

Geomorphological determinants of nekton use of intertidal salt marsh creeks

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ABSTRACT: Spatial variations in nekton use are often attributed to differences in the configuration and composition of habitat. We predicted that differences in nekton use among intertidal creeks were related to certain geomorphological characteristics. We measured or derived 28 features at 8 intertidal creeks in the high salinity North Inlet Estuary, South Carolina, USA. Nekton were collected simultaneously from all creeks once each season for 2 yr. Spatial variations in total abundance and biomass were greater than seasonal variations. Differences of 3- to 30-fold in resident and transient taxa densities occurred among creeks on the same date. Relative use (ranks) was similar among seasons and years. In canonical correlation analyses, depth, steepness, flow, and location were primary factors for total nekton and many taxa. Creeks that were shallow, broad, and filled and emptied slowly supported the greatest use. Total nekton use was not related to creek size, amount of edge, or oyster bottom. Grass shrimp *Palaemonetes* spp., numerically dominant in 83% of the collections, responded most to creek shape. Mummichog *Fundulus heteroclitus* favored shallow creeks with low flow and low proportions of submerged bottom at low tide. Juvenile spot *Leiostomus xanthurus* and pinfish *Lagodon rhomboides* were associated with the same features throughout their seasonal periods of occurrence. Persistent differences in nekton use of adjacent intertidal creeks might be explained by behavioral selection for preferred conditions and reoccupation of selected creeks. Geomorphological variations are significant among sites and must be considered when assessing factors affecting nekton use along salinity and other environmental gradients.

KEY WORDS: Nekton · Intertidal creeks · Salt marsh · Estuaries · Habitat structure · Fish behavior · Oysters · Bio-physical coupling

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INTRODUCTION

Understanding relationships between organisms and habitats is an especially difficult challenge for investigators interested in motile animals in tidal systems. With a wide range of patterns and processes operating simultaneously on many spatial and temporal scales and an inability to measure all relevant abiotic and biotic factors, estuarine ecologists are usually forced to select a subset of conditions for hypothesis testing. Recently, the hierarchical landscape approach provides insights into the importance

of landscape structure at different scales to the distribution of nekton (Pittman et al. 2004), but programs that require simultaneous measurements at multiple spatial scales are difficult to sustain through seasons and years. More often, investigators focus their research efforts on nekton–habitat relationships at fairly fine spatial scales and make repeated measurements over longer periods of time so that changes in taxonomic and life stage composition can be addressed. Many studies in estuarine systems have compared patterns of nekton use between habitat types such as the vegetated marsh surface, non-

vegetated edges and intertidal creeks (see review by Minello et al. 2003).

Intertidal creeks are prominent features of the salt marsh landscape where they connect permanently flooded waterways and the vegetated marsh surface. Creeks that begin flooding shortly after low tide and remain inundated through most of the tidal cycle function as primary conduits for hydrologic and material exchanges between subtidal channels and the intertidal landscape, which often include mudflats, oyster reefs and marsh. Densities, sizes, shapes and bottoms of intertidal creeks vary considerably within and among estuaries. Short-term fluctuations in physical conditions of the water column within flooded creeks generally exceed those in major channels and open waterways. Intertidal creeks closest to the uplands are most variable due to the influences of freshwater runoff and development within adjacent watersheds (Holland et al. 2004).

Fishes and motile invertebrates use flooded intertidal creeks to forage and find refuge from aquatic predators (McIvor & Rozas 1996, Kneib 1997, Gibson 2003). Some nekton use intertidal creeks as corridors to access the marsh (Rozas et al. 1988), but these channels can also serve as terminal destinations for other taxa and life stages that do not move into the marsh at high tide (Cain & Dean 1976). Most tidal migrants return to subtidal areas during low tide, but some remain in permanently submerged portions (pools) of intertidal creeks which may serve as staging areas for animals that move into higher intertidal areas when these are flooded (Webb & Kneib 2002). Whether nekton feed on the marsh (Cicchetti & Diaz 2000, Kneib 2000) or within the creek (Cattrijsse et al. 1994), intertidal creeks play a key role in facilitating the 'trophic transfer' of biomass and energy between the salt marsh, open waters and the coastal ocean (Kneib 1997, Deegan et al. 2000).

Spatial variations in nekton use of creeks have been attributed to salinity (Weinstein et al. 1980, Able et al. 2001), dimensions and stream order (Rozas & Odum 1987, Desmond et al. 2000), and surrounding landscape structure (Webb & Kneib 2002). Despite widespread recognition of the high utilization of intertidal creeks by nekton, relationships between the internal composition and configuration of creeks and nekton use have not been explored. In this study, we quantified relationships between hydrogeomorphological characteristics of intertidal salt marsh creeks and the use of this habitat by fishes, shrimps and crabs. We predicted that: (1) the magnitude of nekton use varies considerably among intertidal creeks, (2) variations in use are related to differences in certain physical characteristics of creeks, and (3) patterns of use and associations with physical features vary among taxa and change seasonally.

MATERIALS AND METHODS

Study site. The study was conducted in North-Inlet Estuary (33° 20' N, 79° 10' W) in Georgetown County, South Carolina, USA. This warm temperate, high salinity, barrier island bounded system is dominated by *Spartina alterniflora* marsh (1650 ha). Creeks, intertidal flats and oyster reefs cover about 850 ha. The system is subject to semidiurnal tides with a mean tidal range of 1.5 m. Due to shallow water depth and tidal currents, the creeks are generally well mixed and vertically homogeneous with respect to dissolved substances (Dame et al. 2000).

For this study, we selected 8 relatively large intertidal creeks that ranged from 153 to 517 m in length. The furthest distance between creeks was 1.3 km (Fig. 1). Four of the intertidal creeks (1 to 4) were associated with Clambank Creek, a major subtidal channel, and the other 4 intertidal creeks (5 to 8) were associated with Town Creek, a larger subtidal channel (Fig. 1). All 8 intertidal creeks were located above the mean low water level, and >90% of the flooded volume flowed into the adjacent subtidal channel during

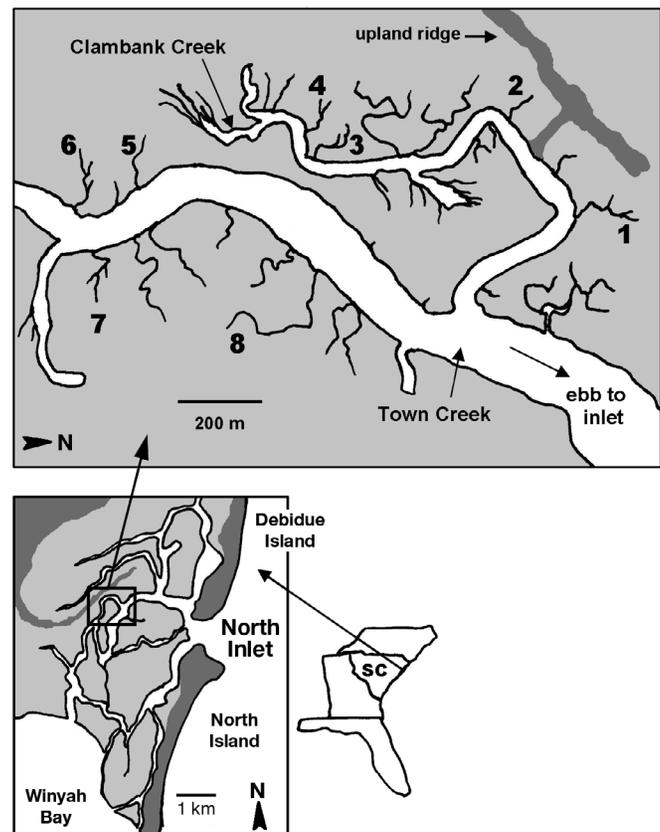


Fig. 1. Location of 8 intertidal creeks in North Inlet Estuary, South Carolina, USA. Uplands (dark grey) border intertidal marshes (light grey), and intertidal creeks (black) are connected to sub-tidal channels (white)

every ebbing tide. Current velocities in the intertidal creeks were $<35 \text{ cm s}^{-1}$ during peak flow.

Experimental design. Our study of relationships between nekton and the hydrogeomorphological features of the intertidal creeks was part of an investigation of the role of oysters in determining the structure and function of these intertidal systems. In that study, we used a replicated Before After Control Impact (BACI) design (Steward-Oaten et al. 1986) in which physical, chemical and biological (oysters and nekton) parameters were measured for 1 yr (March 1997 to February 1998) before the experimental manipulation. In the second year, living oysters were removed by hand from 4 of the 8 creeks and the same variables were measured for another year (March 1998 to February 1999). Dead shell base remained in areas from which live oysters were removed. Specific information about the design, methods and results of the oyster removal experiment on dissolved constituents can be found in Dame et al. (2000, 2002). The following methods include information most relevant to the nekton component.

Geomorphological variables. To characterize and quantify the physical configurations of the intertidal creeks, we measured 11 geomorphological features during topographic and bathymetric surveys (Dame et al. 2000). These were: length, width, cross-sectional area, elevation, number of pools, total bottom area, submerged bottom area, oyster bottom area, mud bottom area and intertidal bottom area outside the creek mouth. Total Station survey equipment (Topcon America, Model GTS2R) was used for standard dimensional variables and elevations. Tape measures and 1 m quadrants were used to classify and quantify the bottom types. We also determined values for 4 other variables (drainage area, location, branches and bends) from high-resolution aerial photographs. These and additional measurements were used to calculate values for 13 additional variables (e.g. volume, slope, roughness, meander, flow, percent submerged area and percent oyster area). There are 28 variables defined in Table 1. Although most live oysters were removed by hand from Creeks 1, 4, 5 and 7 in the second year of the experiment, the shell base and small live oysters remained in place and the percentage of oyster bottom (defined by the presence of shell) in each creek was similar between years.

Nekton sampling. Nekton abundance, biomass and species richness were determined for each creek in March (spring), June (early summer), August (late summer) and November (fall) during both years. Collections were made simultaneously from all 8 creeks using funnel-shaped block nets (3 mm) similar to those designed by Shenker & Dean (1979). Each net was mounted on a rectangular PVC frame (2.0 m \times 1.6 m)

which fitted into a permanently installed frame that oriented the net perpendicular to the creek bed and prevented nekton from escaping from the creek. The block net system covered the wet cross-sectional area near the mouth of the creek. Nets were set at slack high tide and only on early morning tides with predicted peak heights that were not sufficient to flood the marsh surface beyond the creek banks, thus eliminating the possibility of water and nekton exchanges between adjacent creeks at high tide. These tides and tide levels are referred to as bank full. At low tide, catches were removed from the nets and all pools were seined (3 mm). All samples were frozen and subsequently sorted to the lowest possible taxonomic level. Total numbers of individuals and total wet weight were determined for each taxon in all collections. Volume adjusted abundance (ind. m^{-3}) and biomass (g m^{-3}) values were used in all descriptions of patterns and all analyses to represent nekton use. Densities based on volume were considered better indicators of habitat use than area based adjustments for most taxa. Volume and bottom area were strongly correlated among creeks ($p < 0.05$, $r = 0.91$), and our decision does not affect the patterns and relationships reported. Volume based densities can be converted to bottom area based densities using the following multipliers for Creeks 1 to 8, respectively: 1.1, 0.7, 0.8, 0.9, 1.3, 1.2, 1.1, 1.2.

Water temperature, salinity and depth were measured when nets were set in the morning and again at sample retrieval that afternoon. Average water temperatures among creeks were similar in March (10°C), June (25°C) and August (28°C) for both years; they were 16°C in November 1997 and 22°C in November 1998. Water temperature variations among creeks at the time of the high tide net set never exceeded 2°C . Salinities were 31 to 35 psu on all 8 sampling dates; seasonal variations were <5 psu with slightly lower salinities occurring in March. Salinity differences among creeks never exceeded 2 psu on the same date. Bank full levels of flooding were similar in March, June and August (both years) and November 1997 with <20 cm differences being observed among dates. Water levels in November 1998 were about 30 cm higher than the average and thus exceeded bank full status for about 30 min around high tide; this level was not high enough to allow mixing with adjacent marsh basins.

Statistical analysis. Characterization of creek geomorphology: Relationships among geomorphological and associated hydrographical features of the creeks were examined with Spearman correlation analysis. A correlation-based principal components analysis (PCA) with varimax rotation was performed on these variables to explore patterns of association among the variables.

Table 1. Definitions of measured and derived physical variables of intertidal creeks used in the analyses of creek hydrogeomorphology and relationships between physical features and nekton. Bank full elevation refers to the top of the creek banks at the edge of the *Spartina* marsh. Units of measurement are given in Table 3

Variable	Definition
Size	
Length	Length of the main axis plus tributaries. Measurements along the centerlines of the main channel and all tributaries (from the mouths to the ends where the channel bottom rises to the bank full elevation) were summed to create this variable. Doubling of the length values provides a measure of creek edge.
Width	Mean width of the main channel of the creek. Distances between banks were measured every 10 m from the mouth to the end of the main creek to determine mean width. The measurements were made at the bank full elevation.
Depth	Mean depth of the main channel. Vertical distances between the flooded water surface (bank full level) and creek bottom were measured at the same transects used to determine mean width.
Cross-section	Area of the cross-section of the creek mouth. This variable was calculated from multiple linear measurements of the vertical plane that defined the mouth of the creek. Vertical measurements were based on bank full elevation.
Bottom area	Total area of bottom of all types in the main creek and all tributaries. A survey using 1 m ² quadrants and tape measure generated total bottom area. All roughly horizontal surfaces between creek banks were included.
Variables related to tide	
Elevation	Surveyed elevation of the creek mouth relative to the mean low water level.
Volume	Volume of the creek (including tributaries) at bank full tide level. Calculations were based on survey measurements of creek length, width and depth at bank full.
Landscape	
Drainage area	Area of intertidal marsh and mudflats between the edge of the creek and the estimated furthest distance flooding waters move outward before encountering flooding waters from adjacent drainage basins. The boundaries were estimated from high resolution aerial photographs.
Location	Shortest linear distance from the creek mouth to the nearest upland forest edge. Distances were determined from high resolution aerial photographs.
Shape	
Branches	No. of tributaries extending from the main creek channel.
Bends	No. of locations at which the axis of the main channel changes direction by more than 10 degrees.
Slope	Slope of the regression line based on bottom elevation at 10 m intervals from the mouth to the end of the main channel (where the bottom attains bank full elevation).
Bottom features	
Roughness	Irregularity of the bottom based on the coefficient of variation associated with mean depth.
Pools	No. of depressions (>5 m ²) in the intertidal creek bed that hold at least 10 cm of water at low tide.
Submerged area	Area of creek bottom (pools) covered by at least 10 cm of water at low tide.
Oyster area	Area of creek bottom with living oysters and/or whole shell regardless of the composition of the underlying sediment. Qualifying quadrants ranged from dense oyster reef to muddy areas with sparse clusters or shell patches.
Mud area	Area of creek bottom with unconsolidated sediment but without oysters. Qualifying quadrants ranged from uniform areas of soft mud to shelly mud without whole shell. Mud area plus oyster area equals total bottom area.
Outside oyster area	Area of intertidal bottom with living oysters and/or whole shell immediately outside of the creek mouth. The area calculation was based on the distance between the center of the intertidal creek mouth and the low tide mark at the edge of the subtidal creek (width) and a standard 20 m length (10 m either direction from the centerline).
Proportions	
% Submerged bottom	Ratio of submerged bottom area to (total) bottom area at low tide.
% Oyster bottom	Ratio of oyster bottom area to total bottom area.
% Outside oysters	Ratio of area of oysters outside of the creek mouth to total area outside of the creek mouth.
Other ratios	
Conduit	Ratio of drainage area to (total) bottom area. Creeks with high ratios had large drainage areas relative to the size of the creek (as indicated by bottom area).
Axial dominance	Ratio of length of the main channel axis to the cumulative total length of all tributaries.
Steepness	Ratio of total volume of water at bank full level to total bottom area. Creeks with high ratios tended to have square lateral profiles with steeper banks.
Fringe	Ratio of surface area at bank full to total bottom area. Creeks with high ratios tended to have more shallow fringing areas.
Flow	Ratio of cross-sectional area at the mouth to total volume of water at bank full tide. Creeks with high ratios tended to have large mouths relative to the volume of the creek; these creeks filled and emptied more slowly than others.
Meander	Ratio of number of directional changes in the main channel axis (bends) to the length of the main channel.
Split	Ratio of number of branches to the length of the main channel.

Nekton data: A BACI analysis and the SAS-VARCOMP (SAS 1996) procedure were used to assess whether the removal of live oysters in 4 out of the 8 study creeks had an effect on nekton use of those creeks ($p < 0.05$). The statistical analysis of the BACI followed an adaptation of Stewart-Oaten et al. (1986) by Dame et al. (2002). The 8 creeks were considered replicates and assigned to 1 of 4 blocks (1+2, 3+4, 5+6 or 7+8). A repeated-measures ANOVA using the treatment-control differences in each block as the response variables was performed using volume based abundance and biomass data; all data were $\log(n+1)$ transformed prior to the analyses. The contributions of year, season and creek to the overall variation of final densities were assessed with the SAS-VARCOMP procedure. Both the BACI and the VARCOMP analyses were performed for both total nekton and individual taxa.

BACI revealed no significant differences in creek use by nekton before (1997) and after (1998) the removal of live oysters. This outcome was observed for both biomass and abundance for the total nekton and individual taxa. No differences were observed between years for species richness either. VARCOMP showed that spatial and/or seasonal patterns of nekton densities were stronger than inter-annual patterns for the total nekton and most individual taxa (Table 2). Accordingly, the 1997 and 1998 data were combined and treated as a single dataset in analyses that examined relationships between nekton and the geomorphological features of the creeks.

Nekton abundance and biomass densities and species richness were tested for differences among seasons by ANOVA using $\log(n+1)$ transformed data. Partial Spearman correlation analyses were performed on abundance and biomass data by season to determine relationships among the different taxa. The analysis considers the correlation between a pair of variables in a variable set while holding constant the value of each of the other variables. Thereby, it takes the interactions of any of the other variables on the 2 variables in question into account (Zar 1996).

Linking nekton and creek data: Relationships between nekton and creek geomorphology were examined by canonical correlation analysis (SAS-CANCORR). Canonical correlation analyses were conducted

regularly for each season since habitat preferences may change depending on ontogenetic development and seasonal abundance. Densities of total nekton (biomass and abundance) and numbers of taxa (richness) were used in 1 set of analyses. Individual taxa (biomass and abundance) were tested separately. Both the predictor and criterion variables were rank transformed prior to the analyses. To account for the potential of autocorrelation in the input data set, correlation coefficients (r) of individual habitat variables (predictor variables) with the first canonical variable of the nekton variables (criterion variables) were used for the interpretation (Fischer & Eckmann 1997). These values range from -1 to 1 and can be compared to each other by their absolute numerical value. In CANCORR, the number of variables of both variable sets together must be smaller than the number of sites (Jongman et al. 1995), so not all available creek parameters could be included in each analysis. Prior to canonical correlation analyses, Spearman correlations for the creek variables and nekton densities were calculated for both total nekton and individual taxa. Only those creek variables for which significant correlations were revealed were included in the analyses.

Table 2. Temporal and spatial variability for nekton densities in intertidal creeks in North Inlet Estuary. All values are variance component estimates (among years, among seasons, among creeks) calculated using the SAS variance component estimation procedure (PROC VARCOMP)

Species	Abundance			Biomass		
	Year	Seasons	Creeks	Year	Seasons	Creeks
Total catch	317.9	600.5	923.9	1.7	440.1	749.3
Bay anchovy and striped anchovy <i>Anchoa</i> spp.	0.0	11.9	0.0	<0.1	2.9	0.0
Atlantic silverside <i>Menidia menidia</i>	0.1	1.3	2.1	0.0	5.9	3.4
Blue crab <i>Callinectes sapidus</i>	<0.1	<0.1	<0.1	<0.1	4.3	8.1
Brown shrimp <i>Farfantepenaeus aztecus</i>	<0.1	<0.1	<0.1	0.0	<0.1	<0.1
Grass shrimp <i>Palaemonetes</i> spp.	141.1	116.0	426.4	0.3	4.5	16.2
Mummichog <i>Fundulus heteroclitus</i>	<0.1	0.4	0.2	0.0	0.2	0.5
Pinfish <i>Lagodon rhomboides</i>	<0.1	<0.1	0.1	0.1	14.8	19.2
Spot <i>Leiostomus xanthurus</i>	63.8	208.2	2.7	2.2	5.5	36.9
Striped mullet <i>Mugil cephalus</i>	0.2	0.3	0.0	<0.1	0.5	1.6
White mullet <i>Mugil curema</i>	<0.1	0.4	0.1	0.3	9.4	2.9
White shrimp <i>Litopenaeus setiferus</i>	0.0	21.7	0.0	0.0	45.1	4.5

Table 5. Variable loading and percentage of the variance explained in the principal components analysis of geomorphological variables from the intertidal creeks. Column headings represent the first 6 principal components. Variables underlined are those with the highest loading values

Variable	Principal components					
	1	2	3	4	5	6
Length	0.67	0.41	0.32	0.36	-0.35	0.16
Width	<u>0.76</u>	0.61	-0.16	0.08	0.12	0.04
Depth	0.31	-0.11	<u>0.85</u>	0.08	-0.22	0.33
Cross-section	0.74	0.46	-0.08	0.45	0.16	-0.03
Bottom area	<u>0.83</u>	0.36	0.24	-0.01	-0.27	0.15
Elevation	<u>-0.91</u>	0.29	-0.15	-0.14	-0.21	0.00
Volume	0.68	0.53	0.38	0.01	-0.24	0.23
Drainage area	0.02	<u>0.92</u>	0.08	0.28	-0.09	0.12
Location	0.03	-0.28	0.58	0.01	0.18	<u>0.73</u>
Branches	0.20	0.02	0.17	<u>0.94</u>	-0.05	0.18
Bends	-0.06	<u>0.88</u>	0.29	-0.10	-0.18	0.10
Slope	-0.30	-0.13	<u>-0.90</u>	0.14	0.07	0.26
Roughness	<u>0.81</u>	-0.07	0.01	-0.08	0.14	-0.22
Pools	0.24	0.74	0.00	0.38	0.18	-0.40
Submerged area	0.44	0.16	0.27	-0.22	<u>-0.80</u>	0.04
Oyster area	0.14	<u>0.81</u>	-0.51	0.23	-0.11	0.07
Mud area	<u>0.83</u>	0.11	0.43	-0.09	-0.25	0.14
Outside oyster area	0.06	<u>0.87</u>	-0.16	-0.03	0.12	-0.39
% Subm. bottom	-0.16	-0.23	0.10	-0.17	<u>-0.91</u>	-0.10
% Oyster bottom	-0.46	0.42	<u>-0.78</u>	0.05	0.05	0.01
% Outside oyster	0.03	<u>0.85</u>	0.03	-0.40	0.26	0.00
Conduit	<u>-0.87</u>	0.34	-0.25	-0.03	0.23	0.04
Axial dominance	-0.16	-0.04	0.54	<u>-0.74</u>	-0.32	0.17
Steepness	-0.19	0.47	<u>0.76</u>	0.04	0.18	0.24
Fringe	-0.52	0.38	0.08	0.72	0.04	-0.23
Flow	-0.18	-0.06	<u>-0.92</u>	0.11	0.26	-0.13
Meander	-0.01	-0.12	-0.25	<u>0.92</u>	0.23	-0.02
Split	-0.50	0.66	0.09	-0.21	0.42	0.25
% Variance	25.10	24.60	19.10	13.50	9.30	5.30

ables. Creek size was not related to either drainage area or the distance between the creek mouth and the nearest upland edge (location).

Negative relationships between the elevation of the mouth and both volume and bottom area indicated that smaller creeks tended to be perched higher in the tidal range where they started flooding later and finished ebbing earlier in the tidal cycle (Table 4). Depth was not correlated with the elevation of the mouth or with other size variables. Creeks with shallow mean depth and greater slope filled and drained more slowly than others. Deep creeks had larger areas of mud bottom

Results of the principal component analyses using all 28 physical variables indicated that creeks differed in shape, size and relationships with external features (Table 5). In the first principal component, the 4 variables with highest loadings were elevation, conduit, mud bottom area and roughness. Drainage area, bends, depth, slope, flow, branches and percent bottom submerged had the highest loading values among the other components. Together, the 6 principal components explained about 96 % of the overall variance.

Nekton

ANOVA showed that season had a significant effect on nekton, biomass and species richness ($p < 0.05$). Total nekton biomass was not significantly different in March, June and November ($p < 0.05$). Biomass in August was significantly higher ($p < 0.05$), but not distinguishable from June (Fig. 2). Total abundances were similar in March, June and August. Abundance was significantly lower ($p < 0.1$) in November, but could not be distinguished from levels in June. High levels of species richness occurred in June and August (Fig. 2). Richness levels were similar ($p < 0.05$) in March and November, but both were significantly lower than in the summer months.

Seasonal and spatial patterns of occurrence were stronger than inter-annual patterns for total nekton and most individual taxa (Table 2). Within seasons, total abundance among creeks varied by 4 to 28 times and total biomass varied by 3 to 25 times (Fig. 2). Among seasons, the same creeks had consistently higher or lower biomasses than others (Table 6). Biomass in Creek 2 was ranked highest or second highest during all 8 samplings (Fig. 2, Table 6). Creeks 3, 4 and 1 were ranked higher than most other creeks during the 2 yr period. Creek 6 biomass was lowest and Creek 8 ranked last or next to last on almost every date. As a group, Town Creek locations (5 to 8) ranked lower than Clambank Creek locations (1 to 4) on all dates.

At least 77 species of fishes and motile epibenthic crustaceans were collected during the study. Overall, 11 taxa accounted for >93 % of the biomass and >99 % of the abundance. Within seasons, the same group of taxa dominated in all creeks (Fig. 3) Grass shrimp *Palaemonetes* spp. (with *P. pugio*, 21 to 43 mm, accounting for >90 %) was by far the most abundant overall and during each season; it was the only taxon represented in every collection and its abundance exceeded the abundances of all other taxa in 83 % of the collections (Table 7). Composition varied considerably among seasons, but composition by season was similar among years (Fig. 4). In March, resident taxa including grass shrimp *Palaemonetes* spp, mummichog *Fundulus heteroclitus* (24 to 98 mm) and Atlantic silverside *Menidia menidia* (74 to 103 mm) accounted

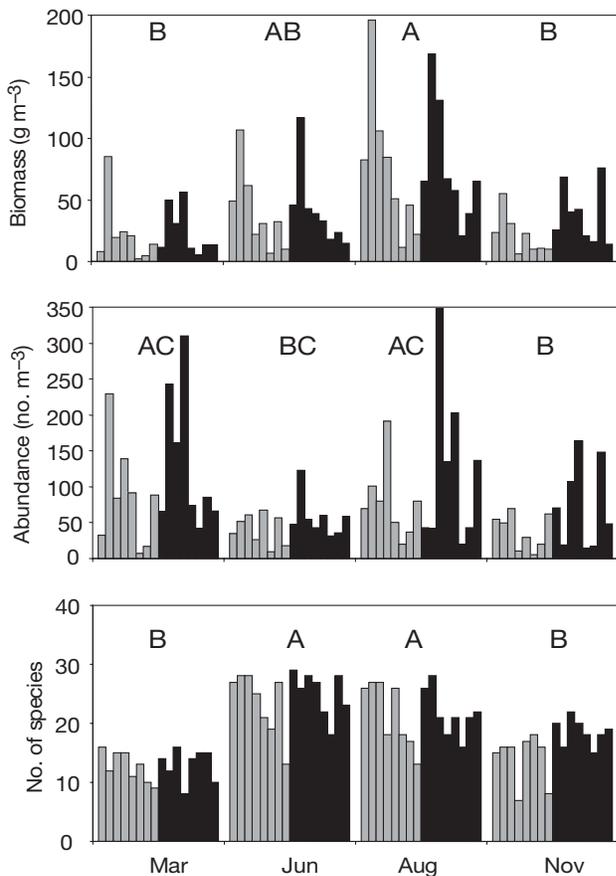


Fig. 2. Biomass, abundance and species richness for 8 intertidal creeks during the March, June, August and November collections in 1997 and 1998. Each bar represents one creek and the 8 creeks are shown in order (1–8). The 1997 (grey bars) and 1998 (black bars) data are paired for each month to facilitate comparison within and between months. Results of post hoc Tukey tests (both years combined, log(n+1) transformed data) comparing months are shown with shared letters indicating no differences. The significance level for the ANOVA was $p < 0.05$ and, for the Tukey tests, they were $p < 0.05$ for biomass and species richness and $p < 0.1$ for abundance

Table 6. Ranks for total nekton biomass densities (g m^{-3}) at the 8 creeks during the quarterly samplings. A rank of 1 indicates the location with the highest value for that sampling period

	Creek							
	1	2	3	4	5	6	7	8
Mar 1997	6	1	4	2	3	8	7	5
Mar 1998	6	2	3	1	7	8	4	5
Jun 1997	3	1	2	6	5	8	4	7
Jun 1998	2	1	3	4	5	7	6	8
Aug 1997	4	1	2	3	5	8	6	7
Aug 1998	5	1	2	3	6	8	7	3
Nov 1997	3	1	2	8	5	7	4	6
Nov 1998	5	2	4	3	6	7	1	8

for the greatest portion of total abundance and biomass. Young of the year spot *Leiostomus xanthurus* (23 to 33 mm) made up most of the rest of the March catches; more spot occupied the creeks in 1998. In June, grass shrimp and mummichog together accounted for the highest portion of the total abundance with spot and anchovy *Anchoa* spp. (35 to 66 mm) accounting for most of the rest. However, June total biomass was more evenly distributed between these abundant, small taxa and less numerous, larger taxa such as blue crab *Callinectes sapidus* (35 to 166 mm), pinfish *Lagodon rhomboides* (65 to 160 mm), striped mullet *Mugil cephalus* (67 to 320 mm) and white mullet *M. curema* (41 to 70 mm). In August, white shrimp *Litopenaeus setiferus* (42 to 122 mm) and anchovy contributed to higher transient than resident species biomass. In November, grass shrimp was again the most abundant with Atlantic silverside, anchovy and mummichog accounting for most of the rest of the catch. November biomass was dominated by resident taxa.

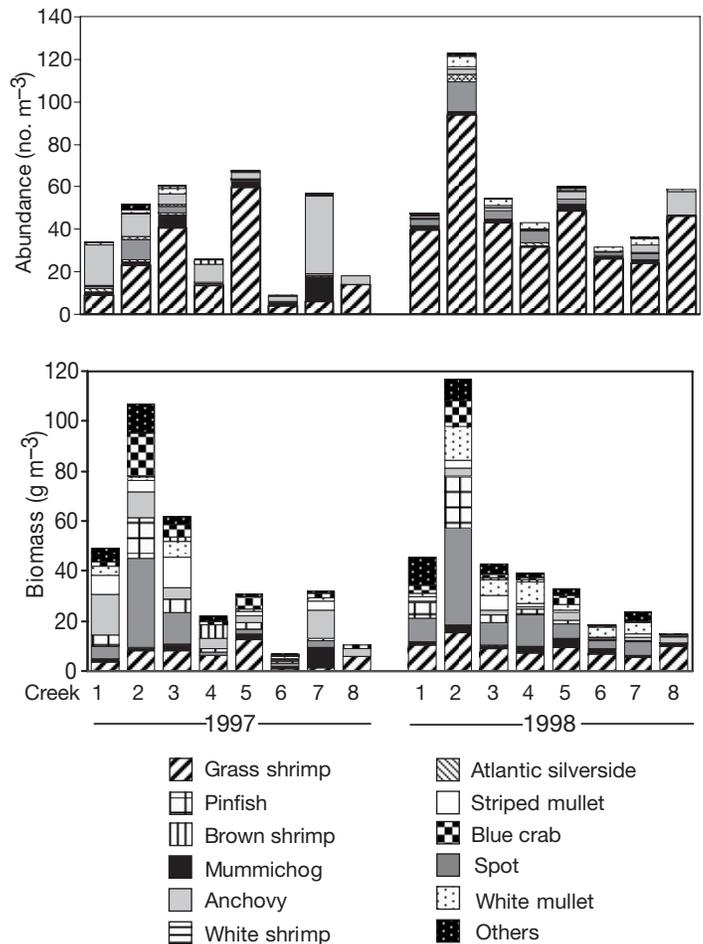


Fig. 3. Abundance and biomass densities for 11 dominant taxa and others in each of the 8 creeks during June 1997 and 1998

Table 7. Summary of abundance density statistics for total nekton and the top 11 taxa in the intertidal creeks. Values are given for percent occurrence in all collections (Freq), peak abundance (Peak) and mean abundance with SE (parentheses) for each of the 4 mo (yr combined)

Taxon	Freq (%)	Peak (no. m ⁻³)	Mean abundance (no. m ⁻³)			
			Mar	Jun	Aug	Nov
Total nekton	100	347.6	108.4 (21.6)	48.7 (6.5)	99.9 (21.8)	55.4 (12.0)
Grass shrimp <i>Palaemonetes</i> spp.	100	291.3	69.0 (13.9)	32.7 (5.9)	63.0 (19.3)	42.8 (10.6)
Mummichog <i>Fundulus heteroclitus</i>	98	11.8	0.3 (<0.1)	2.2 (0.7)	2.3 (0.5)	1.3 (0.4)
Spot <i>Leiostomus xanthurus</i>	95	177.3	35.6 (12.0)	3.1 (0.9)	1.0 (0.5)	0.1 (<0.1)
Pinfish <i>Lagodon rhomboides</i>	94	6.6	0.2 (<0.1)	0.6 (0.2)	0.6 (0.2)	0.1 (<0.1)
Brown shrimp <i>Farfantepenaeus aztecus</i>	25	1.9	0	< 0.2 (< 0.1)	0	0
White shrimp <i>Litopenaeus setiferus</i>	50	164.9	0	0	17.2 (10.0)	4.1 (3.8)
White mullet <i>Mugil curema</i>	77	5.0	<0.1	1.5 (0.3)	1.0 (0.3)	<0.1
Striped mullet <i>Mugil cephalus</i>	74	10.9	1.7 (0.9)	0.2 (< 0.1)	0.3 (0.1)	<0.1
Anchovies <i>Anchoa</i> spp.	98	47.3	0.9 (0.4)	7.1 (2.3)	12.2 (3.6)	3.3 (2.5)
Atlantic silverside <i>Menidia menidia</i>	91	12.3	0.5 (0.2)	0.5 (0.1)	1.6 (0.8)	3.4 (0.9)
Blue crab <i>Callinectes sapidus</i>	86	0.5	<0.1	0.1	0.1	<0.1

Relationships between nekton and geomorphological features

The first canonical correlation linking the nekton and geomorphological variables was highly significant ($p < 0.01$) for total nekton abundance and biomass and species richness. In June, the first canonical correlation value ($r^2 = 0.97$) explained 86% of the variance, and in August, it ($r^2 = 0.96$) explained 77% (Table 8). In both seasons, biomass was explained better than richness or abundance. In June, flow (0.86), depth (-0.76), steepness (-0.74) and location (-0.69) were the geomorphological values most strongly correlated with the first canonical axis. These same 4 variables were also the most strongly correlated with total nekton in August.

For grass shrimp, March was the only season for which a significant first canonical correlation was determined ($r^2 = 0.97$). In the analysis, 99% of the overall variance was explained and abundance and biomass were equally highly correlated to the first canonical axis of the geomorphological variables. Branches (-0.80), location (-0.69), meander (-0.62) and length (-0.55) were the geomorphological variables most

strongly correlated with the first canonical axis of the multivariate nekton dataset (Table 8).

The analyses for mummichog yielded a significant first canonical correlation only in June ($r^2 = 0.94$) when 94% of the variance was explained (Table 8). Abundance was more completely explained by the geomorphological variables than was biomass. Percent of the creek bottom remaining submerged at low tide (-0.75) was by far the most important variable, but flow (0.47) and depth (-0.45) were also important factors.

For spot, significant first canonical correlations were found in August ($r^2 = 0.93$) and November ($r^2 = 0.97$), when 83% and 97% of the overall variance was explained, respectively (Table 8). In August, location (-0.73) and depth (-0.71) and in November, flow (0.87) and depth (-0.84) were the most important factors. Six other factors were more important in August than November.

Analyses of pinfish data demonstrated significant first canonical correlations for 3 seasons. The proportion of the overall variance explained in each analysis was high and both the biomass and abundance were highly correlated with the geomorphological variables in the first canonical correlation (Table 8). In June ($r^2 = 0.98$, 98%), the most important factors were depth (-0.82), flow (0.81), location (-0.76) and steepness (-0.58). In August ($r^2 = 0.94$, 88%), depth (-0.77) was the most important factor and location, length, total bottom area, flow, branches, conduit, elevation and volume were also strongly correlated. In November ($r^2 = 0.95$, 96%), depth (-0.77) and flow (0.76) were again the most important, with length, volume, total bottom area, conduit and elevation being additional strong variables.

Brown shrimp *Farfantepenaeus aztecus* results (not shown) for June ($r^2 = 0.92$, 91%) showed steepness (-0.81) was the most important factor, whereas white shrimp results (not shown) for August ($r^2 = 0.94$, 95%) showed that bends (-0.77) and steepness (-0.75) ranked highest. Biomass and abundance variations were explained well in the analyses for both penaeid shrimps.

For striped mullet (results not shown) in June ($r^2 = 0.93$), 97% of the overall variance was explained and biomass was more completely addressed than abundance. Catches were strongly related to flow (0.89)

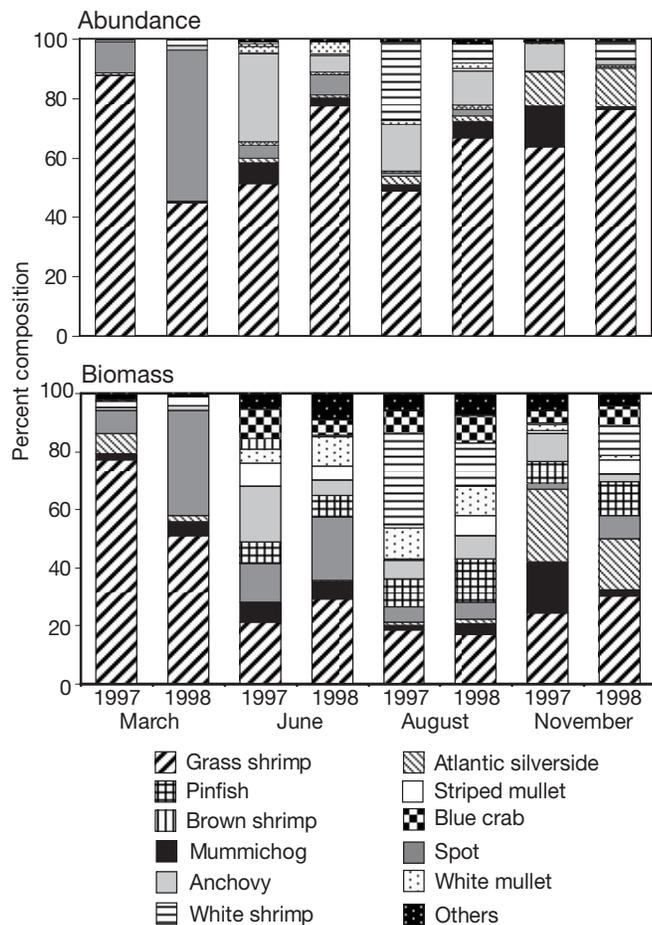


Fig. 4. Percent of total abundance and biomass represented by the 11 dominant taxa and others (all other taxa combined) during each of the sampling periods. Density data from all 8 creeks were used to determine each seasonal value

with depth (-0.67), axial dominance (-0.64), percent submerged bottom area (-0.60), slope (0.56) and steepness (-0.56) being additional strong factors.

For Atlantic silverside in November ($r^2 = 0.96$), 83% of the overall variance was explained but neither biomass nor abundance were well accounted for in the analyses. No correlation of a variable to the first canonical axis of the nekton variables exceeded 0.5. No significant first canonical correlations were found for white mullet, anchovy, or blue crab.

Overall, among the 21 geomorphological variables used in the canonical correlation analyses, 4 physical variables were most important. Flow and depth were the physical features that most strongly correlated with total nekton, mummichog, spot, pinfish and striped mullet. Location and steepness were the next most important features for total nekton as well as for spot, pinfish and brown shrimp. One or more of these 4 factors was among the most important factors for each

of the 11 dominant taxa. Only 2 variables, pools and percent oyster area, were not correlated with total nekton or individual taxa.

The signs or directions of the relationships differed among variables. For taxa in which flow, elevation of the mouth and slope were important factors, positive relationships were indicated (Table 8). Depth, steepness, location, drainage area, bends, meander, branches, splits, length, axial dominance, volume, roughness, total bottom area and percent submerged bottom area were all inversely related to density in analyses in which they were strongly correlated factors.

Rankings of the variables identified as most important to individual species in the CANCOOR analyses were similar to those for the same features among the set of 8 creeks (Table 3). For example, in March, grass shrimp (which were inversely correlated to branches) were least abundant in Creek 6, which had higher numbers of branches than most other creeks. Grass shrimp were inversely correlated to location (distance to upland ridge) and were most abundant in Creek 2, which was closest to the uplands. Location and depth were among the most important factors (negative correlations) for spot and pinfish and their densities were highest in shallow creeks closest to the uplands. The biomass and abundance of both spot and pinfish increased as flow decreased.

DISCUSSION

Recurring patterns and large differences in the magnitude of nekton use among intertidal creeks, combined with evidence of strong relationships between nekton densities and certain hydrogeomorphological features, indicated that selection for favorable conditions played an important role in the distribution of nekton. Because use was not related to the size of the creeks (length, width, bottom area, or volume) and the smallest, slowest flowing creeks supported the highest densities, large inter-creek differences in nekton use could not be explained by passive transport of nekton from low tide refuges in adjacent subtidal channels. Spatial differences were most likely the result of directed movements caused by behavioral responses to certain physical attributes of the creeks. Selection is the non-random use of space resulting from voluntary movements (Kramer et al. 1997) and a mechanism by which choices are made among alternatives (Craig & Crowder 2000). Many tagging and telemetry studies have demonstrated that individual fishes regularly return to or remain in certain locations. Some rocky intertidal pool fishes are able to learn the topography of their environment and return repeatedly to the same locations (Gibson 1999). High site fidelity or extended

Table 8. Results of the canonical correlation analyses for total catch, mummichog, grass shrimp, spot and pinfish. Indicators of the strength of the overall analysis are given for months in which there was a significant relationship between biomass, abundance and/or species richness and geomorphological features. All canonical correlation numbers: I

	Total catch		Grass shrimp <i>Palaemonetes</i> spp.	Mummichog <i>Fundulus</i> <i>heteroclitus</i>	Spot <i>Leiostomus</i> <i>xanthurus</i>		Pinfish <i>Lagodon</i> <i>rhomboides</i>		
	Jun	Aug	Mar	Jun	Aug	Nov	Jun	Aug	Nov
Month	Jun	Aug	Mar	Jun	Aug	Nov	Jun	Aug	Nov
r ²	0.97	0.96	0.97	0.94	0.93	0.97	0.98	0.94	0.95
pr > F	0.0051	0.0049	0.0091	0.0434	0.0154	0.0035	0.0038	0.0271	0.0247
% Variance explained	86	77	99	94	83	97	98	88	96
Criterion:									
Biomass	0.93	0.95	0.96	0.46	0.93	0.71	0.97	0.93	0.81
Abundance	0.35	0.37	0.97	0.94	0.92	0.87	0.93	0.90	0.92
Species richness	0.82	0.67							
Predictor:									
Flow	0.86	0.69		0.47	0.60	0.87	0.81	0.58	0.76
Depth	-0.76	-0.54		-0.45	-0.71	-0.84	-0.82	-0.77	-0.77
Steepness	-0.74	-0.81		0.08	-0.39	-0.45	-0.58	-0.34	-0.37
Location	-0.69	-0.82	-0.69	0.37	-0.73	-0.58	-0.76	-0.69	-0.47
Slope	0.44	0.26	-0.14	0.38					
% Oyster bottom	0.35	0.14			0.54	0.54			
Meander	0.33	-0.05	-0.62						
% Submerged bottom	-0.30	-0.09		-0.75					
Fringe	0.26	-0.06	-0.41						
Length	-0.24	-0.37	-0.55	-0.16			-0.46	-0.63	-0.63
Branches	-0.05	-0.37	-0.80				-0.30	-0.58	-0.33
Elevation	0.04	0.09	0.23	-0.12	0.58	0.26	0.32	0.55	0.48
Conduit			-0.02		0.52	0.38	0.36	0.56	0.53
Volume				-0.07			-0.37	-0.53	-0.62
Bends				-0.29					
Bottom area				-0.05	-0.59	-0.32	-0.40	-0.60	-0.59
Roughness				0.01	-0.58	-0.32			
Cross section							-0.11	-0.33	-0.32
Drainage area							-0.10	-0.02	-0.19

periods of residency have been demonstrated for several estuarine species (Lotrich 1975, Weinstein & O'Neil 1986). Potthoff & Allen (2003) showed that tagged juvenile pinfish moved between intertidal creeks and the adjacent subtidal channel, but not into neighboring intertidal creeks. Stability in spatial patterns of nekton use among creeks over long periods is best explained by the ability of individuals to recognize features and return to specific locations.

Mechanisms by which unequal spatial distributions of nekton are established and maintained are difficult to elucidate and few investigators have addressed the subject (Craig & Crowder 2000). One possibility is that over periods of days and weeks, highly motile individuals visit multiple creeks and select one that they will repeatedly reenter. If some creeks are more attractive and can support higher densities than others, unequal levels of use would result. When densities of regular users approach the carrying capacity of the habitat, other individuals might be expected to use other creeks or habitats that have less suitable conditions. The Ideal Free Distribution model (Fretwell 1972) pre-

dicts that density in each habitat (e.g intertidal creek) will be positively correlated with its intrinsic suitability, some habitats attracting and supporting higher densities than others (Kramer & Chapman 1999). Evidence of persistent differences in nekton use of adjacent estuarine creeks has also been reported by Paterston & Whitfield (2003).

Of the 28 variables used in the analyses, flow (cross sectional area:volume) was the factor that affected nekton biomass and abundance more often than any other. Total nekton, spot, pinfish, mummichogs, white shrimp and striped mullet might have been attracted to slow flowing creeks or they actively avoided creeks in which flow was stronger. Cattrijesse et al. (1994) found that nekton in an intertidal creek in the Netherlands migrated at the beginning and end of the tide when current velocities were lowest. McIvor & Rozas (1996) reported higher abundances with lower flow.

Shallow depth was one of the 4 most important factors. Creeks with shallower mean depths were not necessarily perched higher in the tidal range, however, shallow creeks flooded and emptied more slowly. Shal-

low depths may be attractive to small nekton as refuge from aquatic predators, but Craig & Crowder (2000) concluded that few studies have directly tested this. Using tethering experiments, Ruiz et al. (1993) demonstrated higher mortality of grass shrimps, mummichogs and other small fishes with increasing depth. Large predators were uncommon in flooded intertidal creeks, but they occurred in adjacent subtidal channels (Cain & Dean 1976, Paterson & Whitfield 2003, Bretsch & Allen 2006). Nekton may select shallow depths to find more abundant or preferred prey resources (Kneib 1997).

Steepness was another important feature with low steepness supporting higher nekton use. Creeks with more gently sloped banks had slower flow. This was also reported by McIvor & Odum (1988). We would expect that intertidal creeks with flatter profiles are used more by demersal foragers than creeks with nearly vertical, eroding marsh banks. Low bank steepness was the most important factor affecting brown shrimp in June and white shrimp in August, when they were at peak abundances. Rozas & Zimmerman (2000) found both brown and white shrimps most abundant at low, shoreline marsh sites, and Wenner & Beatty (1993) recognized the importance of sloped intertidal creek (rivulet) banks to juvenile white shrimp. For some species, gently sloped edges may provide better refuges than steep banks (McIvor & Odum 1988, Hettler 1989). Rozas et al. (1988) concluded that depositional (sloped) creek banks were the primary corridors for nekton movements between creeks and the marsh surface. Many fishes were more abundant in California salt marsh creeks with sloped than steep banks (Williams & Zedler 1999).

The length of marsh edge was not an important factor for nekton use of intertidal creeks. Nekton densities in other systems are higher at marsh edges than on adjacent open bottom or interior marshes (Baltz et al. 1993, Minello et al. 1994, Peterson & Turner 1994, Cicchetti & Diaz 2000, Minello et al. 2003). Edge habitat varies geographically with respect to landscape features such as channel network complexity, which increases with tidal range along the Atlantic coast (McIvor and Rozas 1996). Temporally dynamic relationships between edges and adjacent intertidal and subtidal areas also account for high variability in nekton use. Elevation of the bank, characteristics of the adjacent water body, proximity of vegetation to the edge and types and densities of plant stems are some factors that affect the use of edges (Rakocinski et al. 1992, Rozas & Zimmerman 2000). Differences in the relationship between nekton and edges are expected between locations and the spatial and temporal scales of measurements. A significant km scale relationship was reported between densities of white shrimp occu-

pying Georgia creeks near low tide and the amount of intertidal edge (Webb & Kneib 2002). Kneib (2003) reported a strong relationship between production of nekton and the amount of intertidal edge. At the scale of the intertidal creek with whole creek collections being made at bank full high tide, our study indicated that amount of edge was not as important as other features including the slope of the bank (edge).

The association of higher nekton densities with nearness to an upland ridge (location) could not be attributed to differences in internal geomorphology or drainage area of the intertidal creeks, and salinity regimes did not vary among creeks. Dame et al. (1992) concluded that age related differences in physical and geochemical features of the marsh along the continuum from the uplands to the ocean ends of estuaries such as North Inlet may influence the distribution of estuarine species. Other studies have reported that nekton abundances increase with decreasing stream order and proximity to uplands (Rozas & Odum 1987, Desmond et al. 2000, Webb & Kneib 2002). Differences in nekton use between the 2 groups of intertidal creeks may have been related to differences in size, depth, or other characteristics of the adjacent subtidal channels that may have affected predator abundance or refuge availability at low tide.

Strong relationships between nekton and certain geomorphological characteristics suggest that major intertidal creeks serve as more than just corridors for nekton movement. Intertidal creeks are often thought of as conduits connecting permanently flooded and higher intertidal areas (Kneib 1997, Wenner & Beatty 1993). Rozas et al. (1988) demonstrated that compared to edges bordering open water, small creeks (rivulets) were the primary corridors for nekton movements into a tidal marsh. Hettler (1989) reported densities were higher adjacent to a rivulet than adjacent to a major creek bank. McIvor & Rozas (1996) concluded that the proximity of rivulets to the marsh enabled nekton to maximize time on the marsh and that rivulets afforded greater protection from predators. Because intertidal creeks are inundated for longer periods than the adjacent marsh, use by nekton is expected to be important regardless of whether those occupants eventually move onto the flooded marsh. We assumed the tidal migrants were not able to predict the extent to which they could access the marsh from tide to tide, so collections at bank full (20 to 30% of the tides) were representative of regular patterns of use. If so, selection for certain internal characteristics of creeks might be more important than features of the surrounding marsh. In fact, we found that use of the creeks by total nekton, all shrimps and most fishes was related to internal features but not to drainage area. The exceptions (blue crab, white mullet and striped mullet) were commonly

observed foraging on the flooded marsh. Anchovies and Atlantic silversides, pelagic feeders that were abundant in creeks but not on the marsh, were not associated with drainage area and were only weakly influenced by internal features.

Grass shrimp, the overall most abundant tidal migrant every season, did not appear to be strongly influenced by the geomorphological characteristics of the creeks. It was only related to features in March when densities of overwintering shrimps were related to branches, meander and length. Few transient taxa were present in March. The absence of relationships during the warm months suggests that smaller summer generation grass shrimps were not as responsive to physical features when many other taxa co-occupied the creeks.

The importance of slow flow and shallow depth to the mummichog was consistent with other reports (Kneib 1997). The most important factor affecting their use was the proportion of bottom submerged at low tide. This inverse relationship might be explained by their preference for deeper areas of submerged bottom. In this area, creeks with lower percent submergence at low tide have deeper pools. The lack of relationships between mummichog (>15 mm) in creeks and the sizes of adjacent marsh basins during any season suggests that geomorphological differences within creeks (pools) may be more important than the amount of marsh available around high tide.

We did not find evidence that oysters provide essential habitat for nekton within intertidal creeks. Removal of live oysters in the BACI experiment did not affect patterns of use between years and bottom coverage by oyster shell was not an important feature for either total nekton or individual taxa in the multivariate analyses conducted for the 2 yr period. These findings contrast with the results of many reports that identify Eastern oyster reefs as important nekton habitat (Dame 1996, Coen et al. 1999). This may be due to the differences in the configuration of oysters and tidal currents in intertidal creeks compared to those on subtidal reefs (Coen et al. 1999, Lehnert & Allen 2002) or intertidal fringing and island reefs surrounded by open water or flats (Wenner et al. 1996, Glancy et al. 2003). Oysters in intertidal creeks tend to occur in small isolated patches and are not exposed to strong tidal currents and wave action. Other physical features of intertidal creeks appear to influence patterns of nekton use more strongly than the presence of oysters.

Our findings raise an interesting question about the relative importance of geomorphology and water quality to nekton use of tidal creeks. Spatial variations in the abundance of estuarine nekton are often attributed to variations in salinity, dissolved oxygen, or other water quality parameters. Demonstrated relationships between the physical configuration of habitat and nek-

ton use among neighboring creeks with similar and stable salinity suggest caution is necessary in evaluating causes for differences in nekton use of habitat along environmental gradients, regardless of habitat type or geographic location.

It is important to recognize that the hydrology, landscape structure and ecology of marshes and associated creeks on different coasts vary considerably, and that the features found to be important to nekton in this system may not be as important as other features elsewhere. The approach to identifying geomorphological features of importance to nekton used in this study should be useful in other marsh, mangrove and shallow-water systems. Nevertheless, we believe that our finding that shallow average depths, broad lateral profiles, slow tidal flow and close proximity to uplands support the highest densities of nekton has broad applications and can provide guidance for resource managers charged with protecting and restoring salt marsh systems. Creeks with these characteristics should be assigned high priority for protection. Webb & Kneib (2002) recommended a precautionary approach to making land-use decisions that would reduce the structural complexity of marshes and networks of creeks. As components of the intertidal landscape, tidal creeks should be configured to provide essential ecological services to resident and transient species (Desmond et al. 2000, Rozas & Zimmerman 2000, Able et al. 2002). Williams & Zedler (1999) suggested that future restoration projects should mimic natural marsh hydrogeomorphology and diversity more closely. The importance of dendritic tidal channel complexity, habitat matrix heterogeneity and other attributes of estuarine landscape structure is described by Simenstad et al. (2002). Additional investigations of relationships between geomorphological features of creeks, water quality and the behavior and production of nekton populations will be necessary to determine design and management criteria that achieve sustainable functional equivalency for created marshes in different geographic regions.

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