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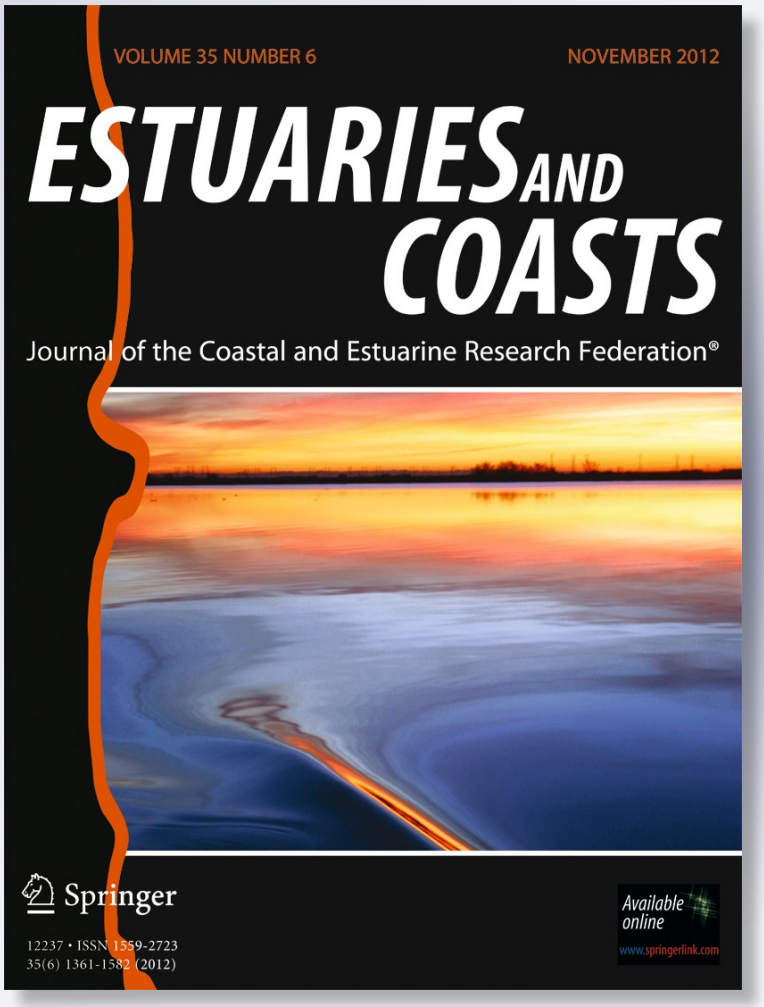

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Comparison of Estuarine Salinity Gradients and Associated Nekton Community Change in the Lower St. Johns River Estuary

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Abstract Salinity is an important determinant of estuarine faunal composition; previous studies, however, have indicated conflicting accounts of continuous vs. relatively rapid change in community structure at certain salinities from geographically distinct estuaries. This study uses a large fisheries monitoring database (n>5,000 samples) to explore evidence for estuarine salinity zonation by nekton in the lower St. Johns River estuary (LSJR). There was little evidence to support the presence of estuarine salinity zones except at the extremes of the salinity gradient (i.e., 0.1–1.0 and 34–39). The LSJR estuarine nekton community exhibits progressively slow ecological change throughout most of the salinity gradient with rapid change at the interfaces with fresh and marine waters—an ecoline bounded by ecotones. This study affirms the rapid change that occurs at the extremes of the salinity spectrum in certain estuaries and is relevant to efforts to manage surface water resources and estuarine ecosystems. Given the disparity in the results of the studies examining biological salinity zones in estuaries, it would be wise to have, at minimum, a regional understanding of how communities are structured along the gradient from freshwater to marine.

Keywords Estuary · Fish · Nekton · Oligohaline · Salinity zones

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Introduction

Estuaries and their biota are often characterized by the environmental salinity gradient from marine to freshwater conditions. The organisms that inhabit estuaries tend to inhabit fairly predictable portions of these salinity gradients because of their innate salinity tolerances or the intersection of a particular salinity range with other necessary ecological features (e.g., habitat, suitable food) that are preferable. Remane and Schlieper (1971) observed that the salinity ranges, and associated biota, from freshwater to marine can be subdivided into distinct stages. The most common and accepted salinity classification scheme is the Venice System, which separates habitats into limnetic (<0.5 psu), oligohaline (0–5 psu), mesohaline (5–18 psu), polyhaline (18–30 psu), euhaline (30–40 psu), and hyper–haline (>40 psu) (Anonymous 1958).

However, some have noted that the criteria used to define the salinity zones in the Venice System were not made explicit (Bulger et al. 1993). In order to create an explicit classification system, Bulger et al. (1993) used principal components analysis (PCA) to analyze salinity range data from fishes and invertebrates along mid-Atlantic (USA) estuaries and defined five overlapping biological salinity zones (0–4, 2–14, 11–18, 16–27, and 24–marine). Christensen et al. (1997) examined several estuaries in the northern Gulf of Mexico, and Farrell et al. (2005) analyzed communities in the Suwannee River watershed (Florida) and found results similar to those of Bulger et al. (1993). More recently, Greenwood (2007) examined nekton communities in Tampa Bay and Charlotte Harbor (Florida) in an effort to find evidence for salinity zone end points (regions of "accelerated

change superimposed on a gradient of continuous change"; Boesch 1977). Greenwood's analysis differed slightly from earlier ones in that he used data on only juvenile abundance and employed nonmetric multidimensional scaling (MDS) to evaluate community structure.

The objective of this study was to explore evidence of estuarine biological salinity zonation by nekton inhabiting the lower St. Johns River estuary (LSJR), Florida, a system with many unique features and observations (see "Methods"). We do so by (a) examining evidence for biological salinity zones in the LSJR and comparing results with other known estuarine biological salinity zonation found elsewhere; (b) examining salinity zone end points for accelerated change in community structure; and (c) identifying species that contribute to community differences between salinity zones. Data from juveniles and adults were analyzed using techniques similar to those presented by Bulger et al. (1993) and Greenwood (2007), facilitating comparison of the presence or absence of distinct salinity zones in light of different analytical approaches.

Materials and Methods

Study Area and Sampling Methods

The present study uses a relatively large database (n>5,000 samples), compiled from nekton sampling in the lower St. Johns River estuary in northeast Florida (Fig. 1). Data for this study were collected from the LSJR from May 2001 through December 2008 by the Fisheries-Independent Monitoring Program (FIM) of the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife

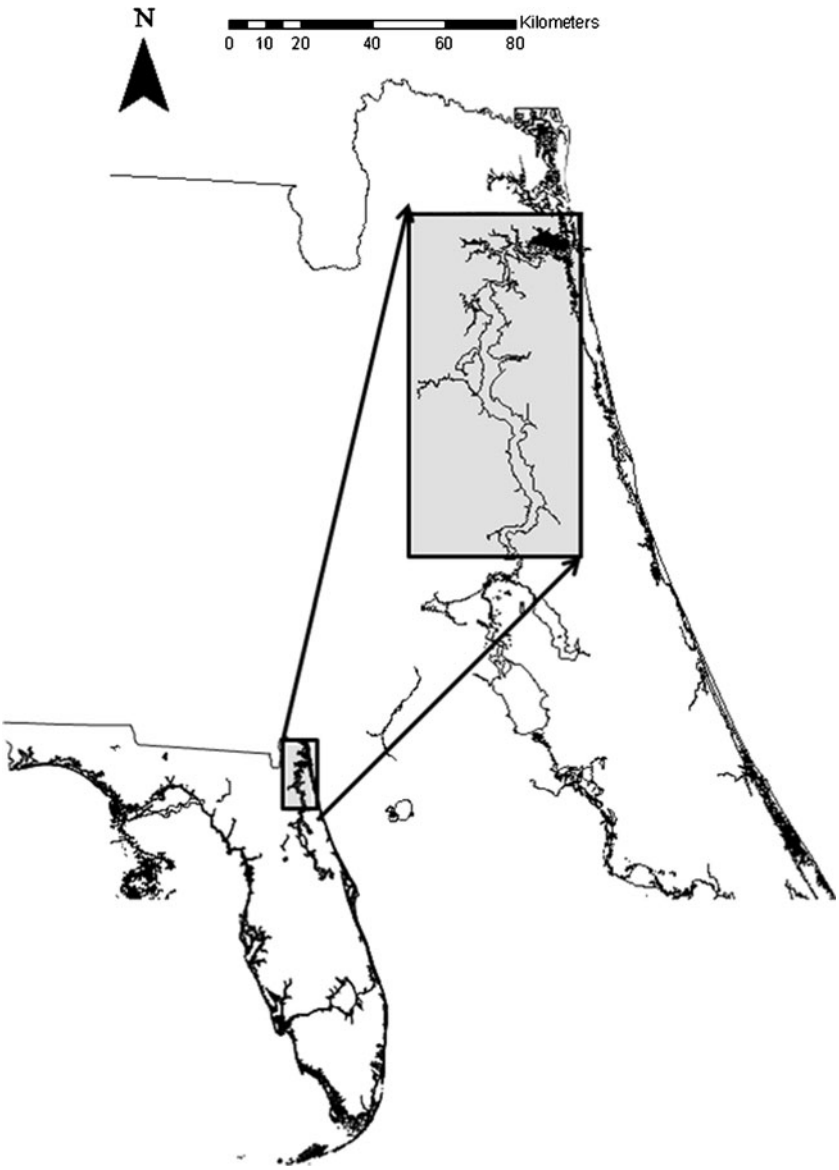

Fig. 1 The lower St. Johns River estuary and the area sampled during this study

Research Institute. Sampling within the LSJR extended 134 km upstream from the mouth and comprised marine, tidal, and freshwater reaches. Tidal influence is evident throughout the LSJR, with tidal amplitudes of 1.5 m at the mouth (Brody 1994) and negative flows occurring frequently as far upriver as Lake George (177 km) of the river (Morris 1995). The St. Johns River estuary is unique among estuaries in that vertical salinity stratification rarely develops; rather, the river remains thoroughly mixed throughout most of the LSJR. Salinities far upriver (134 km from the mouth) are often elevated due to groundwater inflow from springs containing large concentrations of sodium, calcium, and chloride ions (Brody 1994). For more detailed descriptions of the LSJR, refer to Sagan (2009) and the Environmental Protection Board (2009).

A stratified, random, multigear sampling design has been employed on the LSJR by the FIM program since 2001 to develop a comprehensive data set characterizing spatial and temporal patterns in catch rates and community structure of nekton across a wide range of habitats and life history stages. The area sampled in the LSJR ranged from the upper limits of salt penetration in tidal freshwater reaches to marine waters at the river's mouth (salinity >35). Nekton were collected during this study using three types of sampling gear: (a) 21.3-m center-bag seines of 3.2-mm stretched mesh; (b) 183-m center-bag seines of 38-mm stretched mesh; and (c) 6.1-m otter trawls of 38-mm stretched mesh with a 3.2-mm stretched mesh liner. The 21.3-m seines principally target small-bodied animals (e.g., juveniles of larger species and juveniles and adults of smaller species), while the 183-m seine tends to capture larger subadult and adult fishes. The 6.1-m otter trawl samples deeper areas not accessible to either type of seine and tends to collect epibenthic fish and macrocrustaceans. The 21.3-m seines (n=2,277) were used in shoreline habitats and were limited to waters ≤1.8 m deep. The 183-m seines (n=881) were deployed along shoreline habitats and were limited to waters ≤2.5 m deep. The 6.1-m trawls (n=2,346) were used in water from 1.8 to 7.6 m deep. In total, 5,504 samples from the LSJR were included in this analysis (Fig. 2).

At each sampling site, fish and selected macroinvertebrates were identified (usually to species) and enumerated, and a subsample (≤40 individuals per species) was measured (standard length for teleosts, disk width for rays, precaudal length for sharks, carapace width for crabs, and postorbital head length for shrimps). A suite of environmental variables was also recorded at each sample site, salinity being pertinent to this study. Salinity was recorded with a Hydrolab (model MS5) or YSI (model 600QS system) multiprobe at the water's surface and bottom and at every 1-m increment in between. When water depth was ≤0.4 m, only a surface reading was taken. For the purposes of the study, the salinity measurement used was a water-column-averaged salinity because stratification was mostly absent.

Data Analysis

Data from juveniles and adults were analyzed using similar techniques to those of both Bulger et al. (1993) and Greenwood (2007), thus facilitating the comparison of the presence or absence of distinct salinity zones in light of these different analytical approaches. Each of the 5,504 samples was assigned to one of 44 salinity increments (Fig. 2). Following Greenwood (2007), the 0–0.5 range was divided into five increments due to the potential ecological importance of this range (Anonymous 1958). Each species collected was subdivided into size classes to reflect the potential for shifts in salinity tolerance throughout ontogeny (Livingston 1988; Peebles et al. 1991; Able et al. 2001; Greenwood 2007). For this purpose, species were subdivided into 0–30, 31–50, 51–100, and >100 mm size classes (except for pink, *Farfantepenaeus duorarum*, brown, *F. aztecus*, and white, *Litopenaeus setiferus* shrimp, which were divided into 0–15 and >15 mm size classes)

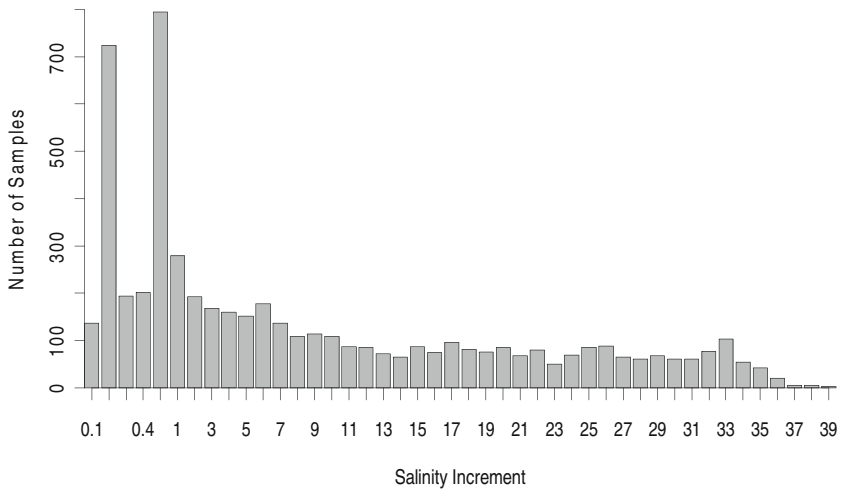

Fig. 2 Sampling effort grouped by salinity increment (0.1=0–0.1, 0.2 = >0.1–0.2,…, 39 = >39)

following Baltz and Jones (2003) and Farrell et al. (2005). This subdivision resulted in 600 species–size combinations, which will henceforth be referred to as *pseudospecies*.

For this study, two nonparametric approaches (nonmetric multidimensional scaling and principal components analysis) were taken to examine estuarine salinity zones as evidenced by the change in nekton community composition along the salinity gradient. Nonmetric MDS and similarity percentages analysis (SIMPER), as detailed by Greenwood (2007), were used in the first analytical approach to identify changes in community structure related to salinity zones. The frequency of occurrence of each pseudospecies by salinity increment was square-root-transformed to reduce the influence of common species. Matrices of pairwise Bray–Curtis similarities (Bray and Curtis 1957) were computed for all contiguous pairs of salinity increments. Nonmetric MDS (Clarke 1993; Clarke and Warwich 2001) was conducted on the Bray–Curtis similarity matrix to produce ordination plots depicting the similarities in community structure between salinity increments. The ordination plots are based on ranked similarities in community structure between salinity increments and as such are nonmetric and plotted on unitless axes. The proximity of the salinity increment labels to each other in the ordination plots is an indication of similarity in community structure over the salinity gradient; large distances between salinity increments indicate greater differences in community structure. Ordination plots were visually inspected for evidence of salinity zones, based on regions of accelerated change.

To allow comparisons with Bulger et al. (1993); Christensen et al. (1997); and Greenwood (2007), the analysis was repeated with defined salinity range data. The data were not transformed since they consisted of presence or absence by salinity increment over a defined salinity range. The salinity range was defined as the maximum and minimum salinity at which a pseudospecies occurred. The maximum, minimum, and all intermediate salinities were assigned a value of one, indicating presence (assumed or actual); otherwise, salinities were assigned a value of zero, indicating absence. In an attempt to interpret differences in observed community structure and to examine the role of species in contributing the average dissimilarity between salinity increments, similarity percentages analysis (Clarke and Warwick 2001) was conducted on both the frequency of occurrence and the salinity range data sets. All nonparametric analyses were computed using PRIMER-E (Clarke and Gorley 2006).

The second analytical approach was to apply PCA to the salinity range data set as detailed by Bulger et al. (1993). For this study, the variables for the PCA were the 44 salinity increments, for which each pseudospecies was scored. The purpose of this analysis was to use incidence data for the 600 pseudospecies to identify estuarine salinity zones (i.e., similarities among the 44 salinity increments, or *PCA variables*). PCA factor loadings (correlation coefficients between salinity increments and the principal components) were examined to determine whether any were especially closely associated with certain salinity ranges. Cases with high loading scores for a principal component are thought to have salinity ranges that overlap in the corresponding salinity zones (Bulger et al. 1993). PCA loadings were plotted against salinity increments in order to visualize correlation

Table 1 Summary of water quality parameters from river sections along the lower St. Johns River estuary

River (km)	Temp. (°C)	Salinity (psu)	Dissolved oxygen (mg/l)	pH	Temp. stratification	Salinity stratification	Dissolved oxygen stratification (mg/l)	pH stratification
0–10	22.63	26.90	7.64	7.71	0.17	0.80	0.23	0.05
11–20	23.02	19.99	8.06	7.70	0.17	0.72	0.32	0.06
21–30	22.71	12.87	8.12	7.67	0.19	0.68	0.38	0.06
31–40	22.97	7.96	7.90	7.72	0.22	0.85	0.43	0.10
41–50	22.93	4.94	8.68	7.81	0.25	0.38	0.40	0.10
51–60	23.25	2.61	9.24	8.01	0.25	0.14	0.51	0.10
61–70	22.78	2.14	8.73	7.96	0.29	0.12	0.43	0.10
71–80	23.21	1.54	9.00	7.91	0.16	0.11	0.32	0.05
81–90	23.42	1.12	9.36	8.01	0.20	0.06	0.44	0.06
91–100	23.63	0.73	9.64	8.09	0.21	0.02	0.39	0.05
101–110	23.35	0.56	9.58	8.11	0.18	0.00	0.47	0.05
111–120	23.58	0.54	9.18	8.03	0.20	0.00	0.43	0.05
121–130	23.61	0.54	8.91	8.06	0.17	0.00	0.51	0.05
131–140	23.90	0.51	8.07	8.10	0.08	0.01	0.26	0.10

Temperature stratification, salinity stratification, dissolved oxygen stratification, and pH stratification represent the difference between the surface and bottom measurements

between increments. PCA analysis was conducted using the R version 2.8.1 software package (R Development Core Team 2008)

The relatively large data set allowed each salinity increment to be treated as a separate sample and frequency of occurrence information to be used. The use of different types of gear precluded the use of relative abundance data. However, given the correlation between frequency of occurrence and relative abundance (Wright 1991), the trends would likely be similar, and the use of frequency of occurrence data is valid. The use of both MDS and PCA allows direct comparisons with the results of Bulger et al. (1993) and Greenwood (2007) and the evaluation of results in light of differing analytical techniques.

Results

Water temperature was fairly consistent throughout the study area, while salinity decreased and dissolved oxygen and pH tended to increase further upstream (Table 1). There was little evidence of temperature or salinity stratification at any point along the sampling universe. Differences in surface and bottom salinity decreased further upstream, while differences in surface and bottom temperature were greatest around 61–70 km of the river (Table 1).

The rate of change in nekton community structure was rapid at both ends of the salinity gradient (Fig. 3a and b). The rate of community change decreased fairly rapidly from 0 to 1 and decreased more slowly from 2 to 10, after which the rate of change was fairly small and consistent through 30–34. The rate of change increased rapidly again from 34 to 39. Following examination of the proximity of salinity increments for the frequency of occurrence data, it is evident that there is a rapid community change at both ends of the salinity gradient (i.e., at 0.1–2 and 32–39), but that there is little definitive evidence for regions of accelerated change at intermediate levels. Similar results are observed when examining the salinity range data set. With the exception of the interfaces of marine and freshwater, clearly defined end points are absent at all intermediate salinity increments. Both MDS ordinations have low stress values (≤0.05) indicating that the two-dimensional plots give excellent representations of the multi-dimensional data. Arch effects were present in both MDS plots, indicating considerable change in community structure along the estuarine salinity gradient (Fig. 3a and b). SIMPER results indicate that lower salinity increments were dominated by stenohaline freshwater penetrants and euryhaline estuarine species (Table 2). Conversely, upper salinity increments were dominated by stenohaline marine and euryhaline estuarine species (Table 2).

Likewise, there is little evidence from the PCA to suggest definitive biological salinity zones for the LSJR. Results

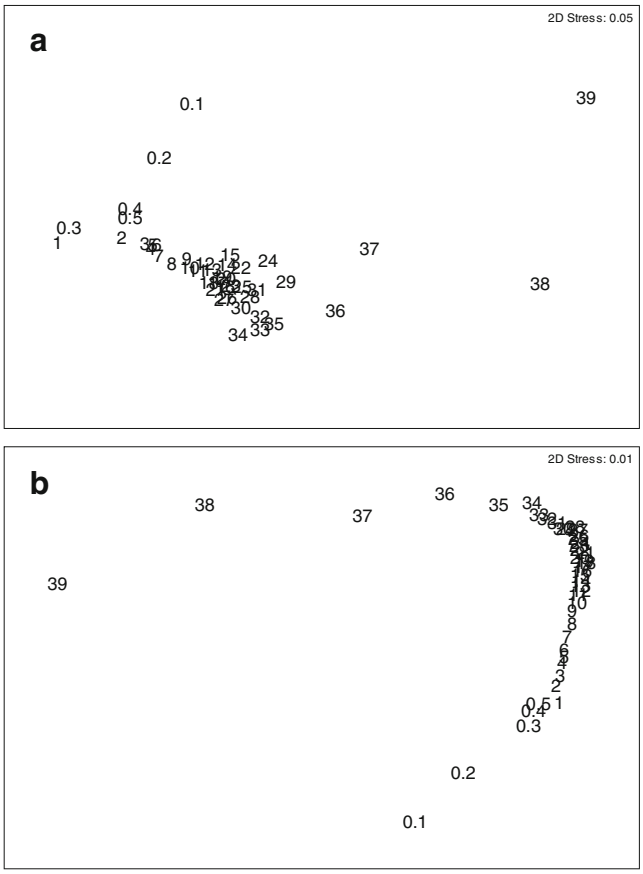

Fig. 3 Nekton community change along estuarine salinity gradient for the lower St. Johns River estuary based on a species' frequency of occurrence and **b** species' salinity ranges. Each label represents the community at that salinity increment (0.1=0–0.1, 0.2 = >0.1–0.2,…, 39 = >39), with the proximity of the labels indicating the relative similarity of the nekton community along the salinity gradient (i.e., labels closer together have communities more similar than those that have labels farther apart)

from the PCA indicate a small amount of artifact called the horseshoe effect that is seen due to presence/absence of data points that occupy only some of the apices of the multidimensional space (Kendall 1971, 1975; Bulger et al. 1993). Only the first three of the five principal components shown in Fig. 4 explain a significant (α=0.05) percentage of the total variation (58, 18, and 6 %, respectively; Table 3). Even though the first three principal components explain a significant percentage of the variation, the individual loadings failed to achieve significant correlations (Fig. 4). As a rule, a principal component with a variable loading of 0.3 or more is considered to represent a meaningful correlation (Tabachnik and Fidell 1989). Even correlations of 0.3 (only 9 % of the variation explained) are considered low by some (Comrey 1973). Therefore, any interpretations from the results of the PCA are considered questionable at best. Loadings from the PCA hint at possible differential use by species at the lowest salinity increments but not at the other end of the spectrum in full marine environments (Fig. 4).

Table 2 SIMPER results for the freshwater (0.1–0.5) and marine (33.0–39.0) salinity increments

Freshwater salinity increments							
Pseudospecies	Frequency	Pseudospecies	Frequency	Pseudospecies	Frequency	Pseudospecies	Frequency
Salinity increment 0.1		Salinity increment 0.2		Salinity increment 0.3		Salinity increment 0.4	
Trinectes maculatus 31–50 mm	0.16	*M. undulatus*≤30 mm	0.22	*M. undulatus*≤30 mm	0.60	*Menidia spp.* 31–50 mm	0.34
T. maculatus≤30 mm	0.15	*C. sapidus* 51–100 mm	0.22	*A. catus*> 100 mm	0.59	*Menidia spp.* ≤ 30 mm	0.30
Callinectes sapidus 51–100 mm	0.13	*L. macrochirus* 31–50 mm	0.21	*M. undulatus* 31–50 mm	0.58	*L. macrochirus* 51–100 mm	0.28
Menidia spp. 31–50 mm	0.13	*Menidia spp.* 31–50 mm	0.21	*Menidia spp.* 31–50 mm	0.58	*M. undulatus* 51–100 mm	0.27
Lepomis macrochirus 51–100 mm	0.13	*L. macrochirus* 51–100 mm	0.21	*A. catus* 51–100 mm	0.55	*Lucania parva*≤30 mm	0.26
L. macrochirus 31–50 mm	0.12	*T. maculatus*≤30 mm	0.21	*M. undulatus* 51–100 mm	0.55	*Microgobius gulosus*≤ 30 mm	0.26
C. sapidus≤30 mm	0.12	*T. maculatus* 31–50 mm	0.21	*C. sapidus*>100 mm	0.52	*Dasyatis sabina*>100 mm	0.25
Micropogonias undulatus≤30 mm	0.11	*C. sapidus*>100 mm	0.20	*T. maculatus* 31–50 mm	0.50	*Mugil cephalus*>100 mm	0.25
Labidesthes sicculus 51–100 mm	0.11	*L. microlophus*>100 mm	0.18	*Menidia spp.* ≤ 30 mm	0.49	*Litopenaeus setiferus*≤ 15 mm	0.25
Ameiurus catus 51–100 mm	0.11	*L. sicculus* 51–100 mm	0.18	*C. sapidus* 51–100 mm	0.49	*M. gulosus* 31–50 mm	0.25
Salinity increment 0.5		Salinity increment 1.0		Salinity increment 2.0			
C. sapidus>100 mm	0.34	*Menidia spp.* 31–50 mm	0.72	*C. sapidus*>100 mm	0.41		
M. undulatus 51–100 mm	0.34	*C. sapidus*>100 mm	0.70	*M. undulatus* 51–100 mm	0.38		
M. undulatus≤30 mm	0.31	*M. undulatus*≤30 mm	0.67	*L. setiferus*≤15 mm	0.38		
Menidia spp. 31–50 mm	0.31	*L. parva*≤30 mm	0.65	*Menidia spp.* 31–50 mm	0.37		
Anchoa mitchilli≤30 mm	0.30	*M. undulatus* 31–50 mm	0.65	*M. undulatus*≤30 mm	0.37		
M. undulatus 31–50 mm	0.30	*M. undulatus* 51–100 mm	0.62	*M. undulatus* 31–50 mm	0.36		
M. gulosus≤30 mm	0.29	*M. gulosus*≤30 mm	0.60	*A. mitchilli* 31–50 mm	0.35		
A. mitchilli 31–50 mm	0.28	*M. gulosus* 31–50 mm	0.59	*C. sapidus* 51–100 mm	0.34		
Leiostomus xanthurus 51–100 mm	0.28	*A. mitchilli*≤30 mm	0.58	*A. catus*> 100 mm	0.33		
L. setiferus≤15 mm	0.27	*A. mitchilli* 31–50 mm	0.58	*L. xanthurus* 51–100 mm	0.33		
Marine salinity increments							
Salinity increment 33.0		Salinity increment 34.0		Salinity increment 35.0		Salinity increment 36.0	
D. sabina>100 mm	0.18	*D. sabina*>100 mm	0.20	*D. sabina*>100 mm	0.16	*A. probatocephalus*> 100 mm	0.13
C. sapidus>100 mm	0.17	*A. probatocephalus*>100 mm	0.17	*Menidia spp.* ≤ 30 mm	0.13	*D. sabina*>100 mm	0.11
Archosargus probatocephalus> 100 mm	0.17	*A. mitchilli* 31–50 mm	0.17	*A. probatocephalus*>100 mm	0.13	*C. sapidus*>100 mm	0.10
L. xanthurus 51–100 mm	0.15	*C. sapidus*≤30 mm	0.15	*A. mitchilli* 31–50 mm	0.13	*L. rhomboides* 51–100 mm	0.10
Menidia spp. 31–50 mm	0.14	*Lagodon rhomboides* 51–100 mm	0.15	*Paralichthys albigutta* 51–100 mm	0.11	*A. mitchilli* 31–50 mm	0.09
A. mitchilli 31–50 mm	0.14	*L. rhomboides*>100 mm	0.15	*Farfantepenaeus* spp. ≤ 15 mm	0.11	*Farfantepenaeus* spp. ≤ 15 mm	0.09
Farfantepenaeus spp. ≤ 15 mm	0.14	*Farfantepenaeus* spp. ≤ 15 mm	0.15	*Achirus lineatus*>100 mm	0.11	*Etropus crossotus* 51–100 mm	0.09

Table 2 (continued)

Eucinostomus spp. ≤ 30 mm	0.13	*L. setiferus*≤15 mm	0.14	*Eucinostomus gula* 51–100 mm	0.11	*Eucinostomus* spp. 31–50 mm	0.09
Menidia spp. 51–100 mm	0.13	*Elops saurus*>100 mm	0.14	*P. albigutta*>100 mm	0.11	*A. mitchilli*≤30 mm	0.08
L. xanthurus 31–50 mm	0.13	*L. xanthurus*>100 mm	0.14	*C. sapidus*≤30 mm	0.10	*P. dentatus*>100 mm	0.08
Salinity increment 37.0		Salinity increment 38.0		Salinity increment 39.0			
L. setiferus≤15 mm	0.12	*Eucinostomus* spp. 31–50 mm	0.04	*L. xanthurus* 51–100 mm	0.04		
Eucinostomus spp. 31–50 mm	0.10	*A. probatocephalus*>100 mm	0.04	*L. rhomboides* 51–100 mm	0.04		
A. probatocephalus>100 mm	0.09	*D. sabina*>100 mm	0.04	*Farfantepenaeus* spp. ≤ 15 mm	0.04		
D. sabina>100 mm	0.09	*E. harengulus* 31–50 mm	0.04	*C. sapidus* 51–100 mm	0.04		
E. harengulus 31–50 mm	0.09	*Menidia spp.* 31–50 mm	0.04	*L. xanthurus* 31–50 mm	0.04		
Menidia spp. 31–50 mm	0.09	*M. cephalus*>100 mm	0.04	*M. cephalus*>100 mm	0.04		
M. cephalus>100 mm	0.09	*Aris felis*>100 mm	0.04	*M. curema*>100 mm	0.04		
C. similis≤30 mm	0.08	*Fundulus majalis*≤30 mm	0.04	*E. gula* 51–100 mm	0.04		
Menidia spp. 51–100 mm	0.08	*Membras martinica* 31–50 mm	0.04	*M. curema* 51–100 mm	0.04		
Selene vomer>100 mm	0.08	*M. martinica* 51–100 mm	0.04	*A. hepsetus*≤30 mm	0.04		

For each salinity increment, frequency of occurrence for the ten pseudospecies contributing the most to differences in community structure is listed

Further examination of the loadings indicates relatively gradual changes in loading values, which differs from the abrupt changes seen in Bulger et al. (1993).

Discussion

The analytical methods used for this study allow direct comparisons with previous studies regarding biological salinity zones. Boesch (1977) found evidence for distinct biological salinity zones at salinities of 5–8 and 18–21 along the York River–Chesapeake Bay estuary (Virginia), while Bulger et al. (1993) found distinct salinity zones at 2–4, 11–14, 16–18, and 24–27 in the Chesapeake Bay and Delaware Bay. Greenwood (2007) found little evidence for distinct biological salinity zones at all but the extreme end points of the salinity gradients in Tampa Bay and Charlotte Harbor (Florida). Our study confirms the Greenwood (2007) hypothesis that rapid change in community composition would most likely occur at the extreme end points of the salinity range and that subdividing the lowest salinity ranges into 0.1 categories was warranted. In the present study, there were relatively rapid or abrupt changes in nekton community structure at the lowest (0.1–2) and highest (32–39) salinity increments, with slow but steady changes at all intermediate levels. These results are similar to those of Greenwood (2007), although in the present study, abrupt changes were more evident at higher salinity increments. The inclusion of a wide range of nekton size classes did not appear to affect the results of the analysis. Greenwood (2007) used data on only small-bodied nekton, whereas Bulger et al. (1993) used data on nekton ranging from eggs to large-bodied adults. In this study of the LSJR, a fairly comprehensive-size spectrum of nekton (from juveniles to large-bodied adults) was used, and there still was no evidence for multiple biological salinity zones. In addition, the PCA analyses, when compared with those of Bulger et al. (1993), further support that there are no distinct biological salinity zones (with the possible exception of the low-salinity increments) present in the LSJR (Fig. 4).

The abrupt changes in community structure at both ends of the salinity gradient are likely attributable to the presence of stenohaline freshwater species upstream and marine species downstream (Bulger et al. 1993) but may also be influenced by river geomorphology and the use of presence/absence, rather than abundance data. Stenohaline freshwater species have limited capabilities of penetrating areas of higher salinities, and stenohaline marine species have limited capabilities of penetrating areas of lower salinity (Bulger et al. 1993). Therefore, rapid change in community structure would be expected at these extremes, as was observed in the present study (Fig. 3). The lack of any intermediate biological salinity zones may be related to the

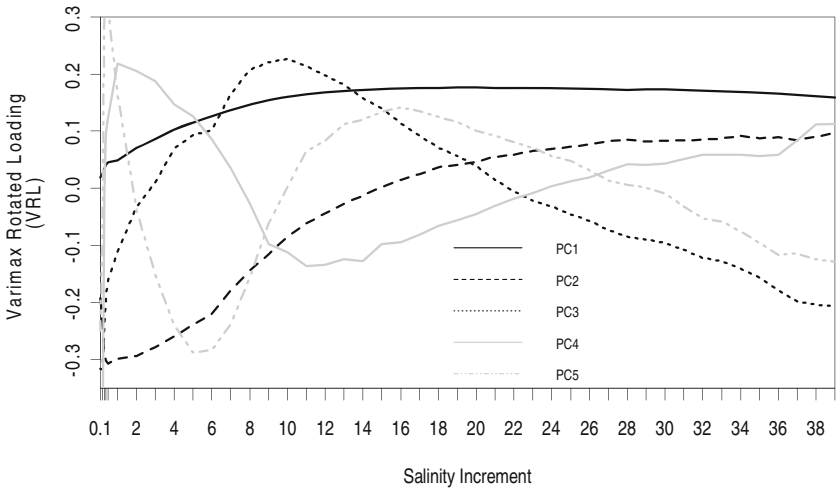

Fig. 4 Varimax-rotated loadings (correlation coefficients) of the 44 salinity increments on the five principal components. *Black lines* indicate the principal components (PC1, PC2, and PC3) that explain a significant (α=0.05) percentage of the variation; *gray lines* (PC4 and PC5) represent principal components that did not explain a significant percentage of the variation

unique characteristics of the LSJR. First, due to tidal ranges and the flow regime of the LSJR (regular and frequent reverse flows; Morris 1995), salinity is rarely static and can vary greatly over large distances. This could lead to temporary residence of nekton in suboptimal salinity environments that they may not normally inhabit. In effect, animals could become "stranded" during periods of reverse flow until the flow regime changes, or they emigrate to areas with a more favorable salinity. Second, several springs within the upper reaches of the LSJR discharge sodium, calcium, and chloride ions (Brody 1994), increasing salinity. The presence of these springs could create refugia for species requiring higher salinities. These unique features of the LSJR could contribute to a complex salinity environment, shifting spatially and temporally, that could mask any distinct biological salinity zones in the intermediate salinity ranges (Fig. 3). The absence of obvious biological salinity zones except at the extreme ranges of salinity may also be inherent in the analyzed metric (presence/absence); it is likely that abundance data would be more sensitive to salinity changes than presence/absence data.

Inherent differences in estuaries in peninsular Florida are likely responsible for reported discrepancies in biological salinity zonation. It is unlikely that differences between peninsular Florida and the other regions can be attributed to size classes of nekton used or analytical techniques since this study used the full-size spectrum of nekton encountered and explored both analytical techniques used previously. Flow regimes in rivers of peninsular Florida are unique. Rivers in the southeastern USA typically follow a flow pattern driven by spring rains with the greatest flows occurring from March through April (Kelly 2004; Kelly and Gore 2008). Rivers of Peninsular Florida typically behave differently, driven by summer rains; the greatest flows typically occur from July through October (Kelly 2004; Kelly and Gore 2008). River slope may also be an important factor in creating distinct biological salinity zones. Rivers of peninsular Florida have a minimal slope compared with more northern rivers, where this slope could create a well-defined region in which rapidly descending freshwater mixes with marine waters. Distinct salinity zones created by abrupt changes from marine to freshwater may be partially responsible for the differences seen in biological salinity zonations between rivers of peninsular Florida and those studied farther north. The discrepancy in flow patterns and river slope may influence the presence/absence and habitat use of nekton utilizing riverine environments, especially estuarine-dependent species, in peninsular Florida and result in the distinct lack of biological salinity zones.

Bulger et al. (1993) and Greenwood (2007) noted that salinity-related habitat changes could influence development of biological salinity zones. Typically, as salinity decreases, dominant shoreline vegetation changes from salt marsh to freshwater marsh to forested wetlands (Estevez et al. 1991). The relative contribution of static (vegetation or structure) and dynamic (salinity) habitats in determining nekton community structure is difficult to determine, but it is likely that both play a critical role and may be influenced by factors such as river slope and hydrology. A slow, continuous change in salinity zonation created by hydrology and a minimal slope would likely

Table 3 Eigenvalues, percent variation, and cumulative percent variation of the five principal components explaining differences in community structure among salinity increments

Principal component	Eigenvalue	Percent variation	Cum. percent variation
1	5.950	58.1	58.1
2	1.880	18.3	76.4
3	0.620	6.1	82.5
4	0.312	3.0	85.5
5	0.242	2.4	87.9

lead to slow, continuous change in static habitats along the longitudinal axis of the estuary. This would likely provide nekton flexibility in static habitat across miles of estuary without abrupt salinity changes, resulting in gradual nekton community change throughout the majority of the estuarine habitat. The estuarine habitat in the system studied here reflects this gradual change in static habitat with shallow salt marsh transitioning to cypress wetland habitats far upstream. Similarly, the Tampa Bay and Charlotte Harbor studies (Greenwood 2007) reflect gradual static habitat change with shallow seagrass and mangrove habitats extending the length of the estuary. Northern river systems tend to exhibit more abrupt changes with hardwood forests extending to the river mouth before transitioning to shallow wetland habitat. When these preferred static and dynamic habitats overlap, estuarine productivity and diversity are maximized (Browder and Moore 1981; Sklar and Browder 1998).

Given the disparity in the studies examining biological salinity zones in estuaries, it would be wise to have, at minimum, a regional understanding of how communities are structured along the freshwater-to-marine gradient. The results of this study are relevant to the management of estuaries, especially where the management of freshwater (withdrawals, impoundments, effluent discharges, etc.) or river morphology alterations (dredging, impoundments, shoreline alteration, etc.) can impact salinity regimes and organism distribution and abundance. Careful consideration is required to avoid situations in which the rate of community change, as a result of shifting salinity regimes, becomes unacceptably rapid. Shifting salinity regimes can have serious and deleterious impacts on estuarine fauna including reduction in oyster populations (Turner 2006), seed clam mortality (Baker et al. 2005), alterations in seagrass distribution and density (Iverson and Bittaker 1986; Quammen and Onuf 1993; McIvor et al. 1997), and reduced biotic diversity (Sklar and Browder 1998). The presence of many estuarine-dependent species utilizing a large portion of the LSJR as nursery and foraging habitat indicates the importance of the LSJR to fisheries production. Given this information, it would be possible to design management practices that maintain isohalines at relevant positions within the estuary to ensure that adequate amounts of habitat are retained.

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