Use of Marsh Edge and Submerged Aquatic Vegetation as Habitat by Fish and Crustaceans in Degrading Southern Louisiana Coastal Marshes

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Understanding habitat value to fish and crustaceans in degrading brackish coastal marshes is important for management of coastal ecosystems. Marshes in coastal Louisiana are undergoing rapid rates of loss. To evaluate change in habitat use in a degrading coastal ecosystem, nekton communities were sampled in three dominant co-occurring habitat types (brackish marsh edge, submerged aquatic vegetation [SAV], and submerged bare substrate) within brackish marshes undergoing rapid fragmentation in Terrebonne Bay, Louisiana. Vegetated habitats supported greater nekton biomass, abundance, and species richness values than non-vegetated habitat. SAV supported greater fish and shrimp abundance than marsh edge, although fish and shrimp biomass were not significantly different. The confirmation that SAV provides equivalent or greater habitat value for some fish and crustacean species than marsh edge, in a moderate to highly fragmented marsh undergoing rapid disaggregation, demonstrates the importance of assessing SAV abundance and structure for sustainable fisheries management in coastal Louisiana.

Resumen: *Entender el valor del hábitat de los peces y crustáceos en los pantanos costeros salobres es importante para el manejo de los ecosistemas costeros. Los pantanos en la costa de Luisiana están experimentando rápidas tasas*

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de pérdida. Para evaluar el cambio en el uso del hábitat en un ecosistema costero degradante, las comunidades de nekton fueron muestreadas en tres tipos de hábitats dominantes coexistentes (margen pantanoso salobre, vegetación acuática sumergida [SAV] y sustrato sumergido) en marismas salobres que sufren fragmentación rápida en la Bahía de Terrebonne , Luisiana. Los hábitats vegetados apoyaron una mayor biomasa de nekton, abundancia y valores de riqueza de especies que el hábitat sin vegetación. SAV apoyó mayor abundancia de peces y camarones que borde de pantano, aunque la biomasa de peces y camarón no fueron significativamente diferentes. La confirmación de que SAV proporciona un valor de hábitat equivalente o mayor para algunas especies de peces y crustáceos que el borde del pantano, en un pantano moderado o altamente fragmentado que está siendo desagregado rápidamente, demuestra la importancia de evaluar la abundancia y estructura del SAV para la ordenación pesquera sostenible en la costa de Luisiana.

KEY WORDS: land loss, wetland, fisheries

PALABRAS CLAVE: pérdida de tierras, humedales, pesquerías

INTRODUCTION

In coastal areas, emergent herbaceous marsh and submerged aquatic vegetation (SAV) provide essential habitat for many fish and invertebrate species (Beck et al. 2001, Gillanders 2006, Battaglia et al. 2012). These plants add structural complexity to aquatic habitat, which provides aquatic animals, and particularly juvenile fish and crustaceans, with a refuge from predators and enhanced food supply (Zimmerman and Minello 1984, Rozas and Odum 1988, Kanouse et al. 2006). As a result, animal abundances are often greater, mortality due to predation is reduced, and individual growth is enhanced in emergent marsh and SAV compared to non-vegetated substrate (Heck and Crowder 1991). In marsh-dominated systems, habitat edge (i.e., the transition zone between interior marsh vegetation and open water; Rakocinski et al. 1992) is particularly important for supporting higher abundances of animals compared to the marsh interior (Minello and Rozas 2002).

Coastal Louisiana is experiencing the greatest areal loss of wetlands in the United States due to a combination of sea level rise, subsidence, saltwater intrusion and reduced sediment inflow (Scavia et al. 2002, Day et al. 2011). Nearly 5,000 km^2 of wetlands were lost from 1932 to 2010, and it is predicted that an additional 2,000 to 4,600 km^2 may be lost over the next 50 years (Couvillion et al. 2013). The majority of this land loss has occurred in coastal marsh ecosystems that provide essential habitats for nearshore aquatic species, including economically important commercially fished species such as brown shrimp (*Farfantepenaeus aztecus*) and blue crabs (*Callinectes sapidus*) (McIver and Rozas 1996). Common marsh types in coastal Louisiana include fresh (0–0.5 ppt), intermediate (0.5–5 ppt), brackish (5–18 ppt), and saline (>18 ppt) marshes, with different suites of dominant emergent and submerged plant species (Visser et al. 1998, Visser et al. 2000, Cho et al. 2012, Pham et al. 2014). In coastal ecosystems, tidal regimes, fresh water input, and tropical storm surge along with other saltwater intrusion events are known to create a dynamic soil salinity gradient which controls vegetation community composition (Battaglia et al. 2012). Dominant and often adjacent habitats in these systems are marsh edge, SAV, bare substrate, and in some areas, oyster reefs (Visser et al. 1998, Visser et al. 2000, Visser et al 2012). Previous studies examining faunal use of coastal marsh systems in Louisiana have reported the importance of each of these habitat types (Castellanos and Rozas 2001, Hitch et al. 2011). However, the role of each habitat can vary across marsh salinity types and there is less known on the use of these habitats by fish and crustaceans as marshes transition between salinity types, or as emergent marsh transitions to open water.

Land loss has resulted in a fragmented coastal landscape consisting of discrete patches varying in size, shape and spatial separation, and variation in the overall degree of fragmentation across the coast (Couvillion et al. 2016). Aggregation index analyses indicate increasing salinity is generally correlated with decreasing aggregation (i.e. increasing fragmentation) among marsh types (Couvillion et al. 2016). Louisiana brackish marshes are experiencing a trend of disaggregation of 0.28 percent per year (Couvillion et al. 2016), however certain basins, such as Terrebonne, have experienced higher rates up to 0.37 percent per year (Couvillion et al. 2016). Even with these high rates of land loss and large scale changes in marsh structure, combined landings of commercial fishery species have remained relatively stable since the 1950's (Chesney et al. 2000). Plausible explanations include an increased abundance of submerged aquatic macrophytes moving into newly created shallow open water with emergent marsh loss which could compensate for the lost habitat function. However, as emergent marsh transitions into shallow open water and marsh edge habitat is lost, nekton populations are expected to decline (Chesney et al. 2000). Understanding relative habitat use within degrading marsh ecosystems in coastal Louisiana will help better inform future fisheries management and coastal restoration decisions. The objective of this study was to compare nekton use of co-occurring brackish marsh edge, submerged aquatic vegetation, and submerged bare substrate in a system where emergent marsh has been shown to be undergoing high rates of disaggregation.

METHODS

Study area

This study was conducted in Terrebonne Basin, Louisiana, a region experiencing marsh disaggregation rates as high as 0.37 percent per year (Couvillion et al. 2016). The study area (2 km × 2 km) was selected using 2015 orthoimagery from the United States Department of Agriculture Farm Service Agency (USDA: FSA 2015). Each pixel within the orthoimagery contained an 8-bit gray-scale value. For color-infrared and natural color, a digital number from 0 to 255 was assigned to each pixel; the number referred to a color look-up table which contained the RGB red, blue and green values. The study area was centered on Louisiana's Coastwide Reference Monitoring Systems (CRMS) Station 0369 (29°17'40.50" N, 90°41'42.08" W), a marsh that has transitioned between brackish and saline marsh over the past six decades and displays heterogeneity in the degree of marsh fragmentation. Emergent vegetation at this site was dominated by the native cordgrass (*Spartina alterniflora)* and submerged aquatic vegetation (SAV) dominated by the introduced Eurasian watermilfoil (*Myriophyllum spicatum)*, both of which are common within brackish marsh areas in Louisiana (Visser et al. 1998, Visser et al. 2000, Visser et al 2012).

Sampling design

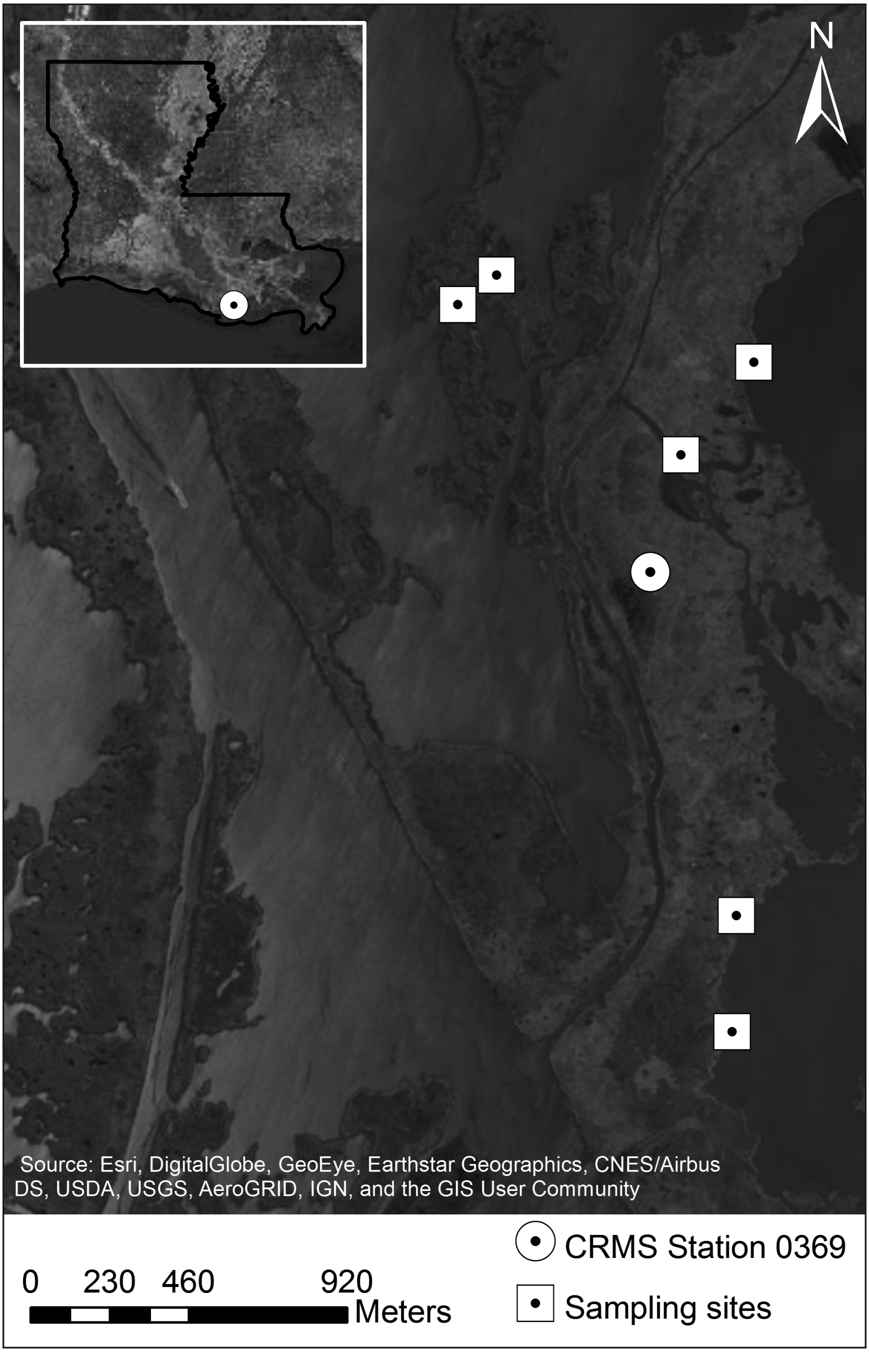
Sampling was conducted in May 2016. Within the study area, six study sites were chosen in degrading (fragmenting) marsh (Figure 1). Sites were chosen based on availability of targeted habitats (see below) and to represent a range of marsh fragmentation levels. Fragmentation (i.e., perimeter to area ratio and land to water ratio) across the study area was quantified using ARCGIS (Geographic Information System; Version 10.2, Environmental Systems Research Institute (ESRI), Redlands, California, U.S.A.) through delineation of orthoimagery (Davidson 1998, USDA: FSA 2015). Within the study area, across the fragmentation gradient, the perimeter to area ratio ranged from 0.02 to 0.12 and the percent land ranged from 38 to 73 percent. Within each study site three habitats were sampled: 1) emergent marsh edge (marsh edge), 2) submerged aquatic vegetation (SAV), and 3) non-vegetated substrate (bare substrate), resulting in a sample size of $n = 6$ per habitat (Figure 2). However, SAV was not found at two of the sites, resulting in an $n = 4$ for the SAV habitat. SAV sites were on average located 9.7 ± 2.4 m away from the marsh edge and bare sites were located 7.3 ± 3.6 m away from the marsh edge. Distance between habitat samples within a study site (i.e., bare, marsh, SAV) ranged from 3.7 m to 51.8 m.

Environmental and habitat characteristics

Salinity (ppt) and water depth (cm) were recorded at each sample location. Salinity was measured using a refractometer (Extech RF20) and water depth (cm) was determined by taking the mean of four depth measurements within the throw trap (i.e., one measurement per quadrant of the throw trap; see below). If depth was unsuitable for sampling with the throw trap, the trap was redeployed in a new location. Contextual salinity, temperature, and water surface elevation data were downloaded for CRMS Station 0369 to assess typical environmental conditions (Figures 3, 4). Percent cover of the dominant marsh edge plants and SAV species were estimated within each 1 m^2 sampling area, with cover being reported as percent vegetated: bare sediment per meter squared (see *Nekton sampling* below).

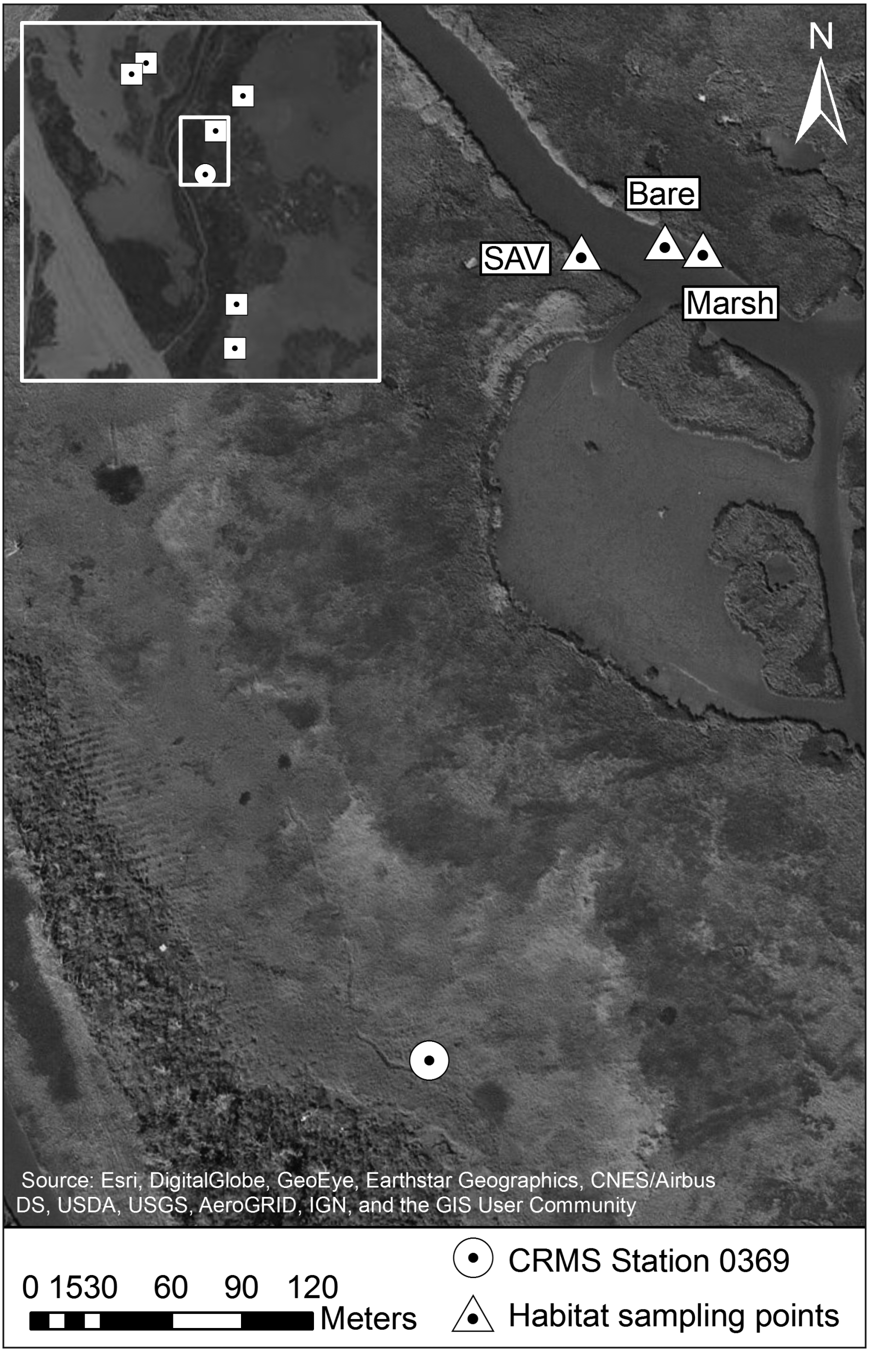
Nekton sampling

Nekton were sampled in each habitat with a 1 m^2 throw trap. The throw trap was constructed of an aluminum frame (1 m × 1 m × 0.7 m tall) with 1.6 mm nylon mesh sides. To enable sampling in deeper water, the nylon mesh was extended above the frame to a total height of 1.25 m and attached to a buoyant PVC square (1 m × 1 m) with floats (La Peyre and Gordon 2012). Marsh edge was sampled by placing the throw trap in the marsh vegetation to water interface (i.e., the transition zone between inner marsh vegetation and open water, Rakocinski et al. 1992). After deployment, the throw trap was immediately pushed into the ground to ensure complete contact with the sediment. If complete contact (i.e., no



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1. Location of six study sites (squares) in a rapidly disaggregating marsh ecosystem in Terrebonne Basin, Louisiana, U.S.A. The black line in the inset map delineates the Louisiana state border and the circle (in both map and inset map) denotes the center of CRMS Station 0369.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 2. Example of habitat sample locations (i.e., SAV, bare, marsh) at one site. The inset map represents Figure 1 and the circle (in both map and inset map) denotes the center of CRMS Station 0369.

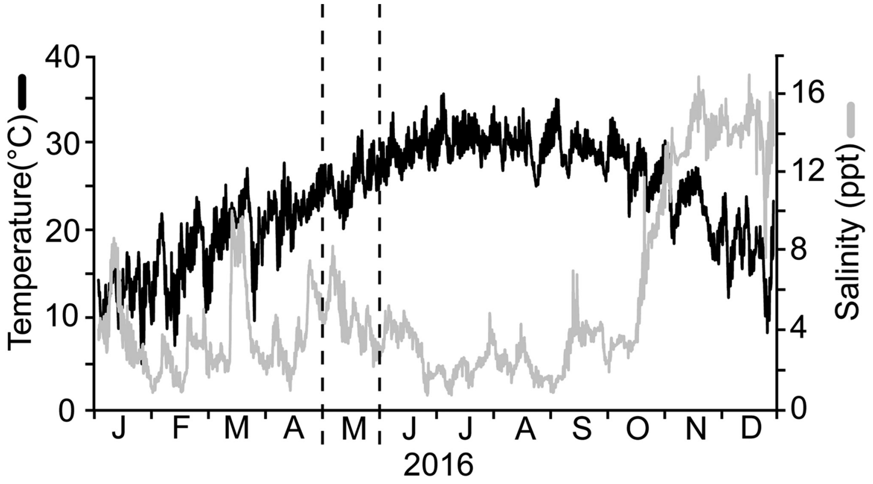


Figure 3. Continuous hourly sampling of temperature and salinity data for CRMS Station 0369 in 2016. Sampling month (May) of the present study is denoted by dotted lines.

gaps between the frame and sediment) was not achieved, the throw trap was removed and redeployed at a new undisturbed nearby location (at least 3 to 5 m away from the initial deployment location) to ensure accurate nekton sampling (Hitch et al. 2011). Marsh vegetation and SAV were removed from the throw trap prior to nekton sampling. The vegetation was placed on ice in 10-gallon Ziploc™ bags and transported to the laboratory where the vegetation was later sorted for nekton. Following vegetation removal, the interior of the throw trap was swept with a 1 m wide bar seine (1.6 mm mesh) to remove all nekton from the trap. The sweeping process continued until five consecutive sweeps of the bar seine yielded no organisms.

Nekton samples were placed on ice and transported to the laboratory, where they were frozen until further processing. Thawed nekton were identified, counted, measured to the nearest mm, and individuals of the same species from a given sample were pooled and weighed to the nearest 0.001 g wet weight. From this, individual species abundance (number of individuals per sample (i.e., per m2)), biomass, species richness, and diversity, calculated as the Shannon-Wiener diversity index, were determined. Organisms were identified to the species level, except for grass shrimp, which were identified to the genus level. Six individual fish could not be accurately identified due to extensive body damage, and were removed from the sample analyses.

Statistical analysis

Statistical analyses were conducted using the R statistical software programming environment (Version 3.2.3, The R Foundation for Statistical Computing, Vienna, Austria). Normality and homogeneity of the variance were tested via Shapiro-Wilk normality test and Levene's Test for homogeneity of variance.

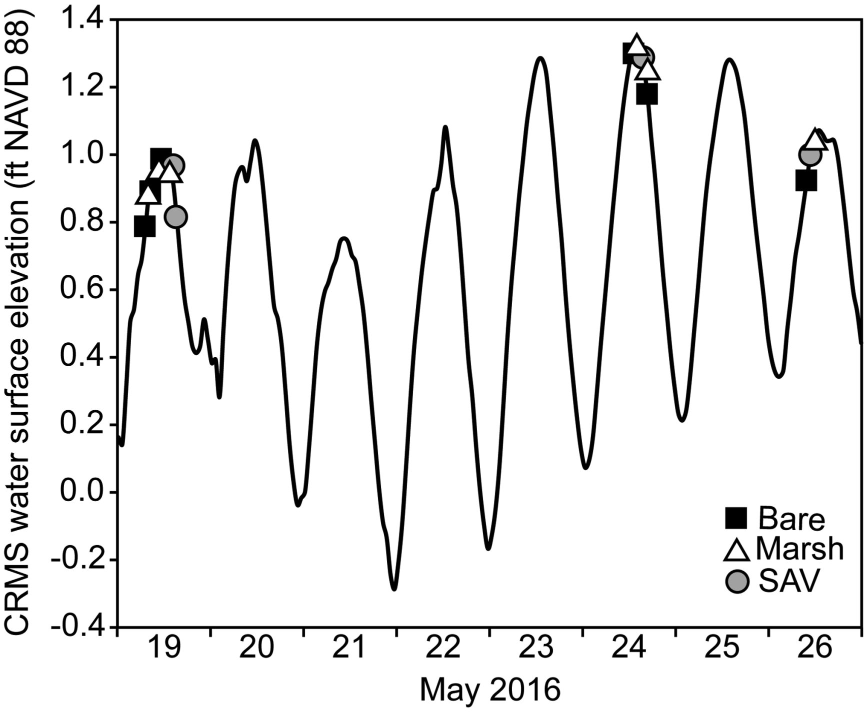


Figure 4. Continuous hourly water surface elevation data for CRMS Station 0369 in 2016. Timing of collection of samples within each habitat is presented.

Subsequently, all nekton and the percent cover data required a $\log_{10}(x+1)$ transformation. Despite transformation, fish abundance, nekton biomass, and species richness data did not meet the given normality assumptions. Data were analyzed using analyses of variance (ANOVA, alpha level $p = 0.05$), which is robust to non-normality, so interpretation of the outcomes is likely unaffected (Underwood 1997).

Separate ANOVAs were conducted on abundance (total nekton, fish, shrimp), biomass (total nekton, fish, shrimp), species diversity, species richness, water depth, water surface elevation, vegetation percent cover, and salinity data across habitats (bare substrate, marsh edge, SAV) (Table 1, Table 2). Pairwise Tukey HSD post-hoc tests were then conducted on significant main effects to test for differences among habitat types. An unpaired two sample T-test was conducted on total length of select nekton species between marsh and SAV habitats. Total length analyses only included species with an appropriate sample size across all three habitats (i.e., > 3 specimens per habitat; *Palaemonetes* spp. (grass shrimp), *Farfantepenaeus aztecus* (brown shrimp), and *Syngnathus scovelli* (gulf pipefish)). An additional unpaired two-sample T-test was performed on the distance to the marsh edge for samples in SAV and bare habitats.

Table 1. Analysis of variance table comparing abundance, biomass, diversity, and species richness metrics across habitat types (bare substrate, marsh edge, SAV). (NS = nonsignificant). See Figures 5 and 6 for Tukey HSD results.

Factor	**DF**	**SS**	**MS**	**F**	**P**
Nekton abundance	2	19.14	9.57	10.33	< 0.01
Fish abundance	2	9.91	4.96	5.38	< 0.05
Shrimp abundance	2	28.15	14.08	21.34	< 0.001
Nekton biomass	2	6.91	3.46	4.22	< 0.05
Fish biomass	2	2.00	1.00	0.73	NS
Shrimp biomass	2	10.14	5.07	10.57	< 0.01
Shannon-Wiener (Diversity Index)	2	0.08	0.04	0.52	NS
Species richness	2	1.87	0.93	4.41	< 0.05

Table 2. Analysis of variance table comparing water depth, vegetation percent cover, water surface elevation at time of sampling (relative to CRMS Station 0369), and salinity across habitat types (bare substrate, marsh edge, SAV). (NS = nonsignificant). Letters indicate significant differences ($p < 0.05$) according to Tukey HSD post hoc tests.

	ANOVA					**Tukey**		
Factor	**DF**	**SS**	**MS**	**F**	**P**	**Bare**	**Marsh**	**SAV**
Water depth	2	9102.80	4551.40	27.09	<0.001	a	b	b
Water surface elevation	2	0.01	0.01	0.19	NS			
Vegetation percent cover	2	53.28	26.64	301.03	<0.001	a	b	b
Salinity	2	0.64	0.32	0.16	NS			

This was conducted to confirm that sampling distance from the marsh edge was not a confounding factor for SAV and bare samples, as previous studies have shown correlations between proximity to marsh edge and nekton abundance (Minello and Rozas 2002).

RESULTS

Environmental and habitat characteristics

Mean water depth was significantly different across habitat types (Table 2). Water depths were greater for bare substrate (90.5 ± 5.3 cm SE [standard error]) than SAV (55.3 ± 6.9 cm SE) and marsh (36.0 ± 5.0 cm SE) (Tukey HSD, $p < 0.05$, Table 2), however SAV and marsh water depths did not significantly differ (Tukey HSD, p = NS [non-significant], Table 2). Distance from marsh edge did not significantly differ between SAV and bare samples (unpaired two sample t-test, $t = -0.608$, $df = 8$, p = NS). Water surface elevation at the time of sampling (Table 2, Figure 4) and water salinity (bare substrate: 3.9 ± 0.6 ppt SE; marsh edge: 3.8 ± 0.6 ppt SE; SAV: 3.9 ± 0.7 ppt SE; Table 2) were not significantly different across habitat types. Annual salinity and temperature data for CRMS Station 0369 is presented for reference in Figure 3. Among the vegetated habitat types, percent cover was not significantly different (marsh edge: 48.0 ± 8.4 percent SE; SAV: 50.0 ± 7.1 percent SE; Tukey HSD, $p = NS$, Table 2). Environmental parameters were representative of conditions in Louisiana brackish marshes in the month of May (Hitch et al. 2011, Table 2).

Species description

A total of 784 organisms, consisting of 12 species of fish and 2 species of shrimp, were collected (Table 3). Overall, crustaceans were 4.6 times more abundant than fish, accounting for 82.3 percent of all organisms collected. Grass shrimp in SAV habitat comprised 59 percent of all organisms collected. Grass shrimp and brown shrimp accounted for 74.6 percent and 7.7 percent of the total nekton abundance, respectively. The dominant fish taxa across habitats included menhaden (*Brevoortia patronus*), speckled worm eels (*Myrophis punctatus*), and sailfin mollies (*Poecilia latipinna*), which represented approximately 5.0 percent, 4.5 percent, and 2.3 percent of the total nekton collected, respectively.

Within habitats, grass shrimp were numerically dominant in marsh edge and SAV, relative to bare substrate (Table 3). In the marsh edge, grass shrimp were approximately 7 and 29 times more abundant than brown shrimp and pinfish (*Lagodon rhomboides*), the second and third most abundant species. In SAV, grass shrimp were approximately 16 and 18 times more abundant than speckled worm eels and brown shrimp, the second and third most abundant species. Conversely, the numerically dominant species in the bare substrate were menhaden, brown shrimp and speckled worm eels, which represented 58.2 percent, 25.4 percent, and 7.5 percent of the organisms within the bare substrate habitat, respectively.

Grass shrimp, brown shrimp and speckled worm eels were collected in all three habitats. Pinfish were found only in bare substrate and marsh edge habitats, while Gulf pipefish, Gulf killifish (*Fundulus grandis*), naked gobies (*Gobiosoma bosc*), and sailfin mollies were only found in the marsh edge and SAV habitats (Table 3). Spot (*Leiostomus xanthurus*) were only found in bare substrate and SAV habitats.

Habitat comparisons

Nekton abundance, fish abundance, shrimp abundance, nekton biomass, shrimp biomass, and species richness values were significantly different among habitat types and were greater in SAV than bare substrate (Tukey HSD, $p < 0.05$, Table 1, Figures 5, 6). Shrimp abundance and shrimp biomass were significantly greater in marsh edge than bare substrate (Tukey HSD, $p < 0.05$, Table 1, Figures 5B, 6B). Shrimp abundance was the only metric that was significantly different across all habitats (SAV $>$ marsh edge $>$ bare substrate; Tukey HSD, $p < 0.05$, Figure 5B). SAV samples had significantly greater abundances of fish, shrimp, and nekton than marsh edge samples (Tukey HSD, $p < 0.05$, Table 1, Figure 5). However, SAV samples were not statistically different to marsh edge samples for species richness,

Table 3. Total species abundance by habitat types (bare substrate, marsh edge, SAV)

Habitat	Common Name	Scientific Name	Abundance
Bare	Menhaden	*Brevoortia patronus*	39
Bare	Brown shrimp	*Farfantepenaeus aztecus*	17
Bare	Speckled worm eel	*Myrophis punctatus*	5
Bare	Bay anchovy	*Anchoa mitchilli*	2
Bare	Pinfish	*Lagodon rhomboides*	1
Bare	Spot	*Leiostomus xanthurus*	1
Bare	Grass shrimp	*Palaemonetes* spp.	1
Total			66
Marsh	Grass shrimp	*Palaemonetes* spp.	116
Marsh	Brown shrimp	*Farfantepenaeus aztecus*	17
Marsh	Pinfish	*Lagodon rhomboides*	4
Marsh	Gulf pipefish	*Syngnathus scovelli*	3
Marsh	Gulf killifish	*Fundulus grandis*	2
Marsh	Naked goby	*Gobiosoma bosc*	1
Marsh	Speckled worm eel	*Myrophis punctatus*	1
Marsh	Sailfin molly	*Poecilia latipinna*	1
Total			145
SAV	Grass shrimp	*Palaemonetes* spp.	468
SAV	Speckled worm eel	*Myrophis punctatus*	29
SAV	Brown shrimp	*Farfantepenaeus aztecus*	26
SAV	Sailfin molly	*Poecilia latipinna*	17
SAV	Gulf pipefish	*Syngnathus scovelli*	10
SAV	Rainwater killifish	*Lucania parva*	7
SAV	Gulf killifish	*Fundulus grandis*	4
SAV	Naked goby	*Gobiosoma bosc*	2
SAV	Clown goby	*Microgobius gulosus*	2
SAV	Spot	*Leiostomus xanthurus*	1
SAV	Atlantic croaker	*Micropogonias undulatus*	1
Total			567

biomass (shrimp and nekton and), or diversity index values (Tukey HSD, $p = NS$, Table 1, Figure 6).

Significant differences in abundance, but not biomass, between marsh edge and SAV habitats suggested a possible difference in nekton size across habitats. To compare nekton sizes between habitats, mean total lengths were calculated for those species with a minimum of three organisms per habitat (i.e., brown shrimp, grass shrimp, and Gulf pipefish; Table 4). Brown shrimp total lengths were greater in the marsh than SAV habitat (unpaired two sample t-test, $t = 5.70$, $df = 23.63$, $p < 0.001$; Table 4). SAV grass

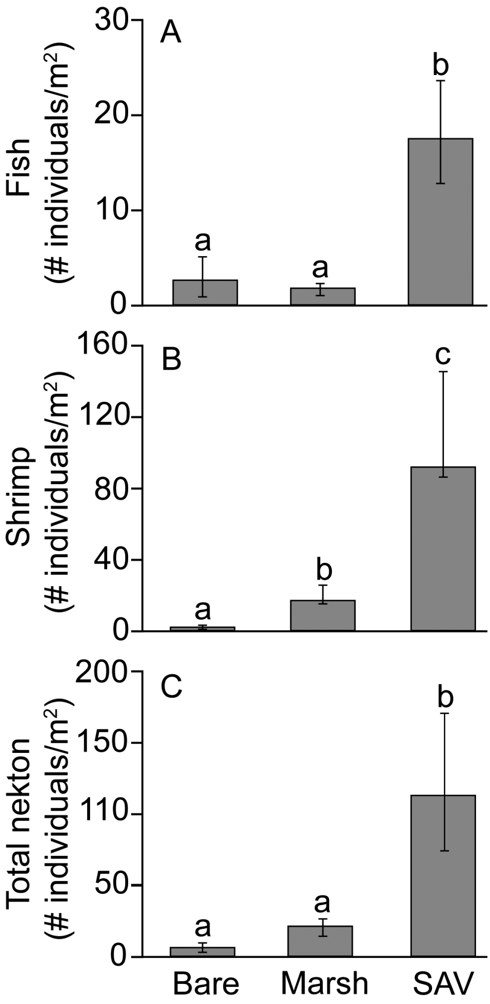


Figure 5. Density of (A) fish, (B) shrimp, and (C) total nekton by habitat type (mean ± S.E.). Letters indicate significant differences ($p < 0.05$) according to Tukey HSD post hoc tests. Note the different scales on the Y-axes, data are back transformed.

shrimp total lengths were greater than marsh grass shrimp total lengths (unpaired two sample t-test, $t = -2.40$, $df = 197.65$, $p < 0.05$). Gulf pipefish total lengths were not significantly different between vegetated habitats (unpaired two sample t-test, $t = 1.31$, $df = 11$, $p = NS$). Gulf pipefish and brown shrimp total lengths were 20.2 percent and 62.2 percent greater in the marsh edge than SAV samples, respectively, whereas the total length of grass shrimp was 8.2 percent greater in SAV than marsh edge (Table 4).

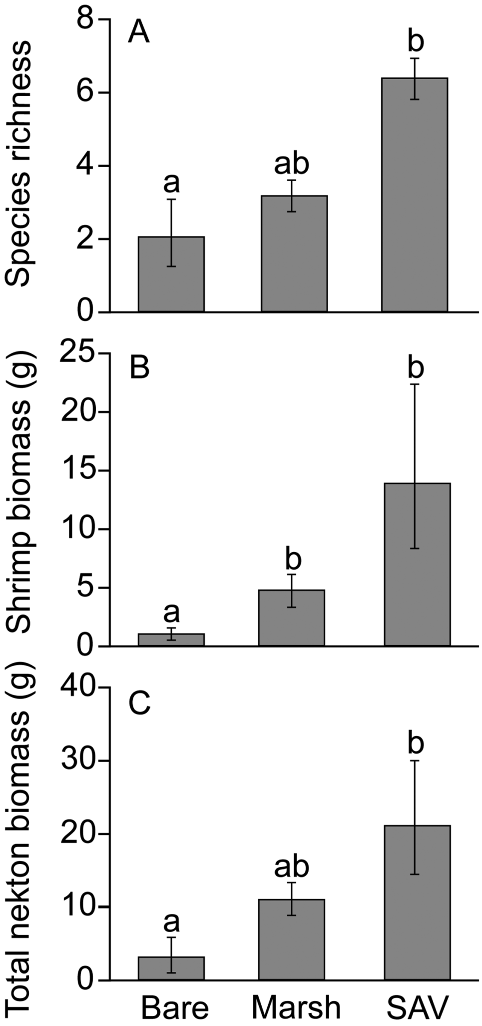


Figure 6. (A) Species richness, (B) shrimp biomass, and (C) total nekton biomass by habitat type (mean ± S.E.). Letters indicate significant differences ($p < 0.05$) according to Tukey HSD post hoc tests. Note the different scales on the Y-axes, data are back transformed.

Table 4. Total length (mean ± 1 SE mm) for nekton species by habitat type. Only those species with at least three individuals per habitat are included.

Common Name	**Scientific Name**	**Marsh**	**SAV**
Brown shrimp	*Farfantepenaeus aztecus*	45.1 ± 2.9	26.6 ± 1.6
Grass shrimp	*Palaemonetes* spp.	23.4 ± 0.7	25.4 ± 0.4
Gulf pipefish	*Syngnathus scovelli*	80.3 ± 7.4	66.8 ± 5.1

DISCUSSION

Nekton species-specific comparisons

The species diversity measured in the present study was typical for brackish areas of a Louisiana estuary (Castellanos and Rozas 2001, Kanouse et al. 2006). The overall numerical dominance of crustaceans (predominately grass shrimp) in the vegetated habitats was consistent with similar studies examining nekton use of coastal submerged and emergent vegetation (Rozas and Odum 1987, Rozas and Minello 1998, Castellanos and Rozas 2001, Kanouse et al. 2006, La Peyre and Gordon 2012). Fish and crustacean density (i.e., individuals per m^2) per habitat also fell within the wide range of previously reported values (Rozas and Odum, 1987, Castellanos and Rozas 2001, Troutman et al. 2007).

Previous studies in south Louisiana have documented speckled worm eels within nekton assemblages of both SAV and marsh edge (Kanouse et al. 2006, Rozas and Minello 2010), but in the present study speckled worm eels were numerically dominant in SAV and rare in marsh edge. Baltz et al. (1993) classified this species as a marsh edge resident, due to its yearlong presence of juveniles in the habitat. When presented with both habitat types, speckled worm eels tend to inhabit SAV over marsh (i.e., eel biomass was significantly greater in *Potamogeton nodosus* than in *Scirpus sp.*) (Castellanos and Rozas 2001). However, the preference for SAV varied with plant species and season, greater eel abundance in SAV was only reported in spring, the season of sampling for the current study (Castellanos and Rozas 2001).

Rainwater killifish have additionally illustrated contradictory trends in habitat abundance. Rainwater killifish are known to be present in both habitats (Castellanos and Rozas 2001, Kanouse et al. 2006, Rozas and Minello 2010), but in the current study were absent from the marsh edge and present in low numbers in the SAV. Nekton such as speckled worm eel and rainwater killifish are known to exhibit species-specific habitat preferences, which may be related to the animal's life history and aspects of the habitats themselves, such as plant architecture or specific chemical cues (Martin 2016). Furthermore, the relative use of marsh edge and SAV as habitat can be species, time, and location specific (Heck and Crowder 1991, Rozas et al. 2012). For example, previous studies have suggested seasonal flooding patterns may affect habitat density because of the subsequent changes in depth and habitat accessibility (Rozas and Minello 1998, Zimmerman and Minello 1984). Several studies have also demonstrated seasonal and species specific nekton habitat preference trends (Rozas and Minello 1998, Castellanos and Rozas 2001).

Two fish species, bay anchovies and gulf menhaden, were exclusively present in the bare substrate habitat. This is similar to previous studies that reported higher bay anchovy abundances in non-vegetated than vegetated habitats (Zimmerman and Minello 1984, Rozas and Minello 1998, Castellanos and Rozas 2001). Species such as bay anchovies and menhaden are classified as nektonic transient fishes and are typically seasonably abundant in the marsh edge habitat. As they are typically aggregated in schools, sampling frequencies can be highly variable (Baltz et al. 1993).

Habitat-specific comparisons

Vegetated habitats (marsh edge and SAV) supported higher nekton abundance, biomass, and species richness values than non-vegetated (bare substrate) areas. This result agrees with previous studies illustrating nekton habitat preference for vegetated habitat over non-vegetated bare substrate (Heck et al. 1989, Rozas and Minello 1998, Beck et al. 2001, Castellanos and Rozas 2001). However, there was a lack of significant differences between the marsh edge and bare substrate habitats for four metrics; this was most likely attributable to the large number of transient menhaden sampled over bare substrate.

Significant differences in nekton abundance, but not biomass, between the SAV and marsh edge habitats can be partially attributed to differences in animal size between habitats. The brown shrimp and Gulf pipefish total length trends support previous studies that reported significantly smaller nekton in SAV than in co-occurring marsh edge habitats (Rozas and Minello 1998, Orth and van Montfrans 1987, Thomas et al. 1990). The size-habitat pattern observed may indicate a change in refuge requirements as juveniles increase in size, enabling larger nekton to explore less protected habitats (Heck and Orth 1980, Heck and Thoman 1984, Orth et al. 1984). Other proposed explanations for size-habitat patterns include differential mortality and growth rates in these habitats, and the inability of small juveniles to effectively travel between habitats with the changing tide (Kneib 1987, Thomas et al. 1990, Rozas and Minello 1998, Rieucau et al. 2015). Furthermore, changes in nutritional requirements and the inability of larger individuals to forage effectively in high density vegetation such as *Myriophyllum spicatum*, may lead to larger juveniles residing in the marsh edge (Heck and Orth 1980, Ryer 1987, Thomas et al. 1990).

Landscape fragmentation

Landscape fragmentation, or the breaking apart of continuous habitat into smaller patches, is a global issue and one of the most influential processes threatening the persistence of species (Lindenmayer and Fischer 2006). Terrebonne Basin is experiencing substantial marsh fragmentation and land loss (Couvillion et al. 2016). Projected land loss in this region is estimated at 11.9 $km^2\ y^{-1}$, which could result in a loss of nearly 50 percent of marsh area by 2050 (Barras et al. 2003). Over time, habitat fragmentation results in the reduction of emergent marsh habitat and a subsequent increase in shallow open water habitat (Bennett and Saunders 2010). The transition to shallow open water habitat also creates potential space for SAV to colonize (Chesney et al. 2000).

A previous nekton study looking at the interactions of salinity, marsh fragmentation, and SAV documented lower nekton densities in fragmented brackish marshes (Hitch et al. 2011). Fragmented marsh was defined by Hitch et al. (2011) as greater than 55 percent open water, while non-fragmented marsh was defined as less than 35 percent open water. They postulated that the reduced role of fragmentation in structuring the nekton community in fresh and intermediate marshes was potentially related to the greater abundance of SAV (Hitch et al. 2011). In the current study, salinity and fragmentation conditions were within the range reported by Hitch et al. (2011).

Despite high rates of land loss and marsh fragmentation, Louisiana's coastal wetlands have remained a productive system, supporting 21 percent of all commercial fish and shellfish landings in the contiguous United States (Chesney et al. 2000). In this area of Louisiana, which is susceptible to wide salinity fluctuations, it is possible that the presence of SAV could lessen the effects of high fragmentation upon nekton communities, prior to total marsh loss. The measured higher fish and shrimp abundances in SAV than marsh edge in the present study suggests the importance of understanding the process of emergent marsh fragmentation, subsequent changes in SAV, and SAV habitat value for commercially important fish and shellfish species. Understanding the extent to which SAV could compensate for marsh loss in areas of rapid disaggregation, such as Terrebonne Basin, is critical to providing accurate scientific support for future management and restoration decisions for Louisiana and the Gulf Coast.

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