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Multiple Determinants of Community Structure in Shallow Marsh Habitats, Cape Fear River Estuary, North Carolina, USA

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Abstract

The nekton of tidal creeks was studied at 17 sampling localities from September 1977 through August 1978, in the Cape Fear River estuary, North Carolina, USA. Prior to these dates, collections were made at 9 stations beginning in January 1977; these data were used to supplement conclusions drawn from the larger effort. Species recruited from the ocean utilized marsh habitats only temporarily and dominated the catches with over 70% of the total abundance. Their distribution was influenced by salinity gradients and to a lesser extent by substrate characteristics. In addition, temporal habitat partitioning with associated size differences of related species played an important role in structuring marsh nekton communities. A clearly defined ecotone was associated with the mesohaline-polyhaline transition zone, in salinities between 14 and 21‰ S. Numerous marine stenohaline forms were restricted to salinities above 16‰ S, thus increasing species richness in high salinity marshes. Despite differences in freshwater flows in 1977 and 1978, major features of the various marsh communities (species associations and relative abundances) exhibited little change throughout the Cape Fear estuary, indicating that these communities were relatively persistent in time. Standing crops for ocean-spawned species at the end of the growing season indicated that considerable annual export in the form of living biomass of fish and shellfish takes place from the marshes. Since most individuals of these species return to the ocean in the fall, an important energy link between the marshes and nearshore marine environment is demonstrated.

Introduction

Shallow marsh habitats rank among the most productive zones of estuaries for standing crops of fish and shellfish (Marshall, 1976; Meredith and Lotrich, 1979; Weinstein, 1979). Transient species, recruited primarily from the ocean and residing in the marshes during their early life stages, form a conspicuous seasonal component of the marsh fauna and may play an important role in the organization of marsh communities. Because they return to the ocean as juveniles or maturing adults, they may also create an important link for energy transfer from the estuary to the marine environment.

The impact of these species on marsh communities is further mediated by their differential utilization of specific portions of the estuary. Selection of ultimate residence zones is partly governed by physicochemical factors: salinity (Remane, 1934; Hedgpeth, 1957; Gunter, 1961, 1967; Khlebovich, 1969; Boesch, 1977) and substrate characteristics (directly or indirectly affecting food supplies–DeSylva, 1975; Mills, 1975). These factors act to create a mosaic of distinct faunal assemblages within the estuary. Their role in governing species distributions within the marsh drainage system (tidal creeks) has been investigated only recently (Dahlberg and Odum, 1970; Dahlberg, 1972; Subrahmanyam and Drake, 1975; Cain and Dean, 1976; Hackney *et al.*, 1976; Weinstein, 1979).

The role transient species play in structuring marsh communities, the influence of salinity gradients and other variables on distributions of these (and other) species, and the measurement of living biomass exported from the marshes in the form of fish and shellfish tissue, is the subject of this paper. We examine the link between the marshes (and other shallow productive zones of the estuary) and the nearshore marine environ, and further establish the interdependence of these 2 areas and the spatial and temporal continuum that exists between them.

Materials and Methods

Seventeen stations were established in tidal creeks and along the river shoals adjacent to the marsh fringe (Fig. 1,

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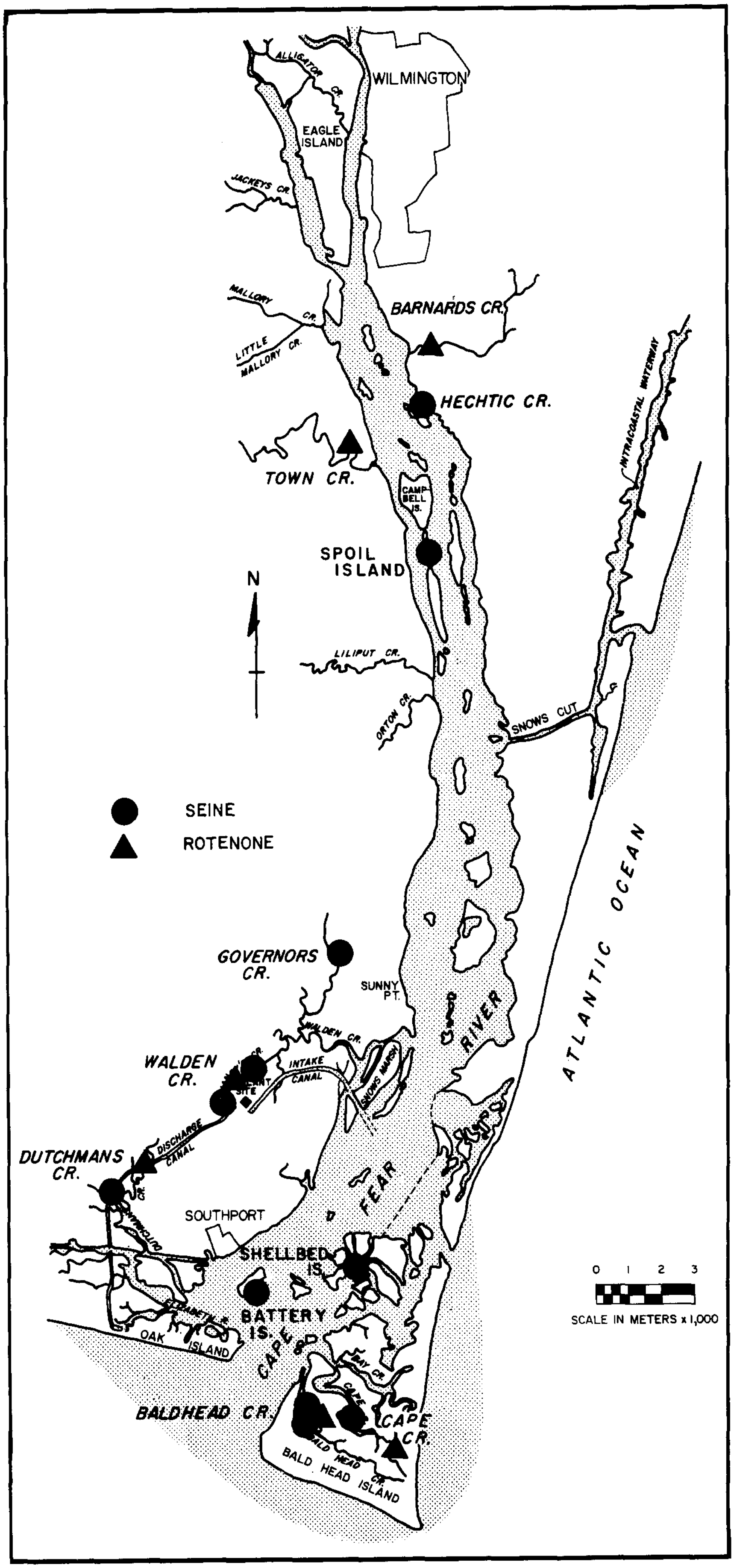

Fig. 1. Seine and rotenone sampling sites, Cape Fear River estuary, North Carolina, USA

Table 1. Sampling localities for collections of fishes and invertebrates, Cape Fear River estuary, North Carolina, including physicochemical data. D = approximate distance from river mouth to creek entrance; SD = standard deviation; MPS = median particle size; SC = sorting coefficient

				Sediment parameters								
Station	Method	Locality	D (km)	Salinity (± SD) ‰	Temperature (± SD) C	Sand (%) Medium	Sand (%) Fine	Silt and clay (%)	Percent organics	MPS (mm)	S.C. (I)	Number of cores
Baldhead Cr. 1	Seine	Tidal Creek	0.9	22.1(6.9)	19.5(8.6)	13	86	1	1.88	0.23	0.65	7
Baldhead Cr. 2	Seine	Tidal Creek	0.9	22.3(6.7)	20.1(9.3)	19	80	1	0.94	0.25	0.75	3
Baldhead Cr	Rotenone	Tidal Creek	0.9	22.0(6.4)	19.9(8.4)	34	65	1	1.13	0.34	0.80	6
Cape Cr.	Seine	Tidal Creek	1.9	22.2(5.5)	19.9(8.0)	17	82	1	0.93	0.26	0.69	6
Cape Cr.	Rotenone	Tidal Creek	1.9	22.4(5.5)	21.1(8.6)	18	75	6	6.17	0.25	1.02	3
Battery Is.	Seine	River Shoal	3.1	24.9(6.1)	19.5(7.8)	28	69	3	2.35	0.28	1.02	2
Shellbed Is.	Seine	River Shoal	4.6	21.4(7.6)	18.6(8.9)	7	93	1	0.77	0.23	0.60	3
Dutchman Cr.	Seine	Tidal Creek	6.6	19.3(5.5)	18.4(8.1)	10	86	4	2.67	0.21	0.79	7
Dutchman Cr.	Rotenone	Tidal Creek	6.6	14.2(6.8)	18.8(7.8)	20	66	14	10.42	0.20	1.31	4
Walden Cr. 1	Seine	Tidal Creek	9.7	5.0(3.2)	19.9(8.0)	12	87	1	0.80	0.22	0.59	6
Walden Cr. 2	Seine	Tidal Creek	9.7	4.4(2.7)	19.3(8.2)	7	81	12	1.53	0.17	0.88	3
Walden Cr.	Rotenone	Tidal Creek	9.7	4.8(3.0)	20.1(8.4)	12	87	1	0.43	0.25	0.56	3
Governors Cr.	Seine	Tidal Creek	9.7	2.2(2.3)	19.7(8.4)	21	78	1	0.67	0.31	0.54	5
Spoil Is.	Seine	River Shoal	28.8	3.0(2.6)	16.8(8.0)	41	58	1	0.30	0.38	0.81	3
Town Cr.	Rotenone	Brackish Stream	30.7	2.2(3.3)	18.1(9.3)	26	59	14	30.50	0.24	1.38	3
Hechtic Cr.	Seine	River Shoal	33.6	2.5(3.2)	19.0(7.9)	27	66	7	2.30	0.28	1.13	6
Barnards Cr.	Rotenone	Brackish Stream	33.9	1.7(2.3)	17.4(7.3)	8	86	6	33.17	0.25	0.72	3

Table 1). Previously, Weinstein (1979) described the study area and reported on the results of the first year's effort at 9 of these stations, sampled monthly from January through December 1977. In September 1977, the program was expanded to include 8 additional sites, although collections were not successful at 2 of them in this month. These collections (September 1977 through August 1978) form the basis of community analysis in this paper. However, the entire 20-month sampling effort will be drawn upon to evaluate changes in the nekton community and to compare the population dynamics of successive year classes of fish and shellfish. Pertinent habitat data for all sites are presented in Table 1.

Approximately 400 m^2 sections of tidal creeks or shoal areas were blocked with 20 m, 1.0 mm mesh seines. These areas were then swept repetitively with seines, or rotenone (Fish-tox) was added to the site and surfacing fish were collected with dipnets. In the latter procedure, dead fish were also collected along the shoreline and from the downstream blocknet. Preliminary seining efforts (Weinstein, 1979; his Fig. 2) indicated that 8 sweeps of a 7.6 m, 6.5 mm mesh seine were sufficient to produce nearly asymptotic species number (S), H' (Shannon and Weaver, 1949), and ENS (Hurlburt, 1971) accumulation curves. To these, 3 additional sweeps of a 7.6 m, 1.0 mm mesh seine were added and this significantly reduced the lower size range of many post-larval fish captured (Weinstein, 1979). Marked fish experiments (Weinstein and Davis, 1979) demonstrated the effectiveness of the blocking procedure. Because all collections were made as close to low tide as possible, the effect of tidal currents on the sampling procedure was also minimized.

The nekton was preserved in 10% formalin, and standard length (carapace width for crabs, total length for shrimp) was recorded for selected species. Subsampling for lengths was employed when sorted collections contained more than 100 individuals of a given species. After sorting, composite wet weight was recorded for each species (separated by age groups whenever possible). Prior to each collection, temperature and salinity were recorded with a Beckman (Model RS5-3) salinometer. The instrument was calibrated prior to each monthly sampling trip by a known resistor, and periodically checked against salinity standards. Densities for all collections were reported as the number of individuals per 400 m^2, the average surface area of the sites.

Sediment Cores

Three to 7 sediment cores (0.01 m^2, 5 cm deep) were collected at each station, the frequency depending on the uniformity of the substratum (Weinstein, 1979). Cores were processed according to procedures described by the American Society for Testing and Materials (ASTM, 1963). Hydrometer analysis was used for the fine sediment fraction. Particle size descriptions and sorting characteristics were based on the unified scale (Corps of Engineers, 1953) and formulae of Folk (1974).

Classification Analysis

General features of Cape Fear estuary marsh communities were compared by numerical classification analysis employing both "normal" and "inverse" classification schemes (Clifford and Stephenson, 1975). The former method groups sites by their species attributes and the latter method groups species according to their site of occurrence (i.e., the sites become the attributes of the species; Clifford and Stephenson, 1975). Similarity between sites or between species was calculated with the Percent Similarity Index (Whittaker and Fairbanks, 1958):

$$\mathrm{PSI} = 100\ \Sigma \min (p_{ia}, p_{ib}),$$

where p_{ia} and p_{ib} are the proportions of species i in samples a and b ("normal"), or the proportion of species a and b at Site i ("inverse"). For each of these comparisons, separate matrices were constructed for pooled monthly data and clustered by the unweighted pair group-averaged method (Sneath and Sokal, 1973). All taxa not identified to species (except *Paralichthys* spp., a dominant taxon) and singletons were eliminated prior to clustering; the data were then log-transformed to give added emphasis to less common species and to decrease the effect of extreme values (Clifford and Stephenson, 1975). Dendrograms of station and species similarity were constructed from seine data comparisons, and also were cross-referenced in a two-way coincidence table (Clifford and Stephenson, 1975).

Ordination

Binary discrimination analysis (BDA) (Strahler, 1978a) and direct ordination (Whittaker, 1967) were employed in this study in an attempt to relate species distributions to salinity gradients. BDA is a multistep procedure which operates on binary (presence-absence) data within ordered categories. It requires initial construction of a 2xK contingency table for each combination of species presence or absence and site factor (salinity category). In our case, the K rows were selected to represent intervals of salinity based on a modified version of the Venice system (Khlebovich, 1969), a scheme chosen to be biologically meaningful in the context of physiological limitations imposed on nekton occupying estuaries (Remane, 1934; Khlebovich, 1969; Gainey and Greenberg, 1977). Pearson χ^2 tests were then applied to these species presence-absence data to determine whether or not species presence was related to any of the salinity categories. When such a relationship was demonstrated, standardized contingency table residuals (Haberman, 1973) were computed and then subjected to a Principal Components Analysis (Morrison, 1967). The conversion to standardized residuals allowed species to be compared on an equal footing and by convention; a positive value was taken to indicate a preference for an environmental group (Strahler, 1978a). Principal components scores for the species involved were subsequently plotted in a two-dimensional array.

Direct ordination consisted of calculating catch-per-unit-effort (CPUE) for 5‰ salinity increments and fitting smoothed curves to the data (Whittaker, 1967). Results of this analysis were then compared to those derived from the BDA.

Ridit Analysis

Because of discontinuities in the gradients for several sediment parameters (Table 1), a less vigorous treatment for relationships with substratum characteristics was employed. Ridit analysis (Bross, 1958) is a computationally simple statistical technique for the analysis of categorical data when the categories are ordered, but no other assumptions can be made. First, a reference distribution was selected; this was the distribution of all samples among the categories of the environmental variable (substratum characteristics). Categories were chosen to provide maximum resolution of relationships with substratum parameters but, at the same time, to avoid zero entry cells. Thus, for example, 5 categories were used for percent organics (Table 1): 0-1, 1-2, 2-3, 3-15 and > 15%.

The ridit for each category is defined to be one-half the proportion of samples in that category plus the proportion of samples in all lesser categories. An average ridit is then computed for each species:

$$\bar{r}_i = \sum_{j=1}^{k} N_{ij}\,\rho_j \Big/ \sum_{j=1}^{K} N_{ij},$$

where P_j is the ridit for category j, and N_{ij} is the number of samples in category j in which species i is present. A species having an average ridit greater than 0.5 demonstrates a positive relationship with the environmental variable. Conversely, an average ridit of less than 0.5 may be taken as a negative relationship. Tests for significant departures (z-tests) from the reference distribution were performed for each species used in the analysis.

Results

Physicochemical Parameters

Salinities at marsh sites generally fell into 2 patterns (Table 1, Fig. 2). Stations at Baldhead Island and vicinity (Battery and Shellbed Islands) and the Dutchman Creek seine station were characterized by values exceeding 16‰ S (reference line in Fig. 2). Exceptions to this trend occured in January and May 1978 during periods of high river flows. Mean salinity at the Dutchman Creek rotenone site, however, was slightly lower than at the seine site (Table 1), mainly as the result of local freshwater input. Salinities in Walden Creek (including Governor's Creek) did not exceed 16‰ S during the study period, although values above this level were reported in July and August of 1977 (Weinstein, 1979). They also did not exceed 16‰ S during the entire 20-month study at upriver marsh sites (Fig. 1). Although the entrance to the Walden Creek system is located only 9.7 km upstream from the river mouth, extensive local drainage maintained reduced salinities at this locale (compare means in Table 1). The lack of full spatial coverage along the estuary axis because of site inacces-

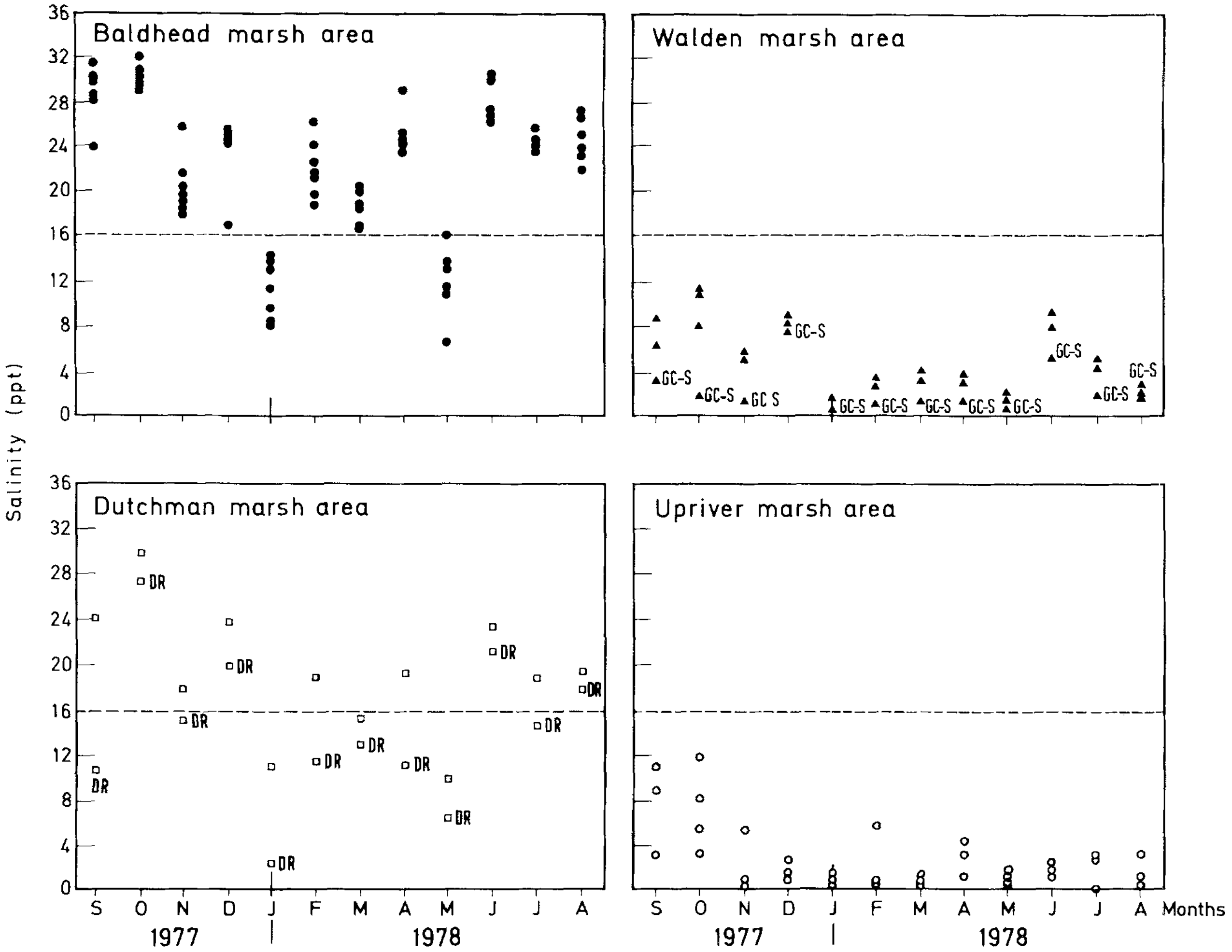

Fig. 2. Monthly salinity values at all stations. A reference line is placed at 16‰ S, between the mesohaline and polyhaline boundary. Dr = Dutchman Creek rotenone site; GC-S = Governor's Creek seine site

sibility or logistical constraints, has created some gaps in the spacing of mean values along the salinity gradient. For example, note the absence of values between approximately 5 and 14‰ S (Table 1). Variability within sites was expectedly high, however, and we concluded that a sufficient range of salinities were covered to yield meaningful results on the role of salinity in influencing Cape Fear estuary nekton communities.

Sediment characteristics varied among the areas sampled (Table 1). Most sites had primarily sandy substrates; however, these were complemented with variable amounts of silts and clays. Fine particles were more prevalent upriver and toward the headwaters of each marsh creek, where flows were reduced.

The major sediment fraction at all stations was fine sand (1.25 to 3.75ϕ), with values varying from 55% at Spoil Island to 92% at Shellbed Island. Silts and clays ($<$ 3.75ϕ), were minor components of the substratum at stations located in the Baldhead Island complex, with a peak value of 6% at the headwater Cape Creek rotenone site. Similarly, higher percentages of silts and clays were found at the Dutchman Creek stations, particularly at the rotenone site (14%). Fine substrate fractions were also more prevalent at the upriver stations, except Spoil Island.

Organic content tended to be highest in sediments with high percentages of silts and clays, i.e., in areas with reduced flows. Thus, peaks in percent organic levels were observed at Town Creek, Barnard Creek, Dutchman Creek, and Cape Creek rotenone stations. The first 2 sites were particularly rich in organic material which comprised nearly one-third (by weight) of the substratum. Both stations were located in areas off the mainstream creek, where tidal flows were lower and where considerable *in situ* decomposition of organic plant material took place.

The best indication of an effect of sediment characteristics on species distributions was derived from comparisons with percent organics (Fig. 3). All species shown on this figure exhibited significant relationships ($\alpha < 0.05$) with this parameter: those appearing to the left of a ridit value of 0.500 had negative correlations with increasing percent organics, and those to the right all had positive relationships. Percent fine sand and sorting

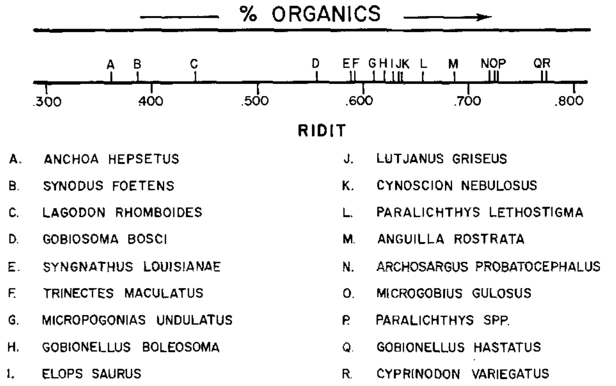

Fig. 3. Ridit analysis comparing the distribution of selected species with percent organic composition of the substrate. All species shown in this figure have a significant relationship ($P < 0.05$) with percent organic matter; those appearing to the left of a ridit value of 0.500 display a negative relationship, those to the right, a positive association

Table 2. Pooled species abundance for all collections at seine and rotenone sites in the Cape Fear River estuary, listed in order of abundance. Only species comprising 0.5% of the total number of individuals and their corresponding percentages are shown. Species appearing in bold italics are recruited primarily from the ocean, other species are considered estuarine endemics

Taxon	Abundance (No./400 m^2)	%
Brevoortia tyrannus	194813	39.3
Leiostomus xanthurus	90889	18.3
Fundulus heteroclitus	53576	10.8
Menidia menidia	37661	7.6
Anchoa mitchilli	29365	5.9
Mugil cephalus	16287	3.3
Mugil curema	10665	2.2
Penaeus aztecus	9330	1.9
Paralichthys sp	8317	1.7
Callinectes sapidus	6267	1.3
Fundulus majalis	4711	1.0
Menidia beryllina	4566	0.9
Bairdiella chrysoura	2882	0.6
Lagodon rhomboides	2865	0.6
Gambusia affinis	2386	0.5
Gobiosoma bosci	2380	0.5
Total	476960	96.2

coefficient were tested in a similar manner and had little effect on the distribution of most species.

Community Patterns

Sixteen taxa comprised 96.2% of the total number of individuals collected between September 1977 and August 1978 (Table 2). Three species within the genus *Paralichthys* were included among this group: *P. lethostigma*, which dominated in the collections, and *P. dentatus* and *P. albigutta*, present in lesser abundance. Because it was difficult to separate smaller individuals (< 15 mm SL) into species, only a single category was recognized for the earliest life stages. Taxa appearing in bold italics in Table 2, are generally recognized as being recruited from the ocean. These species accounted for 70% of the community dominants collected during this program.

Distribution of individuals and species among sites is summarized in Table 3. The extraordinary abundance associated with the Walden Creek (Seine 2) and rotenone site resulted from 2 large collections of yearling (~ 50 to 100 mm) *Brevoortia tyrannus* in June (~ 54000 individuals) and July (~ 89000 individuals). Densities varied considerably among stations and reflected individual habitat characteristics, and perhaps their suitability as residence zones for young fish. For example, the low catch associated with the sand flat station designated Spoil Island, may be due to severe currents throughout most of the tide at this site, and to periodic heavy wave action from the wake of closely passing ships. Care is obviously necessary in making direct comparisons between abundance in seine and rotenone collections, although for several dominant species the efficiency associated with each methodology was similar (Weinstein and Davis, 1979).

Other stations which exhibited relatively high faunal densities, Cape Creek (rotenone) and Battery Island, were located in low flow areas; the former site was a headwater station and the latter a "cul-de-sac" protected by a sandbar. The 2 headwater stations in Dutchman Creek also produced higher catches; however, downstream localities within tidal creeks were also productive,

Table 3. Total number of individuals and species collected at seine and rotenone sampling sites, Cape Fear River estuary, North Carolina

Station	Number of individuals	Number of species	Station	Number of individuals	Number of species
Baldhead Creek (Seine 1)	19,880	56	Walden Creek (Seine 1)	12,014	37
Baldhead Creek (Seine 2)	19,818	42	Walden Creek (Seine 2)	133,953	38
Baldhead Creek (Rotenone)	11,644	54	Walden Creek (Rotenone)	72,171	33
Cape Creek (Seine)	8,232	48	Governors Creek (Seine)	37,964	33
Cape Creek (Rotenone)	32,671	60	Hechtic Creek (Seine)	12,741	46
Shellbed Island (Seine)	12,742	44	Spoil Island (Seine)	4,992	29
Battery Island (Seine)	27,324	63	Town Creek (Rotenone)	22,817	37
Dutchman Creek (Seine)	22,487	34	Barnards Creek (Rotenone)	10,900	38
Dutchman Creek (Rotenone)	33,200	28			

Table 4. Species richness comparisons among seine and rotenone stations, Cape Fear River estuary, North Carolina. The test statistic is the Wilcoxon signed rank test. + = significant at $\alpha = 0.05$, row station > column station; – = significant at α 0.05, column station > row station; o = not significant

Seine Station	Dutchman	Walden 1	Shellbed	Hechtic	Governors	Walden 2	Baldhead 2	Cape	Battery	Spoil Is.
Baldhead Creek 1	+	+	+	o	+	+	+	+	o	+
Dutchman Creek		o	o	–	o	o	–	–	–	o
Walden Creek 1			–	–	o	o	–	–	–	o
Shellbed Island				o	o	o	o	o	–	+
Hechtic Creek					+	o	o	o	o	+
Governors Creek						o	–	–	–	o
Walden Creek 2							–	–	–	o
Baldhead Creek 2								o	–	+
Cape Creek									o	+
Battery Island										+

Rotenone Station	Dutchman	Walden	Barnards	Cape	Town
Baldhead Creek	+	+	+	o	+
Dutchman Creek		o	o	–	o
Walden Creek			–	–	o
Barnards Creek				–	+
Cape Creek					+

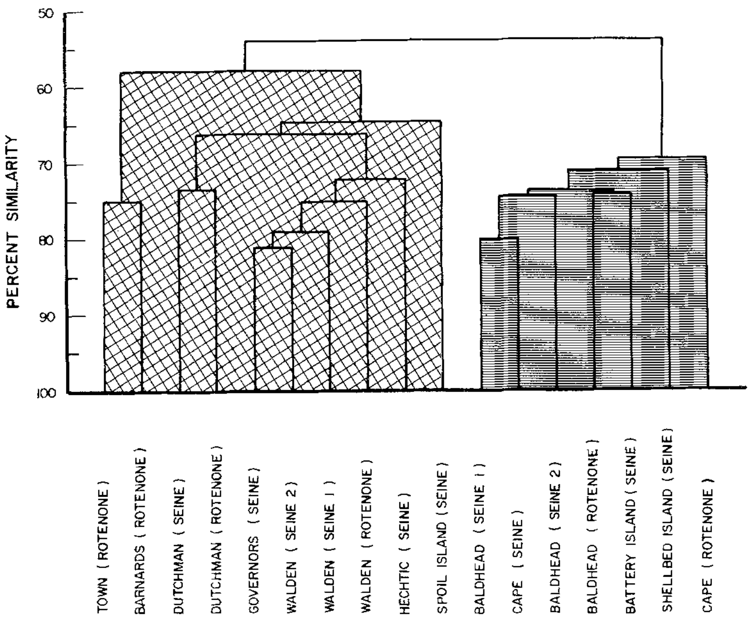

Fig. 4. Percent similarities among all station collected from September 1977 through August 1978. Associations in the dendrogram are based on pooled monthly collections. Samples were not taken at Spoil Island (seine) and Walden (seine 2) in September

as was the case at Governor's and Town Creeks. Thus, clear patterns of spatial abundance were not evident among marsh stations and distributions of individuals were influenced primarily by habitat types.

When the number of species collected each month were compared among sites (Table 4), species richness was generally observed to be greater in the Baldhead Island area (including Shellbed and Battery Islands). Comparisons involving Hechtic Creek, an upriver site, were the primary exceptions to this pattern.

Classification Analysis

Classification analysis produced 2 distinct station clusters (Fig. 4). An association (PSI > 65%) was formed among high salinity sites at Baldhead Island and nearby Shellbed and Battery Islands. Despite higher average salinities (Table 1), stations located in Dutchman Creek formed a second group with Walden marsh and with upriver sites. The 2 upriver rotenone stations in Town and Barnard's Creeks, where soft substrate predominated (Table 1), exhibited the least similarities among stations. Furthermore, more distinct subgroupings were evident at sites in the second cluster, i.e. characteristic differences among stations were greater than at Baldhead Island. Yet, in both instances, seine and rotenone sites were closely allied with their corresponding marsh complex.

To facilitate direct comparisons among stations, seine data alone were used to construct a two-way coincidence table (Table 5). At the 60% PSI level, the 11 seine stations formed 2 distinct groups, designated A and B,

Table 5. Two-way coincidence table comparing dendrograms for station and species associations. The two station clusters, designated A and B are cross-referenced against 22 (I–XXII) species clusters derived from previous calculations. Dendrograms are not shown

		A					B					
	Species	Shellbed Island	Battery Island	Baldhead Creek 2	Cape Creek	Baldhead Creek 1	Spoil Island	Dutchman Creek	Hechtic Creek	Walden Creek 1	Governors Creek	Walden Creek 2
I	*Strongylura marina*	11	36	31	4	7	5		4	6	2	4
	Anchoa mitchilli	1091	2011	320	4003	9397	2874	112	2788	106	93	18
	Penaeus duorarum	29	301	244	137	739	5	64	69	39	125	34
	Bairdiella chrysoura	86	732	413	98	409	5	135	97	34	63	36
	Menidia menidia	2563	7945	10716	1430	3132	26	2007	10	99	7	704
	Mugil curema	198	1430	229	33	512	11	3423	18	73	22	92
	Paralichthys spp.	71	10	45	17	87	150	12	447	121	224	204
	Eucinostomus argenteus	182	317	40	87	153	6	98	6	116	391	134
	Penaeus aztecus	89	91	745	109	492	4	1277	88	1320	2281	2151
	Lagodon rhomboides	140	51	141	63	84	7	58	60	168	180	846
	Fundulus heteroolitus	4080	4855	647	26	802	12	3093	1152	3347	1970	9600
	Callinectes sapidus	163	435	297	169	396	408	1554	510	401	419	823
	Leiostomus xanthurus	3384	3769	4632	446	1229	1050	7689	2344	4379	11547	15735
	Mugil cephalus	61	1911	692	88	141	75	662	1858	640	336	3019
	Brevoortia tyrannus	60	3	37	509	104	138	951	2534	793	16013	99128
	Citharichthys spilopterus	6	1	4	2	1			14	1	6	3
	Fundulus majalis	20	1134	178	207	876	4	1087	19	50		
	Gobiosoma bosci		49	30	329	596	2	6	7	1		7
	Symphurus plagiusa	45	9	67	80	108	7	1	1	2		3
II	*Paralichthys lethostigma*					5	12		12	2	6	
	Trinectes maculatus				2	7	42		7	2		1
	Micropogonius undulatus	4	3		1	1	130	4	126	19	9	3
III	*Syngnathus louisianae*		46	14	7	44		1	8			
	Gobionellus boleosoma		52	57	4	30		3	7			
	Cynoscion nebulosus		11	1	1	7		2	2	1		1
	Lutianus griseus	1	12	3		10			16			
	Caranx latus	5	5		2				2			1
	Membras martinica	12	8		6	1						1
	Paralichthys dentatus	9	24	4	3	1	1			1		
	Prionotus tribulus	11	9			13						
	Monacanthus hispidus	4	3	1		4			1			
	Opsanus tau	1	3	1	2	9						
	Syngnathus fuscus		9	7	6	34				1		
	Gobiosoma ginsburgi	2	13	14	1	10						
	Callinectes similis	12	11	33	21	60						
	Synodus foetens	33	2	14	34	44						
	Prionotus scitulus	5	1	1	2	3						
	Anchoa hepsetus	157	62	1	71	106			1			
	Etropus crossotus	16	5		8	5						
	Orthopristis chrysoptera	147	1585	15	144	100						
	Chilomycterus shoepfi	1	4		2	1						
IV	*Dorosoma cepedianum*							1	11	6	6	4
	Menidia beryllina	5	1				8	11	263	88	2798	713
	Gambusia affinis		10				1	1	10	116	1370	602
	Caranx hippos	1	1	1				2	7	22	1	12
	Anguilla rostrata		1				3	1	107		15	10
	Penaeus setiferus			8				20	51	19	12	1
	Lepomis macrochirus								1		4	1
V	*Pomatomus saltatrix*						2			11	2	7
VI	*Elops saurus*		1		3	1		68	5		6	1
	Sciaenops ocellata		2			2	1	60	2		12	9
VII	*Cyprinodon variegatus*		3					3				1
VIII	*Pogonias cromis*		3	1	34			21		2		
IX	*Mycteroperoa microlepis*		2	1								
	Eucinostomus gula		2	9	1							
	Gobionellus shufeldti		2	2					1		1	
X	*Sphyraena barracuda*			1		1						
XI	*Citharichthys macrops*	1		2								

Table 5. (continued)

	Species	Shellbed Island	Battery Island	Baldhead Creek 2	Cape Creek	Baldhead Creek 1	Spoil Island	Dutchman Creek	Hechtic Creek	Walden Creek 1	Governors Creek	Walden Creek 2
XII	*Ancylopsetta quadrocellata*		3			1						
	Tautoga onitis		1			1						
	Selene vomer		6		1	1						
	Chaetodipterus faber		2		1							
	Hypsoblennius hentzi	2	10									
	Chasmodes bosquianus	1	6									
	Gobiesox strumosus		8									
	Opisthonema oglinum		2									
XIII	*Archosargus probatocephalus*		1						1			
	Evorthodus lyricus		1						12		1	
XIV	*Morone saxatillis*									3		
XV	*Fundulus luciae*		2							2		
XVI	*Diapterus olisthostomus*				1	1				2	4	
	Alosa aestivalis				1					10	1	
XVII	*Lutjanus synagris*					2						
	Astroscopus y-graecum					5						
	Microgobius gulosus		1			7						
XVIII	*Stellifer lanceolatus*	2										
	Urophycis regius	2				1						
	Prionotus carolinus	4				1						
	Scopthalmus aquosus	16				2						
XIX	*Alosa sapidissima*				1							1
	Poecilia latipinna											3
XX	*Hippocampus erectus*				1	1						
	Astroscopus guttatus				2							
	Cynoscion regalis				18	1						
XXI	*Gobionellus hastatus*						1	2				
XXII	*Lepomis gibbosus*										9	

while at this same level of similarity 22 species associations were recognized. Species Groups I through IV comprised > 99% of the total number of individuals captured at seine sites in this study and were, therefore, definitive of the community characteristics in each marsh. However, rarer species appearing in the remaining species associations (Groups V through XXI) also contributed to differences in species richness. For example, there were 10 joint occurrences among species in Groups A and B (station associations), while 5 species occurred at lower salinity sites (Group B) alone, and 22 species were captured only at Group A stations.

Among the dominant species groups, members of Group I were generally ubiquitous in the Cape Fear marshes, yet had centers of abundance clearly associated with specific areas. *Menidia menidia*, for example, were more abundant at polyhaline stations, including Baldhead Island and vicinity and at the Dutchman Creek station. Similarly, *Gobiosoma bosci* and *Fundulus majalis* were more abundant at these sites. The converse was true for catches of *Paralichthys* spp. and *Brevoortia tyrannus*, averaged over all sites within each station group. Of the remaining dominant groups, members of Group III were prevalent in polyhaline and marine salinities, while species Groups II and IV were more numerous at lower salinities.

Similar patterns are reflected in the rotenone collection data of Table 6, which lists species contributing at least 0.5% of the total numbers of individuals collected by rotenone. Rotenone samples also indicated that *Menidia menidia, Gobiosoma bosci* and *Fundulus majalis* were more abundant at Baldhead Island than elsewhere. This pattern, however, was not as distinct for *Symphurus plagiusa* because of the substantial catch at Barnard's Creek where the organic content of the substratum was very high (33.17%). As expected, catches of *Brevoortia tyrannus* and *Paralichthys* spp. were slightly reduced at Baldhead Island compared to those at upriver sites. Rotenone collections also confirmed that many species in the high salinity groups (primarily Group III) were resident mainly in the Baldhead Island vicinity. With the usual caution associated with sample size, it can be reasonably concluded that the following species prefer more saline waters: *Membras martinica, Paralichthys dentatus, Prionotus tribulus, Prionotus scitulus, Opsanus tau, Gobiosoma ginsburgi, Callinectes similis* (not con-

Table 6. Pooled species abundances (number 400 m^{-2}) for all collections at rotenone sites in the Cape Fear River estuary, listed in order of abundance. Only species comprising 0.05% of the total number of individuals and their corresponding percentages are shown

Baldhead Creek			Cape Creek			Walden Creek		
Taxon	No.	%	Taxon	No.	%	Taxon	No.	%
Leiostomus xanthurus	2393	20.6	*Leiostomus xanthurus*	9352	28.6	*Brevoortia tyrannus*	57172	79.2
Fundulus heteroclitus	2117	18.2	*Menidia menidia*	7081	21.7	*Leiostomus xanthurus*	8983	12.5
Menidia menidia	1683	14.5	*Anchoa mitchilli*	4051	12.4	*Fundulus hetercolitus*	2727	3.8
Anchoa mitchilli	1215	10.4	*Fundulus heteroclitus*	3668	11.2	*Mugil cephalus*	789	1.1
Gobiosoma bosci	1049	9.0	*Brevoortia tyrannus*	1853	5.7	*Paralichthys* spp	586	0.8
Fundulus majalis	870	7.5	*Gobiosoma* spp.	935	2.9	*Lagodon rhomboides*	413	0.6
Gobionellus boleosoma	546	4.7	Gobiidae	766	2.3			
Lagodon rhomboides	301	2.6	*Penaeus aztecus*	597	1.8			
Bairdella chrysoura	267	2.3	*Microgobius gulosus*	590	1.8			
Mugil cephalus	172	1.5	*Symphurus plagiusa*	557	1.7			
Eucinostomus argenteus	133	1.1	*Pogonias cromis*	490	1.5			
Brevoortia tyrannus	129	1.1	*Bairdiella chrysoura*	365	1.1			
Paralichthys spp.	120	1.0	*Paralichthys* spp.	264	0.8			
Mugil curema	106	0.9	*Lagodon rhomboides*	239	0.7			
Orthopristis chrysoptera	77	0.7	*Mugil curema*	215	0.7			
Symphurus plagiusa	64	0.6						
Syngnathus louisianae	55	0.5						

Dutchman Creek			Town Creek			Barnards Creek		
Taxon	No.	%	Taxon	No.	%	Taxon	No.	%
Fundulus heteroclitus	14859	44.8	*Brevoortia tyrannus*	13638	59.8	*Paralichthys* spp.	4324	39.7
Leiostomus xanthurus	7841	23.6	*Leiostomus xanthurus*	5053	22.2	*Brevoortia tyrannus*	1644	15.1
Mugil cephalus	5137	15.5	*Paralichthys* spp.	1501	6.6	*Leiostomus xanthurus*	1064	9.8
Mugil curema	4063	12.2	*Anchoa mitchilli*	993	4.4	*Fundulus heteroclitus*	519	4.8
Callinectes sapidus	217	0.7	*Anguilla rostrata*	500	2.2	*Gobionellus boleosoma*	505	4.6
Menidia menidia	163	0.5	*Menidia beryllina*	194	0.8	*Mugil cephalus*	496	4.6
Elops saurus	160	0.5	*Paralichthys lethostigma*	118	0.5	*Micropogonias undulatus*	469	4.3
			Mugil cephalus	103	0.5	*Anguilla rostrata*	348	3.2
			Fundulus heteroclitus	103	0.5	*Anchoa mitchilli*	265	2.4
						Symphurus plagiusa	257	2.4
						Callinectes sapidus	221	2.0
						Menidia beryllina	127	1.2
						Trinectes maculatus	102	0.9
						Paralichthys lethostigma	92	0.8
						Bairdiella chrysoura	83	0.8
						Penaeus duorarum	50	0.5
						Bothidae	50	0.5

sidered quantitatively sampled in rotenone collections), *Synodus foetens, Anchoa hepsetus, Orthopristis chrysoptera, Microgobius gulosus*, and *Eucinostomus gula*.

Conversely, several species listed in the high salinity groups could not be included in this designation when rotenone collections were considered. For example, *Syngnathus louisianae, Gobionellus boleosoma, Lutjanus griseus*, and *G. shulfeldti*, were frequently collected at low salinity rotenone sites; their greater abundance in Baldhead Island seine collections was apparently fortuitous.

Other species restricted to, or preferring, lower salinities, based on both collecting methodologies were: *Dorosoma cepedianum, Menidia beryllina, Gambusia affinis, Anguilla rostrata*, and postlarval and juvenile *Micropogonias undulatus*. Young *Paralichthys lethostigma* and *Trinectes maculatus* were also caught in slightly greater numbers upriver; several freshwater species were occasionally present, including *Micropterus salmoides, Lepomis gibbosus, L. macrochirus, Perca flavescens*, and *Ictalurus catus*. The latter species were not abundant in the estuary but were collected in salinities up to 5.1 $^{\circ}/_{oo}$ S.

When the faunal composition at each station was compared to that of the site with the highest mean salinity, there was a generally decreasing trend in PSI values (Fig. 5) proceeding from the river mouth upstream. This trend, however, was not linear. A striking change in slope was evident in the general salinity range between 14 and 21 $^{\circ}/_{oo}$ S, attributed, in part, to a faunal turnover zone in this region of the estuary. It was surprising that the estuarine endemics (Fig. 5) exhibited essentially the same pattern as the entire nekton community. Like the marine group, they apparently responded strongly to salinity, with several species (e.g., *Menidia menidia, Gobiosoma bosci, Bairdiella chrysoura, Fundulus majalis*, and *Anchoa hepsetus*) having their centers of abundance in the polyhaline zone and less frequently penetrating brackish or freshwaters.

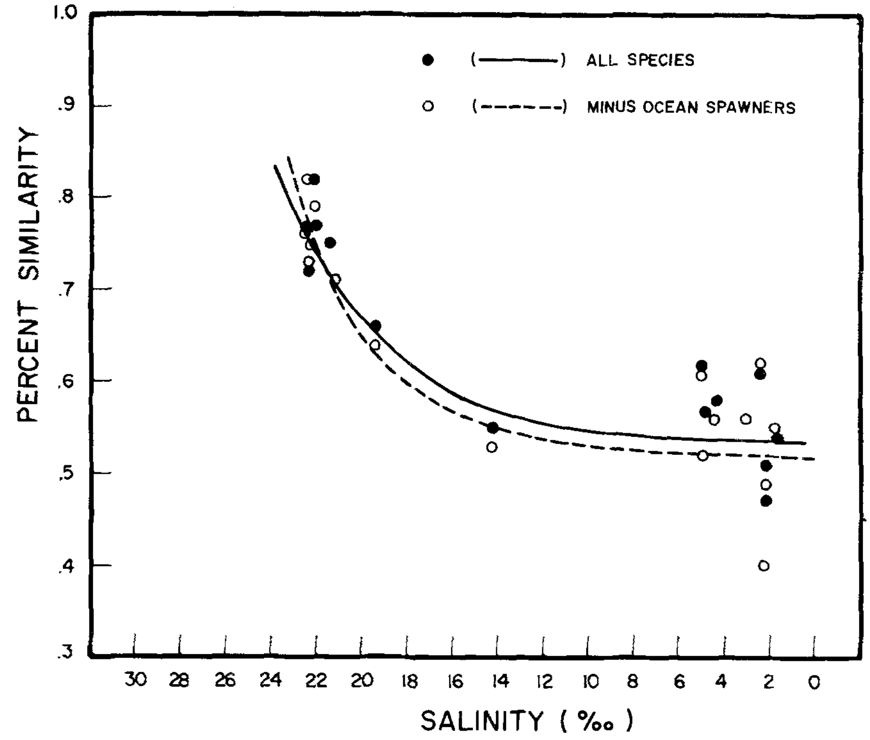

Fig. 5. Interstation similarity based on pooled monthly collections comparing each station (represented by its mean annual salinity) to the station with the highest mean salinity (not shown on graph). Similarity among sites decreased in the upstream direction in a non-linear fashion, the change in slope between 14–20‰ S is interpreted as the presence of an ecotone

Ordinations

In an attempt to further quantify the role of salinity in mediating distributions of dominant Cape Fear estuary nekton, catch data for individual species were combined for the entire 20 month study and subjected to Binary Discriminant Analysis. In all, 29 species were sufficiently abundant to conduct χ^2 tests; of these, 27 species displayed significant ($\alpha \leqslant 0.05$) departures from expected values and, after conversion of their χ^2 residuals, were subjected to principal components analysis. Because they were uniformly distributed in the estuary (i.e, had non-significant χ^2 values), abundance data for *Fundulus heteroclitus* and *Callinectes sapidus* were not included in the latter procedure.

Principal component I (Table 7) accounted for 68.8% of the variance in the total data set and displayed an inverse relationship with increasing salinities. The second principal component, accounting for an additional 20.9% of the variance, had factor loadings which were highly correlated with the middle of the salinity range, particularly the mesohaline zone. The latter relationship was especially useful since it allowed quantification of non-linear species abundance distributions with the salinity gradient as a whole.

Table 7. Results of a binary discriminant analysis (BDA) across ordered salinity intervals. The percent of total variance in the data set explained by each factor is also shown

Category	Factor		
	I	II	III
Freshwater (< 0.5‰ S)	0.440	−0.426	0.570
Oligohaline (0.5 – 8‰ S)	0.506	0.547	−0.547
Mesohaline (8 – 16.5‰ S)	0.211	0.887	0.126
Polyhaline (16.5 – 30‰ S)	−0.516	0.023	0.414
Marine (> 30‰ S)	−0.489	−0.139	−0.435
% Total Variance	68.8	20.9	6.1

Factor score plots for the 27 species are shown in Fig. 6. There were 4 general groupings among the species scores (designated A through D), with *Menidia menidia* and *Brevoortia tyrannus* located in transitional areas between groupings. Individuals recruited from the ocean were generally well separated along the salinity gradient. Species with the highest salinity preferences were *Eucinostomus argenteus* and *Callinectes similis* (Group A), followed by *Mugil curema, Symphurus plagiusa, Penaeus duorarum, Orthopristis chrysoptera,* and *Synodus foetens* in the polyhaline zone (Group B). At intermediate salinities (mesohaline zone), *Mugil cephalus, Lagodon rhomboides*, and *Penaeus aztecus* were most common (Group C), and *Micropogonias undulatus, Paralichthys* spp., *P. lethostigma*, and *Anguilla rostrata* predominated in low salinities (Group D).

Other species appearing in Fig. 6 were members of the dominant estuarine endemic groups and displayed considerable separation of their own. For both the ocean and estuarine endemic groups, congeners had widely separated centers of abundance.

Spatial separations along the salinity gradient for the 27 species appearing in Fig. 6 also were analyzed by subjecting catch per unit effort data (CPUE) to a direct gradient analysis (Fig. 7). The figure is divided into 4 panels to correspond with the groupings shown in the

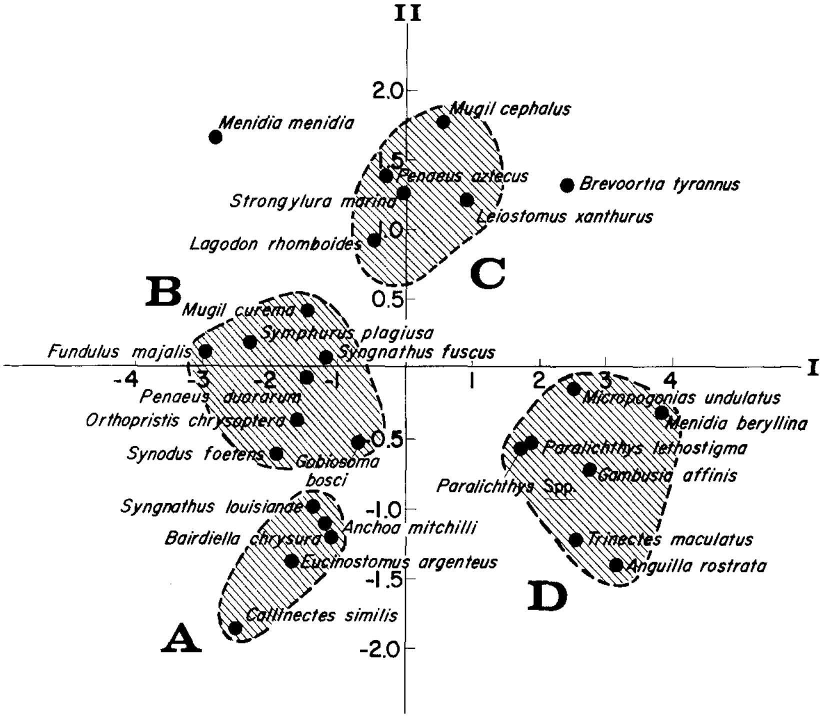

Fig. 6. Species distribution along the salinity gradient as depicted by Binary Discriminant Analysis. Factor I accounted for 68.8% of the total variance and was correlated with the freshwater–oligohaline zones (positive correlation) and negatively correlated with polyhaline and marine salinities. Factor II accounted for an additional 20.9% of the variance and showed a strong positive association with mesohaline salinities

indirect ordination of Fig. 6. Good agreement is evident between the 2 methods, except for the locations of the centroids for *Orthopristis chrysoptera* and *Strongylura marina*. Since these 2 species had relatively low frequency counts in several cells of the Chi-square contingency table, their particular departures from expected values in the BDA could have been the result of chance (Strahler, 1978b).

Discussion

Community Structure

Whether they originated in the ocean (and utilized the marshes temporarily), or were more permanent members of the marsh community, the distribution of many nekton species in the Cape Fear River estuary appeared to be strongly influenced by salinity gradients. Along with other abiotic variables, salinity apparently provides a broad framework of limiting conditions within which biotic interactions (predation, competition, etc.) act to "fine tune" community relationships. Considered in terms of scale, the estuary as a whole may be viewed primarily as a physically controlled environment (Sanders, 1968), while within individual habitats (marshes), biological accommodation seems to play an increasingly important role (Weinstein and Walters, 1980). Despite conspicuous differences in mobility and life history characteristics between nekton and macrobenthos this pattern is similar to one described by Boesch (1977) for benthic macroinvertebrate communities in the Chesapeake Bay and Brisbane River estuary, Australia. In his work, upestuary limits of marine and estuarine organisms were set by tolerance to low salinity, as were the downstream limits of brackish and freshwater forms. However, he also concluded that euryhaline opportunists were apparently disfavored in "equilibrium" polyhaline habitats by biotic interactions. Similar scale effects have been noted for the rocky intertidal by Connell (1972), and are the subject of many studies of terrestrial vegetation along gradients (Whittaker, 1967).

Because the physiological capacity to penetrate upstream is limited in many species of marine fishes, a major transitional zone was centered around the Baldhead Island marsh system. The enhanced species richness in this area was related to the seasonal presence of many marine species which are rarely numerically dominant in the Cape Fear estuary. Apparently, these taxa are not easily able to reside in salinities below 16‰ S, and were absent or rare in upstream marshes. At the same time, however, it is apparent that certain species experienced increased predation pressure in the Baldhead Island area (Weinstein and Walters, 1980), and that this effect may have contributed to enhanced species diversity in this region (Paine, 1966; Connell, 1975). Because some of these predators were restricted to higher salinities, localized predation effects also may have enhanced community differences among marshes (Weinstein, 1979).

Interestingly, species residing permanently in the estuary were distributed in a similar manner to those derived from the open ocean environment (Figs. 6 and 7). This observation contrasts with that of Boesch (1977) for the Chesapeake Bay, where macrobenthic species he referred to as "endemic" were generally excluded from the polyhaline and marine zones. Conversely, zonation of nekton communities in the Cape Fear estuary followed Boesch's (1977) descriptions in 2

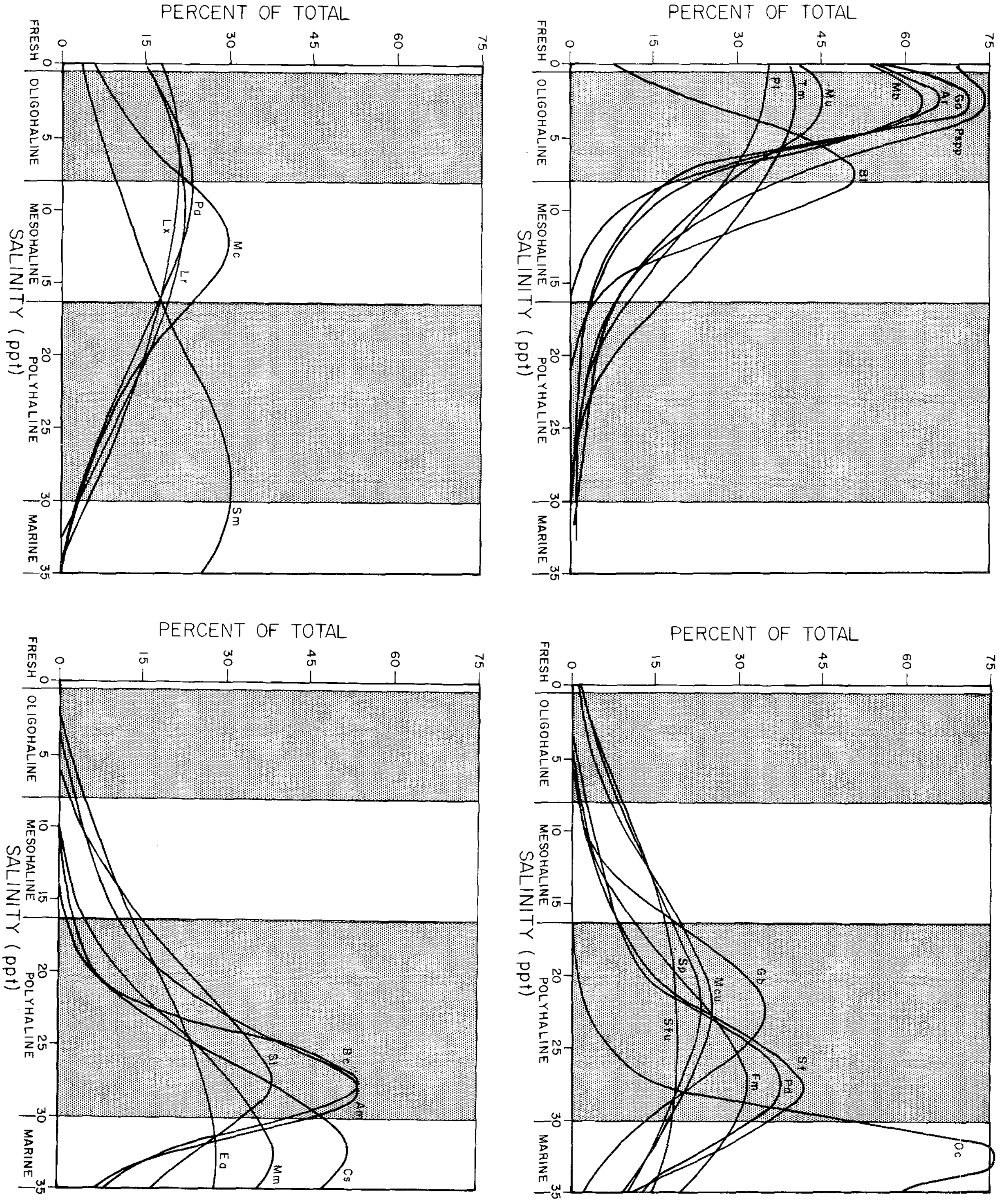

Fig. 7. Direct ordination of species distribution along the salinity gradient. Catch per unit effort (CPUE) was calculated for 5‰ salinity increments and smooth curves fitted to the data. The 4 panels in this figure correspond to the 4 species groupings in Fig. 6. Pspp–*Paralichthys* spp.; Ga–*Gambusia affinis*; Ar–*Anguilla rostrata*; Mb–*Menidia beryllina*; Mu–*Micropogonias undulatus*; Tm–*Trinectes maculatus*; Pl–*Paralichthys lethostigma*; Bt–*Brevoortia tyrannus*; Mc–*Mugil cephalus*; Pa–*Penaeus aztecus*; Lr–*Lagodon rhomboides*; Lx–*Leiostomus xanthurus*; Sm–*Strongylura marina*; Oc–*Orthopristis chrysoptera*; Sf–*Synodus foetens*; Pd–*Penaeus duorarum*; Fm–*Fundulus majalis*; Gb–*Gobiosoma bosci*; Mcu–*Mugil curema*; Sp–*Symphurus plagiusa*; Sfu–*Syngnathus fuscus*; Am–*Anchoa mitchilli*; Bc–*Bairdiella chrysoura*; Cs–*Callinectes similis*; Sl–*Syngnathus louisianae*; Mm–*Menidia menidia*; Ea–*Eucinostomus argenteus*

important ways: (1) faunal turnover zones were not sharply demarcated; even the ecotone effect, described above, occurred only as a gradually accelerating transition zone in salinities between 14 and 21‰ S, and (2) although considerable overlap in spatial distribution for individual species occurred, recognizable and persistent assemblages of organisms appeared along the salinity gradient (Fig. 4, Tables 5, 6). We have not been able to distinguish between the estuarine endemics and euryhaline opportunists of Boesch (1977), perhaps because the latter do not exist in nekton communities (*sensu* Grassle and Grassle, 1974). At any rate, exclusion of the former group from high salinity areas by predation or competition with marine forms did not seem to occur in the Cape Fear estuary.

Despite differences in freshwater flow between 1977 and 1978, community patterns in marshes of the Cape Fear system have remained virtually intact. Apparently, changes in freshwater flow, although sometimes considerable, were not of sufficient magnitude or duration to alter the estuarine coenocline seriously, as was also witnessed by Boesch (1977) during the monsoon season in the Brisbane River estuary, Australia. This is a somewhat puzzling observation, since we have noted a close association between the upestuary presence of certain species of postlarvae, for example, *Leiostomus xanthurus* and *Micropogonias undulatus*, and the localized presence of saltwater intrusion (Weinstein *et al.*, 1979). When river flows exceeded 990 m^3 s^{-1} in the spring of 1978, these species (previously present in high densities in the river channel and shoals) were either swept or migrated downstream and catches were very low. Although there was relatively rapid recovery to pre-high-flow densities as these freshets passed downstream, several species did not fully re-establish themselves in upestuary marshes. Thus, there are documented changes in the presence of certain species in localized areas; but the important observation is that the community as a whole maintains its integrity and may be characterized by readily identifiable species composition and ranking of its dominants. Whether or not larger seasonal freshwater flows would seriously alter community patterns within the Cape Fear estuary remains a point for conjecture. However, we suspect that an event such as that associated with Hurricane Agnes along the Atlantic seaboard in 1972, would have dire consequences for the Cape Fear system (Anderson *et al.*, 1973). Obviously, this is a rare event and recovery would be expected to follow.

DeSylva (1975) has described some of the relationships of estuarine nekton to substrate characteristics, and has related their distributions to prey organisms associated with characteristic sediment types. In some cases, species may make direct use of the organic (detrital) content of the sediments (Darnell, 1958; Odum, 1968). This seems to be the situation for several species appearing in Fig. 3; however, these data must be treated with caution for 2 reasons. First, demonstration of a significant positive (or negative) correlation with percent organics does not necessarily imply that the organic content of the sediment was the underlying causative factor for the observed distribution. Second, some bias was probably introduced into the analysis as a result of softer stations (greater percent organics) being more frequently sampled by rotenone. The presence of several gobies in these locales, therefore, may result from their being more effectively captured by rotenone, rather than by their selecting areas rich in organic matter. However, the latter possibility is not necessarily precluded. Species appearing in Fig. 3 with known or suspected affinities for muddy areas (some because they are detritivores or prefer to feed in these habitats) include *Cyprinodon variegatus* (Kilby, 1955), *Micropogonias undulatus* (Darnell, 1958), *Trinectes maculatus* (Reid, 1954), and *Anguilla rostrata* (Bigelow and Schroeder, 1953). On a broad scale, therefore, substrate characteristics probably exert some influence on the distribution of certain species. Although we have sampled a relatively small area of total marsh creeks in the Cape Fear estuary, and are describing highly mobile organisms, the persistent (albeit seasonal) appearance of certain species over specific substrate types lends credence to this belief.

Species Interactions

Although we cannot present direct evidence for interactions among species, data are available which indicate that potential competitive interactions play an important role in structuring Cape Fear nekton communities. This "evidence" takes 2 forms: First, congeneric or closely related species tended to display less overlap in their distributions (Fig. 7); second, when the meroplanktonic stages of ocean-spawned species were considered separately, it was clearly evident that strong seasonal programming in the form of sequential waves of recruitment took place (Table 8). For the 2 entirely separate year classes surveyed during this study, peak abundance for individual species of postlarvae occurred at very similar times of the year. Perhaps even more important, the temporal sequence for recruitment of different species remained remarkably similar during 1976-1977 and 1977-1978 (Table 8).

Weinstein (1979) discussed the potential for diffuse competition (MacArthur, 1972) among these species. In light of their similar food requirements (Thayer *et al.*, 1974; Kjelson *et al.*, 1975) and the possibility of food limitation within the estuary for the meroplanktonic life stages (Thayer *et al.*, 1974; Houde, 1978), temporal and spatial separation could conceivably act to reduce the potential for competitive interactions. The critical relationship between available food supply for larval and postlarval fishes and the ultimate survival of the year class has been frequently recognized (Hjort, 1914; Marr, 1956; May, 1974; Houde, 1978). Yet, virtually nothing is known concerning niche overlaps and species interactions among postlarval fishes in estuaries.

To a large degree, spatial and temporal separations carried over into the juvenile life stages of the transient

Table 8. Seasonal distribution, mean size and preferred salinity range for selected species of nekton utilizing the Cape Fear River estuary. Recruitment during a 2 yr period is considered in the compilation of this table

Species	Peak recruitment months (s)		Mean size[b] (+ SE)		Preferred salinity range
	1976-77	1977-78	1976-77	1977-78	
Sciaenops ocellata	Oct[a]	Oct	23.4 ± 1.8	24.8 ± 0.2	Polyhaline
Micropogonias undulatus	–	Dec	–	16.2 ± 0.3	Oligohaline
Lagodon rhomboides	Mar	Mar	14.8 ± 0.0	14.6 ± 0.0	Mesohaline
Leiostomus xanthurus	Mar-Apr	Mar-Apr	22.4 ± 0.1	17.6 ± 0.0	Mesohaline
Paralichthys spp.	Feb-Mar	Mar-Apr	13.1 ± 0.2	14.0 ± 0.1	Oligohaline
Brevoortia tyrannus	Apr-May	Apr-May	27.0 ± 0.1	29.6 ± 0.1	Oligohaline
Mugil cephalus	Mar-Apr	Mar-Apr	22.8 ± 0.1	23.3 ± 0.1	Mesohaline
M. curema	May-Jul	Jun-Jul	25.8 ± 0.1	29.6 ± 0.2	Polyhaline
Penaeus aztecus	May-Jun	May-Jun	37.7 ± 0.4	24.3 ± 0.6	Mesohaline
P. duorarum	Jul	Aug	22.2 ± 0.4	25.9 ± 0.4	Polyhaline
P. setiferus	Jul	Jul		29.3 ± 1.4	Oligohaline

[a] Based on preliminary seine surveys at 3 stations from October through December 1976

[b] Earliest recruitment month, where a plateau was evident in the data

marsh residents and were also evident for the adults of some estuarine endemics. For example, spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) maintained a bathymetric separation during the juvenile growth period, with croaker more prevalent in deeper water near the head of the estuary (Weinstein *et al.*, 1979; see also Chao and Musick, 1977). Croaker also displayed a preference for areas with higher organic content in the substrate. Penaeid shrimp were somewhat restricted in their distribution, with brown (*Penaeus aztecus*) and pink (*P. duorarum*) shrimp more abundant in middle and higher salinity reaches, respectively, and white shrimp (*P. setiferus*) taken in the greatest numbers from brackish waters (Table 5, and Weinstein, 1979).

Where related species co-occurred, an additional component, taking the form of a time-size relationship, seemed to reduce the potential for competition effectively. For example, periods of peak abundance for striped (*Mugil cephalus*) and white mullet (*M. curema*) were separated by about 2 months, with the latter species arriving last. When white mullet peaked in May, their average size was 25.8 ± 0.13 (SE) mm, while striped mullet, having reached peak abundance in March, averaged 36.0 ± 0.27 (SE) mm during May. As previously described, these 2 species also had centers of abundance at different salinities and tended to favor substrates rich in organic matter.

Similar sequential appearances in the estuary for the majority of winter-spawned species (which were often recruited to the estuary at different mean sizes), would be expected to aid in maintaining a size gradation through time (Table 8) and might also reduce diet overlap through size-selective predation (George and Hadley, 1979). In addition to displaying particular salinity preferences, older fish, especially those that feed on the epibenthos and infauna, may be "tracking" their relatively sedentary and well zonated food supply in the estuary (Boesch, 1977).

Average Biomass Export at End of the Growing Season

Standing crops for 6 dominant marsh species at the end of the 1977 growing season were determined by computing mean biomass values for the last 2 months of marsh residency (Table 9). Two dates were selected because emigration was believed to be a gradually accelerating event, lasting several weeks. Because the sampling program had terminated before the 1978 year class fully vacated the marshes, data for 1977 alone were used in the mean biomass calculations. In addition, it was necessary to depend on previously published values for wet to dry weight conversions (Thorson, 1961) and for caloric equivalents (Thayer *et al.*, 1973), in order to report the data in kcal m^{-2}. Based on these calculations, a total of 7.02 kcal m^{-2} were available for export to the lower estuary and marine environment in the late summer and fall of 1977. This value represents high quality protein, lipids, etc., directly available to higher trophic levels.

The large potential export of energy to the marine environment in the form of living nekton biomass emigrating from the marshes may be placed in further perspective when considered in light of a study of Cape Fear marsh productivity conducted by Pendleton (1979). In the Walden Creek marsh system, potential export of dissolved organic carbon and detritus (originating primarily from *Spartina alterniflora*), was estimated at 9377 kcal m^{-2}. Assuming that this material passes through at least 3 trophic levels (e.g., bacteria, amphipods, secondary consumers) before it becomes available to marine predators, the equivalent yield of energy to higher trophic levels in the marine environment from transient species growing up in the marshes is similar to that resulting from primary plant productivity. These considerations do not include productivity of other fish species present in the marshes (e.g., permanent marsh residents, older year classes, or gear efficiency factors). Thus, the marshes serve not only as an important nursery area for many marine species, but also provide an

Table 9. Average standing crops near the end of the main period of marsh residency for 6 dominant Cape Fear River estuary species. The range of individual values for all sites is shown in parentheses

Species	Period of marsh residence (months)	Wet weight (g.m^{-2})	Dry weight[a] (g.m^{-2})	Dry weight[b] (k cal m^{-2})
Leiostomus xanthurus	7	0.41 (0.03-2.313)	0.12	0.62
Brevoortia tyrannus	5	0.36 (0.00-2.67)	0.11	0.58
Mugil cephalus	7	0.50 (0.00-1.79)	0.15	0.67
M. curema	5	2.87 (0.00-2.63)	0.84	3.76
Penaeus aztecus	3	0.96 (0.00-2.53)	0.28	1.33
P. duorarum	3	0.03 (0.00-0.06)	0.01	0.06
Total		5.13	1.51	7.02

[a] Conversion value for wet to dry weight based on estimate of 70.8 ± 0.4 (SE) % total body water for 7 species of marine Teleostei (Thorson, 1961)

[b] Conversion values for caloric equivalents of dry weight taken from Thayer *et al.* (1973)

additional important route for the transfer of energy from the estuary to the marine environment. In recent years, the estuarine and nearshore marine environments have become increasingly viewed as a functional continuum with inexorable links in community dynamics and energy processes. It is our conclusion that the 20-month effort in marshes of the Cape Fear estuary strongly supports this thesis.

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