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Complexity and nekton use of marsh edge habitats in Barataria Bay, Louisiana

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**COMPLEXITY AND NEKTON USE OF MARSH EDGE HABITATS IN
BARATARIA BAY, 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
Timothy W. Birdsong
B.S., Southeastern Oklahoma State University, 2002
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ABSTRACT

This study examined the effects of intrahabitat variability on marsh edge use by fishes and decapod crustaceans. The objectives were to (1) identify quantitative measures of habitat complexity that describe the structural design of marsh edge habitats, and (2) examine differences in nekton use between cut-bank and gently sloping marsh edge habitats. The study was conducted in Barataria Bay, Louisiana at 75, 10-m marsh edge study sites. Monthly seining was conducted in fall 2003 and spring 2004 and measures of habitat complexity were recorded at each sample location. Indices of tidal inundation and site exposure to wind and wave action were calculated. Results showed significantly greater complexity (i.e., irregularity, elevation, bank height, bank undercut, vegetation densities and percent vegetated cover) at cut-bank edges over gently sloping edges ($P < 0.0001$). Nekton diversity (fall: $P = 0.0236$, spring: $P = 0.0297$) and mean abundance of bay anchovy *Anchoa mitchilli* (fall: $P = 0.0010$) were also significantly greater at cut-bank edges over gently sloping edges. Lower mean elevation at gently sloping edges resulted in significantly greater levels of inundation over cut-bank edges ($P < 0.0001$), providing earlier and prolonged use of inner marsh habitats. Mean abundances of marsh residents that frequent the vegetated marsh surface (naked goby *Gobiosoma bosc* (fall: $P = 0.0055$), gulf killifish *Fundulus grandis* (fall: $P = 0.0280$), and grass shrimp *Palaemonetes pugio* (fall: $P = 0.0017$) were significantly greater at gently sloping edges over cut-bank edges. Several associations were observed between nekton community parameters and measures of habitat complexity, including strong positive correlations between species diversity (fall: $P < 0.0001$, spring: $P < 0.0001$), species richness (fall $P = 0.0001$, spring $P = 0.0029$), and exposure to wind and wave action. Differences in use between cut-bank and gently sloping edges and associations between nekton variables and measures of habitat complexity suggest that differences in habitat structure exist among marsh edge habitats and that these differences do influence habitat

selection by nekton. This study highlights the need for methods that provide more explicit identification of EFH by determining relationships between productivity and the different habitats used by aquatic organisms.

INTRODUCTION

The Magnuson-Stevens Fishery Conservation and Management Act, passed by congress in 1996, provides a modified approach to fishery management that focuses on identification, conservation, and enhancement of habitats essential to all life stages of species with fishery management plans (FMPs). The purpose of this ecosystem-based approach is to provide links between specific habitat types and the productivity of fishery stocks. Identification of essential fish habitat (EFH) for the 26 species of finfishes and decapods with FMPs in the Gulf of Mexico has presented a unique challenge for marine resource managers. The majority of these species exhibit a range of life-history strategies involving ontogenetic shifts in habitat use, as well as tidal, seasonal, and annual migration patterns. Because these species use resources from a variety of habitats during their life histories, it is important to understand the contribution and relative value of specific habitat types to fisheries production. Description of EFH focuses predominantly on fish use of different macro-scale habitat types (i.e., marsh edge, vegetated bottom). Linking fish use to this level of habitat type assumes that all microhabitats, within each type, are equivalent, despite obvious structural variability. This study seeks to more explicitly identify the value of marsh edge habitats as EFH by examining the effects of intrahabitat structural variability on nekton use.

The importance of marsh edge habitats in support of estuarine and coastal fisheries production is well-documented in the northern Gulf of Mexico (Turner 1977, Boesch and Turner 1984, Zimmerman et al. 2001, Minello and Rozas 2002) and marsh edge habitats are often cited as EFH (Benaka 1999). These habitats serve as productive nursery areas for juvenile finfishes and decapod crustaceans of economic importance and provide productive feeding grounds for resident and transient predators (Boesch and Turner 1984, Peterson 1986, Chambers 1992, Baltz

et al. 1993, Minello 1999, Peterson and Turner 1994, Rozas and Zimmerman 2000, Zimmerman et al. 2000). Marsh edge habitats serve as the defining border between the emergent marsh vegetation and open water and have been referred to as ‘critical transition zones’ that promote the movement of organisms and nutrients between intertidal and subtidal estuarine environments (Levin et al. 2001). It has been estimated that 94-98 % of the commercial fisheries catch from the southeastern coastal-Atlantic states and the northern Gulf of Mexico consists of estuarine-dependent species (Chambers 1992) and commercial yields of these species have been positively correlated with the amount of marsh edge (edge: area ratio) and total area of intertidal marsh habitats (Turner 1977, Zimmerman et al. 2000, Minello and Rozas 2002).

The fisheries value of marsh edge is often evaluated through interhabitat comparisons with other estuarine habitat types (i.e., oyster reef, mud bottom) (Rozas and Zimmerman 2000, Jones et al. 2002, Minello et al. 2003). Interhabitat comparisons often disregard intrahabitat variability, thus assuming that all microhabitats within a given habitat type function similarly (Minello 1999). Marsh edge habitats in Barataria Bay vary structurally from cut-bank erosional edges to gently sloping depositional edges and from relatively straight to more sinuous lengths of shoreline with variation in bank morphology, plant community structure, substrate characteristics, hydrology, and landscape position. It is important to understand how these structural differences influence nekton use and distribution patterns among specific marsh edge habitats.

Measures of habitat complexity provide a means to examine intrahabitat variability by quantifying the variation in habitat structure attributable to size or abundance of specific structural components contained within a habitat (e.g., rocks, coral, sea grass, algae, etc.) (McCoy and Bell 1991). Habitat complexity has been measured in a diversity of environments

in numerous ways and includes measures of topographical, shoreline, and substratum characteristics (Table 1). Although the presence of specific structural components may affect habitat selection (Stoner and Lewis 1985), several studies have shown the effects of habitat complexity to be independent of structural components. For example, Beck (1998) showed that the effects of complexity on gastropods could be measured and compared between rocky intertidal and mangrove habitats. These habitats had very different structural components, but densities of gastropods were positively correlated with measures of complexity. Ohman and Rajasuriya (1998) found that complexity, measured by surface topography, was strongly correlated with fish species diversity in reef fish communities regardless of whether the reef was composed of coral or sandstone.

Regardless of the actual complexity measures used to define intrahabitat variability, complex habitats tend to have greater faunal abundance and diversity than less complex habitats (Ebeling et al. 1980, Bartholomew et al. 2000). These patterns have been associated with decreased physical stress (Dean and Connell 1987), increased resource or niche availability (Orth et al. 1984, Hacker and Steneck 1990, Hixon and Beets 1993), increased food availability (Hacker and Steneck 1990), and decreased competition (Jones 1988) offered by complex habitats. Structurally complex habitats have also been shown to reduce predation rates by providing greater refuge availability and limiting predator access and movement (Orth et al. 1984, Sih et al. 1992, James and Heck 1994).

Measures of habitat complexity have been used to determine the conservation value of specific marine habitats (Jennings et al. 1996) and to zone for marine protected areas (Edinger and Risk 2000). To effectively identify habitats for conservation or management, managers require classification schemes that allow detailed examination and measurement of

environmental variables so that habitats can be characterized accurately, yet can be applied easily at a regional scale (Zacharias et al. 1999). With the abundance of marsh edge habitat in estuarine environments, and the continued restoration of marsh edges, a similar approach could be beneficial to scientists and managers in better understanding the structural characteristics that influence use by important fisheries species.

This study was designed to examine differences in nekton use between marsh edge microhabitats. The specific objectives were to (1) identify quantitative measures of habitat complexity that describe the structural design of marsh edge habitats and (2) examine differences in nekton use between cut-bank and gently sloping marsh edge microhabitats.

Table 1. Indices and measures of habitat complexity that have been applied in marine and estuarine ecosystems.

Index/Measure	Habitat	Study
Fractal dimension (D)	Rocky intertidal/Mangrove	Beck 1998
	Rocky intertidal	Beck 2000
	Laboratory	Berntson and Stoll 1997
Vector dispersion (VD)	Rocky intertidal/Mangrove	Beck 1998
	Rocky intertidal	Beck 2000
Consecutive substratum height difference ($\sum dh^2$)	Rocky intertidal/Mangrove	Beck 1998
	Rocky intertidal	Beck 2000
	Coral Reef	McCormick 1994
Shoreline heterogeneity Index (SHI)	Rocky intertidal/Mangrove	Beck 1998
	Rocky intertidal	Beck 2000
	Estuarine	Archambault and Bourget 1996
	Estuarine	Bergeron and Bourget 1986
Rugosity/Chain-Link/Chain-and-tape	Heterogeneous coastline	Zacharias et al. 1999
	Rocky shore	Ferreira et al. 2001
	Coral reef	Bergman et al. 2000
	Coral reef	Grigg 1994
	Coral reef	McCormick 1994
	Coral Reef	Ohman and Rajasuriya 1998
Interstitial space	Rocky shore	Ferreira et al. 2001
	Coral Reef	Grigg 1994
Exposure to wave activity (Fetch)	Heterogeneous Coastline	Valesini et al. 2003
	Heterogeneous Coastline	Schafer et al. 2002
	Heterogeneous Coastline	Zacharias et al. 1999
Shoreline aspect	Heterogeneous Coastline	Valesini et al. 2003
Slope	Heterogeneous Coastline	Valesini et al. 2003
Distance to reef	Heterogeneous Coastline	Valesini et al. 2003
Refraction coefficient for swell waves	Heterogeneous Coastline	Valesini et al. 2003
Reef continuation	Coral Reef	Valesini et al. 2003
Tidal stream velocity	Heterogeneous Coastline	Zacharias et al. 1999

Table 1 Continued.

Surface Area	Rocky outcrops	Ferreira et al. 2001
	Seagrass beds	Jenkins et al. 2002
	Seagrass beds	Stoner and Lewis 1985
Percent cover	Coral reef	Edinger and Risk 2000
	Coral reef	Bergman et al. 2000
	Salt marsh	Bartholomew et al. 2000
Substrate particle size	Rocky outcrops	Ferreira et al. 2001
	Estuarine	Archambault and Bourget 1996
	Heterogeneous coastline	Valesini et al. 2003
	Seagrass beds	Bostrom and Bonsdorff 2000
	Estuarine	Corona et al. 2000
Elevation	Estuarine	Jones et al. 2002
	Salt marsh	Minello et al. 1994

METHODS

Study Area

The study was conducted in Barataria Bay, a 167,300 ha estuary located in the deltaic plain of southeastern Louisiana (USEPA 1999, Figure 1). Barataria Bay is highly turbid and well-mixed with a mean depth of 1.25 m and salinity levels that vary between 6 and 22 ppt (Day et al. 1973, Conner and Day 1987). Tides are diurnal with a range of 0.32 m and dominated by seasonal winds (Day et al. 1973, Baltz et al. 1993). Barataria Bay contains numerous small interconnected bays and canals with approximately 145,000 ha of saline marsh separated from the northwestern Gulf of Mexico by a chain of barrier islands (Conner and Day 1987). The bay is bordered to the east by the levees of the current course of the Mississippi River, constructed in the 1930s and 1940s for flood protection, and to the west by the abandoned Bayou Lafourche distributary, which was closed to riverine input in 1902 (Conner and Day 1987). Absence of freshwater input and associated sediment, along with subsidence, canal construction for petroleum production, and increased saltwater intrusion due to barrier island erosion have contributed to extensive amounts of wetland loss in the bay (Day et al. 1989). The primary source of freshwater input is precipitation, which averages approximately 160 cm yr⁻¹ (Baumann 1984). Other sources of freshwater input include siphons constructed at Naomi and West Pointe a la Hache, Louisiana, designed to mimic flow into the bay from the Mississippi River through a natural crevasse, and the Davis Pond Freshwater Diversion Structure, located near Luling, Louisiana. The diversion, which is scheduled for use beginning in spring 2005, was designed to divert a maximum discharge of 10,650 CFS from the Mississippi River into Barataria Basin, providing a source of nutrients and sediments to replenish the deteriorating wetlands.

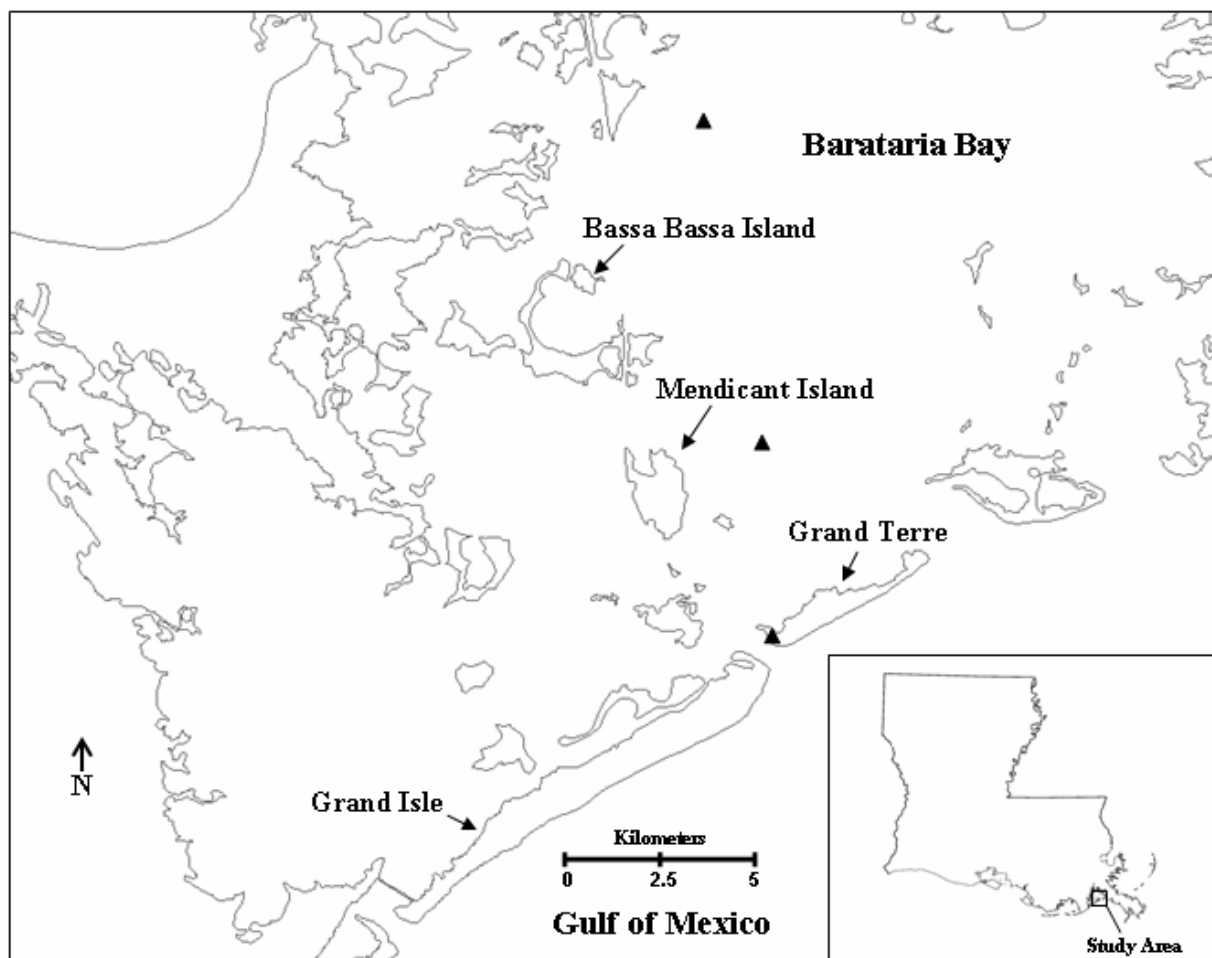


Figure 1. Study islands (Bassa Bassa, Mendicant, Grand Terre) located in Barataria Bay estuary. Triangles represent location of U.S.G.S. meteorological and water quality monitoring stations.

Sampling was conducted in the southwestern portion of Barataria Bay at sites selected on Grand Terre, Mendicant, and Bassa Bassa islands (Figure 1). The islands are evenly dispersed along an 11.5 km transect that extends northwesterly along the Barataria Waterway from Barataria Pass, a major source of saltwater exchange with the Gulf of Mexico located between Grand Isle and Grand Terre Island.

Site Selection

Marsh edge habitats were categorized based on bank morphology and designated as either cut-bank erosional edge (Figure 2), which was characterized as rugged, complex shoreline

with exposed plant root systems and a distinct vertical drop between the emergent vegetated marsh edge and the adjacent open-water substrate, or gently sloping edge (Figure 3), defined as shoreline with a smooth, gentle relief and no distinct difference in elevation between the vegetated edge and the open-water substrate.

In August, 2003, each marsh island was circumnavigated and a surveyor grade Trimble Geo-XT Global Positioning System (GPS) was used to record marsh edge bank morphology. ESRI ArcGIS 8.1 Geographic Information Systems (GIS) software was then used to map marsh edge morphology on Digital Orthophoto Quarter Quadrangle (DOQQ) images analyzed by the United States Geological Survey from color-infrared aerial photographs (1:40,000 scale). Twenty-five, 10-m marsh edge habitats were selected from each island with a stratified random sampling design that was based on proportional representation of each habitat type. A total of 20 gently sloping habitats (Bassa Bassa $n = 9$, Mendicant Island $n = 4$, Grand Terre $n = 7$) and 55 cut-bank habitats were included in the study. Study sites were located with GPS and marked with PVC poles placed 10 m apart (straight-line distance) and flush with the vegetated marsh edge (Figure 4).

Sampling Design

Nekton sampling was conducted monthly in fall 2003 (9/03, 10/03, 11/03) and spring 2004 (3/04, 4/04, 5/04) at all study sites within 2-day sampling periods. Meteorological and water quality variables were measured concurrent with nekton sampling and measurements of marsh edge complexity were taken once seasonally (12/03, 5/04).



Figure 2. Cut-bank marsh edge on Mendicant Island in Barataria Bay, Louisiana.



Figure 3. Gently-sloping marsh edge on Bassa Bassa Island at low tide in Barataria Bay, Louisiana.



Figure 4. Marsh edge study site marked with PVC poles placed 10 m apart (straight-line distance) and flush with the vegetated edge.

Edge Complexity Variables

Numerous physiochemical parameters, including meteorological, water quality, bank morphology, substrate sediments, emergent vegetation, and landscape position (Table 2), were recorded seasonally at all study sites to quantify the complexity of marsh edge habitats.

Meteorological and Water Quality

Hourly meteorological and water quality measurements including wind speed (mph) and direction (degrees), tidal level (ft), salinity (ppt), precipitation (in), and water temperature (°C) were available from U.S.G.S. monitoring stations located adjacent to the study islands (Figure 1). Dissolved oxygen (% and mg L^{-1}), salinity (ppt), and water temperature (°C) were also recorded with a Yellow Springs Instruments (YSI) Model 556 multiprobe adjacent to study islands concurrent with nekton sampling.

Bank Morphology

Quantitative measures of bank morphology including bank height, bank undercut, elevation, shoreline irregularity, and shoreline slope were measured to assess differences in habitat complexity between marsh edge habitat types and examine relationships between measures of bank morphology and nekton community parameters. Bank height, bank undercut, and elevation of the vegetated edge were all measured to the nearest centimeter at three random locations within each study site and averaged to obtain descriptor values. Shoreline slope was calculated from the base of the vegetated edge of the marsh to the substrate at 5 m from the shoreline. Shoreline irregularity was taken by measuring the total sinuous shoreline length at each 10-m (straight-line length) study site. Site elevation and tidal level were used to calculate site inundation, which provided a method of examining differences in potential nekton access to the marsh surface at cut-bank and gently sloping habitats during sample periods. Inundation was calculated as:

$$\text{Inundation} = \text{Tidal level at sampling (cm)} - \text{Site Elevation (cm)}$$

Negative values indicated no access, whereas positive values indicated various levels of potential nekton access to the marsh surface during sampling.

Substrate Characteristics

Sediment composition of the upper five cm of open-water substrate was examined at each site and characterized based on dominant and subdominant components (Baltz et al. 1993, Jones et al. 2002). Component categories consisted of clay, silt, sand, organic detritus, and shell. Samples were taken at 1, 3, and 5 m from the emergent shoreline.

Shoreline Vegetation

Herbaceous stem densities and percent vegetated cover were recorded within 3 m of the vegetated edge at each site. Stem densities were measured inside three randomly thrown 0.1-m quadrats. Percent cover was measured inside three randomly thrown 0.25-m quadrats.

Landscape Position

An index of relative exposure that incorporated wind speed and wind directional fetch at the time of nekton sampling was developed to provide a measure of shoreline protection from wave action and evaluate the effects of landscape position on marsh edge habitat complexity and nekton use.

Wind speed and wind direction during sampling were obtained from U.S.G.S. monitoring stations in Barataria Bay and directional fetch (N, NE, NW, S, SE, and SW) of each study site was measured on DOQQ images of the study area with GIS. Relative exposure ($Exposure_R$) was calculated as:

$$Exposure_R = Wind_R + Fetch_R$$

where $Wind_R$ represented wind speed at time of nekton sampling and $Fetch_R$ represented the directional fetch that corresponded with wind direction at time of nekton sampling. $Wind_R$ was considered low and assigned a value of 1 if wind speed was $< 1.6 \text{ m s}^{-1}$, intermediate and assigned a value of 2 if wind speed was $\geq 1.6 \text{ m s}^{-1}$ or $< 5.5 \text{ m s}^{-1}$, and high and assigned a value of 3 if wind speed was $\geq 5.5 \text{ m s}^{-1}$. Directional fetch at each site was assigned a low, intermediate, or high value based on percent of the maximum fetch recorded in each general direction over all study sites. $Fetch_R$ was considered low and assigned a value of 1 if wind directional fetch at time of nekton sampling was $< \frac{1}{3}$ max directional fetch (km). $Fetch_R$ was considered intermediate and assigned a value of 2 if wind directional fetch was $\geq \frac{1}{3}$ max

directional fetch or $< \frac{2}{3}$ max directional fetch and Fetch_R was considered high and assigned a value of 3 if wind directional fetch $\geq \frac{2}{3}$ max directional fetch. Exposure_R values ranged from 2, indicating highly protected sites, to 6, indicating sites with high exposure to wind and wave activity.

Statistical Analysis

Univariate Analysis of Variance (ANOVA, PROC GLM) was conducted on meteorological and water quality variables to determine if differences existed among months or study islands within months. Multivariate Analysis of Variance (MANOVA) was used to determine if edge complexity variables (Table 2), compared simultaneously, were significantly different between cut-bank and gently sloping shoreline habitat types. ANOVA with Tukey HSD tests were conducted on individual variables following significant MANOVA results. Analyses were conducted with SAS 8.1 software and an alpha level of 0.05 was used to determine significance.

Nekton Assemblages

Nekton Sampling

Adult and juvenile fishes and decapod crustaceans were sampled monthly in fall 2003 (9/03, 10/03, 11/03) and spring 2004 (3/04, 4/04, 5/04) to examine differences in nekton assemblages between cut-bank and gently sloping marsh edge habitats and determine associations between nekton assemblages and specific measures of marsh edge habitat complexity. Nekton were collected with a 5-m by 2-m bag seine composed of 3-mm square delta mesh that was swept parallel against the shoreline between the PVC poles that marked each site (Figure 4). All nekton were removed from the seine, placed on ice, and returned to the laboratory for identification. Nekton were identified to species or lowest taxonomic rank

possible and total length of fishes and shrimp (cm), carapace width of crabs (cm), and wet weight (g) were recorded. Sub-sampling ($n = 30$) was conducted to obtain length and weight measurements of individuals from abundant species. Total abundance and total biomass of all species were recorded.

Table 2. Measures of meteorological conditions, water quality, bank morphology, substrate characteristics, shoreline vegetation, and landscape position recorded at marsh edge habitats in fall 2003 and spring 2004 with method of measure.

Habitat Characteristics (units)	Method of Measure
Meteorological Conditions	Downloadable data from U.S.G.S. monitoring stations
Wind Speed (m s^{-1})	
Wind Direction (degrees)	
Precipitation (cm)	
Water Quality	YSI Model 556 multiprobe and downloadable data from U.S.G.S. monitoring stations
Salinity (ppt)	
Dissolved Oxygen (mg L^{-1} and %)	
Bank Morphology	
Bank Height (cm)	Height of vegetated edge above open-water substrate
Bank Undercut (cm)	Horizontal distance from the outer vegetated edge into the bank
Bank Slope (cm m^{-1})	Vertical drop from vegetated edge to substrate at 5 m from the bank (horizontal)
Shoreline Irregularity (m)	Sinuuous shoreline length per 10-m straight line length
Elevation (cm)	Distance from vegetated edge to water level standardized with tide gauge readings
Inundation	
Substrate Characteristics	Primary and secondary sediment components at 1, 3, and 5 m from the shoreline
Shoreline Vegetation	
Stem Density (stems m^{-2})	Average of three randomly thrown 0.10 m quadrates within 3 m of open-water edge
% Cover	Average of three randomly thrown 0.25 m quadrates within 3 m of open-water edge
Landscape Position	
Relative Exposure Index	Incorporated wind speed and direction with direction fetch (m); measured with GIS

Nekton Community Parameters

Several nekton community parameters including Shannon-Weiner species diversity (H') (Magurran 1988), species richness, and total species abundance of numerically dominant taxa were used to examine differences in nekton use between cut-bank and gently sloping marsh edge habitat types and examine relationships between nekton community parameters and measures of marsh edge habitat complexity.



Figure 5. Bag seine used to collect nekton at marsh edge habitats in Barataria Bay, Louisiana.

Statistical Analysis

MANOVA was used to determine if nekton community parameters (species richness, diversity (H'), and species abundances), compared simultaneously, were significantly different between cut-bank and gently sloping marsh edge habitat types. Individual ANOVAs and Tukey HSD tests were conducted following significant MANOVA results. Multivariate regression (PROC REG) was used to identify and measure associations between nekton community parameters and measures of marsh edge bank morphology.

Decapod crustaceans that composed less than 1 % of the total catch of crustaceans and finfish species that composed less than 1 % of the total finfish catch were excluded from species abundance analyses. Outliers were removed to address assumptions of normality. Individuals from all species were included in analyses of species richness and diversity. An alpha level of 0.05 was used to determine significance.

RESULTS

Edge Complexity Variables

Meteorological and Water Quality

Nekton sampling was conducted over a range of meteorological (Table 3) and water quality conditions (Table 4) typical of coastal Louisiana, with significant differences observed in mean wind speed ($P < 0.0001$), water level ($P < 0.0001$), salinity ($P < 0.0001$), and water temperature ($P < 0.0001$) among sample periods. Significant differences were also observed in mean salinity among islands within sample periods ($P < 0.0001$). No observable differences were recorded in dissolved oxygen in the study area (Table 4) thus the measurement was excluded from statistical analyses.

Table 3. Mean wind speed + 1 SD (m s^{-1}), mean water level + 1 SD (cm), and predominant wind direction observed during monthly nekton sampling periods with total monthly precipitation (cm) recorded at Grand Terre Island.

Month	Wind Speed	Water Level	Wind Direction	Precipitation
September	5.60 ± 1.12	37 ± 12	NW	2.54
October	2.04 ± 1.08	39 ± 10	SW	8.74
November	5.66 ± 2.37	22 ± 12	SW	4.88
March	6.15 ± 1.46	23 ± 13	NW	1.88
April	4.75 ± 1.51	41 ± 19	SW	13.23
May	11.29 ± 1.06	48 ± 18	N	5.49

Bank Complexity

Study sites were represented by a wide range of shoreline configurations with measures of bank complexity that varied both across and within cut-bank and gently sloping marsh edge habitat types. MANOVA showed that cut-bank habitats had greater shoreline irregularity ($P < 0.0001$), higher elevation ($P < 0.0001$), steeper slopes ($P < 0.0001$), higher banks, and greater

bank undercut than gently sloping habitats, with the same patterns and levels of significance observed in fall (Figure 6) and spring (Figure 7) samples. In contrast, inundation of the vegetated marsh edge was considerably greater at gently sloping habitats than at cut-bank habitats in both sample seasons ($P < 0.0001$, Figure 8).

Table 4. Water quality measurements recorded during monthly nekton sampling periods in fall 2003 and spring 2004 at study islands in Barataria Bay, LA.

Date	Study Island	Salinity (ppt)	DO (mg L ⁻¹)	Water Temperature (°C)
Sept. 2003	Bassa Bassa	18	7	28
	Mendicant	20	7	28
	Grand Terre	20	7	28
Oct. 2003	Bassa Bassa	18	7	23
	Mendicant	18	7	23
	Grand Terre	21	7	23
Nov. 2003	Bassa Bassa	20	7	22
	Mendicant	22	7	22
	Grand Terre	23	7	22
March 2004	Bassa Bassa	14	7	22
	Mendicant	20	7	22
	Grand Terre	21	7	22
April 2004	Bassa Bassa	16	7	22
	Mendicant	22	7	22
	Grand Terre	22	7	22
May 2004	Bassa Bassa	2	7	28
	Mendicant	12	7	28
	Grand Terre	13	7	28

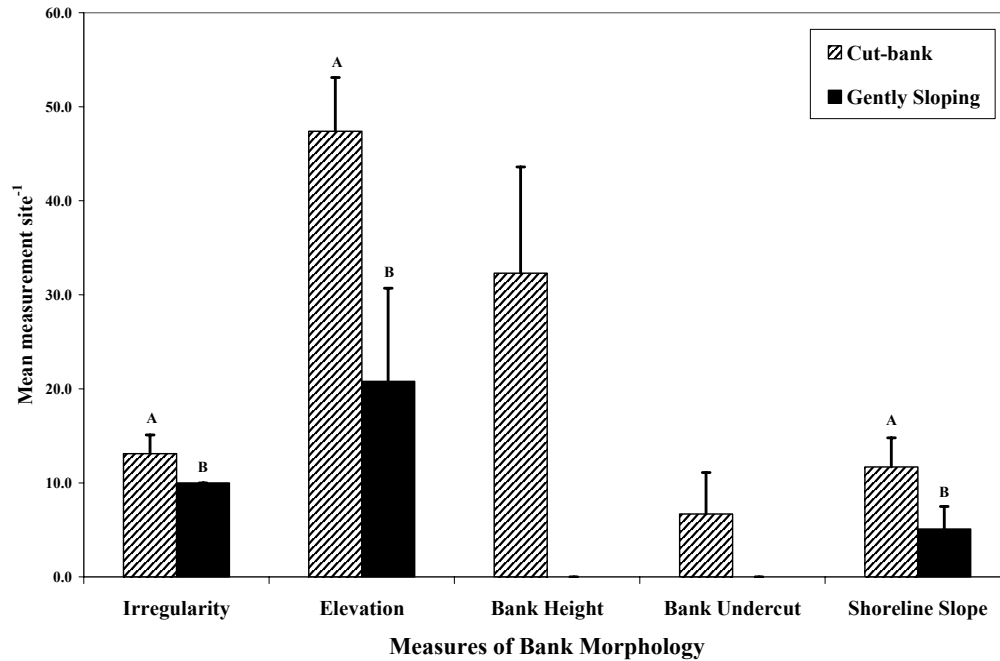


Figure 6. Mean measurements of shoreline irregularity (m), site elevation (cm), bank height (cm), bank undercut (cm), and shoreline slope (cm m^{-1}) + 1 SD recorded in fall 2003 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each measurement ($P < 0.05$).

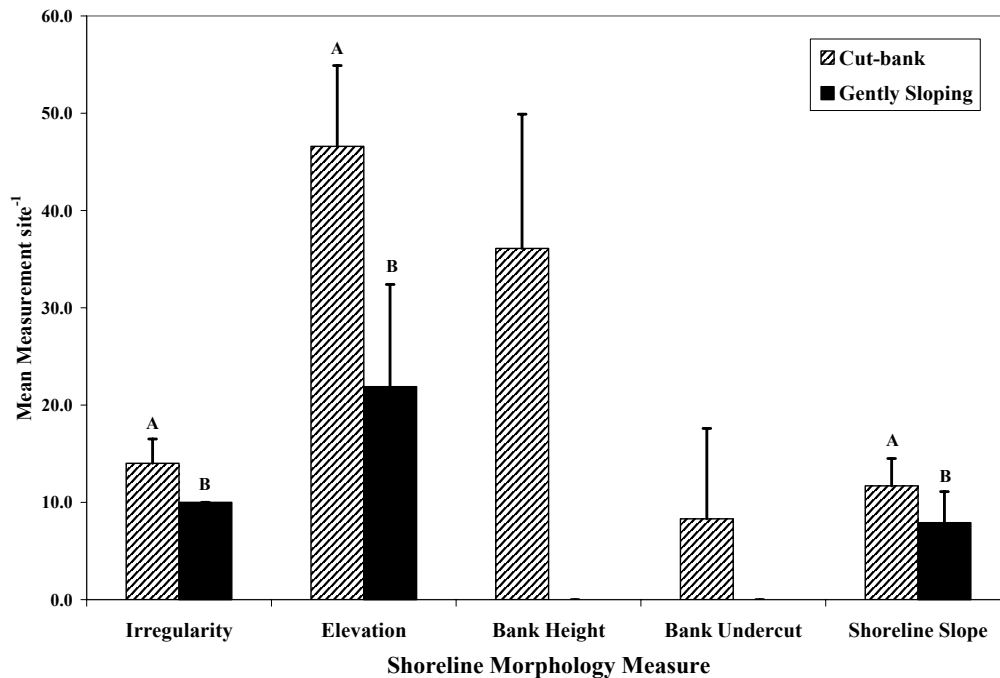


Figure 7. Mean measurements of shoreline irregularity (m), site elevation (cm), bank height (cm), bank undercut (cm), and shoreline slope (cm m^{-1}) + 1 SD recorded in spring 2004 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each measurement ($P < 0.05$).

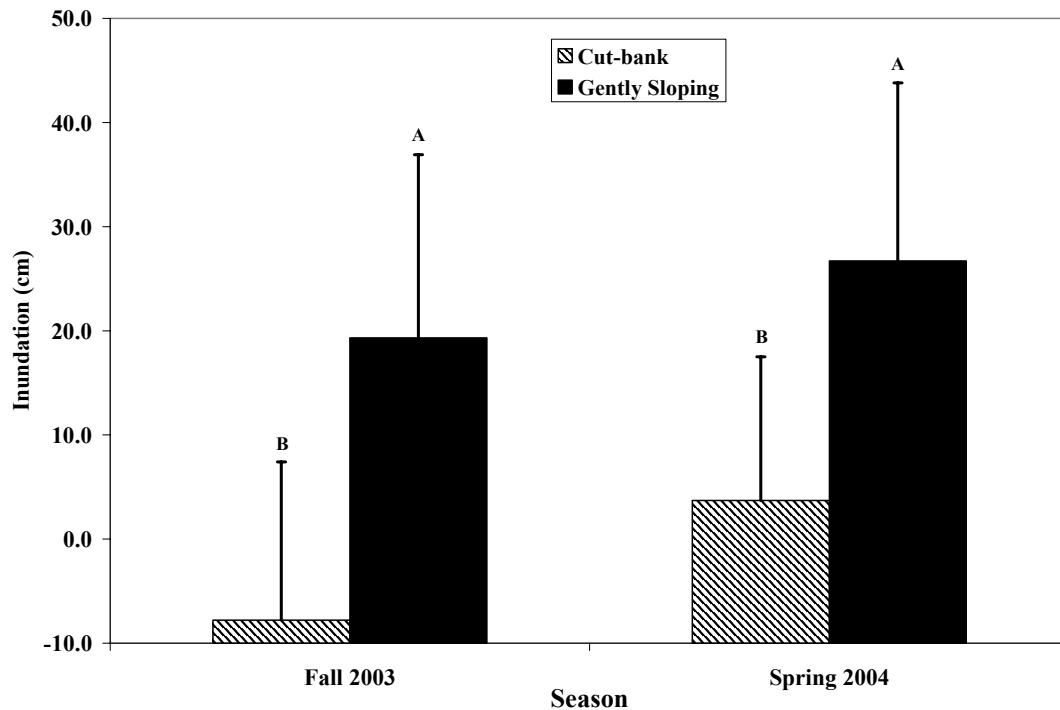


Figure 8. Mean inundation of the marsh edge + 1 SD during fall and spring nekton sampling periods at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each season ($P < 0.05$).

Substrate Characteristics

MANOVA showed significant differences in the adjacent open-water substrate composition between cut-bank and gently sloping shoreline habitats. Presence of compacted fine grain clay sediments was significantly greater at cut-bank habitats at 1 m (fall: $P < 0.0001$, spring: $P = 0.0239$), 3 m (fall: $P < 0.0001$, spring: $P = 0.0188$), and 5 m (fall: $P = 0.0037$, spring: $P = 0.0069$) from the vegetated shoreline than at gently sloping habitats. Detritus, primarily consisting of plant roots, was more abundant at cut-bank habitats at 1 m (fall: $P = 0.0409$) and 3 m (fall: $P < 0.0001$) from the vegetated shoreline than at gently sloping habitats, whereas loosely laden fine grain silts were significantly greater at 1 m (fall: $P < 0.0001$), 3 m (fall: $P < 0.0001$), and 5 m (fall: $P = 0.0022$, spring: $P = 0.0188$) from the shoreline at gently sloping habitats. Cultched

and live oyster shell were also significantly greater at gently sloping habitats at 3 m (fall: $\underline{P} < 0.0001$, spring: $\underline{P} = 0.0054$) and 5 m (fall: $\underline{P} = 0.0359$) from the shoreline than at cut-bank habitats.

Shoreline Vegetation

Vegetation on the emergent marsh edge at study sites consisted of a mixed stand of six species dominated by *Spartina alterniflora*. Similar vegetative composition was observed in fall (Figure 9) and spring samples seasons. Mean herbaceous stem density (Figure 10) and mean percent cover (Figure 11) of the vegetated edge were significantly greater at cut-bank habitats in both sample seasons ($\underline{P} < 0.0001$).

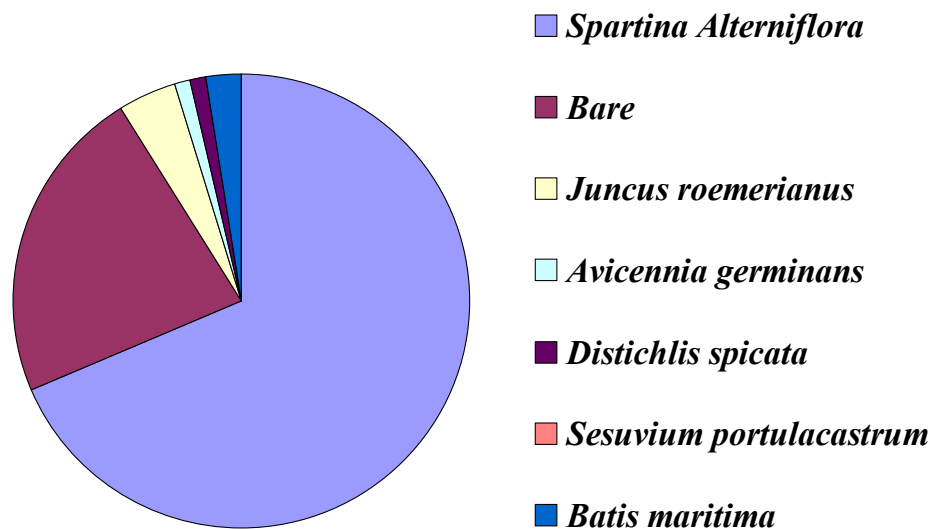


Figure 9. Vegetative composition of the emergent marsh edge recorded in fall 2003 across all study sites.

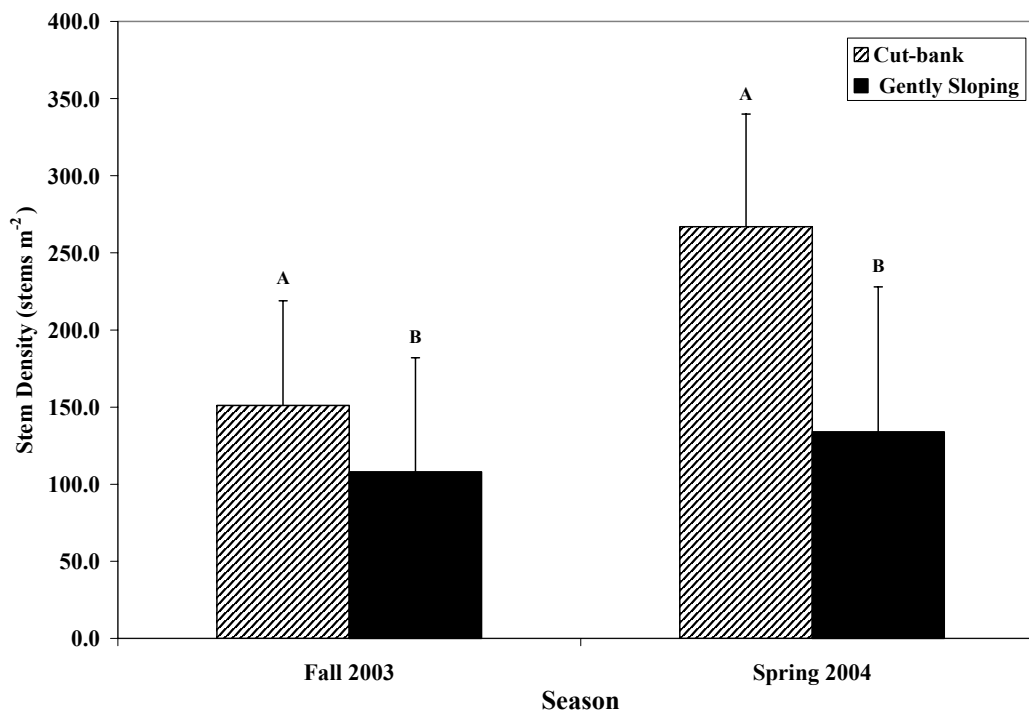


Figure 10. Mean herbaceous stem density of the emergent marsh vegetation + 1 SD within 3 m of the open-water edge in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each season ($P < 0.05$).

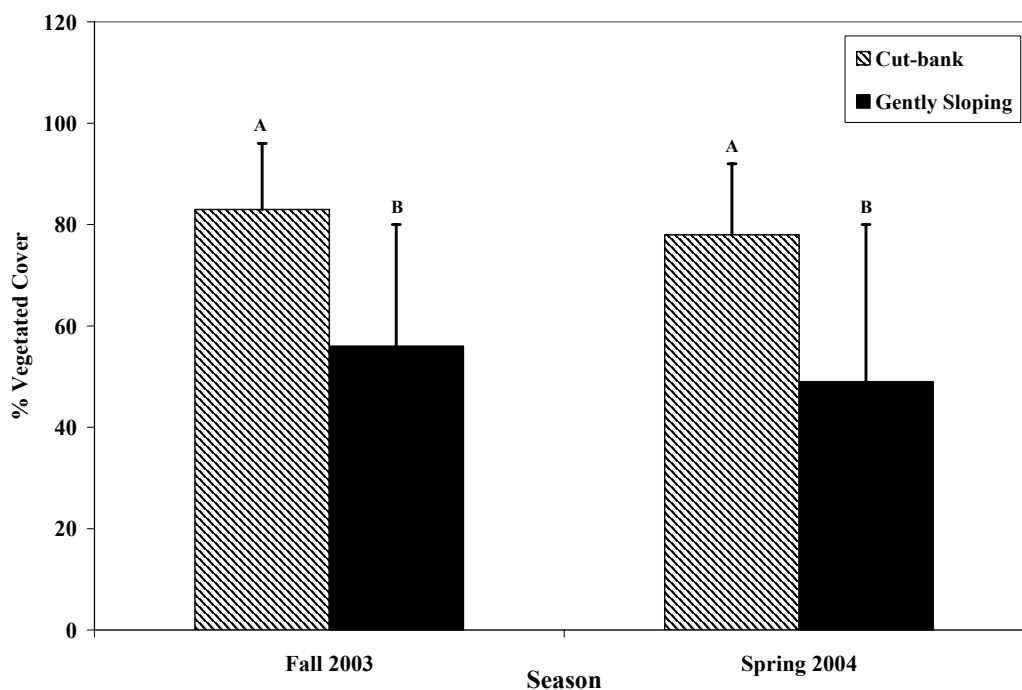


Figure 11. Mean percent vegetated cover of the emergent marsh + 1 SD within 3 m of the open-water edge in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each season ($P < 0.05$).

Landscape Position

Site exposure to wind and wave action, measured with the relative exposure index, was significantly higher in both sample seasons at cut-bank habitats ($P < 0.0001$, Figure 12).

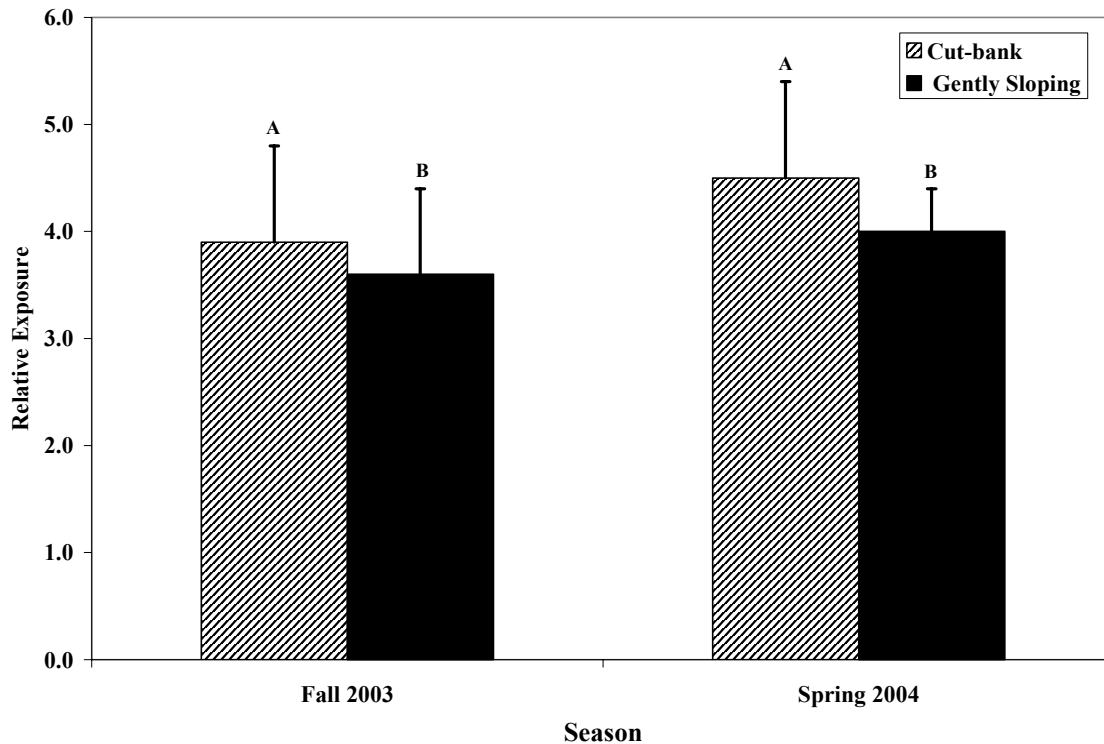


Figure 12. Mean relative exposure + 1 SD of cut-bank and gently sloping sites in fall 2003 and spring 2004. Bars with different letters were significantly different within each season ($P < 0.05$).

Nekton Assemblages

Fall 2003 Catch

A total of 67,873 individuals from 56 species were collected in 220 seine hauls conducted over the course of fall sampling (Table 5). Grass shrimp *Palaemonetes pugio*, white shrimp *Penaeus setiferous*, tidewater silverside *Menidia beryllina*, and bay anchovy *Anchoa mitchilli* composed over 96 % of the total catch and occurred in the majority of collections. Gulf killifish

Fundulus grandis, naked goby *Gobiosoma bosc*, gulf menhaden *Brevoortia patronus*, juvenile red drum *Sciaenops ocellatus*, blue crab *Callinectes sapidus*, silver perch *Bairdiella chrysoura*, and juvenile speckled trout *Cynoscion nebulosus* were also present in the majority of collections and were included in species abundance comparisons between marsh edge habitat types and regression models that examined the association between species abundances and measures of marsh edge bank complexity.

Spring 2004 Catch

In spring 2004, a total of 21,843 individuals were collected in 217 seine hauls from the same 75 stationary study sites (Table 5). Only 31 species were represented in spring samples, which primarily consisted of the same numerically dominant species collected in fall 2003 with the addition of high abundances of juvenile brown shrimp *Penaeus aztecus* and juvenile striped mullet *Mugil cephalus*. Juvenile spot *Leiostomus xanthurus*, juvenile sand trout *Cynoscion arenarius*, juvenile atlantic croaker *Micropogonias undulatus*, and juvenile silver perch *Bairdiella chrysoura* also occurred in most seine samples and were included in analyses of species abundance.

Differences in Habitat Use

MANOVA showed significant differences in several nekton community parameters between cut-bank and gently sloping marsh edge habitats, including species diversity and mean abundances of several numerically dominant nekton species.

In fall 2003, no significant differences in habitat use were observed between cut-bank and gently sloping marsh edge habitats among species of schooling fishes (tidewater silverside *Menidia beryllina*, bay anchovy *Anchoa mitchilli*, and gulf menhaden *Brevoortia patronus*) ($P >$

0.05, Figure 13). In spring 2004, mean abundance of bay anchovy *Anchoa mitchilli* was significantly greater at cut-bank marsh edge habitats ($P = 0.0010$, Figure 14).

In fall 2003, no significant differences in habitat use were observed among the numerically dominant juvenile sciaenids (red drum *Sciaenops ocellatus*, silver perch *Bairdiella chrysoura*, and spotted seatrout *Cynoscion nebulosus*) ($P > 0.05$, Figure 15). Juvenile spot *Leiostomus xanthurus*, juvenile sand trout *Cynoscion arenarius*, and juvenile Atlantic croaker *Micropogonias undulatus* collected in spring 2004 also showed no significant differences in habitat use ($P > 0.05$).

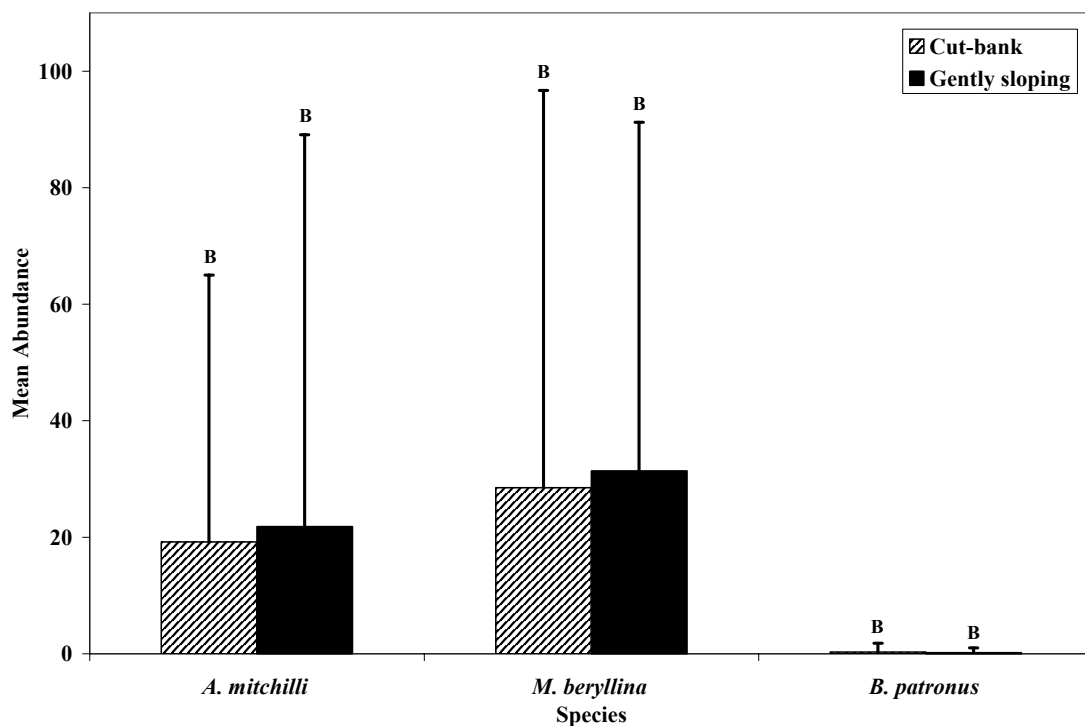


Figure 13. Mean abundance of schooling bait fishes + 1 SD collected in fall 2003 at cut-bank and gently sloping marsh edge habitats. No significant differences were found within species ($P > 0.05$).

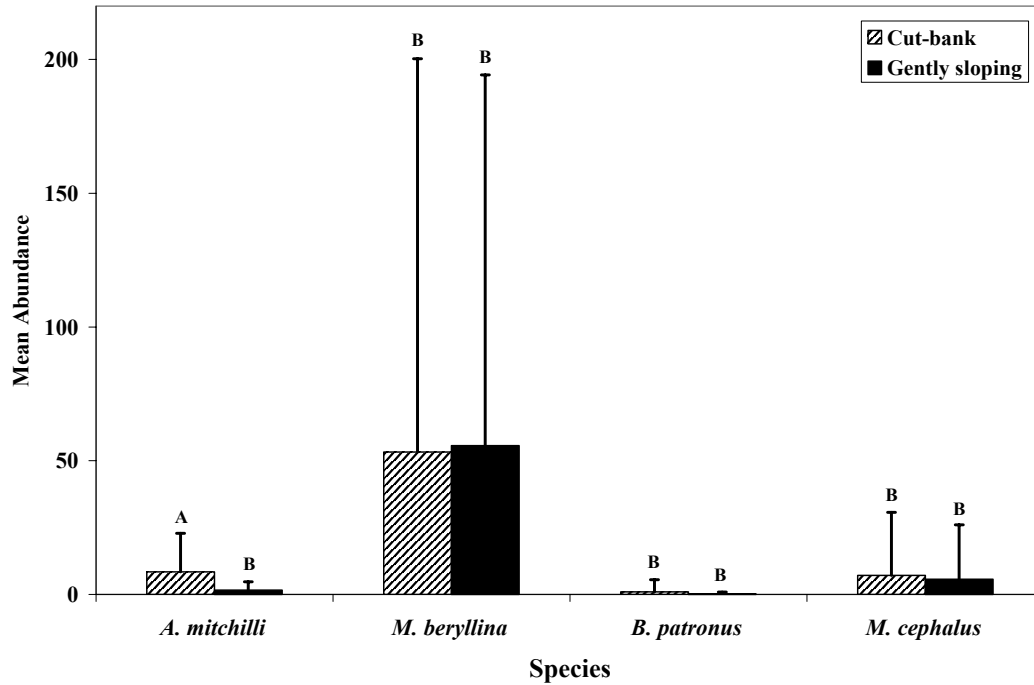


Figure 14. Mean abundance of schooling bait fishes + 1 SD collected in spring 2004 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each species ($P < 0.05$).

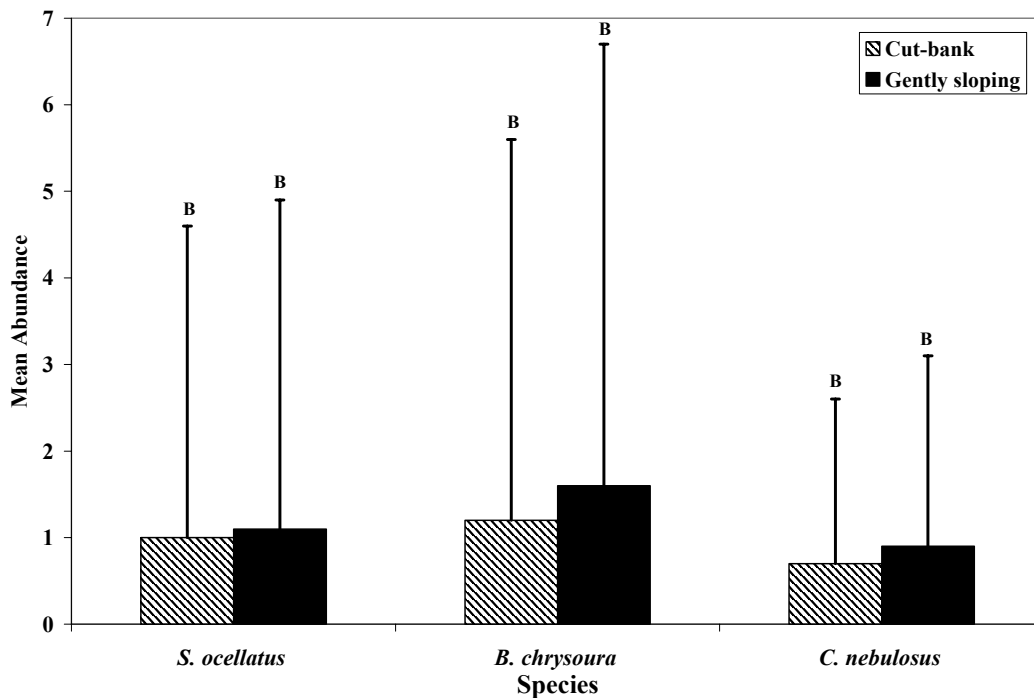


Figure 15. Mean abundance of red drum *Sciaenops ocellatus*, silver perch *Bairdiella chrysoura*, and spotted seatrout *Cynoscion nebulosus* + 1 SD collected in fall 2003 at cut-bank and gently sloping marsh edge habitats. No significant differences were found within species ($P > 0.05$).

Of the decapods collected in fall 2003, similar patterns of habitat use were observed for grass shrimp *Palaemonetes pugio* (Figure 16) and penaeid shrimp (brown shrimp *Penaeus setiferous* and white shrimp *Penaeus aztecus*) (Figure 17), which displayed greater mean abundances at gently sloping habitats with significant effects observed for grass shrimp *Palaemonetes pugio* collected in fall 2003 ($\underline{P} = 0.0017$). No significant difference in habitat use was observed in mean abundance of blue crab *Callinectes sapidus* collected in fall 2003 ($\underline{P} > 0.05$) (Figure 18).

Resident finfishes collected in fall 2003 (gulf killifish *Fundulus grandis* and naked goby *Gobiosoma bosc*) showed significantly greater use of gently sloping marsh edge habitats ($\underline{P} = 0.0280$, $\underline{P} = 0.0055$) (Figure 19). Species diversity (H') was significantly greater at cut-bank sites in fall ($\underline{P} = 0.0236$) and spring ($\underline{P} = 0.0297$) sample seasons (Figure 20). Species richness was not significantly different between habitat types in either season ($\underline{P} > 0.05$, Figure 21).

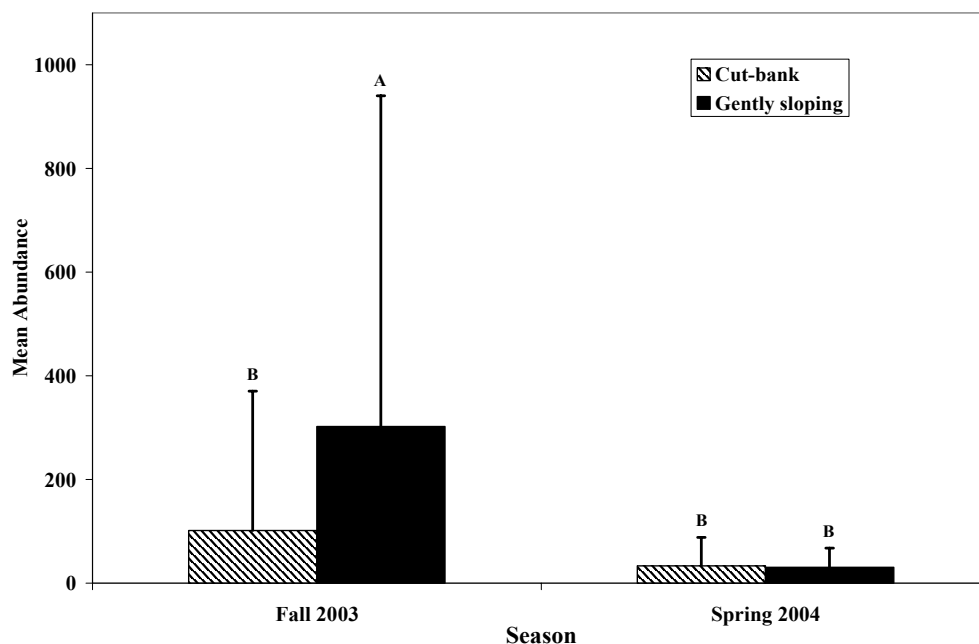


Figure 16. Mean abundance of grass shrimp *Palaemonetes pugio* + 1 SD collected in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each season ($\underline{P} < 0.05$).

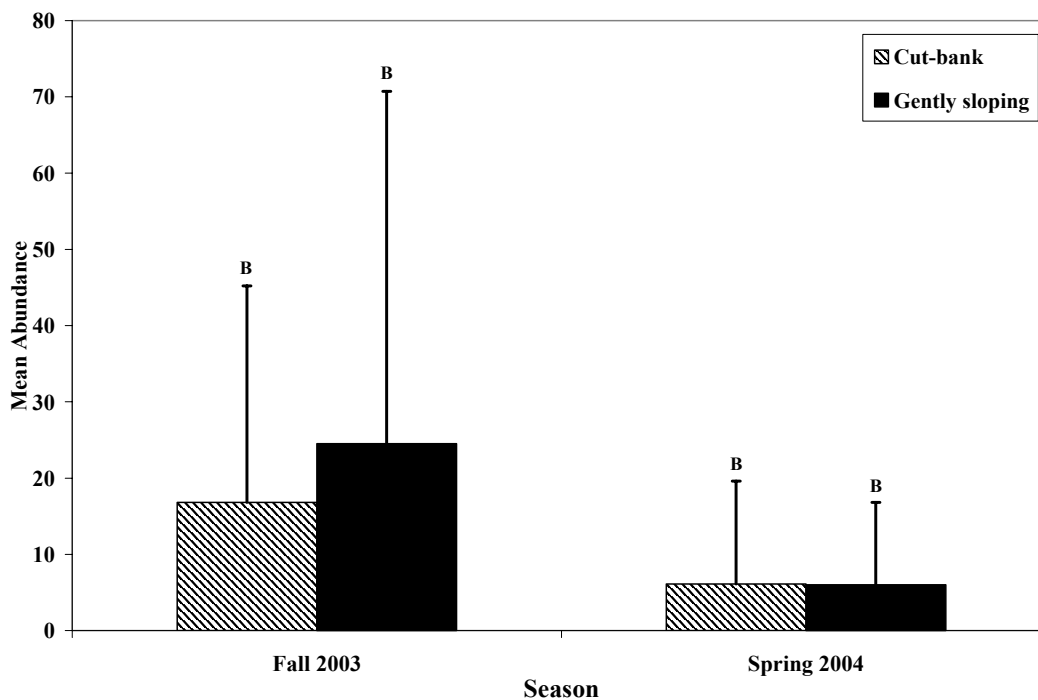


Figure 17. Mean abundance of penaeid shrimp (brown shrimp *Penaeus aztecus* and white shrimp *Penaeus setiferous*) + 1 SD collected in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. No significant differences were found within each season ($P > 0.05$).

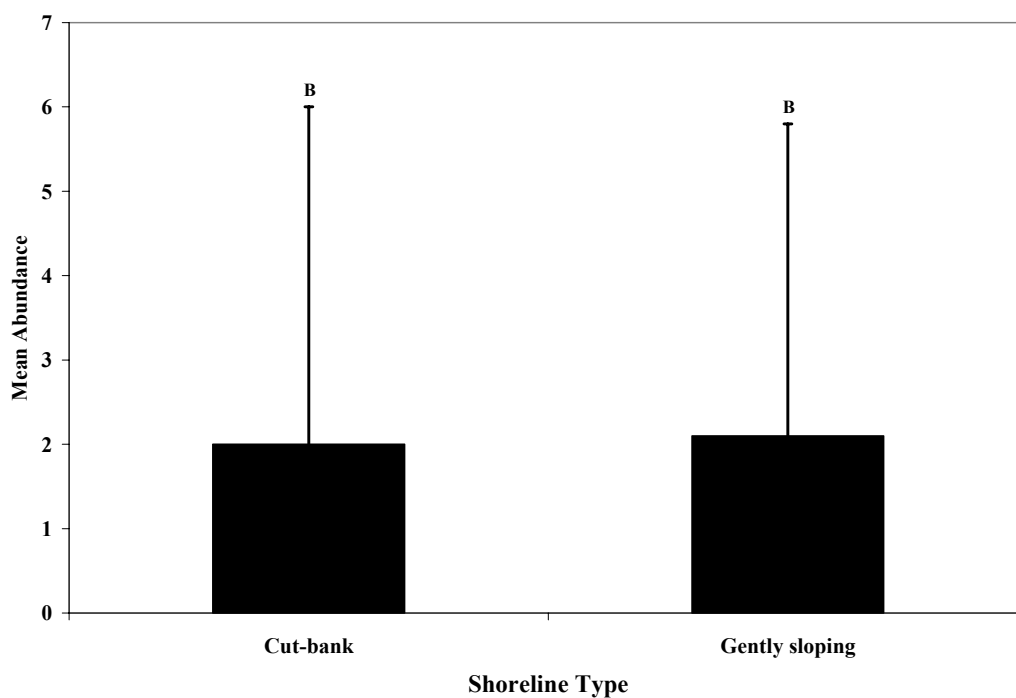


Figure 18. Mean abundance of blue crab *Callinectes sapidus* + 1 SD collected in fall 2003 at cut-bank and gently sloping marsh edge habitats. No significant difference was found between habitats ($P < 0.05$).

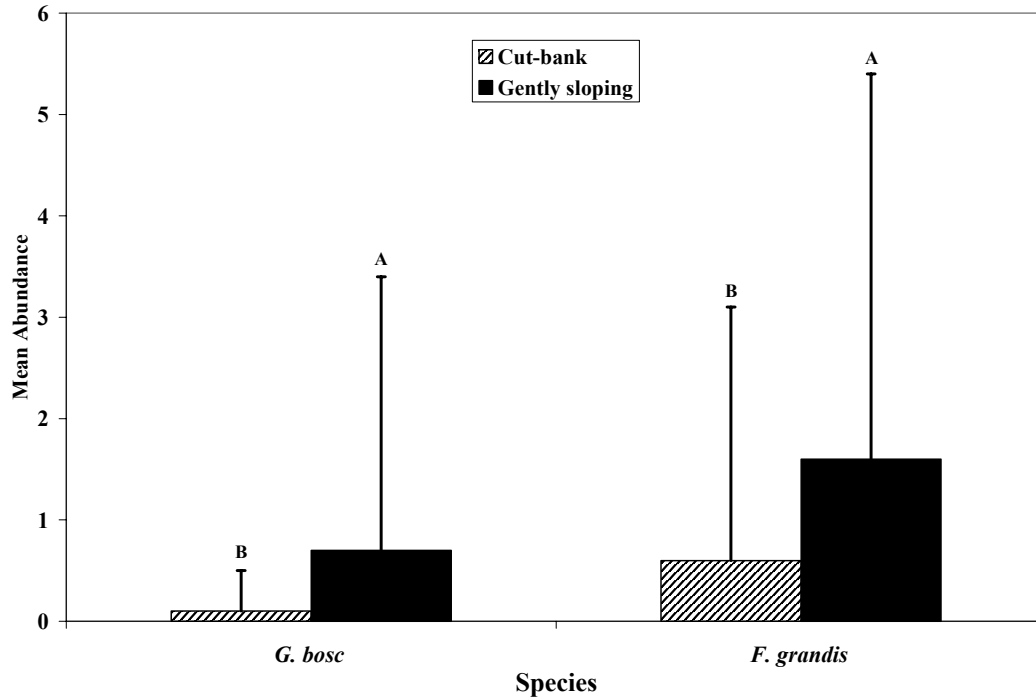


Figure 19. Mean abundance of naked goby *Gobiosoma bosc* and gulf killifish *Fundulus grandis* + 1 SD collected in fall 2003 at cut-bank and gently sloping habitats. Bars with different letters were significantly different within each species ($P < 0.05$).

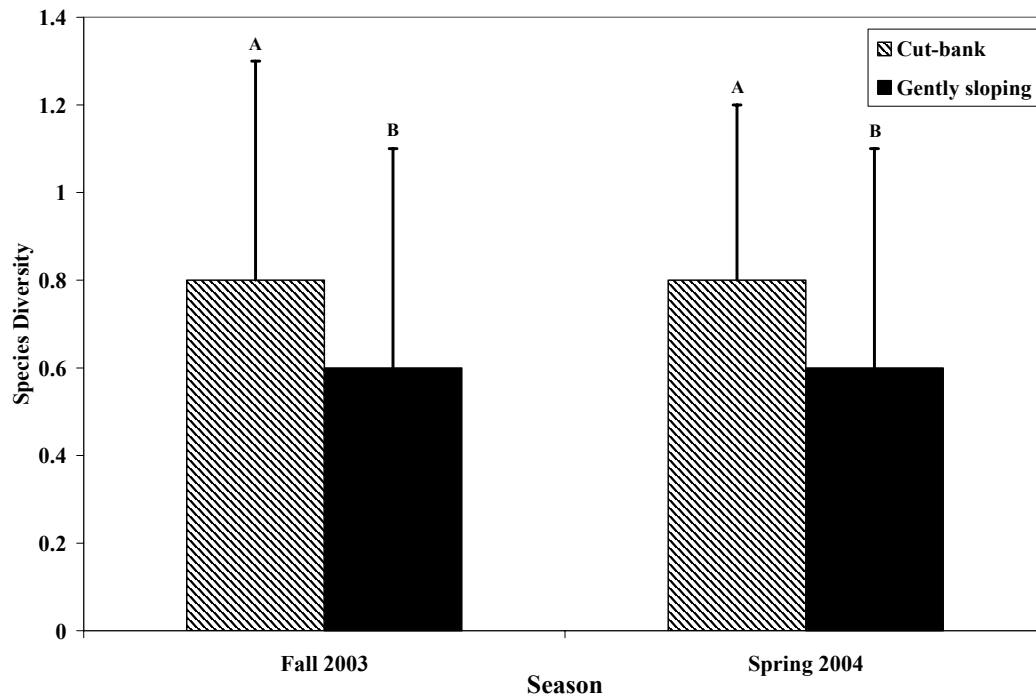


Figure 20. Mean species diversity (H') + 1 SD in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. Bars with different letters were significantly different within each season ($P < 0.05$).

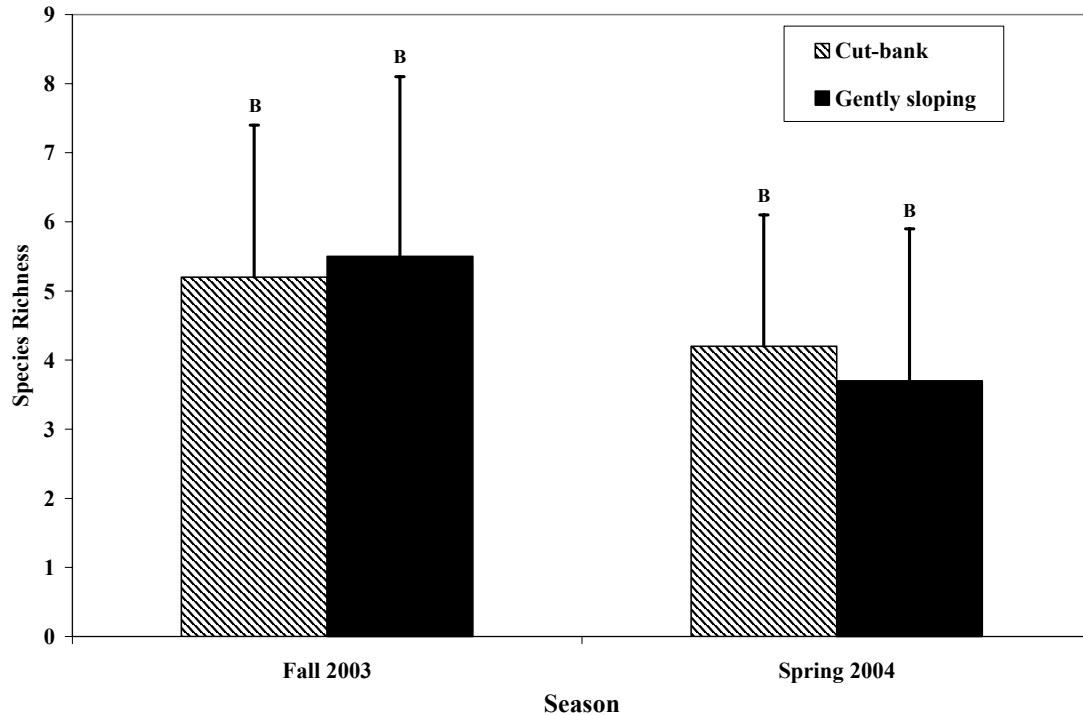


Figure 21. Mean species richness + 1 SD in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. No significant differences were found within each season ($P > 0.05$).

Nekton-Habitat Associations

Multivariate regression models showed several significant relationships between nekton community parameters and measures of marsh edge bank complexity. In fall 2003, tidewater silverside *Menidia beryllina* and gulf killifish *Fundulus grandis* were positively correlated with height of the emergent marsh bank ($P = 0.0006$, $P = 0.0032$ respectively), but negatively associated with site elevation ($P = 0.0038$, $P = 0.0016$). Grass shrimp *Palaemonetes pugio* and species of penaeid shrimp (brown shrimp *Penaeus aztecus* and white shrimp *Penaeus setiferous*) also showed negative associations with site elevation in the fall ($P = 0.0033$, $P = 0.0482$ respectively). In spring 2004, silver perch *Bairdiella chrysoura* showed a positive association

with bank undercut ($\underline{P} = 0.0015$), while species diversity (H') was positively correlated with shoreline slope ($\underline{P} = 0.0391$).

Grass shrimp *Palaemonetes pugio* ($\underline{P} = 0.0136$) and juvenile spot *Leiostomus xanthurus* ($\underline{P} = 0.0043$) collected in spring 2004 were negatively correlated with inundation of the marsh edge. Positive correlations with inundation were observed with tidewater silverside *Menidia beryllina* ($\underline{P} = 0.0304$), silver perch *Bairdiella chrysoura* ($\underline{P} < 0.0002$), spotted seatrout *Cynoscion nebulosus* ($p = 0.0089$), and penaeid shrimp ($\underline{P} = 0.0009$) collected during fall sampling, as well as with tidewater silverside *Menidia beryllina* ($\underline{P} = 0.0009$) and penaeid shrimp ($\underline{P} < 0.0001$) collected during the spring sample season. Species richness was positively correlated with inundation in both fall ($\underline{P} < 0.0001$) and spring ($\underline{P} < 0.0001$) sample seasons, whereas species diversity (H') showed a positive correlation with inundation in the spring ($p = 0.0018$).

Species associations were also observed with site exposure during fall sampling. Tidewater silverside *Menidia beryllina* ($\underline{P} = 0.0443$) and gulf menhaden *Brevoortia patronus* ($\underline{P} = 0.0054$) showed negative associations with exposure, while silver perch *Bairdiella chrysoura* ($\underline{P} = 0.0002$) and spotted seatrout *Cynoscion nebulosus* ($\underline{P} = 0.0358$) displayed positive associations. Species diversity (H') (fall: $p < 0.0001$, spring: $\underline{P} < 0.0001$) and species richness (fall $\underline{P} = 0.0001$, spring $\underline{P} = 0.0029$) were positively correlated with site exposure in both sample seasons.

Table 5. Total catch per unit effort in fall 2003 and spring 2004 at cut-bank and gently sloping marsh edge habitats. Species are listed by family and mean abundance of species \pm 1 standard deviation is provided. Species that represented ≥ 0.01 of the total seasonal finfish or decapod crustacean catch are represented by bold type.

Species	Fall 2003				Spring 2004			
	Cut-bank		Gently Sloping		Cut-bank		Gently Sloping	
	N	Mean \pm 1 SD	N	Mean \pm 1 SD	N	Mean \pm 1 SD	N	Mean \pm 1 SD
Achiridae								
<i>Achirus lineatus</i>	0	0.0 \pm 0.0	6	0.1 \pm 0.8	0	0.0 \pm 0.0	0	0.0 \pm 0.0
Atherinidae								
<i>Membras martinica</i>	10	0.1 \pm 0.8	0	0.0 \pm 0.0	1	0.0 \pm 0.1	2	0.0 \pm 0.3
<i>Menidia beryllina</i>	6027	37.9 \pm 95.4	1696	32.9 \pm 61.2	1684	74.3 \pm 231.5	2892	55.6 \pm 138.6
Balistidae								
<i>Monocanthus ciliatus</i>	0	0.0 \pm 0.0	0	0.0 \pm 0.0	1	0.0 \pm 0.1	0	0.0 \pm 0.0
Batrachoididae								
<i>Opsanus beta</i>	0	0.0 \pm 0.0	2	0.0 \pm 0.2	0	0.0 \pm 0.0	0	0.0 \pm 0.0
Belonidae								
<i>Strongylura marina</i>	6	0.0 \pm 0.2	3	0.1 \pm 0.3	35	0.2 \pm 0.9	12	0.2 \pm 0.8
Bothidae								
<i>Citharichthys spilopterus</i>	1	0.0 \pm 0.0	3	0.0 \pm 0.3	2	0.0 \pm 0.2	12	0.2 \pm 1.2
<i>Paralichthys lethostigma</i>	1	0.0 \pm 0.1	0	0.0 \pm 0.0	1	0.0 \pm 0.1	0	0.0 \pm 0.0
Carangidae								
<i>Caranx hippos</i>	33	0.2 \pm 2.4	0	0.0 \pm 0.0	0	0.0 \pm 0.0	0	0.0 \pm 0.0
<i>Oligoplites saurus</i>	22	0.1 \pm 0.5	8	0.2 \pm 0.6	0	0.0 \pm 0.0	0	0.0 \pm 0.0
<i>Selene vomer</i>	4	0.0 \pm 0.2	0	0.0 \pm 0.0	0	0.0 \pm 0.0	0	0.0 \pm 0.0
<i>Trachinotus falcatus</i>	0	0.0 \pm 0.0	0	0.0 \pm 0.0	3	0.0 \pm 0.2	0	0.0 \pm 0.0
Clupeidae								
<i>Brevoortia patronus</i>	96	0.6 \pm 2.9	9	0.2 \pm 0.9	332	2.1 \pm 9.0	9	0.1 \pm 0.7
<i>Harengula jaguana</i>	22	0.1 \pm 1.5	0	0.0 \pm 0.0	0	0.0 \pm 0.0	0	0.0 \pm 0.0
<i>Sardinella anchovia</i>	8	0.0 \pm 0.0	0	0.0 \pm 0.0	0	0.0 \pm 0.0	0	0.0 \pm 0.0
Cynoglossidae								
<i>Symphurus plagiusa</i>	18	0.1 \pm 0.4	10	0.2 \pm 0.7	6	0.0 \pm 0.3	0	0.0 \pm 0.0

Table 5 Continued.

Cyprinodontidae								
<i>Cyprinodon variegatus</i>	2	0.0 ± 0.1	2	0.0 ± 0.2	0	0.0 ± 0.0	0	0.0 ± 0.0
Dasyatidae								
<i>Dasyatis sabina</i>	6	0.0 ± 0.2	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Engraulidae								
<i>Anchoa mitchilli</i>	5383	33.2 ± 115.9	1177	23.0 ± 69.1	1598	10.2 ± 19.5	164	3.2 ± 11.8
Ephippidae								
<i>Chaetodipterus faber</i>	11	0.1 ± 0.5	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Exocoetidae								
<i>Hyporhamphus meeki</i>	2	0.0 ± 0.2	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0
Fundulidae								
<i>Adinia xenica</i>	1	0.0 ± 0.1	9	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Fundulus grandis</i>	158	0.9 ± 3.9	89	1.4 ± 3.4	1	0.0 ± 0.1	0	0.0 ± 0.0
<i>Fundulus pulverous</i>	0	0.0 ± 0.0	1	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Fundulus similis</i>	6	0.0 ± 0.2	6	0.0 ± 0.5	4	0.0 ± 0.2	0	0.0 ± 0.0
Gerreidae								
<i>Eucinostomus argenteus</i>	20	0.1 ± 0.8	11	0.2 ± 0.9	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>E. melanopterus</i>	24	0.1 ± 1.3	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Gobiesocidae								
<i>Gobiesox strumosus</i>	0	0.0 ± 0.0	0	0.0 ± 0.0	1	0.0 ± 0.1	1	0.0 ± 0.1
Gobiidae								
<i>Gobionellus boleosoma</i>	13	0.1 ± 0.4	3	0.1 ± 0.3	2	0.0 ± 0.2	1	0.0 ± 0.1
<i>Gobiosoma bosc</i>	45	0.3 ± 2.7	69	1.4 ± 4.1	2	0.0 ± 0.2	1	0.0 ± 0.1
<i>Microgobius gulosus</i>	10	0.1 ± 0.4	4	0.0 ± 0.3	2	0.0 ± 0.2	1	0.0 ± 0.1
Haemulidae								
<i>Conodon nobilis</i>	1	0.0 ± 0.1	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0
Ictaluridae								
<i>Arius felis</i>	6	0.0 ± 0.2	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Lutjanidae								
<i>Lutjanus griseus</i>	2	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Lutjanus synagris</i>	1	0.0 ± 0.1	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0

Table 5 Continued.

Mullidae								
<i>Mugil cephalus</i>	3	0.0 ± 0.1	1	0.0 ± 0.1	1357	8.0 ± 27.4	730	14.0 ± 46.6
Palaemonidae								
<i>Palaemonetes pugio</i>	19401	121.9 ± 366.9	27058	478.1 ± 1055.5	6913	45.3 ± 97.5	3139	60.4 ± 127.9
Penaeidae								
<i>Penaeus spp.</i>	3103	19.5 ± 43.5	1608	478.1 ± 1055.5	1133	7.3 ± 16.9	310	6.0 ± 10.8
Poeciliidae								
<i>Poecilia latipinna</i>	21	0.1 ± 0.7	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0
Portunidae								
<i>Callinectes sapidus</i>	377	2.4 ± 5.0	139	2.7 ± 5.1	88	0.6 ± 1.2	8	0.2 ± 0.6
Sciaenidae								
<i>Bairdiella chrysoura</i>	185	1.2 ± 4.4	88	1.7 ± 5.3	215	1.2 ± 4.5	41	0.8 ± 3.0
<i>Cynoscion arenarius</i>	51	0.3 ± 2.0	9	0.2 ± 0.9	332	0.4 ± 1.1	9	0.2 ± 0.9
<i>Cynoscion nebulosus</i>	119	0.8 ± 2.2	46	0.9 ± 2.2	11	0.1 ± 0.5	2	0.0 ± 0.3
<i>Leiostomus xanthurus</i>	3	0.0 ± 0.2	0	0.0 ± 0.0	563	3.7 ± 16.5	41	0.8 ± 2.5
<i>Menticirrhus americanus</i>	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Menticirrhus littoralis</i>	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Micropogonias undulatus</i>	3	0.0 ± 0.0	0	0.0 ± 0.0	85	0.6 ± 1.8	30	0.6 ± 2.0
<i>Pogonias cromis</i>	6	0.0 ± 0.2	1	0.0 ± 0.1	7	0.0 ± 0.2	0	0.0 ± 0.0
<i>Sciaenops ocellatus</i>	468	2.5 ± 12.9	61	0.8 ± 2.5	5	0.0 ± 0.3	12	0.2 ± 1.1
Sparidae								
<i>A. probatocephalus</i>	1	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Lagodon rhomboides</i>	12	0.1 ± 0.3	4	0.1 ± 0.3	13	0.1 ± 0.6	2	0.0 ± 0.2
Sphyraenidae								
<i>Sphyraena guachancho</i>	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Stromateidae								
<i>Peprilus burti</i>	1	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Syngnathidae								
<i>Syngnathus scovelli</i>	5	0.0 ± 0.2	1	0.0 ± 0.1	7	0.0 ± 0.3	7	0.1 ± 0.5
<i>Syngnathus louisianae</i>	23	0.1 ± 0.5	14	0.2 ± 0.5	3	0.0 ± 0.2	5	0.1 ± 0.5
Synodontidae								
<i>Synodus foetens</i>	1	0.0 ± 0.0	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0

Table 5 Continued.

Triglidae								
<i>Prionotus tribulus</i>	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
Tetraodontidae								
<i>Sphoeroides nephelus</i>	2	0.0 ± 0.2	1	0.0 ± 0.1	0	0.0 ± 0.0	0	0.0 ± 0.0
<i>Sphoeroides parvus</i>	1	0.0 ± 0.0	0	0.0 ± 0.0	5	0.0 ± 0.2	0	0.0 ± 0.0

DISCUSSION

Nekton use differed significantly among marsh edge microhabitats. Specifically, community-specific patterns of habitat use (i.e., diversity) were observed between visually distinct cut-bank and gently sloping habitats. However, due to variability in habitat requirements among species, species-specific patterns were better explained by a more detailed structural analysis of marsh edge habitats, which included habitat features such as bank height, marsh elevation, slope, and tidal inundation.

Cut-bank habitats were found to be more complex than gently sloping habitats and, similar to complexity studies conducted in other habitat types, consistently supported greater species diversity (Jones 1988, Connell and Jones 1991, Hixon and Beets 1993, Ferreira et al. 2001, Hovel and Lipcius 2001, Wyda et al. 2002). Ferreira et al. (2001) examined the effects of habitat complexity on fish use of tropical rocky shoreline microhabitats and found that more complex habitats were associated with higher fish diversity and richness. These complex habitats offered greater space between boulders and greater cover in the form of sessile invertebrates than the less complex habitats, thus providing greater refuge availability. Similarly, Ohman and Rajasuriya (1998) found strong correlations between fish diversity and complexity of coral and sandstone reefs.

For juvenile fishes and other small prey, the most important effects of habitat complexity may be on recruitment and survival. Beukers and Jones (1997) found a strong correlation between recruitment and survivorship of juvenile fishes and the abundance of high complexity corals. Russo (1987) also found that more complex habitats were associated with greater rates of prey survivorship, with complexity moderating predation through reduced foraging success by predators. Similar results were observed by Hixon and Menge (1991), who suggested that

complexity may modify the interaction between predation and competition, with more complex habitats offering greater availability of cover and decreased predation and competition. The structurally complex banks and exposed plant root systems associated with cut-bank marsh edge habitats may provide greater refuge and availability of cover for small prey fishes (i.e., bay anchovy *Anchoa mitchilli*) and juveniles over the less complex gently sloping habitats, thus influencing habitat availability and nekton diversity.

In contrast, gently sloping edge habitats, although less complex, were associated with increased inundation of the marsh surface. This increased inundation provides additional habitat complexity from flooded vegetation and apparent benefits over cut-bank habitats for species that exploit the inner marsh by providing earlier and prolonged access across all tidal cycles (Zimmerman et al. 1991, Rozas and Reed 1993). Several small resident finfishes, specifically naked goby *Gobiosoma bosc* (fall) and gulf killifish *Fundulus grandis* (fall), showed greater use of gently sloping sites over cut-bank sites. Resident species have been shown to congregate in shallow subtidal areas that provide earlier access to vegetated intertidal habitats during flood tides (Rozas and Odum 1987, Rozas et al. 1988, Rozas and Zimmerman 2000). Grass shrimp *Palaemonetes pugio* (fall) also showed greater use of gently sloping habitats over cut-bank habitats and the negative association between grass shrimp abundance and tidal inundation in the spring suggests that this species is absent from shallow subtidal open-water edge habitats when water levels allow access to vegetated intertidal habitats. Previous studies of shallow estuarine habitats have suggested that selection of shallow subtidal and vegetated intertidal habitats by juveniles and other small nekton may be linked to predation. Small fishes are often too small to be of interest to avian predators (Kneib 1982) and may seek out shallow water habitats to escape predation by larger piscivorous fishes (Ruiz 1993).

The positive associations between species richness (fall and spring), diversity (spring), abundances of several species of estuarine transients including tidewater silverside *Menidia beryllina* (fall and spring), silver perch *Bairdiella chrysoura* (fall), spotted seatrout *Cynoscion nebulosus* (fall), and penaeid shrimp (fall and spring), and tidal inundation provides evidence to suggest that a high number of species move into these habitats from other estuarine areas during higher water levels to exploit the available resources. Kneib and Wagner (1994) observed that transient species tend to arrive later on flood tides and leave the marsh earlier on ebbing tides and suggested that this timing and behavior was important to avoid stranding and desiccation. With the exception of bay anchovy *Anchoa mitchilli* (fall), no differences were observed in abundances of estuarine transients between cut-bank and gently sloping edges. Because transients arrive later on flood tides, the shallow slopes of gently sloping edges may be just as accessible as the steep slopes associated with cut-bank habitats, thus allowing use of the open-water edge across all marsh edge habitat types.

Similar to the finding of Kentual et al. (1992), marsh edge elevation and shoreline slope seemed to positively influence stem densities and percent cover of shoreline vegetation. The lower stem densities recorded at gently sloping habitats may attract nekton by providing increased foraging surface and success without affecting movement (Rozas and Zimmerman 2000). Higher stem densities and percent cover of cut-bank habitats may limit nekton access to vegetated intertidal habitats and with the added effects from associated patterns of high elevation and low inundation, cut-bank habitats may altogether prevent nekton use of the inner marsh. The dense vegetation at cut-bank habitats may have alternative benefits for larger nekton that rarely move onto the marsh surface. Emergent vegetation provides structural complexity in the coastal

landscape that offers habitat for ambush predators (Whitman and Gilmore 1993, Kneib 1997, Kneib 2003).

The index of exposure to wind and wave action may provide some insight into landscape effects on species richness and diversity. The high diversity and richness of nekton at more exposed microhabitats suggests that these shorelines are more accessible to nekton. The majority of the highly exposed sites were cut-bank habitats located on the outermost edges of the marsh islands and were possibly areas of initial contact for nekton moving into the marsh from other estuarine environments.

Landscape position, although not specifically measured, may provide another type of habitat complexity measure that could be useful in understanding nekton use of marsh edge habitats. The majority of gently sloping habitats included in this study were located in protected areas of the marsh near the shallow mouths of subtidal creeks. Polychaete worms, which are an important food source for small fishes, blue crab, and brown shrimp (McTigue and Zimmerman 1991), have been shown to be most abundant near natural marsh creeks (Kneib 1984) and Minello et al. (1994) showed that abundance of natant macrofauna was correlated with polychaete densities in the associated sediment. Subtidal creeks have also been shown to serve as staging areas for nekton that move into adjacent intertidal habitats during flood tides (Rozas and Odum 1987, Rozas et al. 1988, Rozas and Zimmerman 2000).

Implications for Habitat Restoration

The importance of landscape features, such as tidal creeks, and marsh edge structural features is beginning to be emphasized in restoration projects of marsh environments. Specifically, a number of studies evaluating the value of created marsh edge have suggested that the created marshes, and specifically the edges created, are not functionally equivalent to the

natural marsh habitats in terms of nekton habitat (Minello 2000, Rozas and Minello 2001, Bush Thom et al. 2004). Marsh creation projects that have in fact increased habitat complexity by adding various natural structural components (i.e., tidal creeks) into their architectural design have increased nekton use and function over control areas (Minello et al. 1994). These studies, combined with findings from this study, highlight the need for better understanding of intrahabitat variability, and specifically, of the effects of habitat complexity on nekton use. The identification of structural marsh edge features that enhance nekton use of edge habitats allows for habitat complexity to be incorporated into the architectural design of artificial marshes.

Fisheries Management Implications

A lack of consistent results for many parameters between fall and spring seasons may be due to distinct differences in nekton community composition that often exist between these two seasons (Conner and Day 1987). Presence, absence, or abundance of certain species in the bay may alter habitat use by other organisms between seasons, which could complicate the search for useable measures of marsh edge structure to manage for specific species. However, if EFH designations remain species specific, detailed analyses of species of interest could generate species-specific marsh edge micro EFH identification. For example, a finfish of recreational and economic importance to many regional managers such as spotted seatrout *Cynoscion nebulosus* was found to be positively related to tidal inundation, which is a measure that could be easily calculated over large areas to identify marsh edge microhabitats that are preferred by this species.

Alternatively, findings from this project could be used to identify marsh edge microhabitats that contribute most to species diversity, based on findings of significantly higher diversity at visually distinct cut-bank edges, which were highly correlated with quantitative

measures of site exposure and tidal inundation. These quantitative measures are easily calculated indices that could be applied at a large scale, making it a potentially significant and useful tool for making regional assessments of habitat value. Further testing of these methods should be conducted, but they may provide a useful approach for predicting habitat value and contribute significantly to conservation efforts, which are often aimed at managing habitats that support greater biodiversity (Edinger and Risk 2000).

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