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Habitat use by nekton in a saltmarsh estuary along a stream-order gradient in northeastern Barataria Bay, Louisiana

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**HABITAT USE BY NEKTON IN A SALTMARSH ESTUARY ALONG A
STREAM-ORDER GRADIENT IN NORTHEASTERN 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 Department of Oceanography and Coastal Sciences

by

Pablo Granados-Dieseldorff
B.S., Universidad de San Carlos de Guatemala, 2001
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TO AMREI AND MATTHIAS

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ABSTRACT

Mesohaline estuarine regions in Louisiana play an important role in coastal ecosystems. To begin to understand how nektonic species and communities respond to environmental variables before habitat modification, I examined patterns of habitat use by fishes and decapod crustaceans in a seemingly pristine mesohaline system that drains into Bay Batiste, southeastern Louisiana. The study area was focused on a relatively unaltered core saltmarsh complex drained by intertidal and subtidal streams and it was representative of a larger surrounding system in terms of nekton community structure and associated environmental variables. Stratified monthly sampling (February – November 2004) along a stream-order gradient examined changes in nekton abundance, species richness, and community structure within the study area. Analyses were based on a microhabitat approach used to characterize nekton responses to seasonal and spatial gradients of water depth, temperature, dissolved oxygen concentration, salinity, turbidity, bottom slope, stream width and distance to mouth. In 81 seine samples, 3757 individuals from 30 taxa were collected. Daggerblade grass shrimp was the numerically dominant species (72.7 %), followed by penaeid shrimp (13.4 %), bay anchovy (1.7 %) and inland silverside (1.7 %). Univariate ANOVAs detected the significant effects of stream order and season on nekton abundance and associated environmental variables. Greater numbers of nekton were mainly distributed in streams of low order. Kendall's W tests of ranked abundances indicated that nekton community structure was concordant among stream orders but not among seasons. Seasonal and spatial differences of environmental variables across stream orders and among seasons were attributed to the geomorphological and hydrological characteristics of the study area. A factor analysis resolved eight environmental variables into four orthogonal axes that explained 80 % of environmental variation. Factor one was interpreted as a stream-order axis,

Factor two as a morphological axis, Factor three as a seasonal axis, and Factor four as a salinity axis. Differences in use of the four-dimensional factor space by dominant species reflected habitat selection, species residency status and seasonality of recruitment.

INTRODUCTION

Louisiana estuaries and low salinity coastal waters play an important role in marine ecosystems, most notably because of their high primary and secondary productivity that supports a great abundance and diversity of fishes and invertebrates (Boesch & Turner 1984, Beck et al. 2001). For more than fifty years, our understanding of the recruitment of estuarine fishes and macroinvertebrates has been based on two principles (Able 2005): (1) estuaries are important nursery grounds because of the role they play in providing juveniles a relatively food-rich environment with reduced predation pressure, and (2) many species are estuarine dependent. Ecologists have usually considered the entire estuary to be a nursery, but lately there has been more emphasis on individual habitat types such as salt marshes (Minello et al. 2003). High individual densities in estuaries indicate high quality and preferred habitat (Zimmerman & Minello 1984, Baltz et al. 1993, Rozas & Minello 1998), but the identification of nursery habitat types should require at least a comparison of the densities of early life history stages in other nearby habitat types (Pearcy & Myers 1974).

Physicochemical factors, especially salinity and temperature, as well as biotic factors (e.g., competition and predation) are likely to be responsible for nekton distributional patterns and abundance in estuaries (Rozas & Zimmerman 2000). Because tidal creeks are conduits and staging areas at low tide for nekton that use the flooded marsh surface, their properties may influence the use of adjacent marshes by controlling some species or predators (Rozas & Odum 1987, Rozas et al. 1988, Rozas & Zimmerman 2000). In the context of niche theory (Hutchinson 1957) and competition, an individual uses a resource space to the exclusion of other species, and its tolerance to a particular habitat resource limits the space an individual can occupy (Magnuson et al. 1979). Both shallow water and flooded vegetation at the marsh edge (marsh-water interface) provide protection to small fishes and decapod crustaceans from large, natant predators

(Baltz et al. 1993, Ruiz et al. 1993, Miltner et al. 1995), leading to higher nekton densities in this estuarine ecotone (Minello et al. 1994, Peterson & Turner 1994, Minello 1999, Rozas & Zimmerman 2000).

Each species or life history stage has a particular suite of preferences, requirements, and habits that determine how its population will respond to natural and anthropogenic changes in coastal Louisiana (Baltz et al. 1993, 1998). The specific microhabitat that an individual occupies is limited by the physiological tolerances and interactions with other species (Magnuson et al. 1979, Hurlbert 1981, Magnuson 1991). At the finest scale, the microhabitat of an individual is the site it occupies at a given point in time (Baltz 1990). Individual fishes and decapod crustaceans presumably select sites in response to factors that optimize their net energy gain while minimizing predation risks and competition (Boesch & Turner 1984, Baltz 1990, Baltz et al. 1993). Careful measurements of numerous individuals and associated physicochemical and biological variables should define the response of a population or life history stage to complex environmental gradients (Hurlbert 1981, Livingston 1988, Baltz 1990, Baltz et al. 1993). The structure of a local nektonic community can be viewed as an array of species that have successfully passed through a series of biotic and abiotic filters (e.g., vicariant events, zoogeographic filters, physiological factors, biological interactions, natural and anthropogenic disturbances) to constitute the particular assemblage observed (Smith & Powell 1971). For species that use estuaries, seasonal variation in environmental conditions may serve as ecological filters (Magnuson 1991, Moyle & Cech 2004) or bottlenecks (Wiens 1977, Beck 1995) that define the quantity of suitable habitat for early life history stages and thus influence recruitment into adult populations. A minor reduction in juvenile mortality can be quite important in determining the size of the adult population (Rose et al. 1993). Given the importance of

Louisiana's highly productive estuarine nurseries, it is of interest to determine how fishes and decapod crustaceans use the available coastal estuarine habitat (Switzer et al. 2004).

The geomorphological attributes of estuaries, such as dendritic intertidal stream networks, add elevation and channel complexity that increase edge in saltmarsh landscapes, offering feeding grounds and refuge from predators to nektonic species (Kneib 1994, Desmond et al. 2000, Simenstad et al. 2000). The saltmarsh complex is constituted by different habitat types which vary in microtopography, elevation, and location within the estuarine system. These attributes, in conjunction with tides, submergence, coastal geomorphology and meteorological and climatical events, result in patterned pulses of marsh flooding that control and facilitate habitat use by nekton (Rozas 1995, Rozas & Reed 1993, Zimmerman et al. 2000). On the northern Gulf coast, nekton spatial distributions are irregular and population sizes are difficult to estimate (Minello & Rozas 2002). The approach of combining fine-scale distributions and landscape-scale patterns could facilitate the estimation of populations and the assessment of ecological processes in marsh ecosystems (Kneib 2000). Odum (1984) adapted Horton's (1945) concept of stream order to tidal marsh creeks based on the number of tributaries (i.e., first order streams have no tributaries, second order streams result from the confluence of two first order streams, etc.) and on morphological features (i.e., stream size, drainage basin area, stream width and depth, and tidal flood stage). Essentially, "tidal creeks of the same stream order have similar physical attributes (width, depth, and drainage basin size) which influence their physiochemical and biological properties ... and vary across stream order" (Rozas & Odum 1987).

In the north central Gulf of Mexico, mesohaline estuarine regions have only been studied episodically, for short durations (McIvor & Rozas 1996, Minello 1999), and have generally failed to encompass the entire life cycle of many important species or the duration of environmental disturbances (Jackson et al. 2001). To begin to understand how species and

communities respond to environmental stressors, I selected a core study area of “high quality” habitat nested within more heavily degraded conditions to examine faunal responses to environmental variables with minimal baseline degeneration (Pauly 1995). Within a wider area more strongly modified by human intervention (e.g., infrastructure and canal construction for oil industry), the core area is a more natural mesohaline system characterized by a network of tidal creeks with natural variation in biotic and abiotic conditions, and with little or minimum effects of fishing. I addressed the question of habitat use by nekton by fine scale studies of distribution and abundance at the microhabitat level (Baltz 1990). The overall objective of this study was to describe the effects of stream order, seasonality, and selected environmental variables on the abundance, species richness, and community structure of fishes and decapod crustaceans in a seemingly pristine saltmarsh stream system. An analysis of environmental data and nekton samples collected monthly at 81 different sites across three stream orders draining into Bay Batiste, Louisiana, tested: (1) whether nekton composition (abundance, species richness, and community structure) and habitat structure changed seasonally and/or spatially along a stream-order gradient, and (2) what environmental variables accounted for observed differences in habitat use by dominant species.

MATERIALS AND METHODS

Study Area

Barataria estuary has 55% of the total wetland area surrounding the Gulf of Mexico, most of which is marsh habitat (Turner 2003). The Barataria Basin (Fig. 1) is the first major estuary west of the Mississippi River and is approximately 110 km long and 50 km wide and has a saltmarsh area of 145,000 ha (Conner & Day 1987). Located between the natural levees of the Mississippi River and the abandoned Bayou Lafourche distributary, the basin was increasingly deprived of riverine input of sediment and fresh water by closure of the Bayou Lafourche-Mississippi River connection in 1902 and by an enhanced levee system completed in the 1930s–40s (Conner & Day 1987). The absence of riverine inputs of fresh water, sediments, and nutrients, combined with subsidence, canal construction for petroleum production, drainage, and navigation, and saltwater intrusion, contributed to an estimated wetland loss in southern Louisiana of $65 \text{ km}^2 \text{ yr}^{-1}$ from 1969–1979 (Dunbar et al. 1992, Ning & Abdollahi 2003, Stead & Hill 2004). However, recent models have estimated that the annual wetland loss rate for the region decreased to 25.6 km^2 from 1990–2000 (Morton et al. 2005). The opening of the Davis Pond freshwater diversion in 2002 has provided an additional source of fresh water and sediment in an attempt to reverse the land loss trends in Barataria Basin (Stead & Hill 2004).

Currently the main source of fresh water for the basin is precipitation, which averages 160 cm yr^{-1} (Baumann 1987). The climate is subtropical, hot and humid (Ning & Abdollahi 2003), and the hydrography and salinity are primarily influenced by local precipitation, tidal flux, and prevailing winds (Baumann 1987, Switzer et al. 2004).

The hydrology of the microtidal system (mean tidal range of 0.32 m) is easily dominated by wind stress (Childers et al. 1990), generally associated with winter cold fronts, which minimizes vertical stratification within the shallow bays (Hopkinson et al. 1985).

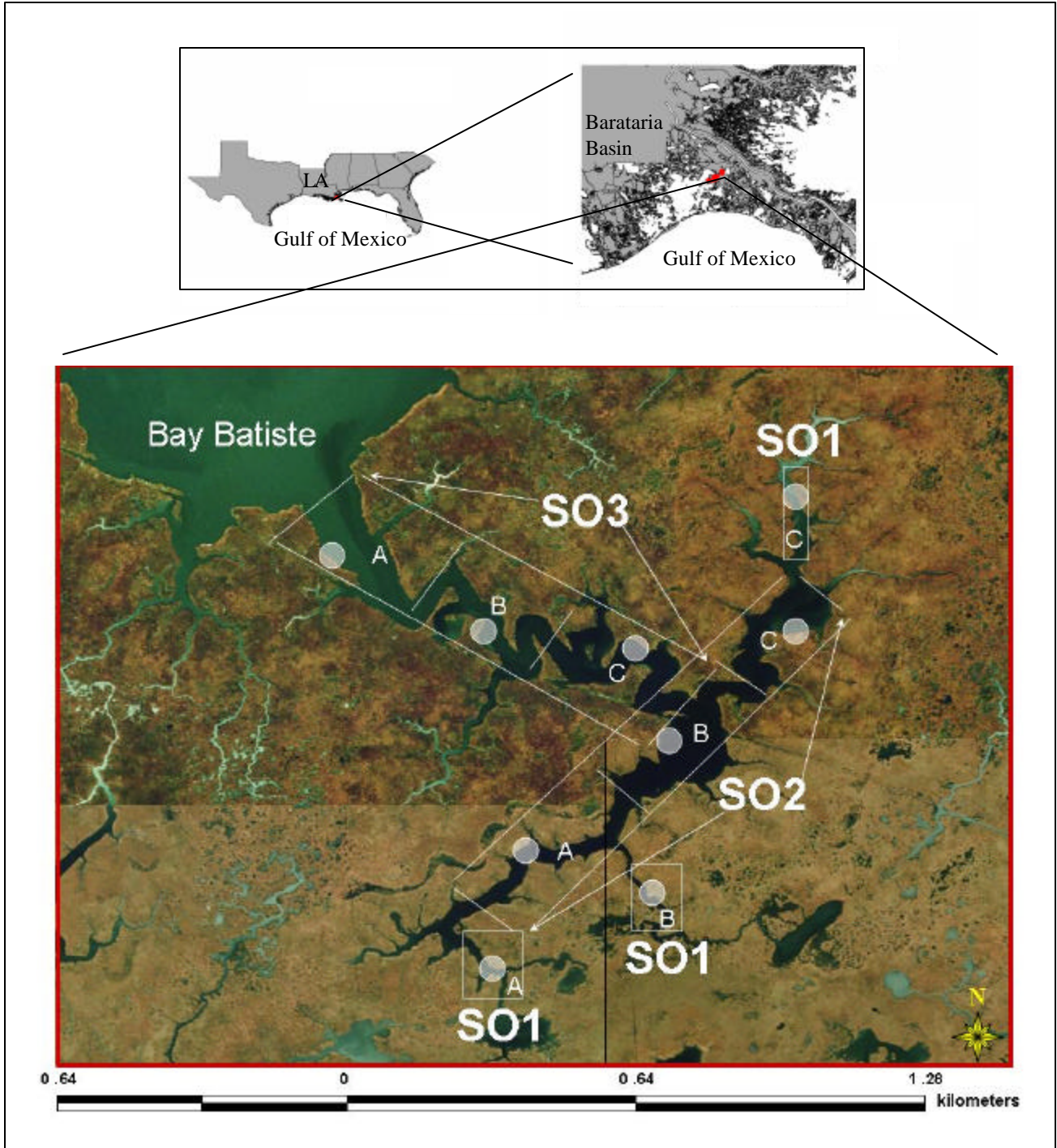


Fig. 1. Study area and reference system in Bay Batiste, northeastern Barataria Bay, coastal Louisiana, with stream-order stratification: stream order 1 (SO1), upper reach; stream order 2 (SO2), middle reach; and stream order 3 (SO3), lower reach open to Bay Batiste. Three randomized locations (A, B, and C) within each stratum were sampled for fishes and decapod crustaceans.

Warmer temperatures and higher humidity are associated with southeasterly winds in spring and summer, and cooler, drier weather accompany the northerly winds that occur predominantly in fall and winter. Water level and the resulting marsh hydroperiod (i.e., the frequency of marsh inundation) in the Barataria Basin are governed by the combined effects of tides and weather events (Baumann 1987, Rozas 1995). In coastal Louisiana, *Spartina alterniflora* marshes are flooded only about 20 % of the time in January, but up to 80 % of the time in September and October (Gosselink 1984). The tidal pattern switches in the area from high tides around noon in late spring and summer to high tides around midnight from late fall to middle spring. Maximum tidal range occurs during summer and winter solstices, and minimum tidal range occurs during spring and fall equinoxes (Baumann 1987). Tides in the basin are diurnal and because of their small range, meteorological events often influence the marsh hydroperiod more than astronomical tides (Rozas 1995). A bimodal distribution of seasonal water level is characteristic of the basin. The substantial change from low wind stress in summer to higher wind stress in fall accentuates the corresponding rise in water level, and the reversal in direction of high wind stress from fall to winter accentuates the corresponding decrease in water level (Baumann 1987, Rozas 1995). Additionally, episodic winter cold fronts generally cause a rapid drop in estuarine water levels (Swenson 2003).

Salinities in the saltmarsh portion of Barataria Bay vary seasonally and spatially between 6 and 22 psu (Baltz et al. 1993). Water in the basin is turbid and shallow, with depths usually not exceeding 2 m (Baltz et al. 1993, Allen & Baltz 1997). The dominant marsh vegetation is *Spartina alterniflora* (smooth cord grass) and other species present include *Juncus roemerianus* (black rush), *Distichlis spicata* (saltgrass), *Batis maritima* (saltwort), and *Salicornia virginica* (glasswort) (Conner et al. 1987).

The study area is centered on a small tidal mesohaline marsh system (i.e., the reference system) that drains into Bay Batiste, northeastern Barataria Bay, Louisiana (Fig. 1). It consists of a relatively unaltered core saltmarsh complex that includes vegetated marsh surface and intertidal and subtidal streams. The reference system is surrounded by a larger area that has been greatly modified by human intervention (e.g., infrastructure and canal construction for oil industry, dredging, and navigation). Based on image analysis and field verifications, the morphology of this seemingly pristine reference system is unique within Bay Batiste and northeastern Barataria Bay basins (Jennifer Spicer, pers. comm.).

Field Methods

Following Rozas & Odum (1987), the reference system was stratified morphologically into three stream orders, first order upper reaches (SO1), second order middle reaches (SO2), and the third order lower reach (SO3) (Fig. 1) to facilitate sampling across the stream-order gradient (about 2 km length) and to describe patterns of habitat use by nekton within the system. Within each stratum, three randomized sites were selected each month (A, B, and C) to sample fishes and decapod crustaceans and associated environmental conditions during daylight hours (Fig. 1).

My intent was to collect 3 samples within each stratum on a monthly basis; however, the tidal regime and the northerly winds associated with cold fronts in the fall and winter precluded access during December 2003 and January 2004 because of extreme low tides during daylight. Winter samples were those collected in February ($n = 8$); spring samples were collected in March ($n = 9$), April ($n = 9$), and May ($n = 9$); summer samples were collected in June ($n = 9$), July ($n = 9$), and August ($n = 9$); fall samples were collected in September ($n = 9$), October ($n = 6$), and November ($n = 4$). First order streams (SO1) were intertidal creeks and only 24 samples were collected. Three different first order (SO1) streams were selected based on sampling accessibility (i.e., stream width > 6 m and maximum depth > 15 cm) and were consequently

located farther from the mouth of the reference system (Fig. 1). Twenty-seven samples were collected in two second order streams (SO2), which were generally subtidal, except for the shallowest areas on extreme low tides during the late fall and the entire winter seasons. The third order stream (SO3) was subtidal and 30 samples were collected.

Samples were collected using a bag seine (6 m long, 1.20 m deep, 1.20x1.20 m bag, 0.6 cm mesh size) with a mudline (i.e., a modified bottom line of 9 strands of 1 cm diameter rope for use on fine substrates), and sampling consisted of making a seine haul along the nonvegetated marsh edge: one seine pole was fixed at the shoreline, while the other was used to stretch the seine toward mid-channel, before moving to shore and closing the net into a semi-circle. Haul duration was carefully timed and short, 1 minute, to minimize habitat heterogeneity and net clogging. Each haul covered an area of approximately 30 m². Surficial substrate was characterized in the field at each haul site in terms of dominant and subdominant bottom types and coded on an ordinal scale of particle size as (1) clay, (2) silt, (3) sand, (4) plant detritus (primarily decaying *S. alterniflora* stems and rhizomes), and (5) fragments or whole shell (Baltz & Jones 2003). Salinity (psu), temperature (°C), and dissolved oxygen concentration (mg l⁻¹) were measured at each sampling site in the water column with a Yellow Springs Instrument (YSI) model 85 meter. Turbidity (NTU) and pore water samples were collected and maintained in cold storage until they were read on a HACH 2100N nephelometer and on a Microtox model 500 analyzer in the laboratory. Microtox was used to screen sample sites for contamination (Long 2000). Minimum and maximum water depths were used to calculate median depth (cm) and to estimate the grade of the bottom slope (%) as the ratio of their difference divided by the seine length. Stream width (m) at each sampling site and distance to mouth (m) were estimated in the field using a Garmin GPS model 72 and corrected in the laboratory with Garmin MapSource and ArcView 3.3.

Seine samples were sorted in the field to separate all fishes and decapod crustaceans. Specimens were iced and returned to the laboratory for identification using keys and descriptions by Heard (1982), Thompson (1986), Hopkins et al. (1989), and Hoese & Moore (1998). Species were counted and measured to the nearest millimeter of standard length (SL) for fishes, of carapace width (CW) for blue crabs, and of total length (TL) for all other decapods, then preserved in 70 % ethanol. Organisms were recorded as juveniles or adults based on literature values for size at maturity published in the US Fish and Wildlife Service species profiles series (1983-1989) and in the FishBase website (www.fishbase.org).

Analytical Methods

Two-factor ANOVAs (3x4 Factorial), using the MIXED procedure (mixed linear model procedure) and the least-square-means method (SAS Institute Inc 2004), were used to test for interactions and separate effects of stream order and season on eight environmental variables (i.e., water depth, bottom slope, temperature, dissolved oxygen concentration, salinity, turbidity, stream width, and distance to mouth) and on six biological variables (i.e., abundance and species richness of decapod crustaceans, fishes, and total individuals combined). In analyses, variables either exhibited homogeneity of variance and were normally distributed, or were transformed by log functions ($\ln(X)$ for environmental variables and $\ln(X+1)$ for biological data) to conform to test assumptions. If interactions between stream order and season were non-significant (p -values > 0.05), the main effects of stream order and season on environmental and biological variables were examined separately. The ten most frequently occurring species (i.e., species that occurred in more than 9 % of total sites) were selected to evaluate patterns of resource use among species. Univariate means and standard errors of environmental variables for species were calculated by treating each seine-haul collection as an independent sample. For among-species comparisons, I generated one record for each species present in each sample and decapods and fishes were

analyzed separately. Main effect means of environmental variables found to differ significantly in ANOVAs were tested using Tukey's adjustment for multiple pairwise comparisons.

To examine spatial and seasonal changes in community structure, I used Kendall's W (Kendall 1955, Landis & Koch 1977, Fleiss 1981, SAS Institute Inc 2004) to test for concordance in numerical ranking of abundant species. Separate tests were conducted across stream orders and seasons. I progressively reduced the number of species included to examine the influence of the most dominant species. Only the 10 most common species were used to assess patterns of community structure because rare species tended to be concordant.

To understand and visualize changing community structure across important environmental axes, I examined variation in patterns of habitat use in a Factor Analysis of eight environmental variables (i.e., temperature, dissolved oxygen concentration, salinity, turbidity, water depth, bottom slope, stream width, and distance to mouth) based on the correlation matrix. The analysis was conducted using the Factor Procedure and the Varimax rotation option to facilitate interpretability (SAS Institute Inc 2004). Environmental variables in 81 samples were used to calculate variable loadings and generate factor scores for each sample. Mean factor scores for each species were calculated by treating each sample as an independent observation and weighting the analysis by abundance. I calculated multidimensional means to plot species centroids in factor space. Confidence intervals (± 1 SE) about the centroids were estimated as the means of standard errors for each of four factor scores for each species, and then were displayed as balloons of 1 SE radii to allow for visual comparisons of resource utilization among species.

To compare the study area with the surrounding systems in terms of nekton abundance, species richness, community structure, and habitat conditions, I conducted two short-term ecological experiments that involved sampling of environmental and biological variables at

increasing distances from the center of the reference system (Fig. 2). During daylight hours at high tide in July 2004, 9 sites were sampled on a 1.6-km radius circle (i.e., reference circle) and another 9 sites were sampled on a concentric circle with a 3.2-km radius (C2). Nekton abundance, species richness and the same suite of associated environmental variables (i.e., water temperature, salinity, dissolved oxygen concentration, turbidity, depth, and bottom slope) were measured at each sampling site. In July 2005, a second experiment was conducted and the same environmental and biological variables were measured. For this occasion, 10 sites were randomly intercepted on the reference circle (RC), and another 10 sites were randomly intercepted on a concentric circle with a 5-km radius (C3). The first experiment tested the representativeness of the reference system to surrounding high quality habitat, and the second experiment tested the reference system against human-altered habitat.

For both experiments (July of 2004 and 2005), I used univariate ANOVAs in SAS to test differences in environmental and biological variables between the reference circle and the larger circles and a series of multivariate 1-way layout ANOSIM (Analysis of Similarities) in PRIMER version 5.2.9 (Plymouth Routines In Multivariate Ecological Research 2000) to test differences in nekton community structure. ANOSIM is a non-parametric hypothesis test analogue of ANOVA (Clarke & Green 1988, Clarke 1993, Clarke & Gorley 2001, Clarke & Warmick 2001) and is based on permutation tests (Mantel 1967), combined with a general randomization approach for the generation of significance levels (Monte Carlo tests, Hope 1968). Basically, ANOSIM tests for differences among groups, defined *a priori*, of multivariate samples from different locations, times, conditions, etc. (Clarke & Green 1988, Clarke 1993, Clarke & Gorley 2001, Clarke & Warmick 2001). ANOSIM is a statistically robust test that operates on similarity matrices and assumes that the primary information on group relationships between samples is summarized in the ranks of the similarity matrix (Clarke & Gorley 2001). Prior to constructing

the rank similarity matrices, data were log-transformed for approximation to multivariate normality and standardized to Bray-Curtis similarity measures for biological data and normalized Euclidean distances for environmental variables. The resulting R-statistic values in ANOSIM, more than the p-values, give an absolute measure of how well the groups are separated (Clarke & Warwick 2001) on a scale from 0 (indistinguishable) to 1 (complete segregation).

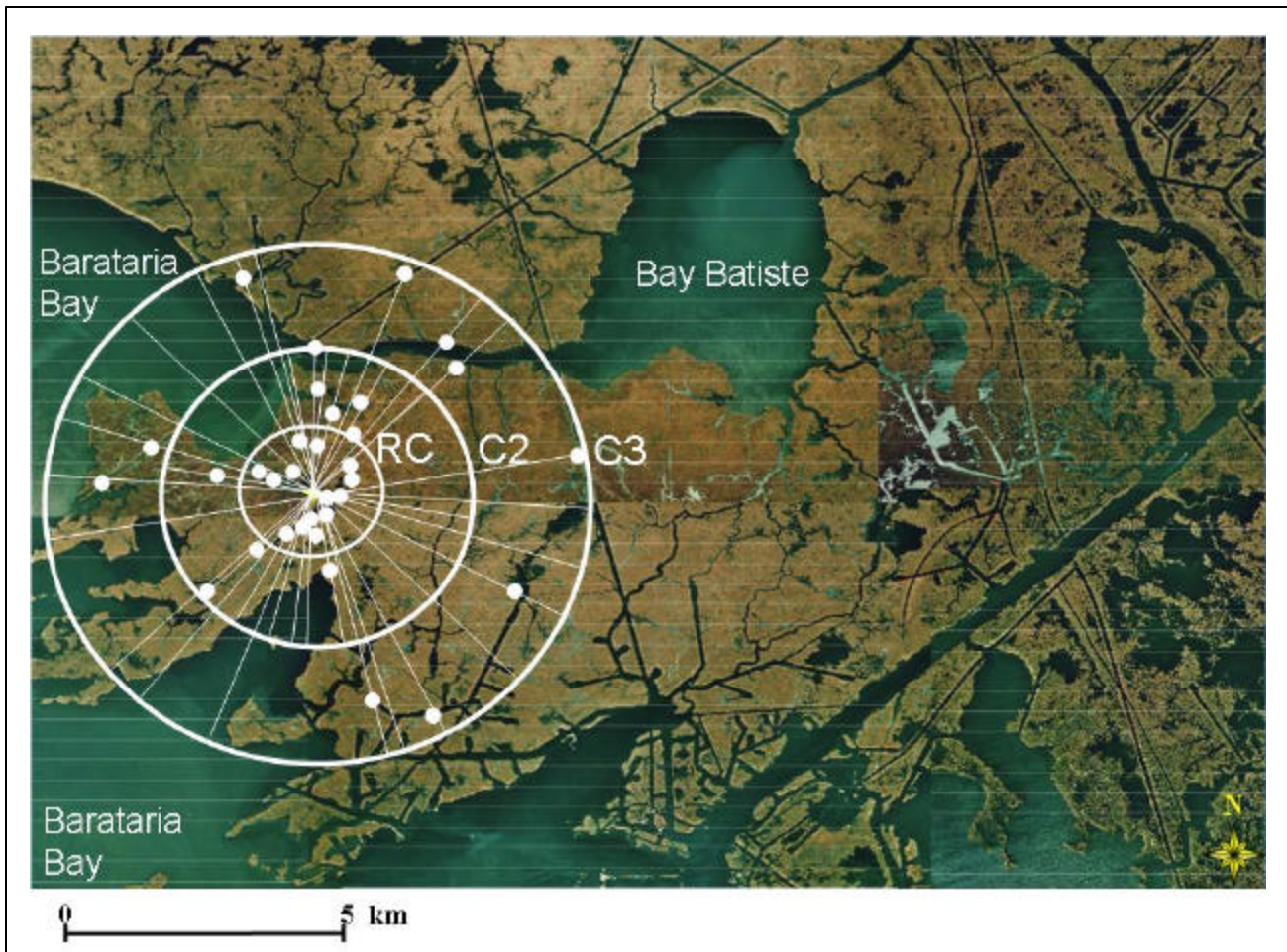


Fig. 2. Sampling design of the two ecological experiments conducted in July of 2004 and 2005 in northeastern Barataria Bay, coastal Louisiana. The lower reach (SO3 in Fig. 1) of the reference system constituted the center of three concentric circles: RC: reference circle with a 1.6-km radius, C2: circle with a 3.2-km radius, and C3: circle with a 5-km radius. In 2004, random radii intercepted 9 sampling sites on RC and another 9 sampling sites on C2. In 2005, random radii intercepted 10 sites on RC and another 10 sites on C3.

RESULTS

Spatial and Seasonal Environmental Variation

Several environmental conditions varied widely over four seasons. Plant detritus, usually mixed with silt, was the dominant surficial bottom type. Thick mats of organic detritus were more common near shore. Detritus decreased with distance from shore and finer sediments, mainly silt, became progressively dominant. Shell was present in only a few hauls and ranged in size from fragments of a few millimeters to live oysters, *Crassostrea virginica*, exceeding 100 mm in longest dimension. Toxicity in sediment pore water was not detected in Microtox screening. None of the stream order-season interaction terms were significant (p -values > 0.05) in two-factor ANOVAs, so I proceeded to test for separate effects of season and stream order. Seasonal variations of environmental conditions were significant (Table 1) for temperature, salinity, dissolved oxygen and water depth (2-way ANOVAs: $F = 9.68$, $df = 3$ and 69 , $p = 0.0001$); however, turbidity, distance to mouth, stream width and bottom slope did not differ significantly (2-way ANOVAs: $F < 2.74$, $df = 3$ and 69 , $p > 0.05$). Water temperature was significantly higher in summer and lower in winter, and did not differ between spring and fall. Dissolved oxygen was significantly higher in winter, lower in fall, and did not differ between spring and summer. Salinities were higher in fall and differed significantly from other seasons. Additionally, water depths were significantly higher in summer, but no differences were detected among other seasons, although low water levels precluded sampling in December 2003 and January 2004.

The effect of stream order on the environmental conditions was also significant (Table 2) for dissolved oxygen, distance to mouth, stream width and bottom slope (2-way ANOVAs: $F = 8.65$, $df = 2$ and 69 , $p = 0.0004$); however, temperature, salinity, turbidity and water depth were not significantly different (2-way ANOVAs: $F < 3.13$, $df = 2$ and 69 , $p > 0.05$). Dissolved

oxygen concentration was higher in the lower reach (SO3) than in the middle and upper reaches (SO2 and SO1, respectively). Bottom slope increased with increasing stream order, and stream widths were greatest within the middle reach (SO2). Distance to mouth decreased with increasing stream order, but this was an artifact of the sampling design.

Species Occurrence and Community Structure

Thirty taxa, generally species, were identified from 3757 individual fishes and decapod crustaceans collected in 81 seine samples (Table 3). Daggerblade grass shrimp was the dominant species and accounted for 72.7 % of the total individuals, followed by penaeid shrimp (13.4 %), which together constituted 86.1 % of the total individuals. Bay anchovy was the dominant fish species (1.9 % of the total individuals), followed by inland silverside (1.7 %), diamond killifish (1.7 %), spot (1.7 %), Gulf killifish (1.5 %), Gulf menhaden (1.3 %), and pinfish (1.2 %), and together accounted for 11 % of the total individuals and 81.3 % of all fishes.

The ten most frequently occurring species (Tables 3 & 4) amounted to 95.7 % of all individuals and were selected for posterior among-species comparisons. These species included the three decapods, daggerblade grass shrimp (60.5 % frequency of occurrence, FO), penaeid shrimp (48.1 % FO), and blue crab (12.3 % FO), and seven fishes - pinfish (24.7 % FO), bay anchovy (22.2 % FO), inland silverside (19.8 % FO), Gulf killifish (19.8 % FO), spot (18.5 % FO), sheepshead minnow (11.1 % FO), and spotted seatrout (9.9 % FO). Most individuals were juveniles, with the exception of three small species (daggerblade grass shrimp, Gulf killifish and sheepshead minnow) that also included adults. For decapod crustaceans, sizes ranged from 10 mm CW for blue crab to 110 mm TL for penaeid shrimp; whereas for the selected fish species, lengths ranged from 16 mm for bay anchovy to 120 mm SL for spot.

The common species were a mixture of residents and transients. Year-round residents included daggerblade grass shrimp, bay anchovy, inland silverside, Gulf killifish, and

Table 1. Seasonal means \pm 1 SE and (ranges) for environmental variables measured at 81 seine sites in the reference system, Bay Batiste, coastal Louisiana, between February and November 2004. Posterior testing of means among seasons for each environmental variable is based on least-square-means pairwise comparisons (Tukey's adjustment). Significant differences ($p = 0.05$) among seasons are indicated by different letters (i.e., A, B, and C), reading horizontally.

Variable	Winter	Spring	Summer	Fall
Temperature ($^{\circ}\text{C}$)	17.5 ± 0.5 A (15.4-19.9)	25.9 ± 0.4 B (22.5-29.0)	31.1 ± 0.1 C (29.9-32.1)	25.0 ± 0.9 B (18.2-30.0)
Salinity (psu)	10.0 ± 0.04 A (9.9-10.2)	10.8 ± 0.4 A (8.2-14.5)	8.6 ± 0.9 A (4.0-18.3)	14.1 ± 0.3 B (11.3-15.1)
Dissolved oxygen (mg l^{-1})	9.6 ± 0.1 A (9.1-10.2)	6.1 ± 0.3 B (3.1-9.2)	5.4 ± 0.3 B (2.1-7.9)	4.4 ± 0.5 C (2.0-8.3)
Turbidity (NTU)	8.4 ± 1.3 (3.6-13.8)	10.3 ± 1.4 (3.0-35.7)	12.8 ± 1.0 (7.4-28.3)	11.4 ± 1.3 (4.4-24.6)
Distance to mouth (m)	1280.0 ± 220.1 (320.0-2080.0)	1315.6 ± 109.5 (320.0-2080.0)	1315.6 ± 109.5 (320.0-2080.0)	1111.6 ± 125.7 (320.0-2080.0)
Stream width (m)	61.8 ± 16.1 (18.0-132.0)	56.7 ± 8.4 (16.0-132.0)	56.7 ± 8.4 (16.0-132.0)	69.9 ± 10.3 (16.0-132.0)
Water depth (cm)	34.8 ± 5.0 A (22.0-61.0)	34.1 ± 2.7 A (10.5-75.0)	57.5 ± 3.2 B (34.5-105.0)	39.8 ± 3.2 A (11.0-71.0)
Bottom slope (%)	5.6 ± 0.4 (26.0-44.0)	6.0 ± 0.6 (11.0-70.0)	7.15 ± 0.7 (9.0-90.0)	8.7 ± 1.2 (4.0-110.0)
Sample size (N)	8	27	27	19

Table 2. Means \pm 1 SE and (ranges) by stream order for environmental variables measured at 81 seine sites in the reference system, Bay Batiste, coastal Louisiana, between February and November 2004. Posterior testing of means among stream orders for each environmental variable is based on least-square-means pairwise comparisons (Tukey's adjustment). Significant differences ($p = 0.05$) among stream orders are indicated by different letters (i.e., A, B, and C), reading horizontally.

Variable	Stream order 1	Stream order 2	Stream order 3
Temperature ($^{\circ}\text{C}$)	27.3 \pm 0.9 (16.3-31.7)	26.4 \pm 0.9 (15.4-32.1)	26.3 \pm 0.9 (17.4-31.8)
Salinity (psu)	10.8 \pm 0.8 (4.2-18.2)	10.9 \pm 0.7 (4.0-18.3)	10.6 \pm 0.7 (4.1-15.1)
Dissolved oxygen (mg l^{-1})	4.8 \pm 0.4 A (2.1-9.8)	5.6 \pm 0.4 A (2.0-9.5)	6.8 \pm 0.3 B (3.0-10.2)
Turbidity (NTU)	12.1 \pm 1.7 (3.0-35.7)	11.5 \pm 1.0 (3.2-27.9)	10.3 \pm 0.9 (4.4-22.9)
Distance to mouth (m)	1878.3 \pm 41.7 A (1600.0-2080.0)	1428.6 \pm 44.3 B (1120.0-1600.0)	640.0 \pm 48.5 C (320.0-960.0)
Stream width (m)	17.4 \pm 0.2 A (16.0-18.0)	78.3 \pm 7.7 B (44.0-132.0)	76.3 \pm 7.3 B (44.0-132.0)
Water depth (cm)	41.8 \pm 4.7 (10.5-105.0)	41.8 \pm 2.3 (18.5-62.5)	45.9 \pm 3.4 (18.5-89.0)
Bottom slope (%)	5.4 \pm 0.8 A (4.0-90.0)	6.6 \pm 0.6 B (13.0-90.0)	8.5 \pm 0.8 B (13.0-110.0)
Sample size (N)	23	28	30

Table 3. Fish and decapod crustacean species listed in order of numerical abundance from 81 seine samples collected in the reference system, Bay Batiste, coastal Louisiana, between February and November 2004. Codes are indicated for the ten most frequently occurring species. Total catch (%) corresponds to the percentage of individuals caught for a taxon relative to the total 3757 individuals collected. Occurrence (N) is the number of samples where a taxon occurred. Occurrence (%) expresses the percentage of number of sites where a taxon occurred divided by the 81 total sampling sites.

Taxon	Code	Total number	% Total catch	Occurrence (N)	% Occurrence
Daggerblade grass shrimp <i>Palaemonetes pugio</i>	GSh	2731	72.7	49	60.5
Penaeid shrimp <i>Penaeidae</i> spp.	PSH	502	13.4	39	48.1
Bay anchovy <i>Anchoa mitchilli</i>	BA	73	1.9	18	22.2
Inland silverside <i>Menydia beryllina</i>	IS	64	1.7	16	19.8
Diamond killifish <i>Adinia xenica</i>		63	1.7	3	3.7
Spot <i>Leiostomus xanthurus</i>	Sp	63	1.7	15	18.5
Gulf killifish <i>Fundulus grandis</i>	GK	55	1.5	16	19.8
Gulf menhaden <i>Brevoortia patronus</i>		49	1.3	2	2.5
Pinfish <i>Lagodon rhomboides</i>	Pi	46	1.2	20	24.7
Sheepshead minnow <i>Cyprinodon variegatus</i>	ShM	28	0.7	9	11.1
Spotted seatrout <i>Cynoscion nebulosus</i>	SpS	18	0.5	8	9.9
Blue crab <i>Callinectes sapidus</i>	BC	16	0.4	10	12.3
Least puffer <i>Sphoeroides parvus</i>		6	0.2	4	4.9
White mullet <i>Mugil curema</i>		6	0.2	3	3.7
Atlantic croaker <i>Micropogonias undulatus</i>		5	0.1	4	4.9
Red drum <i>Sciaenops ocellatus</i>		5	0.1	4	4.9
Black drum <i>Pogonias cromis</i>		4	0.1	1	1.2
Gray snapper <i>Lutjanus griseus</i>		3	0.1	3	3.7
Spotfin mojarra <i>Eucinostomus argenteus</i>		3	0.1	1	1.2
Striped killifish <i>Fundulus majalis</i>		3	0.1	2	2.5
Highfin goby <i>Gobionellus oceanicus</i>		2	0.1	2	2.5
Inshore lizardfish <i>Synodus foetens</i>		2	0.1	2	2.5

(table cont.)

Table 3 cont.

Saltmarsh topminnow <i>Fundulus jenkinsi</i>	2	0.1	2	2.5
Striped mullet <i>Mugil cephalus</i>	2	0.1	1	1.2
Bay whiff <i>Citharichthys spilopterus</i>	1	<0.1	1	1.2
Gulf pipefish <i>Syngnathus scovelli</i>	1	<0.1	1	1.2
Hardhead catfish <i>Ariopsis felis</i>	1	<0.1	1	1.2
Naked goby <i>Gobiosoma bosc</i>	1	<0.1	1	1.2
Sailfin molly <i>Poecilia latipinna</i>	1	<0.1	1	1.2
Sand seatrout <i>Cynoscion arenarius</i>	1	<0.1	1	1.2
Total number	3757			

Table 4. Most frequently occurring fishes and decapods sorted by stream order and season. Species are listed in order of occurrence from 81 seine samples collected monthly in the reference system, coastal Louisiana, between February and November 2004. Effort (N) is the number of seine hauls.

Common name	Frequency of occurrence	Total number	Order 1	Order 2	Order 3	Winter	Spring	Summer	Fall
Daggerblade grass shrimp	49	2731	899	1417	415	76	2354	34	267
Penaeid shrimp	39	502	156	211	135	0	272	30	200
Pinfish	20	46	6	36	4	0	34	11	1
Bay anchovy	18	73	15	28	30	0	39	33	1
Inland silverside	16	64	4	19	41	2	20	41	1
Gulf killifish	16	55	24	13	18	2	11	4	38
Spot	15	63	30	23	10	0	50	13	0
Blue crab	10	16	4	6	6	2	3	1	10
Sheepshead minnow	9	28	2	16	10	1	2	0	25
Spotted seatrout	8	18	3	8	7	0	2	1	15
Effort (N)		81	23	28	30	8	27	27	19

sheepshead minnow. Penaeid shrimp, blue crab, pinfish, spot, and spotted seatrout represented estuarine transients. All of these species occurred in all three stream-orders, and daggerblade grass shrimp, blue crab, inland silverside, and Gulf killifish were collected in all seasons. Penaeid shrimp, pinfish, bay anchovy, and spotted seatrout were absent in winter, sheepshead minnow were absent in summer, and spot occurred only in spring and summer. Daggerblade grass shrimp, penaeid shrimp, and blue crabs are commercially important species, and spot and spotted seatrout are important sport-fishing species.

When testing for separate effects (i.e., none of the interactions were significant) of stream order (2-way ANOVAs: $F = 0.69$, $df = 2$ and 69 , $p = 0.51$) and season (2-way ANOVAs: $F = 6.27$, $df = 3$ and 69 , $p = 0.0008$) on total nekton abundance and species richness, only the seasonal effects were significant (Table 5). Total nekton abundance was higher in spring, followed by fall, winter, and summer. Significant differences were only detected between summer and fall, summer and spring, and spring and winter. Nekton species richness was highest in fall, followed by spring, summer, and winter (Table 5), and all adjacent seasons were significantly different, except summer and fall.

When analyzing decapods separately, their numbers contributed greatly to the patterns of total nekton abundance among stream orders and seasons. Again, only the effect of season was significant (2-way ANOVA: $F = 14.14$, $df = 3$ and 69 , $p < 0.0001$); the stream-order effect was not (2-way ANOVA: $F < 0.01$, $df = 2$ and 69 , $p > 0.99$). Decapods were most abundant in spring, followed in numbers by fall; but significant differences in their abundances were only detected between summer and fall, summer and spring, and spring and winter. Fish abundances were significantly different among seasons (2-way ANOVA: $F = 2.81$, $df = 3$ and 69 , $p = 0.04$), but not among stream orders (2-way ANOVA: $F = 0.14$, $df = 2$ and 69 , $p = 0.87$). Fish were most abundant in fall, declined and decreased through spring, summer, and winter, respectively;

Table 5. Means (± 1 SE) by stream order and season for abundance and species richness of fishes and decapods collected at 81 seine sites in the reference system, coastal Louisiana, between February and November 2004. Posterior testing of means among stream orders and seasons is based on least-square-means pairwise comparisons (Tukey's adjustment). Significant differences ($p = 0.05$) are indicated by different letters (i.e., A, B, and C), reading horizontally.

Biological variable	Order 1	Order 2	Order 3	Winter	Spring	Summer	Fall
Abundance (individuals)							
Decapod crustaceans	46.0 \pm 23.1	58.4 \pm 23.6	18.5 \pm 4.9	9.7 \pm 6.5 A	97.4 \pm 28.7 B	2.4 \pm 0.9 A	25.1 \pm 6.6 AB
Fishes	4.8 \pm 1.3	8.9 \pm 3.0	4.9 \pm 1.4	0.6 \pm 0.3 AC	6.9 \pm 1.5 BC	5.9 \pm 2.1 C	8.2 \pm 3.8 C
Total	50.9 \pm 23.5	67.3 \pm 23.8	23.4 \pm 4.8	10.4 \pm 6.7 A	104.3 \pm 28.9 B	8.4 \pm 2.1 A	33.3 \pm 7.4 AB
Species richness (number of species)							
Decapod crustaceans	1.2 \pm 0.2	1.1 \pm 0.2	1.3 \pm 0.2	0.7 \pm 0.2 C	1.4 \pm 0.1 AC	0.7 \pm 0.2 BC	1.8 \pm 0.2 AC
Fishes	1.6 \pm 0.3	1.9 \pm 0.3	1.7 \pm 0.3	0.5 \pm 0.2 AC	2.2 \pm 0.3 BC	1.5 \pm 0.3 C	2.1 \pm 0.3 C
Total	2.8 \pm 0.4	3.0 \pm 0.4	3.0 \pm 0.3	1.2 \pm 0.4 A	3.6 \pm 0.4 B	2.1 \pm 0.3 AB	3.9 \pm 0.5 B
Seine hauls (N)	23	28	30	8	27	27	19

however, only winter and spring fish abundances were significantly different.

The effects of stream order on the species richness of both fishes and decapods were not significant (2-way ANOVAs: $F = 0.55$, $df = 2$ and 69 , $p = 0.58$). Seasonal differences in fish species richness were detected between winter and spring (2-way ANOVA: $F = 3.21$, $df = 3$ and 69 , $p < 0.03$). Fish species richness was highest in spring, followed by fall, summer, and winter. Decapod species richness differed significantly between summer and fall, and between spring and summer (2-way ANOVA: $F = 8.82$, $df = 3$ and 69 , $p < 0.001$); species richness was highest in fall, followed by spring, but winter and summer were not different.

Kendall's coefficient of concordance (W) for ranked abundances was highly significant when the 15 most common species in the assemblage were included in analyses among stream orders and among seasons (1-way ANOVAs: $W = 0.454$, $F = 2.49$, $df = 13.3$ and 26.7 , $p = 0.013$). However, for the top ten or five species, assemblages among seasons were not concordant (1-way ANOVAs: $W = 0.537$, $F = 3.47$, $df = 3.5$ and 10.5 , $p = 0.05$), while assemblages among stream orders remained significantly concordant (1-way ANOVAs: $W = 0.588$, $F = 2.85$, $df = 3.33$ and 6.67 , $p = 0.03$). For the ten most frequently occurring species (Table 6), the seasonal ranks showed substantial change in assemblage structure over the course of the year (1-way ANOVAs: $W = 0.415$, $F = 2.13$, $df = 8.5$ and 25.5 , $p = 0.068$) but remained concordant across stream order (1-way ANOVAs: $W = 0.750$, $F = 5.99$, $df = 8.33$ and 16.67 , $p = 0.001$). With the exception of pinfish and blue crab, the seasonal rankings of transient species such as penaeid shrimp, spot, and spotted seatrout varied considerably. Juvenile blue crabs showed little difference in their rankings by season. Year-round residents such as daggerblade grass shrimp, Gulf killifish, bay anchovy and sheepshead minnow showed little change in their rankings. Rankings of resident inland silversides varied considerably among seasons. Daggerblade grass shrimp and penaeid shrimp numerically ranked first and second, respectively,

Table 6. Rank of the ten most frequently occurring species overall, by stream order and by season from 81 seine samples collected in the reference system, coastal Louisiana, between February and November 2004.

Taxa	Overall	Order 1	Order 2	Order 3	Winter	Spring	Summer	Fall
Daggerblade grass shrimp	1	1	1	1	1	1	2	1
Penaeid shrimp	2	2	2	2	8*	2	4	2
Bay anchovy	3	5	4	4	8*	4	3	8
Inland silverside	4	7.5	6	3	3	6	1	8
Spot	5	3	5	6.5	8*	3	5	10*
Gulf killifish	6	4	8	5	3	7	7	3
Pinfish	7	6	3	10	8*	5	6	8
Sheepshead minnow	8	10	7	6.5	5	9.5	10*	4
Spotted seatrout	9	9	9	8	8*	9.5	8.5	5
Blue crab	10	7.5	10	9	3	8	8.5	6

*These taxa were absent from samples in at least one season.

in all stream orders. With exception of inland silverside, Gulf killifish and pinfish, all other species showed little change in their rankings among stream orders.

Among-Species Comparisons

Different patterns in the abundances of the most frequently occurring species were evident. Abundances of daggerblade grass shrimp, penaeid shrimp, spot, pinfish, and bay anchovy peaked in spring, whereas those of blue crab, Gulf killifish, sheepshead minnow, and spotted seatrout peaked in fall (Table 4). Inland silverside was the only common species with a summer peak in abundance.

For eight environmental variables tested (Table 7), no significant differences in resource use were detected among decapods (1-way ANOVAs: $F = 2.33$, $df = 2$ and 95 , $p = 0.10$). Among fishes, significant differences (1-way ANOVAs: $F = 3.69$, $df = 6$ and 95 , $p = 0.002$) were detected for temperature, salinity and bottom slope in several posterior pairwise comparisons (Table 7). Sheepshead minnows used lower temperatures than six other fishes. Pinfish and spot used the lowest salinity and sheepshead minnow and spotted seatrout used the highest salinity. Spotted seatrout used steeper bottom slopes than most other fishes.

Factor Analysis

The Factor Analysis resolved eight intercorrelated environmental variables into four orthogonal axes of environmental variation with eigenvalues greater than one. Together, they explained 79.9 % of the variation (Table 8). The first factor explained 22.6 % of the variance, had a large positive loading for stream width and a large negative loading for distance to mouth, and was interpreted as a stream-order axis. The second factor explained 22.3 % of the variance, had large positive loadings for bottom slope and water depth, and was interpreted as a morphological axis. The third factor explained 19.9 % of the variance, had large positive loadings for temperature and turbidity and a large negative loading for dissolved oxygen, and

Table 7. Weighted means (± 1 SE) of environmental variables used by the ten most frequently occurring taxa from 81 seine samples collected in the reference system, coastal Louisiana, between February and November 2004. N is the number of independent samples used in the analysis (species occurrence). Posterior testing ($p = 0.05$) of means among taxa is based on least-square-means comparisons, with significantly different means lacking at least one letter in common (i.e., A, B, C, and D), reading vertically.

Taxon	N	Temperature (°C)	Salinity (psu)	Dissolved Oxygen (mg l ⁻¹)	Turbidity (NTU)	Distance to mouth (m)	Stream width (m)	Water depth (cm)	Bottom slope (%)
Decapod crustaceans									
Daggerblade grass shrimp	49	24.3 \pm 0.3	11.7 \pm 0.3	5.7 \pm 0.2	9.2 \pm 0.6	1515.5 \pm 68.9	52.3 \pm 5.7	32.0 \pm 1.2	6.6 \pm 0.4
Penaeid shrimp	39	25.9 \pm 0.4	11.9 \pm 0.4	4.5 \pm 0.3	10.7 \pm 1.2	1344.4 \pm 91.6	64.9 \pm 7.6	39.8 \pm 2.5	8.2 \pm 0.8
Blue crab	10	24.8 \pm 1.2	12.8 \pm 0.8	4.8 \pm 0.9	9.6 \pm 1.0	1220.0 \pm 172.7	62.1 \pm 14.2	39.1 \pm 3.9	6.4 \pm 1.4
Fishes									
Pinfish	20	26.8 \pm 0.7 ABC	9.3 \pm 0.6 B	5.9 \pm 0.3	11.0 \pm 1.5	1384.3 \pm 88.7	81.4 \pm 10.5	42.1 \pm 2.8	7.5 \pm 0.6 BC
Bay anchovy	18	29.2 \pm 0.5 A	11.2 \pm 0.8 ABC	5.8 \pm 0.3	12.3 \pm 2.1	1196.7 \pm 134.1	65.5 \pm 10.1	54.2 \pm 4.2	7.0 \pm 0.8 BC
Inland silverside	16	29.6 \pm 0.7 ABC	12.1 \pm 0.7 ABC	6.4 \pm 0.3	15.5 \pm 2.1	765.0 \pm 134.2	104.0 \pm 10.9	59.0 \pm 3.8	6.6 \pm 0.8 BC
Gulf killifish	16	23.5 \pm 1.1 BD	12.2 \pm 0.5 ABC	5.2 \pm 0.6	9.6 \pm 0.8	1306.2 \pm 132.2	54.6 \pm 11.7	31.2 \pm 3.0	6.1 \pm 1.0 AC
Spot	15	26.2 \pm 0.7 ABC	11.2 \pm 0.9 B	5.6 \pm 0.2	12.7 \pm 1.8	1452.7 \pm 145.0	56.9 \pm 13.1	35.5 \pm 3.0	5.0 \pm 0.5 BC
Sheepshead minnow	9	22.7 \pm 0.9 D	14.1 \pm 0.4 C	5.1 \pm 0.6	7.6 \pm 1.1	1211.4 \pm 193.9	72.4 \pm 13.7	38.7 \pm 3.1	11.0 \pm 1.5 AC
Spotted seatrout	8	25.0 \pm 0.9 ABCD	14.2 \pm 0.7 AC	3.9 \pm 0.3	11.0 \pm 1.8	1271.1 \pm 158.0	54.2 \pm 11.5	48.4 \pm 4.2	13.4 \pm 1.6 A

was interpreted as a seasonal axis. The fourth factor explained 15.1 % of the variance and had a large positive loading for salinity. The primary environmental influences on community structure in the system were identified: (1) the geomorphological and hydrological effects related to stream order (Factor 1 and Factor 2, which explained together 44.9 % of the variability), and (2) the tidal and meteorological effects related to season (Factor 3 and Factor 4, which explained together 35 % of the variability). Upper reaches (SO1) were narrow, distant to the mouth, generally shallow, with low bottom slope; whereas the middle (SO2) and lower (SO3) reaches were wide, closer to the mouth, deeper and had steeply sloped bottoms.

A plot of species in three-dimensional factor space indicated spatial and seasonal habitat use differences among fishes and decapod crustaceans (Fig. 3A). A second plot in four-dimensional environmental space (Fig. 3B) more clearly reflects differences among the dominant taxa. Daggerblade grass shrimp, pinfish, spot, blue crab and Gulf killifish used similar environmental conditions; individuals typically occurred in streams of low order, with intermediate water temperatures, turbidities, dissolved oxygen concentrations and salinities. Penaeid shrimp, bay anchovy, inland silverside, sheepshead minnow and spotted seatrout were present in higher order streams. Bay anchovy and penaeid shrimp co-occurred in similar habitat conditions, most notably in the middle reaches (SO2) during seasons with warm water temperatures, elevated turbidities and low dissolved oxygen concentrations. Sheepshead minnow and spotted seatrout were mostly abundant in the middle and lower reaches (SO2 and SO3), occurring typically in sites with the highest salinities. Nevertheless, spotted seatrout used steeper bottoms and greater depths in narrow streams, where waters were warmer, more turbid, and less oxygenated than the colder, clearer and more oxygenated waters used by sheepshead minnow in the wide and shallow and more gently sloped streams. Inland silverside typically used the third order stream (SO3), where sites were deepest, widest, and warmest.

Table 8. Variables and factor loadings from a rotated factor analysis of eight environmental variables collected at monthly sampling sites in the reference system, Bay Batiste, coastal Louisiana. Magnitude and signs of loadings indicate strength and direction of each variable's influence on a factor. Variables with loadings = $|0.50|$ are shown in bold and were used to characterize factors.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Stream width	0.90	-0.04	-0.01	0.01
Distance to mouth	-0.88	-0.26	0.13	0.01
Bottom slope	0.10	0.89	-0.13	0.10
Water depth	0.04	0.82	0.28	-0.24
Temperature	-0.09	0.27	0.84	-0.34
Turbidity	0.01	-0.29	0.66	0.26
Dissolved oxygen	0.45	-0.27	-0.58	-0.22
Salinity	-0.02	-0.05	0.04	0.96
Eigenvalue	1.81	1.78	1.59	1.21
% variance explained	22.6	22.3	19.9	15.1
Cumulative % variance explained	22.6	44.9	64.8	79.9

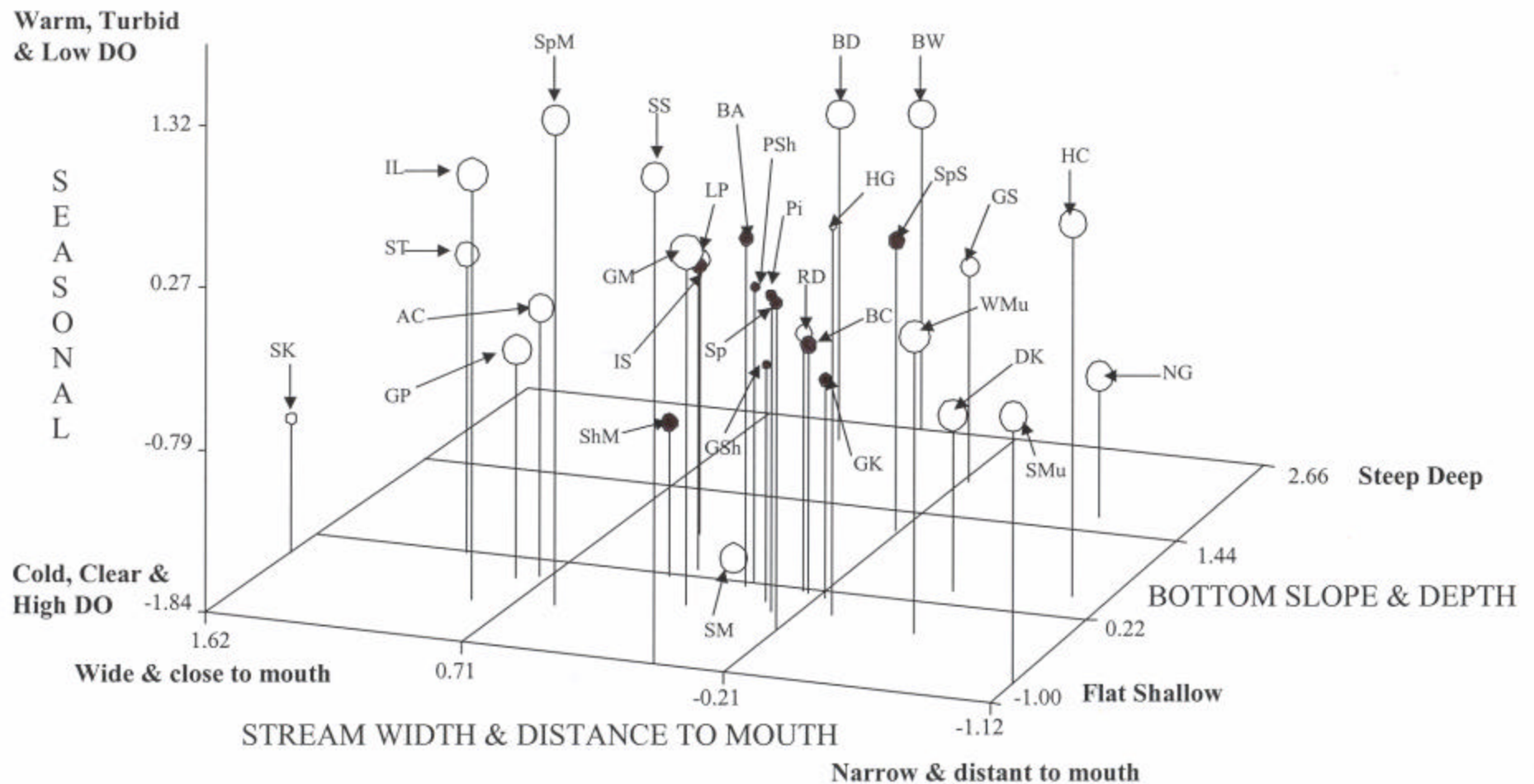


Fig. 3. (A) Representation of the average ten-month pattern of habitat use by the 30 fish and decapod crustaceans species collected in the study reference system. Species centroids are plotted in 3-dimensional factor space with balloon radii representing 1 SE about the mean. Shaded balloons represent the 10 most frequently occurring species. Species codes are AC=Atlantic croaker, BA=bay anchovy, BC=blue crab, BD=black drum, BW=bay whiff, DK=diamond killifish, GK=Gulf killifish, GM=Gulf menhaden, GP=Gulf pipefish, GS=gray snapper, GSh=daggerblade grass shrimp, HC=hardhead catfish, HG=highfin goby, IL=inshore lizardfish, IS=inland silverside, LP=least puffer, NG=naked goby, Pi=pinfish, PSh=penaeid shrimp, RD=red drum, ShM=sheepshead minnow, SK=striped killifish, SM=sailfin molly, SMu=striped mullet, Sp=spot, SpM=spotfin mojarra, SpS=spotted seatrout, SS=sand seatrout, ST=saltmarsh topminnow, WMu=white mullet.

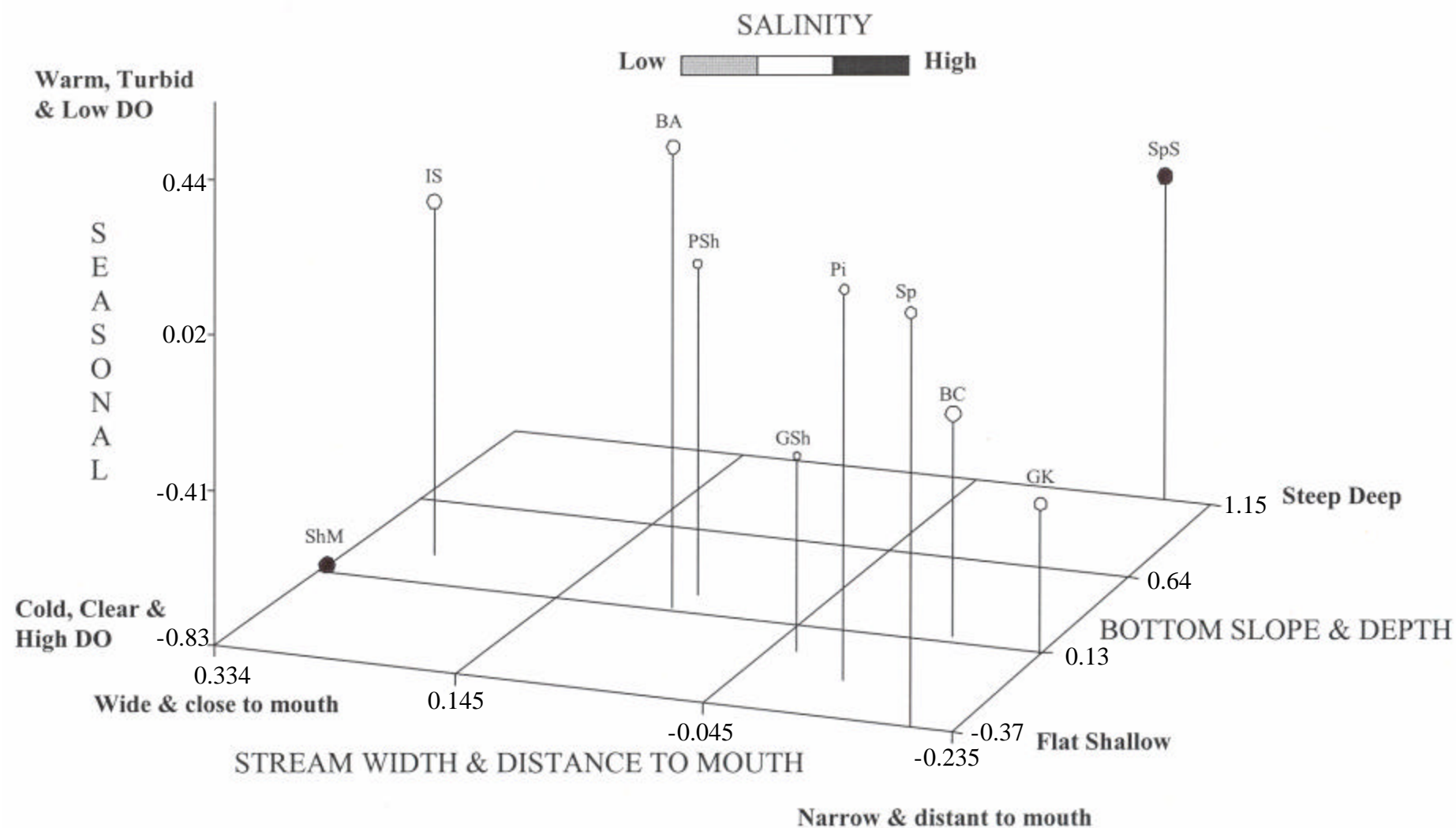


Fig. 3. (B) Resource use patterns of the 10 most frequently occurring species in four-dimensional factor space. Balloons indicate locations of centroids with balloon radii representing 1 SE about the mean. Species codes are BA=bay anchovy, BC=blue crab, GK=Gulf killifish, GSh=daggerblade grass shrimp, IS=inland silverside, Pi=pinfish, PSh=penaeid shrimp, ShM=sheepshead minnow, Sp=spot, SpS=spotted seatrout.

Representativeness of the Study Area

In July of 2004 and 2005 the reference system was compared to sites in the greater study area (Fig. 2). In the 2004 experiment for testing the representativeness of the reference area, a total of 393 juvenile individuals from 14 species were collected from 18 seine samples in the reference and 3.2-km circles (RC and C2). Daggerblade grass shrimp was the numerically dominant species (60.8 % of total individuals), followed by bay anchovy (10.9 %), brown shrimp (9.4 %), and inland silverside (6.1 %). Compared to RC, turbidity was higher and bottom slope was lower in C2 (1-way ANOVAs: $F = 7.78$, $df = 1$ and 16 , $p = 0.013$), but other environmental variables did not differ significantly (1-way ANOVAs: $F = 1.82$, $df = 1$ and 16 , $p = 0.197$). No significant differences were detected for species richness (1-way ANOVA: $F = 0.49$, $df = 1$ and 16 , $p = 0.495$). However, nekton abundances were significantly higher in C2 (1-way ANOVA: $F = 13.49$, $df = 1$ and 16 , $p = 0.002$). When analyzing community structure for 14 species, 9 species and 5 species, I was unable to reject the null hypothesis of no difference in community structure between RC and C2 (1-way layout ANOSIMs: $R < 0.107$, $p > 0.081$).

A total of 87 juveniles of 18 species were collected in 2005 from 20 seine samples in the reference (RC) and 5-km (C3) circles. Inland silverside was the numerically dominant species (46.0 % of total individuals), followed by bay anchovy (17.2 %), Atlantic croaker (8.0 %), and blue crab (4.6 %). No significant differences between RC and C3 were detected in most environmental variables, nekton abundance and species richness (1-way ANOVAs: $F < 4.41$, $df = 1$ and 18 , $p > 0.05$); however, salinity and dissolved oxygen concentrations were higher on C3 (1-way ANOVAs: $F = 5.52$, $df = 1$ and 16 , $p = 0.03$). When analyzing community structure for 18 species, 9 species and 5 species, I was unable to reject the null hypothesis of no difference in community structure between RC and C3 (1-way layout ANOSIMs: $R = 0.011$, $p = 0.478$).

DISCUSSION

Stream order is a geomorphological feature that is relatively easy to determine from topographic maps (Kuehne 1962) and reflects other physical variables (e.g., drainage area, depth, width, topography, and hydrology) which influence the distribution and abundance of species in saltmarsh estuaries (Weinstein 1979, Rozas & Odum 1987, Rozas et al. 1988, Hettler 1989, Kneib 1994, McIvor & Rozas 1996, Desmond et al. 2000). The spatial patterns of ecological processes have been described from a human perspective and from the perspective of the organism or process under study (Kneib 1994). From a fish's eye view (Chesney et al. 2000) the range of environmental conditions used by a species or life history stage should vary with seasonally and spatially changing environmental conditions and with natural and anthropogenic disturbances. In coastal Louisiana, many anthropogenic stresses to natural landscapes, including the effects of fishing and coastal modifications, influence the relative abundance of species and their community structure (Chesney et al. 2000). To understand how anthropogenic stressors are affecting coastal ecosystems in southeastern Louisiana, it is important to identify baselines representative of natural or relatively "unaltered" states of the population and ecosystems in question (Pauly et al. 2005). Within a relatively natural Louisiana estuarine system, two primary axes of environmental variability influencing community structure were identified: (1) the geomorphological and hydrological attributes of the study area related to the stream-order effect, and, (2) the tidal and meteorological events in the region related to the seasonal effect. Nekton abundance was typically higher in low order streams and differences in habitat use among dominant species reflected individual habitat selection, seasonality of recruitment and species residency status. Community structure was concordant among stream orders, but not among seasons.

Environmental Variability

Physical processes and climate continuously shape estuarine landscapes (Kneib 1994). Geomorphological characteristics of salt marshes include a stream order gradient, subtidal geomorphology, marsh elevation and duration of flooding, drainage density, and relative amount of edge (McIvor & Rozas 1996). The significant effects of season and stream order on the environmental variables in this study reflect some of the meteorological, hydrological, and geomorphological characteristics (Tables 1 & 2). The meteorological conditions and the tidal regime, primarily local precipitation, tidal fluxes, and prevailing winds, influence the observed water temperatures that are inversely related to dissolved oxygen concentrations, and salinity and depth (Tables 1 & 8). Salinities also vary with tides and precipitation, increasing during flood tides and decreasing with precipitation during stormy months (Childers et al. 1990, Swenson 2003). The tidal range combined with slope of the intertidal zone determines both the flooded area and the depth of flooding (McIvor & Rozas 1996).

Analogous to other studies (Odum 1984, Rozas & Odum 1987, Kneib 1994, Desmond et al. 2000), the physicochemical characteristics of the system varied along stream order. Dissolved oxygen concentrations increased with stream order, attributable to wide streams (e.g., SO₂ and SO₃), with greater water-atmosphere interface area, carrying more oxygenated waters (Odum 1984). Because of the relatively uniform subtidal geomorphology of the system, water depths and temperatures did not differ among stream orders for sites sampled, in part because only the nonvegetated marsh edge was sampled (i.e., the deep middle channels (> 1.5 m) of SO₂ and SO₃ were not seined).

Turbidity is an environmental variable in Louisiana estuaries that probably plays an important role in nekton predator avoidance, providing refuge to individuals that use nonvegetated habitats (Baltz et al. 1998, Chesney et al. 2000, Jones et al. 2002). Compared to

other studies in coastal Louisiana (Baltz et al. 1998, Chesney et al. 2000, Baltz & Jones 2003), mean turbidity values in the reference system and surrounding human-modified areas were atypically low. The orientation and exposure of the reference system to wind stress and tidal flux along with a low level of commercial and sport trawling may account for low turbidity.

Community Structure and Habitat Use

Differences in the use of environmental variables reflected habitat selection, seasonality of recruitment, and residency status (Table 7, Figs. 3A & 3B). Fish and decapod abundances, species richness, and community structure were affected by season (Tables 5 & 6). As in other studies in the northern Gulf of Mexico salt marshes (Rozas 1992, Baltz et al. 1993, Rozas & Reed 1993, Rozas & Reed 1994, Baltz et al. 1998, Rozas & Zimmerman 2000, Jones et al. 2002, Minello & Rozas 2002, Baltz & Jones 2003), the decapod community, especially daggerblade grass shrimp and penaeid shrimp, constituted more than 75 % of the total nekton abundances (Table 3). Concordance was evident among stream orders, whereas the seasonal ranks of the ten most frequently occurring species showed considerable change in structure over the year (Table 6). The common species (Table 4) were a mixture of small taxa that typically dominate marsh surface habitat types (e.g., daggerblade grass shrimp, sheepshead minnow and Gulf killifish) and the young of open-water species (e.g., bay anchovy, spot and spotted seatrout). Sheepshead minnow, inland silverside, daggerblade grass shrimp, pinfish and Gulf killifish are species that spawn and spend most of their lives within the estuary. These small residents are found throughout the estuary because they tolerate wide salinity and temperature ranges, and shallow waters may provide them with alternate refuge habitat (Ruiz et al. 1993). Bay anchovy, spot, penaeid shrimp and blue crab are transients that occur in the estuary primarily as young of the year, but spawn in coastal or marine areas (Baltz et al. 1993, McIvor & Rozas 1996).

Estuarine geomorphology and hydrodynamics, combined with meteorological and climatical events, influence the location, extent and availability of specific habitats (Rozas & Reed 1993, Rozas 1995, Deegan et al. 2000, Zimmerman et al. 2000, Able 2005). The spatial arrangement of streams within the landscape may control the degree to which nektonic species use potential foraging and refuge habitats in intertidal marshes (Kneib 1994, McIvor & Rozas 1996). Fish and decapod densities tend to be higher in marshes with a developed stream order gradient and individuals show greater use of the marsh edge (Rozas & Odum 1987, Kneib 1994). My results were consistent with the patterns from different geographic locations in which greater numbers of fishes and decapods use low-order streams more than high-order streams (Weinstein 1979, Rozas & Odum 1987, Rozas et al. 1988, Hettler 1989, Kneib 1994, McIvor & Rozas 1996, Desmond et al. 2000) as refuge and foraging habitat. Because nektonic species using the marsh surface need to vacate these sites with the ebbing tide, subtidal geomorphology and bottom slope are relevant to understanding fish community structure. McIvor and Odum (1988) found that marsh-surface sites adjacent to depositional banks supported significantly higher numbers of nekton. Both lower predation risk and higher food availability in the depositional subtidal zone are likely mechanisms producing this pattern. Rozas and Odum (1987) hypothesized that the relationship between stream order and nekton abundance was probably attributable to the distribution of submerged aquatic vegetation (SAV) in tidal marsh creeks. However, my study area was devoid of SAV, so low order streams may serve as preferred corridors between marsh surface and tidal channel habitats for natant organisms because of the food and shelter benefits associated with marshes flooded for longer periods (Rozas et al. 1988). Hettler (1989) recognized that high-order streams bordered steeply bottomed subtidal areas, whereas low-order streams bordered shallow depositional subtidal profiles. Larger natant predators may be limited by their physiological tolerance and by physical constraints of shallow and warm waters

deprived of high oxygen concentrations (Hackney et al. 1976, Shenker & Dean 1979; Rozas & Hackney 1984, Rozas & Odum 1987, McIvor & Odum 1988, Hettler 1989), and/or avian predators (Kneib 1982). Flooding duration and eventually marsh submergence time influence habitat use by nekton because individuals can occupy the habitat only when it is flooded.

The plots of species in factor space simplify a multitude of complex environmental gradients (eight in this study) to a level that can be viewed and examined as a general and realistic pictorial model in just four dimensions. Two different species associations were evident (Fig. 3B). The first, daggerblade grass shrimp, pinfish, spot, blue crab, and Gulf killifish were concentrated in low order shallow streams, and the second, bay anchovy and penaeid shrimp occurred mainly in deeper water of the middle reach. Inland silverside, sheepshead minnow and spotted seatrout were spread out in environmental space, reflecting their particular environmental requirements and spatial and temporal distributions.

Plots of species in factor space also show how individual species respond to a complex of gradients in their environment (Baltz et al. 1993). Species centroids are multidimensional means for all of the variables measured, and are weighted by numerical abundance to reflect the population's patterns of habitat utilization (i.e., a measure of central tendency for essential fish habitat) and can be coupled with confidence limits to display graphically the variance of conditions in which a species is likely to be found and how it relates to other species.

The limited temporal and spatial scales of the study (i.e., a relatively unique small natural stream system in northeastern Barataria Bay sampled over 10 months), in addition to the selectivity of the sampling gear and the difficult accessibility to the entire system restrict the characterization of essential fish habitat (Minello 1999) for many of the most frequently occurring species. I consider the fine-scale definition of environmental conditions used by juvenile and adult nektonic species as potentially important niche dimensions (*sensu* Hurlbert

1981; i.e., energy, materials, and sites) that can be used to assess the quality of nursery habitats, to describe essential characteristics of fish habitats for species, and to provide insights into factors that influence or control population density, community structure (Figs. 3A & 3B), inter- and intra-specific interactions, and patterns of recruitment. Fishes and decapods respond to changing abiotic conditions that test the limits of their physiological tolerance (Magnuson 1991), and they presumably select sites that favor their growth and survival (Boesch and Turner 1984). If we view habitat from a fish's perspective, as the range of environmental conditions used by a species or life history stage (Baltz 1990), we can easily see that the quantity of suitable habitat varies seasonally (Childers et al. 1990) and spatially with changing environmental conditions (Baltz & Jones 2003). Drainage density or the complexity of the natural stream network of the study area may increase the marsh edge available (McIvor & Rozas 1996). Because most species use the marsh edge (Baltz et al. 1993; Peterson & Turner 1994), secondary productivity has been related to the amount of edge habitat contained in *S. alterniflora* marshes (Chesney et al. 2000; Minello & Rozas 2002).

The reference portion of the study area was a unique meandering stream network within a salt marsh heavily modified by human intervention (Fig. 2). As in the rest of coastal Louisiana, human-made canals for pipelines and navigation dominated the landscape in northeastern Barataria Bay. Pipeline canals constructed in coastal wetlands differ from natural tidal systems in several important characteristics. Canals are usually straight, deep and with steep bottomed profiles, and their average depth is considerably greater than nearby natural streams or ponds (Gosselink 1988, Rozas 1992, Rozas & Reed 1994). Contrary to what I expected, differences in nekton community structure were not significant between the reference area and human-modified marshes (Fig. 2). Comparative studies in coastal Louisiana and California (Rozas 1992, Williams & Zedler 1999) document that nekton assemblages and densities of dominant

species in shallow-water and adjacent marsh-surface habitats of canals and natural streams are remarkably similar. Nekton typically occupy narrow strips of marsh along canals at high tide in densities similar to those found on natural marshes. Rozas (1992) concluded that slumping of steep banks after canal construction may be partly responsible for this finding because this process decreases depth and steepness of bottom profiles, creating shallow areas that could be used as subtidal refuge (McIvor & Odum 1988). Other factors that may influence the habitat function of canals in coastal areas include presence or absence of submerged aquatic vegetation and degree of connectivity to surrounding habitat types (Neill & Turner 1987b, Rozas 1992, Kneib 1994).

I have tried to describe patterns of habitat use by nekton in a seemingly pristine mesohaline reference system surrounded by a more heavily human-modified marsh landscape in southeastern Louisiana. Landscape patterns may be affecting nekton populations (Kneib 1994, McIvor & Rozas 1996, Chesney et al. 2000, Minello & Rozas 2002). Depending on their degree of transformation, alteration of natural marshes (e.g., canal construction and artificial marsh construction) combined with subsidence of coastal marshes in Louisiana may benefit nekton by increasing marsh edge (Chesney et al. 2000) and increasing the percentage of time the marsh surface is accessible (Minello & Rozas 2002). However, these short-term benefits will eventually lead to a significant decrease in total marsh habitat (Chesney et al. 2000) that would negatively affect nekton populations. It has been proposed that the addition of some edge in the northern Gulf of Mexico should be a priority in the design of saltmarsh restoration to benefit commercially important species such as shrimp and crabs and to improve the value of created marshes (Chesney et al. 2000, Minello & Rozas 2002). The sinuosity of meandering natural creeks that add habitat complexity (Kneib 1994) and the backfilling of artificial canals (Neill & Turner 1987a) may enhance the nursery value of saltmarsh complexes by increasing marsh edge

(Chesney et al. 2000), by expanding the area of shallow subtidal habitat (Rozas & Reed 1994) and by reducing the density of large predators (McIvor & Odum 1988, Baltz et al. 1993, Ruiz et al. 1993).

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VITA

Pablo Granados-Dieseldorff was born on August 22, 1976, in Guatemala City, Guatemala. Pablo is the son of E. Salvador Granados and Marlene Dieseldorff, and the eldest brother of Diego, Nathalia, and David. He attended the French high school in his home town, graduating in 1994. Pablo married Amrei Baumgarten in 2000 and their son Matthias was born on May 10th, 2006, in Baton Rouge, Louisiana. He graduated with honors in 2001 and earned a Bachelor of Science degree in biology with emphasis in aquatic ecology from the Universidad de San Carlos de Guatemala (USAC) where he worked during his last two years as a teaching assistant in biology and ecology courses. During his senior year at USAC, he was principal investigator of a project assessing the limnology of a karstic lake in northern Guatemala. The United States Agency for International Development in Mexico (USAID-Mexico) funded his project “Basic Limnology of the Lachua Lake National Park” in 2000. The title of his bachelor’s thesis was “Ichthyofauna of the Lachua Lake National Park”. After graduating from USAC, Pablo continued his research on neotropical ichthyofauna and worked in projects related to the conservation and management of coastal and marine ecosystems of the Caribbean and Pacific coasts of Guatemala. While he was working in the Guatemalan Trust for the Conservation of Nature (2002), he received the Russell E. Train Education for Nature Program scholarship awarded by the World Wildlife Fund to pursue a master’s degree in a foreign country. This scholarship allowed him to enter the master’s degree program in the Department of Oceanography and Coastal Sciences at the Louisiana State University in the summer of 2003 under the supervision of Dr. Donald M. Baltz. He will earn his Master of Science degree in Oceanography and Coastal Sciences in December 2006. Following graduation, Pablo will start as a 2007 fellow in the Dean John A. Knauss Marine Policy Fellowship Program in Washington, D.C.