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M. Andres Soto
Gulf Coast Research Laboratory

G. Joan Holt
University of Texas Marine Science Institute

Scott A. Holt
University of Texas Marine Science Institute

Jay Rooker
University of Texas Marine Science Institute

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FOOD HABITS AND DIETARY OVERLAP OF NEWLY SETTLED RED DRUM (*SCIAENOPS OCELLATUS*) AND ATLANTIC CROAKER (*MICROPOGONIAS UNDULATUS*) FROM TEXAS SEAGRASS MEADOWS

M. Andres Soto,[1] G. Joan Holt,[2] Scott A. Holt[2] and Jay Rooker[2]
[1]*Gulf Coast Research Laboratory, Institute of Marine Sciences, University of Southern Mississippi*
703 East Beach Drive, Ocean Springs, Mississippi 39564, USA
[2]*University of Texas Marine Science Institute, 750 Channelview Dr., Port Aransas, Texas 78373, USA*

ABSTRACT Food habits and dietary overlap of newly settled larval and juvenile red drum and Atlantic croaker were examined during the period when the two species co-occur in seagrass nurseries. A total of 274 red drum (4.00 - 19.99 mm SL) and 205 Atlantic croaker (8.00 - 17.99 mm SL) were used for this analysis. Of the red drum stomachs examined, 8.4% were empty while 28.8% of Atlantic croaker stomachs contained no food. Major prey items identified for both species were calanoid copepods, harpacticoid copepods and mysid shrimp across all size classes. Ontogenetic trophic niche shifts were detected for red drum and Atlantic croaker. Type and quantity of food ingested by red drum were similar across all stations (Aransas Bay Station: 1H, 2T and 3H) examined. Atlantic croaker ingested the same types of prey at all stations, but contained varying quantities of food throughout the study area. In general, high dietary overlap was observed between red drum and Atlantic croaker with most overlap values (Schoener's index) exceeding 70%.

INTRODUCTION

Red drum (*Sciaenops ocellatus*) spend most of their adult lives offshore and migrate to tidal passes to spawn in late August through mid-November, whereas adult Atlantic croaker (*Micropogonias undulatus*) occupy gulf coastal waters and congregate offshore to spawn in early October through February (Johnson 1978). Pelagic larvae of both species are transported by currents through tidal inlets and into nursery habitats in bays and estuaries (Rooker et al. 1998). Consequently, larval and juvenile red drum (4 - 20 mm SL) occupy seagrass beds from late September to early December, while larval and juvenile Atlantic croaker (8 - 18 mm SL) are found in seagrass beds from early October to February (Holt et al. 1983, Rooker et al. 1998). Both species concurrently occupy seagrass beds in November at similar sizes.

Conspecifics and morphologically similar species (i.e., confamilials) occupying similar habitats can potentially compete for food particularly during times when fish densities are high and prey is scarce. Intraspecific and interspecific competition among larval fishes can reduce growth rates, which in turn, may increase early-life stage mortality due to starvation or predation (Houde 1987). Therefore, it is important to understand the trophic relationships of early life stages.

Fishes change resource (food) use throughout the course of their lives, especially during larval and juvenile stages. Such ontogenetic niche shifts may divide size-structured populations into ecologically distinct stages based on diet (Olson 1996). Duration of stages and transition among stages has the potential to minimize intraspecific competition for food.

Although several studies have addressed food habits of these two species separately (Bass and Avault 1975, Chao and Musick 1977, Oversteet and Heard 1978, Steen and Laroche 1983, Govoni et al. 1983, Currin et al. 1984, Govoni et al. 1986, and Peters and McMichael 1987), no dietary overlap analysis has been conducted on newly settled red drum and Atlantic croaker. The primary aim of this study was to obtain an understanding of the trophic dynamics of newly settled larval and juvenile red drum and Atlantic croaker occurring in seagrass habitat. Specific objectives were to: 1) quantitatively describe the diets of larval and juvenile red drum and Atlantic croaker; 2) determine ontogenetic changes in diets of the two species; 3) determine if diet varies across different sites and habitats for red drum and Atlantic croaker; 4) determine interspecific dietary overlap between red drum and Atlantic croaker; and 5) determine if red drum and Atlantic croaker feed on equal quantities of food at similar sizes during the co-occurring period.

MATERIALS AND METHODS

Diurnal sampling (0730 - 1700 h) was conducted weekly from October through December 1994. Fish samples were taken from three stations in Aransas Bay (1H, 2T and 3H) and two stations in Redfish Bay (4H and 5T)(Figure 1). Stations 1H, 3H and 4H were in shoal grass (*Halodule wrightii*) while stations 2T and 5T were in turtle grass (*Thalassia testudinum*) (Figure 1). A 1 m (diameter), 505 µm mesh cone net attached to a 0.75 m (length) x 0.56 m (height) epibenthic sled was hand-towed for 20 m across the grassbed sites. Three samples from each site were obtained, picked free of grass, and preserved in 5% formalin. Standard

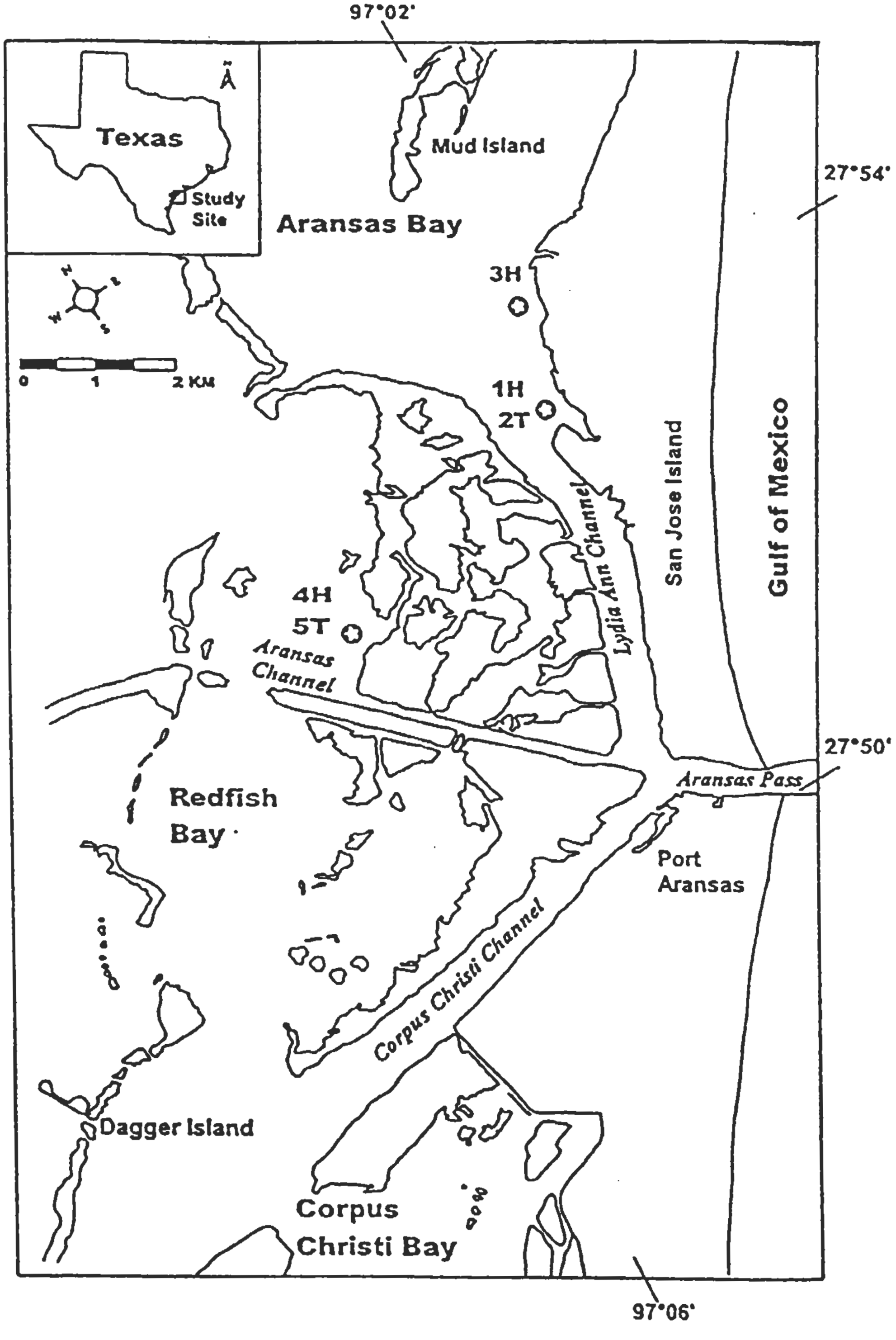

Figure 1. Locations of sampling sites in Aransas Estuary, Texas. Sites were chosen from Shoal grass (*Halodule wrightii* = H) and Turtle grass (*Thalassia testudinum* = T) in Aransas Bay (1H, 2T, 3H) and Redfish Bay (4H, 5T).

length (SL) of red drum and Atlantic croaker were measured using an ocular micrometer scope. No adjustments for shrinkage were made.

Stomach contents were sorted, counted and identified to lowest possible taxon. For red drum, the development of the stomach (determined by the formation of the pyloric sphincter) begins at approximately 7 - 8 mm SL (personal observation). Consequently, gut content analysis before stomach formation was performed on the entire alimentary canal, and after formation, gut analysis was limited to the stomach to minimize differential rates of digestion. For Atlantic croaker, development of the stomach had begun in all fish examined (personal observation); therefore, gut analysis was limited to the stomach.

When prey items were relatively intact, volumes were determined by measuring the longest length, width, and depth of individual prey using an ocular micrometer scope. Average volumes of prey categories were then calculated (Wallace 1981). For mysids and amphipods, total lengths (TL) were taken when measurable and converted to volumes by a length to volume relationship generated from mysids and amphipods obtained from Site 1H in November 1995. If mysids and amphipods were heavily digested and total length could not be taken, they were divided into three categories (small, medium, and large). The length to volume relationship was subsequently divided into three categories, and average volumes were calculated and assigned to the digested specimens.

Miscellaneous prey is a general group composed of prey items that could not be identified. Miscellaneous prey volume was estimated from a standard length of fish to total prey volume (TPV) relationship (where total prey volume is the sum of all prey item volumes in an individual fish's stomach). If a fish consumed only miscellaneous prey, then the fish's standard length was used to estimate volume.

Red drum (4.00 - 19.99 mm) and Atlantic croaker (8.00 - 17.99 mm) were divided into 2 mm size classes. Three dietary measures were taken for each size class: percent composition by frequency of occurrence (%F), percent numerical abundance (%N), and percent of total volume (%V), where %F = (number of stomachs containing prey of one taxon divided by total number of stomachs that contained any prey items) x 100; %N = (number of individuals of one prey taxon divided by total number of all prey individuals) x 100; and %V = (volume of one prey taxon divided by total volume of all prey) x 100. These three prey measures were used to calculate the Index of Relative Importance (IRI) (Pinkas et al. 1971). The IRI is defined as:

$$\mathrm{IRI} = (\%V + \%N)(\%F).$$

This index emphasizes small, numerous prey and de-emphasizes large, less frequently occurring prey and allows for prey items to be ranked quantitatively (Wallace 1981). Empty stomachs were noted and excluded from the above analysis.

Hierarchical cluster analysis was performed to determine ontogenetic trophic patterns across size classes of both red drum and Atlantic croaker (Hartigan 1975). Clustering was based on % IRI values of all prey items from each size class (Table 1 and 2). To determine if rare prey items biased our cluster results, a cluster using the three most important prey items was generated for both red drum and Atlantic croaker. This method produced similar results and, therefore, was excluded from the analysis. Single linkage method (nearest neighbor) was used, and the dissimilarity measure was Euclidean distance. Groupings were determined by cutting the dendrogram at the widest range of Euclidean distance for which the number of clusters remained constant (Romesburg 1984). SYSTAT was used for cluster analysis (Wilkinson 1990).

Schoener's index (1970) is most reliable for measuring dietary overlap when estimates of prey abundance are not available (Wallace 1981, Linton et al. 1981).
Schoener's index is defined as:

$$\alpha = 100\,[1 - 0.5 \sum_{i=1}^{n} | p_{xi} - p_{yi} |],$$

where p_{xi} = proportion (percent IRI) of food category i in the diet of species x; p_{yi} = proportion (percent IRI) of food category i in the diet of species y; n = the number of food categories.

For within-species and between-species overlap comparisons, % IRI values were calculated for prey items from similar-sized fish between stations. Schoener's index was then used to calculate intraspecific and interspecific dietary overlap between stations. When measuring between-species dietary overlap by size-class, red drum and Atlantic croaker from the same size-classes were compared. For this analysis we pooled fish obtained from all habitat types over the three sampling dates when the two fish species co-occurred. For the purposes of discussion, overlap values were classified as: low $\leq$ 33.3%, moderate, 33.3 - 66.6%, and high $\geq$ 66.7%.

Analysis of covariance (ANCOVA) was used to examine the effect of site and habitat on total prey volume (where total prey volume is the sum of all prey item volumes in an individual fish's stomach). ANCOVAs were also used to compare total prey volumes of red drum and Atlantic croaker when the two species co-occured. To reduce "time of day" effect on feeding, only samples from approximately equal times were examined; for example, afternoon samples

TABLE 1

Prey items arranged in descending order of importance by size class (mm SL) of 274 red drum. % IRI = [(% Number + % Volume)(% Frequency)] (100). F = number of fish with food, and E = number of fish with empty guts.

Size Class		I				II				III				IV		
Range (mm SL)		4.00- 5.99				6.00- 7.99				8.00- 9.99				10.00- 11.99		
		F = 14 E = 4				F = 22 E = 5				F = 30 E = 6				F = 39 E = 0		
Prey Categories	%F	%N	%V	%IRI	%F	%N	%V	%IRI	%F	%N	%V	%IRI	%F	%N	%V	%IRI
Mysid shrimp													28.2	6.9	61.4	26.9
Calanoid copepod	14.3	6.9	18.3	7.1	59.1	59.4	45.0	80.4	70.0	69.5	65.1	85.9	48.7	37.3	7.4	30.5
Harpacticoid copepod	21.4	10.3	11.8	9.4	36.4	17.7	5.8	11.1	60.0	13.4	5.4	10.2	71.8	30.9	2.6	33.6
Copepodite species	35.7	44.8	11.5	39.8	13.6	11.5	0.8	2.2	10.0	3.1	0.3	0.3	20.5	5.1	0.1	1.5
Miscellaneous prey	35.7	17.2	23.0	28.5	9.1	2.1	1.7	0.4	3.3	0.3	1.7	0.1	5.1	0.9	1.7	0.2
Copepod species	14.3	17.2	34.6	14.6	22.7	6.3	4.2	3.1	10.0	1.4	1.0	0.2	2.6	0.5	0.1	0.0
Crustacean remains					4.5	1.0	42.4	2.6	0.0	0.0	17.1	0.0	10.3	1.8	19.4	3.0
Amphipod													5.1	0.9	4.6	0.4
Harpacticoid copepodite	7.1	3.4	0.8	0.6	4.5	1.0	0.1	0.1	6.7	0.7	0.1	0.0	17.9	6.0	0.1	1.5
Copepod egg sac					4.5	1.0	0.2	0.1	20.0	3.1	0.6	0.7	23.1	5.5	0.2	1.9
Calanoid copepodite									26.7	7.5	0.8	2.0	7.7	1.8	0.0	0.2
Palaemonetes									6.7	0.7	8.1	0.5	5.1	0.9	2.3	0.2
Cyclopoid copepod													5.1	0.9	0.0	0.1
Penaeus																
Mysid larvae																
Leptochelia																
Hippolydid													2.6	0.5	0.0	0.0
Polychaete																
Copepod nauplius																
Erichsonela																
Total		100.0	100.0	100.0		100.0	100.0	100.0		99.7	100.0	100.0		100.0	100.0	100.0

TABLE 1 (Continued)

Size Class	V				VI				VII				VIII				
Range (mm SL)	12.00- 13.99				14.00- 15.99				16.00- 17.99				18.00- 19.99				
	F = 57 E = 5				F = 36 E = 3				F = 31 E = 0				F = 22 E = 0				
Prey Categories	%F	%N	%V	%IRI	%F	%N	%V	%IRI	%F	%N	%V	%IRI	%F	%N	%V	%IRI	Sum of %IRI
Mysid shrimp	47.4	12.4	63.0	40.8	69.4	23.0	87.8	69.1	80.6	25.1	77.0	69.8	86.4	20.6	81.2	74.8	281.4
Calanoid copepod	47.4	29.7	3.8	18.2	38.9	19.1	1.4	7.2	48.4	30.6	2.1	13.4	36.4	44.6	3.3	14.8	257.5
Harpacticoid copepod	73.7	37.4	2.0	33.2	61.1	38.2	1.2	21.6	58.1	23.5	0.7	11.9	31.8	28.4	0.9	7.9	139.0
Copepodite species	8.8	2.4	0.0	0.2	5.6	1.1	0.0	0.1	6.5	3.3	0.0	0.2					44.2
Miscellaneous prey	1.8	0.3	0.6	0.0	2.8	0.6	0.9	0.0	6.5	1.1	3.3	0.2	4.5	0.5	2.3	0.1	29.6
Copepod species	7.0	5.3	0.5	0.5	2.8	0.6	0.0	0.0	6.5	3.3	0.2	0.2					18.6
Crustacean remains	19.3	3.2	22.0	5.6	5.6	1.1	4.5	0.3	6.5	1.1	2.0	0.2	18.2	2.0	7.7	1.5	13.1
Amphipod	7.0	1.5	7.4	0.7	5.6	1.7	2.8	0.2	25.8	6.0	9.8	3.4	13.6	2.0	3.7	0.7	5.4
Harpacticoid copepodite	14.0	3.5	0.0	0.6	11.1	7.9	0.1	0.8									3.6
Copepod egg sac	7.0	2.4	0.1	0.2	13.9	4.5	0.1	0.6	3.2	0.5	0.0	0.0	4.5	0.5	0.0	0.0	3.4
Calanoid copepodite	3.5	0.6	0.0	0.0					3.2	0.5	0.0	0.0	4.5	0.5	0.0	0.0	2.3
Palaemonetes	1.8	0.3	0.5	0.0	5.6	1.1	1.1	0.1	12.9	2.7	2.4	0.6	9.1	1.0	0.9	0.1	1.6
Cyclopoid copepod	3.5	0.6	0.0	0.0	2.8	0.6	0.0	0.0									0.1
Penaeus									3.2	0.5	2.2	0.1					0.1
Mysid larvae	1.8	0.3	0.0	0.0					3.2	0.5	0.0	0.0					0.0
Leptochelia									3.2	0.5	0.2	0.0					0.0
Hippolydid																	0.0
Polychaete									3.2	0.5	0.0	0.0					0.0
Copepod nauplius					2.8	0.6	0.0	0.0									0.0
Erichsonela	1.8	0.3	0.1	0.0													0.0
Total		100.0	100.0	100.0		100.0	100.0	100.0		100.0	100.0	100.0		100.0	100.0	100.0	

TABLE 2

Prey items arranged in descending order of importance by size class (mm SL) of 205 Atlantic croaker. % IRI = [(% Number + % Volume)(% Frequency)] (100). F = number of fish with food, and E = number of fish with empty guts.

Size Class		I				II				III		
Range (mm SL)		8.00- 9.99				10.00- 11.99				12.00- 13.99		
		F = 6	E = 18			F = 37	E = 14			F = 56	E = 9	
Prey Categories	%F	%N	%V	%IRI	%F	%N	%V	%IRI	%F	%N	%V	%IRI
Harpacticoid copepod	16.7	5.0	3.1	1.5	64.9	26.9	5.9	23.9	69.6	38.6	3.5	34.3
Calanoid copepod	50.0	75.0	94.0	94.2	70.3	48.7	21.5	55.5	30.4	22.8	4.2	9.6
Mysid shrimp					24.3	5.1	59.8	17.7	46.4	12.6	81.1	50.9
Harpacticoid copepodite	16.7	5.0	0.5	1.0	18.9	4.1	0.1	0.9	21.4	8.9	0.1	2.3
Copepodite species	16.7	5.0	0.8	1.1	13.5	4.1	0.2	0.7	19.6	8.9	0.2	2.1
Crustacean remains					5.4	1.0	6.1	0.4				
Calanoid copepodite	16.7	10.0	1.6	2.2	8.1	2.5	0.1	0.2	1.8	0.4	0.0	0.0
Copepod egg sac					5.4	1.0	0.1	0.1	5.4	1.2	0.0	0.1
Palaemonetes species					2.7	0.5	2.6	0.1	5.4	1.2	2.6	0.2
Bivalve												
Copepod species					5.4	4.1	1.5	0.3	1.8	1.2	0.2	0.0
Sagitta species									5.4	1.2	4.6	0.4
Cyclopoid copepod									1.8	0.4	0.8	0.0
Miscellaneous prey									1.8	0.4	1.2	0.0
Amphipod									3.6	0.8	1.0	0.1
Isopod					2.7	0.5	1.1	0.1				
Polychaete									1.8	0.4	0.0	0.0
Alpheus species					2.7	0.5	0.9	0.0				
Copepod nauplius					2.7	1.0	0.0	0.0	1.8	0.4	0.0	0.0
Leptochelia rapax									1.8	0.4	0.4	0.0
Total		100.0	100.0	100.0		100.0	100.0	100.0		100.0	100.0	100.0

TABLE 2 (Continued)

Size Class	IV				V				
Range (mm SL)	14.00- 15.99				16.00- 17.99				
	F = 34	E = 14			F = 13	E = 4			
Prey Categories	%F	%N	%V	%IRI	%F	%N	%V	%IRI	Sum of %IRI
Harpacticoid copepod	70.6	43.0	3.0	42.0	76.0	52.0	7.0	70.0	172.0
Calanoid copepod	5.9	1.0	0.0	0.0					159.0
Mysid shrimp	35.3	12.0	76.0	40.0	7.0	2.0	69.0	8.0	117.0
Harpacticoid copepodite	47.1	21.0	0.0	13.0	30.0	11.0	0.0	5.0	23.0
Copepodite species	8.8	2.0	0.0	0.0	23.0	23.0	0.0	8.0	12.0
Crustacean remains	5.9	2.0	6.0	0.0	15.0	5.0	21.0	6.0	7.0
Calanoid copepodite									2.0
Copepod egg sac	20.6	6.0	0.0	1.0					2.0
Palaemonetes species	5.9	1.0	3.0	0.0					0.0
Bivalve					7.0	2.0	0.0	0.0	0.0
Copepod species	2.9	1.0	0.0	0.0					0.0
Sagitta species									0.0
Cyclopoid copepod	2.9	1.0	3.0	0.0					0.0
Miscellaneous prey	2.9	0.0	3.0	0.0					0.0
Amphipod	2.9	0.0	1.0	0.0					0.0
Isopod									0.0
Polychaete	2.9	0.0	0.0	0.0					0.0
Alpheus species									0.0
Copepod nauplius									0.0
Leptochelia rapax									0.0
Total		100.0	100.0	100.0		100.0	99.0	100.0	

were compared only to afternoon samples. Standard Length was the covariate in all analyses. ANCOVAs were performed when more than 15 fish were present in the sample. Total prey volumes were square-root transformed to approximate a normal distribution and to minimize heteroscedasticity. Analysis of covariance is robust to departures from both normality and homogeniety of variances; therefore, minor deviations from assumptions should not affect results (Underwood 1981). An interactive regression model (SYSTAT 1990) was performed prior to ANCOVA to confirm the homogeneity of slopes assumption. If the homogeneity of slopes assumption was violated, then the interactive regression model results were reported. When making multiple statistical comparisons, alpha levels were adjusted using the sequential Bonferroni test (Rice 1989).

RESULTS

The relationship between total length to volume for mysid shrimp was: $V = 0.02L^{2.89}$ ($R^2 = 0.99$), whereas the relationship between total length to volume for amphipods was: $V = 0.02L^{3.30}$ ($R^2 = 0.97$). These relationships were used to estimate mysid shrimp and amphipod volumes from total length estimates made for mysids and amphipods obtained from gut contents of red drum and Atlantic croaker.

A total of 274 red drum between 4.00 - 19.99 mm SL, and 205 Atlantic croaker between 8.00 - 17.99 mm SL were examined for gut content (Tables 1 and 2). Of the red drum examined, 8.4% had empty guts, while 28.8% of Atlantic croaker guts contained no food. The highest percentage of empty stomachs for red drum occurred in the smallest size class (22.2%). Three size classes of red drum had no fish with empty stomachs (10.00 - 11.99, 16.00 - 17.99, and 18.00 - 19.99). Atlantic croaker from the smallest size-class (8.00 - 9.99) had the greatest proportion of empty stomachs (75 %), while fish from size class (12.00 - 13.99) had the least proportion (13.8%).

Red Drum

Percent Composition of Diet

Twenty taxonomic groups were identified from the guts of red drum (Table 1). Calanoid copepods and harpacticoid copepods were the most numerous prey consumed by fish from all size classes. Mysid shrimp were consumed by the five largest size classes (10.00 - 19.99) and comprised most of the dietary volume in those size classes. Harpacticoid copepodites, copepod egg sacs, and calanoid copepodites occurred in moderate numbers in some size classes (8.00 - 9.99, 10.00 - 11.99), but comprised only a small fraction of the total volume. In the 16.00 - 17.99 mm size class, amphipods comprised 25.81 by % Frequency, 6.01 by % Number, and 9.76 by % Volume, and were the fourth most important prey for that size class.

Relative Importance of Prey

Mysid shrimp, calanoid copepods, and harpacticoid copepods were the three major prey items consumed by red drum and together averaged 84.7% IRI across all size classes (Table 1). Red drum showed ontogenetic shifts in feeding (Figure 2). Calanoid copepods were ingested by red drum in all size classes but were dominant prey for smaller red drum (6.00 - 9.99 mm). Harpacticoid copepods were also ingested by red drum from all size classes and were especially important to fish in the intermediate size classes (10.00 - 15.99 mm). Mysid shrimp were first consumed by fish in the 10.00 - 11.99 mm size class and became the most important prey item thereafter. Prey items from the smallest size class were heavily digested and difficult to identify, and as a result, the general groups copepodites and miscellaneous prey accounted for 39.78 and 28. 45% IRI, respectively. Sixteen of the twenty taxonomic groups found in red drum also occurred in Atlantic croaker. *Penaeus* sp., mysid larvae, Hippolydids, and *Erichsonela* sp. were unique to the diet of red drum, but were of little importance (%IRI = < 1 for each).

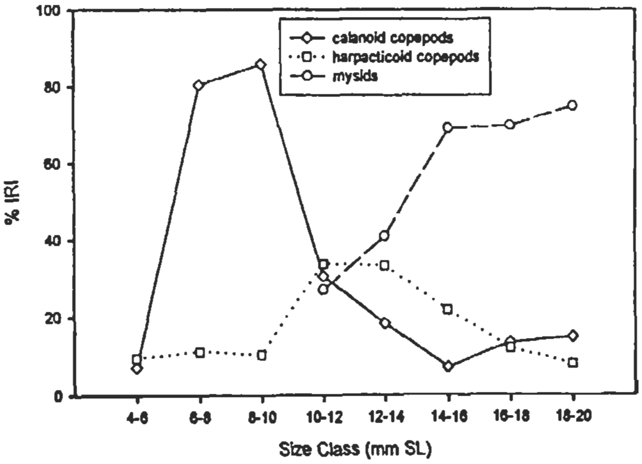

Figure 2. Relative importance values (IRI) by size class (mm SL) of the three major prey items for red drum (*Sciaenops ocellatus*).

Atlantic Croaker

Percent Composition of Diet

Twenty taxonomic groups were identified from Atlantic croaker stomachs (Table 2). Harpacticoid copepods and calanoid copepods were the most numerous and most frequent prey items consumed by Atlantic croaker. Mysid shrimp were not numerous in the stomachs of Atlantic croaker; however, this prey item accounted for most of the total volume. While some prey items had relatively high % Frequency and % Number values in some size classes, their small size reduced % IRI values. For example, harpacticoid copepodites in the 14.00 - 15.99 mm size class accounted for 47.1% Frequency and 21.7% Number, but by volume, represented only 0.3%. In the same size class, copepod egg sacs occurred in 20.6% of fish and accounted for 6.6% by number but only comprised 1.8% by volume.

Relative Importance of Prey

Harpacticoid copepods, calanoid copepods and mysid shrimp were the three major prey items identified in Atlantic croaker, together averaging 89.9% IRI across size classes (Table 2). Ontogenetic shifts in diet composition were detected for Atlantic croaker as well (Figure 3). Harpacticoid copepods were ingested by fish in all size classes. Their consumption increased gradually across the size spectrum and were most important to 14.00 to 17.99 mm fish. Calanoid copepods were dominant prey for smaller Atlantic croaker (8.00 - 11.99 mm). Mysid shrimp were first consumed by Atlantic croaker in the 10.00 - 11.99 mm size class and were the major prey for intermediate-sized fish (12.00 - 13.99 mm). Bivalves, *Sagitta* sp., isopods, and *Alpheus* sp. were unique to Atlantic croaker diet but each accounted for less than one percent IRI.

Hierarchical Cluster Analysis

The eight size classes of red drum clustered to form three trophic groups: 4.00 - 5.99 mm, 6.00 - 9.99 mm, and 10.00 - 19.99 mm (Figure 4). The diets of fish in the 4.00 - 5.99 mm size group were dissimilar to diets of fish from all other groups because of heavily digested prey (miscellaneous prey). Fish from the 6.00 - 7.99 mm and 8.00 - 9.99 mm size classes fed primarily on calanoid copepods (%IRI = 80.43, and 85.91, respectively); consequently, the two size classes grouped together. Red drum greater than 10.00 mm formed a separate cluster. Within this group there appeared to be some evidence for further separation. Fish from the intermediate size classes (10.00 - 11.99 mm, 12.00 - 13.99 mm) fed on relatively equal proportions of mysid shrimp, calanoid copepods, and harpacticoid copepods. Red drum from the larger size classes (14.00 - 15.99 mm, 16.00 - 17.99 mm, and 18.00 - 19.99 mm) clustered to form a group which fed primarily on mysid shrimp (%IRI = 69.10, 69.75, and 74.79, respectively).

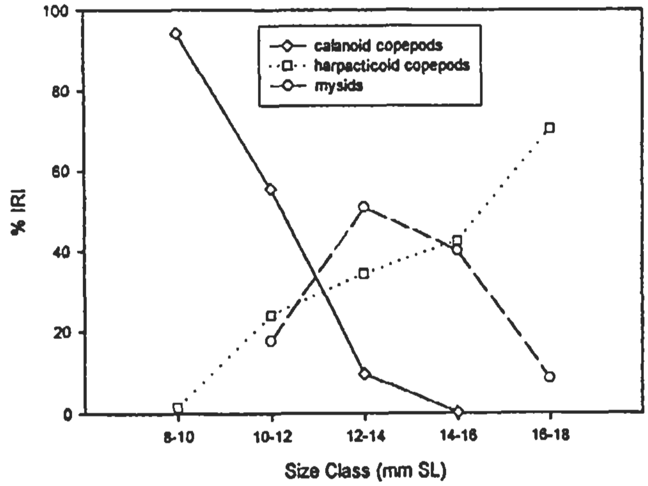

Figure 3. Relative importance values (IRI) by size class (mm SL) of the three major prey items for Atlantic croaker (*Micropogonias undulatus*).

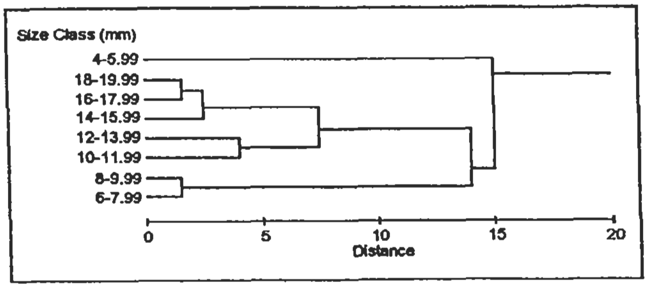

Figure 4. Dendrogram for hierarchical cluster analysis of diet dissimilarity of eight size classes (mm SL) of red drum (*Sciaenops ocellatus*). Clustering was based on% IRI (Index of Relative Importance) of all prey items. Single linkage clustering and Euclidean distance were used.

Four trophic groups were identified for Atlantic croaker (Figure 5). Size classes 8.00 - 9.99 mm, 10.00 - 11.99 mm, and 16.00 - 17.99 mm each had distinct diets (Table 2) and did not cluster with any other size class. The size class, 8.00 - 9.99 mm fed almost exclusively on calanoid copepods (%IRI = 94.2) while the size class, 10.00 - 11.99 mm consumed a combination of mysid shrimp, harpacticoid copepods and calanoid copepods (%IRI = 55.5, 23.9, and 17.7, respectively). Larger Atlantic croaker from size class 16.00 - 17.99 mm ingested mainly harpacticoid copepods (%IRI = 70.4). Intermediate size classes 12.00 - 13.99 mm and 14.00 - 15.99 mm combined to form a group which fed on equal proportions of mysid shrimp and harpacticoid copepods.

Site and Habitat Dietary Comparison

Red drum

Site and habitat did not affect the type or quantity of food ingested by red drum. This species exhibited moderate

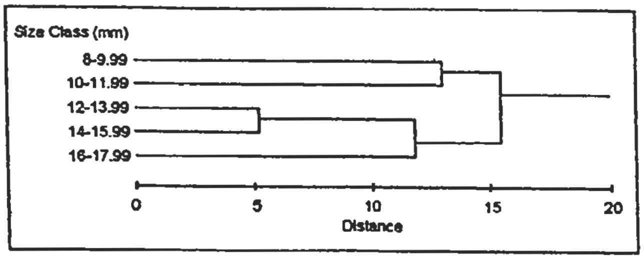

Figure 5. Dendrogram for hierarchical cluster analysis of diet dissimilarity of eight size classes (mm SL) of Atlantic croaker (*Micropogonias undulatus*). Clustering was based on % IRI (Index of Relative Importance) of all prey items. Single linkage clustering and Euclidean distance were used.

intraspecific dietary overlap values between the two seagrass types (Table 3). Moderate and high values were observed between the two *H. wrightii* sites (Table 3).

No significant difference in total prey volume was observed for red drum taken from the two seagrass types (1H versus 2T, Table 4). Moreover, when comparing total prey volume of fish diets taken from the two sites in *H. wrightii* (1H versus 3H), red drum contained similar amounts of food as well (Table 4).

Atlantic croaker

For Atlantic croaker, site and habitat did not affect the type of food but did affect the quantity of food consumed by this species. Atlantic croaker taken from both seagrass types ingested almost identical prey (Schoener = 95%, Table 5). Furthermore, a 73% dietary overlap was observed for Atlantic croaker taken from two sites in *H. wrightii* (1H versus 3H).

Atlantic croaker showed no significant difference in total prey volume between the two seagrass types (Table 6). However, there was a significant difference in total prey volumes between fish from the two sites in *H. wrightii* (1H versus 3H, ANCOVA, $p = .004$).

Interspecific Dietary Comparison

Interspecific dietary overlap (Schoener's index) was calculated for red drum and Atlantic croaker from five size-classes ranging from 8.00 - 17.99 mm SL (Figure 6). Red drum and Atlantic croaker exhibited high overlap values in excess of 70 % in four of the five size classes. However, low dietary overlap (23 %) was observed in the largest size class (16.00 - 17.99 mm SL). Interspecific dietary overlap values were consistently high when red drum and Atlantic croaker from identical samples were compared (Table 7). Four of the five comparisons encompassing three sampling dates (7 November, 16 November and 21 November) and four times (0830 h, 0946 h, 1445 h and 1630 h) had overlap values in excess of 76%. Moderate overlap values (Schoener = 39%) were observed at Site 1H (7 November)(Table 7).

Total prey volumes were significantly higher for red drum than for Atlantic croaker at Site 1H and Site 3H on 7 November and 16 November, respectively (Table 8). At Site 3H (16 November) red drum and Atlantic croaker contained similar amounts of food, but were affected differently with respect to Standard Length (slopes intersected, interactive regression, $P = .000$).

TABLE 3

Estimated dietary overlap (Schoener's index) for red drum between sites. N is sample size, and SL is standard length.

Date (1994) Site	Size	Range (mm SL)	N	% Dietary Overlap
7-Nov	1H	8.0 - 14.1	48	66.0
	2T	8.8 - 15.2	24	
7-Nov	1H	8.0 - 14.1	48	43.8
	3H	8.1 - 13.5	27	
7-Nov	2T	8.8 - 15.2	24	45.2
	3H	8.1 - 13.5	27	
16-Nov	1H	10.5 - 13.4	9	71.7
	3H	9.5 - 13.9	18	

TABLE 4

ANCOVA comparison of Total Prey Volume (TPV) of red drum between sites. N is sample size, SE is Standard Error of the mean, and P is the probability of Type I Statistical error.

Date (1994)	Site	Time	N	SL Mean (mm)	SE	Volume Mean (mm3)	SE	P-value
7-Nov	1H	1430 h	65	12.6	0.3	1.46	0.1	0.414
	2T	1530 h	28	13.1	0.5	1.37	0.2	
7-Nov	1H	1430 h	65	12.6	0.3	1.46	0.1	0.156
	3H	1630 h	33	11.5	0.5	0.97	0.2	
7-Nov	2T	1530 h	28	11.5	0.5	0.97	0.1	0.473
	3H	1630 h	33	13.1	0.5	1.37	0.2	
16-Nov	1H	830 h	16	13.8	0.5	1.85	0.3	0.514
	3H	946 h	23	13	0.5	1.39	0.3	

TABLE 5

Estimated dietary overlap for Atlantic croaker between sites. N is sample size, and SL is standard length.

Date (1994)	Site	Size Range (mm SL)	N	% Dietary Overlap
16-Nov	1H	10.1 - 14.2	37	73.2
	3H	10.7 - 16.0	27	
21-Nov	1H	12.0 - 17.29	17	95.0
	2T	12.0 - 17.8	55	

TABLE 6

ANCOVA comparison of Total Prey Volume (TPV) of Atlantic croaker between sites. N is sample size, SE is Standard Error of the mean, and P is the probability of Type I statistical error.

Date (1994)	Site	Time	N	SL Mean	SE	Volume Mean (mm3)	SE	P-value
16-Nov	1H	830 h	37	12.3	0.2	0.82	0.09	.004[s]
	3H	946 h	27	13.8	0.2	1.38	0.12	
21-Nov	1H	1445 h	17	15.2	0.4	0.14	0.1	0.14
	2T	1345 h	57	14.7	0.2	0.31	0.06	

[s] Significant after alpha adjustment (Rice 1989).

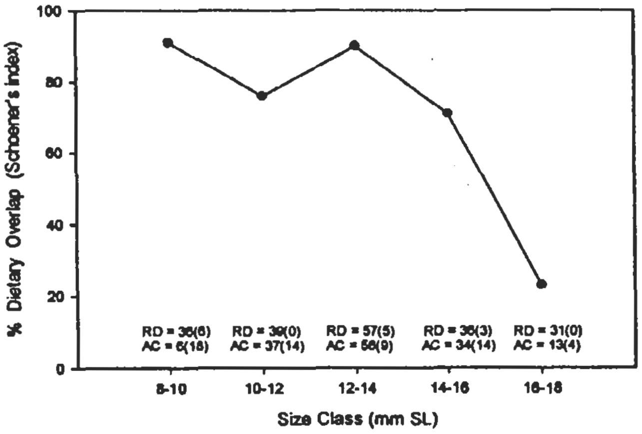

Figure 6. Fish size class (mm SL) versus interspecific dietary overlap (Schoener's index). Parentheses indicate number of fish with empty guts.

DISCUSSION

The proportion of empty stomachs found in red drum (8.4%) was less than that reported in other studies. All fish examined in the present study were obtained from seagrass beds and sampled diurnally. Bass and Avault (1975) reported 11.7% of red drum less than 19 mm SL had empty guts while 17% of red drum (8.00 - 15.00 mm SL) examined by Peters and McMichael (1987) contained no food. Those studies pooled day and night collected fish and did not specify whether the fish used were pelagic or demersal. Both variables have been shown to affect food consumption of larval and juvenile fish (Govoni et al. 1983, Kane 1984). Atlantic croaker from the smallest size class had the highest percentage of empty stomachs (75%). High percentages of empty stomachs (49%) have been reported by Govoni et al. (1983) for pelagic Atlantic croaker (5.01 - 10.00 mm SL). The higher percentage of empty stomachs in Atlantic croaker compared to red drum may be due to these fish feeding in the evening or at night, or to seagrass beds not being primary nursery habitat for Atlantic croaker. Larval and juvenile fish probably do not feed at night (Blaxter 1986). While it has been shown that larval and juvenile red drum prefer seagrass beds as nursery habitat (Rooker and Holt 1997, Holt et al. 1983), seagrass may not be primary habitat for Atlantic croaker since they have been found in high densities at equal sizes in other habitats, such as sand, mud and deeper waters (Holt and Arnold 1989, Chao and Musick 1977).

Of the 20 prey items ingested by larval and juvenile red drum and Atlantic croaker, 16 were common to both species. The same three prey, calanoid copepods, harpacticoid copepods, and mysid shrimp, dominated the diet of both species. Other studies examining demersally caught red drum showed similar patterns (Bass and Avault 1975, Peters and McMichael 1987). These investigations found copepods (calanoids, harpacticoids, and cyclopoids) to be dominant food items for fish less than 8 - 9 mm SL, while mysid shrimp became the principal prey for red drum greater than 9 - 10 mm SL. Steen and Laroche (1983), examining 21 demersally caught red drum between 8.50 - 12.99 mm SL, observed a different pattern. They found decapod postlarvae and a calanoid copepodite to be most important. Sheridan (1979) found insect larvae and

TABLE 7

Estimated dietary overlap (Schoener's index) between red drum and Atlantic croaker by site. N is sample size, and SL is standard length.

Date (1994)	Site	Time	Species	N	Size Range (mm SL)	% Dietary Overlap
7-Nov	1H	1430 h	Atlantic croaker	8	9.2 - 13.2	38.9
			red drum	48	8.0 - 14.1	
7-Nov	3H	1630 h	Atlantic croaker	16	9.3 - 13.4	97.4
			red drum	27	8.1 - 13.5	
16-Nov	1H	830 h	Atlantic croaker	37	10.1 - 14.2	81.3
			red drum	9	10.5 - 13.4	
16-Nov	3H	946 h	Atlantic croaker	27	10.7 - 16.0	85.9
			red drum	23	9.5 - 17.5	
21-Nov	1H	1445 h	Atlantic croaker	17	12.0 - 17.3	76.8
			red drum	7	12.8 - 17.4	

TABLE 8

ANCOVA comparison of Total Prey Volume (TPV) between red drum and Atlantic croaker. N is sample size, SE is standard error of the mean, and P is the probability of Type I statistical error.

Date (1994)	Time	Species	N	SL Mean	SE	Volume Mean (mm^3)	SE	P-value
7-Nov	1630 h	Red drum	33	11.5	0.4	0.97	0.1	0[s]
		Atlantic croaker	16	11.1	0.7	0.33	0.14	
16-Nov	830 h	Red drum	16	13.8	0.4	1.85	0.18	0.001[s]
		Atlantic croaker	37	12.3	0.3	0.82	0.12	
16-Nov	946 h	Red drum	23	12.99	0.34	1.39	0.19	.0000*[s]
		Atlantic croaker	27	13.75	0.38	1.38	0.17	

* Interactive regression results (slopes intersected).

[s] Significant after alpha adjustment (Rice 1989).

polychaetes to be primary prey for Atlantic croaker (10 - 19 mm SL) although calanoid copepods, harpacticoid copepods, and mysid shrimp were also reported.

Prey assemblages differ in a pelagic compared to a demersal environment (Rudnick et al. 1985). Steen and Laroche (1983) described a different trophic pattern for pelagic red drum. They found copepod eggs and a cyclopoid copepodite (*Oithona* sp.) to be most important to fish between 3.00 - 8.49 mm SL. Govoni et al. (1983), examining food of pelagic Atlantic croaker up to 10 mm SL, showed a slightly different pattern as well. Calanoid copepods, copepod fragments, and invertebrate eggs were major prey identified in that study.

Pelagic red drum and Atlantic croaker arrive in seagrass beds at approximately 4 - 5 mm SL and 8 - 9 mm SL, respectively. Consequently, the major prey of both fish at the smaller size classes are calanoid copepods, a more pelagic group of copepods. Conversely, harpacticoid copepods are found in higher concentrations in seagrass beds than in a pelagic environment (Stoner 1980, Orth et al. 1984), and become important prey for intermediate-sized red drum and larger Atlantic croaker. The ontogenetic shift from calanoid copepods to harpacticoid copepods is probably due to a higher abundance of this prey in the seagrass habitat and not to morphological constraints in feeding since harpacticoids in general are smaller than calanoid copepods. Thus, the shift from calanoid copepods to harpacticoid copepods indicates the transition from a pelagic environment to settlement into grassbeds. Steen and Laroche (1983) described a similar settlement pattern for red drum and Sheridan (1979) for Atlantic croaker, occurring at similar sizes.

Red drum can be divided into two distinct trophic niche stages with a transition occurring at the 10.00 - 11.99 mm size class. Red drum, <9.99 mm SL, feed almost exclusively on calanoid copepods, while fish ≥12.00 mm consume primarily mysid shrimp. The transition (10.00 - 11.99 mm) is characterized by the ingestion of relatively equal proportions of calanoid copepods, harpacticoid copepods, and mysid shrimp. Discrete trophic niche stages were also detected for Atlantic croaker. Fish from the 10.00 - 13.99 mm size range marked a transition. Atlantic croaker from this size range showed the greatest diet change. Harpacticoid copepod and mysid shrimp consumption increased while calanoid copepod ingestion decreased. Atlantic croaker <9.99 mm SL, ingested almost entirely calanoid copepods while fish ≥14.00 mm ingested primarily harpacticoid copepods and mysid shrimp. Based on ontogenetic trophic niche shifts, red drum and Atlantic croaker can be divided into ecologically distinct stages that could serve to minimize intraspecific competition for food (Olson 1996).

Site and habitat did not affect the types or quantity of food ingested by red drum. These results support findings by Rooker et al. (1997) that nutritional condition of larval and juvenile red drum did not differ between seagrass type (*H. wrightii* vs. *T. testudinum*) or between various *H. wrightii* sites. Consequently, larval and juvenile red drum appear to be in good nutritional condition in seagrass beds.

Atlantic croaker ingested the same types of prey items regardless of site and habitat which may imply that either prey assemblages are similar at the three sites, or that red drum and Atlantic croaker select the same prey from each of the sites. Atlantic croaker taken from site 3H ingested greater quantities of food compared to other Atlantic croaker at other sites (Table 6), and relatively equal quantities compared to red drum (Table 8). This may indicate spatial variation in prey abundance in seagrass meadows (Orth 1984) or that this particular site (3H) is more suitable habitat for Atlantic croaker. Interestingly, larval and juvenile red drum were shown to have increased growth rates at this particular site (Rooker et al. 1997).

Although previous investigations have demonstrated partitioning of prey among species of larval fish (Laroche 1982, Govoni et al. 1983), little evidence of this was observed for red drum and Atlantic croaker in the present study. High dietary overlap (Schoener's index) was observed throughout most of the size range and at most stations, although a decrease in dietary overlap (23%) was observed at the largest size class (16.0 - 17.9 mm SL). Sheridan (1979) found diets of Atlantic croaker (10 - 59 mm SL) and Spot (*Leiostomus xanthurus*) (20 - 79 mm SL) to be similar.

High dietary overlap values in the present study must be interpreted with caution since identifying prey to lower taxonomic levels could have reduced dietary overlap values given that these fish are able to select for different prey at the lower taxonomic levels (Motta et al. 1995). For example, if one species of fish selected for a particular species of calanoid copepod, then dietary overlap values would almost certainly decrease.

Red drum and Atlantic croaker may also partition resources by feeding at different times of the day. For example, one species may feed nocturnally and the other diurnally. Studies have shown that larval and juvenile fishes at these stages lack appropriate number of neuromast and retinal rod cells (O'Connell 1981, Poling and Fuiman in press); therefore, efficient nocturnal foraging is probably not likely. In addition, diel food habits studies have shown gut fullness declines considerably at night (Kjelson 1975, Archambault and Feller 1991). Furthermore, most fish caught nocturnally have higher proportions of empty guts than fish caught diurnally (Govoni et al. 1983). Resources can also be partitioned by one species foraging more intensely at a different time of the day than the other. Since high dietary overlap was observed throughout the entire day, resource partitioning of this type is probably not likely.

In order for competition for food to occur, prey must be limiting, there must be high dietary overlap, and there has to be a negative effect on one or more species (Schreck and Moyle 1990). No data on prey abundance was taken; therefore, arguments for a limiting resource are difficult to make. Evidence for the latter two requirements is provided. Three cases for high dietary overlap are: 1) the same three prey types were most important to both species; 2) high dietary overlap (Schoener's index) was observed between Atlantic croaker and red drum throughout most of the size range and at most stations; and 3) both species showed similar ontogenetic trophic niche stages during the co-occurring period. Evidence of a negative effect on Atlantic croaker feeding is: 1) there was a greater proportion of empty stomachs found in Atlantic croaker (28.8%) compared to red drum (8.4%); 2) Atlantic croaker are able to ingest as much prey as red drum but did not at times; and 3) there was an absence of mysid shrimp in Atlantic croaker stomachs at the largest size range. Of the three major prey items, mysid shrimp are the largest by volume and probably constitute the greatest caloric gain. Laboratory experiments to support the negative affect on Atlantic croaker feeding should be conducted.

Chao and Musick (1977) have suggested that sciaenid fishes separate use of nursery habitat to potentially reduce interspecific competition for food. Similarly, Rooker et al. (1998) showed that newly settled red drum (4.0 - 30 mm SL) and Atlantic croaker (8.0 - 20 mm SL) stagger occupancy of seagrass beds. The overlap period when similar-sized larval and juvenile red drum and Atlantic croaker co-occur lasts for only a few weeks (Rooker et al. 1998). Thus, red drum and Atlantic croaker may temporarily separate use of seagrass beds to partition food resources. Moreover, these two species may have evolved to spawn at different times of the year or at different distances from nursery habitat to reduce competition for food.

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LITERATURE CITED

Archambault, J.A. and R.J. Feller. 1991. Diel variations in gut fullness of juvenile spot, *Leiostomus xanthurus* (Pisces). Estuaries 14:94-101.

Bass, R.J. and J.W. Avault Jr. 1975. Food Habits, length-weight relationship, condition factor, and growth of juvenile red drum, *Sciaenops ocellatus*, in Louisiana. Transactions of the American Fisheries Society 104:35-45.

Blaxter, J.H.S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Transactions of the American Fisheries Society 115:98-114.

Chao, L.N. and J.A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River Estuary, Virginia. Fishery Bulletin, U.S. 75: 657-701.

Currin, B.M., J.P. Reed and 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.

Govoni, J.J., D.E. Hoss and A.J. Chester. 1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus, Leiostomus xanthurus,* and *Micropogonias undulatus.* Marine Ecology Progress Series 13:189-199.

Govoni, J.J., P.B. Ortner, F. Al-Yamani and L.C. Hill. 1986. Selective feeding of spot, *Leiostomus xanthurus,* and Atlantic croaker, *Micropogonias undulatus,* larvae in the northern Gulf of Mexico. Marine Ecology Progress Series 28:175-183.

Hartigan, J.A. 1975. Clustering algorithms. Wiley, New York. p 351.

Holt, S.A. and C.R. Arnold. 1989. Data synthesis and analysis, nitrogen processes study (NIPS), nursery habitat utilization by finfish and shellfish in Lavaca, San Antonio, and Mesquite Bays and their relationships to freshwater inflow. Section I. Data analysis. Final report to Texas Water Development Board, Bays and Estuaries Program. Technical Report No. TR/89-009.

Holt, S.A., C.L. Kitting and C.R. Arnold. 1983. Distribution of young red drums among different sea-grass meadows. Transactions of the American Fisheries Society 112:267-271.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2:17-29.

Johnson, D.J. 1978. Development of fishes of the mid-Atlantic bight: An atlas of egg, larval and juvenile stages. Volume IV, Carangidae through Ephippidae. Biological Service Program. FWS/OBS-78\12.

Kane, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Marine Ecology Progress Series 16:9-20.

Kjelson, M.A., D.S. Peters, G. Thayer and G.N. Johnson. 1975. The general feeding ecology of postlarval fishes in the Newport River Estuary. Fishery Bulletin U.S. 73:137-144.

Laroche, J.L. 1982. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary. Fishery Bulletin U.S. 80:827-840.

Linton, L.R., R.W. Davies and F.J. Wrona. 1981. Resource utilization indices: An assessment. Journal of Animal Ecology 50:283-292.

Motta, J.M., K.B. Clifton, P. Hernandez, B.T. Eggold, S.D. Giordano and R. Wilcox. 1995. Feeding relationships among nine species of seagrass fishes of Tampa Bay, Florida. Bulletin of Marine Science 56:185-200.

O'Connell, C.P. 1981. Development of organ systems in the northern anchovy, *Engraulis mordax,* and other teleosts. American Zoologist 21:429-446.

Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. Ecology 77:179-190.

Orth, R.J., K.L. Heck and J. Montfrans. 1984. Faunal communities in seagrass beds: A review on the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7:339-350.

Overstreet, R.M. and R.W. Heard. 1978. Food of the red drum, *Sciaenops ocellata,* from Mississippi Sound. Gulf Research Reports 6:131-135.

Peters, K.M. and R.H. McMichael Jr. 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 10:92-107.

Pinkas, L., M.S. Oliphant and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Fish and Game Bulletin 152:1-105.

Poling, K.R. and L.A. Fuiman (in press). Sensory development and concurrent behavioural changes in Atlantic croaker larvae. Journal of Fish Biology.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Romesburg, H.C. 1984. Cluster analysis for researchers. Lifetime Learning Publications, Belmont, California.

Rooker, J.R., G.J. Holt and S.A. Holt. 1997. Condition of larval and juvenile red drum (*Sciaenops ocellatus*) from estuarine nursery habitats. Marine Biology 127:387-394.

Rooker, J.R. and S.A. Holt. 1997. Utilization of subtropical seagrass meadows by newly settled red drum (*Sciaenops ocellatus*) from estuarine nursery habitats. Marine Ecology Progress Series 158:139-149.

Rooker, J.R., S.A. Holt, M.A. Soto and G.J. Holt. 1998. Recruitment of sciaenids to subtropical seagrass meadows: patterns in nursery habitat use. Estuaries "In press".

Rudnick, D.T., R. Elmgren and J.B. Frithsen. 1985. Meiofaunal prominence and benthic seasonality in coastal marine ecosystems. Oecologia 67:157-167.

Schoener, T.W. 1968. The anolis lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49:704-726.

Schrek, C.B. and P.B. Moyle eds., 1990. Methods for fish biology. American Fisheries Society. Bethesda, Maryland.

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

Steen, J.P. and J.L. Laroche. 1983. The food of red drum (*Sciaenops ocellatus)* larvae and early juveniles taken from Mississippi Sound and the northern Gulf of Mexico. p 35-38. in Shabica, S.V., N.B. Cofer and E.W. Cake, Jr., eds., 1983. Proceedings of the northern Gulf of Mexico estuaries and barrier islands research conference. 13-14 June 1983, Biloxi, Mississippi. U.S. Department International National Park Service SE Regional Office Atlanta, Ga. p 191.

Stoner, A. W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bulletin of Marine Science 30:537-551.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Revue 19:513-605.

Wallace, R.K. Jr. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110:72-76.

Wilkinson, L. 1990. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.