp in spring. We also collected most Atlantic croaker from coves in spring (Table 3). Marsh ponds had the highest mean density of white shrimp in fall (Table 3). No white shrimp were taken in shallow bay waters (Table 3).

Nearly 50% of the total molluscs collected at East Bay were marsh periwinkle or eastern melampus. Marsh periwinkle was most abundant in inner *Spartina alterniflora* and *Juncus* marshes, and most eastern melampus occurred in inner *S. alterniflora* marsh.

Infauna

Infaunal taxa taken from marsh and shallow water substrates were mainly annelids, insects, and molluscs in upper Galveston Bay and annelids and small crustaceans in East Bay (Table 4). At the upper Galveston Bay location, infaunal densities were greatest in the spring; most numerically dominant taxa were more abundant in nonvegetated areas, although densities of oligochaetes and chironomids were not significantly different between vegetated and nonvegetated areas (Table 4). Among marsh types, edge *Spartina alterniflora* marsh contained the highest mean densities of most taxa. Edge *S. alterniflora* and marsh ponds were dominated by chironomids and 2 polychaetes (*Capitella capitata* and *Laeonereis culveri*). These 3 taxa also were present, though less abundant, in channels. Channels and coves contained numerous individuals of the polychaete genus *Mediomastus*. Although we could not identify this taxon to species (because few intact organisms were recovered), most were likely *Mediomastus ambiseta*, which is one of the most abundant polychaetes in subtidal areas of Galveston Bay (Harper 1992). Oligochaetes and *C. capitata* also were numerous in coves. Although infaunal densities observed in the other habitat types declined to low values in the fall, densities in the shallow bay were high in fall and consisted mainly of oligochaetes and several taxa of polychaetes (*Mediomastus* spp., *Parandalia ocularis*, and *Streblospio benedicti*) (Table 4).

Most of the numerically dominant taxa at the East Bay location were more abundant in nonvegetated areas than marsh, although oligochaetes and 2 poly-

Table 4. Mean densities as number 60.8 cm^{-2} and (SE, 1 standard error) of common infauna (at least one mean ≥1.0) taken in upper Galveston Bay habitat types sampled in May and October 1993. Each mean is estimated from 5 sediment cores. Within major taxa, species are ranked by overall abundance. Number of taxa was determined from all 5 sediment cores and includes uncommon taxa. Results (p values) are given for ANOVAs comparing mean densities of taxa among the 8 habitat types and *a priori* contrasts testing for significant differences between: 1 = vegetated and nonvegetated habitat types; 2 = edge *Spartina alterniflora* and *Scirpus maritimus*; 3 = edge *S. alterniflora* and *Spartina patens*; 4 = edge *S. alterniflora* and inner *S. alterniflora*; 5 = inner *S. alterniflora* and *S. maritimus*; 6 = inner *S. alterniflora* and *S. patens*; and 7 = *S. patens* and *S. maritimus*. See Table 1 for an example of the ANOVA model. *Probability value was significant after alpha was adjusted as described by Rice (1989)

Species	*Spartina patens* Mean	SE	*Scirpus maritimus* Mean	SE	Inner *S. alterniflora* Mean	SE	Edge *S. alterniflora* Mean	SE	Pond Mean	SE	Channel Mean	SE	Cove Mean	SE	Shallow bay Mean	SE	ANOVA p value	Contrast p values 1	2	3	4	5	6	7
May 1993																								
Annelids	6.0	(2.28)	3.0	(2.26)	6.0	(4.53)	21.8	(10.62)	18.2	(6.48)	26.2	(12.36)	42.0	(11.10)	7.6	(1.97)								
Polychaetes	2.4	(1.12)	0.6	(0.25)	5.4	(4.67)	21.2	(10.66)	18.2	(6.48)	24.6	(11.46)	31.6	(9.32)	4.4	(0.81)	0.0017*	0.0002	0.0131	0.0715	0.0866	0.3963	0.9238	0.4508
Mediomastus spp.	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	0.2	(0.20)	0.2	(0.20)	16.6	(11.95)	21.6	(7.30)	2.4	(0.75)	0.0001*	0.0001	0.7873	0.7873	1.0000	0.7873	0.7873	1.0000
Capitella capitata	1.2	(0.80)	0.0	(0.00)	4.4	(3.91)	7.8	(5.12)	10.4	(1.96)	4.6	(0.98)	7.2	(2.06)	0.6	(0.24)	0.0005*	0.0014	0.0092	0.0955	0.2552	0.1163	0.5799	0.2993
Laeonereis culveri	0.0	(0.00)	0.0	(0.00)	0.4	(0.40)	11.4	(9.51)	7.0	(5.82)	2.6	(1.63)	0.0	(0.00)	0.0	(0.00)	0.1188							
Polydora ligni	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	1.0	(1.00)	0.4	(0.40)	0.2	(0.20)	2.0	(1.09)	0.4	(0.40)								
Oligochaetes	3.6	(1.75)	2.4	(2.40)	0.6	(0.40)	0.6	(0.40)	0.0	(0.00)	1.6	(0.93)	10.4	(3.90)	3.2	(1.59)	0.0159*	0.1912	0.7718	0.1140	1.0000	0.7718	0.1140	0.1921
Insects	0.4	(0.25)	0.4	(0.25)	7.0	(5.32)	9.0	(5.54)	25.6	(6.16)	5.4	(4.91)	0.2	(0.20)	0.0	(0.00)								
Chironomidae	0.2	(0.20)	0.4	(0.24)	6.8	(5.37)	9.0	(5.53)	25.6	(6.15)	5.4	(4.90)	0.0	(0.00)	0.0	(0.00)	0.0001*	0.3361	0.0690	0.0421	0.7198	0.1384	0.0888	0.8151
Molluscs	1.4	(0.93)	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	0.0	(0.00)	1.2	(0.80)	0.4	(0.40)	3.8	(0.92)	0.0001*	0.0144	0.6317	0.0924	0.6317	1.0000	0.0337	0.0337
Tellina texana	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	0.0	(0.00)	1.2	(0.80)	0.4	(0.40)	1.4	(0.40)								
Rangia cuneata	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1.8	(1.11)								
Total infauna	8.0	(2.07)	4.0	(2.76)	13.6	(9.69)	31.0	(15.14)	43.8	(6.21)	32.8	(11.96)	42.8	(10.86)	12.2	(1.66)								
Total number of taxa	5		5		8		8		6		9		8		8									
October 1993																								
Annelids	3.0	(1.05)	2.2	(1.20)	3.6	(2.04)	1.6	(0.51)	2.4	(1.25)	2.4	(1.29)	3.8	(1.59)	16.2	(2.60)								
Polychaetes	2.6	(1.03)	1.4	(0.40)	2.0	(0.89)	0.6	(0.25)	1.6	(0.81)	2.0	(1.10)	3.0	(1.30)	14.2	(2.42)	0.0002*	0.0132	0.3033	0.0831	0.2203	0.8396	0.5939	0.4631
Mediomastus spp.	0.0	(0.00)	0.4	(0.24)	0.0	(0.00)	0.2	(0.20)	0.6	(0.40)	0.6	(0.40)	2.8	(1.39)	9.0	(2.28)	0.0001*	0.0001	0.6548	0.6548	0.6548	0.3735	1.0000	0.3735
Streblospio benedicti	0.0	(0.00)	0.2	(0.20)	0.2	(0.20)	0.0	(0.00)	0.6	(0.60)	1.4	(1.16)	0.0	(0.00)	2.6	(0.98)	0.0103*	0.0103	0.6469	1.0000	0.6469	1.0000	0.6469	0.6469
Nomalycastis quadraticeps	2.2	(0.97)	0.4	(0.24)	0.6	(0.60)	0.2	(0.20)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)								
Parandalia ocularis	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	1.6	(1.36)								
Oligochaetes	0.4	(0.25)	0.8	(0.80)	1.6	(1.16)	1.0	(0.45)	0.8	(0.58)	0.4	(0.24)	0.8	(0.49)	2.0	(0.71)	0.6811							
Insects																								
Chironomidae	0.2	(0.20)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.2	(0.20)	1.6	(1.17)	0.8	(0.80)	0.0	(0.00)								
Total infauna	4.4	(1.03)	2.2	(1.20)	3.8	(1.96)	1.8	(0.66)	2.6	(1.17)	4.0	(2.07)	5.0	(1.18)	16.2	(2.60)								
Total number of taxa	7		5		8		4		5		4		4		7									

chaetes (*Capitella capitata* and *Fabricia* sp.) were most numerous in *Spartina alterniflora* and *Juncus* marshes (Table 5). Amphipods (*Hargeria rapax* and *Corophium* spp.) and 3 polychaetes (*Mediomastus* spp., *Parandalia ocularis*, and *Nereis succinea*) were most numerous in the shallow bay (Table 5). *Mediomastus* spp. also dominated the infaunal assemblages in ponds, channels, and coves (Table 5).

Environmental parameters

At upper Galveston Bay, vegetated habitats had significantly less dissolved oxygen, lower water temperatures, and shallower water depths than nonvegetated areas (Table 6). Turbidity levels were higher in marsh than nonvegetated areas in May, but this pattern was reversed in October. Within vegetated marsh areas, means of most environmental characteristics were not significantly different. However, edge *Spartina alterniflora* marsh flooded more deeply than *S. patens* marsh; and inner *S. alterniflora* and *S. patens* marshes had significantly lower dissolved oxygen concentrations than *Scirpus* marsh in October (Table 6). The average density of plant stems and standing biomass in the marsh types were less in the spring than in the fall at the end of the growing season (Table 6, Fig. 4). In *S. patens* marsh, average stem density was an order of magnitude higher than in other marsh types, and stem densities were significantly greater in this marsh than the other marsh types in both the spring and fall (Fig. 4a). *S. patens* marsh also had significantly higher standing biomass than the other marsh types in the spring (Fig. 4b). In the fall, the standing biomass of *S. patens* was similar to that of the 2 *S. alterniflora* marsh types, and these were significantly greater than the *Scirpus* marsh biomass (Fig. 4b).

At the East Bay location, marsh areas had significantly less dissolved oxygen, lower water temperatures, lower salinity (April only), and shallower water depths than nonvegetated areas (Table 7). Turbidity levels were higher in marsh than nonvegetated areas only in the fall. Some environmental characteristics differed among marsh types as well. For example, inner *Spartina alterniflora* marsh had significantly lower dissolved oxygen levels than edge *S. alterniflora* or *Juncus* marsh in October (Table 7). The average density of plant stems in *Juncus* marsh was significantly greater than in the 2 *Spartina* marsh types in both the spring and fall (Table 7, Fig. 5a). Standing biomass did not differ significantly among habitat types in spring (Fig. 5b). However, in fall when plant biomass peaked, *Juncus* marsh had significantly higher standing biomass than edge *S. alterniflora* marsh (Fig. 5b); the mean standing biomasses of *Juncus* and inner *S. alterniflora* were not significantly different in fall ($p > 0.05$).

Flooding durations differed among habitat types in response to differences in surface elevations (Table 8, Fig. 6a). Among marsh types, edge *Spartina alterniflora* marsh had the lowest surface elevation. In upper Galveston Bay, inner *S. alterniflora*, *Scirpus*, and *S. patens* marshes exceeded the elevation of edge *S. alterniflora* marsh by 5.0, 6.7, and 22.0 cm, respectively. The mean flooding duration in 1993 for edge *S. alterniflora* marsh was over 45%, and monthly flooding durations ranged from 26% in August to 72% in June (Table 8, Fig. 6a). Inner *S. alterniflora* marsh flooded 37% of the time in 1993, and monthly flooding durations ranged from 18 to 63%. *Scirpus* marsh was inundated about 34% of the time (range = 12 to 62%), whereas *S. patens* marsh flooded approximately 13% of the time (range = 0 to 32%). Nonvegetated areas were submerged for longer periods than marsh (Fig. 6b). Shallow bay was inundated 98% of the time in 1993; whereas marsh channels (87%), coves (76%), and ponds (74%) were flooded less (Fig. 6b).

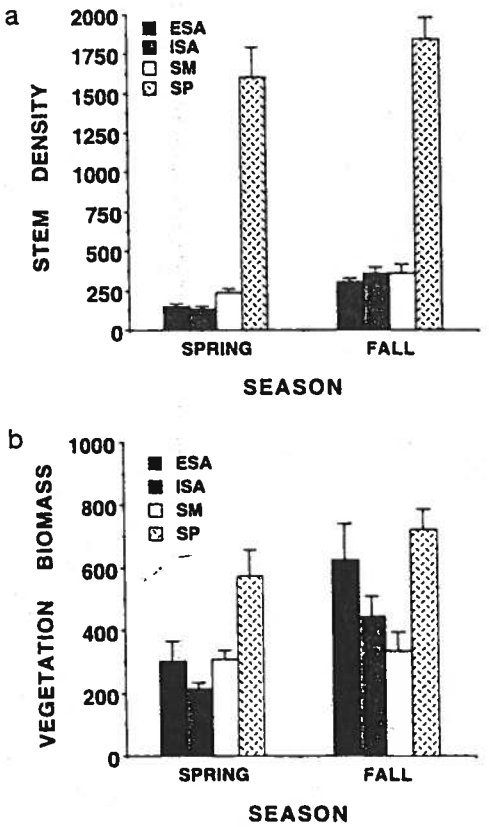

Fig. 4. Average stem densities (plant stems m^{-2}) and plant biomasses (g dry wt m^{-2}) of vegetation sampled from marsh in upper Galveston Bay. ESA: edge *Spartina alterniflora*; ISA: inner *Spartina alterniflora*; SM: *Scirpus maritimus*; SP: *Spartina patens*. Error bars = 1 standard error (SE). Means and SEs were calculated from 8 samples per habitat type

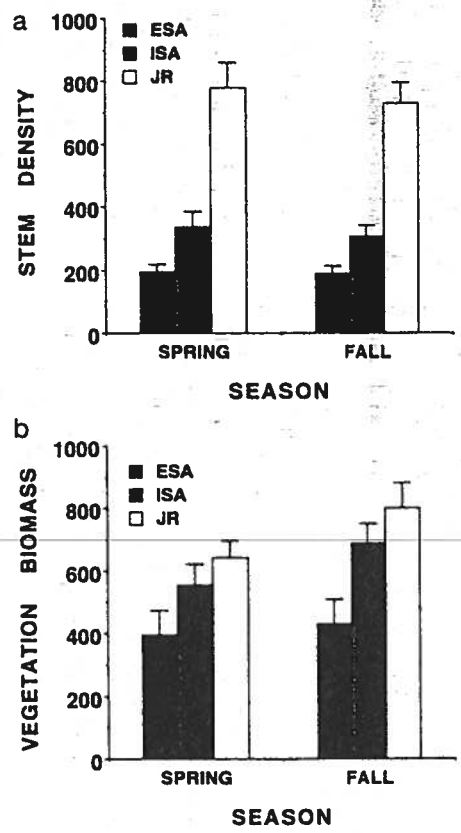

Fig. 5. Average stem densities (plant stems m^{-2}) and plant biomasses (g dry wt m^{-2}) of vegetation sampled from marsh in East Bay. ESA: edge *Spartina alterniflora*; ISA: inner *Spartina alterniflora*; JR: *Juncus roemerianus*. Error bars = 1 standard error (SE). Means and SEs were calculated from 10 samples per habitat type

At East Bay in 1994, habitats were generally flooded longer than upper Galveston Bay sites in 1993. In 1994, edge *Spartina alterniflora* marsh at East Bay was submerged 66% of the time, and flooding durations ranged from 45% in January to 91% in October (Fig. 7a). Inner *S. alterniflora* marsh was inundated 53% of the time in 1994 (range = 29 to 85%), and *Juncus* marsh was submerged only 34% of the time (range = 15 to 71%). The difference in flooding duration between locations (upper Galveston Bay and East Bay) apparently was not due to interannual differences in tide levels. Flooding durations within marsh types were similar in 1993 and 1994 (Table 8). These differences between locations may be the result of differences in the position of the marsh within the tidal frame. The East Bay marsh is located lower in the tidal frame (i.e. the surface elevation is lower relative to Mean Tide Level) than the marsh at upper Galveston Bay (Table 8). Nonvegetated bottom habitats at East Bay were inundated most of the time in 1994 (Fig. 7b). Shallow bay and cove sites were almost continuously submerged (average flooding durations >99%).

Table 5. Mean densities as number 60.8 cm^{-2} and (SE, 1 standard error) of common infauna (i.e. at least one mean ≥1.0) taken in East Bay habitat types sampled in April and September 1994. Each mean is estimated from 6 sediment cores. Within major taxa, species are ranked by overall abundance. Number of taxa was determined from all 6 sediment cores and includes uncommon species. Results (p values) are given for ANOVAs comparing mean densities of taxa among the 7 habitat types and a *priori* contrasts testing for significant differences between: 1 = vegetated and nonvegetated habitat types; 2 = edge *Spartina alterniflora* and *Juncus roemerianus*; 3 = edge *S. alterniflora* and inner *S. alterniflora*; and 4 = *J. roemerianus* and inner *S. alterniflora*. See Table 1 for an example of the ANOVA model. *Probability value was significant after alpha was adjusted as described by Rice (1989)

Species	*Juncus roemerianus* Mean	SE	Inner *S. alterniflora* Mean	SE	Edge *S. alterniflora* Mean	SE	Pond Mean	SE	Channel Mean	SE	Cove Mean	SE	Shallow bay Mean	SE	ANOVA p value	Contrast p values 1	2	3	4
April 1994																			
Annelids	38.3	(12.51)	66.7	(32.01)	35.2	(7.72)	23.2	(7.19)	14.8	(4.30)	21.7	(4.32)	21.5	(8.62)					
Polychaetes	17.7	(7.89)	2.5	(0.72)	19.3	(4.55)	21.3	(6.28)	13.7	(4.03)	18.7	(4.11)	20.8	(8.19)	0.0292*	0.0209	0.2775	0.0040	0.0559
Mediomastus spp.	0.0	(0.00)	0.0	(0.00)	0.2	(0.17)	14.8	(6.93)	8.8	(3.26)	8.8	(2.81)	7.3	(5.95)	0.0002*	0.0001	0.8335	0.8335	1.0000
Fabricia sp.	12.8	(7.01)	0.2	(0.17)	3.3	(1.99)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0012*	0.0005	0.0656	0.0831	0.0008
Capitella capitata	4.0	(2.18)	1.5	(0.62)	8.3	(3.24)	1.8	(1.14)	0.5	(0.34)	0.0	(0.00)	0.0	(0.00)	0.0017*	0.0002	0.1322	0.0203	0.3800
Parandalia ocularis	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	4.8	(0.95)	5.5	(2.09)					
Nereis (Neanthes) succinea	0.0	(0.00)	0.2	(0.17)	2.0	(1.13)	0.0	(0.00)	0.0	(0.00)	0.7	(0.67)	4.7	(0.88)					
Streblospio benedicti	0.0	(0.00)	0.2	(0.17)	0.0	(0.00)	3.0	(1.75)	1.0	(0.63)	0.8	(0.40)	1.0	(0.82)					
Polydora ligni	0.0	(0.00)	0.2	(0.17)	2.5	(1.46)	0.0	(0.00)	0.0	(0.00)	0.5	(0.34)	1.7	(0.67)					
Hobsonia gunneri	0.0	(0.00)	0.0	(0.00)	0.3	(0.33)	0.5	(0.34)	0.8	(0.40)	2.3	(0.96)	0.2	(0.17)					
Eteone heteropoda	0.0	(0.00)	0.2	(0.17)	1.7	(0.76)	0.5	(0.34)	1.0	(0.82)	0.0	(0.00)	0.3	(0.21)					
Heteromastus filiformis	0.0	(0.00)	0.0	(0.00)	0.8	(0.54)	0.5	(0.34)	1.5	(0.96)	0.2	(0.17)	0.2	(0.17)					
Nomalycastis quadraticeps	0.8	(0.65)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					

Table 5 (continued)

Species	*Juncus roemerianus* Mean SE	Inner *S. alterniflora* Mean SE	Edge *S. alterniflora* Mean SE	Pond Mean SE	Channel Mean SE	Cove Mean SE	Shallow bay Mean SE	ANOVA p value	Contrast p values 1	2	3	4
Oligochaetes	20.7 (6.16)	64.2 (31.33)	15.8 (3.39)	1.8 (0.95)	1.2 (0.65)	3.0 (1.27)	0.7 (0.49)	0.0001*	0.0001	0.8287	0.0464	0.0733
Crustaceans	0.5 (0.34)	1.8 (0.40)	7.3 (4.98)	1.7 (0.62)	1.0 (0.52)	8.5 (3.34)	24.5 (18.53)	0.0021*	0.0422	0.0609	0.5399	0.1963
Amphipods	0.5 (0.34)	1.8 (0.40)	2.3 (1.28)	1.3 (0.62)	0.7 (0.33)	6.8 (2.63)	5.7 (3.41)					
Ampelisca abdita	0.2 (0.17)	0.0 (0.00)	0.0 (0.00)	1.3 (0.62)	0.7 (0.33)	6.5 (2.43)	0.5 (0.34)					
Corophium sp.	0.0 (0.00)	0.0 (0.00)	1.2 (0.75)	0.0 (0.00)	0.0 (0.00)	0.3 (0.21)	3.8 (3.64)					
Orchestia cf. *uhleri*	0.3 (0.33)	1.3 (0.49)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)					
Gammarus mucronatus	0.0 (0.00)	0.3 (0.33)	1.2 (0.60)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)					
Isopods	0.0 (0.00)	0.0 (0.00)	0.3 (0.21)	0.3 (0.21)	0.3 (0.21)	0.3 (0.21)	2.3 (0.72)					
Xenanthura brevitelson	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	1.3 (0.88)					
Tanaids												
Hargeria rapax	0.0 (0.00)	0.0 (0.00)	4.7 (4.28)	0.0 (0.00)	0.0 (0.00)	1.3 (1.33)	16.3 (15.74)					
Insects	1.2 (0.48)	7.3 (4.39)	0.5 (0.22)	2.7 (0.96)	0.3 (0.21)	0.0 (0.00)	0.0 (0.00)					
Chironomidae	1.2 (0.48)	7.2 (4.45)	0.3 (0.21)	2.7 (0.96)	0.3 (0.21)	0.0 (0.00)	0.0 (0.00)	0.0196*	0.1290	0.3121	0.0303	0.2261
Molluscs	0.5 (0.22)	0.8 (0.17)	0.0 (0.00)	3.2 (1.25)	2.8 (1.17)	2.5 (0.43)	0.8 (0.40)	0.0008*	0.0001	0.2504	0.0595	0.4412
Tellina texana	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	3.0 (1.16)	2.5 (1.18)	1.0 (0.63)	0.2 (0.17)					
Total infauna	40.5 (12.49)	76.7 (30.12)	43.0 (9.90)	30.7 (9.06)	19.0 (5.29)	33.7 (7.08)	47.0 (27.16)					
Total number of taxa	9	15	16	13	13	23	22					
September 1994												
Annelids	32.8 (10.18)	36.7 (17.99)	20.8 (8.50)	6.7 (3.63)	11.8 (5.02)	37.7 (6.17)	45.2 (15.41)					
Polychaetes	9.2 (2.09)	3.7 (1.09)	10.0 (6.85)	3.7 (2.11)	6.2 (2.32)	30.7 (4.90)	44.0 (15.67)	0.0001*	0.0085	0.0900	0.7794	0.1528
Mediomastus spp.	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.3 (0.21)	1.8 (1.64)	22.2 (6.27)	13.2 (4.09)	0.0001*	0.0001	1.0000	1.0000	1.0000
Nereis (*Neanthes*) *succinea*	0.0 (0.00)	0.3 (0.21)	0.2 (0.17)	0.0 (0.00)	0.0 (0.00)	0.5 (0.34)	21.2 (14.74)	0.0020*	0.0921	0.7916	0.7916	0.5977
Fabricia sp.	8.7 (2.16)	1.5 (1.03)	8.8 (6.45)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	0.0001*	0.0001	0.0216	0.2533	0.0011
Streblospio benedicti	0.0 (0.00)	0.5 (0.22)	0.7 (0.67)	2.8 (1.49)	4.0 (2.35)	2.8 (2.64)	1.5 (1.12)					
Capitella capitata	3.2 (0.91)	1.0 (0.26)	1.7 (1.17)	0.2 (0.17)	0.2 (0.17)	1.0 (0.82)	0.5 (0.50)					
Parandalia ocularis	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	0.0 (0.00)	2.8 (1.66)	4.7 (1.94)					
Polydora ligni	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.7 (1.67)					
Laeonereis culveri	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	0.2 (0.17)	1.0 (0.63)	0.3 (0.33)					
Oligochaetes	23.7 (8.43)	33.0 (17.34)	10.8 (3.08)	3.0 (1.67)	5.7 (3.62)	7.0 (3.34)	1.2 (0.75)	0.0005*	0.0001	0.3708	0.1865	0.6620
Crustaceans	0.2 (0.17)	0.3 (0.33)	0.2 (0.17)	0.0 (0.00)	0.2 (0.17)	4.0 (3.42)	79.0 (46.62)	0.0001*	0.0107	1.0000	0.9041	0.9041
Amphipods	0.2 (0.17)	0.2 (0.17)	0.2 (0.17)	0.0 (0.00)	0.0 (0.00)	1.8 (1.83)	59.7 (36.77)					
Corophium sp.	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.3 (1.33)	54.5 (34.51)					
Grandidierella bonneroides	0.2 (0.17)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.3 (0.33)	3.3 (2.06)					
Ampelisca abdita	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	1.8 (0.83)					
Isopods	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.7 (0.33)	4.8 (2.56)					
Cassidinidea ovalis	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2.8 (2.83)					
Xenanthura brevitelson	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	1.5 (0.96)					
Tanaids												
Hargeria rapax	0.0 (0.00)	0.2 (0.17)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	1.3 (1.33)	14.3 (8.77)					
Insects	0.3 (0.21)	1.2 (0.60)	0.2 (0.17)	0.0 (0.00)	0.3 (0.21)	0.0 (0.00)	0.0 (0.00)					
Molluscs	0.2 (0.17)	0.0 (0.00)	0.0 (0.00)	0.2 (0.17)	0.0 (0.00)	2.0 (1.44)	1.0 (0.45)					
Eulimastima cf. *E. weberi*	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.3 (1.33)	0.0 (0.00)					
Nemerteans	0.3 (0.33)	0.0 (0.00)	0.2 (0.17)	0.3 (0.21)	0.0 (0.00)	0.8 (0.40)	1.7 (0.72)					
Total infauna	37.0 (10.85)	39.2 (18.69)	23.2 (9.15)	7.3 (3.65)	12.5 (5.33)	45.5 (6.95)	127.3 (58.16)					
Total number of taxa	10	12	12	10	8	24	27					

Table 6. Environmental characteristics of upper Galveston Bay habitat types. Mean and (SE, 1 standard error) are given for 8 parameters measured in May and October 1993. Each mean is estimated from 8 samples in each habitat type (exceptions: In May — Turbidity:– Pond [n = 2]; *Spartina patens*, inner *Spartina alterniflora*, and *Scirpus maritimus* [n =4]; Channel [n = 6]; Cove [n = 7]; Water depth:– Shallow bay [n = 7]; Distance to edge:– Cove [n = 6]; Pond and Shallow bay [n = 7]; in October — Distance to edge:– Shallow bay [n = 5]; Channel and Cove [n = 7]; all other parameters: Shallow Bay [n = 7]). *Overall probability value for the test of the main effect Habitat was significant after alpha was adjusted as described by Rice (1989). Means of marsh types with the same letter are not significantly different (ANOVA, contrasts, $p > 0.05$). Means of marsh types versus nonvegetated habitats are significantly different for all parameters except salinity

Parameter	*Spartina patens* Mean SE	*Scirpus maritimus* Mean SE	Inner *S. alterniflora* Mean SE	Edge *S. alterniflora* Mean SE	Pond Mean SE	Channel Mean SE	Cove Mean SE	Shallow bay Mean SE	p value
May 1993									
Dissolved oxygen (ppm)	5.6a (0.34)	5.9a (0.47)	5.5a (0.46)	6.4a (0.18)	6.1 (0.52)	6.8 (0.46)	7.9 (0.27)	9.3 (0.12)	0.0001*
Salinity (‰)	5.1a (0.13)	5.1a (0.13)	5.3a (0.16)	5.0a (0.00)	5.0 (0.00)	4.9 (0.13)	5.0 (0.00)	4.9 (0.13)	0.1862
Temperature (°C)	24.7a (0.71)	24.1a (0.55)	24.2a (0.59)	23.7a (0.36)	24.6 (0.46)	25.7 (0.52)	26.5 (0.47)	27.9 (0.08)	0.0001*
Turbidity (FTU)	312a (69.0)	152a (16.7)	194a (48.3)	148a (14.9)	129 (31.5)	123 (18.2)	142 (39.8)	57 (6.5)	0.0004*
Water depth (cm)	17b (1.6)	27ab (2.4)	26ab (1.9)	35a (4.3)	51 (2.0)	70 (5.8)	52 (8.1)	74 (2.1)	0.0001*
Distance to edge (m)	1.0a (0.20)	1.2a (0.30)	6.8b (0.60)	0.1a (0.10)	6.6 (1.10)	1.8 (0.30)	16.5 (5.30)	21.4 (3.40)	0.0001*
Vegetation biomass (g)	653b (94.6)	362a (33.0)	250a (24.7)	356a (75.5)					0.0010*
Stem density (no. m^{-2})	1603b (190.3)	237a (23.0)	132a (16.3)	149a (20.2)					0.0001*
October 1993									
Dissolved oxygen (ppm)	2.3a (0.27)	5.4b (0.62)	2.6a (0.41)	3.1ab (1.94)	4.7 (0.84)	4.2 (0.48)	6.6 (0.23)	6.5 (0.11)	0.0013*
Salinity (‰)	18a (0.27)	18.3a (0.16)	18.4a (0.26)	17.9a (0.23)	18.6 (0.32)	18.6 (0.26)	18.6 (0.18)	18.1 (0.26)	0.2062
Temperature (°C)	26.2a (0.11)	25.5a (0.54)	26.4a (0.18)	25.8a (0.56)	27.2 (0.19)	26.7 (0.19)	29.0 (0.12)	24.9 (0.53)	0.0001*
Turbidity (FTU)	63a (16.4)	55a (5.3)	44a (10.0)	61a (26.2)	78 (19.7)	60 (14.9)	158 (16.6)	23 (6.1)	0.0001*
Water depth (cm)	15b (2.6)	20ab (3.9)	22ab (2.9)	27a (4.2)	42 (1.2)	62 (7.2)	32 (3.1)	89 (2.6)	0.0001*
Distance to edge (m)	1.5a (0.30)	1.2a (0.50)	5.9a (0.40)	0.2a (0.10)	7.0 (1.10)	1.8 (0.40)	23.4 (8.90)	26.7 (2.60)	0.0001*
Vegetation biomass (g)	810b (75.3)	400a (70.5)	596b (90.4)	849b (154.8)					0.0017*
Stem density (no. m^{-2})	1842b (143.2)	357a (59.5)	358a (37.5)	308a (20.9)					0.0001*

Although flooded less than shallow bay and cove habitats, marsh ponds (95%) and channels (89%) were also submerged for long periods (Fig. 7b).

Results of the discriminant analysis clearly show that we can statistically separate the habitat types we sampled in our study based on environmental characteris-

Table 7. Environmental characteristics of East Bay habitat types. Mean and (SE, 1 standard error) are given for 8 parameters measured in April and September 1994. Each mean is estimated from 10 samples in each habitat type (exceptions: in April — Water temperature:– Shallow bay, [n = 9l and Dissolved oxygen:– *Juncus roemerianus* marsh [n = 9]). *Probability value for the test of the main effect Habitat was significant after alpha was adjusted as described by Rice (1989). Means of marsh types with the same letter are not significantly different (ANOVA, contrasts, $p > 0.05$). Means of marsh types vs nonvegetated habitat types are significantly different for all parameters except turbidity in April and salinity and temperature in September

Parameter	*Juncus roemerianus* Mean SE	Inner *S. alterniflora* Mean SE	Edge *S. alterniflora* Mean SE	Pond Mean SE	Channel Mean SE	Cove Mean SE	Shallow bay Mean SE	p value
April 1994								
Dissolved oxygen (ppm)	6.5b (0.27)	4.9a (0.32)	5.9b (0.28)	5.6 (0.20)	5.8 (0.32)	7.3 (0.23)	7.7 (0.06)	0.0001*
Salinity (‰)	11.1a (0.10)	11.6a (0.22)	11.5a (0.50)	12.2 (0.42)	11.9 (0.38)	14.6 (0.16)	13.3 (0.58)	0.0001*
Temperature (°C)	25.8ab (0.19)	26.2b (0.31)	25.3a (0.26)	25.1 (0.11)	26.3 (0.25)	27.5 (0.20)	26.2 (0.12)	0.0001*
Turbidity (FTU)	25.9a (2.3)	31.8a (3.4)	40a (12.3)	23 (3.1)	27 (3.4)	22 (3.2)	16 (2.1)	0.0791
Water depth (cm)	41b (2.2)	29a (1.6)	38b (3.4)	67 (1.8)	63 (1.9)	95 (3.5)	102 (2.2)	0.0001*
Distance to edge (m)	0.2a (0.10)	6.5b (0.30)	0.1a (0.10)	13.1 (4.10)	1.4 (0.30)	16.4 (3.40)	15.3 (1.60)	0.0001*
Vegetation biomass (g)	532a (67.1)	516a (60.0)	397a (79.6)					0.3381
Stem density (no. m^{-2})	616b (77.0)	253a (30.8)	196a (22.5)					0.0001*
September 1994								
Dissolved oxygen (ppm)	4.2a (0.23)	4.2a (0.38)	4.6a (0.28)	4.8 (0.33)	4.6 (0.33)	5.6 (0.15)	6.1 (0.18)	0.0001*
Salinity (‰)	15.0a (0.00)	15.7a (0.40)	16.1a (0.38)	15.9 (0.46)	15.7 (0.45)	15.1 (0.28)	15.7 (0.60)	0.4340
Temperature (°C)	27.8a (0.37)	28.3a (0.34)	28.2a (0.34)	28.9 (0.40)	28.5 (0.57)	28.6 (0.22)	26.6 (0.33)	0.0018*
Turbidity (FTU)	23a (1.5)	29ab (5.7)	40b (6.4)	23 (3.8)	14 (3.3)	15 (1.2)	24 (7.1)	0.0043*
Water depth (cm)	31a (1.0)	24a (2.5)	32a (4.0)	54 (3.3)	52 (9.1)	87 (2.1)	75 (5.2)	0.0001*
Distance to edge (m)	0.6a (0.10)	5.7b (0.20)	0.7a (0.20)	5.8 (2.40)	1.1 (0.20)	10.7 (1.70)	9.5 (1.00)	0.0001*
Vegetation biomass (g)	721b (82.5)	668b (60.3)	431a (75.3)					0.0215*
Stem density (no. m^{-2})	664b (72.6)	289a (33.8)	186a (21.5)					0.0001*

Table 8. Mean elevation and flooding durations of each habitat type sampled at upper Galveston Bay in 1993 and East Bay in 1994. Elevations are based on a Mean Tide Level (MTL) of 182.9 cm (6.0 ft) for the Morgans Point tide station and an adjusted MTL of 130.1 cm (4.3 ft) for East Bay that was calculated from the MTL at the Pier 21 tide station using an equation from Minello & Webb (1997). Each mean is estimated from 16 (except Shallow bay = 14) and 20 samples in each habitat type at upper Galveston Bay and East Bay, respectively

Habitat type	Elevation MTL (cm)	Flooding durations (%) 1993	1994
Upper Galveston Bay			
Shallow Bay	−52.0	97.5	97.9
Cove	−17.7	76.2	80.9
Channel	−26.7	86.8	89.5
Pond	−12.8	74.4	74.9
Edge *S. alterniflora*	4.4	45.6	45.8
Inner *S. alterniflora*	9.4	37.4	35.8
Scirpus maritimus	11.1	34.3	32.9
Spartina patens	26.4	12.9	9.7
East Bay			
Shallow Bay	−58.3	99.7	99.8
Cove	−53.1	99.3	99.4
Channel	−31.7	95.6	88.5
Pond	−31.4	95.6	94.9
Edge *S. alterniflora*	−6.5	66.6	66.2
Inner *S. alterniflora*	0.8	50.2	52.7
Juncus roemerianus	9.1	31.4	34.3

tics (Figs. 8 & 9). The multivariate model used to discriminate among the 9 habitat types was highly significant (Wilks' lambda = 0.018, df = 64, 1275, $p < 0.0001$). The first 2 canonical variates in the model were responsible for 96% of the separation (Fig. 8), and the predictor variables having the highest standardized discriminant weights were stem density (weights: first canonical variate = −2.274, second canonical variate = 1.405) and water depth (weights: first canonical variate = 0.589, second canonical variate = 1.390). The model accurately classified most habitat types (median accuracy = 90%), although the accuracy of the model was relatively low in classifying marsh channel (18%) and *Scirpus* (33%) sites. Many channel (58%) and *Scirpus* (42%) sites were incorrectly classified as pond and edge *Spartina alterniflora* sites, respectively.

Marsh types also could be clearly separated using discriminant analysis (Wilks' lambda = 0.008, df = 32, 367, $p < 0.0001$). In this analysis, the first 2 canonical variates were responsible for 98% of the separation among habitat types (Fig. 9), and the predictor variables with the highest standardized weights were distance to edge (3.316) and water depth (−0.425) in the first canonical variate and stem density (2.245) in the second canonical variate. Marsh sites were accurately classified for 94, 97, 100, 100, and 33% of edge *Spartina alterniflora*, inner *S. alterniflora*, *Juncus*, *S. patens*, and *Scirpus* sites, respectively. Fifty percent of the *Scirpus* sites we sampled were incorrectly classified as edge *S. alterniflora* sites.

Environmental characteristics and decapod and fish densities

The canonical analysis for the relationship between densities of decapod crustaceans and fishes and environmental characteristics of habitat types was statistically significant (Wilks' lambda = 0.059, df = 144, 1559, $p < 0.0001$). The first canonical variate pair showed that 60% of the variance in animal densities was explained by environmental variables. In this equation, high densities of Atlantic croaker and blackcheek tonguefish and low densities of gulf marsh fiddler crab were associated with deep water, high turbidity levels,

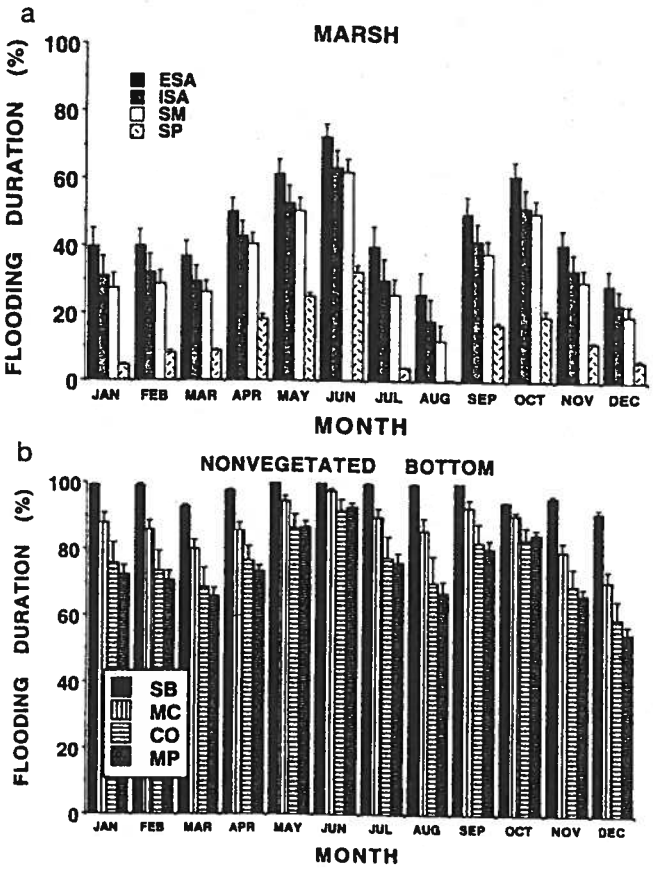

Fig. 6. Average monthly flooding durations ([hours habitat type inundated/total hours in month] × 100) of marsh and nonvegetated areas in upper Galveston Bay. Error bars = 1 standard error (SE). ESA: edge *Spartina alterniflora*; ISA: inner *Spartina alterniflora*; SM: *Scirpus maritimus*; SP: *Spartina patens*; SB: shallow bay; MC: marsh channels; CO: coves; MP: marsh ponds. Means and SEs were calculated from 16 samples from each habitat type (except shallow bay = 14)

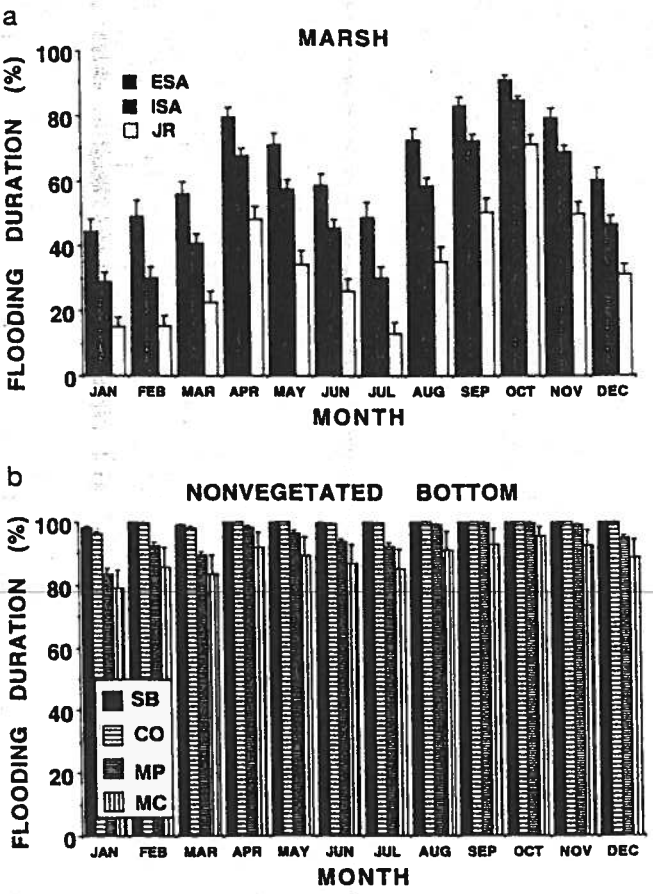

Fig. 7. Average monthly flooding durations ([hours habitat type inundated/total hours in month] × 100) of marsh and nonvegetated areas in East Bay. ESA: edge *Spartina alterniflora*; ISA: inner *Spartina alterniflora*; JR: *Juncus roemerianus*; SB: shallow bay; CO: coves; MP: marsh ponds; MC: marsh channels. Error bars = 1 standard error (SE). Means and SEs were calculated from 20 samples from each habitat type

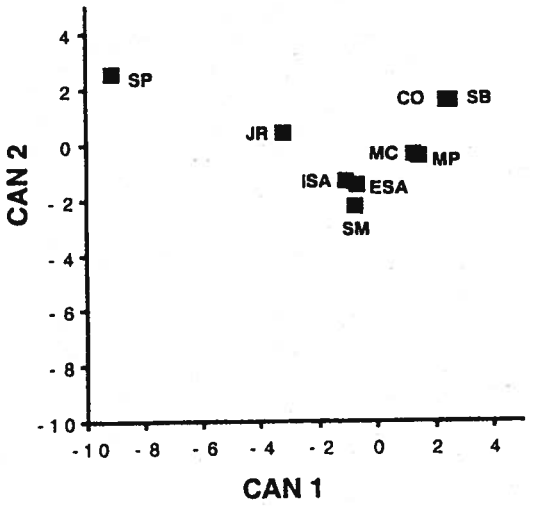

Fig. 8. Separation of habitat types using environmental characteristics. This plot of class means from the discriminant model shows the relative position of each habitat type along the canonical axes. Heavily weighted variables in both canonical variates were water depth and stem density. ESA: edge *Spartina alterniflora*; ISA: inner *Spartina alterniflora*; SM: *Scirpus maritimus*; SP: *Spartina patens*; JR: *Juncus roemerianus*; MP: marsh ponds; MC: marsh channels; CO: coves; SB: shallow bay

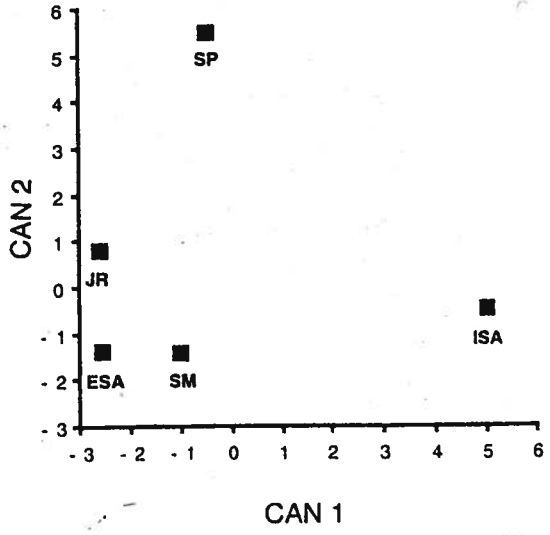

Fig. 9. Separation of marsh types by environmental characteristics. This plot of class means from the discriminant model shows the relative position of each marsh type along the canonical axes. Heavily weighted variables were distance to edge and water depth in CAN 1 and stem density in CAN 2. ESA: edge *Spartina alterniflora*; ISA: inner *Spartina alterniflora*; SM: *Scirpus maritimus*; SP: *Spartina patens*; JR: *Juncus roemerianus*

and high salinity (Table 9). The second variate pair explained an additional 23% of the variance; in this equation, high densities of white shrimp and blue crab and low densities of brown shrimp were associated with high values for salinity, elevation, and temperature. This second equation is influenced by a strong seasonal signal. Relatively high temperature and salinity occurred in the fall and coincided with high densities of white shrimp and relatively low densities of brown shrimp. White shrimp were not collected in spring. The high canonical weight given to elevation in the second variate pair is an indication that higher densities of white shrimp and blue crab were taken at marsh sites than in nonvegetated areas; marsh sites were generally higher in elevation than nonvegetated areas.

The canonical analysis for the relationship between densities of decapod crustaceans and fishes at marsh sites and environmental parameters also was statistically significant (Wilks' lambda = 0.021, df = 112, 636, $p < 0.0001$). The first canonical variate pair showed that 73% of the variance in animal densities within marsh was explained by environmental variables. In

this equation, high densities of brown shrimp, heavy marsh crab, naked goby, and daggerblade grass shrimp were associated with low elevation and small values of distance to edge (Table 10). The second variate pair explained an additional 15% of the variance; in this equation, high densities of white shrimp and low densities of brown shrimp were associated with high temperature, high salinity, and low values of distance to edge. This second equation is influenced by a strong seasonal signal that masked the importance of elevation in explaining the occurrence of white shrimp when both seasons were combined into 1 analysis. When the analysis was repeated using only fall data, the relationship between animal densities and environmental variables was significant (Wilks' lambda = 0.021, df = 88, 291, $p < 0.0001$), and the results indicate that high densities of white shrimp and other species were associated with low elevation and low values of distance to edge. In this analysis, high positive standardized canonical weights for the variables white shrimp (0.290), heavy marsh crab (0.283), darter goby (0.249), and naked goby (0.245) were associated with high negative weights for the variables distance to edge (−0.539) and elevation (−0.414).

Table 9. Standardized canonical weights of potential relationships between animal densities and environmental characteristics of habitat types. Weights are shown only when absolute values exceed 0.250. First and second variate pairs explained 60 and 23% of the variance, respectively. In this analysis, we included data from all habitat types, both locations, and both seasons. Number of cases = 236; 31 observations were omitted in the analysis because of missing data

Variable Set	Variable	Canonical variate pairs First	Second
First	Salinity	0.320	0.715
	Temperature		0.407
	Dissolved oxygen		
	Turbidity	0.379	
	Distance to edge		
	Depth	0.993	
	Stem density		
	Elevation		0.498
Second	Gulf menhaden		
	Atlantic croaker	0.328	
	Striped mullet		
	Spot		
	Gulf killifish		
	Blackcheek tonguefish	0.268	
	Naked goby		
	Darter goby		
	Sheepshead minnow		
	Bay anchovy		
	Daggerblade grass shrimp		
	Brown shrimp		−0.471
	Gulf marsh fiddler crab	−0.508	
	Blue crab		0.255
	Heavy marsh crab		
	White shrimp		0.524
	Marsh grass shrimp		
	Squareback marsh crab		

Table 10. Standardized canonical weights of potential relationships between animal densities and environmental characteristics of marsh habitat types. Weights are shown only when absolute values exceed 0.250. First and second variate pairs explained 73 and 15% of the variance, respectively. Only data from marsh samples were used in this analysis (both locations and both seasons were included). Number of cases = 111; 13 observations were omitted in the analysis because of missing data

Variable Set	Variable	Canonical variate pairs First	Second
First	Salinity	−0.261	0.294
	Temperature		0.794
	Dissolved oxygen		
	Turbidity		
	Distance to edge	−0.603	−0.347
	Depth	0.288	
	Stem density		
	Elevation	−0.416	
Second	Gulf menhaden		
	Striped mullet		
	Gulf killifish		
	Naked goby	0.253	
	Darter goby		
	Sheepshead minnow		
	Daggerblade grass shrimp	0.280	
	Brown shrimp	0.370	−0.466
	Gulf marsh fiddler crab	−0.315	
	Blue crab		
	Heavy marsh crab	0.453	
	White shrimp		0.450
	Marsh grass shrimp		
	Squareback marsh crab		

DISCUSSION

Our study allows unbiased comparisons of the use of marsh and shallow nonvegetated bottom by decapod crustaceans and fishes in Galveston Bay because we sampled all areas at similar water levels using quantitative methods (Rozas & Minello 1997). Our results show that no single habitat type was consistently selected over others by all species, and no species used only one habitat type exclusively. Nonetheless, most species of nekton frequently taken on the marsh surface were concentrated in low marsh located at the marsh-water interface. Thus, for these species, apparent habitat selection within emergent marsh was influenced most by 2 factors: marsh elevation and the proximity of the marsh to open-water areas (Zimmerman &

Minello 1984, Rozas 1993, Rozas & Reed 1993, Peterson & Turner 1994). In our study, high densities of brown shrimp, white shrimp (fall), daggerblade grass shrimp, naked goby, and darter goby (fall) were strongly associated with low, shoreline marsh sites.

One of the major differences among habitat types in our study was elevation. The mean elevation of *Spartina patens* marsh and *Juncus* marsh exceeded that of edge *S. alterniflora* marsh by 22 and 16 cm, respectively. The effect of elevation in our results was evident from differences in nekton use between edge *S. alterniflora* marsh and these 2 high marsh types (*S. patens* and *Juncus*). In our study, striped mullet, daggerblade grass shrimp, white shrimp, and blue crab appeared to select edge *S. alterniflora* marsh over high *S. patens* marsh, whereas gulf killifish was significantly more abundant in *S. patens* marsh. Striped mullet, daggerblade grass shrimp, brown shrimp, and blue crab also were more numerous in edge *S. alterniflora* marsh than *Juncus* marsh. Similarly, in a previous study, brown shrimp and white shrimp seemed to prefer low *S. alterniflora* marsh, whereas gulf killifish and diamond killifish appeared to favor high *Distichlis spicata* marsh over low *S. alterniflora* marsh (Rozas & Reed 1993). In another study, densities of daggerblade grass shrimp and brown shrimp were 1.2 to 4.3 times higher on low than high *S. alterniflora* marsh, but elevation did not seem to affect the abundance of white shrimp (Minello et al. 1994). Although apparently not the preferred habitat type of these organisms, high marsh in our study was exploited by several species of economic importance. *Juncus* marsh, in particular, contained modest densities of brown shrimp (>3 m^{-2} in spring) and blue crab (>1 m^{-2} in fall) and relatively high densities of white shrimp (>12 m^{-2} in fall). The highest elevation sites we sampled, within *S. patens* marsh, contained modest densities of brown shrimp (>3 m^{-2} in spring) and blue crab (1 m^{-2} in fall).

We examined how habitat selection was affected by the proximity of a marsh to open water (i.e. the edge effect) by comparing animal densities in *Scirpus* marsh and inner *Spartina alterniflora* marsh. Although others have examined the edge effect within *S. alterniflora* marsh (Peterson & Turner 1994, Minello et al. 1994, Minello & Webb 1997), elevation and proximity to marsh edge were confounded in these studies. Elevation within a *S. alterniflora* marsh generally increases with distance from the shoreline. For example, in our study, the mean elevation of inner *S. alterniflora* marsh was 5 to 7 cm higher than edge *S. alterniflora* marsh. In contrast, the mean elevation of inner *S. alterniflora* marsh was slightly less (1.7 cm) than that of *Scirpus* marsh; therefore, a comparison of nekton densities between these 2 marsh types (inner *S. alterniflora* marsh and *Scirpus* marsh) should be a conservative test of the edge effect. Even though these 2 habitat types were separated laterally by only a few meters and they had similar elevations, we found significant differences in animal densities between marsh types. In our study, gulf killifish and striped mullet were more numerous in inner *S. alterniflora* marsh, but brown shrimp in spring and daggerblade grass shrimp, white shrimp, and blue crab in fall were significantly more abundant in *Scirpus* marsh. We found even more differences in animal densities between marsh types when we compared inner *S. alterniflora* marsh and edge *S. alterniflora* marsh. We believe that this result is a response to a combination of the edge and elevation effects. Peterson & Turner (1994) found that resident marsh species (mostly grass shrimp and killifishes) used inner *S. alterniflora* marsh, and most other nekton was concentrated in marsh within 3 m of the waters edge. In both natural and created marshes of Galveston Bay, brown shrimp (spring) and blue crab (fall) were significantly more abundant in edge than inner *S. alterniflora* marsh (Minello & Webb 1997). Because many fishery species prefer marsh edge, increasing this habitat in solid stands of *S. alterniflora* marsh should enhance its habitat value and cause a substantial increase in its use by these species. Constructing channels in a transplanted *S. alterniflora* marsh increased densities of brown shrimp and white shrimp near the channels by a factor of 4.6 to 13 (Minello et al. 1994). Adding channels also significantly raised the densities of polychaete worms and daggerblade grass shrimp in the marsh edge. These animals are an important food of nekton predators such as small fishes, blue crab, and brown shrimp (Harrington & Harrington 1961, Gleason & Wellington 1988, Minello et al. 1989, Thomas 1989, McTigue & Zimmerman 1991).

Distributions of decapod crustaceans and fishes also may be affected by differences in structural complexity of vegetation among habitat types. Plant stem density and standing biomass in our study area generally increased with marsh surface elevation. Predatory fishes and decapod crustaceans may be attracted to sparse vegetation if foraging success is greater there than in dense vegetation. The relatively sparse vegetation of *Spartina alterniflora* and *Scirpus* marshes may have provided more foraging surface than nonvegetated areas, yet may have interfered less with movement and foraging activity than dense *S. patens* or *Juncus roemerianus* vegetation (Vince et al. 1976, Van Dolah 1978, West & Williams 1986).

The marsh surface and contiguous shallow nonvegetated areas generally supported higher densities of fishes and decapod crustaceans than the nearby shallow bay. Few of the dominant species collected in our study were abundant in shallow bay waters, although the shallow bay occasionally had densities of gulf men-

haden and bay anchovy similar to those in nonvegetated areas contiguous with marsh.

In nonvegetated areas, water depth and proximity to vegetation may influence nekton densities. Predation risk is high in deep, nonvegetated areas, especially in Gulf coast estuaries (Heck & Coen 1995). Open bay waters were usually deeper than the other areas we sampled. Mean water depth in the shallow bay was always significantly greater than the average water depths of the marsh surface; it was greater than all other habitat types in fall. In the absence of submerged aquatic vegetation, small fishes and decapod crustaceans may select shallow water to avoid large natant predators (Baltz et al. 1993, Ruiz et al. 1993, Miltner et al. 1995, Kneib 2000). In a study of a subestuary of Chesapeake Bay, Ruiz et al. (1993) found that several small species including daggerblade grass shrimp, naked goby, and 2 killifishes were significantly more abundant in shallow water (<70 cm), and the proportion of small juvenile blue crabs decreased with depth. They attributed this habitat segregation by depth to predator avoidance by small vulnerable nekton. Known predators (e.g. large spot, Atlantic croaker, and blue crab) were often more abundant in waters >70 cm, and the mortality rates of tethered daggerblade grass shrimp, killifish, and small blue crabs significantly increased with depth (Ruiz et al. 1993). Submerged vegetation was absent from our study area, and the shallow water of marsh ponds, channels, and coves may have afforded some protection from large natant predators. In addition, animals in nonvegetated areas adjacent to marsh have access to the nearby emergent marsh vegetation when it floods, which would provide protection as well (Minello & Zimmerman 1983, Minello et al. 1989, Minello 1993). Highest densities of 15 abundant species in nonvegetated areas were collected near the marsh edge, and Baltz et al. (1993) attributed this pattern to the protection provided by both the shallow water and flooded *Spartina alterniflora* at the marsh-water interface.

The paucity of available prey in the shallow bay may also have contributed to the low densities of most nekton predators. In Galveston Bay, infaunal densities generally peak in spring (between February and May) and decline to a low level in fall (October and November); however, a second peak may occur in the fall (Harper 1992, Whaley 1997). In our study during spring, average total infaunal densities in the shallow bay were lower than those in both *Spartina alterniflora* marsh types and other nonvegetated areas contiguous with marsh. In addition, at this time the shallow bay was dominated by the polychaete *Mediomastus* spp. and oligochaetes, which are subsurface, deposit feeders (Gaston & Nasci 1988, Whaley 1997) that may be unavailable to most predators. In contrast, *S. alterniflora* marsh, ponds, and channels were dominated by chironomids, which are available and often consumed by estuarine predators (Sheridan 1979, Laughlin 1982, Rozas & LaSalle 1990). Although infaunal densities in the shallow bay peaked in the fall and surpassed average densities in other habitat types, *Mediomastus* spp. continued to dominate the assemblage. The availability of prey in the shallow bay at this time, however, may have increased with the rise in densities of the polychaete *Streblospio benedicti*, which is a surface deposit feeder.

Factors that influence the abundance of infaunal prey populations in shallow estuarine areas are complex. The decline of infaunal densities in marsh and adjacent nonvegetated areas that we observed between spring and fall in our study may have resulted from grazing by predators (Cammen 1979, Kneib 1984). However, many environmental conditions (e.g., temperature, desiccation, sediment oxygen concentration) that vary with flooding patterns, elevation, and distance to edge also may control abundance of infaunal prey (Kneib 1984, Whaley 1997, Flynn et al. 1998). A combination of biotic or abiotic factors are likely responsible for the infaunal distributional patterns that we observed in our study. The identification of specific controlling factors will require further research that incorporates controlled experiments.

In summary, we observed distinct utilization patterns for different species of fishes and decapod crustaceans in a shallow region of Galveston Bay. None of the marsh or shallow nonvegetated habitat types we sampled was preferred by all species. However, the marsh surface and adjacent nonvegetated areas contained much higher densities of most animals than the shallow bay. Most fishery species that use the marsh surface were found in greatest abundance in low, shoreline marsh vegetation. In applying our results to habitat restoration in estuaries, we recommend creating a variety of marsh and contiguous shallow habitat types to enhance nekton biodiversity. To maximize fishery habitat, we recommend that within this mix of habitat types, greater emphasis be given to constructing low marsh edge by creating large areas of low marsh interspersed with a dense network of shallow channels and interconnected ponds.

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