Temporal and Spatial Distribution of Marsh-edge and Tidal Creek Fishes in the Savannah River Estuary, Georgia and South Carolina.

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Abstract: Assessments of how the fish assemblage in the Savannah River Estuary (SRE) might be affected from a proposed harbor expansion and deepening project for the Port of Savannah, Georgia, were hindered by the lack of information about the temporal and spatial distribution of fishes in the estuary. Accordingly, we conducted a year-long investigation to determine the temporal and spatial distribution of estuarine-dependent fishes along marsh edges and in tidal creeks of the SRE. We used various seines to sample the fishes monthly at eight, 2-km long reaches of the SRE. During the fish sampling, we also measured temperature, salinity, dissolved oxygen, conductivity, and pH just below the surface (<1m) at sample sites. We used two-way ANOVA to evaluate species density and richness among seasons (spring, summer, fall, and winter) and habitats (polyhaline >15‰; mesohaline 5–15‰; oligohaline 1–5‰; and tidal freshwater <1‰). Fish sampling yielded 74 species and 21,739 individuals. Fish density and richness varied either among habitats or seasonally (P <0.01). Fish density and species richness were low in fall, increased in late winter, and peaked in spring. Spatial patterns in fish distribution were less recognizable. Most members of the fish community were estuarine generalists capable of tolerating a wide range of salinities (5.0‰–15.0‰). Marine species whose distribution was limited to areas with higher salinities (>10‰) comprised a smaller subset of the assemblage. These species occasionally invaded the estuary as the salt wedge moved inland during periods of low river discharge. Obligate freshwater species and those intolerant of salinities above 5.0‰ were a small component of the assemblage. Members of this latter group may be at the greatest risk of range contraction or population declines in the advent of increased salinities in the estuary, which would be expected if the harbor were deepened.

Key words: salinity, harbor development, fish density, species richness

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The U.S. Army Corps of Engineers operates the Savannah Harbor Navigation Project at Savannah, Georgia, and currently maintains a 12.8-m deep navigation channel for commercial deep-draft traffic. Georgia Ports Authority (GPA) operates port facilities in the upper harbor and is the largest single terminal operator in the port. The current navigation channel cannot accommodate the largest ocean-going container barges, and the GPA believes that an expanded harbor (i.e., deepening and other navigational improvements) would expand the capabilities of the port (GPA 1998). Based on a GPA-prepared feasibility report, the U.S. Congress conditionally authorized the proposed harbor deepening to accommodate ships whose draft is >12.8 m (Water Resources Development Act, WRDA 1999). Initiation of the deepening was contingent on the completion of environmental impact assessments, including potential adverse affects to the estuarine wetlands and the biota they support.

Information about the use of Savannah River Estuary (SRE) habitats by fishes and invertebrates for feeding, reproduction, and refuge from predators is limited. The scarcity of information about the system is especially acute given the size of the system and the human population base in the area. Most research and monitoring efforts have been species-specific (e.g., striped bass [*Morone saxatalis*], shortnose sturgeon [*Acipenser brevirostrum*]) (Van Den Avyle and Maynard 1994, Collins et al. 2002). In the early 1990s, two estuary-wide studies focused on the SRE. Nelson et al. (1991) compiled survey data from regional and local biologists; however, the data obtained was from expert opinion instead of actual field sampling. Concurrently, Patrick (1991) surveyed parts of the SRE to determine the extent to which the Front and Back rivers were being used by fishes for spawning, nursery area, migratory use, and residency. However, Patrick's (1991) survey did not include a complete spatial survey of the estuary or document temporal variability in fish populations; it also did not document the fish habitat required by the estuarine-dependent species present.

Evaluation of the potential effects of the proposed harbor deepening on fishes in the SRE has been hampered by the lack of recent (i.e., <10 years) data on the estuarine fish assemblage and species temporal or spatial distribution. The scarcity of recent information led to investigations of fish habitat use and distribution in the SRE as part of the environmental impact assessment of the proposed Sa-

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vannah River Harbor Expansion Project. The data presented here are the results of one aspect of this study. The goal of the present investigation was to ascertain the spatial and seasonal use of habitats by estuarine-dependent species along marsh-edge habitats and tidal creeks within the SRE. Specific objectives were: 1) determine fish density in marsh-edge and tidal creek habitats and 2) determine fish richness in marsh-edge and tidal creeks.

Study Area

The Savannah River serves as a boundary between South Carolina and Georgia and flows about 500 km in a southeasterly direction to the Atlantic Ocean. The SRE encompasses about 117,363 ha and includes the Savannah Harbor, which is a major industrial complex. The SRE also encompasses the 10,927-ha Savannah National Wildlife Refuge (NWR) and adjacent lands. The Savannah NWR and adjacent lands originally contained 21% of the tidal freshwater marsh in South Carolina and Georgia, which in turn contained one quarter of the freshwater tidal marsh along the eastern coast of the United States (Pearlstine et al. 1990). The hydrology of SRE is a complex, tidally-driven system that ties together a web of deltaic channels (Front, Middle, and Back rivers) and habitats.

Methods

Sample Locations

Eight reaches (~2.0 km long each) in the SRE were sampled monthly along marsh edges and in tidal creeks for water quality and fishes. Four reaches (SR09, SR17, SR22, and SR26) were in the main Savannah River channel (i.e., Front River), two reaches were in the Middle River (MR02 and MC0.75), and two reaches were in the Back River (BR06 and BR10). The number of the sample station (e.g., 09, 17, 22, and 26) represents the river mile from either the mouth of the Savannah River (Tybee Island) (Savannah/Front River) or the confluence of the deltaic channels (Middle and Back rivers) with the main Savannah River Channel. Exact coordinates for each sample reach as well as specific descriptions of habitat and substrates at each station are given in Jennings and Weyers (2003).

Fish Sampling

Marsh-edge Fish Assemblages.—At each reach, marsh-edge fish assemblages were sampled with a tide-assisted seine method during spring tides from June 2001 to May 2002. There were two replicates (i.e., two different seine sets) within each reach. On each sampling occasion, the seines (0.63-cm mesh, 15.2-m in length x 1.8-m in height) were set parallel to the shoreline at slack high tide in 0.5–2.0 m water depth and allowed to fish for about 1.5–3.0 h. Each seine set was made by anchoring the lead and float lines to a pair of 5-cm diameter, 3-m long, polyvinyl chloride (PVC) pipes that were driven about 0.5 m into the substrate. Juvenile and adult fishes were trapped behind the seine as the tide ebbed and water level dropped 1–2 m. The seine was retrieved by detaching the lead and float lines from the PVC posts and pulling the lead line to shore (usually < 0.5 m). The seine was then stretched out on shore or onboard a boat, and fauna were removed by hand. Large fish (>150mm) were identified, measured, and released. All other fishes were preserved in 10% formalin and returned to the laboratory at the University of Georgia for identification and enumeration. Non-fish fauna (e.g., shrimp, crabs) were released unharmed.

Tidal Creek Fish Assemblages.—Tidal Creek fish assemblages were sampled on the same days as marsh-edge seines from June 2001 to May 2002. There were two replicates (i.e., two separate tidal creeks) within each sampling station. The creeks were medium-sized (5–15 m width at high tide) and were sampled with seines (0.63-cm mesh, 9.1-m long x 2.4-m high) that contained a 2.4- x 2.4- x 2.4-m bag in the center section.

Bag seines were set at slack, high tide by stretching them across the mouths of tidal creeks and attaching the ends to PVC pipes positioned as described earlier. Bag seines were fished with a similar method to the marsh-edge seines and retrieved by detaching one end from the PVC post and pulling the free end to the other post. This action encircled fishes near the seine and forced them into the bag section. Data on fish identification and enumeration were collected as described for marsh-edge fishes.

Water Quality Sampling

Water quality data (temperature, salinity, dissolved oxygen, conductivity, and pH) at marsh edge and tidal creek sites were measured with either a YSI 6820 Multi-parameter Data Sonde or a YSI Model 85 Temp/Sal/DO/Cond meter at about 1 m depth before each fish sample was collected. These data were used to measure changes in temporal and spatial water quality parameters that could affect fish abundance, species composition, and distribution.

Seasonal and Habitat Partitioning

Seasons.—Temperatures measured during fish during surveys were used to quantify monthly and seasonal temperature regimes in the estuary. Minimum and maximum temperatures recorded in sample reaches for each month were plotted on a graph, and values showed low variability (<1 C) during a sample period. Sample temperatures within each month were used to calculate mean monthly temperatures, which were used to determine seasonal groupings Mean monthly temperatures among the seasonal groupings were compared with ANOVA. Most of the variation (P <0.0003) was explained by the seasonal groupings of fall (October, November, and December), winter (January, February), spring (March, April), and summer (May, June, July, August, and September).

Salinity-defined Habitat Zones.—Salinity data were used to partition the fish samples into salinity-defined habitat zones. The habitat zones used were a hybridization of the Venice, Biologically-Based, and NOAA estuarine-habitat classification systems and were defined as: tidal freshwater (<1.0‰), oligohaline (1.0‰–5.0‰), mesohaline (5.1‰–15.0‰), and polyhaline (>15.0‰) (Nelson et al. 1991, Bulger et al. 1993). Because tide and discharge affect salinity, samples were grouped in habitat zones based on the salinity recorded during sampling, regardless of spatial position in the estuary. This method more accurately reflected the habitat used by fishes at the time of collection.

Data Analysis

Fish density (number of fishes $2h^{-1}$), species richness (number of species $2h^{-1}$), and water quality (temperature and salinity) were used to evaluate the effects of habitat and season on fish distributions in the SRE. All data were analyzed with SAS (SAS Institute 2001) and JMP (SAS Institute 2000) software. Data were tested for homogeneity of variances with an F-max test and for normality with a Shapiro-Wilks Test (Sokal and Rohlf 1981). Variances were unequal across some of the data sets, and none of the variables were distributed normally. Transformation of values did not achieve equal variances or a normal distribution.

ANOVA has been shown to be a robust statistical test even when data do not exhibit a normal distribution (Netter et al. 1990). Therefore, group means for fish density and species richness were evaluated with two-way ANOVA ($\alpha = 0.10$) to determine the effects of habitat and season on these variables. Temporal trends in fish density and species richness were evaluated by analyzing seasonal differences within each habitat (e.g., polyhaline-fall, polyhaline-winter, polyhaline-spring, and polyhaline-summer). Spatial trends in fish density and species richness were evaluated by analyzing habitat differences within each season (e.g., fall-polyhaline, fall-mesohaline, fall-oligohaline, and fall-tidal fresh).

Results

Water Quality

Water temperatures throughout the estuary were stable within habitats but varied among seasons. Mean water temperatures in the sample reaches of the SRE ranged from 13.8 ± 1.1 C in winter to 27.2 ± 1.6 C during summer. Mean temperature was lowest (13.1 ± 0.78 C) in February and highest (29.3 ± 0.80 C) in August.

Surface salinities in the SRE were highly variable at most of the sample stations and generally decreased with increasing river mile (i.e., going upstream). This variability was based on tidal cycle (increased during high tide and decreased during low), and the change was sufficiently large to cause the sample reach's salinity classification to change (i.e., polyhaline to mesohaline). Salinities at stations at the up- and downstream ends of the study reach tended to be less variable than salinities at stations in the middle of the study reach.

Fish Sampling

Marsh-edge Fish Surveys.—One hundred ninety-two marsh-edge seine sets (96 sampling occasions with 2 replicates per reach) were conducted in the SRE. Of these 96 samples, most were from mesohaline (39) and tidal freshwater (24) habitats (Table 1). Twenty-seven families comprising 56 species and 4,182 individuals were caught between June 2001 and May 2002. Most of the fishes (77%) were captured at BR10, SR26, MR02, and BR06. Mesohaline-spring had the highest fish abundance and mesohaline-summer was the most speciose (Table 1). Bay anchovy *Anchoa mitchelli* (1,344), spot *Leiostomus xanthurus* (765), Atlantic menhaden *Brevoortia tyrannus* (668), silver perch *Bairdiella chrysoura* (250), freshwater goby *Gobionellus shufeldti* (228), and southern flounder *Paralichthys lethostigma* (198) were the most abundant species caught in the seines and comprised 83% of the fishes collected. Many species were caught from multiple habitats; 12 species oc-

Table 1. Total number of species and individuals collected in each habitat and season during marsh-edge seine surveys conducted in the Savannah River Estuary, Georgia and South Carolina from June 2001 to May 2002.

	Number of species					Number of individuals				
Habitat (*n* samples)	Total	Fall	Winter	Spring	Summer	Total	Fall	Winter	Spring	Summer
Polyhaline (11)	29	8	9	8	20	360	49	40	55	216
Mesohaline (39)	33	14	10	14	23	1,898	136	101	1,319	342
Oligohaline (22)	27	11	8	14	16	1,367	264	282	600	221
Tidal freshwater (24)	28	7	5	6	21	557	133	13	86	325
Total all (96)	56	21	16	21	44	4,182	582	436	2,060	1,104

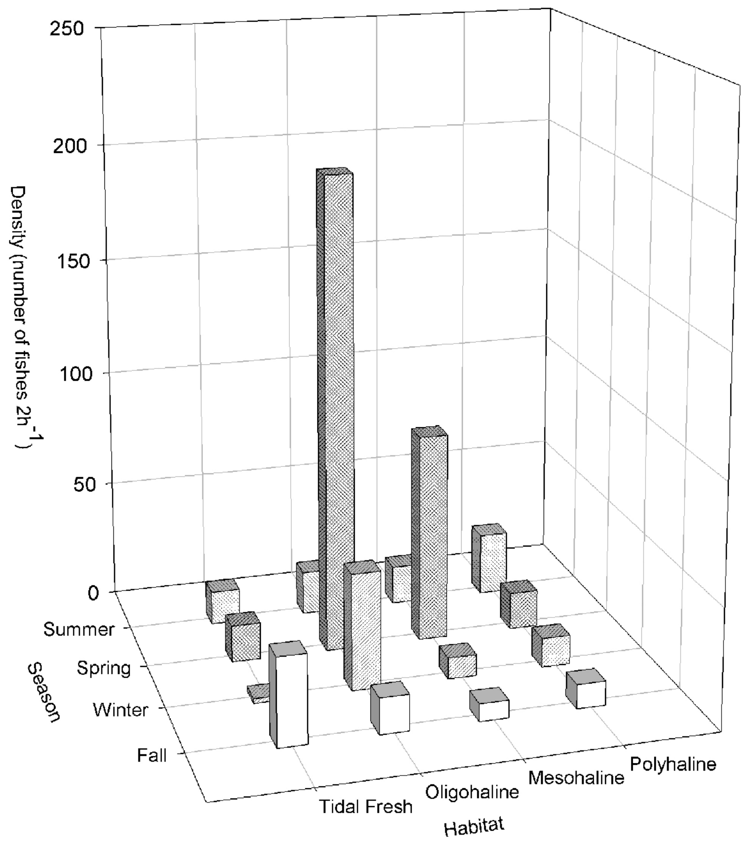

Figure 1. Mean fish density by habitat and season estimated from marsh-edge surveys conducted in the Savannah River Estuary, Georgia and South Carolina from June 2001 to May 2002.

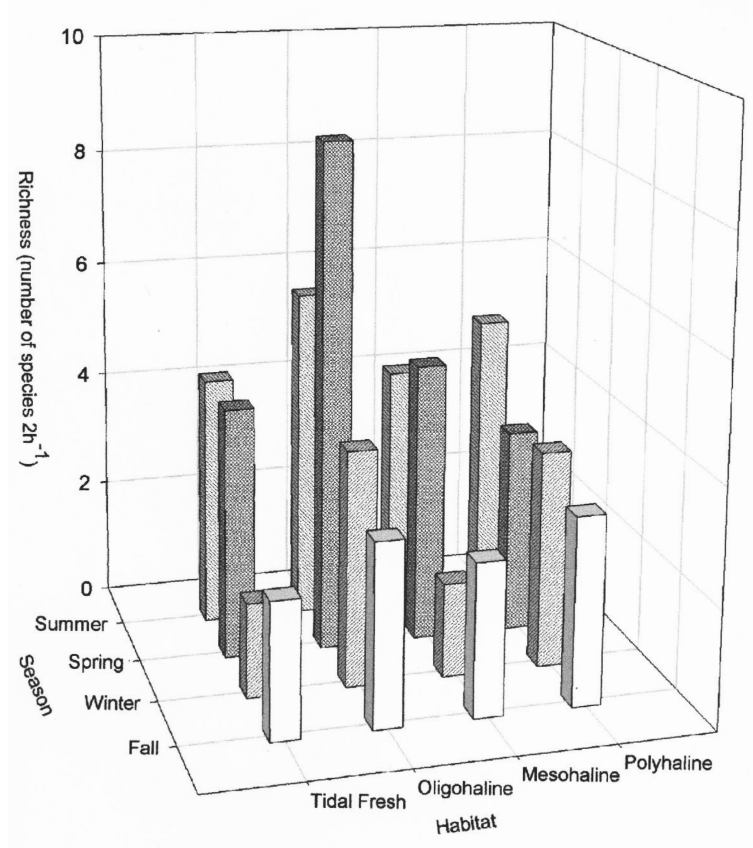

Figure 2. Mean fish species richness by habitat and season estimated from marsh-edge surveys conducted in the Savannah River Estuary, Georgia and South Carolina from June 2001 to May 2002.

curred across all habitats, and 27 species were found exclusively in a single habitat. Most species (31) were collected only in a single season, but seven species occurred in all four seasons. A complete list of species captured (by season and by habitat) in marsh-edge habitats of the SRE is given in Jennings and Weyers (2003).

Mean fish density ranged from 200.5 ± 134.0 in oligohaline-spring samples to 1.9 ± 0.3 in tidal freshwater-winter samples. Mean fish density did not differ among habitats ($P = 0.12$), but was significantly higher ($P = 0.005$) in spring compared to densities in fall, winter, and summer (Figure 1). There also were significant differences among the habitat-season interactions ($P = 0.02$). Densities in mesohaline- and oligohaline-spring were higher than densities in mesohaline- and oligohaline-fall, -winter, and -summer seasons. In polyhaline and tidal freshwater habitats, densities were similar in all seasons (Figure 1). Density in spring-oligohaline habitats was higher than densities in spring-polyhaline, -mesohaline, and -tidal freshwater habitats. Density in spring-mesohaline habitats was higher than densities in spring-polyhaline and -tidal freshwater habitats. In the other three seasons, density was similar for all habitat types (Figure 1).

Mean species richness ranged from 8.7 ± 0.8 in oligohaline-spring to 1.6 ± 0.3 in mesohaline- and 1.6 ± 0.5 in tidal freshwater-winter samples. Mean species richness was similar among habitats ($P = 0.21$) and among habitat*season interactions (P=0.89), but spring and summer richness were significantly higher than fall and winter richness ($P = 0.03$; Figure 2).

Tidal Creek Fish Surveys.—One hundred ninety-two tidal creek sets (96 sampling occasions with 2 replicates per reach) were conducted in the SRE. Of these 96 samples, most were from mesohaline (39) and tidal freshwater (24) habitats (Table 2). Thirty families comprising 66 species and 17,557 individuals were caught between June 2001 and May 2002 (Table 2). Most of the fishes (72%) were captured at BR10, BR06, SR17, and MR02 . Bay anchovy (5,567), spot (5,021), blueback herring *Alosa aestivalis* (1,596), mummichog *Fundulus heteroclitus* (1,233), and striped mullet *Mugil cephalus* (1,180) were the most abundant species caught in the tidal creeks and comprised 83% of the total catch. Many species were collected from multiple habitats, 10 species occurred across all habitats, and 29 species were found exclusively in a single habitat.

Table 2. Total number of species and individuals collected in each habitat and season during tidal creek surveys conducted in the Savannah River Estuary, Georgia and South Carolina from June 2001 to May 2002.

	Number of species					Number of individuals				
Habitat (*n* samples)	**Total**	**Fall**	**Winter**	**Spring**	**Summer**	**Total**	**Fall**	**Winter**	**Spring**	**Summer**
Polyhaline (11)	20	11	8	6	13	1,139	38	55	472	574
Mesohaline (39)	46	27	14	18	37	7,942	958	314	3,697	2,973
Oligohaline (22)	37	15	11	18	27	6,358	792	953	1,964	2,649
Tidal freshwater (24)	34	16	7	12	28	2,118	246	58	21	1,793
Total all (96)	66	38	20	25	54	17,557	2,034	1,380	6,154	7,989

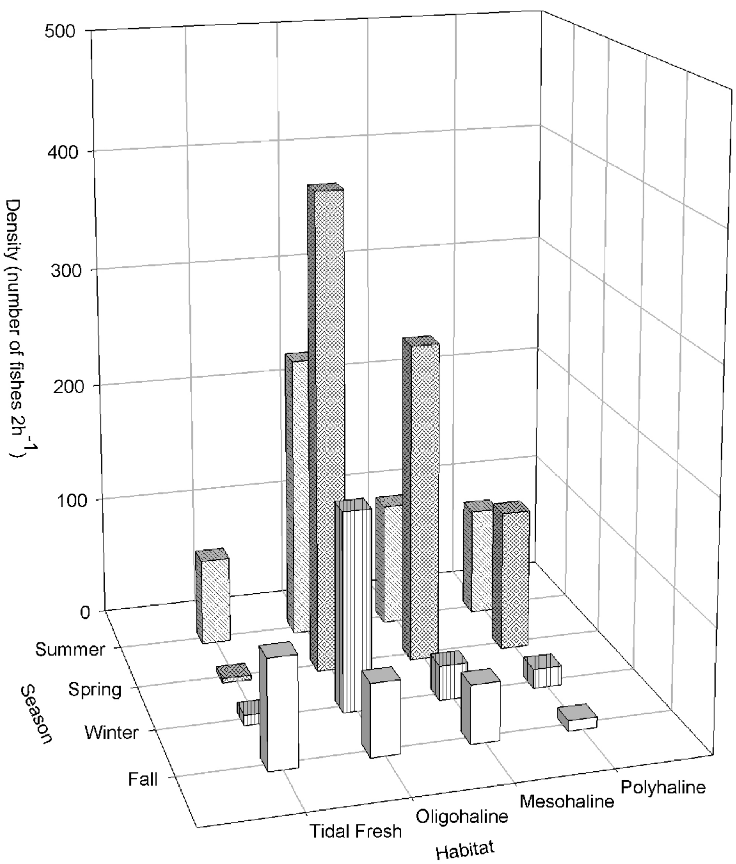

Figure 3. Mean fish density by habitat and season estimated from tidal creek surveys conducted in the Savannah River Estuary, Georgia and South Carolina from June 2001 to May 2002.

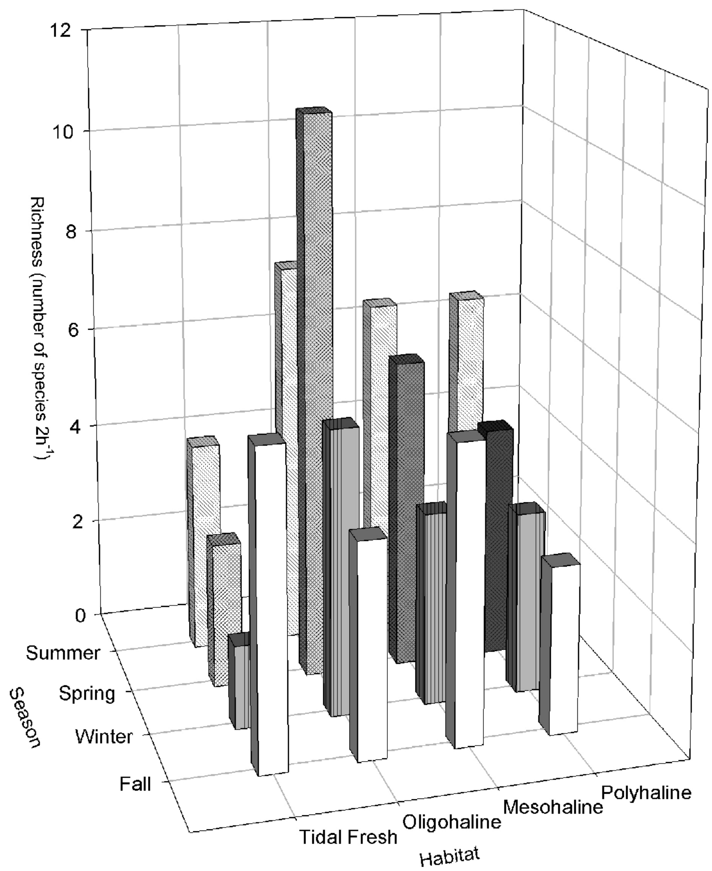

Figure 4. Mean fish species richness estimated from tidal creek surveys conducted in the Savannah River Estuary, Georgia and South Carolina from June 2001 to May 2002.

Fourteen species occurred in all four seasons, and 26 species were exclusive to a single season. A complete list of species captured (by season) in tidal creeks of the SRE is given in Jennings and Weyers (2003).

Mean density ranged from 393.8 ± 328.5 in oligohaline-spring samples to 3.7 ± 1.2 in the tidal freshwater-winter samples. Mean fish density in tidal creeks was significantly higher in oligohaline habitat compared to mean fish density in polyhaline and tidal freshwater habitats ($P = 0.07$; Figure 3). Mean fish densities were not different among seasons ($P = 0.13$) or the habitat*season interactions ($P = 0.81$).

Mean species richness ranged from 10.9 ± 1.1 in oligohaline-spring samples to 1.6 ± 0.4 in tidal freshwater-winter samples. Mean species richness in tidal creeks was significantly higher in oligohaline habitat than richness in polyhaline and tidal freshwater habitats; richness in mesohaline habitats also was significantly higher than richness in tidal freshwater habitats different among habitats ($P = 0.009$; Figure 4). Seasonally, richness during summer was higher than richness during fall and winter, and richness in spring was significantly higher than richness during winter ($P = 0.02$; Figure 4). Mean species richness was not different for habitat*season interactions ($P = 0.13$).

Discussion

Fish Distribution-temporally

Surface temperature in the SRE was consistent spatially among sample reaches and across habitats over short-term temporal scales. For each sample period, temperatures recorded at the farthest down river reach (SR09) were similar to measurements at the farthest up river reach (SR26). Likewise, temperatures at Back River reaches and Middle River reaches were similar to Front River reaches. Polyhaline habitat had similar temperatures to mesohaline, oligohaline, and tidal freshwater habitats. Because differences in temperature were small (<2.0 C), temperature probably did not affect short-term distribution of fish populations.

Temperature did vary considerably from season to season, and this seasonal variability probably influenced fish distribution in the SRE. Seasonal changes in the distribution of estuarine fishes have been documented in other estuaries worldwide (Hoff and Ibara 1977, Loneragan et al. 1989, Yoklavich et al. 1991, Rakocinski et al. 1992, Yoklavich et al. 1992). Moderate temporal variability (i.e., seasons) can affect fish distributions by increasing or decreasing abundances of some species. In this study, mean fish density and species richness in the SRE were significantly lower during fall than in other seasons. Some abundant species (e.g., Atlantic croaker *Micropogonias undulatus*, Atlantic menhaden, bay anchovy, blueback herring, spot, and striped mullet) were present in fall, but occurred at much lower abundances than in other seasons. Many species caught in other seasons virtually disappeared from sample reaches in fall. These taxa (e.g., drums and seatrouts (Sciaenidae), porgies (Sparidae), gobies (Gobiidae), jacks (Carangidae), hogchokers *Trinectes maculatus,* mummichogs, and tonguefish *Symphurus plagiusa*) either declined in numbers or completely left sample reaches in late summer and early fall, and their abundances did not increase again until the following spring and summer.

The decline in fish density and species richness in fall probably was related to a decline in spawning activity and some emigration of species from the sample area. Spawning activity in estuarine environments generally declines when water temperatures rise above 27 C (Lippson and Moran 1974, Able and Fahay 1998). These temperatures were recorded estuary-wide in the SRE in late summer.

Fish Distribution-Spatially

Variability of habitat use by estuarine species in sample reaches probably can be attributed to the dynamic nature of salinity distribution. Surface salinity in sample reaches varied considerably and was affected most by tidal fluctuation and to some extent river discharge. In the SRE, all sample reaches experienced a 2.3- to 2.9-m tidal fluctuation depending on tidal period (spring or neap), and habitat classification (e.g., polyhaline, mesohaline, oligohaline, tidal freshwater) for most reaches changed at high and low tide. In reaches such as SR17 and BR06, salinity at high tide was sometimes 5‰–10‰ higher than salinity at low tide, which indicates that several different salinities had dominated the same area in a 6-h period. Although still tidally influenced, salinity rarely increased above 1‰ in reaches SR26 and MC0.75, which resulted in extended periods of freshwater habitat in these areas. Low river discharge during many months of the 12-month study resulted in increased salinities estuary-wide, including upper estuary areas around SR22, MR02, and BR10 (Jennings and Weyers 2003).

Salinity can affect species assemblages and fish abundances in estuarine environments (Hoff and Ibara 1977, Yoklavich et. al. 1991, Paperno et. al. 2001). Many of the fishes collected during the present study seemed to be estuarine generalists {(e.g., anchovies (Engraulidae), shad and herrings (Clupeidae), drums (Sciaenidae), and flatfishes (Bothidae, Cynoglossidae)}. Juveniles and adults of these species were present in the SRE most of the year, and they used most of the habitats in the sample reaches.

The temporal and spatial extent of various habitats in the SRE can be critical to the degree of spawning success of some species in the system (e.g., striped bass) (Van Den Avyle and Maynard 1994). Further, spawning success or the lack thereof among some species could determine the fate of other estuarine species. For example, many estuarine generalists are major prey for larger commercial and recreational fishes, and temporal and spatial differences in peak abundance of various prey species probably provide high biomass for year-round predators. Changes in temporal and spatial patterns that affect survival and growth of prey species could result in changes in the abundance of economically important species.

Migratory marine species typically enter estuaries during summer to exploit the productivity of the estuarine environment (Dando 1984, Loneragan et al. 1989, Yocklavich et al. 1991, Able and Fahay 1998). These fishes are capable of tolerating salinities that are lower than salinities in marine habitats and can use polyhaline and mesohaline habitats of an estuary. In polyhaline and mesohaline habitat, fish density and species richness increased in late spring and summer with the influx of marine opportunist species such as Atlantic bumper, blackcheek tonguefish, filefish *Monacanthus hispidus,* leatherjacket *Oligoplites saurus*, rough silverside *Menidia martinica,* Atlantic silverside *Menidia menidia,* sea robin *Prionotus* sp., and striped burrfish *Chilomycterus schoepfi*. These species were collected only in the high-salinity habitats at BR06, SR17, and SR09 and occurred in low abundances.

Predominantly freshwater fishes such as largemouth bass *Micropterus salmoides*, catfish *Ictalurus spp.*, black crappie *Pomoxis nigromaculatus*, longnose gar *Lepisosteus osseus*, minnows Cyprinidae, and sunfish *Lepomis* spp. were found in low salinity oligohaline and tidal freshwater areas. Abundances for freshwater fishes were highest in spring. High river discharge in spring and early summer probably made conditions favorable for these species to move down the river and exploit the tidal freshwater areas of the upper estuary around SR22, SR26, MC0.75, MR02, and BR10. Spatial changes in salinity distribution might either expand or contract ranges of these species.

Conclusions

The Savannah River Estuary is a dynamic system characterized by high tidal fluctuation, which causes spatial shifts in various salinity-defined habitats. Changes in habitat in many areas occurred every six hours, and these habitats also were influenced by seasonal changes in river discharge. As a result, the SRE supported a diverse and abundant fish community that was dependent on the availability of these specific salinity-defined habitat zones. If the planned harbor expansion and deepening project proceeds at the Port of Savannah, then salinities in the SRE will increase. The degree of salinity increase and potential changes to the fish assemblage will be dependent on the extent of river channel modification. Increased salinities in the SRE will have somewhat predictable consequences for the fish community, most of which were estuarine generalists capable of tolerating a wide range of salinities (1‰–15‰). A smaller subset of the assemblage can be characterized as marine species whose distribution was limited to areas with higher salinities (>10‰); these species occasionally invade the estuaries as the salt wedge moves inland during periods of low river discharge. Obligate freshwater species and those that could not tolerate salinities above 5.0‰ were not as abundant as the euryhaline species. Therefore, the salinity-intolerant species in the SRE would be at the greatest risk of range contraction or population declines in the advent of increased salinities in the estuary. Finally, the fate of freshwater species or marine species may be useful indicators for evaluating the degree and directionality of changes to the various salinity-defined habitat zones in the SRE and fate of the fish communities the system supports.

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Literature Cited

Able, K. W. and M. P. Fahay. 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press. New Brunswick, New Jersey.

Bulger, A. J., B. P. Hayden, M. E. Monaco, D. M. Nelson, M. G. McCormick-Ray. Biologically-based estuarine salinity zones derived from a multivariate analysis. Estuaries 16:311–322.

Collins, M. R., W. C. Post, D. C. Russ, and T. I. J. Smith. 2002. Habitat use and movements of juvenile shortnose sturgeon in the Savannah River, Georgia–South Carolina. Transactions of the American Fisheries Society 131: 975–979.

Dando, P. R. 1984. Reproduction in estuarine fish. Pages 155–170 *in* G. W. Potts and R. J. Wooton, editors. Fish reproduction strategies and tactics. Academic Press. London.

Georgia Ports Authority (GPA). 1998. Savannah Harbor Expansion Feasibility Study Report. Savannah, Georgia.

Hoff, J. G. and R. M. Ibara. 1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a Southeastern New England estuary. Estuarine and Coastal Marine Science 5:665–678.

Jennings, C. A. and R. S. Weyers. 2003. Spatial and temporal distribution of estuarine-dependant species in the Savannah River Estuary. Report of the Georgia Cooperative Fish and Wildlife Research Unit to Georgia Ports Authority. Savannah, Georgia.

Lippson, A. J. and R. L. Moran. 1974. Manual for the identification of early developmental stages of fishes of the Potomac River Estuary. Maryland Department of Natural Resources. Baltimore, Maryland.

Loneragan, N. R., I. C. Potter, and R. C. J. Lenanton. 1989. Influence of site, season, and year on contributions made by marine, estuarine, diadromous, and freshwater species to the fish fauna of a temperate Australian estuary. Marine Biology 103:461–479.

Nelson, D. M., E. A. Irlandi, L. R. Settle, M. E. Monaco, and L. Coston-Clements. 1991. Distribution and Abundance of Fishes in Southeast Estuaries. Estuarine Living Marine Resources Report No. 9. National Oceanic and Atmospheric Administration (NOAA)/ National Ocean Service (NOS) Strategic Environmental Assessments Division, Silver Spring, Maryland.

Netter, J., W. A. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs, third edition. Irwin Publishing Co. Homewood, Illinois.

Paperno, R., K. J. Mille, and E. Kadison. 2001. Patterns in species composition of fish and selected invertebrate assemblages in estuarine subregions near Ponce de Leon Inlet, Florida. Estuarine, Coastal and Shelf Science 52:117–130.

Patrick, R. 1991. Biological Studies of the Savannah Estuary, Georgia, for the Savannah Chamber of Commerce. Parts 1, 2, and 3, 1989–1990. Division of Environmental Research. The Academy of Natural Sciences. Philadelphia, Pennsylvania.

Pearlstine, L., P. Latham, W. Kitchens and R. Bartleson. 1990. Development and application of a habitat succession model for the wetland complex of the Savannah National Wildlife Refuge. Volume II. Final Report. U.S. Fish and Wildlife Service, Savannah, Georgia.

Rakocinski, C. F., D. M. Baltz, and J. W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. Marine Ecology Progress Series 80: 135–148.

SAS Institute. 2000. JMP Statistics Version 4.0. Cary, North Carolina.

———. 2001. SAS User Version 8. Cary, North Carolina.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research, Second edition. W. H. Freeman and Co. New York.

Van Den Avyle, M. J. and M. A. Maynard. 1994. Effects of saltwater intrusion and flow diversion on reproductive success of striped bass in the Savannah River Estuary. Transactions of the American Fisheries Society 123:886–903.

Water Resources Development Act (WRDA). 1999. Publication L 106–053. 17 August 1999. STAT 269. Federal Register 74 (161).

Yoklavich, M. M., G. M. Cailliet, J. P. Barry, D. A. Ambrose, and B. S. Antrim. 1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. Estuaries 14:465–480.

———, M. Stevenson, and G. M. Cailliet. 1992. Seasonal and spatial patterns of ichthyoplankton abundance in Elkhorn Slough, California. Estuarine, Coastal, and Shelf Science 34:109–126.