

# Nekton density patterns and hurricane recovery in submerged aquatic vegetation, and along non-vegetated natural and created edge habitats

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## ARTICLE INFO

### Article history:

Received 17 May 2011

Accepted 7 December 2011

Available online 14 December 2011

### Keywords:

SAV  
mesohaline  
nekton  
fishery habitats

## ABSTRACT

We compared nekton habitat value of submerged aquatic vegetation, flooded non-vegetated natural and man-made edge habitats in mesohaline interior marsh areas in southwest Louisiana using a 1-m<sup>2</sup> throw trap and 3-mm bag seine. When present, SAV habitats supported close to 4 times greater densities and higher species richness of nekton as compared to either natural or man-made edge habitats, which supported similar densities to one another. Three species of concern (bayou killifish, diamond killifish, chain pipefish) were targeted in the analysis, and two of the three were collected almost entirely in SAV habitat. During the course of the study, Hurricanes Ike and Gustav passed directly over the study sites in September 2008. Subsequent analyses indicated significant reductions in resident nekton density 1-mo post hurricanes, and only limited recovery 13-mo post-hurricane. Possible alteration of environmental characteristics such as scouring of SAV habitat, deposition of sediment over SAV, edge erosion and marsh loss, and extended high salinities may explain these lasting impacts.

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## 1. Introduction

Debate over the relative value of dominant shallow-water estuarine habitat types in support of nekton productivity remains a central issue affecting fisheries management and coastal restoration. Estuaries are composed of an assortment of shallow-water habitat types (i.e., salt marsh, oyster reefs, submerged aquatic vegetation, non-vegetated bottom), many of which have been identified as extremely productive areas that support dense populations of nekton (e.g., Weinstein, 1979; Boesch and Turner, 1984; Kneib, 1997; Minello, 1999; Minello et al., 2003; Shervette and Gelwick, 2008; Stunz et al., 2010). In the northern Gulf of Mexico, extensive coastal marsh loss affects both the amount and location of all of the shallow-water habitat types. Within this changing landscape, efforts to protect, enhance and restore habitat further affect the distribution of habitat types across the coast. For management and restoration of these habitats, the relative value of these changing and created habitats is of increasing importance given the scale of coastal restoration in the northern Gulf of Mexico.

Interhabitat comparisons are critically important in helping to define conservation priorities, but results are rarely comparable

between studies, and parameters of interest vary depending on the management question of interest. For example, at the species level, Minello (1999) examined data from over 20 studies taken from six habitat types in Texas and Louisiana and concluded that each of the six habitat types was of highest relative importance for at least one species. At the community level, studies often rank relative value of habitats based on the tenet that high animal densities indicate high quality or preferred habitat, and while conclusions vary, they tend to rank habitats providing structure (i.e., submerged aquatic vegetation, oyster reefs) above those without structure (i.e., non-vegetated bottom) (Baltz et al., 1993; Rozas and Minello, 1998; Plunket and La Peyre, 2005; Shervette and Gelwick, 2008; Stunz et al., 2010).

Mixed within this diverse assortment of shallow-water habitat types are man-made or enhanced habitats. There remains much uncertainty as to how well these restored or created habitats function in comparison to their natural counterparts. For nekton in particular, conclusions differ as to the equivalency of these created habitats with some study results suggesting equivalency based on density, abundance, biomass, or growth of nekton, and some finding that the created habitats fail to provide equivalent services at the time each study was conducted (Minello and Webb, 1997; Minello, 2000; Rozas and Minello, 2001a,b; Bush Thom et al., 2004; La Peyre et al., 2007; Zeug et al., 2007; Llewellyn and La Peyre, 2010). Given the substantial investment of effort and money in restoration, enhancement and creation of habitats,

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relative interhabitat comparisons that include both “natural” and man-made habitats are essential in determining relative habitat values and helping set conservation priorities (Beck et al., 2001).

In southwest Louisiana, numerous management and restoration projects target the enhancement of SAV beds and the creation of marsh edge (LCPRA, 2007). However, few published studies have compared nekton assemblage between SAV beds, natural and man-made marsh edge habitats to identify priorities for either protection or restoration. We use the term “natural” to refer to habitats that were not intentionally created by humans; “man-made” edges are those created through terracing projects in marshes, or levees. Specific objectives of our study were to quantify and compare nekton assemblages among naturally occurring submerged aquatic vegetation beds, natural marsh edges and man-made marsh edge (<1 m on the water side of the water–marsh interface composed of flooded mud-bottom) in southwest Louisiana using multiple measures including nekton density, abundance, biomass, assemblage composition, and abundance of three listed species of concern (*Syngnathus louisianae*, *Fundulus pulvereus*, *Adinia xenica*) (Lester et al., 2005). We also examined if these observed patterns varied seasonally. Furthermore, Hurricanes Ike and Gustav impacted our sites during the study which allowed us to compare habitat recovery and nekton assemblage 12-mo pre, 1-mo post and 13-mo post-hurricane.

## 2. Methods

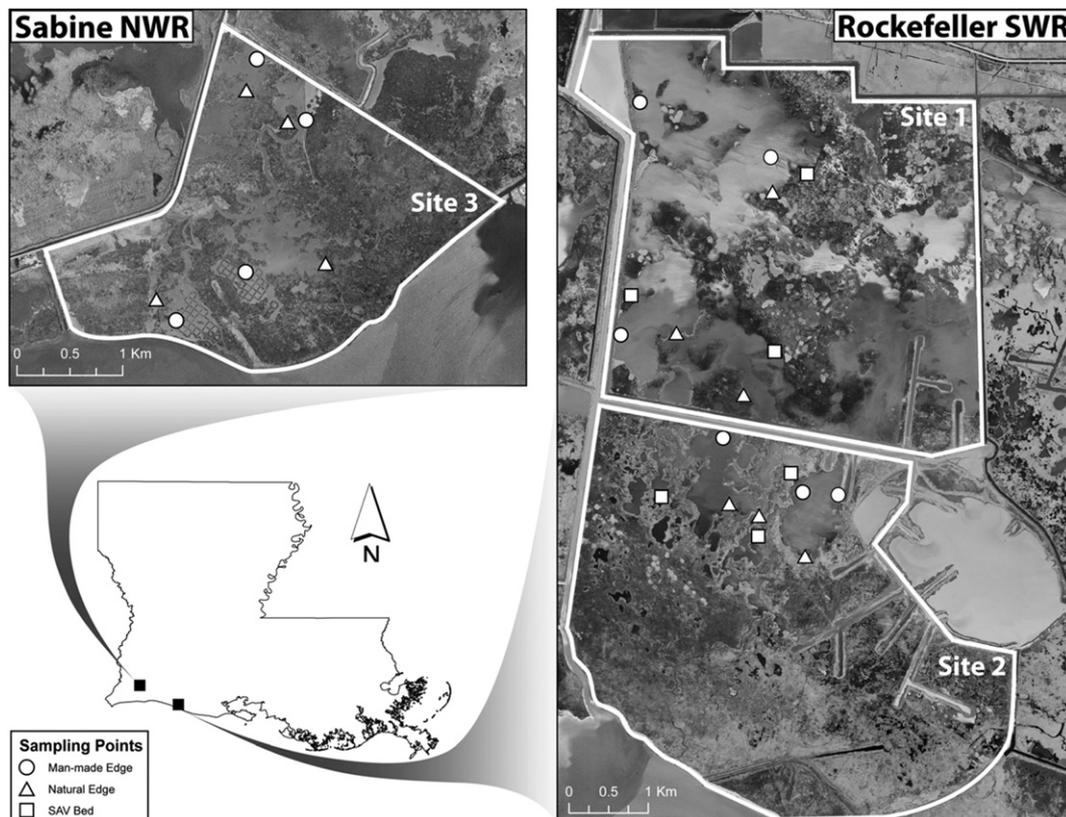
### 2.1. Study area

Sites were selected at three study units, two located at Rockefeller State Wildlife Refuge (RWR; 29°40′30″N, 92°48′45″W) and one located at Sabine National Wildlife Refuge (SWR; 29°54′N,

93°32′W) in southwest Louisiana (Fig. 1). All sites are brackish water with long-term salinity ranging between 8 and 15 (LOCPR, 2011). Site 1 is located in Unit 4 of RWR, which is a 2,400-ha impoundment managed via two variable-crest flap-gated structures. The area is dominated by saltmeadow cordgrass *Spartina patens* marsh (Flynn et al., 1999). *Ruppia maritima*, *Potamogeton pusilus*, and *Myriophyllum spicatum* occur in this area (Chabreck, 1970; Gossman, 2005). Site 2 is located in Unit 5 of RWR, which is a 1,982 ha impoundment directly south of Unit 4. The area is composed of *S. patens* dominated marsh. Levees are constructed around 3 sides of the impoundment, while the southern end is a broad beach rim at the Gulf of Mexico. *R. maritima* and *P. pusilus* occur in this unit (Chabreck, 1970; Gossman, 2005). Site 3 is located in SWR, south of Hog Island Gully and along the western edge of Lake Calcasieu. The marsh is dominated by *Spartina alterniflora*. The area includes terraces built in 1990. Several species of SAV are reported in the shallow water areas (*R. maritima*, *Halodule wrightii*, *Thalassia testudinum*) (LDNR, 1993).

### 2.2. Sampling design

The three study sites were sampled using a stratified random sampling design. Within each study site, triplicate sample sites were randomly selected within each of the three pre-identified habitat types (SAV, natural edge, man-made edge). Sample sites were a minimum of 500 m from one another, and SAV sites were a minimum of 100 m from a shoreline edge of any kind. Samples were taken in June and October 2007, January, March, June, and October 2008 and October 2009. The 2009 sampling was added because our sites experienced a direct hit from both Hurricanes Gustav and Ike on Sept. 1 and Sept 13, 2008 respectively. October 2008 sampling was 1 month post-hurricane while October 2009 sampling occurred 13



**Fig. 1.** Study site locations in southwest Louisiana. All study sites were located in interior mesohaline marsh. Study sites 1 and 2 were both located at Rockefeller State Wildlife Refuge. Study site 3 was located at Sabine National Wildlife Refuge.

months post-Hurricane. During several sample periods (Winter 2008, Spring 2008, Fall 2008, Fall 2009), SAV was not detectable at several of our study sites and thus no SAV samples were taken. In total, 157 throw trap and 157 seine samples were taken (63 natural edge, 63 man-made edge, 31 SAV for each gear type described below). All samples were taken during daylight hours.

### 2.3. Environmental characteristics

Salinity, temperature ( $^{\circ}\text{C}$ ), and dissolved oxygen ( $\text{mg L}^{-1}$ ) were measured with a YSI model 556 water quality meter (Yellow Springs Instruments, Yellow Springs, OH) at each sample point. Turbidity (NTU) was measured with a Turner Designs Aquafluor turbidimeter (Turner Designs, Sunnyvale, CA). Water depth was determined by calculating the mean of three random depth measurements (cm) taken within each throw trap sample. Water levels were taken from nearby continuous data recorders (CRMS 0581, 0685; LOCPR, 2011) and used to calculate marsh flooding status (flooded, not flooded). Soil cores were collected for organic matter content and bulk density determination. Three 10-cm diameter soil cores were collected from the top 5 cm of soil at each sampling point. Cores were stored on ice until processing. Upon return to the laboratory, the soil cores from each sampling point were homogenized into one composite sample. Composite samples were placed in crucibles and dried at  $60^{\circ}\text{C}$  in a forced air drying oven to constant weight. The samples were then ground with a mortar and pestle and split into 5 sub-samples. The sub-samples were weighed to the nearest 0.001 g (initial dry weight), fired in a muffle furnace at  $500^{\circ}\text{C}$  for 4 h, and weighed again (final dry weight). Percent organic matter was calculated as: % organic matter =  $[1 - (\text{final dry weight}/\text{initial dry weight})] \times 100$ .

All submerged aquatic vegetation (SAV) was collected from each SAV habitat type throw trap samples only; marsh edge samples categorically excluded SAV. Prior to nekton removal, all SAV was collected by hand, and placed on ice for transport to the laboratory where they were sorted according to species, dried in a forced air drying oven at  $60^{\circ}\text{C}$  to constant weight, and weighed to the nearest 0.001-g dry weight to determine SAV biomass ( $\text{g m}^{-2}$ ). Emergent marsh vegetation was sampled within 1 m of the water's edge near each marsh edge (natural and created) sample point only. Marsh edge vegetation biomass, species composition, and percent cover were quantified at each sample site using three randomly thrown  $0.25\text{ m}^2$  quadrats. Samples were returned to the laboratory where they were sorted according to species, dried in a forced air drying oven at  $60^{\circ}\text{C}$  to constant weight and weighed to the nearest 0.01 g dry weight to determine biomass ( $\text{g m}^{-2}$ ).

### 2.4. Nekton

Nekton was quantitatively sampled at each sample station with a  $1\text{-m}^2$  throw trap and with a bag seine. The seine consisted of a 5-m long by 2-m deep bag seine with 3-mm square delta mesh. The seine was swept parallel to the marsh edge along the 10-m microhabitat, and in a random 10 m line within SAV sites. The trap consisted of a  $1\text{-m} \times 1\text{-m} \times 0.66\text{-m}$  aluminum frame with 1.6-mm knotless nylon mesh sides. To facilitate sampling in water greater than 0.66 m deep the nylon mesh was extended above the frame to a total height of 1.25 m. A  $1\text{-m}^2$  PVC square was integrated into the top of the extended netting and buoyed by net floats. The interior of the throw trap was swept with a 1-m wide bar seine (1.6-mm mesh) to clear all nekton from the trap. The trap was considered cleared when 5 consecutive sweeps of the bar seine yielded no organisms. Samples were placed on ice for transport to the laboratory, where they were frozen until processing.

Upon returning to the laboratory, samples were sorted, identified to species or lowest feasible taxon, measured, counted to determine density (individuals  $\text{m}^{-2}$ ), and weighed to determine biomass ( $\text{g m}^{-2}$ ). Fish and shrimp were measured to the nearest 0.1-mm total length and crabs were measured to the nearest 0.1-mm carapace width. All nekton were weighed to the nearest 0.001-g wet-weight using an Ohaus Adventurer model top-loading laboratory balance (Ohaus Corp., Pinebrook, NJ).

## 3. Data analyses

All data were tested for normality, by examining model residuals, and homogeneity of variance. Subsequent logarithmic ( $\log_{10}(x + 1)$ ) transformation was necessary only for nekton density, vegetation biomass and SAV biomass. Data are reported as mean  $\pm$  SE, and significance level used was an alpha level of 0.05 unless indicated otherwise. All nekton data were analyzed separately by gear type. Seasons were defined as winter (December, January, February), spring (March, April, May), summer (June, July, August) and fall (September, October, November). However, because of the hurricanes passing in fall 2008, all sample periods (season, year) were analyzed separately and seasons were not grouped by years for analysis.

### 3.1. Environmental variables

Multivariate analysis of variance (MANOVA) was used to test whether environmental habitat characteristics (salinity, temperature ( $^{\circ}\text{C}$ ), DO ( $\text{mg L}^{-1}$ ), turbidity (NTU), water depth (cm), soil bulk density ( $\text{g cm}^{-3}$ ), SAV biomass ( $\text{g m}^{-2}$ ), emergent vegetation biomass ( $\text{g m}^{-2}$ ), compared simultaneously, differed among habitats and sample periods (season and year). ANOVA with Student-Newman-Keuls (SNK) tests were conducted on individual variables following significant MANOVA results ( $p < 0.05$ ; soil bulk density ( $\text{g cm}^{-3}$ )).

### 3.2. Nekton species abundance, diversity and biomass

All nekton data were analyzed separately by gear type. Nekton density and CPUE were highly correlated with nekton biomass, so only density data are presented. Repeated measures ANOVA was used to test whether nekton abundance (seine), density (throw trap), species richness, species diversity ( $H'$ ), and individual abundance of the three species of concern (*S. louisianae*, *F. pulvereus*, *A. xenica*) differed among habitat types (man-made edge, natural edge, SAV), and marsh flooded status (flooded, not flooded) blocking on study unit. Significance levels were adjusted using the Bonferroni algorithm to account for the use of response variables in multiple tests. Total CPUE was run with and without the dominant species *Palaeomonetes pugio* included ( $\sim 50\%$  total overall abundance).

Multivariate analyses of nekton communities were performed for each gear type, by habitat and sample period, on a full species abundance matrix. A two-way crossed analysis of similarity (ANOSIM) was performed to test for differences in habitat type (SAV, natural edge, man-made edge) and sample period (season and year) using PRIMER software (Clarke and Gorley, 2006). ANOSIM was performed on a Bray–Curtis dissimilarity matrix computed on the fourth-root transformed abundances on  $\log(x + 1)$  transformed data. When significant effects were found, SIMPER analysis was performed to examine which species were most responsible for similarities within and between groups.

Canonical correlation analysis (CCA) was performed on the full species abundances to examine the nekton assemblages along with environmental data listed in Table 1.

**Table 1**

Environmental variables by season and year. There were no significant differences by habitat type. SAV and emergent vegetation were not compared among all habitat types; SAV habitats did not include emergent vegetation and edge habitats did not include SAV. Mean (SE) are presented for each sample period. In gray are fall sample periods used to compare Hurricane effects (Fall 2008 1 mo- post Hurricanes Ike and Gustav; Fall 2009: 13-mo post Hurricanes Ike and Gustav. ND indicates no data were collected due to the absence of submerged aquatic vegetation.

	Summer 2007	Fall 2007	Winter 2008	Spring 2008	Summer 2008	Fall 2008	Fall 2009
<b>SAV habitat</b>							
Salinity	8.0 (1.5)	4.9 (2.0)	ND	ND	11.0 (2.7)	ND	ND
Temperature (°C)	29.0 (0.9)	28.0 (0.7)	ND	ND	29.5 (0.5)	ND	ND
DO (mg L <sup>-1</sup> )	3.7 (0.6)	4.5 (0.7)	ND	ND	3.3 (0.3)	ND	ND
Turbidity (NTU)	12.1 (2.4)	0.8 (0.4)	ND	ND	1.2 (0.3)	ND	ND
Water depth (cm)	31.7 (2.6)	44.2 (3.6)	ND	ND	30.8 (1.8)	ND	ND
Soil bulk density (g cm <sup>-3</sup> )	0.1 (0.0)	0.3 (0.0)	ND	ND	0.3 (0.0)	ND	ND
SAV biomass (g m <sup>-2</sup> )	0.1 (0.0)	0.2 (0.1)	ND	ND	0.1 (0.0)	ND	ND
Emergent vegetation (g m <sup>-2</sup> )	0	0	ND	ND	0	ND	ND
<b>Natural edge habitat</b>							
Salinity	13.7 (1.8)	11.0 (2.5)	14.0 (2.0)	10.4 (1.2)	12.2 (1.7)	19.2 (0.2)	16.4 (2.2)
Temperature (°C)	28.5 (0.5)	24.2 (1.4)	18.2 (0.1)	27.0 (0.5)	29.6 (0.4)	18.2 (0.4)	25.8 (0.3)
DO (mg L <sup>-1</sup> )	3.9 (0.3)	11.9 (5.4)	4.4 (0.3)	5.5 (0.2)	4.1 (0.3)	14.2 (8.2)	4.8 (0.7)
Turbidity (NTU)	9.3 (1.1)	5.9 (2.0)	8.4 (3.3)	6.2 (2.0)	2.0 (0.6)	8.1 (1.2)	.
Water depth (cm)	31.8 (1.9)	33.6 (3.6)	17.0 (2.4)	16.0 (2.7)	27.1 (2.3)	42.8 (2.3)	39.7 (2.9)
Soil bulk density (g cm <sup>-3</sup> )	0.2 (0.0)	0.3 (0.0)	0.3 (0.1)	0.3 (0.0)	0.3 (0.0)	0.3 (0.0)	0.3 (0.0)
SAV biomass (g m <sup>-2</sup> )	0	0	0	0	0	0	0
Emergent vegetation (g m <sup>-2</sup> )	2001.7 (357.8)	1789.5 (380.9)	1192.7 (297.7)	776.9 (173.2)	746.4 (98.2)	1369.6 (246.5)	1502.6 (597.4)
<b>Created edge habitat</b>							
Salinity	13.5 (1.9)	9.8 (2.0)	12.5 (2.1)	10.4 (1.4)	11.6 (1.7)	18.9 (0.3)	15.8 (2.0)
Temperature (°C)	28.9 (0.5)	24.5 (1.4)	17.9 (0.2)	26.8 (0.6)	29.7 (0.5)	18.5 (0.2)	25.6 (0.3)
DO (mg L <sup>-1</sup> )	4.5 (0.4)	6.1 (0.4)	4.3 (0.4)	5.0 (0.5)	4.1 (0.5)	6.0 (0.1)	4.8 (0.4)
Turbidity (NTU)	11.6 (2.6)	1.9 (0.4)	6.0 (1.2)	6.9 (2.1)	2.7 (0.5)	4.9 (0.9)	.
Water depth (cm)	31.5 (2.7)	35.3 (5.2)	16.0 (1.9)	18.3 (3.7)	28.9 (4.7)	47.6 (4.4)	44.8 (2.8)
Soil bulk density (g cm <sup>-3</sup> )	0.2 (0.0)	0.5 (0.1)	0.4 (0.0)	0.4 (0.0)	0.4 (0.0)	0.5 (0.1)	0.5 (0.1)
SAV biomass (g m <sup>-2</sup> )	0	0	0	0	0	0	0
Emergent vegetation (g m <sup>-2</sup> )	1743.8 (439.0)	2201.4 (435.9)	1145.5 (262.6)	645.1 (128.4)	798.4 (144.0)	1485.1 (371.3)	1056.1 (374.6)

### 3.3. Hurricane effects

To explicitly examine the immediate and longer term effects of the passage of Hurricanes Ike and Gustav, we compared fall 2007, 2008 and 2009 data separately. SAV samples were only available in fall 2007, so only edge samples were compared. To test explicitly for hurricane effects, fall environmental variables were examined separately using a two-factor MANOVA (year, habitat), blocking on study unit, followed by ANOVA with SNK for significant results. Comparisons of nekton variables using the two-factor ANOVA indicated no differences between natural and man-made edge so further analyses were completed as a two-factor ANOVA (factors = year, flooded status), blocking on study unit. LS Means was used when significant differences were found. Multivariate analyses of nekton communities were performed by year on a full species abundance matrix using PRIMER software (Clarke and Gorley, 2006). CCA was performed on the full species abundances to examine the nekton assemblages along with environmental data.

## 4. Results

### 4.1. Habitat measures

The only significant habitat type difference was in soil characteristics ( $p < 0.0001$ ). Mean bulk density differed significantly by habitat type and was highest at man-made edge habitat ( $0.42 \pm 0.02$  g cm<sup>-3</sup>) as compared to natural edges ( $0.29 \pm 0.01$  g cm<sup>-3</sup>) or SAV ( $0.24 \pm 0.02$  g cm<sup>-3</sup>) habitats. Percent organic matter and bulk density were highly and negatively correlated.

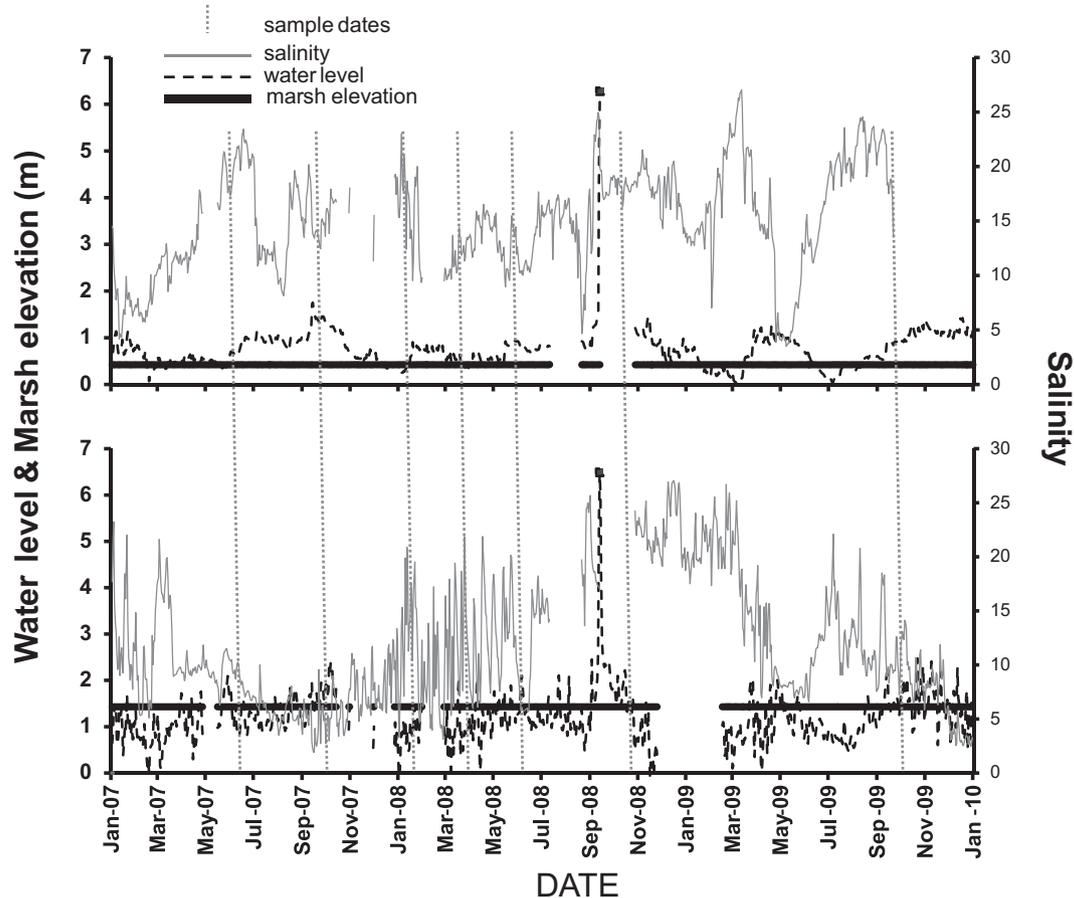
There were no significant habitat differences for salinity, water depth, temperature, dissolved oxygen or water depth (Table 1, Fig. 2), but all varied by sample period, following expected seasonal trends.

Between marsh edge habitat types, emergent vegetation did not vary. There were seasonal differences with greatest live biomass in the summer and greatest dead biomass in the winter. Submerged aquatic vegetation biomass was only measured in SAV habitats as it was avoided in edge samples in order to avoid confounding effects, so analysis was performed to evaluate differences only between sample periods. SAV was only located within our study areas in Summer 2007, Fall 2007 and Summer 2008 sample periods. There were no significant differences in SAV biomass between sample periods when SAV was collected (Summer 2007, Fall 2007, Summer 2008).

### 4.2. Nekton

#### 4.2.1. Species assemblages and composition - throw trap

A total of 157 throw trap samples were collected over 7 sampling periods. In total, 6,655 individuals, consisting of thirty-six species of fish and invertebrates were collected using the throw trap (Table 2). The most abundant organisms were daggerblade grass shrimp (*P. pugio*), accounting for 42% of the total catch by abundance. Fifty-two percent of the total abundance consisted of 9 other species (*Menidia beryllina*, *Poecilia latipinna*, *Cyprinodon variegatus*, *Farfantepenaeus aztecus*, *Callinectes sapidus*, *Anchoa mitchilli*, *Litopenaeus setiferus*, *Gambusia affinis*, *Lucania parva*). The remaining species accounted for less than 6% of total catch. Repeated measures ANOVA analyses indicated that total nekton density varied among habitat types, within ( $F_{2, 131} = 24.1$ ,  $p < 0.0001$ ) and across sample periods (with and without *P. pugio*) ( $F_{4, 262} = 14.2$ ,  $p < 0.0001$ ), but not by marsh flooded status ( $p = 0.6137$ ). Specifically, nekton densities measured from SAV habitats in summer and fall 2007 were significantly greater than those in natural or man-made edge habitats, but not significantly different from those measured in SAV habitats in summer 2008 (Table 2). Species richness did not



**Fig. 2.** Salinity, water level and marsh elevation data taken from on-site continuous data recorders are presented for the study sites, Hurricanes Gustav (9/1/2008) and Ike (9/13/2008) passed directly over the sites during the course of the study. Data from CRMS Stations 0581 and 0685 located within each refuge were used (LOCPR 2011: Retrieved from Strategic Online Natural Resource Information System (SONRIS) database. <http://dnr.louisiana.gov/crm/coastres/monitoring.asp>).

vary by habitat, but diversity ( $H'$ ) was found to be significantly lower in man-made edge habitat as compared to SAV habitat ( $p = 0.05$ ;  $0.84 \pm 0.05$  vs  $1.13 \pm 0.1$ ). Species diversity was also lower in natural edge ( $H' = 0.88 \pm 0.06$ ) as compared to SAV habitat but not significant ( $p = 0.07$ ).

A two-way crossed analysis (ANOSIM, PRIMER) indicated differences in species composition only by sample period and not by habitat type. (Global  $R = 0.149$ ,  $p = 0.001$ ). Specifically, the fall 2008 assemblages, immediately following the two hurricanes, differed significantly from all other sample periods, with the exception of fall 2009, but fall 2009 did not differ from any other sample period. A SIMPER analysis was performed to test which species were mostly responsible for similarities within sample periods, and differences between sample periods. Differences between fall 2008 and other sample periods were largely due to fall 2008 having lower densities of *P. pugio* and *L. setiferus*, with these species accounting for over 30% of the difference in all cases. Other species that consistently were in the top five species (50% of change) explaining differences between sample periods included *C. sapidus*, *F. aztecus* and *A. mitchilli*.

#### 4.2.2. Species assemblages and composition – seine

Over 49,400 individuals of 35 species of fish and invertebrates were collected using seine gear during this study. Of these, 54% of the sample consisted of the daggerblade grass shrimp, and over 42% consisted of 15 other species (*M. beryllina*, *P. latipinna*, *C. variegatus*, *F. aztecus*, *C. sapidus*, *A. mitchilli*, *L. setiferus*, *Micropogonias*

*undulatus*, *Brevoortia patronus*, *G. affinis*, *Mugil cephalus*, *Mugil gulosus*, *Gobiosoma bosc*, *L. parva*, *Sciaenops ocellatus*). The remaining species all accounted for less than 4% of the total catch. Repeated measures ANOVA indicated that total nekton abundance varied among habitat types, within ( $F_{2, 149} = 405.11$ ) and across sample periods (with and without *P. pugio*) ( $F_{4, 298} = 20.4$ ,  $p < 0.0001$ ). Nekton abundances in SAV samples were approximately 4 times greater as compared to either edge type habitats (SAV:  $1131.3 \pm 206.7$ ; natural edge:  $250.2 \pm 42.7$ ; man-made edge:  $148.5 \pm 23.0$ ). Furthermore, there were significant differences in species richness, with higher richness in SAV samples ( $9.4 \pm 0.8$ ) as compared to either edge type (natural:  $6.3 \pm 0.3$ ; man:  $5.7 \pm 0.3$ ). Diversity ( $H'$ ) did not differ significantly by habitat or sample period.

A two-way crossed analysis (ANOSIM, PRIMER) indicated differences in species composition only by sample period and not by habitat type. (Global  $R = 0.267$ ,  $p = 0.001$ ). Specifically, the fall 2008 and 2009 assemblages, following the two hurricanes, differed significantly from all other 2008 sample periods (winter, spring, summer) which differed from the 2007 summer sample periods. A SIMPER analysis was performed to test which species were mostly responsible for similarities within sample periods, and differences between sample periods. Differences between fall 2008 and 2009 and other sample periods were largely due to fall 2008 and 2009 having lower densities of *P. pugio*, *L. setiferus*, *M. beryllina*, *A. mitchilli* and *C. sapidus* with these species accounting for over 50% of the difference in all cases.

**Table 2**

Mean (SE) by habitat type and sample period (season, year) for throw-trap catch data. Seine data followed the same trends and are not presented. Nekton density, richness, diversity and density of dominant species captured are presented. In gray are fall edge data used for Hurricane effect comparisons. ND indicates no data were collected due to the absence of submerged aquatic vegetation at the study sites.

	Summer 2007	Fall 2007	Winter 2008	Spring 2008	Summer 2008	Fall 2008	Fall 2009
<b>SAV habitat</b>							
Density (#m <sup>-2</sup> )	145.5 (46.9)	176.8 (40.5)	ND	ND	98.7 (42.3)	ND	ND
Residents	137.0 (46.0)	161.8 (47.0)	ND	ND	93.2 (43.1)	ND	ND
Transients	8.5 (6.1)	15.0 (19.9)	ND	ND	5.5 (2.4)	ND	ND
Richness	6.2 (0.5)	6.5 (0.5)	ND	ND	8 (0.7)	ND	ND
H'	0.9 (0.1)	1.1 (0.1)	ND	ND	1.3 (0.2)	ND	ND
<i>Anchoa mitchilli</i>	0.2 (0.2)	0	ND	ND	0	ND	ND
<i>Cyprinodon variegatus</i>	1.8 (1.4)	6.3 (3.6)	ND	ND	3.8 (1.5)	ND	ND
<i>Gambusia affinis</i>	1.3 (1.0)	9.3 (4.5)	ND	ND	16.0 (15.4)	ND	ND
<i>Lucania parva</i>	3.5 (2.5)	3 (1.7)	ND	ND	19.2 (12.6)	ND	ND
<i>Menidia beryllina</i>	7.5 (3.3)	1.7 (1.2)	ND	ND	4.8 (4.8)	ND	ND
<i>Poecelia latipinna</i>	2.8 (1.6)	83.2 (41.2)	ND	ND	13.5 (11.8)	ND	ND
<i>Callinectes sapidus</i>	6.2 (4.4)	10.2 (9.6)	ND	ND	2.2 (0.8)	ND	ND
<i>Litopenaeus setiferus</i>	0.8 (0.8)	8.5 (8.3)	ND	ND	0.8 (0.7)	ND	ND
<i>Palaeomonetes pugio</i>	116.5 (40.9)	51.8 (14.5)	ND	ND	32.3 (20.6)	ND	ND
<i>Penaeus aztecus</i>	0.8 (0.8)	0.8 (0.7)	ND	ND	1.3 (1.0)	ND	ND
<b>Natural edge habitat</b>							
Density (#m <sup>-2</sup> )	18.5 (7.1)	65.3 (17.4)	27.5 (9.3)	30.8 (8.8)	32.0 (5.4)	12.5 (4.8)	46.1 (15.8)
Residents	15.8 (8.9)	49.0 (19.0)	15.5 (4.7)	17.2 (6.2)	25.7 (5.6)	2.7 (1.3)	15.6 (7.8)
Transients	5.8 (1.9)	16.3 (6.7)	12.0 (5.2)	13.6 (4.7)	6.3 (1.8)	9.8 (3.6)	35.4 (17.0)
Richness	3.1 (0.5)	5.4 (0.7)	3.1 (0.4)	3.4 (0.7)	4.6 (0.7)	3.4 (0.7)	19.3 (15.8)
H'	1.0 (0.2)	0.9 (0.2)	0.7 (0.1)	1.0 (0.2)	0.9 (0.1)	1.0 (0.2)	0.7 (0.1)
<i>A. mitchilli</i>	1.2 (0.5)	1.3 (0.6)	1.8 (1.8)	0.7 (0.6)	0	1.1 (0.6)	6.2 (4.1)
<i>C. variegatus</i>	3.0 (2.8)	0.9 (0.8)	1.0 (0.7)	0	3.7 (2.4)	0	1.7 (1.7)
<i>G. affinis</i>	0	1.1 (0.7)	0	0.2 (0.2)	1.2 (0.6)	0	0
<i>L. parva</i>	0	2.7 (2.1)	0.7 (0.6)	1.2 (1.2)	0.7 (0.4)	0	0
<i>M. beryllina</i>	4.2 (3.3)	1.8 (1.2)	0	0	1.4 (0.7)	1.3 (1.3)	5.6 (4.8)
<i>Poecelia latipinna</i>	0.3 (0.3)	7.9 (7.5)	0	3.7 (3.5)	2.6 (1.7)	0	0
<i>C. sapidus</i>	0.8 (0.4)	3.2 (1.6)	1.0 (0.3)	2.8 (1.1)	0.9 (0.4)	2.1 (0.8)	2.7 (1.6)
<i>L. setiferus</i>	2.6 (1.4)	10.9 (4.9)	0	5.5 (2.4)	0.1 (0.1)	4.2 (2.2)	32.1 (13.7)
<i>P. pugio</i>	7.2 (2.5)	23.3 (7.9)	13.1 (4.6)	11.2 (4.2)	13.1 (4.3)	0.2 (0.2)	5.7 (3.8)
<i>P. aztecus</i>	0.7 (0.4)	1.3 (0.7)	0	0	4.7 (1.4)	1.4 (1.0)	0.7 (0.5)
<b>Created edge habitat</b>							
Density (#m <sup>-2</sup> )	14.3 (4.4) B	29.3 (12.3) B	34.0 (10.7) B	19.1 (6.3) B	25.1 (8.4) B	14.3 (3.2) B	19.3 (3.3) B
Residents	9.2 (5.1)	29.0 (14.8)	28.9 (8.9)	13.0 (5.4)	19.2 (8.3)	3.8 (1.7)	11.6 (3.8)
Transients	5.1 (1.5)	5.4 (3.2)	5.1 (2.7)	6.1 (2.7)	5.9 (1.8)	10.5 (1.9)	7.7 (2.5)
Richness	2.6 (0.3)	3.7 (0.3)	2.2 (0.4)	2.2 (0.7)	4.4 (0.7)	4.8 (0.9)	3.8 (0.6)
H'	0.7 (0.1)	0.7 (0.1)	0.5 (0.1)	0.7 (0.1)	1.0 (0.1)	1.2 (0.2)	1.0 (0.1)
<i>A. mitchilli</i>	1.7 (0.6)	0.1 (0.1)	0	0.5 (0.5)	0	2.4 (1.1)	2.0 (0.8)
<i>C. variegatus</i>	0	0	1.0 (1.0)	0	0	0	0.1 (0.1)
<i>G. affinis</i>	0.1 (0.1)	0	0	0.3 (0.3)	0	0	0
<i>L. parva</i>	0	0.1 (0.1)	0.8 (0.6)	0.1 (0.1)	3.5 (2.8)	0	0
<i>M. beryllina</i>	1.0 (0.7)	1.7 (0.9)	0.2 (0.2)	0	0.7 (0.6)	0.2 (0.1)	6.1 (3.0)
<i>Poecelia latipinna</i>	0	0	0	0	0.1 (0.1)	0	0
<i>C. sapidus</i>	0.2 (0.1)	0.8 (0.4)	1.4 (0.9)	2.4 (1.7)	1.6 (0.6)	3.0 (1.1)	0.9 (0.4)
<i>L. setiferus</i>	1.2 (0.9)	3.8 (2.3)	0	1.1 (1.0)	0.7 (0.4)	3.5 (0.9)	9.3 (3.9)
<i>P. pugio</i>	8.1 (4.6)	19.9 (12.4)	24.7 (8.2)	11.9 (4.9)	9.8 (3.8)	1.5 (1.3)	4.0 (1.4)
<i>P. aztecus</i>	1.1 (0.8)	0.1 (0.1)	0	0	2.3 (1.1)	1.4 (0.5)	0.1 (0.1)

#### 4.2.3. Species composition-environment relationships – throw trap

Patterns were similar between gear types, so only throw trap data results are presented. Canonical correlation analysis (CCA) indicates that differences in nekton assemblages were most strongly driven by the presence of SAV (57.8% of the species-environment relation; eigenvalue = 0.125; F-ratio = 5.284,  $p = 0.004$ ) (Table 3; Fig. 3). Salinity and temperature are the dominant differences along the second axis. *P. latipinna*, *Oligoplites saurus* and *F. pulvereus* were most closely associated with the SAV habitats.

#### 4.2.4. Species of concern

Individuals of three listed species of concern (Lester et al., 2005) were collected during this study. Two *S. louisianae* were caught in total; both in Summer 2007 in SAV habitat. Forty-seven *F. pulvereus* were collected, 45 of which were from SAV and two from natural edge habitat. Forty-three *F. pulvereus* were caught

during Fall 2007 and four were collected during Summer 2008. Eight *A. xenica* were collected in edge habitat; six from natural edge, and two from man-made edge. Five were caught in Spring 2008, and three in Winter 2008.

## 5. Hurricane effects

### 5.1. Environmental characteristics

Environmental characteristics from natural and man-made edge habitats collected during fall 2007, 2008 and 2009 were compared using a two-factor ANOVA (year, habitat). Data from SAV habitat were removed from this analysis because SAV was only present during fall 2007 (Table 2). There were no significant edge habitat differences, so only year was used in the final model. Salinity, temperature, water depth and vegetation differed significantly by year (Table 1). Salinity was highest in fall 2008, immediately after

**Table 3**  
List of species code for presentation of canonical correlation analysis (Fig. 3).

Code	Species name
AM	<i>Anchoa mitchilli</i>
AR	<i>Anguilla rostrata</i>
AX	<i>Adinia xenica</i>
BC	<i>Bairdiella chrysoura</i>
BP	<i>Brevoortia patronus</i>
CA	<i>Cynoscion arenarius</i>
CB	<i>Ctenogobius boleosoma</i>
CN	<i>Cynoscion nebulosus</i>
CR	Crawfish
CS	<i>Callinectes sapidus</i>
CV	<i>Cyprinodon variegatus</i>
DM	<i>Dormitator maculatus</i>
FG	<i>Fundulus grandis</i>
FP	<i>Fundulus pulvereus</i>
GA	<i>Gambusia affinis</i>
GB	<i>Gobiosoma bosc</i>
GO	<i>Gobionellus oceanicus</i>
LP	<i>Lucania parva</i>
LR	<i>Lagodon rhomboides</i>
LS	<i>Litopenaeus setiferus</i>
LX	<i>Leiostomus xanthurus</i>
MB	<i>Menidia beryllina</i>
MC	<i>Mugil cephalus</i>
MG	<i>Microgobius gulosus</i>
MP	<i>Myrophis punctatus</i>
MU	<i>Micropogonias undulatus</i>
OS	<i>Oligoplites saurus</i>
PA	<i>Farfantepenaeus aztecus</i>
PC	<i>Pogonias cromis</i>
PL	<i>Poecilia latipinna</i>
PP	<i>Palaemonetes pugio</i>
PS	<i>Pomatomus saltatrix</i>
RH	<i>Rhithropanopeus harrissii</i>
SL	<i>Syngnathus louisianae</i>
SO	<i>Sciaenops ocellatus</i>
SS	<i>Syngnathus scovelli</i>

passage of the two hurricanes, and lowest in fall 2007. Temperature was also significantly lower in 2008 as compared to the other years. Water depth measured at each sample point was greater in 2008 and 2009 as compared to 2007 but not significant when tested as covariate.

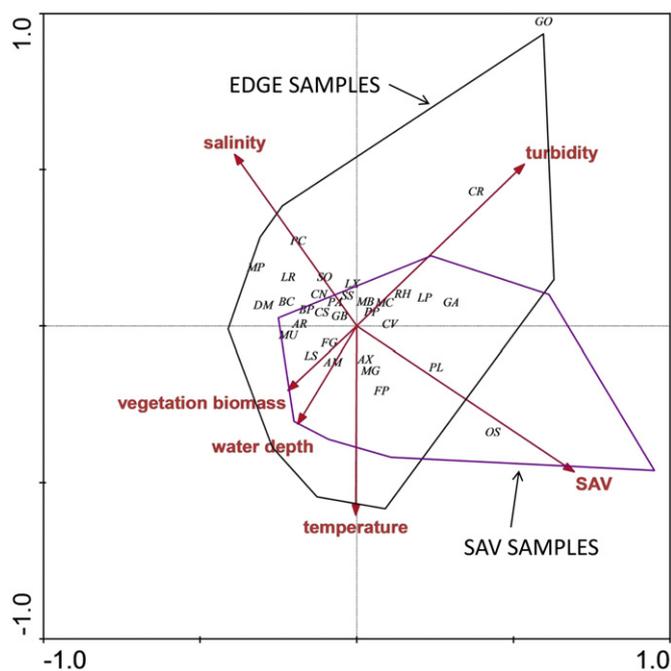
## 5.2. Nekton abundance and communities

Nekton density (ind m<sup>-2</sup>) at edge habitats was more than three as high in fall 2007 (Throw-trap (TT): 94.3 ± 17.4; Seine (S): 290.3 ± 89.9) as compared to fall 2008 (TT: 26.8 ± 4.8; S: 70.4 ± 11.4), with fall 2009 density falling in the middle range (TT: 65.4 ± 15.8; S: 120.3 ± 24.5) (Table 2). Most of the reduction in density was due to a reduction in resident species; transient abundances appeared to not be affected by the recent hurricane in 2008. Individual species response varied by gear type making it difficult to discern a clear pattern. For example, throw trap catches indicated notable decreases of *P. pugio* decreasing in edge habitats from 2007 (TT: 21.6 ± 7.2) to 2008 (TT: 0.9 ± 0.7) and beginning to increase in 2009 (TT: 4.9 ± 2.0), and *L. setiferus* increasing significantly in 2009 (TT: 19.7 ± 6.8) as compared to 2007 and 2008 (TT: 7.4 ± 2.7, 3.9 ± 1.2 respectively). In contrast, seine data indicate little change in abundances of either *P. pugio* (07: 24.9 ± 0.3; 08: 25.3 ± 0.4; 09: 20.9 ± 0.7) or *L. setiferus* (07: 64.6 ± 3.9; 08: 54.6 ± 1.0; 09: 65.3 ± 4.6) between the years. Seine data did however capture large increases in *P. latipinna*, *B. patronus* and *M. undulatus* which were present in 2008, but not in 2007 or 2009 (2008: 48.0 ± 0.01; 28.8 ± 1.0; 22.1 ± 0.6 respectively). While there were differences in overall catch rates, there were no nekton community differences between years for fall nekton data using either throw trap or seine data (ANOSIM, PRIMER: TT: Global  $R = 0.076$ ,  $P = 0.7$ ). Canonical correlation analysis (CCA) indicates that differences in nekton catch were most strongly driven by salinity (46.4% of the species–environment relation; eigenvalue = 0.16; F-ratio = 3.31,  $p = 0.05$ ). Water depth is the dominant influence on the second axis.

## 6. Discussion

When present, submerged aquatic vegetation habitats supported close to 4 times greater densities of nekton as compared to either natural or created marsh edge habitats, and tended to support a higher richness of species, including support of two estuarine species of concern. Nekton assemblages differed only by sample period, with the greatest difference in the sample taken 1-mo after Hurricanes Ike and Gustav crossed the sample areas resulting in significant reductions in dominant resident species only. Salinity and SAV biomass were the dominant habitat variables influencing species assemblages, both of which were significantly different at the study sites following passage of the two hurricanes which resulted in immediate higher salinity and a prolonged absence of SAV. These differences were detected up to 13-mo after the hurricanes indicating lasting effects from the hurricanes in these interior ponds. While the natural and created non-vegetated marsh edges supported nekton, most nekton species sampled were more abundant at SAV habitat when it was available, suggesting that SAV habitats should be a priority for conservation and protection of mesohaline shallow-water habitats.

In general, SAV habitat is assumed to be valuable because it provides both refuge from predators and a rich source of food for resident and estuarine dependent nekton (Orth et al., 1984; Rozas and Odum, 1988; Heck et al., 2003). The structural heterogeneity of SAV habitats provides a structural refuge from predators for juvenile nekton (e.g. Rozas and Odum, 1988; Woodley and Peterson, 2003). Our study found a four-fold increase in nekton density when SAV was present, regardless of salinity or marsh flood



**Fig. 3.** CCA for species–environment relationships for throw-trap nekton and habitat samples for all years and seasons. The box delineates samples taken from SAV habitats while the black box delineates samples taken from natural and man-made edge habitats. Table 3 indicates species codes used in this figure.

status, and 2 of the three estuarine species of concern were caught predominantly in SAV habitat (100% *S. louisianae*, 96% *F. pulvereus*). *S. louisianae* have known habitat preferences for SAV or estuarine seagrass beds, in coastal waters from Florida to Mexico (Hubbs et al., 1991), so its association with SAV is not surprising. Other studies in Louisiana and Texas over the last couple decades have found the chain pipefish along natural marsh edge in Barataria Bay, LA (La Peyre and Birdsong, 2005), and in low densities in a range of habitats including SAV and marsh edge (Minello, 1999). *F. pulvereus* is listed as a resident brackish marsh species, and appears to be more ubiquitous having been collected in SAV, vegetated edges, and inner marshes in Texas and Louisiana (Gunter, 1950; Minello, 1999; Bush Thom et al., 2004). Interestingly, we collected few *A. xenica*, which may not be surprising as in a metadata analysis, it was found in the highest densities in inner marsh samples (Minello, 1999), which we did not collect. Past studies have concluded that SAV habitats support greater nekton use than do shallow-water non-vegetated habitats (e.g. Castellanos and Rozas, 2001; Stunz et al., 2002; Kanouse et al., 2006; Rozas and Minello, 2006). Three studies have reported positive relationships between SAV and nekton density in oligohaline and mesohaline marshes (Kanouse et al., 2006; Rozas and Minello, 2010; Hitch et al., 2011).

An alternative structured habitat to SAV that is available to nekton regardless of water level, is that of the flooded mud-bottom adjacent to vegetated marsh edge. In comparing these mud bottoms with submerged aquatic vegetation in our study, we are comparing two habitats that are always available to nekton, but their use may be influenced by inundation of nearby marsh as nekton may assemble to this high quality ephemeral habitat (Rozas, 1995; Kneib, 2000; Castellanos and Rozas, 2001; Gillanders and Kingsford, 2002; Rozas et al., 2005; Piazza and La Peyre, 2007). Along the northern Gulf of Mexico, resident nekton species have been shown to congregate in shallow subtidal areas that provide earlier access to vegetated intertidal habitats during flood tides (Rozas and Zimmerman, 2000; Minello and Rozas, 2002). Sampling in this study was not restricted by water levels, and occurred over a range of water levels including flooded and non-flooded marsh conditions. Analysis failed to indicate an effect of marsh inundation on nekton density by habitat type suggesting that, regardless of the availability of other valuable emergent vegetation habitat, high nekton densities remain closely associated with SAV habitat, and nekton consistently use the non-vegetated marsh edge areas. Several studies completed in the northern Gulf of Mexico have concluded that vegetated habitats (i.e., SAV and vegetated marsh) may support similar densities of nekton (Rozas and Minello, 1998, 2006, 2010) when the vegetated marsh is inundated, although different species may assemble to the different habitats.

While management and restoration with an eye towards maximizing SAV may be a goal for supporting nekton in mesohaline environments, there is a paucity of information and understanding about the annual and seasonal cycles of submerged aquatic vegetation species in these environments. In fact, while some very early studies suggested two growing seasons for *R. maritima*, the dominant species in Louisiana brackish marshes (Joanen and Glasgow, 1965; Pulich, Jr. 1985), a recent study showed no clear seasonal pattern, nor the expected winter decline in SAV abundance (Merino et al., 2005). While it's difficult with our current understanding regarding expected SAV patterns in this region, the absence of SAV where SAV previously existed, for 13 months post-hurricanes Ike and Gustav indicates that physical scouring, sediment deposition and/or water quality impacts (i.e., salinity) from the hurricanes may be extremely destructive to SAV in these shallow-water interior ponds and have long lasting effects. Clearly, more specific work needs to be completed regarding SAV growth and distribution in order to provide managers with concrete actions for management

and restoration activities that produce valuable SAV habitat that can support nekton. Furthermore, there are limited data to compare the relative presence and potential value of SAV between mesohaline and oligohaline waters along the northern Gulf of Mexico, possibly due to its spatially and temporally limited presence (Merino et al., 2005, 2009).

While the difference in nekton density and catch per unit effort (CPUE) between natural and man-made edge habitats was not statistically significant, there was a clear trend with higher density and CPUE in the natural edge, and, interestingly, species of concern collected along edge habitats were predominantly collected along natural edge habitats. While a number of water quality, and geomorphological characteristics were compared to identify why there might be a difference, the only significant result was that soil percent organic matter was lower in the man-made edges. This finding is supported by numerous past studies which have found that created marshes, and their edges tend to have lower percent organic matter, even when all else appears equal. Differences in soil organic matter between natural and constructed marshes have been positively linked to differences in benthic infaunal communities (Moy and Levin, 1991; Sacco et al., 1994; Levin et al., 1996; Zeug et al., 2007). Located at the base of the estuarine food web, marsh infauna are an important component linking the primary production of the marsh to surrounding waters and are needed for a marsh to reach full functional equivalency (Sacco et al., 1994; Craft et al., 2003). While vegetation has been found to be equivalent in created and natural marshes within 3–5 years (Craft et al., 1999), benthic invertebrate communities and soil properties can take more than 15 years to develop (Craft et al., 1999). Restoration projects may consider means of boosting initial organic matter in created marshes and their edges, or inoculating edges with benthic invertebrate communities from donor areas.

### 6.1. Hurricane effects

Similar to past studies (Sallenger et al., 2006; Cahoon, 2006; Tomasko et al., 2006), lasting effects on the physical habitat were evident at some but not all of our sites. Land-water analysis using 2005 and 2008 post-hurricane data indicated minimal change in land:water ratio from a ratio of 2.44 to 2.3 at the Rockefeller site and a change in land:water from 2.7 to 2.63 at the Sabine site (LOCPR, 2011).

In addition to visible emergent vegetation and erosion impacts, lack of SAV at all of the sites post-hurricane may potentially be a result of the hurricanes; past research has found mixed results on large storm effects on SAV, with some finding no impacts (Byron and Heck, 2006), and others finding more longer-lasting effects resulting from either physical or salinity changes (Lapointe et al., 2006), or runoff related impacts (Carlson et al., 2010). Aside from potential physical scouring of SAV at our sites, which we were not able to document, significant immediate high salinity occurred that likely would have negatively impacted SAV survival and growth (Frazer et al., 2006). Specifically, salinity increased from  $10.4 \pm 1.6$  to a mean of  $19.1 \pm 0.2$  between 2007 and 2008 (immediately post-hurricanes) (Fig. 2; LOCPR, 2011). While porewater salinities were not taken in this study, other studies in coastal Louisiana have noted elevated porewater salinities in interior marsh ponds resulting from storm surges that appear to leach out over long time periods to maintain these elevated salinities beyond the period of the storm event (Tobias, 2010).

In contrast to past studies on hurricane impacts which indicate that most components of coastal systems, including the nekton communities, appear to be highly resilient to the acute effects of severe hurricanes (i.e. Burkholder et al., 2004; Greening et al., 2006; Switzer et al., 2006), we found that impacts on overall nekton

abundance extended to 13 mo post-hurricane with reduced numbers of resident nekton in all our samples. Differences in water levels by site and years failed to explain the reduced resident species numbers from 2007 to 2008, or the increase from 2008 to 2009. Changes in nekton communities in other studies, either short or long-term, appear to be related to storm impacts on salinity (Paerl et al., 2001; Switzer et al., 2006), dissolved oxygen (Tomasko et al., 2006; Engle et al., 2009), or physical scouring (Greenwood et al., 2007; Engle et al., 2009). However, most studies identify very short-term impacts (<3 mo), with nekton populations returning to pre-storm levels as salinity, or dissolved oxygen levels rebound. Interestingly, many of the studies conducted on the east coast of the United States showed lowered salinity events from the storms (i.e., rainfall run-off), with an immediate declines in marine species, which returned as salinity returned (e.g., Paerl et al., 2001; Switzer et al., 2006; but see; Andrews, 1973). Our sites were different in that the salinity drastically increased and remained high following the passage of the storm, thus maintaining the transient fish populations, but reducing our catch of resident fish. Furthermore, due to the nature of the interior ponds, and managed marsh areas, salinity did not recover to its pre-storm range until the end of 2009 (LOCPR, 2011). Thus, long-term salinity impacts, along with potential loss of SAV in the sample areas, or a combination of these factors may explain the longer term impacts of the hurricane on the nekton communities in our study.

## 7. Conclusions

With coastal Louisiana experience extensive loss and fragmentation of coastal marshes, along with extensive restoration activities, the potential impacts on nekton populations overall may be enormous. These potential impacts have been proposed to occur through several mechanisms including simply loss of productive habitat such as marsh and SAV (Hovel and Lipcius, 2001; Jackson et al., 2006; Long and Burke, 2007), but also through changes in the configuration of the landscape, including changes in the amount and type of edge habitat (i.e., Browder et al., 1985, 1989; La Peyre and Birdsong, 2005). Among the three habitat types (natural and man-made) compared in this study, submerged aquatic vegetation habitat provided valuable habitat supporting significantly greater density of species, and greater numbers of three estuarine species of concern than the other habitats studied. Both natural and man-made edge habitats supported similarly diverse and species rich nekton assemblages, but not the same density of organisms as SAV habitat.

These findings are informative as they suggest that in terms of overall nekton community support, (1) man-made edges are providing similar support as the natural edges, and (2) SAV habitat, when present, supports high densities of nekton and may be serving as valuable feeding or nursery grounds. However, given that SAV was not present anywhere near the study sites more than 50% of the time sampled, it is difficult to assess its actual value in supporting nekton throughout the year. SAV appears to be ubiquitous geographically across the region (Merino et al., 2009), but not always temporally (Joanen and Glasgow, 1965; Merino et al., 2005), and the consequences of this for nekton remain unclear. While shifts in SAV distribution have been used to indicate ecological changes (Orth et al., 2006), not enough is known to understand if the absence of SAV at our study sites is indicating an ecological shift at our sites related to lasting hurricane impacts, simply a reflection of natural variability (given the lack of SAV at our sites in Winter, Spring 2008 and a return in Summer 2008), or an indicator of some other ecological shift.

Clearly however, in considering responses to habitat loss or conversion of habitats, in particular as they relate to nekton

populations, requires a better understanding of what controls the presence and growth of SAV in the region. With further habitat loss and fragmentation, the conversion of SAV habitats, regardless of their temporal or geographic distributions would likely have a significant effect on nekton populations (Zimmerman and Minello, 1984; Hitch et al., 2011). Similarly, changes in available edge habitat have been shown through theoretical modeling to influence the ratio of marsh surface (Browder et al., 1985), and thus, continued fragmentation of the landscape could also have significant effects on nekton populations through this mechanism. The finding that the created and man-made flooded edge habitats supported similar nekton densities provides hope.

Recovery of environmental and nekton parameters following impacts from two Hurricanes (Ike and Gustav) indicated a slow response (> 13 mo) which may be linked to the fact that the areas sampled were interior marsh and salinity and water levels were not quickly restored once the hurricanes had passed. Future analyses of hurricane impacts may need to consider differentiating between exposed (coastal) and interior marsh sites, which may be more prone to extended impacts, and consider marsh management options for these interior sites.

## Acknowledgments

This was partially funded by U.S. Fish & Wildlife Service, State Wildlife Grant T-51-R. This grant was administered by the Louisiana Department of Wildlife and Fisheries. Thanks to Whitney Gayle and Anna Cattalanello for processing the bulk of samples in the laboratory. Thanks also to Bryan Piazza, Shannon Martin, Austin Humphries, Bryan Gossman, April Mason, Sandra Casas, Shea Miller, and Mason Piehler who helped with field sampling. Thanks to Sarai Piazza (USGS) for providing early access to CRMS data. Comments from Dr. Andy Nyman (LSU), Chris Llewellyn (EPA) and two anonymous reviewers significantly improved early versions of this manuscript. The use of trade, product, industry or firm names, or products is for informative purposes only and does not constitute an endorsement by the US Government or the US Geological Survey.

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