2010

Impacts of marsh loss and fragmentation on microhabitat use by estuarine nekton in southwest Louisiana

John Alexander Gordon
Louisiana State University and Agricultural and Mechanical College

IMPACTS OF MARSH LOSS AND FRAGMENTATION ON MICROHABITAT USE BY ESTUARINE NEKTON IN SOUTHWEST LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The School of Renewable Natural Resources

by
John Alexander Gordon
B.S., University of Delaware, 2007
August 2010

DEDICATION

I dedicate this work to my parents, John and Jane Gordon.

They put me first.

I can’t thank them enough.

ACKNOWLEDGEMENTS

This project was funded by the Louisiana Department of Wildlife and Fisheries through the USGS Louisiana Fish and Wildlife Cooperative Research Unit. The completion of this project would not have been possible without the generous contribution of personal time by many volunteers. Shannon Martin, Bryan Piazza, and Vanessa Tobias provided their invaluable airboat driving expertise. Post-doctoral research associate Sandra Casas, research associate Lainey Pitre, and graduate students Kelly Henry, Austin Humphries, Sung-Ryong Kang, April Newman, and Jonathan West provided assistance collecting samples. Undergraduate assistants Anna Catalanello and Whitney Gayle collected and processed field samples.

I would also like to thank the faculty and staff of the School of Renewable Natural Resources and the Department of Oceanography and Coastal Science for their role in the quality education I have received at LSU. In particular, I thank Cheryl Duplechain for providing logistical support. I thank Dr. James P. Geaghan and Dr. Michael Kaller for their statistical advice. I thank my committee members, Dr. Donald M. Baltz and Dr. John A. Nyman for their time and contributions to this study. Finally, I express my greatest gratitude to my major professor, Dr. Megan La Peyre, for her advice, optimism, and endless encouragement throughout this LONG process.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

In Louisiana, the extensive loss and fragmentation of coastal marshes has prompted inquires into the impacts these processes may have on estuarine-dependant nekton. To date, research on nekton response to marsh loss and fragmentation has been limited to landscape-level studies which focus on the relationship between nekton productivity and the availability of marsh edge. These studies have relied on the assumption that marsh edges provide the same level of support to nekton regardless of the degree of surrounding marsh loss or fragmentation. This study tested this assumption by investigating the impacts of marsh loss and fragmentation on marsh-edge characteristics and their associated nekton assemblages. The effects of marsh loss at the 1 km^2 scale were examined by stratifying three brackish marsh management units located in the Chenier Plain of western Louisiana into three 1 km^2 treatment squares, each representing one of three levels of marsh loss: Low (10%-35% water), Medium (40%-65% water), and High (70-95% water). Within each treatment square, nekton assemblage (density, diversity, body condition) and marsh-edge characteristics (water quality, submerged aquatic vegetation biomass, sediment organic matter, and emergent stem density) were sampled concurrently at six randomly established sampling points during the spring and fall of 2008. Variables representing marsh loss and fragmentation were also quantified within 1 ha squares centered on each sampling point. Relationships between nekton assemblage characteristics and environmental variables were explored with a canonical correspondence analysis. Data analysis revealed differences in sediment organic matter, ha scale percent marsh, and ha scale fragmentation in the spring sampling season. The passage of Hurricane Ike between sampling seasons may explain why only ha scale percent marsh differed between treatments in the fall. Despite differences in these environmental variables between treatments, nekton assemblage characteristics were not found

to differ between treatments. This may be partially explained by the lack of strong relationships between nekton assemblage characteristics and environmental variables as indicated by the canonical correspondence analysis. The results of this study do not indicate that nekton support provided by marsh edges is influenced by the degree of marsh loss at the 1 km^2 scale.

INTRODUCTION

Habitat loss and fragmentation are widely recognized as principle causes of habitat alteration in many terrestrial (Chen and Franklin 1990, Saunders et al. 1991, Andrén 1994, Watson et al. 2004) and aquatic ecosystems (Hovel and Lipcius 2001, Jackson et al. 2006, Long and Burke 2007). Because habitat modifications resulting from habitat loss and fragmentation often alter habitat quality for fauna (Saunders et al. 1991), describing these habitat changes and the associated faunal response is essential to ecological conservation efforts in heavily fragmented ecosystems. In Louisiana, coastal marshes have become increasingly fragmented; a process which is driven by the loss of over 4,856 km^2 of marsh surface since the 1930's (Boesch et al. 1994). These ecosystems are important for the production of many ecologically and economically valuable species of fish and crustaceans. In fact, it has been estimated that greater than 94 percent of the commercial saltwater fisheries catch from the southeastern United States consists of estuarine-dependent species (Chambers 1992). Despite this, it remains unknown what effect marsh loss and fragmentation may have on marsh characteristics and consequently, nekton assemblages. Answering this question should improve estimates of nekton productivity in coastal ecosystems as they become increasingly impacted by marsh loss and fragmentation.

Considerable debate about the appropriate definition and usage of the term habitat fragmentation has stemmed largely from confusion over the characteristics which distinguish habitat fragmentation from habitat loss. Habitat loss simply refers to the reduction of total habitat within a specified area. Habitat fragmentation "per se" is best defined as the division of contiguous habitat into multiple smaller habitat patches (Farhig 2003). The rationale for distinguishing between these two terms is twofold. First, although habitat loss must occur for fragmentation to take place, not all habitat loss results in fragmentation. A common example of

this is the erosion of shorelines. Secondly, it is important to determine whether the ecological impacts often attributed to habitat fragmentation are indeed caused by fragmentation, or actually by habitat loss. Several studies have attempted to isolate the ecological effects of habitat fragmentation "per se" from the effects of habitat loss by either expanding the area of the study to compensate for habitat loss (Collins & Barrett 1997, Caley et al. 2001), or by statistically controlling for the amount of habitat in each study area (McGarigal and McComb 1995, Villard et al. 1999). The results of these studies suggest that although habitat fragmentation may have a small influence on faunal assemblages, habitat loss is typically the dominant force driving major ecological changes. Thus, failing to properly define fragmentation and segregate its effects from those of habitat loss may result in misleading conclusions.

An additional definition of habitat fragmentation exists in the literature that should not be confused with the one used in this study. This alternate form is characterized as the isolation of habitat by extensive impassable structures (Layman et al. 2004, Layman et al. 2007, Valentine-Rose et al. 2007, Rypel and Layman 2008). In the case of coastal marshes, these structures typically include elevated man-made barriers such as roads or levees. This type of habitat isolation is distinguishable from the definition of fragmentation used in this study because elevated barriers are capable of preventing migration by nekton under normal water level conditions. Conversely, when marsh habitat is fragmented by marsh loss, the newly created open water which segregates marsh patches may actually facilitate migration by nekton.

The causes of marsh loss and fragmentation in coastal Louisiana are believed to be composed of an assortment of both natural and anthropogenic processes including subsidence, storm surge, erosion, sea level rise, canal dredging, levee construction, and subsurface fluid withdrawal (Penland et al. 1990). Relative sea level rise, a consequence of the combined effects of

subsidence and rising sea levels, is considered to be of chief importance among these processes. Rates of relative sea level rise often surpass natural marsh accretion rates resulting in excessive inundation of marsh vegetation and thus, widespread plant death and marsh loss. Rates of relative sea level rise exceed 1 cm/yr in the deltaic plain and 0.5 cm/yr in the Chenier plain (Boesch et al. 1994). The disparity between these two regions is attributable to higher rates of subsidence in the deltaic plain (~ 0.8 cm/yr) than in the Chenier plain (~0.3 cm/yr) (Ramsey and Penland 1989). Predictably, the highest marsh loss rates found along the Louisiana coast occur within the deltaic plain which lost approximately 0.57 % of its total area annually between 1956 and 2006. The Chenier plain lost just 0.41 % of total area annually during the same time period (Barras et al. 2008).

With over 40 landscape metrics associated with habitat loss and fragmentation described in the literature (McGarigal and Cushman 2002), it would appear that no shortage of options exists for quantifying these processes. McGarigal and Marks (1995) condensed this unwieldy number of metrics into a more manageable eight basic categories. Two of these categories, area and nearest neighbor distance, are good measures of habitat loss. Three of these categories: patch density, contagion, and edge metrics, represent effective methods for quantifying aspects of habitat fragmentation. The remaining categories: diversity, shape, and core area metrics are not true measures of habitat loss or fragmentation despite occasionally being regarded as such. Although representing marsh loss and fragmentation with single metrics may be adequate, it may be wiser to employ multiple metrics to represent each. Few metrics are arguably perfect indicators of marsh loss or fragmentation, and each presents unique ecological implications as well.

Area metrics, which measure the area occupied by a specified habitat type, are generally considered to be the most straightforward indicators of habitat loss (Farhig 2003). Landscapes with low amounts of habitat are assumed to have experienced the greatest amount of habitat loss. Habitat area is a key controlling factor for virtually all species including estuarine-dependant nekton. For example, Turner (1977) found a positive relationship between penaeid shrimp productivity and the area of Spartina spp. marsh.

Nearest-neighbor distance metrics, which measure the distance from a patch to the nearest neighboring patch of the same type, are also effective indicators of habitat loss. The mean distance between nearest neighboring patches positively relates to the amount of habitat removed from the landscape (Farhig 2003). Further, an abundance of literature on population dynamics and species interactions within meta-populations suggests nearest-neighbor indices may have additional ecological implications. Results suggest that the dynamics of sub-populations within patches are influenced by their proximity to other sub-populations of the same or competing species (Kareiva 1990). Johnson and Heck (2006) found that juvenile blue crab densities were significantly influenced by the distance from the nearest seagrass patch. They hypothesized that the high risk of predation associated with unstructured seafloor (Orth et al. 1984, Micheli and Peterson 1999) may have limited inter-patch movement.

Patch density metrics measure the number of patches of a particular habitat type within a given area. Patch density is an effective indicator of habitat fragmentation because the division of contiguous habitat directly results in an increased number of patches. Patch density may have additional ecological importance because the number of patches can determine the number of sub-populations within a meta-population. This in turn may influence the dynamics and persistence of the meta-population (Gilpin and Hanski 1991). Small resident marsh fishes may

be particularly responsive to changes in the number of patches because their small home ranges (> 40 m) (Lotrich 1975, Potthoff and Allen 2003) may make inter-patch migration infrequent.

Contagion metrics measure the contiguity of patches within the landscape. The fragmentation process reduces habitat contiguity by interspersing at least two landscape types. In coastal marshes, fragmentation intersperses new marsh creeks and ponds throughout previously contiguous marsh. Isolated marsh ponds may provide habitat with fewer predators to small marsh fishes that colonize them during high water events (Halpin 1997, Paterson and Whitfield 2000), but also may expose nekton to high water temperatures and extremely low dissolved oxygen (Smith and Able 2003).

Edge metrics measure the length of edge habitat within the area of interest. Edge metrics are an effective indicator of fragmentation because the division of contiguous habitat results in the creation of new edge. Within coastal marsh ecosystems, most species of small nekton congregate near the flooded edge of sub-aerial marsh. The physical and biological characteristics of marsh edge have been shown to enhance the growth and recruitment of many important forage species and juvenile piscivores by providing feeding ground and escape cover (Boesch and Turner 1984, Rozas and Odum 1988, Zimmerman et al. 2000). By comparison, open water ponds and marsh interiors have been shown to support a much lower density and diversity of fishes and crustaceans (Baltz et al. 1993, Minello 1999, Minello et al. 2008).

It is important to note that because most small marsh nekton species rely primarily on marsh edge, marsh loss does not necessarily equate to habitat loss. Marsh loss frequently results in the fragmentation of the marsh surface, thereby creating new edge. Browder et al. (1985, 1989) described a theoretical parabolic relationship between the percentage of landscape occupied by marsh surface and the availability of marsh edge (Fig 1). Marsh edge availability is believed to

be maximized when approximately 50 percent of the marsh surface had been removed from the landscape. Marsh edge then declines as marsh-surface approaches zero percent of the landscape.

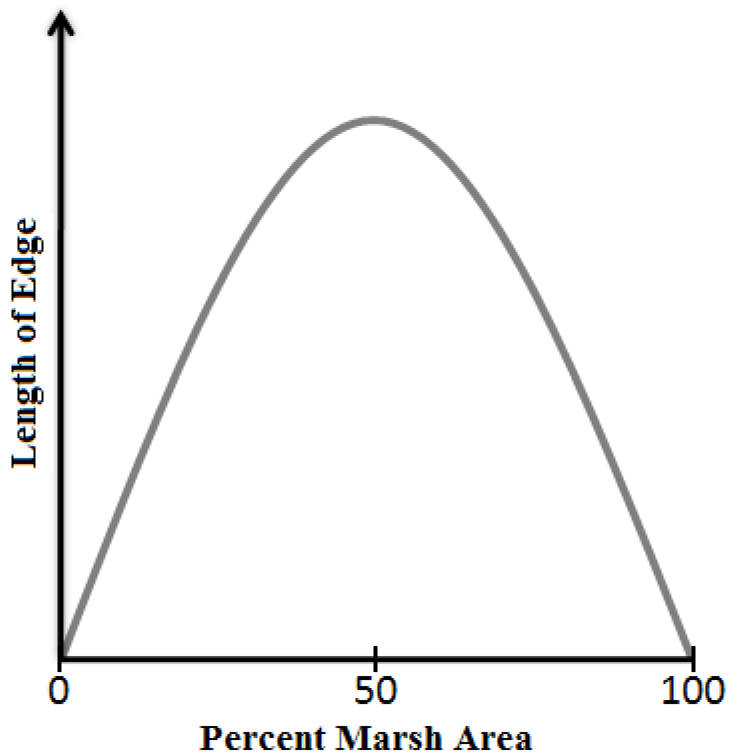

Figure 1. The theoretical relationship between the percentage of area occupied by marsh surface and the total length of marsh edge as proposed by Browder et al. (1985).

Much of the previous research that has investigated nekton response to marsh loss and fragmentation has focused on providing empirical evidence for the hypothesized positive relationship between nekton productivity and the total length of marsh edge per unit area (Faller 1979, Dow 1982, Browder et al. 1989, Minello and Rozas 2002, Roth et al. 2008). This work relies on the assumption that all marsh edges provide equivalent support to all species of nekton. However, recent research has demonstrated that variation within the physical characteristics of marsh edges can significantly influence the composition of nekton assemblages at the micro-scale (1 m^2) level. For example, La Peyre and Birdsong (2008) found differences in nekton assemblages associated with bank geomorphology. Bank geomorphology may affect the duration and frequency of flooding on the adjacent marsh surface. Because marsh inundation is

believed to be a critical factor in determining the total nekton productivity of marsh ecosystems (Roth et al. 2008), geomorphic characteristics that limit flooding will likely reduce the value of marsh edge as habitat for nekton. This is supported by studies that have shown resident species often congregate in shallow sub-tidal areas that provide earlier access to vegetated intertidal habitats during rising tides (Rozas and Odum 1988, Rozas and Reed 1993). Similarly, the stem density of marsh-edge vegetation may influence the ability of nekton to use the marsh surface. Vegetation which exhibits high stem densities may serve as a barrier against both movement and foraging by nekton (Vince et al. 1976, Jacobus and Webb 2005). Finally, wave fetch and the associated wave energy reaching marsh edge have been linked to increased nekton diversity at the marsh edge (La Peyre and Birdsong 2008). If marsh-edge characteristics differ significantly between marshes exhibiting different levels of marsh loss, then previous estimates of nekton productivity in fragmented marsh ecosystems may be inaccurate.

The goal of this study was to determine if the physical characteristics of marsh edge and the associated nekton assemblages are influenced by coastal marsh loss and fragmentation. Specifically, this study asked, (1) do the physical characteristics of marsh edge differ between marshes exhibiting low, medium, and high levels of 1 km^2 scale marsh loss; (2) do marsh-edge nekton assemblage characteristics (species density, Shannon-Wiener diversity, assemblage structure, or Relative Condition Factor) differ between marshes exhibiting low, medium, and high levels of 1 km^2 scale marsh loss; and (3) do relationships exist between nekton assemblage characteristics and marsh-edge characteristics or ha scale landscape variables.

METHODS

Study Areas

This study was conducted within two wildlife refuges located in the Chenier Plain of southwestern Louisiana. Rockefeller State Wildlife Refuge (29°40'93" N, 92°48'45" W) is a 42,400 ha refuge located in Vermillion Parish, wedged between Highway 82 and the Gulf of Mexico (Fig. 2). Rockefeller State Wildlife Refuge is heavily managed by the Louisiana Department of Natural Resources to promote waterfowl habitat. Thus, it consists of 17 impoundments which allow for control of both water level and salinity through flap gates, weirs, and gated culverts (Wicker et al. 1983). Sabine National Wildlife Refuge (29°55'08" N, 93°35'15" W) is a 50,388 ha area located in Cameron Parish between Calcasieu and Sabine Lakes (Fig. 3). Much like Rockefeller State Wildlife Refuge, Sabine National Wildlife Refuge has been divided into management units by a system of levees and canals which allow water level and salinity to be controlled via water control structures. Within these two refuges, marsh management units exhibiting accessible areas of low, moderate, and high marsh loss were selected to serve as study units.

Within Rockefeller State Wildlife Refuge, the Unit Six management area was selected to serve as the first study unit (Fig 2). Unit Six is a 7,200 ha intermediate to brackish impoundment dominated by saltmeadow cordgrass *Spartina patens* and common coontail *Typha latifolia.* Much of the marsh loss that occurred in this unit took place between 1956 and 1978. In addition, this unit recently suffered substantial marsh loss in 2005 due to storm damage inflicted by Hurricane Rita (Barras et al. 2008).

Within Sabine National Wildlife Refuge, two study units were selected. The first included the easternmost portion of the refuge known as "Hog Island Gully" which is bordered to the west by

Route 27 and to the east by Calcasieu Lake (Fig 3). This 1,600 hectare area is not impounded by levees, and is thus influenced by wind driven tidal exchange with Calcasieu Lake. This brackish marsh is dominated primarily by smooth cordgrass *Spartina alterniflora*, with lesser amounts of *Spartina patens,* black needlerush *Juncus roemerianus,* and saltgrass *Distichlis spictata* also present. The majority of the marsh loss that has taken place in this area occurred between 1956 and 1978 (Barras et al. 2008). However, sediment slurry dredged from the Calcasieu Ship Channel was pumped in to restore several areas of the study unit between the years 1983 and 1999. Restored sections of the study unit were avoided when selecting locations for sampling.

The third study unit, located in the northwest corner of Sabine NWR, is the Unit Five management unit (Fig. 3). This roughly 10,000 ha area is surrounded by impoundment levees to the south, east, and west which promote intermediate salinity conditions in this *Spartina patens* dominated marsh. Much of the marsh loss that has occurred in this unit took place between 1956 and 2008.

On September 13th, 2008, just prior to the fall sampling period of this study, Hurricane Ike made landfall near the southwestern Louisiana coast affecting all study units. Storm surge gauges near Rockefeller Refuge Unit Six (29°38'27" N, 92°25'37" W) measured storm surge heights up to 2.3 m. Gauges near Sabine NWR Hog Island Gully (29°48'15" N, 93°20'56" W) measured storm surge heights up to 3.1 m. Finally, gauges near Sabine NWR Unit Five (29°45'52" N, 93°20'56" W) measured storm surge heights up to 3.3 m (East et al. 2008). An inspection of post-hurricane aerial imagery (October, 2008) revealed visible damage to the marsh surface was evident only within the Sabine NWR Unit Five management area (Fig. 4) (Barras et al. 2008).

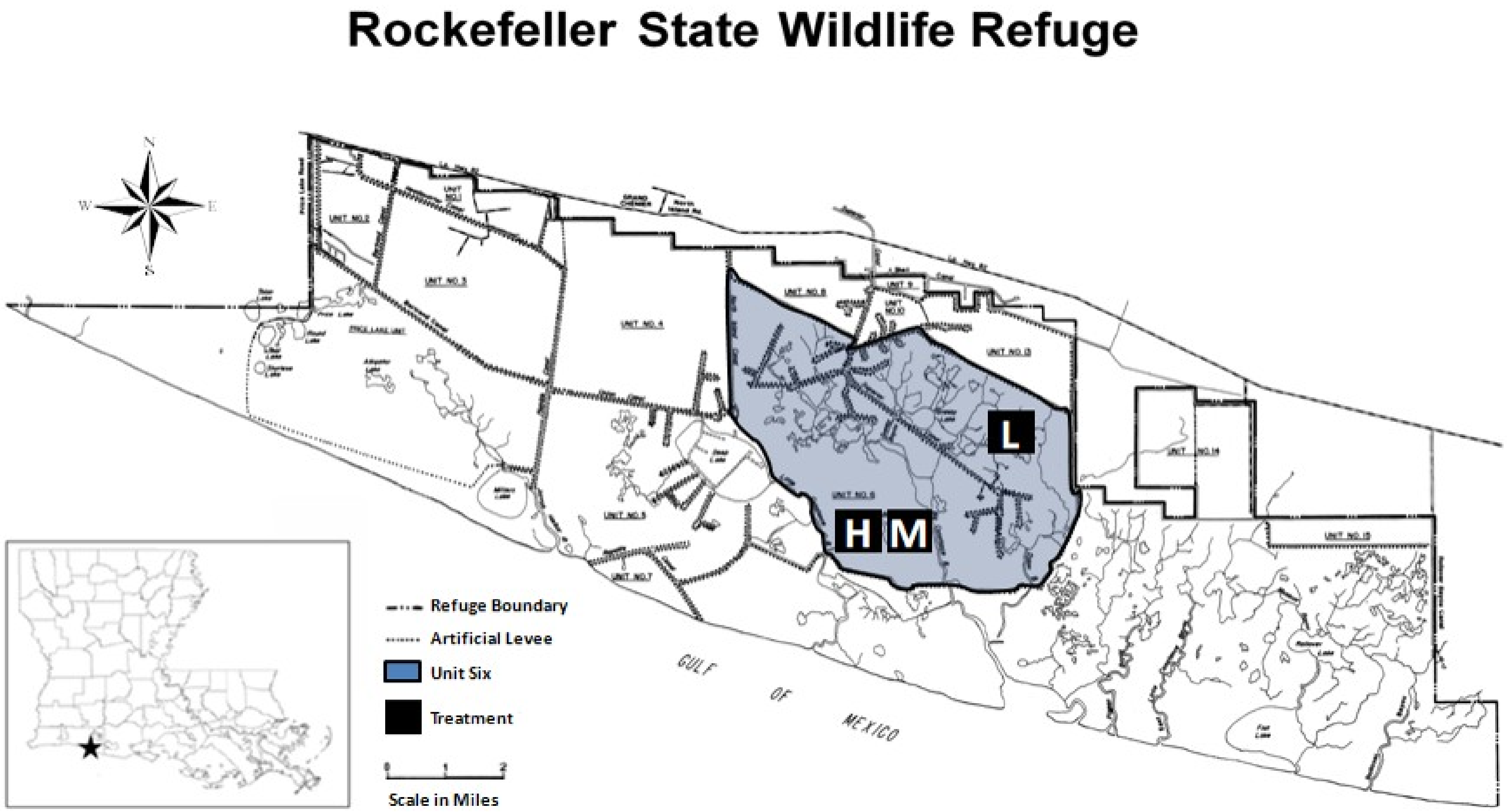

Figure 2. The Unit Six management area within Rockefeller State Wildlife Refuge. Black squares represent the location of the three 1 km^2 marsh loss treatments: L (Low), M (Medium), and H (High).

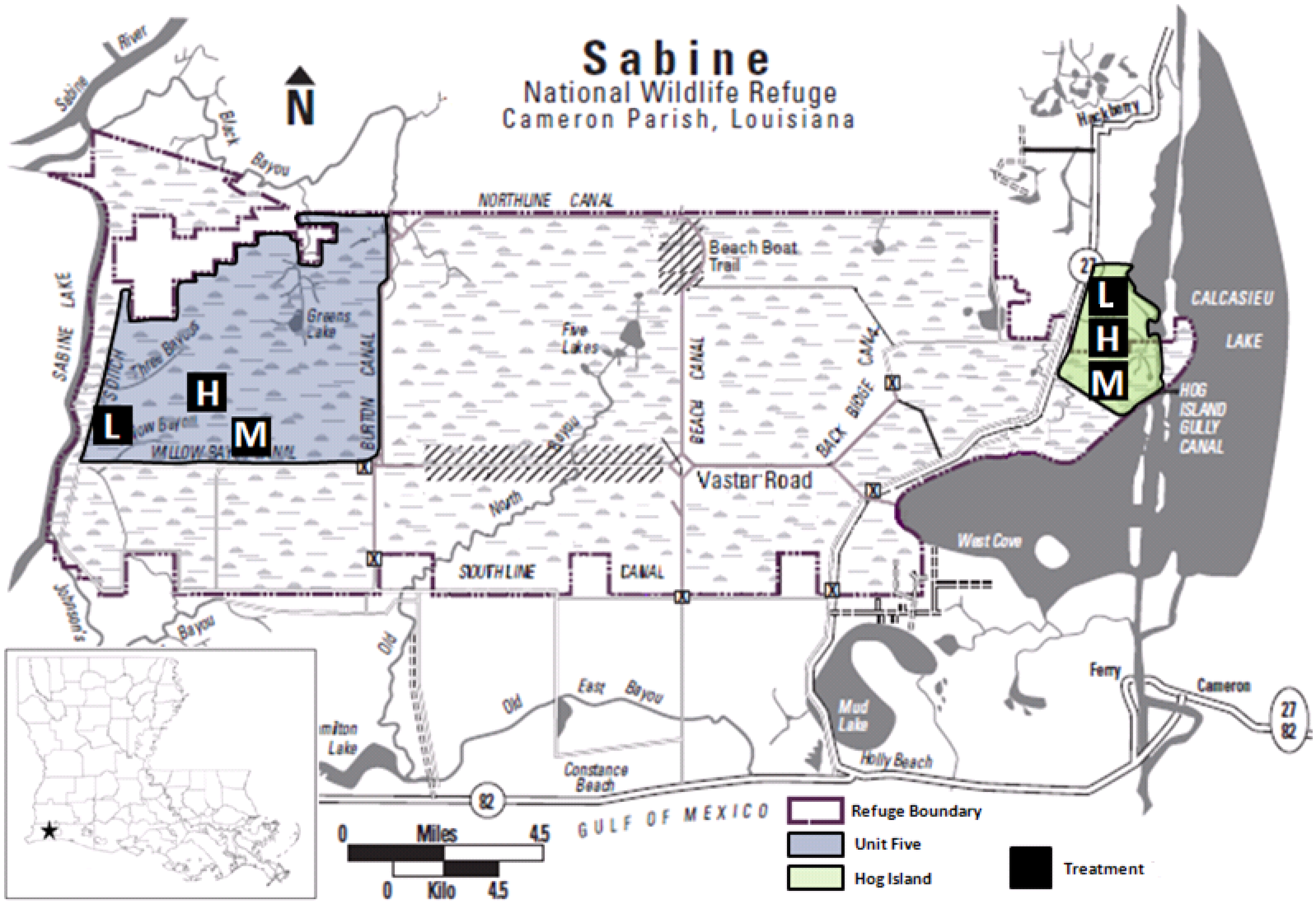

Figure 3. The Unit Five management area and Hog Island Gully area of Sabine National Wildlife Refuge. Black squares represent the location of the three 1 km^2 marsh loss treatments: L (Low), M (Medium), and H (High).

Sampling Design

Each study unit was stratified by selecting a 1 km^2 treatment square for each of three levels of marsh loss. In this study, the percentage of area occupied by water was used as an indicator of marsh loss. Historical maps of coastal Louisiana indicate that nearly all open water present within the 1 km^2 marsh loss treatments at the beginning of this study was the result of marsh loss that occurred after 1956 (Barras et al. 2008). Thus, the marsh loss treatments were defined as: Low (10%-35% water), Medium (40%-65% water), and High (70-95% water) (Fig. 4 - 6). To randomly select locations for treatments within each study unit, a grid with 1 km^2 cells was placed over a georeferenced 2007 Digital Orthophoto Quarter Quadrangle (DOQQ) aerial map of each study unit. A random number generator was then used to select grid cells until a cell fitting each marsh loss treatment level was obtained. When selecting locations for marsh loss treatments, percent water was estimated visually.

Within each 1 km^2 treatment square, six sampling points were randomly established along the marsh edge. To select locations for each sampling point, a grid with 50 m^2 cells was overlaid on 2007 DOQQ aerial maps of each treatment square. A random number generator was then used to select grid cells. The nearest marsh edge to the selected grid cell was chosen as the sampling point. If access to the selected sampling point was not possible due to impassable terrain, an alternate sampling point was chosen.

At each sampling point, triplicate sub-samples of the nekton assemblage and marsh-edge variables were taken. Sub-samples were then averaged for each sampling point to promote normality. Therefore, each of the three study units contained three 1 km^2 treatment squares in which 6 sampling points composed of three sub-samples were established for a total of 54

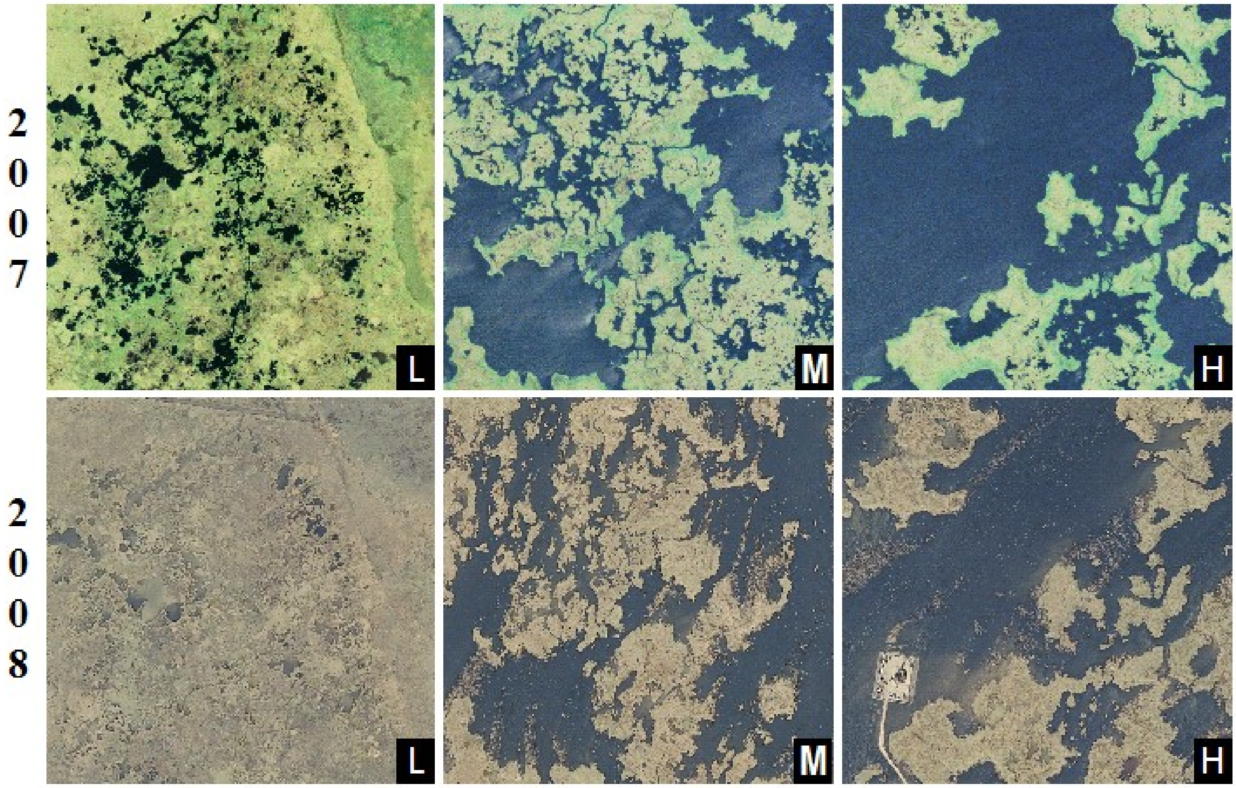

Figure 4. Pre (2007) and post (2008) hurricane imagery of marsh loss treatments from Sabine NWR Unit Five. Treatments are indicated as L (Low), M (Medium) and H (High). Significant hurricane damage is visible in the medium and high loss treatments.

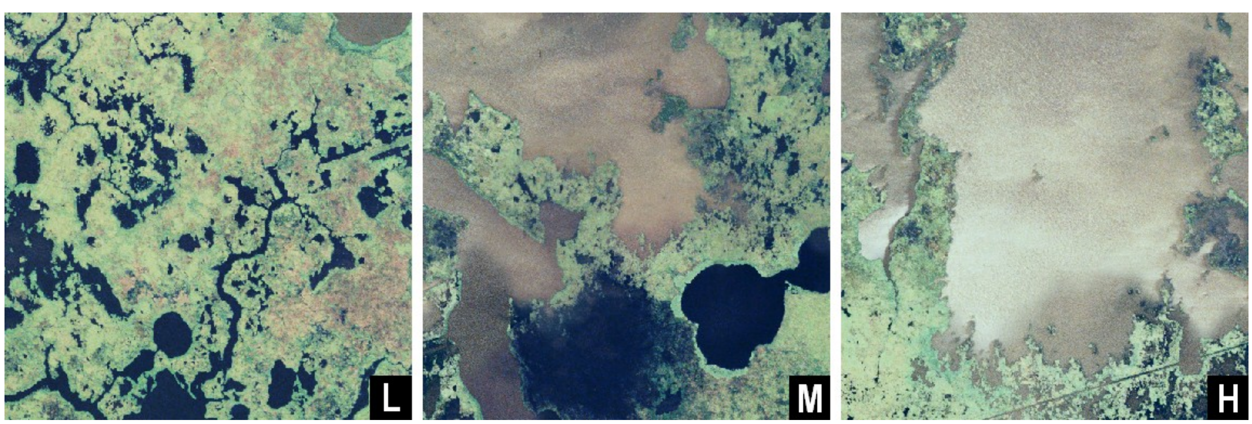

Figure 5. 2007 imagery of marsh loss treatments from Rockefeller Refuge Unit Six. Marsh loss levels are indicated as L (Low), M (Medium) and H (High). No hurricane-related damage was evident between sampling seasons.

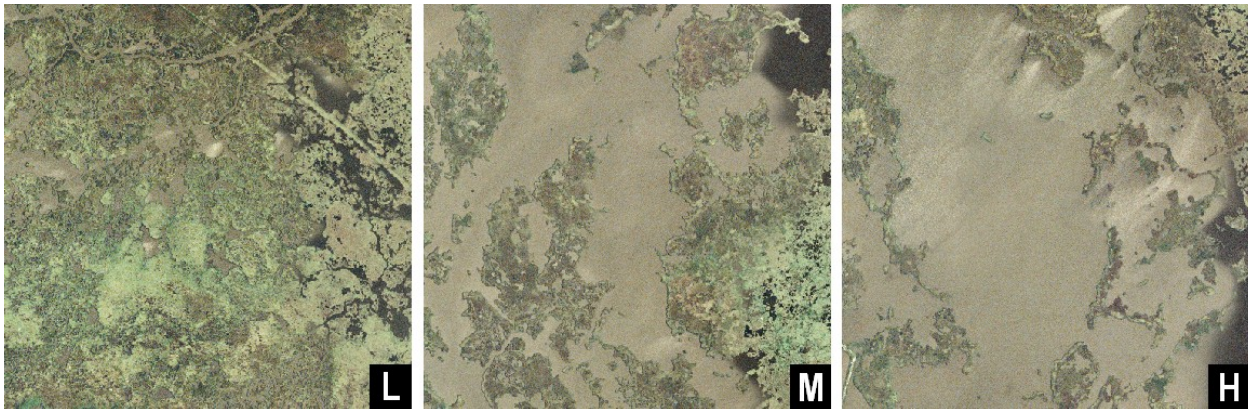

Figure 6. 2007 imagery of marsh loss treatments from the Hog Island Gully area at Sabine NWR. Marsh loss treatments are indicated as L (Low), M (Medium) and H (High). No hurricane-related damage was evident between sampling seasons.

samples per season. Sampling occurred in late spring (June) and fall (October-November) of 2008 to allow for the capture of seasonal transient nekton in addition to resident species.

<u>Nekton Sampling</u>

Nekton were collected at each sampling point using a 1 m^2 throw trap with 3 mm mesh netting sides similar to the one described by Kushlan (1981). The throw trap is an effective quantitative sampling tool designed for shallow water environments including coastal marshes. At each sampling point, the trap was thrown three times randomly to control high variances often associated with throw trap sampling. Each of the three throws was made approximately 10 m apart to reduce the likelihood that site disturbance would influence nekton samples.

To deploy the trap, each sampling point was cautiously approached by airboat until the trap could be thrown from the bow into the flooded mudflat within 1 m of the marsh edge. The trap then sunk into the substrate forming a seal around its base which prevented captured organisms from escaping. Captured nekton were removed from the throw trap by sweeping a 1 m bar seine with 3 mm mesh netting across the inside of the trap. When five consecutive sweeps of the bar seine yielded zero organisms, the trap was considered clear. Captured nekton were placed on ice

and returned to the laboratory at Louisiana State University where they were frozen until they could be identified, counted, and measured for length and weight. The total lengths of all fish and shrimp and the carapace widths of all crabs were measured to the nearest 1 mm. The wet weights of all nekton were taken to the nearest 0.001 g. If more than 30 individuals of the same species occurred in one throw trap sample, measurements of length and weight were limited to a sample of 30 randomly selected individuals.

For each throw trap sample, nekton assemblage characteristics were calculated. Density (individuals/m^2) was determined for each species and the combined nekton assemblage. In addition, nekton diversity was calculated using the Shannon Wiener diversity index (H') (Magurran 1988). Finally, mean body condition of each captured fish species was estimated using the relative condition factor (K_n) (Anderson and Neumann 1996).

Marsh-Edge Characteristics

Marsh-edge characteristics at each sampling point were estimated from triplicate sub-samples taken in conjunction with the triplicate throw trap sub-samples (Table 1). For each throw trap deployment, all marsh-edge characteristics were measured once in close proximity (< 1 m) to the throw trap location. Water quality variables were sampled only once at each sampling point because they were expected to be nearly uniform throughout the vicinity of the sampling point.

Water quality parameters including dissolved oxygen (mg/L), temperature (°C), and salinity were measured with a Yellow Springs Instruments (YSI) water quality meter model 556. Water depth within each throw trap (cm) was estimated by calculating the mean of three depth measurements taken inside each throw trap.

Both emergent marsh-edge vegetation and submerged aquatic vegetation (SAV) were measured at each sampling point. To quantify emergent marsh-edge vegetation, 0.25 m^2

sampling quadrats were placed on the marsh surface (<1 m from the water edge) adjacent to each throw trap location. Stem percent cover was then determined by visually estimating the percentage of each quadrat that was occupied by emergent stems. SAV was collected from each thrown 1 m^2 throw trap by hand until it could no longer be detected. Collected SAV was then placed on ice, returned to the laboratory at Louisiana State University and refrigerated until it could be sorted to species and dried in a forced air drying oven at 50°C. SAV dry weight aboveground biomass was then measured to the nearest 0.001 g.

The percent organic matter of the top 5 cm of sub-tidal substrate was measured from 10 cm diameter sediment cores taken at each throw trap location. To determine percent organic content, sediment cores were first dried in a forced air drying oven at 50°C and then ground to a fine powder with a mortar and pestle. Three 3 g sub-samples of each ground core were burned in a muffle furnace at 500°C for 4 hours resulting in the combustion of all organic matter. The burned sub-samples were then weighed again to acquire a post-burn mass. All mass measurements were made to the nearest 0.001 g. Percent organic matter was calculated as:

$$\text{Percent Organic Matter} = [1 - (\text{Post-Burn Mass} / \text{Pre-Burn Mass})] \times 100$$

The mean percent organic matter of the three core sub-samples was used to represent the sediment organic matter of each sediment core.

Landscape Variables

Landscape characteristics commonly associated with marsh loss and fragmentation were calculated by analyzing infrared or true color 1 m^2 resolution DOQQ imagery from 2007 and 2008. All calculations for spring data were completed using 2007 imagery. Following Hurricane Ike, post-hurricane imagery (October 2008) of treatment squares was visually assessed to determine if and where storm damage had occurred. For treatment squares that were deemed

to be damaged, all landscape characteristics taken within the square were recalculated for the fall data set from post-hurricane imagery. To prepare imagery for analysis, a supervised classification of landscape types was performed on DOQQ imagery using the multi-spectral image analysis software MULTISPEC (Landgrebe and Biehl 2007). Multi-spectral image analysis programs allow different landscape types to be distinguished based upon the color of the raster grid cells. A supervised classification involves user guided sampling of each landscape type within the raster image (i.e., 'training areas'). From these samples, the software is able to identify colors that are characteristic of each landscape type. After associations between landscape type and cell color have been defined, the software assigns numerical values corresponding to each landscape type to raster grid cells based on color. Thus, the classification process results in the conversion of a raster image to a numerical grid which can then be analyzed by other software programs.

In this study, MULTISPEC was used to classify cells as either marsh surface or water. Raster grid cells defined as water were assigned a 1. Grid cells defined as marsh were assigned a 2. These numerical grids were then analyzed with the landscape analysis software FRAGSTATS (McGarigal et al. 2002). FRAGSTATS has been successfully used to calculate marsh landscape characteristics including percent vegetated marsh, total length of edge, and marsh clumpiness (Roth et al. 2008).

In this study, FRAGSTATS was used to measure several marsh landscape indices including percent water, mean water patch nearest neighbor distance, number of marsh patches, mean marsh patch clumpiness, and total edge (Table 1). All landscape variables were measured within 1 ha squares centered on each sampling point. FRAGSTATS was also used to calculate percent

water within the 1 km^2 marsh loss treatment squares to confirm the treatment assignments which were originally made visually.

Percent water (PWATER) is simply the percentage of the area of interest occupied by water. PWATER is a direct indicator of the amount of marsh loss that has taken place.

Mean water patch nearest neighbor distance (NEIGHBOR) measures the average straight line distance between all water patches within the area of interest.

Number of marsh patches (MPTCH) is the total number of marsh patches segregated by water within the boundaries of the area of interest. The 'Eight Neighbor Rule' was used in this study which states that in a raster grid, two cells of the same classification (marsh or water) are considered to be of the same patch if they are adjacent either horizontally, vertically, or diagonally. MPTCH serves as a simple indicator of landscape fragmentation.

Mean marsh patch clumpiness (CLUMP) measures the degree of marsh patch contiguity within the landscape. Landscapes with large contiguous sections of marsh receive scores approaching 1. Landscapes with a high degree of interspersion between marsh and water patches receive scores approaching -1. CLUMP is calculated as follows:

$$\text{For } G_i < P_i \text{ and } P_i < 0.5: \quad CLUMP = \frac{G_i - P_i}{P_i}$$

$$\text{Else:} \quad CLUMP = \frac{G_i - P_i}{1 - P_i}$$

Where G_i equals the proportion of cells bordered by a cell of the same patch type and P_i equals the proportion of the area of interest occupied by marsh.

Total edge (EDGE) is the summed length of all cell segments that form the perimeter of patches in the landscape. The boundary of each 1 ha area was not included as edge in this metric.

Table 1. Summary of marsh-edge and ha scale landscape variables measured for each sampling point.

Type	Variable Name	Units	Abbreviation
Marsh-Edge			
	Trap Depth	cm	DEPTH
	Dissolved Oxygen	mg/L	D.O.
	Water Temperature	°C	TEMP
	Salinity	N/A	SALINITY
	Marsh Vegetation Stem Cover	%	COVER
	Submerged Aquatic Vegetation Biomass	g/m^2	SAV
	Sediment Organic Matter	%	ORGANIC
Landscape (Ha Scale)			
	Percent Water	%	PWATER
	Number of Marsh Patches	N/A	MPTCH
	Mean Marsh Patch Clumpiness	N/A	CLUMP
	Total Edge	m	EDGE
	Water Patch Nearest Neighbor Distance	m	NEIGHBOR

Data Analysis

Analysis was based on a randomized block design where study unit served as the block and 1 km^2 treatment squares representing three levels of marsh loss were the treatments (Table 2). With the exception of the factor analysis, analyses were separated by season. A significance of $\alpha < 0.05$ was required to reject the null hypotheses. All analyses were performed with SAS statistical analysis software (Version 9.3; SAS Institute, Cary, North Carolina) unless otherwise noted.

Table 2. A summary of the randomized block design used in this study.

Source	Degrees of Freedom
Treatment (Marsh Loss Levels = 3)	2
Block (Study Units = 3)	2
Experimental Error	4
Sampling Error (N = 54)	45
Total	53

To prepare data for analysis, tests for the assumptions of normality and homogeneity of variance were conducted. To better meet these assumptions, natural log transformations ln(x+1) were performed upon all nekton abundance and condition data and the following habitat variables: SAV Biomass, Total Edge, Number of Marsh Patches, and Mean Water Patch Nearest Neighbor Distance. For several of these variables, transformation was insufficient to fully meet these assumptions. However, it is unlikely that the results of the robust statistical techniques used in this study were substantially influenced by this.

Factor analysis (Proc Factor) was used to reduce the total number of 1 ha scale landscape variables to be analyzed. Factors with eigenvalues greater than 1.0 were retained for further analysis. Varimax rotation was employed to facilitate interpretation of factors. Loading values of 0.4 or greater were considered meaningful.

Marsh-edge characteristics and retained landscape factors were entered into a multivariate analysis of variance (MANOVA; Proc Mixed) to test whether they differed between 1 km^2 treatment squares (low, medium, and high marsh loss). Following significant MANOVA results, individual one-way analysis of variance (ANOVA; Proc Mixed) tests were performed. Significant ANOVA effects were tested using post-hoc comparisons of Tukey's adjusted least squared means.

MANOVA was also used to determine if the density, diversity, or body condition of the most abundant fish and crustacean species differed between marsh-loss treatments. Following significant MANOVA results, individual one-way ANOVA tests were performed. Significant ANOVA effects were tested using post-hoc comparisons of Tukey adjusted least squared means.

Kendall's W was used to examine shifts in assemblage structure across marsh loss treatments

(Kendall 1955, Landis & Koch 1977, Fleiss 1981). Tests for concordance in nekton assemblages were run for the most commonly captured fishes and crustaceans and the top five most commonly captured species. Rare species were excluded from this analysis because they tend to be concordant.

Canonical correspondance analysis (CCA) was used to relate marsh-edge characteristics and ha scale landscape factors to nekton species densities and assemblage diversity (CANOCO; ter Braak & Smilauer 2002). The effect of study unit was blocked to eliminate variance associated with different study units. The statistical significance of the canonical axes was examined with Monte Carlo tests. Marsh-edge characteristics and ha scale landscape factors which were found to be highly correlated with canonical axes ($r = 0.3$) were considered meaningful.

Density and condition indices of rare species were excluded from analyses because rare species have been shown to contribute little to the explanative value of analyses (Gauch 1982). However, abundances of rare species were included when calculating total nekton density and the Shannon-Wiener Diversity Index. Rare fishes were considered to be any species that accounted for less than 1.0 percent of the total fish abundance, or any crustacean that accounted for less than 1.0 percent of the total crustacean abundance. Rare species were determined for each season separately.

RESULTS

Post-Hurricane Treatment Calculations

Visual inspection of imagery taken after the landfall of Hurricane Ike indicated the need to recalculate 1 km^2 marsh loss and 1 ha landscape variables for the medium and high loss treatments in Sabine NWR Unit Five using post-hurricane imagery. The percentage of area occupied by water increased in the 1 km^2 medium loss treatment from 49 % to 60 % as a result of storm-related marsh damage. This new value is still within the defined range of a medium loss treatment (40% - 65%). However, the percentage of area occupied by water in the high loss treatment declined from 70 % percent to 63 %. This decrease in open water appeared to be the result of deposition of large quantities of marsh rack into the treatment square. This new value no longer met the definition of a high loss treatment (70% - 95%), but the high loss classification of this treatment was retained for fall data analysis.

Variable Reduction

The factor analysis run on all ha scale landscape variables accounted for 80.0 percent of the total variance and reduced the five original landscape variables to two landscape factors (Table 3). Factor 1 (F1), which accounted for 51.8 percent of the variance, was positively correlated to MPTCH and EDGE, while negatively correlated with CLUMP. Because high values of MPTCH and EDGE and low values of CLUMP indicate a highly fragmented landscape, F1 was interpreted as a measure of fragmentation and was renamed FRAGMENT. Factor 2 (F2), which accounted for 28.2 percent of the variance, was positively correlated with NEIGHBOR and negatively correlated with PWATER. Because large distances between water patches and a low percent area covered by water both imply large marsh areas, F2 was interpreted to be a measure

of the area occupied by marsh surface and was renamed MARSH. MARSH is expected to be inversely related to marsh loss.

Table 3. Factor analysis loadings for the five ha scale landscape variables. Two principle components explained 80.0 percent of variance in the data. Shading indicates interpreted loadings.

INITIAL VARIABLE	F1	F2
PWATER	-0.3832	-0.8143
MPTCH	0.8206	-0.1972
NEIGHBOR	-0.183	0.846
CLUMP	-0.9017	-0.0867
EDGE	0.8731	0.3813
EIGENVALUE	3.26	1.88
PERCENT VARIANCE	51.8	28.2
CUMULATIVE VARIANCE	51.8	80.0

Environmental Characteristics

MANOVA tests for differences in marsh-edge characteristics and ha scale landscape factors between marsh loss treatments were significant for both the spring ($p < 0.0001$) and fall ($p < 0.0001$). Subsequent one-way ANOVA tests on spring variables found significant differences between treatments for MARSH ($p = 0.0379$), organic matter ($p = 0.0245$), and FRAGMENT ($p = 0.0260$) (Table 4). One-way ANOVA tests on fall variables found only MARSH differed between treatments ($p = 0.0353$) (Table 5).

Following significant ANOVA tests, comparisons of Tukey adjusted least squares means revealed that in both seasons, values of MARSH were higher in the low loss treatments than the high loss treatments (Spring: $p = 0.0379$, Fall: $p = 0.0353$) (Fig 7 and 8 respectively). Spring FRAGMENT values were higher in the low loss treatment than in the high loss treatments (p =

0.0233) (Fig 9). Finally, spring organic matter was a smaller percentage of the substrate in the low loss treatment than the high loss treatment ($p = 0.0217$) (Fig 10).

Table 4. Mean ± SE values for spring 2008 (pre-hurricane) environmental characteristics by treatment. Significant p-values are in bold type.

Environmental Variable	Low	Medium	High	Mean	Pr > F
FRAGMENT	0.5 ± 0.2	-0.4 ± 0.2	-0.9 ± 0.2	-0.3 ± 0.1	**0.0260**
MARSH	0.6 ± 0.2	0.1 ± 0.2	-0.4 ± 0.3	0.1 ± 0.1	**0.0379**
Dissolved Oxygen (mg/L)	3.9 ± 0.4	4.5 ± 0.4	4.8 ± 0.4	4.5 ± 0.3	0.31
Salinity (ppt)	7.1 ± 0.9	5.5 ± 1.1	5.1 ± 1.0	5.9 ± 0.6	0.41
Temperature (°C)	29.5 ± 0.4	31.1 ± 0.5	30.1 ± 0.5	30.3 ± 0.3	0.37
Emergent Cover (%)	57.6 ± 4.1	57.8 ± 4.3	54.6 ± 5.2	56.7 ± 2.6	0.35
SAV Dry Biomass (g/m^2)	0.9 ± 0.3	0.3 ± 0.1	0.2 ± 0.1	2.9 ± 1.2	0.11
Soil Organic Matter (%)	21.1 ± 2.7	29.5 ± 2.7	34.3 ± 3.3	28.6 ± 1.8	**0.0217**
Trap Depth (cm)	30.0 ± 1.7	29.0 ± 3.6	30.2 ± 2.1	29.7 ± 1.5	0.98

Table 5. Mean ± SE values for fall 2008 (post-hurricane) environmental characteristics by treatment. Significant p-values are in bold type.

Environmental Variable	Low	Medium	High	Mean	Pr > F
FRAGMENT	0.5 ± 0.2	0.2 ± 0.2	0.1 ± 0.3	0.3 ± 0.1	0.89
MARSH	0.6 ± 0.2	-0.3 ± 0.1	-0.5 ± 0.2	-0.1 ± 0.1	**0.0353**
Dissolved Oxygen (mg/L)	3.8 ± 0.2	4.1 ± 0.3	5.1 ± 0.4	4.3 ± 0.2	0.19
Salinity (ppt)	17.3 ± 0.8	18.0 ± 1.4	17.9 ± 1.0	17.7 ± 0.6	0.93
Temperature (°C)	20.2 ± 0.3	20.2 ± 0.7	21.7 ± 0.4	20.7 ± 0.3	0.54
Emergent Cover (%)	58.9 ± 4.0	52.8 ± 4.6	51.0 ± 5.1	54.2 ± 2.6	0.47
SAV Dry Biomass (g/m^2)	0.4 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	1.2 ± 0.3	0.90
Soil Organic Matter (%)	21.1 ± 1.9	26.2 ± 2.8	28.9 ± 2.8	25.4 ± 1.5	0.12
Trap Depth (cm)	35.8 ± 3.4	43.8 ± 2.3	43.9 ± 3.8	41.2 ± 1.9	0.24

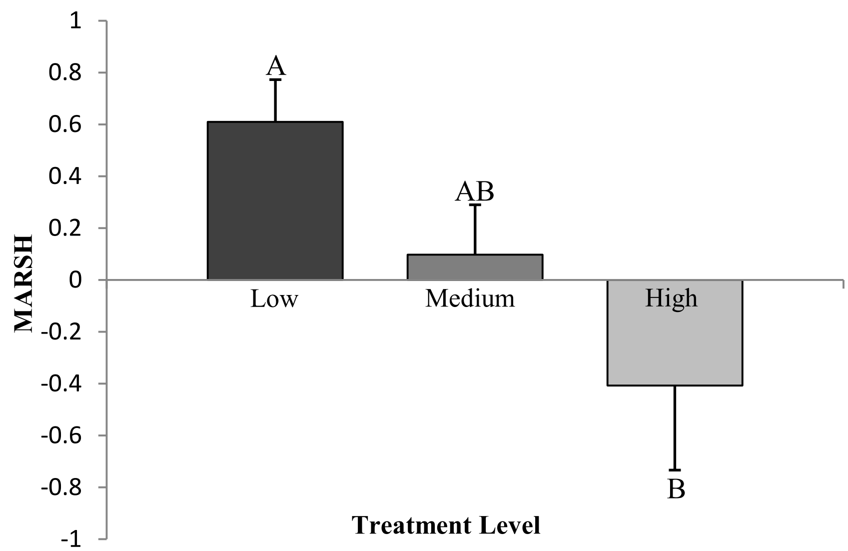

Figure 7. Spring 2008 (pre-hurricane) MARSH values by marsh loss treatment. Different letters indicate significant difference ($p < 0.05$).

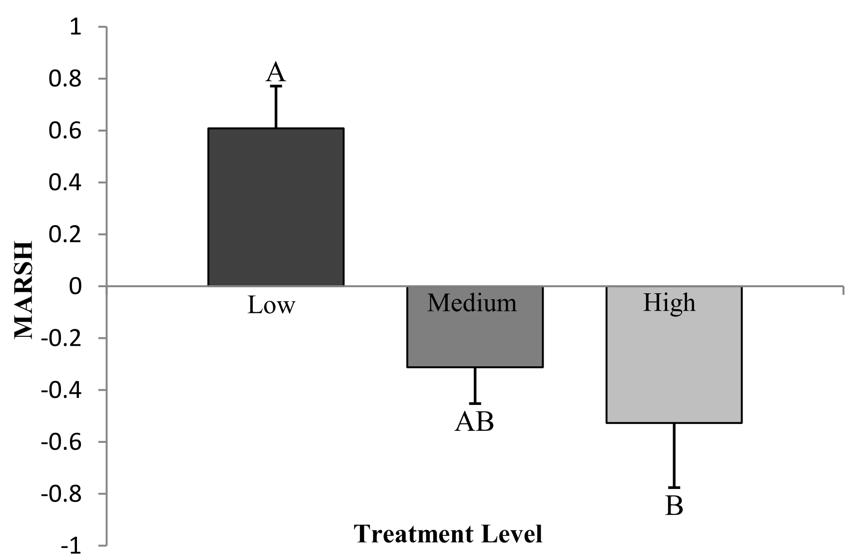

Figure 8. Fall 2008 (post-hurricane) MARSH values by marsh loss treatment. Different letters indicate significant difference ($p < 0.05$).

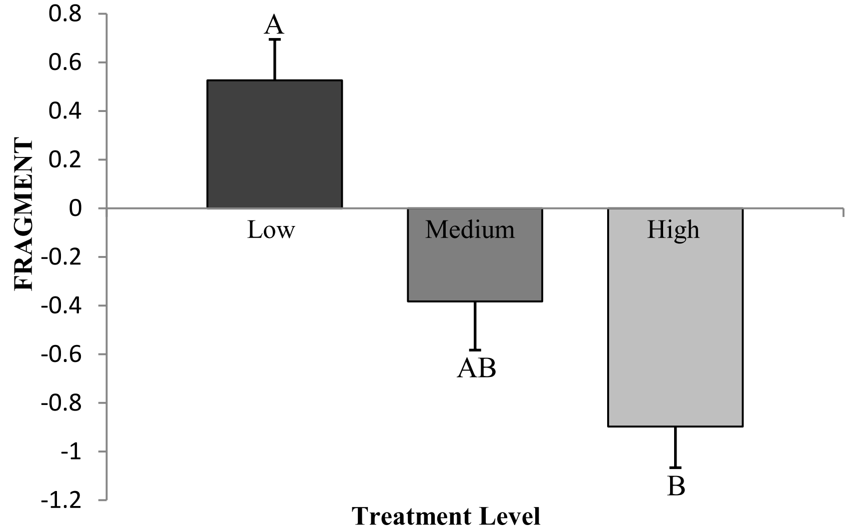

Figure 9. Spring 2008 (pre-hurricane) FRAGMENT values by marsh loss treatment. Different letters indicate significant difference ($p < 0.05$).

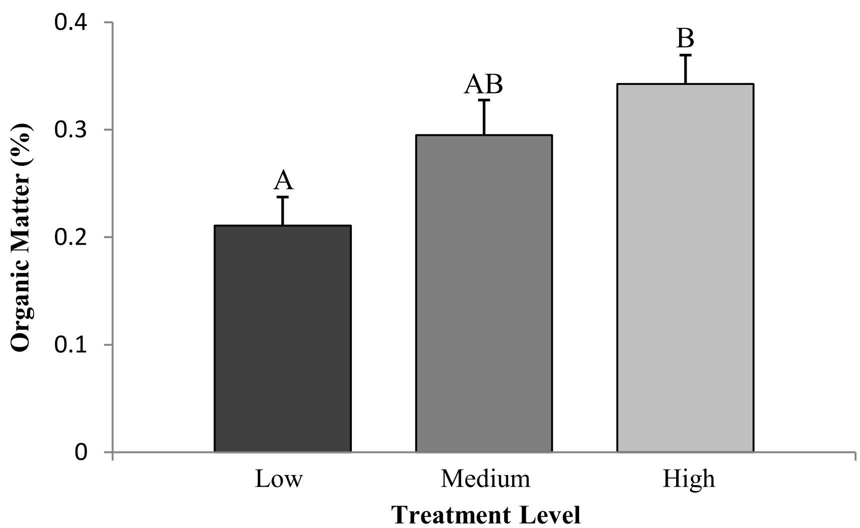

Figure 10. Spring 2008 (pre-hurricane) soil organic matter values by marsh loss treatment. Different letters indicate significant difference ($p < 0.05$).

Nekton Catch Summary

A total of 18,659 organisms representing 39 distinct taxa were caught over the course of this study. Spring sampling accounted for 10,383 individuals of 30 species with eleven species sufficiently abundant to be included in the analysis (Table 6). Fall sampling accounted for 8,276 individuals of 32 species with fourteen species being sufficiently abundant to be included in the analysis (Table 7).

Nekton Response to Marsh Loss

MANOVA tests for differences in nekton assemblage characteristics between marsh loss treatments were significant for spring ($p < 0.0001$) and fall ($p < 0.0001$). However, subsequent one-way ANOVAs found no significant differences between treatments for nekon species densities, total density, or Shannon-Wiener diversity (Tables 6-7). Results from one-way ANOVAs also indicated that relative condition factor scores did not differ between marsh loss treatments for any of the most commonly captured fishes (Tables 8-9).

Kendall's test for concordance (W) for ranked densities was highly significant in both sampling seasons for the most common species of fishes and crustaceans in the assemblage across marsh loss treatments (Spring: W = 0.822, Num df = 9.3, Den df = 18.7, $p < 0.001$), (Fall: W = 0.609, Num df = 12.3, Den df = 24.6, p = 0.0079). For the top five species, tests for concordance were significant in the spring (W = 0.867, F = 13.0 Num df = 3.3, Den df = 6.6, p = 0.0032, but not the fall (W = 0.444, Num df = 3.3, Den df = 6.7, p = 0.2781). In the spring sampling season, variation in rank across treatments was most apparent in brown shrimp *Farfantepenaeus aztecus* (Table 10). In the fall, variation between treatments were more apparent with sailfin molly *Poecilia latipinna*, white shrimp *Litopenaeus setiferus*, rainwater

Table 6. Spring (pre-hurricane) nekton catch summary displayed by marsh loss treatment. Tests for differences between treatments were run for all taxa that represented > 1.0 percent of the total finfish or decapod catch.

Scientific Name	**Season Total**	**Low Loss**		**Medium Loss**		**High Loss**		**Pr > F**
		N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	
Palaemonetes spp.	5915	999	20.8 ± 9.4	3755	69.5 ± 21.6	1161	21.5 ± 6.3	0.17
Poecilia latipinna	1229	491	10.2 ± 5.1	405	7.5 ± 3.4	333	6.2 ± 3.0	0.63
Gambusia affinis	889	388	8.1 ± 3.5	387	7.2 ± 3.8	114	2.1 ± 1.2	0.23
Cyprinodon variegatus	597	462	9.6 ± 3.9	87	1.6 ± 0.7	48	0.9 ± 0.4	0.55
Lucania parva	582	276	5.6 ± 3.0	249	4.6 ± 1.6	57	1.1 ± 0.3	0.19
Farfantepenaeus aztecus	230	58	1.2 ± 0.6	90	1.7 ± 0.6	82	1.5 ± 0.6	0.38
Anchoa mitchilli	189	63	1.3 ± 0.6	55	1.0 ± 0.8	71	1.3 ± 0.6	0.71
Menidia beryllina	158	85	1.8 ± 0.9	36	0.7 ± 0.3	37	0.7 ± 0.5	0.41
Gobiosoma bosc	119	1	0.1 ± 0.0	85	1.6 ± 0.7	33	0.6 ± 0.2	0.32
Callinectes sapidus	100	39	0.8 ± 0.2	39	0.7 ± 0.2	22	0.4 ± 0.1	0.32
Fundulus pulvereus	77	71	1.5 ± 1.0	5	0.1 ± 0.1	1	0.0 ± 0.0	0.34
Litopenaeus setiferus	51	30	0.6 ± 0.5	17	0.3 ± 0.2	4	0.1 ± 0.1	.
Family Xanthidae	43	0	0.0 ± 0.0	6	0.1 ± 0.0	37	0.7 ± 0.3	.
Microgobius gulosus	38	1	0.0 ± 0.0	20	0.4 ± 0.2	17	0.3 ± 0.2	.
Myrophis punctatus	28	19	0.4 ± 0.2	5	0.1 ± 0.1	4	0.1 ± 0.0	.
Syngnathus scovelli	23	5	0.1 ± 0.1	16	0.3 ± 0.1	2	0.0 ± 0.0	.
Bairdiella chrysoura	22	2	0.0 ± 0.0	2	0.0 ± 0.0	18	0.3 ± 0.2	.
Brevoortia patronus	21	4	0.1 ± 0.1	4	0.1 ± 0.0	13	0.2 ± 0.2	.
Mugil cephalus	19	6	0.1 ± 0.1	10	0.2 ± 0.1	3	0.1 ± 0.1	.
Fundulus grandis	18	7	0.1 ± 0.1	5	0.1 ± 0.0	6	0.1 ± 0.1	.
Leiostomus xanthurus	10	3	0.1 ± 0.0	7	0.1 ± 0.1	0	0.0 ± 0.0	.
Micropogonias undulatus	6	6	0.1 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	.
Procambarus clarkii	5	4	0.1 ± 0.1	1	0.0 ± 0.0	0	0.0 ± 0.0	.
Lagodon rhomboides	5	3	0.1 ± 0.0	1	0.0 ± 0.0	1	0.0 ± 0.0	.
Gobionellus boleosoma	4	0	0.0 ± 0.0	0	0.0 ± 0.0	4	0.1 ± 0.3	.
Cynoscion arenarius	1	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	.
Citharichthys spilopterus	1	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	.
Atractosteus spatula	1	1	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	.
Pogonias cromis	1	1	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	.
Uca spp.	1	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	.
Total Abundance	10383	3025	63.0 ± 14.4	5287	97.9 ± 27.7	2071	38.4 ± 9.5	0.39
Shannon Diversity (H')			1.0 ± 0.1		0.9 ± 0.1		0.9 ± 0.1	0.49

Table 7. Fall (post-hurricane) nekton catch summary displayed by marsh loss treatment. Tests for differences between treatments were run for all taxa that represented > 1.0 percent of the total finfish or decapod catch.

Scientific Name	**Season Total**	**Low Loss**		**Medium Loss**		**High Loss**		**Pr > F**
		N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	
Palaemonetes spp.	2438	910	16.7 ± 4.8	688	12.7 ± 3.3	840	15.6 ± 5.4	0.99
Poecilia latipinna	1377	1219	22.3 ± 14.1	133	2.5 ± 1.9	25	0.5 ± 0.4	0.13
Callinectes sapidus	1221	172	3.2 ± 0.7	527	9.8 ± 2.2	522	9.7 ± 2.2	0.48
Litopenaeus setiferus	1077	44	0.8 ± 0.3	265	4.9 ± 1.0	768	14.2 ± 7.7	0.26
Menidia beryllina	402	60	0.9 ± 0.4	175	3.2 ± 1.6	167	3.1 ± 1.2	0.34
Lucania parva	372	131	1.9 ± 0.7	194	3.6 ± 1.3	47	0.9 ± 0.4	0.43
Microgobius gulosus	211	17	0.3 ± 0.2	115	2.1 ± 0.8	79	1.5 ± 0.6	0.55
Gobiosoma bosc	203	6	0.1 ± 0.1	59	1.1 ± 0.4	138	2.6 ± 0.9	0.28
Farfantepenaeus aztecus	197	8	0.1 ± 0.1	91	1.7 ± 0.4	98	1.8 ± 0.7	0.21
Gambusia affinis	194	169	3.1 ± 1.4	17	0.3 ± 0.2	8	0.1 ± 0.1	0.15
Cyprinodon variegatus	147	124	2.3 ± 1.2	16	0.3 ± 0.2	7	0.1 ± 0.1	0.06
Anchoa mitchilli	144	2	0.0 ± 0.0	44	0.8 ± 0.5	98	1.8 ± 0.9	0.26
Micropogonias undulatus	68	5	0.1 ± 0.1	48	0.9 ± 0.4	15	0.3 ± 0.1	0.39
Gobionellus boleosoma	59	9	0.2 ± 0.1	11	0.2 ± 0.1	39	0.7 ± 0.3	0.33
Family Xanthidae	28	0	0.0 ± 0.0	2	0.0 ± 0.0	26	0.5 ± 0.4	.
Fundulus pulvereus	27	27	0.5 ± 0.2	0	0.0 ± 0.0	0	0.0 ± 0.0	.
Syngnathus scovelli	26	0	0.0 ± 0.0	10	0.2 ± 0.1	16	0.3 ± 0.1	.
Fundulus grandis	20	15	0.3 ± 0.1	3	0.1 ± 0.1	2	0.0 ± 0.0	.
Myrophis punctatus	14	2	0.0 ± 0.0	10	0.2 ± 0.1	2	0.0 ± 0.0	.
Gobionellus oceanicus	13	8	0.1 ± 0.1	2	0.0 ± 0.0	3	0.1 ± 0.0	.
Cynoscion nebulosus	8	0	0.0 ± 0.0	3	0.1 ± 0.0	5	0.1 ± 0.0	.
Mugil cephalus	6	2	0.0 ± 0.0	2	0.0 ± 0.0	2	0.0 ± 0.0	.
Bairdiella chrysoura	4	1	0.0 ± 0.0	1	0.0 ± 0.0	2	0.0 ± 0.0	.
Cynoscion arenarius	4	0	0.0 ± 0.0	4	0.1 ± 0.1	0	0.0 ± 0.0	.
Symphurus plagiusa	4	0	0.0 ± 0.0	2	0.0 ± 0.0	2	0.0 ± 0.0	.
Eucinostomus argentus	3	0	0.0 ± 0.0	3	0.1 ± 0.0	0	0.0 ± 0.0	.
Citharichthys spilopterus	2	0	0.0 ± 0.0	0	0.0 ± 0.0	2	0.0 ± 0.0	.
Dormitator maculatus	2	1	0.0 ± 0.0	1	0.0 ± 0.0	0	0.0 ± 0.0	.
Trichiurus lepturus	2	0	0.0 ± 0.0	2	0.0 ± 0.0	0	0.0 ± 0.0	.
Adinia zenica	1	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	.
Paralichthys lethostigma	1	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	.
Stellifer lanceolatus	1	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.0	.
Total Abundance	8276	2932	53.1 ± 16.9	2428	45.0 ± 7.5	2916	54.0 ± 12.0	0.94
Shannon Diversity (H')			0.9 ± 0.1		1.3 ± 0.1		1.3 ± 0.1	0.57

killifish *Lucania parva*, mosquitofish *Gambusia affinis*, sheepshead minnow *Cyprinodon variegatus*, and bay anchovy *Anchoa mitchilli* fluctuating greatly in rank across treatments (Table 11).

Table 8. Mean Relative Condition Factor (K_n) ± SE by treatment level for finfish species which accounted for > 1.0 percent of the total spring (pre-hurricane) finfish catch.

Species	Low	Medium	High	Mean	Pr > F
Anchoa mitchilli	1.05 ± 0.04	1.13 ± 0.11	0.99 ± 0.08	1.03 ± 0.04	0.59
Cyprinodon variegatus	1.09 ± 0.07	1.05 ± 0.02	0.96 ± 0.03	1.05 ± 0.03	0.47
Fundulus pulvereus	1.02 ± 0.04	1.15 ± 0.21	1.15 ± 0.00	1.08 ± 0.07	0.71
Gambusia affinis	1.07 ± 0.03	1.01 ± 0.02	1.09 ± 0.15	1.05 ± 0.04	0.69
Gobiosoma bosc	0.77 ± 0.00	1.02 ± 0.02	1.04 ± 0.04	1.01 ± 0.03	0.30
Lucania parva	1.17 ± 0.09	1.04 ± 0.03	1.02 ± 0.04	1.07 ± 0.04	0.32
Menidia beryllina	1.00 ± 0.03	1.01 ± 0.02	1.00 ± 0.10	1.00 ± 0.03	0.92
Poecilia latipinna	1.01 ± 0.04	0.99 ± 0.03	0.97 ± 0.03	0.99 ± 0.02	0.94

Table 9. Mean Relative Condition Factor (K_n) ± SE by treatment level for finfish species which accounted for at least 1.0 percent of the total fall (post-hurricane) finfish catch.

Species	Low	Medium	High	Mean	Pr > F
Anchoa mitchilli	0.85 ± 0.04	1.11 ± 0.25	0.90 ± 0.04	0.97 ± 0.09	0.51
Cyprinodon variegatus	0.96 ± 0.02	0.99 ± 0.12	1.05 ± 0.06	0.98 ± 0.03	0.64
Gambusia affinis	0.95 ± 0.05	0.97 ± 0.04	1.14 ± 0.06	1.01 ± 0.04	0.08
Gobionellus boleosoma	0.94 ± 0.01	1.08 ± 0.09	1.23 ± 0.06	1.14 ± 0.04	0.35
Gobiosoma bosc	0.96 ± 0.09	1.15 ± 0.05	1.05 ± 0.06	1.07 ± 0.04	0.38
Lucania parva	1.12 ± 0.07	1.14 ± 0.15	1.04 ± 0.04	1.10 ± 0.06	0.62
Menidia beryllina	1.05 ± 0.05	0.99 ± 0.03	0.98 ± 0.03	1.00 ± 0.02	0.20
Microgobius gulosus	1.02 ± 0.04	1.07 ± 0.05	1.07 ± 0.05	1.06 ± 0.03	0.40
Micropogonias undulatus	1.12 ± 0.09	1.03 ± 0.07	1.32 ± 0.18	1.16 ± 0.08	0.73
Poecilia latipinna	1.02 ± 0.06	1.05 ± 0.04	0.97 ± 0.06	1.02 ± 0.08	0.74

Table 10. Spring 2008 (pre-hurricane) ranks of the most frequently captured fishes and crustaceans by marsh loss treatment level.

Taxa	Low	Medium	High
Palaemonetes spp.	1	1	1
Poecilia latipinna	2	2	2
Gambusia affinis	4	3	3
Cyprinodon variegatus	3	6	7
Lucania parva	5	4	6
Farfantepenaeus aztecus	9	5	4
Anchoa mitchilli	8	8	5
Menidia beryllina	6	10	8
Gobiosoma bosc	11	7	9
Callinectes sapidus	10	9	10
Fundulus pulvereus	7	11	11

Table 11. Fall 2008 (post-hurricane) ranks of the most frequently captured fishes and crustaceans by marsh loss treatment level.

Taxa	Low	Medium	High
Palaemonetes spp.	2	1	1
Poecilia latipinna	1	6	11
Callinectes sapidus	4	2	3
Litopenaeus setiferus	8	3	2
Menidia beryllina	7	5	5
Lucania parva	5	4	9
Microgobius gulosus	9	7	8
Gobiosoma bosc	6	9	4
Farfantepenaeus aztecus	8	8	6
Gambusia affinis	3	12	13
Cyprinodon variegatus	6	13	14
Anchoa mitchilli	12	11	6
Micropogonias undulatus	11	10	12
Gobionellus boleosoma	10	14	10

Nekton Environment Associations

The results of the spring canonical correspondence analysis (CCA) indicated significant relationships between measured environmental variables and nekton assemblage characteristics during the spring sampling period (1^{st} axis: p = 0.004, All axes: p = 0.002) (Fig. 11). However, eigenvalues for the first and second axes accounted for only 1.6 and 1.1 percent of the variation within the nekton assemblage respectively (Table 12). The first axis, which accounted for 47.9 percent variance, was most related to dissolved oxygen (r = -0.60), organic matter (r = -0.42), FRAGMENT (r = 0.43), SAV biomass (r = 0.41), and MARSH (r = 0.38). Species such as naked goby *Gobiosoma bosc* (GB), bay anchovy (AM), and inland silverside *Menidia beryllina* (MB) were most negatively associated with axis 1. Bayou killifish *Fundulus pulvereus* (FP), sheepshead minnow (CV), western mosquitofish (GA), and sailfin molly (PL) were most positively associated. The second axis accounted for 31.0 percent of the variance and was most related to temperature (r = -0.49) and trap depth (r = 0.45). Bay anchovy and bayou killfish were most positively associated with axis two, while rainwater killifish (LP), blue crab *Callinectes sapidus* (CS), and the Shannon-Wiener Diversity index were most negatively associated.

The canonical correspondence analysis for fall relationships between measured environmental variables and nekton assemblage characteristics was also significant (1^{st} axis: p = 0.002, All axes p = 0.002) (Fig. 12). However, eigenvalues for the first and second axes were once again weak, accounting for only 3.5 and 1.3 percent of the variation within the nekton assemblage respectively (Table 13). The first axis, which accounted for 59.0 percent of the variance, was best related to MARSH (r = -0.55), SAV biomass (r = -0.50), organic matter (r = 0.50), FRAGMENT (r = -0.48), and dissolved oxygen (r = 0.42). Bay anchovy and naked goby

were the most positively associated with this axis. Sheepshead minnow western mosquitofish, and sailfin molly were the most negatively associated with this axis. The second axis, which accounted for 22.0 percent of the variance, was not strongly related to any variables entered in the factor analysis. Atlantic croaker *Micropogonias undulatus* (MU) and bay anchovy were the most positively correlated species to this axis. Rainwater killifish and inland silverside were the most negatively associated species to this axis.

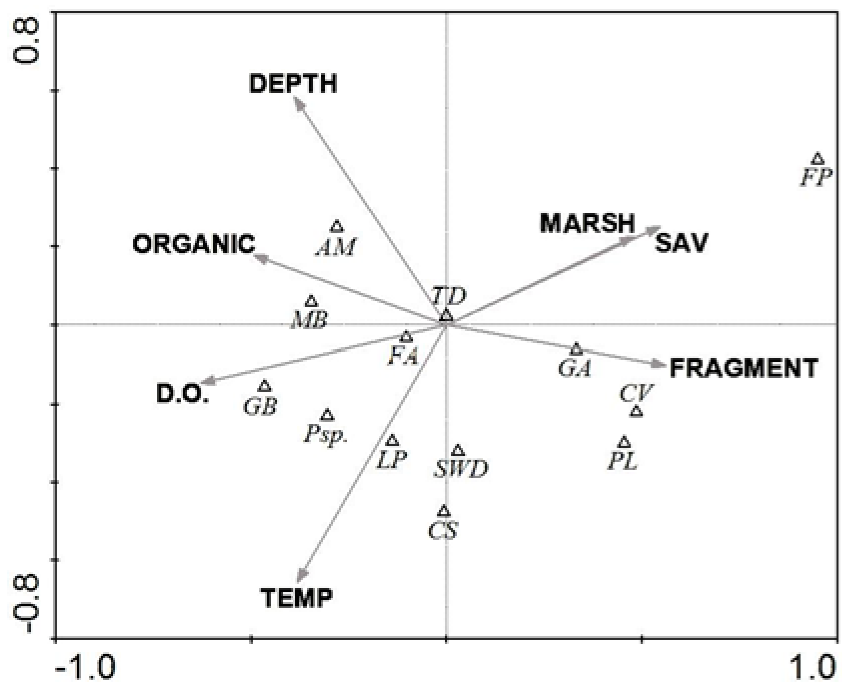

Figure 11. Association of nekton assemblage characteristics to ha scale landscape factors and marsh-edge characteristics from a canonical correspondence analysis from spring 2008 (pre-hurricane). Environmental variable and taxa codes are summarized in Table 12.

Table 12. Spring 2008 (pre-hurricane) canonical correspondence analysis results of nekton assemblage characteristics and environmental variables. Presented are eigenvalues and cumulative percentage variance of species–environment relationships.

Axis	Eigenvalue	Cumulative % Variance
1	0.016	47.9
2	0.011	78.9
3	0.003	87.5
4	0.002	93.4

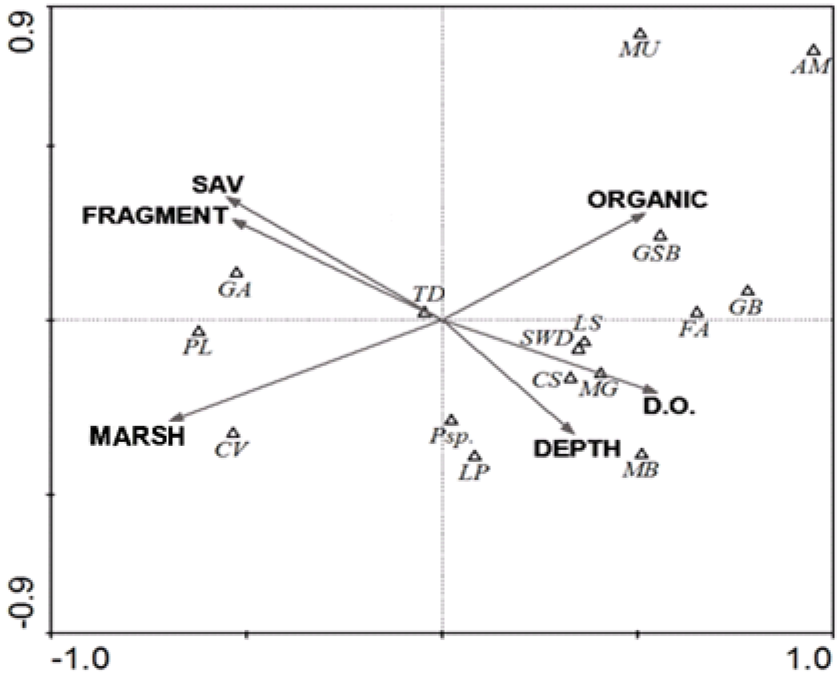

Figure 12. Association of nekton assemblage characteristics to ha scale landscape factors and marsh-edge characteristics from a canonical correspondence analysis from Fall 2008 (post-hurricane). Environmental variable and taxa codes are summarized in Table 13.

Table 13. Fall 2008 (post-hurricane) canonical correspondence analysis results of nekton assemblage characteristics and environmental characteristics. Presented are eigenvalues and cumulative percentage variance of species–environment relationships.

Axis	Eigenvalue	Cumulative % Variance
1	0.035	59.0
2	0.013	81.0
3	0.005	89.8
4	0.003	94.7

Table 14. Key to nekton and environmental variable codes from the spring and fall canonical correspondence analyses.

Taxa		Environmental Variables	
Code	**Scientific Name**	**Code**	**Description**
AM	*Anchoa mitchilli*	DEPTH	Trap Depth
CS	*Callinectes sapidus*	D.O.	Dissolved Oxygen
CV	*Cyprinodon variegatus*	TEMP	Temperature
FA	*Farfantepenaeus aztecus*	SAV	Submerged Aquatic Vegetation
FP	*Fundulus pulvereus*	ORGANIC	Sediment Organic Matter
GA	*Gambusia affinis*	MARSH	Area of marsh surface (ha scale)
GSB	*Gobionellus boleosoma*	FRAGMENT	Fragmentation (ha scale)
GB	*Gobiosoma bosc*		
LP	*Lucania parva*		
MB	*Menidia beryllina*		
MG	*Microgobius gulosus*		
MU	*Micropogonias undulatus*		
PL	*Poecilia latipinna*		
PS	*Litopenaeus setiferus*		
Psp.	*Palaemonetes spp.*		
SWD	Shannon Wiener Diversity		
TD	Total Density		

DISCUSSION

The results of this study indicate that coastal marsh loss at the 1 km^2 scale may significantly influence environmental characteristics within Louisiana's coastal ecosystems. Sediment organic matter, FRAGMENT, and MARSH differed significantly between 1 km^2 scale marsh loss treatments in at least one sampling season (Tables 4 and 5). Despite these differences in environmental characteristics, a clear and consistent difference in nekton assemblages between treatments was not evident in this study. No significant differences between treatments were detected for either species density, total density, Shannon-Wiener Diversity (H'), or Relative Condition Factor (K_n) (Tables 6 – 9). Kendall's test for concordance (W) found that only the top five most frequently captured species from the fall season were not concordant across treatments. Collectively, these results indicate that marsh loss at the 1 km^2 scale may not play an important role in shaping nekton assemblages along the marsh edge. They further suggest that the environmental variables which differed between treatments may not be important influences on nekton assemblages; a finding which is supported by the low percentage of variance in nekton assemblages accounted for by the axes of the canonical correspondence analysis in (Tables 12 and 13).

The lack of a clear nekton response to marsh loss at the 1 km^2 scale may be attributable to several possible explanations. Perhaps the most likely of these may be that marsh loss treatments were defined by the percentage of area occupied by open water. Small nekton may be unlikely to respond to shifts in the area of open water because this environment is infrequently used by small nekton due to increased risk of predation by larger fishes (Boesch and Turner 1984). Similarly, the marsh interior is rarely accessible to nekton in many areas due to the low frequency and duration of flooding events. The tendency of small nekton to avoid these

environments was illustrated by Minello (2008) who found that densities of crustaceans were roughly ten times greater on the marsh edge than in either open water or marsh surface areas greater than 10 m from the marsh edge. Marsh area may play a more significant role in shaping nekton assemblages in marshes where flooding frequency and duration are high. For example, in a restored New Jersey marsh which experienced semi-diurnal flooding averaging 2-3 hours in duration, Teo and Able (2003) found that mummichogs (*Fundulus heteroclitus*) used up to 15 ha of marsh surface despite having strong fidelity to a particular marsh creek during low tide. The use of such an extensive area suggests that small patches of marsh surface may be insufficient to maximize fitness. Although access to the marsh surface has been shown to increase growth rates in small fishes (Javonillo et al. 1997), it remains unclear exactly how much marsh area is needed to maximize growth rates or total fitness. It is likely however to be contingent upon an assortment of other factors such as flooding regime and availability of prey items.

Environmental differences between treatments were not limited to infrequently used habitats such as open water or marsh interior. Nekton assemblages also failed to respond to greater marsh edge availability (as indicated by FRAGMENT values) in the low marsh loss treatment during the spring season ($p = 0.0260$) (Fig 9). In conjunction with previous research, this may indicate that the area or availability of frequently used habitats may not have a substantial influence on nekton assemblages at micro-scales (1 m^2). Rozas and Minello (2007) found that reducing marsh terrace cell size and therefore increasing density of marsh terraces had no effect on micro-scale (1 m^2) densities of small nekton on the marsh edge. Additionally, Johnson and Heck (2006) found that only mud crab (Xanthidae) density differed between seagrass patches of different sizes. Johnson and Heck reasoned that the weak nekton response to habitat availability

may be due to the generalist nature of most species of small nekton in regards to habitat selection.

The issue of scale could be another possible explanation for the lack of a detectable nekton response to 1 km^2 scale marsh loss. The influence of habitat loss and fragmentation on fauna has been shown to be scale dependant (Debinski and Holt 2000, Stephens et al. 2003, Cerezo et al. 2010). Thus, it may be wisest to design studies at a scale which most closely reflects the ecological characteristics of the taxa of interest. The selection of 1 km^2 marsh loss treatments may be inappropriate for some species of small marsh nekton because it does not closely reflect the size of their home ranges (10 m – 15 ha) (Lotrich 1975, Potthoff and Allen 2003, Teo and Able 2003). The landscape factor MARSH, which provides an inverse measure of marsh loss at the 1 ha scale, was significantly greater in the low loss treatment in both seasons (Spring: $p = 0.0379$, Fall: $p = 0.0353$). Nekton assemblages did not appear to respond to this difference however, suggesting that marsh loss at the 1 ha scale may not be an important controlling factor on nekton assemblages.

The results of the canonical correspondence analysis provide further statistical support to the notion that landscape factors FRAGMENT and MARSH, as well as marsh-edge characteristics, do not strongly influence nekton assemblages. Eigenvalues associated with canonical axes in both sampling seasons accounted for only 1-3 percent of the variance within nekton assemblages (Tables 12 and 13). Although the CCA indicates only very weak relationships between environmental variables and nekton assemblage characteristics, several of these relationships were consistent across seasons and with previous research suggesting further discussion is warranted (Fig 11 and 12). Common marsh resident fishes (sailfin molly, sheepshead minnow, and western mosquitofish) were consistently associated with MARSH, FRAGMENT, and

submerged aquatic vegetation biomass in both seasons. Areas of low marsh loss may be attractive to many species of small nekton because narrow channels are believed to provide refuge from predators (Weinstein 1979, Werme 1981, Odum 1984, Paterson and Whitfield 2000). Additionally, the association of SAV biomass with these areas may further improve the value of these habitats for small nekton. Submerged aquatic vegetation is widely believed to support greater densities of nekton than adjacent un-vegetated substrate due to the more productive feeding ground and greater degree of protection from large predators that these habitats provide (Rozas and Odum 1988, Heck et al. 2003, Kanouse et al. 2006). Several species were consistently associated with the opposing end of the first axis. Bay anchovies may be avoiding areas occupied by submerged aquatic vegetation in favor of open water habitats (Wyda et al. 2002). Demersal feeding species such as gobies and crustaceans may be attracted to areas of higher marsh loss in search of prey. Sediment organic matter, which was associated with the high loss end of the axis, is linked to the density and diversity of benthic infaunal prey (Moy and Levin 1991, Sacco et al. 1994).

Possible associations between nekton assemblage characteristics and environmental variables may help to explain the results of Kendall's test for concordance (W). Kendall's W found nekton assemblages to be concordant across treatments with the exception of the top five most abundant taxa from the fall season. In conjunction with the ANOVA tests, the results of Kendall's W tests indicate a lack of clear treatment effect on nekton assemblages. Random variation may be the cause of the discordance amongst the top five most abundant taxa in the fall season, but this could also be the result of relationships between taxa and environmental variables. Discordance in the top five species of the fall season was primarily caused by variation across treatments in sailfin molly and white shrimp (Table 11). Sailfin molly was

ranked higher in the low loss treatment (1st) than in the high loss treatment (11th). This concurs with the association seen between sailfin molly and MARSH, which was significantly greater in the high loss treatment in the fall ($p = 0.0353$). White shrimp were ranked higher in the high loss treatment (2nd) than in the low loss treatment (8th). This may be a response to sediment organic matter which was significantly greater in the high loss treatment in the spring ($p = 0.0217$) and nearly greater in the high loss treatment in the fall ($p = 0.12$).

The CCA also provided some insight into the relationships between environmental variables. For both seasons, the first axis appeared to describe two inversely related environments. On one end of the first axis, MARSH formed a variable cluster with FRAGMENT and SAV. FRAGMENT was likely associated with MARSH in this study because no sampling points were surrounded with more than ~ 85 % marsh surface. This resulted in a more positive linear relationship between marsh surface and marsh edge (See Appendix B) rather than the complete quadratic relationship described in Browder (1985) (Fig. 1). Submerged aquatic vegetation biomass may associate with areas of low marsh loss due to low fetches and wave energy which is known to suppress the establishment and size of submerged aquatic vegetation (Dan et al. 1998, Robbins and Bell 2000).

On the opposing end of axis 1, a variable cluster was formed by sediment organic matter and dissolved oxygen. Dissolved oxygen may be negatively associated with MARSH because high wave energy associated with greater fetches can facilitate the mixing of oxygen with water. The negative relationship between sediment organic matter and MARSH is likely related to the finding that sediment organic matter was higher in the high marsh loss treatment than in the low loss treatment in the spring. Higher sediment organic content found in the high loss treatment suggests these areas also possessed low percent mineral content. Although mineral matter alone

is unrelated to sediment strength (McGinnis 1997), it has been shown to stimulate growth in marsh plants including *S. alterniflora* (Delaune et al. 1979) and *S. patens* (Nyman et al. 1994). Greater root biomass in turn has been shown to relate to soil strength (McGinnis 1997), and thus may reduce the probability of marsh damage due to storms and erosion. An alternative hypothesis relating sediment characteristics with marsh loss was supported by work by DeLaune et al. (1994). The authors suggest that the decomposition of organic peat deposits could be a major cause of marsh loss. Therefore, marsh sediments composed of higher percent organic content could be more susceptible to increased rates of marsh loss. Additional hypotheses indicate that high organic matter in sub-tidal sediments could be the result of marsh loss caused by processes independent of organic matter. Highly organic sub-tidal sediments could merely be the remnants of subsided or eroded marsh surface.

A difference in sediment organic matter between treatments was not detected in the fall data set largely due to substantial changes in sediment organic content in all treatments of the Sabine Hog Island Gully study unit. Hurricane storm surge has been shown to be capable of redistributing organic matter between marsh locations (Chabreck and Palmisano 1973). Hog Island Gully was the only study unit not impounded by levees and thus may have experienced greater flushing action during the passing of Hurricane Ike. It is possible that landward flowing storm surge may have flushed organic matter northward from large marsh ponds in the medium and high loss treatments to the low loss treatment.

The influence of Hurricane Ike was also likely responsible for observed changes in the variable FRAGMENT between seasons. FRAGMENT was originally found to be greatest in the low marsh loss treatment during the spring sampling period. However, analysis of post-hurricane (Fall) data failed to detect this difference. Hurricane damage appeared to increase

edge in the medium and high loss treatments of Sabine NWR Unit Five by cutting new channels and depositing small chunks of marsh wrack into open water.

The pre-hurricane (Spring) finding that FRAGMENT was highest in the low loss treatment conflicts with previous research which demonstrates that marsh edge should be greatest when marsh surface covers fifty percent of total area (Browder et al. 1985). Several possible explanations exist for the disagreement between these two studies. First, the work by Browder et al. (1985) was based upon mathematical simulations rather than actual imagery from Louisiana's coast. Later work by Browder et al (1989) which did use marsh area and edge data collected from thematic imagery of Louisiana's coast found a relationship which suggests that marsh edge peaks when water occupies 30-50 percent of the landscape. However, this trend may have been distorted by a lack of data in the 80-100 percent water area range. Perhaps a more likely explanation for the discrepancy between this study and Browder (1985) is that the relationship between marsh area and edge availability is heavily influence by the pattern of marsh loss (Browder et al. 1985, Browder et al. 1989). This allows for wide variation in marsh area/edge relationships between marshes and may explain why the expected relationship between marsh loss and edge was not seen in the 1 km^2 marsh loss treatments.

Hurricane influence on other variables including salinity, trap depth, and SAV biomass were suspected in this study but could not be confirmed due to confounding seasonal effects. However, the influence of hurricanes has been shown in previous studies to have a substantial impact on salinity, emergent and submerged aquatic vegetation, and dissolved oxygen (Chabreck and Palmisano 1973, Steward et al. 2006, Maiaro 2007, Piazza and La Peyre 2009). These changes in environmental characteristics have been implicated as the primary cause of hurricane-related shifts in nekton assemblages. For example, Piazza and La Peyre (2009) found greater

nekton density, biomass, and richness on the marsh surface six months after a direct hit by Hurricane Katrina. Increases in density and biomass were largely attributed to grass and mysid shrimps which may have responded to increased marsh breakup and the availability of decomposing marsh wrack. The observed increase in richness may have resulted from elevated salinity levels which likely attracted estuarine migrants. Similarly, Steward et al. (2006) found that decreases in salinity due to increased freshwater discharge altered assemblage structure by attracting freshwater migrants into the estuary. Maiaro (2007) found that hurricane-related damage to seagrass beds altered nekton assemblage structure by reducing the abundance of several seagrass dependant species (rainwater killifish, gulf pipefish, grass shrimp).

Despite the substantial influence of hurricanes on nekton and their habitats, the effects of hurricane landfall did not appear to alter nekton response to marsh loss or fragmentation. In both sampling seasons, nekton assemblages did not clearly respond to 1 km^2 marsh loss treatments. Further, the canonical correspondence analysis appeared to demonstrate similar nekton response to environmental variables through both sampling seasons. The effects of hurricane landfall on nekton densities in this study did not appear to be extensive when compared to the natural variability in nekton densities between locations and years; a finding which concurs with the results of several other studies (Greenwood et al. 2006, Paperno et al. 2006). A review of studies which sampled sub-tidal marsh edges within study units similar to those used in this study revealed nekton densities as high as 34.5 individuals/m^2 (La Peyre and Gossman 2007) and as low as 5-10 individuals/m^2 (Bush Thom et al. 2004, Llewellyn 2008). Densities for this study (Spring: 72.1/m^2, Fall: 51.1/m^2) were more comparable to those of Kanouse and La Peyre (2006) who reported densities of 77.0 individuals / m^2 from SAV habitats within 1 m of the marsh edge. Although this study did not target SAV habitats near the marsh edge, SAV was frequently

detected in the throw trap in various quantities and may have been partially responsible for the high densities detected in this study.

It has been well established that marsh loss and fragmentation affect the availability of marsh-edge habitat. Many studies have used the availability of marsh edge as a primary indicator of nekton production in coastal marshes. These studies have relied on the assumption that marsh edges support equivalent nekton densities per meter of edge regardless of the degree of loss or fragmentation of the surrounding marsh landscape. This study tested this assumption in an effort to improve these estimates. Results show that although marshes exhibiting different degrees of marsh loss did exhibit slightly different habitat conditions, marsh-edge nekton assemblage characteristics did not differ significantly between treatments. This finding implies that efforts to estimate nekton productivity in coastal marshes should continue to rely on the assumption that marsh edges support equivalent nekton assemblages regardless of the degree of marsh loss. Although this study did provide some weak evidence that several nekton species may respond to 1 ha scale differences in marsh loss and fragmentation, most estimates of marsh nekton productivity must be performed at scales much larger than 1 ha to be valuable for fishery production estimates.

LITERATURE CITED

Anderson, R. O. and R.M. Neumann. 1996. Length, weight, and associated structural indices. pp. 447-476 In: Murphy, B.R. and Willis D.W. editors. Fisheries techniques. 2nd ed. Bethesda, Maryland: American Fisheries Society.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71:355-366.

Baltz, D.M., C.F. Rakocinski, and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36:109-126.

Barras, J.A., J.C. Bernier, and R.A. Morton. 2008. Land area change in coastal Louisiana−A multi-decadal perspective (from 1956 to 2006): U.S. Geological Survey Scientific Investigations Map 3019, scale 1:250,000, 14 p. pamphlet.

Boesch, D. F., M. N. Josselyn, J. M. Ashish, J. T. Morris, W. K. Nuttle, C. A. Simenstad, and D. J. P. Swift. 1994. Scientific Assessment of Coastal Wetland Loss, Restoration and Management in Louisiana. Journal of Coastal Research. Special Issue no. 20. 103 pp.

Boesch, D.F. and R.E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7:460-468.

Browder, J.A., H.A. Bartley, and K.S. Davis. 1985. A probabilistic model of the relationship between marshland-water interface and marsh disintegration.

Browder, J.A., L.N. May, A. Rosenthal, J.G. Gosselink, and R.H. Baumann. 1989. Modeling future trends in wetland loss and brown shrimp production in Louisiana using thematic mapper imagery. Remote Sensing of Environment 28:45-59.

Bush Thom, C.S., M.K.G. La Peyre, and J. A. Nyman. 2004. Evaluation of nekton use and habitat characteristics of a restored Louisiana marsh. Ecological Engineering 23:63-75.

Caley M.J., K.A. Buckley, and G.P. Jones. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. Ecology 82:3435–3448.

Cerezo A., S. Perelman, and C.S. Robbins. 2010. Landscape-level impact of tropical forest loss and fragmentation on bird occurrence in eastern Guatemala. Ecological Modeling 221:512-526.

Chabreck, R. H. and A.W. Palmisano. 1973. The effects of Hurricane Camille on the marshes of the Mississippi River Delta. Ecology 54:1118-1123.

Chambers, J. R. 1992. Coastal degradation and fish population losses. P. 45-51. In R. H. Stroud (Ed.), Stemming the Tide of Coastal Fish Habitat Loss. National Coalition for Marine Conservation, Inc., Savannah, Georgia.

Chen, J. and J. F. Franklin. 1990. Microclimatic configuration and basic biological responses at the clear-cut edges of old-growth Douglas-fir stands. Northwest Environmental Journal 6:424-425.

Collins R.J. and G.W. Barrett. 1997. Effects of habitat fragmentation on meadow vole (Microtus pennsylvanicus) population dynamics in experiment landscape patches. Landscape Ecology 12:63–76

Dan, A., A. Moriguichi, K. Mitsuhashi, and T. Terawaki. 1998. Relationship between Zostera marina and bottom sediments, wave action offshore in Naruto, Southern Japan. Fisheries Engineering 34:229–204.

Debinski, D.M. and R.D. Holt. 2000. Review. A survey and overview of habitat fragmentation experiments. Conservation Biology 14:342-355.

Dow, D.D. 1982. Software programs to measure interface complexity with remote sensing data, with an example of a marine ecosystem application. NASA Rep. 219. National Aeronautics and Space Administration, Earth Resources Laboratory, National Space Technology Laboratories, NSTL, MS, 25 pp.

East, J.W., Turco, M.J., and Mason, R.R., Jr., 2008, Monitoring inland storm surge and flooding from Hurricane Ike in Texas and Louisiana, September 2008: U.S. Geological Survey Open-File Report 2008–1365 [http://pubs.usgs.gov/of/2008/1365/].

Farhig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Faller, K.H. 1979. Shoreline as a controlling factor in commercial shrimp production. NASA Tech. Memo, 72-732 33 pp.

Fleiss J.L. 1981. Statistical methods for rates and proportion, 2nd edn. John Wiley & Sons Inc, New York

Gauch, H. G. Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York. 298 p.

Gilpin, M. E., and I. Hanski. 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, San Diego. 336 pp.

Greenwood, M. F. D., P. W. Stevens, and R. E. Matheson, Jr. 2006. Effects of the 2004 hurricanes on the fish assemblages in two proximate southwest Florida estuaries: change in the context of inter-annual variability. Estuaries and Coasts 29:985-996.

Halpin P.M. 1997. Habitat use patterns of the mummichog, Fundulus heteroclitus, in New England. I. Intramarsh variation. Estuaries & Coasts 20:618–625.

Haunert, D.E. and J.R. Startzman. 1980. Some seasonal fisheries trends and effects of a 100 cfs fresh water discharge on the fishes and macro-invertebrates in the St. Lucie estuary, Florida. South Florida Water Management District Technical Publication No. 80-3, West Palm Beach, Florida.

Hovel, K.A. and R.N. Lipcius. 2001. Habitat fragmentation in a seagrass landscape: Patch size and complexity control blue crab survival. Ecology 82:1814-1829.

Jackson, E.L., M.J. Attrill, and M.B. Jones. 2006. Habitat characteristics and spatial arrangement affecting the diversity of fish and decapods assemblages of seagrass beds around the coast of Jersey (English Channel). Estuarine, Coastal, and Shelf Science 68:421-432.

Jacobus, J. and P.W. Webb. 2005. Using fish distributions and behavior in patchy habitats to evaluate potential effects of fragmentation on small marsh fishes: A case study. Journal of Great Lakes Research. 31:197-211.

Javonillo, R., L. Deagan, K. Chiaravalle, J. Hughes. 1997. The importance of access to salt-marsh surface to short term growth of Fundulus heteroclitus in a New England Salt Marsh.

Johnson, M.W. and K.L. Heck. 2006. Effects of habitat fragmentation per se on decapods and fishes inhabiting seagrass meadows in the northern Gulf of Mexico. Marine Ecology Progress Series 306:233-246.

Kanouse, S., M.K. La Peyre, and J.A. Nyman. 2006. Nekton use of Ruppia maritima and non-vegetated bottom habitat types within brackish marsh ponds. Marine Ecology Progress Series 327:61-69.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Phil. Trans. R. Soc. Lond. B 330:175-190.

Kendall, M.G. 1955. Rank correlation methods, 2nd edn. Charles Griffin & Co Ltd, London

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

Landgrebe, D. and L. Biehl. 2007. MULTISPEC: a multispectral imagery data analysis system. Computer software program produced by the authors at Purdue University. Available at http://cobweb.ecn.purdue.edu/~biehl/MultiSpec/

Landis, J.R. and G.G. Koch. 1977. The measurement of observer agreement for categorical data. Biometrics 33:159-174

La Peyre, M.K., B. Gossman, and J.A. Nyman. 2007. Assessing functional equivalency of nekton habitat in enhanced habitats: Comparison of terraced and unterraced marsh ponds. Estuaries and Coasts 30:526-536.

La Peyre, M.K. and T. Birdsong. 2008. Physical variation of non-vegetated marsh-edge habitats, and use patterns by nekton in Barataria Bay, Louisiana, USA. Marine Ecology Progress Series 356:51-61.

Layman, C.A., D.A. Arrington, R.B. Langerhans, and B.R. Silliman. 2004. Degree of fragmentation affects fish assemblage structure in Andros Island Estuaries. Caribbean Journal of Science 40:232-244.

Layman, C.A., J.P. Quattrochi, C.M. Peyer, and J.P. Allgeier. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters 10:937-944.

Llewellyn, C.B. 2008. Evaluating ecological equivalence in created marshes, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge, LA, USA

Long, W.C. and R.P. Burke. 2007. Habitat size, flora, and fauna: Interactions in a tidal saltwater marsh. Journal of Experimental Marine Biology and Ecology 353:80-88.

Lotrich, V. A. 1975. Summer home range and movements of Fundulus heteroclitus in a tidal creek. Ecology 56:191–198.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey 179 pp.

Maiaro, J. L. 2007. Disturbance effects on nekton communities of seagrasses and bare substrates in Biloxi marsh, Louisiana. M.S. Thesis. Louisiana State University, Baton Rouge, LA, USA.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA For. Serv. Gen. Tech. Rep. PNW-351.

McGarigal, K. and S.A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12:335-345.

McGarigal, K., S.A. Cushman, M.C. Neel, and E. Ene . 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at www.umass.edu/landeco/Research/fragstats/fragstats.html

McGarigal, K. and W.C. McComb 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs. 65:235–260

McGinnis, T. E. 1997. Factors of soil strength and shoreline movement in a Louisiana coastal marsh. M.S. Thesis. University of Louisiana, Lafayette, LA, USA.

Micheli, F. and C.H. Peterson. 1999. Estuarine vegetated habitats as corridors for predator movements. Conservation Biology 4:869–881.

Minello, T.J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. American Fisheries Society Symposium 22: 43-75.

Minello, T.J. and L.P. Rozas. 2002. Nekton in gulf coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. Ecological Applications 12:441-455.

Minello, T.J., L.P. Rozas, G.A. Matthews, and P.A. Caldwell. 2008. Population and production estimates for decapods crustaceans in wetlands of Galveston Bay, Texas. Transactions of the American Fisheries Society 137:129-146.

Moy, L. D. and L. A. Levin. 1991. Are Spartina marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries 14:1-6.

Nyman, J.A., M. Carloss, R.D. DeLaune, and W.H. Patrick, Jr. 1994. Erosion rather than plaint dieback as the mechanism of marsh loss in an estuarine marsh. Earth Surface Processes and Landforms. 19:69-84.

Odum, W.E. 1984. Dual-gradient concept of detritus transport and processing in estuaries. Bulletin of Marine Science 35:510-531.

Orth, R.J., K.L. Heck, and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7:339–350.

Paperno, R., D. M. Tremain, D. H. Adams, A. P. Sebastian, J. T. Sauer, and J. Dutka-Gianelli. 2006. The disruption and recovery of fish communities in the Indian River Lagoon, Florida, following two hurricanes in 2004. *Estuaries and Coasts*29:1004-1010.

Paterson, A.W. and A.K. Whitfield. 2000. Do shallow-water habitats function as refugia for juvenile fishes? Estuarine Coastal and Shelf Science 51:359–364

Penland, S., H. H. Roberts, S. J. Williams, A. H. Sallenger Jr., D. R. Cahoon, D. W. Davis, and C. G. Groat. 1990. Coastal land loss in Louisiana. Transactions of the Gulf Coast Associations of Geological Societies 90:685-699.

Piazza, B.P. and M. K. La Peyre. 2009. The effect of Hurricane Katrina on nekton communities in the tidal freshwater marshes of Breton Sound, Louisiana, USA. Estuarine, Coastal, and Shelf Science 83:97-104.

Potthoff, M.T. and D.M. Allen. 2003. Site fidelity, home range, and tidal migrations of juvenile pinfish, Lagodon rhomboides, in salt marsh creeks. Environmental Biology of Fishes 67:231-240.

Ramsey, K.E. and S. Penland. 1989. Sea-level rise and subsidence in Louisiana and the Gulf of Mexico. Gulf Coast Association of Geological Societies Transactions. 39:491-500.

Robbins, B. D. and S. S. Bell. 2000. Dynamics of a subtidal seagrass landscape: Seasonal and annual changes in relation to water depth. Ecology 81:1193–1205.

Roth, B.M., K.A. Rose, L.P. Rozas, and T.J. Minello. 2008. Relative influence of habitat fragmentation and inundation on brown shrimp Farfantepenaeus aztecus production in northern Gulf of Mexico salt marshes. Marine Ecology Progress Series 359:185-202.

Rozas, L.P., and D.J. Reed. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. Marine Ecology Progress Series 96:147–157.

Rozas, L.P. and T.J. Minello. 2007. Restoring coastal habitat using marsh terracing: The effect of cell size on nekton use. Wetlands 27:595-609.

Rozas, L.P. and W. E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77:101-106.

Rypel, A.L. and C.A. Layman. 2008. Degree of aquatic ecosystem fragmentation predicts population characteristics of gray snapper (Lutjanus griseus) in Caribbean tidal creeks. Canadian Journal of Fisheries and Aquatic Science 65:335-339.

Sacco, J. N., E. D. Seneca, and T. R. Wentworth. 1994. Infaunal community development of artificially established salt marshes in North Carolina. Estuaries 17:489-500.

Saunders, D. A., R. T. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Smith, K.J. and K.W. Able. 2003. Dissolved oxygen dynamics in salt marsh pools and its potential impacts on fish assemblages. Marine Ecology Progress Series 258:223–232

Stephens, S.E., D.N. Koons, J.J. Rotella, and D.W. Willey. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101-110.

Steward, J. S., R. W. Virnstein, M. A. Lasi, L. J. Morris, J. D. Miller, L. M. Hall, and W. A. Tweedale. 2006. The impacts of the 2004 hurricanes on hydrology, water quality, and seagrass in the central Indian River Lagoon, Florida. Estuaries and Coasts 29:954-965.

Syms, C. and G.P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81:2714–2729.

Teo, S.L.H. and K.W. Able. 2003. Habitat use and movement of the Mummichog (Fundulus heteroclitus) in a restored salt marsh.

ter Braak, C.J.F. and P. Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, NY

Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106:411-416.

Valentine-Rose, L., C.A. Layman, D.A. Arrington, and A.L. Rypel. 2007. Habitat fragmentation decreases fish secondary production in Bahamian tidal creeks. Bulletin of Marine Science 80:863-877.

Villard, M.A., M.K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13:774–83.

Vince, S., I. Valiela, and N. Backus. 1976. Predation by the salt-marsh killifish Fundulus heteroclitus (L.) in relation to prey size and habitat structure: Consequences for prey distribution and abundance. Journal of Experimental Marine Biology and Ecology 23:255-266.

Watson, J.E.M, R.J. Whittaker, and T.P. Dawson. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependant birds in tropical coastal forests of southeastern Madagascar. Biological Conservation 120:311-327

Weinstein, M.P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fisheries Bulletin 77:339-357.

Werme, C.E. 1981. Resource partitioning in a salt marsh fish community. Ph.D. Dissertation. Boston University.

Wicker, K.M., D. Davis, and D. Roberts. 1983. Rockefeller State Wildlife Refuge and Game Preserve: evaluations of wetland management techniques. Coastal Management Division, Louisiana Department of Natural Resources, Baton Rouge, Louisiana

Wyda, J.C., L.A. Deegan, J.E. Hughes, M.J. Weaver. 2002. The response of fishes to submerged aquatic vegetation complexity in two ecoregions of the mid-atlantic bigt: Buzzards Bay and Chesapeake Bay. Estuaries 25:85-100.

Zimmerman, R.J., T.J. Minello, and L.P. Rozas. 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. P. 293-314: In Weinstein, M.P. and D.A. Kreeger (eds.) Concepts and controversies in tidal marsh ecology: Kluwer Academic Publishers. Dordrecht, Netherlands.

APPENDIX A

PROPOSAL OF AN ALTERNATE STUDY DESIGN

The original goals of this study were to investigate the influence of marsh loss and fragmentation at multiple scales on marsh nekton assemblages and the environmental characteristics which support them. This study does present a sound design for investigating the impact of 1 km^2 scale marsh loss on nekton and microhabitat variables, but fails to provide definitive answers regarding fragmentation at the 1 km^2 scale as well as 1 ha scale marsh loss and fragmentation. Therefore, a new study design should be developed to address these weaknesses. Achieving all of these goals would require an elaborate design that may be difficult to analyze and interpret. Thus, it may be wisest to employ multiple studies to address all of these questions. Nevertheless, the following design attempts to achieve all of the afore mentioned goals in a single study.

The basic study design involves a replicated 3x3 factorial split by a second 3x3 factorial. This design would be built with four orthogonal factors: 1 km^2 marsh loss, 1 km^2 fragmentation, 1 ha marsh loss, and 1 ha fragmentation. Three levels (low, medium, and high) of each factor would be included in this study. The first 3x3 factorial would be built by the 1 km^2 marsh loss and 1 km^2 fragmentation factors. This alone would test for effects of 1 km^2 marsh loss and 1 km^2 fragmentation (FIG A.1). To test for 1 ha scale effects, each cell in the preceding factorial would be split by an additional 3x3 factorial consisting of all possible level combinations of the two ha scale factors. This design could then be replicated at a different location with location serving as a block (Fig A.2).

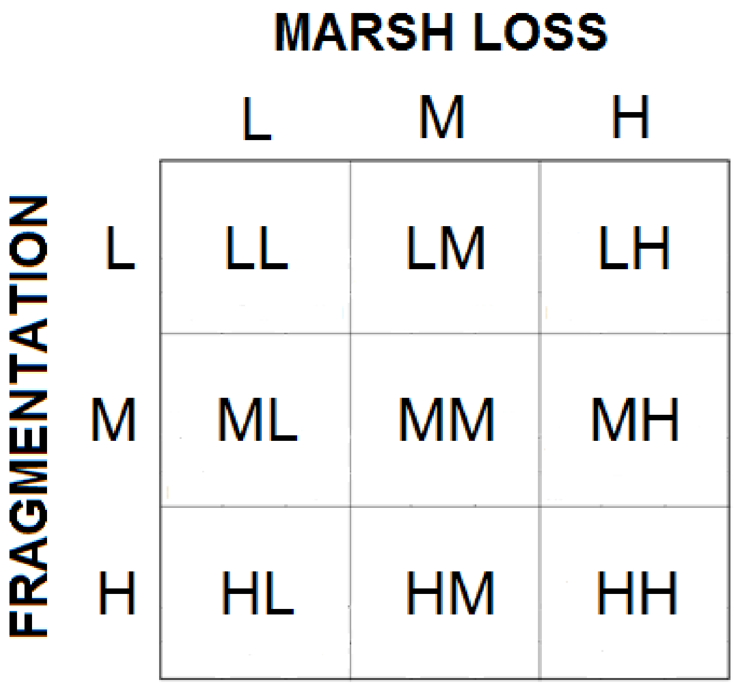

Figure A.1. Diagram of proposed new study design for evaluating the effects of 1 km^2 marsh loss and fragmentation factors only (L= Low, M = Medium, H = High).

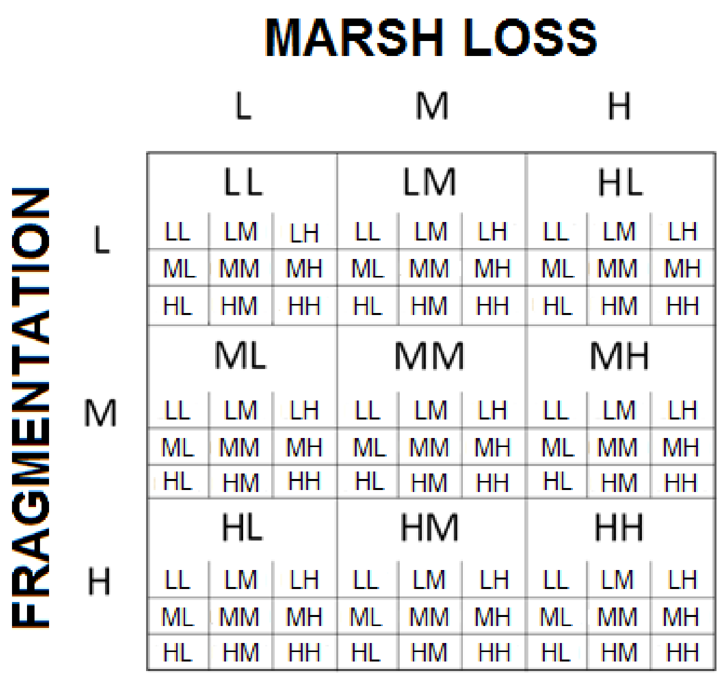

Figure A.2. Diagram of proposed new study design for evaluating the effects of 1 km^2 and 1 ha scale marsh loss and fragmentation factors. Large letters indicate 1 km^2 scale treatment, small letters indicate 1 ha cells of the split-plot factorial (L=Low, M = Medium, H = High).

APPENDIX B

RELATIONSHIPS BETWEEN MARSH AREA AND EDGE

Limited hard data exist to support the theoretical quadratic relationship between the percentage of a landscape occupied by marsh surface and the amount of marsh edge proposed by Browder (1985). In this study, data for percent marsh area and length of marsh edge (m) was calculated for 54 1 ha landscapes. Twelve of these landscapes were recalculated for the fall data set due to hurricane-related damage.

Regressions run on the spring (pre-hurricane) data revealed that a linear effect was statistically significant ($p < 0.001$) but a quadratic effect was not ($p = 0.09$) (Fig. B.1.). The model, which can be described as: Total Length of Edge = 277.60 + 13.03(Percent Marsh), explained 33 percent of the variance ($R^2 = 0.33$). A positive linear model does not support the relationship proposed by Browder. If the quadratic effect is accepted (Fig. B.2.) as significant ($\alpha < 0.1$) the model continues to describe 33 percent of the variance ($R^2 = 0.33$) and is described

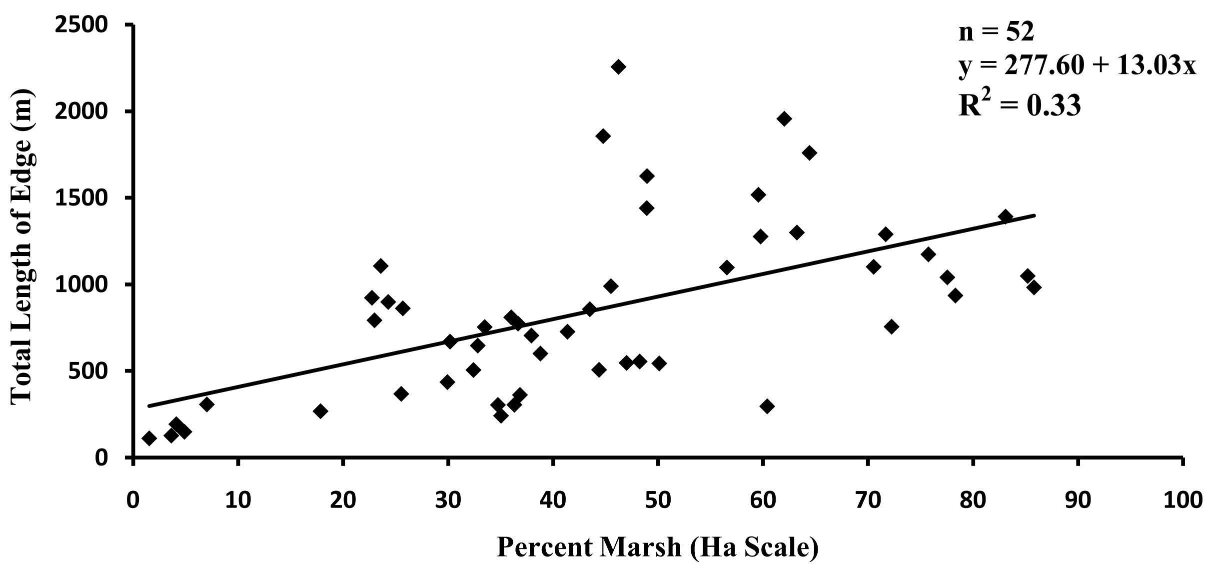

Figure B.1. A linear relationship was found in the spring (pre-hurricane) data between the percentage of area occupied by marsh surface and the total length of marsh edge (m). A quadratic effect was not considered significant $p = 0.09$.

as: Total Length of Edge = 18.46 + 28.40(Percent Land) – 0.17(Percent Land)^2. This incomplete parabola also fails to approximate the expected relationship between marsh area and marsh edge. The accuracy of both models may be limited by a lack of data in the 85-100 percent marsh range. Should landscapes from this range have close to zero edge, a more parabolic relationship would be likely.

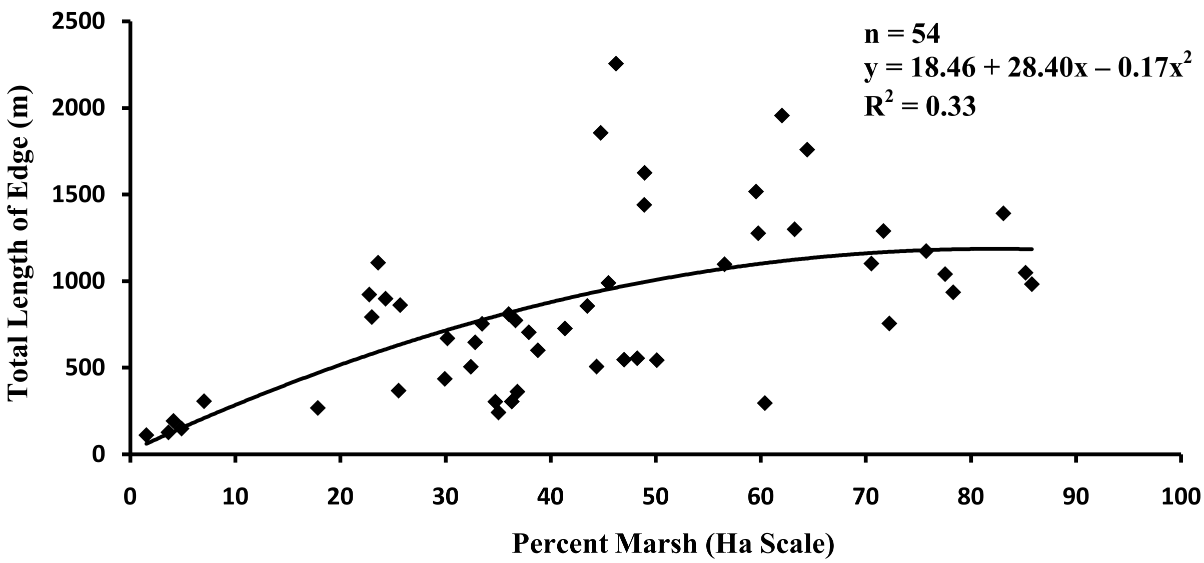

Figure B.2. A quadratic relationship was found in the spring (pre-hurricane) data between the percentage of area occupied by marsh surface and the total length of marsh edge (m) when α is accepted < 0.1

Regressions run on the fall (post-hurricane) data revealed that a quadratic effect was significant ($p = 0.0137$) (Fig. B.3.). This model, which can be described as: Total Length of Edge = 22.37 + 44.02(Percent Marsh) – 0.37(Percent Marsh)^2, explained 23 percent of the variance ($R^2 = 0.23$). This model is similar to the one proposed by Browder et al. (1985). However, like the spring data, this model lacks data from the 85-100 percent marsh range. This model is also influenced by at least one outlier (edge > 3,500 m) which is known to be the result of a marsh rack deposit.

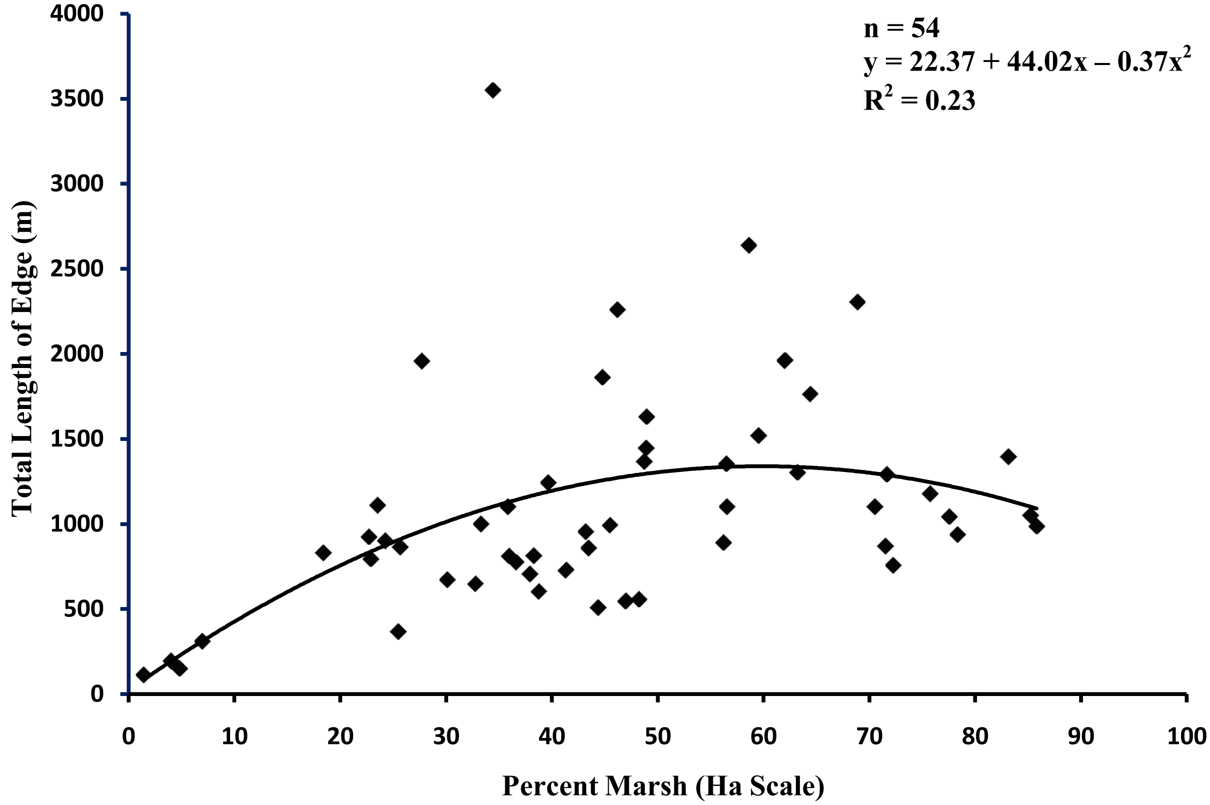

Figure B.3. A quadratic relationship was found in the fall (post-hurricane) data between the percentage of area occupied by marsh surface and the total length of marsh edge (m). The quadratic effect was significant $p = 0.0137$.

VITA

John Alexander Gordon was born in Harrisburg, Pennsylvania, in 1985 to John and Jane Gordon. He graduated from Smyrna High School in Smyrna, Delaware, in 2003. John then attended the University of Delaware where he earned a Bachelor of Science degree in wildlife conservation in 2007. Upon graduation, he departed for Baton Rouge, Louisiana, in June of 2007 to pursue a Master of Science in fisheries at Louisiana State University under the direction of Dr. Megan La Peyre.