

# Fish Assemblage Structure in Relation to Environmental Variation in a Texas Gulf Coastal Wetland

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**ABSTRACT:** We described seasonal fish-assemblages in an estuarine marsh fringing Matagorda Bay, Gulf of Mexico. Habitat zones were identified by patterns of fish species abundance and indicator species optima along gradients in salinity, dissolved oxygen (DO), and depth in our samples. Indicators of the lower brackish zone (lower lake and tidal bayou closest to the bay) were gulf menhaden (*Brevoortia patronus*), bay anchovy (*Anchoa mitchilli*), silver perch (*Bairdiella chrysoura*), and spotted seatrout (*Cynoscion nebulosus*) at salinity > 15‰, DO 7–10 mg l<sup>-1</sup>, and depth < 0.5 m. Indicators of the upper brackish zone (lake and fringing salt marsh) were pinfish (*Lagodon rhomboides*) and spot (*Leiostomus xanthurus*) at salinity 10–20‰, DO > 10 mg l<sup>-1</sup>, and depth < 0.5 m. In the freshwater wetland zone (diked wetland, ephemeral pool, and perennial scour pool), indicators were sheepshead minnow (*Cyprinodon variegatus*), rainwater killifish (*Lucania parva*), mosquitofish (*Gambusia affinis*), and sailfin molly (*Poecilia latipinna*) at salinity < 5‰, DO < 5 mg l<sup>-1</sup>, and depth ≥ 1 m. In the freshwater channelized zone (slough and irrigation canal), indicators were three sunfish species (*Lepomis*), white crappie (*Pomoxis annularis*), and gizzard shad (*Dorosoma cepedianum*) at salinity < 5‰, DO < 5 mg l<sup>-1</sup>, and depth > 1.5 m. In brackish zones, seasonal variation in species diversity among sites was positively correlated with temperature, but assemblage structure also was influenced by depth and DO. In the freshwater zones, seasonal variation in species diversity among sites was positively correlated with depth, DO, and salinity, but assemblage structure was weakly associated with temperature. Species diversity and assemblage structure were strongly affected by the connectivity between freshwater wetland and brackish zones. Uncommon species in diked wetlands, such as tarpon (*Megalops atlanticus*) and fat sleeper (*Dormitator maculatus*), indicated movement of fishes from the brackish zone as the water level rose during natural flooding and scheduled (July) releases from the diked wetland. From September to July, diversity in the freshwater wetland zone decreased as receding waters left small isolated pools, and fish movement became blocked by a water-control structure. Subsequently, diversity was reduced to a few species with opportunistic life histories and tolerance to anoxic conditions that developed as flooded vegetation decayed.

## Introduction

Organisms in coastal wetlands are affected by spatial and temporal dynamics of salinity within these complex, terrestrial-freshwater-marine ecotones (Bulger et al. 1993). Physiological tolerance to salinity and other physiochemical parameters, and life-history strategies determine how animals respond to habitat heterogeneity and dynamics. Fish communities of coastal salt marshes generally represent a mixture of ecological groupings that contain euryhaline species adapted to brackish environments, plus others more typical of either marine or freshwater systems (Rozas and Hackney 1983; Odum 1988; Peterson and Meador 1994; Wagner and Austin 1999). Renfro (1959) concluded that survival of freshwater fishes in saline habitats of the Aransas River, Texas was generally short-term. He suggested that low abundance of freshwater fishes was likely due to stress associated with frequent salinity fluctuations, and that freshwater fishes either moved to less saline waters or died. In

other systems (Perry 1967; Peterson and Ross 1991; Wagner and Austin 1999), freshwater fish can withstand short-term exposure to salinities > 10‰, but occur most often at < 5‰. Freshwater predators such as largemouth bass (*Micropterus salmoides*) and longnose gar (*Lepisosteus osseus*) enter tidal creeks to forage (Meador and Kelso 1989). However, different species and life-stages of freshwater and estuarine fishes vary greatly in their salinity tolerances (Chipman 1959; Renfro 1959; Griffith 1974; Hollander and Avault 1975; Meador and Kelso 1990a; Susanto and Peterson 1996).

Beyond individual response to physiochemical variation, populations also respond through biotic interactions that influence community structure across these complex ecotones (Dunson and Travis 1991; Winemiller and Leslie 1992; Wagner and Austin 1999). Habitat structure and the interaction of fishes and other aquatic fauna with terrestrial predators, also influences composition and biomass of aquatic biota (Vince et al. 1976; Kneib 1987). Availability of aquatic prey for waterfowl, wading birds, and other animals depends on temporal change in habitat quality and quantity for

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aquatic organisms (Kahl 1964; Kushlan 1976; Willard 1977; Browder 1978). Submerged aquatic vegetation influences prey availability and predation risk for fish and aquatic invertebrates (Rozas and Odum 1987a,b, 1988; Meador and Kelso 1990b). Also, schedules for accumulation of detritus in salt marshes and tidal creeks influences community structure, productivity, and transfer of energy between freshwater and marine systems (Odum 1984). Because of the natural spatial and temporal dynamics in water level and habitat conditions in coastal systems, the role of connectivity among habitats also should be understood. Diked wetlands (often used for restoration) provide deep-water refugia for fishes (Toth et al. 1998). However, when these reduce spatial connectivity among aquatic habitats, dikes can isolate aquatic organisms, influence water quality, and affect community dynamics (Johnson et al. 1997). For example, despite identical water-level dynamics, diked wetlands in Florida did not support a fish fauna as rich as that of restored wetlands that were connected to natural open-water habitat (Toth et al. 1998).

The use of terrestrial and freshwater resources by a growing human population has impacted the ecological integrity and health of Texas coastal wetlands (McKinney 1997). Reduction of freshwater flow to estuaries has obvious effects on salinity and a host of related abiotic environmental factors. The Nature Conservancy of Texas manages the Mad Island Marsh Preserve (MIMP) on the edge of Matagorda Bay (Gulf of Mexico). Management goals include augmenting freshwater inflows and enhancement of coastal salt-marsh and prairie ecosystems through erosion control, prescribed burning, mowing, grazing, and impoundment. Though focused on benefits to terrestrial wildlife, wading birds, and migratory water fowl, management actions also are relevant to habitat use and production of fishes, many of which are prey for birds. Connectivity among estuarine habitats in MIMP and management of freshwater inflows (e.g., dikes for roads and rice fields, water-control structures, and irrigation canals) likely influence spatial dynamics of physiochemical factors and habitat use by fishes.

Because fishes respond to both terrestrial and aquatic environmental factors, fish assemblage composition can indicate biological integrity of aquatic systems (Karr 1991). In order to plan monitoring and management to restore natural ecosystems and their functions (e.g., flood control, nutrient dynamics, food production for terrestrial wildlife) in MIMP, relationships between habitat attributes and assemblage structure of fishes were quantified. Assemblage structure (e.g., species composition, diversity, life-history strategies) was

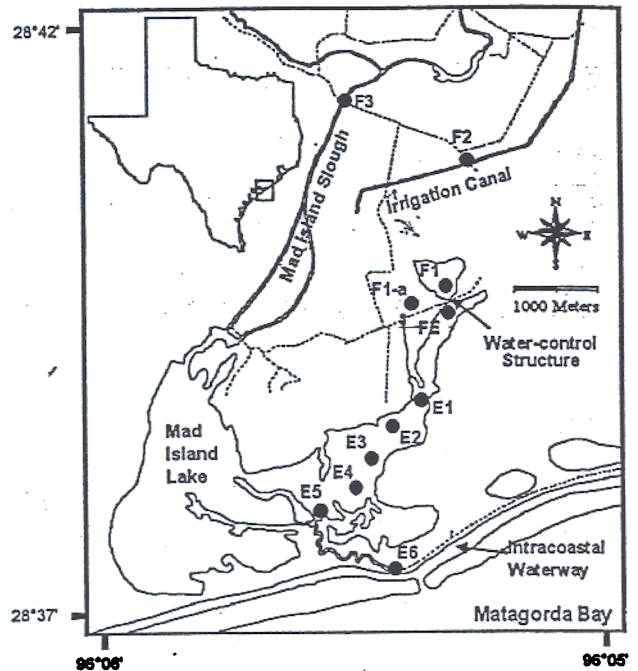


Fig. 1. Mad Island Marsh Preserve. Sites E1-E6 were brackish estuarine habitats, and sites FE and F1-F3 were freshwater habitats. An irrigation canal diverted water from the Colorado River, 20 km east of Mad Island Marsh Preserve. Dotted lines indicate roads. The area between FE and E1 was dry in March and May, and F1-a was dry from March through July. A water-control structure at the road culvert between F1 and FE was closed from September to July.

evaluated across seasonal and spatial gradients of depth, water quality (dissolved oxygen, salinity, and temperature), and connectivity (diked and open systems). In addition, habitat zones were identified based on fish-assemblage composition, and characterized by indicator species and their optima across measured physiochemical factors. This study also provided baseline data and locations for monitoring and evaluating environmental conditions and biotic integrity of MIMP.

## Methods

### STUDY AREA AND SAMPLING PROTOCOL

The MIMP is located on the northwestern coast of the Gulf of Mexico, in Matagorda Bay (Fig. 1). Aquatic habitats in MIMP span physiochemical gradients, from freshwater Mad Island (MI) Slough and diked wetlands, to oligo-mesohaline MI Lake and salt marsh, and a polyhaline tidal bayou. Before initial sampling, heavy rainfall caused flooding in October 1997 that over-topped diked roads and wetlands throughout MIMP, connecting all aquatic habitats. Winter samples were made at four sites when they were accessible in December 1997, and other sites were added in March 1998 as access was

established. Spring, summer, and fall samples were made in May, July, and October 1998, respectively. Sites were located in the dominant aquatic habitats of MIMP (Fig. 1). MI Bayou (E6) was a tidal system connecting brackish MI Lake to the Intracoastal Waterway. Five sites were located along MI Lake and fringing salt marsh (Fig. 1, E1-E5). Among these, only E2 was sampled in December 1997, but it and other sites in MI Lake and Bayou were sampled in the four other months, representing the four seasons. An irrigation canal from the Colorado River (F2) and MI Slough (F3) represented channelized open freshwater systems, but only F3 was connected to MI Lake (Fig. 1) while the Colorado River entered the intracoastal waterway about 20 km east of MIMP. Sampling at F2 began in March, but the May sample was omitted by mistake. Sampling at F3 was possible in May, July, and October. A diked freshwater wetland (F1) retained water from October 1997 through June 1998. In July 1998, scheduled releases of water drained F1 as riser boards blocking a road culvert were removed, and water flowed into the upper salt marsh. This reduced the size of F1 from about 100 m<sup>2</sup> to a 12-m<sup>2</sup> pool adjacent to the culvert. In September, scheduled closure of the culvert allowed rainfall and runoff to refill the wetland. A small ephemeral pool (F1-a, ca. 6 m<sup>2</sup>; Fig. 1) was sampled when it retained overflow from F1 in December 1997, and again in October 1998 after it had dried and refilled. A perennial scour pool (FE, ca. 15 m<sup>2</sup>) had formed at the outflow of the culvert from the diked wetland. During March and May (culvert closed), FE was sampled but the downstream reach was dry, and thus, it was disconnected from both the upper salt marsh and the diked wetland. During July and August (culvert open), flow reconnected FE to both F1 and E1.

For each sample, water depth was measured (0.01 m), and temperature (°C), dissolved oxygen (DO, mg l<sup>-1</sup>), and salinity (‰) were measured with a Hydrolab Datasonde3 or a Yellow Springs Instruments YSI Model 85 during daytime (0900–1600). Measurements were intended to represent among-site and within-site variation at the time of sampling, rather than diel extremes actually experienced by fishes. Fishes were collected using a combination of active and passive gear to maximize number of species captured. Because seining consistently captured more species, as well as individuals, than other methods, those data were selected for statistical analyses of assemblage structure. Seines were 6-m long, 1.2-m tall, with 4.5-mm mesh, and 1.2-m by 1.2-m bag. Brails were kept about 3 m apart during seine hauls parallel to shore, and distance seined was recorded. Seining continued until no new fish species were encoun-

tered in three consecutive hauls. Higher density of vegetation (*Ruppia*, *Spartina*) generally reduced the distance covered per seine haul, and total distance seined was reduced in very small habitats. Across all seasons and sites, total distance seined at a site ranged from 5 to 105 m. Captured fish were anesthetized in MS-222, fixed in a 10% formalin solution in the field, then sorted and counted in the laboratory. Data were standardized to catch per unit of effort (CPUE, calculated as number per meter of distance seined) and log<sub>10</sub> transformed for analyses.

#### DATA ANALYSIS

Shannon diversity ( $H'$ ) based on natural logarithm of CPUE was calculated for each sample and tested for correlation with each environmental variable (marginal effects) and partial correlations (conditional, or independent additive effects) of each environmental variable. Variables were tested for fit to normal distributions using the univariate procedure of SAS to test the Kolomogorov D statistic (SAS 1996). Normally distributed variables were tested using Pearson's correlation coefficient, and others were tested using Spearman's Rank correlation coefficient (SAS 1996).

Canonical Correspondence Analysis (CCA), a multivariate method of direct gradient analysis, was run on species CPUE across all samples using CANOCO (ter Braak and Smilauer 1998). To compare the importance of the gradients separately in freshwater and brackish zones identified by the initial CCA and cluster analyses (see below), additional analyses were run for MI Lake and salt marsh (E1-E6), and MI Slough, irrigation channel, and freshwater wetland (FE, F1-3). To focus analyses on responses by common species to environmental gradients, species were restricted to those with total CPUE  $\geq 1\%$  of total CPUE across all species and samples. Each canonical axis was derived from an iterative reciprocal weighted averaging of species CPUE among samples, with the additional constraint that ordination scores for species and sites were linear combinations of environmental variables. This method of ordination is particularly useful for species that show a unimodal (humped) relationship to environmental gradients and zero values in many samples (ter Braak and Smilauer 1998). Hill's scaling of scores with a focus on species was chosen so that distances between species were generalized Mahalanobis distances, and distances between sites represented species turnover across samples (beta diversity) in standard deviations (SD; ter Braak and Smilauer 1998). Monte Carlo simulations (199 iterations), tested the significance ( $p \leq 0.05$ ) of the variation in fish distribution among samples that was represented along

TABLE 1. Fishes in families and species that were collected by seining in Mad Island Lake from December 1997 to October 1998. Values are numbers of individuals  $m^{-1}$  of shoreline seined. Group membership was determined by cluster analysis using these values and those for fishes from Mad Island Slough (Table 2).

Family	Species	Common	Lower Brackish Habitat Zone 1										
			E6				E5						
			Mar	May	Jul	Oct	Mar	May	Jul	Oct			
Lepisoteidae	<i>Atractosteus spatula</i>	alligator gar											
Clupeidae	<i>Brevoortia patronus</i>	gulf menhaden	4.57	20.40	0.12	0.03	4.37	181.27			0.02		
	<i>Dorosoma cepedianum</i>	gizzard shad		0.40				0.23			0.02		0.04
Engraulidae	<i>Anchoa mitchilli</i>	bay anchovy	0.23	0.43	0.67	1.00	0.21	30.87			0.67		5.24
Cyprinodontidae	<i>Adinia xenica</i>	diamond killifish											
	<i>Cyprinodon variegatus</i>	sheepshead minnow		0.27	0.01								
	<i>Fundulus grandis</i>	gulf killifish	0.02		0.09								
	<i>Fundulus pulvereus</i>	bayou killifish		0.10									
	<i>Lucania parva</i>	rainwater killifish	0.02										
Poeciliidae	<i>Poecilia latipinna</i>	sailfin molly											
Atherinidae	<i>Menidia beryllina</i>	Inland silverside	0.05		0.80		0.03						0.11
Sparidae	<i>Lagodon rhomboides</i>	pinfish	0.02		0.11	0.07	0.15	0.13	0.11				
Sciaenidae	<i>Bairdiella chrysoura</i>	silver perch		0.17	0.05	0.12		0.97	0.02	0.01			
	<i>Cynoscion nebulosus</i>	spotted seatrout			0.03	0.04			0.04				
	<i>Leiostomus xanthurus</i>	spot	0.42	0.07	0.04	0.01	1.32	0.10	0.64	0.04			
	<i>Micropogonias undulatus</i>	Atlantic croaker	0.03				0.65						
	<i>Pogonias cromis</i>	black drum	0.02	0.03	0.01	0.05				0.02	0.01		
	<i>Sciaenops ocellatus</i>	red drum				0.03		0.03					
Mugilidae	<i>Mugil cephalus</i>	striped mullet	0.10	0.53	0.20	0.11		0.50					
Gobiidae	<i>Gobiosoma bosc</i>	naked goby					0.03						0.01
Bothidae	<i>Paralichthys lethostigma</i>	southern flounder				0.01		0.03					
Total distance seined (m)			60	30	75	75	60	30	45	90			

the first (canonical) axis (a gradient of physiochemical factors). In addition, a partial CCA was run for each physiochemical variable (remaining variables as covariables) in order to quantify variation among samples that was due to independent additive effects of each variable, and significance ( $p \leq 0.05$ ) was tested using Monte Carlo simulation (199 iterations).

To evaluate overall use of sites by fishes and influence of environmental factors, a cluster analysis of sites identified habitat zones based on mean CPUE (across seasons) for each species in the ordination using PC-ORD (McCune and Mefford 1997). Because winter samples were unevenly distributed among sites in December and March, separate analyses were run to compare results with and without December data. Euclidean distance and Ward's hierarchical method of clustering produced the best definition of clusters, as indicated by low percentage of sequentially added small clusters or individual sites to produce one or two large clusters. The selected number of clusters minimized the loss of information contained in the original data matrix and maximized the number of significant indicator species (see below) of these clusters (hereafter referred to as habitat zones).

Species that best discriminated among habitat zones were determined using Indicator Species Analysis (Dufrene and Legendre 1997) included in PC-ORD. The indicator value for a species is the

product of its relative proportional abundance and its relative frequency of occurrence in samples within a defined group (here, our habitat zones). Indicator species values can range from zero (no indication) to 100 (perfect indication). The latter indicates that species presence identifies a particular group without error (at least for the data used). Monte Carlo simulations (1,000 iterations) tested the null hypothesis that the maximum indicator value for a species was no larger than expected by chance. In addition, the probability of occurrence across gradients for measured environmental variables was calculated for each indicator species using CanoDraw (Smilauer 1992). The best-fit generalized linear model (using a logit link function, and assuming a binomial distribution for species and gamma distribution for environmental variables) was tested ( $p \leq 0.05$ ) for each species to determine environmental values for species optimal or maximal occurrence in each habitat zone.

## Results

Sixty-one fish species (24 families) were sampled in MIMP. Distribution and CPUE of 26 species met criteria for analyses. This represented 21 of 36 species sampled in MI Lake and salt-marsh (Table 1), and 15 of 36 species sampled in MI Slough and other freshwater habitats (Table 2). Across all samples, Shannon diversity was related to temperature ( $r = 0.636$ ,  $p < 0.01$ ) and depth ( $r = 0.087$ ,  $p =$

TABLE 1. Extended.

Lower Brackish Habitat Zone 1 (extended)				Upper Brackish Habitat Zone 2												
E4				E3				E2					E1			
Mar	May	Jul	Oct	Mar	May	Jul	Oct	Dec	Mar	May	Jul	Oct	Mar*	May*	Jul	Oct
23.31			0.03	20.67			0.12						0.04			
			0.01				0.01						0.19	27.41		0.08
0.16		0.07	0.41	0.30	0.08		0.76						0.01			0.02
								0.21	0.07				1.19			0.13
						0.02	0.02	0.63			0.63				0.23	
						0.03				0.08	1.18			0.10	3.30	
	0.03									0.08					0.12	
						0.04	0.03			90.03	0.05			0.07	0.05	
										0.03	0.25			0.03		
0.02				0.10	0.36	0.03	0.03			2.03			0.05	0.07		
0.02	0.87	0.23	0.01	0.03	0.84	0.02	0.05		0.03	0.15			0.01	0.23	1.53	0.01
	0.10				0.54		0.01									
			0.13										0.02			
	2.23	0.17	0.03	3.13	0.18	0.48	0.03		6.90	0.20			2.29	0.20		0.10
0.67	0.23			0.83												
0.07			0.01			0.05			0.03							
			0.01				0.01		0.03							
	1.33	0.07				0.02			0.03							
		0.10				0.05			0.23	0.35	0.45		0.49	0.03	0.05	
0.02		0.07					0.01	0.01						0.07		
45	30	30	75	30	50	60	75	75	30	40	60	90	75	30	60	105

\* Dry area from E1 to FE.

0.05; Table 3 and Fig. 2). Across samples only in MI Lake and salt-marsh, diversity was correlated to temperature ( $r = 0.865$ ,  $p < 0.01$ ). Among these brackish sites, the only significant partial correlation of diversity with any environmental variable was at E2 for salinity ( $r = 0.99$ ,  $p = 0.01$  with December data included;  $r = 0.99$ ,  $p = 0.04$  with December omitted). At E1 and E3, partial correlation of salinity to diversity was at a lower significance level than at E2 (for each  $r = 0.99$ ,  $p = 0.07$ ). This reflected higher salinities in May and July (Table 3) when salt-tolerant killifishes (Cyprinodontidae) entered uplake sites (Table 1, E1-E3). Among samples in MI Slough and the freshwater wetland, diversity was correlated to depth ( $r = 0.768$ ,  $p < 0.01$ ), DO ( $r = 0.255$ ,  $p = 0.05$ ), and salinity ( $r = 0.422$ ,  $p = 0.01$ ). At FE and F1 (each having data for all five sample dates), the only significant relationship with diversity was for partial correlation of DO ( $r = 0.96$ ,  $p = 0.04$ ) at F1, where lowest DO values were measured in July and October (Table 3), when assemblages were reduced to a few species tolerant of anoxia (Table 2).

Results for CCA with and without December (post flood) samples were similar, so December samples are included for completeness. The strongest gradient (CA 1; eigenvalue = 0.565,  $p = 0.01$ ) explained 15.1% of species variation related to salinity, DO, and depth (indicated by environmental

vectors at acute angles to CA 1; Fig. 3). Vectors point toward increasing values for an environmental variable, with a longer vector indicating greater range of variation for a variable along the canonical axes. Vectors point toward increasing values for an environmental variable with a longer vector indicating greater range of variation in species distributions for the variable. Thus, important variables tend to be represented by longer arrows. The more acute the angle between the vector and the canonical axis, the greater the correlation between them. Distribution of sites along this complex primary gradient represented a complete turnover (5 SD) of species, ranging from those having optima in deeper water of the irrigation canal and MI Slough (F2 and F3), and at lower DO and salinity (Fig. 3 left side of CA 1), to those species with optima at intermediate values for variables in diked wetland and scour pool (F1 and FE, Fig. 3 middle of CA 1), and finally to those species in MI Lake with optima in shallower water and at higher DO and salinity (Fig. 3 right side of CA 1).

Correlation of temperature to CA 2, indicated seasonal change in assemblage structure, which explained 4.5% of species distribution. This represented a less-extensive turnover of species (3 SD) than that along the primarily spatial gradient of CA 1 (Fig. 3, bottom to top of each panel). In December and March 1998 (Fig. 3 lower center) after the

TABLE 2. Fishes in families and species that were collected by seining in Mad Island Slough from December 1997 to October 1998. Values are number of individuals  $m^{-1}$  of shoreline seined. Group membership was determined by cluster analysis of sites using these values and those for fishes from Mad Island Lake (Table 1).

Family	Species	Common	Freshwater Wetland Habitat Zone 3			
			FE			
			Dec <sup>c</sup>	Mar <sup>o*</sup>	Jul <sup>*</sup>	Oct <sup>*</sup>
Lepisosteidae	<i>Atractosteus spatula</i>	alligator gar				
Clupeidae	<i>Dorosoma cepedianum</i>	gizzard shad				
Cyprinodontidae	<i>Adinia xenica</i>	diamond killifish	3.00			
	<i>Cyprinodon variegatus</i>	sheepshead minnow	1.50		3.50	4.50
	<i>Fundulus grandis</i>	gulf killifish	18.50			
	<i>Fundulus pulvereus</i>	bayou killifish	3.00			13.00
	<i>Lucania parva</i>	rainwater killifish	0.50			69.00
Poeciliidae	<i>Gambusia affinis</i>	mosquitofish	1.50	0.50	25.00	96.50
	<i>Poecilia latipinna</i>	sailfin molly	16.50			20.00
Atherinidae	<i>Menidia beryllina</i>	inland silverside			11.50	13.50
Centrarchidae	<i>Lepomis macrochirus</i>	bluegill				
	<i>Lepomis megalotis</i>	longear sunfish				
	<i>Lepomis symmetricus</i>	bantam sunfish				
	<i>Pomoxis annularis</i>	white crappie			0.50	
Mugilidae	<i>Mugil cephalus</i>	striped mullet				
	Total distance seined (m)		5	5	5	5

<sup>c</sup> culvert between FE and F1 closed.

<sup>o</sup> culvert open.

\* dry area from E1 to FE.

October 1997 flood, shallow upper reaches of MI Lake and salt marsh (E1–E3) as well as freshwater MI Slough, scour pool, and diked wetland (F3, FE, F1, F1-a, respectively) were nearly optimal for killifish (Cyprinodontidae). In March, sites closer to the intracoastal canal (E4–E6, Fig. 3 lower right) were nearly optimal for Gulf menhaden, croaker (Sciaenidae), and naked goby (*Gobiosoma bosc*). In

May and July (Fig. 3 upper left), the irrigation canal and MI Slough (F2 and F3, respectively) were nearly optimal for sunfishes (*Lepomis*) and white crappie (*Pomoxis annularis*), while shallower freshwater sites (F1 and FE) were nearly optimal for livebearers (Poeciliidae) and inland silverside (*Menidia beryllina*). The warmest temperatures and highest DO values for our samples in MI Lake occurred during May in the shallow salt marsh (Table 3, E1–E3), and were nearly optimal for silver perch (*Bairdiella chrysoura*), red drum (*Sciaenops ocellatus*), and pinfish (*Lagodon rhomboides*) (Fig. 3 upper right). In October, temperature and DO were low in shallower freshwater sites (FE, F1, F1-a, Fig. 3 left; Table 3) nearly optimal for killifish and livebearers, while sites in MI Lake were nearly optimal for inland silverside, spotted seatrout (*Cynoscion nebulosus*), bay anchovy, and red drum (Fig. 3 right).

Overall, measured environmental variables explained 21.8% of spatial and temporal variation in assemblage composition (canonical eigenvalues = 0.818; total eigenvalues = 3.747). Partial CCA showed variation was correlated with additive effects of salinity (5.0%,  $p = 0.01$ ), temperature (4.2%,  $p = 0.02$ ), and DO (3.7%,  $p = 0.04$ ), as well as interactions among environmental variables (7.6%), but not significantly with depth (1.4%,  $p = 0.75$ ). Ranges for total species variation in separate CCA of freshwater (eigenvalues = 1.985) and brackish samples (eigenvalues = 2.241) were smaller than for all samples combined but a higher percentage of species variation was correlated with en-

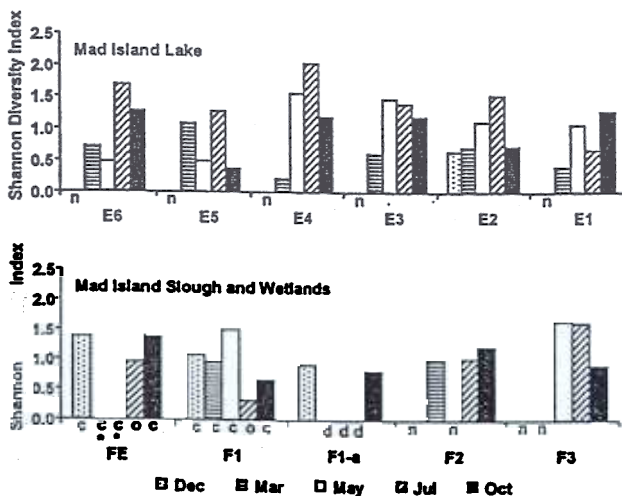


Fig. 2. Shannon diversity indices for fishes seine samples from December 1997 to October 1998 in brackish estuarine habitats (E) and freshwater habitats (F) of Mad Island Marsh Preserve. Site codes follow Fig. 1, and Tables 1 and 2. Lowercase letters indicate months when no sample was collected (n), when the water-control structure was closed (c) or open (o), and when F1-a was dry (d). Asterisks indicate when the area from E1 to FE was dry.

TABLE 2. Extended.

Freshwater Wetland Habitat Zone 3 (extended)							Freshwater Channelized Habitat Zone 4					
F1					F1-a		F2			F3		
Dec <sup>a</sup>	Mar <sup>a</sup>	May <sup>a</sup>	Jul <sup>a</sup>	Oct <sup>a</sup>	Dec	Oct	May	Jul	Oct	Mar	Jul	Oct
					14.50		1.00	3.25		2.40	0.20	0.80
	1.60	16.00	1.20		309.00	0.50		1.88	2.00			
		1.80			44.50							
3.60		1.00			15.00	1.00			0.88			
10.80	5.80	3.00	18.40	9.60	12.00	19.00	0.88	2.75	51.00			3.20
0.60	0.40	3.00		16.20	10.50	7.50	0.63	9.50	40.38			
	0.60	1.40										
	0.20	0.20						1.25		0.20		8.80
0.60		0.20						0.13		0.20	0.60	3.20
		2.20	0.40				0.38	2.38	1.63			
								0.13		0.40	0.40	0.40
35	45	40	5	35	5	5	30	30	30	30	30	30

environmental variables in the separate analysis for brackish sites. For brackish MI Lake (E1–E6), canonical axes explained 32.5% ( $p = 0.01$ ) of species variation, which was primarily correlated with additive effects of depth (11.5%,  $p = 0.01$ ) and DO (9.1%,  $p = 0.02$ ), but not significantly related to temperature (5.5%,  $p = 0.80$ ) or salinity (3.6%,  $p = 0.39$ ), and with the remaining correlated with interactions (2.8%). For freshwater scour pool, diked wetland, irrigation canal, and slough (FE, F1–F3) canonical axes explained 24.1% of species variation but significance was low for temperature (9.7%,  $p = 0.07$ ), salinity (6.6%,  $p = 0.33$ ), DO (4%,  $p = 0.64$ ), and depth (3.4%,  $p = 0.81$ ).

As in the CCA, cluster analyses were similar with and without December samples, and results using December samples are presented. Four habitat zones were identified along the spatial gradient from intracoastal canal and lower MI Lake (Zone 1, E5 and E6), to upper MI Lake (Zone 2, E1–E4), to freshwater wetlands (Zone 3, FE, F1, and F1-a), and to MI Slough and the irrigation canal (Zone 4, F2 and F3). The superscript on a species label in the CCA plot (Fig. 3) corresponds to the habitat zone indicated by a species. Probability of occurrence plotted along gradients of measured environmental variables showed significant optima for indicator species of the lower brackish zone (Fig. 3 right side, Zone 1). These species were small-bodied, and found along shallow (< 0.5 m) shorelines, or across wide ranges of salinity and DO in our samples but were most likely to occur at salinity > 15‰ and DO 7–10 mg l<sup>-1</sup> (Fig. 4). Two indicators of the upper brackish zone (Fig. 3, Zone 2) were estuarine dependent, pinfish and spot (*Leiostomus xanthurus*), and were most likely to occur at salinity 10–20‰, DO > 10 mg l<sup>-1</sup>, and depth < 0.5 m (Fig. 4). Indicators of the freshwater wetland zone (Fig. 3, Zone 3) included mosquitofish, which were most likely to occur at lower salinity (< 5‰) and DO (< 5 mg l<sup>-1</sup>), and three euryhaline species, bayou killifish (*Fundulus pulvereus*), sheepshead minnow (*Cyprinodon variegatus*), and sailfin molly (*Poecilia latipinna*), which were most likely to occur at DO < 5 mg l<sup>-1</sup> and depth > 1 m (Fig. 4). In the freshwater channelized zone (Fig. 3, Zone 4), five indicator species, including three sunfish species (*Lepomis macrochirus*, *L. megalotis*, *L. symmetricus*), white crappie, and gizzard shad (*Dorosoma cepedianum*), occurred across a wide range of depth and DO, but were most likely to occur at salinity < 5‰, DO < 5 mg l<sup>-1</sup>, and depth > 1.5 m (Fig. 4).

#### Discussion

As expected, salinity had the strongest association with fish assemblages along a spatial gradient from mesohaline MI Lake and fringing salt marsh to oligohaline habitats of the freshwater diked wetland and MI Slough. A study of Chesapeake and Delaware Bays using multivariate analysis of presence/absence data for fish and invertebrates determined biologically-based estuarine salinity zones useful for long-term monitoring of estuarine ecosystem health (Bulger et al. 1993). Our analyses were based on seine CPUE across seasonal samples, and identified indicator species that had maximal occurrence (in our samples) within three salinity zones (< 5‰, 10–20‰, and > 20‰). These corresponded to zones 0–4‰, 11–18‰, and 16–

TABLE 3. Values of environmental variables measured for fish samples at sites in Mad Island Marsh Preserve from December 1997 to October 1998.

System/Site	Month	Temp (°C)	Sal (‰)	DO (mg l <sup>-1</sup> )	Depth (m)
<b>Brackish Habitats</b>					
E6	Mar	20.00	12.0	7.17	0.53
	May	29.05	13.5	5.70	0.50
	Jul	32.40	29.4	4.95	0.41
	Oct	28.50	12.8	6.50	0.74
E5	Mar	19.74	12.0	6.55	0.30
	May	31.51	12.5	7.32	0.40
	Jul	28.00	12.0	3.67	0.20
E4	Mar	19.10	12.0	7.01	0.27
	May	34.67	12.1	9.66	0.40
	Jul	29.30	13.9	4.51	0.21
E3	Mar	18.88	3.6	7.10	0.29
	May	33.26	13.5	12.85	0.40
	Jul	30.10	15.1	5.02	0.21
E2	Mar	18.88	3.5	7.52	0.25
	May	32.17	14.9	9.86	0.30
	Jul	31.50	18.2	5.40	0.17
E1	Mar <sup>d</sup>	16.48	3.7	7.85	0.30
	May <sup>d</sup>	36.08	15.0	12.75	0.30
	Jul	37.20	21.1	2.85	0.14
	Oct	30.30	9.7	9.33	0.54
<b>Freshwater Habitats</b>					
FE	Dec <sup>c</sup>	13.50	0.3	4.50	1.00
	Mar <sup>c*</sup>	13.00	0.3	3.20	1.00
	May <sup>c*</sup>	28.09	0.0	4.82	0.40
	Jul <sup>c</sup>	28.70	0.4	7.72	0.40
F1	Dec <sup>c</sup>	27.20	0.2	0.20	1.00
	Mar <sup>c</sup>	13.50	0.3	4.50	0.50
	May <sup>c</sup>	15.30	0.0	5.30	1.50
	Jul <sup>c</sup>	28.15	0.9	5.41	0.15
F1-a	Dec <sup>c</sup>	28.70	0.4	0.50	0.25
	Oct <sup>c</sup>	27.30	0.2	2.40	1.50
	Dec	14.00	0.0	4.50	0.50
F2	Oct	27.50	0.6	2.32	0.50
	May	28.83	0.0	1.07	2.00
F3	Jul	30.10	0.3	1.30	2.00
	Oct	28.40	0.3	4.34	0.50
	Mar	15.00	0.0	4.00	1.00
	Jul	31.70	0.3	2.98	0.45
Oct	29.40	0.2	5.15	1.00	

<sup>c</sup> culvert between FE and F1 closed.

<sup>c\*</sup> culvert open.

<sup>d</sup> dry area from E1 to FE.

27% identified for Chesapeake and Delaware Bays (Bulger et al. 1993). As previously suggested (Bulger et al. 1993), gradients for variables other than salinity further differentiated our assemblages. Occurrence of species along combined gradients of DO, depth, and salinity delineated four habitat zones. Salinity and DO explained the greatest percentage of variation in overall species distribution across these zones, and is consistent with findings from studies of other North American coastal salt

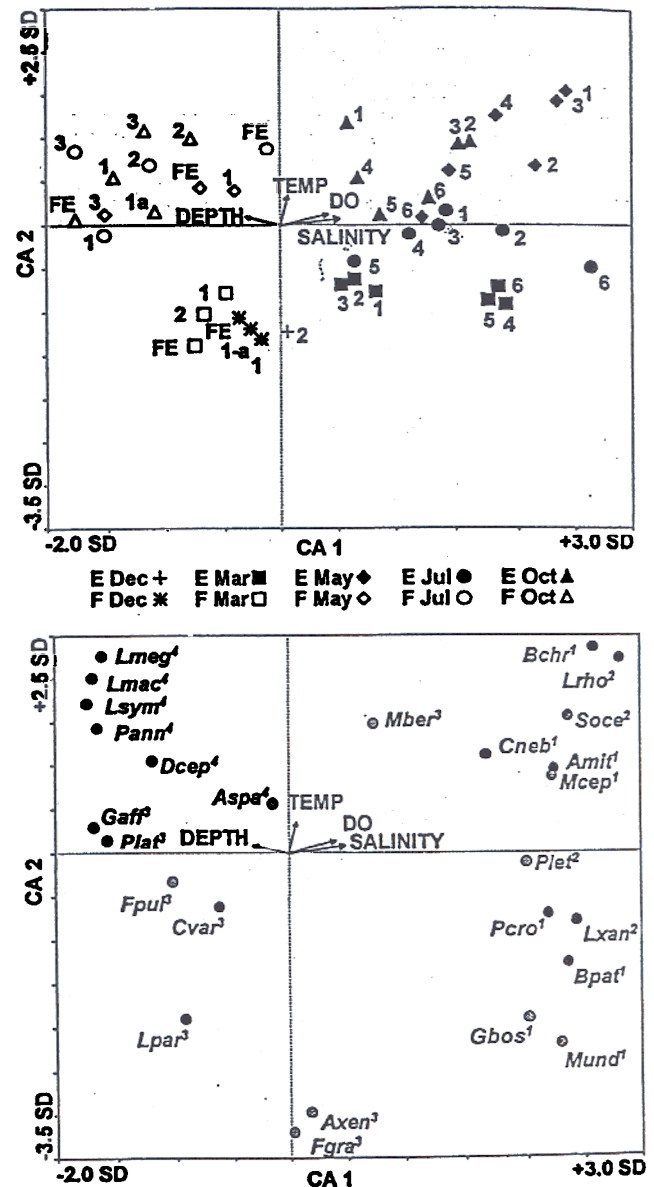


Fig. 3. Plot of sample scores (symbols in upper panel) and species centroids (circles in lower panel) on the first two (canonical) axes (CA1, CA2) for the correspondence analysis of fishes in seine samples from brackish estuarine habitats (E) and freshwater habitats (F) of Mad Island Marsh Preserve in December 1997 (E = +, F = \*) and March (E = ■, F = □), May (E = ◆, F = ◇), July (E = ●, F = ○), and October (E = ▲, F = △) of 1998. Arrows indicate direction of increasing value for environmental variables. More acute angles between arrow and axis indicate stronger correlation of variables with the axis. Numbers in upper panel correspond to site codes in Fig. 1. In the lower panel, centroids indicate approximate centers of species' distributions relative to environmental variables. Species codes are the first letter of the genus and first three letters of the specific name. Superscripts identify the habitat zone (Tables 1 and 2) that was best indicated by a species' occurrence and abundance, and centroids indicate significant (filled circle) and nonsignificant (shaded circle) indicator species.



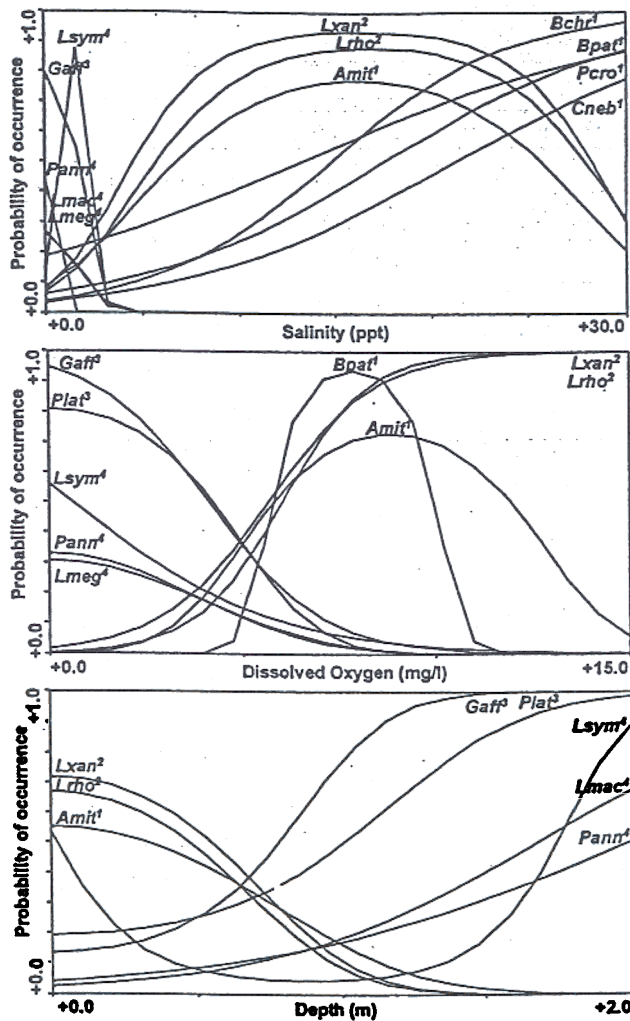


Fig. 4. Probability of occurrence for indicator species that had significant relationships to measured gradients for salinity (upper panel), DO (middle panel), and depth (lower panel) in samples of fishes at Mad Island Marsh Preserve. Species are those that indicated habitat zones identified by cluster analysis of fishes. Labels indicate location of maximum probability of occurrence for each species along gradients. Codes for species labels are those in Fig. 3.

marshes (Keup and Bayless 1964; Parrish and Yerger 1974; Weinstein et al. 1980; Peterson and Ross 1991).

Although transition between freshwater and marine faunas is bound to occur, the temporal and spatial scale of the transition will vary depending on geography, topography, and composition of regional faunas. Within the relatively small spatial scale of the MIMP (ca. 6 km from F3 to E6), a considerable turnover from freshwater to marine faunas was observed across habitat zones. The only species in seine samples occurring at each end of the salinity gradient were gizzard shad, sheepshead minnow, bayou killifish, and striped mullet. A

range of temporal dynamics characterized assemblages across this physiochemical ecotone. Overall, assemblages were most similar when saltwedge intrusion was minimal (December 1997 and March 1998, following flood conditions of October 1997), and were least similar when it was maximal (July 1998). Overall diversity was positively correlated with temperature and depth, both of which tended to be positively correlated with seasonal changes in salinity in the upper brackish zone and with DO and salinity in the freshwater zones. In the lower brackish zone, salinity was less variable and diversity declined with seasonal dominance by gulf menhaden and bay anchovy. In freshwater zones, diversity was positively correlated with depth, DO, and salinity. In a study of a similar coastal salt marsh on the Gulf coast of Mississippi, Peterson and Ross (1991) found that tidal freshwater and oligohaline habitats had greater fish diversity than a mesohaline site located on the edge of Biloxi Bay. They concluded that species richness at low-salinity coastal sites was enhanced by the presence of freshwater species, as well as species which tolerate low salinity, and euryhaline marine species with broad salinity tolerance.

Citing findings by Hackney et al. (1976), Peterson and Ross (1991) also suggested that habitats experiencing frequent and large fluctuations in salinity also might support fewer fish species. For example, if sites are predominantly freshwater, then downstream mesohaline sites would have lower species richness if obligate freshwater species are excluded, whereas euryhaline marine species would not be excluded from upstream sites. Alternatively, if sites are predominantly mesohaline, then lowest species richness would be associated with upstream sites if they experience great environmental fluctuations. In our study, additive and synergistic effects of salinity, depth, and DO on species richness and diversity similarly depended on site location and dynamics of environmental variation across the landscape. Variation among assemblages in the freshwater zones was related to species tolerances or physiological optima along gradients of DO and depth; among these sites more species and families occurred at the most inland freshwater site (MI Slough), which was continuously connected to MI Slough. The lake contained a range of primary-division freshwater fishes (Ostariophysi) including Cyprinidae, Catastomidae, and Ictaluridae (unpublished data this study), as well as marine species (striped mullet) that penetrate Gulf coast rivers hundreds of kilometers inland (Riggs 1957). The lake's upper brackish zone contained euryhaline marine species, pinfish, sciaenids, striped mullet, and southern flounder (*Paralichthys lethostigma*), as well as

freshwater species that tolerate low salinity, alligator gar, and gizzard shad. No species in MI Lake and its fringing salt marsh had maximal occurrence at salinity 5–10‰. Indicator species of the upper brackish zone (where salinity fluctuated across this range) had optima > 10‰. Our results are similar to those for summer fish assemblages across longer reaches (up to 150 km) of lower Chesapeake Bay tributaries (Wagner 1999), where a species-richness minimum occurred at 8–10‰, across a range of 0–18‰. In contrast, Peterson and Ross (1991) sampling seasonally at three sites across a longer distance (17 km) but along a similar salinity gradient to that in MIMP, reported no significant relationship between combined freshwater-estuarine/marine species richness and salinity at each site. They related this to compensatory shifts in assemblage structure from primarily freshwater to increasing estuarine/marine species richness with increasing salinity.

Aquatic macrophytes provide cover and a source of invertebrate prey for salt marsh fishes (Rozas and Odum 1987b, 1988). Emergent shoreline macrophytes (e.g., *Spartina* spp., *Typha latifolia*) and submergent forms (e.g., *Ruppia maritima*, *Chara* sp.) occurred in MIMP, although dominant plant species varied over the topographic/salinity gradient. In freshwater tidal salt marshes in Virginia, fish abundance was greater at low-order sites, apparently associated with greater macrophyte density (Rozas and Odum 1987a). Temporal as well as spatial patterns determine how a given habitat feature influences biota. For example, greater amplitude and duration of water-level fluctuation in a marsh should lead to extended periods of emergent macrophyte production, followed by periods of hypoxia associated with plant decay during reflooding. In tropical-river floodplains, this cycle is driven by seasonal flood pulses, followed by fish emigration and mortality (Howard-Williams and Junk 1976; Winemiller 1996). In shallow MI Lake, DO was sufficiently high during most of our sampling to support even those species most sensitive to hypoxia. In contrast, low DO (< 3 mg l<sup>-1</sup>) was recorded for several samples in the freshwater channelized zone and in the October 1998 sample in the freshwater wetland zone, as macrophyte decay proceeded. Dominating those samples were small-bodied fishes (killifishes, livebearers) that efficiently use aquatic-surface respiration as compensation for hypoxic conditions (Lewis 1970). Impoundment of freshwater runoff in the diked wetland when the culvert was closed (September to July) likely increased the amplitude and duration of normal flood conditions, and consequently decreased habitat quality for organisms sensitive to aquatic hypoxia. This also was illustrated in July,

after the culvert was open to drain the diked wetland, and more fishes were present in the scour pool (DO = 7.7 mg l<sup>-1</sup>) than in the residual wetland (DO = 0.5 mg l<sup>-1</sup>).

Despite the fact that shallow coastal salt marshes serve as important nursery habitats for numerous marine-estuarine dependent fishes and invertebrates, high predation mortality can occur when water level declines. The abundant small fishes of coastal salt marshes provide a food resource for alligators, wading birds, and piscivorous fishes, such as gar and red drum. Periodic concentrations of small fishes, such as those we encountered in the ephemeral wetland pool, can be an important resource for nesting piscivorous birds (Kahl 1964; Kushlan 1976; Willard 1977; Browder 1978). Such conditions apparently favored small-bodied cyprinodontiform fishes with an opportunistic life history strategy that allows them to quickly increase population sizes and recolonize disturbed habitats (Winemiller and Rose 1992). Killifishes and livebearers (Poeciliidae) dominated all freshwater sites, except the irrigation canal. In our study, 7 killifish and livebearer species were collected in the ephemeral pool in December 1997 (after the October 1997 flood), and 4 of these were again collected in October 1998, despite the fact that it had dried and refilled in the interim. Even in deeper habitats of the channelized freshwater zone, these small fishes were abundant in shallow margins where they could probably consume zooplankton and smaller macroinvertebrates. May and July samples in MI Slough contained 6 and 8 species respectively, but only 5 in October. Five species present in the earlier samples, most of them relatively larger-bodied (alligator gar, gizzard shad, and three sunfishes), were absent in the latter samples when water was shallower. In the irrigation canal, Bayou killifish, another small-bodied euryhaline species that moves inland with rising floodwaters, was sampled only in October.

Movement of fishes in the lower, brackish lake zone shifted assemblage composition, but this change was uncorrelated with salinity. Large schools of marine fishes, such as juvenile gulf menhaden, seasonally migrate into and out of shallow estuarine habitats, and likely influenced correlation of measured environmental variables to assemblage composition and diversity. Although not as numerous other marine species moved in and out of MI Lake on variable time scales. For example, large piscivorous red drum and spotted seatrout entered MI Lake from the bay in pursuit of abundant shrimp, crabs, mullet, and small fishes (Akin unpublished data). Densities of red drum were highest in October when water temperature was moderate and prey were near their peak densities

after the summer growing season (Akin unpublished data, Dumesnil personal communication).

Synergism of environmental variability and habitat connectivity undoubtedly influences spatiotemporal assemblage patterns (Gelwick et al. 1997; Johnson et al. 1997; Toth et al. 1998). Reduction of aquatic habitats that periodically concentrates fishes, can increase their competition for resources (Lowe-McConnell 1987; Winemiller 1989) and facilitate predation by wading birds (Kushlan 1976; Browder 1978). During low-water periods in the freshwater wetland zone, rooting by feral hogs (*Sus scrofa*) disturbed the damp soil and remaining vegetation, and wading birds were common. The perennial scour pool below the water-control culvert retained fishes that might otherwise have moved toward the upper brackish zone as water level receded across the fringing salt marsh. For example, a juvenile tarpon (*Megalops atlanticus*) collected in the diked wetland in October, and fat sleepers (*Dormitator maculatus*) collected in the scour pool and diked wetland in July, indicated use of the freshwater zones by fishes from brackish zones. However, even when water level would otherwise have allowed movement of fishes between these zones, the nearly year-round (September to July) closure of the culvert restricted fish movement. During years without pervasive flooding to connect habitats, water level fluctuations at MIMP were influenced by management primarily for production of rice and waterfowl forage (i.e., draining, burning, irrigation, and mowing). Alternative scenarios for the management of surface hydrology and vegetation growth at MIMP and other coastal marshes could be explored to increase connectivity among wetlands, and synchronize water-level manipulations to natural flood regimes in favor of enhanced aquatic, as well as terrestrial, biodiversity.

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#### SOURCE OF UNPUBLISHED MATERIALS

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