HABITAT USE AND DIETS OF JUVENILE SPOT (*LEIOSTOMUS XANTHURUS*) AND ATLANTIC CROAKER (*MICROPOGONIAS UNDULATUS*) IN A SMALL ESTUARY AT MAD ISLAND MARSH, TEXAS

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ABSTRACT.–Spatial and temporal variation in feeding of immature stages (10-130 mm standard length) of two sciaenids, spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*), was investigated at Mad Island Marsh on the Texas Gulf coast from March 1998 through August 1999. Periods of peak abundance of each species were different (December for croaker, March for spot). The two species were dissimilar in diet and habitat use along the longitudinal gradient of a small estuary, except for the winter months of both years when postlarvae dominated samples and dietary overlap was high. Low dietary overlap occurred despite the fact that both species consumed mostly benthic organisms (amphipods, gastropods, nematodes, polychaetes), pelagic copepods, and detritus. Overall, spot consumed greater proportions of copepods, nematodes and chironomid larvae, and croakers had broader diets that included most of the abundant invertebrates in the habitat (e.g., amphipods, shrimp, blue crabs) plus smaller percentages of fish. Regardless of season and body size, the spot diet was dominated by copepods and nematodes. The croaker had a more pronounced ontogenetic diet shift, with the smallest size classes (10-25 mm) consuming mostly copepods, and larger juveniles having diets dominated by amphipods, polychaete worms, shrimp, crabs, and fish. Ontogenetic diet shifts resulted in low interspecific dietary overlap among larger size classes when they co-occurred in the estuary, which could be interpreted as niche complementarity in response to competition past or present.

Many marine fishes enter productive estuarine habitats to forage on abundant zooplankton, meiofauna, molluscs, crustaceans and fishes. Seagrass beds and brackish marshes are particularly important habitats for early life stages of estuarine-dependent marine fishes (Thiel & Potter 2001; Ross 2003; Dahlgren et al. 2006; Sheppard et al. 2011). Along the U.S. southeastern Atlantic coast and the northern Gulf of Mexico, two sciaenid species, the spot (*Micropogonias undulatus*) and Atlantic croaker (*Leiostomus xanthurus*), are among the most widespread and abundant fishes in

shallow estuarine habitats (McErlean et al. 1973; Shenker & Dean 1979; Cowan & Birdsong 1985; Paperno et al. 2001; Akin et al. 2003; Jung & Houde 2003; Ross 2003; Nemerson & Able 2004). Spot spawn offshore from December through May, and larvae are transported by inshore currents into shallow estuaries (Chao & Musick 1977; Pattillo et al. 1997). The spot has been characterized as an opportunistic trophic generalist (e.g., Currin et al. 1984), a selective predator (e.g., Nelson & Coull 1989), or both (e.g., O'Neil & Weinstein 1987). Larvae feed on zooplankton, fish eggs and invertebrates; postlarvae and juveniles consume copepods, nematodes and polychaete worms; and adults consume mostly amphipods, polychaetes, mysid shrimp, and mollusks (Roelofs 1954; Parker 1971; Sheridan 1979; Hodson et al. 1981; Govoni & Chester 1990; Pattillo et al. 1997; Street et al. 1998; Nemerson & Able 2004; Zapfe & Rakocinski 2008).

Atlantic croakers spawn in coastal waters of the northern Gulf of Mexico from September to May, depending on the region, and postlarvae are transported into estuaries where they take residence in marshes and seagrass beds. Larvae and early juveniles feed on zooplankton (Parker 1971; Pattillo et al. 1997; Soto et al. 1998). Older juveniles and adults are reported to feed on polychaetes, mollusks, crustaceans, and fish (Roelofs 1954; Parker 1971; Sheridan 1979; Nemerson & Able 2004). Feeding habits of adults are similar to those of juveniles, but adults ingest larger invertebrates, such as mussels and shrimp, and greater proportions of fish (Overstreet & Heard 1978).

Here we examine temporal and spatial patterns of occurrence, population size structure, and feeding ecology of spot and Atlantic croaker, the two most abundant sciaenids at Mad Island Marsh on the Texas Gulf coast. We surveyed a small estuary fringed with salt marsh that drains into eastern Matagorda Bay. Two previous studies compared diets of spot and croaker in Gulf estuarine habitats; Darnell (1958) investigated Lake Pontchartrain, Louisiana, and Parker (1971) studied Lake Borgne, Louisiana and Clear Lake/Galveston

Bay, Texas. Both of those studies described the two species as having generalist diets that overlapped broadly and seemed to reflect non-selective feeding. While acknowledging differences in foraging behavior (Roelofs 1954), both of these authors, nonetheless, concluded that high dietary overlap results in food resource competition between the spot and croaker. The current study examines similarities and differences in temporal and spatial patterns of occurrence, population size structure, and feeding ecology of spot and Atlantic croaker in Mad Island Marsh to assess potential niche overlap.

MATERIALS AND METHODS

Study system and field sampling.—The field study was conducted at Mad Island Marsh Preserve (MIM), a small polyhaline estuary that drains into the eastern portion of Matagorda Bay, Texas, located on the northwestern coast of the Gulf of Mexico (Fig. 1). A detailed description of the estuary, including a map and values for physicochemical variables, appears in Akin (2001) and Akin et al. (2003). Aquatic habitats of MIM consist of freshwater marshes that drain into a shallow (≤ 0.75 m) mesohaline lake (survey sites 1-5 were positioned along a longitudinal transect through the lake) fringed with salt marsh and a polyhaline tidal creek (site 6) that connects the lake with Matagorda Bay. Smooth cordgrass *(Spartina alterniflora)* and gulf cordgrass *(Spartina spartinae)* are dominant aquatic macrophytes of the salt marsh. Submergent aquatic vegetation, especially widgeon grass *(Ruppia maritima)* and *Chara* sp., occurs seasonally and was especially dominant at the upper portion of the mesohaline region of the lake (sites 1-3). The substrate at sites 1-5 was a mud-sand mixture covered by an approximately 5-cm layer of decomposing vegetation. The substrate at site 6 was mud, sand, and crushed oyster shell. Small patches of oyster reef also were present at sites 4 and 5.

Fishes were collected bimonthly from March 1998 through August 1999 from six sites located along the longitudinal estuarine
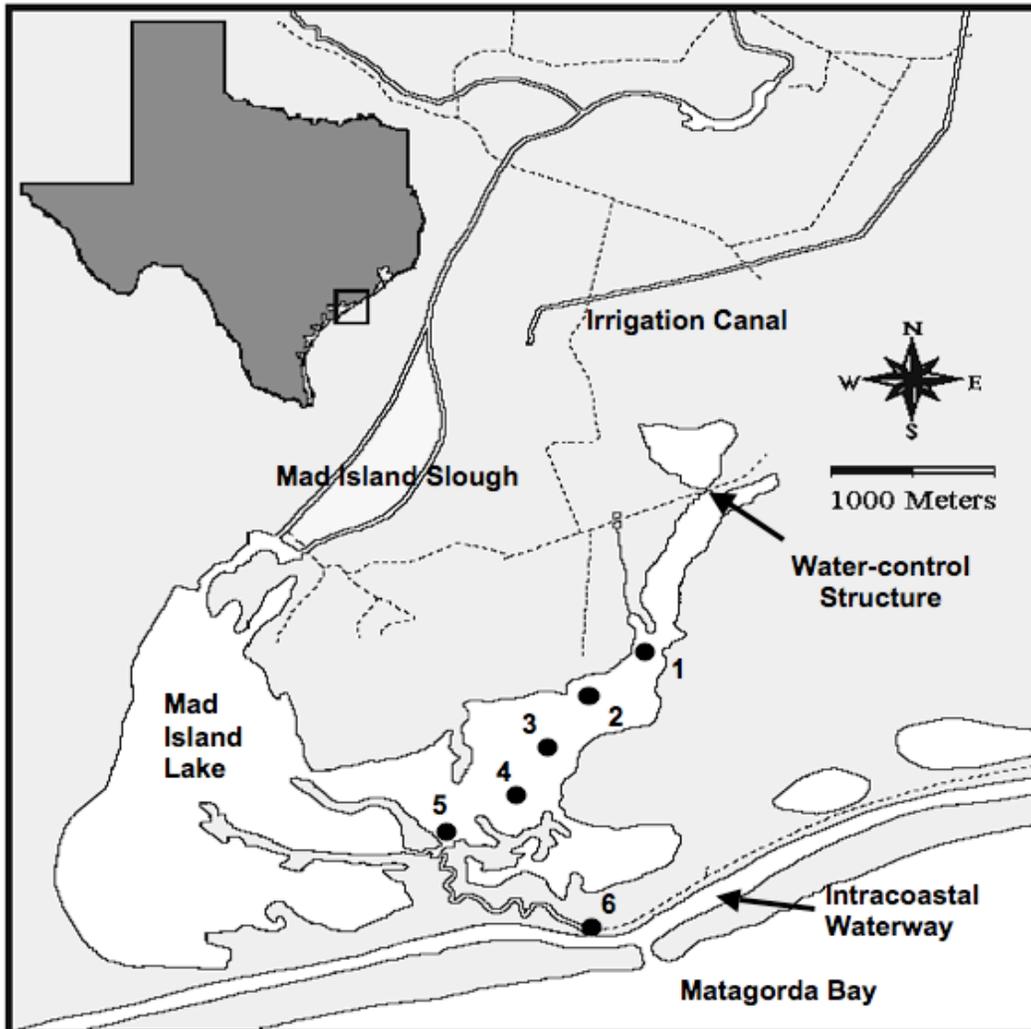
Figure 1. Map of study area at Mad Island Marsh on the edge of Matagorda Bay on the Texas Gulf Coast. Survey sites (black dots) are located along a natural fluvial gradient.

gradient using a bag seine (6 m x 1.2 m, 4.5 mm mesh, bag 1.2 x 1.2 m). Seine hauls were perpendicular to the shoreline, and the distance of each haul (range 20-40 m) was recorded in order to calculate catch per unit effort (CPUE) of fishes. All captured specimens of spot and Atlantic croaker were anesthetized in MS 222 and then fixed in a 10% formalin solution in the field. On each survey date, water depth and physicochemical variables were recorded and multiple benthic invertebrate samples were collected at each survey site with a drop

sampler, and those data are reported in Akin (2001) and Akin & Winemiller (2006).

Laboratory analyses.–In the laboratory, specimens of the two fish species were identified, counted, measured (SL to nearest 0.1 mm), and weighed (to nearest 0.1 g). When sufficient specimens were present in a given survey sample, at least 30 individuals were dissected for stomach contents analysis. When a sample contained >30 specimens, individuals were selected for dissection so that size classes were represented in proportions approximating those in the field sample. Water displacement methods for volumetric estimation of items contained in stomachs followed those described in Akin (2001) and Winemiller et al. (2007).

Data analyses.–For each species, abundance in seine samples was compared according to sampling site and period using the Kruskal-Wallis test (H). Tukey's 1 degree of freedom test was used to test the possible interaction between the fixed factors 'site' and 'month' (the latter were treated as independent samples given that consecutive surveys were separated by 1-2 mo.). No site x month interaction was detected for either species.

In order to ascertain whether a given sample for a species and size class adequately described diet, the number of food items was plotted against sample size to produce an accumulation curve (Toepfer and Fleeger 1995). The sample size needed to represent diet diversity reliably is the value where the curve begins to approach an asymptote. For the purpose of constructing diet accumulation curves, 50 gut contents samples from each species were randomly selected for plotting, and food categories were tallied based on the highest level of taxonomic resolution. Accumulation curves attained asymptotes at 21 and 16 food categories corresponding to 28 and 37 individual croaker and spot, respectively (Fig. 2).

The percentage relative importance value (PRIV) (Coetzee 1986; Mariani et al. 2002) was used to determine the dietary importance of
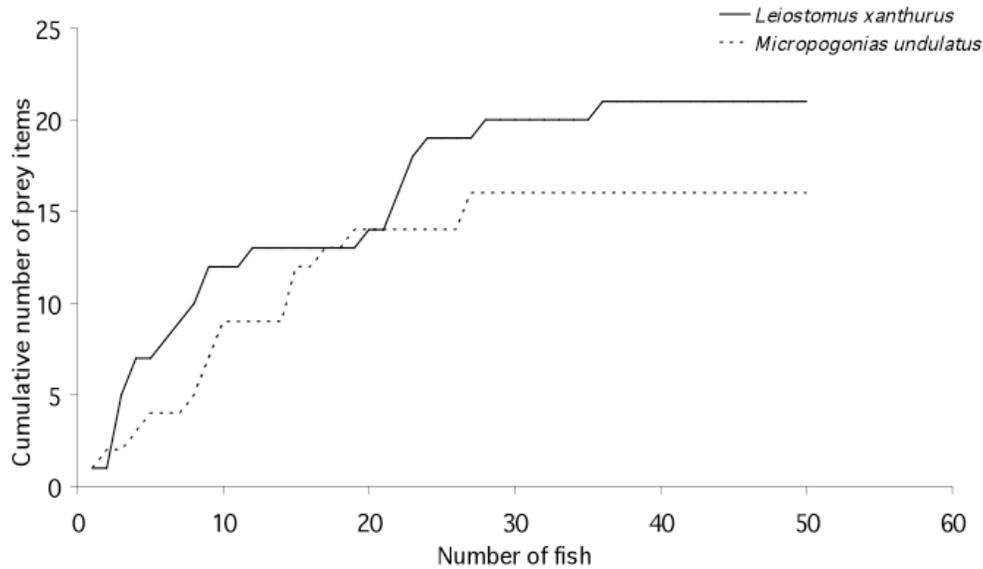
Figure 2. Dietary richness accumulation curves as a function of sample size for spot and Atlantic croaker.

individual food items. PRIV is a derivation of the relative importance index that accounts for both frequency of occurrence and volume of food items; PRIV is standardized on a percentage scale that yields values from 0 to 100 for enhanced between-group comparisons. The *PRIV* of the ith prey item is given by:

$$PRIV_i = 100 V_i(\%) F_i(\%) \left[\sum_i^n V(\%) F(\%) \right]^{-1}$$

where $V_i(\%)$ is the volumetric percentage of each prey item relative to the total volume of all prey items in a sample of consumer stomach contents. $F_i(\%)$ is the percentage occurrence of each prey item relative to the total occurrence of all prey items in stomachs.

Diets of both species were analyzed using canonical correspondence analysis (CCA; ter Braak et al., 1986). CCA is a direct ordination technique designed for analysis the relationship

between the observations (in this case samples of a given species obtained at a given site on a given date) and a set of variables that could be correlated with patterns among the observations (ter Braak & Verdonschot 1995). In the present study, CCA assessed the multivariate diet response by each sample to a number of potential explanatory variables. Prey data were converted to relative values (% of diet by volume) for each sample and subsequently arcsine square-root transformed, which is suitable for percentages and proportions (Zar 1996) to normalize data and to reduce heterogeneity of variance. Mean fish size and mean depth of the water were input as continuous variables, whereas the month and site of collection were regarded as categorical variables. Month and site were recorded as sets of dummy variables (Legendre & Legendre 1998). The most important explanatory variables were identified using a forward selection procedure (ter Braak & Verdenschot 1995). Each variable to be included in the model was tested for significance (5% significance level) using a Monte Carlo permutation test. CCA was performed using CANOCO (version 4.5).

Diet breadth (B), an index of diet diversity, was calculated using Levins' (1968) measure:

$$B = \left[\sum_{i=1}^{n} p_i^2 \right]^{-1}$$

where p_i is the volumetric proportion of food category i in the diet and n is the number of food categories in the diet. B values vary from 1.0 (when the species uses for one resource category exclusively) to the number of all resource categories (when the species uses all categories in equal proportions). Levins's standardized index of niche breadth (B_A) was also calculated:

$$B_A = \frac{B-1}{n-1}$$

where B is Levins' niche breadth and n is the maximum number of

food categories. B_A provides a measure of the evenness of prey utilization (Hurlbert 1978).

Dietary similarity (dietary niche overlap) was calculated between samples based on species, site, and sampling period. Schoener's (1970) percent similarity index (θ_{xy}) was used to quantify dietary overlap between two species:

$$\theta_{xy} = 1 - 0.5\left(\sum_{i=1}^{n} P_{xi} - P_{y_i}\right)$$

where P_{xi} and P_{yi} are the volumetric proportions for the ith food category for consumer samples x and y, respectively. Overlap values range from 0 (no overlap) to 1 (complete overlap). The same index was used to indicate similarity in habitat use based on species abundance data from zones of the estuary during specified periods (in this case, P_{xi} and P_{yi} correspond to the proportional use of the ith habitat zone for species samples x and y).

RESULTS

Spatial and temporal patterns of abundance.–Spot and Atlantic croaker abundance in seine samples from MIM showed large temporal variation (Fig. 3). Spot abundance was significantly higher during March than October, December, and August ($H= 32.05$, $P< 0.001$). Site 4 (mid-lower reach of the estuary and adjacent to the tidal creek) yielded the most individuals, however between-site differences in abundance were not statistically significant. Croakers were more abundant during December than May, August, October, and July ($H= 38.71$, $P< 0.001$). Sites 3, 4 and 5 (mid-lower estuary but not adjacent to the tidal creek) yielded more croakers than other sites, however, none of the between-site statistical comparisons were significant (Fig. 3). Overall, there was low spatial variation in abundance within and between these species, however temporal variation was large, with croakers having greatest abundance in the system during winter and spot having greatest abundance in spring.
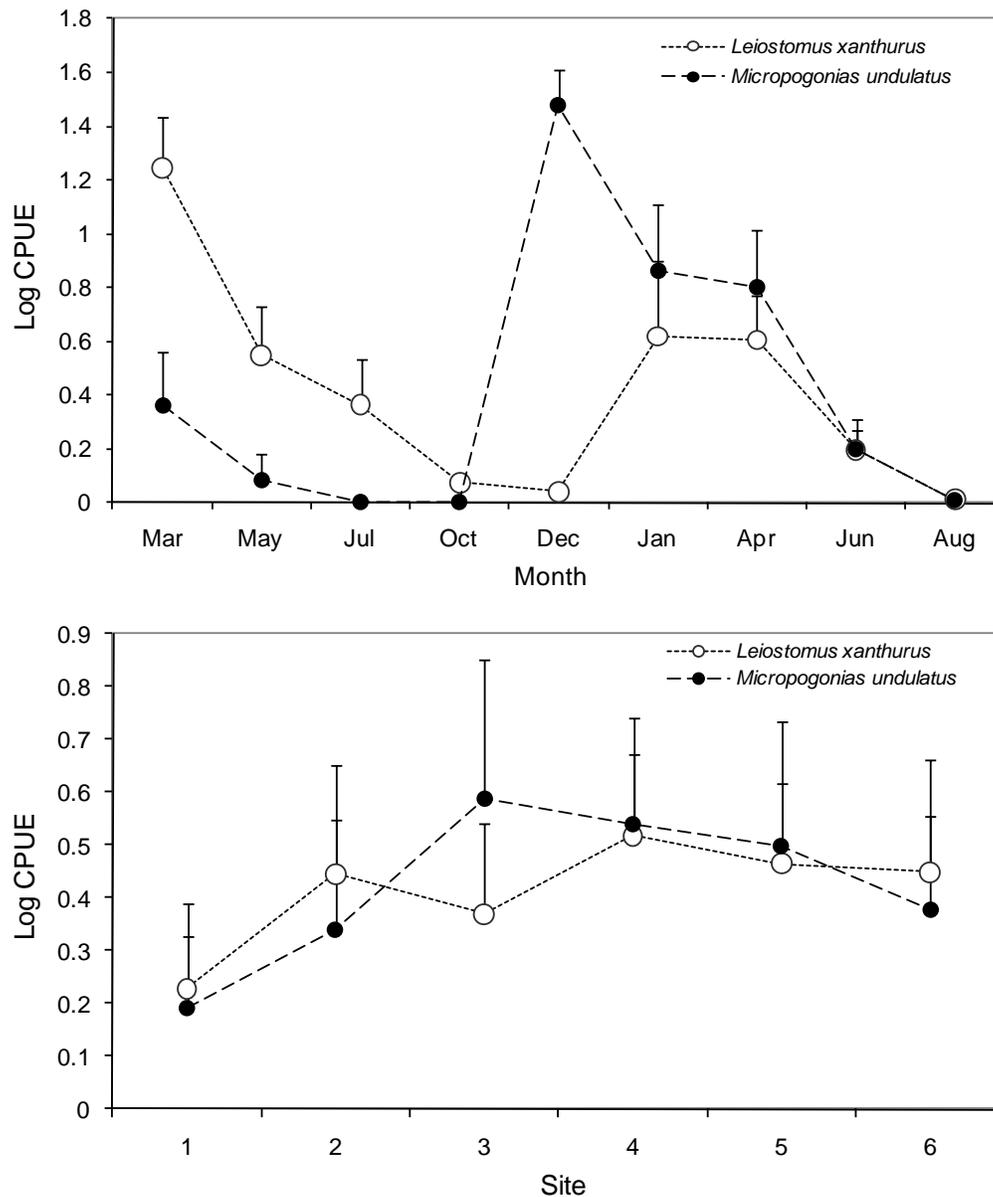
Figure 3. Temporal (top) and spatial (bottom) variation in abundance of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, at Mad Island Marsh. Site 1 is located at the top of the estuarine gradient and site 6 is located near the outlet to Matagorda Bay.

Dietary patterns.–From the total catches of Atlantic croaker (3,004) and spot (1,361), subsamples of 514 and 538 specimens of croaker and spot, respectively, were selected for stomach contents analysis. Size distributions of specimens selected for dissection were

proportional to size distributions of the overall catch for each survey period (Fig. 4). The standard length of individuals dissected for stomach contents analysis ranged from 11.8 to 180 mm for croaker, with a mean of 29.9 mm ($\pm$16.6 SD), and from 10.7 to 135 mm for spot, with a mean of 38.7 mm ($\pm$15.6). The most abundant size interval for the croaker was 15-35 mm (365 individuals), and for spot was 15-35 mm (398 individuals). The overall percentage of empty stomachs was 13.4% for croaker and 8.4% for spot (Table 1). The croaker diet consisted of 41 food categories compared to 50 for spot. The mean number of food categories per stomach was 1.7 $\pm$1.9 for croaker and 3.2 $\pm$1.8 for spot (Table 1). Despite these differences in number of food categories, diet diversity and evenness were similar for the two species, with B= 9.25 and B_A= 0.21) for croaker overall, and B= 9.74 and B_A= 0.18) for spot overall (Table 1).

Overall, copepods (PRIV= 23.1%), detritus (PRIV= 20.4%), chironomid larvae (PRIV= 18.3%), amphipods (PRIV= 13.4%), shrimps (PRIV= 8.5% consisting of approximately equal amounts of palaemonids and penaeids), polychaetes (PRIV= 8.4%), and fish (PRIV= 3.35%) were the principal food items consumed by croakers (Table 1). Some of the same food items dominated the diet of spot but to different magnitudes, e.g., copepods (PRIV= 31.4%), chironomid larvae (PRIV= 7.4%), and detritus (PRIV= 4.4%). The most important food item for spot was nematodes (PRIV= 47.3%), a food item that was relatively unimportant for croakers (PRIV= 0.75%) (Table 1).

The mean volume of stomach contents of spot changed significantly over time (F= 2.76, P< 0.01), with the highest (0.008 ml $\pm$ 0.003) and lowest (0.002 ml $\pm$ 0.004) values obtained for April-June and December-January, respectively (Table 2). Mean volume of stomach contents of Atlantic croakers also changed significantly over time (F= 38.00, P< 0.0001), with mean volume highest in July (0.32 $\pm$0.43 SD) and lowest during December (0.002 $\pm$0.006) (Table 2). The highest percentage of the empty stomachs was encountered during December for both species (Table 2). No empty stomachs
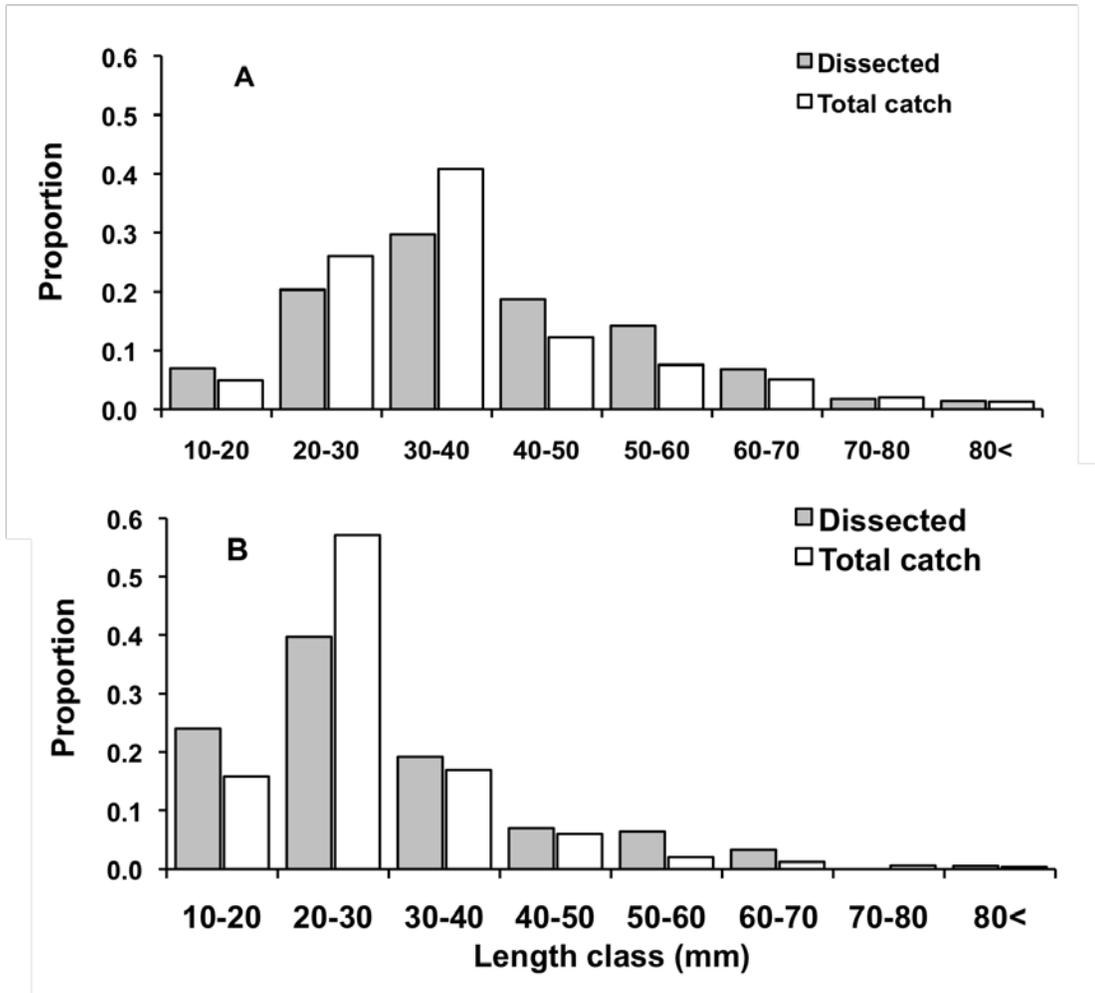
Figure 4. Length frequency histogram of spot (A) and Atlantic croaker (B) specimens analyzed for stomach contents and specimens in the field samples from which those were selected.

were encountered among spot specimens collected during June or among croaker specimens collected during July and May (Table 2). The mean number of food items recovered from the spot stomachs also showed significant seasonal variation ($F= 24.49$, $P< 0.0001$), with the values ranging from 2.7 (±1.9) to 4.55 (±2.2) for December and May, respectively (Table 2). The monthly mean number of food items from croaker stomachs varied from 0.8 (±0.45) to 3.9 (±1.5)

Table 1. Volumetric percentage (VP) and frequency of occurence (FO) of aggregated prey items consumed by spot (*L. xanthuru*s) and Atlantic croaker (*M. undulatus*) at Mad Island Marsh.

Food item	*Leiostomus xanthurus*			*Micropogonias undulatus*		
	VP(%)	FO(%)	PRIV (%)	VP(%)	FO(%)	PRIV (%)
Detritus	**6.59**	**26.77**	**4.43**	**5.22**	**33.03**	**20.44**
Algae	**0.57**	**17.44**	**0.13**	**0.03**	**2.47**	**<0.01**
diatoms	0.34	12.17	0.10	0.01	2.02	<0.01
other algae	0.22	5.27	0.03	0.02	0.45	<0.01
Protozoa	**2.85**	**21.30**	**0.00**	**0.02**	**1.80**	**<0.01**
Nematoda	**24.17**	**78.09**	**47.41**	**0.33**	**19.10**	**0.75**
Crustacea	**28.76**	**82.96**	**33.11**	**60.65**	**86.07**	**47.30**
Amphipoda	1.71	2.64	0.11	7.19	15.73	13.41
Ostracoda	0.03	1.01	0	0	0	0.00
Isopoda	0.01	0.41	0.00	9.93	0.45	0.53
Copepoda	22.59	55.38	31.41	3.74	52.13	23.13
Mysidacea	0.18	0.41	<0.01	0.38	1.80	0.08
Palaemonidae (*P. pugio*)	1.08	0.20	0.01	5.60	6.29	4.18
Penaeidae	3.03	20.69	1.57	4.14	8.99	4.40
Portunidae (*C. sapidus*)	0.00	0.00	0.00	29.55	0.45	1.57
(*Brachyura* sp.)	0.15	2.23	0.01	0.12	0.22	<0.01
Annelida	**1.55**	**5.27**	**0.11**	**11.23**	**7.64**	**8.45**
Polychaetes	0.52	2.23	0.03	10.49	6.74	8.37
Oligochaetes	1.03	3.04	0.08	0.74	0.90	0.08
Insecta	**19.60**	**42.60**	**9.26**	**8.21**	**33.03**	**19.60**
Diptera (chrinomid larvae)	13.31	22.11	7.39	6.09	25.39	18.32
other Diptera	5.49	12.37	1.71	1.74	5.84	1.20
unidentified insects	0.79	8.11	0.16	0.38	1.80	0.08
Mollusca	**5.51**	**51.93**	**3.58**	**1.14**	**5.62**	**0.09**
Bivalvia	3.28	25.56	2.10	0.14	3.82	0.06
Gastropoda	2.23	26.37	1.48	0.01	1.57	0.00
other mollusks	0	0	0	0.98	0.22	0.03
Chordata	**9.02**	**7.71**	**0.17**	**13.12**	**5.84**	**3.35**
Teleostei *(B. patronus)*	0	0	0	10.28	1.57	1.92
Teleostei *(M. cephalus)*	8.58	0.41	0.09	0	0	0
other fishes	0.44	7.30	0.08	2.84	4.27	1.44
unidentified material	**5.60**	**39.96**	**2.07**	**0.13**	**5.39**	**0.01**
mean std. length (mm ± s.d.)	38.7 ±15.6			29.9 ±16.6		
stomachs examined	538			514		
empty stomachs	45			69		
mean volume/stomach (ml)	0.05 ±0.01			0.09 ±0.05		
diet breadth	9.7 (0.18)			9.25 (0.21)		
dietary overlap			0.27			

Table 2. Temporal variation in feeding indices of *Leiostomus xanthurus* and *Micropogonias undulatus* from Mad Island Marsh. ± indicates standard deviation; values in parentheses are standardized values of Levin's diet breadth.

Month	*Leiostomus xanthurus*					Between - species dietary overlap	*Micropogonias undulatus*				
	Mean standard length (mm)	No. stomachs examined	No. stomachs with food	Mean no. prey items per stomach	Diet breadth (standard)		Mean standard length (mm)	No. stomachs examined	No. stomachs with food	Mean no. prey items per stomach	Diet breadth (standard)
1998											
Mar	32.2 ±2.3	174	167	4.0 ±1.9	4.5 (0.12)	0.29	28.1 ±6.9	61	57	1.8 ±1.2	5.3 (0.36)
May	43.5 ±3.1	58	53	4.5 ±2.2	1.5 (0.03)	0.02	55.9 ±11.0	7	7	3.9 ±1.5	2.6 (0.27)
Jul	51.2 ±2.2	66	57	3.1 ±2.0	3.3 (0.12)	0	163.2 ±7.5	5	5	0.8 ±0.45	1.0 (0.14)
Oct	86.0 ±5.1	12	9	3.2 ±2.1	1.8 (0.10)	-	-	-	-	-	-
Dec	78.7 ±3.3	7	5	2.7 ±1.9	3.0 (0.34)	0.57	23.2 ±6.1	154	116	1.8 ±1.5	3.8 (0.17)
1999											
Jan	20.6 ±2.1	80	69	2.8 ±1.8	3.3 (0.16)	0.27	19.6 ±4.3	123	119	2.5 ±1.5	6.4 (0.30)
Apr	41.9 ±3.8	120	112	3.9 ±1.9	5.1 (0.25)	0.09	38.3 ±14.9	135	116	1.5 ±1.1	5.9 (0.29)
Jun	52.9 ±2.8	21	21	4.4 ±1.9	1.4 (0.04)	0.22	51.0 ±6.2	29	23	1.6 ±1.3	2.4 (0.14)

for July and May, respectively (main effect of month, $F = 6.43$, $P < 0.01$). Spot diet breadth was highest during December and lowest during May (Table 2), whereas the highest and lowest diet breadth for croakers during March and July, respectively (Table 2).

The first two CCA axes together explained 23.7 percent of the variation in the spot diet. The results of CCA indicate that diet of spot partly changed according to season. The first and second axes were strongly influenced by seasons, with April (1999) having the highest loading (0.64) on the first axis and May (1998) having the highest loading (0.62) on the second axis (Fig. 5). Fish size was not strongly correlated with the first two axes. Spot fed on polychaetes, other zooplankton, bivalves, oligochaetes and fish during April (Fig. 5) and on arachnids, nematodes, gastropods and algae during May of the preceding year. Fishes consumed several food resources, including copepods, isopods, diatoms, chironomids and other dipteran larvae, that were not strongly correlated with either axis 1 or 2 and that showed no strong temporal pattern of variation.

The first two CCA axes explained 25.7 percent of variation in the croaker diet, several components of which varied seasonally and according to location along the estuarine gradient. March had the highest loading on axis 1 (0.52) which described a dietary gradient dominated by shrimps and insects. December (-0.63), April (0.47) and June (-0.31) were the survey periods with highest loadings on axis 2 which described a gradient influenced by copepods, dipteran larvae, diatoms, protozoa, fish and bivalves (Fig. 6). Fish size (0.68) and water depth (0.42) also were correlated with axis 2. Croakers were larger during April and June, and they tended to consume more gastropods, polychaetes and isopods (Fig. 6).

Ontogenetic dietary patterns.–The mean volume of stomach contents of spot ranged from 0.0005 (±0.000) to 0.014 (±0.006) ml for size classes of 10-15 and 30-35 mm, respectively (Table 3). The differences in the mean volume of food consumed varied significantly among size classes for spot ($F = 2.22$, $P < 0.025$), but did
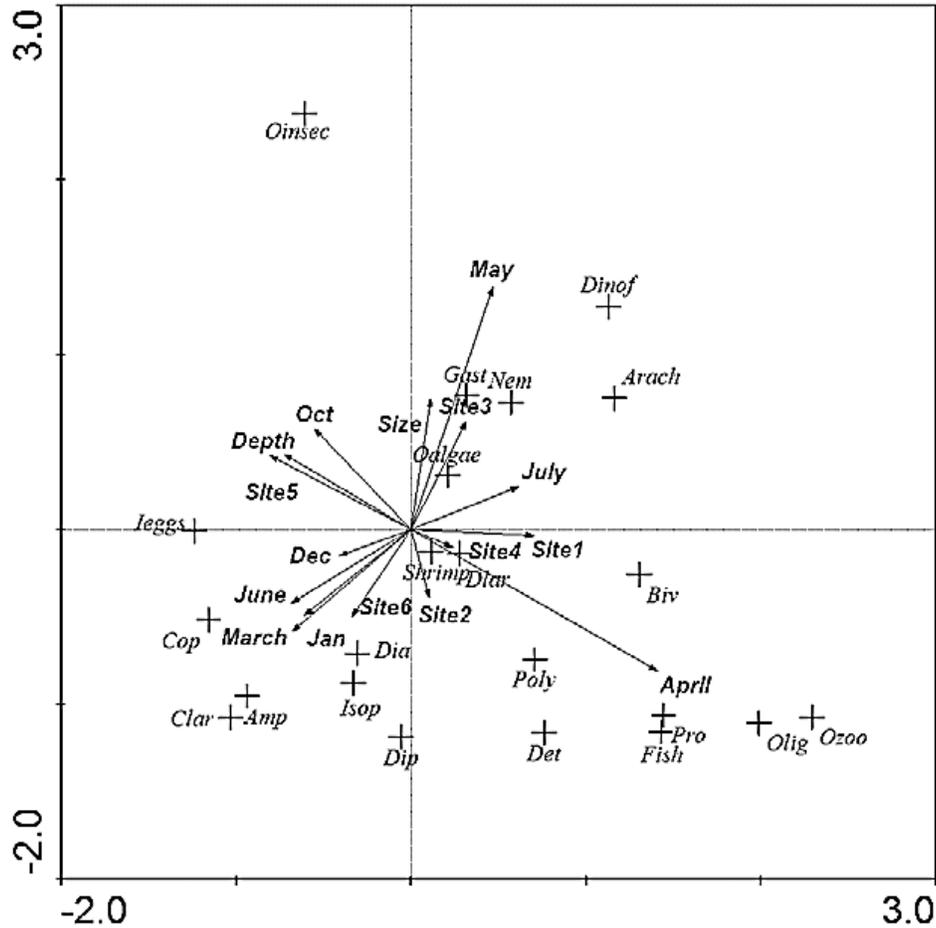
Figure 5. CCA ordination plot based on volumetric proportions of foods consumed by spot at Mad Island Marsh. Diet items were coded as follows: Oinsec: other insect, Dinof: dinoflagellata, Arach: Arachnida, Gast: Gastropoda, Nem: Nematoda, Oalgae: other algae, Ieggs: invertebrate eggs, Shrimp: shrimp, Dlar: Decopada larvae, Biv: Bivalvia, Cop: Copepoda, Amp: Amphipoda, Dia: diatoms, Isopoda: Isopoda, Poly: polychaetes, Det: detritus, Fish: fish, Pro: protozoa, Olig: oligochaetes, Ozoo: other zooplankton, Dip: dipteran larvae, Clar: chironomid larvae. Coordinates at the tips of vectors reveal the magnitudes of variable loadings (correlations) on the x and y axis; sample size for stomach contents analysis: spot = 493, croaker = 445.

not vary significantly for croaker ($F = 1.67$, $P = 0.08$), with the spot values ranging from 0.0004 ml (± 0.001) to 0.042 ml (± 0.175) ml for 10-15 and >65 mm size classes, respectively. The mean number of food items significantly changed with the size of spot ($F = 7.85$, $P < 0.0001$), with the lowest (2.19 ± 0.27) and highest (4.04 ± 0.22) values obtained for size classes 15-20 mm and 40-50 mm, respectively. In
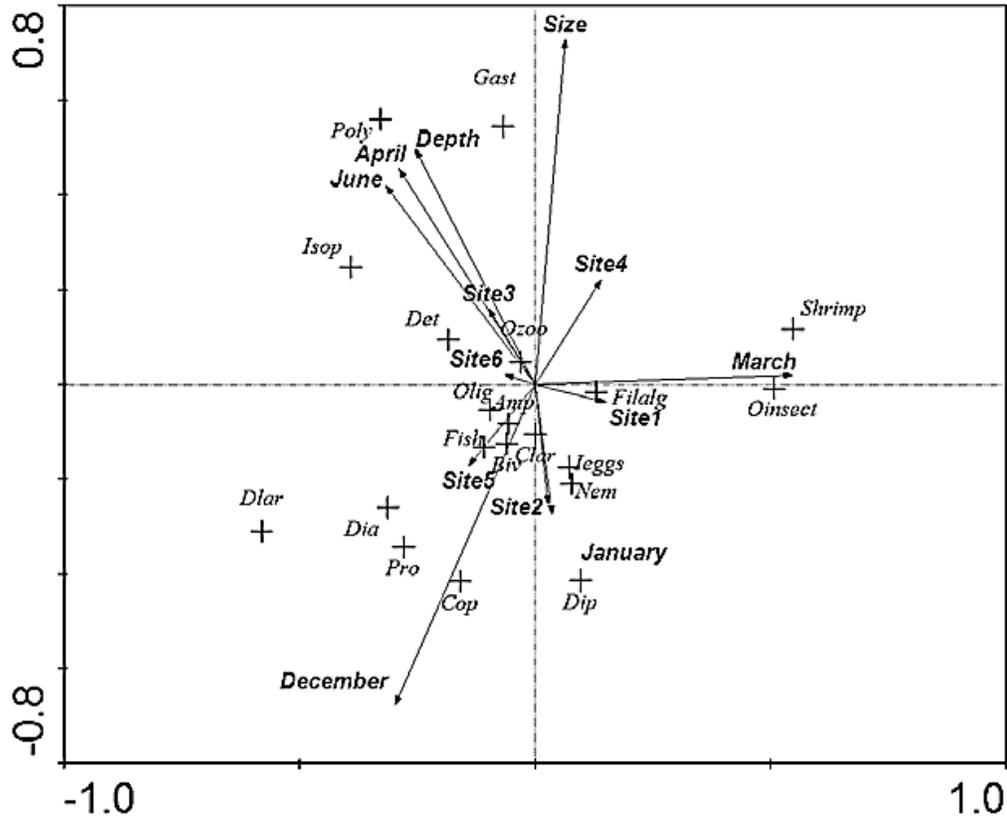
Figure 6. CCA ordination plot based on volumetric proportions of foods consumed by croaker at Mad Island Marsh. Diet items were coded as follows: Oinsec: other insect, Dinof: dinoflagellata, Arach: Arachnida, Gast: Gastropoda, Nem: Nematoda, Oalgae: other algae, Ieggs: invertebrate eggs, Shrimp: shrimp, Dlar: Decopada larvae, Biv: Bivalvia, Cop: Copepoda, Amp: Amphipoda, Dia: diatoms, Isopoda: Isopoda, Poly: polychaetes, Det: detritus, Fish: fish, Pro: protozoa, Olig: oligochaetes, Ozoo: other zooplankton, Dip: dipteran larvae, Clar: chironomid larvae. Coordinates at the tips of vectors reveal the magnitudes of variable loadings (correlations) on the x and y axis; sample size for stomach contents analysis: spot = 493, croaker = 445.

contrast, the mean number of prey items did not change significantly with size for croaker ($F= 1.07$, $P= 0.38$), with mean values ranging from 1.35 ± 0.23 for the 40-45 mm size class and 2.00 ± 0.37 and 2.00 ± 0.68 for the 50-55 and 60-65 mm classes, respectively. Diet breadth of spot decreased from 0.31 for the 1-15 mm size classes to 0.07 for the 60-65 mm size class, and diet breadth of croaker decreased from 0.45 for the 40-45 mm class to 0.10 for the >65 mm size class. The percentage of the empty stomachs was lowest (3.85%) for the

Table 3. Size-based feeding indices of spot (*L. xanthurus*) and Atlantic croaker (*M. undulatus*) from Mad Island Marsh (± indicates standard deviation; values in parentheses are standardized values of Levin's diet breadth).

Length class	*Leiostomus xanthurus*				Between species dietary overlap	*Micropogonias undulatus*			
	No. stomachs examined	No. stomachs with food	Mean no. prey items per stomach	Diet breadth (standard)		No. stomachs examined	No. stomachs with food	Mean no. prey items per stomach	Diet breadth (standard)
10-14.9	13	12	2.5 ±0.4	3.2 (0.31)	0.99	24	23	1.7 ±0.2	2.1 (0.21)
15-19.9	26	25	2.2 ±0.3	3.1 (0.18)	0.93	100	90	1.9 ±0.1	6.2 (0.34)
20-24.9	55	47	2.2 ±0.2	4.15 (0.29)	0.85	124	105	1.8 ±0.1	7.2 (0.28)
25-29.9	58	51	2.9 ±0.2	6.1 (0.25)	0.84	81	66	1.6 ±0.1	7.6 (0.39)
30-34.9	112	106	3.8 ±0.2	5.4 (0.17)	0.57	60	49	1.4 ±0.1	7.6 (0.33)
35-39.9	53	50	3.6 ±0.2	5.8 (0.21)	0.66	39	35	1.7 ±0.2	7.3 (0.42)
40-44.9	51	50	4.0 ±0.2	6.0 (0.22)	0.84	17	15	1.35 ±0.2	4.6 (0.45)
45-49.9	53	46	3.2 ±0.3	4.7 (0.17)	0.89	19	17	1.7 ±0.2	5.5 (0.41)
50-54.9	51	48	3.3 ±0.2	5.0 (0.24)	0.52	23	21	1.5 ±0.3	2.3 (0.16)
55-59.9	28	25	3.9 ±0.3	3.3 (0.23)	0.87	10	9	2.0 ±0.4	3.6 (0.29)
60-64.9	13	0	3.6 ±0.4	1.8 (0.07)	0.81	6	5	2.0 ±0.7	2.65 (0.24)
65<	25	20	2.6 ±0.3	3.15 (0.18)	0.11	11	10	1.55 ±0.5	2.25 (0.10)

15-20 mm size class of spot and highest (20%) for the >65 mm size class. For croaker, the percentage of the empty stomachs ranged from 4.2% to 18.5% for 10-15 and 25-30 mm size classes, respectively (Table 3).

Copepods and nematodes were the most important prey for spot of every size class, with PRIV exceeding 45% in each case. Spot >25 mm also consumed moderate proportions of chironomids, other diptera, gastropods, bivalves, and protozoa, with spot 60-65 mm SL consuming comparatively high volumetric percentages of juvenile mullet. Copepods were also important prey for croakers <30 mm (PRIV > 40%). For croaker size classes between 30 and 60 mm SL, food categories with relatively high PRIV (>20%) were amphipods, isopods, grass shrimp, and polychaete worms. Croakers >65 mm consumed large percentages (PRIV >25%) of menhaden and other fishes.

Niche overlap.–Overall dietary overlap (similarity) between spot and croaker was highest during December, reflecting a predominance of copepods and detritus in diets of both species (Fig. 7). Lowest dietary overlap occurred during late spring and summer (April–July), however few croakers were collected from May to July. Low dietary overlap also was observed during January–March, a period when the two species consumed different volumetric percentages of copepods, amphipods, nematodes, and detritus.

Throughout the year, interspecific habitat overlap, calculated based on species abundance data from the six survey sites along the longitudinal estuarine gradient, tended to be higher than dietary overlap (Fig. 7). December was the exception; during this month interspecific habitat overlap was low and dietary overlap was high, a pattern suggesting niche complementarity. Highest habitat overlap was during April, a period when both species were abundant in the system and dietary overlap was low.

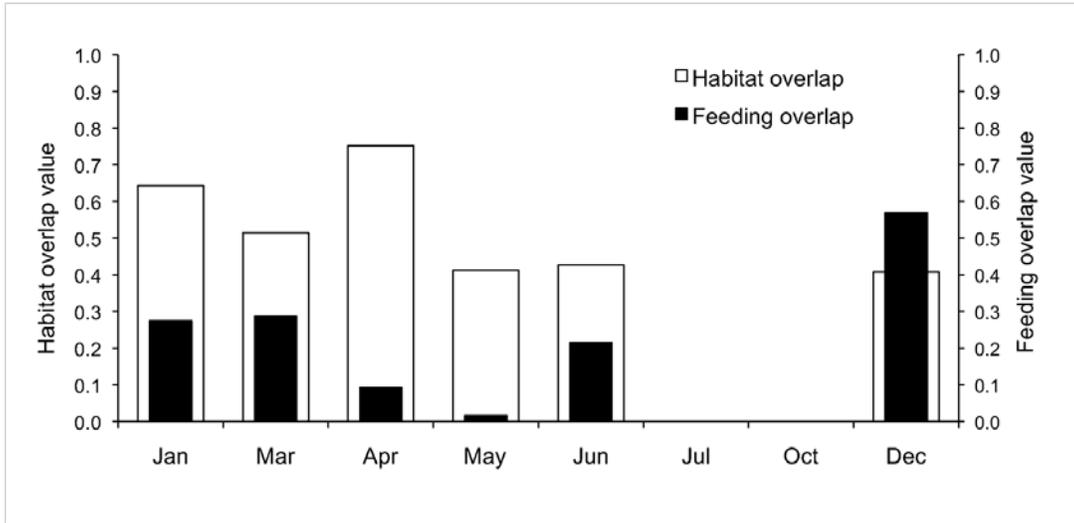Spatio-temporal variation in dietary similarity was examined at a

Figure 7. Monthly variation in dietary and habitat overlap between spot and Atlantic croaker at Mad Island Marsh. No croakers were captured between July and October.

Table 4. Spatio-temporal variation in dietary overlap of spot (*L. xanthurus*) and Atlantic croaker (*M. undulatus*) at Mad Island Marsh.

Month	Site					
	1	2	3	4	5	6
Mar	-	0.21	0.38	0.31	-	-
May	-	-	0.03	-	-	-
July	-	-	-	-	-	-
Oct	-	-	-	-	-	-
Dec	-	0.68	0.38	-	-	-
Jan	-	0.30	-	0.40	0.23	0.21
Apr	0.00	0.05	0.14	0.08	0.26	0.02
June	-	-	0.45	-	0.14	<0.01
Aug	-	-	-	<0.01	-	-

finer scale of resolution by calculating between-species overlap using site-specific data for each survey month. Overall, these overlap values were moderate to low (Table 4). The highest value (0.68) was obtained for December at site 2, whereas the lowest (<0.01) was obtained for April and August at sites 1 and 4.

DISCUSSION

Many, if not most, estuarine-dependent fish species enter estuaries as postlarvae and use brackish estuarine habitats, including oligohaline upper reaches, as nursery grounds (Shenker & Dean 1979; Weinstein 1979; Currin et al. 1984; Rogers et al. 1984; Sheridan et al. 1984; Nemerson & Able 2004). Spot and Atlantic croaker provide clear examples of this life history strategy. The use of upper estuarine reaches by these sciaenids during their early life stages could be due to preferences for low salinities (Miglarese et al. 1982; Rogers et al. 1984) and physically complex habitats that provide cover from predators (Ross 2003). These species' broad salinity tolerances and occurrence of juveniles of both species in open water habitats have been documented (Diaz 1982; Hales & Van Den Avyle 1989), however, for spot in particular, larger individuals tend to occur in deeper habitats. Another factor could be high availability of food resources in productive estuarine habitats (Weinstein 1979; Diaz 1982). Densities of zooplankton and infauna, two important food resources for postlarvae and small juveniles, were higher at the oligohaline upper sites of MIM (e.g., annual mean density of organisms from a drop sampler at sites 1-4 averaged 549.7 m^{-2} compared to 379.5 m^{-2} in samples from more saline lower sites 5 and 6; Akin 2001). The abundance of both species was positively associated with relatively low salinity, beds of submerged macrophytes, and high abundance of benthic invertebrates that are potential prey, and a manipulative experiment would be required to determine which variable had strongest influence.

The diet of spot at MIM changed over the course of the annual cycle, which is consistent with studies from other locations that reveal ontogenetic niche shifts in this species (summarized in Hales & Van Den Avyle 1989). Larvae and postlarvae feed on zooplankton, mainly pelagic copepods (Govoni & Chester 1990, Ocaña-Luna & Sanchez-Ramirez 1998), whereas juveniles are demersal and have been reported to consume mostly mollusks, crustaceans, nematodes, and polychaete worms (Livingston 1984;

Nemerson & Able 2004; Zapfe & Rakocinski 2008). Spot postlarvae at MIM fed mostly on calanoid copepods soon after their arrival in the estuary during winter; however, consumption of polychaetes during the demersal postlarval and juvenile stages was uncommon. The low consumption of polychaete worms by this species likely resulted from low abundance of polychaetes in the upper oligohaline reaches of the estuary (Akin, 2001; Akin & Winemiller 2006). Densities of polychaete worms were greater (annual mean density= 42.6 m^{-2} at sites 5-6) in sediment from drop samples taken from lower estuarine reaches, where spot were less abundant, compared with polychaete densities at upper sites (annual mean density= 29.8 m^{-2} at sites 1-4) (Akin 2001; Akin & Winemiller 2006). Instead, juvenile spot at MIM mostly consumed nematodes, copepods (calanoid and harpactacoid), and chironomid larvae.

Atlantic croakers at MIM revealed stronger ontogenetic dietary shifts than spot. Young croakers have been reported to feed on copepods, mysids and polychaete worms, and larger individuals feed principally on macrocrustaceans (shrimps and crabs), mollusks (snails and bivalves), and fish (Sheridan 1979; Sheridan et al. 1984; Soto et al. 1998). Mercer (1989) reported that small juvenile Atlantic croakers (15-30 mm), which have already shifted to a demersal mode, fed mostly on zooplankton and later shift to feeding on infaunal and epibenthic organisms. During December and January, when croakers at MIM averaged about 20 mm, the main diet items were harpactacoid copepods, amphipods, and immature aquatic insects (mainly chironomid and other dipteran larvae). During the spring and early summer, croakers grew and their gape size increased, and this was associated with consumption of greater volumetric percentages of oligochaetes, polychaetes, shrimp, juvenile menhaden, and detritus. Our findings thus imply that both juvenile and subadult croakers are opportunistic and generalist feeders. Regardless of their size, croakers seemed to use pelagic and benthic food resources according to gape size, food particle size, and relative food availability in the habitat. High volumetric proportions of immature insects (mostly chironomid larvae), polychaete and

oligochaete worms in the croaker diet during late spring and summer corresponded with high abundance of these items in sediments samples.   For example croakers consumed large volumes of polychaete worms during April when mean abundance of these worms was high (83.3 m^{-2}) compared to their annual average abundance (34.4 m^{-2}) (Akin 2001; Akin & Winemiller 2006).

The seasonal use of estuaries by migratory fishes and crustaceans has been postulated to reduce the competition for food and space (Miller et al. 1985; Mariani et al. 2002). Time segregation among juvenile marine fishes in estuaries is a function of differential spawning periods and recruitment from coastal marine waters (Mariani et al. 2002; Hagan & Able 2003). In the northern Gulf of Mexico, spot and Atlantic croaker have different peak periods of reproduction that result in different periods of peak abundance of early life stages in shallow estuarine habitats, a pattern that has been noted for these and other estuarine-dependent fishes in other coastal regions of eastern North America (e.g., Weinstein 1983; Hagan & Able 2003).   Postlarval (<30 mm SL) spot appeared in high abundance within upper reaches of MIM during spring (March 1998, April 1999) and abundance of croaker postlarvae peaked in MIM during winter (December 1998, January 1999), a finding similar to those obtained by Parker (1971) from Galveston Bay, Texas. The two species, however, had similar abundance in April. Closer examination of the spatial distribution patterns during April reveal that croakers occurred mainly in the upper reaches of the estuary (sites 3 and 4), while spot were more common in the tidal creek (site 6). Thus there appeared to be a high degree of spatial segregation during the period when these species co-occurred in greatest numbers within the estuary. Low dietary overlap also was observed during these months. A similar pattern of niche complementarity involving diet and habitat was found in a study of sparid fishes inhabiting rocky habitats of the Mediterranean coast (Sala & Ballesteros 1997). *Diplodus puntazzo* and *D. vulgaris* shared the same near-shore habitat but had low dietary overlap, *D. vulgaris* and *D. sargus* had high diet overlap but the latter occurred in the surf zone, and *D.*

puntzzo and *D. sargus* had low overlap in both diet and habitat. Such patterns of niche complementarity imply adaptive responses to interspecific competition, either past or present. It is uncertain whether or not competition currently plays a role in producing patterns of niche complementarity among estuarine fishes. Although estuaries generally are considered to be among the most productive ecosystems and food resources should be abundant, it should be noted that not all food is necessarily available for small fishes, due to constraints of gape size, prey defenses and refugia, and risk sensitive foraging due to the presence of predators. The fact that relatively low numbers of individual prey items were encountered within many spot and croaker stomachs could indicate food limitation during some times and places.

Spot and Atlantic croaker have both been reported to consume detritus (Parker 1971; Sheridan 1979; Sheridan et al. 1984), and detritus was an important food item collected from stomachs of both species in MIM. Although ingested, detritus probably has little nutritional value for these fishes that lack apparent morphological and physiological adaptations for digesting and assimilating plant material. For example the alimentary canals of both species are relatively short and lack structures such as caeca that increase surface area and retention time for digestion and absorption. Even considering the potential for bacteria and fungi to be associated with detritus particles and thus provide significant nutritional benefits (Tenore 1983; Wilson 2002), detritus mostly likely was ingested incidentally by spot and croakers while foraging for benthic invertebrates (e.g., nematodes, protozoa, dipteran larvae, polychaete worms, and bivalves).

Fishes commonly undergo shifts in diet composition as they grow (Werner & Gilliam 1984, Ross 1986). Ordination plots of spot and croaker diet composition indicated seasonal patterns of variation, and shifts were strongly associated with changes in the size structure of the two populations. For spot these shifts were smaller and less related to body size, because many important food items (e.g.,

nematodes, copepods, bivalves, gastropods) were consumed through most of the year. The much greater dietary shifts observed in the Atlantic croaker seemed to be related to both body size and patterns of resource availability. Compared to spot, croaker had greater diet breadth during all months except May–July, suggesting that the croaker has more flexible feeding habits that allow response to changes in availability of a wide range of food resources. For example, consumption of polychaetes, blue crabs and menhaden by croakers during spring and early summer reflected the high abundance of these prey items in the drop samples during these periods (Akin 2001).

Smallest juveniles of both species, which were present at MIM during winter and spring months, tended to have broader diets than larger conspecifics that were more common during summer. This pattern could have been influenced by differences in prey availability, gape limitation, or optimal foraging. Optimal foraging theory predicts that consumers select food items that yield highest rates of energy acquisition at lowest cost. Therefore, larger fish can maximize energy intake by increasing their consumption of larger prey (Werner & Hall, 1977). CCA results revealed that spot from different seasons (having different average body sizes) had similar diets. In contrast, larger juvenile croakers consumed larger prey items that are undoubtedly less abundant than small prey but provide higher energetic returns. However, it remains unclear why the spot, a morphologically similar sciaenid, did not switch to larger prey. Competition from the croaker is one possible explanation, however it was already noted that the principal food resources for both species tended to be abundant in benthic samples.   The interspecific difference in proportional mouth width increases during growth, with larger croakers having a larger relative mouth width than larger spot (Chao & Musick 1977). Species differences in foraging efficiency for prey of different sizes based on gape limitation could represent adaptive divergence in response to interspecific competition during one or more periods in the evolutionary histories of the two lineages. Behavior differences, such as differences in the ability to winnow

prey from soft sediments, also could account for observed differences in ontogenetic dietary shifts.

CONCLUSIONS

Diets of both the spot and Atlantic croaker in the MIM estuary were broad with compositions similar to those reported for populations in other estuarine systems in the Gulf of Mexico (Sheridan 1979; Sheridan et al. 1984; Govoni & Chester 1990; Ocaña-Luna & Sanchez-Ramirez 1998). Dietary overlap between species was generally low, with the exception being postlarvae that had high interspecific dietary overlap. Temporal niche partitioning was apparent among postlarvae and small juveniles, with the two species having different periods of recruitment into the estuary. Larger size classes present later in the year partitioned both food resources and habitats along the estuarine longitudinal gradient. Spot revealed lower temporal and spatial diet variation than croaker, and this may be associated with size limitation (spot do not grow as large) or subtle morphological and perhaps behavioral differences. Future studies should examine habitat use and feeding of these species and other sympatric sciaenids using finer scales of resolution for food resources and habitats, as well additional methods for studying trophic ecology, such as stable isotope and fatty acid analyses. Field experiments that manipulate fish densities at different locations along fluvial estuarine gradients while monitoring food resources could reveal changes in fitness or niche shifts in response to competition.

ACKNOWLEDGEMENTS

LITERATURE CITED

Akin, S. 2001. Ecological dynamics of the aquatic community in a Texas coastal salt marsh. PhD Dissertation, Texas A&M University, College Station, Texas, 444 pp.

Akin, S. and K.O. Winemiller. 2006. Seasonal variation in food web composition and structure in a temperate tidal estuary. Estuaries and Coasts 29:552-567.

Akin, S., K.O. Winemiller & F.P. Gelwick. 2003. Seasonal and spatial variation in fish and macrocrustacean assemblage structure in Mad Island Marsh estuary, Texas. Estuar. Coast. Shelf Sci. 56:1-14.

Chao, N.L. & J.A. Musick. 1977. Life history, feeding habits and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. U.S. Fish B-NOAA 75:657-702.

Coetzee, P.S. 1986. Diet composition and breeding cycle of blacktail, *Diplodus sargus capensis* (Pisces: Sparidae), caught off St Croix Island, Algoa Bay, South Africa. S. Afr. J. Zool. 21:237–243.

Cowan, J.H. & R.S. Birdsong. 1985. Seasonal occurrence of larval and juvenile fishes in a Virginia Atlantic coastal estuary with emphasis on drums (family Sciaenidae). Estuaries 8:48-59.

Currin, B.M., J.P. Reed & J.M. Miller. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker, a comparison of tidal and nontidal nursery areas. Estuaries 7:451-459.

Dahlgren, C.P., G.T. Kellison, A.J. Adams, B.M. Gillanders, M.S. Kendall, C.A. Layman, J.A. Ley, I. Nagelkerken & J.E. Serafy. 2006. Marine nurseries and effective juvenile habitats: concepts and applications. Mar. Ecol. Prog. Ser. 312:291-295.

Darnell, R.M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, and estuarine community. Publications of the Institute of Marine Sciences, University of Texas 5:353-416.

Diaz, R.J. 1982. Habitat suitability index models: juvenile Atlantic croaker. U.S. Department of the Interior, Fish and Wildlife Service, FWS/OBS-82/10.21, 22 pp.

Gisbert, E., L.Cardona & F. Castello. 1995. Competition between mullet fry. J. Fish Biol. 47:414-420.

Govoni, J.J. & A.J. Chester. 1990. Diet composition of larval *Leiostomus xanthurus* in and about the Mississippi River plume. J. Plankton Res. 12:819-830.

Hagan, S.M. & K.W. Able. 2003. Seasonal changes of the pelagic fish assemblage in a temperate estuary. Estuar. Coast Shelf Sci. 56:15-29.

Hales, L.S. & M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) – spot. U.S. Fish and Wildlife Service Biological Report 82(11.91). U.S. Army Corps of Engineers TR EL-82-4, 24 pp.

Hodson, R.G., J.O. Hackman & C.R. Bennett. 1981. Food habits of young spot in nursery areas of the Cape Fear River estuary, North Carolina. Trans. Am. Fish. Soc. 110:495-501.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67-77.

Jung, S. & E.D. Houde. 2003. Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. Estuar. Coast. Shelf Sci. 58:335-351.

Legendre, P. & L. Legendre. 1998. Numerical Ecology, 2nd Edition, Elsevier Science Amsterdam, 853 pp.

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, New Jersey, 115 pp.

Livingston, R.J. 1984. Trophic response of fishes to habitat variability in coastal seagrass systems. Ecology 65:1258-1275.

Mariani, S., A. Maccaroni, F. Massa, M. Rampacci & L. Tancions. 2002. Lack of consistency between the trophic interrelationships of five sparid species in the two adjacent central Mediterranean coastal lagoons. J. Fish Biol. 61:138-147.

McErlean, A.J., S.G. O'Connor, J.A. Milhursky & C.I. Gibson. 1973. Abundance, diversity and seasonal patterns of estuarine fish populations. Estuar. Coast. Mar. Sci. 1:19-36.

Mercer, L.P. 1989. Fishery Management plan for Atlantic croaker (*Micropogonias undulatus*). Fishery Management Report No. 10, Atlantic States Marine Fisheries Commission, Washington, D.C., 90 pp.

Miglarese, J.V., C.W. McMillan & M.H. Shealy, Jr. 1982. Seasonal abundance of Atlantic croaker (*Micropogonias undulatus*) in relation to bottom salinity and temperature in South Carolina estuaries. Estuaries 5:216-223.

Miller, J.M., L.B. Crowder & M.L. Moser. 1985. Migration and utilization of estuarine nurseries by juvenile fishes, an evolutionary perspective. Contrib. Mar. Sci. 27:338-342.

Nelson, A.L. & B.C. Coull. 1989. Selection of meiobenthic prey by juvenile spot (Pisces): and experimental study. Mar. Ecol. Prog. Ser. 53:51-57.

Nemerson, D.M. & K.W Able. 2004. Spatial patterns in diet and distribution of juveniles of four fish species in Delaware Bay marsh creeks, factors influencing fish abundance. Mar. Ecol. Prog. Ser. 276:249-262.

Ocaña-Luna, A. & M. Sanchez-Ramirez. 1998. Feeding of sciaenid (Pisces, Sciaenidae) larvae in two coastal lagoons of the Gulf of Mexico. Gulf Caribbean Res. 10:1-10.

O'Neil, S.P. & M.P. Weinstein. 1987. Feeding habitats of spot, *Leiostomus xanthurus*, in polyhaline versus meo-haline tidal creeks and shoals. Fish B-NOAA 85:785-796.

Overstreet, R.M. & R.W. Heard. 1978. Food of the Atlantic croaker, *Micropogonias undulatus*, from Mississippi Sound and the Gulf of Mexico. Gulf Res. Rep. 6:145-152.

Paperno, R., K.J. Miller & E. Kadison. 2001. Patterns in species composition of fish and selected invertebrate assemblages in estuarine subregions near Ponce de Leon Inlet, Florida. Estuar. Coast. Shelf Sci. 58:117-130.

Parker, J.C. 1971. The biology of spot, *Leiostomus xanthurus* Lacepede, and the Atlantic croaker, *Micropogon undulatus* (Linnaeus), in two Gulf of Mexico nursery areas. Ph.D. thesis, Texas A&M University, College Station, Texas, 213 pp.

Pattillo, M. E., T.E. Czapla, D.M. Nelson & M.E. Monaco. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries. Volume II. Species life histories summaries. Estuarine Marine Living Resource Program Report No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD, 337 pp.

Roelofs, E.W. 1954. Food studies of young sciaenid fishes, *Micropogonias* and *Leiostomus* from North Carolina. Copeia 1954:151-153.

Rogers, S.G., T.E. Targett & S.B. Von Sant. 1984. Fish nursery use in Georgia salt marsh estuaries: the influence of springtime freshwater conditions. Trans. Am. Fish. Soc. 113:595–606.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 1982:352-368.

Ross, S.W. 2003. The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes. Fish. B-NOAA 101:384-404.

Sala, E. & E. Ballesteros. 1997. Partitioning of space and food resources by three fish of genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. Mar. Ecol. Prog. Ser. 152:273-283.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.

Shenker, J.M. & J.M. Dean, J.M. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes, abundance, diversity and temporal variation. Estuaries 2:154-163.

Sheppard, J.N., N.C. James, A.K. Whitfield & P.D. Cowley. 2011. What role do beds of submerged macrophytes play in structuring estuarine fish assemblages? Lessons from a warm-temperate South African estuary. Estuar. Coast Shelf Sci. 95:145–155.

Sheridan, P.F. 1979. Trophic resource utilization by three species of sciaenid fishes in a northwest Florida estuary. Northeast Gulf Sci. 3:1-15.

Sheridan, P.F., D.L. Trimm & B.M. Baker. 1984. Reproduction and food habits of seven species of northern Gulf of Mexico fishes. Contrib. Mar. Sci. 27:175-204.

Soto, M.A., G.J. Holt, S.A. Holt & J. Rooker. 1998. Food habits and dietary overlap of newly settled red drum (*Scieanops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*) from Texas seagrass meadows. Gulf Caribbean Res. 10:41-56.

Street, G.T., B.C. Coull, G.T. Chandler & D.M. Sanger. 1998. Predation on meiofauna by juvenile spot *Leiostomus xanthurus* (Pisces) in contaminated sediments from Charleston Harbor, South Carolina, USA. Mar. Ecol. Prog. Ser. 170:261-268.

Tenore, K.R. 1983. What controls the availability to animals of detritus derived from vascular plants: organic nitrogen enrichment or caloric availability? Mar. Ecol. Prog. Ser. 10:307-309.

ter Braak, C.F.F. & P.F.M. Verdonschot 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. 57: 255-268.

ter Braak, C.F.F. & P.F.M. Verdonschot 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

Thiel, R. & I.C. Potter. 2001. The ichthyofaunal composition of the Elbe estuary, an analysis in space and time. Mar. Biol. 138:603-616.

Toepfer, C.S. and J.W. Fleeger. 1995. Diet of juvenile fishes *Citharichythys spilopterus, Symphurus plagiusa* and *Gobionellus boleosoma*. Bull. Mar. Sci. 56:238-249.

Weinstein, M.P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. B-NOAA, U.S. 77:339-357.

Weinstein, M. P. 1983. Population dynamics of an estuarine-dependent finfish along a tidal creek-seagrass meadow coenocline. Can. J. Fish. Aquat. Sci. 40:1633-1638.

Werner, E.E. & D.J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869-876.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15:393–425.

Wilson, S. 2002. Nutritional value of detritus and algae in blenny territories on the Great Barrier Reef. J. Exp. Mar. Biol. Ecol. 271:155-169.

Winemiller, K.O., S. Akin & S.C. Zeug. 2007. Production sources and food web structure of a temperate tidal estuary: integration of dietary and stable isotope data. Mar. Ecol. Prog. Ser. 343:63-76.

Zapfe, G.A. & C.F Rakocinski. 2008. Coherent growth and diet patterns in juvenile spot (*Leiostomus xanthurus* Lacepéde) reflect effects of hydrology on access to shoreline habitat. Fish. Res. 91:107-111.

Zar, J.H. 1996. Biostatistical Analysis, 3rd Edition. Prentice Hall, Upper Saddle River, New Jersey, 662 pp.

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