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Fish and Decapod Crustacean Assemblages from the Ashepoo-Combahee-Edisto Basin, South Carolina (1993–1999)

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ABSTRACT

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The spatial and temporal distributions of decapod crustacean and juvenile fish species in the Ashepoo, Combahee, and South Edisto (ACE) rivers in the ACE Basin National Estuarine Research Reserve were examined from 1993 to 1999. Nekton samples were collected monthly during slack low to early flood tide by bottom trawl from 12 fixed stations (four stations/river) along the salinity gradient in the reserve. During the 6-year survey, 79 species of fish and 26 decapod crustacean species were caught. Coastal marine species represented more than 80% of the species collected during the survey; the remaining finfish were permanent residents, freshwater, and diadromous species. Star drum (*Stellifer lanceolatus*), Atlantic croaker (*Micropogonias undulatus*), bay anchovy (*Anchoa mitchilli*), and spot (*Leiostomus xanthurus*) constituted >68% of the total number of individual fishes collected. White shrimp (*Litopenaeus setiferus*) and brown shrimp (*Farfantepenaeus aztecus*) constituted ~87% of the total number of individual decapods collected. Fish and decapod crustacean assemblage structure in the three rivers were analyzed for spatial and seasonal patterns. Spatial distribution of the species assemblages in the estuarine systems appeared to be strongly influenced by the physiological tolerances of the individuals to salinity gradients in the study area. Seasonal variations in species diversity and abundance appeared to be related to migration and recruitment of species to the estuarine system, and there were two annual recruitment cycles: winter–spring (October to March) and summer–fall (April to September). The variations in species diversity among the stations in the mesohaline zone were driven by the abundance of the dominant species.

ADDITIONAL INDEX WORDS: *Decapod crustaceans, fish, distributions, ACE Basin.*

INTRODUCTION

Two of the most important taxonomic groups to the ecology and commercial viability of coastal South Carolina are fishes and decapod crustaceans. These taxa have been investigated more intensively than other taxa within the subtidal estuarine habitats of the Ashepoo-Combahee-Edisto River (ACE) Basin in South Carolina. Monthly trawl sampling was first conducted in the ACE Basin from 1953–64 (Lunz, 1970), and another bottom trawl survey was done in the North and South Edisto Rivers from 1974–75 (Shealy, 1974; Shealy, Miglarese, and Joseph, 1975; Wenner *et al.,* 1991).

Information on community assemblages of fishes and decapod crustaceans has not been previously available for the three major rivers of the ACE Basin. This study was conducted to examine the species assemblages, abundance, and selected life-history aspects fish and decapod crustaceans along a salinity gradient in the ACE Basin National Estuarine Research Reserve (NERR). Species richness and species composition are examined with regard to salinity regime and seasonality.

STUDY AREA

The study was conducted in the ACE Basin NERR from 1993–99 (Figure 1). Located approximately 96 km southeast of Charleston, South Carolina, the reserve encompasses more than 56,657 ha, of which ~24,282 ha constitute open water, and 28,329 ha are covered by salt marsh communities. Freshwater wetlands and upland communities, such as pine forests and maritime forests, cover the remaining acreage. The core area comprises nine marsh and barrier islands, encompassing more than 6880 ha of wetlands and uplands. The buffer zone is ~51,801 ha and is characterized by a diverse array of natural and managed communities.

The Ashepoo, Combahee, and South Edisto rivers are the major drainage systems of the ACE Basin NERR. From northeast to southwest, the area is divided by the South Edisto, Ashepoo, and Combahee rivers and associated tributaries flowing through extensive wetland acreage into St. Helena Sound.

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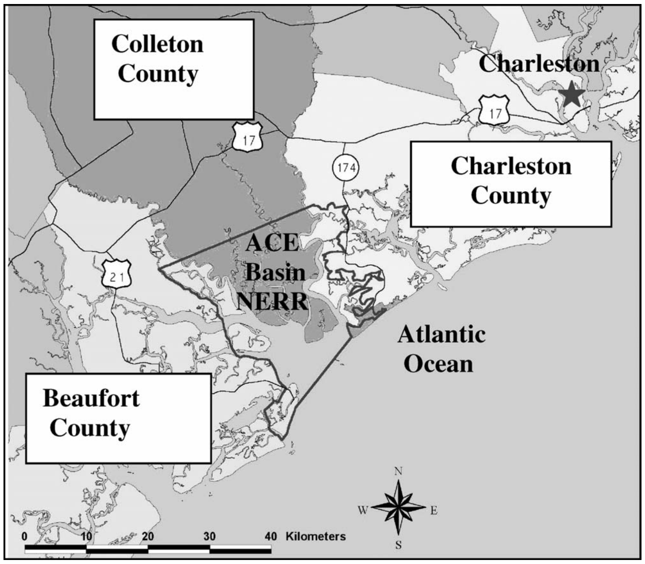

Figure 1. Location of ACE Basin (NERR) in South Carolina.

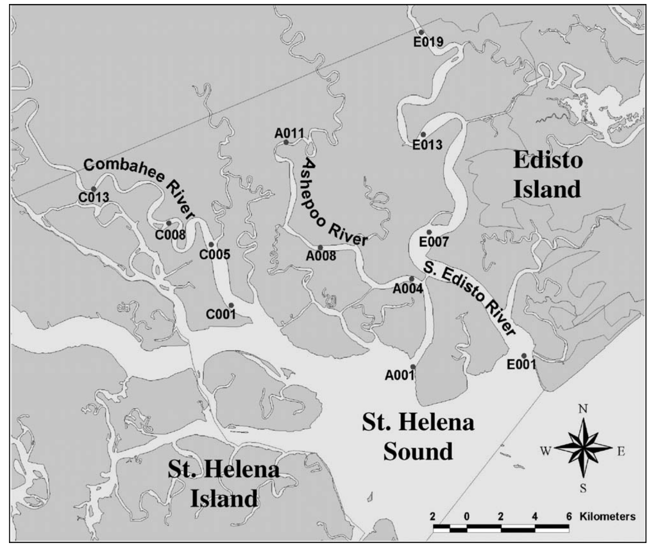

Figure 2. Locations of sampling sites in the Ashepoo, Combahee, and South Edisto rivers.

The Ashepoo River, created by the confluence of Great Swamp and Bluehouse Swamp in Colleton County, drains an area of ~204,267 ha (SCDHEC, 2003). The river originates in the Great Swamp system that lies west of Walterboro, South Carolina. The estuarine portion of the river extends from the mouth upstream ~58 km, which is approximately 26 km upriver from the inland boundary of the reserve. No stream-flow records exist for this river. Salt marshes of smooth cordgrass (*Spartina alterniflora*) dominate the wetlands in the polyhaline and mesohaline, and waterfowl impoundments are the dominant land cover in the oligohaline limnetic waters.

The Combahee River originates at the confluence of the Big and Little Salkehatchie rivers and flows southeastwardly to St. Helena Sound, and the river has a drainage area of ~414,203 ha (SCDHEC, 2003). Average annual streamflow on the river is 9.8 m^3/s (recorded at the Miley, South Carolina, gaging station on the Salkehatchie River) (Cooney *et al.,* 1998). The estuarine system extends from the mouth upstream ~61 km, which is ~38 km upriver from the inland boundary of the reserve. The presence of abandoned rice fields within the estuarine system (24–53 km upriver) suggests that the freshwater discharge to the river changed during the last century. Salt marshes of smooth cordgrass (*Spartina alterniflora*) dominate the wetlands in polyhaline and mesohaline waters, and waterfowl impoundments are the dominant land cover in oligohaline limnetic waters.

The South Edisto River has a drainage area of ~394,176 ha, encompassing the area between Four Holes Swamp and St. Helena Sound (SCDHEC, 2004). The river receives considerable input of freshwater (average annual streamflow is 74 m^3/s (Cooney *et al.,* 2005). The official saltwater-freshwater boundary line on the river lies at ~32 km upriver; however, during periods of very low flow, the saltwater interface can intrude ~51 km upriver, which is ~19 km upriver from the inland boundary of the reserve (Johnson, 1977). Salt marshes of smooth cordgrass (*Spartina alterniflora*) dominate the wetlands in polyhaline and mesohaline waters, and waterfowl impoundments are the dominant land cover in oligohaline limnetic waters.

METHODS AND MATERIALS

Study Design

Samples were collected from 12 fixed stations located in the Ashepoo, Combahee, and South Edisto rivers (Figure 2). These stations represent a gradient in salinity from polyhaline conditions near the mouth to oligohaline/limnetic conditions farthest upriver. The South Edisto River stations are also in proximity to those sampled during the 1973–75 survey (Wenner *et al.,* 1991).

Stations were sampled monthly during a 6-year period (August 1993 to July 1999). Collections were made with a 7.62-m semiballoon otter trawl composed of 0.64-cm stretch mesh. Wenner, Shealy, and Sandifer (1982) discussed the bias of this net toward selective capture of juvenile fishes. Ten-minute tows were made against a flood tide during daylight hours at a speed of approximately 0.183 m/s (0.356 knots), which resulted in coverage of 0.11 ± 0.006 km during a tow.

Basic surface-water parameters were measured before trawling. Water temperature was measured with a stem thermometer and salinity with a refractometer. Water depth was recorded with the onboard depth finder. Meteorological conditions (*i.e.,* precipitation and wind speed and direction) during the tow were noted. Monthly river discharge and gage height for the Combahee and South Edisto rivers were obtained from the U.S. Geological Survey for the period of 1993–99. Parametric procedures were used when appropriate. For consistency with previous studies in the ACE Basin (Wenner, Shealy, and Sandifer, 1982; Wenner *et al.,* 1991), seasons are defined as follows: winter is January, February, and March; spring is April, May, and June; summer is July, August, and September; and fall is October, November, and December.

All samples were processed within 24 hours of collection. Specimens were identified, counted, measured (total or fork length for fish, carapace width [distance between tips of final anterolateral spines] of crabs, and total length [tip of rostrum to tip of telson] of shrimp) and weighed to the nearest 1 g. A maximum of 30 individuals of each species was measured.

The species were placed in categories based on known information about their life history (NORDLIE, 2003). Species that spawn outside the estuary and whose young are not dependent on the estuarine habitat for successful development are classified as *Marine Transients.* Species that spawn outside the estuary but whose young must reside in the estuary for a period of time for successful development are considered *Marine Nursery* species. Species that spend most of their time in the estuary are placed in the *Permanent Resident* category, but some are known to migrate elsewhere for a portion of the life cycle, including spawning. The *Freshwater Transient* category contains species that are rarely known to enter waters as concentrated as those of saltwater, and the *Diadromous Species* category contains those forms that migrate to saltwater (anadromous) or freshwater (catadromous) to spawn.

Data Analysis

Cluster analysis was used to examine the relationship among stations along the salinity gradients in the three rivers. Before calculations of similarity matrices, species that only occurred in one or two collections taken during a sampling period, and collections that only contained one species, were eliminated (CHAO, 1987). The data were logarithmically transformed by $\log_{10}(x + 1)$, where x is the number of individuals for a given species, to emphasize less-common species and decrease dominance of extremely abundant species in the data matrix (CLIFFORD and STEPHENSON, 1975). Matrices were constructed for each river on combined, transformed data from the 6-year sampling period, with site (collection) as individuals and species as attributes (normal analysis). The sites were classified into groups by means of an agglomerative, hierarchical, "intense" clustering strategy (STEPHENSON, WILLIAMS, and COOKE, 1972; WILLIAMS, 1971), using flexible sorting (LANCE and WILLIAMS, 1967) with $\beta = -0.25$. The degrees of similarity among collections were determined using the Bray-Curtis similarity coefficient (CLIFFORD and STEPHENSON, 1975). The cluster calculations were performed using the Community Analysis Package 3.1 software program (PISCES CONSERVATION LTD., 2004).

Detrended Correspondence Analysis (DCA) was used to examine the grouping of species along the spatial gradient in the three rivers. This indirect ordination method uses a weighted average algorithm to ordinate sampling stations based on the occurrence and abundance of species (HILL and GAUGH, 1980). The ordination calculations were performed using the Community Analysis Package 3.1 software program (PISCES CONSERVATION LTD., 2004).

Four diversity indices were selected to assess the differences in community composition among the stations and rivers: Shannon-Wiener, species richness, evenness, and species dominance. The Shannon-Wiener function increases as both the number of species and the equitability of species abundance increase. The Shannon-Wiener function is defined as $H = \Sigma\, p_i \log_e p_i$ (where p_i = the proportion of individuals in the ith species). The evenness, or equitability, index represents the ratio of species numbers to number of individuals/species, and it compares the observed Shannon-Wiener index against the distribution between the observed species. The Equitability J index (PIELOU, 1969), $J = H'/H_{max} = H'/\log S$ (where $\log S$ is the maximum possible value of H'; $H' = H_{max}$ when all species are equally abundant) was selected to calculate the evenness index. The dominance measure, Berger-Parker Dominance, was used because it expresses the proportional importance of the most abundant species, and it is expressed as $d = N_{max}/N$, where N_{max} is the number of individuals in the most abundant species (BERGER and PARKER, 1970). A randomization test, as described by SOLOW (1993), was run to compare differences in the Shannon index between two stations. The diversity calculations were performed using the Species Diversity and Richness III software program (PISCES CONSERVATION LTD., 2002).

RESULTS

Hydrographic Variables

Surface-water temperatures did not differ significantly ($p \leq 0.001$) among the stations in the study area (Figure 3a). Seasonal variations in temperatures were detected in the study area ($p \leq 0.001$), and the lowest water temperatures occurred during the winter ($\beta = 13.5$°C) with highs during summer ($\bar{x} = 28.3$°C) (Table 1).

Marked differences between salinities at the most downstream and upstream stations occurred in the three rivers ($p < 0.001$) (Figure 3b). On the Ashepoo and S. Edisto Rivers, mean salinities were highest at the most downriver stations, A001 ($\bar{x} = 21.3$‰) and E001 ($\bar{x} = 24.1$‰), and lowest at the most upstream stations A011 ($\bar{x} = 6.2$‰) and E019 ($\bar{x} = 1.4$‰). On the Combahee River, the mean salinity at the most upriver station, C013, was significantly lower than the salinities at the other stations, but there was considerable overlap in mean salinities at the downstream stations.

Salinities at the stations varied among seasons (Table 1). The highest mean salinities were observed during the summer, and the lowest mean salinities were observed during the winter ($p \leq 0.001$). Annual differences in seasonal salinities also were encountered in all three rivers, and it appeared to correlate to river flow. Significantly lower salinities were encountered at all stations during periods of high river discharge on the South Edisto and Combahee rivers during the summer of 1995 and the winter of 1998 ($p \leq 0.001$).

Salinity conditions at the stations were based on seasonal extremes in salinities (seasonal mean salinities), and characterization of the salinity at each station by the Venice System (ANONYMOUS, 1958) yielded the following designations: A001 (17.3–23.5‰) and E001 (19.7–28.3‰) as polyhaline; C001 (12.8–20.7‰), A004 (11.4–19.0‰), and C005 (8.9–18.7‰) as poly-mesohaline; A008 (8.3–15.1‰), C008 (7.9–

Table 1. *Seasonal mean temperature (SE) and salinity (SE) at the 12 fixed sampling stations on the ACE rivers, 1993–99.*

Sampling Stations	Winter	Spring	Summer	Fall
Mean temperatures (SE)				
A001	13.38 (0.72)	24.21 (0.84)	27.71 (0.53)	17.12 (0.81)
A004	14.25 (1.02)	23.17 (1.14)	27.43 (0.84)	16.35 (1.06)
A008	14.4 (0.98)	23.39 (0.93)	27.23 (1.16)	15.94 (1.15)
A011	14.19 (1.01)	21.41 (1.8)	26.62 (1.42)	14.7 (1.52)
C001	13.26 (0.64)	24.32 (0.91)	27.43 (0.78)	17.13 (0.94)
C005	13.46 (0.64)	24.47 (0.91)	27.34 (0.83)	16.83 (0.99)
C008	13.76 (0.78)	24.41 (0.92)	27.63 (0.84)	16.46 (1.18)
C013	14.2 (0.96)	24.42 (0.91)	27.19 (1.39)	15.56 (1.56)
E001	12.26 (0.76)	24.09 (0.95)	27.82 (0.28)	16.98 (1.03)
E007	12.52 (0.52)	22.93 (1.07)	26.94 (1.03)	15.6 (1.23)
E013	13.0 (0.64)	21.98 (1.49)	26.41 (1.59)	14.59 (1.5)
E019	12.44 (0.98)	19.87 (2.24)	26.28 (1.6)	13.84 (1.54)
Mean salinities (SE)				
A001	17.25 (1.53)	21.18 (1.94)	23.74 (1.17)	23.71 (1.77)
A004	11.36 (1.59)	15.66 (2.11)	19.3 (1.44)	18.48 (1.83)
A008	8.29 (1.57)	12.09 (1.87)	15.61 (1.42)	14.65 (2.42)
A011	3.85 (1.37)	5.61 (1.13)	9.08 (1.39)	10.1 (2.58)
C001	12.84 (1.76)	19.15 (1.6)	21.06 (1.15)	19.61 (1.9)
C005	8.87 (1.61)	16.6 (1.54)	18.84 (1.11)	16.88 (1.94)
C008	7.9 (1.45)	13.75 (1.44)	17.15 (1.22)	14.56 (1.96)
C013	4.32 (1.26)	8.71 (1.74)	13.72 (1.41)	10.26 (1.9)
E001	19.67 (2.28)	24.4 (1.95)	28.35 (1.33)	23.81 (1.71)
E007	8.02 (2.1)	13.59 (2.11)	16.98 (1.81)	13.03 (2.21)
E013	3.17 (1.52)	4.89 (1.54)	6.83 (1.8)	5.04 (1.47)
E019	0.76 (0.65)	1.02 (0.81)	2.89 (1.37)	1.19 (0.48)

16.9‰), and E007 (8.0–16.6‰) as mesohaline; A011 (3.9–8.9‰), C013 (4.3–13.2‰), and E013 (3.2–6.5‰) as oligomesohaline; and E019 (0.7–2.7‰) as oligohaline.

Species Composition

During the study period, 79 species of fish, totaling 76,937 individuals, and a total of 26 decapod crustacean species, totaling 51,724 individuals, were collected (Table 2). Approximately 60% of the finfish species and 38% of the decapod crustaceans were marine transient species. These species represented <10% of the total catch, and they generally were seasonal visitors in the study area, migrating to the estuary during the warmer months and moving offshore during the winter months. Their absence from the estuaries during the winter is attributed to offshore migration to warmer deeper waters (Hildebrand and Cable, 1938).

Marine nursery finfish represented 23% of fish species collected during the study, and 36% of the decapod crustaceans were marine nursery species. Marine nursery finfish accounted for over 70% of the individuals caught throughout the year. Four of the marine nursery finfish species (star drum [*Stellifer lanceolatus*], Atlantic croaker [*Micropogonias undulatus*], bay anchovy [*Anchoa mitchilli*], and spot [*Leiostomus xanthurus*]) constituted >68% of the total number of individual fishes collected. Two of the marine nursery decapod crustaceans species, white shrimp (*Litopenaeus setiferus*) and brown shrimp (*Farfantepenaeus aztecus*), constituted ~87% of the total number of individual decapods collected.

Eight percent of the finfish species were permanent residents, whereas ~26% of the decapod crustaceans were permanent residents. One permanent resident species, blue crab (*Callinectes sapidus*), constituted 4% of the total number of individual decapods collected. In South Carolina, mummichog (*Fundulus heteroclitus*), skilletfish (*Gobiesox strumosus*), highfin goby (*Gobionellus oceanicus*), naked goby (*Gobiosoma bosci*), feather blenny (*Hypsoblennius hentzi*), and oyster toadfish (*Opsanus tau*) are considered permanent residents of the estuary (Cain and Dean, 1976; Crabtree and Middaugh, 1982; Lehnert and Allen, 2002).

The remaining 9% of the finfish were freshwater transients. Diadromous species in the study area were finfish. The highest numbers of freshwater species (*Ameiurus catus, Dorosoma petenense, Esox americanus, Ictalurus furcatus, Ictalurus punctatus,* and *Lepisosteus osseus*) generally occurred at the oligomesohaline stations (A011, C013 and E013) and the oligohaline station E019.

Species Distribution

Site groups were related to location along the salinity gradient in the three rivers, as identified by the cluster dendrogram (Figure 4). At an arbitrarily chosen similarity level of 75%, four distinct groupings were clearly evident. The polyhaline and poly-mesohaline stations (A001, A004, C001 and E001) were grouped together. The mesohaline stations (A008, C005, C008, and E007) formed a second group, and the oligomesohaline stations, A011, C013, and E013, formed a third group. The lone oligohaline station, E019, was placed in a separate group.

Species scores relative to axis 1 of the DCA ordination plot generally reflected the tolerance of the species along the salinity gradient that was identified by the cluster dendrogram (Figure 4). For example, marine and freshwater finfish and

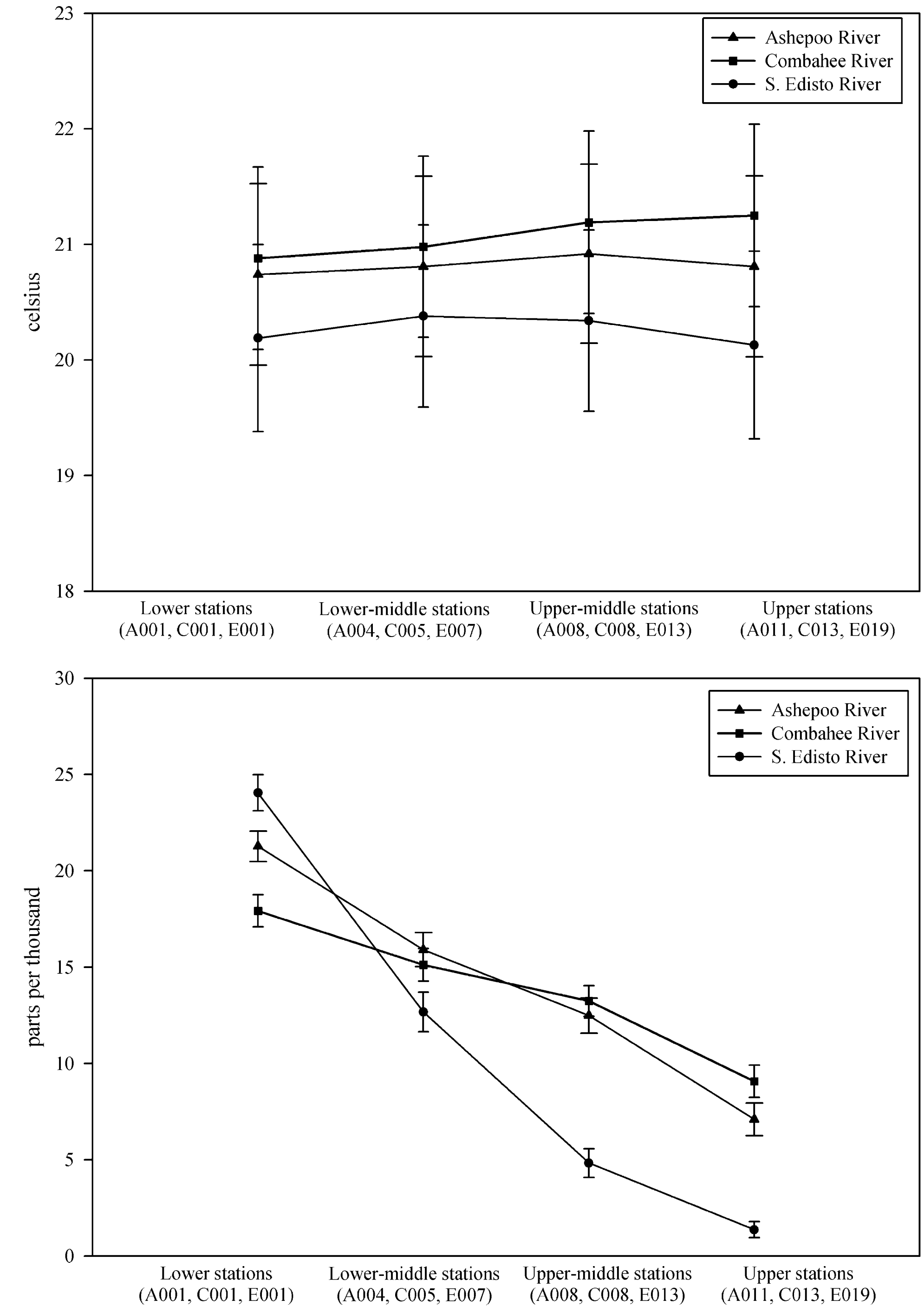

Figure 3. Mean salinities (SE) at stations in the three rivers during the study, 1993–99.

decapod crustacean species (*e.g., Rhizoprionodon terraenovae* and *Libinia dubia,* respectively) with narrow salinity tolerance were found at opposites ends of axis 1, whereas species with broader salinity tolerance, such as *Micropogonias undulatus* and *Callinectes sapidus,* fell at intermediate positions on axis 1.

Four discrete assemblages for finfish species could be identified in the DCA ordination plot (Figure 5a). The stenohaline coastal marine finfish, such as *Anchoa hepsetus, Centropristis striata, Gobiesox strumosus, Rhizoprionodon terraenovae,* and *Urophycis floridana,* were more abundant at the polyhaline stations (A001 and E001) where salinities rarely fell below

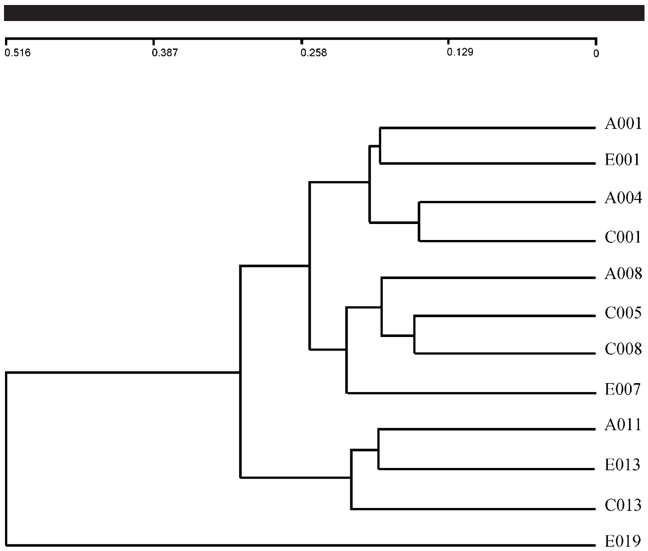

Figure 4. Normal cluster dendrogram showing relationship of sampling stations according to species collected during the study.

18‰. Finfish species such as *Chaetodipterus faber, Chloroscombrus chrysurus, Hypsoblennius hentzi,* and *Prionotus tribulus* were more abundant at poly-mesohaline stations (A004, C005, and E007), whereas *Arius felis, Citharichthys spilopterus, Menticirrhus americanus, Opsanus tau, Urophycis regia, Gobiosoma bosci,* and *Bagre marinus* exhibited similar association with the mesohaline stations (A008, C008, and E007). Freshwater species (*e.g., Ameiurus catus, Ictalurus furcatus,* and *Lepisosteus osseus*) were found in higher numbers at the stations with salinities below 10‰ (A011, C013, E013, and E019).

Only three discrete assemblages for decapod crustaceans could be identified in the DCA ordination plot (Figure 5b). The stenohaline coastal marine decapods (*Clibanarius vittatus, Cancer irroratus, Libinia dubia, Ovalipes ocellatus, Pagurus longicarpus* and *Portunus spinimanus*) were more abundant at the stations with salinities above 15‰ (A001, A004, C001, C005, and E001). The majority of the decapods collected during the study (*Alpheus heterochaelis, Callinectes sapidus, Callinectes similis, Farfantepenaeus aztecus, Farfantepenaeus duorarum, Litopenaeus setiferus, Menippe mercenaria, Trachypenaeus constrictus,* and *Xiphopenaeus kroyeri*) were more abundant at the mesohaline stations (A008, C005, and E007). Permanent residents (*Dyspanopeus sayi, Palaemonetes pugio, Palaemonetes vulgaris, Panopeus herbstii,* and *Rhithropanopeus harrisii*) were found in higher numbers at the oligomesohaline stations (A011, C013, and E013).

Species Diversity

Spatial patterns in species diversity were noted along the salinity gradients within the three rivers (Table 3). Species richness (number of species) for finfish and decapod crustaceans assemblages on all three rivers was observed at the stations with the highest salinities of the four stations (A001, C001, and E001) on each river, and the lowest numbers of species were collected at the most upriver stations (A001, C013, and E019).

Shannon-Wiener index for finfish and decapod crustacean assemblages in the Ashepoo and South Edisto rivers showed that the stations with the highest salinities, A001 and E001, had the highest diversity of the four stations on the respective rivers; stations A008 and E013 were second, A004 and E007 third, and finally, A011 and E019 ($p \leq 0.05$). On the Combahee River, the Shannon index for finfish showed that the station with the lowest salinity, C013, had the highest diversity of the four stations; station C008 was second, station C005 third, and finally, station C001; for the decapod crustaceans, diversity was highest at station C001 and lowest at station C013 ($p \leq 0.05$).

There appeared to be a positive relationship between the Shannon-Wiener and evenness values, which reflects the distribution of individuals among the species in the assemblages. In the Ashepoo and South Edisto rivers, evenness for finfish and decapod crustacean species was lower at the mesohaline stations (A004, A008, E007, and E013) compared with the polyhaline stations (A001 and E001). In the Combahee River, evenness for fish species was lower at the mesohaline stations (C001, C005, and C008) compared with the oligohaline station C013; for decapod crustaceans, evenness was higher at the mesohaline stations compared with the oligohaline station. The influx and exodus of juvenile marine species to the mesohaline stations resulted in the depression of evenness in assemblages with the dominant species (represented by many individuals). In the three rivers, star drum (*Stellifer lanceolatus*), Atlantic croaker (*Micropogonias undulatus*), and white shrimp (*Litopenaeus setiferus*) reached peak numbers in the assemblages at the mesohaline stations.

Berger-Parker's index of dominance, which represents the proportion of the most common species in the assemblage, was higher at the mesohaline stations. The fauna was not normally diverse, and collections were consistently dominated by the three species. The more "even" distribution of individuals among the species at C001 accounted for the low dominance for finfish and decapod crustaceans compared with the downstream stations. At A001 and E001, prevalence of rare marine transient species in the assemblages resulted in the low dominance for finfish, whereas the low numbers of the white shrimp resulted in the depressed dominance for decapod crustacean assemblages at the two sites.

Seasonal pulses in Shannon-Wiener were exhibited for fish and decapod crustacean species (Table 4). Fish assemblages on the Ashepoo River were more diverse during the summer at the A001 and A008 stations and during the fall at the A004 and A011 stations ($p \leq 0.05$). Lows in diversity occurred during the spring at three stations (A004, A008, and A011) and during the winter at station A001 ($p \leq 0.05$). In the Combahee River, diversity at three stations (C001, C005, and C008) generally was highest during the winter and lowest during the fall, whereas the assemblage at station C013 was more diverse during the fall with lows occurring in winter ($p \leq 0.05$). Diversity at station E001 was highest during the fall and lowest during the summer, whereas station E007 was more diverse during the summer and less diverse during the fall ($p \leq 0.05$). Highest diversity at station E013 occurred

Table 2A. *Fish species and total individuals collected in the study area and the occurrence of the species in the three rivers 1993–99. MT = marine transient, MN = marine nursery, PR = permanent resident, FT = freshwater transient, D = diadromous.*

Species Name	Common Name	Life History Category	No. of Individuals	River Occurrence		
				Ashepoo	Combahee	S. Edisto
Anchoa hepsetus	Striped anchovy	MN	98		X	X
Anchoa mitchilli	Bay anchovy	MN	9835	X	X	X
Bairdiella chrysoura	Silver perch	MN	1872	X	X	X
Brevoortia tyrannus	Atlantic menhaden	MN	1825	X	X	X
Cynoscion nebulosus	Spotted sea trout	MN	31	X	X	X
Cynoscion nothus	Silver sea trout	MN	45	X	X	X
Leiostomus xanthurus	Spot	MN	2423	X	X	X
Menidia menidia	Silverside	MN	14	X	X	
Micropogonias undulates	Atlantic croaker	MN	21,331	X	X	X
Mugil cephalus	Striped mullet	MN	19	X		X
Mugil curema	White mullet	MN	2	X		
Ophichthus gomesi	Shrimp eel	MN	2	X		
Pogonias cromis	Black drum	MN	2	X	X	
Prionotus tribulus	Bighead sea robin	MN	473	X	X	X
Sciaenops ocellatus	Red drum	MN	2			
Stellifer lanceolatus	Star drum	MN	22,174	X	X	X
Symphurus plagiusa	Blackcheek tonguefish	MN	4171	X	X	X
Trinectes maculates	Hogchoker	MN	3640	X	X	X
Ancylopsetta quadriocellata	Ocellated flounder	MT	105	X	X	X
Arius felis	Hardhead catfish	MT	120	X	X	X
Astroscopus guttatus	Northern stargazer	MT	21	X	X	X
Bagre marinus	Gafftopsail catfish	MT	177	X	X	X
Centropristis ocyurus	Bank Sea Bass	MT	23	X	X	X
Centropristis philadelphica	Rock sea bass	MT	9		X	X
Centropristis striata	Black sea bass	MT	5	X	X	X
Chaetodipterus faber	Atlantic spadefish	MT	86	X	X	X
Chilomycterus schoepfi	Striped burrfish	MT	26	X		X
Chloroscombrus chrysurus	Atlantic bumper	MT	151	X	X	X
Citharichthys spilopterus	Bay whiff	MT	133	X	X	X
Cynoscion regalis	Weakfish	MT	3180	X	X	X
Dasyatis Sabina	Atlantic stingray	MT	31	X	X	X
Etropus crossotus	Fringed flounder	MT	631	X	X	X
Eucinostomus argenteus	Spotfin mojarra	MT	9			X
Eucinostomus sp.	Mojarras	MT	14			X
Gymnura micrura	Smooth butterfly ray	MT	29	X	X	X
Lagocephalus laevigatus	Smooth puffer	MT	3	X		X
Lagodon rhomboids	Pinfish	MT	3		X	X
Larimus fasciatus	Banded drum	MT	14	X		X
Lutjanus griseus	Grey snapper	MT	2			X
Menticirrhus americanus	Southern kingfish	MT	776	X	X	X
Menticirrhus littoralis	Kingfish	MT	1			X
Monacanthus hispidus	Planehead filefish	MT	10	X	X	X
Ophidion marginata	Cusk eel	MT	27	X	X	X
Ophistonema oglinum	Atlantic thread herring	MT	4	X		
Orthopristis chrysoptera	Pigfish	MT	2	X		X
Paralichthys dentatus	Summer flounder	MT	156	X	X	X
Paralichthys lethostigma	Southern flounder	MT	495	X	X	X
Peprilus alepidotus	Harvestfish	MT	126	X	X	X
Pomatomus saltatrix	Bluefish	MT	5	X	X	X
Prionotus evolans	Searobin	MT	1	X		
Prionotus scitulus	Leopard searobin	MT	2	X		
Rhinoptera bonasus	Cownose ray	MT	9	X		X
Rhizoprionodon terraenovae	Atlantic sharpnose shark	MT	8	X	X	X
Scophthalmus aquosus	Windowpane	MT	17			
Selene setapinnis	Atlantic moonfish	MT	10	X		X
Selene vomer	Lookdown	MT	48	X	X	X
Sphyraena barracuda	Great barracuda	MT	1			X
Syngnathus louisianae	Chain pipefish	MT	10	X	X	X
Syngnathus scovelli	Gulf pipefish	MT	1	X		
Trichiurus lepturus	Atlantic cutlassfish	MT	9	X		X
Urophycis floridana	Southern hake	MT	96	X	X	X
Urophycis regia	Spotted hake	MT	977	X	X	X
Fundulus heteroclitus	Mummichog	PR	1	X		
Fundulus majalis	Striped killifish	PR	3	X		
Gobiesox strumosus	Skilletfish	PR	12	X	X	X

Table 2A. *Continued.*

Species Name	Common Name	Life History Category	No. of Individuals	River Occurrence		
				Ashepoo	Combahee	S. Edisto
Gobionellus oceanicus	Highfin goby	PR	51	X	X	X
Gobiosoma bosci	Naked goby	PR	6	X	X	X
Hypsoblennius hentzi	Feather blenny	PR	23		X	X
Opsanus tau	Oyster toadfish	PR	98	X	X	X
Ameiurus catus	White catfish	FT	960	X	X	X
Dorosoma petenense	Threadfin shad	FT	4	X		X
Esox americanus	Redfin pickerel	FT	15			X
Lepisosteus osseus	Longnose gar	FT	29	X	X	X
Ictalurus furcatus	Blue catfish	FT	193	X	X	X
Ictalurus punctatus	Channel catfish	FT	6			X
Acipenser oxyrhynchus	Atlantic sturgeon	D	2			X
Alosa sapidissima	American shad	D	3	X		X
Anguilla rostrata	American eel	D	3	X	X	
Morone saxatilis	Striped bass	D	4			X

during the summer with lows in spring; and diversity at station E019 was highest during the winter and lowest during the fall ($p \leq 0.05$).

Shannon-Wiener index for decapod crustaceans also varied seasonally (Table 4). Highest diversity (Shannon-Wiener) for decapod crustaceans assemblages occurred at station A001 during the winter and at stations A004, A008, and A011 during the spring ($p \leq 0.05$), whereas, lows in diversity at stations on the Ashepoo River occurred during the fall ($p \leq 0.05$). In the Combahee River, diversity was highest at all of the stations during the spring, with lows during the fall at the mesohaline stations (C001, C005, and C008) and during the spring at the oligohaline station C013 ($p \leq 0.05$). Shannon-Wiener was highest at stations E001, E007, and E013 during the spring and at E019 during the summer ($p \leq 0.05$).

Evenness tended to follow the same seasonal trend as the Shannon-Wiener index (Table 4). Seasonal lows in evenness for finfish coincided with the migration of star drum, Atlantic croaker, and hogchoker to the study area. For decapod crustaceans, seasonal lows in evenness on three rivers occurred during the periods of peak abundance (number of individuals) of white shrimp (*Litopenaeus setiferus*). The low evenness at

Table 2B. *Decapod crustacean species and total individuals collected in the study area and the occurrence of the species in the three rivers 1993–99. MT = marine transient, MN = marine nursery, PR = permanent resident, FT = freshwater transient, D = diadromous.*

Species Name	Common Name	Life History Category	No. of Individuals	River Occurrence		
				Ashepoo	Combahee	S. Edisto
Callinectes sapidus	Blue crab	MN	2026	X	X	X
Farfantepenaeus aztecus	Brown shrimp	MN	2872	X	X	X
Farfantepenaeus duorarum	Pink shrimp	MN	109	X	X	X
Libinia dubia	Longnose spider crab	MN	39	X	X	X
Libinia sp.	Spider crab	MN	11	X		X
Litopenaeus setiferus	White shrimp	MN	41,869	X	X	X
Trachypenaeus constrictus	Roughneck shrimp	MN	432	X	X	X
Callinectes ornatus	Shelligs	MT	1			X
Callinectes similis	Lesser blue crab	MT	1212	X	X	X
Cancer irroratus	Atlantic rock crab	MT	6	X		X
Clibanarius vittatus	Thinstripe hermit crab	MT	19	X		X
Pagurus longicarpus	Longwrist hermit crab	MT	56	X	X	X
Pagurus pollicaris	Flatclaw hermit crab	MT	4			X
Portunus gibbesii	Iridescent swimming crab	MT	2	X		
Portunus spinicarpus	Swimming crab	MT	1			X
Portunus spinimanus	Blotched swimming crab	MT	44	X		X
Xiphopenaeus kroyeri	Seabob	MT	96	X	X	X
Alpheus heterochaelis	Big claw snapping shrimp	PR	51	X	X	X
Dyspanopeus sayi	Say mud crab	PR	26	X	X	X
Menippe mercenaria	Florida stone crab	PR	19	X	X	X
Ovalipes ocellatus	Lady crab	PR	33	X	X	X
Palaemonetes pugio	Dagger blade grass shrimp	PR	629	X	X	X
Palaemonetes vulgaris	Marsh grass shrimp	PR	1839	X	X	X
Panopeus herbstii	Atlantic mud crab	PR	25	X	X	X
Panopeus occidentalis	Furrowed mud crab	PR	1	X		
Rhithropanopeus harrisii	Mud crab	PR	296	X	X	X

the oligohaline station E019 was probably related more to the low species richness, rather than to the distribution of individuals among the species, of the assemblages.

Periods of peak abundance of marine species were attributed to the seasonal variations in dominance (Berger-Parker) for finfish at the stations. On the Ashepoo River, the influx of weakfish (*Urophycis regia*) during the cooler months resulted in an elevated dominance for fish species at station A001, and dominance was higher at the mesohaline stations during the spring when the greatest numbers of Atlantic croaker were caught. High dominance on the Combahee River occurred during peak abundance of star drum (*Stellifer lanceolatus*) at the stations. Low dominance at stations E001 and E007 occurred when the greatest numbers of star drum were caught, and peak numbers of Atlantic croaker resulted in low dominance at station E013.

DISCUSSION

The structure of faunal communities in the ACE Basin estuary was similar to that of other estuarine systems along the mid-Atlantic region (Able *et al.,* 2001; Martino and Able, 2003; Nordlie, 2003; Pierce and Mahmoudi, 2001; Rogers, Targett, and Van Sant, 1984; Wenner *et al.,* 1981, 1984). Coastal marine species represented more than 80% of the species collected during the survey; the remaining finfish were permanent residents, freshwater forms, and diadromous species. The majority of the coastal marine transient fish species in the study area were summer visitors (Powles and Stender, 1978; Sedberry and Van Dolah, 1984). Marine transients represented <10% of the total catch, and the majority of these species were collected near the mouth of the river. Weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and brown shrimp (*Farfantepenaeus aztecus*) exhibited a wider tolerance to salinity in the ACE rivers and were present in collections from all stations with the exception of the limnetic-oligohaline station on the South Edisto River. Similar composition of high-salinity assemblages was noted in other estuarine systems (Martino and Able, 2003; Pierce and Mahmoudi, 2001; Wenner *et al.,* 1981, 1984, 1991).

The second largest group of marine species in the ACE rivers was dependent on the estuary for successful development; it was present year-round. Star drum (*Stellifer lanceolatus*), Atlantic croaker (*Micropogonias undulatus*), bay anchovy (*Anchoa mitchilli*), and white shrimp (*Litopenaeus setiferus*) were the top-ranking marine nursery species, accounting for more than 70% of the individuals caught throughout the year. Star drum (*Stellifer lanceolatus*) has previously been shown to be a highly abundant estuarine species in South Carolina (Wenner *et al.,* 1984; Wenner *et al.,* 1991) as well as Georgia (Dahlberg and Odum, 1970). Although the range of star drum extends from Chesapeake Bay to Texas (Powles and Stender, 1978), it is found in low numbers in large estuarine systems at the northern range end of its range, suggesting that the species may be a marine transient species in the mid-Atlantic. Young-of-the-year star drum have been shown to have a preference for mesohaline salinities (10–18‰) in the North Edisto River estuary (Wenner *et al.,* 1991), a smaller tidal estuary with a narrow salinity range (16–30‰). However, the star drum was rare in the North Inlet Estuary, South Carolina, which is a small, tidally driven, primarily euhaline (30–35‰) system (Allen *et al.,* 1992; Ogburn *et al.,* 1988). This observation suggests that the star drum cannot tolerate higher salinity (>30‰) conditions, which agrees with the evidence from this study. Atlantic croaker (*Micropogonias undulatus*) and bay anchovy (*Anchoa mitchilli*) were also abundant species in Cooper River-Charleston Harbor and the Winyah Bay systems in South Carolina as well as in other large estuarine systems within its range. The low numbers of Atlantic croaker in the smaller systems of North Inlet and North Edisto River are attributed to the lack of suitable habitat for the larvae (Allen and Barker, 1990; Ogburn *et al.,* 1988; Wenner *et al.,* 1991).

Estuarine species, those that spawn and use the estuary as a nursery habitat, represented less than 10% of the faunal community in the ACE rivers. Blue crab (*Callinectes sapidus*), mummichog (*Fundulus heteroclitus*), blennies (*i.e., Gobiosoma bosci*), and grass shrimp (*Palaemonetes* sp.) were the most common permanent residents in the study area as well as in other South Carolina estuarine systems. Blue crab and grass shrimp were the most abundant permanent residents in the study area, although grass shrimp generally were more abundant in the low salinity (<10‰) region of the ACE rivers. Mummichogs and blennies were not as abundant in the subtidal habitats of the South Carolina estuaries, being more abundant in intertidal habitats of South Carolina estuaries (Cain and Dean, 1976; Hettler, 1989), whereas blennies reportedly preferred the tidal pools and oyster reef habitats (Coen, Luckenbach, and Breitburg, 1999; Crabtree and Dean, 1982).

Another minor component of the community in the ACE rivers was that of freshwater finfish transient species. The most common species were the euryhaline white catfish (*Ameiurus catus*), blue catfish (*Ictalurus furcatus*), channel catfish (*Ictalurus furcatus*), and longnose gar (*Lepisosteus osseus*). Stenohaline freshwater species, such as redfin pickerel (*Esox americanus*), and diadromous species, such as threadfin shad (*Dorosoma petenense*), were only collected in low numbers at the limnetic-oligohaline station on the South Edisto River. White catfish is the most common freshwater species in large estuarine systems along the Atlantic coast (Keup and Bayless, 1964; Rogers *et al.,* 1984; Rozas and Hackney, 1984; Wenner *et al.,* 1981, 1984), and was the only freshwater species that was part of the dominant catch in this study.

Spatial distribution of the species assemblages in the estuarine systems appeared to be strongly influenced by the physiological tolerances of the individuals to salinity gradients in the systems. Site groups formed by normal classification of species revealed distinct groupings associated with major salinity regimes in the ACE rivers. The most pronounced difference in species assemblages was observed between the stations at or near the mouth of the rivers and the stations farthest upriver. Coastal marine transient species (*e.g., Centropristis striata, Anchoa hepsetus, Ovalipes ocellatus*) that spend a portion of their time outside of the estuary, were strongly associated with stations A001, C001, and E001,

Table 3. *Overall species diversity indices for stations in the three rivers, 1993–99.**

Station	Finfish				Decapod Crustaceans			
	Species Richness	*H*	*J*	Parker-Berger	Species Richness	*H*	*J*	Parker-Berger
A001	55	2.36	0.54	0.25	18	1.08	0.33	0.71
A004	47	1.95	0.44	0.32	19	1.08	0.33	0.72
A008	42	2.05	0.47	0.30	15	0.60	0.18	0.87
A011	29	1.70	0.39	0.52	14	0.85	0.26	0.80
C001	47	1.63	0.37	0.58	15	1.04	0.32	0.75
C005	35	1.81	0.41	0.43	15	0.71	0.22	0.84
C008	33	1.82	0.41	0.41	12	0.86	0.26	0.77
C013	31	1.96	0.45	0.29	13	0.97	0.30	0.76
E001	57	2.13	0.48	0.35	22	1.35	0.41	0.61
E007	34	1.55	0.35	0.41	17	0.41	0.13	0.92
E013	35	2.02	0.46	0.33	11	0.31	0.09	0.95
E019	21	1.25	0.29	0.57	9	1.18	0.36	0.65

* $H = H$ as defined in the Shannon-Wiener diversity index; $J = J$ as defined in the Equitability J diversity index.

where salinities generally were above 20‰, whereas freshwater species (*e.g., Ameiurus catus, Dorosoma petenense, Esox americanus,* and *Lepisosteus osseus*) formed clusters at stations with salinities below 10‰. Examinations with ordination techniques of data from studies conducted in the Chesapeake Bay (Wagner and Austin, 1999), Mullica River-Great Bay Estuary (Martino and Able, 2003), and Hudson River (Hurst, McKown, and Conover, 2004) revealed similar distribution of stenohaline freshwater and marine species along salinity gradients.

The physiological impediments of movement by stenohaline species into brackish or fresh waters partly explained the coenoclinal nature of species assemblages in estuarine systems. Marine transients were rare or absent from stations upstream of the upper mesohaline regions, indicating that salinities below 11‰ may pose a physicochemical barrier for the upstream movement in tidal rivers (Khlebovich, 1969; Kinne, 1971; Schmidt-Nielsen, 1975). It is generally accepted that marine species begin to experience osmotic stress (*i.e.,* imbalance of internal water levels) at salinities below 11‰, and stenohaline marine species lack the ability to osmoregulate efficiently in brackish waters with osmotic concentrations at one-quarter to one-third of the level of full seawater.

Stenohaline freshwater species, such as redfin pickerel (*Esox americanus*) and diadromous threadfin shad (*Dorosoma petenense*), were strongly associated with station E019, where salinities rarely rose above 0.5‰. Stenohaline freshwater species generally were more constrained by the freshwater interface (0–2‰) compared with their marine counterparts (Darlington, 1957; Moyle and Czech, 1988). Deaton and Greenberg (1986) and Bulger *et al.* (1993) contend that movement of stenohaline freshwater species can be hindered by ionic ratios at salinities between 0 and 2‰. Most freshwater species in estuaries along the Atlantic (Keup and Bayless, 1964; Rogers, Targett, and Van Sant, 1984; Rozas and Hackney, 1984; Wenner *et al.,* 1981, 1984) and the Gulf of Mexico (Peterson and Ross, 1991) coast generally occur at salinities below 5‰. In the tributaries of Chesapeake Bay, stenohaline freshwater species have not been found at salinities greater than 0.5‰ (Wagner, 1999).

The minimum zone of species, or Artenminimum (Remane, 1934), reached at the limnetic-oligohaline station on the South Edisto River (E019) probably was the result of a physicochemical barrier at salinities between 0 and 2‰. This station had the lowest numbers of marine species compared with the brackish stations in the Ashepoo and Combahee Rivers. The marine component of the assemblage comprised freshwater species (*i.e.,* white catfish, redfin pickerel, and longnose gar) and the young-of-the-year of the most salt-tolerant marine species (*i.e.,* Atlantic croaker and hogchoker) caught in the study area. A decrease in the number of species occurred in the upper mesohaline (10–15‰) waters in the tributaries of Chesapeake Bay (Wagner and Austin, 1999) and the Mullica River-Great Bay (Martino and Able, 2003) estuarine systems because the study areas did not extend to the tidal freshwater interface (0–2‰).

Temporal distributional patterns of fish and decapod crustaceans strongly influenced the assemblage structure in the three rivers. The seasonal variation in the number of species appeared to be related to migration and recruitment of species. There were two annual recruitment cycles: winter-spring (October to March) and summer-fall (April to September). Species number started to increase with the influx of marine species to the study area during the late winter and early spring, primarily due to the arrival of Atlantic croaker in late winter. Marine species and juvenile marine transients, weakfish (*Cynoscion regalis*) and southern hake (*Urophycis regia*), first appeared in catches in spring. Peak species numbers in the study area coincided with peak collections of marine transient and marine nursery species in the estuary during the summer. The low number of species during the winter months coincided with the temperature induced seaward migration of stenohaline marine species to warmer waters offshore, which accounted for more than 50% of the species collected during the study (Bearden, 1964). Similar seasonal trends in species distribution have been observed in other estuaries (Able and Fahay, 1998; Able *et al.,* 2001; Dahlberg, 1972; Holliday, 1971; Merriner *et al.,* 1976; Wenner *et al.,* 1981, 1984).

The use of the ACE rivers relative to life-history stage and age of the fauna also varied with season, as indicated by the size extremes of year-round residents. The new recruits of Atlantic croaker (~40 mm length from mouth to tail [TL]) to

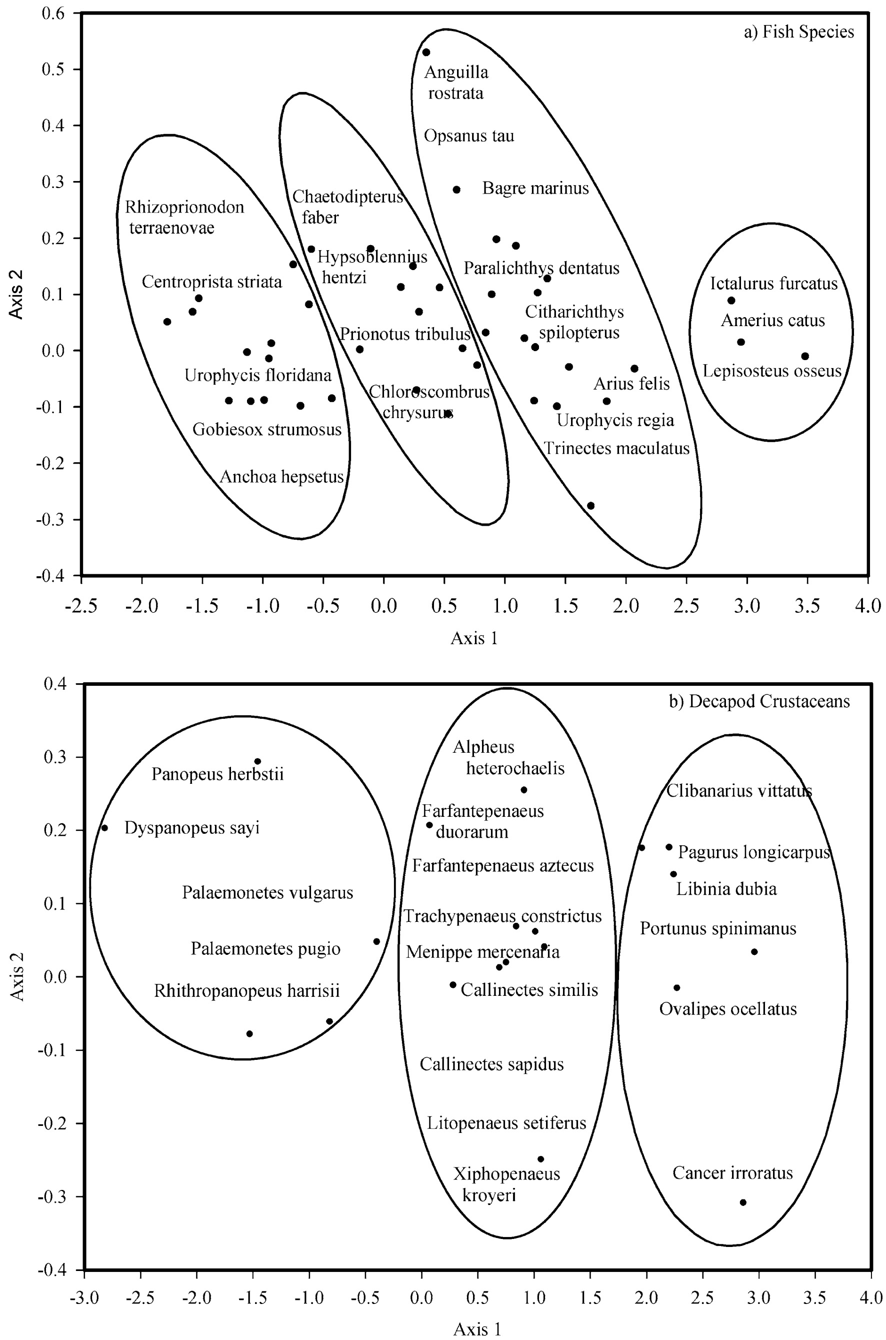

Figure 5. Detrended correspondence analysis ordination plots showing species in relation to salinity gradients in the ACE Basin study area. Ovals outline the species groupings, as interpreted by the author.

the estuary during the winter and spring were most abundant at salinities below 10‰, whereas 1-year-old Atlantic croaker (>100 mm TL) were collected in higher numbers at salinities above 10‰ during the summer and fall. Young-of-the year (~50 mm TL) star drum were abundant throughout the mesohaline (5–18‰) region during summer and fall, whereas the older fishes were present during the spring at stations with salinities above 15‰. Similar patterns were observed in other large estuarine systems in the southeast and mid-Atlantic regions (Able *et al.,* 2001; Rogers *et al.,* 1984; Rozas and Hackney, 1984). Differences in monthly fluctuations in the abundance of bay anchovy (*Anchoa mitchilli*) during the survey indicated little, if any, seasonality was associated with catches of bay anchovy, although highest catches occurred during late fall and winter (December–March). Peak abundance of white shrimp (*Litopenaeus setiferus*) in

Table 4. *Diversity indices by season for all stations in the ACE Basin study area, 1993–99.**

Station	Season	Finfish				Decapod Crustaceans			
		Species Richness	*H*	*J*	Berger-Parker	Species Richness	*H*	*J*	Berger-Parker
A001	Winter	31	1.72	0.41	0.36	14	1.42	0.45	0.36
	Spring	32	1.85	0.44	0.38	13	1.24	0.40	0.63
	Summer	32	2.42	0.57	0.23	13	0.59	0.19	0.86
	Fall	33	2.01	0.47	0.40	13	0.28	0.09	0.95
A004	Winter	30	1.74	0.41	0.43	14	1.41	0.45	0.42
	Spring	23	1.41	0.33	0.62	12	1.66	0.53	0.45
	Summer	26	1.66	0.39	0.55	12	0.71	0.23	0.81
	Fall	27	1.76	0.41	0.34	14	0.35	0.11	0.93
A008	Winter	26	1.53	0.36	0.42	11	1.31	0.42	0.52
	Spring	19	1.32	0.31	0.66	10	1.52	0.48	0.39
	Summer	26	2.07	0.49	0.37	10	0.35	0.11	0.93
	Fall	22	1.64	0.39	0.50	9	0.26	0.08	0.95
A011	Winter	20	1.75	0.41	0.40	8	0.93	0.30	0.76
	Spring	15	0.89	0.21	0.80	12	1.55	0.49	0.56
	Summer	17	1.54	0.36	0.56	11	0.37	0.12	0.93
	Fall	16	1.82	0.43	0.34	7	0.25	0.08	0.95
C001	Winter	32	1.88	0.47	0.36	10	0.96	0.34	0.72
	Spring	25	1.76	0.44	0.48	11	1.76	0.62	0.36
	Summer	27	1.44	0.36	0.66	10	0.68	0.24	0.84
	Fall	24	0.78	0.19	0.84	10	0.46	0.16	0.91
C005	Winter	22	1.74	0.44	0.45	9	0.98	0.35	0.71
	Spring	21	1.57	0.39	0.59	10	1.53	0.54	0.49
	Summer	22	1.43	0.36	0.65	9	0.73	0.26	0.83
	Fall	18	1.25	0.31	0.69	9	0.15	0.05	0.98
C008	Winter	21	2.05	0.51	0.23	7	0.75	0.26	0.75
	Spring	20	1.44	0.36	0.65	9	1.54	0.54	0.37
	Summer	21	1.27	0.32	0.70	11	0.39	0.14	0.93
	Fall	17	1.16	0.29	0.69	8	0.21	0.07	0.96
C013	Winter	16	1.11	0.28	0.74	8	0.64	0.23	0.85
	Spring	17	0.94	0.23	0.78	8	1.63	0.58	0.45
	Summer	21	1.74	0.43	0.46	11	0.59	0.21	0.88
	Fall	16	2.18	0.54	0.31	9	1.01	0.35	0.60
E001	Winter	27	2.05	0.48	0.46	18	1.45	0.45	0.43
	Spring	37	1.87	0.44	0.40	14	1.81	0.56	0.40
	Summer	34	1.36	0.32	0.68	11	0.78	0.24	0.80
	Fall	36	2.33	0.55	0.33	13	1.00	0.31	0.65
E007	Winter	18	1.58	0.37	0.41	11	1.26	0.39	0.53
	Spring	23	1.02	0.24	0.76	8	1.48	0.46	0.42
	Summer	21	1.66	0.39	0.53	7	0.44	0.14	0.91
	Fall	21	0.92	0.22	0.78	7	0.09	0.03	0.99
E013	Winter	17	1.87	0.44	0.31	6	1.14	0.35	0.59
	Spring	19	1.28	0.30	0.46	7	1.70	0.53	0.30
	Summer	22	2.22	0.52	0.23	8	0.09	0.03	0.99
	Fall	19	2.08	0.49	0.23	7	0.54	0.17	0.87
E019	Winter	4	0.61	0.14	0.82	5	1.45	0.45	0.29
	Spring	14	0.99	0.23	0.52	5	1.09	0.34	0.62
	Summer	14	1.38	0.32	0.55	8	1.05	0.33	0.70
	Fall	13	0.94	0.22	0.79	3	0.70	0.22	0.75

* $H = H$ as defined in the Shannon-Wiener diversity index; $J = J$ as defined in the Equitability J diversity index.

the study area during the fall resulted in lower diversities for decapod crustacean assemblages. White shrimp are recruited as postlarvae to the estuaries and sounds of South Carolina in late spring and early summer. They grow rapidly to juvenile and subadult stages in estuarine nursery areas and emigrate to coastal waters in fall (WENNER and BEATTY, 1993). During mild winters, white shrimp can overwinter in deep, high-salinity areas, but their survival is dependent on temperatures >6°C (FARMER, WHITAKER, and CHIPLEY, 1978).

The findings of the study demonstrate that there is a need to assess relative habitat value through interhabitat comparisons of nekton densities to fully understand the importance of the estuary as a nursery habitat. The stratification of star drum and Atlantic croaker by size along the estuarine salinity gradient in the ACE rivers indicates the importance of the estuary as nursery habitats for a wide array of marine species at varying stages of development. A study of a larval fish population in North Inlet by CAIN and DEAN (1976) revealed that species shift trophic levels (primary consumers, omnivores, detritivores) from season to season and as they grow. Some larval species prefer the intertidal creeks that traverse the salt marshes (CAIN and DEAN, 1976; KNEIB, 1997), whereas others prefer larger creeks (HETTLER and CHESTER, 1990; WEINSTEIN and BROOKS, 1983). Many larval marine fishes and permanent estuarine residents move onto the marsh during high tide to feed and return to creeks during low tide (CAIN and DEAN, 1976; HETTLER, 1989). Thus, the reticulated network of rivulets and creeklets across the marsh surface in the ACE Basin estuarine system are important nursery habitats for larval marine and estuarine fauna. For future examination of assemblage structure, different age groups should be considered as distinct observational units to understand the spatial use of the estuary by fishes (LIVINGSTON, 1988).

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