

Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence

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ABSTRACT: We used lift nets from April through November 1991 in Louisiana (USA) deltaic marshes to compare nekton densities in 3 marsh-surface habitats undergoing submergence and having different surface elevations (*Distichlis spicata* marsh = high elevation; intact *Spartina alterniflora* marsh = intermediate elevation; and hummocky *S. alterniflora* marsh = low elevation). Daggerblade grass shrimp *Palaemonetes pugio*, gulf killifish *Fundulus grandis*, sheepshead minnow *Cyprinodon variegatus*, diamond killifish *Adinia xenica*, striped mullet *Mugil cephalus*, blue crab *Callinectes sapidus*, brown shrimp *Penaeus aztecus*, and white shrimp *P. setiferus* numerically dominated samples from all 3 marsh types and accounted for 93 % of the total catch. These dominant species exhibited 3 distinct patterns of spatial distribution among habitats. Gulf killifish and diamond killifish were most abundant on *D. spicata* marsh, whereas highest densities of brown shrimp and white shrimp were found on hummocky *S. alterniflora* marsh. Densities of daggerblade grass shrimp, sheepshead minnows, striped mullet, and blue crabs were similar among the 3 marsh types. Although in an advanced state of deterioration, hummocky *S. alterniflora* marsh did not lose its habitat function. Submergence of coastal Gulf of Mexico marshes may benefit marsh nekton, especially penaeid shrimp, by increasing the percentage of time the marsh surface is available for use. However, these benefits will be short-lived in regions where rapid submergence leads to a significant decrease in total marsh habitat.

INTRODUCTION

The loss of wetlands caused by coastal submergence is a serious problem in many regions of the United States (Gornitz et al. 1982, Clark 1986, Stevenson et al. 1986, Hackney & Cleary 1987). In Louisiana, the highest rate of coastal land loss occurs in the Mississippi River deltaic plain, where between 1983 and 1990 land was converted to open water at an average rate exceeding $50 \text{ km}^2 \text{ yr}^{-1}$ (Dunbar et al. 1992). The Mississippi River deltaic plain consists of a series of overlapping Holocene deltas which have been sequentially built up and then abandoned by the river as it changed its course to the Gulf of Mexico (Coleman & Gagliano 1964). A major cause of the current land loss

problem was the leveeing of the Mississippi River and the channelizing and stabilizing of its outlet in the early part of this century, which severely curtailed freshwater and sediment inputs to the deltaic marshes (Baumann et al. 1984). New sediment is no longer supplied by the river during spring floods, and the abandoned Holocene deltaic deposits are rapidly subsiding. Consequently, deltaic marshes in coastal Louisiana are experiencing a relative sea level rise of approximately 1 cm yr^{-1} (Penland & Ramsey 1990). As subsidence proceeds, marsh sediments become waterlogged, stressing marsh vegetation and reducing net primary productivity (Mendelssohn & McKee 1988). Where subsidence continues without compensating marsh-surface accretion, waterlogging leads to a buildup of toxic sulfides in sediments, which eventually causes plant death (Mendelssohn & McKee 1988).

In salt marshes undergoing submergence, the process of vegetation deterioration and conversion of

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marsh to open water is gradual. Deterioration usually begins in the marsh interior (Smith 1970, Sasser et al. 1986, Mendelssohn & McKee 1988) where sediment accretion rates are less than at streamside locations (Baumann & DeLaune 1982, Hatton et al. 1983), and submergence is therefore increased. As more and more plants die, the character of the marsh surface changes from uniform, intact stands of vegetation to bare substrate interspersed by small patches of vegetation. In these bare areas where vegetation is no longer present to bind the substrate, to trap new sediment, or to add below-ground biomass, the rate of submergence accelerates. Eventually, the marsh surface takes on a hummocky appearance as the difference in surface elevation between vegetated patches and bare substrate becomes pronounced. In the final stage of deterioration bare areas deepen, expand, and merge to form ponds (Sasser et al. 1986). Ultimately, large areas that were once vegetated intertidal habitat (salt marsh) are converted into shallow, unvegetated subtidal environments.

Estuarine marshes provide nursery habitat for numerous species of nekton (Zimmerman & Minello 1984, Rozas & Odum 1987, McIvor & Odum 1988, Hettler 1989, Kneib 1991, Rozas 1992b), and many of the species that depend on these marshes support important coastal fisheries. For example, brown shrimp *Penaeus aztecus* Ives are dependent on marsh-surface habitat during their post-larval and early juvenile stages (Minello & Zimmerman 1991). Blue crabs *Callinectes sapidus* Rathbun and striped mullet *Mugil cephalus* Linnaeus also use the marsh surface as small juveniles (Hettler 1989, Thomas et al. 1990, Rozas 1992a). In addition, this habitat is essential for forage species such as grass shrimp and killifishes, which are eaten by predatory fishery species, and therefore support fishery stocks through the food chain.

Although the use of coastal marshes by nekton is well documented, we know very little about how habitat use might change as coastal marshes undergo submergence and deterioration. The purpose of our research was to document patterns of nekton use among salt marsh habitats in a region of coastal Louisiana undergoing rapid submergence. Nekton densities were quantified and compared among 3 adjacent marsh-surface habitats having different elevations.

MATERIALS AND METHODS

The study area was within the Terrebonne-Timbalier estuary near latitude 29° 14' N and longitude 90° 40' W, approximately 4 km southwest of the Louisiana Universities Marine Consortium (LUMCON) Marine Center at Cocodrie (Fig. 1). Tides in the estuary are predominantly diurnal and have a mean range of approximately 0.4 m (Shirzad et al. 1989, U.S. Department of Commerce 1990). Chabreck & Linscombe (1991) classified the area as saline marsh. *Spartina alterniflora* Loisel dominated the vegetation except at higher elevations (e.g. on natural levees of tidal creeks) where *Distichlis spicata* (L.) Greene grew in dense stands.

Along each of 3 natural channels (A, B, and C; Fig. 1), we selected 3 marsh types having different surface elevations: *Distichlis spicata* marsh was highest in elevation; intact *Spartina alterniflora* marsh was intermediate in elevation; and hummocky *S. alterniflora* marsh was lowest in elevation. We surveyed surface el-



Fig. 1 Study area showing its location relative to Louisiana. Marsh sampling sites were located along Channels A, B, and C. (▲) Location of water level recorder

evaluations of sites in relation to local benchmarks and staff gauges located on each channel; these were tied into the National Oceanic and Atmospheric Administration/National Ocean Service (NOAA/NOS, Rockville, Maryland 20852) Cocodrie tide station (No. 876-2928) at the LUMCON Marine Center. In addition, a water level recorder was installed in a pipeline canal near the study sites in September 1991 (Fig. 1). Elevation data and tide gauge records were used with a software package, PEAKBASE, to calculate duration of marsh flooding (Reed & Cahoon 1992). We also measured plant-stem density within each sampling area in October 1991, near the period of peak standing crop (Hopkinson et al. 1978), and the distance from each site to the channel. When sampling nekton, we measured water temperature and salinity in the channels adjacent to each site with a Beckman RS5-3 salinometer.

Sampling. We sampled nekton on marshes using 9 lift nets (Rozas 1992a), one in each marsh type along the 3 channels. Briefly, lift nets (2 × 3 × 1 m deep) were bottomless with walls constructed of 3 mm mesh nylon netting. Between sampling events the net walls were buried in the marsh substrate. To collect a sample at slack high tide, 2 persons simultaneously pulled the net walls into an upright position from remote locations, trapping organisms inside the enclosed area. As the marsh drained, organisms accumulated in a collecting pan located in one corner of each sampling area. We retrieved samples at low tide by temporarily removing each collecting pan and placing its contents into a sample bag. We collected nekton at each sample site on 15 occasions from April through November

1991: once in April, May, and October; twice in August, September, and November; and 3 times in June and July. Sampling occurred on tropical tides to insure that marshes at all sites were flooded. In July, the 3 lift nets on Channel B had to be moved about 100 m, outside an area of vegetation dieoff. The cause of the vegetation dieoff is unknown, but it followed a period of unusually high tides in the spring of 1991. Prolonged flooding of the area may have caused sufficient waterlogging of the marsh soils to kill the vegetation.

Samples were preserved in 20 % formalin for at least 72 h, washed in running water for 24 h, and placed into 70 % ethanol for storage. Organisms were later separated from detritus, identified to species, and counted. All individuals of each species in a sample were weighed together to the nearest 0.1 g (wet weight).

Statistical analyses. Our statistical design was a repeated measures multivariate analysis of variance (MANOVA) with the lift net the unit of observation (O'Brien & Kaiser 1985, Norusis 1990). The between-subjects factor was elevation or marsh type, the within-subjects factor was sampling date. Data for each numerically dominant species were analyzed for differences in catch (number of individuals) among marsh habitats. Catch data were $\ln(x+1)$ -transformed prior to analyses to meet the MANOVA assumption of homogeneity of variances (Green 1979). When significant results were found among treatments, the data were analyzed with *a posteriori* contrasts (Norusis 1990). A significance level of 0.10 was used for *a posteriori* contrasts to increase the power of this analysis, and 0.05 was used for all other analyses; these values

Table 1. Characteristics of lift-net sites in *Distichlis spicata* and *Spartina alterniflora* marsh. Elevations are based on a Mean Tide Level of 95.1 cm (3.12 ft.) for the NOAA Cocodrie tide station located at the LUMCON Marine Center. Distances were measured from the edge of the net to the nearest tidal channel. B2 sites replaced B1 sites in July 1991

Site	Elevation above Mean Tide Level (cm)	Distance to channel (m)	Stem density (culms per 0.062 m ²)
A <i>D. spicata</i>	20.4	1.7	58
A Intact <i>S. alterniflora</i>	11.3	4.1	23
A Hummocky <i>S. alterniflora</i>	4.3	3.3	19
B1 <i>D. spicata</i>	17.1	11.8	–
B1 <i>S. alterniflora</i>	13.4	13.6	–
B1 <i>S. alterniflora</i>	3.4	22.5	–
B2 <i>D. spicata</i>	20.7	3.5	75
B2 Intact <i>S. alterniflora</i>	13.1	4.8	17
B2 Hummocky <i>S. alterniflora</i>	7.6	7.0	9
C <i>D. spicata</i>	14.6	3.6	32
C Intact <i>S. alterniflora</i>	13.7	4.9	21
C Hummocky <i>S. alterniflora</i>	7.0	3.0	8

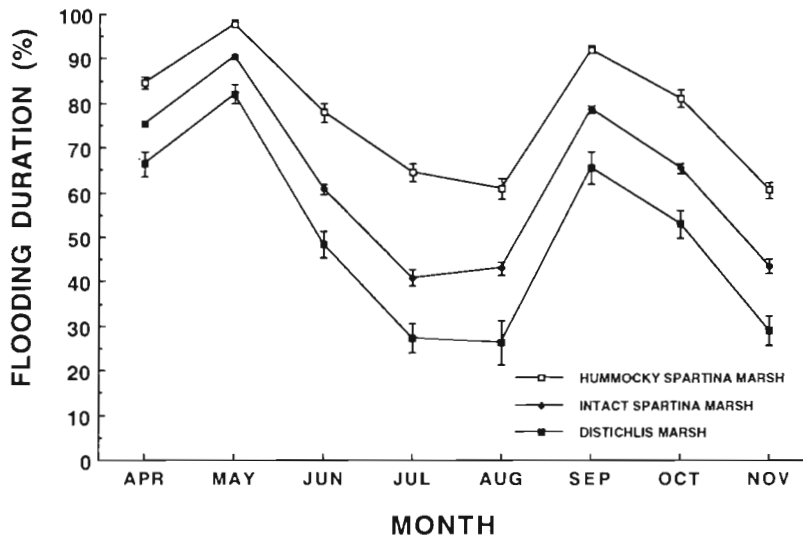


Fig. 2. Average monthly flooding durations [(hours marsh inundated)/(total hours in month) \times 100] of *Distichlis spicata*, intact *Spartina alterniflora*, and hummocky *S. alterniflora* marshes from April to November 1991. Error bars = 1 SE

were adjusted using the method of Rice (1989) to correct for the error introduced by making multiple statistical comparisons.

RESULTS

Distichlis spicata marsh contained the greatest density of plants and was on average 5 and 13 cm higher than intact and hummocky *Spartina alterniflora* marshes, respectively. Hummocky *S. alterniflora*

marsh, which was in an advanced stage of submergence and vegetation deterioration, generally contained the sparsest vegetation and was approximately 7 cm lower than intact *S. alterniflora* marsh (Table 1).

Data obtained from our 2 sources of water-level records were coherent for the 3 months in which both collected data (R^2 : Sep = 0.80, Oct = 0.93, Nov = 0.83). Because the LUMCON gauge provided water-level data for the entire study period, we used data from it to estimate flooding duration of study marshes. Flooding durations differed substantially among marshes, even though elevational differences were relatively small. For example, *Distichlis spicata* marsh flooded <30% of the time during July, August and November, and <55% of the time in 5 of the 8 months it was sampled, whereas hummocky *Spartina alterniflora* marsh was inundated more than 60% of the time during each month (Fig. 2). The average water temperature peaked in the summer months (32 °C in June and July); lowest temperatures occurred in November (Fig 3). Above-average rainfall in the spring kept salinities below 5‰ well into summer, but salinity in the area increased to 18.8‰ in October (Fig. 3).

In 135 lift-net samples we collected 8229 organisms having a preserved wet weight of 14.3 kg. We identified 25 species (13 families) of fishes and 4 species (3 families) of decapod crustaceans from these samples (Table 2). Daggerblade grass shrimp *Palaemonetes pugio* Holthuis, gulf killifish *Fundulus grandis* Baird & Girard, sheepshead minnow *Cyprinodon variegatus* Lacepede, diamond killifish *Adinia xenica* (Jordan & Gilbert), striped mullet, blue crab, brown shrimp, and white shrimp *Penaeus setiferus* (Linnaeus) numerically dominated catches and accounted for 93 and 95% of the total catch and biomass, respectively (Table 2).

The spatial distribution of nekton on marshes varied with species, but 3 distinct patterns were observed. Four species showed a preference for either *Distichlis spicata* marsh or hummocky *Spartina alterniflora* marsh (Fig. 4). Gulf killifish and diamond killifish were most abundant on *D. spicata* marsh (Tables 3, 4 & 5, Fig. 4), and were occasionally collected on marshes inundated as little as 5 cm deep.

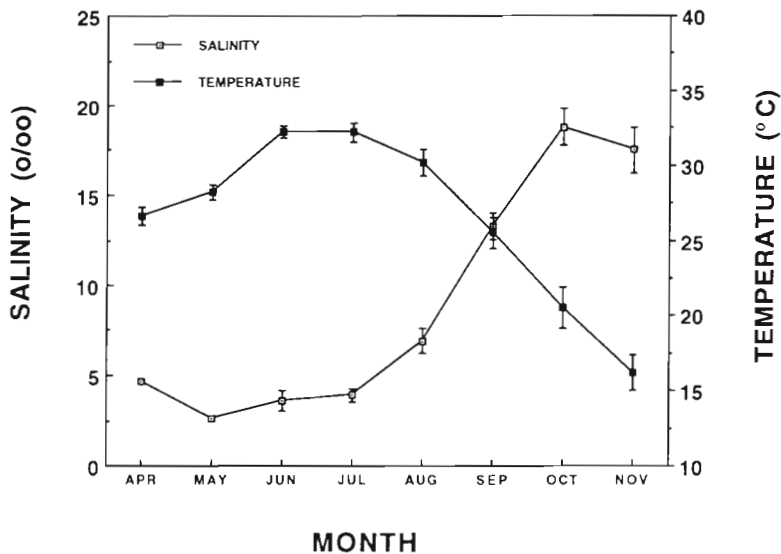


Fig. 3. Average monthly salinity and water temperature (all sample sites combined), April to November 1991. Error bars = 1 SE

Table 2. List of fishes and decapod crustaceans collected on *Distichlis spicata* and *Spartina alterniflora* marsh surface from April to November 1991 using lift nets. Total number and biomass (g wet wt. in parentheses) for each marsh type represent pooled data for 45 samples of 6 m² each. Relative abundance and biomass for all marsh types combined are given only when equal to at least 1 %

Scientific and common name	Totals by habitat			Relative abundance and biomass (%)
	<i>D. spicata</i>	Intact <i>S. alterniflora</i>	Hummocky <i>S. alterniflora</i>	
<i>Palaemonetes pugio</i> Holthuis Daggerblade grass shrimp	1052 (166.5)	540 (82.9)	1461 (219.5)	37.1 3.3
<i>Fundulus grandis</i> Baird & Girard Gulf killifish	1069 (2028.2)	234 (575.8)	128 (264.3)	17.4 20.0
<i>Cyprinodon variegatus</i> Lacepede Sheepshead minnow	604 (696.3)	281 (390.9)	88 (76.1)	11.8 8.1
<i>Adinia xenica</i> (Jordan & Gilbert) Diamond killifish	418 (130.9)	216 (88.4)	84 (29.4)	8.7 1.7
<i>Mugil cephalus</i> Linnaeus Striped mullet	107 (909.9)	239 (1937.3)	253 (1338.5)	7.3 29.2
<i>Callinectes sapidus</i> Rathbun Blue crab	205 (2298.1)	103 (1004.0)	168 (992.5)	5.8 30.0
<i>Penaeus aztecus</i> Ives Brown shrimp	28 (27.5)	51 (48.6)	140 (126.7)	2.7 1.4
<i>Penaeus setiferus</i> (Linnaeus) White shrimp	7 (1.9)	39 (25.7)	167 (117.1)	2.6 1.0
<i>Menidia beryllina</i> (Cope) Inland silverside	27 (24.3)	117 (58.5)	45 (35.8)	2.3 -
<i>Fundulus pulvereus</i> (Evermann) Bayou killifish	98 (76.6)	10 (5.8)	7 (3.4)	1.4 -
<i>Fundulus similis</i> (Baird & Girard) Longnose killifish	70 (48.2)	20 (46.8)	1 (0.0)	1.1 -
<i>Gobiosoma bosc</i> (Lacepede) Naked goby	6 (2.8)	14 (9.0)	23 (9.3)	- -
<i>Evorthodus lyricus</i> (Girard) Lyre goby	15 (23.0)	8 (23.9)	18 (32.3)	- -
<i>Gobionellus shufeldti</i> (Jordan & Eigenmann) Freshwater goby	8 (2.1)	3 (1.5)	5 (1.3)	- -
<i>Poecilia latipinna</i> (Lesueur) Sailfin molly	4 (5.7)	3 (1.8)	8 (5.1)	- -
<i>Bairdiella chrysoura</i> (Lacepede) Silver perch	2 (0.1)	0 (0.0)	5 (8.2)	- -
<i>Cynoscion nebulosus</i> (Cuvier) Spotted seatrout	2 (13.1)	1 (56.5)	3 (13.5)	- -
<i>Myrophis punctatus</i> Lutken Speckled worm eel	3 (57.3)	1 (37.8)	0 (0.0)	- -
<i>Citharichthys spilopterus</i> Gunther Bay whiff	0 (0.0)	0 (0.0)	3 (13.5)	- -
<i>Fundulus jenkinsi</i> (Evermann) Saltmarsh topminnow	1 (0.1)	2 (0.6)	0 (0.0)	- -
<i>Gobionellus boleosoma</i> (Jordan & Gilbert) Darter goby	3 (0.9)	0 (0.0)	0 (0.0)	- -
<i>Lucania parva</i> (Baird & Girard) Rainwater killifish	0 (0.0)	0 (0.0)	3 (4.5)	- -
<i>Dormitator maculatus</i> (Bloch) Fathead per	2 (21.1)	0 (0.0)	0 (0.0)	- -
<i>Archosargus probatocephalus</i> (Walbaum) Sheepshead	0 (0.0)	0 (0.0)	1 (2.7)	- -

(Table continued on next page)

Table 2 (continued)

Scientific and common name	Totals by habitat			Relative abundance and biomass (%)
	<i>D. spicata</i>	Intact <i>S. alterniflora</i>	Hummocky <i>S. alterniflora</i>	
<i>Arius felis</i> (Linnaeus) Hardhead catfish	0 (0.0)	0 (0.0)	1 (9.5)	-
<i>Eucinostomus argenteus</i> Baird & Girard Spotfin mojarra	0 (0.0)	0 (0.0)	1 (4.0)	-
<i>Lagodon rhomboides</i> (Linnaeus) Pinfish	1 (0.1)	0 (0.0)	0 (0.0)	-
<i>Lutjanus griseus</i> (Linnaeus) Gray snapper	0 (0.0)	0 (0.0)	1 (31.2)	-
<i>Sciaenops ocellatus</i> (Linnaeus) Red drum	0 (0.0)	0 (0.0)	1 (50.5)	-
Total: Number = 8229 Biomass = 14319.4 g				

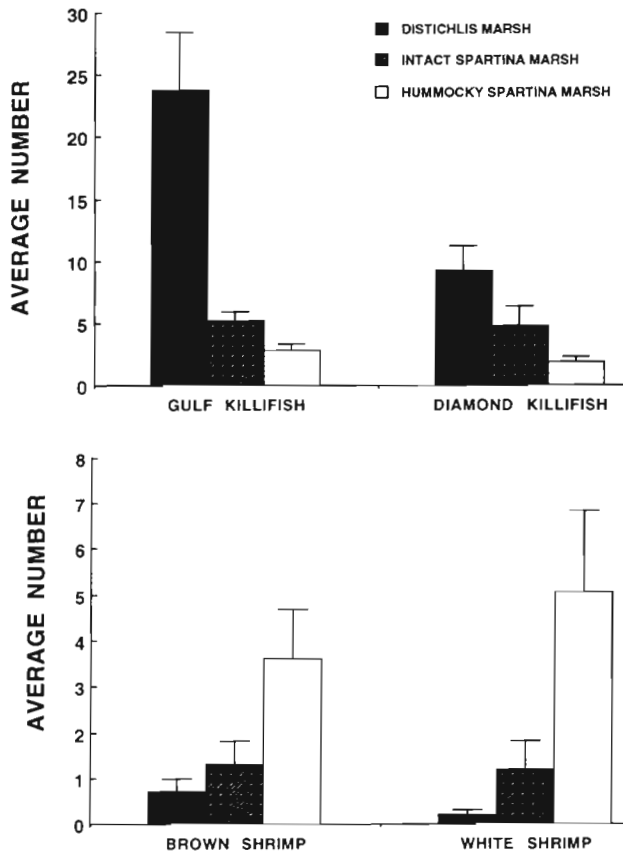


Fig. 4. Average number of gulf killifish *Fundulus grandis*, diamond killifish *Adinia xenica*, brown shrimp *Penaeus aztecus*, and white shrimp *Penaeus setiferus* collected in 6 m² samples on the 3 marsh types. Means for gulf killifish and diamond killifish are calculated from 45 samples collected from April to November 1991. Means for brown shrimp and white shrimp are calculated from 39 samples (April to October 1991) and 33 samples (June to October 1991), respectively. Samples taken during months when penaeids were not collected in marsh habitats were not used to calculate means for these species. Error bars = 1 SE

In contrast to these killifishes, brown shrimp and white shrimp were found in greatest densities on hummocky *S. alterniflora* marsh (Tables 3, 4 & 5, Fig. 4), and penaeids were never collected on any marsh flooded < 10 cm deep. Densities of daggerblade grass shrimp, sheepshead minnow, striped mullet, and blue crab were not significantly different among marsh types (Tables 3 & 4).

Most of the dominant marsh nekton reached peak abundance in late summer to early fall (Table 3). However, white shrimp and gulf killifish were most numerous later in the year (September–October). Only 2 species, brown shrimp and daggerblade grass shrimp, were seasonally abundant on marshes in the spring.

DISCUSSION

Salt marshes undergoing submergence, even marshes in an advanced state of vegetation deterioration, continue to provide habitat for estuarine species. The process of submergence not only enhances access to the marsh surface, but it may also improve marsh habitat, at least over the short term, for some species. In our study both brown shrimp and white shrimp were strongly associated with hummocky *Spartina alterniflora* marsh (Fig. 4, Tables 3, 4 & 5), a habitat-type characteristic of Gulf coast salt marshes in a late stage of submergence. Rather than moving into the shallowest habitat available, penaeid shrimp selected the low-elevation *S. alterniflora* marsh. Zimmerman & Minello (1984) reported densities even higher than those reported here for penaeids and other decapods on a similarly deteriorated *S. alterniflora* marsh near Galveston Bay (Texas, USA). Selectively exploiting deteriorated marshes may have several advantages. Because they are lower in elevation, they are flooded deeper and

Table 3. Comparisons of monthly average catches (no. of individuals per 6 m² sample area) of numerically dominant species among different habitats. Means ± standard errors are listed for each habitat (D = *Distichlis spicata* marsh, IS = intact *Spartina alterniflora* marsh, HS = hummocky *S. alterniflora* marsh)

Species	Habitat type	Month							
		Apr n = 3	May n = 3	Jun n = 9	Jul n = 9	Aug n = 6	Sep n = 6	Oct n = 3	Nov n = 6
Daggerblade grass shrimp	D	20.7 ± 11.3	39.7 ± 29.2	37.9 ± 14.0	16.4 ± 7.5	16.7 ± 7.0	17.3 ± 4.9	17.0 ± 12.1	21.2 ± 9.3
	IS	19.7 ± 9.1	22.7 ± 12.1	15.1 ± 5.4	7.4 ± 2.3	9.0 ± 3.0	6.5 ± 2.8	3.7 ± 1.5	17.7 ± 3.8
	HS	30.3 ± 17.9	28.0 ± 13.3	36.7 ± 12.6	24.6 ± 5.7	19.7 ± 11.5	27.8 ± 14.9	40.7 ± 19.4	54.7 ± 14.8
Gulf killifish	D	7.0 ± 1.5	13.7 ± 5.4	8.6 ± 2.2	7.2 ± 1.7	33.8 ± 8.0	62.2 ± 20.4	62.7 ± 36.0	16.8 ± 6.0
	IS	4.0 ± 1.0	7.7 ± 3.7	4.8 ± 1.1	4.1 ± 1.3	9.7 ± 2.8	2.0 ± 0.9	3.0 ± 2.0	6.7 ± 1.6
	HS	6.7 ± 2.6	2.7 ± 2.2	1.8 ± 0.8	3.1 ± 1.6	3.3 ± 1.3	2.0 ± 1.5	2.3 ± 1.5	2.8 ± 1.1
Sheepshead minnow	D	2.7 ± 1.8	7.3 ± 3.8	12.0 ± 4.3	17.9 ± 7.8	16.5 ± 6.4	26.0 ± 9.8	10.3 ± 4.3	3.2 ± 1.1
	IS	6.0 ± 1.5	0.0 ± 0.0	4.9 ± 3.7	9.8 ± 3.3	15.2 ± 7.1	3.0 ± 1.1	1.0 ± 1.0	3.2 ± 0.9
	HS	1.3 ± 0.9	2.0 ± 2.0	0.1 ± 0.1	1.8 ± 0.9	4.5 ± 1.3	1.8 ± 1.8	1.0 ± 0.6	3.3 ± 1.2
Diamond killifish	D	2.0 ± 1.0	4.3 ± 1.5	9.8 ± 5.6	8.2 ± 4.3	12.7 ± 7.5	14.0 ± 5.5	11.3 ± 8.1	7.2 ± 2.7
	IS	1.3 ± 0.9	0.0 ± 0.0	0.4 ± 0.3	9.7 ± 6.2	12.5 ± 4.6	1.5 ± 1.0	1.3 ± 0.7	5.5 ± 3.6
	HS	0.7 ± 0.3	0.0 ± 0.0	0.7 ± 0.4	1.9 ± 1.0	3.3 ± 1.9	2.3 ± 1.3	4.7 ± 2.9	1.8 ± 1.2
Striped mullet	D	3.7 ± 2.7	2.3 ± 1.2	1.2 ± 0.6	1.6 ± 1.2	0.8 ± 0.8	8.3 ± 2.3	0.0 ± 0.0	1.5 ± 1.5
	IS	5.7 ± 2.0	1.3 ± 0.9	4.8 ± 3.7	6.9 ± 4.4	6.8 ± 3.8	7.5 ± 2.0	5.0 ± 2.5	2.0 ± 0.7
	HS	6.0 ± 3.1	1.0 ± 1.0	4.7 ± 2.6	9.9 ± 7.5	12.5 ± 9.7	3.3 ± 1.1	2.0 ± 0.6	0.0 ± 0.0
Blue crab	D	2.0 ± 1.2	4.0 ± 1.0	5.4 ± 0.9	3.7 ± 1.0	5.8 ± 2.1	8.2 ± 4.5	2.7 ± 1.2	2.2 ± 0.6
	IS	1.0 ± 0.0	0.0 ± 0.0	1.8 ± 0.4	2.1 ± 0.5	2.5 ± 0.6	4.2 ± 1.2	3.0 ± 0.6	2.7 ± 0.6
	HS	5.0 ± 3.5	0.3 ± 0.3	2.1 ± 0.7	1.9 ± 0.5	4.2 ± 1.3	5.7 ± 1.2	8.0 ± 3.1	5.5 ± 1.2
Brown shrimp	D	1.3 ± 0.7	4.7 ± 2.4	0.8 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	0.0 ± 0.0	0.0 ± 0.0
	IS	6.3 ± 4.9	6.0 ± 3.0	1.0 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.2	0.7 ± 0.7	0.0 ± 0.0
	HS	14.0 ± 10.7	13.7 ± 2.9	4.8 ± 1.4	0.4 ± 0.2	0.8 ± 0.8	0.2 ± 0.2	1.3 ± 0.9	0.0 ± 0.0
White shrimp	D	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.3 ± 0.3	0.5 ± 0.5	0.3 ± 0.3	0.0 ± 0.0
	IS	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	5.3 ± 3.0	2.0 ± 1.2	0.0 ± 0.0
	HS	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.3	0.1 ± 0.1	0.8 ± 0.5	20.2 ± 6.5	11.7 ± 3.2	0.0 ± 0.0

Table 4. Results of the MANOVA tests of differences in catch among habitats for the April to November 1991 sampling period. *Significant result (adjusted $p < 0.05$ as described by Rice 1989)

Species	df	F	Sig. of F
Gulf killifish	2,4	78.82	0.001*
White shrimp	2,4	28.04	0.004*
Diamond killifish	2,4	21.06	0.008*
Brown shrimp	2,4	18.51	0.010*
Sheepshead minnow	2,4	11.16	0.023
Blue crab	2,4	4.43	0.097
Daggerblade grass shrimp	2,4	1.80	0.277
Striped mullet	2,4	0.83	0.500

Table 5. Results of the MANOVA *a posteriori* comparisons of mean catches among habitats (D = *Distichlis spicata*, IS = Intact *Spartina alterniflora*, HS = hummocky *S. alterniflora*) for the April to November 1991 sampling period. *Significant result (adjusted $p < 0.10$ as described by Rice 1989)

Species	Comparison	df	F	Sign. of F
Gulf killifish	D vs IS	1,2	183.14	0.005*
	D vs HS	1,2	77.24	0.013*
Diamond killifish	D vs IS	1,2	32.29	0.030*
	D vs HS	1,2	24.62	0.038*
White shrimp	HS vs D	1,2	66.58	0.015*
	HS vs IS	1,2	16.03	0.057*
Brown shrimp	HS vs D	1,2	20.23	0.046*
	HS vs IS	1,2	18.68	0.050*

longer than other marsh habitats (Fig. 2). Therefore, deteriorated marsh is accessible for longer periods than higher marsh, giving penaeids more time to forage and find concealment from predators. Even sparse vegetation, which is characteristic of this habitat, may afford more protection from avian and large natant predators than bare substrate (Minello & Zimmerman 1983, Minello et al. 1989)

A lengthy hydroperiod not only allows more time for marsh-surface exploitation, but it also influences the density of prey organisms found on marshes (Kneib 1984). For example, in the intertidal zone, the spionid polychaete *Streblospio benedicti* Webster occurs most abundantly in low, frequently flooded areas (Kneib 1984, Rader 1984, LaSalle & Rozas 1991), and it is a preferred prey of brown shrimp foraging on Gulf coast salt marshes (T. A. McTigue,

National Marine Fisheries Service, Galveston Laboratory, pers. comm.). Brown shrimp may have been drawn to hummocky *Spartina alterniflora* marsh by high densities of this favored prey. Marsh hydroperiod also influences the species diversity and density of vegetation, which in turn may affect habitat quality. For example, *S. alterniflora* stem density decreases in subsiding marshes as hydroperiod increases (Linhurst & Seneca 1980, Mendelssohn & Seneca 1980). Scattered patches of *S. alterniflora* culms are less of an impediment to swimming organisms than thick vegetation, and sparse vegetation may provide more foraging surface and interfere less with the foraging activity of penaeid shrimp and other predators (Vince et al. 1976, Van Dolah 1978). Controlled experiments are now needed to further elucidate the specific mechanisms by which changes in hydroperiod alter the habitat function of *S. alterniflora* marshes.

Variations in hydroperiod may also influence differences in marsh-nekton densities on a regional scale. Zimmerman et al. (1991) have postulated that nekton exploit Gulf coast marshes in greater numbers than Southeastern U.S. Atlantic coast marshes, because Gulf coast marshes have longer hydroperiods. Quantitative estimates of nekton densities on Gulf and Atlantic coast marshes are few, but the available data are consistent with the hypothesis of greater marsh

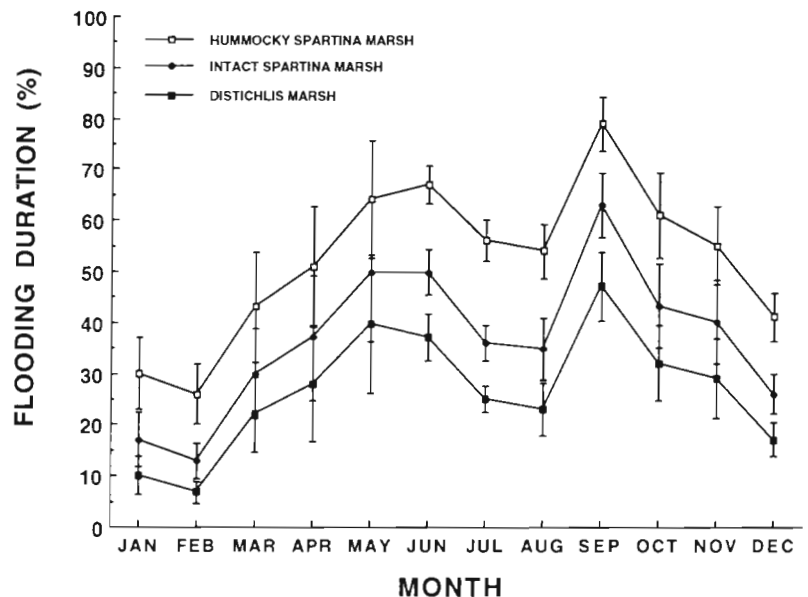


Fig. 5. Estimated 5 yr average monthly flooding durations [(hours marsh inundated)/(total hours in month) \times 100] of *Distichlis spicata*, intact *Spartina alterniflora*, and hummocky *S. alterniflora* marshes for the period 1987 to 1991. Error bars = 1 SE

utilization on the Gulf coast. For example, densities of dominant species collected in our study and those reported by Zimmerman & Minello (1984) are 1 to 2 orders of magnitude greater than those reported by Mense & Wenner (1989) in South Carolina, by Hettler (1989) in North Carolina, and by Kneib (1991) and Fitz & Wiegert (1991) in Georgia. Furthermore, Gulf coast marshes are flooded for long periods of time, especially during the late spring/early summer and fall. During 1991 *Distichlis spicata*, intact *Spartina alterniflora*, and hummocky *S. alterniflora* marshes in our study area were flooded 39, 51 and 68 % of the time, respectively. Sasser (1977) reported very similar mean annual flooding durations for *S. alterniflora* (54 %) and *D. spicata* (40 %) growing in coastal Louisiana. Based on 5 yr of data (Fig. 5), we estimate that maximum monthly flooding durations occurred in our hummocky *S. alterniflora* marshes in June (68 %) and September (78 %). Intact *S. alterniflora* marshes flooded 49.8, 49.8, and 61 % of the time in May, June and September, respectively (Fig. 5). Similar maximum flooding durations of 75 and 80 % were reported for salt marshes of Barataria Bay, Louisiana (Baumann 1980) and Galveston Bay, Texas (Zimmerman et al. 1991), respectively. However, lengthy flooding durations (annual mean > 50 %, maximum = 64 to 74 % in September) have also been recorded for some Atlantic coast marshes (D. L. Childers, National Marine Fisheries Service, Galveston Laboratory, pers. comm.). Unfortunately, hydroperiod data for coastal marshes are too limited, and the variation in flooding duration within marshes is so high, that comparisons of hydroperiod between the 2 regions are impossible to make at this time. Regional comparisons of marsh utilization and studies that examine the factors (including hydroperiod) that may influence differences in habitat use require further study.

Temporal variations in hydroperiod may also affect the abundance of marsh nekton. Seasonal changes in water levels explained most of the variability in brown shrimp collected on Galveston Bay salt marshes, and densities of white shrimp and blue crabs were also correlated with seasonal hydroperiods (Zimmerman & Minello 1984). Likewise, highest densities of these decapods on our study marshes coincided with seasonally high water levels in the spring (brown shrimp) and fall (white shrimp and blue crab) (Table 3, Fig. 2). Marsh nekton populations may also be influenced by year-to-year variations in sea level. Commercial landings of penaeid shrimp and menhaden *Brevoortia tyrannus* (Latrobe) and *B. patronus* Goode have been correlated with interannual fluctuations in coastal water levels, suggesting a relationship between the degree of marsh flooding and productivity of these fisheries species (Childers et al. 1990, Morris et al.

1990). Evidence that brown shrimp grow faster and experience lower mortality rates when high water levels allow greater access to the marsh surface (Minello et al. 1989, Minello & Zimmerman 1991) is consistent with these models.

Although the most abundant species did not show a preference for hummocky *Spartina alterniflora* marsh over other marsh types, they probably occupy this habitat during low water periods when other habitats are not accessible. For example, grass shrimp and blue crab, which showed no significant habitat preference at high tide in our study (Fig. 4), exhibit strong selection for marsh vegetation when given a choice between unvegetated bottom and salt marsh (Zimmerman & Minello 1984, Thomas et al. 1990). Gulf killifish and diamond killifish, which were associated with *Distichlis spicata* marsh at high tide (Fig. 4), apparently use the marsh surface whenever it is flooded (Hastings & Yerger 1971, Lipcius & Subrahmanyam 1986). In our study, gulf killifish were not constrained by shallow water in the *D. spicata* marsh; they were collected on marsh flooded < 5 cm deep, and their abundance was not related to water depth ($R^2 = 0.038$, $p = 0.201$). The other numerically dominant cyprinodonts exhibited similar behavior. Gulf killifish and diamond killifish undoubtedly use *S. alterniflora* marsh when it is first inundated but move onto higher *D. spicata* marsh when it becomes accessible later in the tidal cycle. *Fundulus heteroclitus* (Linnaeus) exhibit similar behavior on Atlantic coast marshes; they occupy intermediate and upper intertidal marsh at slack high tide, and occur in low intertidal marsh only on early advancing and late receding portions of the tidal cycle (Kneib 1976, 1984). However, for extended periods each month (during equatorial tides) when high marshes do not flood, killifishes and other marsh nekton must rely entirely on low *S. alterniflora* marshes. Gulf killifish and diamond killifish may be selecting *D. spicata* marsh when it is available because it contains high densities of favored prey, or perhaps the dense vegetation and shallow water found there provide added protection from predators. Adult killifishes may also use high marshes to locate suitable spawning sites (Greeley & MacGregor 1983).

Gosselink (1984), Zimmerman et al. (1984), Browder et al. (1989), and others have postulated that coastal submergence enhances nekton access to Gulf coast marshes and secondary productivity, at least over the short term, by accelerating marsh disintegration and increasing the amount of marsh edge (marsh-water interface) in this region. However, coastal submergence also increases the percentage of time the marsh surface is available for use by aquatic species by lowering marsh-surface elevation and increasing hydroperiod. This may be especially beneficial to penaeid

shrimp which seem to prefer low, deeply and frequently flooded *Spartina alterniflora* marshes that are in a late stage of submergence. The presence of low *S. alterniflora* marshes may be important for maintaining the high productivity of marsh nekton because they provide habitat during periods of low water when higher marshes are not flooded. However, the productivity of species that are dependent on marshes will surely begin to decline at some point in regions where the rate of submergence is high enough to cause a significant decrease in the total area of marsh habitat (Zimmerman et al. 1991).

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