



# Seasonal and spatial variations in fish and macrocrustacean assemblage structure in Mad Island Marsh estuary, Texas

S. Akin, K.O. Winemiller\*, F.P. Gelwick

*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA*

Received 20 May 2002; accepted 23 August 2002

## Abstract

Fish and macrocrustacean assemblage structure was analyzed along an estuarine gradient at Mad Island Marsh (MIM), Matagorda Bay, TX, during March 1998–August 1999. Eight estuarine-dependent fish species accounted for 94% of the individual fishes collected, and three species accounted for 96% of macrocrustacean abundance. Consistent with evidence from other Gulf of Mexico estuarine studies, species richness and abundance were highest during late spring and summer, and lowest during winter and early spring. Sites near the bay supported the most individuals and species. Associations between fish abundance and environmental variables were examined with canonical correspondence analysis. The dominant gradient was associated with water depth and distance from the bay. The secondary gradient reflected seasonal variation and was associated with temperature, salinity, dissolved oxygen, and vegetation cover. At the scales examined, estuarine biota responded to seasonal variation more than spatial variation. Estuarine-dependent species dominated the fauna and were common throughout the open waters of the shallow lake during winter–early spring when water temperature and salinity were low and dissolved oxygen high. During summer–early fall, sub-optimal environmental conditions (high temperature, low DO) in upper reaches accounted for strong spatial variation in assemblage composition. Small estuarine-resident fishes and the blue crab (*Callinectes sapidus*) were common in warm, shallow, vegetated inland sites during summer–fall. Estuarine-dependent species were common at deeper, more saline locations near the bay during this period. During summer, freshwater species, such as gizzard shad (*Dorosoma cepedianum*) and gars (*Lepisosteus* spp.), were positively associated with water depth and proximity to the bay. The distribution and abundance of fishes in MIM appear to result from the combined effects of endogenous, seasonal patterns of reproduction and migration operating on large spatial scales, and species-specific response to local environmental variation.

© 2003 Elsevier Science B.V. All rights reserved.

**Keywords:** aquatic vegetation; biotic community; canonical correspondence analysis; environmental gradient; estuary; Gulf of Mexico; salinity; species diversity

## 1. Introduction

Estuarine systems undergo short-term, seasonal, and inter-annual changes in physical parameters (Livingston, 1976). Among these, salinity and temperature are most frequently cited as having the strongest influence on the structure of aquatic assemblages (Allen & Horn, 1975; Araujo, Bailey, & Williams, 1999; Hoff & Ibara, 1977; Loneragan, Potter, Lenanton, & Caputi, 1986; Loneragan, Potter, Lenanton, & Caputi, 1987; Marshall

& Elliot, 1998; Peterson & Ross, 1991; Weinstein, Weiss, & Walters, 1980). Natural salinity gradients in estuaries may represent a continuum of physiological stress for aquatic organisms (Peterson & Ross, 1991). Dissolved oxygen (DO) concentration influences species distributions (Maes, Van Damme, Taillieu, & Ollevier, 1998; Rozas & Hackney, 1984; Whitfield, 1999), including effects on predator–prey and competitive interactions (Breitburg, Lohor, Pecay, & Gerstein, 1997). Water depth influences fish and invertebrate distribution and abundance. Water level was strongly associated with seasonal changes in the density of brown shrimp (*Farfantepenaeus aztecus*) in an estuary on the northern Gulf of Mexico (Zimmerman & Minello, 1984). Other

\* Corresponding author.

E-mail address: [k-winemiller@tamu.edu](mailto:k-winemiller@tamu.edu) (K.O. Winemiller).

physical factors, such as distance to the estuary mouth, tidal pass obstructions, and current velocity, can affect estuarine populations (Loneragan et al., 1987; Loneragan, Potter, & Lenanton, 1989).

Biotic factors have obvious potential to influence community patterns (Barry, Yoklavich, Cailliet, Ambrose, & Antrim, 1996). Rozas and Hackney (1984) concluded that Atlantic croaker (*Micropogonias undulatus*), bay anchovy (*Anchoa mitchilli*), mummichog (*Fundulus heteroclitus*), grass shrimp (*Palaemonetes pugio*) and other common estuarine species do not select habitats primarily on the basis of salinity, but instead select areas associated with abundant food and low densities of competitors and predators. Kneib (1997a) argued that biotic factors, such as reproduction, food limitation, and predation, can be important determinants of recruitment in estuaries. In addition, aquatic vegetation can influence species interactions by creating structurally complex habitats (Levin, Petrik, & Malone, 1997; Rozas & Odum, 1987). Abundance of certain fish species is strongly associated with vegetation (Killgore, Morgan, & Rybicki, 1989; Rozas & Minello, 1998; West & King, 1996; Zimmerman & Minello, 1984), and grass shrimp abundance increased in marshes when artificial submerged vegetation was added (Rozas & Odum, 1987).

Local population abundance is influenced by response to changes in local environmental conditions as well as large-scale seasonal migrations of immature life stages (Blaber & Blaber, 1980; Drake & Arias, 1991; Potter, Claridge, & Warwick, 1986; Subrahmanyam & Coultas, 1980). Potter et al. (1986) and Drake and Arias (1991) concluded that estuarine fish communities change primarily in response to extreme environmental conditions. Yet, many estuarine species show regular, seasonal patterns of occurrence inconsistent with this view, and seasonally resident marine species are common in virtually all estuarine communities (Dahlberg & Odum, 1970; McErlean, O'Connor, Mihursky, & Gibson, 1973; Moore & Reis, 1983; Peterson & Ross, 1991; Potter et al., 1986; Rogers, Targett, & Von Sant, 1984; Rozas & Hackney, 1984; Yoklavich, Cailliet, Barry, Ambrose, & Antrim, 1991; Garcia, Vieira, & Winemiller, 2001). Day, Hall, Kemp, and Yáñez-Arancibia (1989) classified estuarine fishes into three categories based on life history patterns: estuarine residents (complete their life cycle in the estuary), estuarine-dependent (spawn offshore and larvae and/or juveniles move thorough passes into estuaries where they reside for variable periods), and occasional visitors (usually adults). In addition, freshwater fishes typically inhabit upper reaches of estuaries, but some move to lower reaches depending on their salinity tolerance (Dando, 1984; Loneragan et al., 1989).

Our study investigates relationships between physical variables and spatiotemporal variation in fish and

macrocrustacean assemblage structure in Mad Island Marsh (MIM), a shallow estuary that enters Matagorda Bay in the northern Gulf of Mexico. During 1997, Gelwick, Akin, Arrington, and Winemiller (2001) investigated fish assemblage structure in MIM across a gradient between a freshwater marsh and polyhaline tidal bayou. Using two collecting methods, the present study focuses on both fish and macrocrustacean assemblage structure in the lower, mesohaline reach of MIM over a longer time interval (March 1998–August 1999). Our objectives are twofold: to identify the degree to which variation in the distribution and abundance of fishes and invertebrates are related to spatial and temporal variations in environmental variables along the longitudinal estuarine gradient; and to determine if species richness and diversity are primarily associated with these local-scale factors, or if they more likely influenced by seasonal migrations linked to endogenous cycles or macro-scale environmental variation.

## 2. Materials and methods

### 2.1. Study area

MIM is located on the northwestern coast of the Gulf of Mexico, in Matagorda Bay, Texas (Fig. 1). Aquatic habitats include freshwater marshes (Mad Island Slough and diked wetlands), a mesohaline lake and surrounding salt marsh, a polyhaline tidal bayou, and the main body of the bay. Dominant vegetation of the marsh includes smooth cordgrass (*Spartina alterniflora*) and gulf cordgrass (*Spartina spartinae*). Submergent aquatic vegetation, such as widgeon grass (*Ruppia maritima*) and *Chara* spp., occurs seasonally and is especially dominant at the upper portion of the mesohaline region (e.g. sites 1–3; Fig. 1). Aquatic habitats of the marsh range in depth from 0.1 to 0.75 m. Substrate of sites 1 through 5 is a mud–sand mixture covered by an approximately 5-cm layer of decomposing vegetation. Substrate at site 6 consists of mud, sand, and crushed oyster shell. Small patches of oyster reef occur at sites 4 and 5.

### 2.2. Sampling protocol

Samples were collected every 2 months between March 1998 and August 1999 at six sites located along the longitudinal estuarine gradient. Five sites (1–5) were located within a brackish lake (Fig. 1). Site 6 was a tidal bayou connecting the lake to the intracoastal waterway and main body of Matagorda Bay.

Fishes and invertebrates were collected using a bag seine (6 m × 1.2 m, 4.5 mm mesh, bag 1.2 m × 1.2 m) mostly for small organisms and monofilament experimental gillnets (38 m, five panels of 25, 38, 50, 64, and 76 mm mesh) for larger organisms. Seine hauls were

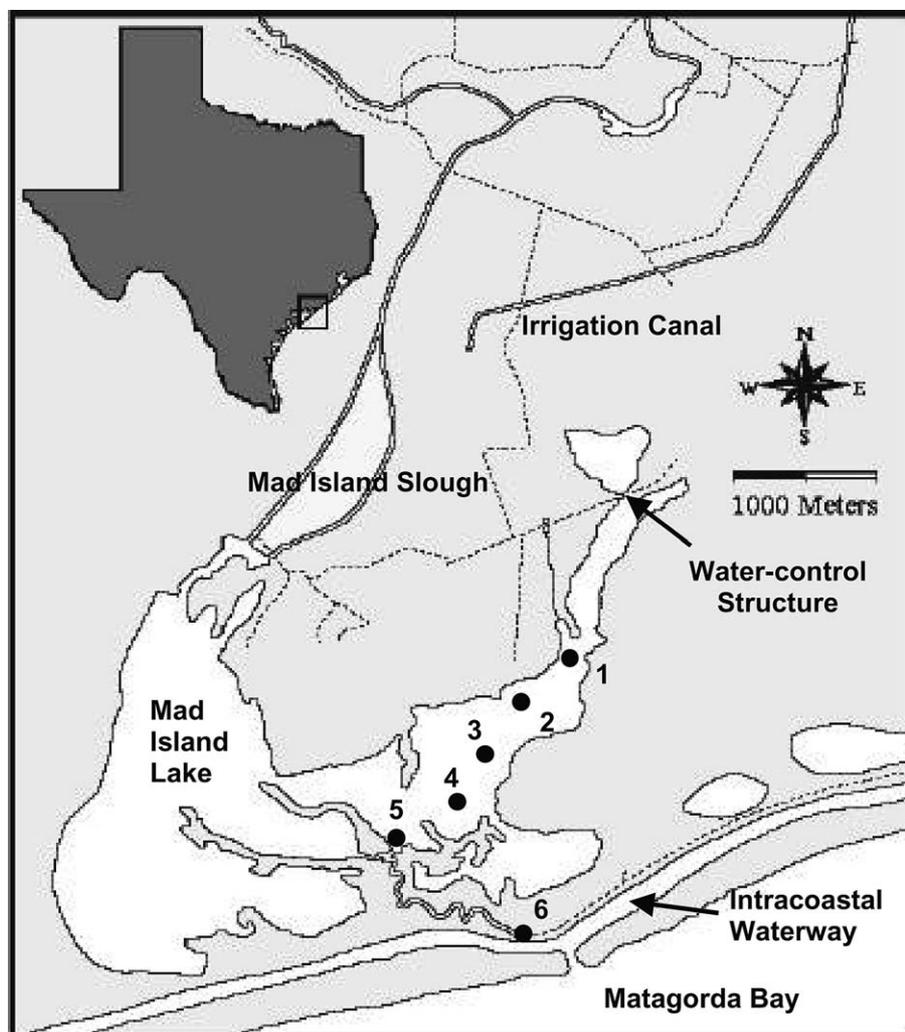


Fig. 1. Map of MIM on the Texas Gulf of Mexico coast with locations of survey sites.

perpendicular to the shoreline (from deeper water to shore). Seining continued at each site until no new species were encountered in three consecutive hauls. To calculate species catch per unit effort (CPUE), distances seined and numbers of hauls were recorded. Gillnets were deployed at sites within 1 h of one another, and remained in place from ca. 0830 to 2130 h. Duration of each gillnet set was recorded, and catch data were recorded as number of individuals captured per hour. Captured fish and invertebrates were anesthetized in MS-222 then fixed in 10% formalin in the field. In the laboratory, samples were sorted, and organisms were identified to species, measured (SL to nearest 0.1 mm), and weighed (to nearest 0.1 g).

Prior to seining each site (typically 0900–1300 h), water depth (to nearest 0.01 m), temperature ( $^{\circ}\text{C}$ ), dissolved oxygen (DO, mg/l), and salinity were measured with a Hydrolab Datasonde or YSI Model 85. These measurements characterized among-site variation at the time of sampling rather than diel extremes, and

interpretations of biotic associations with environmental parameters are interpreted in this context. In doing so, it is acknowledged that conditions for variable periods prior to sampling can influence biota. Percent areal coverage of aquatic macrophytes was estimated visually at each site.

### 2.3. Data analysis

Taxon numerical abundance for seine and gillnet data was standardized to CPUE (abundance per 100 m seined, and abundance per gillnet hour). Survey site and period mean values for Shannon–Wiener diversity index ( $H'$ ), species richness ( $S$ ), and species evenness ( $J = H'/H_{\max}$ ) were calculated based on species CPUE. Spatial and temporal variations in environmental variables and fish/macrocrustacean abundance (log-transformed CPUE), diversity, richness, and evenness were analyzed using two-way ANOVA. Interactions between sites and months for each variable were tested

using Tukey's 1-degree-of-freedom test (Winer, 1962). Only three variables (temperature, vegetation cover, and CPUE for gillnet) indicated significant month  $\times$  site interactions, hence these variables were not tested with ANOVA. When a significant difference for main effects was detected ( $P < 0.05$ ), Student–Newman–Keuls (SNK) multiple comparison test was used to test for significant mean differences. In almost all cases, environmental and biological data met assumptions of normality (Kolmogorov–Smirnov test) and homogeneity of variances (Cochran test). Variables that did not meet these assumptions were tested using the Kruskal–Wallis test. Spearman's rank correlation was used to examine simple relationships between environmental variables and log-transformed CPUE and diversity indices ( $H'$ ,  $S$ ,  $J$ ).

Associations between species CPUE and environmental variables were examined with canonical correspondence analysis (CCA) using CANOCO. CCA is a weighted averaging method that directly relates community data to environmental variables by constraining species ordination to a pattern that correlates maximally with environmental variables. To minimize effects of rare species, CCA only included species with CPUE  $\geq 1\%$  of the total based on all species and samples collected in both the seine and gillnets. To eliminate effects of sampling gear (seine and gillnets) on CCA, the assemblage matrix consisting of rows (sites) and columns (taxa) was transformed into a matrix in which each gear had equal weight following the method described in Weaver and Magnuson (1993). Correlations between environmental variables (temperature, salinity, DO, vegetative cover, and water depth) and CCA axes were used to assess each variable's contribution (Rakocinski, Lyczkowski-Shultz, & Richardson, 1996). Statistical significance of the contribution of each variable to each CCA axis was tested using Monte Carlo simulation and the forward selection option in CANOCO.

### 3. Results

#### 3.1. Environmental variation

During the study period, water temperature ranged from 16.5°C (March 1998 at site 1) to 37.2°C (July 1998 at site 1) and peaked during late spring and summer both years (Fig. 2). Lowest (18.8°C) and highest (32.7°C) mean temperatures were recorded in 1998 during March and May, respectively. Spatial variation in temperature was more pronounced during late spring–summer compared with other periods (Fig. 2). Temperature tended to decrease towards the lower reaches of the estuary.

Salinity ranged from 3.5 (March 1998 at site 2) to 29.4 (July 1998 at site 6) and was correlated with

temperature ( $r = 0.71$ ,  $P < 0.01$ ). Mean salinity differed significantly among months ( $H = 40.99$ ,  $P < 0.0001$ ), with highest (18.3) and lowest (5.2) mean values in July 1998 and December 1998, respectively (Fig. 2). In general, upper reaches (sites 1–3) had lower salinity than lower reaches (sites 4–6), but the between-reach mean difference was not statistically significant ( $H = 2.52$ ,  $P = 0.77$ ). Spatial variation in salinity was greatest during March 1998, July 1998, October 1998, and August 1999.

As expected, DO was higher during colder months. Mean DO ranged from 2.66 mg/l (August 1999 at site 1) to 13.9 mg/l (January 1999 at site 5), and variation among months was significant ( $F_{8,5} = 5.13$ ,  $P = 0.05$ ), with highest concentrations during May 1998 and January 1999, and lowest values during July 1998 and August 1999 (Fig. 2). When values were aggregated across seasons, DO was not significantly different among sites ( $F_{1,26} = 0.47$ ,  $P = 0.79$ ).

Water depth ranged from 0.14 m (July 1998 at site 1) to 0.74 m (October 1998 at site 6), and varied significantly among sampling periods ( $F_{8,5} = 16.0$ ,  $P < 0.005$ ), reaching highest and lowest values during October 1998 (0.56 m) and July 1998 (0.22 m), respectively (Fig. 2). In general, water depth increased from site 1 to 6 ( $F_{5,8} = 10.07$ ,  $P < 0.005$ ), but water depths at other sites (2–5) were not statistically different from those recorded at either site 1 or 6 (Fig. 2). Water depth was significantly correlated with distance from the estuary mouth ( $r = -0.39$ ,  $P < 0.01$ ).

Widgeon grass was the most abundant form of submerged aquatic vegetation in the study area. Percent cover of widgeon grass ranged from 0 to 95% and was highest between sites 1 and 4 from late spring through early fall (Fig. 2), with a significant site  $\times$  time interaction (ANOVA). Percent cover was correlated with temperature ( $r = 0.57$ ,  $P < 0.01$ ) and distance from the estuary mouth ( $r = 0.47$ ,  $P < 0.01$ ).

#### 3.2. Overall dominance pattern of fishes and macrocrustaceans

A total of 49,534 individual fish representing 43 species and 19 families was captured with the seine between March 1998 and August 1999 (Table 1). Due to identification challenges, juveniles of three taxa were identified only to family (Sciaenidae, Gobiidae, and Poeciliidae), and few juveniles were captured by our gear. Twenty-two estuarine-dependent species (Day et al., 1989) contributed 94% of numerical abundance of seine samples. Estuarine residents (18 species) accounted for only 5.5% of individuals in seine samples. The two most abundant estuarine-dependent species, Gulf menhaden and bay anchovy, comprised 42.6 and 36.4% of individuals in seine samples, respectively. Other species, in order of abundance, were Atlantic croaker, spot,

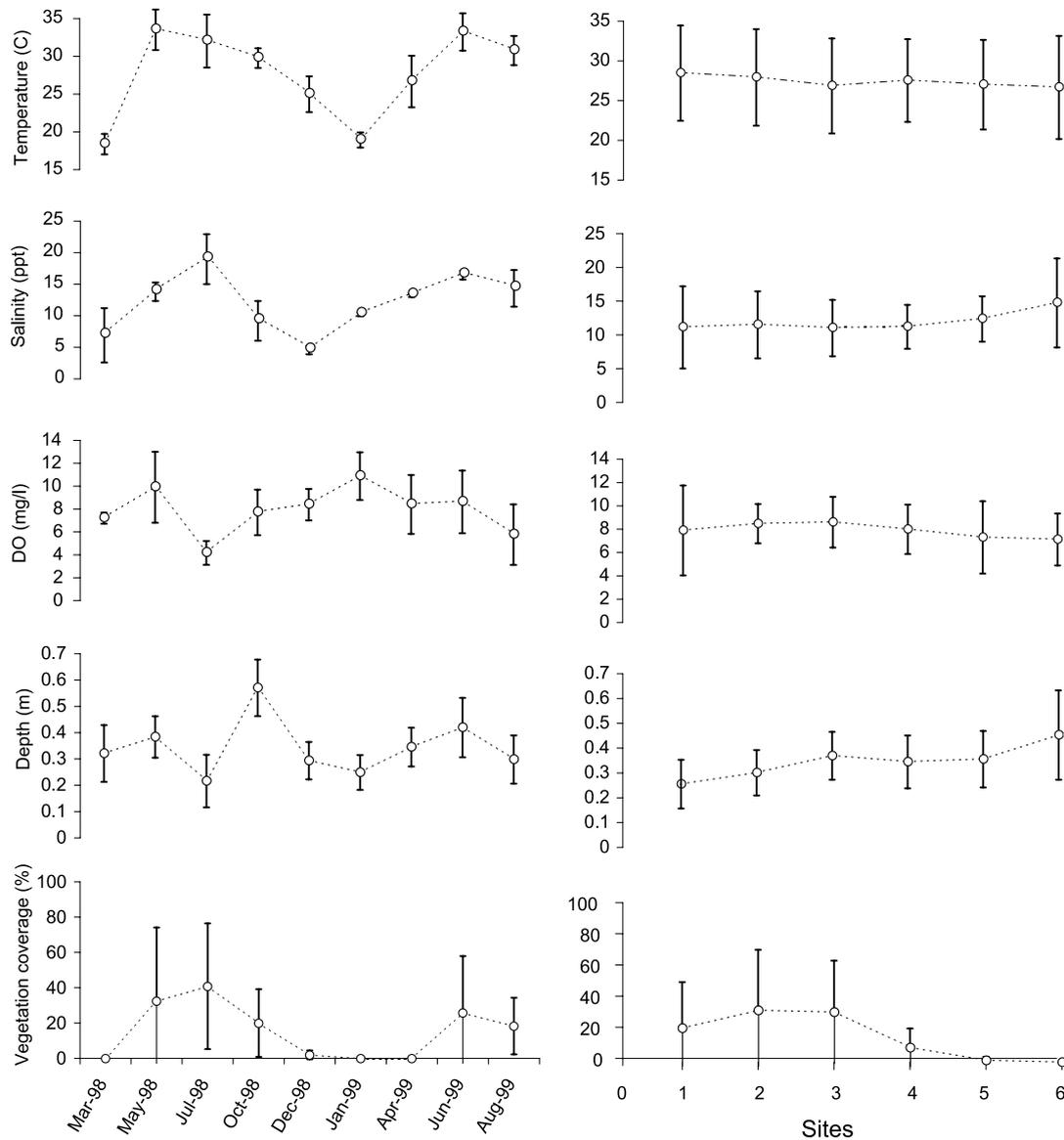


Fig. 2. Temporal and spatial variations in mean water temperature, salinity, DO, depth, and aquatic vegetation cover at MIM (bars =  $\pm 1$  SE).

inland silversides, striped mullet, and pinfish. Each of these species contributed 1–7% of the total seine catch. A total of 55,229 macrocrustaceans representing 10 species was collected with the seine (Table 1). The most abundant species was grass shrimp (88.3%; samples were mostly *P. pugio* but probably also contained *Palaemonetes vulgaris* and *Palaemonetes intermedius*), followed by brown shrimp (6.9%), white shrimp (3.1%), and blue crab (1.1%).

Gillnet samples yielded 824 fishes from 20 species and 10 families (Table 1). Of the 20 species, 13 were captured in the seine also. Estuarine-dependent species (16) contributed 71% of total gillnet samples; however, contribution of freshwater species was 29%. Striped mullet (34.0%), gizzard shad (24.3%), red drum

(11.8%), hardhead catfish (9.8%), black drum (5.7%), southern flounder (4%), and alligator gar (3.8%) were the most abundant species in gillnet samples (Table 1).

### 3.3. Spatial and temporal variations in abundance of fishes and macrocrustaceans

Fish and macrocrustacean abundance was greatest in seine samples during May 1998, December 1998, April 1999, and August 1999, with the latter yielding the largest collection (7809 individuals/100 m) (Fig. 3). Abundance peaks were largely due to high densities of bay anchovy, grass shrimp, and Gulf menhaden. Grass shrimp were largely responsible for the peaks in December 1998, and Gulf menhaden for peaks in April

Table 1

Frequency, CPUE rank, mean, minimum, and maximum values of species from seine samples (#/100 m) and gillnet samples (values in parentheses; number/h) at MIM

Scientific name	Common name	Frequency	CPUE rank	Mean CPUE	Minimum CPUE	Maximum CPUE
<b>Sciaenidae</b>						
<i>Leiostomus xanthurus</i>	Spot (D)	100 (22)	8 (13)	50.67 (0.06)	0.36 (0.02)	202 (0.09)
<i>Micropogonias undulatus</i>	Atlantic croaker (D)	78 (33)	6 (12)	85.11 (0.06)	0.36 (0.02)	353.01 (0.09)
<i>Sciaenops ocellatus</i>	Red drum (D)	(100)	(3)	0.28	0.15	0.60
<i>Bairdiella chrysoura</i>	Silver perch (D)	67 (22)	15 (19)	13.78 (0.03)	1.63 (0.02)	39.73 (0.03)
<i>Cynoscion nebulosus</i>	Spotted sea trout (D)	56 (56)	21 (11)	4.3 (0.06)	0.33 (0.02)	8.93 (0.09)
<i>Cynoscion arenarius</i>	Sand trout (D)	22 (11)	28 (10)	1 (0.06)	0.36 (0.06)	1.63 (0.06)
<i>Pogonias cromis</i>	Black drum (D)	44 (89)	30 (6)	0.92 (0.14)	0.49 (0.04)	1.37 (0.28)
Unidentified Sciaenidae		33	25	2.08	0.35	4.42
<b>Cyprinodontidae</b>						
<i>Fundulus grandis</i>	Gulf killifish (R)	89	20	4.98	0.33	20.00
<i>Cyprinodon variegatus</i>	Sheepshead minnow (R)	67	13	19.96	0.49	82.12
<i>Lucania parva</i>	Rainwater killifish (R)	78	16	13.06	0.35	31.79
<i>Fundulus pulvereus</i>	Bayou killifish (R)	44	27	1.07	0.49	1.82
<i>Fundulus majalis</i>	Striped killifish (R)	11	49	0.23	0.23	0.23
<i>Fundulus jenkinsi</i>	Saltmarsh topminnow (R)	11	43	0.36	0.36	0.36
<i>Adinia xenica</i>	Diamond killifish (R)	44	19	5.04	0.49	15.76
<i>Fundulus confluentus</i>	Marsh killifish (R)	33	26	1.47	0.55	2.42
<b>Atherinidea</b>						
<i>Menidia beryllina</i>	Inland silverside (R)	100	10	38.53	2.35	123.93
<i>Menidia peninsulae</i>	Tidewater silverside (D)	33	5	100.33	2.47	292.14
<b>Engraulidae</b>						
<i>Anchoa mitchilli</i>	Bay anchovy (D)	100	3	663.15	1.75	5095.36
<b>Clupeidae</b>						
<i>Brevoortia patronus</i>	Gulf menhaden (D)	89 (11)	2 (16)	887.62 (0.03)	2.73 (0.03)	2975.12 (0.03)
<i>Dorosoma cepedianum</i>	Gizzard shad (F)	11 (89)	38 (2)	0.49 (0.62)	0.49 (0.05)	0.49 (2.59)
<b>Sparidae</b>						
<i>Lagodon rhomboids</i>	Pinfish (D)	100 (11)	12 (17)	28.66 (0.03)	0.16 (0.03)	149.3 (0.03)
<i>Archosargus probatocephalus</i>	Sheepshead (M)	(22)	(18)	0.03	0.03	0.03
<b>Mugilidae</b>						
<i>Mugil cephalus</i>	Striped mullet (D)	89 (100)	11 (1)	33.02 (0.75)	0.81 (0.03)	114.88 (1.62)
<b>Gobiidae</b>						
<i>Gobiosoma bosc</i>	Naked goby (R)	89	24	2.10	0.20	8.93
<i>Gobionellus boleosoma</i>	Darter goby (R)	56	18	5.76	0.36	19.30
<i>Gobiosoma robustum</i>	Code goby (R)	33	41	0.43	0.20	0.81
<i>Microgobius gulosus</i>	Clown goby (R)	33	34	0.71	0.49	0.93
Unidentified Gobiidae				0.16	0.16	0.16
<b>Achiridae</b>						
<i>Achirus lineatus</i>	Lined sole (D)	33	36	0.53	0.30	0.71
<b>Bothidae</b>						
<i>Paralichthys lethostigma</i>	Southern flounder (D)	56	37 (7)	0.51 (0.10)	0.16 (0.02)	1.16 (0.24)
<i>Citharichthys spilopterus</i>	Bay whiff (D)	33	22	4.06	0.27	10.93
<i>Citharichthys macrops</i>	Spotted whiff (D)	11	47	0.35	0.35	0.35
<b>Ariidae</b>						
<i>Arius felis</i>	Hardhead catfish (D)	(78)	(4)	0.25	0.02	0.56
<b>Lepisosteidae</b>						
<i>Atractosteus spatula</i>	Alligator gar (F)	(100)	(8)	0.08	0.02	0.14
<i>Lepisosteus oculatus</i>	Spotted gar (F)	(33)	(15)	0.05	0.02	0.10
<i>Lepisosteus platostomus</i>	Shortnose gar (F)	(11)	(20)	0.02	0.02	0.02
<b>Elopidae</b>						
<i>Elops saurus</i>	Lady fish (D)	22 (44)	31 (14)	0.84 (0.05)	0.27 (0.02)	1.4 (0.11)
<b>Poeciliidae</b>						
<i>Poecilia latipinna</i>	Sailfin molly (R)	44	17	7.18	1.79	14.29
Unidentified Poeciliidae		11	44	0.36	0.36	0.36
<b>Dasyatidae</b>						
<i>Dasyatis sabina</i>	Atlantic stingray (M)	22 (22)	45 (9)	0.36 (0.08)	0.23 (0.06)	0.49 (0.10)
<b>Carangidae</b>						
<i>Hemicaranx amblyrhynchus</i>	Bluntnose jack (M)	22	23	3.35	0.36	6.34
<i>Oligoplites saurus</i>	Leathearjacket (M)	22	42	0.38	0.36	0.39
<b>Syngnathidae</b>						
<i>Syngnathus scovelli</i>	Gulf pipefish (R)	44	32	0.77	0.23	1.90
<i>Syngnathus louisianae</i>	Chain pipefish (R)	11	29	0.98	0.98	0.98

Table 1 (continued)

Scientific name	Common name	Frequency	CPUE rank	Mean CPUE	Minimum CPUE	Maximum CPUE
Tetraodonidae						
<i>Sphoeroides pachygaster</i>	Bluntnose puffer (M)	11	39	0.49	0.49	0.49
Gobiesocidae						
<i>Gobiesox strumosus</i>	Skilletfish (D)	22	51	0.20	0.16	0.23
Carcharhinidae						
<i>Carcharhinus limbatus</i>	Blacktip shark (M)	(11)	(21)			
Synodontidae						
<i>Synodus foetens</i>	Inshore lizard fish (M)	11	50	0.23	0.23	0.23
Gerreidae						
<i>Eucinostomus argenteus</i>	Spotfin mojarra (D)	11	35	0.71	0.71	0.71
Macrocrustacea						
<i>Callinectes sapidus</i>	Blue crab (D)	100	14 (5)	19.17 (0.18)	5.67 (0.06)	47.67 (0.49)
<i>Callinectes similis</i>	Lesser blue crab (D)	11	7	70.23	70.23	70.23
<i>Eurypanopeus debressus</i>	Mud crab (D)	11	53	0.16	0.16	0.16
<i>Neopenope sayi</i>	Mud crab (D)	44	40	0.44	0.23	0.70
<i>Pagurus</i> sp.	Hermit crab (D)	22	46	0.36	0.23	0.49
<i>Uca rapax</i>	Fiddler crab (D)	11	48	0.33	0.33	0.33
<i>Farfantepenaeus aztecus</i>	Brown shrimp (D)	89	4	139.96	3.00	480.23
<i>Litopenaeus setiferus</i>	White shrimp (D)	89	9	46.11	0.49	133.33
<i>Palaemonetes</i> spp.	Grass shrimp (R)	100	1	1355.37	35.25	3106.01

1999 and May 1998. The March 1998 peak, however, was largely due to an influx of Gulf menhaden and spot. The June 1999 peak was strongly influenced by grass shrimp and bay anchovy. In contrast, the August 1999 peak was mostly due to an influx of juvenile bay anchovy. Grass shrimp and sheepshead minnows comprised the largest portion of the July 1998 seine sample that yielded 681 individuals/100 m. October 1998 seine samples yielded 318 individuals/100 m and were dominated by bay anchovy. During January 1999, seine samples (1337 individuals/100 m) were dominated by grass shrimp and Gulf menhaden, and, to a lesser extent, Atlantic croaker (Fig. 3).

Gillnets yielded highest abundance of fishes and macrocrustaceans between spring and early fall, with the single largest sample in October 1998 (4.97 individuals/h) (Fig. 3). High gizzard shad abundance was largely responsible for the peak in October 1998. Gillnet samples during October 1998, April 1999, and August 1999 were dominated by striped mullet, red drum, and hardhead catfish.

Based on seine data aggregated across sampling periods, fish and macrocrustacean abundance tended to increase from sites 1 to 6 (Fig. 3). Site 6 yielded highest mean density for seine samples (6397 individuals/100 m), followed by sites 4, 5, and 3. High densities at sites 4, 5, and 6 were primarily influenced by grass shrimp, bay anchovy, and Gulf menhaden. Several species (e.g. grass shrimp, Atlantic croaker, spot, brown shrimp, inland silversides, bay anchovy, and Gulf menhaden) also were common at sites 2 and 3. The most inland site (site 1) was dominated by grass shrimp and Gulf menhaden. Overall, abundance in seine samples was inversely correlated with distance from estuary mouth ( $r = -0.38$ ,  $P < 0.01$ ) and vegetation cover ( $r = -0.44$ ,  $P < 0.01$ ), and abundance in gillnet samples was inversely correlated only with distance from the estuary mouth ( $r = -0.31$ ,  $P < 0.05$ ). Site 6 yielded the largest gillnet catches (3.5 individuals/h), followed, in decreasing order, by sites 5, 4, 3, 2, and 1 (Fig. 3).

#### 3.4. Spatial and temporal variations in species richness, diversity, and evenness

Species richness ranged from 4 to 23 (January 1999 at site 1 and August 1999 at site 4, respectively). Between-survey differences in mean species richness for combined

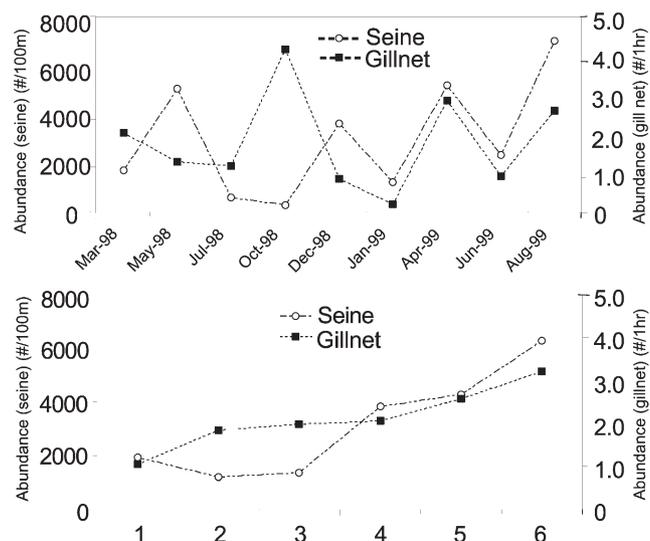


Fig. 3. Temporal and spatial variations in total abundance of fishes and macrocrustaceans collected in seine and gillnets.

seine and gillnet samples were significant ( $F_{8,5} = 8.59$ ,  $P < 0.05$ ). April 1999 and August 1999 seine samples yielded the highest averages (both = 16.67), and the January 1999 seine samples yielded the lowest average (8.17) (Fig. 4). Differences in species richness among sites also were statistically significant ( $F_{5,8} = 8.69$ ,  $P < 0.005$ ). Species richness tended to increase from site 1 to site 6 (Fig. 4), with highest (16.44) and lowest (9.44) values recorded at sites 6 and 1, respectively. Species richness showed significant spatial variation within individual survey periods. Numbers of species recorded at sites 1 through 4 during March 1998, May 1998, October 1998, December 1998, and January 1999 tended to be lower than values recorded at sites 5 and 6 during the same periods. In contrast, nearly equal numbers of species were recorded at all sites during the months of April 1999, June 1999, and August 1999 (Fig. 4). Across all sites, species richness was correlated with abundance ( $r = 0.68$ ,  $P < 0.01$ ), evenness ( $r = -0.42$ ,  $P < 0.01$ ), distance from the estuary mouth ( $r = -0.49$ ,  $P < 0.01$ ), and salinity ( $r = 0.27$ ,  $P < 0.05$ ).

Species richness in gillnet samples ranged from 0 (several sites during January 1999 and March 1998) to 12 (June 1999 at site 6). As observed for seine samples, species richness in gillnet samples revealed significant temporal variation ( $F_{8,5} = 5.74$ ,  $P < 0.01$ ). Total species richness was highest in June 1999 (6.83) and lowest in January 1999 (0.83) (Fig. 4). Although species richness in gillnet samples tended to increase from sites 1 to 6, this pattern was not statistically significant ( $H = 3.67$ ,  $P = 0.60$ ) (Fig. 4). When data were aggregated across all sampling periods, highest and lowest mean richness values were recorded at sites 6 (5.22) and 1 (3.44), respectively. Across all samples, species richness for gillnets was correlated with abundance ( $r = 0.74$ ,  $P < 0.01$ ),

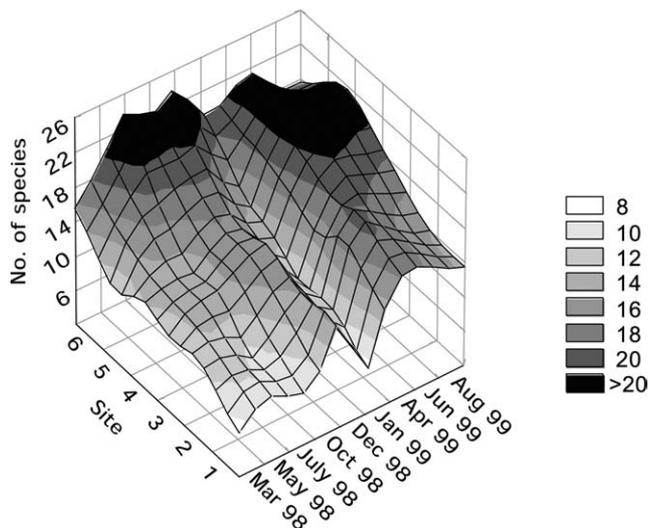


Fig. 4. Temporal and spatial variations in species richness in combined seine and gillnet samples.

$H'$  ( $r = 0.94$ ,  $P < 0.01$ ),  $J'$  ( $r = 0.48$ ,  $P < 0.01$ ), depth ( $r = 0.48$ ,  $P < 0.01$ ), salinity ( $r = 0.32$ ,  $P < 0.05$ ), and temperature ( $r = 0.40$ ,  $P < 0.01$ ).

3.5. Canonical correspondence analysis

Eigenvalues (indicating strength of the model) for the first four multivariate axes were 0.223 (CCA1), 0.195 (CCA2), 0.078 (CCA3), and 0.043 (CCA4). Total model inertia (sum of unconstrained eigenvalues) was 2.37, and the sum of all canonical eigenvalues was 0.57. Species–environment correlation coefficients for the first four pairs of axes (CCA 1–4) were 0.87, 0.80, 0.685, and 0.58. For the first four assemblage axes, cumulative percent variance of species data was 23%. The first two assemblage axes modeled 10 and 8 percent of variation, respectively, and the first two sets of axes explained 79% of cumulative variance in the species–environment relationship modeled by CCA, therefore results for these two axes are plotted (Fig. 5).

Correlations between all five environmental variables and the first four canonical axes were statistically significant ( $P < 0.05$ ). Water depth was strongly correlated (0.79) with the first axis (axis 1 explained 39.4% of species–environment relation). Vegetation cover (0.55) and water temperature (0.42) had highest correlations with the second axis (24% of species–environment relation). The first CCA axis models a

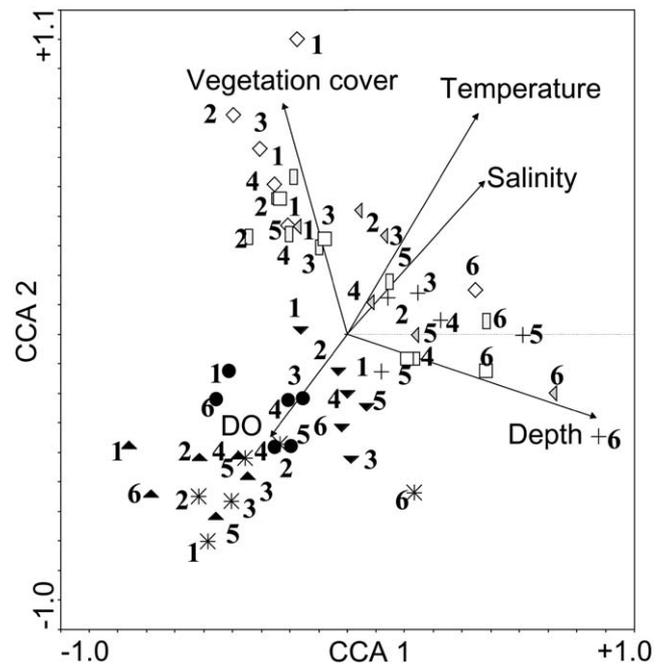


Fig. 5. Plot of sample/site scores on the first two axes from CCA with environmental and species assemblage data at MIM: March 1998 (○), May 1998 (□), July 1998 (◇), October 1998 (+), December 1998 (●), January 1999 (▲), April 1999 (▼), June 1999 (○), and August 1999 (○). Numbers correspond to sample sites along the estuarine gradient (1 upper–6 lower).

spatial gradient that distinguishes deeper sites (high scores) from shallower sites (low scores) (Table 2). The second axis represents a temporal gradient that separated summer and autumn samples (high scores) from winter and spring (low scores). Summer samples were associated with warmer temperatures, more aquatic vegetation, higher salinity, and lower DO and depth (Table 2). Samples plotted in the upper-left panel of the ordination plot were dominated by killifishes, pinfish, inland silverside, blue crab, adult striped mullet, and alligator gar. These species were common during summer months at shallow sites where widgeon grass was dense. Silver perch, bay anchovy, tidewater silverside, southern flounder, spotted sea trout, gizzard shad, black drum, and hardhead catfish were associated with higher salinities at deeper sites during summer–autumn (lower-right panel, Fig. 5). Darter goby, naked goby, spot, Atlantic croaker, and Gulf menhaden were common as larvae and juveniles in the upper reaches of the estuary during winter and early spring (lower-left panel, Fig. 5). Grass, brown and white shrimp, blue crab, and red drum had relatively low loadings on both of the first two CCA axes (Table 2), an indication of weak relationship with environmental parameters or strong association with intermediate levels of these parameters.

## 4. Discussion

### 4.1. Species composition

The fish assemblage at MIM was dominated by estuarine-dependent species common in estuaries along the southern and southeastern US coast (Kneib, 1997b; Sheridan, 1983). Even though species richness of estuarine-dependent and resident species was nearly equal during the study, the abundance of estuarine-dependent species was greater. Most of these species feed low in the food web, with detritivores/planktivores (Gulf menhaden, striped mullet), planktivores (bay anchovy), omnivores (pinfish), and invertivores (spot and Atlantic croaker) represented. Adult red drum, southern flounder, and other large predatory fishes enter MIM to feed (S. Akin, unpublished data). Most estuarine-resident fishes common at MIM (e.g. inland silversides, gobies, and several cyprinodontids) have broad temperature, salinity, and DO tolerances (Nordlie, 1985). Only four freshwater species were collected during the study (gizzard shad and three gar species). Grass shrimp, the numerically dominant macrocrustacean, was abundant throughout the study at all times. Occasional visitors included sheepshead and blacktip shark (a single juvenile captured at site 6).

Table 2

Species and environmental variable eigenvalues (loadings) associated with the first two axes from CCA (gillnet samples designated by G)

Species	Axis 1	Axis 2	Variable	Axis 1	Axis 2
<i>Menidia peninsulae</i>	1.31	0.20	Depth	0.87	−0.28
<i>Micropogonias undulatus</i> (G)	1.31	−0.16	Salinity	0.48	0.52
<i>Dorosoma cepedianum</i> (G)	0.85	−0.08	Temperature	0.46	0.75
<i>Arius felis</i> (G)	0.76	−0.14	Vegetation cover	−0.22	0.78
<i>Bairdiella chrysoura</i>	0.75	0.16	Dissolved oxygen	−0.27	−0.35
<i>Cynoscion nebulosus</i>	0.54	−0.16			
<i>Anchoa mitchilli</i>	0.50	0.01			
<i>Pogonias cromis</i>	0.34	0.05			
<i>Paralichthys lethostigma</i> (G)	0.30	0.01			
<i>Elops saurus</i> (G)	0.27	0.68			
<i>Mugil cephalus</i>	0.20	−0.34			
<i>Farfantepenaeus aztecus</i>	0.05	0.11			
<i>Litopenaeus setiferus</i>	0.02	−0.11			
<i>Sciaenops ocellatus</i>	−0.06	−0.06			
<i>Mugil cephalus</i> (G)	−0.08	0.15			
<i>Lagodon rhomboides</i>	−0.14	0.15			
<i>Brevoortia patronus</i>	−0.15	−0.84			
<i>Fundulus grandis</i>	−0.16	0.59			
<i>Palaemonetes</i> spp.	−0.18	−0.13			
<i>Callinectes sapidus</i>	−0.19	0.12			
<i>Menidia beryllina</i>	−0.23	0.16			
<i>Gobionellus boleosoma</i>	−0.36	−0.67			
<i>Atractosteus spatula</i> (G)	−0.36	0.02			
<i>Lucania parva</i>	−0.50	0.37			
<i>Cyprinodon variegatus</i>	−0.56	1.12			
<i>Gobiosoma bosc</i>	−0.56	−0.26			
<i>Leiostomus xanthurus</i>	−0.62	−0.73			
<i>Micropogonias undulatus</i>	−0.63	−0.88			
<i>Poecilia latipinna</i>	−0.70	1.21			

The high productivity and dense vegetative cover of shallow estuarine habitats presumably enhance growth and survival of juvenile estuarine-dependent species (Gunter, 1938; McErlean et al., 1973). During periods of high freshwater inflow, upper estuarine reaches may experience high recruitment of estuarine-dependent species (Grimes & Kingsford, 1996; Rogers et al., 1984). Gelwick et al. (2001) concluded that species diversity at MIM responded to runoff from the adjacent freshwater wetland. This effect was greater in the upper oligohaline reaches of the marsh than in the lower mesohaline zone examined in the present study. Freshwater inflow has been hypothesized to transport catchment olfactory cues that facilitate orientation to estuaries (Whitfield, 1999). At MIM, freshwater inflow did not appear to be associated with the appearance of greater numbers of estuarine-dependent species in upper reaches of the mesohaline zone. A water control structure diverts freshwater for rice production and reduces freshwater inflow to lower reaches (Gelwick et al., 2001). Salinity decline in the upper reaches during winter and spring occurred mostly in response to local precipitation, a pattern common in the southern US (Rakocinski, Baltz, & Fleeger, 1992). Three estuarine-dependent species (Gulf menhaden, spot, and Atlantic croaker) were particularly common in upper reaches, an area where detritus (derived from widgeon grass) and associated microorganisms were abundant (S. Akin, unpublished data).

#### 4.2. *Spatial and temporal variations in relation to environmental variables*

Several estuarine studies have emphasized the importance of environmental factors affecting seasonal and spatial changes in fish and macrocrustacean assemblage structure (Blaber & Blaber, 1980; Gelwick et al., 2001; Livingston, 1976; Marshall & Elliot, 1998; Peterson & Ross, 1991; Rakocinski et al., 1996; Subrahmanyam & Coultas, 1980; Weinstein et al., 1980). The suite of environmental variables measured in our study was significantly associated with seasonal and spatial changes in assemblage structure. CCA revealed a dominant spatial gradient spanning shallow upper reach to deeper sites closer to the bay. Spatial variation in assemblage structure was strongest during summer when upper sites apparently had sub-optimal environmental conditions for aquatic fauna. The second CCA axis (influenced by vegetation cover, salinity, temperature, and DO) represented a temporal gradient that separated samples taken during winter–early spring from those collected during summer–early autumn. Declines in temperature and salinity, and an increase in DO during winter–spring were accompanied by an increase in abundance of estuarine-dependent species (e.g. spot, Gulf menhaden, and Atlantic croaker). When salinity,

temperature, and vegetation cover increased during late spring–summer, bay anchovy, pinfish, cyprinodontids, and a different group of scianids (e.g. spotted sea trout and silver perch) dominated the system, a pattern consistent with the findings from a Louisiana estuary (Rakocinski et al., 1992). Seasonal changes in species dominance may constitute temporal resource partitioning that reduces competition for food, or it may reflect species responses to sub-optimal physical environmental conditions, or some combination of both.

Variation in species distribution explained by the first four CCA axes was only 22.7%, an indication that other factors influence community structure at MIM. Sediment characteristics (Marchand, 1993), food availability (Barry et al., 1996), turbidity (Araujo et al., 1999; Blaber & Blaber, 1980; Cyrus & Blaber, 1992), pH (Maes et al., 1998; Rozas & Hackney, 1984; Whitfield, 1999), and distance from the estuary mouth (Loneragan et al., 1987) have shown associations with fish and invertebrate distributions in other estuarine systems. Density of larval fishes and microinvertebrates at MIM was twice as high during summer compared with that during winter (S. Akin, unpublished data), which might have contributed to high species richness during summer. Tides influence the entry of nekton into estuaries and subsequent patterns of habitat use (Kneib & Wagner, 1994; Rozas, 1995). The predictable seasonal and temporal variations in water depth observed during both years (1998, 1999) suggest fluctuations in water were not strongly affected by tidal variation. Maximum diel variation in water depth recorded on our survey dates was only 10 cm.

Another potential factor driving seasonal changes in estuarine assemblages is reproductive biology (Drake & Arias, 1991; Potter et al., 1986; Potter et al., 2001; Subrahmanyam & Coultas, 1980; Thiel & Potter, 2001; Yoklavich et al., 1991). Seasonal changes in assemblage composition could be influenced by seasonal recruitment dynamics and/or migration as much as by response of local populations to environmental factors. Seasonal patterns of abundance of several species at MIM were consistent with those from other studies, which suggests endogenous reproductive cycles and/or migrations associated with large-scale environmental variation (e.g. weather fronts, coastal currents) influenced temporal patterns of abundance and distribution. For example, high abundance of juvenile Gulf menhaden during winter–spring is consistent with offshore spawning during late autumn (Marotz, Herke, & Rogers, 1990). Two common sciaenids, Atlantic croaker and spot, peaked in abundance during winter–spring, a reflection of autumn spawning (Ditty, Zieske, & Shaw, 1988). Rogers et al. (1984) recorded peak occurrence of croaker and spot during December and February–March, respectively, a pattern that agrees with our findings.

Species richness and abundance increased at MIM during late spring and summer, a pattern consistent with findings from other US estuaries (e.g. Allen & Horn, 1975; Hoff & Ibara, 1977). High species richness during this period was positively correlated with salinity. Predictable seasonal patterns of variation in salinity and temperature were observed during both years of our study, yet, the pattern of elevated species richness was not present in seine samples during May and July of 1998. Temperature also affects estuarine organisms, but temperature was not significantly correlated with species richness at MIM. High water temperature coupled with low water depth during summer and winter sometimes resulted in sub-optimal environmental conditions. For example, low depth and high salinity and temperature during July 1998 at upper sites (sites 1–3) probably excluded intolerant species, such as spot, bay anchovy, and pinfish. During summer, upper sites were dominated by cyprinodontids and other tolerant species (see also Nordlie, 1985). Sub-optimal conditions also were observed at site 1 in January 1999 when only four species were collected. During this period, upper sites were very shallow, which probably restricted most species to the lower parts of the estuary.

Overall, species richness was higher in lower reaches than upper reaches, especially at sites 1 and 2. Lone-ragan et al. (1987) argued that large numbers of species at lower estuarine sites may be a function of sampling during intervals when many small fishes have recently entered the estuary and not yet penetrated inland locations. Yoklavich et al. (1991) related this pattern to the fact that lower reaches are strongly influenced by marine processes, and warm temperatures at upper sites exclude thermally intolerant marine species. Yoklavich et al. (1991) further argued that habitat complexity (rock pilings, commercial oyster racks) in lower estuarine reaches supported the greatest number of species. In MIM, habitat heterogeneity of upper and lower sites was increased by the presence of widgeon grass and oyster reefs, respectively. However, certain marine species probably avoid vegetated habitats during summer due to the sub-optimal abiotic environment. CCA results supported the view that thermally intolerant marine species were excluded from upper sites during summer due to high temperatures and lower depths. Marine species, such as spotted sea trout, silver perch, and tidewater silversides, were strongly associated with greater depth and higher salinity. Oyster reefs and associated invertebrates provide food and refuge for certain fish and invertebrate species such as, skillethead gobies, and grass shrimp (discussed subsequently), so the presence of oyster reef patches in the lower sites could have contributed to higher species richness.

Unlike species richness, species diversity did not show a seasonal pattern at MIM. Species diversity patterns were strongly influenced by abundant species such as

Gulf menhaden, grass shrimp, and bay anchovy. Average species richness (seine data) was lowest in October 1998 despite the fact that mean diversity was highest during this period. This apparent paradox was mostly due to the relatively even distribution of abundant species (Gulf menhaden, bay anchovy, and grass shrimp) across sites during this period. Although not significant, upper sites had higher evenness values than lower sites that were dominated by a few abundant species. Peterson and Ross (1991) found higher evenness at sites nearer freshwater in a Mississippi estuary, and they also found a higher abundance of species at these sites, a finding not consistent with our results.

The distribution and abundance of large fishes captured in gillnets were more influenced by environmental variables (water depth, salinity, distance from the estuary mouth) than were those of small fishes and macrocrustaceans. Species richness, diversity, and abundance in gillnet samples were correlated with salinity, temperature, and depth at MIM. Like species richness in seine samples, total abundance in gillnet samples was inversely related to distance from the estuary mouth, which suggests that movement to upper sites may have been inhibited by the combination of shallow depth, high temperature, and low DO.

#### 4.3. Resident species

Occurrence of estuarine-resident species (e.g. sheepshead minnow, Gulf killifish, rainwater killifish, sailfin molly, and inland silversides) was positively associated with lower depth, higher salinity, and greater vegetation cover at upper sites during summer. Like other studies (Kneib, 1997b; Ley, McIvor, & Montague, 1999; Weinstein, 1979), our study revealed that resident species dominate shallow, vegetated coastal habitats. Unlike other resident species, naked and darter gobies were common at lower sites during winter months when salinities and depth were relatively low. Naked gobies are known to inhabit oyster reefs (Hoese & Moore, 1998) like those in the lower marsh (sites 5, 6).

Although inland silversides were fairly abundant during summer months, they did not seem to be influenced by any of the variables we measured. This suggests that, like grass shrimp, silversides are highly tolerant of physical environmental variation. CCA revealed an association between inland silversides and aquatic vegetation. In contrast, abundance of tidewater silversides, an estuarine-dependent congener, was correlated with salinity, temperature, and depth, all of which were high during summer months in lower reaches of the estuary. These spatial patterns indicate habitat segregation between two closely related species. Inland silversides at MIM had a broad diet that included insects, annelid worms, phytoplankton, zooplankton, chironomid larvae, and fish (S. Akin, unpublished data). In

contrast, tidewater silversides fed on crab zoea, calanoid copepods, gastropods, and diatoms. Low dietary overlap indicates low probability of competition for food between these congeners.

Grass shrimp (*Palaemonetes* spp.), the dominant macrocrustacea throughout the estuary during the study, showed peak abundance during summer and early winter, which reflects recruitment during spring and fall reproductive periods (Wood, 1967). Abundance of grass shrimp was not correlated with any of the environmental variables measured. *P. pugio* is tolerant of low DO and high temperature and variable salinity (Rozas & Hackney, 1984; Welsh, 1975). Shrimp seek physical structure, such as oyster reefs (commonly associated with *P. vulgaris*) and vegetation that provides food and protection from predators (Morgan, 1980; Welsh, 1975; Zimmerman & Minello, 1984). High grass shrimp abundance at site 6 could have been due to the presence of oyster reefs.

#### 4.4. Estuarine-dependent species

Pinfish were abundant during spring–summer at upper sites, and positively associated with vegetation cover. Levin et al. (1997) found that recruitment of pinfish was higher in vegetated habitats than in open sandy areas, and concluded that pinfish use vegetated areas for both feeding and refuge from predators. Pinfish at MIM consumed both widgeon grass and associated microinvertebrates, such as amphipods (S. Akin, unpublished data). In contrast, other abundant estuarine-dependent species, such as bay anchovy, tidewater silversides, and silver perch, occupied lower marsh reaches during summer when these sites had greater depths, temperatures, and salinities. Weinstein (1979) found that estuarine-dependent species similarly dominated deep, unvegetated tidal creeks in salt marshes. Young-of-the-year silver perch are reported to concentrate in more seaward zones with higher salinity (Chao & Musick, 1977; Weinstein et al., 1980).

Most estuarine-dependent species enter estuaries as postlarvae and use brackish habitats as nursery grounds (Rogers et al., 1984). Atlantic croaker and spot recruited into MIM during the same period observed for these species in the Ogeechee River estuary in Georgia (Rogers et al., 1984). Spot and Atlantic croaker were recorded in high abundance during spring (March 1998, April 1999) and winter (December 1998, January 1999) when temperature was relatively low. Spot and Atlantic croaker were negatively associated with both temperature and vegetation cover. Spot abundance was not correlated with salinity, and Atlantic croaker abundance was negatively correlated with salinity. Moser and Gerry (1989) found that Atlantic croaker avoided areas where salinity was less than 10, but spot did not. Based on these patterns, they concluded that rapid change in

osmoregulatory response was energetically more costly for croaker than spot. From December 1998 through April 1999 when Atlantic croaker abundance at MIM was highest, salinity variation was minimal (0.4–1.6 between sites 1 and 6). Abundance of spot peaked during March 1998 when salinity differed by 8.3 between sites 1 and 6.

Young-of-the-year Gulf menhaden were abundant in the estuary from winter through early summer, and absent during the remainder of the year. The smallest individuals (20–30 mm TL) appeared in December 1998 in the upper reaches of the estuary. Subsequent samples obtained larger cohort members in deeper sites of the lower reach. The same movement pattern has been observed in other estuaries (Deegan, 1990; Marotz et al., 1990; Shaw, Cowan, & Tillman, 1985; Shaw, Wiseman, Turner, Rouse, & Condrey, 1985). Deegan (1990) and Marotz et al. (1990) claimed that movement to deeper sites might be a response to physicochemical environmental conditions.

White shrimp and brown shrimp are morphologically and ecologically similar, but they occurred in the marsh during different seasons. White shrimp were most common during autumn and winter, and brown shrimp were abundant during spring and summer. Similar temporal patterns of abundance for these species were observed in salt marshes of Galveston Island, Texas (Zimmerman & Minello, 1984). Postlarval white shrimp enter the estuaries during late spring and summer (Baxter & Renfo, 1967). White shrimp abundance was inversely correlated with salinity, and brown shrimp abundance was positively correlated with temperature and salinity. Similar associations with physicochemical variables have been observed in other estuaries. Gunter (1961) found that white shrimp tolerated low salinity better than brown shrimp, and white shrimp are less affected than brown shrimp by sudden declines in salinity (Minello & Zimmerman, 1991). Blue crabs were common throughout the estuary during our study. Blue crab abundance had highest correlation with temperature and salinity, a finding consistent with other studies (Killam, Hochberg, & Cripe, 1992).

## 5. Conclusions

Co-occurrence of seasonal changes in physicochemical variables and fish/macrocrustacean assemblage structure makes it difficult to ascertain whether assemblage dynamics were driven by species response to local environmental conditions, or whether they were a result of species life histories and regional migrations. Seasonal co-occurrence of peak abundance of juveniles of several estuarine-dependent species, such as spot, Gulf menhaden, bay anchovy, and Atlantic croaker, was consistent with other estuarine studies in the Gulf of

Mexico, and supports the idea that temporal variation in assemblage structure results from seasonal large-scale migrations and reproduction inside and outside the estuary. Offshore spawning by many species precedes migration of larvae into the estuary. Once immatures arrive in the estuary, species-specific responses to abiotic environmental conditions apparently influence patterns of species distribution and abundance at the local scale.

In summary, seasonal variation in both environmental conditions and the biota was stronger than spatial variation at the scale of our study. Seasonal occurrence of estuarine-dependent species suggested that endogenous migrations are an important factor influencing assemblage structure. Weak spatial patterns may have been influenced by our relatively small study region as well as limited freshwater discharge into the estuary. The strongest spatial patterns were associated with sub-optimal environmental conditions during summer in shallow, upper reaches of the estuary. Distance from the estuary mouth seemed to be a major factor driving spatial variation in community structure, possibly because movement of larvae and juveniles to inland sites was limited by insufficient freshwater inflow at this location.

### Acknowledgements

The Nature Conservancy of Texas and M. Dumesnil provided access to field sites and facilities at MIM Preserve. We thank A. Arrington, J. Arrington, S. Aydin, Y. Bolek, T. Lantz, H. Lopez, M. Morgan, M. Robertson, S. Tarim, and J. Walther for assistance with data and specimen collection in the field. W. Neill and J. Calvin provided helpful analytical advice. Funding was provided by the Nature Conservancy of Texas, International Sportfish Fund, and Gaziosmanpasa University fellowship (S.A.).

### References

- Allen, L. G., & Horn, M. H. (1975). Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. *Estuarine and Coastal Marine Science* 3, 371–380.
- Araujo, F. G., Bailey, R. G., & Williams, W. P. (1999). Spatial and temporal variation in fish populations in the upper Thames estuary. *Journal of Fish Biology* 55, 836–853. doi:10.1006/jfbi.1999.1042.
- Barry, J. P., Yoklavich, M. M., Cailliet, G. M., Ambrose, D. A., & Antrim, B. S. (1996). Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980. *Estuaries* 19, 115–118.
- Baxter, K. N., & Renfo, W. C. (1967). Seasonal distribution and size distribution of postlarval brown shrimp and white shrimp, near Galveston, Texas, with notes on species identification. *US Fish and Wildlife Service Fishery Bulletin* 66, 149–158.
- Blaber, S. J. M., & Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* 17, 143–162.
- Breitburg, D. L., Lohor, T., Pecay, C. A., & Gerstein, A. (1997). Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecological Monographs* 67, 489–507.
- Chao, L. N., & Musick, J. A. (1997). Life history, feeding habitats and functional morphology of juvenile sciaenid fishes in the New York Estuary, Virginia. *US Fish and Wildlife Service Fishery Bulletin* 75, 657–702.
- Cyrus, D. P., & Blaber, S. J. M. (1992). Turbidity and salinity in a tropical Northern estuary and their influence on fish distribution. *Estuarine, Coastal and Shelf Science* 35, 545–563.
- Dahlberg, M. D., & Odum, E. P. (1970). Annual cycles of species occurrence, abundance, and diversity in Georgia estuarine fish populations. *American Midland Naturalist* 83, 382–392.
- Dando, P. R. (1984). Reproduction in estuarine fish. In G. W. Potts, & R. J. Wootton (Eds.), *Fish reproduction* (pp. 155–170). London: Academic Press.
- Day, J. W. Jr., Hall, C. A. S., Kemp, W. M., & Yáñez-Arancibia, A. (1989). *Estuarine ecology*. New York: Wiley.
- Deegan, L. A. (1990). Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. *Marine Ecology Progress Series* 68, 195–205.
- Ditty, J. G., Zieske, G. G., & Shaw, R. F. (1988). Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above latitude 26°00'N. *US Fish and Wildlife Service Fishery Bulletin* 86, 396–404.
- Drake, P., & Arias, A. M. (1991). Composition and seasonal fluctuations of ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S. W. Spain). *Journal of Fish Biology* 39, 347–364.
- Garcia, A. M., Vieira, J. P., & Winemiller, K. O. (2001). Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. *Journal of Fish Biology* 59, 1218–1238.
- Gelwick, F. P., Akin, S., Arrington, D. A., & Winemiller, K. O. (2001). Fish assemblage structure in relation to environmental variation in a Texas Gulf coastal wetland. *Estuaries* 24, 285–296.
- Grimes, C. B., & Kingsford, M. J. (1996). How do riverine plumes of different size influence fish larvae: do they enhance recruitment? *Marine and Freshwater Research* 47, 191–208.
- Gunter, G. (1938). Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana, with particular reference to life histories. *Ecological Monographs* 8, 313–346.
- Gunter, G. (1961). Some relations of estuarine organisms to salinity. *Limnology and Oceanography* 6, 182–190.
- Hoese, H. D., & Moore, R. H. (1998). *Fishes of the Gulf of Mexico* (2nd ed.). College Station: Texas A&M University Press.
- Hoff, J. G., & Ibara, R. M. (1977). Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. *Estuarine and Coastal Marine Science* 5, 665–678.
- Killam, K. A., Hochberg, R. J., & Cripe, C. R. (1992). *Synthesis of basic life histories of Tampa Bay species*. Tampa Bay National Estuary Program, Technical Publication Number, 10-92.
- Killgore, K. J., Morgan, R. P. II., & Rybicki, N. B. (1989). Distribution and abundances of fishes associated with submerged aquatic plants in Potomac River. *North American Journal of Fisheries Management* 9, 101–111.
- Kneib, R. T. (1997). Early life stages of resident nekton in intertidal marshes. *Estuaries* 20, 214–230.
- Kneib, R. T. (1997). The role tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology* 35, 163–220.
- Kneib, R. T., & Wagner, S. L. (1994). Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* 106, 227–238.
- Levin, P., Petrik, R., & Malone, J. (1997). Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* 112, 55–63.

- Ley, J. A., McIvor, C. C., & Montague, C. L. (1999). Fishes in mangrove prop-root habitats of northeastern Florida Bay: distinct assemblages across an estuarine gradient. *Estuarine, Coastal and Shelf Science* 48, 701–723. doi:10.1006/ecss.1998.0459.
- Livingston, R. J. (1976). Diurnal and seasonal fluctuations of organisms in a north Florida estuary. *Estuarine and Coastal Marine Science* 4, 373–400.
- Loneragan, N. R., Potter, I. C., Lenanton, R. C., & Caputi, N. (1986). Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. *Marine Biology* 92, 575–586.
- Loneragan, N. R., Potter, I. C., Lenanton, R. C., & Caputi, N. (1987). Influence of environmental variables on fish fauna of the deeper waters of large Australian estuary. *Marine Biology* 94, 631–641.
- Loneragan, N. R., Potter, I. C., & Lenanton, R. C. J. (1989). Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Marine Biology* 103, 575–586.
- Maes, J., Van Damme, P. A., Taillieu, A., & Ollevier, F. (1998). Fish communities along an oxygen-poor salinity gradient (Zeeschelde Estuary, Belgium). *Journal of Fish Biology* 52, 534–546. doi:10.1006/jfbi.1997.0602.
- Marchand, J. (1993). The influence of seasonal salinity and turbidity maximum variations on nursery function of the Loire estuary (France). *Netherlands Journal of Aquatic Ecology* 27, 427–436.
- Marotz, B. L., Herke, W. H., & Rogers, B. D. (1990). Movement of gulf menhaden through three marshland routes in southern Louisiana. *North American Journal of Fisheries Management* 10, 408–417.
- Marshall, S., & Elliot, M. (1998). Environmental influences on the fish assemblages of the Humber Estuary, U.K. 1998. *Estuarine, Coastal and Shelf Science* 46, 175–184. doi:10.1006/ecss.1997.0268.
- McErlean, A. J., O'Connor, S. G., Mihursky, J. A., & Gibson, C. I. (1973). Abundance, diversity and seasonal patterns of estuarine fish populations. *Estuarine and Coastal Marine Science* 1, 19–36.
- Minello, T. J., & Zimmerman, R. J. (1991). The role of estuarine habitats regulating growth and survival of juvenile penaeid shrimp. In P. DeLoach, W. J. Dougherty, & M. A. Davidson (Eds.), *Frontiers in shrimp research* (pp. 1–16). Amsterdam: Elsevier.
- Moore, H. R., & Reis, R. R. (1983). Analysis of spatial and temporal variations in biomass and community structure of motile organisms in Town Creek, a South Carolina tidal pass. *Contributions in Marine Science* 26, 111–125.
- Morgan, M. D. (1980). Grazing and predation of the grass shrimp *Palaemonetes pugio*. *Limnology and Oceanography* 25, 896–902.
- Moser, M. L., & Gerry, L. R. (1989). Differential effects of salinity changes on two estuarine fishes, *Leiostomus xanthurus* and *Microponias undulatus*. *Estuaries* 12, 35–41.
- Nordlie, F. G. (1985). Osmotic regulation in the sheepshead minnow *Cyprinodon variegatus* Lacépède. *Journal of Fish Biology* 26, 161–170.
- Peterson, M. S., & Ross, S. T. (1991). Dynamics of littoral fishes and decapods along a coastal river-estuarine gradient. *Estuarine, Coastal and Shelf Science* 33, 467–483.
- Potter, I. C., Bird, D. J., Claridge, P. N., Clarke, K. R., Hyndes, G. A., & Newton, L. C. (2001). Fish fauna of the Severn Estuary. Are there long-term changes in abundance and species composition and are the recruitment patterns of the main marine species correlated? *Journal of Experimental Marine Biology and Ecology* 258, 15–37.
- Potter, I. C., Claridge, P. N., & Warwick, R. M. (1986). Consistency of seasonal changes in an estuarine fish assemblages. *Marine Ecology Progress Series* 32, 217–228.
- Rakocinski, C. F., Baltz, D. M., & Fleeger, J. W. (1992). Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series* 80, 135–148.
- Rakocinski, C. F., Lyczkowski-Shultz, J., & Richardson, S. L. (1996). Ichthyoplankton assemblage structure in Mississippi sound as revealed by canonical correspondence analysis. *Estuarine, Coastal and Shelf Science* 43, 237–257.
- Rogers, S. G., Targett, T. E., & Von Sant, S. B. (1984). Fish nursery use in Georgia salt marsh estuaries: the influence of springtime freshwater conditions. *Transactions of American Fisheries Society* 113, 595–606.
- Rozas, L. P. (1995). Hydroperiod and its influence on nekton use of the salt-marsh: a pulsing ecosystem. *Estuaries* 18, 579–590.
- Rozas, L. P., & Hackney, C. T. (1984). Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. *Estuaries* 7, 213–224.
- Rozas, L. P., & Minello, T. J. (1998). Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bulletin of Marine Science* 63, 481–501.
- Rozas, L. P., & Odum, W. E. (1987). The role of submerged aquatic vegetation in influencing the abundance of nekton on contiguous tidal fresh-water marshes. *Journal of Experimental Marine Biology Ecology* 114, 289–300.
- Shaw, R. F., Cowan, J. H. Jr., & Tillman, T. L. (1985). Distribution and density of *Brevoortia patronus* (gulf menhaden) eggs and larvae in the continental shelf waters Louisiana. *Bulletin of Marine Science* 36, 96–103.
- Shaw, R. F., Wiseman, W. J. Jr., Turner, R. E., Rouse, L. J. Jr., & Condrey, R. E. (1985). Transport of larval gulf menhaden *Brevoortia patronus* in continental shelf waters of western Louisiana: a hypothesis. *Transactions of American Fisheries Society* 114, 452–460.
- Sheridan, P. F. (1983). Abundance and distribution of fishes in Galveston Bay system, 1963–1964. *Contributions in Marine Sciences* 26, 143–163.
- Subrahmanyam, C. B., & Coultas, C. L. (1980). Studies on the animal communities in two north Florida salt marshes. Part III. Seasonal fluctuations of fish and macroinvertebrates. *Bulletin of Marine Science* 30, 790–818.
- Thiel, R., & Potter, I. C. (2001). The ichthyofaunal composition of the Elbe Estuary: an analysis in space and time. *Marine Biology* 138, 603–616.
- Weaver, M. J., & Magnuson, J. J. (1993). Analyses for differentiating littoral fish assemblages with catch data from multiple sampling gears. *Transactions of the American Fisheries Society* 122, 1111–1119.
- Weinstein, M. P. (1979). Shallow marsh habitats as primary nursery for fishes and shellfish in Cape Fear River estuary, North Carolina, USA. *US Fish and Wildlife Service Fishery Bulletin* 77, 339–357.
- Weinstein, M. P., Weiss, S. L., & Walters, M. F. (1980). Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, USA. *Marine Biology*: 58, 227–243.
- Welsh, B. L. (1975). The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. *Ecology* 56, 513–530.
- West, R. J., & King, R. J. (1996). Marine, brackish, and freshwater fish communities in vegetated and bare shallows of an Australian coastal river. *Estuaries* 19, 31–41.
- Whitfield, A. K. (1999). Ichthyofaunal assemblages in estuaries: a South African case study. *Reviews in Fish Biology and Fisheries* 9, 151–186.
- Winer, B. J. (1962). *Statistical principles in experimental design*. New York: McGraw-Hill.
- Wood, C. E. (1967). Physioecology of the grass shrimp, *Palaemonetes pugio*, in the Galveston Bay estuarine system. *Contributions in Marine Science* 12, 54–79.
- Yoklavich, M. M., Cailliet, G. M., Barry, J. B., Ambrose, D. A., & Antrim, B. S. (1991). Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. *Estuaries* 14, 465–480.
- Zimmerman, R. J., & Minello, T. J. (1984). Densities of *Penaeus aztecus*, *Penaeus setiferus* and other natant macrofauna in a Texas salt marsh. *Estuaries* 7, 421–433.