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ABSTRACT: Flume nets of various lengths and a 3-m seine were used to sample the fishes and macrocrustaceans using a flooded Louisiana salt marsh and the adjacent tidal creek. The experiment allowed for species-specific comparisons of the flooded marsh at the creek edge versus the interior. Of the 37,667 organisms collected in flume nets from January through November 1989, 89% were decapods (nine species) and 11% were fish (29 species). An additional 18,539 organisms (75% decapods and 25% fish) were collected from concurrent seine samples taken from July through November. Comparison of catches among different flume lengths and low tide versus high tide seine collections revealed distinct patterns of marsh habitat utilization. Densities of most organisms were highest within 3 m of the water's edge, but significant numbers of marsh-resident fish species used the interior marshes. The edge marshes appeared to be used by both transient and resident species; however, the interior marshes were used primarily by marsh-resident species (Cyprinodontiformes and *Palaemonetes* sp.) that are excellent food sources for adult transient-species. Four zonations of marsh use are described for transients, residents, and rare species.

Introduction

Shallow-water, salt-marsh habitats are known to be important nursery areas for estuarine fish and crustaceans (Herke 1971; Weinstein 1979; Bozeman and Dean 1980; Turner 1992). The traditionally accepted role of emergent marsh vegetation supporting estuarine fisheries productivity via detrital-based food chains (Darnell 1958, 1961, 1967; Odum and Heald 1975) has been questioned (Nixon 1980; Boesch and Turner 1984), and more recent attention has focused on the direct use of intertidal marshes by fishes and invertebrates for feeding, reproduction, and refuge from predators. Recently developed methods for sampling in emergent vegetation, including pit traps (Kneib and Stiven 1978), drop samplers (Zimmerman et al. 1984), flume nets (McIvor and Odum 1986), block-nets (Hettler 1989), flume-weirs (Kneib 1991), and lift nets (Rozas 1992a) have shown that juvenile and small adult fishes and invertebrates use flooded marsh habitats.

Results from the new gear types are not necessarily comparable. Pit traps are effective for catching killifishes (Cyprinodontidae) and other marsh-resident species that use flooded marshes and return to marsh ponds and ditches at low tide (Kneib and Stiven 1978; Kneib 1984; Talbot and Able 1984). Pit traps are probably not effective at catching transient species that move from tidal creeks and bays up onto the marsh at high tide and return to open-water areas on ebbing tides. Studies in Texas that utilized paired drop samplers on flooded salt marshes reported higher densities of grass shrimp, blue crabs, and brown shrimp in vegetated marsh habitats when compared to adjacent nonvegetated habitats (Zimmerman et al. 1984; Zimmerman and Minello 1984). Drop samplers are very quantitative but sample a relatively small area (0.5–2.8 m^2), and, because they are usually dropped from a boat, they are only effective for sampling the edge of marshes. McIvor and Odum (1986) developed flume nets to passively sample fish from intertidal freshwater marshes in Virginia. They reported extensive use of flooded marshes by resident, freshwater species, as well as by some estuarine, transient fishes and crustaceans. Hettler (1989) collected fish coming off a flooded salt marsh in North Carolina with a modified block-net and reported extensive use of these marshes by both resident and transient fishes and crustaceans. Both flume nets and block nets utilize tidal action to passively (and nondestructively)

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sample large areas of vegetated marsh, and have proven effective in marshes that flood regularly. These two approaches cannot determine which fish utilize only the edge marshes and which (if any) penetrate into the interior marshes because the entire catch is consolidated into one net at the creekbank.

Two new gear types were described after this study was initiated that quantitatively and nondestructively sample fish on the flooded marsh surface. These two passive methods enclose the marsh at high tide and concentrate the sample into pit traps located at the lowest elevation inside the enclosure as the marsh drains. The flume-weir (Kneib 1991), enclosing 100 m^2 of marsh, uses screen panels inserted into frames from a boardwalk. The lift net gear (Rozas 1992a) is buried in the marsh and is remotely lifted to enclose 6 m^2 of marsh. These gear are without permanent walls to block access to the marsh and can discretely sample the edge and interior marshes. They are, therefore, probably more effective than flumes and block nets for sampling fishes using interior marshes.

Data were collected using flumes and seines to address three objectives: to quantify the temporal and spatial use of the flooded marsh surface by fishes and crustaceans in a natural Louisiana saline marsh; to compare the relative importance of the marsh habitat at the creek edge versus the interior marshes; and to identify species-specific differences in marsh habitat use. We were particularly interested in comparing spatial marsh use by resident and estuarine-dependent species. Our basic hypothesis was that there are species-specific differences in marsh use, that is, not all species will use the marsh edge exclusively and not all species distribute themselves homogeneously over the marsh during flooding (Hypothesis #1). We further hypothesized that the edge marshes are more important to fishes and crustaceans (particularly transient, estuarine-dependent species) than are the interior marshes (Hypothesis #2), and the interior marshes are utilized primarily by marsh-resident species (Hypothesis #3).

Materials and Methods

Study Area, Sample Gear, and Site Selection

The study area was in a saline marsh approximately 2 km NNW of the Louisiana Universities Marine Consortium (LUMCON) Marine Center in Cocodrie, Louisiana (Fig. 1). The streamside edge and interior marsh vegetation is dominated by *Spartina alterniflora* and along the natural levee is a mixed *S. alterniflora, Spartina patens* and *Distichlis spicata* community. The experiment used flume nets of different lengths to allow comparisons between edge and interior marshes. Samples were also collected by seining at high and low tides along the creek edge adjacent to the flumes to allow comparisons of the species composition at the creek edge with that of the adjacent flooded marsh. Flume nets were constructed in a relatively uniform marsh adjacent to a nearly straight stretch of creek bank (approximately 175 m long) with a gradual sloping shoreline profile. This site was chosen to increase the chances that all flumes would sample similar habitats (shoreline conditions, vegetation stem density and biomass). Results from flume net studies in Virginia tidal freshwater marshes report that stream-order, shoreline profiles (erosional vs depositional), and drainage features (rivulets vs creekbanks) have significant effects on the densities of nekton utilizing the adjacent marshes (Rozas and Odum 1987; McIvor and Odum 1988; Rozas et al. 1988). Rozas et al. (1988) reported densities of fish to be three times greater in rivulet flumes than in creekbank flumes, but because of the relatively low density of rivulets, they estimated that 88% of fishes reached the marsh surface via creekbanks; therefore, all flumes used in this study were constructed on creekbanks without rivulets. Because marshes adjacent to gradually sloping shorelines (depositional) are utilized more by fish than those adjacent to steep erosional shorelines (McIvor and Odum 1988), a site was selected along a straight stretch of creekbank to assure that all flumes had similar shoreline profiles.

Flume Net Sampling

Flume nets, modified from the design by McIvor and Odum (1986), were used to quantitatively and nondestructively sample the fishes and macrocrustaceans using the flooded marsh surface. The flume nets consisted of parallel walls of 3-mm-mesh plastic aquaculture netting oriented perpendicular to the creek axis. The net walls were attached to 5 cm × 5 cm wooden posts spaced 2 m apart and the bottom 10–15 cm was buried in the marsh sediment, resulting in walls approximately 0.75 m high. These flume walls remained in the marsh throughout the study. The ends of the flumes remained open except when they were being "fished." At this time a cod-end net constructed from 3-mm-mesh nylon netting attached to a rectangular PVC-pipe frame (2 m × 0.915 m) was attached to each end of the flume using a sliding PVC track similar to that described by McIvor and Odum (1986). An A-frame was added (after 2 mo of sampling) at each end of the flumes to suspend the cod-end net over the opening and to allow remote setting of the nets, thus minimizing organism disturbance. The nets were suspended in the slid-

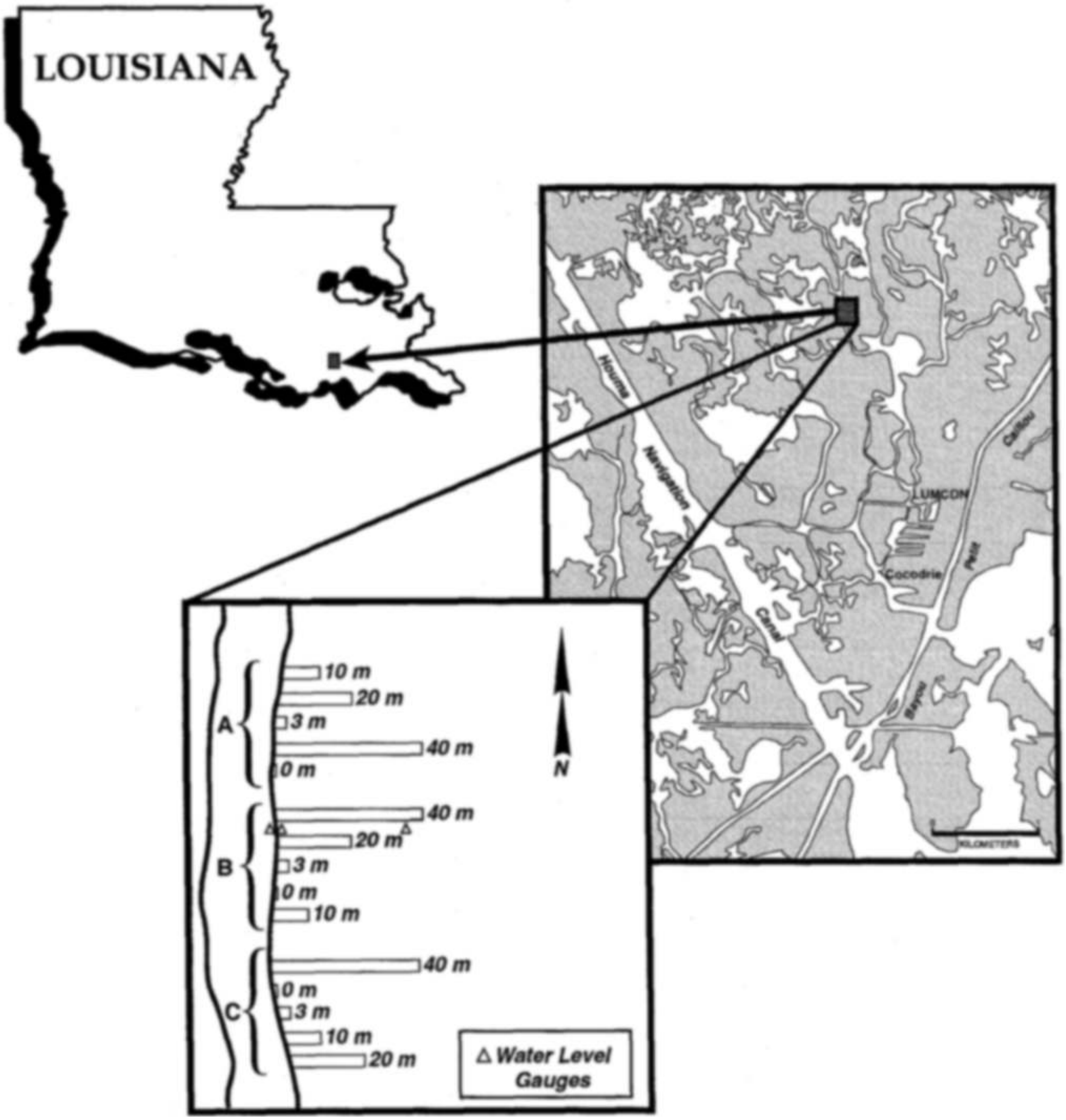

Fig. 1. Location of the study area and water-level gauges, and a diagram of the experimental design showing the randomized placement of five flume length treatments within three blocks (A, B, C).

ing tracks by bridles and attached to the A-frames with release pins that were tripped remotely with a 4.5-m long cord.

The flume nets used in this study differed from those described by McIvor and Odum (1986). The mesh size was smaller (3 mm vs 6 mm), the flumes wider (2 m vs 1.5 m), the length varied (0 m, 3 m, 10 m, 20 m, and 40 m vs 20 m), and both ends remained open during the flood tide (as opposed to being open only at the creek bank). The experiment was a randomized block design with three blocks of five treatments, consisting of flumes extending 0 m (no flume), 3 m, 10 m, 20 m, and 40 m into the marsh (Fig. 1). Flumes were spaced approximately 10 m apart within treatment blocks, with approximately 20 m between blocks.

Each flume had a boardwalk to minimize damage to the marsh during construction and monthly inspection. Walkway planks were used only during the construction, on monthly inspections, and while setting and retrieving of nets to eliminate the possible effects of shading.

The flumes were "fished" by letting both ends of the flume remain open during flood tides, closing both ends at or near slack high tides, and then picking up the cod-end nets after the marsh drained (at or near low tide). Because the "natural levee" of the creek (approximately 3 m in from the edge) had a slightly higher elevation than the interior marshes, it was necessary to use cod-end nets on both ends of the long flumes (10 m, 20 m, and 40 m). The 3-m flumes had a cod-end net on the creek end and a flat block-net on the marsh end. The no-flume (0 m) treatment consisted of a cod-end net attached to end posts placed at the edge of the creek (with no flume walls attached).

The underlying assumptions for making comparisons between flume lengths were that access to all flumes (3 m, 10 m, 20 m, and 40 m) was equal for organisms entering the marsh from the creek bank (or from the interior marsh), and that these flumes neither attract nor deter aquatic organisms to use the marsh. Because both ends remain open until the nets are set at high tide, an organism entering the marsh from the creek could move inland unrestrained and would only be captured if it remained within that particular flume (i.e., a fish entering a 3-m flume will not be captured if it moves inland 10 m). Therefore, if an organism entered the marsh over the creek bank and used the edge and interior marshes homogeneously, catches will be proportional to length. Conversely, catches will be equal in all flume lengths if only the edge marshes (<3 m from the creek) are used.

Catches are reported as numbers and biomass per 2 m of marsh edge (as did McIvor and Odum 1986) not per unit area of marsh. This was done because the flume walls restrict the lateral movement of fish over the marsh surface. Because all flumes had the same width (regardless of length), comparisons among treatments were made with actual numbers (log-transformed) captured.

Sampling was conducted approximately monthly during the tidal cycle with the highest predicted tidal height and range. The sampling dates were selected based on tides predicted by the United States Department of Commerce, National Ocean Survey from the gauge at the LUMCON Marine Center. Samples were collected monthly from all 15 flumes beginning in January 1989; in March 1989, net deployment was modified to allow remote setting of the nets. Data from January through November 1989 are presented here.

Seine Sampling

Some fish captured in flume nets may not have been on the marsh surface because the design of the flume nets (straight net frame along an irregularly shaped marsh edge) results in a small amount of creek-edge habitat being sampled. Species that are infrequently caught in flumes may be a result of this phenomenon. This design flaw became evident after a few months of sampling. We therefore supplemented the flume sampling with high-tide and low-tide seine sampling along the creek-edge habitat beginning in July 1989.

Our working assumptions about the results from the seining were that fish using the marsh surface at high tide will be scarce in high-tide samples and much more abundant in low-tide samples when they are forced out of the marsh, that species using only the creek-edge habitat will be equally abundant at high and low tides, and that species preferring deeper, more open-water habitats will be rare in low-tide seine samples but more abundant in high-tide samples when the water at the edge is deeper.

Seine samples were collected adjacent to the flumes at high and low tide every time the flume nets were fished to allow comparisons of the species composition and abundance at different tide stages and between these two gear types. Two seine stations were permanently established along the creek edge adjacent to the flumes, one north and one south of the flumes on the same side of the creek. One seine sample was collected at each station at high tide, immediately after setting the flume nets, and again at low tide, immediately before retrieving the flume net samples. Seine samples were collected with a 3 m × 2 m straight seine with 3.2-mm nylon ace mesh pulled along the creek edge by two persons, one walking on the marsh edge and one in the creek approximately 2 m from shore. Each sample covered 30 m of creek edge and was collected in three short drags (approximately 10 m each) that were pooled together.

All animals collected in flume or seine samples were preserved in the field in 10% formalin and transported to the laboratory where they were sorted, identified, counted, measured, and weighed.

Physical Data Collection

Endeco® Type 1152 Density Compensating Water-Level Recorders were installed 1 m into the creek, 1 m into the marsh, and 35 m into the marsh alone one boardwalk near the center of the flume site (Fig. 1). An identical gauge was installed approximately 2 km away in the creek near the

LUMCON Marine Center. These gauges provided a continuous record of the frequency, amplitude, and duration of flooding events, as well as water salinity and temperature. A water-salinity sample was taken from the creek at the flume site at high tide (when the flume nets were set) and again at low tide (when the nets were retrieved). Salinity was measured in the laboratory with a Haake-Buchler Digital Chloridometer.

DATA ANALYSIS

Analysis of the data was on the Louisiana State University (LSU) mainframe computer using the Statistical Analysis System package (SAS Institute Inc. 1985a, b, c). All analysis of variance (ANOVA) and regression models were run with the general linear models (GLM) procedure. All catch data was log-transformed prior to analysis. Comparisons of catches were made between flume length treatments (FLENGTH) with a factorial ANOVA model to test the hypothesis that the edge marshes are more important to transient fishes and decapod crustaceans than are interior marshes. Comparisons were also made between catches from front (creek bank) nets and back (interior marsh) nets from those flumes that had both front and back nets (10-m, 20-m, and 40-m flumes only). Because the flume net experiment was set up in a randomized block design, all ANOVA models included REP as a blocking factor to remove any block effects (and as a test of the sampling error). An ANOVA was also used to test for differences between high-tide and low-tide catches from seine samples. Because seasonal differences in species abundance were expected, DATE was included as a main effect in all models as was its interaction with other main effects. These ANOVA models were run on various subsets of the data including log-transformed numbers of decapods only, fish only, "transient" fish only, "resident" fish only, and individual species. Because of the potential problem of finding a significant result by chance alone when running multiple ANOVAs, a Bonferroni-adjusted alpha level was used to assure a 95% confidence level for the individual species ANOVAs ($p < 0.0025$ for flume data; $p < 0.0036$ for seine data). ANOVA tables are not presented here; instead, F-values and probability levels are given when appropriate.

Resident species are generally defined as those that spend their entire life cycle in the estuary; transient species are those that spend only some life stages (e.g., juvenile) in the estuary. In this report, fish species were classified as either "resident" or "transient" based on an ecological classification in Thompson and Forman (1987), who classified fish from the Barataria Bay basin into four groups. The resident classification included any species listed in their "estuarine" and "freshwater" classifications; the transient classification included those fish species classified as "estuarine-marine" or "marine" in Thompson and Forman (1987).

Results

PHYSICAL DATA

The data presented here are from the LUMCON Marine Center gauge that had the most complete data set. There were data collection problems with the three gauges (located in the creek, at the marsh edge, and in the interior marshes) at the flume site. Several months of water-level data from these gauges were usable and were compared with data from the gauge in the bayou at LUMCON. Water levels at the two sites were highly coherent at diurnal tidal frequencies ($R^2 > 0.95$). A nearly complete continuous record (15-min intervals) of water levels from January through December 1989 is presented in Fig. 2. This figure illustrates the frequency, depth, and duration of flooding events, and the times when flume net samples were taken. The horizontal line on Fig. 2 (at 0-cm water level) approximates the average interior marsh elevation (the level at which the 35-m inland gauge was set). The maximum water depth on the marsh at high tide (typically diurnal) ranged from less than zero (not flooded) to approximately 54 cm during the period of study (January through November 1989). The maximum water depths during the tidal cycles when flume net samples were collected ranged from 6.9 cm in February to 34.5 cm in November 1989.

Figure 3A illustrates the mean marsh-elevation profiles for each flume (each line is a mean of two profiles within each flume). Although individual flume profiles are not readily distinguishable from this figure (all five flumes within each block have the same line pattern), the variation in flume elevations along the transects is generally <10 cm. A well-defined natural levee, approximately 10–15 cm higher than the interior marsh elevation, is evident with its peak located about 3 m from the creek edge. Since the "zero elevation" reference line in Fig. 3A corresponds to the "zero water level" reference line in Fig. 2, it is obvious that a high tide flooding depth <10–15 cm would not flood the natural levee. However, even at these lower water levels, the interior marsh does flood "from the back" through small drainage features such as rivulets and muskrat trails.

Salinity and temperature data from the LUMCON gauge were also recorded for January through December 1989. Salinity during that time

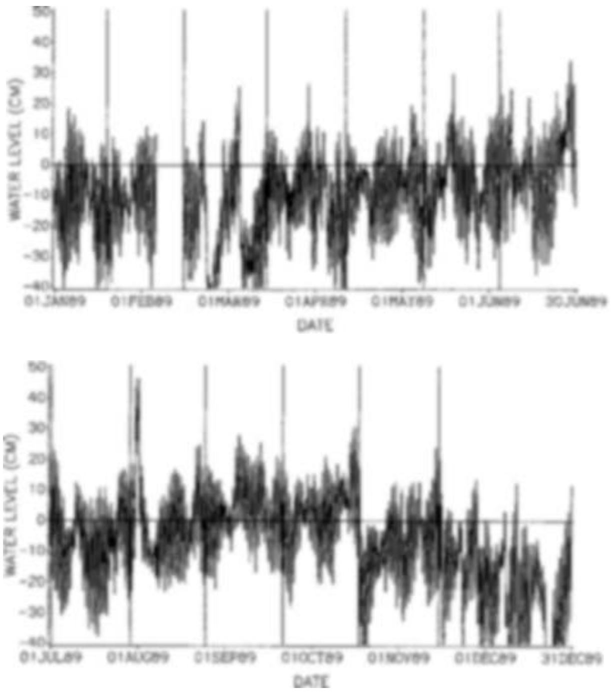

Fig. 2. Water-level data for 1989 at the LUMCON gauge. The horizontal line represents the approximate marsh surface elevation at the flume site. The vertical lines indicate the times when the flume net samples were collected.

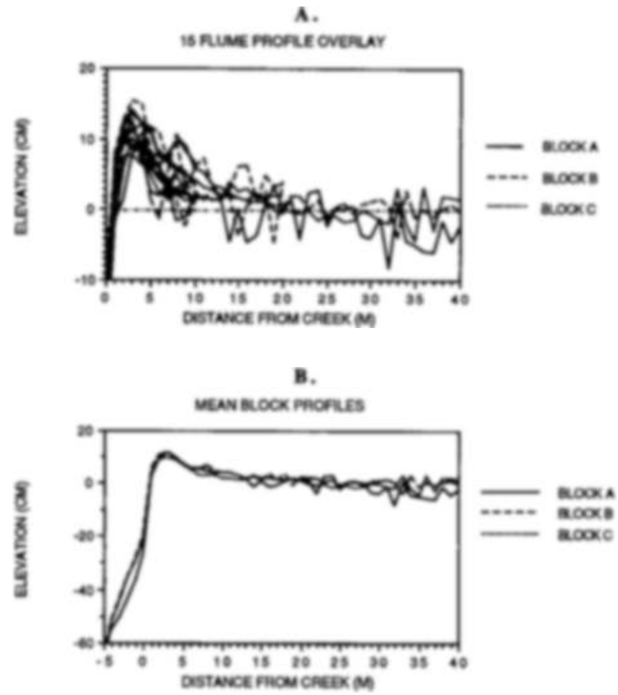

Fig. 3. Elevation levels at the flume net sites. A. Average marsh elevation profiles (two replicate profiles) for each of 15 individual flumes, identified by flume block (A, B, or C). B. Mean marsh and adjacent creek elevation profiles of five flumes within each flume block (each flume has two replicates).

ranged from 0.8‰ in July to 20.6‰ in October. Actual salinities at the site during flume net collections varied from 2.0‰ in April to 18.1‰ in October. Temperatures at the LUMCON gauge ranged from 34.4°C in August to 0°C in December.

Flume Net Data

Species Composition

A total of 37,667 organisms (fish and decapod crustaceans) with a total preserved wet weight of 29.1 kg were collected in the flume nets from January through November 1989 (Table 1). The total catch included 29 species of fish (4,124 individuals, 6.9 kg preserved wet weight) representing 14 families and at least 9 species of decapod crustaceans (33,543 individuals, 22.3 kg preserved wet weight). Other taxa of invertebrates, including Amphipoda, Isopoda, Mysidacea, Gastropoda, Bivalvia, Polychaeta, Arachnida, Insecta, and Hirudinea, and even Gulf salt-marsh snakes (*Nerodia clarkii*), were captured in the flume nets but were not included in the summaries and analysis of catch data. The species composition in flume net catches varied with season (Table 2). In general, marsh-resident species were more abundant and always present. Transient species were only seasonally present.

The total catch was dominated by decapod crustaceans that made up 89.0% of the total number and 76.4% of the total biomass (Table 1 and Fig. 4). Grass shrimp (*Palaemonetes* sp.) were the most abundant organisms caught in the flumes, comprising 74.9% by number (25.4% biomass) of the total catch; blue crabs (*Callinectes sapidus*) were the next most abundant at 9.9% by number (42.9% biomass). Fish species made up only 11.0% of the total catch by number but 23.6% of the total biomass. Naked goby (*Gobiosoma bosc*) was the most abundant fish caught (4.4% of total) but was fifth in biomass (1.6% of total). The Gulf killifish (*Fundulus grandis*) was the second most abundant fish species (1.8% of total) but had the highest biomass (7.5% of total). A single specimen of southern flounder (*Paralichthys lethostigma*) represented more biomass (1.7% of total) than all 1,649 naked gobies. Because of the problem of single large specimens dominating biomass, all comparisons and analysis are done on counts rather than biomass.

Comparison of Flume Catches From Front and Back Nets

Among those flumes that had both front and back nets (10-m, 20-m, and 40-m flumes only), sig-

TABLE 1. List of fishes and decapod crustaceans collected from flume nets from January through November 1989. The total number, total biomass (preserved wet weight), and percentage of total catch by number and biomass are given for each species. Fish and decapod species are listed separately in order of decreasing numerical abundance.

Species	Total Number		Total Biomass	
	Number	Percent	Weight (g)	Percent
Fishes				
Gobiosoma bosc	1,649	4.4	480.6	1.6
Fundulus grandis	663	1.8	2,182.6	7.5
Adinia xenica	450	1.2	178.4	0.6
Fundulus pulvereus	336	0.9	165.0	0.6
Gobionellus boleosoma	171	0.5	56.4	0.2
Poecilia latipinna	169	0.4	116.6	0.4
Lucania parva	132	0.4	34.6	0.1
Cyprinodon variegatus	116	0.3	119.6	0.4
Fundulus jenkinsi	102	0.3	63.3	0.2
Menidia beryllina	67	0.2	42.0	0.1
Cynoscion nebulosus	64	0.2	485.4	1.7
Mugil cephalus	47	0.1	1,742.2	6.0
Anchoa mitchilli	39	0.1	10.9	<0.1
Myrophis punctatus	27	0.1	245.3	0.8
Bairdiella chrysoura	20	0.1	58.3	0.2
Archosargus probatocephalus	18	<0.1	178.9	0.6
Gambusia affinis	9	<0.1	0.6	<0.1
Citharichthys spilopterus	9	<0.1	39.8	0.1
Achirus lineatus	9	<0.1	5.2	<0.1
Micropogonias undulatus	6	<0.1	5.1	<0.1
Lagodon rhomboides	5	<0.1	75.9	0.3
Gobionellus shufeldti	4	<0.1	2.2	<0.1
Symphurus plagiusa	4	<0.1	1.6	<0.1
Sciaenops ocellatus	3	<0.1	32.0	0.1
Cynoscion arenarius	1	<0.1	0.8	<0.1
Syngnathus floridae	1	<0.1	0.7	<0.1
Syngnathus scovelli	1	<0.1	0.6	<0.1
Paralichthys lethostigma	1	<0.1	504.1	1.7
Opsanus beta	1	<0.1	47.3	0.2
Decapod crustaceans				
Palaemonetes sp.	28,221	74.9	7,390.0	25.4
Callinectes sapidus	3,714	9.9	12,505.4	42.9
Uca sp.	804	2.1	1,737.2	6.0
Penaeus setiferus	307	0.8	141.3	0.5
Penaeus aztecus	252	0.7	353.5	1.2
Xanthidae	207	0.5	45.9	0.2
Sesarma sp.	35	0.1	90.2	0.3
Macrobrachium sp.	2	<0.1	0.2	<0.1
Paguridea	1	<0.1	2.8	<0.1
Total fish	4,124	11.0	6,876.2	23.6
Total decapods	33,543	89.0	22,266.5	76.4
Total fish and decapods	37,667	100.0	29,142.7	100.0

nificantly higher numbers of decapods ($F = 1708.74$, $p < 0.0001$) were caught in the front nets (94.3%) than in the back nets. Some grass shrimp and blue crabs were caught in back nets, but most (98.9% and 90.9% respectively) were caught in the front nets (Table 3). Almost all (99.9%) of the fiddler crabs (*Uca* sp.) and 39.3% of the wharf crabs (*Sesarma* sp.) were caught in the back nets. Penaeid shrimp and Xanthid crabs were caught exclusively in the front nets.

Significantly higher numbers of fish ($F = 183.87$, $p < 0.0001$) were caught in the front nets (68.6%) than in the back nets (Table 4). The 10 most abundant fish species (naked goby, *Gobiosoma bosc*; gulf killifish, *Fundulus grandis*; diamond killifish, *Adinia xenica*; bayou killifish, *F. pulvereus*; sailfin molly, *Poecilia latipinna*; rainwater killifish, *Lucania parva*; sheephead minnow, *Cyprinodon variegatus*; darter goby, *Gobionellus boleosoma*; saltmarsh topminnow, *F. jenkinsi*; and tidewater silverside, *Menidia beryllina*) accounted for 94.4% of the total fish catch from the 10-m, 20-m, and 40-m flumes (Table 4). These 10 species were classified as resident species and represent four families (Cyprinodontidae, Gobiidae, Poecilidae, and Atherinidae). Resident fish species were caught in significantly higher num-

TABLE 2. Seasonal occurrence of fish and decapod crustaceans collected from flume net samples from January through November 1989. Species are classified as either marsh resident (R) or transient (T) and listed in order of decreasing numerical abundance.

Species	Sample Date											
	January	February	March	April	May	June	July	July	August	September	October	November
Palaemonetes sp. (R)	3,898	2,885	2,292	1,300	1,190	1,914	1,635	2,668	3,660	2,375	2,375	2,029
Callinectes sapidus (T)	150	168	228	81	171	158	206	211	597	671	625	448
Gobiosoma bosc (R)	76	123	126	23	99	254	154	147	179	134	205	129
Uca sp. (R)		14	48		70	110	130	189	172	42	3	26
Fundulus grandis (R)	77	11	10	97	37	24	40	38	55	108	122	44
Adinia xenica (R)	4	5	36	43	5	28	29	82	64	28	89	37
Fundulus pulvereus (R)	20	10	49	2	3	45	25	53	39	17	46	27
Penaeus setiferus (T)			1			1	51	71	61	110	7	5
Penaeus aztecus (T)	1	1		1	69	52	87	25	2	8	4	2
Xanthidae (R)	1	5	18	4	22	48	25	23	14	12	27	8
Gobionellus boleosoma (R)	13	7	12						1	26	40	72
Poecilia latipinna (R)						1		6	13	10	135	4
Lucania parva (R)			27		18	3	5	17	12	3	13	34
Cyprinodon variegatus (R)	4		1	6	6	10	12	8	6	11	33	19
Fundulus jenkinsi (R)	13	10	23	11	2	1	2	8	8	11	11	2
Menidia beryllina (R)	1					11	25	3	10	7	8	2
Cynoscion nebulosus (T)	1					6	12	8	14	9	5	9
Mugil cephalus (T)	14		4				8	2	5	7	5	2
Anchoa mitchilli (T)	1					2	16	20				
Sesarma sp. (R)			1		4	10	3	6	6	3	1	1
Myrophis punctatus (T)	4	10	2			2	1	6	1			1
Bairdiella chrysoura (T)					2	9	5	1	1			2
Archosargus probatocephalus (T)					5	3	3	3	3	1		
Gambusia affinis (R)							1		2	1	3	2
Citharichthys spilopterus (T)	1				2	4	1	1				
Achirus lineatus (T)								2		5	1	1
Micropogonias undulatus (T)	4											2
Lagodon rhomboides (R)				1	1		1		2			
Gobionellus shufeldti (R)		1								1	2	
Symphurus plagiusa (T)										4		
Sciaenops ocellatus (T)	1		1	1								
Macrobrachium sp. (R)							2					
Cynoscion arenarius (T)								1				
Syngnathus floridae (T)						1						
Syngnathus scovelli (R)					1							
Paralichthys lethostigma (T)				1								
Opsanus beta (T)										1		
Paguridea (R)											1	
Total resident species	10	10	12	9	13	13	15	13	16	16	17	15
Total transient species	9	3	5	4	5	10	10	12	8	9	6	9
Total resident individuals	4,107	3,071	2,643	1,487	1,458	2,459	2,089	3,248	4,243	2,789	3,114	2,436
Total transient individuals	177	179	236	84	249	238	390	351	684	816	647	472

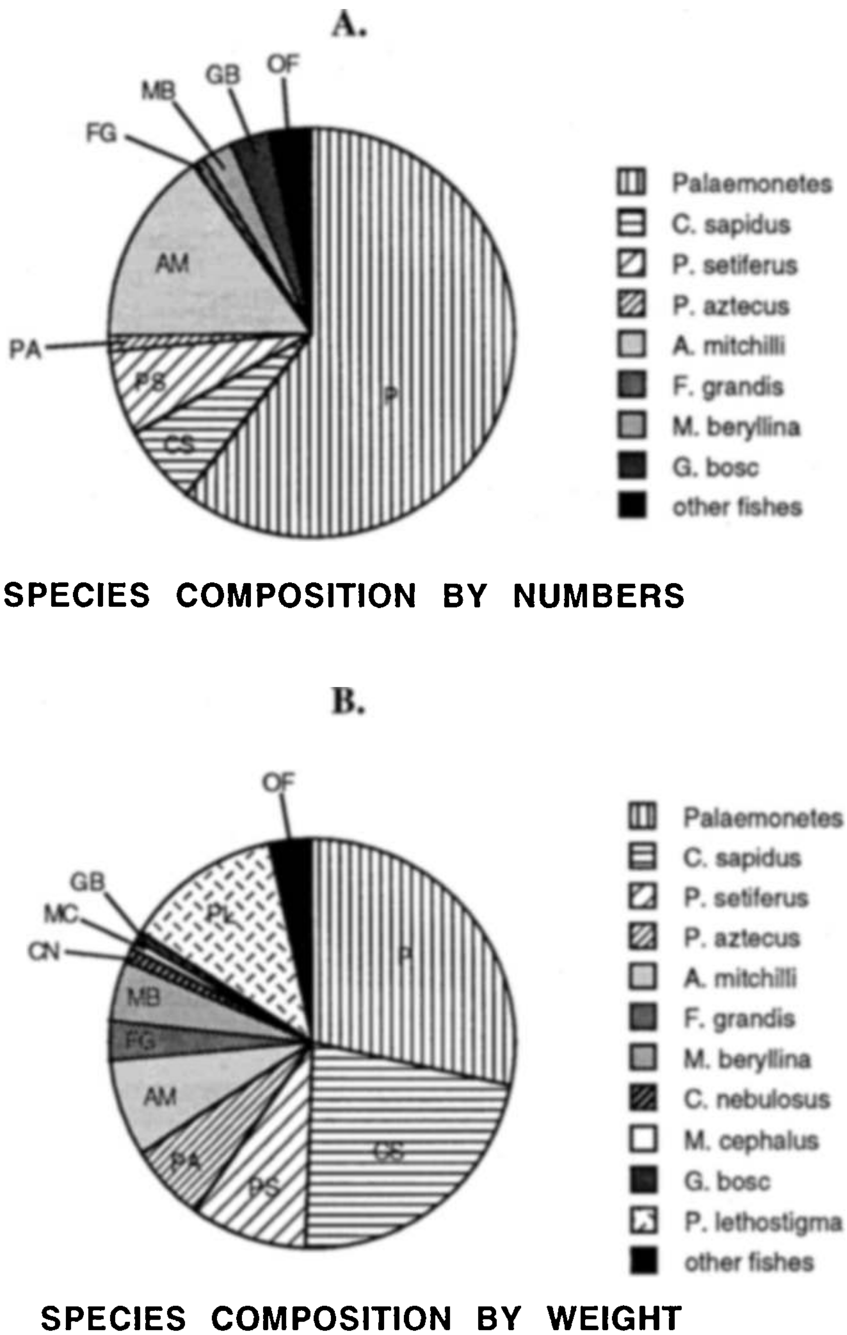

Fig. 4. Pie charts illustrating the proportion of total flume net catch represented by the most abundant fish and decapod species. A. Species composition by numbers. B. Species composition by wet weight.

bers ($F = 162.90$, $p < 0.0001$) in front nets than in back nets. The transient fish species were much less abundant in flume catches. These species made up 6% of the total fish number and 49% of the total fish biomass, and were caught exclusively in the front nets.

Only eight species of fish were caught in back nets and all belonged to the order Cyprinodontiformes (families Cyprinodontidae and Poecilidae), except for one *Menidia beryllina* (Table 4). Five of these eight species (*Fundulus pulvereus, Gambusia affinis, Poecilia latipinna, Adinia xenica,* and *Cyprinodon variegatus*) were more abundant in the back nets than in the front nets. Two other Cyprinodontid species (*Lucania parva* and *Fundulus grandis*) were commonly caught in back nets but were

TABLE 3. Number and percent of each decapod species caught in front and back nets, and total number caught in flume net collections from January through November 1989 from only those flumes (10, 20, and 40 m) with front and back nets. Species are listed in order of decreasing numerical abundance.

Taxa	Front Nets		Back Nets		Total	
	Number	Percent[a]	Number	Percent[a]	Number	Percent[b]
Palaemonetes sp.	17,665	98.9	196	1.1	17,861	83.4
Callinectes sapidus	2,102	90.9	211	9.1	2,313	10.8
Uca sp.	1	0.1	802	99.9	803	3.8
Penaeus setiferus	143	100.0	0	0.0	143	0.7
Penaeus aztecus	133	100.0	0	0.0	133	0.6
Xanthidae (fam.)	126	100.0	0	0.0	126	0.6
Sesarma sp.	17	60.7	11	39.3	28	0.1
Macrobrachium ohione	1	100.0	0	0.0	1	0.0
Paguridea (fam.)	1	100.0	0	0.0	1	0.0
Total decapods	20,189	94.3	1,220	5.7	21,409	100.0

[a] Percentage of that species caught in front or back nets.
[b] Percentage of total decapods (caught in 10-m, 20-m, and 40-m flumes only) represented by that species.

more abundant in front nets. The saltmarsh topminnow (*Fundulus jenkinsi*) was the only Cyprinodontid species that was never caught in a back net. All other fish species, including a few estuarine residents (primarily Gobiids) and all transient fish species, were caught exclusively in the front nets (Table 4).

Block Effect

The experiment was set up in a randomized-block design with three adjacent blocks (REP) of flume-length treatments (FLENGTH). Microhabitat differences among the three treatment blocks may have led to the occasional differences among adjacent blocks. In general, REP A (the northernmost block) produced higher total catches of fish and decapods than REPs C and B. On a species level, this same trend was apparent for *Gobiosoma bosc* and *Palaemonetes* sp., the most abundant fish and decapod species. These differences may have been due to slight differences in elevation profiles in the marsh; however, these elevation differences averaged less than 5 cm (Fig. 3B) and are highly variable, with no clear trends by block. The adjacent creek (0–5 m from the edge) had a slightly steeper bottom profile and a small oyster reef in front of flumes 3 and 4 (REP A). This reef could have had some unknown effect on organisms using the adjacent marsh. In contrast, three species that were commonly caught in back nets (*Cyprinodon variegatus, Adinia xenica,* and *Lucania parva*) were significantly more abundant in REP C than in other blocks. The other three species that were commonly caught in back nets (*Fundulus grandis, F. pulvereus,* and *Poecilia latipinna*) were also most abundant in REP C but not significantly so. The higher catch of Cyprinodontid species in REP C is probably an effect of several muskrat trails close to the back openings of flumes 14 and 15 (REP C). These muskrat trails provided access and refuge to marsh-resident species.

Date Effect

The variable DATE was included in all ANOVA models to remove the expected source of variation caused by seasonal differences in species abundance. In almost all cases this DATE effect was found to be highly significant ($p < 0.01$). These seasonal differences in species abundance may result from the migration of species in and out of marsh areas, or from changes in behavior with seasonal changes in hydrology (depth of flooding), temperature, or salinity.

Comparisons of Flume Length Treatments

The total catch of each species by flume length (treatment) is listed in Table 5. The total catch of fish and decapods (front and back nets combined) varied significantly between treatments. Similar results were found only for decapods since decapods dominate the total catch. In both cases, significantly higher mean numbers were caught in the 40-m flumes than in other flume lengths. The next highest catches were in the 10-m flumes followed by the no-flume treatment (0 m), the 20-m flume treatment, and the 3-m flume treatment; however, these four treatments were not significantly different from each other. When catches in the long flumes (10 m, 20 m, and 40 m; pooled) and short flumes (3 m) were compared, the long flume catches were significantly higher for total fish and decapods and for decapods only (Fig. 5). These results indicate use of the interior marshes by some fish and decapods.

When the catches of fish only were compared, the differences between treatments were also significant. Catches from the 40-m, 10-m, and 20-m flumes were greater than catches from the 3-m and

TABLE 4. Number and percent of each fish species caught in front and back nets, and total number caught in flume net collections from January through November 1989 from only those flumes (10, 20, and 40 m) with front and back nets. Species are listed in order of decreasing numerical abundance.

Fish Species	Ecological[a] Classification	Front Nets		Back Nets		Total	
		Number	Percent[b]	Number	Percent[b]	Number	Percent[c]
Gobiosoma bosc	R	968	100.0	0	0.0	968	33.3
Fundulus grandis	R	455	90.8	46	9.2	501	17.2
Adinia xenica	R	74	20.2	293	79.8	367	12.6
Fundulus pulvereus	R	15	4.8	298	95.2	313	10.8
Poecilia latipinna	R	21	12.5	147	87.5	168	5.8
Lucania parva	R	68	61.3	43	38.7	111	3.8
Cyprinodon variegatus	R	30	28.0	77	72.0	107	3.7
Gobionellus boleosoma	R	90	100.0	0	0.0	90	3.1
Fundulus jenkinsi	R	66	100.0	0	0.0	66	2.3
Menidia beryllina	R	52	98.1	1	1.9	53	1.8
Cynoscion nebulosus	T	43	100.0	0	0.0	43	1.5
Mugil cephalus	T	41	100.0	0	0.0	41	1.4
Myrophis punctatus	T	17	100.0	0	0.0	17	0.6
Archosargus probatocephalus	T	12	100.0	0	0.0	12	0.4
Anchoa mitchilli	T	9	100.0	0	0.0	9	0.3
Gambusia affinis	R	1	11.1	8	88.9	9	0.3
Bairdiella chrysoura	T	8	100.0	0	0.0	8	0.3
Achirus lineatus	T	5	100.0	0	0.0	5	0.2
Micropogonias undulatus	T	3	100.0	0	0.0	3	0.1
Lagodon rhomboides	R	3	100.0	0	0.0	3	0.1
Gobionellus shufeldti	R	3	100.0	0	0.0	3	0.1
Citharichthys spilopterus	T	3	100.0	0	0.0	3	0.1
Symphurus plagiusa	T	3	100.0	0	0.0	3	0.1
Cynoscion arenarius	T	1	100.0	0	0.0	1	0.0
Sciaenops ocellatus	T	1	100.0	0	0.0	1	0.0
Syngnathus floridae	T	1	100.0	0	0.0	1	0.0
Opsanus beta	T	1	100.0	0	0.0	1	0.0
Total resident fish	R	1,846	66.9	913	33.1	2,759	94.9
Total transient fish	T	148	100.0	0	0.0	148	5.1
Total fish		1,994	68.6	913	31.4	2,907	100.0

[a] Ecological classification: R = resident; T = transient.
[b] Percentage of that species caught in front or back nets.
[c] Percentage of total fish (caught in 10-m, 20-m, and 40-m flumes only) represented by that species.

0-m flumes. The apparent trend of lower fish catches in the shorter flumes to higher catches in the longer flumes indicates some use of the interior marshes by fishes. ANOVA test results for marsh-resident fish showed significant differences in catches between treatments with higher catches in long flumes when contrasted with short flumes (Fig. 6). Transient fish showed no differences in catch between treatments or between long and short flumes (Fig. 7), indicating that transient fish are not using the interior marsh habitats.

Effectiveness of No-Flume Treatment. There were no significant differences in decapod catches between the no-flume treatment and the flumes (all lengths were pooled) suggesting that the nets without flumes were just as effective at catching these organisms as those with flumes. However, fish (resident and transient) were caught in significantly higher numbers in nets with flumes (all lengths were pooled) than in the no-flume treatment, indicating a possible avoidance of nets without flumes. These generalizations did not always hold when individual species were tested.

Species Differences in Catch by Flume Length. Because habitat-use patterns vary between species, it is illustrative to analyze the data at a species level. This was done for the 20 most abundant species (13 fish, 7 decapod) caught in the flumes (species total catch >30). A Bonferonni-adjusted alpha level ($p < 0.0025$) was used to reduce the probability of finding a significant result by chance alone. Because the Bonferroni adjustment is extremely conservative, a few species ANOVAs had significant results at $p < 0.01$, which were not significant with the Bonferroni-adjusted alpha level. These cases are reported as such, because there may be some biological significance that may be overlooked using such a conservative approach.

Of the 20 species tested, only four fish species (*C. variegatus*, *F. grandis*, *F. pulvereus*, and *P. latipinna*) and two decapod species (*Palaemonetes* sp. and *Uca* sp.) were found to have significantly greater

TABLE 5. Total number of each species (fish and decapods) caught by flume length treatment (total for three flumes) from January through November 1989. Species listed in order of decreasing numerical abundance.

Species	Flume Length Treatment					Total
	No Flume	3-m	10-m	20 m	40-m	
Palaemonetes sp.	5,608	4,752	5,429	4,852	7,580	28,221
Callinectes sapidus	751	650	679	687	947	3,714
Gobiosoma bosc	344	337	314	229	425	1,649
Uca sp.	0	1	240	233	330	804
Fundulus grandis	103	59	160	178	163	663
Adinia xenica	6	77	143	148	76	450
Fundulus pulvereus	5	18	118	133	62	336
Penaeus setiferus	123	41	62	42	39	307
Penaeus aztecus	38	81	42	39	52	252
Xanthidae (fam.)	51	30	48	22	56	207
Gobionellus boleosoma	38	43	36	26	28	171
Poecilia latipinna	0	1	29	96	43	169
Lucania parva	8	13	19	55	37	132
Cyprinodon variegatus	3	6	7	61	39	116
Fundulus jenkinsi	20	16	19	19	28	102
Menidia beryllina	3	11	8	13	32	67
Cynoscion nebulosus	9	12	12	14	17	64
Mugil cephalus	2	4	8	20	13	47
Anchoa mitchilli	1	29	2	3	4	39
Sesarma sp.	0	7	8	16	4	35
Myrophis punctatus	7	3	5	4	8	27
Bairdiella chrysoura	7	5	0	1	7	20
Archosargus probatocephalus	0	6	4	3	5	18
Gambusia affinis	0	0	2	2	5	9
Citharichthys spilopterus	0	6	1	2	0	9
Achirus lineatus	3	1	2	1	2	9
Micropogonias undulatus	1	2	2	0	1	6
Lagodon rhomboides	0	2	0	0	3	5
Gobionellus shufeldti	0	1	0	3	0	4
Symphurus plagiusa	1	0	1	2	0	4
Sciaenops ocellatus	2	0	0	1	0	3
Macrobrachium ohione	1	0	0	1	0	2
Cynoscion arenarius	0	0	1	0	0	1
Syngnathus floridae	0	0	0	0	1	1
Syngnathus scovelli	1	0	0	0	0	1
Paralichthys lethostigma	0	1	0	0	0	1
Opsanus beta	0	0	0	1	0	1
Paguridea (fam.)	0	0	0	1	0	1
Total resident fish	531	584	855	963	941	3,874
Total transient fish	33	69	38	52	58	250
Total fish	564	653	893	1,015	999	4,124
Total decapods	6,572	5,562	6,508	5,893	9,008	33,543
Total fish and decapods	7,136	6,215	7,401	6,908	10,007	37,667

catches in the long flumes when contrasted with the 3-m flumes, indicating a significant use of interior marshes by these species. The four fish species are all resident Cyprinodontiform species. Two other Cyprinodontid species, *L. parva* and *A. xenica*, were not significantly more abundant in long flumes when contrasted with short flumes. However, both species were commonly caught in the back nets (Table 4), thereby documenting the frequent use of interior marshes by these species as well.

All other abundant fish species (total catch >30) that were tested with ANOVA were found to have no significant differences between catches from long vs short flumes. These included four resident species (*F. jenkinsi, G. bosc, G. boleosoma,* and *M. beryllina*) and three transient species (*C. nebulosus, M. cephalus,* and *A. mitchilli*). Three of these species, *A. mitchilli* ($p = 0.11$), *M. beryllina* ($p = 0.23$), and *M. cephalus* ($p = 0.40$), had nonsignificant ANOVA models (REP, DATE, FLENGTH), probably because of the low numbers caught. The relative abundance of these seven fish species in flume catches indicates that the marsh surface may be utilized by these fish at high tide; however, the uniformity of catches among flumes of different lengths and the absence of these species from back nets (except for one individual of *M. beryllina*

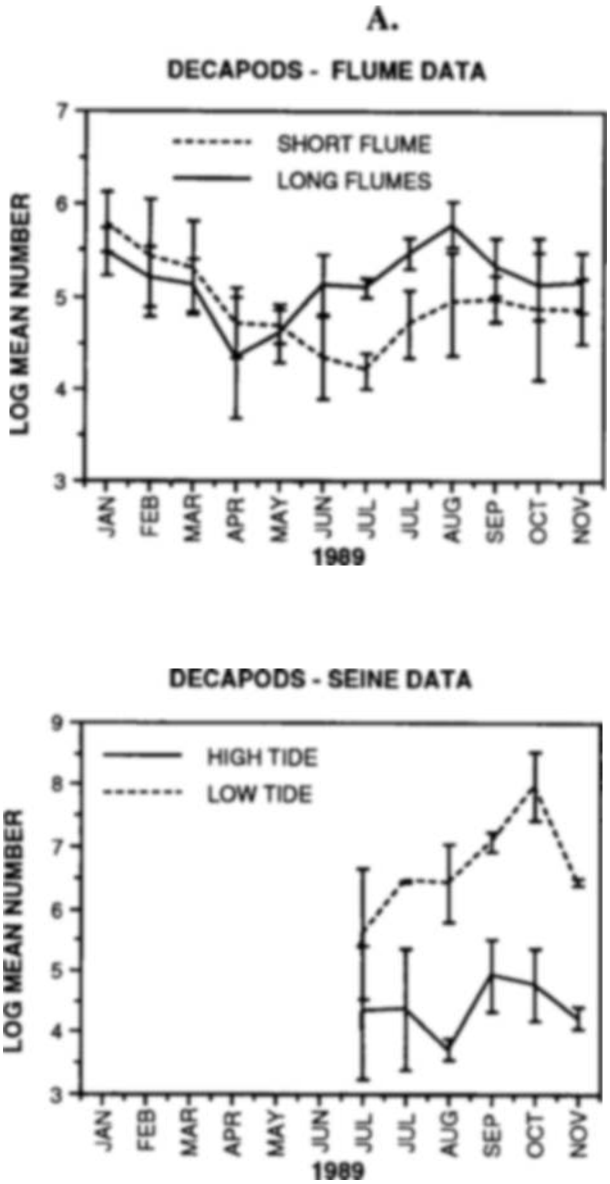

Fig. 5. The log mean numbers of decapods caught by sample date. A. In short flumes (3 m) vs long flumes (10-m, 20-m, and 40-m flumes). B. At low and high tide with seines. The vertical bars represent one standard error of the mean.

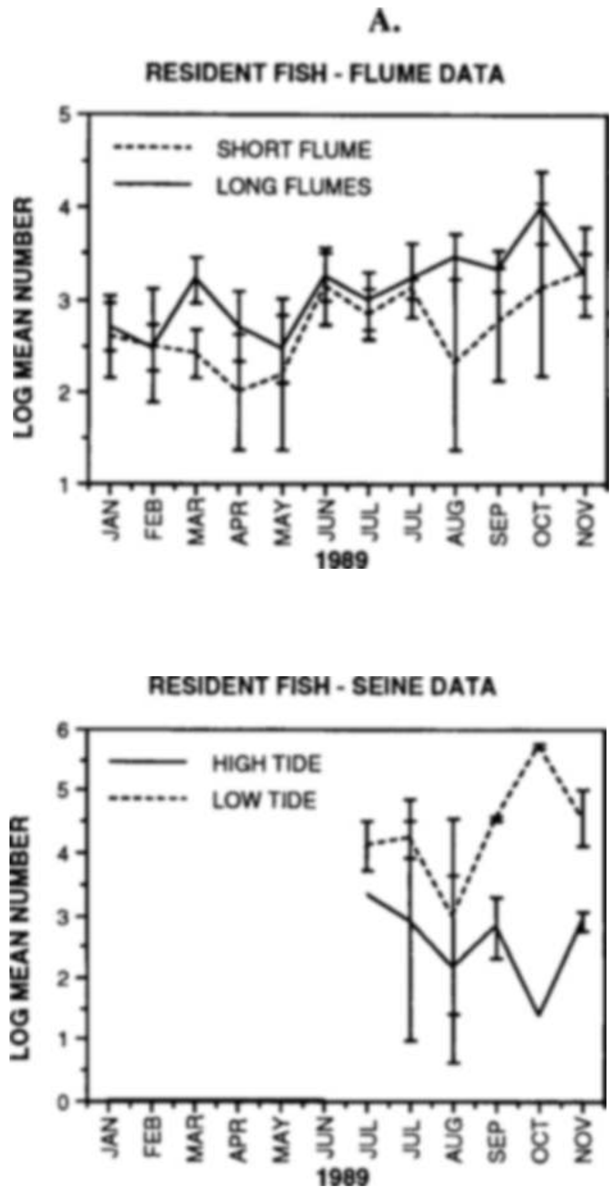

Fig. 6. The log mean numbers of resident fish caught by sample date. A. In short flumes (3 m) vs long flumes (10-m, 20-m, and 40-m flumes). B. At low and high tide with seines. The vertical bars represent one standard error of the mean.

caught in a 40-m back net) indicates that these species mostly use the edge marshes (<3 m) or possibly only the adjacent creek-edge habitat.

Palaemonetes sp. and *Uca* sp. were significantly more abundant in long flumes than short flumes among the decapod species tested; however, the proportions of each caught in front nets vs back nets (Table 3) suggests completely different patterns of interior marsh use. Grapsid crabs (*Sesarma* sp.) were caught in back nets, but there were no significant differences in catches between long and short flumes or between front and back nets. Blue crabs (*Callinectes sapidus*) were significantly more abundant in 40-m flumes than in all other flume lengths; however, catches were not significantly different when long flumes (10 m, 20 m, and 40 m) were contrasted with 3-m flumes for log-transformed numbers ($p = 0.14$). Blue crabs were commonly caught in back nets (Table 3), especially as small juveniles, documenting that blue crabs do utilize interior marshes.

Penaeid shrimp and Xanthid crabs were also

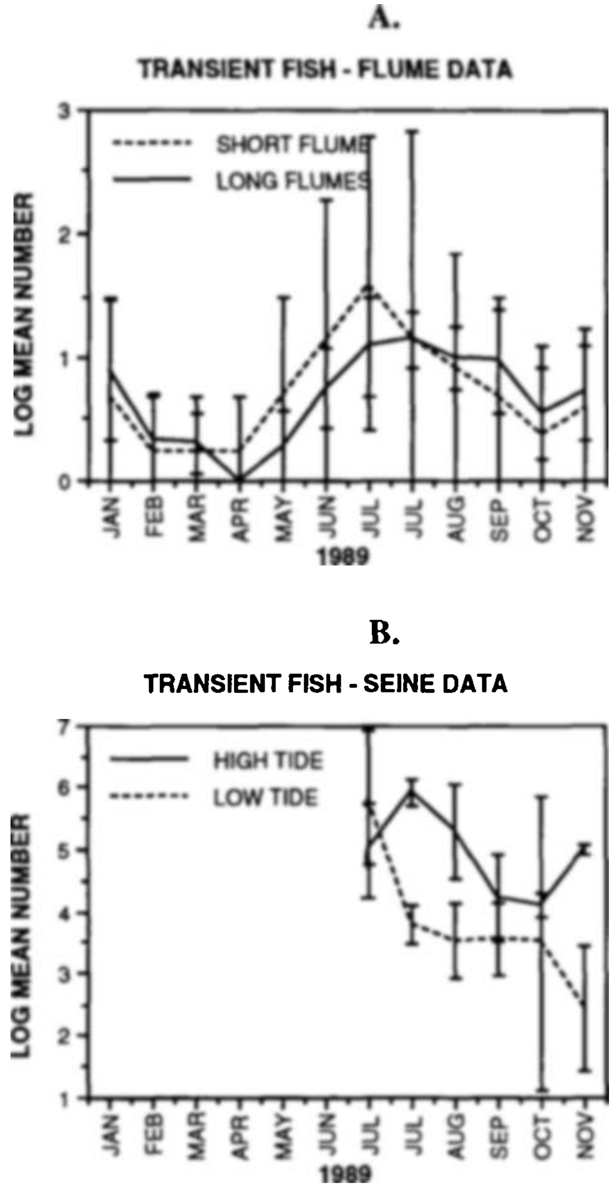

Fig. 7. The log mean numbers of transient fish caught by sample date. A. In short flumes (3 m) vs long flumes (10-m, 20-m, and 40-m flumes). B. At low and high tide with seines. The vertical bars represent one standard error of the mean.

abundant in flume net samples, but the data suggests that their use of the marsh is restricted to the edge marshes (<3 m from creek). ANOVA test results show no differences between long and short flumes for Xanthid crabs and *Penaeus setiferus*. *Penaeus aztecus* was significantly ($p = 0.008$) more abundant in 3-m flumes than in long flumes, but this difference is not significant with the Bonferroni-adjusted alpha level ($p = 0.0025$). None of these three species were ever caught in back nets (Table 3).

All other fish and decapod species, most of which were transient species, were not caught in sufficient numbers to test with ANOVA. This in itself is an indication that these species are infrequently or rarely using the marsh-surface habitat. The relative abundance of some of these species in seine samples suggests that they are present in the area but not using the marsh surface. One exception may be *Gambusia affinis,* a mostly freshwater marsh resident that was caught infrequently but almost exclusively in back nets, suggesting it may use interior marshes in areas where it is more abundant.

Seine Data

Species Composition

A total of 18,539 organisms (fish and decapod crustaceans) with a total preserved wet weight of 7.1 kg were collected in the seine samples from July through November 1989 (Table 6). The total catch included 29 species of fish (4,699 individuals, 2.4 kg preserved wet weight) representing 16 families and at least 7 species of decapod crustaceans (13,840 individuals, 4.7 kg preserved wet weight). The number of fish species caught in flumes and seines was the same (29), but the species composition was different because of the different habitats sampled by each gear and seasonal differences in sampling (seine samples were only collected from July to November).

The total seine catch was dominated by decapod crustaceans, which made up 74.6% of the total number and 65.8% of the total biomass (Table 6 and Fig. 8). Grass shrimp (*Palaemonetes* sp.), the dominant species in the flume net experiments, dominated the seine catches, comprising 60.4% by number and 28.4% by biomass. Other decapods that were abundant in seine samples include the Penaeid shrimp and blue crabs.

Compared with flume catch data, fish species made up a larger proportion of the total seine catch (25.3% by number, 23.6% biomass), and were dominated by bay anchovy (*Anchoa mitchilli*), which represented 15.6% of the total catch by numbers (7.7% of biomass). Naked goby (*Gobiosoma bosc*) was the next most abundant fish species caught (3.0% of total), followed by tidewater silversides (*Menidia beryllina*). A single specimen of southern flounder (*Paralichthys lethostigma*) represented more biomass (12.5% of total) than all 2,901 bay anchovies, the most abundant fish in seine samples.

High Tide vs Low Tide

The total catch (log-transformed) was significantly higher in low-tide seine samples than high-tide seine samples. This same relationship (low >

high tide) held true for decapods only and resident fish only (Figs. 5 and 6). This provides supporting evidence that these organisms are using the marsh surface at high tide and returning to the creek at low tide. In contrast, transient fish were significantly more abundant in high-tide samples (Fig. 7). This pattern could result from fish moving from deeper water to the marsh edge at high tide. Differences in fish species abundance were apparent among seine samples collected from July through November. When the total fish catch was tested with ANOVA, there was no difference in catch between high and low tide samples; however, a shift in fish abundance between low-tide and high-tide samples with season resulted in a significant DATE-TIDE interaction. This interaction resulted primarily from the abundance of *Anchoa mitchilli* in high tide samples in July and August and the abundance of *Gobiosoma bosc* and *Fundulus grandis* in low tide samples in October.

Species Differences in Catch by Tide Stage. Because habitat-use patterns vary between species, the seine catch data were analyzed with ANOVA for the 14 most abundant species (10 fish and 4 decapod species with total catches >30). Again, as with the flume data analysis, a Bonferroni-adjusted alpha level ($p < 0.0036$) was used to reduce the problem of finding a significant result by chance alone. Of the 14 species tested, four fish species (*G. bosc, F. grandis, G. boleosoma,* and *L. parva*) and two decapod species (*Palaemonetes* sp. and *C. sapidus*) were significantly more abundant in low-tide samples when compared to high-tide samples. Two other fish species, *C. nebulosus* and *M. beryllina,* were more abundant in low tide samples ($p = 0.018$), but this difference was not significant with the more conservative Bonferroni alpha level ($p < 0.0036$). This pattern of higher abundance in low-tide seine samples, combined with the relative abundance of these eight species in flume samples, is strong evidence that these species use the marsh-surface habitat (at least at the edge) when it is flooded.

The total catch of *Penaeus aztecus* from low-tide samples was approximately double that from high-tide samples (Table 6), but this difference was not statistically significant ($p = 0.08$) with log-transformed catch data. White shrimp (*Penaeus setiferus*) were not significantly more abundant in low-tide than in high-tide samples. Both penaeid species were commonly caught in flume nets.

Twice as many *Achirus lineatus* were caught in low-tide samples as in high-tide samples, but this difference was not significant ($p = 0.11$). Another flatfish, *Symphurus plagiusa,* was equally abundant in high-tide and low-tide seine samples. Both of these species were rarely caught in flume nets.

TABLE 6. List of species collected from seine samples along edge from July through November 1989 in order of decreasing numerical abundance. Number caught at high tide and low tide, and total number and percentage of total catch are given for each species.

Species	High Tide	Low Tide	Total	Percent[a]
Palaemonetes sp. (R)[b]	304	10,893	11,197	60.40
Anchoa mitchilli (T)	1,904	997	2,901	15.65
Penaeus setiferus (T)	526	701	1,227	6.62
Callinectes sapidus (T)	187	994	1,181	6.37
Gobiosoma bosc (R)	41	524	565	3.05
Menidia beryllina (R)	130	329	459	2.48
Penaeus aztecus (T)	71	144	215	1.16
Fundulus grandis (R)	0	160	160	0.86
Gobionellus boleosoma (R)	20	128	148	0.80
Lucania parva (R)	0	125	125	0.67
Symphurus plagiusa (T)	38	36	74	0.40
Achirus lineatus (T)	20	40	60	0.32
Cynoscion nebulosus (T)	8	33	41	0.22
Brevoortia patronus (T)	24	13	37	0.20
Fundulus jenkinsi (R)	1	23	24	0.13
Cynoscion arenarius (T)	11	11	22	0.12
Micropogonias undulatus (T)	17	4	21	0.11
Bairdiella chrysoura (T)	13	7	20	0.11
Xanthidae (R)	1	16	17	0.09
Citharichthys spilopterus (T)	6	7	13	0.07
Membras martinica (R)	7	0	7	0.04
Mugil cephalus (T)	3	1	4	0.02
Syngnathus scovelli (R)	0	3	3	0.02
Sciaenops ocellatus (T)	0	2	2	0.01
Syngnathus louisianae (T)	1	1	2	0.01
Sphoeroides parvus (T)	1	1	2	0.01
Prionotus tribulus (T)	1	1	2	0.01
Macrobrachium ohione (R)	1	1	2	0.01
Poecilia latipinna (R)	0	1	1	0.01
Strongylura marina (T)	0	1	1	0.01
Stellifer lanceolatus (T)	1	0	1	0.01
Gobionellus shufeldti (R)	1	0	1	0.01
Arius felis (T)	1	0	1	0.01
Paralichthys lethostigma (T)	1	0	1	0.01
Microgobius thalassinus (R)	1	0	1	0.01
Sesarma sp. (R)	1	0	1	0.01
Total resident individuals	508	12,203	12,711	68.56
Total transient individuals	2,834	2,994	5,828	31.44
Total fish and decapods	3,342	15,197	18,539	100.00

[a] Percentage of total catch represented by that species.
[b] Ecological classification (in parentheses): R = resident, T = transient.

Anchoa mitchilli, the most abundant fish species in seine samples, was significantly more abundant in high-tide samples. Gulf menhaden (*Brevoortia patronus*), another abundant filter-feeder, had slightly higher catches in high-tide seine samples (Table 6), but the differences were not significant. The relatively low numbers of menhaden caught in seines is a function of the absence of complete seasonal sampling. Catches would have been much greater if seine samples had been collected in the winter and early spring when postlarval and juvenile menhaden are abundant in the estuaries.

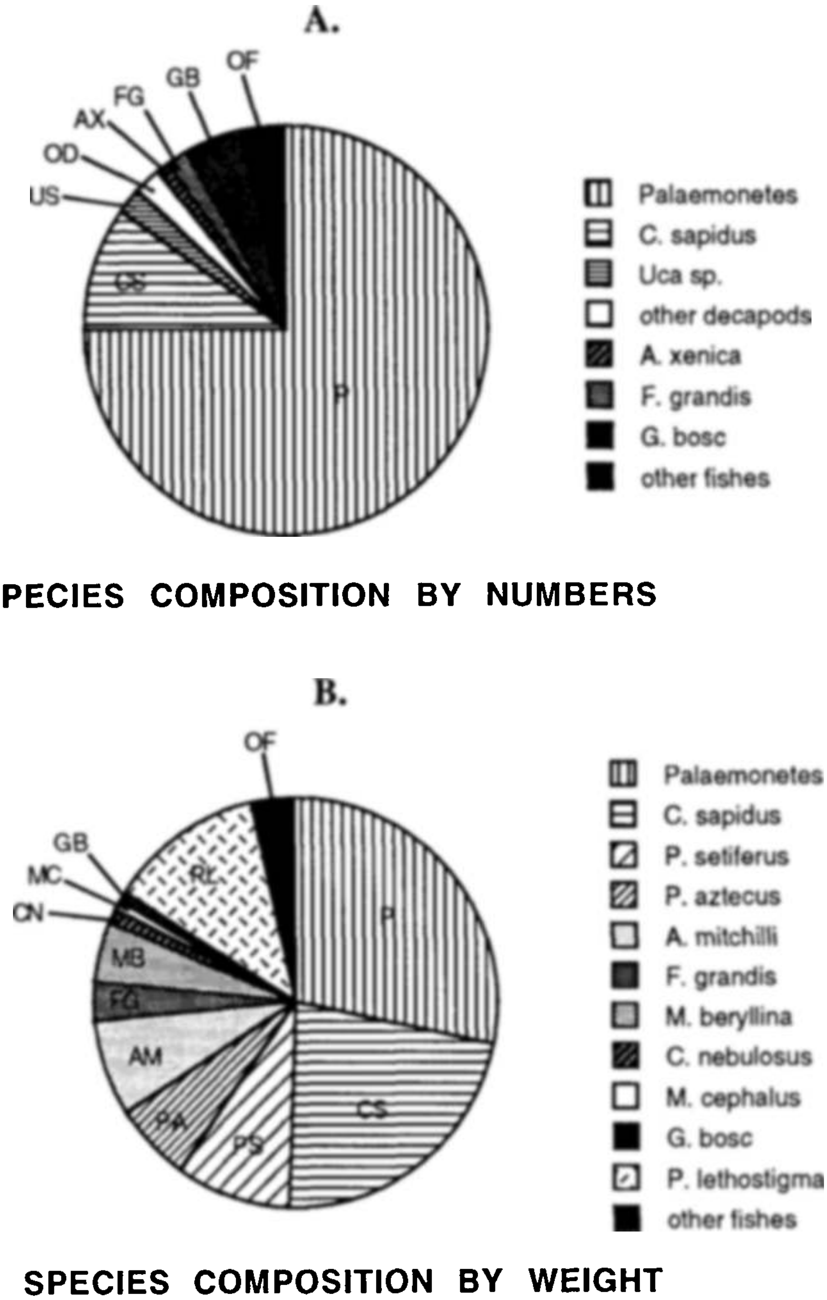

Fig. 8. Pie charts illustrating the proportion of the total seine catch represented by the most abundant fish and decapod species. A. Species composition by numbers. B. Species composition by weight.

Combining Flume Net and Seine Data

Flume and seine catch data are not quantitatively comparable because of the differences in the methods of fishing (passive vs active), the habitats sampled (marsh surface vs creek edge), and the size of the areas sampled. However, by comparing (qualitatively) the relative abundance and distribution (spatial and temporal) of species caught by these two gears, we can begin to see how marsh and edge habitats are utilized. These relationships are shown in Fig. 9. For example, several species (fish: *A. xenica, F. pulvereus, P. latipinna, C. variegatus*; decapods: *Uca* sp., *Sesarma* sp.) were rare or absent in seine samples but were abundant in flumes, especially in the back (interior) nets. These represent true marsh-resident species that forage on the flooded interior marsh and take ref-

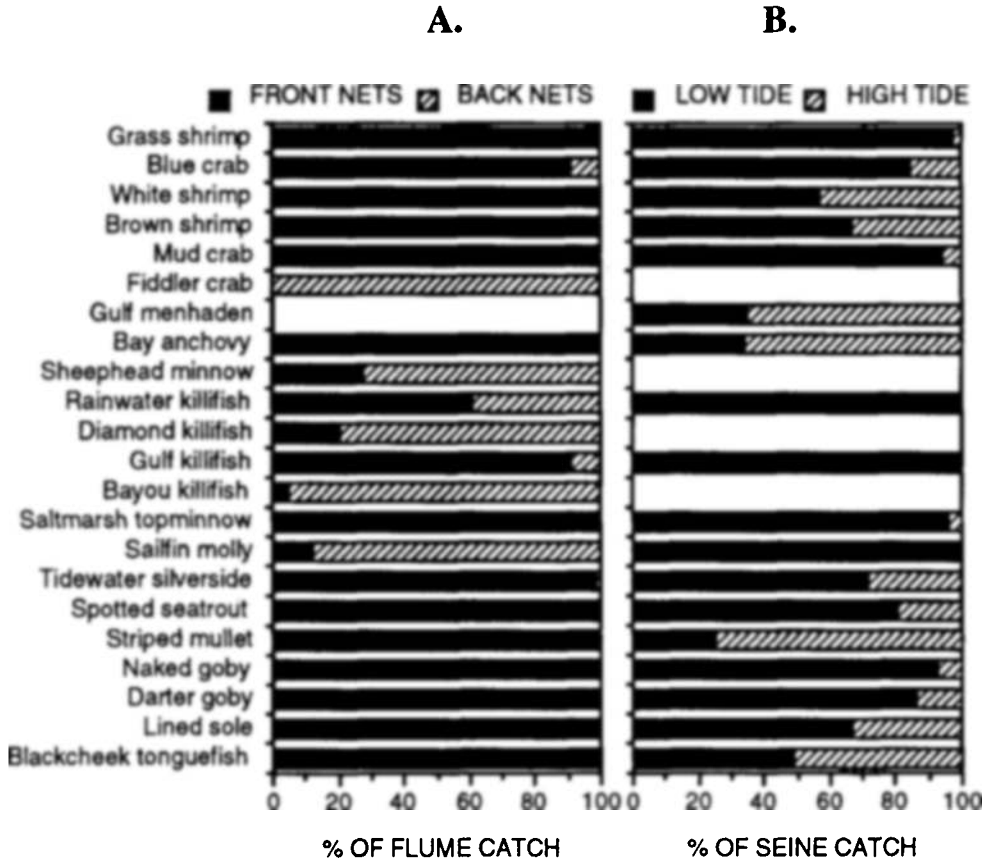

Fig. 9. Relative proportions (percent of total catch) of most abundant species caught in A. front versus back nets of flumes and B. low versus high tide seine samples.

uge in small ponds, potholes, burrows, muskrat trails, and rivulets at low tide, and only rarely retreat to the open water of the creek. *Mugil cephalus, Myrophis punctatus,* and Xanthid crabs were also more abundant in flumes than in seine samples; however, this could result from their ability to avoid seines, either by burrowing in mud (worm eels and mud crabs) or by swimming fast or jumping (mullet). On the other extreme are open-water estuarine species (e.g., *Anchoa mitchilli, Brevoortia patronus, Micropogonias undulatus*) that were relatively common in seines, especially at high tide, but were rarely or never caught in flumes, indicating that the flooded marshes are not utilized as nursery habitat by these species.

The catch data by gear and the results of ANOVA tests for the most abundant fish and decapod species (> 30 individuals with one gear) collected from flume nets and seines are summarized in Table 7. The ANOVA results are summarized for the comparisons of (log-transformed) catches between front and back nets, and between long and short flumes for flume net data, and between high-tide and low-tide catches for seine data.

Marsh Habitat Utilization Patterns

Not all estuarine species utilize flooded marsh habitat to the same extent. A qualitative comparison of the results given in Table 7 indicated four general patterns of marsh utilization. The 10 most abundant fish species captured in flume nets (Table 4) are considered resident species because they spend their entire lives within the estuary. We assigned a species to one of four general patterns of marsh habitat utilization. Figure 10 shows a typical profile of a creek edge and adjacent marsh with the area of utilization delineated for each category.

(A) Interior Marsh Residents. The first habitat-use pattern describes species that move into interior marshes whenever they are flooded and then retreat to potholes, muskrat trails or small ponds at low tides. These species probably gain access to interior marshes through small rivulets or muskrat trails and seek refuge in these low wet areas during normal low tides. These species may burrow in the mud or find their way back to the creek during extreme low-water levels. These species represent the true marsh-resident species that are adapted to

TABLE 7. Summary of catch data and ANOVA results for the most abundant fish and decapod species collected from flume nets and seines from January through November 1989. The total catch (number) of each species is given for each gear. Results of ANOVA tests are summarized for comparisons between front and back nets (NET) and flume length treatments (FLENGTH) for flume data, and between tide stages (TIDE) for seine data. (only or >) = significantly greater at a Bonferroni adjusted alpha level ($p < 0.0025$); (≥) = significantly greater at $p < 0.05$, but not at Bonferroni adjusted alpha level ($p < 0.0025$); (=) = not significantly different ($p > 0.05$); (*) = not tested ($n < 30$).

Species	Flume Net Data			Seine Data		Habitat Use Category[d]
	Number	NET[a]	FLENGTH[b]	Number	TIDE[c]	
Fishes						
Cyprinodon variegatus	116	B ≥ F	L > S	0	*	A
Adinia xenica	450	B > F	L = S	0	*	A
Fundulus pulvereus	336	B > F	L > S	0	*	A
Poecilia latipinna	169	B > F	L > S	1	L only*	A
Lucania parva	132	F = B	L = S	125	L only	B
Fundulus grandis	663	F > B	L > S	160	L only	B
Fundulus jenkinsi	102	F only	L = S	24	L > H*	C
Menidia beryllina	67	F > B	L = S	459	L ≥ H	C
Cynoscion nebulosus	64	F only	L = S	41	L ≥ H	C
Mugil cephalus	47	F only	L = S	4	*	C
Gobiosoma bosc	1,649	F only	L = S	565	L > H	C
Gobionellus boleosoma	171	F only	L = S	148	L > H	C
Achirus lineatus	9	F only*	*	60	H = L	D
Symphurus plagiusa	4	F only*	*	74	H = L	D
Anchoa mitchilli	39	F only	L = S	2,901	H > L	D
Brevoortia patronus	0	*	*	37	H = L	D
Decapod crustaceans						
Uca sp.	804	B > F	L > S	0	*	A
Sesarma sp.	35	F = B	L = S	1	*	A
Palaemonetes sp.	28,221	F > B	L > S	11,197	L > H	B
Callinectes sapidus	3,714	F > B	L = S	1,181	L > H	B
Penaeus aztecus	252	F only	S ≥ L	215	L = H	C
Penaeus setiferus	307	F only	L = S	1,227	L = H	C
Xanthidae	207	F only	L = S	17	L only*	C

[a] NET: F = front net vs B = back net.
[b] FLENGTH: L = long flumes (10, 20, and 40 m) vs S = short flumes (3 m).
[c] TIDE: L = low tide vs H = high tide.
[d] See Fig. 10.

surviving (or escaping) the adverse environmental conditions (e.g., extremes of temperature, salinity, and dissolved oxygen) likely to occur if these organisms were to become trapped in a small pothole or burrow. Organisms in this classification were abundant in flumes and the majority were caught in the back nets of the long flumes. These organisms were more abundant in long flumes than in short flumes (3 m) and were rare or absent in seine samples since they rarely venture out into the "open" water of the creek. Fish in this group were all from the order Cyprinodontiformes, specifically: *Fundulus pulvereus, Cyprinodon variegatus, Poecilia latipinna,* and *Adinia xenica.* Of the common decapods caught, *Uca* sp. and possibly *Sesarma* sp. best fit into this category.

(B) Interior Marsh Users. These species utilize the interior marshes (but may require slightly deeper water than the first group) and have a tendency to return to the creek edge at low tide. These species were also abundant in flumes and were more abundant in long flumes than in short flumes. Organisms in this group were commonly caught in back nets but were more abundant in front nets. These organisms were common in seine samples with higher catches from low-tide samples as compared to high-tide samples. The fish species that fit into this group, *Fundulus grandis,* and possibly *Lucania parva,* also belong to the family Cyprinodontidae. The two most abundant decapod species, *Palaemonetes* sp. and *Callinectes sapidus,* also fit into this category.

(C) Edge Marsh Users. The third habitat-use pattern describes both resident and transient species that utilize the marshes along the creek edge at high tide but apparently do not penetrate into the interior marshes (>3 m from the creek), except possibly during extreme flooding events. These species return to the creek and many remain in the shallow water along the creek edge during low tide. Species in this category were abundant in flumes and caught only in front nets. Catches of these species were not significantly different between long flumes and short flumes, indicating no significant use of interior marshes. These organisms were abundant in seine samples along the

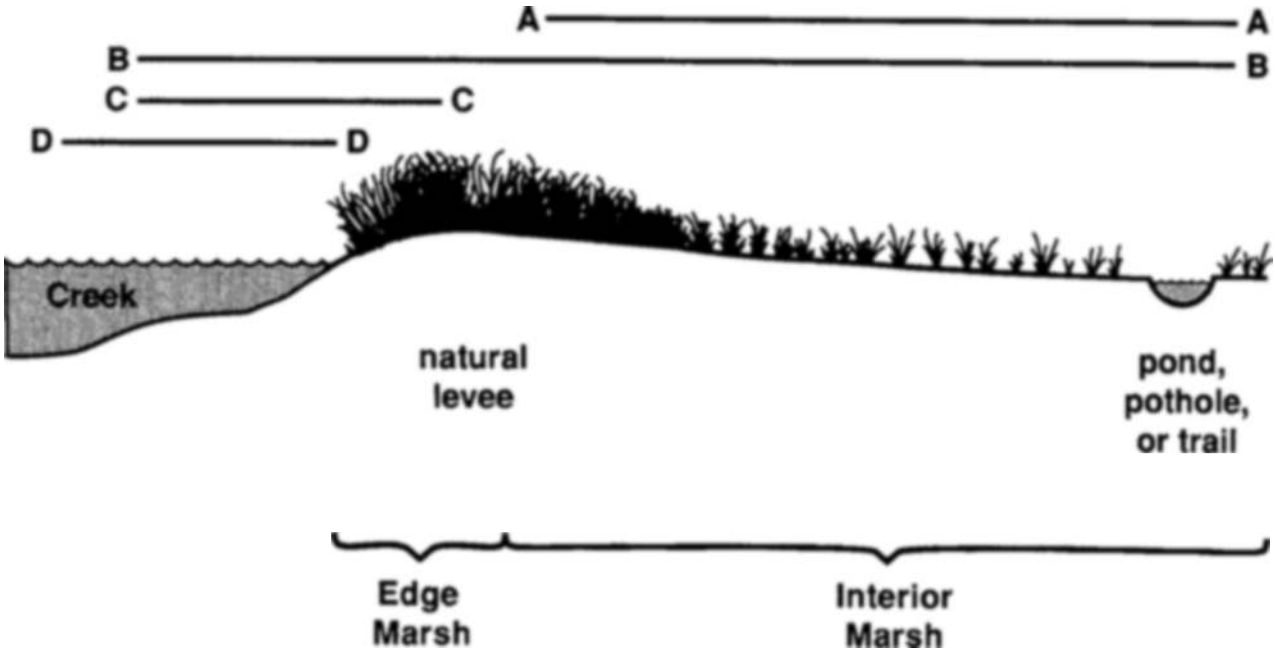

Fig. 10. A schematic elevation profile of the marsh creek bank with streamside effect (natural levee). Lines A-A, B-B, C-C, and D-D represent patterns of marsh utilization by fish and decapod assemblages described in the text and in Table 7 (habitat use categories A, B, C, and D, respectively).

marsh edge and were generally more abundant in low-tide samples. Included in this category were resident species such as *Fundulus jenkinsi, Gobiosoma bosc, Gobionellus boleosoma,* and *Menidia beryllina,* and Xanthid crabs. Commercially important transient species, including spotted seatrout (*Cynoscion nebulosus*), Penaeid shrimp (*Penaeus aztecus* and *P. setiferus*), and possibly striped mullet (*Mugil cephalus*), were also included in this group.

(D) Marsh Subtidal Group. The last habitat-use pattern describes species that utilize estuarine open-water habitats, including the shallow-water creek edge, but apparently do not utilize the flooded marsh surface. Organisms in this category rarely, if ever, ventured onto the flooded marsh surface, based on their absence or rarity in flumes (occasionally found in front nets only). However, seine sampling results suggest that species within this category utilize the shallow-water creek-edge habitat to varying degrees. Species within this category could be divided into two subgroups of creek-edge habitat utilization based on differences between high-tide and low-tide seine catches. The first subgroup included two flatfish species, *Symphurus plagiusa* and *Achirus lineatus,* that were common in seine samples from the creek edge but had no significant differences between high-tide and low-tide seine samples. Fish in the second subgroup were more abundant in high-tide than in low-tide seine samples, and included important transient species such as *Anchoa mitchilli* and probably *Brevoortia patronus* and some Sciaenid species.

Discussion

Based on these results we accept all three hypotheses stated in the Introduction. The results of the flume net and seine sampling indicate that flooded marshes are utilized primarily by decapod crustaceans (shrimp and crabs) and resident fish (Cyprinodontidae and Gobiidae; Hypothesis #3). Transient fishes were less abundant on flooded marshes and primarily used the edge marshes (Hypothesis #2). Utilization of flooded marsh habitats is highly variable among species in these wetlands. Some species stay in the marsh as long as it is flooded and take refuge in small ditches and potholes at low tide; others only use the edge marshes or venture into the interior marshes and return to the creek as the water drops; other species rarely, if ever, get up on the marsh. Therefore, we conclude that there are important species-specific patterns of marsh use by estuarine organisms (Hypothesis #1). Here we summarize the individual species uses of the marsh and integrate our results with the results of others.

Species Comparisons of Marsh Use: Decapods

Grass shrimp (*Palaemonetes* sp.) were the dominant organism using the flooded marsh surface in this and other studies (Zimmerman and Minello 1984; McIvor and Odum 1986; Rozas and Odum 1987; Zimmerman 1989; Rozas 1992a, b). All life stages, from the smallest juveniles that could be retained in the mesh to gravid adult grass shrimp, were caught in flume and seine samples. Grass shrimp were not identified to species because they were so abundant and identification to species is difficult and time consuming; however, from those that were identified and from the salinity range sampled, it appears that *Palaemonetes pugio* was the dominant species. Zimmerman (1989) listed three species of grass shrimp (*P. pugio, P. vulgaris,* and *P. intermedius*) in a higher salinity site in Louisiana and found that they all showed a similar preference for vegetated over nonvegetated habitat. Grass shrimp were significantly more abundant in long flumes than in short flumes and in low-tide vs high-tide seine samples. Some were caught in back nets (up to 40 m inland), although most (99%) were caught in front nets. Grass shrimp apparently use the marsh surface including the interior marsh whenever it is flooded, and most return to the creek at low tide. The use of flooded interior marshes by grass shrimp was also documented by Kneib (1991) and Rozas (1992a). Because of the abundance of *Palaemonetes* species, their ability to accelerate the breakdown of detritus, and their importance as forage for other estuarine species, this movement of grass shrimp on and off the marsh surface with the tides may provide a major biological mechanism for the transport of energy (primary productivity) from intertidal marshes to the open estuary (Welsh 1975).

Penaeid shrimp were common in flume net and seine samples but were much less abundant (by two orders of magnitude) than grass shrimp. Only juvenile penaeids were caught and these were transient species that move out of the estuaries as adults. White shrimp (*P. setiferus*) were equally abundant in long and short flumes, but unexplainably, brown shrimp (*P. aztecus*) were more abundant in short flumes. Also, these two penaeid species were never caught in back nets, indicating that their use of the flooded marsh is limited to the edge (<3 m). Greater numbers of both species were caught in low-tide seine samples, but the numbers were not significantly higher than high-tide catches when log-transformed data were tested with an ANOVA.

Studies in flooded Texas salt marshes (Zimmerman and Minello 1984; Zimmerman et al. 1984) showed that brown shrimp have a strong selection bias for vegetated habitat, particularly as small juveniles, whereas white shrimp were equally abundant in vegetated and nonvegetated areas. A similar pattern was found in the laboratory, where the selection of vegetative cover by brown shrimp was shown to be an advantage for avoiding some predator species (Minello and Zimmerman 1983). Kneib (1991) used a "flume-weir" to sample nekton in the interior of a Georgia salt marsh, and reported white shrimp to be the most numerically important transient species. Rozas (1992a) often caught penaeid shrimp in his lift nets located on the marsh surface, and reported brown and white shrimp to be equally abundant.

Blue crabs (*Callinectes sapidus*) were caught in flume nets mostly as juveniles, but some adults were also caught in the front nets. Although differences between long and short flumes were not as pronounced as for grass shrimp, blue crabs were most abundant in 40-m flumes and several juveniles were caught in back nets, thus documenting the use of interior marshes by juvenile blue crabs. The higher abundance of blue crabs in low-tide seine samples indicates that flooded marshes are important habitats for blue crabs; however, the edge marshes are probably utilized more than interior marshes, especially by larger juveniles and adults. Studies in Texas salt marshes (Zimmerman and Minello 1984; Thomas et al. 1990) reported that juvenile blue crabs were always significantly more abundant in flooded vegetated habitat than in adjacent nonvegetated areas. Other studies have found blue crabs (especially juveniles) to be one of the more abundant species using the flooded marsh surface in salt marshes (Hettler 1989; Zimmerman 1989; Kneib 1991; Rozas 1992a, b) as well as in tidal freshwater marshes (McIvor and Odum 1986; Rozas and Odum 1987).

Mud crabs (Xanthidae) were relatively common in the flume samples and apparently use only the edge marshes, since they were caught in equal abundance in all flume lengths and never caught in a back net. Although they were uncommon in seine samples (probably because of their ability to burrow to avoid seines), the mud crabs caught in seines were caught almost exclusively in low-tide samples. This observation provides evidence that mud crabs utilize the flooded marsh surface. Mud crabs were rare or only occasionally caught in Atlantic coast marshes (Rozas and Odum 1987; Hettler 1989) but were commonly found in flooded vegetation in another Louisiana salt marsh by Zimmerman (1989).

Fiddler crabs (*Uca* sp.) were commonly caught in flumes and almost exclusively in the back nets of the long flume treatments. Fiddler crabs were never caught in seine samples along the edge of the creek. Fiddler crabs use interior marshes and apparently avoid the open water of the creek, instead seeking refuge in burrows or potholes in the interior marsh at low tide. Wharf or marsh crabs (*Sesarma* sp.) were commonly caught in back nets (39%), but there were no significant differences in catches between front and back nets or between long and short flumes. Only one wharf crab was caught in a seine sample (at high tide). Wharf crabs apparently use interior marshes but seem to show some preference for creek edge (natural levee) marshes. Both *Uca* sp. and *Sesarma* sp. were commonly seen on the marsh surface at low tide, and tend to scurry away or retreat to burrows or potholes when approached. Because of their amphibious and burrowing behaviors and their ability to climb out of flumes, fiddler and wharf crab abundances are probably underestimated since they are not forced into the cod-end nets as the water ebbs. Zimmerman (1989) collected 100% of fiddler crabs and 96% of wharf crabs from vegetated habitat in his study comparing vegetated to adjacent nonvegetated habitats in a Louisiana salt marsh.

Species Comparisons of Marsh Use: Resident Fishes

Gobiosoma bosc was the most abundant fish caught in flume nets and the second most abundant fish caught in the seine samples. This resident species was only caught in front nets. There were no significant differences between catches from long and short flumes and they were more abundant in low-tide seine catches (Category C, Table 7). Naked gobies apparently move onto the marsh surface when it floods but remain near the creek edge. Naked gobies were also the most numerous and frequently caught fish species found in drop samples along the marsh edge in the Barataria Basin, Louisiana (Rakocinski et al. 1992; Baltz et al. 1993). In a Texas salt marsh, naked gobies were the most abundant fishes in drop samples, with 81% caught in vegetated (vs adjacent nonvegetated) samples at high tide (Zimmerman and Minello 1984). Other studies that sampled the saline marsh and edge habitats have found this species to be one of the more abundant fishes utilizing this habitat (Peterson 1986; Hettler 1989; Rozas 1992b).

Another resident goby, *Gobionellus boleosoma*, was somewhat less abundant than *G. bosc* in the flume and seine samples but showed the same pattern of marsh utilization. This species was also commonly caught along the salt-marsh edge and on the flooded marsh surface in other studies (Peterson 1986; Hettler 1989; Zimmerman 1989; Baltz et al. 1993).

Several species of Cyprinodontid fishes were commonly caught in both front and back nets of the flumes. The use of flooded marshes by this group of fishes is well documented (Butner and Brattstrom 1960; Kneib and Stiven 1978; Weisberg et al. 1981; Talbot and Able 1984; Kneib 1984, 1986, 1991; McIvor and Odum 1986; Lipcius and Subrahmanyam 1986; Rozas and Odum 1987; Rozas et al. 1988; Hettler 1989; Rozas 1992a, b). Differences in marsh utilization patterns among the different cyprinodontid species can be inferred from the flume and seine catch results. Three species (*Cyprinodon variegatus, Adinia xenica,* and *Fundulus pulvereus*) utilized the interior marshes and residual pools of water at both high and low tides (Category A, Table 7). Another cyprinodontiform fish (*Poecilia latipinna,* Fam. Poecilidae) also fits into this pattern of marsh utilization. *Fundulus grandis* and *Lucania parva* also utilized the interior marshes at high tide but apparently returned to the creek at low tide (Category B, Table 7). *Fundulus jenkinsi* was the only cyprinodontid species that was commonly caught along the marsh edge, but it apparently did not utilize the interior marshes (Category C, Table 7).

These different patterns of marsh utilization may reflect an evolutionary partitioning of this habitat that allows these ecologically similar species to coexist. Weisberg (1986) compared four sympatric species of *Fundulus* on the Atlantic Coast (Delaware) and suggested that competitive exclusion, rather than physiological barriers, may be the more important factor in controlling spatial segregation of these species. Forman (1968) suggested that differences in anatomy and feeding behaviors defined separate niches for five Cyprinodontid species and allowed for the coexistence of these species on a Louisiana barrier island. The factors controlling the habitat partitioning among the Gulf of Mexico cyprinodontid species need more investigation.

On the Atlantic Coast, *Fundulus heteroclitus* has been shown to move on and off the marshes with the tides to feed on invertebrates on the flooded marsh surface (Kneib and Stiven 1978; Weisberg et al. 1981; Rozas et al. 1988). These fish in turn are preyed upon by larger predators (fish, crabs, and birds), thereby providing an important link (mechanism) in energy transfer between the intertidal marsh and adjacent subtidal waters (Valiela et al. 1977; Weisberg and Lotrich 1982; Kneib 1986). *Fundulus grandis,* the Gulf Coast ecological equivalent to *F. heteroclitus,* is reported to feed on the flooded intertidal marshes (Rozas and LaSalle 1990), and therefore probably performs a similar function in the energy dynamics of Gulf Coast estuaries.

Several cyprinodontid species, *F. grandis* (Greeley and McGregor 1983), *F. heteroclitus* (Taylor et al. 1977, 1979), *F. pulvereus* and *Adinia xenica* (Greeley 1984), reportedly utilize the flooded intertidal marshes for spawning and have evolved a spawning pattern that is correlated with the biweekly spring tides during the breeding season.

Menidia beryllina were less abundant in flume samples than the other resident species but were often caught in flumes and were abundant in seine samples, especially at low tide, indicating some marsh surface utilization. Catches from long and short flumes were not significantly different, and all but one of the 67 *M. beryllina* caught in the flumes came from the front nets. These results imply that their use of the marsh is mostly limited to the edge. *Menidia beryllina* have been reported to be abundant along the marsh edge (Peterson 1986; Rozas 1992b; Baltz et al. 1993) and common on the marsh surface (McIvor and Odum 1986; Rozas 1992a, b). However, when adjacent vegetated and nonvegetated habitats were sampled at high tide (with drop samplers), *M. beryllina* were more abundant in nonvegetated habitats (Zimmerman and Minello 1984; Zimmerman 1989). A similar species, *Menidia menidia,* has also been collected from flooded salt marshes along the Atlantic Coast (Hettler 1989; Kneib 1991). *Menidia menidia* is generally an open-water schooling species found in tidal creeks and near-shore estuarine zones but is reported to spawn in the flooded intertidal vegetation (Butner and Brattstrom 1960; Fay et al. 1983).

SPECIES COMPARISONS OF MARSH USE: TRANSIENT FISHES

Transient fishes are those that spend only a portion of their life cycle (usually the juvenile stage) in the estuary, and include many economically important species. Only two transient species (*Cynoscion nebulosus* and *Mugil cephalus*) were caught in sufficient numbers in the flumes to infer direct use of the flooded marsh habitat. Both of these species were only caught in the front nets and were equally abundant in long vs short flumes. This result suggests they use the marsh surface only at the edge (<3 m from creek).

Seagrass beds are reported to be the preferred nursery habitat for juvenile *Cynoscion nebulosus* throughout much of their range (Perret et al. 1980; Lassuy 1982; Mercer 1984). In estuaries where extensive seagrass beds are lacking, shallow, saline-marsh shoreline areas are probably the primary nursery habitat for juvenile *C. nebulosus* (Peterson 1986). Several recent studies have reported capturing juvenile spotted seatrout from the flooded marsh surface (Hettler 1989; Kneib 1991; Rozas 1992b), and others have reported greater catches in flooded vegetation when compared to adjacent nonvegetated habitats along the marsh edge (Zimmerman and Minello 1984; Zimmerman 1989; Rakocinski et al. 1992). Small juvenile spotted seatrout apparently utilize the shallow water along the marsh edge at low tide and move onto the marsh surface when it floods probably to feed and to avoid predators. Marsh use by spotted seatrout is probably restricted to the edge, because they were equally abundant in short and long flumes. Interior marshes may be more important in marshes that are inundated more often or deeper, such as those on the Atlantic Coast where spotted seatrout have been reported from interior marshes (Kneib 1991).

Although not extremely abundant, juvenile striped mullet (*Mugil cephalus*) were commonly caught in flumes in these marshes and from a nearby marsh (Rozas 1992b). These results indicate that mullet utilize the flooded marsh surface to some extent. The data from this study suggests that marsh use by mullet is limited to the edge; however, we have observed large juvenile mullet in the interior of other marshes during deep (>0.5 m) flood tides. In a follow-up to this study, we captured several mullet in pit traps within flumes on the marsh (15 m from the creek) at a site closer to the Gulf of Mexico that floods deeper and more often than the present study site. In another Louisiana study, Rozas (1992a) reported that *M. cephalus* was one of the more abundant fish species caught on the marsh surface in lift nets. Kneib (1991) reported that *Mugil* spp. are the most abundant transient fish species in his flume-weirs located in the interior of a salt marsh in Georgia. Hettler (1989) reported that *Mugil curema* and *M. cephalus* were the sixth and ninth most abundant fish species (respectively) in his block-net samples from a flooded salt marsh in North Carolina, but he was unable to determine their extent of penetration into the interior marshes. Although the present study indicates that mullet utilize the marsh only near the edge (Category C, Table 7), other studies suggest that mullet may be one of the few transient fishes that utilize interior marshes (Category B).

Two nektonic filter-feeders, *Anchoa mitchilli* and *Brevoortia patronus,* and two demersal flatfishes, *Achirus lineatus* and *Symphurus plagiusa,* were common in seine samples but were rarely or never caught in flumes (Category D, Table 7). This result indicates that they utilized the shallow water along the marsh edge but rarely, if ever, utilized the flooded marsh surface. *Anchoa mitchilli* was the most abundant fish species in seine samples and was significantly more abundant in high-tide samples. *Brevoortia patronus* were also more abundant in high-tide seine samples, but the differences were not significant because the total numbers caught were small. A relatively low number of menhaden were caught in seines in this study because seine samples were not collected in the winter and early spring when postlarval and juvenile menhaden are abundant in the estuaries. *A. mitchilli* and *B. patronus* are two of the more abundant species found in estuarine, open-water habitats (Gunter 1936, 1938; Herke 1971; Perret 1971; Wagner 1973) and along the marsh edge (Peterson 1986; Rozas 1992b; Baltz et al. 1993) in Louisiana estuaries. Anchovies and menhaden are frequently caught in drop-samples along the marsh edge but are rarely caught in samples containing vegetation (Zimmerman and Minello 1984; Zimmerman 1989; Rakocinski et al. 1992). These are mostly open-water species that may utilize the shallow creek-edge habitats at high tide, when the water at the edge is deeper, possibly to avoid predators or strong currents. Fore and Baxter (1972) reported increased catches of *Brevoortia patronus* larvae on ebb tides along the edge of a tidal pass in Texas, and suggested that these immigrating larvae moved to the slower moving waters along the shore to avoid being swept back out of the estuary during ebb tides.

Although bay anchovies were caught in flumes, the numbers were low relative to their abundance in high-tide seine samples. In Atlantic Coast marshes with a greater tidal range, bay anchovies were commonly taken from the flooded marshes with flume nets (Rozas et al. 1988) and block nets (Hettler 1989), but none were caught on the interior marsh with flume-weirs (Knieb 1991). Rozas et al. (1988) reported that bay anchovy was the only common fish species that was more abundant in creek-bank flumes than in rivulet flumes. Bay anchovies are open-water, filter-feeders that may utilize the shallow-water marsh-edge habitat at high tide but probably do not penetrate into the flooded marsh vegetation except perhaps in sparsely-vegetated, deeply-flooded marsh edges. A close association with the marsh edge at high tide could account for the presence of bay anchovies in flume net and block net samples, since these passive sample gears are set at high tide and, by design limitations, may sample a small amount of open-water (nonvegetated) habitat at the creek edge.

No Gulf menhaden were caught in flumes. However, Rozas (1992b) captured 226 small Gulf menhaden in his flumes. Like bay anchovies, juvenile Gulf menhaden are filter-feeders and may be incidentally captured in flumes if they feed along the marsh edge at high tide. Gulf menhaden undergo a distinct transformation in morphology and feeding habits during the time they are in the estuary. Pre-transformed larval menhaden (<30–33 mm TL) are carnivores that selectively feed on zooplankton, whereas post-transformed juveniles and adults are omnivorous filter-feeders (Lassuy 1983). A selective feeding strategy would seem to be more effective among the stems of vegetation, but there was no evidence of utilization of the flooded marsh surface by small postlarval menhaden. In studies conducted along the Atlantic Coast, Hettler (1989) did not report any *Brevoortia tyrannus* from his block-nets, but Knieb (1991) caught a few (most >30-mm TL) in his flume-weirs in the interior marsh. The low abundance of menhaden collected from marsh-surface as compared to more open-water habitats is evidence that this important "estuarine-dependent" species does not significantly utilize the flooded marsh habitat.

Achirus lineatus and *Symphurus plagiusa* and other flatfish species have been captured from the flooded marsh surface in small numbers with block nets (Hettler 1989) and flumes (Rozas 1992b; this study) but not from the interior marshes (Kneib 1991; Rozas 1992a; this study). *Symphurus plagiusa* are relatively common along the marsh edge in shallow-water marsh habitats but are more often caught in samples with no vegetation (Zimmerman and Minello 1984; Zimmerman 1989; Rakocinski et al. 1992; Baltz et al. 1993). These and other small flatfish species are relatively common in estuarine, open-water habitats, as they often show up in estuarine trawl surveys (Herke 1971; Perret 1971; Wagner 1973) and in the bycatch of shrimp trawl fisheries (Gunter 1936). Morphologically, the flatfishes appear to be better designed for feeding in open-water habitats than among the closely spaced stems on the marsh surface, but the shallow-water, mud-flat habitat along the marsh edge may be very important to these flatfishes.

Several other transient fish species were caught in flumes and/or seines, but their numbers were too low to confidently assign them to any habitat-use categories. Many common sciaenids (e.g., *Micropogonias undulatus, Leiostomus xanthurus, Cynoscion arenarius, Bairdiella chrysoura, Sciaenops ocellatus*) and other species (*Lagodon rhomboides, Arius felis*) that are commonly caught in trawl and seine surveys in Louisiana estuaries (Gunter 1936, 1938; Norden 1966; Herke 1971; Perret 1971; Wagner 1973; Peterson 1986) were rare or absent in flume samples. These are all considered to be estuarine-dependent transient species, but the analysis of flume data indicates that they do not directly utilize the flooded marsh habitat or they were not present in this area of the estuary during this study. None of these species were abundant in seine samples, although no samples were taken during the winter and spring when juvenile Atlantic croaker, spot, and red drum are most abundant in the estuaries. Some of these species may be more abundant in higher salinity portions of the estuary and could possibly utilize the marsh surface in marshes that flood deeper and more regularly.

Spot (*Leiostomus xanthurus*) are reported to be one of the most abundant estuarine transients utilizing the tidal creeks (Weinstein 1979; Weinstein and Brooks 1983) and flooded salt marshes (Hettler 1989; Knieb 1991) on the Atlantic Coast. On the Gulf Coast, spot are abundant in shallow open-water areas (Herke 1971) and along the edges of salt marshes (Zimmerman and Minello 1984; Peterson 1986; Rozas 1992b), but none were caught in our flume or seine samples. Rozas (1992b) caught only seven spot in his flumes but caught 97 in beam trawl samples along the marsh edge. In drop samples along the marsh edge, spot were more often caught in samples without vegetation (Zimmerman and Minello 1984; Baltz et al. 1993). Spot may not utilize flooded marsh vegetation to the same extent on the Gulf Coast as they do on the Atlantic Coast because of our smaller tidal range.

Unlike spot, juvenile Atlantic croaker (*Micropogonias undulatus*) are rarely found in shallow-water tidal creeks or flooded marshes on the Atlantic Coast but are common in deeper channel habitats (Weinstein 1979; Weinstein and Brooks 1983; Hettler 1989). This apparent spatial segregation may reduce competition between these two morphologically similar species that are both abundant in the estuary during the same season. This mechanism may be less important in the microtidal estuaries on the Gulf Coast, where salinity may play a more important role in habitat partitioning. Although these two species are often caught in the same trawl samples, particularly in mesohaline open-water areas in Gulf estuaries, spot are often more abundant in higher salinity portions of the estuary, whereas croakers are more abundant in lower (oligohaline) salinities (Perret 1971; Thompson and Forman 1987; Zimmerman et al. 1990). Atlantic croaker are often the most abundant sciaenid caught in Louisiana estuarine surveys in shallow marsh creeks and small lakes, as well as in open bays and channels (Gunter 1938; Norden 1966; Herke 1971; Perret 1971). Juvenile croaker are also relatively common along the marsh edge in Louisiana but not usually as abundant as juvenile spot in this habitat (Peterson 1986; Baltz et al. 1993). The absence (or rarity) of Atlantic croaker in flumes and other collections from the flooded marsh (Hettler 1989; Knieb 1991; Rozas 1992a, b; this study) indicates that flooded marsh surfaces are not a primary nursery habitat for this species.

Juvenile sand seatrout (*Cynoscion arenarius*) are one of the more abundant species in Louisiana estuarine surveys and in the bycatch of shrimp trawl fisheries (Gunter 1936, 1938; Norden 1966; Perret 1971; Herke et al. 1984), yet they are uncommon or rare in samples from the flooded marsh and edge habitats (Peterson 1986; Rozas 1992a, b; Baltz et al. 1993; this study). The primary nursery habitats for juvenile sand seatrout are probably the open-water estuarine bottoms and therefore they are susceptible to capture in trawls. In contrast, juvenile spotted seatrout, as discussed above, utilize the flooded marsh and shallow waters along the edge as a primary nursery habitat. This spatial segregation presumably reduces competition between these two morphologically similar species and allows them to coexist in the estuary during the same (summer) season. The segregation of these two *Cynoscion* species by habitat has been documented in Louisiana marshes (Peterson 1986) as well as in Florida grass bed habitats (Springer and Woodburn 1960).

Hardhead catfish (*Arius felis*) is another species that, like Atlantic croaker and sand seatrout, is seasonally common in open-water estuarine trawl surveys (Gunter 1938; Perret 1971; Wagner 1973) but is much less common along the marsh edge (Peterson 1986; Baltz et al. 1993). Hardhead catfish have never been reported from the flooded marsh surface (Hettler 1989; Knieb 1991; Rozas 1992b; this study).

Pinfish (*Lagodon rhomboides*) are reported to utilize the flooded marshes adjacent to channels in a North Carolina salt marsh (Hettler 1989) but were not found in the interior of a salt marsh in Georgia (Knieb 1991). We caught only five pinfish in flumes and none in seine samples; however, Rozas (1992b) caught 84 in flumes and 126 in trawls along the marsh edge at a nearby marsh of higher salinity. Pinfish showed a preference for flooded vegetation and were most abundant in mesohaline and polyhaline marsh habitats in Galveston Bay, Texas (Zimmerman and Minello 1984; Zimmerman et al. 1990). Pinfish are common along the salt-marsh edges in Louisiana (Peterson 1986; Baltz et al. 1993) and may utilize the flooded edges of marshes in higher salinity marshes.

Silver perch (*Bairdiella chrysoura*) are common along salt-marsh edges in the Barataria estuary, Louisiana (Peterson 1986; Baltz et al. 1993). Although rare in our flume and seine samples, Rozas (1992b) reported silver perch to be relatively abundant in his flume and beam trawl samples from a higher salinity marsh within the same estuary. On the Atlantic Coast, silver perch were commonly found on the flooded marsh surface (Hettler 1989; Kneib 1991), and although they were not as numerous as spot, they were more abundant than spotted seatrout in both of these studies. It therefore seems likely that in areas where they are abundant, silver perch will utilize the flooded marsh habitat, at least near the edge.

Juvenile red drum (*Sciaenops ocellatus*) are also common along salt-marsh edges in the Barataria estuary, Louisiana, particularly in higher salinity marshes close to the Gulf of Mexico (Peterson 1986; Baltz et al. 1993). Only three red drum were caught in flumes and only four in seines during this study. In a higher salinity area, Rozas (1992b) caught only seven red drum in his flumes, but caught 66 in beam trawl samples along the marsh edge. Hettler (1989) reported a few red drum in his block-net samples from a salt marsh in North Carolina, and Kneib (1991) caught only two red drum in 271 samples from the interior of a salt marsh in Georgia. Zimmerman and Minello (1984) reported 12 out of 13 red drum were caught in drop samples containing vegetation. Larger juveniles and subadult red drum forage among sparse vegetation along the marsh edge and juveniles are caught in seines along the edge in high salinity marshes (Peterson 1986). Juvenile red drum are rarely, if ever, caught in trawl samples away from the marsh edge in estuarine surveys (Gunter 1938; Norden 1966; Herke 1971; Perret 1971; Wagner 1973). The marsh-edge habitat is very important to juvenile red drum (Peterson 1986), but their use of the flooded marsh surface is apparently limited to the sparse vegetation at the edge, at least in Louisiana.

Conclusions and Management Implications

In Louisiana estuaries, the flooded interior marsh surface is an important habitat for marsh-resident fish (Cyprinodontiformes) and decapods (*Palaemonetes* sp. and *Uca* sp.) but is probably not directly utilized by most transient fish and decapod species. Of those transient species that do use the marsh surface at high tide, most are only using the edge marshes (<3 m into the marsh). This is not to say that these interior marshes are not important to the survival of transient "estuarine-dependent" organisms. The importance of emergent marshes as a source of detritus for detrital-based food chains is well documented (e.g., Darnell 1958, 1961, 1967; Harrington and Harrington 1961; Day et al. 1973; Deegan and Thompson 1985). The small resident fishes and grass shrimp that utilize the interior marshes provide a very important food source for larger estuarine-transient carnivores (e.g., spotted seatrout and red drum), especially in the fall and winter when cold fronts cause extremely low tides forcing these forage species into open waters. Furthermore, we did not determine the relative value of the marsh interior vs the edge for its use as a refuge or food source for organisms smaller than caught by the nets (3-mm mesh). Further, we measured biomass and numbers, not growth and predation rates. It is possible that species rarely found on the marsh surface are nonetheless dependent on the marsh for a brief period to sustain their populations. More importantly, the segregation of the marsh into spatial parts that are more or less important in terms of fisheries production is premature, in our opinion. Wetland-water couplings are complex. Knowledge of fisheries habitat use is not complete without understanding of, for example, the evolutionary relationships, predator-prey feeding networks, sediment resuspension and deposition, and microbial interactions.

Because the vegetation is so dense on the natural levee and the water depth, even at the highest levels sampled, never exceeded 25–30 cm, it is likely that most fish entering this marsh from the creek did not cross the natural levee and therefore were not utilizing the interior marsh surface. Those fish that are using the interior marshes are marsh-resident species that probably gain access through rivulets, muskrat trails, and small ponds and retreat to these areas at low tide. The densities of these marsh-resident species were probably underestimated because flume walls restrict lateral movement over the marsh and because several potholes and muskrat trails within the flumes held water and provided refuge for these fish at low tide where they could avoid being captured in cod-end nets. These marsh-resident species probably would have been more effectively sampled with pit traps, similar to those used in flume-weirs (Kneib 1991) and lift nets (Rozas 1992a), placed in low areas within the flumes.

A follow-up study is now in progress to compare utilization of marshes with and without well-developed natural levees, and to sample higher salinity marshes that are closer to the Gulf of Mexico and have a greater depth, frequency, and duration of flooding. This follow-up study is a test of the organism use of the edge vs the interior marshes using only two flume length treatments and using pit traps within these flumes to more effective sample the interior marshes.

Much emphasis is being placed on marsh management and restoration projects in Louisiana as a response to the rapid loss of marshes in Louisiana. Most marsh management plans in operation (or proposed) involve alterations of the marsh hydrology through impoundment or semi-impoundment via levees and water-control structures. Levees placed along a shoreline create obvious barriers to the movement of fish or crustaceans between the open-water and the marsh behind the levee. Water-control structures, such as fixed-crest weirs, have been shown to create barriers to the transport of estuarine-dependent fish and crustaceans that may result in decreased fishery productivity of the marsh open-water areas (Herke et al. 1992). Water-control structures also tend to dampen the daily tidal range in the marshes behind the structure and it is not known what impact this change in hydrology has on the use of these marshes by fish or on the overall productivity of the marsh. Besides altering fish access to the marsh surface, a change in the tidal regime of the marsh may also effect the export of primary (detritus) and secondary production from the marsh surface to the adjoining estuarine waters. Many economically important estuarine-dependent species (shrimp, crabs, and finfish) have adapted their feeding patterns to this daily tidal pattern. A change in the hydrology of a marsh could result in a change of the community structure of organisms using that marsh. More information is needed on how fish utilization of marsh habitats is influenced by different hydrological regimes before we can begin to predict the full impacts of marsh management on fisheries. This type of information is also essential for planning marsh creation or restoration projects, if the objective is to create a marsh that functions as a fisheries habitat. A well-vegetated marsh that is not regularly inundated and not accessible to fishes and invertebrates may look like a successful project, but will not be as productive as a natural stable or deteriorating deltaic marsh. The results of this study (and others) suggest that man-made marshes should be designed to maximize the edge habitat, have a gradual sloping edge profile (minimize levee effect), be well dissected by small drainage features, and flood and drain on a regular tidal schedule. In other words, man-made marshes should mimic the natural marsh morphology and hydrology.

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