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A Profile of the Fish and Decapod Crustacean Community in a South Carolina Estuarine System Prior to Flow Alteration

Elizabeth Lewis Wenner, Malcolm H. Shealy, Jr.,
and Paul A. Sandifer

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U.S. DEPARTMENT OF COMMERCE
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National Marine Fisheries Service

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ELIZABETH LEWIS WENNER, MALCOLM H. SHEALY, JR., and PAUL A. SANDIFER[2]

ABSTRACT

The seasonal distribution and abundance of fishes and decapod Crustacea collected by 6 m otter trawl from the North and South Santee Rivers, South Carolina, were examined over a 2-year sampling period. Species richness was greatest during summer and at stations located in proximity to the river mouths. Although species richness was found to be related to salinity, temperature, depth, and dissolved oxygen, it was most noticeably affected by a spring freshet which considerably lowered richness and abundance.

Eleven species accounted for 93% of the number and ~70% of the total fish biomass taken in both rivers: *Micropogonias undulatus, Anchoa mitchilli, Bairdiella chrysoura, Stellifer lanceolatus, Ictalurus catus, Cynoscion regalis, Dorosoma petenense, Leiostomus xanthurus, Trinectes maculatus, Brevoortia tyrannus,* and *Symphurus plagiusa*. White shrimp, *Penaeus setiferus*; brown shrimp, *P. aztecus*; and blue crabs, *Callinectes sapidus*, comprised over 96% by number and weight of the decapod fauna collected in both rivers. Dominant fishes were present in fairly equal abundance throughout the year and utilized the Santee system as either a residential or nursery area, while *P. setiferus* and *P. aztecus* were more seasonal in their pattern of appearance and abundance.

Length-frequency analysis showed the Santee system fish fauna to be composed mostly of juvenile specimens. Their presence throughout the year indicated that the Santee is a temporally stable and relatively nonstressed system and an important nursery area.

The predominance of juveniles accounted for lower biomass (kg/ha) of fishes in the Santee system compared to values for other estuaries along the Atlantic coast of the United States. The continued importance of juvenile fishes and shrimp in the Santee system is questionable in view of salinity changes in the nursery habitat following proposed river rediversion.

INTRODUCTION

A number of published accounts are available on community ecology of estuarine fauna along the northeastern and southeastern coasts of the United States. Despite this, few comprehensive studies exist on distributional patterns and faunal composition of estuarine megafauna, such as fishes and decapods, from a system which has experienced as many manipulations as the Santee River, S.C. The drainage basin of the Santee encompasses 41,000 km^2 in North and South Carolina. The Santee was the fourth largest river on the U.S. east coast prior to diversion of most of its flow into the Cooper River in 1942. Diversion not only lowered the annual mean discharge from 525 m^3/s to 74 m^3/s but also caused severe shoaling in Charleston Harbor at the mouth of the Cooper River (Kjerfve and Greer 1978). Changes in the amount of freshwater flow completely altered the supply and deposition of sediments, erosion patterns, salinity regime, flooding characteristics, and floral and faunal communities (Kjerfve 1976). After diversion, the salinity in the Santee distributaries, the North and South Santee Rivers, increased sharply. In addition, large quantities of fine-grained suspended sediments were transported into the Cooper River and, eventually, into Charleston Harbor.

The costly necessity to dredge Charleston Harbor continuously prompted a rediversion project begun in 1975 whereby 80% of the Cooper River flow eventually will be directed back into the Santee system (Kjerfve 1976). Upon projected completion of rediversion on the North and South Santee Rivers is purely 428 m^3/s (Kjerfve and Greer 1978). Although the impact of rediversion on the North and South Santee Rivers is purely speculative, it is likely to reduce the net salinity in the Santee system and increase amounts of fine-grained suspended sediments. Kjerfve and Greer (1978) cautioned that these combined changes may ultimately end the economically important American oyster, *Crassostrea virginica*, and hard clam, *Mercenaria mercenaria*, fisheries flourishing at present in this river. The effect of rediversion on fishes and decapod Crustacea also may be substantial. Shealy and Bishop (1979) suggested that population changes in penaeid shrimp may occur, and the extent of nursery areas may be affected. Fishes such as *Ictalurus catus, I. punctatus, Morone saxatilis,* and *Anguilla rostrata*, which are frequently encountered in lower salinity regions of estuaries, may increase in abundance in the Santee system; however, the effect on most species, such as the euryhaline sciaenid fishes which are numerically dominant in South Carolina estuaries (Shealy et al. 1974), cannot be predicted.

The present study examines quantitative annual and seasonal variability, diversity, and species assemblages of fishes and decapod Crustacea found in the channel of the lower North and South Santee Rivers. Our primary consideration is to describe the megafaunal community as it currently exists and to relate distributional patterns to abiotic factors which may influence the community after rediversion.

STUDY AREA

All sampling stations were located within the Santee River system (Fig. 1). The Santee River provides the major headwaters

[1]Contribution No. 139 from the South Carolina Marine Resources Center.
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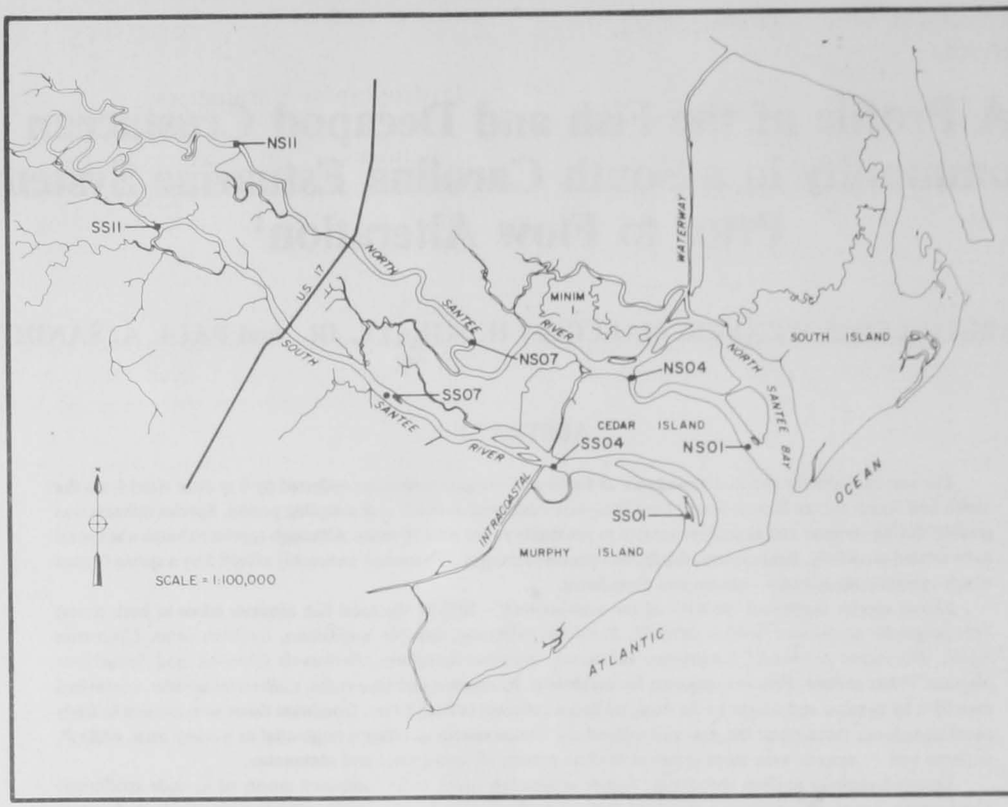

Figure 1.—Station locations in North and South Santee Rivers, S.C.

supplying Lakes Marion and Moultrie. About 23 km from the ocean, the Santee River bifurcates to form the North and South Santee Rivers.

The Santee system has been classified by Kjerfve and Greer (1978) as a partially mixed estuary with weak-to-moderate salinity stratification and gravitational circulation. However, this classification is variable due to tidal fluctuations as well as variations in saltwater intrusion and freshwater discharge (Cummings 1970[3]; Stephens et al. 1975; Kjerfve 1976; Nelson 1976; Burrell 1977; Calder et al. 1977). The South Santee River receives less freshwater drainage, with the result that saltwater intrusion is greater than in the North Santee River.

The two distributaries differ somewhat with regard to bathymetry since the North Santee River is slightly deeper than the South Santee River. Substrate in both rivers is very similar, being predominately coarse to fine-grained sand and shell of oceanic origin at the mouths, and hard mud and sand mix in the intermediate reaches of the estuary, replaced by fine-grained sand of inland origin in the upper estuary (Calder et al. 1977).

Dissolved oxygen values fluctuate seasonally, being usually 9-14 mg/liter in winter and ≥ 4 mg/liter in summer (Cummings footnote 3; Nelson 1976; Mathews[4]).

MATERIALS AND METHODS

Data Collection

We sampled eight stations which were located in the channel at 1, 4, 7, and 11 river miles from the mouths of the North and South Santee Rivers (Fig. 1). Hereafter, we will refer to these stations as NS01, NS04, NS07, and NS11 in the North Santee River and SS01, SS04, SS07, and SS11 in the South Santee River. Stations were sampled monthly over a 2-yr period from January 1975 through December 1976, with the following exceptions which were not included in our analysis: SS11 was not sampled in 1975; NS11 was sampled with a 5 m (16 ft) trawl in May and July 1975; and NS07 was not successfully trawled in May 1975.

All collections were made with a 6 m (12 ft) semiballoon otter trawl with 8 m headrope, composed of 2.5 cm (1 in) stretch mesh throughout. A complete description of the trawl is given by Shealy et al. (1974). Twenty-minute tows were made against floodtide during daylight hours at a speed of 1.3 m/s (2.5 kn), which resulted in a coverage of 1.5 ± 0.4 km during a tow.

Bottom-water samples were collected with 6 liter capacity Van Dorn bottles 0.3 m above the bottom at each station prior to trawling. Water temperature was read from stem thermometers mounted within the Van Dorn bottles. Salinity was measured in the laboratory with a Beckman RS7B induction salinometer. Dissolved oxygen was determined by the Winkler-Carpenter method (Strickland and Parsons 1968). Turbidity was determined with a Hach Model 2100A turbidimeter. Specimens were either processed in the field or preserved in 10% Formalin and returned to the laboratory for identification, measuring, and weighing. All specimens were weighed to the nearest 0.1 g and counted. We also recorded measurements (total length for fishes, carapace width for crabs, and total length for shrimps) for all species numbering ≤ 50 specimens per tow. At stations where the trawl caught larger numbers of organisms, we subsampled the catch as follows: If ≥ 50 to ≤ 250 individuals were collected, then a minimum of 50 randomly selected specimens were measured; if >250 to ≤ 500 individuals were caught, then

[3]Cummings, T. R. 1970. A reconnaissance of the Santee River estuary, South Carolina. A report prepared by United States Geological Survey, Water Resources Division, Columbia, S.C., 96 p.

[4]T. Mathews, Assistant Marine Scientist, South Carolina Marine Resources Research Institute, Charleston, SC 29412, pers. commun. December 1979.

20% of the catch was measured; when >500 were caught, 10% of the catch was measured.

Data Analysis

Cluster analysis was used to define assemblages of fishes and decapod crustaceans and to determine degree of similarity among stations. Prior to cluster analysis, data were logarithmically transformed by $\log_{10}(x + 1)$, where x is number of individuals for a given species. We reduced data by elimination of species which occurred in fewer than three collections during a sampling period and by elimination of collections which contained only one species.

The methods of cluster analysis used are described in detail by Boesch (1977). The Bray-Curtis coefficient (Clifford and Stephenson 1975) was used to compute similarity values. Symmetrical similarity matrices were computed for both the North and South Santee Rivers on data from the 2-yr sampling period with collections as entities and species as attributes (normal analysis), and with species as entities and sites as attributes (inverse analysis). Entities were classified into related groups by using flexible sorting (Lance and Williams 1967) with $\beta = -0.25$.

Two separate dendrograms were generated for each river: A dendrogram which indicated association of all collections during the 2-yr sampling period based on their faunal content and a dendrogram which indicated association of all species from the collections made during the 2-yr sampling period. We used postclustering techniques of nodal analysis (Williams and Lambert 1961; Lambert and Williams 1962) to examine species and station coincidences. Nodal analysis diagrams were made by using patterns of constancy (a measure of how consistently a species is found in a site group) and fidelity (a measure of how restricted a species is to a site group).

An index of abundance (Musick and McEachran 1972; Elliott 1977) was used to compare numbers and weights of selected dominant species and is expressed as:

$$\text{Index of Abundance} = \frac{1}{n}\sum_{l}^{n} \log_{10}(x + 1),$$

where x = number or weight of individuals of a given species and n = number of collections in a chosen time frame.

We determined biomass and density estimates for fishes and decapods from computations of area swept for trawl gears. Estimates of area swept (a) were determined by the following equation given by Roe (1969):

$$a = \frac{K \times M \times (0.6\,H)}{10{,}000\ \text{m}^2/\text{ha}},$$

where K is speed in meters per hour, M is time in hours fished, and H is headrope length in meters (Klima[5]). Roe (1969) assumed an effective swath of about 60% of the headrope length as established by Wathne (1959). The area swept by our 6 m otter trawl was estimated to be 0.72 ha/tow based on the method described by Roe (1969).

[5]Klima, E. F. 1976. A review of the fishery resources in the western central Atlantic. West. Cent. Atl. Fish. Comm. Publ. 3, 77 p.

RESULTS

Hydrographic Parameters

Bottomwater temperatures were very similar between rivers and among stations. Temperatures were lowest in both the North and South Santee Rivers during February and March 1975 and January and February 1976. In the North Santee River, temperatures gradually increased from April to reach a peak in either August (1976) or September (1975). The warmest month in the South Santee River during both years of sampling was August. Based on temperature over the 2-yr sampling period, winter encompassed January, February, and March; spring, April, May, and June; summer, July, August, and September; and fall, October, November, and December.

Salinities were extremely variable both seasonally and among stations. Freshwater outflow increased in the Santee watershed from 14.2 m^3/s to an average of 679.3 m^3/s between mid-March and mid-April 1975 and to 238.5 m^3/s from mid-May until late June 1975 (Burrell 1977). These freshets considerably lowered salinities at stations in both rivers. Salinities were also variable in 1976 but the extreme fluctuations caused by freshwater outflow were not as evident as in 1975. Except during periods of high runoff when freshwater was found throughout the system, salinity decreased from stations located at the river mouth to those located upstream. Salinities at stations SS01 and NS01 ranged from 0.2 to 32.9‰, which characterized these stations as limnetic-euhaline by the Venice System (Symposium on the Classification of Brackish Waters 1958). Stations SS04 and NS04 were limnetic-polyhaline (0.1-26‰), while SS07 and NS07 were limnetic-mesohaline (0.1-15.9‰). Salinities at NS11 and SS11 ranged from <0.1 to 1.4‰ and were within the limnetic-oligohaline salinity regime.

Community Composition and Diversity

Eighty species of fishes were collected from the South Santee River and 64 species from the North Santee River during the 1975-76 sampling period (Table 1). Eleven species accounted for 93% of the total number of specimens and 70% of the total fish biomass taken in both rivers: Atlantic croaker, *Micropogonias undulatus*; bay anchovy, *Anchoa mitchilli*; silver perch, *Bairdiella chrysoura*; star drum, *Stellifer lanceolatus*; white catfish, *Ictalurus catus*; weakfish, *Cynoscion regalis*; threadfin shad, *Dorosoma petenense*; spot, *Leiostomus xanthurus*; hogchocker, *Trinectes maculatus*; Atlantic menhaden, *Brevoortia tyrannus*; and blackcheek tonguefish, *Symphurus plagiusa*. In both rivers, *M. undulatus* was the most abundant species collected. With regard to biomass, however, *M. undulatus* was outranked by *I. catus* in the North Santee River and *Bairdiella chrysoura* in the South Santee River.

The decapod crustaceans were represented by 22 species in the North Santee River and 18 species in the South Santee River. Although fewer species of decapods than fish were collected, the decapods dominated in terms of total number of individuals captured (Table 2). The numerical dominance of the decapods was due to extremely large catches of the white shrimp, *Penaeus setiferus*, especially in the South Santee River. This species was by far the most abundant decapod collected in both rivers and also dominated other decapods in terms of biomass. *Penaeus setiferus*, together with the brown shrimp, *P. aztecus*, and the blue crab, *Callinectes sapidus*, comprised over 96% by number and weight of the total decapod fauna collected in both rivers.

Table 1.—Total number and total weight (kg) of fishes collected from 1975 and 1976 in estuaries of the North and South Santee Rivers, S.C. Species are listed in order of abundance, and data are pooled for the 2-yr sampling period.

Species	Total no.	Percent of total catch	Total weight	Percent weight
North Santee River:				
Micropogonias undulatus	3,535	23.68	20.282	10.12
Trinectes maculatus	3,233	21.66	15.251	7.61
Ictalurus catus	1,975	13.23	58.429	29.16
Anchoa mitchilli	1,502	10.06	2.895	1.44
Brevoortia tyrannus	824	5.52	13.600	6.79
Stellifer lanceolatus	766	5.13	3.651	1.82
Cynoscion regalis	555	3.72	2.528	1.26
Bairdiella chrysoura	531	3.56	8.621	4.30
Dorosoma petenense	467	3.13	1.831	0.91
Symphurus plagiusa	418	2.80	5.387	2.69
Leiostomus xanthurus	207	1.39	9.135	4.56
Ictalurus punctatus	150	1.00	3.623	1.81
Ictalurus furcatus	142	0.95	7.785	3.88
Paralichthys lethostigma	131	0.88	15.664	7.82
Menticirrhus americanus	57	0.38	0.531	0.26
Urophycis regia	50	0.33	0.339	0.17
Arius felis	49	0.33	1.024	0.51
Opsanus tau	29	0.19	1.502	0.75
Paralichthys dentatus	25	0.17	0.840	0.42
Etropus crossotus	25	0.17	0.075	0.04
Anguilla rostrata	19	0.13	2.301	1.15
Alosa sapidissima	17	0.11	0.114	0.06
Urophycis floridana	17	0.11	0.582	0.29
Cyprinus carpio	16	0.11	2.793	1.39
Cynoscion nebulosus	13	0.09	0.327	0.16
Chloroscombrus chrysurus	13	0.09	0.028	0.01
Alosa aestivalis	12	0.08	0.295	0.15
Dasyatis sabina	12	0.08	10.851	5.41
Gobiesox strumosus	11	0.07	0.047	0.02
Prionotus tribulus	11	0.07	0.022	0.01
Peprilus triacanthus	9	0.06	0.045	0.02
Pomatomus saltatrix	9	0.06	0.220	0.11
Morone saxatilis	8	0.05	0.070	0.03
Peprilus alepidotus	8	0.05	0.045	0.02
Astroscopus y-graecum	7	0.05	0.067	0.03
Anchoa hepsetus	7	0.05	0.055	0.03
Hypsoblennius hentzi	6	0.04	0.045	0.02
Centropristis striata	6	0.04	0.228	0.11
Lagodon rhomboides	6	0.04	0.044	0.02
Mugil cephalus	5	0.03	0.199	0.10
Ictalurus platycephalus	5	0.03	0.717	0.36
Ancylopsetta quadrocellata	4	0.03	0.037	0.02
Dorosoma cepedianum	4	0.03	1.243	0.62
Ophidion marginatum	4	0.03	0.149	0.07
Lepisosteus osseus	3	0.02	5.213	2.60
Selene vomer	3	0.02	0.013	0.01
Membras martinica	2	0.01	0.005	<0.01
Eucinostomus argenteus	2	0.01	0.021	0.01
Citharichthys spilopterus	2	0.01	0.005	<0.01
Gobionellus hastatus	2	0.01	0.093	0.05
Hypsoblennius ionthas	2	0.01	0.007	<0.01
Chaetodipterus faber	1	0.01	0.223	0.11
Prionotus scitulus	1	0.01	0.002	<0.01
Archosargus probatocephalus	1	0.01	0.338	0.17
Morone americana	1	0.01	0.484	0.24
Centropristis philadelphica	1	0.01	0.144	0.07
Bagre marinus	1	0.01	0.007	<0.01
Acipenser oxyrhynchus	1	0.01	0.300	0.15
Prionotus sp.	1	0.01	0.001	<0.01
Gobionellus shufeldti	1	0.01	0.001	<0.01
Eucinostomus sp.	1	0.01	0.008	<0.01
Scophthalmus aquosus	1	0.01	0.002	<0.01
Perca flavescens	1	0.01	0.017	0.01
Chilomycterus schoepfi	1	0.01	0.002	<0.01
Total	14,929		200.403	
South Santee River:				
Micropogonias undulatus	4,385	31.72	23.815	13.90
Anchoa mitchilli	2,944	21.29	4.259	2.49
Bairdiella chrysoura	2,187	15.82	33.547	19.58
Stellifer lanceolatus	636	4.60	3.419	2.00
Ictalurus catus	625	4.52	25.443	14.85
Cynoscion regalis	595	4.30	2.478	1.45
Dorosoma petenense	400	2.89	2.102	1.23
Leiostomus xanthurus	348	2.52	9.100	5.31
Trinectes maculatus	304	2.20	1.657	0.97
Brevoortia tyrannus	291	2.10	11.039	6.44
Symphurus plagiusa	220	1.59	2.193	1.28
Paralichthys lethostigma	155	1.12	13.274	7.75
Opsanus tau	85	0.61	7.470	4.36
Hypsoblennius ionthas	60	0.43	0.187	0.11
Hypsoblennius hentzi	58	0.42	0.246	0.14
Paralichthys dentatus	42	0.30	1.502	0.88
Menticirrhus americanus	34	0.25	0.284	0.17
Cynoscion nebulosus	30	0.22	1.033	0.60
Centropristis striata	29	0.21	0.627	0.37
Urophycis regia	28	0.20	0.351	0.20
Peprilus triacanthus	26	0.19	0.203	0.12
Gobiesox strumosus	25	0.18	0.076	0.04
Peprilus alepidotus	23	0.17	0.130	0.08
Chloroscombrus chrysurus	21	0.15	0.196	0.11
Alosa aestivalis	20	0.14	0.057	0.03
Alosa sapidissima	19	0.14	0.149	0.09
Etropus crossotus	19	0.14	0.206	0.12
Citharichthys spilopterus	18	0.13	0.118	0.07
Ictalurus furcatus	17	0.12	0.632	0.37
Archosargus probatocephalus	17	0.12	3.861	2.25
Urophycis floridana	16	0.12	0.432	0.25
Lagodon rhomboides	13	0.09	0.405	0.24
Dasyatis sabina	9	0.07	7.515	4.39
Lepisosteus osseus	8	0.06	8.075	4.71
Pomatomus saltatrix	8	0.06	0.285	0.17
Prionotus tribulus	8	0.06	0.011	0.01
Selene vomer	7	0.05	0.046	0.03
Anchoa hepsetus	7	0.05	0.057	0.03
Ancylopsetta quadrocellata	6	0.04	0.382	0.22
Prionotus evolans	6	0.04	0.009	0.01
Ictalurus punctatus	6	0.04	0.227	0.13
Opisthonema oglinum	5	0.04	0.014	0.1
Caranx hippos	4	0.03	0.008	<0.01
Centropristis philadelphica	4	0.03	0.172	0.10
Ophidion marginatum	4	0.03	0.166	0.10
Lutjanus griseus	4	0.03	0.041	0.02
Morone saxatilis	3	0.02	0.054	0.03
Dorosoma cepedianum	3	0.02	0.143	0.08
Arius felis	3	0.02	0.418	0.24
Eucinostomus sp.	3	0.02	0.042	0.02
Prionotus scitulus	3	0.02	0.007	<0.01
Scomberomorus maculatus	2	0.01	0.043	0.03
Eleotris pisonis	2	0.01	0.024	0.01
Astroscopus y-graecum	2	0.01	0.011	0.01
Bagre marinus	2	0.01	0.158	0.09
Orthopristis chrysoptera	2	0.01	0.112	0.07
Chaetodipterus faber	2	0.01	0.176	0.10
Mugil cephalus	1	0.01	0.100	0.06
Sciaenops ocellata	1	0.01	0.002	<0.01
Larimus fasciatus	1	0.01	0.001	<0.01
Eucinostomus argenteus	1	0.01	0.002	<0.01
Morone americana	1	0.01	0.338	0.20
Syngnathus louisianae	1	0.01	0.008	<0.01
Menidia menidia	1	0.01	0.002	<0.01
Membras martinica	1	0.01	0.004	<0.01
Strongylura marina	1	0.01	0.075	0.04
Trachinotus falcatus	1	0.01	0.004	<0.01
Trachinotus carolinus	1	0.01	0.005	<0.01
Urophycis earlli	1	0.01	0.001	<0.01
Brevoortia smithi	1	0.01	0.268	0.16

Table 1.—*Continued.*

Species	Total no.	Percent of total catch	Total weight	Percent weight
South Santee River.—*Cont.*				
Anguilla rostrata	1	0.01	0.150	0.09
Mugil curema	1	0.01	0.040	0.02
Gobionellus hastatus	1	0.01	0.009	0.01
Prionotus carolinus	1	0.01	0.001	<0.01
Prionotus sp.	1	0.01	0.002	<0.01
Cyprinus carpio	1	0.01	1.562	0.91
Gobionellus shufeldti	1	0.01	0.002	<0.01
Diapterus olisthostomus	1	0.01	0.022	0.01
Chilomycterus schoepfi	1	0.01	0.085	0.05
Monacanthus hispidus	1	0.01	0.003	<0.01
Total	13,826		171.372	

The total number of species of fishes and decapods varied over the 2-yr sampling period with the greatest number occurring in summer in both rivers (Fig. 2). Fewest species were collected during spring of 1975 when freshwater input and riverflow drastically increased. The dramatic drop in number of species was most noticeable at stations located upriver (NS07, NS11, and SS07). The total number of species captured was much lower during this time period than in spring of 1976 when no freshet occurred. During the 2-yr sampling period, more species were collected at stations nearest the mouths of both rivers.

The number of individual fish and decapod crustaceans, expressed in logarithms, showed patterns similar to the number of species when plotted over time (Fig. 2). In both rivers, numbers of individuals were greater during 1975, with peaks occurring in summer.

The number of species and number of individuals were compared to environmental factors such as bottom temperature, salinity, oxygen, turbidity, and depth using Pearson's product-moment correlation coefficient (Table 3). Based on these analyses, we found the number of species in the North Santee River to be significantly associated with bottom temperature and salinity in 1975 and with salinity and depth in 1976. In the South Santee River, the number of species was significantly associated with salinity during both years.

In the North Santee system, the number of individuals was positively correlated with bottom temperature in 1975, but there were no significant associations detected between number of individuals and environmental factors in 1976 (Table 3). The number of individuals captured in the South Santee system was positively correlated with bottom temperature and negatively correlated with oxygen in 1975 and 1976. A positive correlation with depth was found also in 1976.

Normal cluster analysis revealed that no strong differentiation of collections existed by river mile. Rather, collections made in the limnetic-euhaline zone were grouped with those from the limnetic-oligohaline zone indicating little stratification of the fauna according to salinity regime. In addition, an examination of the allocation of collections according to station and month indicated that association of the collections was not related to time of year. Based on similarity of faunal composition, we discerned three primary station groups by cluster analysis of data from the North Santee River: 1) a group in which collections at station NS01, NS04, and NS07 were represented by nearly equal numbers of collections; 2) a group in which collections at station NS01 predominated; and 3) a group which was most distinct from the other groups and was dominated by collections made at station NS11. Two major groupings of stations were indicated by cluster analysis for the South Santee River: 1) a group consisting mostly of collections from stations SS01 and SS04, and 2) a group consisting predominantly of collections from stations SS07 and SS11.

Table 2.—Total number and total weight (kg) of decapod Crustacea collected from 1975 and 1976 in the North and South Santee Rivers. Species are listed in order of abundance and data are pooled over the 2-yr sampling period.

Species	Total no.	Percent of total catch	Total weight	Percent weight
North Santee River:				
Penaeus setiferus	34,998	90.08	121.703	48.38
Penaeus aztecus	1,556	4.00	13.393	5.32
Callinectes sapidus	1,318	3.39	114.709	45.60
Palaemonetes vulgaris	510	1.31	0.228	0.09
Palaemonetes pugio	255	0.66	0.125	0.05
Penaeus duorarum	95	0.24	1.036	0.41
Panopeus herbstii	23	0.06	0.085	0.03
Portunus gibbesii	19	0.05	0.016	0.01
Callinectes similis	18	0.05	0.161	0.06
Trachypenaeus constrictus	18	0.05	0.019	0.01
Rhithropanopeus harrisii	17	0.04	0.013	0.01
Clibanarius vittatus	13	0.03	0.024	0.01
Portunus spinimanus	5	0.01	0.008	<0.01
Macrobrachium ohione	3	0.01	0.028	0.01
Xiphopenaeus kroyeri	2	0.01	0.004	<0.01
Panopeus occidentalis	2	0.01	0.002	<0.01
Panopeus sp.	1	<0.01	0.001	<0.01
Alpheus heterochaelis	1	<0.01	0.001	<0.01
Total	38,854		251.556	

Species	Total no.	Percent of total catch	Total weight	Percent weight
South Santee River:				
Penaeus setiferus	10,431	78.80	44.333	44.98
Penaeus aztecus	1,726	13.04	10.242	10.39
Callinectes sapidus	568	4.29	42.763	43.39
Macrobrachium ohione	120	0.91	0.414	0.42
Palaemonetes pugio	90	0.68	0.047	0.05
Palaemonetes vulgaris	89	0.67	0.052	0.05
Trachypenaeus constrictus	83	0.63	0.071	0.07
Callinectes similis	31	0.23	0.184	0.19
Penaeus duorarum	17	0.13	0.077	0.08
Clibanarius vittatus	16	0.12	0.024	0.02
Pagurus longicarpus	12	0.09	0.006	0.01
Xiphopenaeus kroyeri	12	0.09	0.030	0.03
Rhithropanopeus harrisii	10	0.08	0.134	0.14
Portunus spinimanus	7	0.05	0.104	0.11
Callinectes similis or *ornatus*[1]	7	0.05	0.018	0.02
Callinectes ornatus	5	0.04	0.031	0.03
Panopeus herbstii	4	0.03	0.006	0.01
Portunus gibbesii	3	0.02	0.007	0.01
Alpheus heterochaelis	2	0.02	0.002	<0.01
Acetes americanus	1	0.01	0.001	<0.01
Ovalipes ocellatus	1	0.01	0.002	<0.01
Eurypanopeus depressus	1	0.01	0.001	<0.01
Xanthidae[2]	1	0.01	0.008	0.01
Total	13,237		98.557	

[1]Field identification.

[2]Specimen damaged and unidentifiable, not included in analyses.

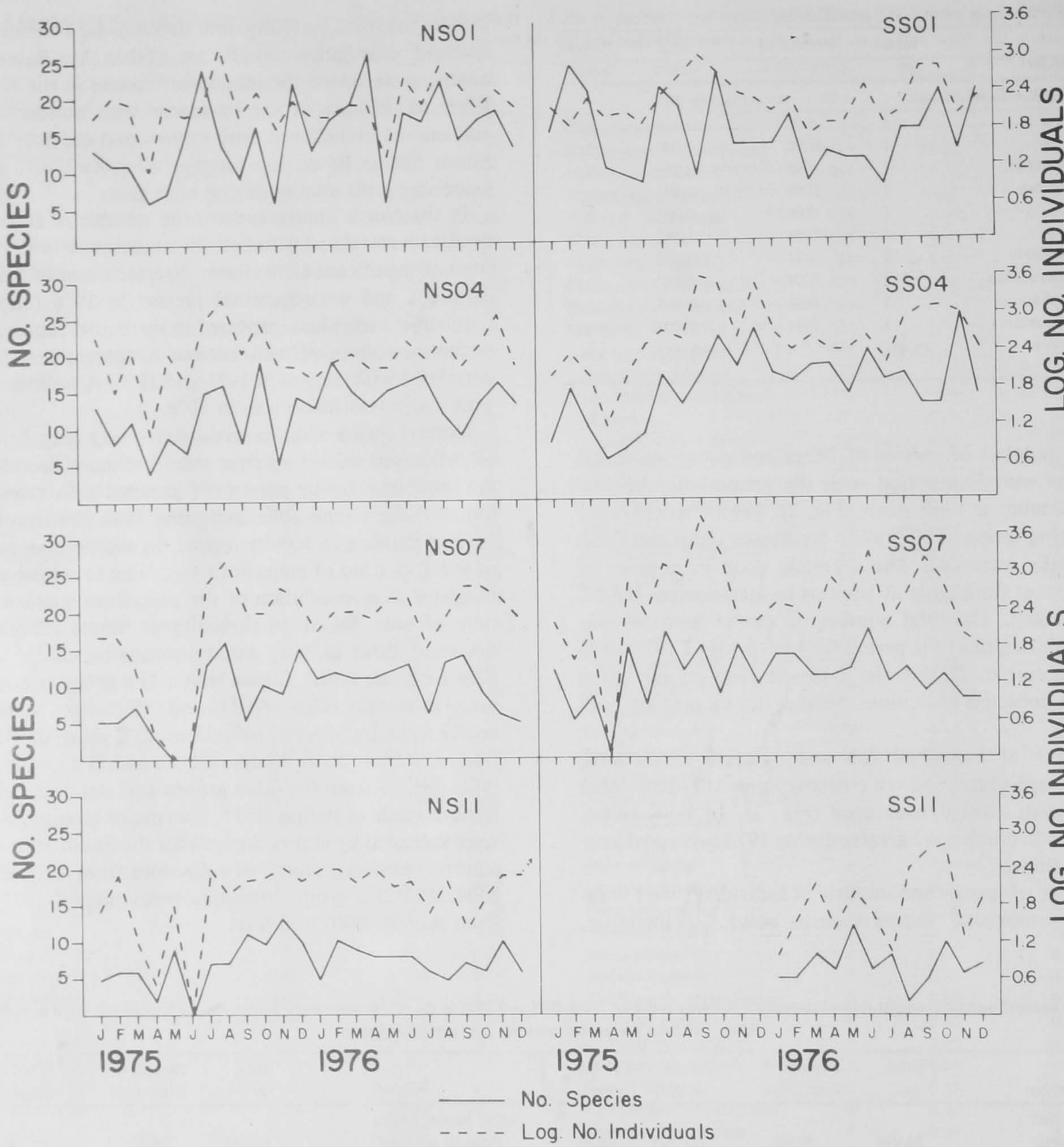

Figure 2.—Monthly fluctuations in number of species and number of individuals (log transformed) of fishes and decapod crustaceans at sampling sites in the North and South Santee Rivers, 1975-76.

Table 3.—Correlation between ln (n + 1) transformed values of number of species and number of individuals of fishes and decapods in relation to environmental factors. r = Pearson product-moment correlation coefficient; n = number of observations.

	1975				1976			
	North Santee		South Santee		North Santee		South Santee	
Environmental factor	r	n	r	n	r	n	r	n
	Number of species				Number of species			
Bottom temperature (°C)	0.4270*	45	0.1646	36	−0.0225	48	−0.0769	48
Salinity (‰)	0.3984*	45	0.4185*	36	0.5437*	48	0.5929*	48
Oxygen (mg/liter)	−0.1575	45	−0.0457	36	−0.0110	48	0.0074	48
Turbidity (FTU)**	0.2972	45	0.0849	36	−0.0550	48	−0.2213	48
Depth (m)	−0.3045	45	0.0170	36	−0.6029*	48	0.2420	48
	Number of individuals				Number of individuals			
Bottom temperature (°C)	0.5003*	45	0.5158*	36	0.0239	48	0.3385*	48
Salinity (‰)	0.2006	45	0.1605	36	0.0187	48	0.2766	48
Oxygen (mg/liter)	−0.0768	45	−0.3710*	36	−0.0614	48	−0.3089*	48
Turbidity (FTU)	0.1575	45	−0.2985	36	0.0142	48	−0.0146	48
Depth (m)	−0.1624	45	−0.1052	36	−0.1766	48	0.4652*	48

*Significant ($\rho \neq 0$) at $\alpha = 0.05$.

**FTU = Formazin Turbidity Units.

Table 4.—Groups formed from cluster analysis of species of fishes and decapod Crustacea collected in the North and South Santee Rivers from 1975 and 1976. Dendrograms are not shown.

North Santee R.	South Santee R.
Group A	Group A
Lagodon rhomboides	*Ophidion marginatum*
Alpheus heterochaelis	*Ancylopsetta quadrocellata*
Eucinostomus argenteus	*Urophycis regia*
Group B	*Urophycis floridana*
Prionotus tribulus	*Etropus crossotus*
Dasyatis sabina	*Alosa sapidissima*
Callinectes similis	*Cynoscion nebulosus*
Gobiesox strumosus	*Archosargus probatocephalus*
Etropus crossotus	*Lutjanus griseus*
Hypsoblennius hentzi	*Lagodon rhomboides*
Xiphopenaeus kroyeri	Group B
Group C	*Dasyatis sabina*
Astroscopus y-graecum	*Citharichthys spilopterus*
Ancylopsetta quadrocellata	*Caranx hippos*
Ophidion marginatum	*Eucinostomus* sp.
Urophycis floridana	*Centropristis philadelphica*
Centropristis striata	Group C
Urophycis regia	*Hypsoblennius ionthas*
Penaeus duorarum	*Trachypenaeus constrictus*
Group D	*Menticirrhus americanus*
Arius felis	*Clibanarius vittatus*
Peprilus alepidotus	*Hypsoblennius hentzi*
Callinectes ornatus	*Penaeus duorarum*
Selene vomer	*Centropristis striata*
Portunus gibbesii	*Opsanus tau*
Pagurus longicarpus	*Symphurus plagiusa*
Clibanarius vittatus	*Gobiesox strumosus*
Opsanus tau	*Paralichthys dentatus*
Trachypenaeus constrictus	Group D
Menticirrhus americanus	*Pomatomus saltatrix*
Group E	*Peprilus triacanthus*
Alosa sapidissima	*Anchoa hepsetus*
Paralichthys dentatus	*Chloroscombrus chrysurus*
Cynoscion nebulosus	*Panopeus herbstii*
Mugil cephalus	Group E
Dorosoma petenense	*Cynoscion regalis*
Gobionellus hastatus	*Penaeus aztecus*
Rhithropanopeus harrisii	*Stellifer lanceolatus*
Peprilus triacanthus	*Callinectes similis*
Anchoa hepsetus	*Peprilus alepidotus*
Panopeus herbstii	*Selene vomer*
Pomatomus saltatrix	*Lepisosteus osseus*
Chloroscombrus chrysurus	*Rhithropanopeus harrisii*
Group F	*Macrobrachium ohione*
Lepisosteus osseus	Group F
Cyprinus carpio	*Ictalurus punctatus*
Palaemonetes pugio	*Ictalurus furcatus*
Alosa aestivalis	*Alosa aestivalis*
Ictalurus punctatus	Group G
Ictalurus furcatus	*Anchoa mitchilli*
Macrobrachium ohione	*Bairdiella chrysoura*
Anguilla rostrata	*Callinectes sapidus*
Morone saxatilis	*Penaeus setiferus*
Group G	*Paralichthys lethostigma*
Ictalurus catus	*Brevoortia tyrannus*
Trinectes maculatus	*Leiostomus xanthurus*
Micropogonias undulatus	*Micropogonias undulatus*
Anchoa mitchilli	*Trinectes maculatus*
Penaeus setiferus	*Ictalurus catus*
Bairdiella chrysoura	*Palaemonetes vulgaris*
Cynoscion regalis	*Palaemonetes pugio*
Stellifer lanceolatus	*Dorosoma petenense*
Penaeus aztecus	
Symphurus plagiusa	
Callinectes sapidus	
Paralichthys lethostigma	
Brevoortia tyrannus	
Leiostomus xanthurus	
Palaemonetes vulgaris	

The classification based on the quantitative similarities of distribution of species found in the North and South Santee Rivers produced the species groups shown in Table 4. In order to determine affinity of species assemblages along the estuarine gradient, we compared species group constancy and fidelity among the eight stations occupied in the North and South Santee Rivers during 1975 and 1976 (Fig. 3). This was deemed preferable to comparing site groups determined by cluster analysis with species groups because site groups broadly overlapped and were not clearly separated by cluster analysis according to salinity regimes within the estuary.

In the North Santee River, one species group (G) was consistently encountered at stations NS01 and NS04, with slight decline in constancy at NS07 and NS11 (Fig. 3). Species in this group were not restricted in their distribution to any station location but were ubiquitous over the sites sampled, which is an indication of their apparent euryhalinity. The other species groups were not consistently collected at any of the stations, as indicated by low constancy. Species group B, which is largely composed of coastal marine fishes, was entirely restricted to station NS01, which suggests the stenohaline nature and transient occurrences of these fishes within the estuary. Other groups (A and D) were also apparently composed of marine species which were not able to penetrate far into the estuary. Group E species were associated with intermediate to higher salinities and did not

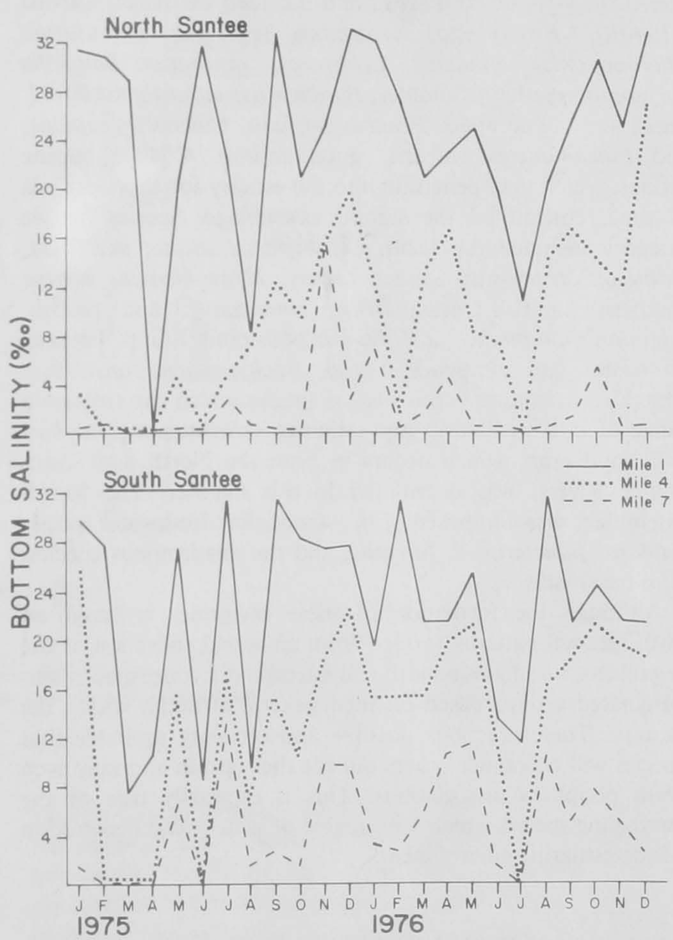

Figure 3.—Two-way coincidence tables of constancy and fidelity which compare species associations with stations in the North and South Santee Rivers, 1975-76. The species associations, designated alphabetically, resulted from cluster analysis of species (dendrogram not shown) collected from the Santee system. Species comprising these associations are listed in Table 5.

occur at stations upriver from NS04. Members of group F were not found downestuary of station NS07.

In the South Santee River, species in group G were considered to be ubiquitous over all sites. The constancy of these species ranged from high at stations SS04 and SS07 to moderate at SS01 and SS11; however, species in this group were not restricted to any station location. Groups A, C, and D included species which were associated with higher salinity areas in proximity to the river mouth. Stenohaline marine species in these groups included sheepshead, *Archosargus probatocephalus*; black sea bass, *Centropristis striata*, butterfish, *Peprilus triacanthus*; and Atlantic bumper, *Chloroscombrus chrysurus*. Group B species were not consistently collected at any station location and displayed low fidelity to stations SS04 and SS11. These species are generally considered to be marine in origin and their penetration as far as SS11 is unusual. Species which were associated with higher and intermediate salinities constituted group E. These were found at all stations except SS11, but were not consistently collected at any site. Group F contained the stenohaline freshwater species, *Ictalurus punctatus* and *I. furcatus*, and the anadromous species, blueback herring, *Alosa aestivalis*, which were restricted to station SS11.

Based on results of the two-way coincidence table (Fig. 3), it was possible to distinguish four assemblages of fishes and decapod Crustacea in both the North and South Santee Rivers. The first assemblage consisted of euryhaline species which occurred throughout both rivers and included the fishes *Anchoa mitchilli*; *Brevoortia tyrannus*; *Trinectes maculatus*; *Micropogonias undulatus*; *Leiostomus xanthurus*; *Bairdiella chrysoura*; southern flounder, *Paralichthys lethostigma*; and *I. catus*; and the decapods *Penaeus setiferus, Callinectes sapidus,* and *Palaemonetes vulgaris*, grass shrimp. Coastal marine species, which may penetrate into the estuary for short periods of time, constituted the second assemblage. Species in this category included the fishes *Centropristis striata*; skilletfish, *Gobiesox strumosus*; feather blenny, *Hypsoblennius hentzi*; southern kingfish, *Menticirrhus americanus*; and pinfish, *Lagodon rhombiodes*—and the decapods pink shrimp, *Penaeus duorarum*, and humpback shrimp, *Trachypenaeus constrictus*. The third assemblage consisted of species which can tolerate a range of intermediate to low salinities. *Rhithropanopeus harrisii*, mud crab, which occurs in both the North and South Santee Rivers, was distributed in this manner. The fourth assemblage was composed of the stenohaline freshwater species *Ictalurus punctatus, I. furcatus*, and the anadromous species, *Alosa aestivalis*.

Although the formation of these categories is based on distributional patterns formed from an actual collection of the organisms, it remains an artificial attempt at forcing species into designated groups based on their general affinities within the estuary. Therefore, it is possible and certainly probable that species will encounter others outside their group and may even form peripheral associations. This is especially true of the euryhaline species which are capable of widespread penetration of the estuarine environment.

Temporal and Spatial Distributions—Fishes

Temporal and spatial distributions for four abundant species of fishes—*Micropogonias undulatus, Anchoa mitchilli, Ictalurus catus, Bairdiella chrysoura*, and *Trinectes maculatus*—are compared in Figures 4-6. A summary table of the distribution and lengths for all species collected is available from the authors.

Micropogonias undulatus, **Atlantic croaker.**—The Atlantic croaker was found throughout both rivers, although its presence at stations varied over the 2-yr sampling period (Fig. 4A). In the North Santee River, number and biomass of the Atlantic croaker were greatest during spring 1976 at NS07. This is in marked contrast to spring 1975 when none were collected at this station or at NS11 further upriver. The absence of croaker at these stations in 1975 may be attributed to the significant alteration of physicochemical properties by the freshet in spring 1975. A similar decrease in abundance was not noted in the South Santee River, but failure to occupy SS11 during 1975 precludes a true assessment of freshet effects far upriver. The apparent absence of Atlantic croaker at upriver stations in the North Santee River during fall 1976 cannot be readily attributed to any hydrographic parameter but may reflect a lag in recruitment of young fish during this period.

Length-frequency distributions (not shown) indicated that sizes of most Atlantic croaker available to our bottom trawls were <10 cm in both rivers during all seasons. The predominance of smaller fish accounts for the low biomass observed for Atlantic croaker. Young fish, 4-16 cm, were prevalent in both rivers during fall and winter. A few larger fish which ranged from 12 to 26 cm were also present, but their numbers were low, which could reflect gear avoidance, movement away from the channel, or emigration from the estuary. Size of young Atlantic croaker had increased to a mode of 8-9 cm by summer and abundance had increased. Others (Haven 1957; Hansen 1969; Hoese 1973; Shealy et al. 1974; Chao and Musick 1977) have noted that small Atlantic croakers are present in different estuarine systems along the east coast throughout much of the year. The abundance of young fish in the Santee system is probably related to the long spawning season of the Atlantic croaker (Chao and Musick 1977), which may be more protracted in South Carolina waters than in temperate northern estuaries, although our choice of sampling gear, biased toward capture of smaller fish, is undoubtedly also a factor.

Anchoa mitchilli, **the bay anchovy.**—*Anchoa mitchilli* was found at all stations in both the North and South Santee Rivers sometime during the 2-yr sampling period, but catches were generally greater in the South Santee River (Fig. 4). Abundance of *A. mitchilli* appeared to be lowest at low-salinity stations located further upriver in both rivers. This decreased abundance was especially noticeable in spring and summer. During these seasons, bay anchovy were found at more seaward stations within the estuary. This distributional pattern is similar to that observed in the Edisto and Cooper Rivers, S.C. (Shealy et al. 1974), and York River, Va. (Markle 1976).

Length-frequency distributions for *A. mitchilli* were strongly bimodal with smaller (20-35 mm) and larger (50-75 mm) fish cooccurring during most seasons (not shown). These data do not indicate an influx of small fish into the population during a particular season, such as summer (Hoese 1973; Shealy et al. 1974), but suggest that small fish are present in the Santee system throughout the year. Multiple spawns (Hoese 1965) or a protracted spawning season (Hildebrand and Cable 1930) best explain the bimodality of frequencies observed for bay anchovy in the Santee system. Similar findings were noted by Hoese (1965), who believed that *A. mitchilli* spawns during all seasons in Texas and probably is short-lived. In addition, Mansueti and

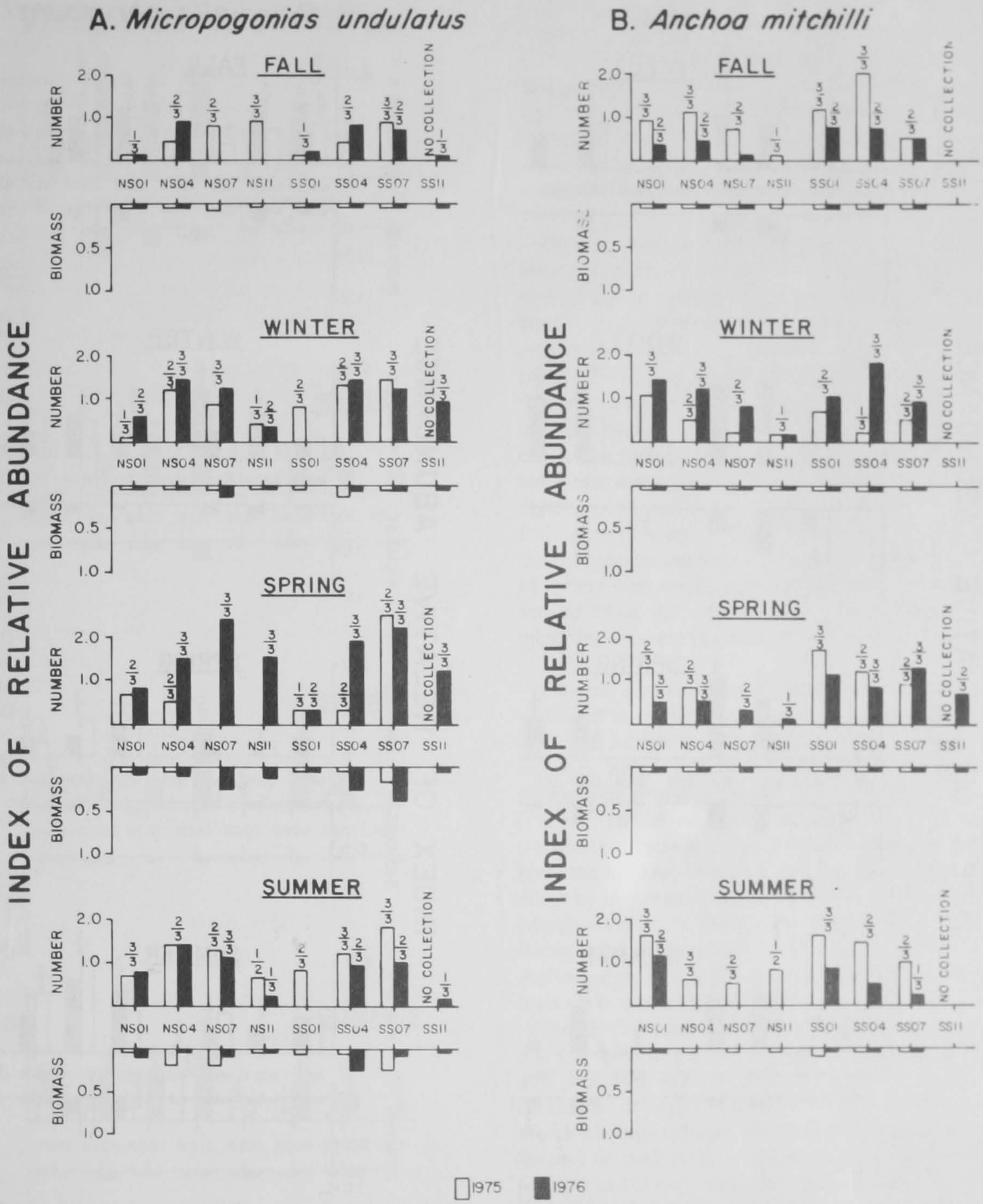

Figure 4.—Abundance of A) ***Micropogonias undulatus*** **and B)** ***Anchoa mitchilli*** **by station and season for the North and South Santee Rivers. Ratios over bars indicate number of collections where fishes were captured to total number of collections at a station.**

Hardy (1967) found sexually mature individuals at 2.5 mo of age in the Chesapeake Bay system.

***Ictalurus catus*, white catfish.**—The distribution of *I. catus* was obviously influenced by salinity since catches declined markedly at higher salinity stations (Fig. 5A). In the North Santee River, catches of *I. catus* were greatest during all seasons at stations furthest upriver. Distributional patterns in the South Santee River were similar in that *I. catus* seldom occurred at higher salinity stations. Shealy et al. (1974) found no *I. catus* at estuary mouths of the North and South Edisto or Charleston Harbor-Cooper Rivers. The infrequent occurrence of white catfish at the mouth of the Santee River probably reflects the often low-salinity nature of the Santee River and the subsequent penetration by lower salinity species. High biomass of *I. catus* corresponded with peak numerical abundance in both rivers. Length-frequency distributions (not shown) showed that most white catfish collected in the Santee system were < 100 mm, although the length range extended from 10 to 370 mm. Based on an age-growth study of *I. catus* from South Carolina (Stevens 1959), the fishes < 100 mm are not older than 2 yr. In the North Santee River, young-of-the-year fish (< 50 mm) were

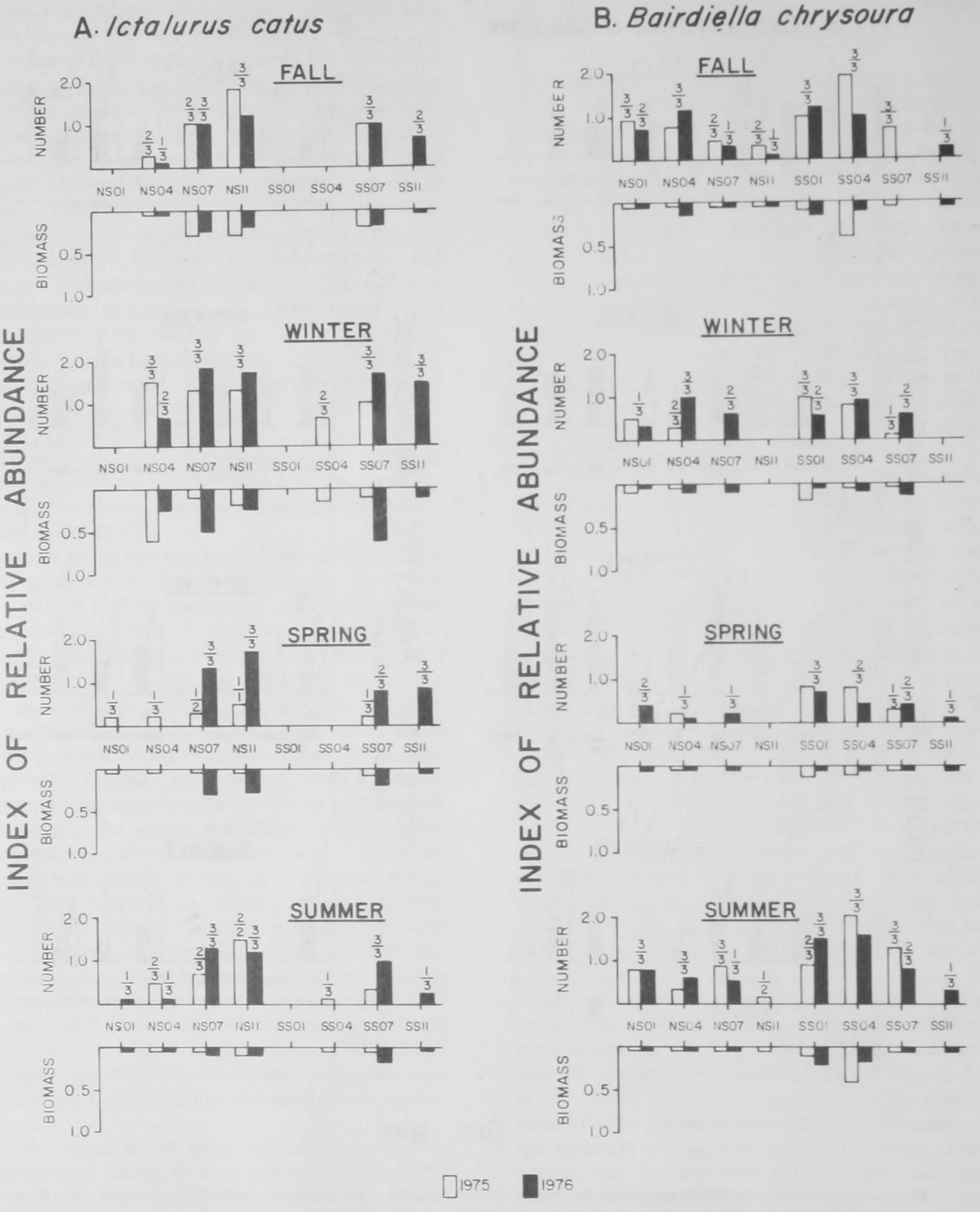

Figure 5.—Abundance of A) *Ictalurus catus* and B) *Bairdiella chrysoura* by station and season for the North and South Santee Rivers. Ratios over bars indicate number of collections where fishes were captured to total number of collections at a station.

prevalent in summer, which is coincidental with the spawning period of *I. catus* in South Carolina (Stevens 1959).

Bairdiella chrysoura, **the silver perch.**—*Bairdiella chrysoura* was present in the Santee system during all seasons, although abundance tended to increase during fall and summer in the South Santee River (Fig. 5). Silver perch showed no apparent preference for a particular portion of the salinity regime in the middle and lower reaches of the estuary since they were collected at all stations; however, catches did decline at the stations located further upriver (NS11 and SS11). *Bairdiella chrysoura* taken from the Santee system were young-of-the-year fish (Shealy et al. 1974; Chao and Musick 1977) within the size range of 20-100 mm.

Trinectes maculatus, **hogchoker.**—*Trinectes maculatus* was ubiquitous in the Santee system during all seasons (Fig. 6). Catches were greatest during fall in both the North and South Santee Rivers. Lower catches tended to be associated with sta-

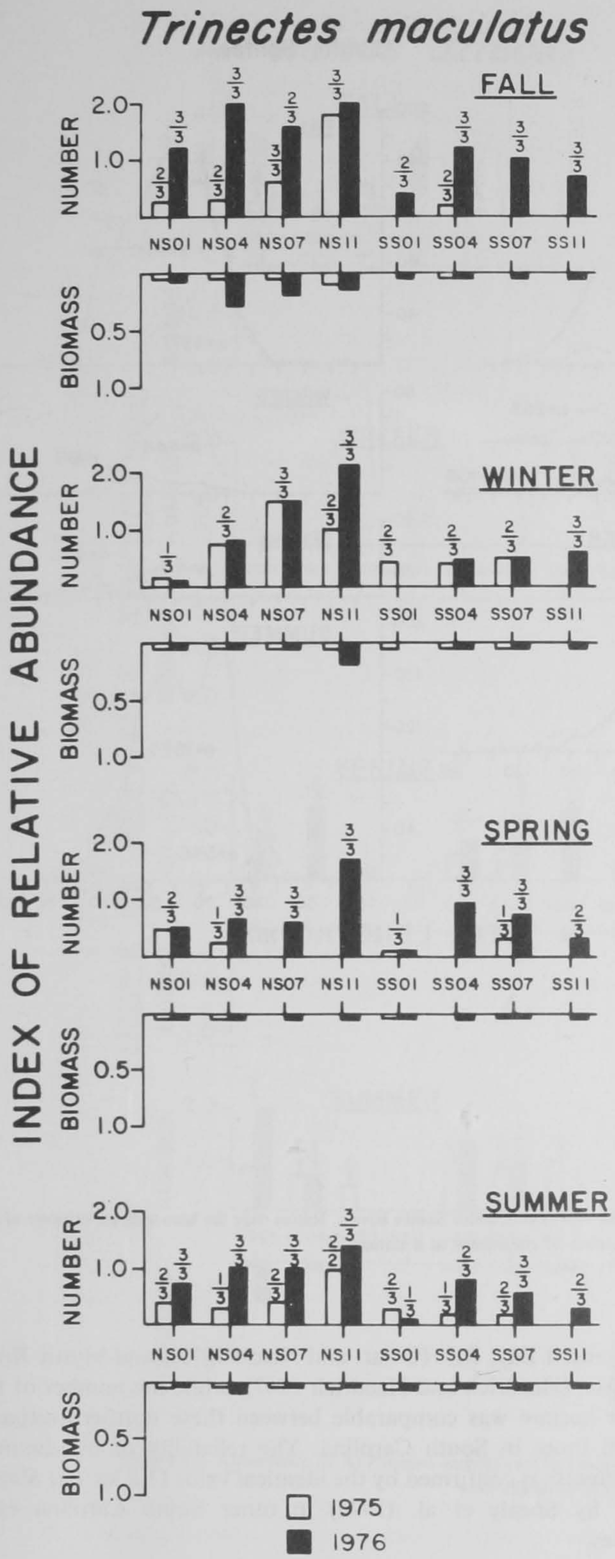

Figure 6.—Abundance of *Trinectes maculatus* by station and season for the North and South Santee Rivers. Ratios over bars indicate number of collections where fishes were captured to total number of collections at a station.

tions in proximity to the river mouths, which suggests an avoidance of euhaline areas by this fish. Lengths of hogchokers ranged from 20 to 175 mm, but most individuals were <80 mm. These specimens probably represent young-of-the-year fish (Dovel et al. 1969) which appear during all seasons due to the extended spawning season of this species in the Carolinas (Hildebrand and Cable 1938).

Temporal and Spatial Distributions—Decapods

Distributional patterns of the most abundant decapod crustaceans, *P. setiferus, P. aztecus*, and *Callinectes sapidus*, are shown in Figures 7 and 8.

Penaeus setiferus, **white shrimp.**—Catches of white shrimp were seasonal, with most individuals occurring in the Santee system during the fall and summer. Though common in both rivers, numerical abundance and biomass of white shrimp were greater in the South Santee River (Table 2), and catches appeared to be lower at the extreme upriver stations. This was particularly evident during winter and spring. Length-frequency distributions showed young-of-the-year white shrimp were present during summer in both rivers (Fig. 7). Sizes of shrimp collected increased during the other seasons, with the largest individuals collected in the spring. Similar findings were noted by Bishop and Shealy (1977) in a study of penaeid shrimp from South Carolina estuaries. They found that the largest numbers of shrimp were small, whereas larger individuals, which may be derived from the overwintering population or from an immigrating offshore population, occurred during fall and spring.

Penaeus aztecus, **brown shrimp.**—Brown shrimp were most abundant in spring and summer (Fig. 8). These brown shrimp were rare in winter trawl collections. In other South Carolina estuaries, Bishop and Shealy (1977) noted that catches of brown shrimp were strongly seasonal, with most individuals collected in summer. The absence of brown shrimp in trawl catches during the winter months does not indicate that they are absent entirely from the estuary. Postlarval shrimp first enter South Carolina estuaries in January and are most abundant in February and March (Bearden[6]). Because it appears that postlarval white shrimp, and perhaps also brown shrimp, primarily occupy the shallow edges and creeks of estuaries where cover and preferred food are available (Bishop and Shealy 1977), we may have failed to sample this component of the shrimp population by restricting our collecting to the channel. It is also probable that 9-12 mm postlarvae are not retained by our 6 m otter trawl. Examination of length-frequency distributions (not shown) for brown shrimp collected in the Santee system showed a total absence of postlarvae in our trawl collections. Shrimp ranged from 30 to 145 mm, with most individuals in the 55-90 mm size range. The abundance of brown shrimp was also related to station location and, hence, salinity as reflected in only one occurrence of *P. aztecus* at the extreme upriver sites.

Callinectes sapidus, **blue crab.**—The blue crab was caught throughout the North and South Santee Rivers during all seasons. Catches did not reflect strong seasonal changes, although fewer blue crabs were collected in summer in the North Santee River. Catches also appeared to be related to sampling location, with fewer blue crabs being caught at upriver stations. Size-frequency distribution of blue crabs covered a wide range of sizes from 15 to 195 mm, with smaller crabs (≤60 mm) occurring in fall.

[6]Bearden, C. M. 1961. Notes on postlarvae of commercial shrimp (*Penaeus*) in South Carolina. Contrib. Bears Bluff Lab. No. 33, 8 p.

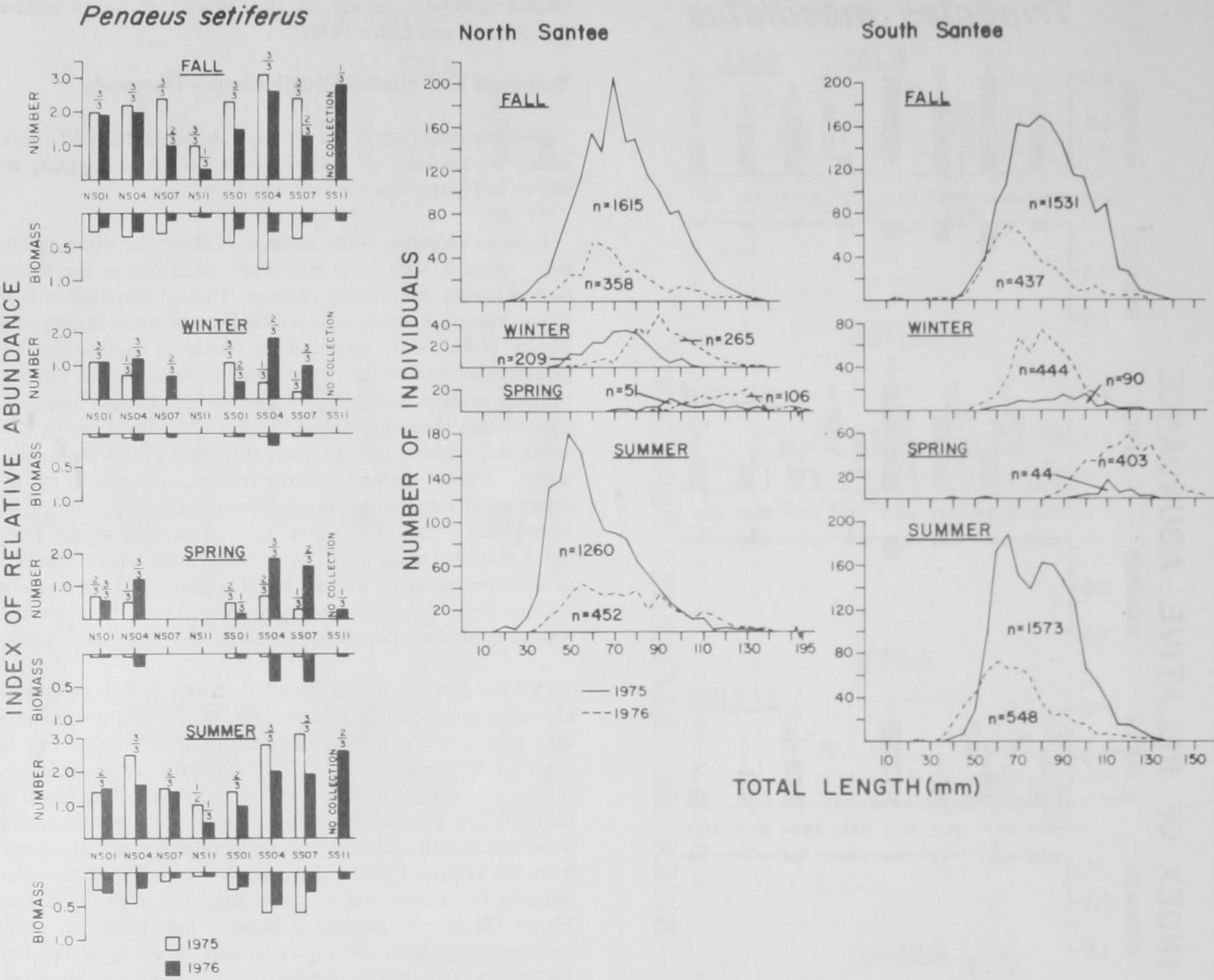

Figure 7.—Seasonal abundance and length-frequency distribution of *Penaeus setiferus* within the North and South Santee Rivers. Ratios over the bars indicate number of collections where shrimp were captured to total number of collections at a station.

Biomass Estimates

The estimated biomass, expressed in kg/ha, for fishes from the North and South Santee Rivers was lower than biomass estimates reported for other estuarine systems along the Gulf and east coasts of the United States (Table 5). Greatest biomass was obtained for northern temperate estuaries such as Narragansett Bay, R.I. (Oviatt and Nixon 1973), and Mystic River, Mass. (Haedrich and Haedrich 1947), while the number of fish per hectare was comparable between these northern estuaries and those in South Carolina. The reliability of our biomass estimates is confirmed by the identical value (3.8 kg/ha) obtained by Shealy et al. (1974) in other South Carolina estuaries.

Table 5.—Estimates of density and number of individuals/hectare for fishes caught by trawls from estuaries along the Gulf and east coasts of the United States.

Geographic area	Biomass (kg/ha)	Density (no./ha)	Gear	Reference
Mystic River, Mass.	26.16	462	4.8 m semiballoon trawl	Haedrich and Haedrich (1974)
Narragansett Bay, R.I.	31.68	290	9.2 m balloon trawl	Oviatt and Nixon (1973)
North Santee River, S.C.	3.9	287	6 m semiballoon trawl	present study
South Santee River, S.C.	3.8	303	6 m semiballoon trawl	present study
Cooper River — Charleston Harbor and Edisto system, S.C.	3.8	433	6 m semiballoon trawl	Shealy et al. (1974)
Doboy Sound, Ga.	10.7	4,190	12.2 m balloon shrimp trawl	Hoese (1973)
Galveston Bay, Tex.	16.57	8,511	3 m otter trawl	Bechtel and Copeland (1970)

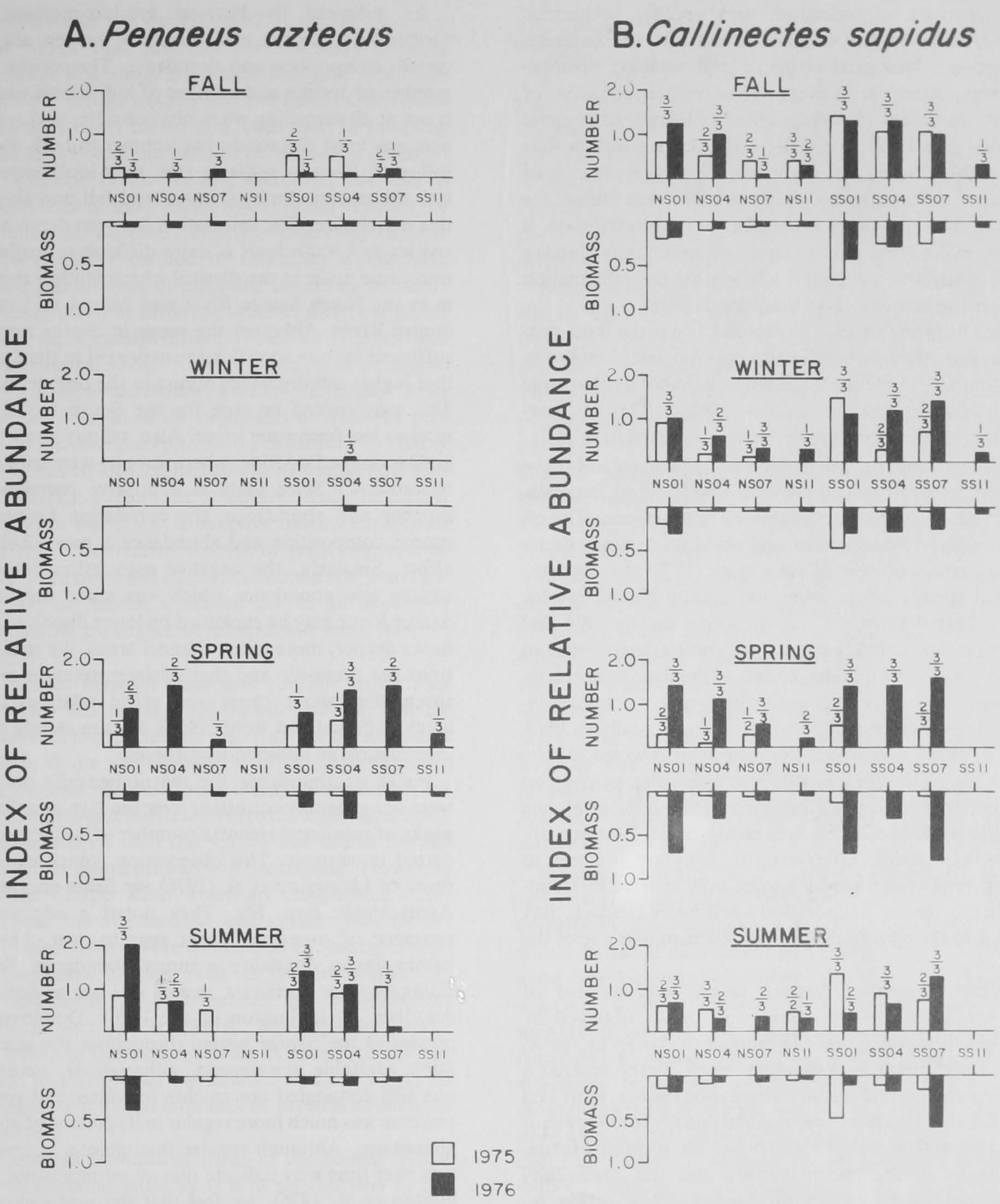

Figure 8.—Abundance of A) *Penaeus aztecus* and B) *Callinectes sapidus*. Ratios over the bars indicate number of collections where shrimp were captured to total number of collections at a station.

We obtained the following density estimates of decapod Crustacea from the Santee system:

	Biomass (kg/ha)	*Density (no./ha)*
South Santee	5.5	836
North Santee	1.9	255

These estimates are comparable to 6.1 kg/ha and 1,190 individuals/ha reported by Hoese (1973) for all invertebrates collected from Doboy Sound, Ga.

DISCUSSION

The distributional patterns of estuarine fishes and decapod Crustacea are influenced by numerous environmental factors. Factors such as salinity (e.g., Gunter 1938, 1945, 1961; Kilby 1955; Kinne 1966; Copeland and Bechtel 1974), temperature (Gunter and Hildebrand 1951; Reid 1954; Kinne 1963), substrate and detritus (Carr and Adams 1973; Mills 1975; Livingston et al. 1977), and river discharge (Aleem 1972; Ruello 1973; Livingston et al. 1977; Glaister 1978) influence animal distributions, with the extent of these influences dependent on spatial (habitat) dimensions as well as individual and specific tolerances. Laboratory studies are generally concerned with the interrelationships between biological response and multiple environmental factors acting in concert. However, application of laboratory methodology to ecological field studies is often quite difficult (Alderdice 1972), especially when dealing with mobile organisms such as fishes and decapods. The interpretation of results concerning distribution of these organisms within the Santee system is no exception to this difficulty. Nevertheless, it is possible to make some interpretation of community stability and specific distributional patterns based on the information collected over the intensive 2-yr sampling period.

The freshet in spring of 1975 appeared to have the most pronounced singular effect on species composition and abundance. The total number of species collected was lower at that time than at any other during the sampling period. This was particularly noticeable at the upriver stations. Abundance of individual species such as *Micropoganias undulatus*, *Anchoa mitchilli*, and *Trinectes maculatus* were also lower at these stations, which also may be attributable to flood effects. The effects on the decapod crustaceans and other numerically dominant fishes were not obvious. Calder et al. (1977) also reported alterations of species composition and density among benthic organisms collected from the Santee system during 1975 and 1976; however, they noted that the flood most affected benthos in the lower, usually more saline reaches of the river where an increase in species normally associated with greater freshwater intrusion into the lower estuary occurred. Others (Andrews 1973; Boesch et al. 1976) have noted that effects of lowered salinity from floods are greatest among meso- or polyhaline species, but the magnitudes of the effects differ for epifaunal, infaunal, and highly motile organisms. The depressed species number observed by us may reflect the tendency of fishes and decapods to escape from areas whose salinity is drastically lowered by floodwaters or, in the case of juveniles and small-bodied species, may be attributed to their being flushed downstream and out of the system.

The positive correlation between salinity and number of species in the Santee system agrees with results obtained by Gunter (1961), who noted that the number of species increased toward the lower reaches of estuaries where there occurred a mixture of euryhaline and marine stenohaline species. Hoff and Ibara (1977) found that in a New England estuary the number of species was greatest at stations which had the greatest fluctuation in salinity. Both species number and the community assemblages defined by us for the Santee system reflect increased diversity with proximity to the river mouth. Also, most assemblages defined for the Santee system consisted partially of euryhaline species. This is not an unusual occurrence within estuaries. Pearse (1936) noted that the estuarine fauna consists of marine or marine-derived species, and Weinstein (1979) stressed how depauperate the shallow marsh estuarine fauna would be if all transient marine species were removed. The distribution of the endemic estuarine species appeared to be more restricted than that of the marine transients. Nevertheless, we observed no abrupt faunal changes along the salinity gradient in the Santee system. Rather, the faunal assemblages overlap and do not exist as sharply delineated groups. This no doubt results from the different tolerances of juveniles and adults; the effect of salinity, in concert with other factors, on reproduction; and the highly compressed nature of salinity regimes in South Carolina estuaries as compared with many estuaries elsewhere.

As indicated by Pearson product-moment correlations, temperature, depth, and dissolved oxygen also affect community composition and abundance. The positive correlation of number of species and number of individuals with temperature is not at all surprising when one considers that species composition was most diverse during summer in both rivers. The huge influx of *Penaeus setiferus* and, to a lesser extent, *P. aztecus* into the estuary during summer and fall probably accounts for this correlation. The association between depth and number of species and individuals is more difficult to explain. All collections were made in the channel where depths ranged from 2 to 8 m in the North Santee River and from 1 to 5 m in the South Santee River. Although the range in depths sampled is slight, sufficient salinity stratification may exist in the Santee system so that higher salinity water occurs in the deeper channel regions. This may indeed be true for the South Santee River which receives less freshwater input. Also, salinity stratification may be greater on the floodtide, where samples were collected (Mathews footnote 4.) Since there is a positive correlation of species number and abundance, the correlation between depth and species composition and abundance is most likely a secondary effect. Similarly, the negative association between dissolved oxygen and abundance which was noted only for the South Santee River may be explained by lower dissolved oxygen values in the deeper, more saline channel areas. We realize the correlations are simplistic and that misinterpretation can result from speculating about cause and effect relations in correlation analysis (Sokal and Rohlf 1969). We are merely presenting this information as untested hypotheses.

Peaks of abundance for the numerically dominant species were not generally consistent over the 2-yr sampling period, but peaks of maximum richness (number of species) consistently occurred in summer. This observation compares favorably with those of Livingston et al. (1976) for fishes and invertebrates of Apalachicola Bay, Fla. They noted a relatively stable appearance of organisms from year to year, but considerable within-species variability in annual abundance. Temporal partitioning by our dominant species was not as noticeable as that described by Livingston et al. (1976). Dominant fishes were present in the Santee system throughout the year and showed fairly equitable abundances, although *M. undulatus* and *A. mitchilli* dominated our catches in winter and spring. *Penaeus setiferus* was much more regular in its pattern of appearance and abundance. Although regular fluctuations in species composition over time may indicate that an estuary is not stressed (Livingston et al. 1976), we feel that the year-round presence of stress-tolerant estuarine species better indicates temporal stability than overall stability of the estuarine system. We relate such occurance to a protracted spawning season in warm temperate areas which enable some element of the population, probably juveniles, to be present in the estuary year-round.

As the length-frequency polygons for selected species showed, the Santee system fish fauna captured during this study are primarily composed of immature fishes. Some larger mature individuals were collected, but the Santee system functions strongly as a juvenile fish habitat. The importance of estuaries as nursery areas is well documented (Gunter 1961; Wallace and Van der Elst 1975; Livingston et al. 1976; Weinstein 1979), and the attraction of young fish to estuaries is attributed to physiological suitability in terms of physiochemical features, an abundance of food, and protection from predators (Gunter 1961; Van Engel and Joseph 1968[7]; Wallace and Van der Elst 1975).

Although Wallace and Van der Elst (1975) and Livingston et al. (1976) also found that juveniles predominated in their samples, we suspect that sampling design and gear selectivity may have biased our results toward juvenile fishes. Our choice of fixed stations is certainly biased and lends itself to sampling error that would have been eliminated or reduced by a stratified random design (Markle 1976). We are, therefore, not able to determine the influence of movements by the fauna between the shoals and the channel. Because trawling is inherently variable (Taylor 1953), a repetitive method of collection would have allowed for statistical analysis of sampling efficiency to determine whether hauls taken at different times in different places did indeed have significantly different catches (Barnes and Bagenal 1951; Livingston 1976). However, even with successive samples, it is difficult to determine whether variability arises from the spatial distribution of the organisms or from the gear utilized (Taylor 1953). The susceptibility of organisms to fishing gear undoubtedly has influenced perception of spatial and temporal patterns (Markle 1976). The relatively small, fine-mesh bottom trawl used in our study is selective toward capture of slower, smaller fish. The relative absence of great numbers of older, larger fish from our trawl catches cannot be attributed entirely to migration or habitat selection, but in all likelihood reflects at least partial avoidance or escapement from the 6 m trawl (Shealy et al. 1974).

Habitat differences between adult and juvenile fishes may also account for the lack of large fish in our samples. Habitat preference varies with the species and also with age (Wallace and Van der Elst 1975; White and Chittenden 1976), so that feeding and residential grounds of adult fishes often are separate from their spawning grounds and nurseries. If spatial separation exists in South Carolina waters, then our survey was biased toward collection of juveniles found primarily in the channel. However, tidal creeks of the Cooper River which are comparable in salinity to those near the intermediate and upriver stations occupied in the Santee system were dominated by young-of-the-year marine euryhaline species such as *M. undulatus, A. mitchilli, L. xanthurus, B. chrysoura*, and *Paralichthys lethostigma* (Turner and Johnson 1974). Although the importance of tidal creeks in the Santee system as nursery areas can only be inferred, it is likely that the limitation of our survey to the channel resulted in minimal estimates of juvenile abundance for the river system.

The lower estimated biomass of fishes in the Santee system and other South Carolina estuaries is a direct function of the predominance of juvenile fishes in our catches and the efficiency of the sampling gear used. Whereas the density of fish from this area compares favorably with other regions, the biomass is much less. The large biomass of fishes in New England estuaries is primarily due to large catches of winter flounder, *Pseudopleuronectes americanus* (Oviatt and Nixon 1973; Haedrich and Haedrich 1974). A comparison of biomass and density estimates from this study and others (see Table 5) which used small trawls towed in the channel with investigations which incorporated shallow tidal creek and marsh sampling (e.g., Turner and Johnson 1974) indicates that the most productive areas are the marsh-creek habitat. Because these areas of the system were not sampled and the efficiency of our gear was low, our biomass and density estimates should also be considered minimal.

The presence of juvenile fishes in the Santee system is especially important in considerations concerning the effects of rediversion. Juvenile stages of resident species and many estuarine transient species are tolerant of and may even be most abundant in lower salinity water (Gunter 1961). Therefore, we believe that the nursery habitat for resident estuarine fishes will not be detrimentally affected and may be increased by rediversion.

Because rediverted flow of water through the Santee system will be moderate compared with the tremendous discharge of freshwater (9,100 m^3/s) put into the Chesapeake Bay estuarine system by Hurricane Agnes (Chesapeake Bay Research Council 1973), we do not anticipate that juvenile fishes will be passively swept from the Santee Rivers into the coastal area. In contrast, the food supply of fishes may be altered in that supplies of benthic organisms could increase in oligohaline and brackish water areas but decrease in lower reaches of the river. This effect could be particularly detrimental if it occurred during summer. Andrews (1973) noted that floods during warm seasons cause silting and an influx of excessive nutrients and organic matter, with consequent algal blooms and stratification of waters. These factors may, in turn, lead to low dissolved oxygen conditions. During other seasons, increased accumulations of detritus caused by increased riverflow and salinity alterations could actually be beneficial to microorganisms and detritivores such as isopods, amphipods, and some decapods. Detritus also serves as the major energy base utilized by juveniles of most fish species from sea grass beds (Carr and Adams 1973) and is probably important as a direct or indirect source of food for many fishes in the Santee system.

Sustained abundance of *Penaeus setiferus* in the Santee system is questionable following rediversion. Shrimp are known detritivores, and large areas of brackish/salt marsh and estuary with substantial land runoff are considered to be conducive to good shrimp production (Bishop and Shealy 1977). Rediversion will cause waters to inundate many areas and should result in a seaward progression of freshwater and brackish water plant communities. Because the total area of estuarine habitat should effectively be moved seaward, a decrease in actual acreage available as nursery habitat may result; yet lower salinity conditions are still likely to exert the greatest influence on shrimp production. Young *P. setiferus* are most abundant in salinities $<10‰$, whereas young *P. aztecus* are most abundant in salinities from 10 to 20‰ (Gunter et al. 1964). Despite these optimum ranges, Barrett and Gillespie (1973, 1975) have suggested that an inverse relationship exists between the amount of freshwater introduced into coastal Louisiana and the catches of brown and white shrimp. Also, increased turbidity and hypertrophy may inhibit photosynthesis so that an initial reduction in oxygen may occur in bottom waters. Others (Hildebrand and Gunter 1953; Copeland 1966; Aleem 1972; Glaister 1978) have noted a positive relationship between shrimp abundance and river discharge, but not all of these studies indicated that abundance was increased within the estuary.

Blue crabs will probably be little affected by rediversion because of their high mobility and tolerance of low-salinity conditions, but increased siltation from rediversion could hamper their respiration. Although blue crab populations sustained little damage following Hurricane Agnes, mortalities in Chesapeake Bay were attributed to increases siltation, low dissolved oxygen levels, and red tide (Chesapeake Bay Research Council 1973).

[7]Van Engel, W. A., and E. B. Joseph. 1968. Characterization of coastal and estuarine fish nursery grounds as natural communities. U.S. Fish Wildl. Serv. Final Rep., 43 p.

From the available data and published literature, it appears that abundance of resident species of decapod crustaceans and fishes from the Santee system will be enhanced by rediversion if riverflow increase is gradual and properly regulated during natural freshets and warm weather periods. Such regulation will insure that salinities do not reach levels below tolerance and that hypertrophic conditions do not occur. On the other hand, the effect of rediversion on transient species such as sciaenid fishes and penaeid shrimps may not be beneficial. A decrease in nursery habitat following rediversion would lower abundance of these species. This is indicated by two aspects of our results: Both biomass and density of the South Santee River, which currently receives less freshwater input, were higher than that of the North Santee River; and both abundance and biomass of dominant species appear to be generally lower at the stations furthest upriver. Species diversity will undoubtedly decrease due to decreased utilization of the lower portion of the Santee Rivers by marine stenohaline species. Lower salinity conditions at and near the mouth should deter penetration of the estuary by these species. Whether decreased abundance of marine transients in the vicinity of the upriver stations following rediversion will be offset by more optimum salinity conditions and increased abundance nearer the mouths of the rivers is supposition. It appears that rediversion is certain; therefore, it is imperative that careful monitoring of biological and hydrographic conditions occur during and after rediversion in order to ascertain effects on the estuarine biota.

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